The best of both worlds: Why antipredator traits are lost in predator free havens and how to keep them

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Abstract

As a response to the current biodiversity crisis, active management of threatened species has become more frequent, with predator-free havens an increasingly common conservation management strategy. In Australia, where introduced predators such as cats and foxes are one of the largest threats to native fauna, havens have played a key role in maintaining viable populations of endemic marsupials. Concerns, however, have been increasingly raised that populations in predator-free havens, or similarly those that are captive bred or on predator-free islands, rapidly lose antipredator traits. Here we suggest that some of the selective pressures and mechanisms that may explain the rapid loss of these traits may have been overlooked. There is convincing evidence within the animal production literature that a fearful, high anxiety temperament (typically associated with anti-predator behaviours) is genetically associated with reduced fecundity; a relationship that may explain the rapid loss of fearful antipredator traits as a byproduct of strong selection for fecundity in havens. We also propose mechanisms by which antipredator behaviour could be maintained in populations that are expected to evolve predator naivety. There is the potential for haven and captive bred populations to be managed to ensure the best of both worlds: anxious, predator-wary individuals selectively maintained for release into the wild, and low anxiety, high fecundity individuals removed for island refuges and public-facing conservation education.

Introduction

The current biodiversity crisis has resulted in many species experiencing rapid population declines and in need of active management (Hoffmann et al., 2010; Legge, Rumpff, et al., 2023). Such management has increasingly included using predator-free ‘havens’ in which predators are actively excluded by fencing discrete areas or peninsulas (Innes et al., 2019; Legge, Hayward, & Weeks, 2023), or by utilising islands that are naturally predator-free or have had predator eradication programs (Jones et al., 2016; Legge et al., 2018). In Australia, where introduced predators such as cats (Moseby et al., 2015) and foxes (Radford et al., 2018) are one of the largest threats to native fauna, havens have played a key role in maintaining viable populations of endemic mammals (Legge et al., 2018; Woinarski et al., 2023), and are credited with preventing the extinction of at least five Australian marsupial species (Legge, Hayward, & Weeks, 2023). There are now 75 island and 32 fenced havens in Australia protecting nearly ~180 populations of marsupial species and subspecies (Legge, Hayward, & Weeks, 2023). There has been increasing concern however, that populations in predator free havens, or similarly those that are captive bred or moved to islands, rapidly lose antipredator traits (Blumstein & Daniel, 2005; Harrison, Phillips, et al., 2023; Smith & Blumstein, 2008). The loss of antipredator traits in species long isolated on islands is well known (Beauchamp, 2004; Blumstein & Daniel, 2005; Curio, 1966), but the loss of antipredator traits in havens has been very rapid; declines have been observed in havened woylies (Harrison, Phillips, et al., 2023), northern quolls recently moved to an island sanctuary (Jolly et al., 2018), and sanctuary brush-tailed possums (Bannister et al., 2018).

Why antipredator traits may have been rapidly lost in havens is much debated (Harrison, Phillips, et al., 2023; Harrison, Wayne, et al., 2023; Kanowski et al., 2023). Leaving aside, and acknowledging a role for plasticity (Kanowski et al., 2023), the loss of such traits is typically ascribed to direct selection on these traits being relaxed (Beauchamp, 2004; Blumstein & Daniel, 2005; Harrison, Phillips, et al., 2023; Jolly & Phillips, 2021; Jolly et al., 2018; Smith & Blumstein, 2008). In the absence of predators, behaviours associated with wariness and shyness would no longer be selected for, and if such traits persist, it is assumed to be due to the low cost of their continued expression (Blumstein & Daniel, 2005; Jolly & Phillips, 2021). It has also been highlighted that resource competition can be exacerbated by high population densities that can arise in the absence of predation (Butler et al., 2019; Jolly & Phillips, 2021; Jolly et al., 2018; Moseby et al., 2018; Treloar et al., 2021), and that this may then become the dominant selection pressure with predator-wary, shy individuals losing out in resource competition (Jolly & Phillips, 2021). What may have been underappreciated however, is that a predator-wary fearful temperament also comes at a direct fecundity cost due to the genetic covariance between fecundity and fearful behaviour (Figure 1). Here, we suggest that selection for fecundity and parental ability in captive populations (the very thing that captive breeders want to enhance) selects, through a common dependence on the neuroendocrine system, for less anxious individuals that are prone to fall prey to predators. Importantly, this means that selection on fecundity alone can drive down antipredator behaviours (Figure 2).

There is convincing evidence in the animal production literature that behavioural traits associated with antipredator responses (e.g. wariness, shyness) trade off against fecundity. For example, a 20-year temperament selection experiment on merino sheep resulted in higher fecundity in calm compared to nervous ewes (van Lier et al., 2017). Nervous ewes had significantly reduced sexual interest (Gelez et al., 2003), lower rates of ovulation and fewer multiple pregnancies (van Lier et al., 2017). Trading off with these fecundity related traits, nervous ewes had offspring with traits that would clearly be a selective advantage in a predator rich environment, showing a shorter latency to stand up in newborn lambs (Bickell et al., 2010), increased locomotor activity, vocalisations and escape behaviours (Bickell et al., 2009). Notably, none of these traits, fecundity nor predator-wariness, were under direct selection; agitation score, taken from two different measures, was the only subject of the artificial selection. The two lines of sheep correspondingly diverged genetically in temperament into ‘calm’ and ‘nervous’ ewes (Bickell et al., 2009), with divergence between lines corresponding to single nucleotide polymorphisms (SNPs) associated with temperament in an outbred flock (Ding et al., 2021).

Independent support for this fecundity/anxiety trade-off also comes from other sheep flocks selected instead for maternal ability, such as twinning rate and lamb survival

(Kilgour & Szantarcoddington, 1995). These lines of sheep were found to differ in arena tests where they were exposed to a human threat, with fertility selected sheep remaining closer to the threat, vocalising less, and moving less than their unselected counterparts (Cloete et al., 2020; Kilgour & Szantarcoddington, 1995). Several other large studies of merino sheep confirm moderate genetic correlations between calm temperament and maternal behaviour scores and the number of lambs weaned (Brown et al., 2016). Together these experiments indicate that selection on fecundity indirectly affects the fear responses of a population. While the recent (Wilkins et al., 2014) interest in the neural crest cell hypothesis, at least in some manifestations (Gleeson & Wilson, 2023), discounts ‘cryptically-shared mechanisms of pleiotropic trait association’, the evidence for a genetic correlation between fearful temperament and fecundity appears to be genetically and mechanistically well founded.

The domestication literature also adds evidence, and a mechanism, for a relationship between fecundity and nervousness. Although the notion of a ‘domestication syndrome’ is controversial (Gleeson & Wilson, 2023; Lord et al., 2020), one of the most well documented examples of selection for low levels of fear is in the silver fox domestication experiment (Belyaev et al., 1985; Dugatkin, 2020; Trut, 1999). In these experiments the behavioural response of foxes to humans were subject to selection, resulting in a diversity of domestic traits in the tameness-selected lineages. The link between tameness and fertility was proposed by Belyaev (referenced by Klotchkov et al., 1998) and appears to arise through the common basis of both, on the neuroendocrine system. For example, tame foxes lost their seasonal reproductive cycles with females entering oestrus outside the breeding season (Trut, 1999); similarly, docile-selected captive mink entered oestrous earlier (Klotchkov et al., 1998).

The link with between tameness and fertility in the above studies is most likely explained by neurotransmitters, with both mink and foxes that were diverged for tameness also showing divergence in serotonin levels in the brain (Klotchkov et al., 1998). Genomic analysis confirms the role of these neurotransmitters in the divergence of the fox lineages, in particular serotonin and glutamate pathways (Kukekova et al., 2018; Lindberg et al., 2005; Wang et al., 2018). Similarly, temperament divergence in sheep was also associated with neuroendocrine changes in serotonin receptors and transporters, and tryptophan 5-hydroxylase (the rate-limiting enzyme in the synthesis of serotonin) (Ding et al., 2021). The neuroendocrine axis between stress and reproduction is phylogenetically ancient among vertebrates (Lovejoy & Hogg, 2021), and across mammal species is strongly associated both with female reproductive hormone profiles (Nakamura et al., 2024), and maternal care as opposed to offspring rejection and mortality (Pawluski et al., 2019). Similarly, in wild birds peripheral serotonin levels have been shown to be positively associated with earlier egg laying, clutch size and parental reproductive behaviours (Tilgar, 2023). In domestic fowl production systems (Cheng et al., 2001; Cheng & Muir, 2007), selecting for productivity and longevity, similar to mammalian studies, found divergence in serotonin levels. Cheng and Muir (2007) suggest that the serotonin receptor "5-HT could serve as a physiological indicator of the animal's coping ability to stress as well as a biological trait marker for domestic behaviours". Given what we know about the role of serotonin in reproductive physiology (Nakamura et al., 2024; Pawluski et al., 2019), this strongly implicates selection for fecundity to changes in predator wariness traits. Due to the conserved nature of the neuroendocrine axis between stress and reproduction, it would be worthwhile to replicate the genomic comparisons of the divergence in the foxes (Kukekova et al., 2018; Lindberg et al., 2005; Wang et al., 2018) and merino sheep (Ding et al., 2021) in haven/island populations that have lost antipredator behaviours versus their corresponding predator-exposed populations. Divergence at SNP loci associated with neurotransmitters that have known effects on fecundity in populations that have lost antipredator behaviour, would confirm the conserved nature of these relationships and the extent to which conservation management needs to address this trade-off.

A general relationship between nervousness and fecundity across wild species is more difficult to establish due to the challenges in accurately quantifying the role of nervousness in species-specific anti-predator traits, as well as ruling out confounding influences on fecundity. So called 'personality' research in behavioural ecology, however, has found boldness to be repeatable and heritable, across taxa as diverse as mammals, fish, birds, reptiles and invertebrates (Réale et al., 2007). Further, meta-analysis shows a positive effect of boldness on reproductive success in captive/domestic animals, with no relationship in wild populations, presumedly due to a survival disadvantage (Smith & Blumstein, 2008). If bold individuals obtain more food resources in predator-free environments (Biro & Stamps, 2008; Jolly & Phillips, 2021), this may add further environmentally induced variation that aligns to any underlying genetic correlation, further strengthening selection for low anxiety individuals in these environments. Recent findings that artificially induced predator anxiety results in fecundity and population declines in field experiments also support the hypothesis (Allen et al., 2022; Zanette et al., 2024).

It has been argued that predator-wary traits can persist in populations without predators if they are selectively neutral (Lahti et al., 2009). Whilst this is true, as we have outlined here, it may be uncommon given the ancient relationship between anxiety and fecundity. This is supported in the number of havened species that have lost rather than maintained predator wariness (Harrison, Phillips, et al., 2023; Jolly & Phillips, 2021; Legge, Hayward, & Weeks, 2023). Recent work has highlighted the value of keeping predators with havened species for maintaining antipredator behaviours (Harrison et al., 2024; Moseby et al., 2023; Moseby et al., 2016; Moseby et al., 2024); predators should effectively remove low anxiety, high fecundity individuals and prevent their offspring swamping the population. There will be circumstances however, where including predators in enclosures may not be viable for numerous logistical reasons (e.g. animal ethics, conservation status, small haven size, no appropriate predator). In such situations, it may be prudent to supplement haven populations with wild individuals that show high agitation scores when trapped; using metrics such as those measured in woylie's (Harrison et al., 2022; West et al., 2019) or brush-tail possums (May et al., 2016).

An additional approach that doesn't involve introducing predators to havens, could be the targeted removal of low anxiety individuals, which may be sufficient to maintain a selective pressure in favour of anxious, predator-wary individuals (Figure 2). Such removal could be relatively simple if low anxiety individuals tend to be more trap-happy or have assessable behavioural differences when trapped such as low agitation scores (Allen et al., 2022; Brehm & Mortelliti, 2018; May et al., 2016; Réale et al., 2000), though species-specific assessments and techniques would be required (i.e. Harrison et al., 2022). Traps could also be modified to require bold/calm behaviour to enter, for example through their positioning (e.g. in the open), or association with predator scent, vocalisation or taxidermy models. These low anxiety individuals could be moved to predator-free islands for which their traits are well aligned, and which, in Australia also frequently act as species' insurance populations (Legge, Hayward, & Weeks, 2023). Removed low anxiety individuals could be used in public education in zoos and for outreach with private conservation organisations or government conservation departments. Such a strategy would also benefit from the expectation that calm individuals should experience less stress than other individuals when exposed to humans, thus also directly addressing animal ethics concerns in human/animal interactions. In Australia the vast majority of the most threatened marsupials are never seen by the public. Allowing zoo's and similar organisations access to the calm individuals removed from havens (and unhampered by reintroduction concerns) may assist in conservation education through the public's direct engagement with species that have been traditionally less visible and thus harder to connect with (Gaston & Soga, 2020; Hughes et al., 2005; Whitburn et al., 2020). For example, the Western Australian conservation department runs a semi-natural enclosure, *Barna Mia*, where the public can enter the enclosure and closely observe rare marsupials such as the bilby (*Macrotis lagotis*), boodie (*Bettongia lesueur*), mala (*Lagorchestes hirsutus*), and woylie (*Bettongia penicillata*); with a very high level of public satisfaction reported (Hughes et al., 2005).

Conclusion

Whilst captive breeding programs and havens understandably aim to rapidly increase population numbers, there is evidence that such rapid growth likely selects for fecundity and thereby comes at the cost of nervousness and associated antipredator behaviours. In understanding the underlying selective mechanisms at play in these populations, selection could be directed to ensure traits such as nervousness, which are valuable in a predator rich environment, are maintained. Ultimately, there is the potential for havens and captive bred populations to be managed to ensure the best of both worlds: nervous, predator-wary individuals selectively maintained for release into the wild, and low anxiety, high fecundity individuals for island refuges and public-facing conservation education.

Acknowledgements

We acknowledge funding from the Australian Research Council DP220100120.

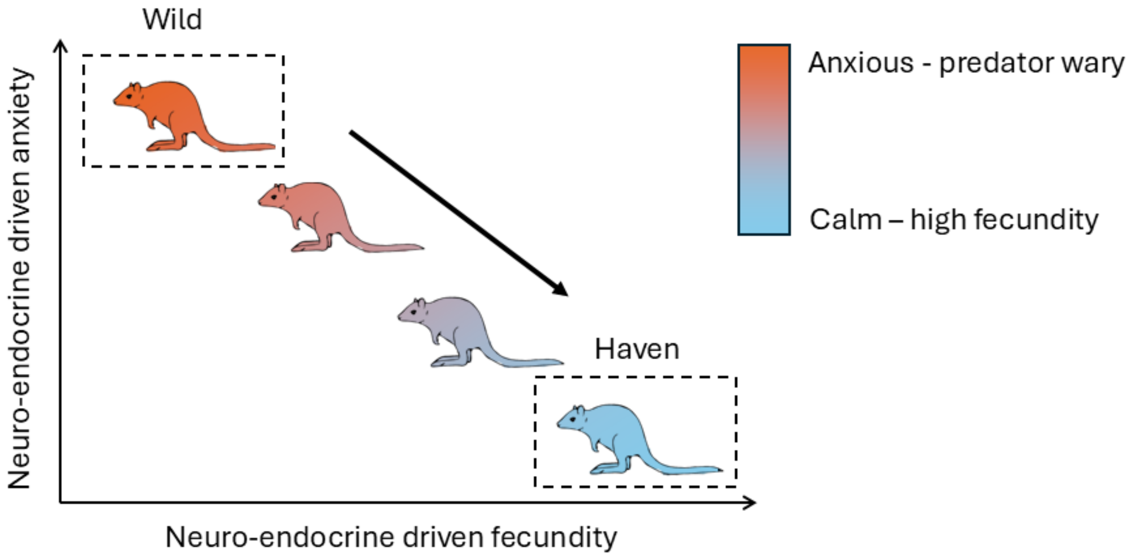

Figure 1. Trade-off between anxious, predator-wary traits and fecundity mediated by their common dependence on the neuroendocrine system. Anxious, predator-wary individuals have low fecundity (red), and calm, less predator-wary individuals have high fecundity (blue). In havens the predominance of fecundity selection may rapidly select for high fecundity, less predator-wary individuals.

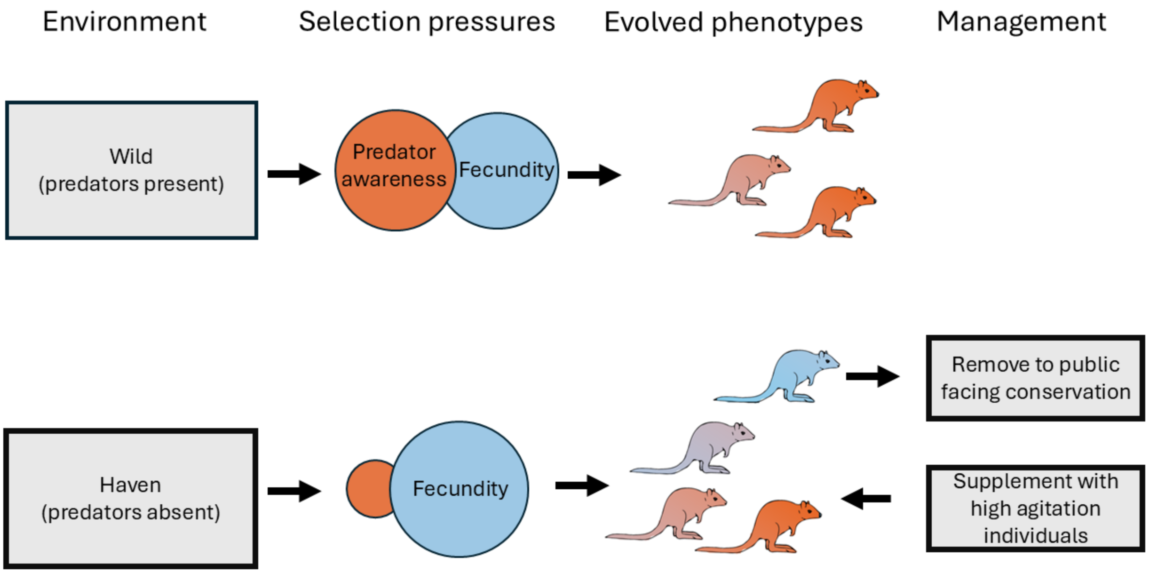

Figure 2. Hypothesis for the consequences of selection on fecundity in havens. If there is a trade-off between predator-wariness and fecundity (Figure 1), differences in selection in 'wild' populations where predators are present, and 'havens' where predators are absent, will lead to the evolution of divergent phenotypes. The size of the circles represents the strength of selection acting on the population, with wild populations balancing predator anxiety and fecundity, whereas in havened populations fecundity is released from the trade-off by the absence of predators, and predator anxiety traits diminish under selection for fecundity. The phenotypes of the resultant populations are coloured to represent their bias/balance between anxious (red), predator-wary traits and fecundity (blue). Selective removal of low anxiety individuals for public facing conservation, and supplementation with anxious, predator-wary wild animals, may help ameliorate selection for fecundity in havens.

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