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 (Hoffmann et al., 2010), with predator free havens an increasingly common conservation management strategy (Legge et al., 2022). 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). Concerns, however, have been increasingly raised that populations in predator free havens, or similarly those that are captive bred or on islands, rapidly lose antipredator traits (Beauchamp, 2004; Blumstein & Daniel, 2005; Harrison, Phillips, et al., 2023; Jolly & Phillips, 2021; Jolly et al., 2018; Smith & Blumstein, 2008). 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 linked to reduced fecundity; a relationship that may explain the rapid loss of fearful antipredator traits as a byproduct of selection for increased fecundity. We also propose a mechanism by which antipredator behaviour could be maintained in populations that are expected to evolve predator naivety.

Introduction

The loss of antipredator traits in havens, whilst debated (Harrison, Phillips, et al., 2023; Harrison, Wayne, et al., 2023; Kanowski et al., 2023), 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 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 linkage between fecundity and fearful behaviour. The 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.

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 correspondingly diverged genetically (Bickell et al., 2009) in temperament into 'calm' and 'nervous' ewes, 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 relaxed 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). More recent 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 (Pawluski et al., 2019), 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 (Cheng & 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 wild populations. A SNP divergence at 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 bold 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 et al., 2022). Recent work has suggested the value of keeping predators with havened species and this is perhaps the most obvious solution (Harrison et al., 2024; Moseby et al., 2016; Moseby et al., 2024), as this should effectively remove bold and fecund individuals and prevent their offspring swamping the population. There will be circumstances however, where this may not be viable for numerous logistical reasons (e.g. animal ethics, conservation status, small haven size). In such situations, the targeted removal of bold individuals could be sufficient to maintain a selective pressure for anxious predator-shy individuals. Such removal could be relatively simple if bold individuals tend to be more trap-happy (Brehm & Mortelliti, 2018; Réale et al., 2000), though species-specific assessments and techniques would be required (i.e. (Harrison et al., 2022). Regardless, traps could be modified to require bold behaviour to enter through their positioning (e.g. in the open), or association with predator scent, vocalisation or taxidermy models. Bold 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. Removed bold individuals could also be used in public education in zoos and for outreach with private conservation organisations or government conservation departments. Such strategies would also benefit from the expectation that bold individuals should experience less stress than other individuals when exposed to humans, thus also directly addressing animal ethics concerns in human/animal interactions.

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 that 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, and potentially, bold, low stress 'domesticated' individuals for island refuges and public-facing conservation education.

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