Fear and stressing in predator-prey ecology: considering the twin stressors of introduced predators and people (#41203)

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Fear and stressing in predator-prey ecology: considering the twin stressors of introduced predators and people

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Introduced predators have strongly deleterious effects on biodiversity in many parts of the world. Exponential growth of human populations is, at the same time, causing degradation of natural habitats and increasing the interaction rates of humans and wildlife, such that conservation management now is beginning to consider the effects of human impacts as tantamount to or surpassing the impacts of introduced predators. The need to simultaneously manage both of these threats is particularly acute in urban areas that are, increasingly, being recognized globally as hotspots of wildlife activity. Australia is a good example of this, as 89% of the human population lives in urban areas that also host introduced mesopredators that are driving extinctions of native wildlife. Pressure from introduced predators and human activity may both initiate fear responses in prey species above those that are triggered by natural stressors in ecosystems. If fear responses are experienced by prey at elevated levels, on top of responses to multiple environmental stressors, chronic stress impacts may occur. Despite common knowledge of the negative effects of stress, however, it is rare that stress management is considered in conservation management. We propose that mitigation of stress impacts on wildlife will be crucial for preserving biodiversity, especially as the value of habitats within urban areas increases. As such, we aim to highlight the need for future studies to consider fear and stress in predator-prey ecology to preserve both biodiversity and ecosystem functioning. We suggest that modern methods allow non-invasive in-situ investigations of endocrinology and ethology, along with habitat influences, to conduct cumulative effects assessments that include considerations of fear and stress impacts.

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Abstract

Introduced predators have strongly deleterious effects on biodiversity in many parts of the world. Exponential growth of human populations is, at the same time, causing degradation of natural habitats and increasing the interaction rates of humans and wildlife, such that conservation management now is beginning to consider the effects of human impacts as tantamount to or surpassing the impacts of introduced predators. The need to simultaneously manage both of these threats is particularly acute in urban areas that are, increasingly, being recognized globally as hotspots of wildlife activity. Australia is a good example of this, as 89% of the human population lives in urban areas that also host introduced mesopredators that are driving extinctions of native wildlife. Pressure from introduced predators and human activity may both initiate fear responses in prey species above those that are triggered by natural stressors in ecosystems. If fear responses are experienced by prey at elevated levels, on top of responses to multiple environmental stressors, chronic stress impacts may occur. Despite common knowledge of the negative effects of stress, however, it is rare that stress management is considered in conservation management. We propose that mitigation of stress impacts on wildlife will be crucial for preserving biodiversity, especially as the value of habitats within urban areas increases. As such, we aim to highlight the need for future studies to consider fear and stress in predator-prey ecology to preserve both biodiversity and ecosystem functioning. We suggest that modern methods allow non-invasive in-situ investigations of endocrinology and ethology, along with habitat influences, to conduct cumulative effects assessments that include considerations of fear and stress impacts.

Introduction

Biodiversity is declining globally as human populations increase and agricultural, industrial, and urban development expand, altering and destroying natural habitats (Madsen *et al.*, 2010). Due to such expansions, human activities are increasingly becoming an additional stressor that influences ecosystem function. Pressures exerted both directly and indirectly by human activities have been likened to the pressures exerted by the presence of a top predator on prey (e.g. Frid and Dill, 2002; Rehnus, Wehrle, and Palme, 2014; Patten and Burger, 2018). Predators in many systems influence the local distribution and abundance of their prey (e.g. Polis *et al.*, 1998; Ayal, 2007; Estes *et al.*, 2011; Weissburg *et al.*, 2014), and can indirectly influence the functioning of whole ecosystems via trophic cascades (Prugh *et al.*, 2009; Ritchie *et al.*, 2009; Estes *et al.*, 2011; Ripple *et al.*, 2014). While predation may contribute to ecosystem function, predators often elicit fear responses in prey that affect their behaviour, energy budget and the way they interact with their environment (Brown and Kotler, 2004; Clinchy *et al.,* 2004; Romero, 2004). These effects arise due to the '*landscape of fear'* that prey individuals perceive – that is, the costs and benefits that prey must balance while pursuing food and safety (Laundré *et al*., 2001). Natural predation pressures coupled with human-imposed predation-like pressures and / or additional exogenous stressors, such as pollution, arising from anthropogenic activities are likely to negatively affect prey species by increasing their levels or frequency of stress. If predators are introduced, their impacts on prey are likely to be exacerbated owing to prey naïveté (Doherty *et al*., 2016). Such impacts have been shown to be particularly acute on wildlife in Australia, where eutherian carnivores are recent arrivals (Salo *et al*., 2007).

Current research is developing a more nuanced understanding of the effects of human activity and predator presence on prey stress (e.g. Arlettaz *et al.,* 2015; Jaatinen, Seltmann, and

Öst, 2014, respectively). However, relatively few studies in terrestrial ecosystems consider both of these pressures simultaneously or consistently correlate observed behavioural responses with endocrinological evidence of stress. Despite this, advances in endocrinology make it possible to fill this knowledge gap with minimally invasive in-field techniques (see Sheriff *et al.*, 2011; Cook, 2012; Palme, 2019). Conservation management and the associated scientific research is often viewed from a single discipline perspective, which may have its strengths in finding biological conclusions. However, the ecological problems arising from anthropogenic influences, including the introduction of novel species and the creation of novel species interactions, call for ~~multidiscipline~~ solutions. Globally, urban edge habitats are becoming increasingly valuable as hotspots of wildlife activity (Ives *et al.*, 2016), and human ~~activity /~~ influences are spreading further into natural habitats (Otto, 2018). There is growing evidence that human activity can ~~impose stress impacts~~ akin to predation pressures, or worse, (Clinchy *et al.*, 2016) and that multiple introduced stressors (e.g. introduced predators and disturbance from humans) can have compounding impacts on wildlife especially when interacting with stressors naturally found in an ecosystem (Geary *et al.*, 2019). For these reasons, we felt it pertinent to bring together relevant information from the broad knowledge bases of conservation physiology and ecology to communicate the urgent need for wildlife managers and future urban conservation ~~scientific~~ studies to routinely consider fear and stress effects from multiple sources, particularly those created by introduced predators and human activities, and their roles in ecosystem functioning.

The central tenet of this review is to illustrate the importance of considering fear and stress in wildlife conservation, particularly when it is imposed by the multiple stressors of human activity and introduced predators. To do this we first illustrate the physiological responses of wildlife to fear and stress, then argue that the landscape of fear theorem supports our contention, and that human activity should be considered as part of the ecosystem so that overall stress impacts can be managed accordingly. We use Australia as an example of a system that would benefit from considering cumulative fear and stress impacts, as wildlife there are subject to adverse impacts from both introduced eutherian predators and human activity. We demonstrate finally how fear and stress can influence habitat use, and conversely how vegetation and microhabitat management potentially may be used to alleviate stress for target wildlife species.

Review method

This is not a systematic review, but instead is a carefully researched and, hopefully, thought-provoking synthesis of existing knowledge. It seeks to extend ideas on the physiological impacts of fear and stress, behavioural ecology, predator-prey dynamics, and conservation management to look at the influence of humans and introduced predators in the urban environment. This review was compiled in a logical order, historical definitions were first reviewed and then further reviews stemmed from them to build on each topic, as new information arose. Numerous literature searches where conducted via Google Scholar ©, Web of Science ©, JSTOR ©, and Wiley Interscience Online Library ©. All manuscripts were mined for their relevant information to wildlife fear and stress in terms of ecological management under anthropogenic pressures, including introduced predators. The literature searches were undertaken using the following key terms as part of their title, keywords, and / or within the abstract: “acute stress”, “chronic stress”, “homeostasis”, “cumulative stress”, “multiple stressors”, “multiple threats”, “allostatic load”, “allostatic overload”, “acclimitisation”, “glucocorticoid response”, “hypothalamic pituitary adrenal axis”, “fear arousal”, “fear evolution”, “fear predation”, “amygdala” “fear”, “Pavlovian fear conditioning”, “glucocorticoid assay”, “f(a)ecal glucocorticoid”, “non-invasive glucocorticoid assay", "reactive scope model", "landscape(s) of fear", "risk allocation hypothesis", "olfaction" + "fear" + "mammal", "post-traumatic stress disorder", "predator" + "odo(u)r" + "fear", "predator cue(s)", "predation stress hypothesis", "predator-sensitive food hypothesis", "human activity" + "stress" + "wildlife", "human disturbance", "interactive stress", "multiple stress(ors)", "additive stress impacts", "synergistic stress impacts", "antagonistic stress impacts", "human" + "wildlife" + "resource subsidies", "predator trophic cascade", "wildlife urban adaptation", "urban ecology" + "wildlife", "Australian mammal extinction", "critical weight range mammal", "diet" + "change" + "Australian" + "predator", "red fox" + "Australia", "domestic cat" + "Australia", "human activity" + "wildlife" + "Australia", "Australia" + "biodiversity" + "conservation policy" + "urban hotspot", "Australian environment protection and biodiversity conservation act" + "cumulative stress", "Australia" + "conservation" + "glucocorticoids", "introduced predator control", "habitat structural complexity", "habitat structural diversity", "vegetation diversity", "vegetation heterogeneity", "habitat heterogeneity hypothesis", "cumulative effects assessments".

Physiological responses to fear and stress

An individual animal experiences stress in response to ecological conditions that threaten its survival or compromise its ability to maintain homeostasis. Examples include acute or chronic encounters with predators, inclement weather, significant natural disturbances including fire and flood, reduced oxygen availability, and depleted food resources (Lima, 1998; King and Bradshaw, 2010; Malcolm *et al.*, 2014; Santos *et al.*, 2014; Crocker, Khudyakov, and Champagne, 2016). If two or more stressors are present, the resultant combined stress may present severe challenges to an individual's physiological systems (Johnstone *et al.,* 2012;

Brearley *et al.*, 2013; Malcolm *et al.*, 2014; Arlettaz *et al.*, 2015; Geary *et al.*, 2019; Legge *et al.*, 2019). Exposure to a stressor(s) that is prolonged, constant, or recurring can have chronic impacts, as recovery from a stressor cannot occur whilst the threat remains (Sapolsky, Romero and Munck, 2000). Acute stress occurs as the initial response to a threat to sustain fitness in the short term; it subsides once the responding action—be it freezing, fighting, or fleeing—diminishes the threat (Wingfield and Kitaysky, 2002). The activation of the hypothalamic-pituitary-adrenal (hereafter HPA) axis in an acute stress response has rapid effects that increase immune system function, energise muscles via enhanced cardiovascular tone, and heighten cognition, including memory (Sapolsky, Romero, and Munck, 2000). These responses occur via increased cerebral perfusion rates and use of glucose, all of which come at the cost of decreased appetite and reproductive behaviours (Sapolsky, Romero, and Munck, 2000). Effectively, the acute stress response suspends non-essential behaviours in favour of altered behaviours that aid in minimizing the threat (Wingfield and Kitaysky, 2002).

Continued exposure to a stressor, or stressors, creates a state of chronic stress, which is classically described as allostatic overload (Dantzer *et al.*, 2014). Allostatic load describes the body's ability to maintain homeostasis in response to a stressor (Sterling and Eyer, 1988; McEwen and Stellar, 1993; McEwan and Wingfield, 2003). Allostatic overload, by extension, refers to the inability to maintain homeostasis and thus an organism's increased susceptibility to external stressors (Sterling and Eyer, 1988; McEwen and Stellar, 1993; McEwan and Wingfield, 2003). Chronic stress reduces an organism's resilience to future stressors by inducing extended behavioural changes in feeding, fighting, and mating, as well as suppression / impairment of the reproductive system and decreasing physiological resistance to pathogens and toxins through the suppression of immune function (Dhabhar and McEwan, 1999; McEwan and Wingfield, 2003; Romero, 2004; Mineur, *et al.*, 2006; Travers, *et al.*, 2010; Feng, *et al.*, 2012).

Cases of acclimatisation to chronic or repeated acute stressors have been observed, although the process often results in enhanced activation of the HPA axis to novel stressors, and thus may not be beneficial to fitness (Romero, 2004). Instead of acclimatising to a chronic or repeated stressor, ~~glucocorticoid levels~~ can remain the same, ~~or~~ become chronically elevated, or ~~the HPA axis can shut down completely and~~ ~~render an animal vulnerable to stressors~~ (Romero, 2004). Physiological impairment of the neurological, cardiovascular and musculoskeletal systems may also result from chronic stress: neurons of the brain can atrophy and impair memory, or grow and enhance fearfulness with extensive releases of adrenaline and cortisol (Roozendaal, 2000; McEwan, 2004); atherosclerotic plaques also may form and impede blood flow from repeated elevation of blood pressure (Manuck *et al.*, 1988), and skeletal muscle can suffer severe protein loss (Wingfield and Kitaysky, 2002).

Activation of the HPA axis may vary depending on the nature of the stressor (Mason, 1971), and it is important to consider this when assessing stress impacts on a system. Changes in abiotic conditions, such as to food and shelter resources, and the introduction of toxins or diseases can be stressful, but do not induce fear arousal. However, a stress response, of peripheral autonomic and neuroendocrine changes (Yates, 1971; Sapolsky, Romero, and Munck, 2000; McEwan and Wingfield, 2003), can be initiated by fear arousal (LeDoux, 2003; LaBar and LeDoux, 2011). Animals with sophisticated nervous systems have a central motive state between threat stimulus and response that is driven by the amygdala (Pitkanen, 2000) and can be identified as ‘fear’ (Mineka, 1979; Öhman, 2000). The development of successful defense mechanisms to fear-inducing stressors has clear survival benefits for animals, and thus fear can be seen as a driver of evolutionary adaptations (Tooby and Cosmides, 1990). Common strategies of escape and avoidance are designed to deal with recurrent stressors, such as the fear-inducing threat of predation (see Lima and Dill, 1990).

The sections of the amygdala associated with fear behaviour serve as an interface between sensory input and information transport and processing, endocrine response, and motor output (Davis and Whalen, 2001). These interactions are associated with learning and memory via the involvement of the lateral and basal nuclei, as demonstrated on captive rodents using neurotoxic lesions on the basal and lateral nuclei of the amygdala (e.g. Wallace and Rosen, 2001), and are evident in Pavlovian fear conditioning paradigms (Davis, 1992; Maren, 2001). Activation of glucocorticoids and norepinephrine in stress responses initiated by fear arousal provides feedback to the brain that influences emotion control and cognition, which contributes to fear conditioning (Rodrigues *et al.,* 2009). Fear responses may, therefore, be both conditioned as aversive learnt behaviours (e.g. Fanselow and Poulos, 2005), and unconditioned as innate freezing responses (e.g. Schulkin *et al.*, 2003). Given that fear motivates a stress response – initiating the freeze, and fight or flight actions – quantifying glucocorticoid outputs from the autonomic nervous and HPA systems, through the use of minimally invasive techniques that assay the level of glucocorticoids present in faeces, fur, or feather (see Sheriff *et al.*, 2011; Cook, 2012; Palme, 2019), should yield a measurable indication of fear from predation as a stressor. Using minimally invasive methods to measure glucocorticoid levels in the wild does not necessarily yield an isolated 'output' of a fear or predator~~/~~human-induced stress response (Rosen and Schulkin, 2004). Nevertheless, such methods could ~~usefully compare~~ responses among habitats or along gradients with variable exposure to predators, be these animal or human-induced, to yield estimates of relative physiological stress.

Behavioural responses to fear and stress: the landscape of fear theorem

A high perceived predation risk can shape adaptive behavioural responses that allow for a prepared response in prey, improving their likelihood of survival (Bókony *et al.*, 2009). However, chronic stress impacts that are sufficient to affect reproduction and long-term survival can be experienced by prey species perceiving recurring predation risks (Thomson *et al.*, 2010; Clinchy *et al* 2011). Chronic perceived predation risk may also result in altered foraging activity driven by prey fear. This can affect where and what prey eat (Schmitz *et al.*, 2004), causing them to move from exploiting risky to sheltered microhabitats (Trussell *et al.*, 2006), in turn altering the distribution and availability of resources. Fear-based adaptive behavioural responses such as these are the premise of the landscape of fear theorem.

The landscape of fear theorem (Laundré *et al.,* 2001) postulates that prey are aware of microhabitat patches associated with high and low predation risk, where predators are either active and ubiquitous or scarce (Laundré *et al.*, 2001; Shrader *et al.*, 2008; van der Merwe and Brown, 2008). Theoretically, landscape of fear effects increase exponentially with increasing landscape homogeneity, as simple landscapes offer less opportunity for hiding and more open hunting access for predators (Bleicher, 2017; Gaynor *et al.,* 2019). However, this relationship can depend on the species and condition of the habitat and, for some species, simple habitats can be the safest (e.g. Hammerschlag, *et al.,* 2015; Schmidt, and Kuijper, 2015; Atuo and O'Connell, 2017). Landscape of fear effects will also be more pronounced in systems where interactions between predators and prey are less frequent (Schmitz, 2008), as is evident in findings from Pavlovian fear conditioning, and the '*risk allocation hypothesis*' – which states that animals exposed to constant high predation risk will increase their foraging risks over time (Lima and

Bednekoff, 1999; Van Buskirk *et al.,* 2002). Fear arousal in a landscape of fear results in two predictable outcomes: either avoidance of high risk areas, or modulation of behaviour (e.g. increased vigilance) to reduce predation risk when foraging in such areas (Gaynor *et al.,* 2019). These outcomes indicate the importance of considering fear arousal and stress levels in ecological management, and the direct and indirect cues that may trigger these effects (Atkins *et al.*, 2017).

Fear arousal can be triggered both directly from a predator and indirectly via a predator cue, such as an associated scent. Olfaction is believed to be a key driver of fear arousal (Soso *et al.*, 2014; Banks *et al.*, 2016; Jones *et al.*, 2016; Parsons *et al.*, 2017). ~~The mechanics of this are best understood in mammals, where odours are assessed for threat by the accessory olfactory bulb that transmits information directly to the amygdala and hypothalamus, where fight or flight responses are developed~~ (Fogaca *et al.*, 2012; Canteras, Pavesi, and Carobrez, 2015). Laboratory studies exploring the effects of post-traumatic stress disorder exposed animals to predators or their cues in order to induce stress, and in doing so revealed that exposure to predator cues alone can affect the neural circuitry associated with fear (Rosen and Sculkin, 1998, 2004).

Subtle cues such as predator odours may precede threats and allow for a prey animal's fear state to be conditioned to a cue that occurs before, or in correlation with, a previously encountered predation threat (Rescorla and Solomon, 1967; Rosen, 2004). Predation risk may, therefore, be perceived by prey species eavesdropping on predator scent marks, such as urine, faeces, or fur left in the environment (Banks and Bytheway, 2016; Jones *et al.*, 2016). Such odours have been observed experimentally to induce fear-like responses of freezing (Wallace and Rosen, 2000), vigilance (Nersesian, Banks, and McArthur, 2012), fleeing (Anson and Dickman, 2013), and avoidance (Hayes, Nahrung, and Wilson, 2006), across a wide range of species in both field and laboratory experiments (Apfelbach *et al.*, 2005, 2015). Consequently, landscape of fear topography, where predators indirectly influence prey behaviour across a range of microhabitats, can arise from the influence of predator olfactory cues on prey foraging behaviour as much as it can from the direct threat of predation (e.g. Persons and Rypstra, 2001; Brown and Kotler, 2004; Parsons and Blumstein, 2010; Cremona *et al.*, 2014; Mella *et al.*, 2014; Hoffman *et al.*, 2016). Fear arousal to predator presence or cues alike can deplete a prey individual's energy budget, resulting in poor reproduction and health either via energy exhaustion from stress (i.e. the predation stress hypothesis: Boonstra *et al.,* 1998; Clinchy *et al.,* 2004; Romero, 2004; Støen *et al.*, 2015), or reduced nutrition from foraging compromises (i.e. the predator-sensitive food hypothesis: Sinclair and Arcese, 1995; Brown and Kotler, 2004; Clinchy *et al.*, 2016). Mitigating the trigger of fear arousal, where possible, through mapping landscapes of fear (e.g. van der Merwe and Brown, 2008; Kauffman *et al.*, 2010; Iribarren and Kotler, 2012) to identify, protect and extend safe foraging areas, could assist in the conservation of wildlife subject to multiple stressors, such as human activity and predators.

Human activity as a fear inducing stressor

Fear and acute/chronic stress may be constant hurdles faced by wildlife, but adding the effects of anthropogenic activities could result in the elevation of numerous acute stress responses to widespread chronic stress, and upscale the possible impacts from individuals to populations (Rehnus, Wehrle, and Palme, 2014). There is ample evidence that human activity alone can both indirectly and directly create landscapes of fear and influence existing landscapes of fear through interactive effects. Interactive effects are context dependent (Belarde and Railsback, 2016). They can be additive and combine the multiple impacts, synergistic whereby the presence of one threat amplifies another (Doherty *et al.*, 2015), or antagonistic whereby one threat cancels the effects of the other; reduced activity of mesopredators in the presence of humans provides an example of antagonism (Clinchy *et al.*, 2016). Additive, synergistic, and antagonistic reactions have each been observed in prey in natural systems in response to exposure to multiple stressors (Crain *et al.*, 2008; Côté *et al.*, 2016; Gunderson *et al.*, 2016; Jackson *et al.,* 2016; Geary *et al.*, 2019; Legge *et al.,* 2019). Thus, predator presence and human activity can interact to alter ecosystem structure and / or increase or decrease the predation risk perceived by prey species.

It has been postulated that humans may impose widespread effects on ecosystem function, as they induce greater fear responses in ubiquitous small predators than top-predators do (Clinchy *et al.*, 2016). In general, human activity can be comparable to the impacts of predation (Hofer and East, 1998; Frid and Dill, 2002; Rehnus, Wehrle, and Palme, 2014; Patten and Burger, 2018), and perhaps even stronger where foraging regimes are disrupted dramatically more than when influenced by natural stressors (Ciuti *et al.*, 2012; Clinchy *et al.*, 2016), or where top down cascading effects occur in response to humans acting as “super predators” disproportionately killing carnivores (Darimont *et al.*, 2015). Trophic cascade effects can also occur when predators avoid human activity, and prey seek refuge behind a “human shield” (Kuijper *et al.*, 2015; Leighton, Horrocks and Kramer, 2010). Conversely, provision of food subsidies, in areas of human activity, can increase predator activity and alter their foraging regimes (Iossa *et al.*, 2010; Bateman and Fleming, 2012; Fischer *et al.,* 2012; Newsome *et al.*, 2014, 2015). The negative effects of human activity can therefore differ between different species groups within trophic systems, as the effects of such disturbance on one species may result in positive consequences for its prey or competing species (e.g. Gill, Sutherland and Watkinson, 1996; Crooks and Soulé, 1999; Leighton, Horrocks and Kramer, 2010). These effects, however, are strongly dependent on the availability of the required resources within the human occupied / disturbed areas, and may be unique in each system.

A common response to increased exposure to human activity is a temporal shift in activity patterns, from diurnal to crepuscular or nocturnal to avoid interaction with humans (McClennen *et al.,* 2001; Tigas *et al.*, 2002; Riley *et al.*, 2003; Ditchkoff, Saalfeld, and Gibson, 2006); the same or reverse may occur too, to reduce predator interactions (Brown, 2000; Laundré *et al.*, 2001). Such temporal shifts can have dire effects if they limit the forager's ability to locate and capture prey (Ditchkoff, Saalfeld, and Gibson, 2006). Regardless of the response, it is evident that human activity has profound indirect effects on community interactions through altering individual behaviour, particularly those contiguous to foraging, through either fear arousal or a stress response (e.g. Frid and Dill, 2002; Werner and Peacor, 2003).

Human activity can influence predator distributions in various ways (e.g. Albert and Bowyer, 1991; Bowyer et al., 1999), depending on the type of activity. For example, high levels of disturbance or active interference can completely displace predators (Kloppers, St Clair, and Hurd, 2005; Berger, 2007). In contrast resource subsidies for shelter, water and food with year-round primary production, can outweigh the stress of human disturbance and influence community behaviours (Parris, 2016), resulting in urban colonisation by wildlife (Shochat *et al.*, 2010; Jokimäki, *et al.,* 2011).

Synurbanisation, that is the adaptation of wildlife to urban environments, can occur through behavioural shifts in foraging, food preferences, predator avoidance, and in reproductive shifts that alter the timing of breeding (Ditchkoff *et al.*, 2006; Møller, 2009; Shochat *et al.*, 2010; Rodriguez *et al.*, 2010; Otto, 2018; Santini *et al.*, 2019). Human activity, can therefore, impose a form of natural selection on behaviour and endocrine traits (Bonier, 2012; Snell-Rood and Wick, 2013), and may select for bold individuals with reduced stress responses to human activity (Atwell *et al.*, 2012) that habituate over time (Sih, 2013).

As the human population continues to grow, pressures on ecosystems from human activity are likely to increase in reach and intensity (Tilman *et al.*, 2017). Ecosystem functioning will be influenced both directly and indirectly by human activities; namely: disturbance from human presence (Fernandez-Juricic and Telleria, 2000), displacement and habitat loss (Fahrig, 2003), introduced chemicals and pollutants, (Schwarzenbach *et al.*, 2006), reverse zoonotic disease transmission (Messenger *et al.,* 2014), increased input of nutrients (Hobbie *et al.,* 2017), food resource subsidies (Newsome *et al.*, 2014, 2015), introduced light and sound (Navara and Nelson, 2007; Shannon *et al.*, 2016), traffic (Blumstein *et al.*, 2005; Jayakody *et al.*, 2008; Stankowich, 2008; Scott, Hume & Dickman, 1999), introduction and continued spread of introduced species including cattle and domestic pets (Scott, Hume & Dickman, 1999; Schlaepfer *et al.,* 2005; Morgan, 2009; Bino *et al.*, 2010; Butchart *et al.*, 2010: Young *et al.*, 2011; Doherty *et al.,* 2015, 2016, 2017), overexploitation (Pirotta and Lusseau, 2015; Verma, 2016), and climate change effects (Rastandeh, Zari, and Brown, 2018). These stressors often co-occur and have interactive effects (Côté *et al.*, 2016; Gunderson *et al.*, 2016; Jackson *et al.*, 2016) that erode biodiversity (Butchart *et al.,* 2010). The combination of stress resulting from the combined pressures of human activities and introduced predators is yet to be investigated. Understanding the effects that both may impose is critical for effective conservation of wildlife in an increasingly human-influenced world.

Fear and stressing in small mammal ecology in Australia; the need to consider the twin stressors of introduced predators and people in biodiversity management

Small mammals are presumed to be somewhat resilient to threatening processes owing to their high population growth rates (Cardillo *et al.*, 2005, 2006). However, in Australia small mammals are declining quickly and due to causes dissimilar to those driving global declines (Woinarski *et al.* 2015). These declines have been attributed to a wide range of habitat stressors: habitat loss; altered fire regimes; disease; increasing temperatures; decreasing water availability; depleted soil quality, and salinity (Woinarski *et al.*, 2015). However, mammals within a 'critical weight range' (CWR) of 35 to 5550 g are particularly vulnerable (Chisholm and Taylor, 2007; Woinarski *et al.*, 2015) owing to the effects of predation by two introduced carnivores, the red fox (*Vulpes vulpes*) and domestic house cat (*Felis catus*) that arrived in Australia some 150+ years ago (Johnson, 2006). Although CWR mammals are of high conservation concern, predation from introduced predators poses a threat also to all native predators by reducing their food resources, which in turn may increase predation and predation-associated stress on alternative food sources such as smaller (< 35 g) or larger (> 5550 g) mammal species. For example, a study examining the diet of a nocturnal, avian predator, the sooty owl (*Tyto tenebricosa*) before and after red fox introduction, revealed a dietary shift post introduction, with owls consuming more arboreal than terrestrial prey species after fox arrival. This shift to consuming arboreal prey has increased dietary overlap with the sympatric powerful owl (*Ninox strenua*), providing disproportionate predation pressure on prey in the ecosystems of East Gippsland, Victoria (Bilney, Cooke, and White, 2006).

Predation by red foxes and cats is prevalent not only in natural habitats but also in agricultural and urban habitats (Dickman, 1996; Morgan, 2009; Bino, 2010). The paths and roads that typically fragment urban and agricultural habitats are used frequently by these predators, which exacerbates their predation pressure on prey species by combining with impacts imposed by human activities (Latham *et al.*, 2011, Červinka *et al.*, 2013). Consequently, this can result in increased abundances of red foxes and cats in human modified landscapes that border or include natural habitats (Towerton *et al.*, 2011; Graham *et al.*, 2012). Urban and agricultural habitats present many threats to wildlife, but they may also offer food and shelter opportunities (Pickett *et al.,* 2001; Gaston *et al.,* 2005; Hobs, Higgs and Harris, 2009). As reported by Ives *et al.* (2016), 46 percent of threatened Australian animals occur in or near Australian cities. Thus, the fate of many species could depend on management that accommodates their needs in urban and agricultural habitats (Ives *et al.*, 2016). A recent assessment of data collected at the Wildlife Rehabilitation Centre in Queensland Zoo, Australia, revealed that pet cat or dog attack, car strike, and entanglement in human-placed objects represented 56.4% of the causes of submission of injured wildlife; mortality rates associated with these traumas were also high, with 61.3% of admitted animals dying from their injuries (Taylor-Brown *et al.*, 2019). These threats may contribute to landscapes of fear, through fear arousal, altered foraging behaviour, post-traumatic stress reactions, and cumulative stress exposures resulting in chronic stress responses.

Despite growing knowledge of anthropogenic impacts on threatened species, Australian conservation planning continues to exclude urban and agricultural habitats from consideration (Dales, 2011). There is recognition of the scope of this issue in Australia (e.g. Hill *et al.*, 2007; Carthey and Banks, 2012; Threlfall *et al.*, 2012; McCauley *et al.*, 2013; Banks and Smith, 2015; Ives *et al.*, 2016), but few studies have explored the interactive effects of introduced predators and human activity on the survival of prey species. Despite the development of glucocorticoid analysis techniques to determine stress in animals dating back to the 1960s (Jones *et al.*, 1964), only six of the 60 extant small mammals of conservation concern in Australia have been subject to studies seeking to better understand their glucocorticoid response to stressors, such as predation by introduced species or human activity (Hing *et al.*, 2014). Conservation management that considers stress from the combined impacts of introduced predators, human activity, and those that naturally occur in ecosystems, is a logical and progressive response towards preserving many species of Australian small mammals.

Alleviating fear and stress for conservation

As we have illustrated, fear can produce stress and simultaneous multiple stressors can have chronic effects that impact populations. Introduced stressors, such as human activity/disturbance (Patten and Burger, 2018) and introduced predators (Woinarski *et al.*, 2015) can have cumulative impacts, either with each other or with stressors that occur naturally in ecosystems (Allan *et al.*, 2013), as outlined in Figure 1. Such cumulative stress impacts can result in homeostatic overload, or failure (as defined by Romero, Dickens, and Cyr, 2009), that may result in population collapses. If prey species face multiple interacting stressors, they may take greater foraging risks, or be less able to allocate energy to vigilance or fleeing behaviours, and thus become more susceptible to predation or additional stressors. In the case of population-impacting stressors, the local population may be impacted to a high degree such that it becomes threatened (e.g. Sweitzer, 1996; Doherty *et al.*, 2015). As such, conservation action in areas where simultaneous introduced stressors occur in addition to natural ecosystem pressures, like in urban and peri-urban habitats, is urgently needed. The most direct way to alleviate stress in wildlife is to remove or reduce the stressors that can be controlled for, especially those imposed by human presence and disturbance. However, as the needs of the expanding human population often usurp those of wildlife, this is rarely, if ever, possible. Similarly, there are difficulties with the control of numbers of introduced predators, which is usually problematic, costly and ineffective (Glen and Dickman, 2005; Rayner *et al.,* 2007; Bergstrom *et al.,* 2009; Norton, 2009; Warburton and Norton, 2009; Carroll, 2011; Newsome *et al.*, 2017). Alternative solutions that offer some reprieve from fear and stress for wildlife therefore need to be considered. Managing vegetation structure, density and heterogeneity may well be such a solution, as it increases refuge potential and facilitates resource partitioning. In order to mitigate introduced fear and stress effects, it is important that future studies investigate whether the management of vegetation complexity can alleviate some of the pressures associated with multiple introduced stressors for target species.

Managing habitat to alleviate fear and stress

The impact of predators (or human activity) may be mitigated by changing the configuration of risky areas in a habitat (Hopcraft, Sinclair, and Packer, 2005; Lone *et al.*, 2014). Food availability is often a dominant factor in habitat selection by species (e.g. Sherman, 1984; Johnson and Sherry, 2001), but predation risk, and similarly impactful human activity, affects a suite of correlated factors such as movement decisions (Turcotte and Desrochers, 2003), foraging patterns (Gil *et al.*, 2017), social organisation (Rodríguez *et al.*, 2001), and reproductive success (Zanette *et al.*, 2011). Prey population survivorship, in the face of predation stressors, is often positively correlated with increased structural complexity of a habitat (Hopcraft, Sinclair, and Packer, 2005; Lone *et al.*, 2014; Leahy *et al.*, 2016). This has been demonstrated in many studies to be a consequence of the increased opportunities for prey to escape and hide, thereby mediating the predator-prey dynamics by reducing encounter rates, as only a proportion of the total prey population remains available to predators (e.g. Holt, 1984; Kotler and Brown, 1988; Taylor and Pekins, 1991; Bowers and Matter, 1997; McIntyre, and Wiens, 1999; Garb, Kotler, and Brown, 2000; Bartholomew, 2002; Creel *et al.*, 2005; Hernández and Laundré, 2005; Warfe and

Barmuta, 2006; Rilov, Figueira, Lyman, and Crowder, 2007; Bianchi, Schellhorn, and Van Der Werf, 2009; Rieucau *et al.*, 2009 Valinoti, Ho, and Armitage, 2011; Klecka and Boukal, 2014; ; Laundré *et al.*, 2014; Grutters, Pollux, Verberk, and Bakker, 2015).

The extensive research surrounding the benefits to prey of habitat structural complexity has been built on the '*habitat heterogeneity hypothesis,'* which postulates that structurally complex habitats can support increased species diversity by offering a wide range of niches and diverse ways of exploiting resources (Bazzaz, 1975). Habitat complexity, by extension, has been generalized to be a primary driver of biodiversity (Pianka, 2011). The landscape of fear theorem accepts this principle too, in that a wide range of microhabitat types offers multiple foraging conditions with varied predation risks for species. For example, northern quolls (*Dasyurus hallucatus*) of the semi-arid Pilbara region in Western Australia utilise complex rocky habitats in preference to open grasslands where the threat of predation from feral cats is greater (Hernandez-Santin, Goldizen and Fisher, 2016).

Animals in habitats with high predation pressures may display foraging preferences for microhabitats or times that they perceive to be safe (Brown, 2000; Laundré *et al.*, 2001). Some small mammals seek structurally complex vegetation owing to the reduced risk of predation and increased reward of foraging they find there (Lima and Dill, 1990; Andruskiw *et al.*, 2008). Others, such as the Australian hopping mouse *Notomys alexis*, have the ability to exhibit bursts of speed in open habitat, and due to their biomechanics are not so adept at moving through complex vegetation (Spencer *et al.*, 2014). No matter the species, in landscape of fear habitats a prey species' use of the topography, refuges, and escape substrates can indicate animals' perceived risk of predation (Brown and Kotler, 2004; van der Merwe and Brown, 2008; Shrader *et al.*, 2008), and the associated fear and stress that may arise or be alleviated due to habitat structure. The same principle may be relevant to reducing stress in proximity to human activity, considering that prey responses to human activity and predators are similar.

Human activity and disturbance can quickly accelerate the reduction of habitat complexity (Western, 2001). However, enhancing habitat complexity and heterogeneity is increasingly being incorporated into restoration and management efforts, with some success (Brown, 2003; Bernhardt and Palmer, 2007; Palmer *et al.*, 2010), and is likely to be of particular importance in such management in the future. In order to balance the needs of people and biodiversity, local planning procedures are increasingly incorporating green spaces and urban greening initiatives into urban areas. As habitat complexity and diversity are of particular importance in supporting biodiversity and population sustainability, it is important that this has some weight in the ecological engineering of wildlife habitats in urban and urban-adjacent habitats (Threlfall *et al.*, 2016). The effectiveness of any management regime depends on recognising the direct and indirect flow-on impacts that occur across balanced ecosystems. Consequently, habitat complexity as a management objective requires that each landscape is approached as an independent case that requires a full ecosystem assessment before the habitat is ecologically engineered (Tews *et al*., 2004).

Management tools to observe and alleviate fear and stress for conservation

Speculative cumulative stress analyses that map human activity and stressors that occur naturally in ecosystems have maximized returns on restoration investments by efficiently indicating areas in need of intervention to prevent them from becoming high stress areas for wildlife (Allan *et al.*, 2013). Several methods are now available to measure stress in wildlife, many of which are also cost efficient and accessible. These include techniques developed in conservation physiology to assess faecal/urine/fur/feather glucocorticoid metabolites (see Cook, 2012; Cooke *et al.*, 2013; Sheriff *et al.*, 2011; Palme, 2019), infrared motion sensor cameras that film giving-up density (Brown, 1988) trials to monitor landscape of fear effects (e.g. Leo *et al.,* 2015), and habitat quality assessments that spatially correlate mapping resources (e.g. Willems and Hill, 2009). Assaying faecal glucocorticoid metabolites from fresh faecal samples collected opportunistically across habitat gradients of high human activity to connected protected areas, allows insight into the stress impacts from human activity based on the relative stress and sex hormone levels compared across the gradient (Rehnus, Wehrle, and Palme, 2014). This method could be applied similarly to comparing the effects on prey of living in areas of high and low predator activity. Such methods undoubtedly allow for better-informed conservation decisions to be made by mapping pathways of fear and stress, where/when they may be cumulative, and where conservation managers should intervene to effectively preserve populations.

Cumulative Effects Assessments (CEA) were developed in the 1990's amid growing concerns that Environmental Impact Assessments (EIA) did not consider all the effects of urban and peri-urban construction developments (Smit and Spaling, 1995). Numerous countries have since mandated that CEA be incorporated into all EIAs (Therivel and Ross, 2007). Despite the legal requirement and the concept of CEA being widely defined in scientific literature, it is rarely applied in practice (Ma *et al.*, 2009; Foley *et al.*, 2017). However, CEA has the potential to be a powerful tool to mitigate cumulative impacts, including human-imposed stressors, on wildlife if the results are adopted by on-ground practitioners (Duinker *et al.*, 2013).

We propose that the principles of the '*reactive scope model*' may be used to develop CEAs that consider where cumulative stressors occur, and thus better inform conservation management initiatives in areas where wildlife is subject to homeostasis overload or failure (Figure 2). The reactive scope model (Romero, Dickens, and Cyr, 2009) provides a useful insight into the range of physiological mediators available in response to a stressor. It maps the homeostasis range of a given species to four stages: 1) predictive – changes in response to routine environmental changes, such as seasons or day to night; 2) reactive – a change in response to an unpredictable change, to allow survival via classic stress responses; 3) overload – consistent changes in response to a stressor, chronic stress impacts start to occur; and 4) failure – inability to sustain homeostasis, very susceptible to additional stressors and death (Romero, Dickens, and Cyr, 2009). If our proposed CEA, based on the reactive scope model, were to be applied to the cumulative stressors problem for small mammals in urban, urban adjacent, and peri-urban ecosystems in Australia, for example, then areas of conservation concern could be identified where the additive or synergistic impacts of human disturbance and introduced predators combine with stressors that occur naturally. Appropriate management could then be implemented to alleviate these stressors.

Conclusion

Considering ongoing global urbanization and the acknowledged importance of urban areas to biodiversity conservation there is need for increased focus on the management of urban biodiversity. Management decisions require information about fear and stress impacts on wildlife, including impacts from both human activities and predators, especially if they are introduced. An understanding of the impacts of human activities is a research priority for modern science (Schindler 2001; Fleishman *et al*., 2011). There are many gaps in our current understanding of the associated fear and stress impacts, and of associated impacts of predation pressures and the persistence of target populations. For the future sustainability of biodiversity in urban and urban-adjacent green space habitats and reserves, it is vital that we establish a better understanding and management of the multiple stressors that operate in these systems.

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Figure 1

A Venn diagram showing two main categories of stressor.

On the left are stressors that occur naturally in ecosystems, such as native predators, social and breeding interactions, availability of refuge and burrow/den microhabitats, availability of food and water, and disease / parasite prevalence. On the right are introduced stressors, primarily those arising from anthropogenic disturbances and introduced predators. Where both categories of stressor occur together, as in many urban environments, cumulative stress impacts can result in homeostatic overload or failure (as defined by Romero, Dickens, and Cyr, 2009). In these situations populations may be at particular risk of collapse and conservation action will be most urgent.

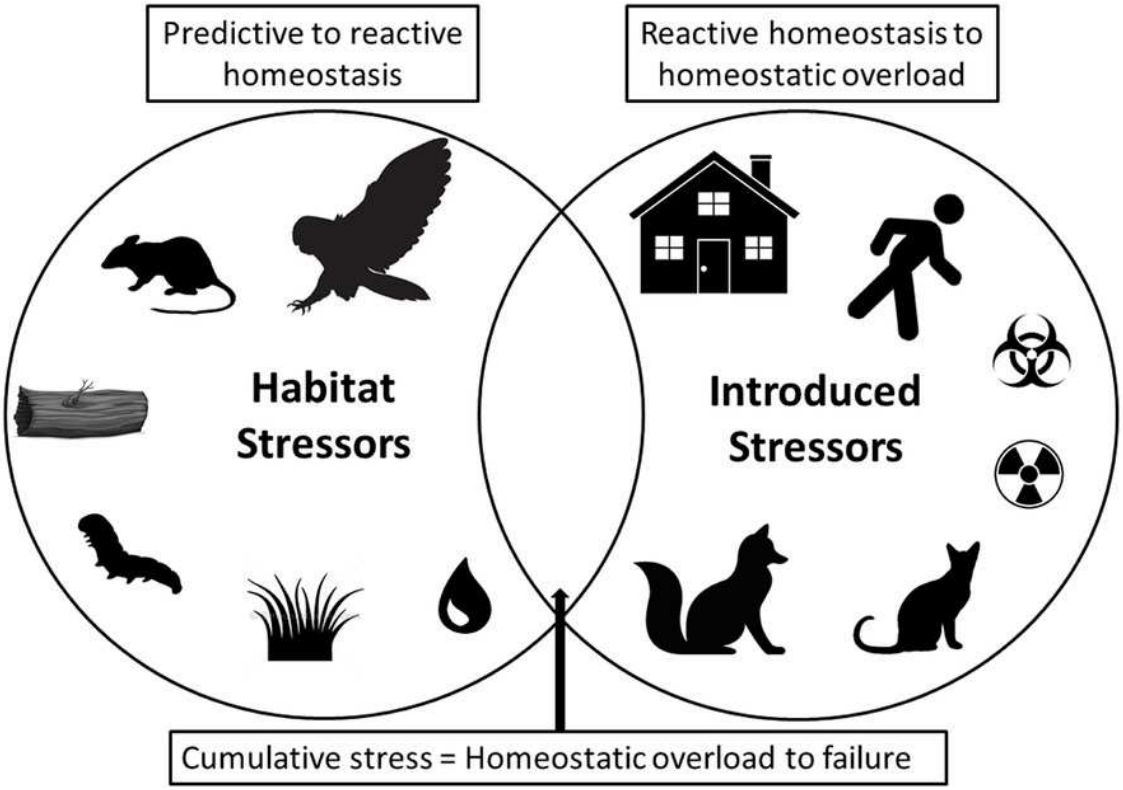
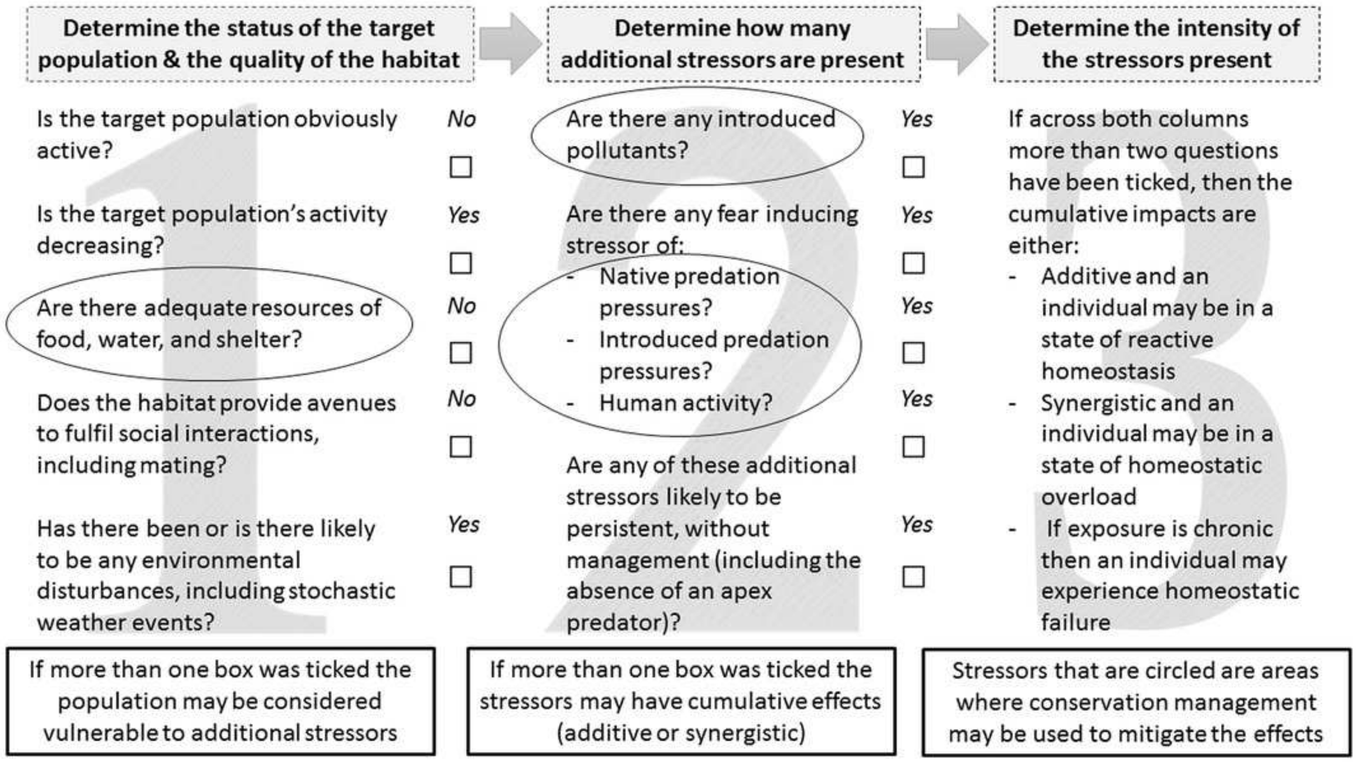


Figure 2

A conservation management approach that outlines the key steps for assessing if cumulative stress impacts are occurring between stressors that occur naturally in ecosystems and introduced stressors.

The circled areas indicate where conservation management initiatives may be used to mitigate these effects through management of vegetation complexity or supplementation materials such as water stations or nest boxes.



Determine the status of the target population & the quality of the habitat

Is the target population obviously active? *No* ☐

Is the target population's activity decreasing? *Yes* ☐

Are there adequate resources of food, water, and shelter? *No* ☐

Does the habitat provide avenues to fulfil social interactions, including mating? *No* ☐

Has there been or is there likely to be any environmental disturbances, including stochastic weather events? *Yes* ☐

If more than one box was ticked the population may be considered vulnerable to additional stressors

Determine how many additional stressors are present

Are there any introduced pollutants? *Yes* ☐

Are there any fear inducing stressor of: *Yes* ☐
- Native predation pressures? *Yes* ☐
- Introduced predation pressures? *Yes* ☐
- Human activity?

Are any of these additional stressors likely to be persistent, without management (including the absence of an apex predator)? *Yes* ☐

If more than one box was ticked the stressors may have cumulative effects (additive or synergistic)

Determine the intensity of the stressors present

If across both columns more than two questions have been ticked, then the cumulative impacts are either:
- Additive and an individual may be in a state of reactive homeostasis
- Synergistic and an individual may be in a state of homeostatic overload
- If exposure is chronic then an individual may experience homeostatic failure

Stressors that are circled are areas where conservation management may be used to mitigate the effects