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Ecology and Neurobiology of Fear in Free-Living Wildlife

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Keywords

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Abstract

The ecology of fear concerns the population-, community-, and ecosystem-level consequences of the behavioral interactions between predators and prey, i.e., the aggregate impacts of individual responses to life-threatening events. We review new experiments demonstrating that fear itself is powerful enough to affect the population growth rate in free-living wild birds and mammals, and fear of large carnivores—or the human super predator—can cause trophic cascades affecting plant and invertebrate abundance. Life-threatening events like escaping a predator can have enduring, even lifelong, effects on the brain, and new interdisciplinary research on the neurobiology of fear in wild animals is both providing insights into post-traumatic stress (PTSD) and reinforcing the likely commonality of population- and community-level effects of fear in nature. Failing to consider fear thus risks dramatically underestimating the total impact predators can have on prey populations and the critical role predator-prey interactions can play in shaping ecosystems.

1. INTRODUCTION

The "ecology of fear" (Brown et al. 1999, p. 385) concerns quantifying the population-, community-, and ecosystem-level impacts of the behavioral interactions between predators and prey, i.e., measuring the aggregate consequences of individual responses to life-threatening events (Brown et al. 1999, Brown 2019). We define what is meant by fear and the ecology of fear. We then review the progress made in experimentally testing the population- and community-level effects of fear in free-living wildlife, focusing specifically on birds and mammals, and report the complementary effect sizes found in experimental and non-experimental (i.e., observational) studies. We end by describing new research demonstrating enduring neurobiological and behavioral effects of fear in wild animals that mirror those diagnostic of post-traumatic stress (PTSD) in humans.

We focus on experimental tests of the ecology of fear in free-living wildlife, and wild birds and mammals in particular, for a number of reasons. Early observational studies (e.g., Ripple & Beschta 2004, Creel et al. 2007) suggested that behavioral interactions between predators and prey can have substantial population- and community-level impacts in free-living wildlife. However, the weak inference intrinsic to observational studies, given that the patterns documented are open to many alternative explanations (Sibly & Hone 2002), meant that many in the scientific community remained unconvinced (Ford & Goheen 2015, Say-Sallaz et al. 2019). Elegant experiments on numerous invertebrate and aquatic species have definitively established that behavioral, physiological, and morphological responses of prey to predators can affect populations and communities (Schmitz et al. 1997, Preisser et al. 2005, Hawlena & Schmitz 2010), but because most of these experiments have been conducted on captive animals in artificial mesocosms (typically table-top terrariums or aquariums), there have been repeated questions regarding "how the results generalize to natural conditions" (Creel & Christianson 2008, p. 199) experienced by free-living wildlife (Ford & Goheen 2015, Say-Sallaz et al. 2019).

We focus specifically on wild birds and mammals because there has been no prior comprehensive review of experiments testing the ecology of fear in these taxa as there has been in other taxa (e.g., Preisser et al. 2005) and because four facets of the biology of birds and mammals warrant specific attention. First is the central role parental care [which is rare in other taxa (Royle et al. 2012)] plays in the development of birds and mammals—and the resulting potentially cumulative and compounding demographic consequences of frightened parents providing poorer care. Second is the significance of being principally preyed upon by the human "super predator" (Darimont et al. 2015, p. 858). Third is the importance of retaining a memory of fear in long-lived, cognitively sophisticated species and the resulting relevance of animal models of PTSD to the ecology of fear. And finally, questions concerning predator-prey interactions in birds and mammals frequently have very direct and often controversial implications for wildlife conservation and human-wildlife conflict (Estes et al. 2011, Ripple et al. 2014, Ford & Goheen 2015, Say-Sallaz et al. 2019).

2. WHAT IS FEAR, AND WHAT IS MEANT BY THE ECOLOGY OF FEAR?

2.1. Fear Is Observable in Behavior and in the Brain

Fear can be readily seen, for example, when observing a prey fleeing from its predator. Darwin (1839) was struck by not seeing fear in birds on the Galápagos Islands, noting that they did not flee at the approach of a dangerous predator (himself), causing him to write in *The Voyage of the Beagle* about the "fear of man [as] an acquired instinct" (Darwin 1839, p. 453). Referring to anti-predator behavior as fear is thus something students of nature, like Darwin, have been doing for centuries.

Fear can refer to behaviors observable in humans or other animals, and it is also observable in the structure and functioning of the "neuronal circuits for fear" located in, but not limited to, two

subcortical brain areas, the amygdala and the hippocampus (Tovote et al. 2015, p. 317; LeDoux 2017). The amygdala is responsible for fear processing and fear memories and the hippocampus for the formation of declarative, episodic, and spatial memories (Heller 2019). Not only can fear be measured in the brain, but specific types of fear can be measured; for example, fear of predators and fear of pain are processed by distinct neuronal pathways (Gross & Canteras 2012). New neurobiological research has begun to focus on fear being far more complex than a simple stimulus-response reaction in cognitively sophisticated species like birds and mammals, involving not only subcortical fear circuits in the amygdala and hippocampus but also higher-level cognitive information processing, primarily in the prefrontal cortex (LeDoux & Pine 2016, LeDoux 2017, Deslauriers et al. 2018, Fanselow 2018, Heller 2019) [the homologous nidopallium caudolaterale in birds (Güntürkün & Bugnyar 2016)]. This greater emphasis on cognitive information processing affected by learning and memory better incorporates the individual differences in life experience that determine how debilitating fear may be. Only a subset of people from among those exposed to the same life-threatening event will develop PTSD, for example, and the best predictor of who does is whether the individual experienced previous childhood trauma (Daskalakis et al. 2013).

2.2. What Is Meant by the Ecology of Fear?

The phrase ecology of fear was first used by Brown et al. (1999) in a paper integrating foraging theory into traditional models of predator-prey population dynamics. Brown et al. began with the straightforward fact that frightened prey eat less (Sih 1980, Lima & Dill 1990) and modeled the effects on population dynamics, assuming prey fecundity is affected by reduced food intake resulting from the fear of predators. Population dynamics may be further affected because frightened prey can also be expected to feed their offspring less (Fontaine & Martin 2006, Zanette et al. 2011), with consequences that may include not only some offspring dying (Zanette et al. 2011) but also the survivors potentially being permanently handicapped, leading to carry-over effects causing reduced survival in subsequent life stages (Moore & Martin 2019), possibly extending to transgenerational impacts reducing offspring fecundity or survival in adulthood (Yin et al. 2019). The ecology of fear concerns both populations and communities because most prey are predators of something else (Brown 2019), and hence not only the prey's abundance but that of its prey may be affected by predator-induced reductions in prey foraging (**Figure 1**).

Critically, the ecology of fear is about whether and how behavioral responses affect the number of individuals, be it the number of prey, predators, or the prey's prey (Brown et al. 1999, Brown 2019), and studies of the ecology of fear must thus necessarily involve quantification of effects on population abundance or its determinants, i.e., fecundity, survival, and recruitment to the next generation (Sibly & Hone 2002). Equally critical is that the ecology of fear is about effects in "ecological time" (Lima & Dill 1990, p. 619), i.e., experiences, behavioral responses, and reproductive success within the lifetime of an individual and its offspring, not changes resulting from natural selection over multiple lifetimes.

Establishing that population abundance and/or its determinants are affected by fear poses two fundamental challenges. The first is demonstrating that changes in abundance are not due to bottom-up (food) limitation. If prey fecundity is affected by fear reducing prey food intake, the more parsimonious alternative must first be excluded, i.e., that reduced food intake is simply due to food shortage (Creel & Christianson 2008). The second challenge, which is as much of a challenge with regard to the effects of direct killing by predators as it is to the impacts of fear, is demonstrating that changes in abundance are due to top-down (predator) limitation. Until fairly recently the Erringtonian view of predators (that predators kill only the doomed surplus) predominated,
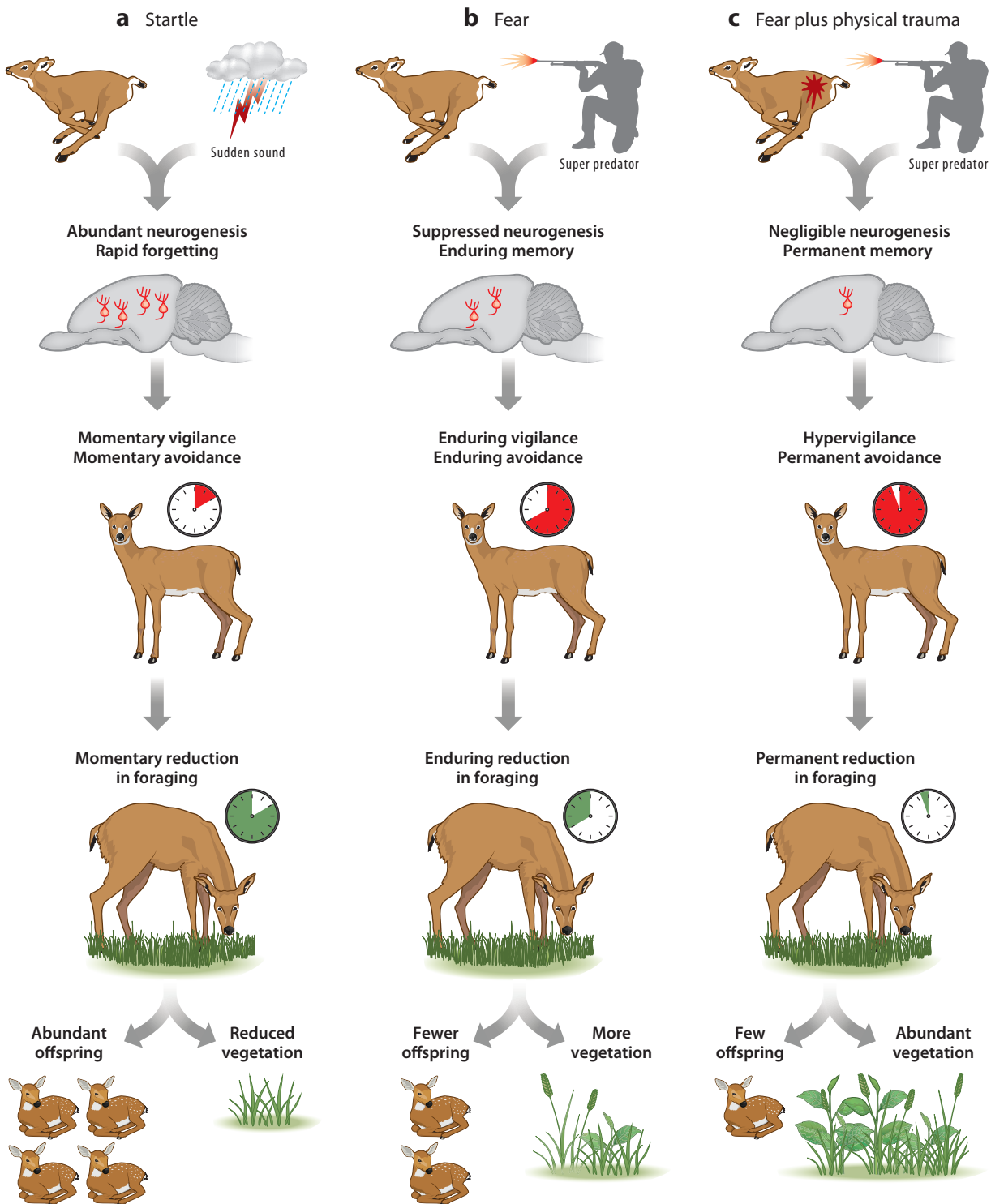
Fecundity: the proportion of females breeding or the number of eggs laid or offspring born per female

Population abundance: the number of individuals of a given species in a given area or category at a given time

Recruitment to the next generation: the number of offspring produced per female that survive to join the adult breeding population

a Startle   **b** Fear   **c** Fear plus physical trauma

Sudden sound   Super predator   Super predator

Abundant neurogenesis
Rapid forgetting

Suppressed neurogenesis
Enduring memory

Negligible neurogenesis
Permanent memory

Momentary vigilance
Momentary avoidance

Enduring vigilance
Enduring avoidance

Hypervigilance
Permanent avoidance

Momentary reduction
in foraging

Enduring reduction
in foraging

Permanent reduction
in foraging

Abundant
offspring   Reduced
vegetation

Fewer
offspring   More
vegetation

Few
offspring   Abundant
vegetation

(Caption appears on following page)

Figure 1 (*Figure appears on preceding page*)

Conceptual illustration contrasting the duration of the neurobiological and behavioral effects and the consequent population- and community-level impacts expected to result from (*a*) a transient startle response to a sudden loud noise like a thunderclap, (*b*) fear induced by a life-threatening predator encounter (exemplified by encountering the most dangerous predator of all—the human super predator), and (*c*) fear and physical trauma caused by an unsuccessful predator attack. The more intensely life-threatening the experience is, the greater and longer the expected effect will be on neurobiological processes such as neurogenesis (the birth of new neurons) and the more enduring (or even permanent) the memory of the experience and its effects on behavior. These behavioral effects entail enduring vigilance and avoidance of encounter-related situations, and in extreme cases, animals may display hypervigilance and more or less permanent avoidance of trauma-related situations, mirroring the behaviors diagnostic of PTSD in humans. The more enduring or permanent the activity cost of devoting time to anti-predator behavior (i.e., vigilance and avoidance), the more enduring the reduction in time spent foraging will be, the anticipated consequences of such a protracted reduction in foraging being a reduction in the number of offspring produced and a reduction in the impact on the abundance of the animal's food (vegetation in this example). The ecology of fear concerns the aggregate impacts of such individual responses to life-threatening events on populations, communities, and ecosystems.

meaning all killing is compensatory, and predators thus never limit bird and mammal populations (Errington 1956). Refuting both the bottom-up and Erringtonian alternatives required conducting experiments that involved adding or removing predators. Consequently, the fact that top-down limitation of prey populations by predators does occur in terrestrial vertebrates was definitively established only as recently as 2010—by the publication of comprehensive reviews of predator manipulation experiments (Lavers et al. 2010, Salo et al. 2010).

Importantly, Errington (1956) was not wrong in asserting that killing by predators can be compensatory and that simple estimates of kill rates are thus not sufficient to draw conclusions. What matters is who is killed and when and not just how many are killed. Taking a recent example, le Roux et al. (2019) used three decades of data to show that although African buffalo (*Syncerus caffer*) are the favored prey of lions (*Panthera leo*), comprising more than 25% of their diet, the population growth rate of buffalo is not affected by lion numbers because most buffalo killed by lions are solitary, old, post-reproductive males, who are thus doomed surplus with respect to population growth (see the sidebar titled Population Growth Rate).

Predation is the proximate cause of death of 87% of all adult birds and 68% of all adult mammals according to a new worldwide analysis of cause-specific mortality (Hill et al. 2019). As just explained, knowing this is insufficient to conclude that predators limit bird and mammal populations. However, this does clearly establish the paramountcy of anti-predator behavior for individual survival and suggests an important modification of how best to view anti-predator behavior. If being preyed upon is the fate of almost every individual, then anti-predator behavior is better described as delaying predation, rather than avoiding it. In species in which longevity is correlated with lifetime reproductive success, as in most birds and mammals (Gaillard et al. 1989), the ecology of fear is thus best envisaged as resulting from individuals endeavoring to delay predation until they are either post-reproductive or have maximized their lifetime reproductive success. Fear effects on current reproductive success, and consequently population growth, may thus be expected to be common whenever lower reproductive success over a longer period provides the surest means of achieving higher lifetime reproductive success (Lima & Dill 1990, Ghalambor &

POPULATION GROWTH RATE

The population growth rate (lambda, λ) refers to the change in number of individuals in a population over a given time, expressed as a fraction of the initial population. It is estimated from censuses over time or determined from demographic (fecundity and survival) data (Sibly & Hone 2002).

Martin 2001, Christianson & Creel 2014, LaManna & Martin 2016). That is, if being more vigilant or avoiding areas with more predators reduces food intake and so lowers current reproductive success (fecundity or offspring survival), this is a cost worth paying if these anti-predator behaviors succeed in delaying predation to some future time, thereby ensuring the individual survives to breed another day (Brown et al. 1999, Brown 2019).

3. POPULATION-LEVEL EFFECTS OF FEAR IN FREE-LIVING WILDLIFE

3.1. Experimental Evidence of Population-Level Effects of Fear

Experimentally testing what limits population growth or its demographic determinants (fecundity, survival, and recruitment) requires adding or removing the factor of interest (Sibly & Hone 2002), e.g., adding or removing food (Boutin 1990) or predators (Salo et al. 2010) or both (Krebs et al. 1995, 2018). The limiting factor of interest in the ecology of fear concerns the behavioral responses of prey to predators caused by the presence of predators and the killing they do. The experiments conducted to date on free-living wildlife have accordingly (*a*) removed predators, (*b*) 'added' predators by simulating their presence, or (*c*) 'added' predation by removing prey [i.e., culling; sensu Okuyama & Bolker (2007)]. Predator responses to dangerous prey are also part of the ecology of fear (Brown 2019), but our search, described below, revealed no experiments on the consequences.

We identified the experiments conducted to date that have tested the population-level effects of fear in free-living wild birds and mammals by searching Web of Science for the terms "predation risk," "fear," "experiment," "fecundity," "survival," "recruitment," "reproduct*," "bird*," and "mammal*" in various combinations and by searching for these same terms in papers citing the foundational works on the topic, e.g., Lima & Dill (1990) and Brown et al. (1999). We found 10 experiments reporting significant effects on one or more of the determinants of population growth: 8 on a total of 15 songbird species and 2 on small mammals (arctic ground squirrels, *Spermophilus parryii*, and gray-sided voles, *Clethrionomys rufocanus*). In **Table 1** we report the effects demonstrated in these experiments, together with the effect sizes [ln(mean for fear treatment/mean for control), after Salo et al. (2010)]. **Table 2** additionally lists results from 11 observational studies contrasting sites or time periods with or without predators, or with few or many predators, that have reported effects on the determinants of population growth that were apparently attributable to fear.

Half of the experiments to date testing population-level effects of fear in free-living wild birds and mammals have focused exclusively on fecundity, and a further three have reported fear effects on fecundity plus some facet of offspring survival (**Table 1**). In all eight experiments demonstrating effects on fecundity, the effect sizes were modest and, while being predominantly negative, included one positive (i.e., fear led to an increase in fecundity). Most (7 out of 8) of these experiments were on songbirds, and moderately negative and occasionally positive effects on fecundity (egg number) were similarly demonstrated in a predator-removal experiment on a further 11 songbird species (Fontaine & Martin 2006) and in a study of the effects of natural variation in predation risk involving 8 additional species (LaManna & Martin 2016). Fontaine & Martin (2006) analyzed all species together rather than individually and found no significant overall effect on egg number, which is why their experiment is not included in **Table 1**. Rather than egg number it was egg mass that Fontaine & Martin found showed a significant overall effect.

'Adding' predation (culling) and 'adding' predators by simulating their presence have both been experimentally demonstrated to affect fecundity (**Table 1**). The effects in the two culling

Table 1 Experiments demonstrating population-level effects of fear in free-living wildlife

Taxa	Reference	Method	Measure	Effect size[a]
Fecundity				
Bird	Doligez & Clobert 2003	'Added' predation (culling)	Egg number	−0.02
Bird	Eggers et al. 2006	'Added' predator (playback)	Egg number	−0.19
Bird	Travers et al. 2010	'Added' predation (culling)	Egg number	−0.12
Bird	Zanette et al. 2011	'Added' predators (playback)	Egg number	−0.09
Bird	Hua et al. 2014	'Added' predator (playback)	Egg number	−0.08
Bird	Malone et al. 2017	'Added' predator (playback)	Egg number	0.11
Bird	Dillon & Conway 2018	'Added' predator (caged predator)	Egg number	−0.08
Mammal	Fuelling & Halle 2004	'Added' predator (odor)	Proportion of females breeding	−0.16
Offspring survival during parental care				
Bird	Zanette et al. 2011	'Added' predators (playback)	Early parental care (egg survival to hatching)	−0.11
Bird	Hua et al. 2014	'Added' predator (playback)	Early parental care (egg survival to hatching)	−0.21
Bird	LaManna & Martin 2016	'Added' predator (playback)	Early parental care (egg survival to hatching)	−0.38
Bird	Zanette et al. 2011	'Added' predators (playback)	Mid-stage parental care [nestling (hatchling) survival to fledging]	−0.23
Bird	M.C. Allen, M. Clinchy & L.Y. Zanette, manuscript in preparation	'Added' predators (playback)	Late parental care (fledgling survival to independence)	−0.30
Cumulative impact on fecundity and facets of offspring survival during parental care				
Bird	Zanette et al. 2011	'Added' predators (playback)	Fledglings per female	−0.47
Bird	Hua et al. 2014	'Added' predator (playback)	Fledglings per female	−0.44
Mammal	Karels et al. 2000	Removed predators (exclusion)	Juveniles leaving burrow per female	−0.43
Mammal	Fuelling & Halle 2004	'Added' predator (odor)	Juveniles trapped per female	−0.75
Recruitment to next generation, population growth rate, and transgenerational impacts				
Bird	M.C. Allen, M. Clinchy & L.Y. Zanette, manuscript in preparation	'Added' predators (playback)	Recruitment to next generation (breeding recruits per female parent)	−0.72
Bird	M.C. Allen, M. Clinchy & L.Y. Zanette, manuscript in preparation	'Added' predators (playback)	Population growth rate (surviving female parents plus breeding recruits)	−0.15
Bird	M.C. Allen, M. Clinchy & L.Y. Zanette, manuscript in preparation	'Added' predators (playback)	Transgenerational impact (projected offspring survival in adulthood)	−0.20

[a]Effect size calculated as ln(mean for fear treatment/mean for control), after Salo et al. (2010).

Table 2 Observational studies reporting population-level effects of fear in free-living wildlife

Taxa	Reference	Method	Measure	Effect size[a]
Fecundity				
Bird	Julliard et al. 1997	Predator (before versus after exclusion)	Egg number	−0.06
Bird	Zanette et al. 2006b	Predator (high versus low number)	Egg number	−0.09
Bird	Scheuerlein et al. 2001	Predator (present versus absent)	Proportion of parents initiating a second breeding attempt	−0.85
Mammal	Krebs et al. 1995	Predator (high versus low number)	Offspring born per female per year	−1.60
Mammal	Cherry et al. 2016	Predator (high versus low number)	Proportion of females ovulating	−0.47
Mammal	Dulude-de Broin et al. 2020	Predator (high versus low number)	Proportion of females giving birth	−0.55
Offspring survival during parental care				
Bird	Zanette et al. 2006a	Predator (high versus low number)	Early parental care (egg survival to hatching)	−0.12
Bird	LaManna & Martin 2016	Natural risk gradient	Early parental care (egg survival to hatching)	−0.22
Bird	Zanette et al. 2006a	Predator (high versus low number)	Mid-stage parental care [nestling (hatchling) survival to fledging]	−0.20
Bird	LaManna & Martin 2016	Natural risk gradient	Mid-stage parental care [nestling (hatchling) survival to fledging]	−0.28
Bird	Dudeck et al. 2018	Relative parental fearfulness	Late parental care (fledgling survival to independence)	−0.27
Offspring survival post–parental care				
Mammal	Bourbeau-Lemieux et al. 2011	Predator (present versus absent)	Post-weaning offspring survival overwinter	−0.19
Cumulative impact on fecundity and facets of offspring survival				
Bird	Zanette et al. 2003	Predator (high versus low number)	Fledglings per female	−0.43
Bird	LaManna & Martin 2016	Natural risk gradient	Fledglings per female	−0.49
Mammal	Christianson & Creel 2014	Predator (before versus after)	Juveniles seen per female in midwinter	−0.18
Mammal	DeWitt et al. 2017	Predator (before versus after)	Juveniles trapped per female	−0.42

[a]Effect size calculated as ln(mean for fear condition/mean for control), after Salo et al. (2010).

experiments our search identified (Doligez & Clobert 2003, Travers et al. 2010) testify to the complexities of what animals find fearful and how they may respond. Doligez & Clobert (2003) removed every nestling from collared flycatcher (*Ficedula albicollis*) nests and measured the effect on clutch size in birds nesting in the same area the following year. Clutch size was lower in areas where there had been culling the previous year among both birds whose previous nests had been culled and those whose nests had not been, pointing to fear being socially communicated at a neighborhood level (Doligez & Clobert 2003). In the second culling experiment (Travers et al. 2010), all eggs were removed from the nests of song sparrows (*Melospiza melodia*), and either the

nest was left empty, simulating predation, or artificial eggs were substituted, which females subsequently incubated, indicating that they did not perceive having suffered any egg loss. To control for bottom-up effects, all birds had a feeder placed in the center of their territory that was kept filled with supplemental food, the use of which prior experiments had demonstrated improved physiological condition (Clinchy et al. 2004) and increased fecundity (Zanette et al. 2006b) and offspring survival (Zanette et al. 2006a). Females whose nests were left empty (i.e., culled) did not go to the feeder, testifying to the fear induced by the simple disappearance of their eggs (Zanette et al. 2013). Most importantly, with regard to the ecology of fear, as a consequence of their forgoing use of the supplemental food (Zanette et al. 2013), females whose nests were culled (left empty) suffered physiological dysregulation and laid fewer eggs in their subsequent nests (Travers et al. 2010).

Directly measured effects of fear on one or more facets of offspring survival have been demonstrated in three experiments, all on songbirds (**Table 1**), two of which reported cumulative impacts of fear on both fecundity and offspring survival (Zanette et al. 2011, Hua et al. 2014). In gray-sided voles, 'adding' predators by simulating their presence using predator odor had a modest effect on fecundity (the proportion of females breeding)—and a substantially greater effect on the number of juveniles entering traps, indicative of a cumulative impact on both fecundity and offspring survival (Fuelling & Halle 2004). In arctic ground squirrels, removing predators [lynx (*Lynx canadensis*) and coyote (*Canis latrans*)] increased the proportion of females with offspring leaving the natal burrow, similarly reflective of a cumulative impact on both fecundity and offspring survival (Karels et al. 2000). Some direct predation of offspring could have contributed to there being fewer in control areas in this experiment, but the sampling intensity suggests direct predation was minimal or nonexistent (Karels et al. 2000). Critically, in contrast to the modest effect sizes demonstrated in the eight experiments reporting fear effects on fecundity (median = −0.08; **Table 1**), the demonstrated effects on offspring survival were larger (median = −0.23), and still larger effect sizes (median = −0.45) were demonstrated in the four experiments that quantified cumulative impacts of fear on both fecundity and facets of offspring survival (**Table 1**).

New experimental research comprehensively quantifying the effects on all of the determinants of population growth (fecundity, survival, and recruitment) demonstrates that fear itself is powerful enough to reduce the population growth rate in free-living wildlife, extending to and including transgenerational impacts that reduce the survival of offspring as adults (Zanette et al. 2011; M.C. Allen, M. Clinchy & L.Y. Zanette, manuscript in preparation). The presence of 'added' predators was simulated by intermittently broadcasting predator (or non-predator control) vocalizations across multiple song sparrow territories over three annual breeding seasons on several small coastal islands. The impacts of this experimental manipulation were comprehensively quantified by enumerating egg number (fecundity), using nest cameras and radio-tags to continuously monitor the fate of offspring from hatch to independence (survival during parental care), exhaustively censusing every island for recruits the next year (survival from independence to first breeding), and testing for transgenerational impacts by recording the song number sung by male recruits [it having been previously shown that reduced song number is indicative of impaired brain development resulting from offspring being fed less (MacDonald et al. 2006, Pfaff et al. 2007) and is accordingly predictive of poorer adult survival (Reid et al. 2005)]. Fear reduced egg number (effect size = −0.09), hatching success (−0.11), nestling survival (−0.23), and post-fledging survival to independence (−0.30), resulting in a very considerable cumulative compounding adverse effect on recruitment (−0.72) and consequent reduction in the population growth rate (−0.15). The reduction in population growth was furthermore projected to extend to the next generation due to the reduced survival of offspring as adults (−0.21) caused by the transgenerational impact of frightened parents feeding their offspring less (Zanette et al. 2011; M.C. Allen, M. Clinchy & L.Y. Zanette, manuscript in preparation) (**Table 1**).

Experiments enable strong inference concerning causation (Sibly & Hone 2002), but they must also have external validity, corroborated by demonstrating effect sizes corresponding to observational studies. In the experiment described above demonstrating that fear can affect population growth (Zanette et al. 2011; M.C. Allen, M. Clinchy & L.Y. Zanette, manuscript in preparation), the methodology and magnitudes of effect sizes demonstrated all accord with reported levels of natural variation. Predator (and non-predator) vocalizations were broadcast at a rate (9.3 min/h) that was comparable to naturally occurring predator vocalizations (9.5 min/h) recorded at naturally high predation risk sites in a study by LaManna & Martin (2016) that measured the effects of natural variation in predation risk on fecundity and facets of offspring survival in 10 species of songbirds. Broadcasting playbacks at naturally maximal rates is consistent with the methodology of other playback experiments (e.g., Dantzer et al. 2013). The size of the effect on fecundity in the experiment (−0.09; **Table 1**) was identical to that in a previous study of song sparrows (−0.09) that compared naturally high versus low predation risk sites (Zanette et al. 2006b) (**Table 2**). Similarly, the effect size in the experiment concerning hatching success (−0.11) was comparable to that in response to natural variation in predation risk in song sparrows (−0.12) (Zanette et al. 2006a) and the 10 species of songbirds (−0.22) studied by LaManna & Martin (2016); the same was true for the magnitude of effect on nestling survival (−0.23, −0.20, and −0.28, respectively; **Tables 1** and **2**). Likewise, the effect on post-fledging survival to independence in the experiment (−0.30; **Table 1**) accords well with that reported in a study of natural variation in parental fearfulness (−0.27; **Table 2**) (Dudeck et al. 2018).

Predator manipulation experiments were critical to demonstrating that predators can limit bird and mammal populations, as established in the aforementioned reviews by Salo et al. (2010) and Lavers et al. (2010). Salo et al. (2010) reported a mean effect size of 0.68 on reproductive responses (e.g., mean recruitment), and Lavers et al. (2010) reported a mean effect size of 0.11 on the population growth rate. Both these values correspond closely with the absolute value of the effects on recruitment (0.72) and the population growth rate (0.15) demonstrated in the experiment testing the effect of fear on population growth (Zanette et al. 2011; M.C. Allen, M. Clinchy & L.Y. Zanette, manuscript in preparation) (**Table 1**). One principal purpose of an experiment is to demonstrate the possible, and the experiments reviewed in **Table 1** demonstrate that it is entirely possible that fear alone could be responsible for some or all of the population-level effects of experimentally adding or removing predators reported by Salo et al. (2010) and Lavers et al. (2010).

3.2. Observational Evidence of Population-Level Effects of Fear

Fear can be confidently concluded to commonly affect some or all of the determinants of population growth in free-living wild songbirds, given the accumulated wealth of experimental and corresponding observational evidence reviewed in **Tables 1** and **2** and other supporting results (Fontaine & Martin 2006, Ibáñez-Álamo et al. 2015). What about other birds and mammals? Tropical songbirds differ from north temperate species (all those in **Table 1**) in ways suggested to increase the likelihood and strength of population-level effects of fear (Ghalambor & Martin 2001). Just such a large effect size (−0.85) was reported in an observational study on tropical stonechats (*Saxicola torquata*) in which the proportion of parents initiating a second breeding attempt was much lower among those with a predatory bird resident in their territory (Scheuerlein et al. 2001) (**Table 2**). The two experiments on small mammals reviewed in **Table 1** both demonstrated considerable effect sizes. Far and away the largest purported population-level effect of fear (−1.60; **Table 2**) concerns the "collapse of reproduction" in snowshoe hares (*Lepus americanus*) reported by Krebs et al. (1995, p. 1114) that was attributed to the extreme frequency of

unsuccessful predator chases during the decline phase of the 10-year snowshoe hare cycle (Krebs et al. 2018). Though reported as part of an exemplary experiment, there was no contemporaneous comparison between control and predator removal areas (Krebs et al. 1995), which is why this result is classified as observational (**Table 2**).

Fear has recently been proposed to be partially responsible for a decline in juveniles per female in porcupines (*Erethizon dorsatum*) following the 'addition' (recolonization) of fishers (*Pekania pennanti*) (DeWitt et al. 2017). The size of the effect attributable to fear (−0.42; **Table 2**) was estimated from the observation that mean porcupine mass declined by 19.6% coincident with fisher recolonization, taken together with the fact that the number of juveniles per female is strongly correlated with female mass. In large carnivore-ungulate systems, fear has been reported to affect fecundity, offspring survival, and both together (in some unknown combination). Fecundity, as measured by the proportion of females ovulating, was considerably lower in white-tailed deer (*Odocoileus virginianus*) in years when coyotes were abundant (effect size = −0.47; **Table 2**) (Cherry et al. 2016). A comparable effect on fecundity (effect size = −0.55; **Table 2**), as measured by the proportion of females giving birth, has also been reported in mountain goats (*Oreamnos americanus*) in response to inter-annual variation in the abundance of the large carnivores that prey on them (Dulude-de Broin et al. 2020). Overwinter lamb survival was lower in bighorn sheep (*Ovis canadensis*) in years when cougars (*Puma concolor*) were present, which was partly attributable to fear (effect size = −0.19; **Table 2**) because cougar presence impeded the growth of lambs, and smaller lambs were less able to survive overwinter (Bourbeau-Lemieux et al. 2011). Similar to porcupines, the number of juveniles per female declined in elk (*Cervus elaphus*) following the 'addition' (reintroduction) of wolves (*Canis lupus*); the size of the effect attributable to fear (−0.18; **Table 2**) in this case was determined from the deficit in juveniles that could not be explained by direct predation, winter severity, or growing season precipitation (Christianson & Creel 2014). Prior research indicated that this deficit was largely due to fear reducing the pregnancy rate (fecundity) (Creel et al. 2007), but an additional fear effect on offspring survival cannot be ruled out.

4. COMMUNITY-LEVEL EFFECTS OF FEAR IN FREE-LIVING WILDLIFE

Whereas most of the experiments to date that have demonstrated population-level effects of fear in free-living wildlife have been conducted on songbirds (**Table 1**), the fear large carnivores inspire in large herbivores and medium-sized carnivores has been the focus of most of the recent experiments that have now demonstrated that fear can also have community-level effects in free-living wildlife. Just as with population-level effects, the factor of interest concerns the behavioral interactions between predators and prey, but here the impact of interest is whether this affects the number of individuals in species other than the interacting predator and prey, e.g., the prey's prey (its food) or the prey's competitors (Ripple & Beschta 2004, Terborgh & Estes 2010, Brown 2019).

Ford et al. (2014) experimentally thinned vegetation to demonstrate that impala (*Aepyceros melampus*) prefer more open areas, and they then used impala exclosures to further experimentally demonstrate that this preference mediates the abundance of competing species of *Acacia* trees. Ford et al. reported correlational evidence indicating that fear of large carnivores [leopards (*Panthera pardus*) and African wild dogs (*Lycaon pictus*)], which lurk more in woody cover, was the mechanism responsible for this preference of impala for open areas, and thus the resulting trophic cascade. This preference of impala and other African herbivores for more open areas has been replicated in subsequent vegetation-thinning experiments (Riginos 2015, le Roux et al. 2018). H. Epperly, M. Clinchy, L.Y. Zanette & R.A. McCleery (manuscript in preparation) also replicated this result, and they experimentally verified that fear of large carnivores was the mechanism. The

authors conducted a bifactorial experiment in which the presence of 'added' large carnivores [leopards, spotted hyena (*Crocuta crocuta*) and domestic dogs (*Canis lupus familiaris*)] was simulated by broadcasting their vocalizations (or non-predator controls) in experimentally thinned and shrubby control sites. Impala and other herbivores fled more or were more vigilant in response to hearing large carnivores in shrubby control sites, consistent with fear mediating the preference for open areas.

In another new experiment on an African ungulate (Atkins et al. 2019), the cascading impact of a shift in habitat use by bushbuck (*Tragelaphus sylvaticus*) on plants (waterwort, *Bergia mossambicensis*) was experimentally demonstrated using exclosures. It was then experimentally verified that fear of large carnivores was the mechanism by demonstrating that bushbuck reacted more fearfully in one habitat than another to 'added' large carnivores, whose presence was simulated using leopard vocalizations and artificial carnivore excreta (with suitable non-predator sounds and excreta as controls). Like impala, the bushbuck is a woodland species, and in the experiment by H. Epperly, M. Clinchy, L.Y. Zanette & R.A. McCleery (manuscript in preparation) mentioned in the previous paragraph, it was demonstrated that, like impala, bushbuck preferred experimentally open areas— in a system where large carnivores are present in the environment. Where Atkins et al. (2019) conducted their experiments, in Mozambique's Gorongosa National Park, leopards and African wild dogs had been 'removed' (extirpated) during the Mozambican civil war. The behavioral shift investigated involved bushbuck moving into a wide-open floodplain habitat, one they had never been reported to use anywhere else, which Atkins et al.'s experiment verified occurred because there were no longer any large carnivores to fear.

Megaherbivores, like rhinoceroses (*Ceratotherium simum*) and elephants (*Loxodonta africana*), have little to fear from large carnivores, in contrast to other African herbivores like impala and wildebeest (*Connochaetes taurinus*). Le Roux et al. (2018) experimentally demonstrated that this in-terspecific contrast in the fear of large carnivores can have complex cascading impacts on herbivore feeding pressure on plants and the resulting nutrient dynamics. Le Roux et al. (2018) conducted a vegetation-thinning experiment and found a preference for open areas among most herbivores, just as in the comparable experiments described above. The preference for open areas among impala, wildebeest, and other species led to there being elevated nutrient inputs from the dung of these species in open areas. However, because of the much greater impact from rhinoceroses and elephants, which showed no preference for open areas (consistent with their having little to fear from large carnivores), there was no overall difference in feeding pressure between experimentally open and shrubby control sites.

The fear large carnivores inspire in medium-sized carnivores has also recently been experimentally demonstrated to cause a trophic cascade (Suraci et al. 2016). The presence of 'added' large carnivores (domestic dogs), simulated by intermittently broadcasting their vocalizations (or non-predator controls) along lengths of shoreline on small coastal islands, reduced the time raccoons (*Procyon lotor*) spent feeding in the intertidal by 66%, significantly impacting the abundance of intertidal fish and invertebrates (Suraci et al. 2016). Importantly, the effect sizes caused by the fear-induced 'removal' of raccoons from the intertidal documented in this experiment were similar or identical to those reported in an observational study contrasting islands on which raccoons were present or absent (Suraci et al. 2014). The 'removal' or absence of raccoons had respective effects of 0.59 or 2.67 on intertidal fish abundance, 0.68 or 2.14 on intertidal crab abundance, and the same effect, 0.48, on the number of large subtidal red rock crabs (*Cancer productus*).

Community-level effects of fear have now been demonstrated in free-living wildlife beyond birds and mammals in an experiment on free-living wild lizards on small Bahamian islands (Pringle et al. 2019). In the absence of predators, insectivorous brown and green anole lizards (*Anolis sagrei*

and *Anolis smaragdinus*, respectively) occupy fairly distinct habitats, with brown anoles feeding on the ground or tree trunks and green anoles feeding in the canopy. Experimentally adding (introducing) ground-dwelling, predatory, curly-tailed lizards (*Leiocephalus carinatus*) caused brown anoles to shift their habitat use to high up on tree trunks due to fear of curly-tailed lizards. This brought brown anoles into closer competition with green anoles, suppressing the population growth of green anoles and causing their extinction on two of four islands.

5. FEAR OF THE HUMAN SUPER PREDATOR IN FREE-LIVING WILDLIFE

Community- and landscape-level effects of fear in free-living wildlife have been demonstrated in other new experiments, also involving large carnivores, but here it is the fear humans inspire in large and medium-sized carnivores, and the cascading impacts on large herbivores and small mammals, which have been documented. Two recent worldwide analyses have established that humans, as predators, have a unique ecology that includes disproportionately killing medium and large carnivores (Darimont et al. 2015) and generally killing larger species of birds and mammals (Hill et al. 2019) at greater rates than non-human predators, meriting humans being termed a "super predator" (Darimont et al. 2015, p. 858).

Fear of the human super predator has recently been experimentally demonstrated to cause a trophic cascade in a large carnivore-ungulate system. Smith et al. (2015) reported correlational results pointing to fear of humans apparently disturbing cougars from their kills, causing cougars to spend less time feeding at each cached deer carcass (effect size = −0.54), thus necessitating their killing more deer per year to compensate (effect size = 0.31). That fear of humans was the mechanism disturbing cougars from their kills was then experimentally verified by demonstrating that the presence of 'added' humans near kill sites, simulated by broadcasting playbacks of people speaking conversationally (or non-predator controls), reduced the total time per 24 h that cougars spent feeding at their caches (effect size = −0.82) (Smith et al. 2017).

Fear of the human super predator has since been demonstrated to have cascading, landscape-scale impacts across wildlife communities, from large carnivores to small mammals. Suraci et al. (2019a) conducted a large-scale, repeated-measures experiment in which the presence of 'added' humans was simulated by intermittently broadcasting playbacks of people speaking (or non-predator controls) across two 1-km^2 blocks of forest for 5 weeks, following which the treatments were switched between blocks and broadcast for 5 more weeks. Fear of humans affected where and when carnivores moved through the landscape, causing avoidance and cautiousness in cougars, increased nocturnality in bobcats (*Lynx rufus*), reduced activity in skunks (*Mephitis mephitis*), and reduced foraging in opossums (*Didelphis virginiana*). The fear induced in the carnivores alleviated fear in small mammals, as evident from deer mice (*Peromyscus* spp.) expanding their habitat use and deer mice and woodrats (*Neotoma fuscipes*) foraging more. Importantly, the simulated density of humans (25 per km^2) was substantially less than in the jurisdiction (California, USA) as a whole (94 per km^2), and comparable effects on the same carnivores were reported in previous observational studies (Wang et al. 2015, Suraci et al. 2019a). Suraci et al.'s (2019a) use of a repeated-measures design meant that while the perception of predation risk was manipulated, the physical landscape and actual mortality risk were unchanged, and what was thus demonstrated were changes in where and when animals moved through the same physical landscape—caused solely by fear itself. Consequently, Suraci et al.'s (2019a) results experimentally demonstrate that a "landscape of fear" (Laundré et al. 2001, p. 1401), defined as spatial variation in the perception of predation risk alone (Gaynor et al. 2019) (see the sidebar titled Landscape of Fear), can have pervasive effects across wildlife communities.

Related to but distinct from the ecology of fear is the concept of the "landscape of fear" (Laundré et al. 2001, p. 1401), which posits that where, when, and how prey move through a landscape is affected by spatial and temporal variation in their perception of predation risk, influenced by, but distinct from, both the physical landscape and the actual risk of mortality from predators (Gaynor et al. 2019).

Two recent meta-analyses have documented that, worldwide, anthropogenic activity is affecting the movement (Tucker et al. 2018) and nocturnality (Gaynor et al. 2018b) of mammals of every size and type, and the results of the landscape-level experiment by Suraci et al. (2019a) demonstrate that fear of the human super predator could be a contributing factor causing this pervasive global pattern. Consistent with fear of the human super predator being pervasive across the planet, European badgers (*Meles meles*) (Clinchy et al. 2016), cougars in California (Suraci et al. 2019b), and white-tailed deer in North America (D.A. Crawford, M. Clinchy, L.Y. Zanette, L.M. Conner & M.J. Cherry, manuscript in preparation) have all recently been experimentally demonstrated to fear hearing humans more than non-human predators. Moreover, new research experimentally demonstrates that fear of the human super predator is pervasive throughout entire mammal communities in Africa, with fear of hearing humans exceeding the fear of hearing the top non-human predator, lions, in everything from impala to giraffes (*Cervus camelopardalis*) to rhinoceroses and even elephants (McComb et al. 2011, 2014; L.Y. Zanette, M. Clinchy, N. Frizzelle, C.B. Keller, S. Huebner, et al., manuscript in preparation). This pervasive fear of humans can have significant conservation consequences. Rhinoceroses and elephants have little to fear from large carnivores but much to fear from humans (Gaynor et al. 2018a, le Roux et al. 2018). Elephants in Gorongosa National Park, for example, were so heavily poached during the Mozambican civil war that the survivors demonstrate PTSD-like behaviors, including aggression toward vehicles, that inspire fear in the human occupants, hindering ecotourism and thus the recovery of the park (Bradshaw et al. 2005, Shannon et al. 2013, Gaynor et al. 2018a).

6. NEUROBIOLOGY AND PSYCHOLOGY OF FEAR IN WILD ANIMALS

Life-threatening events can have enduring, even lifelong, effects on the brain and behavior, as shown most clearly by PTSD. Over 600 animal model (laboratory rodent) studies of PTSD have been conducted, with exposure to a predator (or predator stimuli) being the most common paradigm employed because it constitutes a life-threatening event that induces enduring effects mirroring those in humans (Deslauriers et al. 2018). To meet the criteria to be considered an animal model of PTSD, these effects must endure for 7–90 days, and include alterations in the structure or function of the neuronal circuits for fear involving the amygdala and hippocampus, together with diagnostic changes in behavior (Daskalakis et al. 2013, Diamond & Zoladz 2016, Deslauriers et al. 2018, Mitra 2019). Both the cause—predator-induced fear—and the diagnostic behaviors, which are hypervigilance and the avoidance of trauma-related situations, provide a direct link to the ecology of fear, because these are the same two behaviors (vigilance and avoidance in reaction to predators) that Brown et al. (1999) and others (Sih 1980, Lima & Dill 1990, Creel 2018) have focused on as interfering with foraging—and thus potentially reducing fecundity or survival. This link suggests that fear effects on populations and communities may be commonplace, because if predator exposure in nature causes long-lasting changes in behavior interfering with foraging over weeks to months, this greatly increases the

likelihood of impacts on abundance (Brown et al. 1999; Clinchy et al. 2011, 2013; Zanette et al. 2019).

Enduring effects on the brain and behavior meeting the criteria to be considered an animal model of PTSD—in a wild animal—have recently been demonstrated in an experiment using standard laboratory rodent model of PTSD procedures and measures, conducted on wild-caught birds (black-capped chickadees, *Poecile atricapillus*) (Zanette et al. 2019). Individuals heard intermittent playbacks of predator or non-predator vocalizations over 2 days, and were then housed together in flocks in outdoor aviaries for 7 days, before being assayed. Differences in behavior were assayed by testing the reactions of all birds to hearing a signal of predator danger (conspecific alarm calls), not among the vocalizations any of them heard the week previously. Birds that heard predators 7 days before demonstrated a sixfold greater increase in time spent freezing (vigilant and immobile) in reaction to hearing the alarm calls, behaviorally manifesting an enduring memory of fear. This enduring memory of fear was also evident in the brain. Birds that heard predators 7 days before had 48% higher levels of ΔFosB in the amygdala and 42% higher levels in the hippocampus (ΔFosB being a transcription factor known to modify genes associated with chronic stress) (Zanette et al. 2019).

Enduring predator-induced effects on the brain have subsequently been demonstrated in another experiment on wild birds (brown-headed cowbirds, *Molothrus ater*), conducted under near-natural conditions on flocks living in large (200 m^2) outdoor aviaries complete with natural vegetation for cover (L.E. Witterick, J. Hrynkiewicz, S.A. MacDougall-Shackleton, C.D.C. Bailey, M. Clinchy & L.Y. Zanette, manuscript in preparation). As in the chickadee experiment, individuals heard intermittent playbacks of predator or non-predator vocalizations, followed by no further playbacks for 7 days, before being assayed. Here, a measure of neuronal activation more directly linked to memory was assayed, doublecortin, which is indicative of the presence of immature neurons and so used to assess neurogenesis (the birth of new neurons) in humans and other animals (Kempermann et al. 2018). Neurogenesis facilitates forgetting by aiding the overwriting of existing memories; the suppression of neurogenesis thus being to ensure memories are retained (Frankland et al. 2013). Neuroimaging studies of people with PTSD consistently report reduced hippocampal volume (Algamal et al. 2018, Butler et al. 2018), and suppressed neurogenesis is thought to be a contributing factor (Schoenfeld et al. 2017), leading to the long-lasting retention of traumatic memories seen in PTSD (Algamal et al. 2018, Butler et al. 2018). Fear of predators has been shown to suppress neurogenesis in laboratory rodents (Tanapat et al. 2001, Vignisse et al. 2017, Wu et al. 2019). The experiment on cowbirds demonstrated that fear of predators can induce the same enduring effect in wild animals living in near-natural conditions; birds that heard predators 7 days previously had 30% lower levels of doublecortin in the amygdala and 26% lower levels in the hippocampus (L.E. Witterick, J. Hrynkiewicz, S.A. MacDougall-Shackleton, C.D.C. Bailey, M. Clinchy & L.Y. Zanette, manuscript in preparation).

Reduced doublecortin expression indicative of suppressed neurogenesis in response to predator-induced fear has recently been demonstrated in an experiment on free-living wild rodents (deer mice, *Peromyscus maniculatus*). Predator or non-predator vocalizations were intermittently broadcast across four blocks of forest for three weeks. At the end of this time, a well-established field test of fearful behavior was conducted [the giving-up density of food remaining in foraging trials (Brown 2019)], and mice were then trapped to assess the effects on their physiology and neurobiology (L.Y. Zanette, M. Clinchy, P. MacCallum, J. Blundell & M.J. Sheriff, manuscript in preparation). Mice that heard predator playbacks demonstrated more fearful behavior, higher stress hormone (glucocorticoid) levels, and 55% lower doublecortin expression in the dentate gyrus of the hippocampus (L.Y. Zanette, M. Clinchy, P. MacCallum, J. Blundell & M.J. Sheriff, manuscript in preparation). Notably, there was no interval between the end of the manipulation

and sampling, so this was not a test of enduring effects, but the reduced doublecortin indicative of suppressed neurogenesis in the hippocampus provides compelling evidence consistent with predator exposure inducing an enduring memory of fear (Tanapat et al. 2001, Vignisse et al. 2017, Wu et al. 2019).

Predator-induced suppression of neurogenesis has also been shown in field observations and lab experiments on electric fish (*Brachyhypopomus spp.*). In the field, lower brain cell proliferation indicative of suppressed neurogenesis was documented in fish from populations where predators were abundant and, within populations, in individuals that had tail injuries from predator attacks (Dunlap et al. 2016). Corroborating the conclusion that predator-induced fear was the causal mechanism, experiments in the lab demonstrated that simulated predator chases induced a 48% reduction in brain cell proliferation, and 17 days following experimental tail amputation, there was an enduring 55% reduction (Dunlap et al. 2017).

The physical trauma resulting from an unsuccessful predator attack need not be as severe as tail amputation to induce a memory of fear. Marzluff et al. (2012) measured brain activation in crows (*Corvus brachyrhynchos*) shown people wearing masks molded from the face of the person that captured them (predator) or the person that cared for them (non-predator). Capture and release with no visible injury was itself traumatic enough that crows shown the 'predator' mask demonstrated elevated activation in the amygdala and related neuronal fear circuits. The complexity of what wild animals find fearful is here illustrated not only by differences in fear memories being induced by an apparently quite mild trauma but also the fact that the crows discriminated different human faces. Prey discriminating between dangerous and harmless members of the same predator species has similarly been demonstrated in field experiments on harbor seals (*Phoca vitulina*) and elephants. Harbor seals responded fearfully to playbacks of the vocalizations of mammal-eating killer whales (*Orcinus orca*) but not fish-eating ones (Deecke et al. 2002). Elephants likewise responded fearfully to playbacks of people speaking Maasai but not Kamba, languages which are spoken by people who do and do not hunt elephants, respectively (McComb et al. 2014).

Retaining a memory of a physical trauma resulting from an unsuccessful predator attack is obviously useful if this improves the chances of surviving subsequent predator attacks. This was recently demonstrated in an experiment on wild-caught squid (*Doryteuthis pealei*) subjected to a minor experimental injury (removal of 5–10 mm from the tip of an arm); some squid were not anesthetized and so had a memory of the pain, while others were anesthetized and thus had no such memory (Crook et al. 2014). Individuals from both treatments were then placed together with a predatory fish. Those with a memory of suffering a physical trauma (not anesthetized during injury) demonstrated longer alert and flight-initiation distances in response to the predator and consequently had a 2.4-fold higher probability of survival.

Natural populations of free-living wildlife may commonly contain a large proportion of individuals that have suffered a physical trauma due to a predator attack and can thus be expected to retain a memory of this trauma, like the electric fish, crows, and squid in the previous experiments. Most predator attacks are unsuccessful (Vermeij 1982, Packer & Ruttan 1988), meaning most prey escape, but there is growing evidence that they do not necessarily escape unharmed, resulting in considerable numbers of walking wounded. For example, recent studies have shown that up to 32% of living adult female giraffes bear scars from lions (Strauss & Packer 2013), 25% of harbor porpoises (*Phocoena phocoena*) bear claw and bite marks from gray seals (*Halichoerus grypus*) (Leopold et al. 2015), and 100% of manta rays (*Manta alfredi*) bear multiple bite wounds from sharks (Marshall & Bennett 2010).

Fear is governed by cognitive information processing, as emphasized in the new focus on the neurobiological complexities of fear (LeDoux & Pine 2016, LeDoux 2017). Information is not a physical substance, and it is thus not possible to literally overdose on it; it is either used or not

depending on whether it is useful. Just as retaining a memory can be useful, it can be equally useful to forget, and as explained above, neurogenesis appears integral to both remembering—and forgetting (Frankland et al. 2013, Kempermann et al. 2018). Forgetting is reflected in habituation, i.e., the attenuation of responding to information that experience indicates is useless, because responding is costly. Habituation is governed in part by the time between exposures to an aversive stimulus; irregularity and infrequency lessen the likelihood of habituation (Blumstein 2016). Importantly, if exposure to the aversive stimuli is paired with pain, i.e., physical trauma, habituation (forgetting) is far less likely and may never occur at all (Blumstein 2016). This interplay of memory and forgetting in relation to life experiences means that, as in humans (Daskalakis et al. 2013), there are likely to be immense individual differences among animals in their responses to life-threatening events. With respect to responses to predators, animal populations may be expected to consist of some combination of naïve individuals, such as juveniles, who have yet to learn what to fear; individuals with an enduring memory of fear who may or may not be habituating depending upon the circumstances of subsequent exposures; and individuals who have suffered both physical and psychological trauma whose behavior has been more or less permanently transformed (**Figure 1**).

The ecology of fear posits that effects on abundance result from the activity cost of devoting time to anti-predator behavior rather than foraging (Brown et al. 1999, Brown 2019). By establishing that the activity cost of a predator encounter can be far greater than that entailed by a transient fight-or-flight reaction, and can instead persist in affecting the brain and behavior for weeks or even permanently, the growing experimental evidence of enduring PTSD-like changes in wild animals provides a compelling mechanism strongly supporting the supposition that population- and community-level effects of fear are indeed commonplace in nature.

7. FUTURE PROGRESS

Fear itself clearly can have population- and community-level effects in free-living wildlife, as demonstrated by the experiments we have reviewed. What is equally clear is the need for more experiments—and the means to accomplish them. The success of vegetation-thinning experiments in demonstrating community-level effects of fear in large carnivore systems points to the ready feasibility of removing cover (or adding it; e.g., Fležar et al. 2019) to test for population-level effects in these systems. This is not untried, as removing vegetative cover was shown to reduce reproductive success by inducing fear, in a semi-natural experiment on small mammals (Dehn et al. 2017). In species that rely on group vigilance, like many large herbivores (Creel et al. 2019, Say-Sallaz et al. 2019), culling ('adding' predation) (e.g., Travers et al. 2010) could be particularly effective in inducing fear by reducing the dilution effect (Brown et al. 1999). Food supplementation can corroborate that effects are due to fear by eliminating bottom-up limitation as an alternative explanation (Travers et al. 2010, Krebs et al. 2018). 'Adding' predators by simulating their presence using various means has proven effective in both community- and population-level experiments, and the new research on fear of humans indicates the 'added' predator most likely to induce population-level effects of fear in large carnivore systems is the human super predator. The enduring effects of fear, and the complexity of what cognitively sophisticated species like birds and mammals find fearful, which are both being revealed by the new research on the neurobiology and psychology of fear in wild animals, respectively reinforce the likely commonality of population- and community-level effects of fear, and the necessity of conducting field experiments to corroborate observational results regarding the ecology of fear. The imperative for conducting further carefully designed field experiments concerns the many conservation consequences of fear, well-illustrated by the recent research in Gorongosa National Park, reviewed in Sections 4 and 5 (Gaynor et al. 2018a, Atkins et al. 2019).

DISCLOSURE STATEMENT

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