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

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Predators induce stress in prey and can have beneficial effects in ecosystems, but can also have negative effects on biodiversity if they are overabundant or have been introduced. The growth of human populations is, at the same time, causing degradation of natural habitats and increasing interaction rates of humans with wildlife, such that conservation management routinely considers the effects of human disturbance as tantamount to or surpassing those of predators. The need to simultaneously manage both of these threats is particularly acute in urban areas that are, increasingly, being recognized as global hotspots of wildlife activity. Pressures from altered predator-prey interactions and human activity may each 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, except in intensive *ex situ* situations such as in captive breeding facilities or zoos. We propose that mitigation of stress impacts on wildlife is crucial for preserving biodiversity, especially as the value of habitats within urban areas increases. As such, we highlight the need for future studies to consider fear and stress in predator-prey ecology to preserve both biodiversity and ecosystem functioning, especially in areas where human disturbance occurs. We suggest, in particular, that non-invasive *in situ* investigations of endocrinology and ethology be partnered in conservation planning with surveys of habitat resources to incorporate and reduce the effects of fear and stress on wildlife.

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23   **Abstract**

24   Predators induce stress in prey and can have beneficial effects in ecosystems, but can also have

25   negative effects on biodiversity if they are overabundant or have been introduced. The growth of

26   human populations is, at the same time, causing degradation of natural habitats and increasing

27   interaction rates of humans with wildlife, such that conservation management routinely considers

28   the effects of human disturbance as tantamount to or surpassing those of predators. The need to

29   simultaneously manage both of these threats is particularly acute in urban areas that are,

30   increasingly, being recognized as global hotspots of wildlife activity. Pressures from altered

31   predator-prey interactions and human activity may each initiate fear responses in prey species

32   above those that are triggered by natural stressors in ecosystems. If fear responses are

33   experienced by prey at elevated levels, on top of responses to multiple environmental stressors,

34   chronic stress impacts may occur. Despite common knowledge of the negative effects of stress,

35   however, it is rare that stress management is considered in conservation, except in intensive *ex*

36   *situ* situations such as in captive breeding facilities or zoos. We propose that mitigation of stress

37   impacts on wildlife is crucial for preserving biodiversity, especially as the value of habitats

38   within urban areas increases. As such, we highlight the need for future studies to consider fear

39   and stress in predator-prey ecology to preserve both biodiversity and ecosystem functioning,

40   especially in areas where human disturbance occurs. We suggest, in particular, that non-invasive

41   *in situ* investigations of endocrinology and ethology be partnered in conservation planning with

42   surveys of habitat resources to incorporate and reduce the effects of fear and stress on wildlife.

44   **Introduction**

45   Predators in many systems positively influence the local distribution and abundance of their prey

46   (e.g. Polis *et al.*, 1998; Ayal, 2007; Estes *et al.*, 2011; Weissburg, Smee & Ferner, 2014), and

47   indirectly but positively influence the functioning of whole ecosystems via trophic cascades

48   (Prugh *et al.*, 2009; Ritchie & Johnson, 2009; Estes *et al.*, 2011; Ripple *et al.*, 2014). Predators

49   often elicit fear responses in prey that affect prey behaviour, energy budgets and the way they

50   interact with the environment (Brown & Kotler, 2004; Clinchy *et al.,* 2004; Romero, 2004). For

51   example, the fear response of an individual of a prey species to a predator may be to change the

52   locations or times in which they forage, which can have positive impacts on the structure of the

53   environment (Laundré, Hernández & Ripple, 2010). Such fear responses can in turn influence

54   ecosystem function (Schmitz, Krivan & Ovadia, 2004, Schmitz *et al.* 1997, Hawlena *et al.*,

55   2012). These effects arise due to the '*landscape of fear*' that prey individuals perceive – that is,

56   the spatial distribution of perceived predation risk that influences prey movement and behaviour

57   as prey individuals attempt to mitigate risk and obtain essential resources (Laundré, Hernández

58   & Altendorf, 2001; Laundré, Hernández & Ripple, 2010).

59   Recent studies suggest that the effects of predators are being altered, and often amplified,

60   by human activities. For example, the demise of top predators in many parts of the world has

61   'released' populations of smaller predators, or mesopredators that have since become

62   overabundant and now exert strong pressure on smaller species (Prugh *et al.,* 2009). Predators

63   that have been introduced to new areas also exert much stronger pressure on prey populations

64   than do native predators (Salo *et al*., 2007). Climate change and associated shifts in primary

65   productivity can also have bottom-up impacts on predator-prey interactions (Laws, 2017). Such

66   novel alterations to predator-prey dynamics can depress prey populations and disrupt community

67   structure, and as such require novel approaches to recognize and manage their effects (Carthey &

68   Blumstein, 2018; Fleming & Bateman, 2018; Guiden *et al.*, 2019).

69   Altered predator-prey interactions may contribute to declines in biodiversity, but a

70   primary cause of biodiversity loss is the rapid global increase in human populations, driving

71   agricultural, industrial, and urban expansions that change or destroy natural habitats (Madsen *et*

72   *al.*, 2010). Such expansions are resulting in novel human – wildlife interactions and secondary

73   impacts that arise from human activities in close proximity to natural environments, and thus

74   increasingly are becoming an additional stressor that influences ecosystem function. Pressures

75   exerted both directly and indirectly by human activities have been likened to the pressures

76   exerted by the presence of a top predator on prey (e.g. Frid & Dill, 2002; Rehnus, Wehrle &

77   Palme, 2014; Patten & Burger, 2018). Natural predation pressures coupled with human-imposed

78   predation-like pressures and / or additional exogenous stressors, such as pollution, arising from

79   anthropogenic activities are likely to negatively affect prey species by increasing their levels or

80   frequency of stress. Current research is developing a more nuanced understanding of the effects

81   of human activity and predator presence on the stress of prey (e.g. Arlettaz *et al.,* 2015; Jaatinen,

82   Seltmann & Öst, 2014, respectively). However, few studies in terrestrial ecosystems have

83   considered both of these pressures simultaneously or have linked behavioural responses with

84   endocrinological evidence of stress. In one instructive recent study, human activity was shown to

85   be positively correlated with physiological stress in ungulates, whilst in areas occupied by large

86   predators stress was found to be lower and less variable (Zbyryt *et al.*, 2017).

87   Conservation management and associated scientific research is often viewed from the

88   perspective of a single discipline. However, ecological changes arising from anthropogenic

89   disturbances, including the alteration of predator-prey encounter rates, creation of novel species

90   interactions (including between people and wildlife), introduction of novel species, and the

91   alteration of natural habitats, call for multidisciplinary solutions. This is particularly pertinent as

92   urban edge habitats are becoming increasingly valuable global hotspots of wildlife activity (Ives

93   *et al.*, 2016), and human influences are spreading further into natural habitats (Otto, 2018). There

94   is growing evidence that multiple introduced stressors (e.g. altered predator-prey interactions and

95   disturbance from humans) can have compounding impacts on wildlife, especially when

96   interacting with natural stressors in ecosystems (Geary *et al*., 2019). For these reasons, it is

97   timely to review relevant information from the broad knowledge bases of conservation

98   physiology, ethology, and ecology to communicate the urgent need for wildlife managers and

99   urban planners to routinely consider how fear and stress effects from multiple sources,

100   particularly novel predator interactions and human activities, can affect prey species and

101   ecosystem functioning in increasingly altered systems. Our focus in this review is on mammals

102   because of the wealth of information on this group, but we note relevant studies from other

103   groups where appropriate. We begin our review by describing physiological responses of

104   mammals to fear and stress, then we consider the behavioural responses of mammals to these

105   factors, and argue that human activity should be considered as part of the ecosystem so that

106   overall stress impacts can be managed accordingly. We then demonstrate how fear and stress can

107   influence habitat use, how vegetation and microhabitat management potentially may be used to

108   alleviate stress, and how to monitor for fear and stress to then create management change.

109   Finally, we use Australia as an example to show the benefits of considering cumulative fear and

110   stress impacts to mitigate the effects of introduced eutherian predators, increased human activity,

111   and the possible interactive effects of the two.

112

113 **Review method**

114 This is not a systematic review, but rather a novel synthesis of existing knowledge. It seeks to

115 extend ideas on the physiological impacts of fear and stress, behavioural ecology, predator-prey

116 dynamics, and conservation management to explore the influence of humans and altered

117 predator-prey interactions in the urban environment. To ensure that all key topic areas were

118 thoroughly covered we conducted literature searches via: Google Scholar©, Web of Science©,

119 JSTOR©, and Wiley Interscience Online Library©. Manuscripts were mined for information

120 relevant to wildlife fear and stress in terms of ecological management under anthropogenic

121 pressures, including introduced predators and altered predator-prey interactions. The literature

122 searches were undertaken using the following key terms as part of their title, keywords, and / or

123 within the abstract: "acute stress", "chronic stress", "homeostasis", "cumulative stress",

124 "multiple stressors", "multiple threats", "allostatic load", "allostatic overload", "acclimitisation",

125 "glucocorticoid response", "hypothalamic pituitary adrenal axis", "fear arousal", "fear

126 evolution", "fear predation", "amygdala" "fear", "Pavlovian fear conditioning", "glucocorticoid

127 assay", "f(a)ecal glucocorticoid", "non-invasive glucocorticoid assay", "reactive scope model",

128 "landscape(s) of fear", "risk allocation hypothesis", "olfaction" + "fear" + "mammal", "post-

129 traumatic stress disorder", "predator" + "odo(u)r" + "fear", "predator cue(s)", "predation stress

130 hypothesis", "predator-sensitive food hypothesis", "human activity" + "stress" + "wildlife",

131 "human disturbance", "interactive stress", "multiple stress(ors)", "additive stress impacts",

132 "synergistic stress impacts", "antagonistic stress impacts", "human" + "wildlife" + "resource

133 subsidies", "predator trophic cascade", "wildlife urban adaptation", "urban ecology" +

134 "wildlife", "Australian mammal extinction", "critical weight range mammal", "diet" + "change"

135 + "Australian" + "predator", "red fox" + "Australia", "domestic cat" + "Australia", "human

136 activity" + "wildlife" + "Australia", "Australia" + "biodiversity" + "conservation policy" +

137 "urban hotspot", "Australian environment protection and biodiversity conservation act" +

138 "cumulative stress", "Australia" + "conservation" + "glucocorticoids", "introduced predator

139 control", "habitat structural complexity", "habitat structural diversity", "vegetation diversity",

140 "vegetation heterogeneity", "habitat heterogeneity hypothesis", "cumulative effects

141 assessments". Supplementary articles supporting the review narrative, suggested by reviewers on

142 earlier versions of the manuscript, have also been included.

143

144 **Mammalian physiological responses to fear and stress**

145 Physiological stress can be broadly defined as a change in the physiological well-being of an

146 individual following exposure to an aversive extrinsic stimulus - frequently referred to as a

147 stressor (Seyle, 1936). The physiological stress response that follows aims to restore internal

148 homeostasis (Cannon, 1932). An individual animal experiences stress in response to conditions

149 that threaten its survival or compromise its ability to maintain homeostasis. Examples include

150 acute or chronic encounters with predators, inclement weather, significant natural disturbances

151 including fire and flood, reduced oxygen availability, and depleted food resources (Lima, 1998;

152 King & Bradshaw, 2010; Malcolm *et al.*, 2014; Santos *et al.*, 2014; Crocker, Khudyakov &

153 Champagne, 2016).

154 In mammals, activation of the hypothalamic-pituitary-adrenal (HPA) axis is a common

155 stress response, but this may vary depending on the nature of the stressor (Mason, 1971); it is

156 important to consider this when assessing stress impacts. Changes in abiotic conditions, such as

157 in food availability, or the introduction of toxins or diseases can be stressful, but such changes do

158   not arouse fear. However, a stress response involving peripheral autonomic and neuroendocrine

159   changes (Yates, Russell & Maran, 1971; Sapolsky, Romero & Munck, 2000; McEwen &

160   Wingfield, 2003), can be initiated by fear arousal (LeDoux, 2003; LaBar & LeDoux, 2011).

161   Animals with sophisticated nervous systems, such as mammals, exhibit a central motive state

162   between threat stimulus and response that is driven by the amygdala (Pitkanen, 2000) and can be

163   identified as 'fear' (Mineka, 1979; Öhman, 2000). Fear has been defined as a psychological state

164   that triggers physiological responses to avoid or escape from a stressor (Epstein, 1972; LeDoux,

165   1996). The development of successful defense mechanisms to fear-inducing stressors has clear

166   survival benefits for animals, and thus fear can be seen as a driver of evolutionary adaptations

167   (Tooby & Cosmides, 1990). Common strategies of escape and avoidance allow animals to cope

168   with recurrent stressors, such as the fear-inducing threat of predation (Lima & Dill, 1990).

169   The sections of the mammalian amygdala associated with fear behaviour serve as an

170   interface between sensory input and information transport and processing, endocrine response,

171   and motor output (Davis & Whalen, 2001). These interactions are associated with learning and

172   memory via the involvement of the lateral and basal nuclei, as demonstrated on captive rodents

173   using neurotoxic lesions on the basal and lateral nuclei of the amygdala (e.g. Wallace & Rosen,

174   2001), and are evident in Pavlovian fear conditioning paradigms (Davis, 1992; Maren, 2001).

175   Activation of hormones, specifically glucocorticoids and norepinephrine in stress responses

176   initiated by fear arousal provides feedback to the brain that influences emotion control and

177   cognition, which contributes to fear conditioning (Rodrigues, LeDoux & Sapolsky, 2009). Fear

178   responses may, therefore, be both conditioned as aversive learnt behaviours (e.g. Fanselow &

179   Poulos, 2005), and unconditioned as innate freezing responses (e.g. Schulkin, Thompson &

180   Rosen, 2003).

181   Given that fear motivates a stress response – initiating the freeze, and fight or flight

182   actions – quantifying glucocorticoid outputs from the autonomic nervous and HPA systems

183   should yield a measurable indication of fear from predation as a stressor. Minimally invasive

184   techniques are available that assay glucocorticoid levels in faeces, fur, or feathers (Sheriff *et al.*,

185   2011; Cook, 2012; Palme, 2019). Using minimally invasive methods to measure glucocorticoid

186   levels in the wild does not necessarily yield an isolated 'output' of a fear or predator/human-

187   induced stress response (Rosen & Schulkin, 2004). This situation results from glucocorticoids

188   not being a molecule of fear *per se* but having a fundamental role in maintaining energy balance

189   (Rosen & Schulkin, 2004). As such, glucocorticoids may change not just because of fear but also

190   in response to other exogenous stressors, like food shortage (McEwen & Wingfield, 2003).

191   Nevertheless, such methods could usefully compare longer-term stress responses among habitats

192   or along disturbance gradients with variable exposure to predators, by following experimental

193   designs that are considerate of additional stressors that may be present (see: MacDougall-

194   Shackleton *et al.*, 2019).

195   If two or more stressors are present, the resultant combined stress may present severe

196   challenges to an individual's physiological systems (Johnstone, Lill & Reina, 2012; Brearley *et*

197   *al.*, 2013; Malcolm *et al.*, 2014; Arlettaz *et al.*, 2015; Geary *et al*., 2019; Legge *et al.*, 2019).

198   Interactive fear and stress effects are context-dependent (Belarde & Railsback, 2016). They can

199   be additive and combine the multiple impacts, synergistic whereby the presence of one threat

200   amplifies another (Doherty *et al.*, 2015), or antagonistic whereby one threat cancels the effects of

201   the other. A reduction in the activity of mesopredators in the presence of humans provides an

202   example of antagonism (Clinchy *et al.*, 2016). Additive, synergistic, and antagonistic reactions

203   have each been observed in mammalian prey in natural systems in response to exposure to

204   multiple stressors (Crain *et al.*, 2008; Côté, Darling & Brown, 2016; Gunderson *et al.*, 2016;

205   Jackson *et al.,* 2016; Geary *et al*., 2019; Legge *et al.,* 2019).

206   Exposure to a stressor(s) that is prolonged, constant, or recurring can have chronic

207   impacts, as recovery from a stressor cannot occur whilst the threat remains (Sapolsky, Romero &

208   Munck, 2000). Acute stress occurs as the initial response to a threat to sustain fitness in the short

209   term; it subsides once the responding action—be it freezing, fighting, or fleeing—diminishes the

210   threat (Wingfield & Kitaysky, 2002). Activation of the HPA axis in an acute stress response has

211   rapid effects that increase immune system function, energise muscles via enhanced

212   cardiovascular tone, and heighten cognition, including memory (Sapolsky, Romero & Munck,

213   2000). These responses occur via increased cerebral perfusion rates and use of glucose, all of

214   which come at the cost of decreased appetite and reproductive behaviours (Sapolsky, Romero &

215   Munck, 2000). Effectively, the acute stress response suspends non-essential behaviours in favour

216   of altered behaviours that minimize the threat (Wingfield & Kitaysky, 2002).

217   Continued exposure to a stressor, or stressors, creates a state of chronic stress, which is

218   classically described as allostatic overload (Dantzer *et al.*, 2014). Allostatic load describes the

219   body's ability to maintain homeostasis in response to a stressor (Sterling & Eyer, 1988; McEwen

220   & Stellar, 1993; McEwen & Wingfield, 2003). Allostatic overload, by extension, refers to the

221   inability to maintain homeostasis and thus an organism's increased susceptibility to external

222   stressors (Sterling & Eyer, 1988; McEwen & Stellar, 1993; McEwen & Wingfield, 2003).

223   Chronic stress reduces an organism's resilience to future stressors by inducing extended

224   behavioural changes in feeding, fighting, and mating (Mineur *et al.*, 2006). Chronic stress also

225   affects an organism's physiological state by suppressing or impairing the reproductive system

226   and decreasing physiological resistance to pathogens and toxins through the suppression of

227   immune function (Dhabhar & McEwen, 1999; McEwen & Wingfield, 2003; Romero, 2004;

228   Travers *et al.*, 2010; Feng *et al.*, 2012). Repeated exposure to a stressor can have population and

229   community level consequences as homeostasis is compromised, and it increases susceptibility to

230   additional stressors and can have flow-on effects. For example, chronic risk of predation, which

231   facilitates changes in nutrient demand for prey species and thus changes in the elemental

232   composition of their excreta, can alter nutrient cycling in the community and ecosystem

233   (Hawlena & Schmitz, 2010).

234   Cases of acclimatisation to chronic or repeated acute stressors have been observed,

235   although the process often results in enhanced activation of the HPA axis to novel stressors, and

236   thus may not be beneficial to fitness (Romero, 2004). Instead of acclimatising to a chronic or

237   repeated stressor, glucocorticoid levels can remain the same, or become chronically elevated, or

238   the HPA axis can shut down completely and render an animal vulnerable to future threats

239   (Romero, 2004). Physiological impairment of the neurological, cardiovascular and

240   musculoskeletal systems may also result from chronic stress: neurons of the brain can atrophy

241   and impair memory, or grow and enhance fearfulness with extensive releases of adrenaline and

242   cortisol (Roozendaal, 2000; McEwen, 2004); atherosclerotic plaques also may form and impede

243   blood flow from repeated elevation of blood pressure (Manuck *et al.*, 1988), and skeletal muscle

244   can suffer severe protein loss (Wingfield & Kitaysky, 2002).

245   Although chronic and acute stress responses have been well defined for mammals in

246   laboratory studies, results from *in situ* studies show that reactions vary with the stressor type that

247   animals are exposed to, as well as habituation potential, food availability, social interactions, and

248   density (Dickens & Romero, 2013). *In situ* mammalian endocrine responses to a consistent

249   stressor, such as human activity, have not been studied sufficiently to be able to determine if

250   there is a particular pattern of response. Avian endocrine responses to such stressors have been

251   more extensively studied and they reveal that urban habitats, perceived as a consistent stressor,

252   can shape endocrine responses in birds. However, a consistent stress response pattern has yet to

253   be observed in birds (Bonier, 2012). Inconsistent behavioural responses of mammals and other

254   animals to human activities that are often observed can perhaps be linked to modulating factors

255   such as the level of human activity, the species and condition of the animal being observed, and

256   the spatio-temporal context (Tablado & Jenni, 2017).

257

258   **Mammalian behavioural responses to fear and stress: the landscape of fear concept**

259   The landscape of fear concept (Laundré, Hernández & Altendorf, 2001) postulates that prey are

260   aware of microhabitat patches associated with high and low predation risk, where predators are

261   either active and ubiquitous, or scarce (Laundré, Hernández & Altendorf, 2001; Shrader *et al.*,

262   2008; van der Merwe & Brown, 2008; Laundré, Hernández & Ripple, 2010). Theoretically,

263   landscape of fear effects should increase with landscape heterogeneity, since the differences

264   between high and low risk sites become more pronounced and prey can more easily avoid high-

265   risk sites (Bleicher, 2017; Gaynor *et al.,* 2019). However, this relationship can depend on the

266   species and condition of the habitat and, for some species, simple habitats can be the safest (e.g.

267   Hammerschlag, *et al.,* 2015; Schmidt & Kuijper, 2015; Atuo & O'Connell, 2017). Landscape of

268   fear effects will also be more pronounced in systems where interactions between predators and

269   prey are less frequent (Schmitz, 2008), as is evident in findings from Pavlovian fear

270   conditioning, and the '*risk allocation hypothesis*' – which states that animals exposed to constant

271   high predation risk will increase their foraging risks over time (Lima & Bednekoff, 1999; Van

272   Buskirk *et al.,* 2002). Fear arousal in a landscape of fear results in two predictable outcomes:

273   either avoidance of high risk areas, or modulation of behaviour (e.g. increased vigilance) to

274   reduce predation risk when foraging in such areas (Gaynor *et al.,* 2019). These outcomes indicate

275   the potential positive benefits to conservation management of considering fear arousal and stress

276   levels, and the direct and indirect cues that may trigger these effects (Atkins *et al.*, 2017).

277   The likelihood of survival of a prey species is improved by having a well-developed

278   perception of high predation risk, as it allows adaptive behavioural responses to be established

279   (Bókony *et al.*, 2009). Habitat shifts, temporal shift, grouping, vigilance, and freeze, fly, and

280   fight responses are the most studied such responses to the non-consumptive effects of predators

281   (Say-Sallaz *et al.*, 2019). These often develop due to increased interaction rates between

282   predators and prey. However, chronic stress impacts that are sufficient to affect reproduction and

283   long-term survival can be experienced by prey species perceiving recurring predation risks

284   (Thomson *et al.*, 2010; Clinchy *et al.*, 2011). Chronic perceived predation risk may also result in

285   altered foraging activity driven by fear. This can affect where and what prey eat (Schmitz,

286   Krivan & Ovadia, 2004), causing them to move from risky to sheltered microhabitats (Trussell,

287   Ewanchuk & Matassa, 2006), in turn altering the distribution and availability of resources. Fear-

288   based adaptive behavioural responses such as these underlie the landscape of fear concept.

289   For mammals, fear arousal can be triggered both by a predator's presence or by a

290   predator cue, such as an associated scent. Olfaction can be a key driver of fear arousal (Soso *et*

291   *al.*, 2014; Banks, Daly & Bytheway, 2016; Jones *et al.*, 2016; Parsons *et al.*, 2017). The

292   mechanics of this are best understood in mammals: odours are detected by the accessory

293   olfactory bulb that transmits information directly to the amygdala and hypothalamus, where fight

294   or flight responses are developed (Fogaca *et al.*, 2012; Canteras, Pavesi & Carobrez, 2015).

295   Laboratory studies exploring the effects of post-traumatic stress disorder have exposed small

296   mammals to predators or their cues to induce stress, and in doing so revealed that exposure to

297   predator cues alone can affect the neural circuitry associated with fear (Rosen & Sculkin, 1998,

298   2004).

299   Subtle cues such as predator odours may precede threats and allow for a mammalian prey

300   animal's fear state to be conditioned to a cue that occurs before, or in correlation with, a

301   previously encountered predation threat (Rescorla & Solomon, 1967; Rosen, 2004). Predation

302   risk may, therefore, be perceived by prey species eavesdropping on predator scent marks, such as

303   urine, faeces, or fur in the environment (Banks, Daly & Bytheway, 2016; Jones *et al.*, 2016).

304   Such odours have been observed experimentally to induce fear-like responses of freezing

305   (Wallace & Rosen, 2000), vigilance (Nersesian, Banks & McArthur, 2012), fleeing (Anson &

306   Dickman, 2013), and avoidance (Hayes, Nahrung & Wilson, 2006), across a wide range of

307   species in both field and laboratory experiments (Apfelbach *et al.*, 2005, 2015). Consequently,

308   landscape of fear topography, where predators indirectly influence prey behaviour across a range

309   of microhabitats, can arise from the influence of predator olfactory cues on mammalian prey

310   foraging behaviours as much as it can from the direct threat of predation (e.g. Brown & Kotler,

311   2004; Parsons & Blumstein, 2010; Cremona, Crowther & Webb, 2014; Mella, Banks &

312   McArthur, 2014; Hoffman, Sitvarin & Rypstra, 2016). It is worth noting, however, that whilst

313   predator olfactory cues can elicit a fear or stress response, they do not always do so (Apfelbach

314   *et al.*, 2005). This may be because predators often leave the site after depositing a cue, and the

315   cue intensity diminishes. Predator cues elicit responses that are modulated according to the

316   differential intensity of the perceived threat, prior experience, or pending further information

317   gathering, and thus can be perceived as a low risk by prey (Bedoya-Pérez *et al.*, 2019).

318   Fear arousal due to predator presence or cues can deplete a prey individual's energy

319 budget, resulting in poor reproduction and health either via energy exhaustion from stress (i.e.

320 the predation stress hypothesis: Boonstra *et al.,* 1998; Clinchy *et al.,* 2004; Romero, 2004; Støen

321 *et al.*, 2015), or reduced nutrition from foraging compromises (Brown & Kotler, 2004; Clinchy *et*

322 *al.*, 2016). As food resources become limited, additionally, prey may take greater risks to meet

323 nutritional needs (i.e. the predation-sensitive food hypothesis: Sinclair & Arcese, 1995), but at a

324 possible cost of additional stress. In areas of high human activity, this may result in wildlife

325 increasing the stressors they are exposed to as they seek human-based food sources, such as

326 waste or pet food, and in doing so increase their exposure to domestic pets, altered light,

327 increased sound, and vehicles (Navara & Nelson, 2007; Morgan *et al*., 2009; Riley *et al*., 2014;

328 Shannon *et al.*, 2016; Doherty *et al.*, 2017). For managers mitigating fear arousal, mapping

329 landscapes of fear (e.g. van der Merwe & Brown, 2008; Kauffman, Brodie & Jules, 2010;

330 Iribarren & Kotler, 2012, Smith *et al.*, 2019) to identify, protect and extend safe foraging areas,

331 could assist in the conservation of wildlife subject to human activity or multiple stressors such as

332 human activity and predators.

333

334 **Human activity as a fear-inducing stressor**

335 Human activity can influence wildlife in a wide variety of ways (e.g. Albert & Bowyer, 1991;

336 Bowyer *et al*., 1999). Pressure from increased proximity to human activity or development that

337 encroaches upon animal home ranges, result in wildlife becoming either: 1) 'urban avoiders' that

338 move away from human activity; 2) 'urban adapters' that make some use of anthropogenic

339 resources but still rely largely upon those found naturally; or 3) 'urban exploiters' that are

340 synanthropic and make full use of anthropogenic resources (McKinney, 2006). The effects of

341   human activity can therefore differ between species and trophic levels, and even within the same

342   species, depending on personality. Furthermore, the negative effects of a disturbance on one

343   species may result in flow-on responses of positive consequences for its prey, predators, or

344   competing species (e.g. Gill, Sutherland & Watkinson, 1996; Crooks & Soulé, 1999; Leighton,

345   Horrocks & Kramer, 2010). These effects, however, depend strongly on the availability of

346   necessary resources within the human occupied / disturbed areas, and will often differ between

347   systems.

348   It has been postulated that humans may impose widespread effects on ecosystem function

349   if they induce greater fear responses in ubiquitous small predators than in top predators (Clinchy

350   *et al.*, 2016), or by increasing physiological stress in large ungulates through antagonistic

351   behaviours (Vijayakrishnan *et al.*, 2018). Indeed, human activity can be comparable to the

352   above-mentioned impacts of predation, creating landscapes of fear (Hofer & East, 1998; Frid &

353   Dill, 2002; Rehnus, Wehrle & Palme, 2014; Patten & Burger, 2018), and disrupting foraging

354   (Ciuti *et al.*, 2012; Clinchy *et al.*, 2016). Humans can also act as "super-predators" that

355   disproportionately kill carnivores and drive trophic cascades (Darimont *et al.*, 2015). Trophic

356   cascades can also arise when human activity has non-consumptive effects on the ecological roles

357   of large predators (Smith *et al.*, 2017). For example, large predators may increase their hunting

358   efforts in urban areas: if their own fear response to human activity results in less time spent

359   consuming a kill, this in turn may increase their kill rate of prey in urban areas to meet their

360   energy needs (Smith *et al.*, 2017). When large predators avoid human activity, and / or meso-

361   predators reduce their foraging around human activity, prey species may respond by increasing

362   their own foraging activity (Suraci *et al.*, 2019), effectively taking refuge behind the "human

363   shield" that is reducing predation pressure for them (Berger, 2007; Leighton, Horrocks &

364   Kramer, 2010; Kuijper *et al.*, 2015).

365   Human activity can affect the trophic structure of communities not only via top-down

366   pressure, but also by exerting bottom-up pressure through the constant provision of alternative

367   resources (Fischer *et al.,* 2012), such as subsidies of shelter, water and food with year-round

368   primary production. These resources can outweigh the stresses of human disturbance and

369   influence population and community behaviours (Parris, 2016), resulting in urban colonisation

370   by wildlife (Shochat, Lerman & Fernández-Juricic, 2010; Jokimäki, *et al.,* 2011). As such,

371   human activity does not always result in fear responses, particularly for prey species that benefit

372   from the human shield and access to food, water or shelter subsidies (Lyons *et al.*, 2017). It is

373   possible that, given these conditions, and provided that resource subsidies are nutritionally rich

374   and accessing them does not increase pathogen transmission risk (Murray *et al.*, 2016), prey

375   species like small mammals would experience fitness benefits in urban areas. Resource subsidies

376   can also be exploited by predators, resulting in increased predator activity in urban areas but also

377   in altered foraging behaviours that either decrease or increase predation on small prey (Iossa *et*

378   *al.*, 2010; Bateman & Fleming, 2012; Fischer *et al.,* 2012; Newsome *et al.*, 2014, 2015).

379   Despite such positive effects of human activity on wildlife, negative impacts are more

380   pervasive for many species. The negative effects of high levels of disturbance, for example from

381   roads and vehicles, or of active interference from recreational activities conducted in designated

382   conservation areas, can lead to physiological stress or displacement, countervailing any positive

383   effects of humans on wildlife (Kloppers, St Clair & Hurd, 2005; Banks & Bryant, 2007; Berger,

384   2007; Ciuti *et al.*, 2012; Rehnus, Wehrle & Palme, 2014; Arlettaz *et al.*, 2015; Patten & Burger,

385   2018; Vijayakrishnan *et al.,* 2018).

386   A common response in mammals to increased exposure to human activity is a temporal

387   shift in activity patterns, from diurnal to crepuscular or nocturnal, to avoid interaction with

388   humans (McClennen *et al.,* 2001; Tigas, Van Vuren & Sauvajot, 2002; Riley *et al.*, 2003;

389   Ditchkoff, Saalfeld & Gibson, 2006; Gaynor *et al.*, 2018); the same or reverse may occur too, to

390   reduce interactions with predators (Brown, 2000; Laundré, Hernández & Altendorf, 2001; Kohl

391   *et al.*, 2018; Smith *et al.*, 2019). Temporal shifts can have strongly negative effects if they limit a

392   forager's ability to locate and capture prey (Ditchkoff, Saalfeld & Gibson, 2006). Regardless of

393   the response, it is evident that human activity can have profound indirect effects on community

394   interactions through altering individual behaviour, particularly foraging, through either fear

395   arousal or a stress response (e.g. Frid & Dill, 2002; Werner & Peacor, 2003).

396   The ability of wildlife to cope with urban environments can occur through either plastic

397   or evolved shifts in behaviour, foraging, food preferences, or predator avoidance, and in shifts in

398   the timing of breeding (Ditchkoff, Saalfeld & Gibson, 2006; Møller, 2009; Shochat, Lerman &

399   Fernández-Juricic, 2010; Rodriguez, Hausberger & Clergeau, 2010; Alberti, 2015; McDonnell &

400   Hahs, 2015; Otto, 2018; Santini *et al.*, 2019). It is most common for urban-occupying species to

401   plastically adjust to human imposed stressors (Donihue & Lambert, 2015), with some ultimately

402   evolving tolerance to urban environments. Human activity can therefore impose pressures that

403   are strong enough to influence changes in behaviour and in physiology — endocrinology in

404   particular (Bonier, 2012; Snell-Rood & Wick, 2013; Otto, 2018). Bolder individuals are most

405   likely to exploit novel opportunities and have reduced stress responses to human activity (Atwell

406   *et al.*, 2012). Animals that routinely encounter human activity, typically provide parental care,

407   and are capable of reproducing multiple times across their life span may produce offspring that

408   are acclimated to human activity and accordingly show lower fear/stress responses (Schell *et al.*,

409   2018). Habituation of groups of animals to human activity is being increasingly observed, often

410   as a result of bold individuals spending significant amounts of time around human-disturbed

411   areas and displaying reduced fear responses (Stillfried *et al*., 2017). This counters the idea that

412   human activity always imposes landscapes of fear, but may reflect the combination of reduced

413   resource availability and bold personalities that allow for urban habituation (Lowry, Lill &

414   Wong, 2012). In some instances this may be problematic for humans if increased interactions

415   with habituated animals increase vehicle accidents and / or transfer of zoonotic diseases; this

416   highlights the potential need to manage some mammalian prey species in urban areas (Honda *et*

417   *al.*, 2018).

418   Fear and acute/chronic stress may be constant hurdles faced by wildlife, but adding the

419   effects of anthropogenic disturbance could result in the elevation of acute stress responses to

420   prolonged and widespread chronic stress, and upscale the possible impacts from individuals to

421   populations (Rehnus, Wehrle & Palme, 2014). As we have outlined, human activity can both

422   indirectly and directly create landscapes of fear, influencing and amplifying existing landscapes

423   of fear through interactive effects. Predator presence and human activity can also interact to alter

424   ecosystem structure and modify the predation risk perceived by prey species, with either positive

425   or negative impacts dependent upon the circumstances. The combination of stress resulting from

426   the pressures of altered predator-prey interactions and human activities is yet to be investigated

427   extensively. Understanding the cumulative effects that both may impose is critical for effective

428   conservation of wildlife in an increasingly human-influenced world.

429

430   **Alleviating fear and stress for wildlife conservation**

431 As we have illustrated, fear can produce stress and simultaneous multiple stressors can have

432 chronic effects that negatively influence both predator and prey species populations (Allan *et al.*,

433 2013). To synthesize these impacts, we note that in modern urban situations both habitat

434 stressors and introduced stressors now collide (Figure 1). Habitat stressors result from naturally

435 occurring environmental factors such as native predator presence (especially for prey), social and

436 reproductive pressures, limited access to refuges / nests resource, food and water, disease and

437 parasite prevalence, and produce predictive homeostasis responses by prey species (Figure 1).

438 Introduced stressors, by contrast, are additional stressors that are imposed by human actions that

439 result in reactive homeostasis responses. These introduced anthropogenic stressors include

440 structural developments that change landscapes, human recreational activities in natural habitats

441 (including use of vehicles), introduced pollutants and toxins that alter landscapes and resource

442 quality, and introduced predators and altered predator-prey interactions (Figure 1). The

443 combination of impacts from both naturally occurring and introduced anthropogenic stressors

444 has the potential to cause a cumulative stress response that can result in homeostatic overload or

445 failure, as defined by Romero, Dickens and Cyr (2009), and may result in population collapses

446 due to increased susceptibility of individuals to the additional stressors (as we have demonstrated

447 above, and Figure 1). Cumulative stress may be additive or synergistic, and is likely to be

448 particularly detrimental for prey species. For example, if prey species face multiple stressors,

449 they may take greater foraging risks, or be less able to allocate energy to vigilance or flight

450 behaviours, and thus become more susceptible to predation or additional stressors. In the case of

451 population-impacting stressors, the local population may be impacted to a high degree such that

452 it becomes threatened (e.g. Sweitzer, 1996; Doherty *et al.*, 2015). As such, conservation action in

453   areas where simultaneous introduced stressors occur in addition to natural ecosystem pressures,

454   like in urban and peri-urban habitats, may urgently needed.

455   The most direct way to alleviate stress in wildlife is to remove or reduce the key

456   stressors. This may be difficult if the stressors are anthropogenic, as the needs of the expanding

457   human population often usurp those of wildlife; alternative solutions then need to be considered.

458   A suite of activities related to managing vegetation structure, density, and/or heterogeneity may

459   well provide such an alternative solution. These activities result in increased availability of

460   potential refuge sites and may be readily achieved through ongoing habitat engineering that, for

461   example, supports the growth of structurally complex plants or adds logs / rock piles to reduce

462   areas of open space. In order to mitigate introduced fear and stress effects, it is important that

463   future studies investigate whether vegetation management and other habitat components can

464   alleviate some of the pressures associated with multiple introduced stressors for target species.

465

466   **Managing habitat to alleviate wildlife fear and stress**

467   The impact of predators (or human activity) can be mitigated by changing the configuration of

468   risky areas within a habitat (Hopcraft, Sinclair & Packer, 2005; Lone *et al.*, 2014). Food

469   availability often drives habitat selection (e.g. Sherman, 1984; Johnson & Sherry, 2001), but

470   predation risk and human activity affect a suite of correlated factors such as movement decisions

471   (Turcotte & Desrochers, 2003), foraging patterns (Gil, Zill & Ponciano, 2017), social

472   organisation (Rodríguez, Andrén & Jansson, 2001), and reproductive success (Zanette *et al.*,

473   2011). Supplementation of essential resources including refuges, nests or roosts, food, and water

474   to wildlife is a growing conservation method due to its ease of implementation, immediate

475   results, and favourable portrayal in the media (Sergio *et al.*, 2018). One example of positive

476   results includes increased parasite resistance in nestling birds after supplementation with high-

477   quality food during the stressful young-rearing stage (Knutie, 2020). Another example is the

478   reduction in impact from introduced predators on small desert mammals following the addition

479   of artificial refuge structures (Bleicher & Dickman, 2020). Despite these successes, negative

480   impacts can also ensue following supplementation. Built-up refuges may be primarily

481   investigated by invasive species, such as the black rat (*Rattus rattus*), which could potentially

482   deter commensal native species and support the population growth of invasive species (Price &

483   Banks, 2018). Artificial nests or roosts can support increased predation rates owing to the

484   structure supporting a sit-and-wait predator at the exit (e.g. McComb *et al.*, 2019). Food and

485   water subsidies can increase pathogen transmission, reduce movement and migratory behaviours,

486   increase predator-prey interaction rates, and competitor aggression interactions (Murray *et al*.,

487   2016). However, owing to the benefits of supplementation, especially during times of stress, it

488   may be used as a tool to mitigate the negative impacts of stress on wildlife if conducted in a

489   targeted, monitored and well-considered manner (e.g. Freeman *et al*., 2020).

490   Considering the existing knowledge base on food and water supplementation, meta-

491   analyses have suggested that the associated disease risk may be managed by focusing on specific

492   natural food sources and pathogen groups subject to the target ecosystem and by increasing the

493   spatial extent of feeding stations across potential linked habitats, which also limits microparasite

494   host aggregations (see: Becker, Streicker, & Altizier, 2015; Becker *et al.*, 2018). In considering

495   the specific needs of target animals and ecosystems, chainsaw-carved cavities have more

496   favourable thermodynamic properties for small mammals and birds than do artificial next boxes

497   (Griffiths *et al.*, 2018). As they mimic natural hollows they are also less likely to increase rates

498   of predation. Supplementation projects are therefore moving forward using this growing

499   knowledge base to adaptively tailor methods to specific conditions, and to orchestrate pre- and

500   post-monitoring that ensures successful stress mitigation (Civitello *et al.*, 2018).

501   Survivorship of prey, in the face of predation stressors, is often positively correlated with

502   increased structural complexity of the habitat (Hopcraft, Sinclair & Packer, 2005; Lone *et al.*,

503   2014; Leahy *et al.*, 2016). This has been demonstrated in many studies to be a consequence of

504   the increased opportunities for prey to escape and hide, thereby mediating predator-prey

505   dynamics by reducing encounter rates, as only a proportion of the total prey population remains

506   available to predators (e.g. Holt, 1984; Kotler & Brown, 1988; Bianchi, Schellhorn & Van Der

507   Werf, 2009; Rieucau, Vickery & Doucet, 2009; Klecka & Boukal, 2014; Laundré *et al.*, 2014).

508   The extensive research on the benefits to prey of habitat structural complexity builds on the

509   '*habitat heterogeneity hypothesis,*' which postulates that structurally complex habitats support

510   increased species diversity by offering a wide range of niches and diverse ways of exploiting

511   resources (Bazzaz, 1975). Habitat complexity, by extension, has been generalized to be a

512   primary driver of biodiversity (Pianka, 2011). The landscape of fear concept accepts this

513   principle too, in that a wide range of microhabitat types offers multiple foraging and shelter

514   conditions with varied predation risks for species. For example, northern quolls (*Dasyurus*

515   *hallucatus*) of the semi-arid Pilbara region in Western Australia utilise complex rocky habitats in

516   preference to open grasslands where the threat of predation from feral cats (*Felis catus*) is greater

517   (Hernandez-Santin, Goldizen & Fisher, 2016).

518   Animals in habitats with high predation pressure may display foraging preferences for

519   microhabitats or times that they perceive to be safe (Brown, 2000; Laundré, Hernández &

520   Altendorf, 2001; Laundré, Hernández & Ripple, 2010). Some small mammals seek structurally

521 complex vegetation owing to the reduced risk of predation and increased reward of foraging they

522 find there (Lima & Dill, 1990; Andruskiw *et al.*, 2008). Others, such as the Australian hopping

523 mouse (*Notomys alexis*) that exhibit bursts of speed in open habitat, are less adept at moving

524 through complex vegetation (Spencer, Crowther & Dickman, 2014). No matter the species, in

525 landscapes of fear a prey species' use of the topography, refuges, and escape substrates can

526 indicate its perceived risk of predation (Brown & Kotler, 2004; van der Merwe & Brown, 2008;

527 Shrader *et al.*, 2008), and the associated fear and stress that may arise or be alleviated due to

528 habitat structure. The same principle should be relevant to reducing stress in proximity to human

529 activity, considering that prey responses to human activity and predators are similar.

530   Human activity and disturbance can quickly reduce habitat complexity (Western, 2001).

531 However, enhancing habitat complexity and heterogeneity is being incorporated increasingly

532 into restoration and management efforts, with some success (Brown, 2003; Bernhardt & Palmer,

533 2007; Palmer, Menninger & Bernhardt, 2010). To balance the needs of people and biodiversity,

534 local planning procedures are at times now incorporating green spaces and greening initiatives

535 into urban areas. As habitat complexity and diversity are of particular importance in supporting

536 biodiversity and population sustainability, it is important that habitat structure underpins the

537 engineering of wildlife habitats in urban and urban-adjacent areas (Threlfall *et al.*, 2016). The

538 effectiveness of any management regime depends on recognising the direct and indirect impacts

539 that occur across sustainable ecosystems. Consequently, habitat complexity as a management

540 objective requires that urban landscapes are approached on a case by case basis, with full

541 assessment before the habitat is ecologically engineered (Tews *et al.*, 2004).

542

543 **Management tools to observe and alleviate fear and stress for wildlife conservation**

544   Cumulative stress maps of human activity and stressors that occur naturally in ecosystems have

545   allowed returns on restoration investments to be maximized by indicating key areas that will or

546   do need intervention to mitigate the effects of severe stress on wildlife, as opposed to

547   unsuccessful piecemeal management that focuses on one or two stressors broadly (Allan *et al.*,

548   2013). Physiological and behavioural stress in wildlife may be cost-effectively and

549   straightforwardly observed by comparing the outcomes of simultaneous measurements taken

550   across a disturbance gradient where multiple stressors are both abundant and low, using several

551   well-established methods. Specifically, assays of faecal/urine/fur/feather glucocorticoid

552   metabolites can provide insight into the level of physiological stress an animal is experiencing

553   under comparative circumstances (see Cook, 2012; Cooke *et al.*, 2013; Sheriff *et al.*, 2011;

554   Palme, 2019). Pairing such results for each location with those of giving-up density surveys

555   (Brown, 1988) that can also be filmed by infrared motion sensor cameras to observe foraging

556   behavioural responses (e.g. Leo*, Reading & Letnic*, 2015), yields an understanding of both

557   physiological stress responses and foraging responses. Comparing these results may further

558   indicate if behavioural responses are changing to moderate physiological stress impacts (e.g.

559   Carlstead, Brown, & Seidensticker, 1993; Carlstead, Brown, & Strawn, 1993). Simultaneous

560   measurements of habitat quality that include vegetation cover, refuges, distance to food / water

561   source, and distance to disturbances (e.g. human activity or predator sighting based on

562   spotlighting or in-field camera traps) will build a dataset for spatial correlation analyses that can

563   geographically map the landscape of fear. Such measurements should also identify what factors

564   influence the landscape, such as by use of behavioural data (e.g. Willems & Hill, 2009) and / or

565   giving-up density data (e.g. van der Merwe & Brown, 2008).

566   Spatial mapping of the physiological stress response, based on the collection locations of

567   samples, could be overlaid and compared to these results also. Such spatially mapped results may

568   clarify important areas that are in need of protection or the habitat types that could be extended

569   to mitigate stress impacts. It is worth noting that several authors have emphasized that these

570   methods need to be used correctly to ensure that stress and habitat factors are linked (e.g.

571   McMahon *et al.*, 2018; Bleicher, 2017; Bedoya-Perez *et al.*, 2013; MacDougall-Shackleton *et*

572   *al.*, 2019). For example, collection of fresh faecal samples of a target species along a gradient of

573   high to low human activity would allow glucocorticoid metabolites to be assayed, providing

574   insight into potential stress induced by human activity along the gradient (Rehnus, Wehrle &

575   Palme, 2014). A similar approach could be used to assay stress perceived by prey species in

576   areas of high and low predator activity, and sex hormones also could be assayed to explore sex-

577   related effects of stress. By allowing pathways of fear and stress to be mapped, including sites

578   where stressors from predators and human activity occur simultaneously, such methods should

579   allow managers to reliably identify where best to intervene to preserve at-risk populations and

580   maintain community stability. We consider potential interventions in more detail below.

581   If cumulative stressors occur and are suspected to have detrimental effects on target

582   wildlife populations or communities, we suggest that a potentially powerful mitigation approach

583   could be developed based on Cumulative Effects Assessments (CEA). Devised in the 1990s amid

584   growing concerns that Environmental Impact Assessments (EIA) did not consider all the effects

585   of urban and peri-urban developments (Smit & Spaling, 1995), CEAs have been advocated as an

586   effective tool for use by on-ground practitioners (Duinker *et al.*, 2012). Numerous countries have

587   mandated that CEAs be incorporated into EIAs, namely: the United States of America, Canada,

588   Europe, New Zealand, and Australia each advocate some level of CEAs (Therivel & Ross,

589   2007). Despite this legal requirement, and the CEA concept being widely known in scientific

590   literature, it is rarely applied in practice (Ma, Becker & Kilgore, 2009; Foley *et al.*, 2017).

591   We propose further that the principles of the '*reactive scope model*' be used to develop

592   CEAs, to identify where cumulative stressors occur, and thus better inform conservation

593   management initiatives in areas where wildlife is subject to homeostasis overload or failure

594   (Figure 2). The results from the above mentioned methods and / or other applicable established

595   methods may be used to answer our suggested CEA questions. The reactive scope model

596   (Romero, Dickens & Cyr, 2009) provides useful insight into the range of physiological mediators

597   available in response to a stressor. It maps the homeostasis range of a given species in four

598   stages: 1) predictive – change occurs in response to routine environmental change, such as

599   seasons or day to night; 2) reactive – change occurs in response to an unpredictable change,

600   allowing survival via classic stress responses; 3) overload – consistent changes occur in response

601   to a stressor, and chronic stress impacts start to occur; and 4) failure – the species shows inability

602   to sustain homeostasis, and is very susceptible to additional stressors and death (Romero,

603   Dickens & Cyr, 2009). If our proposed CEA approach (Figure 2), based on the reactive scope

604   model, were applied to small mammals in urban, urban adjacent, and peri-urban ecosystems, for

605   example, then areas of conservation concern could be identified where the additive or synergistic

606   impacts of human disturbance and introduced predators combine with stressors that occur

607   naturally. Appropriate management, such as increasing habitat complexity or reducing human

608   activity in conservation areas (e.g. Bleicher & Dickman 2020), could then be implemented to

609   alleviate these stressors.

610

611 **Fear and stressing in small mammal ecology in Australia; the need to consider the twin**

612 **stressors of introduced predators and people in wildlife management**

613 Small mammals are often somewhat resilient to threatening processes owing to their high

614 population growth rates (Cardillo *et al.*, 2005, 2006). However, in Australia small mammal

615 populations are declining quickly, and due to causes dissimilar to those driving global declines

616 (Woinarski *et al.* 2015). Declines in Australia have been attributed to a wide range of habitat

617 stressors: habitat loss, altered fire regimes, disease, increasing temperatures, decreasing water

618 availability, depleted soil quality, and salinity (Woinarski *et al.*, 2015). However, mammals

619 within a 'critical weight range' (CWR: 35 to 5550 g) are particularly vulnerable (Chisholm &

620 Taylor, 2007; Woinarski, Burbidge & Harrison, 2015) owing to the effects of predation by two

621 introduced carnivores, the red fox (*Vulpes vulpes*) and domestic house cat (*Felis catus*) that

622 arrived in Australia over 150 years ago (Johnson, 2006). If predators are introduced, their

623 impacts on prey are likely to be exacerbated owing to prey naïveté (Doherty *et al*., 2016). Such

624 impacts have been particularly acute on wildlife in Australia, where eutherian carnivores are

625 recent arrivals (Salo *et al*., 2007). However, the question of Australian native animal stress

626 responses and the extent of their naiveté to these introduced eutherian predators is debatable (see:

627 Banks & Dickman, 2007; Carthey & Banks, 2016). Although CWR mammals are of high

628 conservation concern, predation from introduced predators poses a threat also to all native

629 predators by reducing their food resources, which in turn may increase predation and predation-

630 associated stress on alternative food sources such as smaller (< 35 g) or larger (> 5550 g)

631 mammal species. For example, a study examining the diet of a nocturnal, avian predator, the

632 sooty owl (*Tyto tenebricosa*) before and after red fox introduction, revealed a dietary shift post

633 introduction, with owls consuming more arboreal than terrestrial prey species after fox arrival

634   (Bilney, Cooke & White, 2006). This shift to consuming arboreal prey increased dietary overlap

635   with the sympatric powerful owl (*Ninox strenua*), providing disproportionate predation pressure

636   on prey in the ecosystems of East Gippsland, Victoria.

637   Predation by red foxes and cats is prevalent not only in natural habitats but also in

638   agricultural and urban habitats (Dickman, 1996; Morgan *et al*., 2009; Bino *et al*., 2010). The

639   paths and roads that fragment urban and agricultural habitats are used frequently by these

640   predators, which exacerbates their predation pressure on prey species by combining with impacts

641   imposed by human activities (Latham *et al.*, 2011, Červinka *et al.*, 2013). Consequently, this can

642   result in increased abundances of red foxes and cats in human-modified landscapes that border or

643   include natural habitats (Towerton *et al.*, 2011; Graham, Maron & McAlpine, 2012). Urban and

644   agricultural habitats present many threats to wildlife, but they may also offer food and shelter

645   opportunities (Pickett *et al.,* 2001; Gaston *et al.,* 2005; Hobbs, Higgs & Harris, 2009). As

646   reported by Ives *et al.* (2016), 46 percent of threatened Australian animals occur in or near

647   Australian cities. Thus, the fate of many species could depend on accommodating their needs in

648   urban and agricultural habitats (Ives *et al.*, 2016). A recent assessment of data collected at the

649   Wildlife Rehabilitation Centre in Queensland Zoo, Australia, revealed that pet cat or dog attack,

650   car strike, and entanglement in human-placed objects represented 56.4% of the causes of

651   submission of injured wildlife; mortality rates associated with these traumas were also high, with

652   61.3% of admitted animals dying from their injuries (Taylor-Brown *et al.*, 2019). These threats

653   may contribute to landscapes of fear, through fear arousal, altered foraging behaviour, post-

654   traumatic stress reactions, and cumulative stress exposures resulting in chronic stress responses.

655   Despite growing knowledge of anthropogenic impacts on threatened species, Australian

656   conservation planning continues to exclude urban and agricultural habitats from consideration

657   (Dales, 2011). There is recognition of the scope of this issue in Australia (e.g. Hill *et al.*, 2007;

658   Carthey & Banks, 2012; Threlfall, Law & Banks, 2012; McCauley *et al.*, 2013; Banks & Smith,

659   2015; Ives *et al.*, 2016), but few studies have explored the interactive effects of introduced

660   predators and human activity on the survival of prey species. Despite the development of

661   glucocorticoid analysis techniques to determine stress in animals dating to the 1960s (Jones *et*

662   *al.*, 1964), only six of the 60 extant small mammals of conservation concern in Australia have

663   been subject to studies seeking to better understand their glucocorticoid response to stressors

664   (Hing *et al.*, 2014), such as predation by introduced species or human activity.

665   There is a need for alternative management regimes to mitigate the additional stressors of

666   human-imposed impacts on wildlife, and the situation we have outlined in Australia underlines

667   the urgency of this need. As there are difficulties with the current control of introduced predators

668   in Australia (Glen & Dickman, 2005; Rayner *et al.,* 2007; Bergstrom *et al.,* 2009; Norton, 2009;

669   Warburton & Norton, 2009; Carroll, 2011; Newsome *et al.*, 2017), there is also an urgent need

670   for alternative management regimes to mitigate the additional stressors of introduced predator-

671   imposed impacts. As we have argued throughout this review, it is logical that biodiversity

672   conservation managers consider stress from the combined impacts of introduced predators,

673   altered predator interactions, human activity, and stressors that occur naturally in ecosystems.

674   Using the example methods to conduct our proposed CEA, based on the reactive scope model, to

675   draft appropriate management plans, such as increasing habitat complexity or reducing human

676   interaction in areas, would be a progressive response towards preserving many species of

677   Australian small mammals and their constituent communities.

678

679   **Conclusion**

680 Considering ongoing global urbanization and the acknowledged importance of urban areas to

681 biodiversity conservation, there is a great need for increased focus on the management of urban

682 biodiversity. Management decisions require information about fear and stress impacts on

683 wildlife, including impacts from both human activities and predators, especially if they are novel

684 or introduced. Understanding the impacts of human activities is a research priority for modern

685 science. There are many gaps in our current understanding of fear and stress impacts on wildlife,

686 and of associated impacts of altered predation pressures and the persistence of target populations.

687 To sustain biodiversity in urban and urban-adjacent green space habitats, reserves and

688 conservation areas, it is vital that we establish better understanding and management of the

689 multiple stressors that operate in these systems.

690

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1352

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, disease / parasite prevalence, and availability of food and water. On the right are introduced stressors, primarily those arising from anthropogenic disturbances, such as: urban developments, human activity, introduced toxins and introduced predators. Where both categories of stressor occur together simultaneously, 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.
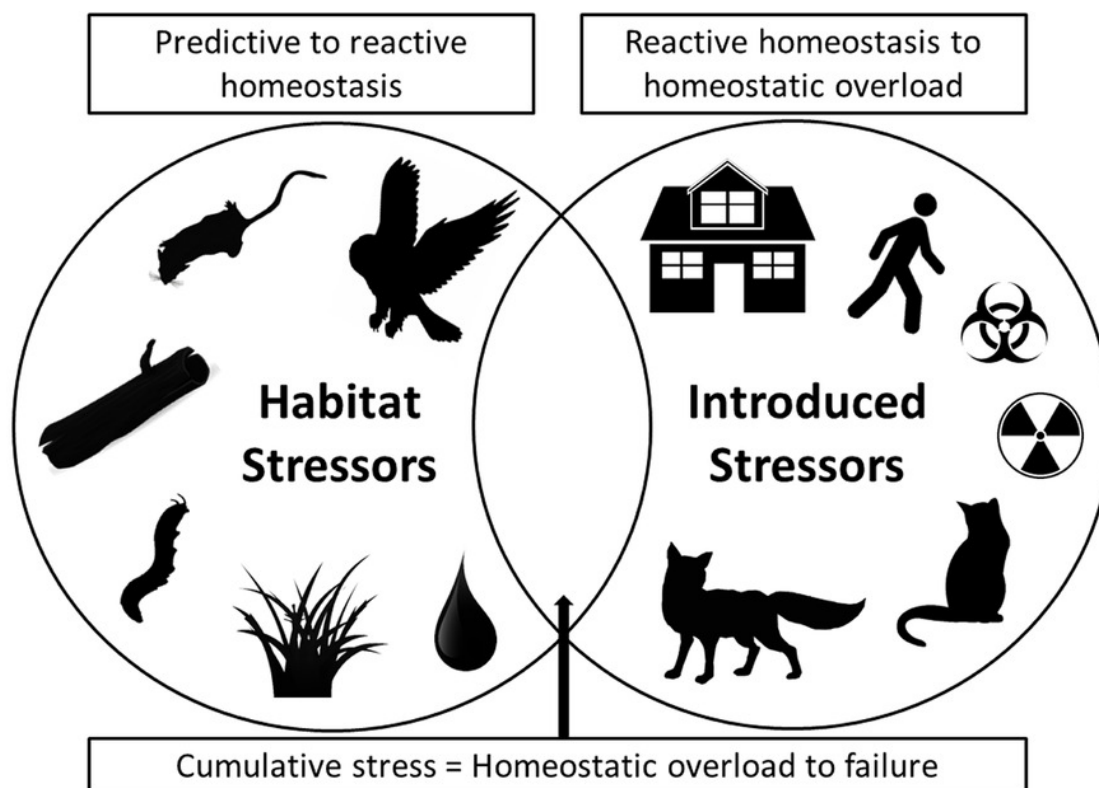
Figure 2

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 those that are introduced.

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 carved 'tree-hollow' cavities.

Figure 3

Graphical Abstract

Why wildlife conservation needs to measure: *Fear and stressing in predator-prey ecology: considering the twin stressors of predators and people on mammals*