

Research



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Animal behaviour

The perils of paradise: an endangered species conserved on an island loses antipredator behaviours within 13 generations

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When imperilled by a threatening process, the choice is often made to conserve threatened species on offshore islands that typically lack the full suite of mainland predators. While keeping the species extant, this releases the conserved population from predator-driven natural selection. Antipredator traits are no longer maintained by natural selection and may be lost. It is implicitly assumed that such trait loss will happen slowly, but there are few empirical tests. In Australia, northern quolls (*Dasyurus hallucatus*) were moved onto a predator-free offshore island in 2003 to protect the species from the arrival of invasive cane toads on the mainland. We compared the antipredator behaviours of wild-caught quolls from the predator-rich mainland with those from this predator-free island. We compared the responses of both wild-caught animals and their captive-born offspring, to olfactory cues of two of their major predators (feral cats and dingoes). Wild-caught, mainland quolls recognized and avoided predator scents, as did their captive-born offspring. Island quolls, isolated from these predators for only 13 generations, showed no recognition or aversion to these predators. This study suggests that predator aversion behaviours can be lost very rapidly, and that this may make a population unsuitable for reintroduction to a predator-rich mainland.

1. Introduction

Species regularly find themselves isolated from the predators with which they co-evolved. This scenario plays out naturally in island populations but also occurs when threatened species are moved into captivity, predator-free enclosures or islands for conservation. In isolation from predators, costly and redundant antipredator behaviours may vanish from a population's repertoire [1–3]. The possibility that conservation measures may cause a loss of antipredator behaviour is rarely considered: the implicit assumption of such isolationist conservation measures is that antipredator traits are lost slowly, on time scales irrelevant to conservation [1,2,4]. As predation is the greatest cause of reintroduction failure [5], loss of antipredator behaviour may have dramatic consequences when populations from predator-free 'islands' are reintroduced to a predator-rich mainland.

The spread of toxic cane toads (*Rhinella marina*) in Australia has seen populations of some large native predators rapidly decline [6]. Northern quolls (*Dasyurus hallucatus*), a native marsupial predator, lack immunity to toad toxins [7] and die when they prey on toads. This has resulted in local extinctions of quolls from many parts of their range [8]. In 2003, populations of northern quolls were established on two toad- and predator-free islands in Arnhem Land, Northern Territory, with hopes that one day they could help repopulate

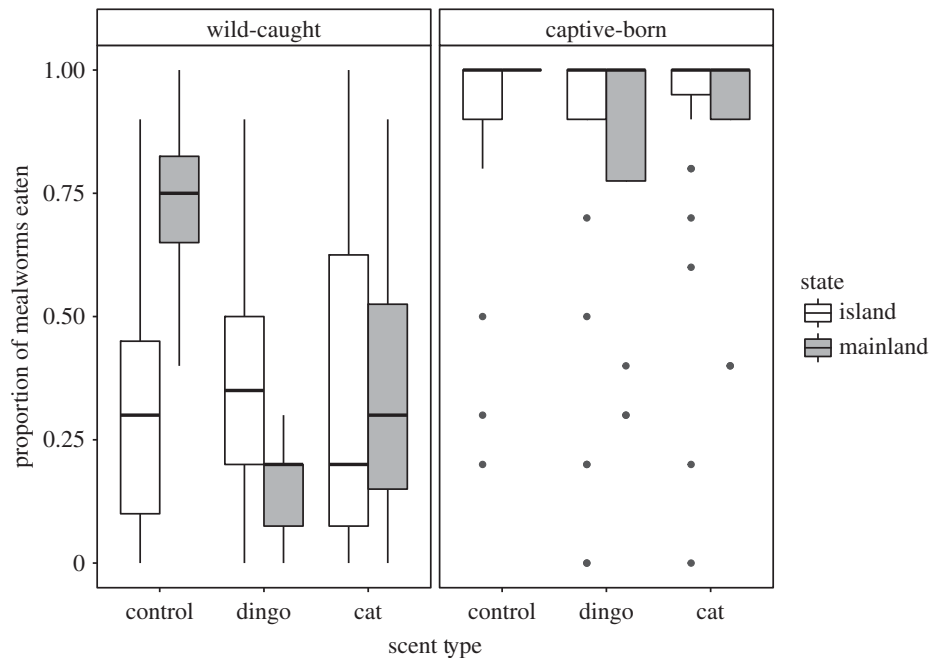


Figure 1. The proportion of mealworms eaten from giving-up density boxes fitted with one of three treatment scent types during a 2 h period. Boxes show median and interquartile range of the raw data; whiskers represent 1.5 times the interquartile range (IQR), or the range of the data, whichever is smaller. Results shown for both predator-exposed (mainland) and predator-naïve (island) quolls and the captive-born offspring of both mainland and island quolls.

the mainland [9]. The founders of these populations were sourced from locations across the Northern Territory, including Kakadu National Park [9]. Quolls proliferated on these islands [10] and in 2016, a reintroduction of toad-trained quolls from Astell Islands to Kakadu was trialled [11]. Toad-trained quolls mostly avoided toads, but they did not survive long-term because they were predated by dingoes (*Canis familiaris dingo*), a predator with which quolls have co-evolved for at least 3500 years [12]. Potentially, the isolation of quolls on these 'island arks' resulted in the loss of predator recognition and aversion [11]. We compared the behavioural responses of wild-caught quolls from the mainland (predator-exposed) and predator-free Astell Island (predator-naïve), as well as the captive-born (predator-naïve) young of both populations, to the scents of both naturalized (dingoes) and invasive (feral cats) predators. Antipredator behaviours can be innate (genetically based), learnt through experience, or a combination of the two: innate priming with the behaviour then triggered by experience. Our design allows us to test whether experience (predator naivety) or population background (island versus mainland) best explains differing responses. We predicted that the loss of antipredator behaviours of island-isolated quolls would be driven by experience rather than population history.

2. Material and methods

Northern quolls (*Dasyurus hallucatus*) are native marsupial predators with a historic distribution across much of northern Australia. Owing to toad-induced population declines, quolls are currently listed as Endangered. Northern quolls are semelparous marsupials, with both sexes maturing at 11 months and males typically dying soon after reproduction [13]. Rapid generation times mean that evolution can proceed quickly in this species. As a consequence, environmental changes, such as loss of predators, may result in rapid trait shift.

We used a giving-up density experiment to test for differences in the antipredator behaviour of quolls. We examined four groups of quolls, from two populations (see electronic

supplementary material, S1): wild-caught quolls from northern Queensland ($n = 8$), where both dingoes and feral cats are common, and where toads have been present for approximately 70 years; wild-caught quolls from predator-free Astell Island, where toads and predators are absent ($n = 16$; see electronic supplementary material, S2); and the captive-born offspring of both cohorts ($n = 12$ and 27 , respectively: see electronic supplementary material, S3).

The responses of all individual quolls to predator scents were tested independently. Each quoll was offered three plastic boxes simultaneously, each containing a matrix of 2 l of wood shavings and 10 mealworms. A hole (15 cm diameter) was cut into the top of each box, the inside of which was fitted with a rolled fly-mesh collar. We filled collars with either dingo fur or cat fur or no fur (control; see the electronic supplementary material). The behavioural responses of each quoll were video recorded for the first 2 h of each night. The following morning, we counted the remaining mealworms. From these videos, we scored behavioural traits (see electronic supplementary material, S4). Videos were scored by a single observer who was blind to quoll origin.

We used generalized linear models to analyse the effect of origin (levels: mainland and island), captivity status (levels: wild-caught and captive-born) and scent type (levels: control, dingo and cat) on the response variables (proportion of mealworms consumed, and time spent investigating predator scents). p -Values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect. This analysis was performed using R with the *lme4* software package (see electronic supplementary material, S5). Because data were not normally distributed, we log-transformed the 'time spent investigating' variable. For proportion of mealworms consumed, we used a generalized linear model with a quasi-binomial error distribution to account for overdispersion in this variable. We calculated relative risk to generate an intuitive metric for effect sizes between cohorts.

3. Results

There was no interaction between quoll origin, captivity status and scent type, and the proportion of mealworms

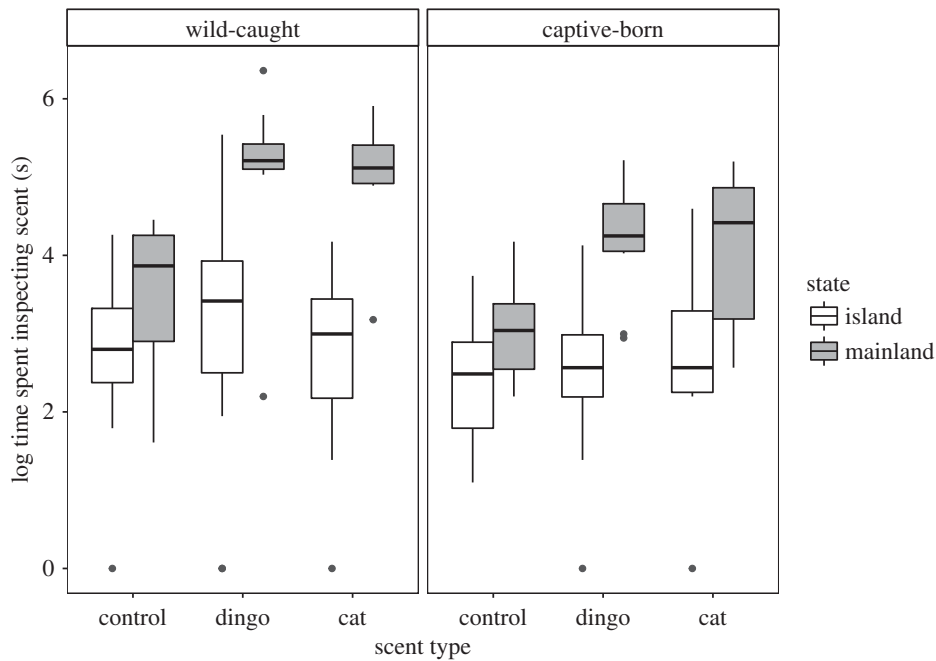


Figure 2. Log of time spent investigating ($\ln[\text{time} + 1]$) three treatment scent types in a 2 h period (in seconds). Boxes show median and interquartile range of the raw data; whiskers represent 1.5 times the IQR, or the range of the data, whichever is smaller. Results shown for both predator-exposed (mainland) and predator-naïve (island) quolls, and the captive-born offspring of both populations.

consumed ($\chi^2_5 = 814.1$, $p = 0.723$; figure 1). The model without this three-way interaction revealed a significant two-way interaction between quoll origin (mainland or island) and scent type (control, dingo or cat) for the proportion of mealworms consumed ($\chi^2_2 = 862.90$, $p < 0.001$; figure 1). Mealworms in a control box were 3.22 times more likely (relative risk, 95% confidence interval [2.91, 8.37]) to be eaten by a wild-caught mainland quoll than mealworms in a dingo-scented box. Comparatively, mealworms in a control box were 1.11 times more likely (95% CI [1.10, 1.34]) to be eaten by a captive-born mainland quoll than mealworms in a dingo-scented box (figure 1; also see electronic supplementary material, S6).

For the amount of time quolls spent investigating the predator scents, there was no interaction between quoll origin, captivity status and scent type ($\chi^2_5 = 164.63$, $p = 0.42$; figure 2). After removing this three-way interaction, there was, however, a significant interaction between quoll origin (mainland or island) and scent type (control, dingo or cat; $\chi^2_2 = 175.42$, $p < 0.01$; figure 2). The direction of these interactions is such that the effects of scent type are stronger for mainland quolls (figure 2).

4. Discussion

Our results provide strong evidence that wild-caught northern quolls from predator-rich populations recognize and avoid the scents of two important mammalian predators (figures 1 and 2). By contrast, quolls conserved on a predator-free island showed no recognition and no aversion to the scent of either predator. Importantly, the offspring of our wild-caught quolls—born and raised in captivity, and naïve to predators—exhibit an identical pattern of behaviour to their parents: in the mainland animals, wariness of these predator's scents; in the island animals, no response to predator scent (figures 1 and 2). This suggests a genetic basis to predator response in quolls.

While the pattern of responses in captive-born animals was similar to patterns expressed by their parents, there was an apparent reduction in the strength of predator aversion expressed by mainland captive-born quolls (relative to the control). For the proportion of mealworms consumed, this effect could be an artefact of the measurement scale (0–1) and a higher overall proportion of mealworms consumed (often reaching the maximum proportion) by captive-born animals potentially having truncated the full expression of their response. This higher overall consumption is likely an artefact of captivity: boldness increases and neophobia decreases in captive-born animals when compared with their wild counterparts [14]. Results from time spent investigating the scent, however, argue against this interpretation. Despite no constraint on the measurement scale, a similar reduction in response (versus control) was seen. Collectively, the lowered relative response of captive-born mainland quolls suggests that while predator response has a genetic basis, the full expression of predator aversion may only be exhibited after experience with predators [2]. What the quolls inherit from their parents is likely a priming for predator aversion; full aversion is expressed upon experience with predators.

In the absence of predators, antipredator behaviours can be costly to maintain. The loss of these behaviours in populations long-isolated on islands is well documented [1,2,14,15], but the rate at which they are lost is unknown. Ours is a two-population comparison, so ideally we would provide evidence that Astell Island quolls expressed antipredator behaviours before their translocation to the island. We cannot provide this evidence directly, but the Astell founders likely exhibited antipredator behaviours analogous to those of quolls from Queensland. Dingoes and cats are major predators in the mainland populations from which the Astell Island quolls were sourced [11,13], and likely have been for at least 3500 [12] and 130 years [16], respectively. After only 13 generations on Astell Island, however, this population now shows no recognition of a predator it

co-evolved with for millennia (see also electronic supplementary material, S7 and S8). While unnecessary and costly antipredator behaviours may be lost over time, we anticipated predator recognition (or priming for predator aversion) to have incurred little fitness cost and be lost gradually. The rapid loss of this trait suggests that predator aversion has been directly selected against. This might be expected where competition for food is limiting [10]. Here, timid behaviour and time spent on vigilance simply reduce access to limited resources.

The main cause of reintroduction failure worldwide is predation of predator-naive species [4]. Clearly, it is paramount to gain a clearer understanding of the mechanisms that dictate how and why antipredator traits are lost and gained from vulnerable prey species' behavioural repertoire. Our study shows that antipredator responses can be lost remarkably quickly, even when they have a genetic basis. Our results highlight the perils of conserving threatened species in complete isolation from important agents of selection, such as predators (see electronic supplementary material, S2). Our results also support the multi-predator hypothesis [14,15] which posits that retention of a single predator can maintain antipredator traits. Our island quolls had no contact with any predators, and consequently, they did not react to dingoes or cats, a result consistent with antipredator behaviour as a genetic trait coded across a linked set of loci. Irrespective of the genetic architecture, however, relaxed selection [3] may result in isolated populations proceeding down an evolutionary pathway at odds with that required for survival on the mainland, and our results indicate that populations may move down this path very

rapidly. Wherever possible, particularly in Australia where managers are increasingly relying on predator-free environments to conserve many native mammals, threatened species should be maintained in the presence of predators and the selective pressures these enforce. This is crucial for ensuring that threatened species do not evolve traits incompatible with survival in their original range; and that they do not succumb to the perils of a predator-free paradise.

Ethics. This study was conducted under Ethics protocol ACEC 2015000175 from the University of Technology Sydney.

Data accessibility. Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.j83258j> [17].

Authors' contributions. C.J.J. conceived, designed and executed the study, and analysed data; J.K.W. contributed to experimental design; B.P. contributed to experimental design and data analysis. All authors contributed to the preparation and revision of this manuscript, gave final approval for publication and agree to be accountable for the content.

Competing interests. We have no competing interests.

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