Fear in Wildlife Food Webs: Large Carnivore Predation Risk Mediates the Impacts of a Mammalian Mesopredator

by

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B.S., University of Virginia, 2006
M.Sc., Simon Fraser University, 2011

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Supervisory Committee

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Abstract

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Mounting evidence suggests that large carnivores regulate the abundance and diversity of species at multiple trophic levels through cascading top-down effects. The fear large carnivores inspire in their prey may be a critical component of these top-down effects, buffering lower trophic levels from overconsumption by suppressing large herbivore and mesopredator foraging. However, the evidence that the fear of large carnivores cascades through food webs has been repeatedly challenged because it remains experimentally untested.

My collaborators and I exploited a natural experiment – the presence or absence of mesopredator raccoons (*Procyon lotor*) on islands in the Gulf Islands of British Columbia, Canada – to examine the breadth of mesopredator impacts in a system from which all native large carnivores have been extirpated. By comparing prey abundance on islands with and without raccoons, we found significant negative effects of raccoon presence on terrestrial (songbirds and corvids), intertidal (crabs and fish) and shallow subtidal (red rock crabs *Cancer productus*) prey, demonstrating that, in the absence of native large carnivores, mesopredator impacts on islands can extend across ecosystem boundaries to affect both terrestrial and marine communities.

To test whether fear of large carnivores can mitigate these community-level impacts of mesopredators, we experimentally manipulated fear in free-living raccoon populations using month-long playbacks of large carnivore vocalizations and monitored the effects on raccoon behaviour and the intertidal community. Fear of large carnivores reduced raccoon foraging to the benefit of the raccoon's prey, which in turn affected a competitor and prey of the raccoon's prey. By experimentally restoring the fear of large carnivores in our study system, we succeeded in reversing the impacts of raccoons, reinforcing the need to protect large carnivores given the conservation benefits the fear of them provides.

Our experimental work demonstrated that fine-scale behavioural changes in prey in response to predation risk can have community-level effects relevant to biodiversity conservation. However, experimentally testing animal responses to predators and other sources of risk in free-living wildlife presents considerable logistical challenges. To address these challenges, my collaborators and I developed an Automated Behavioural Response system, which integrates playback experiments into camera trap studies, allowing researchers to collect experimental data from wildlife populations without requiring the presence of an observer. Here I describe tests of this system in Uganda, Canada and the USA, and discuss novel research opportunities in ecology and conservation biology made available by this new technology.

Table of Contents

Supervisory Committee .... **ii**

Abstract .... **iii**

Table of Contents .... **v**

List of Tables .... **vii**

List of Figures .... **viii**

Acknowledgments .... **xi**

Dedication .... **xiii**

Chapter 1 - Introduction **1**

Chapter 2 - Mammalian Mesopredators on Islands Directly Impact both Terrestrial and Marine Communities **8**

- **2.1 Abstract** **9**
- **2.2 Introduction** **9**
- **2.3 Methods** **12**
  - 2.3.1 Overview, study species, and area 12
  - 2.3.2 Quantifying raccoon predation on song sparrow nests 13
  - 2.3.3 Surveying for raccoon presence or absence in the Gulf Islands 15
  - 2.3.4 Design of the mensurative experiment 16
  - 2.3.5 Quantifying raccoon impacts on bird abundance 17
  - 2.3.6 Quantifying raccoon impacts on intertidal fish 18
  - 2.3.7 Quantifying raccoon impacts on intertidal shore crabs 18
  - 2.3.8 Quantifying raccoon impacts on red rock crabs 18
  - 2.3.9 Quantifying raccoon shoreline use where apex predators persist (Clayoquot Sound) 21
  - 2.3.10 Statistical analyses 21
- **2.4 Results** **23**
  - 2.4.1 Raccoon predation on song sparrow nests 23
  - 2.4.2 Raccoon presence and abundance in the Gulf Islands and Clayoquot Sound 23
  - 2.4.3 Effects of raccoon presence on bird abundance 24
  - 2.4.4 Effects of raccoon presence on intertidal fish 25
  - 2.4.5 Effects of raccoon presence on shore crabs 25
  - 2.4.6 Effects of raccoon presence on red rock crabs 26
- **2.5 Discussion** **29**
  - 2.5.1 Raccoon impacts on terrestrial bird communities 29
  - 2.5.2 Raccoon impacts on nearshore marine communities 30
  - 2.5.3 Mesopredator release in an island system 31
  - 2.5.4 Conservation implications 32

Chapter 3 – Fear of Large Carnivores Causes a Trophic Cascade **34**

- **3.1 Abstract** **35**
- **3.2 Introduction** **35**
- **3.3 Methods** **40**

3.3.1 Study area.....40
3.3.2 Motivation and objectives.....40
3.3.3 Preparing the playbacks.....41
3.3.4 Raccoon immediate reaction to large carnivore vocalizations.....42
3.3.5 Raccoon long-term response to the fear of large carnivores.....43
3.3.6 Measuring cascading effects of fear.....47
3.3.7 Statistical analyses.....49
3.4 Results.....54
3.5 Discussion.....59
Chapter 4 – A New Automated Behavioural Response System to Integrate Playback Experiments into Camera Trap Studies.....63
4.1 Abstract.....64
4.2 Introduction.....65
4.3 Technical Description.....67
4.4 Methods.....70
4.4.1 Field Tests.....70
4.4.2 Measuring ABR System Success.....78
4.4.3 Statistical Analyses.....79
4.5 Results.....81
4.6 Discussion.....87
Chapter 5 – Discussion.....92
Bibliography.....99

List of Tables

Table 2.1. Island area and occurrence of raccoons and raccoon sign on the 12 Gulf Islands study islands. 16
Table 3.1. Overview of methods used in this study to test hypotheses and specific predictions 39
Table 3.2. Model results for raccoon immediate reactions to 10 s playbacks 54
Table 3.3. Model results for raccoon responses to month-long playback manipulations 55
Table 3.4. Results from Generalized Linear Models testing the effect of month-long predator and non-predator treatments on raccoon intertidal prey. 55
Table 3.5. Results from (a) Generalized Linear Mixed Effects Model, (b) Linear Mixed Effects Model and (c) Tukey's Post-Hoc Test describing the indirect effect of month-long predator and non-predator treatments on shallow subtidal red rock crab abundance. 56
Table 3.6. Results from (Generalized) Linear Mixed Effects Models testing the cascading effects of month-long predator and non-predator treatments on intertidal and subtidal species not directly eaten by raccoons.......... 57
Table 4.1. Species from which trials were obtained during field tests of the ABR system in Bwindi and Clayoquot. The body mass and functional group of each species is shown, along with species-specific values for each of three metrics of ABR system success: *proportion triggered*, *proportion observable*, and *overall success rate* (defined in the text) 75
Table 4.2. Results from ANCOVA models testing the effects of species body mass, field test location and functional group on ABR system success at both Bwindi and Clayoquot. P-values shown in bold are significant at $\alpha = 0.05$. 82
Table 4.3. Results from Generalized Linear Mixed Effects Models testing the effects of pre-playback behaviour, species body mass, and functional group on ABR system success at Bwindi Impenetrable National Park. P-values shown in bold are significant at $\alpha = 0.05$. 85
Table 4.4. Results from Generalized Linear Mixed Effects Models testing the effects of ABR system design (Mark 1 or Mark 2) and species body mass on system success at Clayoquot. P-values shown in bold are significant at $\alpha = 0.05$. 85

List of Figures

Figure 2.1. Distribution of raccoons on the Gulf Islands, B.C., Canada. Islands shown in black indicate those on which the presence of raccoons was established, whereas no raccoons or raccoon latrines were observed on islands shown in white. Islands shown in grey were not surveyed. Labeled islands represent the 6 raccoon-present (P1-P6) and 6 raccoon-absent (A1-A6) study islands compared in the 2012 mensurative experiment.. 14

Figure 2.2. Shrub- and ground-nesting songbird (a) and corvid (b) abundance per hectare on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Values are means ± SE. The asterisk denotes a significant difference of $P < 0.05$..................... 24

Figure 2.3. (a) Prickleback and (b) northern clingfish abundance (per m^2) in the mid (Mid) and high (High) intertidal zones on raccoon-present (grey bars) and raccoon-absent (white bars) islands. No clingfish were observed in the high intertidal zone on any island. Data are presented as standard box plots: the bold horizontal black lines indicate median values, the box edges represent the 25% and 75% quartiles, and the whiskers signify the range. 25

Figure 2.4. (a) Large (> 2.0 cm carapace width) and (b) medium-sized (1.31 - 2.0 cm carapace width) shore crab abundance (per m^2) in the mid (Mid) and high (High) intertidal zones on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Data are presented as standard box plots, as described in the caption to Fig. 2.3. The two asterisks denote a significant difference of $P < 0.01$........................... 26

Figure 2.5. (a) Intertidal and (b) shallow subtidal red rock crab abundance, considering red rock crabs live-captured per tide cycle, and live-trapped per 24 hrs (two full tide cycles), respectively, on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Data are presented as standard box plots, as described in the caption to Fig. 2.3. The single asterisk denotes a significant difference of $P < 0.05$; two denote a significant difference of $P < 0.01$ 27

Figure 2.6. Shallow subtidal red rock crab carapace size (cm) comparing males and females live-trapped on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Values are means ± SE. For comparison, the carapace size of red rock crabs freshly preyed-upon by raccoons is indicated by the horizontal solid (mean) and dashed (± SE) lines. The asterisk denotes a significant difference of $P < 0.05$......... 28

Figure 3.1. Fear of large carnivores caused a trophic cascade. Diagram illustrating how broadcasting playbacks of large carnivore vocalizations affected multiple lower trophic levels. Green and red arrows represent positive and negative effects respectively on foraging, abundance or survival. Solid arrows connect predator and prey; dashed arrows connect species affected, but not directly eaten, by another...... 37

Figure 3.2. Raccoon behaviour scoring. Examples of the protocol used to score time spent foraging or vigilant based on raccoon head position in video recordings of 10 s playback trials and in 30 s time-lapse photos from month-long playback manipulations. Videos (10 s playbacks) or photos (month-long playbacks) were scored as: (a) foraging if the head angle (angle between a line connecting the ears and nose of a raccoon head in profile and the horizontal) was > 45° *or* if the tops of the

ears were below the rump; or (b) vigilant if the head angle was ≤ 45° *and* the tops of the ears were in line with or above the rump. 46

Figure 3.3. Fear of large carnivores reduced mesocarnivore foraging. (a) Probability of remaining in the intertidal (% of trials), and (b) time spent foraging (out of 60 s) immediately following 10 s predator and non-predator playbacks. (c) Time spent in the intertidal (per occurrence on camera), and (d) proportion of time spent foraging (per occurrence on camera) during month-long predator and non-predator playbacks. Values are means ± SE. 53

Figure 3.4. Fear of large carnivores benefited the mesocarnivore's prey. Abundance of (a) intertidal crabs, (b) intertidal fish, (c) intertidal polychaete worms, and (d) subtidal red rock crabs following month-long predator and non-predator playbacks. Values are means ± SE... 53

Figure 3.5. Fear of large carnivores affected a competitor and prey of the mesocarnivore's prey. (a) Change in abundance of staghorn sculpins over one month and (b) survival of periwinkle snails per tide cycle during month-long predator and non-predator playbacks. Values are means ± SE. 57

Figure 3.6. Fear of large carnivores affects red rock crab abundance. Red rock crab abundance compared between the pre-treatment, predator and non-predator playback periods sampled in the course of the more intensive red rock crab sampling conducted in 2014. Red rock crabs were trapped once prior to the start of any playback treatments (pre-treatment, n = 10), and then weekly during month-long predator (n = 40) and non-predator (n = 40) treatments (Linear Mixed Effects Model with Tukey's Post-Hoc Test; n.s. = not significant, $*P < 0.05$, $**P < 0.001$). Values are means ± SE... 58

Figure 4.1. Design of the Automated Behavioural Response (ABR) system. (a) Block diagram illustrating the major components of both Mark 1 and Mark 2 ABR designs. (b) The full Mark 1 ABR system, deployed in the field, illustrating the pairing of a speaker unit ('Speaker') and attached motion sensor ('Sensor') with a commercially available camera trap ('Camera'). (c) Inside of the ABR speaker unit, illustrating the custom microcontroller, which allows the user to program the delay between triggering of the motion senor and playback start ('Delay'), as well as the duration of the playback ('Duration'; see detail in c). (d) Outside of the ABR speaker unit illustrating the commercially available, weatherproof speaker ('Speaker'), which as been modified to be triggered by an external motion sensor, and the custom battery pack ('Battery Pack'), which extends the lifespan of both the speaker and the audio player it broadcasts. 69

Figure 4.2. The effect of focal animal body mass (log base 10-transformed) on ABR system success at Bwindi (gray symbols) and Clayoquot (black symbols). ABR system success was measured as (a) *proportion triggered*, (b) *proportion observable*, and (c) *overall success rate* (see text for success metric definitions). Each data point represents the proportion of successful trials for a single mammal species. Solid lines represent a significant, positive relationship between focal animal body mass and ABR system success within a given site, as estimated by weighted linear regression. Dashed lines represent ± 1 SE of model estimates. 83

Figure 4.3. The effect of pre-playback behaviour on ABR system success, measured as (a) *proportion observable* ($P = 0.017$) and (b) *overall success rate* ($P = 0.055$) (see

text for success metric definitions). Animals engaged in “Foraging” behaviours were assumed to be investigating and/or eating the bait, while animals engaged in “Non-Foraging” behaviours were not. Height of the bars represents the proportion of successful trials across all mammal species at Bwindi and error bars represent proportional standard error. 84
Figure 4.4. The effect of species functional group on the *proportion triggered* for all species at Bwindi. Height of the bars represents the proportion of successful trials across all mammal species of a given functional group and error bars represent proportional standard error. Different letters above bars denote significant differences between functional groups, as determined by Generalized Linear Mixed Effects Models and Tukey’s Post Hoc test. 86

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Dedication

To my grandmother, Joann Booth Ovack, who has been encouraging me for years to get a Ph.D. so that she can refer to her grandson the doctor

Chapter 1 - Introduction

The growing recognition that apex predators play a critical role in structuring ecosystems, affecting processes as diverse as community composition (Crooks and Soulé 1999, Croll et al. 2005), disease dynamics (Packer et al. 2003), and geomorphology (Beschta and Ripple 2012), has been called a "paradigm shift in ecology" (Estes et al. 2011, p. 306) and has focused attention on the ecological ramifications of the near global extirpation of many apex predator species (Estes et al. 2011, Ripple et al 2014). At the same time, ecologists have begun to move away from the traditional view that predator-prey dynamics are solely the product of numerical reductions in prey populations (i.e., through direct killing by predators), and to appreciate that behavioural interactions between predators and prey, mediated by the fundamental trade-off between feeding and avoiding predators (Lima and Dill 1990, Schmitz et al. 2004), can be a major driver of ecological processes (Abrams 1995, Preisser et al. 2005, Schmitz 2010). The goal of this dissertation is build on these shifting perspectives in ecology, using geographical comparisons and manipulative experiments to directly test the role of prey behavioural changes in driving the community-level effects of apex predators.

Apex predators may influence communities and ecosystems through the initiation of trophic cascades (Terborgh and Estes 2010), indirectly affecting whole food webs through direct suppression of their prey. In terrestrial habitats, large carnivores are suggested to affect multiple lower trophic levels by suppressing large herbivores and mesocarnivores, thereby initiating both "tri-trophic cascades" (large carnivore – large herbivore – plant) and "mesopredator cascades" (large carnivore – mesopredator – mesopredator's prey) (Ripple et al. 2014, Ford and Goheen 2015). Wolves (*Canis lupus*) and cougars (*Puma concolor*) in North America provide an excellent example of this dual role of large carnivores. Numerous studies indicate that these predators positively affect the abundance, growth and recruitment of woody plant species by suppressing large ungulates (e.g., elk [*Cervus elaphus*], moose [*Alces alces*] and mule deer [*Odocoileus hemionus*]; Hebblewhite et al. 2005; Ripple and Beschta 2006, 2008; Peterson et al. 2014), and, in the case of wolves, provide refuge for smaller vertebrates (e.g., pronghorn antelope [*Antilocarpa Americana*, Berger et al. 2008], red foxes [*Vulpes vulpes*, Newsome and Ripple 2015], various small mammals [Miller et al. 2012]), by suppressing coyotes (*Canis latrans*). The maintenance of biodiversity and ecosystem function (e.g., primary productivity) in some terrestrial habitats may therefore depend on large carnivore suppression of their prey (Letnic et al. 2012, Ritchie et al. 2012).

Even so, there is considerable debate about the nature and biological importance of trophic cascades in terrestrial ecosystems (Strong 1992, Polis and Strong 1996, Schmitz et al. 2004, Shurin et al. 2006). While partially a matter of definitions (e.g., 'species-level' vs. 'community-level' cascades; Polis et al. 2000), concerns have been raised regarding the strength of cascading effects in complex terrestrial food webs (Polis and Strong 1996, Shurin et al. 2006), particularly those involving large carnivores, where experimental evidence for trophic cascades is currently scarce (Ford and Goheen 2015). If predation by large carnivores is compensatory (Boyce et al. 1999), or otherwise affects only a small proportion of the prey population, any cascading effects of large carnivores may be overwhelmed by other ecosystem processes (Ford and Goheen 2015). Nonetheless, compelling examples of cascading effects in terrestrial ecosystems have accumulated in the literature, revealed by the loss or reintroduction of large carnivores (Terborgh and Estes 2010, Estes et al. 2011, Ripple et al. 2014). This apparent discrepancy may be overcome by recognizing the role of predator-induced fear (i.e., perceived risk of death) in terrestrial food webs, which has the potential to affect entire prey populations (Werner and Peacor 2003), even when the numerical effects of predators on prey are relatively minor (Schmitz et al. 2004).

Trophic cascades are typically thought to result when predators reduce prey population sizes through direct killing and consumption, thereby benefitting the prey's resource (Oksanen et al. 1981, Peckarsky et al. 2008). However, predators don't just kill prey. Fear of predation induces changes in prey behaviour (Lima 1998) and physiology (Hawlena and Schmitz 2010, Zanette et al. 2014) that can severely impact prey survival and reproduction (Sheriff et al. 2009, Zanette et al. 2011), and recent work suggests that fear may be equally or more important than direct killing in projecting the effects of predators across multiple trophic levels (Abrams 1995, Schmitz et al. 2004, Preisser et al. 2005). Scared prey eat less (Lima and Dill 1990) and, by altering prey foraging behaviour and habitat use, fear of predators may itself lead to significant positive effects on the prey's resource (Werner and Peacor 2003, Schmitz et al. 2004). Such behaviourally mediated trophic cascades (BMTC) have been well demonstrated in several aquatic and invertebrate systems (e.g., Turner and Mittelbach 1990; Beckerman et al. 1997; Trussell et al. 2006a,b; Alexander et al. 2013; reviewed in Preisser et al. 2005), often through the use of non-functional "fear-only" predators (e.g., spiders with disabled mouth parts; Beckerman et al. 1997) or predator chemical cues (e.g., Trussell et al. 2006a, Alexander et al. 2013), which allow researchers to eliminate actual predation and isolate the effects of fear alone on prey and their resource populations. These laboratory and mesocosm experiments have shown powerful effects of the fear of predators on the energetics (Trussell et al. 2006b, 2008) and survival (Werner and Anholt 1996, Beckerman et al. 1997, Reynolds and Bruno 2013) of prey, with cascading effects on the abundance (Schmitz et al. 1997, Trussell et al. 2006a, Reynolds and Bruno 2013), diversity (Schmitz 2003) and chemical composition (Reynolds and Sotka 2011, Hawlena et al. 2012) of lower trophic levels, which can in turn affect ecosystem function (e.g., decomposition [Hawlena et al. 2012], energy transfer [Trussell et al. 2008]).

Fear may also be a major component in large carnivore suppression of large herbivores and mesopredators, with cascading effects on plants and lower trophic level animals. Indeed, several herbivore species have been shown to alter their foraging behaviour and habitat use in response to large carnivore presence (Laundré et al. 2001, Creel et al. 2005, Fortin et al. 2005), or to avoid habitat types associated with increased large carnivore predation (Ripple and Beschta 2004, Ford et al. 2014), and these behavioural changes have in some cases been suggested to lead to fundamental changes in the plant community (Ripple and Beschta 2012, Ford et al. 2014). However the existence of such cascading fear effects initiated by large carnivores remains highly controversial. Current evidence for fear-based trophic cascades in wildlife comes largely from observational studies, which suffer from an inability to exclude compelling alternative hypotheses (Dobson 2014, Peterson et al. 2014, Ford and Goheen 2015). In a well-known example, the reintroduction of wolves to Yellowstone National Park, USA, has been suggested to lead to fear-induced changes in elk reproductive success (Creel et al. 2007) and foraging behaviour (Creel et al. 2005), with resulting benefits for woody browse species, such as aspen (*Populus termuloides*) (Ripple and Beschta 2004, 2012; Fortin et al. 2005).

However, the suggested BMTC from wolves to aspen remains experimentally untested, and the existence of the indirect benefit to woody plants has been repeatedly challenged (e.g., Kauffman et al. 2010; Winnie 2012, 2014; Middleton et al. 2013), with several authors contending that bottom-up factors (e.g., prolonged drought) and high human harvest rates of elk better explain observed changes in both elk and aspen populations (Vucetich et al. 2005, Kauffman et al. 2010, Dobson 2014). Experimentally isolating the effects of large carnivore-induced fear on prey and testing for cascading effects at lower trophic levels would provide crucial evidence toward resolving this debate, but the logistical challenges associated with conducting experiments on free-living wildlife have so far precluded such research.

Where large carnivore populations have been reduced or extirpated, outbreaks of middle trophic level species can lead to the dramatic reorganization of ecosystems (Terborgh et al. 2001, Colman et al. 2014). The effects of large carnivore loss may cascade through food webs, mediated by relaxed suppression of prey, and potentially result in alternative, low diversity states (Scheffer 2010) dominated by invasive species (Wallach et al. 2010). The "mesopredator release hypothesis" (Prugh et al. 2009, Elmhagen et al. 2010, Gordon et al. 2015) describes one potential consequence of large carnivore loss: outbreaks of smaller mesopredators and subsequent declines and extinctions among the mesopredator's prey. Mesopredator release has been repeatedly implicated in the loss of small vertebrates (Ritchie and Johnson 2009, Brashares et al. 2010), including in Australia, where lethal control of dingos (*Canis dingo*) is associated with increased abundance of introduced mesopredators (red foxes and cats), and declines in the abundance and diversity of Australia's native small mammals (Johnson et al. 2007, Letnic et al. 2009, Colman et al. 2014). Where they co-occur with large carnivores, mammalian mesopredators are known to alter their activity patterns (e.g., Brook et al. 2012) and habitat use (e.g., Durant 2000, Broekhuis et al. 2013, Swanson et al. 2014), behaviours that may limit impacts on lower trophic levels by reducing the temporal and spatial extent of mesopredator foraging. By releasing mesopredators from behavioural suppression, the loss of fear associated with large carnivore extirpation may be a major driver of declines in abundance and diversity of lower trophic level animals (Ritchie and

Johnson 2009, Brashares et al. 2010, Ritchie et al. 2012), though the role of fear in mediating mesopredator release remains experimentally untested.

Many mammalian mesopredators are opportunistic omnivores (Prugh et al. 2009, Brashares et al. 2010), with broader diets than their large carnivore predators (which are more likely to specialize on large vertebrate prey; Carbone et al. 2007), and release of these omnivorous mesopredators from top-down suppression may therefore lead to impacts on a broad range of prey species (Brashares et al. 2010). Indeed the impacts of mammalian mesopredators may be more pervasive than is typically described, with most mesopredator release studies focusing on impacts to terrestrial vertebrate populations (e.g, Elmhagen et al. 2010, Colman et al. 2014; for reviews, see Ritchie and Johnson 2009, Brashares et al. 2010). In coastal habitats and on islands, the expected omnivory of mammalian mesopredators may allow them to exploit nearshore resources such as intertidal vertebrates and invertebrates (Carlton and Hodder 2003), providing the potential for the impacts of mesopredator release to extend across ecosystems, affecting both terrestrial and marine species.

The bulk of the work presented here seeks to understand the role of large carnivore-induced fear in mediating the impacts of mammalian mesopredators, and, more generally, to provide the first direct experimental test of the cascading effects of fear in a wildlife system. My collaborators and I used comparative studies and large-scale field manipulations in the Gulf Islands of British Columbia, Canada to (1) estimate the impacts of mammalian mesopredator populations on both terrestrial and marine prey in the absence of now extirpated native large carnivores, and (2) experimentally test whether restoring the fear of large carnivores where it has been lost could reverse these impacts. As described in detail in Chapter 2, all native large carnivores (wolves, cougars and black bears [*Ursus americanus*]) have been extirpated from the Gulf Islands over the past century (Golumbia 2006), which, according to the mesopredator release hypothesis (Elmhagen et al. 2010, Gordon et al. 2015), may have freed mesopredator raccoons (*Procyon lotor*) to significantly increase their impacts on prey. Evidence from nearby Vancouver Island – where healthy populations of wolves, cougars and black bears persist (Hansen et al. 2010) – suggests that raccoons experience significant top-down control where they co-occur with their native large carnivore predators (see Chapter 2). The absence of such top-down control in the Gulf Islands provides a novel opportunity to experimentally reintroduce just the fear of large carnivores and directly test the role of predator-induced fear in mediating the impacts of mesopredator release.

In Chapter 2, I examine the breadth and severity of mammalian mesopredator impacts in an island system lacking native apex predators. Mammalian mesopredators have been implicated in the decline and extinction of terrestrial vertebrates in many island systems (e.g., Atkinson 2001, Blackburn et al. 2004, Salo et al. 2008), and here I test whether these impacts extend to the surrounding marine community. Drawing on a survey of 44 Gulf Islands that established raccoon presence or absence across the entire archipelago, my collaborators and I compared the abundance of both terrestrial and marine prey between islands with and without raccoons. We show that raccoon presence on an island is associated with substantial reductions in terrestrial and marine prey, indicative of dramatic impacts of this mesopredator that extend across the terrestrial-marine boundary. By comparing shoreline counts of raccoons between the Gulf Islands and Clayoquot Sound on Vancouver Island, where large carnivores persist, we provide evidence that the extirpation of native large carnivores from the Gulf Islands is a major driver of the observed impacts of raccoons.

In Chapter 3, I describe large-scale, replicated field experiments designed to test whether fear itself of large carnivores, independent of actual killing and consumption of mesopredators, can mitigate the impacts of mesopredators on their prey. Using month-long playback manipulations, my collaborators and I found that fear of large carnivores can indeed reverse raccoon impacts on prey, which in turn sets off cascading effects across the marine community. This work provides the first direct experimental test of the role of large carnivore-induced fear in initiating a trophic cascade and strongly supports the contention that the fear large carnivores instill in their prey directly contributes to the maintenance of biodiversity and ecosystem function. This finding has significant implications for the conservation of large carnivores, which I discuss in Chapter 3.

The work described in Chapter 3 demonstrates that relatively fine-scale behavioural changes (e.g., a reduction in the proportion of time raccoons spent foraging in response to perceived predation risk) can, in the aggregate, have community-level effects (e.g., a measurable increase in raccoon prey abundance), suggesting that a full understanding of predator-prey interactions and their relevance to conservation requires detailed knowledge of such fine-scale behavioural changes (Lima 1998; Anthony and Blumstein 2000; Buchholz 2007; Schmitz 2010). However, behavioural interactions between predators and prey are rarely observed events in many wildlife populations, and the study of such cryptic behaviours presents considerable logistical challenges. Concurrent with (and informed by) the field studies described in Chapters 2 and 3, my collaborators and I designed a novel system to address the logistical challenges of studying behavioural interactions among free-living animals. This new methodology combines camera traps, the current method of choice for non-invasive wildlife monitoring (Linkie et al. 2013, Burton et al. 2015), with playback experiments, a powerful technique for directly testing the behavioural responses of animals to myriad inter- and intraspecific cues, including those associated with predation risk. In Chapter 4, I describe the design of this new Automated Behavioural Response (ABR) system and field tests conducted in Uganda, British Columbia and California.

Collectively, the work presented in this dissertation aims to advance both our understanding of the community-level effects of behavioural interactions between predators and prey, as well as our ability to collect detailed information on these interactions in the field. Determining the degree to which processes observed in laboratory and mesocosm experiments scale up to affect open systems and free-living wildlife is a major goal in ecology, and the work presented here attempts to contribute to that goal through the development and application of empirical methods for wildlife research.

Chapter 2 - Mammalian Mesopredators on Islands Directly Impact both Terrestrial and Marine Communities

Adapted from: Justin P. Suraci[1,2], Michael Clinchy[3], Liana Y. Zanette[3], Christopher M. A. Currie[1], Lawrence M. Dill[4]. (2014) *Oecologia*,176:1087–1100.

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2.1 Abstract

Medium-sized mammalian predators (i.e., mesopredators) on islands are known to have devastating effects on the abundance and diversity of terrestrial vertebrates. Mesopredators are often highly omnivorous, and on islands, may have access not only to terrestrial prey, but to marine prey as well, though impacts of mammalian mesopredators on marine communities have rarely been considered. Large apex predators are likely to be extirpated or absent on islands, implying a lack of top-down control of mesopredators that, in combination with high food availability from terrestrial and marine sources, likely exacerbates their impacts on island prey. We exploited a natural experiment – the presence or absence of raccoons (*Procyon lotor*) on islands in the Gulf Islands, B.C., Canada – to investigate the impacts that this key mesopredator has on both terrestrial and marine prey in an island system from which all native apex predators have been extirpated. Long-term monitoring of song sparrow (*Melospiza melodia*) nests showed raccoons to be the predominant nest predator in the Gulf Islands. To identify their community-level impacts, we surveyed the distribution of raccoons across 44 Gulf Islands, and then compared terrestrial and marine prey abundances on 6 raccoon-present and 6 raccoon-absent islands. Our results demonstrate significant negative effects of raccoons on terrestrial, intertidal, and shallow subtidal prey abundance, and point to additional community-level effects through indirect interactions. Our findings show that mammalian mesopredators not only affect terrestrial prey, but that, on islands, their direct impacts extend to the surrounding marine community.

2.2 Introduction

Medium-sized mammalian predators have been implicated in declines in the abundance and diversity of prey in habitats across the globe (Atkinson 2001, Courchamp et al 2003, Blackburn et al. 2004, Schmidt 2003, Johnson et al. 2007, Prugh et al. 2009, Ripple et al. 2013). These mammalian predators are generally species that would be subject to top-down regulation by apex predators in intact ecological communities, and are thus defined here as ‘mesopredators’ (Crooks and Soulé 1999, Prugh et al. 2009). Their impacts have in many cases been attributed to (1) widespread omnivory among mesopredators (Carbone et al. 2007, Prugh et al. 2009), allowing them to impact a broad range of prey species (Brashares et al. 2010), and (2) the extirpation or absence of apex predators, which may free mesopredators from top-down control (Crooks and Soulé 1999, Johnson et al. 2007, Ritchie and Johnson 2009). Mammalian mesopredator impacts may be expected to be particularly severe on islands, where their expected omnivory may provide access to abundant food in the form of both terrestrial and marine prey, and where the limited land area means that larger apex predators are more likely to be extirpated or absent (Brown 1971, Marquet and Taper 1998, Terborgh et al. 2001). Indeed, dramatic impacts of mammalian mesopredators (including cats *Felis catus*, red foxes *Vulpes vulpes*, mink *Mustela vison* and raccoons *Procyon lotor*) on terrestrial biodiversity have been found in many island systems, including impacts on land birds (Atkinson 2001, Blackburn et al. 2004, Galetti et al. 2009), nesting seabirds, (Hartman and Eastman 1999), mammals (Burbidge and Manly 2002, Banks et al. 2008), reptiles (Iverson 1978) and amphibians (Banks et al. 2008, Salo et al. 2008). Given their omnivory, it stands to reason that mammalian mesopredators on islands may additionally impact the surrounding nearshore marine community. However, few studies have yet considered the potential impacts of mammalian mesopredators on intertidal and shallow subtidal prey.

Islands provide ample opportunity for omnivorous mammalian mesopredators to exploit marine prey (Carlton and Hodder 2003), and mesopredators may benefit substantially from such marine subsidies (Rose and Polis 1998). Consumption of marine prey has been suggested to exacerbate mesopredator impacts on terrestrial communities, although there is a paucity of data demonstrating that mammalian mesopredators whose diet is substantially subsidized by marine prey do indeed significantly impact terrestrial prey (Polis and Strong 1996, Polis et al. 1997, Rose and Polis 1998). Moreover, whereas it is clear that mesopredators may benefit from marine subsidies, to our knowledge no study to date has shown that mesopredator consumption of marine prey has a measurable impact on the abundance of the marine species consumed, i.e., that the impacts of terrestrial mammalian predators extend from terrestrial prey across the terrestrial-marine boundary to affect populations and communities of intertidal and subtidal organisms. Indeed research concerning the effects of terrestrial mammals on the diversity, abundance and distribution of marine prey has been identified as a conspicuous gap in the ecological literature (Carlton and Hodder 2003).

The likely extirpation or absence of large apex predators from islands, as a consequence of limited land area (Brown 1971, Marguet and Taper 1998, Terborgh et al. 2001), may further exacerbate mesopredator impacts on their prey through effects on both mesopredator abundance and behaviour. One of the most well established principles in behavioural ecology is that animals spend more time foraging in the absence of predators (Lima and Dill 1990, Lima 1998, Zanette et al. 2013). This increase in foraging may result from either decreased time allocation to antipredator behaviour, or increased use of profitable but risky habitats (Schmitz et al. 2004), which, in the case of mesopredators on islands, may include increased use of exposed shoreline habitats when apex predators are absent. When combined with high food availability (a likely scenario for mesopredators on islands with access to both terrestrial and marine prey), this increased foraging where predators are absent has been shown to have greater than additive effects on demography in both birds (Zanette et al. 2003, 2006) and mammals (Krebs et al. 1995, Karels et al. 2000). This may lead to very high abundances of mesopredators on islands, likely playing a major role in mediating the impacts of mammalian predators on terrestrial island prey (Atkinson 2001; Burbidge and Manly 2002; Blackburn et al. 2004, 2005; Towns, Atkinson and Daugherty 2006), and potentially driving direct impacts on the intertidal and shallow subtidal communities surrounding these islands.

In this study, we investigated the impacts of raccoons (*Procyon lotor*) on terrestrial, intertidal, and shallow subtidal prey in an island system. Raccoons are archetypical mesopredators with highly omnivorous diets (Gehrt 2003), and are known to exert strong impacts on terrestrial prey in continental systems where their apex predators are absent (Soulé et al. 1988, Rogers and Caro 1998, Crooks and Soulé 1999, Schmidt 2003). Raccoons are also among the most common terrestrial mammals observed foraging in intertidal habitats (Carlton and Hodder 2003), and are thus an ideal model species with which to investigate the impacts of insular mammalian mesopredators at the terrestrial-marine interface. Raccoons occur on a subset of islands in the Gulf Islands of British Columbia, Canada, providing the opportunity to isolate their impacts on prey communities through the direct comparison of islands with and without raccoons. Moreover, all native mammalian predators of raccoons – cougars (*Puma concolor*), wolves (*Canis lupus*), and black bears (*Ursus americanus*) – have been extirpated from the Gulf Islands over the last century (Golumbia 2006), and Gulf Islands raccoons likely experience effectively no predation. In contrast, raccoons are heavily preyed upon by large carnivores on nearby Vancouver Island, occurring in up to a quarter of both cougar and wolf scats (Hansen et al. 2010). Here we report the findings of (1) an 8-year study of raccoon predation on the nests of native songbirds (i.e. song sparrow *Melospiza melodia*), (2) a survey of 44 Gulf Islands to determine raccoon distribution, and (3) a mensurative experiment comparing raccoon-present and raccoon-absent islands, which revealed significant impacts of raccoons on both terrestrial and marine prey.

2.3 Methods

2.3.1 Overview, study species, and area

We studied the impacts of raccoons on the Gulf Islands, B.C., Canada (Fig. 2.1), from 2004 to 2012. During that time, raccoon predation on songbird nests was quantified on 4 small Gulf Islands, as part of a long-term study on the effects of predation risk on the demography of song sparrow prey (Zanette, et al. 2006, 2011; Travers et al. 2010). The high levels of raccoon predation on song sparrow nests (detailed here) implicate raccoons as the dominant nest predator in this system, and led us to undertake a survey of 44 Gulf Islands in 2011 to determine whether raccoons were present or absent, as a first step in identifying their community-level impacts. In 2012, we conducted a mensurative experiment to determine if the presence of raccoons affects the abundance of both terrestrial and marine prey, by selecting 6 raccoon-present and 6 raccoon-absent islands from among the 44 surveyed in 2011, and quantifying the abundance of selected species of birds, intertidal fish, and both intertidal and shallow subtidal invertebrates. In 2013 we conducted a methodologically comparable but less extensive survey of the relative abundance of raccoons along shorelines in Clayoquot Sound, B.C., on adjacent Vancouver Island where large carnivores (cougars, wolves and black bears) remain common and are known to regularly eat raccoons.

The apex mammalian predators (cougars, wolves and black bears) that were formerly present throughout the Gulf Islands have largely been extirpated from all islands by humans over the last century (Golumbia 2006). Their former presence is indicated by (1) museum specimens of wolves, and (2) the fact that cougars and black bears occasionally reappear on some Gulf Islands. All of these large carnivores are capable of swimming between islands (Lindzey and Meslow 1977, Darimont and Paquet 2002, Elbroch et al. 2010) and annual sightings throughout the archipelago number between 6 and 20 for cougars and 0 to 34 for black bears (records from 2009 on; B.C. Ministry of Environment, unpublished data). There are no resident animals or viable populations of large carnivores on these islands, and the individuals sighted are almost certainly all migrants from adjacent Vancouver Island. These contemporary sightings are generally restricted to the larger Gulf Islands (i.e., >2000 ha), and are responded to by attempted removal by Provincial Conservation Officers.

The Gulf Islands constitute a network of ecologically similar islands located in the north Pacific between Vancouver Island and the North American mainland (Fig. 2.1), lying between 48°33'59" N, 123°16'33" W; and 49°09'17" N, 123°47'31" W. Vegetation falls mainly into the coastal Douglas fir (*Psuedotsuga menziesii*) biogeoclimatic zone, and elevation ranges from 0 to 360 m above sea level. The islands as a whole are classified as approximately 70% forested, 13% rural, 6% agricultural, 2% suburban, and 9% other (Jewell et al. 2007). A quarter of the islands surveyed in 2011 lie within the Gulf Islands National Park Reserve, and on the other three-quarters there are a further 21 Provincial Parks and Ecological Reserves.

2.3.2 Quantifying raccoon predation on song sparrow nests

We monitored predation on song sparrow nests by continuously video-recording nests on 4 small islands (including Portland Island, used in the mensurative experiment described below) each year from 2004 to 2012. We previously reported that the average nest predation rate in the Gulf Islands is 53% (Zanette et al. 2006) and that raccoons are the principal nest predator in this system (Travers et al. 2010). Here we quantify the percentage of nest predation events attributable to raccoons and other predators, including corvids, the second most important nest predator (see Results). In addition to attacks on song sparrow nests, raccoons were filmed attacking the nests of fox sparrows (*Passerella iliaca*), white-crowned sparrows (*Zonotrichia leucophrys*), and spotted towhees (*Pipilo maculatus*). Details concerning the video recording procedures can be found in Zanette et al. (2011).

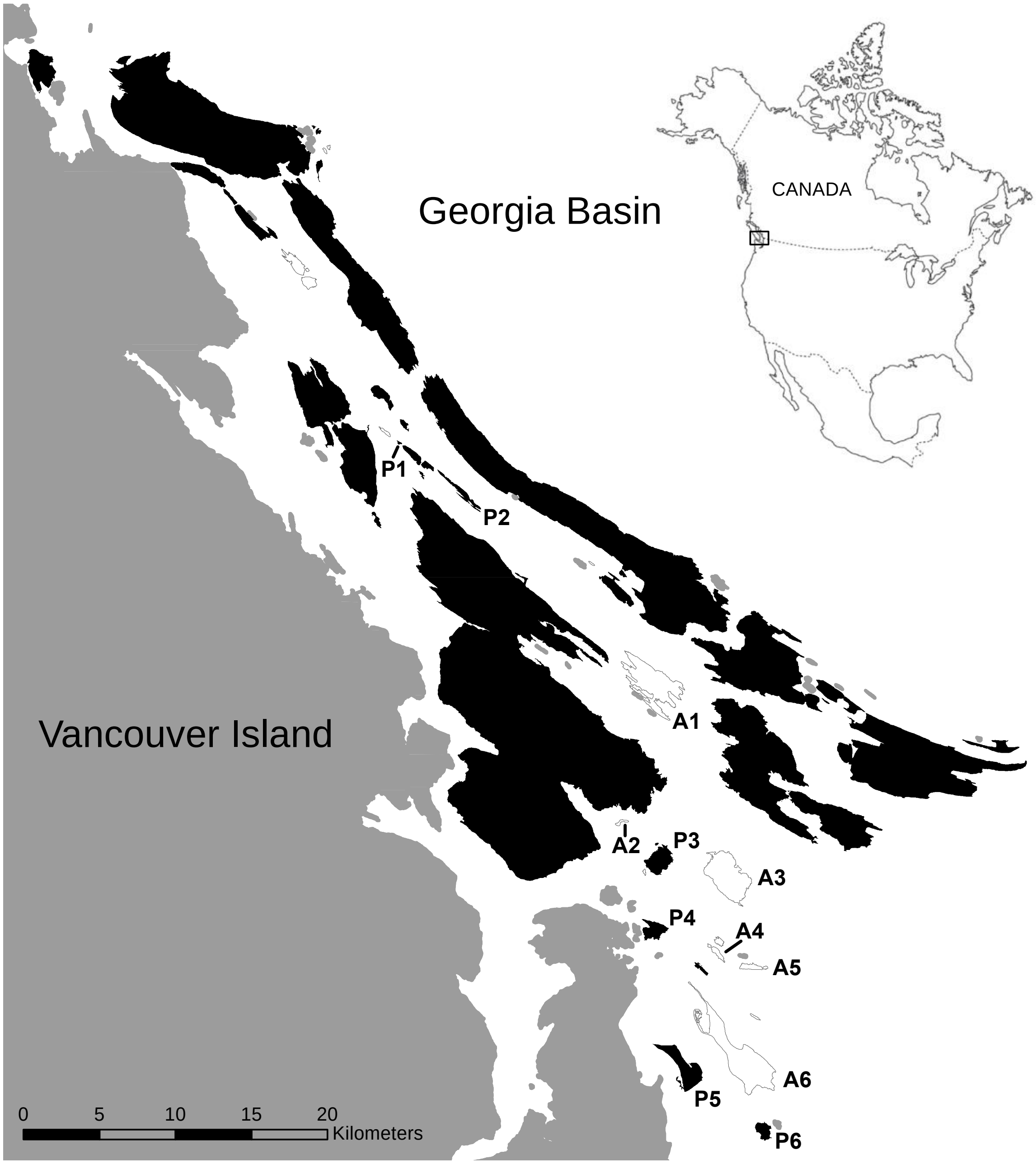

Figure 2.1. Distribution of raccoons on the Gulf Islands, B.C., Canada. Islands shown in black indicate those on which the presence of raccoons was established, whereas no raccoons or raccoon latrines were observed on islands shown in white. Islands shown in grey were not surveyed. Labeled islands represent the 6 raccoon-present (P1-P6) and 6 raccoon-absent (A1-A6) study islands compared in the 2012 mensurative experiment

2.3.3 Surveying for raccoon presence or absence in the Gulf Islands

Two independent methods were used to assess raccoon presence and estimate relative abundance among the Gulf Islands: we counted the number of (1) raccoons directly observed in or near the intertidal zone both day and night; and (2) raccoon scat piles (i.e. latrines) at the bases of trees along the shoreline (Hartman and Eastman 1999). Direct counts provide unambiguous evidence of the presence of raccoons, but are essentially a snapshot of the moment the count is conducted. Latrine transects provide information on raccoon presence over a longer timeframe and thus augment the 'snapshot' provided by direct counts. Nocturnal and diurnal direct count surveys were conducted by searching along the shoreline of all islands from an outboard-powered boat (Zodiac Pro 12) approximately 20 m off shore, and covered a minimum of 8 km of shoreline or the entire circumference of the island. Nocturnal surveys were conducted with the aid of spotlights (Hartman and Eastman 1999), and species identifications were confirmed by at least two observers. Two km latrine transects (Hartman and Eastman 1999) were walked along the tree line within ~15 m of the high tide line and observers recorded the total number of latrines and the total number of trees checked for scat piles (Table 1). Direct counts of raccoons were conducted on a total of 44 Gulf Islands between 10-May and 11-Aug-2011, and latrine transects were conducted on 37 of these islands.

The 12 Gulf Islands compared in our mensurative experiment in 2012 were chosen based on 2011 surveys, with further latrine transects and diurnal (1 per island) and nocturnal (2 per island) boat-based surveys conducted for each island (between 10-May and 21-Aug-2012) to verify the pattern of raccoon presence or absence observed in 2011 (Table 1). On the 6 islands designated raccoon-present, raccoons were invariably detected during both nocturnal surveys. No raccoons were detected during any survey of the 6 islands designated raccoon-absent. The absence of raccoons on these 6 islands is further supported by our own long-term observations, as well as those of island residents and ecologists working for the Gulf Islands National Park Reserve.

Table 2.1. Island area and occurrence of raccoons and raccoon sign on the 12 Gulf Islands study islands.

Island Name (Figure 1 Label)	Area (ha)	Raccoons km^{-1} Nocturnal[a]	Raccoons km^{-1} Diurnal[a]	Max Adults Seen	Max Adults and Juveniles Seen	Latrines Per Tree
Mowgli (P1)	4	2.5	0	4	10	0.18
D'Arcy (P6)	83	0.5	0	3	4	0.07
Wallace (P2)	87	3.5	0.4	36	51	0.10
Coal (P4)	140	3.7	3.7	25	25	0.36
Portland (P3)	225	5.0	2.0	46	46	0.28
James (P5)	335	0.2	0	2	4	0.11
Russell (A2)	12	0	0	0	0	0
Domville (A4)	31	0	0	0	0	0
Rum-Gooch (A5)	49	0	0	0	0	0
Moresby (A3)	594	0	0	0	0	0
Prevost (A1)	674	0	0	0	0	0
Sidney (A6)	854	0	0	0	0	0

[a] Number of raccoons observed per km during boat-based transects. Two nocturnal transects were run for each island, and values presented here are from the transect on which the most raccoons were observed.

2.3.4 Design of the mensurative experiment

To quantify the impacts of raccoons on both terrestrial and marine prey, we selected 6 raccoon-present and 6 raccoon-absent Gulf Islands (hereafter, “study islands”) from those surveyed in 2011, with present and absent islands matched for: (1) size (Table 1); (2) geographic distribution (Fig. 2.1); (3) human land use; and (4) land tenure. All 12 study islands are predominantly wilderness. Land use consisted of public campgrounds (3 raccoon-present islands [P], 3 raccoon-absent islands [A]), sparsely distributed private cottages (4 P, 5 A), and small hobby farms (one per island on 2 P and 2 A). Six of the 12 islands (2 P, 4 A) are wholly or partially part of the Gulf Islands National Park Reserve, and a seventh (P) is partly a Provincial park. Islands were balanced for land tenure, with wholly public (2 P, 1 A), wholly private (3 P, 2 A), or partly public-partly private islands (1 P, 3 A). We alternated sampling of raccoon-present and raccoon-absent islands, and there was consequently no difference in median sampling date (median date for both raccoon-present and raccoon-absent islands = 3-Jul-2012; n = 132, Mann-Whitney U = 2269, P = 0.672).

On all 12 study islands we quantified the abundance of selected species of birds, intertidal fish, and both intertidal and shallow subtidal invertebrates. The bird species selected were those whose nests we had directly observed (from video) being attacked by raccoons, along with those whose nests were likely equally vulnerable based on location. During our survey of the presence of raccoons, we directly observed raccoons foraging on intertidal fish (e.g., pricklebacks, family Stichaeidae), shore crabs (*Hemigrapsus nudus* and *H. oregonensis*), and red rock crabs (*Cancer productus*), and accordingly focused on these species in our assessment of the impacts of raccoons on marine prey abundance.

2.3.5 Quantifying raccoon impacts on bird abundance

To quantify the effects of the presence of raccoons on bird abundance, we focused on small passerines that, like song sparrows (Zanette et al. 2011), nest < 1 m from the ground. We included those species that were directly observed to be victims of raccoon nest predation (song sparrows, fox sparrows, white-crowned sparrows, and spotted towhees), as well as orange-crowned warblers (*Vermivora celata*), and dark-eyed juncos (*Junco hyemalis*), which nest on the ground and may therefore be expected to be at least as vulnerable to raccoon attack as those listed above. We additionally quantified the abundance of corvids (northwestern crows, *Corvus caurinus*, and common ravens, *C. corax*) because, as the second most important nest predator (as determined from video data), their abundance might be expected to affect songbird abundance (Weidinger 2002). Moreover, corvid abundance could be affected by the presence of raccoons because corvids themselves are potential victims of raccoon nest predation (Chamberlain-Auger et al. 1990).

We quantified raccoon impacts on bird abundance using point counts (Hutto et al. 1986; Morley and Winder 2013). Each point count lasted 10 minutes and surveyed a circular area of 50 m radius (i.e., 0.79 ha); all point count data are presented as the number of birds detected per unit area surveyed. All point counts (n = 16 per island) were performed between 1 and 2 hours after sunrise, and each island was surveyed on two dates between 19-May and 29-Jun-2012. Point counts were conducted within 50 m of the high tide line and were spaced approximately 200 m apart (mean ± SD distance between points = 203.3 ± 11.9 m). The same two observers performed all counts. The observers performed the first point count on an island together, and an audio recording of this first point count was made using a portable audio recorder (H2 Handy Recorder, Zoom Corp., Tokyo, Japan) to permit verification of accuracy. Abundance estimates from both observers were significantly correlated with those from audio recordings (Spearman Rank Correlation; Observer 1: $r_s = 0.69$, $P = 0.002$; Observer 2: $r_s = 0.50$, $P = 0.036$; n = 18).

For each point count location, the observer estimated percent cloud cover, rain intensity, wind speed, forest cover, and shrub cover (Zanette and Jenkins 2000). There were no systematic differences between raccoon-present and raccoon-absent islands in any of these variables (Mann-Whitney U Tests, all $P \geq 0.2$).

2.3.6 Quantifying raccoon impacts on intertidal fish

As noted, foraging raccoons were directly observed feeding on intertidal fish, and we therefore quantified the abundances of pricklebacks and northern clingfish (*Gobiesox maeandricus*) in both the mid and high intertidal zones using standard intertidal quadrat methods (Scrosati and Heaven 2007). The mid intertidal zone is characterized by macroalgal cover (predominantly *Ulva* sp. and *Fucus gardenarii*), whereas the drier high intertidal zone is dominated by barnacles (predominantly *Balanus glandula* and *Semibalanus cariosus*). In each zone, we chose a random starting point in boulder-cobble habitat and laid a 50 m transect line parallel to the water line. Ten 0.25 m^2 quadrats were then sampled at 5 m intervals along this transect by searching under rocks down to the substrate (either sand or bedrock).

2.3.7 Quantifying raccoon impacts on intertidal shore crabs

Also as noted, we directly observed raccoon predation on shore crabs (both *Hemigrapsus nudus* and *H. oregonensis*) and therefore quantified intertidal shore crab abundance using the same methods as described for intertidal fish. Shore crabs were grouped into three size classes based on carapace width: small ≤ 1.3 cm; medium = 1.31 to 2.0 cm; large > 2.0 cm. We focused our sampling effort on medium and large shore crabs, as these were the size classes that raccoons were observed to consume. All quadrat sampling was conducted between 20-May and 17-Aug-2012.

2.3.8 Quantifying raccoon impacts on red rock crabs

Based on direct observations of raccoons consuming red rock crabs in the intertidal and large amounts of red rock crab shell observed in raccoon scat, it is evident that red rock crabs are frequently preyed upon by Gulf Islands raccoons. Because red rock crabs are not adapted to tolerate air exposure (deFur and McMahon 1984), raccoons must wade into the ocean to capture them. Red rock crabs occur in large subtidal populations and, during each tide cycle, they migrate from the shallow subtidal into the intertidal as the tide rises, and migrate out again as the tide falls (Robles et al.1989). Out-migrating individuals that linger too long in shallow water as the tide recedes are vulnerable to predation by wading raccoons. Data on the size and sex of red rock crabs killed by raccoons (below) are consistent with smaller individuals, and females (being smaller), being more vulnerable to raccoon predation because they are physically able to remain submerged and so linger longer at shallower depths. Though the loss of individuals to raccoon predation may significantly reduce the abundance of red rock crabs in the intertidal in a given tide cycle, this may not constitute a large loss when considering the shallow subtidal red rock crab population as a whole (Ellis et al. 2005).

We assessed the effects of the presence of raccoons on the abundance of red rock crabs in four ways: (1) we quantified raccoon predation on red rock crabs in a given tide cycle by counting the number of freshly preyed-upon carapaces and measuring and sexing those carapaces that were sufficiently intact; (2) we gauged the abundance of red rock crabs accessible to raccoons in the intertidal by wading in and hand-capturing crabs ourselves; (3) we assessed the effect of raccoons on the abundance of red rock crabs in the shallow subtidal by setting crab traps in the shallow subtidal over a 24-hour period (i.e., over two full tide cycles); and (4) we measured the carapace size of all red rock crabs captured to determine if there was a size bias consistent with raccoons being more likely to prey upon smaller individuals, as suggested by the size of freshly preyed-upon carapaces. If smaller crabs are more likely to be preyed upon and larger crabs are more likely to escape raccoon predation, then one would expect the average size of live-caught crabs to be smaller on raccoon-absent islands, where smaller crabs have a better chance of survival.

Remains of red rock crabs killed by raccoons are readily distinguished by their location and the condition of the carapace. Raccoons leave red rock crab remains *in situ* in the intertidal. Gulls are the only other predator in this area that do this and gull kills are easily distinguished by characteristic square-shaped holes left in the carapace from beak punctures (Ellis et al. 2005). Freshly preyed-upon carapaces are readily differentiated from older remains and molts because bits of flesh remain attached to the inside of the carapace, which is often associated with a pile of appendages (Ellis et al. 2005). To estimate the number of red rock crabs killed by raccoons during a given tide cycle, we followed procedures developed by Ellis et al. (2005), walking 2 km transects along the shoreline 10 min after daily low tide and counting the number of freshly preyed-upon red rock crab carapaces encountered. All transects were conducted by the same two observers between 17-Jun and 4-Aug-2012. In 78 cases, carapaces were sufficiently intact that we could measure the carapace width, and in 39 cases the abdomen remained attached, allowing us to identify the sex of the victim. As described in the Results, the small average carapace size in this sample of 78 red rock crabs killed by raccoons (relative to the average size of live-trapped red rock crabs) is consistent with smaller crabs being more vulnerable to raccoon predation.

To gauge the abundance of red rock crabs in the intertidal that are accessible to raccoons, the same observer each time waded into the water to a depth of 15-20 cm and searched 5 x 2 m line transects. All crabs encountered were caught with the aid of a small dip net, and then measured (carapace width), sexed, and individually marked with a paint pen, before being returned to the water. Twenty transects were searched over 1 km of shoreline with each separated by 50 m. Each transect was searched twice between 15-Jun and 17-Aug-2012, with at least 24 hours separating searches. For each transect, we recorded percent algal cover and the predominant substrate type (four-point scale based on particle size: 1 = bedrock, 2 = boulder, 3 = cobble, 4 = sand), since these variables could affect the observer's ability to locate crabs. However, correlations between the number of crabs detected on a given transect and both algal cover and substrate type were very low (Spearman Rank Correlation; algal cover: $r_s = 0.12$, $P = 0.01$; substrate type: $r_s = -0.01$, $P = 0.80$; n = 467 [all transects surveyed]), indicating that these variables did not affect counts. Moreover, neither variable differed significantly between raccoon-present and raccoon-absent islands (Mann-Whitney U Test; algal cover: $U = 27$, $P = 0.116$; substrate type: $U = 23$, $P = 0.388$).

To assess the effect of the presence of raccoons on the abundance of red rock crabs in the shallow subtidal we set collapsible mesh crab traps (2 cm mesh) baited with ~200 g of frozen herring just below the low tide line for a period of 24 hours, thus capturing two full tide cycles and the corresponding in and out migrations from the shallow subtidal to the intertidal and back. Ten traps were deployed over at least 1 km of shoreline, with 100 m separating each trap. All crabs captured were measured (carapace width), sexed, and individually marked with a paint pen, before being returned to the water. Trapping was conducted between 18-Jun and 2-Aug-2012.

2.3.9 Quantifying raccoon shoreline use where apex predators persist (Clayoquot Sound)

To begin exploring the potential role of apex predators in mediating raccoon impacts on intertidal and shallow subtidal communities, in 2013 we conducted a methodologically comparable but less extensive survey of the relative abundance of raccoons along shorelines in Clayoquot Sound, B.C., on the central west coast of Vancouver Island (between 49°23’10” N, 128°13’42” W; and 49°04’50” N, 125°45’02” W; approximately 140 km from our Gulf Islands study sites). Large carnivores (cougars, wolves and black bears) remain common in Clayoquot Sound, and here raccoons are heavily preyed upon by these predators, occurring in a quarter of both cougar and wolf scats (Hansen et al. 2010). Vegetation in Clayoquot Sound falls mainly into the coastal Western Hemlock (*Tsuga heterophylla*) biogeoclimatic zone, and areas surveyed in 2013 lie within the Clayoquot Sound Biosphere, a UNESCO Biosphere Reserve. Our 2013 survey was conducted on uninhabited islands and coastal areas in sheltered waters to the east of Tofino, B.C., where the intertidal and shallow subtidal communities are generally comparable to those in the Gulf Islands. Between 10-Aug and 13-Aug 2013, we conducted boat-based nocturnal and diurnal direct count surveys in Clayoquot Sound using methods identical to those used in the Gulf Islands, and covering a total of 33 km of shoreline. We also walked 2 km of latrine transects in Clayoquot Sound in areas where we had observed raccoons to be present.

2.3.10 Statistical analyses

Bird abundance data were analyzed using mixed effects ANOVAs with a Poisson error distribution (i.e., Poisson GLMM, Zuur et al. 2009). Data from each point count were used as the dependent variable in these analyses to test for a fixed effect of raccoon presence on bird abundance. Island was included as a random effect in all analyses to account for multiple observations taken on each island (n = 12). We conducted separate analyses testing the effect of the presence of raccoons on the abundance of (1) small shrub- and ground-nesting songbirds, and (2) corvids. We also estimated a main effect of observer in each analysis, and tested for an interaction between observer and raccoon presence. To ensure that our results were robust, we further conducted a much more simplified model, using data calculated at the level of the island (i.e., island-level mean values of bird abundance). In this two-way ANOVA, we tested for island-level effects of raccoon presence, observer, and their interaction on bird abundance, and found identical results (not shown).

All intertidal and shallow subtidal prey abundance data were analyzed using island-level means per quadrat (intertidal fish and shore crabs) or total individuals counted per island (red rock crabs) (n = 12 in all cases) and Mann-Whitney *U* tests. Because the mid and high inter-tidal zones constitute distinct environments (as described above) with a different community composition (Irons et al. 1986), data from these zones were analyzed separately when considering fish and shore crab abundance. To test if there was a difference in the size of red rock crabs between raccoon-present and raccoon-absent islands, consistent with raccoons being more likely to prey upon smaller individuals, we used transect-level (crabs hand captured in the intertidal) or trap-level (crabs trapped in the shallow subtidal) size values for each sex and conducted mixed effects ANOVAs, with island as a random effect to account for multiple samples taken on each island (n = 12). We conducted separate analyses of the data on (1) crabs hand captured in the intertidal and (2) crabs trapped in the shallow subtidal. If the mixed effects ANOVA revealed a significant interaction between sex and raccoon presence, we then tested for a difference in crab size within each sex using separate mixed-effects ANOVAs, again including island as a random effect. As with the bird abundance data described above, simple two-way ANOVAs using island-level mean crab size values tested for the effects of raccoon presence, crab sex, and their interaction on crab size, which again yielded identical results.

2.4 Results

2.4.1 Raccoon predation on song sparrow nests

As noted in the Methods, our long-term data showed that the average nest predation rate in the Gulf Islands is 53% (Zanette et al. 2006), and thus approximately half of all nests monitored suffered nest predation. We directly observed 48 attacks by predators on song sparrow nests, and raccoons accounted for 47.9% of these attacks. Consequently, approximately one quarter of all song sparrow nests initiated fell victim to raccoon predation. Corvids accounted for a further 27.1%, and Mink (*Neovison vison*, 12.5%), brown-headed cowbirds (*Molothrus ater*, 6.3%), owls (4.2%), and garter snakes (*Thamnophis elegans*, 2.1%) accounted for the remaining nest predation events.

2.4.2 Raccoon presence and abundance in the Gulf Islands and Clayoquot Sound

Figure 1 presents the results of our 2011 survey, showing Gulf Islands on which raccoons were deemed to be present based on either direct observation or the presence of latrines. There was a highly significant association between these two methods (two-tailed Fisher's Exact Test, $P < 0.001$). There were 22 islands on which raccoons were directly observed and latrines were found, and 10 on which neither was observed. Consistent with latrines providing additional, independent information, there were 5 islands where latrines were found but no raccoons were seen, and no islands where the opposite was the case. For the 22 islands on which both raccoons and latrines were observed, estimates of relative raccoon abundance based on both methods (raccoons per km; latrines per tree) were significantly correlated (Spearman Rank Correlation: $r_s = 0.70$, $P < 0.001$).

Our 12 Gulf Islands study islands were resurveyed in 2012, and the results are reported in Table 1. We surveyed 77 km of shoreline across the 12 study islands, with the total distance being roughly equally divided between raccoon-present and raccoon-absent islands. The 33 km of shoreline surveyed in apex predator-present Clayoquot Sound in 2013 is thus comparable to the length of shoreline surveyed on the 6 raccoon-present Gulf Islands. Taking the total number of raccoons seen divided by the total length of shoreline surveyed (77 km in the Gulf Islands and 33 km in Clayoquot Sound), there were 9 times as many raccoons seen per km at night and 18 times as many seen per km during the day in the Gulf Islands (1.77 km^{-1} night, 0.54 km^{-1} day) compared to Clayoquot Sound (0.20 km^{-1} night, 0.03 km^{-1} day). Our latrine transects on our 12 Gulf

Islands study islands resurveyed in 2012 corroborate our direct count results, there being no latrines found on raccoon-absent islands (Table 1). We walked a total of 24 km conducting latrine transects on our 12 study islands, half of which (12 km) were on raccoon-present islands. As described in the Methods, we also walked 2 km of latrine transects in Clayoquot Sound. The average number of latrines per tree found on raccoon-present Gulf Islands (0.18) was 6 times the number found in Clayoquot Sound (0.03), consistent with the shoreline abundance of raccoons being much reduced where apex predators persist.

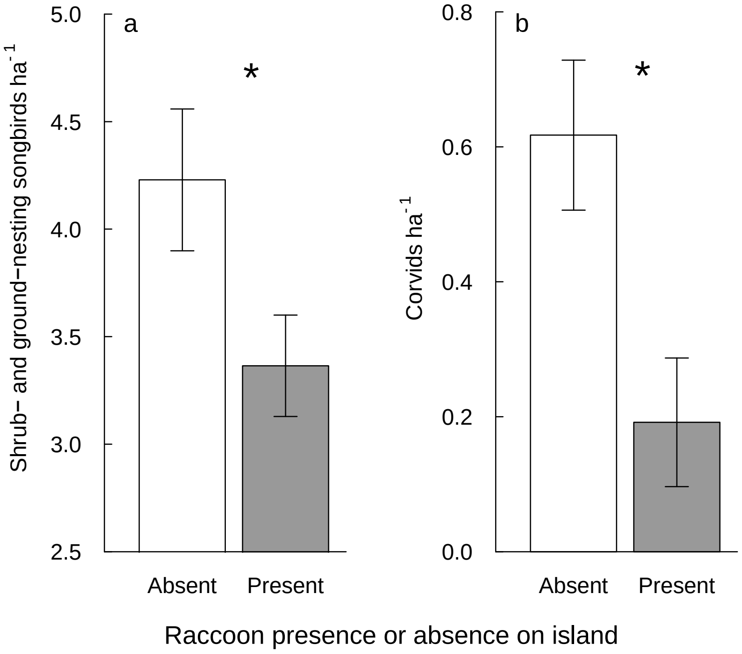

Figure 2.2. Shrub- and ground-nesting songbird (a) and corvid (b) abundance per hectare on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Values are means ± SE. The asterisk denotes a significant difference of $P < 0.05$.

2.4.3 Effects of raccoon presence on bird abundance

Considering our 12 Gulf Islands study islands, there were significantly (21%) fewer shrub- and ground-nesting songbirds counted (raccoon presence: $F_{1, 10} = 6.4$, $P = 0.012$; presence x observer interaction: $F_{1, 10} = 0.03$, $P = 0.860$; Fig. 2.2a), as well as significantly (69%) fewer corvids counted (raccoon presence: $F_{1, 10} = 5.4$, $P = 0.020$; presence x observer interaction: $F_{1, 10} = 3.7$, $P = 0.083$; Fig. 2.2b), on raccoon-present, as compared to raccoon-absent islands.

2.4.4 Effects of raccoon presence on intertidal fish

There were significantly (94%) fewer pricklebacks (Mann-Whitney $U = 32$, $P = 0.025$; Fig. 2.3a) on raccoon-present islands in the mid intertidal zone. Northern clingfish were also significantly less abundant on raccoon-present islands in the mid intertidal zone (Mann-Whitney $U = 32$, $P = 0.016$), being virtually absent where raccoons were present (Fig. 2.3b). In the high intertidal zone, clingfish were absent, while pricklebacks were rare, and tended to be rarer on raccoon-present islands, though not significantly so (Mann-Whitney $U = 27$, $P = 0.059$; Fig. 2.3a).

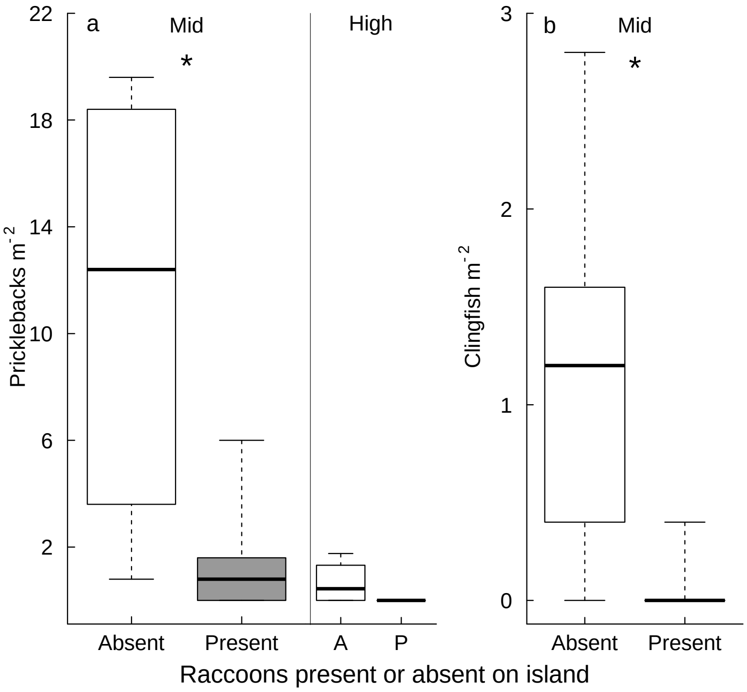

Figure 2.3. (a) Prickleback and (b) northern clingfish abundance (per m^2) in the mid (Mid) and high (High) intertidal zones on raccoon-present (grey bars) and raccoon-absent (white bars) islands. No clingfish were observed in the high intertidal zone on any island. Data are presented as standard box plots: the bold horizontal black lines indicate median values, the box edges represent the 25% and 75% quartiles, and the whiskers signify the range. The asterisk denotes a significant difference of $P < 0.05$.

2.4.5 Effects of raccoon presence on shore crabs

There were significantly fewer shore crabs (*Hemigrapsus* spp.) in the large (90% fewer; Mann-Whitney $U = 36$, $P = 0.004$; Fig. 2.4a) and medium (89% fewer; Mann-Whitney U

= 35, *P* = 0.006; Fig. 2.4b) size classes on raccoon-present islands in the high intertidal. Both large and medium shore crabs tended to be rare in the mid intertidal and both tended to be rarer on raccoon-present islands (Fig. 2.4), but not significantly so (large, Mann-Whitney *U* = 27.5, *P* = 0.114; medium, Mann-Whitney *U* = 27, *P* = 0.180).

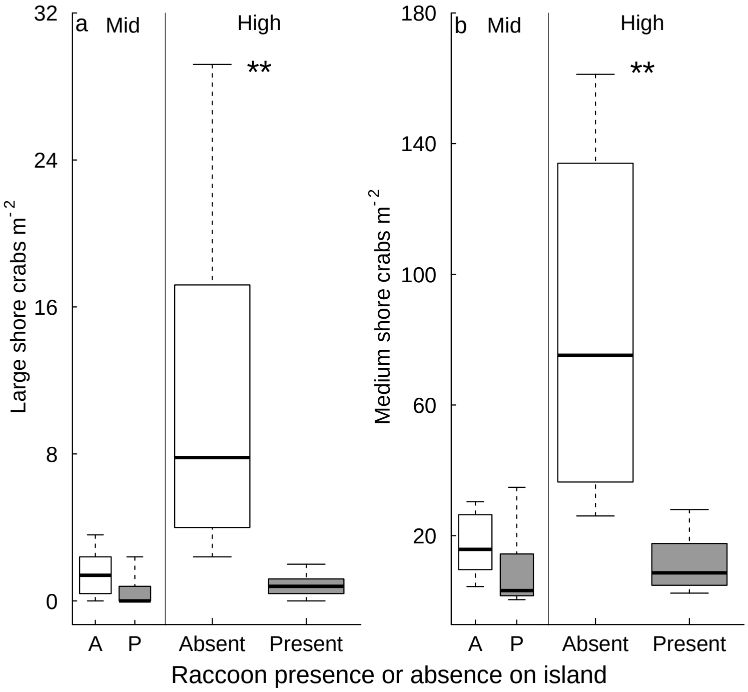

Figure 2.4. (a) Large (> 2.0 cm carapace width) and (b) medium-sized (1.31 - 2.0 cm carapace width) shore crab abundance (per m^2) in the mid (Mid) and high (High) intertidal zones on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Data are presented as standard box plots, as described in the caption to Fig. 2.3. The two asterisks denote a significant difference of *P* < 0.01

2.4.6 Effects of raccoon presence on red rock crabs

On raccoon-present islands, we counted a median of 7.4 red rock crab carapaces per km (range = 0.5-16.0) diagnosed as having been freshly killed by raccoons during that tide cycle. As expected, we found no carapaces freshly killed by raccoons on raccoon-absent islands. The average carapace size of red rock crabs freshly killed by raccoons was 8.3 (± 2.16 SD) cm, and most victims were female (82.1 %), consistent with smaller crabs being more vulnerable to raccoon predation (details below).

There were significantly (51%) fewer red rock crabs in the intertidal on raccoon-present islands (Mann-Whitney *U* = 36, *P* = 0.004; Fig. 2.5a) in any given tide cycle. There were also significantly (38%) fewer red rock crabs in the shallow subtidal on raccoon-present islands (Mann-Whitney *U* = 31, *P* = 0.037; Fig. 2.5b) during any given 24-hour period (i.e., over any two full tide cycles).

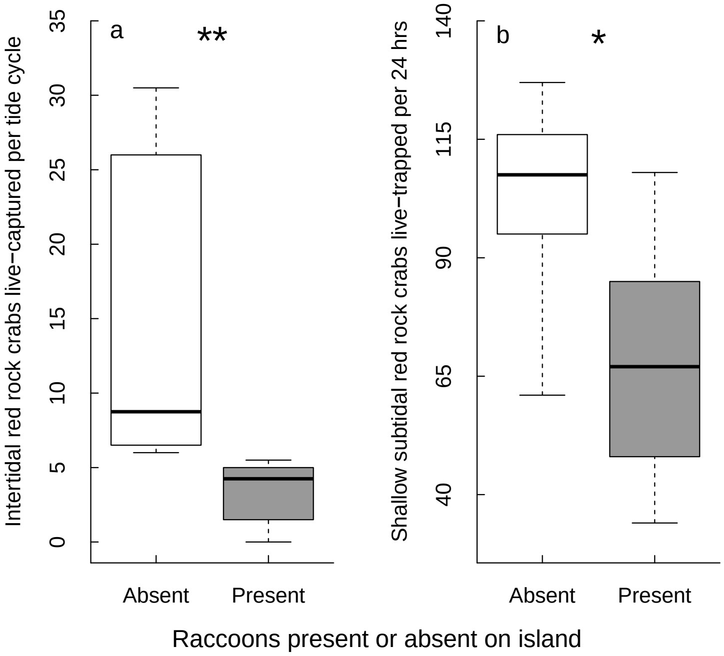

Figure 2.5. (a) Intertidal and (b) shallow subtidal red rock crab abundance, considering red rock crabs live-captured per tide cycle, and live-trapped per 24 hrs (two full tide cycles), respectively, on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Data are presented as standard box plots, as described in the caption to Fig. 2.3. The single asterisk denotes a significant difference of *P* < 0.05; two denote a significant difference of *P* < 0.01

The average size of live-caught red rock crabs tended to be smaller on raccoon-absent islands, consistent with the freshly preyed-upon red rock crab carapace data indicating that raccoons are more likely to prey upon smaller individuals (horizontal solid and dashed lines in Fig. 2.6), and that smaller red rock crabs are thus likely to have a better chance of survival on islands without raccoons. Data on the sizes of red rock crabs hand captured in the intertidal and those live-trapped in the shallow subtidal were analyzed separately. Considering red rock crabs accessible to raccoons in the intertidal, there was a significant raccoon presence by crab sex interaction ($F_{1,\,10} = 9.7$, $P = 0.014$), wherein males were indeed significantly smaller on raccoon-absent islands ($F_{1,\,10} = 4.09$, $P = 0.043$; raccoon-present = 12.69 ± 0.35 cm, raccoon-absent = 10.02 ± 0.60; mean ± SE), but females were not ($F_{1,\,10} = 1.75$, $P = 0.186$; raccoon-present = 7.76 ± 0.45 cm, raccoon-absent = 8.15 ± 0.37). Considering red rock crabs live-trapped in the shallow subtidal (Fig. 2.6), there was a significant main effect of the presence of raccoons ($F_{1,\,10} = 4.47$, $P = 0.034$), wherein both males and females were smaller on raccoon-absent islands (presence by sex interaction, $F_{1,\,10} = 0.07$, $P = 0.795$), consistent with smaller red rock crabs having a better chance of survival on raccoon-absent islands.

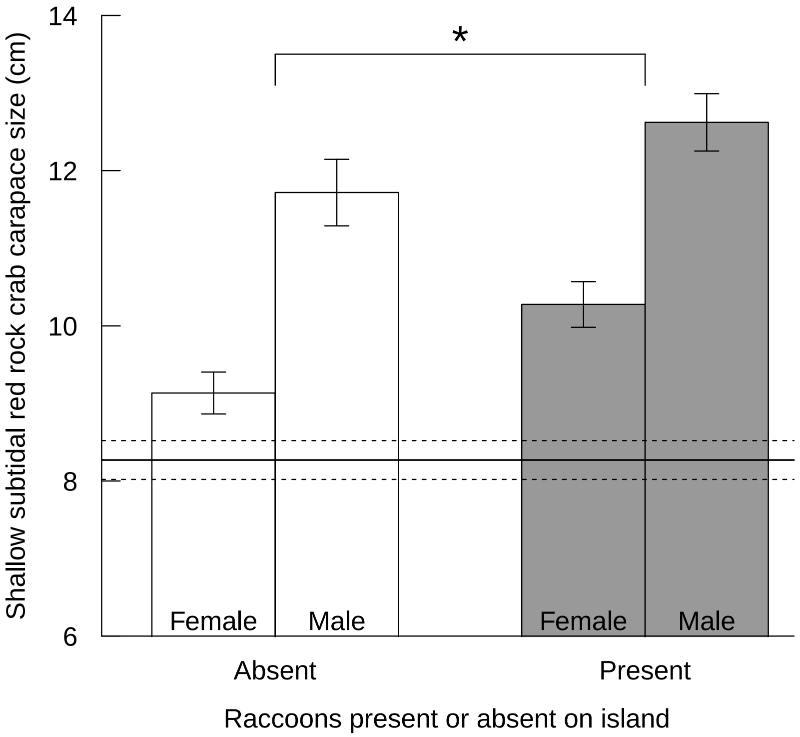

Figure 2.6. Shallow subtidal red rock crab carapace size (cm) comparing males and females live-trapped on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Values are means ± SE. For comparison, the carapace size of red rock crabs freshly preyed-upon by raccoons is indicated by the horizontal solid (mean) and dashed (± SE) lines. The asterisk denotes a significant difference of $P < 0.05$

2.5 Discussion

Our results show that mammalian mesopredators on islands may not only affect terrestrial communities, but can directly impact marine communities as well.   We found significant effects of raccoon presence on terrestrial birds (Fig. 2.2), intertidal vertebrates (Fig. 2.3) and invertebrates (Fig. 2.4), and both intertidal and shallow subtidal red rock crab populations (Figs 5 and 6). These findings corroborate the broad breadth of the impacts mammalian mesopredators are anticipated to have on island communities.

2.5.1 Raccoon impacts on terrestrial bird communities

Raccoons are known to negatively affect songbird populations in continental systems (Wilcove 1985; Small and Hunter 1988; Schmidt and Whelan 1999), particularly in areas where apex predators are absent (Soulé et al. 1988, Rogers and Caro 1998, Crooks and Soulé 1999, Schmidt 2003). Our video data demonstrate a clear impact of raccoon predation on song sparrow nests in the Gulf Islands, and our finding that both shrub- and ground-nesting songbirds and corvids are less abundant on raccoon-present islands (Fig. 2.2) is consistent with the hypothesis that mammalian mesopredators on islands negatively affect bird abundance. Taken together with our findings concerning intertidal and shallow subtidal prey these negative effects on bird abundance corroborate that mammalian mesopredators whose diet is substantially subsidized by marine prey may significantly impact terrestrial prey (Rose and Polis 1998).

As outlined above, our video data indicate that, after raccoons, corvids are the second most important predator on song sparrow nests, accounting for more than a quarter of all nest predation events, and this was the principal reason for quantifying corvid abundance. Though we knew from the literature that corvids could also be affected by raccoon nest predation (Chamberlain-Auger et al. 1990), it was nonetheless surprising to find a strong effect of the presence of raccoons on corvid abundance (Fig. 2.2b). This discovery raises interesting questions about trophic interactions among the terrestrial predators on these islands, as the presence of raccoons is evidently reducing the abundance of a competitor for other songbird nests. Conceivably, this putative interaction between the predators may have attenuated the difference in abundance of shrub- and ground-nesting songbirds between raccoon-present and raccoon-absent islands.

Direct killing as a primary cause of reduced bird abundance on raccoon-present islands is supported by our observations of high levels of raccoon predation on song sparrow nests, as well as an extensive literature implicating raccoons in songbird declines (Wilcove 1985; Small and Hunter 1988; Schmidt and Whelan 1999). However, it is possible that the lower number of birds detected on raccoon-present islands partially results from changes in bird behaviour. Passerines are able to assess landscape-level predation risk and adjust breeding territory selection (among other reproductive strategies) accordingly (Fontaine and Martin 2006, Lima 2009, Forsman et al. 2013). Both shrub- and ground-nesting songbirds and corvids may be able to assess raccoon presence (potentially through the detection of excrement; Forsman et al. 2013) and preferentially nest on islands where raccoons are absent. As discussed in the previous paragraph, the presence of raccoons affects corvid abundance, and shrub- and ground-nesting songbirds may also conceivably use auditory cues (Zanette et al. 2011) from corvids to assess the likely abundance of raccoons.

2.5.2 Raccoon impacts on nearshore marine communities

Our results indicate that terrestrial mammalian mesopredators on islands may directly impact both the intertidal and shallow subtidal marine communities. Input from marine sources may strongly influence terrestrial populations and communities (e.g., Polis and Hurd 1996, Rose and Polis 1998, Stapp and Polis 2003, Field and Reynolds 2011). However such marine subsidies are generally viewed as one-way (i.e., donor-controlled, Polis and Strong 1996) interactions in which the terrestrial receivers benefit, but have no effect on the marine populations and communities that support them. Here we show that raccoon populations with access to marine resources impact the local abundance of their marine prey. Furthermore, the role of terrestrial predators in structuring intertidal communities has received surprisingly little attention (Carlton and Hodder 2003), with most studies of intertidal communities focusing exclusively on marine organisms (Ellis et al. 2007). In a rare counterexample, Kurle et al. (2008) found that Norway rat (*Rattus norvegicus*) predation on nesting seabirds on Alaska’s Aleutian Islands indirectly affects the intertidal community through a trophic cascade, demonstrating the breadth of the impact of small mammals on island ecosystems. In our system, raccoons have been promoted to the top of both the terrestrial and nearshore marine food chains and thereby have a direct impact on both nesting birds and intertidal and subtidal species. This direct effect may in turn initiate trophic cascades both within the terrestrial (as discussed above) and intertidal communities. Trophic cascades within the intertidal community may be anticipated because large crab species, such as the red rock crab, are themselves major intertidal predators (Behrens Yamada and Boulding 1996, Ellis et al. 2007).

Our results suggest that the level of predation exerted by raccoons on red rock crabs present in the intertidal at low tide leads to significant reductions in the size of the shallow subtidal source populations (Fig. 2.5b). We found (1) substantial numbers of freshly preyed-upon carapaces in any given tide cycle on raccoon-present islands, (2) lower numbers of live-trapped red rock crabs in the shallow subtidal on raccoon-present islands, and (3) a smaller average size of subtidal red rock crabs on raccoon-absent islands (consistent with the anticipated higher survival of smaller individuals on these islands). Taken together, these results indicate that direct killing of red rock crabs (particularly small individuals) by raccoons leads to measurable changes in shallow subtidal red rock crab abundance. Nonetheless, our results do not rule out the possibility that the lower number of red rock crabs trapped on raccoon-present islands is partially due to changes in red rock crab habitat use (e.g., fewer individuals may migrate into the intertidal on raccoon-present islands) (Dill et al. 2003).

2.5.3 Mesopredator release in an island system

Several factors likely drive the strong impacts of raccoons observed in this study, including the current absence of native apex predators that were formerly widespread throughout the Gulf Islands, which has likely resulted in the relaxation of both direct predation and behavioural suppression of raccoons. Our results may therefore be partially attributable to the effects of mesopredator release, broadly defined as the ecological phenomena that occur when a mesopredator is ‘released’ from top-down control (Prugh et al. 2009, Elmhagen et al. 2010). Several studies from continental systems have documented mesopredator-driven declines in the abundance and diversity of terrestrial species at lower trophic levels following reductions in apex predator numbers (Prugh et al. 2009, Ritchie and Johnson 2009, Brashares et al. 2010). Our study demonstrates strong impacts on terrestrial prey in an island system that additionally extend to the surrounding marine community, impacting intertidal and shallow subtidal prey. Our comparison of the relative abundance of raccoons along shorelines in the Gulf Islands with that in apex predator-present Clayoquot Sound indeed suggests that apex predator presence could potentially mitigate raccoon impacts on intertidal and shallow subtidal prey, either by locally reducing raccoon numbers or by reducing their use of risky shoreline habitats (or both). This is not a direct test of the effect of apex predator presence on raccoon impacts, but strongly indicates that such a test may provide a promising avenue for future research.

The impacts of mesopredator release may be particularly severe on islands precisely because island mesopredators can exploit both terrestrial and marine prey. Dramatic increases in abundance are known to result from the combination of high food availability, and increased time spent foraging in the absence of predators (Krebs et al. 1995, Karels et al 2000, Zanette et al. 2003, 2006). Such dramatic increases in abundance may be expected to be common in the case of mesopredator release because mesopredators are typically omnivores and so likely always have access to abundant food of some sort (Brashares et al. 2010), which they can spend virtually all their time eating in the absence of apex predators. Given the opportunity to exploit both terrestrial and marine prey, island mesopredators may be particularly likely to increase in abundance when enabled to spend more time foraging in the absence of apex predators. We suggest that our results provide some support for this scenario. Gulf Islands raccoons are definitely exploiting both terrestrial (Fig. 2.2) and marine (Figs 2.3 to 2.6) prey, providing them access to abundant food; and our evidence suggests that they may be spending more time foraging given that we observed considerable diurnal activity (Table 1) in this generally nocturnal species (Gehrt 2003), and that the level of diurnal activity was 18 times higher than in apex predator-present Clayoquot Sound. This combination of factors could lead to substantial increases in raccoon abundance, potentially contributing to the markedly (at least 9 times) greater number of raccoons observed along shorelines in the Gulf Islands compared to apex predator-present Clayoquot Sound.

2.5.4 Conservation implications

Globally, island bird and mammal communities have been severely impacted by mammalian mesopredators (Burbidge and Manly 2002; Blackburn et al. 2004), and our results suggest that marine communities may be similarly affected. The loss of native apex predators is considered by some to be “humankind’s most pervasive influence on the natural world” (Estes et al. 2011, p. 301), and we stress that a focus on the loss or absence of native apex predators in island systems may help elucidate why the impacts of mammalian mesopredators on islands have been so dramatic. Our results highlight two important objectives for the conservation of island ecosystems. Firstly, preventing the spread of mammalian mesopredators to currently unoccupied islands should be a major conservation priority (Morley and Winder 2013), and implementation of eradication programs, which have shown marked success on islands (Zavaleta et al. 2001), may be warranted when new introductions occur. This is of immediate relevance to our study system since our results clearly indicate that preventing the spread of raccoons to currently unoccupied Gulf Islands (Fig. 2.1) is crucial to maintaining the ecological integrity of the Gulf Islands National Park Reserve, and should be prioritized by Park managers. Secondly, as we have outlined, the role apex predators play in suppressing the foraging behaviour of mesopredators (Ritchie and Johnson 2009, Brashares et al. 2010, Wilson et al. 2010, Hudgens and Gracelon 2011) may be particularly critical in island systems, meaning that where mesopredator eradication is inappropriate (e.g., because the mesopredator is native), maintaining or restoring native apex predators in island systems may be even more essential than elsewhere (Prugh et al. 2009, Ritchie and Johnson 2009, Brashares et al. 2010).

Chapter 3 – Fear of Large Carnivores Causes a Trophic Cascade

Adapted from: Justin P. Suraci[1,2,], Michael Clinchy[3], Lawrence M. Dill[4], Devin Roberts[1], Liana Y. Zanette[3] (2016) *Nature Communications*, DOI: 10.1038/ncomms10698.

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Author Contributions: All authors originally conceived of the study, and J.P.S. and D.R. conducted the fieldwork, with the assistance of M.C. and L.Y.Z. J.P.S. and M.C. performed the data analysis and drafted the manuscript. All authors discussed the results and commented on the manuscript.

3.1 Abstract

The fear large carnivores inspire, independent of their direct killing of prey, may itself cause cascading effects down food webs potentially critical to conserving ecosystem function, particularly by affecting large herbivores and mesocarnivores. However, the evidence of this has been repeatedly challenged because it remains experimentally untested. Here we show that experimentally manipulating fear itself in free-living mesocarnivore (raccoon) populations using month-long playbacks of large carnivore vocalizations caused just such cascading effects, reducing mesocarnivore foraging to the benefit of the mesocarnivore's prey, which in turn affected a competitor and prey of the mesocarnivore's prey; and we report that by experimentally restoring the fear of large carnivores in our study system, where most large carnivores have been extirpated, we succeeded in reversing this mesocarnivore's impacts. We suggest that our results reinforce the need to conserve large carnivores given the significant "ecosystem service" the fear of them provides.

3.2 Introduction

Large carnivores are fearsome predators that pose real and perceived threats to human life (Packer et al. 2005) and livelihoods (Packer et al. 2005, Dickman et al. 2011, Chapron et al. 2014, Treves and Bruskotter 2014, Woodroffe and Redpath 2015), which is why humans have attempted, and largely succeeded, at extirpating them everywhere (Packer et al. 2011, Chapron et al. 2014, Ripple et al. 2014). The loss of large carnivores is now being recognized as possibly "humankind's most pervasive influence on nature" (Estes et al. 2011), in part because the fear (perceived predation risk; Brown et al. 1999, Laundré et al. 2001, Brown and Kotler 2004) they inspire in other animals may constitute a significant "ecosystem service" critical to conserving biodiversity and ecosystem function (Creel and Christianson 2008, Prugh et al. 2009, Terborgh and Estes 2010, Ripple et al. 2014). Being at the top of the food chain, large carnivores can play a dual role in structuring ecosystems by affecting both large herbivores and mesocarnivores, causing both 'tri-trophic cascades' (large carnivore – herbivore – plant) and 'mesopredator cascades' (large carnivore – mesopredator – mesopredator's prey), affecting diverse species at multiple lower trophic levels (Creel and Christianson 2008, Prugh et al. 2009, Terborgh and Estes 2010, Estes et al. 2011, Ripple et al. 2014). By both killing and frightening their prey, large carnivores could have a dual impact on these dual cascades, for the straightforward reason that frightened prey (in this case large herbivores and mesocarnivores) eat less (Lima and Dill 1990, Laundré et al. 2001, Brown and Kotler 2004, Terborgh and Estes 2010). The mere presence of large carnivores may therefore give rise to a "landscape of fear" (Laundré et al. 2001), buffering lower trophic levels from overconsumption by large herbivores and mesocarnivores. Failing to consider fear risks dramatically underestimating the role large carnivores play, since fear may be as or more important than direct killing in causing trophic cascades, according to current theory and experiments primarily on captive invertebrates (Schmitz et al. 1997, 2004; Preisser et al. 2005, Railsback and Harvey 2013). Given the potential for human-large carnivore conflict, there have been justifiable calls for direct experimental evidence that the fear large carnivores inspire can provide a significant 'ecosystem service' (Dobson 2014, Woodroffe and Redpath 2015). The absence of such direct evidence to date is due to the challenge of experimentally manipulating fear in free-living wildlife, it being only very recently experimentally demonstrated that fear itself is powerful enough to affect wildlife population dynamics (Zanette et al. 2011).

To test whether the fear of large carnivores can itself cause cascading effects on mesocarnivore foraging and multiple lower trophic levels, we conducted a spatially and temporally replicated field experiment in which we manipulated fear using month-long playbacks of large carnivore vocalizations (Fig. 3.1 and Table 3.1). The experiment was conducted on wild, free-living raccoons (*Procyon lotor*) on several small coastal Gulf Islands (B.C., Canada). The raccoon is a mesocarnivore subject to much research regarding 'mesopredator release' (Prugh et al. 2009, Suraci et al. 2014). Most of the large carnivores known to hunt (wolf [*Canis lupus*], cougar [*Puma concolor*]) or harass (black bear [*Ursus americanus*]) raccoons were extirpated from the Gulf Islands last century (Suraci et al. 2014, Golumbia 2006), the sole remaining large carnivore being the domestic dog (*Canis lupus familiaris*), which harasses and kills raccoons here, and has been present for millennia, having always been kept by local aboriginal peoples (Hanson 1995). In a previous mensurative experiment comparing Gulf Islands with and without raccoons (Suraci et al. 2014), we documented that raccoons impact multiple marine species, reducing the abundance of intertidal crabs and fish, and even subtidal red rock crabs (*Cancer productus*).

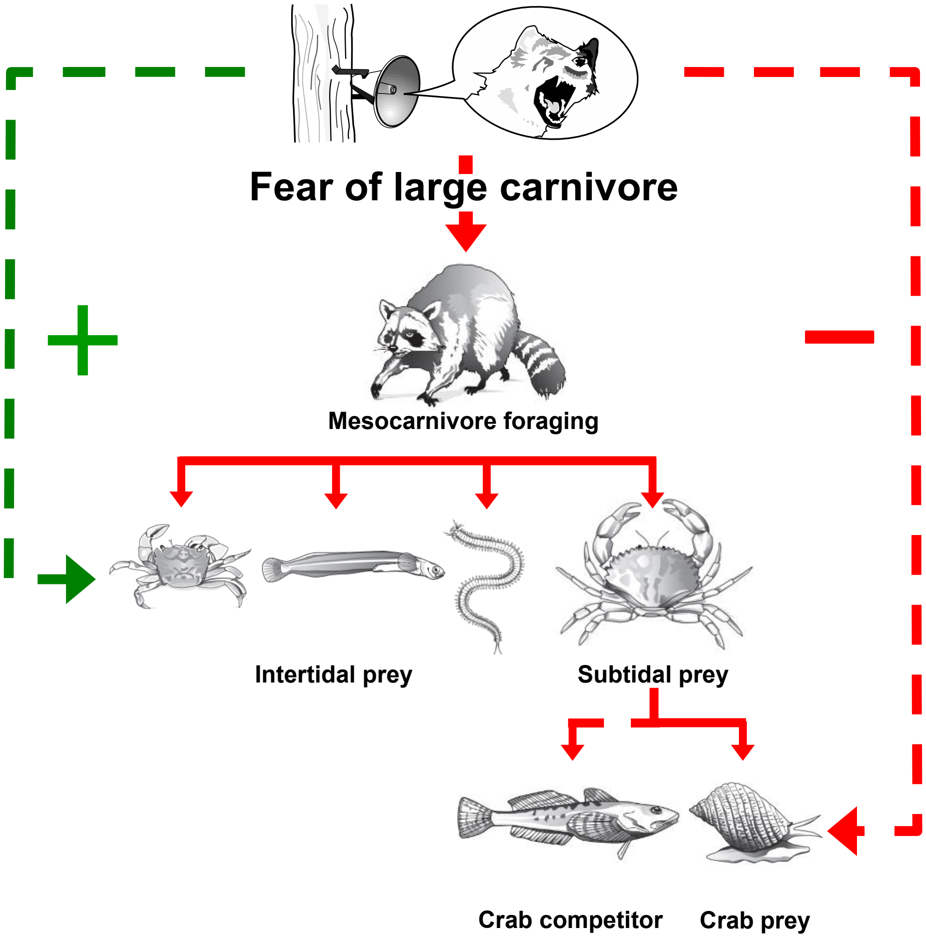

Figure 3.1. Fear of large carnivores caused a trophic cascade. Diagram illustrating how broadcasting playbacks of large carnivore vocalizations affected multiple lower trophic levels. Green and red arrows represent positive and negative effects respectively on foraging, abundance or survival. Solid arrows connect predator and prey; dashed arrows connect species affected, but not directly eaten, by another.

To experimentally test if the fear of large carnivores could itself mediate the impacts of raccoons on marine biota, we broadcast large carnivore predator (dog) or non-predator (local pinnipeds; harbour seal [*Phoca vitulina*], Steller sea lion [*Eumetopias jubatus*]) vocalizations over two large sections of shoreline for one month, and then reversed the treatments for a second month, using a repeated-measures design to spatially replicate our results; which we further spatially and temporally replicated, by repeating the same manipulation on a different island the following year. We assayed the immediate reaction of raccoons to the large carnivore predator and non-predator vocalizations by directly observing their reactions to 10 s playbacks, and assessed their response to the month-long playbacks using multiple video surveillance and time-lapse cameras to continuously film both experimental sections of shoreline over both entire month-long playback periods

To test the cascading effects of our experiment on lower trophic levels we utilized the same methods (intertidal quadrats and subtidal crab trapping) used in our previous mensurative experiment to evaluate effects on raccoon prey (Suraci et al. 2014); and we conducted fish trapping and a mark-recapture experiment additionally quantifying effects on species not directly eaten by raccoons, that are instead a competitor (staghorn sculpin [*Leptocottus armatus*]) and prey (periwinkle snail [*Littorina scutulata*]) of the prey (red rock crab) of raccoons (Tasto 1975, Behrens Yamada and Boulding 1996). Staghorn sculpins are subtidal fish that, like red rock crabs, enter the intertidal at high tide to feed on small invertebrates (Tasto 1975), but unlike red rock crabs, evidently successfully escape being eaten by raccoons (see Methods). Periwinkle snails are too small to be food for raccoons but are eaten by red rock crabs, which use a distinctive method of dispatching them, permitting the level of mortality to be quantified using standard mark-recapture procedures (Behrens Yamada and Boulding 1996).

Here we report significant cascading effects of the fear of large carnivores across multiple trophic levels in an intertidal food web, which effectively reversed the impacts of mesocarnivore populations on marine biota by dramatically suppressing mesocarnivore foraging. These results indicate that the fear large carnivores inspire in their prey can account for a major component of their role in structuring ecosystems, reinforcing the value of large carnivore conservation in ensuring the continuation of this critical ecosystem service.

Table 3.1. Overview of methods used in this study to test hypotheses and specific predictions

Hypothesis	Prediction	Methods
(1) Raccoons reduce intertidal foraging in response to perceived predation risk from large carnivores	(i) Raccoons will react to immediate risk of predation by either abandoning intertidal foraging altogether or reducing foraging in favour of vigilance	10 s playbacks of predator or non-predator vocalizations to free-living raccoons foraging in the intertidal across multiple Gulf Islands. Video recording behaviour immediately prior to and immediately following playback
	(ii) Raccoons will reduce time allocation to intertidal foraging as a long-term response to high perceived risk of predation by large carnivores	Month-long playbacks of predator or non-predator vocalizations presented over sections of shoreline across two Gulf Islands. Raccoon behaviour continuously monitored by surveillance video and time-lapse cameras
(2) By reducing raccoon foraging, fear of large carnivores indirectly benefits raccoon intertidal and shallow subtidal prey	Abundance of intertidal vertebrates and invertebrates and shallow subtidal red rock crabs will be higher following month-long predator treatments, relative to non-predator treatments	- Intertidal quadrat sampling to monitor abundance of intertidal crabs, fish and polychaete worms - Shallow subtidal crab trapping to monitor red rock crab abundance
(3) By benefiting raccoon prey, effects of large carnivore-induced fear will further cascade to negatively affect species not directly eaten by raccoons	(i) Abundance of staghorn sculpins (red rock crab competitors) will decrease during predator treatments	Intertidal fish trapping of staghorn sculpins throughout month-long fear manipulations
	(ii) Increased abundance of red rock crabs will lead to increased predation on periwinkle snails	Snail mark-recapture experiments nested within month-long fear manipulations, quantifying the proportion of snails surviving crab predation over a single tide cycle

3.3 Methods

3.3.1 Study area

Vegetation in the Gulf Islands falls within the Coastal Douglas Fir (*Psuedostuga menziesii*) biogeoclimatic zone, and the region experiences a mild Mediterranean climate (Jewell et al. 2007). This work was conducted on four Gulf Islands. Coal Island (140 ha; 48°41’03” N, 123°22’32”W) is a single-owner private island consisting of approximately 78% forest. Portland Island (225 ha; 48°43’33”N, 123°22’20”W) and Wallace Island (87 ha; 48°56’34”N, 123°33’04”W) are both fully forested parkland, being entirely within the Gulf Islands National Park Reserve (Portland), or mostly BC Provincial Park (Wallace, 83% of land area). Penelakut Island (954 ha; 48°57’30”N, 123°38’34”W) is the traditional territory of the Penelakut First Nation and home to approximately 350 people, all residing in a small village on the north end of the island. The majority of Penelakut Island (approximately 86%) is forested. Domestic dogs were present on all Gulf Islands on which this study was conducted, either as the pets of permanent residents (Coal and Penelakut Islands) or accompanying park visitors (Portland and Wallace Islands), though study sites were chosen well away from areas of high human and dog use to minimize interference.

3.3.2 Motivation and objectives

We experimentally manipulated the fear of large carnivores over two years and at multiple sites in the Gulf Islands, achieving both temporal and spatial replication of our results. In 2013, we tested the immediate reaction of raccoons to 10 s playbacks of large carnivore vocalizations on Coal, Portland and Wallace Islands. We then used month-long playbacks of large carnivore vocalizations to test for long-term behavioural responses by raccoons and cascading effects on marine biota, on Coal Island in 2013 and on Penelakut Island in 2014. The objectives in these two years were similar but complementary. In 2013, we focused on testing whether the fear of large carnivores was sufficient to mitigate the impacts of raccoons on intertidal and shallow subtidal prey. In 2014 we sought to (1) replicate the results from the Coal Island experiment concerning raccoon prey abundance, while expanding the focus of the study to (2) test whether the effects of fear on raccoon behaviour observed in 10 s playback experiments persisted throughout our month-long treatments, and (3) to test for further cascading effects of fear among intertidal and shallow subtidal species not directly eaten by raccoons. All work was conducted in compliance with the guidelines of the Canadian Council on Animal Care, and was approved by the Animal Care and Use Committees of the University of Victoria and the University of Western Ontario.

3.3.3 Preparing the playbacks

We manipulated the fear of large carnivores using playbacks of domestic dog (large carnivore predator) and local pinniped (harbour seal and Steller sea lion; non-predator) vocalizations. Pinniped vocalizations provide an excellent control for dogs; the two call types are qualitatively similar, and Gulf Islands raccoons are certain to be as familiar with pinniped as with dog vocalizations. Most importantly, pinnipeds represent no threat to raccoons, and analyses of red rock crab abundance data verified there was no difference between pinniped playbacks and silence with respect to raccoon impacts on marine prey (see Fig. 3.6). Sound files were acquired from online audio and video databases, and library archives. In testing the immediate reaction of raccoons to large carnivore vocalizations, we used multiple 10 s exemplars of predator and non-predator vocalizations (10 dog and 5 pinniped), and matched the temporal properties (duration, attack, number of staccato elements) of these two groups of playbacks by visually inspecting the spectrograms and waveforms of all exemplars (Blumstein et al. 2008). We ensured that there were no differences in overall frequency characteristics between the two groups by using t-tests to compare each of four frequency characteristics (peak: $t_{1,13} = -0.36$, $P = 0.735$; minimum: $t_{1,13} = 1.46$, $P = 0.180$; maximum: $t_{1,13} = 0.63$, $P = 0.551$; range: $t_{1,13} = 0.62$, $P = 0.556$; n = 10 [predator] and 5 [non-predator] for all tests). We broadcast 10 s calls at a mean (±SD) volume of 78.0 (±2.1) dB at 1 m, with no difference in volume between predator and non-predator treatments ($t_{1,13} = -1.3$, $P = 0.234$; n = 10 and 5). All playbacks were broadcast using identical speakers (Nexxtech Mini Cube 2.0) and mp3 players (Coby Electronics MP301).

To test the long-term response of both raccoons and the nearshore marine community to the fear of large carnivores, we again used playbacks of dog (predator) and pinniped (non-predator) vocalizations. We composed playlists using multiple exemplars of both call types (n = 11 predator and 9 non-predator exemplars) ranging in duration from 8 to 79 s, with no difference in duration between the two treatments (predator [mean ± SD]:

34.1 ± 20.6 s; non-predator: 26.8 ±18.3 s; $t_{1,18} = 0.84$, $P = 0.412$). These two sets of playbacks were again matched for temporal properties using visual inspection of spectrograms and waveforms, and we used t-tests to confirm that there were no differences in overall frequency characteristics between predator and non-predator playlists (peak frequency: $t_{1,18} = -0.03$, $P = 0.973$; minimum: $t_{1,18} = -1.44$, $P = 0.180$; maximum: $t_{1,18} = 0.76$, $P = 0.459$; range: $t_{1,18} = 0.86$, $P = 0.400$; n = 11 [predator] and 9 [non-predator] for all tests). All calls were broadcast at a mean (± SD) volume of 86.1 (±2.9) dB at 1 m, with no difference in volume between predator and non-predator treatments ($t_{1,18} = -0.13$, $P = 0.895$; n = 11 and 9). All playbacks were broadcast using identical speakers (Nexxtech Mini Cube 2.0) and mp3 players (The Source HeadRush 2GB mp3 player).

3.3.4 Raccoon immediate reaction to large carnivore vocalizations

All 10 s playback trials were conducted by two researchers (JPS and DR) between 15-May and 16-September 2013. We located diurnally active raccoons foraging in the intertidal and broadcast a randomly selected predator or non-predator playback from a concealed location. The raccoon’s behaviour was video-recorded immediately prior to and immediately following the 10 s playback using a handheld digital video camera with a 70 x optical zoom (Sony DCR-SX45 Handycam). Immediately following each trial, the distance between the speaker and the focal animal’s location at the time of the playback was measured using a rangefinder (Bushnell Sport 450). Calls were broadcast at an average (± SD) distance of 35 (± 16) m, and the distance between the speaker and the focal animal did not differ between predator and non-predator treatments (One-way ANOVA; $F_{1,70} = 0.96$, P = 0.33; n = 45 [predator] and 27 [non-predator]). Habitat variables that could potentially impact the raccoon’s ability to hear the playback – including wind speed, rainfall and wave action – were measured for each trial, and showed no difference between treatments (Wilcoxon rank sum test; 0.18 > P > 0.87 for all variables; n = 45 and 27 for all tests). As the reaction of conspecifics to our playback treatments could conceivably have influenced the focal animal’s behaviour, we also quantified the number of conspecifics within 50 m of the focal animal at the time of the playback. In general, raccoons were > 50 m from any conspecific during playback trials (median [range] conspecifics within 50 m = 0 [0, 5]), and there was no difference in the number of conspecifics present between the two treatments (Wilcoxon rank sum test, W = 687, P = 0.27, n = 45 and 27). To minimize the likelihood of repeated sampling of raccoons, playback locations on a given island were separated by a median linear distance of 266 m, comparable to the spacing of sampling points (273 m) commonly utilized in raccoon live-trapping studies (Gehrt and Prange 2007). The minimum distance between trials of the same treatment did not differ between predator and non-predator treatments (ANOVA; *P* = 0.17; n = 45 [predator] and 27 [non-predator]). Each playback type was only played once at a given location.

A single researcher (DR), who was blind to the playback treatment, scored all video recordings of 10 s playback trials, and estimated three behavioural measures. First, we scored whether or not the focal raccoon fled the intertidal (i.e., moved from the exposed shoreline into the surrounding forest) within the 3 min immediately following the playback. For those individuals that did not flee, we calculated the amount of time (s) devoted to foraging and to vigilance (Fig. 3.2) in the 60 s immediately prior to and immediately following the playback. Gulf Islands raccoons spent < 1 s of every minute vigilant in the 60 s prior to the playback (0.9 ± 0.3 s [Mean ± SE.], range = 0-14), and instead spent the great majority of their time foraging. We calculated the change in foraging as the time spent foraging following the playback minus time spent foraging prior to the playback. An identical calculation was made for the change in vigilance. We report that raccoons significantly decreased foraging in response to the predator playback, relative to the non-predator playback. We found a correspondingly strong increase in vigilance in the 60 s following the predator playback (vigilance increased by 27.1 ± 1.7 [SE] s, relative to pre-playback, n = 22 raccoons), as compared to the non-predator playback (vigilance increased by 9.7 ± 1.7 s, n = 17; see Table 3.2).

3.3.5 Raccoon long-term response to the fear of large carnivores

The month-long playback manipulations were conducted on Coal Island in 2013 (10-May to 13-July) and Penelakut Island in 2014 (28-June to 25-August). On each island, we chose two shoreline sites separated by sufficient distance (1.2 km on Coal and 2.7 km on Penelakut) that sounds were not detectable between sites. We used a repeated measures design, presenting both predator and non-predator treatments at all sites and alternating the order of treatment presentation between sites on each island, allowing us to control for the effects of site and seasonality on raccoon behaviour and intertidal community data. On a given island, each site received either the predator or non-predator treatment for 28 d (Treatment Period 1), followed by the opposite treatment for a subsequent 28 d (Treatment Period 2), with less than a week separating the two treatment periods. Starting treatment (predator or non-predator) was randomly assigned. Throughout each treatment period, we monitored raccoon behaviour (Penelakut), the abundance of intertidal prey (Coal) and subtidal prey (Coal and Penelakut), and the survival and abundance of marine species not directly eaten by raccoons (Penelakut).

At all sites, five identical sets of speakers and mp3 players housed in weatherproof boxes were deployed at regular intervals along sections of shoreline, attached to trees just above the high water line. Speakers played multiple exemplars of large carnivore predator (dog) or non-predator control (pinniped) vocalizations at regular intervals throughout each 28-d treatment period. On Coal Island in 2013, the speaker systems were deployed at 25 m intervals across 100 m of shoreline, and broadcast either predator or non-predator playbacks 24 h d^{-1} (raccoons on Coal were active both day and night; JPS, pers. obs.). Each speaker played a randomized playlist of calls interspersed by periods of silence, broadcasting calls 40% of the time and remaining silent for 60% of the time. To reduce the likelihood of raccoon habituation to the playbacks, speakers were intermittently turned off completely for 1 to 4 d at a time during each 28-d treatment period (Zanette et al. 2011) such that speakers were active for a total of 19 d during Treatment Period 1 and 18 d during Treatment Period 2.

On Penelakut Island in 2014, the five speaker systems were deployed at 50 m intervals across 200 m of shoreline and broadcast calls only at night (19:00 to 09:00), as this is the period when raccoons on Penelakut are most active (JPS, pers. obs.). Speakers remained on for the full 28 d of each treatment period and played randomized playlists of either dog or pinniped calls 20% of the time, remaining silent for 80% of the time. In addition, two motion-sensitive speaker systems were deployed at each site, one at each end of the 200 m treatment area. These custom-built speaker systems used identical components to those described above, but were modified to incorporate a motion sensor, which activated a 10 s playback (using the same sets of calls described above) when triggered by a raccoon passing within approximately 5 m of the sensor. These speaker systems were always active, but remained silent unless triggered.

In an effort to minimize raccoon habituation to predator cues, we also presented predator and non-predator scent at each treatment site on Penelakut Island in 2014. Predator scent (wolf urine) or non-predator scent (rabbit urine) was presented at six scent stations spaced at regular intervals across each 200 m treatment site. Scent stations consisted of small plastic containers with perforated lids attached to vegetation along the high water line. Each sent station contained a cotton ball to which we applied approximately 10 ml of scent every third day throughout both 28-d treatment periods.

There is no evidence that the minor methodological differences in our fear manipulations between the two years of the experiment had any effect on our results. In particular we have no evidence that the use of scent in 2014 had an effect on raccoon behaviour or the impacts of raccoon foraging on intertidal prey beyond those caused by the presentation of predator and non-predator vocalizations. Indeed, the effect size of our predator and non-predator treatments on subtidal red rock crab abundance was identical in both years of the experiment (see below), suggesting that the minor differences between years in fear manipulation did not affect the impacts of raccoons on their prey.

We measured the long-term effects of the fear of large carnivores on several aspects of raccoon foraging on Penelakut Island in 2014, using a network of cameras deployed at each treatment site. Two colour/infrared, video surveillance cameras (Speco Technologies HT7915DNV Bullet Cameras), recording to custom-built digital video recording systems (Zanette et al. 2011), were deployed within each treatment site and spaced 100 m apart. We estimated the duration of time raccoons spent in the intertidal for all independent raccoon occurrences on camera as the time (s) from an individual raccoon first entering a camera's field of view to when it exited the field of view. Two time-lapse cameras (Moultrie Game Spy M-990i trail cameras set to "time-lapse" mode) spaced 100 m apart were deployed within each treatment site and programmed to record one photograph every 30 s. For each time-lapse image in which a raccoon's entire body was visible, we scored the raccoon's behaviour as either foraging or vigilant (Fig. 3.2). For each individual raccoon, we determined the total number of photos in which it appeared, and calculated the proportion of those photos scored as foraging. A single individual (JPS) scored all images of raccoons taken from time-lapse cameras. To determine whether these scores were repeatable, five independent observers, blind to the fear manipulation treatment, re-scored a total of 184 time-lapse photos (21% of all photos). Agreement between the original scores (used in the analyses presented here) and those made by the five observers was 80%.

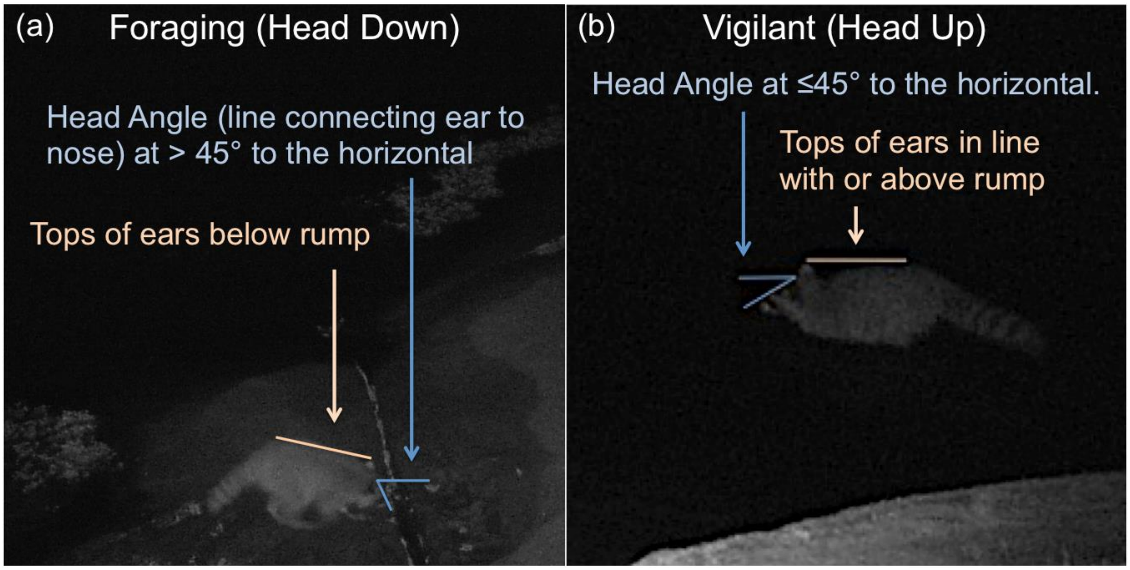

Figure 3.2. Raccoon behaviour scoring. Examples of the protocol used to score time spent foraging or vigilant based on raccoon head position in video recordings of 10 s playback trials and in 30 s time-lapse photos from month-long playback manipulations. Videos (10 s playbacks) or photos (month-long playbacks) were scored as: (a) foraging if the head angle (angle between a line connecting the ears and nose of a raccoon head in profile and the horizontal) was > 45° *or* if the tops of the ears were below the rump; or (b) vigilant if the head angle was ≤ 45° *and* the tops of the ears were in line with or above the rump.

For both camera types (video and time-lapse), we only used data from raccoons recorded between 19:00 and 09:00, when playback systems on Penelakut Island were active. Unless multiple raccoons occurring on a single camera could be classified with certainty as unique individuals, raccoon occurrences on camera were only treated as independent if they were separated by > 30 min (O’Brien and Kinnaird 2011, Brook et al. 2012). All raccoon behaviour variables were calculated per camera per night of the treatment period (Brook et al. 2012, Bowkett et al. 2008); “camera night” is therefore the unit of replication in all behavioural analyses (see below). Camera placement remained constant throughout the duration of the experiment, and we therefore analyzed all behavioural data using mixed effects models with Camera ID included as a random effect to account for variation due to camera placement.

3.3.6 Measuring cascading effects of fear

In 2013, we used standard quadrat sampling methods to test whether our month-long playback manipulations affected the abundance of raccoon intertidal prey. Based on previous work (Suraci et al. 2014) and direct observations of raccoon foraging, our *a priori* prediction was that our fear manipulations would affect the abundances of small (< 5 cm carapace width) intertidal crabs (shore crabs [*Hemigrapsus oregonensis, H. nudus*], black-clawed crabs [*Lophopanopeus bellus*], porcelain crabs [*Petrolisthes* spp.], and juvenile northern kelp crabs [*Pugettia producta*]), intertidal fish (pricklebacks [family Stichaeidae] and northern clingfish [*Gobiesox maeandricus*]), and polychaete worms (families Terebellidae, Orbiniidae, Nereidae, and Glyceridae). Following methods described in Suraci et al. (2014), we quantified species abundance in ten 0.25 x 0.25 m quadrats at each treatment site on Coal Island at the end of each 28-d treatment period.

To test whether our playback manipulations affected red rock crab abundance, we trapped crabs across 200-m sections of shoreline centered at each treatment site by setting five collapsible mesh crab traps per site just below the low intertidal zone, spaced 50 m apart and left in place for 24 h (Suraci et al. 2014). On Coal Island in 2013, crab traps were set at the end of each month-long treatment period. Sampling effort was intensified on Penelakut Island in 2014 such that crab trapping was conducted once prior to the application of any playback treatments (on 11-June 2014) to establish a pre-treatment baseline crab abundance, and then at the end of each week during both month-long treatment periods (i.e., four times per treatment period). In both years trap locations remained constant across all trapping sessions at a given site.

The effects of the fear of large carnivores may extend beyond those species directly subject to raccoon predation to affect the competitors and prey of the raccoons’ prey. Red rock crabs are major intertidal predators, and may compete for resources with other intertidal predators of similar body size, including the staghorn sculpin, the most common sculpin on the Pacific Coast of North America (Tasto et al. 1975). Diets of red rock crabs and staghorn sculpins overlap considerably, with both species preying on a range of arthropods, bivalves and gastropods, and scavenging dead fish (Tasto et al. 1975, Carroll and Winn 1989, Robles et al. 1989, Armstrong et al. 1996, Behrens Yamada and Boulding 1996, Smith et al. 1999, Meyer et al. 2005). Red rock crab and staghorn sculpin habitat use also overlaps substantially (Tasto et al. 1975, Carroll and Winn 1989), suggesting the potential for strong competition between these two intertidal predators. However, unlike red rock crabs, we have no evidence that staghorn sculpins are preyed upon by raccoons. Staghorn sculpins are comparatively large (c. 15 cm), free-swimming, fast-moving, fish (Tasto et al. 1975). Based on our many hundreds of hours recording raccoon foraging, raccoon predation on fish is limited to smaller species that remain in the intertidal at low tide, hidden under rocks (e.g., prickleback and northern clingfish), and we have never encountered staghorn sculpins under rocks at low tide during intertidal quadrat sampling (JPS, pers. obs.). Indeed staghorn sculpins may even benefit from raccoon presence due to increased scavenging opportunities, as raccoons regularly leave the carcasses of freshly killed crabs in the intertidal (Suraci et al. 2014). We tested whether our fear manipulation treatments affected staghorn sculpin abundance by setting conical fish traps (minnow traps) across both treatment sites on Penelakut Island in 2014. Five traps, spaced 50 m apart and baited with ~100 g of frozen herring, were set in the mid intertidal zone at each site and left in place for 24 h. Traps were deployed three times per 28-d treatment period, once immediately prior to the start of each treatment period and again at the mid-point and end of each treatment period. The same trap locations were used for all fish trap deployments at both sites.

Red rock crabs are known to affect the abundance of several species of gastropod prey, including periwinkle snails. We hypothesized that, during predator treatments, reduced raccoon predation on red rock crabs would result in increased red rock crab predation on periwinkle snails relative to non-predator treatments. To test this, we performed 4 replicate short-term snail mark-recapture experiments nested within our fear manipulation experiment on Penelakut Island in 2014, comparing the proportion of marked snails killed by red rock crabs during predator and non-predator treatments. Periwinkle snails were collected from high intertidal beds of *Fucus* algae at each site and transported back to the laboratory where they were marked with a small dab of acrylic paint on the apex of the shell, and held overnight in seawater tanks. Following Rochette and Dill (2000), snails were released the next day at each of four release points (spaced 30 to 50 m apart) within the 200-m treatment area at each site. All release points were located at the same tide level (1.0 m above mean lower low water) on areas of flat rock away from large boulders or crevices (Rochette and Dill 2002). Twenty snails were released within a 5 cm radius of each release point during afternoon rising tides when release points were submerged under at least 1.5 m of water. The following morning at low tide, immediately following exposure of the release points, two researchers searched a 4 m radius around each point, recovering marked live snails and the marked apices of crushed snail shells. Red rock crab predation on snails produces a characteristic shell crushing pattern (Behrens Yamada and Boulding 1996), allowing one to reliably diagnose snail mortality due to red rock crab predation, and counting only shell apices rather than all crushed shell fragments ensures that each crushed snail is only counted once (Rochette and Dill 2002). We estimated the proportion of marked snails surviving red rock crab predation over one tide cycle as the number of live snails recovered divided by the total number of live snails and crushed apices recovered at each release point (the fate of snails not recovered could not be reliably ascribed to red rock crab predation). To minimize potential bias due to low recovery rates, we only used data from trials for which at least 50% of the 20 released snails were recovered, alive or dead (n = 18 trials). For these trials, the average recovery rate was 71% (range = 50% to 95%), and did not differ between predator and non-predator treatments ($t_{1,16} = -0.04$, $P = 0.97$). This snail mark-recapture study was replicated four times on Penelakut Island in 2014, at the mid-point and end of each month-long treatment period, using the same four release points at each site throughout both treatment periods.

3.3.7 Statistical analyses

All model assumptions were checked using statistical tests for normality and homogeneity of variance, and the fit of all models was visually inspected using residual vs. fitted value plots and quantile-quantile plots (Zuur et al. 2009). Where appropriate, means and standard errors were calculated on normalized data, and back-transformed to the original scale of the data for presentation in figures. All (Generalized) Linear Mixed Effects Models were fit using the ‘lme4’ package in R (R Core Team 2014).

We used a Log-Linear analysis to test whether playback treatment affected the proportion of trials in which the focal raccoon fled the intertidal following 10 s playbacks, using a model that included terms for treatment, island and a treatment x island interaction. Data on both the change in foraging and the change in vigilance exhibited by raccoons that did not flee the intertidal following 10 s playbacks were Box-Cox transformed and analysed using separate two-way ANOVA models including the main effects of treatment and island, and a treatment x island interaction (Table 3.2).

We estimated the duration of time spent in the intertidal during month-long playback treatments for all independent raccoon occurrences on video surveillance cameras, and then used the median duration per camera night in our analysis. Median duration data were natural log-transformed and analyzed using a Linear Mixed Effects Model (LMM; Table 3.3). We estimated the proportion of time that raccoons spent foraging when present in the intertidal from time-lapse camera data, as described above, and then calculated the average of these “proportion foraging” values for all individuals on a given camera night, weighted by the total number of photos of each individual. Raccoon occurrences on camera that produced fewer photos were thereby devalued relative to occurrences with many photos and thus more information. Nightly weighted mean proportions of time spent foraging were then analyzed using LMM (Table 3.3). The significance of model terms was tested using Likelihood Ratio Tests (LRT, Zuur et al. 2009). In both behavioural analyses, we tested for main effects of treatment and study site as well as a treatment x site interaction. We also tested for a main effect of time since the start of the treatment period (“night”, measured in days: 1 to 28) and an interaction between treatment and night. This allowed us to determine whether raccoon behavioural responses to the treatments changed over the course of the treatment period (e.g., due to habituation) and whether any such changes differed between predator and non-predator treatments. Finally, we tested for a three-way treatment x site x night interaction. We found no evidence for raccoon habituation to predator playbacks across the month-long treatment periods in either behavioural measure; the effect of night and the treatment x night interaction were non-significant in both analyses (Table 3.3).

Quadrat data on the abundances of intertidal prey were analyzed using Generalized Linear Models (GLM) with a Poisson distribution. All models were checked for overdispersion (Zuur et al. 2009), and those showing evidence of overdispersion (intertidal crabs and polychaete worms) were refit using the Quasi-Poisson distribution. Treatment, site and their interaction were included as fixed effects in all GLM (Table 3.4). Following Zuur et al. (2009), the significance of all main effects and interactions was tested using LRT for models fit with the Poisson distribution (intertidal fish), and F-tests for models fit with the Quasi-Poisson distribution (intertidal crabs and polychaete worms).

We analyzed the effect of the fear manipulation treatments on shallow subtidal red rock crab abundance across the two years of the experiment, using as our response variable the number of red rock crabs caught per trap at the end of Treatment Periods 1 and 2 in both 2013 and 2014. These data were analyzed using a Generalized Linear Mixed Effects Model (GLMM) with a Poisson distribution and checked for overdispersion (ratio of null to residual deviance = 1.17). We tested for main effects of treatment and year, and their interaction. Within a given year, sites and trap locations remained constant across treatment periods, so site and trap location were included in the analysis as nested random effects (trap location nested within site). The significance of main effects and interactions in the GLMM was tested using Type II Wald's χ^2 test (Bolker et al. 2009; Table 3.5).

The above analysis required using a subset of the data on red rock crab abundance collected in 2014 (in which crab abundance was sampled prior to the experiment and weekly during each treatment period; see above), to match data collection in 2013 (when crab abundance was sampled only during the last week of each treatment period). We subsequently analyzed the full 2014 dataset separately, allowing us to compare the abundance of red rock crabs measured across the two treatment periods with baseline levels of crab abundance measured prior to the application of any playback treatment. The response variable for this analysis was the number of red rock crabs per trap, and we tested for the main effects of treatment (a three level factor: "pre-treatment", "non-predator" and "predator") and site, as well as a treatment x site interaction. Within each site, trap locations remained constant throughout all pre-treatment and treatment trapping sessions, and trap location was therefore included in the analysis as a random effect. Due to overdispersion in the dataset, we were unable to achieve adequate model fit using a

Generalized Linear Mixed Effects Model with a Poisson distribution. We therefore natural log + 1 transformed the response variable and analyzed the data using a Linear Mixed Effects Model. We then performed a Tukey's pairwise comparison *post hoc* test to test for significant differences between each combination of treatment levels (Table 3.5).

We calculated the change in staghorn sculpin abundance across each treatment period by subtracting the number of sculpins caught in each trap at the mid-point and end of each treatment period from the number caught in the same trap immediately prior to that treatment period. These data were analyzed using LMM, including trap location (constant across sampling events) as a random effect. We tested for the main effects of treatment and site, and a treatment x site interaction (Table 3.6).

The effect of our playback treatments on the proportion of marked periwinkle snails escaping crab predation was determined by scoring all surviving snails as 1 and all crushed snails as 0 in each trial of the mark-recapture experiment, and analyzing these data using GLMM with a binomial error distribution. There was no evidence for overdispersion in these data (ratio of null to residual deviance = 1.10). Snail release point (constant across all trials at a given site) was included as a random effect. We tested for the main effects of treatment and site, and a treatment x site interaction (Table 3.6).

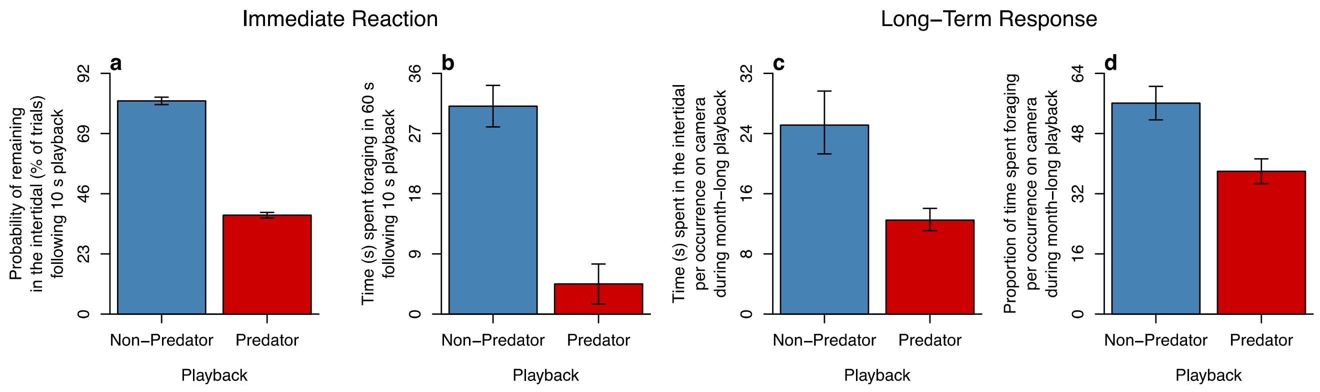

Figure 3.3. Fear of large carnivores reduced mesocarnivore foraging. (a) Probability of remaining in the intertidal (% of trials), and (b) time spent foraging (out of 60 s) immediately following 10 s predator and non-predator playbacks. (c) Time spent in the intertidal (per occurrence on camera), and (d) proportion of time spent foraging (per occurrence on camera) during month-long predator and non-predator playbacks. Values are means ± SE.

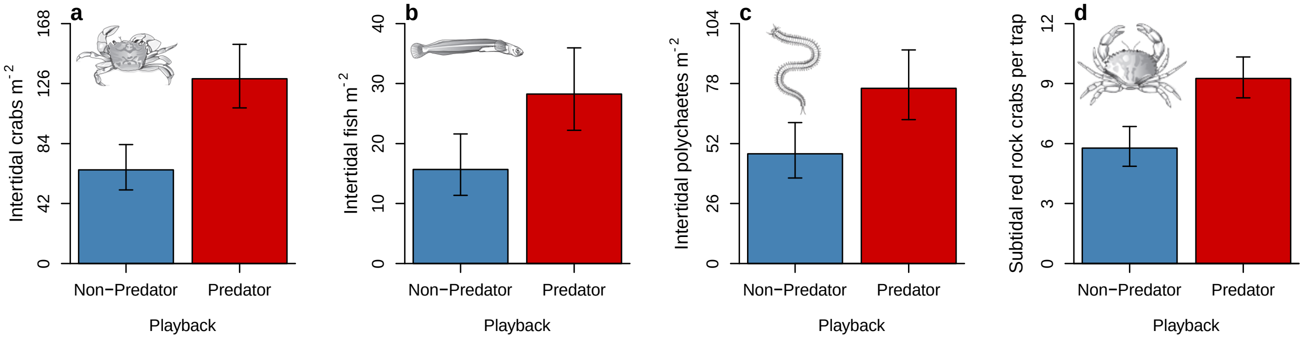

Figure 3.4. Fear of large carnivores benefited the mesocarnivore's prey. Abundance of (a) intertidal crabs, (b) intertidal fish, (c) intertidal polychaete worms, and (d) subtidal red rock crabs following month-long predator and non-predator playbacks. Values are means ± SE.

3.4 Results

Fear of large carnivores dramatically reduced mesocarnivore foraging (Fig. 3.3 and Tables 3.2 and 3.3). The immediate reaction of raccoons to the 10 s predator playbacks was to either abandon foraging entirely by leaving the intertidal (Log-Linear Test, χ^2_1 = 11.96, P < 0.001; n = 45 [Predator] and 27 [Non-Predator]; Fig. 3.3A), or reduce foraging (ANOVA, $F_{1,33}$ = 15.85, P < 0.001; n = 22 and 17; Fig. 3.3B) and increase vigilance. Critically, these same responses persisted throughout the month-long playbacks. Large carnivore playbacks caused raccoons to spend less time in the intertidal (LMM, Likelihood Ratio [LR] χ^2_1 = 9.66, P = 0.002; n = 51 and 43; Fig. 3.3C), and less time feeding when they were present (LMM, LR χ^2_1 = 11.86, P = 0.001; n = 62 and 52; Fig. 3.3D), with the cumulative consequence that they spent 66% less time foraging over the course of the month.

Table 3.2. Model results for raccoon immediate reactions to 10 s playbacks. Results from Log Linear (probability of remaining in the intertidal) and Two-way ANOVA (change in time spent foraging and change in vigilance) models for raccoon immediate reactions to 10 s playbacks.

	Probability of remaining in the intertidal		Change in time spent foraging		Change in vigilance	
	χ^2	P-value	F-value	P-value	F-value	P-value
Treatment	11.957	***<0.001***	15.848	***<0.001***	11.761	***0.002***
Island	0.270	0.873	0.135	0.874	4.126	***0.025***
Treatment x Island	1.530	0.465	1.648	0.208	1.399	0.261

Table 3.3. Model results for raccoon responses to month-long playback manipulations. Results from Linear Mixed Effects Models for raccoon long-term behavioural responses to month-long predator and non-predator treatments.

	Time spent in intertidal		Proportion of time spent foraging	
	LRT[1] χ^2	P-value	LRT χ^2	P-value
Treatment	9.661	***0.002***	11.285	***0.001***
Site	0.822	0.365	0.156	0.693
Night	0.096	0.870	2.563	0.109
Treatment x Site	0.027	0.346	2.626	0.105
Treatment x Night	0.462	0.497	1.654	0.198
Site x Night	1.698	0.193	0.092	0.762
Treatment x Site x Night	2.435	0.119	3.322	0.068

[1] Likelihood Ratio Test

This dramatic reduction in mesocarnivore foraging in turn dramatically benefitted the mesocarnivore's prey (Fig. 3.4 and Tables 3.4 and 3.5). Following the month-long large carnivore playbacks there were 97% more intertidal crabs (Quasi-Poisson GLM, $F_{1,36}$ = 12.11, P = 0.001; n = 20 [Predator] and 20 [Non-Predator]; Fig. 3.4A), 81% more intertidal fish (Poisson GLM, Likelihood Ratio χ^2_1 = 5.15, P = 0.023; n = 20 and 20; Fig. 3.4B), 59% more polychaete worms (Quasi-Poisson GLM, $F_{1,36}$ = 4.54, P = 0.039; n = 20 and 20; Fig. 3.4C) and 61% more subtidal red rock crabs (Poisson GLMM; Wald's χ^2_1 = 10.83, P = 0.001; n = 20 and 20; Fig. 3.4D; see also Fig. 3.6), compared to after the non-predator playbacks.

Table 3.4. Results from Generalized Linear Models testing the effect of month-long predator and non-predator treatments on raccoon intertidal prey.

	Intertidal crabs		Intertidal fish		Polychaete worms	
	F-value	P-value	LRT χ^2	P-value	F-value	P-value
Treatment	12.110	***0.001***	5.148	***0.023***	4.541	***0.039***
Site	2.369	0.133	3.994	***0.046***	1.686	0.202
Treatment x Site	0.544	0.465	0.131	0.717	0.003	0.955

Table 3.5. Results from (a) Generalized Linear Mixed Effects Model, (b) Linear Mixed Effects Model and (c) Tukey's Post-Hoc Test describing the indirect effect of month-long predator and non-predator treatments on shallow subtidal red rock crab abundance.

(a) 2013 and 2014 data pooled

	Wald's χ^2	P-value
Treatment	10.828	***0.001***
Year	2.814	0.093
Treatment x Year	0.577	0.448

(b) 2014 data only

	LRT χ^2	P-value
Treatment	17.365	***<0.001***
Site	4.778	***0.029***
Treatment x Site	3.973	0.137

(c) Tukey's Pairwise Post-Hoc Test comparing treatments for 2014 data

	Z-value	P-value
Pre-Treatment vs. Non-Predator	0.095	0.995
Pre-Treatment vs. Predator	2.532	***0.029***
Predator vs. Non-Predator	4.154	***<0.001***

Finally, fear of large carnivores clearly had cascading effects on multiple lower trophic levels (Fig. 3.1), as the reduction in raccoon foraging (Figs. 3.3C and 3.3D) that produced the increased relative abundance of red rock crabs (Fig. 3.4D) was associated with a decreased abundance of the red rock crab's competitor (staghorn sculpin; LMM, LR χ^2_1 = 21.17, $P < 0.001$; n = 20 [Predator] and 20 [Non-Predator]; Fig. 3.5A) and led to lower survival of the red rock crab's prey (periwinkle snail; Binomial GLMM, Wald's χ^2_1 = 9.51, $P = 0.002$; n = 10 and 8; Fig. 3.5B and Table 3.6).

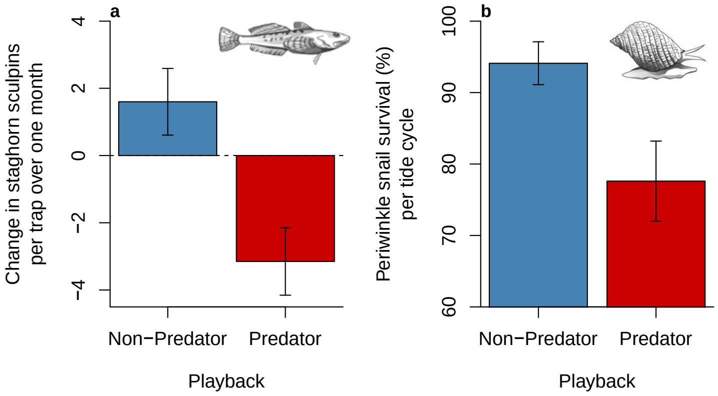

Figure 3.5. Fear of large carnivores affected a competitor and prey of the mesocarnivore's prey. (a) Change in abundance of staghorn sculpins over one month and (b) survival of periwinkle snails per tide cycle during month-long predator and non-predator playbacks. Values are means ± SE.

Table 3.6. Results from (Generalized) Linear Mixed Effects Models testing the cascading effects of month-long predator and non-predator treatments on intertidal and subtidal species not directly eaten by raccoons.

	Change in staghorn sculpins per trap		Periwinkle snail survival	
	LRT χ^2	P-value	Wald's χ^2	P-value
Treatment	21.174	***<0.001***	9.508	***0.002***
Site	6.812	***0.009***	2.921	0.087
Treatment x Site	2.690	0.101	1.224	0.268

We found a remarkable degree of repeatability in our experimental results, as the differences in red rock crab abundance between predator and non-predator treatments were identical in both years of the experiment. There were on average 2.9 more red rock crabs per trap following predator treatments than following non-predator treatments in each year (SE: ± 2.2 [2013] and ± 1.5 [2014]). When considering red rock crab abundance from 2014 only (see Methods), we found a significant overall effect of treatment on the number of red rock crabs per trap (Table 3.5, Fig. 3.6). Tukey's *post* *hoc* test revealed that the predator playback treatment led to a significant increase in crab abundance relative to both the non-predator treatment ($Z = 4.15$, $P < 0.001$) and the pre-treatment baseline ($Z = 2.53$, $P = 0.029$). However, crab abundance did not differ between the pre-treatment baseline and the non-predator treatment ($Z = 0.10$, $P = 0.995$; Table 3.5, Fig. 3.6), confirming the validity of our pinniped playbacks as a non-threatening control. When integrated across the entire month-long treatment period, the magnitude of the effect of large carnivore-induced fear on crab abundance was even greater than when crabs were only sampled at the end of each treatment period – the mean (± SE.) difference in the number of crabs per trap between predator and non-predator treatments was 3.9 (± 1.1) crabs (Fig. 3.6).

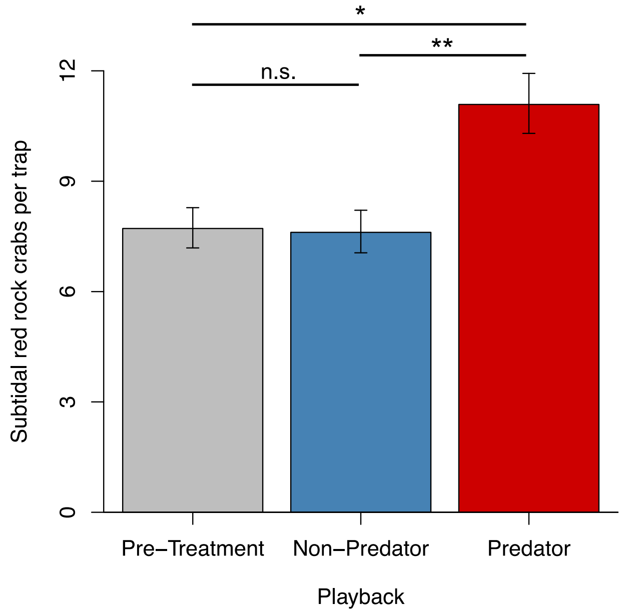

Figure 3.6. Fear of large carnivores affects red rock crab abundance. Red rock crab abundance compared between the pre-treatment, predator and non-predator playback periods sampled in the course of the more intensive red rock crab sampling conducted in 2014. Red rock crabs were trapped once prior to the start of any playback treatments (pre-treatment, n = 10), and then weekly during month-long predator (n = 40) and non-predator (n = 40) treatments (Linear Mixed Effects Model with Tukey's Post-Hoc Test; n.s. = not significant, $*P < 0.05$, $**P < 0.001$). Values are means ± SE.

3.5 Discussion

Our results unambiguously experimentally demonstrate that the fear of large carnivores can itself cause a trophic cascade. Manipulating fear itself – by hanging a speaker from a tree – caused cascading effects on predation and competition at multiple trophic levels in the ocean (Fig. 3.1). Moreover, there were likely many more effects than we measured, potentially cascading down to the level of primary producers, as red rock crabs are themselves significant predators (Behrens Yamada and Boulding 1996) and periwinkle snails are significant grazers (Mrowicki and O'Connor 2015).

As intertidal predators, red rock crabs affect the abundance of several species of gastropod prey (Robles et al. 1989, Bourdeau 2012), including periwinkle snails (McCormack 1982, Behrens Yamada and Boulding 1996, Behrens Yamada et al. 1998, Rochette and Dill 2000). Periwinkle snails are in turn major intertidal grazers (Lindegarth 2001, Mrowicki and O'Connor 2015) with the ability to control algal cover and diversity (Lubchenco 1978, 1983; Bertness et al. 1983), particularly on sheltered coastlines (Mrowicki and O'Connor 2015) like those studied here. The local periwinkle species (*Littorina scutulata* and *L. sitkana*) are among the most abundant grazers along coastlines in and near the Gulf Islands (Behrens Yamada and Boulding 1996, JPS, pers. obs.), and red rock crabs are likely their most important predators in many areas (Boulding et al. 1999, Rochette and Dill 2000). The strength of red rock crab predation on periwinkle snails therefore likely has significant cascading effects on the diversity and abundance of primary producers in this region.

Our results additionally demonstrate that failing to consider the fear large carnivores inspire risks dramatically underestimating their role, given the striking magnitude of the effects (Figs. 3.4 and 3.5), and that these were comparable in magnitude to those documented in our previous mensurative experiment comparing islands with and without raccoons. The presence of raccoons on an island reduces the respective abundance of intertidal crabs and fish, and subtidal red rock crabs, by 90%, 94% and 38% (Suraci et al. 2014); impacts all reversed by the 97%, 81% and 61% relative increase in each (Fig. 3.4) resulting from the reduction in raccoon foraging caused by the fear of large carnivores (Fig. 3.3). That the fear of large carnivores could itself be powerful enough to reverse these impacts corresponds with the fact that the human extirpation of most large carnivores from the Gulf Islands means raccoons here no longer have much to fear, and act accordingly, as they forage night and day (being more normally nocturnal) far from cover (deep into the intertidal; Suraci et al. 2014), and rarely look up from eating, spending < 1 s vigilant per minute (see Methods). Our experiment reversed this now unrestrained foraging by restoring the fear of large carnivores to a system from which it has largely been lost, revealing the significance of the ecosystem service the presence of the now extirpated large carnivores (wolves, cougars and black bears) provided, solely through the fear they inspired.

Similar restorative effects of the fear of large carnivores have been attributed to the reestablishment of a "landscape of fear" accompanying the reintroduction or recolonization of large carnivores (Fortin et al. 2005, Creel and Christianson 2008, Berger et al. 2008, Laundré et al. 2011, Ripple et al. 2014); and broad-scale impacts accompanying the loss of large carnivores that cannot be explained by the reduction in direct killing alone, have likewise been attributed to the associated loss of the fear of large carnivores (Creel and Christianson 2008, Prugh et al. 2009, Terborgh and Estes 2010, Ritchie et al. 2012, Ripple et al. 2014). The evidence to date that the fear of large carnivores can play a central role in structuring ecosystems comes largely from "natural experiments" (Creel and Christianson 2008, Dobson 2014, Ripple et al. 2014), and compelling alternative explanations often exist for the patterns observed (Dobson 2014). Our results in no way refute these alternatives, but our being able to cause a trophic cascade by directly manipulating fear does conclusively demonstrate such a thing is possible, and so corroborates that the fear of large carnivores can play the role attributed to it.

Experimentally manipulating the fear of large carnivores demonstrably affected mesocarnivore behaviour (Fig. 3.3), which in turn evidently caused a "fear cascade" affecting the behaviour of at least some of the mesocarnivore's prey. Red rock crab abundance increased significantly over the course of the month-long large carnivore playbacks (Fig. 3.6), which could only be due to a behavioural change in habitat use, as reproduction in this species requires at least a year (Orensanz and Gallucci 1988). Red rock crabs occur in large subtidal populations and move into the intertidal to forage, where they are killed and eaten by raccoons, which leave the remains, and thus chemical cues, of dead crabs in the water (Suraci et al. 2014). Surviving red rock crabs may modify their habitat use in response to these chemical cues, as has been demonstrated experimentally in other crab species (Hill and Weissburg 2014). The "fear cascade" evident from the increased abundance of red rock crabs may therefore have resulted from straightforward mechanisms: increasing the fearfulness of raccoons reduced their foraging (Fig. 3.3), which presumably led to reduced fearfulness in red rock crabs by decreasing chemical cues in the water, in turn leading to the red rock crabs' increased use of the intertidal (Fig. 3.6).

The loss of large carnivores from habitats across the globe has been linked to far-reaching ecosystem-level consequences – including biodiversity loss and changes in habitat structure – caused by outbreaks of large herbivores and mesocarnivores (Laundré et al. 2001, Fortin et al. 2005, Berger et al. 2008, Prugh et al. 2009, Estes et al. 2011, Ritchie et al. 2012, Ripple et al. 2014). Our results suggest that restoration of these ecosystems will require more than just addressing the overabundance of these middle trophic level species, e.g., through hunting or removal programs. Such numerical suppression may only affect a subset of hyper-abundant large herbivore and mesocarnivore populations, while the remaining individuals are free to engage in unrestricted foraging. Effective ecological restoration may depend on re-establishing the fear of large carnivores in these ecosystems, which has the potential to affect entire populations of their prey (rather than just those individuals subject to direct killing or removal; Werner and Peacor 2003, Schmitz et al. 2004), suppressing prey foraging behaviour and thereby mitigating the impacts of overconsumption on lower trophic level species. The potential ecosystem-level benefit of the mere presence of large carnivores, and the "landscape of fear" they produce, should therefore be a central consideration in making informed management decisions regarding large carnivore populations.

Our experimental results support the contention that, when it comes to conserving biodiversity and maintaining healthy ecosystems, fear has its uses (Creel and Christianson 2008, Prugh et al. 2009, Terborgh and Estes 2010, Ripple et al. 2014). By inspiring fear, the very existence of large carnivores on the landscape, in and of itself, can provide a critical ecosystem service human actions cannot fully replace, making it essential to maintain or restore large carnivores for conservation purposes on this basis alone (Prugh et al. 2009, Terborgh and Estes 2010, Ritchie et al. 2012, Ripple et al. 2014). Ensuring the continuation of this critical ecosystem service the fear of large carnivores provides requires attenuating our own fear of them, which can be accomplished by promoting tolerance and coexistence with large carnivores as an accompaniment to other programs to reduce human-large carnivore conflicts (Packer et al. 2005, 2013; Chapron et al. 2014; Ripple et al. 2014; Woodroffe et al. 2014).

Chapter 4 – A New Automated Behavioural Response System to Integrate Playback Experiments into Camera Trap Studies

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Author Contributions: JPS, MC, MD and LYZ conceived of and designed the Automated Behavioural Response system. JPS, BM, MC, DWM, JAS, CCW and LYZ conceived of and executed the field tests. JPS contributed directly to field test in Clayoquot Sound and Santa Cruz and conducted all data analysis. JPS and MC wrote the manuscript.

4.1 Abstract

How animals respond to human disturbances, predators and competitors are central questions in ecology and conservation biology. Camera traps have rapidly become a critical tool in addressing these questions in free-living wildlife, providing data on rarely observed species and interactions without requiring the presence of an observer, but the typically coarse-scale, correlational nature of camera trap data often permits only relatively weak inferences regarding animal behavioural responses. Playback experiments provide a powerful means of directly testing the behavioural responses of animals, but suffer logistically from the need to have an observer present. We developed and tested an Automated Behavioural Response (ABR) system, which combines all the advantages of camera traps with the ability to conduct playback experiments, allowing researchers to rigorously test hypotheses regarding wildlife behavioural responses without the confounding effects of observer presence. We describe field tests in Uganda, Canada and the USA, in which the unique capacity of the ABR system to collect detailed behavioural data from diverse and often cryptic species permitted us to successfully test hypotheses that would have otherwise been infeasible to address experimentally. Factors influencing the performance of the ABR system were largely the same as those affecting camera trap studies *per se*: success of ABR trials was positively related to species body size and dependent on animal behaviour immediately prior to the playback. However, our field test results demonstrate that these impediments to system performance can be fully overcome through refinements of experimental set-up, which we discuss. By incorporating the experimental rigor of playback studies into non-invasive camera trap methods, the ABR system has the potential to greatly expand the range of research questions addressed by wildlife ecologists and conservation biologists, permitting the collection of experimental behavioural data across the full range of species and habitats currently included in camera trap studies. We provide suggestions on how to optimize performance of the ABR system for various field applications, and discuss novel research opportunities made available by this new technology.

4.2 Introduction

How animals respond to humans, their commensals (e.g. dogs), and anthropogenic disturbances, are central questions in conservation biology (Caro 1999, 2007; Frid and Dill 2002; Valeix et al. 2012; Cristescu et al. 2013; Francis and Barber 2013; Ordiz et al. 2014; Oriol-Cotterill et al. 2015b; Smith et al. 2015); and quantifying how animals respond to predators and competitors is similarly central to behavioural, population and community ecology (Lima and Dill 1990; Lima 1998; Creel and Christianson 2008; Sheriff et al. 2009; Berger 2010; Schmitz 2010; Zanette et al. 2011; Suraci et al. 2016). Camera traps have rapidly become a critical tool in both conservation biology and wildlife ecology in large part because they provide a fully-automated means of observing wildlife that avoids the potentially confounding effects and logistical challenges of needing to have an observer present, and can thus capture information on rare or elusive species and infrequent events (O'Connell et al. 2011; Rowcliffe et al. 2011, 2012, 2014; Hamel et al. 2013; Mugerwa et al. 2013; Burton et al. 2015; Heinicke et al. 2015; Weinstein 2015). Snapshots from camera traps have been used to interpret how animals may be responding to, e.g., humans, predators or competitors, by avoiding them in space and time; but such coarse-scale, correlational data permit only relatively weak inferences (Bridges and Noss 2011; Rowcliffe et al. 2012, 2014; Burton et al. 2015). Most modern camera traps are capable of recording both audio and video, making it readily feasible to quantify more than simply presence or absence, though only a very small subset of camera trap studies have yet made use of this capability to directly record the behavioural responses of animals in real time (Rowcliffe et al. 2012; Weinstein 2015). A Web of Science^{TM} search for "camera trap*" conducted on 15 December 2015 found 922 entries, only 32 of which were returned when "video" was added as an additional search term.

Playback experiments provide a powerful, comparatively easily-implemented and readily-interpretable means of directly testing the behavioural responses of animals (Durant 2000; Clinchy et al. 2011; Zanette et al. 2011; Suraci et al. 2016), and have accordingly been employed in hundreds of wildlife studies to quantify how animals respond to the sounds of humans (e.g., langurs, Yorzinski and Ziegler 2007; elephants, McComb et al. 2014; deer, Padié et al. 2015), dogs (e.g., raccoons, Suraci et al. 2016), anthropogenic noise (Francis and Barber 2013), predators (180 experiments on everything from toads to elephants, reviewed in Hettena et al. 2015), competitors (e.g., lions, Heinsohn and Packer 1995; hyenas and African wild dogs, Webster, McNutt and McComb 2012), potential mates (e.g., lions, McComb et al. 1993) and numerous other stimuli (King 2015). To date, the principal logistical constraint on conducting such experiments has been the need to have an observer present to locate subjects and operate the equipment, with the result that most playback experiments have been restricted to quantifying the responses of relatively common, diurnally-active animals, that are not hyper-sensitive to the presence of humans. This constraint has largely precluded the use of playback experiments in conservation biology (Thuppil and Coss 2013, 2015), as well as studies of more elusive wildlife like large carnivores living in remote or heavily forested habitats.

Here we describe an Automated Behavioural Response (ABR) system, which combines all the advantages that camera trapping derives from not needing to have an observer present, with the power playback experiments provide to directly and rigorously test hypotheses about how animals respond to humans, predators, competitors or conspecifics. The ABR system is designed to be easily integrated into existing camera trap protocols, permitting collection of experimental behavioural data across the full range of species and habitats currently included in camera trap studies. We describe our successful use of ABRs in three experiments that would have been infeasible to conduct without the use of these systems. In the first we addressed a preeminent question in conservation biology concerning how to quantify the extent and intensity of illegal hunting (DeFries et al. 2010; Conteh et al. 2015; Hegerl et al. 2015), by assaying the behavioural responses of wildlife to playbacks of humans and hunting dogs. In the other two experiments we examined interactions among large carnivores that are next to impossible to observe directly, quantifying how other large carnivores respond to playbacks of cougars, and vice versa. These three experiments were respectively conducted in tropical montane forest in Uganda (Bwindi Impenetrable National Park), remote coastal temperate rainforest in Canada (Clayoquot Sound Biosphere Reserve, British Columbia) and coastal montane habitats in the USA (Santa Cruz Mountains, California). Utilizing these ABR systems we successfully quantified the responses of animals from the size of elephants (5250 kg) to black bears (89.5 kg) to squirrels (0.2 kg).

We provide a technical description of two versions of the ABR system, and compare and contrast the factors influencing how effective these two variants were at quantifying the responses of animals to playbacks in the experiments conducted in Uganda and Canada. We then describe using the lessons learned to maximize the performance of the system in the USA experiment. The successfulness with which the ABRs can be integrated into camera trap studies is demonstrated by the fact that most of the factors influencing the performance of the ABRs were the same as those affecting camera trap studies *per se*, such as animal body size and movement speed, camera set-up and the use of attractants (Rowcliffe et al. 2011; Hamel et al. 2013; Burton et al. 2015). The critical difference being that, whereas the correlational nature of standard camera trapping means such factors represent potential confounds that may invalidate the interpretation of the data (Rowcliffe et al. 2011, 2012, 2014; Burton et al. 2015), the new capacity the ABRs provide to conduct experiments mean these simply represent potential impediments to maximizing the performance of the system in a particular context, which can be overcome with the help of the suggestions we provide.

4.3 Technical Description

The ABR system is comprised of a custom-made, motion-sensitive speaker unit, designed to be used in conjunction with any commercially available, audio- and video-enabled camera trap (Fig. 4.1). The speaker unit consists of an off-the-shelf shockproof and waterproof speaker (Ecoextreme, Grace Digital Inc., USA) modified to incorporate a custom microcontroller (Atmel ATTiny85, Fig. 4.1c) and input port for an external motion sensor (Fig. 4.1d). The microcontroller detects an incoming digital trigger from an attached sensor; either a standalone motion sensor (Mark 1; Fig. 4.1a,b), or a separate circuit designed to detect camera trap activity (Mark 2; Fig. 4.1a), the details regarding both of which are described below. This trigger activates the speaker by permitting current to pass from a custom battery pack (Fig. 4.1d) to the terminals in the speaker's battery compartment. The microcontroller allows the user to set two playback parameters: (1) the duration of the playback (duration), and (2) the delay between triggering of the motion sensor and the start of the playback (delay). The inclusion of the delay setting permits researchers to record a predetermined amount of baseline behaviour prior to broadcasting a playback, thus allowing for powerful comparisons of each individual animal's behaviour immediately prior to and immediately following exposure to the stimulus (e.g., Blumstein et al. 2008), thereby reducing statistical noise by accounting for within individual variation in behaviour. Both duration and delay are controlled by potentiometers (see detail in Fig. 4.1c), and the range of parameter values can be pre-programmed by the user.

The custom speaker is designed for use with any AAA-battery powered audio player with a standard 3.5 mm phone connector output (i.e., headphone jack). A custom battery pack, housed in a weatherproof case (Fig. 4.1a; Pelican 1010 Micro Case, Pelican Products Inc., USA), takes 12 AA batteries and provides extended battery life to both the speaker and the audio player (via a custom dummy battery inserted into the audio player's battery compartment). When first powered on, most digital audio players require several seconds and interaction with a menu screen before actually playing a sound file. For this reason, the ABR system is designed such that the audio player is continuously active (i.e., not connected to the motion sensor), but the system remains silent unless the speaker is triggered by the motion sensor. In the field trials described below, we used inexpensive mp3 players (RCA-TH1814WM, VOXX Accessories Corp., USA), which ran continuously for up to 7 days. Speaker battery life will depend on how frequently the system is triggered, but was considerably longer than that of the mp3 player in our field tests. As noted, this custom speaker unit is designed to be paired with any audio and video-enabled camera trap. In all field tests described here, we used Moultrie M-990i (Moultrie Products, LLC, USA) camera traps.

We designed the custom speaker to be activated by either a standalone motion sensor (Mark 1 design), or a separate circuit designed to detect camera trap activity (Mark 2 design). In the Mark 1 design, the speaker is connected by a 6 m cable to a pyroelectric infrared (PIR) motion detector module (Qunqi HC-SR501) housed within a weather-proof casing (see "Sensor" in Fig. 4.1b). These commercially available PIR units include a sensitivity control, allowing the user to set the sensitivity of the motion detector. With the motion detection system of the speaker separate from that of the camera, it is possible that a passing animal will trigger one of these components but not the other, which has advantages in certain applications, as discussed below. In the Mark

2 design, the speaker is connected directly to the camera trap via the camera's DC power supply port, and is triggered by the camera itself. Between camera and speaker, a weather-proof case (Pelican 1010 Micro Case) houses a battery pack to power the camera and a custom current detector circuit, which sends a digital trigger to the speaker whenever the camera draws power from the battery pack to record video. The Mark 2 design thereby ensures that the speaker will trigger whenever the camera triggers.

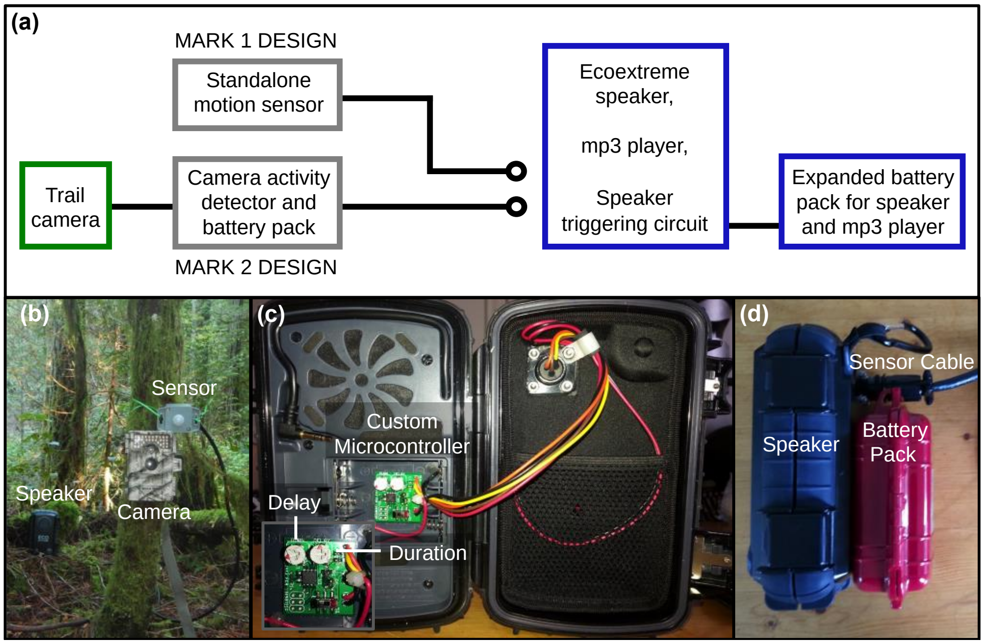

Figure 4.1. Design of the Automated Behavioural Response (ABR) system. (a) Block diagram illustrating the major components of both Mark 1 and Mark 2 ABR designs. (b) The full Mark 1 ABR system, deployed in the field, illustrating the pairing of a speaker unit ('Speaker') and attached motion sensor ('Sensor') with a commercially available camera trap ('Camera'). (c) Inside of the ABR speaker unit, illustrating the custom microcontroller, which allows the user to program the delay between triggering of the motion senor and playback start ('Delay'), as well as the duration of the playback ('Duration'; see detail in c). (d) Outside of the ABR speaker unit illustrating the commercially available, weatherproof speaker ('Speaker'), which as been modified to be triggered by an external motion sensor, and the custom battery pack ('Battery Pack'), which extends the lifespan of both the speaker and the audio player it broadcasts.

4.4 Methods

4.4.1 Field Tests

4.4.1.1 Bwindi Impenetrable National Park, Bwindi

Bwindi Impenetrable National Park (hereafter ‘Bwindi’) is located in the Kanungu district of southwestern Uganda (0°53′ to 1°08′ S, 29°35′ to 29°50′ E). This 321-km^2 park consists of both medium-altitude moist evergreen forest and high altitude submontane forest, and is surrounded by a high-density human population, which legally and illegally enters the park to access forest resources, including poaching wildlife (Mugerwa *et al.* 2013). Bwindi hosts a large diversity of mammals and birds, including rare and cryptic species such as the mountain gorilla (*Gorilla beringei*), forest elephant (*Loxodonta africana*) and African golden cat (*Profelis aurata*; Mugerwa *et al.* 2013), and was designated as a UNESCO World Heritage site in 1994. The present study covered an area of approximately 27 km^2 in the southern, high altitude section of the park.

As noted in the *Introduction*, the field tests conducted in Bwindi were part of an experiment testing the behavioural responses of animals to the sounds of humans and hunting dogs (*Canis lupus familiaris*) as a means of assaying the extent and intensity of illegal hunting; dogs are strictly prohibited in protected areas in Uganda, and only ever present in the company of poachers (Lindsey et al. 2013; Mugerwa et al. 2013). We prepared playlists of humans speaking, dogs barking, and a non-threatening control (cicadas and crickets), using multiple exemplars of each call type broadcast at a consistent volume of 90 dB at 1 m. We programmed all camera traps to record 30 s videos, and to retrigger after 5 s if the animal remained in front of the camera. The speakers were programmed to broadcast a 10-s playback following a 10-s delay. We were thereby able to record several seconds of the focal animal’s behaviour immediately prior to the playback (hereafter, “pre-playback behaviour”; median [range] = 9 [1 to 30] s, the variation being due to the fact that, with the Mark 1 design, speaker and camera are not always triggered simultaneously).

ABR systems were set at 27 pre-established sample points used by the Tropical Ecology Assessment and Monitoring network (TEAM, www.teamnetwork.org) in a long-term camera trap-based biodiversity monitoring study (Ahumada et al. 2011, 2013). Following TEAM protocols, systems were deployed at a density of one system per km^2, and positioned 2 m from active game trails at a height of 50 cm (Mugerwa et al. 2013). The Mark 1 system was used in all field tests in Bwindi, and the speaker motion sensor was attached (via elastic band) to the top of the camera trap to maximize overlap between the camera's and the motion sensor's detection areas. We placed the speaker approximately 3 m from the camera and motion sensor, and changed the speaker position every three days to minimize habituation. All ABR systems were baited, with bait stations placed immediately adjacent to the game trail at a maximum distance of 2 m from the camera trap and speaker motion sensor. Bait stations consisted of a small pile of dried fish and peanuts on which animals could actively feed, as well as a perforated tin can filled with dried fish attached to a pole at a height of 10 cm. Dried fish provided a pungent scent lure, was readily available in the local villages, did not spoil in the heat, and has been shown to be a useful attractant of omnivores, such as jackals (Thorn et al. 2009). Peanuts were similarly available in local villages, did not spoil, and provided bait suitable for herbivores. All bait stations were replenished every three days. The dried fish in the tin could not be consumed, ensuring that the scent lure persisted between days when the bait was replenished. The ABR systems were deployed between 17 February and 3 April 2015, being set for six days at each of the 27 sample points, and provided a total of 162 camera nights.

4.4.1.2 Clayoquot Sound Biosphere Reserve, Canada

Clayoquot Sound Biosphere Reserve (hereafter 'Clayoquot') is located on the central west coast of Vancouver Island, British Columbia, Canada (49°23′ to 49°04′ N, 126°13 to 125°45′ W). Terrestrial habitat consists of old growth and second growth temperate rainforest dominated by coastal western hemlock (*Tsuga heterophylla*), and the adjacent shoreline is a complex of rocky intertidal and mudflat habitat. In contrast to Bwindi this area is remote and far-removed from any considerable concentration of humans, being occupied by fewer than two thousand people engaged in ecotourism or small-scale fisheries. Correspondingly, this region continues to support a relatively diverse and high-density assemblage of mammalian carnivores (Suraci et al. 2014), including three species of large carnivore (cougars [*Puma concolor*], black bears [*Ursus americanus*] and wolves [*Canis lupus*]), and several species of mesocarnivore (raccoons [*Procyon lotor*] and multiple mustelid species) (Hatler et al. 2008). The present study covered approximately

156 km^2 in the southeastern section of Clayoquot Sound (primarily in Lemmens Inlet, Fortune Channel and Tofino Inlet), occurring entirely within the Clayoquot Sound Biosphere Reserve, a UNESCO World Heritage Site.

The Clayoquot field tests were conducted as part of an ongoing study investigating interactions between mammalian carnivores in coastal British Columbia and their effects on intertidal community structure. It has recently been experimentally demonstrated that the fear of large carnivores is itself powerful enough to cause a trophic cascade in such systems (Suraci et al. 2016), and the aim of the current study was to experimentally test the behavioural responses of other large carnivores and mesocarnivores to cougar vocalizations. We prepared playlists of cougar (large carnivore competitor/predator) and pinniped (harbour seal [*Phoca vitulina*] and Stellar's sea lion [*Eumatopias jubatus*]; non-threatening control) vocalizations comprised of seven exemplars of each call type, which were broadcast at a consistent volume of 80 dB at 1 m. We programmed all camera traps to record 90 s (day) or 30 s (night) videos, and to retrigger after 5 s if the animal remained in front of the camera. We tested both the Mark 1 (separate motion sensors for camera and speaker) and Mark 2 (speaker motion sensor integrated with camera, see above) ABR systems in Clayoquot. All systems were programmed to play a 10 s playback following either a 0 s (Mark 1) or 3 s (Mark 2) delay.

We deployed ABRs along shorelines at the level of the highest tide line, 0-3 m from the forest edge, at a height of 1 m and pointed seawards, to collect data on mammalian carnivores foraging and/or transiting in the intertidal zone. Both Mark 1 and 2 ABR systems were deployed. As at Bwindi, when utilizing the Mark 1 system the speaker motion sensor was positioned to maximize the overlap between the camera's and the motion sensor's detection areas. Also as at Bwindi, the speaker was positioned 3 m from the camera/motion sensor for all trials. Unlike at Bwindi it was not possible to establish bait stations because the ABRs were so close to the water's edge that the high tide would wash away any bait placed there. Systems were set in or immediately adjacent to cobble-boulder shorelines, an intertidal habitat type in which we directly observed every carnivore species, including cougars. When setting up ABRs along shorelines, we attempted to use topographical features (e.g., narrow sections of shoreline) to funnel animals towards the ABR system. However, given the large tidal fluctuations in

Clayoquot, the distance between the ABR's location at the high tide line and the edge of the water line varied considerably over each tide cycle, and at low tide it was often possible for animals to pass by the system at a distance of up to 20 m. We deployed the ABRs at 32 sites in Clayoquot between 8 April and 27 August 2015, for a total of 908 camera nights. Mark 1 systems were deployed throughout the duration of the study for a total of 453 camera nights at 22 sites. Mark 2 systems were deployed between 1 July and 27August 2015 for a total of 455 camera nights at 11 sites.

4.4.1.3 Santa Cruz Mountains, USA

The Santa Cruz Mountains (hereafter 'Santa Cruz') lie in the Central Coast region of California, USA (37°38′ to 36°54′ N, 122°31 to 121°37′ W). The 17,000 km^2 study area is bounded by the city of San Francisco to the north, several urban municipalities to the east, mixed farmland and residential development to the south, and the Pacific Ocean to the west, with an elevation ranging from sea level to 1155 m. Vegetation is dominated by redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*), with grassland and coastal scrub immediately adjacent to the ocean. Land use within the study area is highly varied, ranging from relatively vast and intact areas of native vegetation in state and county parks and privately-held estates, bisected by varying amounts of development, from urban to rural, with a major freeway and numerous roads interspersed throughout (Wilmers et al. 2013).

The Santa Cruz field tests were conducted as part on an ongoing study addressing the behavioural responses of cougars to anthropogenic disturbances (Wilmers et al. 2013; Smith et al. 2015). The objective of the current study was to experimentally test the behavioural responses of cougars to large carnivore commensals of humans, i.e. domestic dogs. We prepared playlists of dogs barking and a non-threatening control (Pacific tree frogs [*Pseudacris regilla*]), using multiple exemplars of each call type broadcast at a consistent volume of 80 dB at 1 m. All camera traps were programmed to record 30 s videos, and to retrigger after 5 s if the animal remained in front of the camera. In this experiment we used only Mark 2 ABR systems, which were thus triggered by the camera trap's activation. Because we were able to use a powerful attractant (next paragraph) we were confident would keep the animal in view, we programmed a 10 s delay into the speaker prior to its broadcasting for 10 s; permitting us to record both pre-playback and post-playback behaviour, thereby taking advantage of the powerful capacity that the ABRs provide to compare an individual's response to its baseline behaviour.

In this application of the ABR system we were able to use the cougar's own food cache as an attractant. Every cougar in the study was fitted with GPS/radio telemetry collars which permitted us to locate prey kill sites within as little as 4 hours (for details see Wilmers et al. 2013 and Smith et al. 2015). ABR systems were set up at every accessible deer (*Odocoileus hemionus*) kill site, as cougars commonly return to feed on deer carcasses on successive nights (Wilmers et al. 2013). Carcasses were roped to adjacent trees or staked to the ground to prevent returning cougars from moving the carcass out of view of the camera trap, and an extra deer leg was similarly roped in place, to encourage the cougar to feed in cases where little remained of the original carcass. The camera trap connected to the ABR system was positioned 3 m from the center of the carcass at a height of 1 m, the speaker being positioned 3 m from the camera trap as at Bwindi and Clayoquot. To ensure the cougar's response was filmed regardless of the direction from which it approached, a second camera trap not connected to the ABR system was positioned 4 m from the center of the carcass (at a height of 1 m), on the side of the carcass opposite to the camera trap with the ABR system attached. The line of sight between the two cameras was offset slightly to avoid each being 'blinded' by the other's infrared lights. The ABR systems were deployed between 3 and 8 December 2015 at five kill sites, for multiple nights at some sites, providing a total of 9 camera nights.

Table 4.1. Species from which trials were obtained during field tests of the ABR system in Bwindi and Clayoquot. The body mass and functional group of each species is shown, along with species-specific values for each of three metrics of ABR system success: *proportion triggered*, *proportion observable*, and *overall success rate* (defined in the text)

			Total Videos		**Proportion Triggered**[2]	**Proportion Observable**		**Overall Success Rate**	
	Body Mass (kg)[1]	**Functional Group**[1]	**Mark 1**	**Mark 2**	**Mark 1**	**Mark 1**	**Mark 2**	**Mark 1**	**Mark 2**
Bwindi									
ORDER ARTIODACTYLA									
Black-fronted duiker (*Cephalophus nigrifrons*)	13.9	Herbivore	11	---	0.82	0.89	---	0.73	---
Bushpig (*Potamochoerus larvatus*)	70.6	Omnivore	1	---	1.00	1.00	---	1.00	---
Yellow-backed duiker (*Cephalophus silvicultor*)	69.3	Herbivore	164	---	0.77	0.96	---	0.74	---
ORDER CARNIVORA									
African golden cat (*Caracal aurata*)	9.3	Carnivore	7	---	0.86	0.17	---	0.14	---
Honey badger (*Mellivora capensis*)	7.7	Carnivore	2	---	1.00	1.00	---	1.00	---
Large-spotted genet (*Genetta maculata*)	1.8	Carnivore	32	---	0.91	0.76	---	0.69	---
Marsh mongoose (*Atilax paludinosus*)	3.4	Carnivore	62	---	0.74	0.85	---	0.63	---
Side-striped jackal (*Canis adustus*)	8.5	Omnivore	76	---	0.70	0.94	---	0.66	---
Two-spotted palm civet (*Nandinia binotata*)	2.0	Omnivore	11	---	0.91	0.50	---	0.45	---

Table 4.1. *Continued*

	Body Mass (kg)[1]	**Functional Group**[1]	**Total Videos**		**Proportion Triggered**[2]	**Proportion Observable**		**Overall Success Rate**	
			Mark 1	**Mark 2**	**Mark 1**	**Mark 1**	**Mark 2**	**Mark 1**	**Mark 2**
ORDER PRIMATES									
Chimpanzee (*Pan troglodytes*)	38.1	Omnivore	5	---	0.60	0.67	---	0.40	---
L'Hoest's monkey (*Allochrocebus lhoesti*)	4.8	Omnivore	2	---	0.00	---	---	0.00	---
Mountain gorilla (*Gorilla beringei*)	115.5	Herbivore	2	---	0.50	0.00	---	0.00	---
ORDER PROBOSCIDAE									
Elephant (*Loxodonta africana*)	5250	Herbivore	17	---	0.76	0.77	---	0.59	---
ORDER RODENTIA									
Ground squirrel (*Funisciurus carruthersi*)	0.2	Herbivore	20	---	0.90	0.83	---	0.75	---
Giant pouched rat (*Cricetomys emini*)	0.9	Herbivore	16	---	0.63	0.70	---	0.44	---
Forest African dormouse (*Graphiurus murinus*)	0.02	Omnivore	1	---	0.00	---	---	0.00	---
Unidentified small rodents	0.06	Omnivore	226	---	0.63	0.85	---	0.54	---
ORDER GALLIFORMES									
Handsome francolin (*Pternistis nobilis*)	0.8	Herbivore	6	---	0.50	0.67	---	0.33	---

Table 4.1. *Continued*

	Body Mass (kg)[1]	Functional Group[1]	Total Videos		Proportion Triggered[2]	Proportion Observable		Overall Success Rate	
			Mark 1	**Mark 2**	**Mark 1**	**Mark 1**	**Mark 2**	**Mark 1**	**Mark 2**
Clayoquot									
ORDER ARTIODACTYLA									
Black-tailed deer (*Odocoileus hemionus*)	60.8	Herbivore	1	2	1.00	1.00	1.00	1.00	1.00
ORDER CARNIVORA									
American black bear (*Ursus americanus*)	89.5	Omnivore	14	117	0.93	0.85	0.90	0.79	0.90
Cougar (*Puma concolor*)	53.6	Carnivore	0	1	---	---	1.00	---	1.00
American marten (*Martes americana*)	0.8	Omnivore	2	0	1.00	1.00	---	1.00	---
American mink (*Neovison vison*)	1.0	Carnivore	61	33	0.48	0.55	0.33	0.26	0.33
River otter (*Lontra canadensis*)	11.4	Carnivore	2	1	1.00	0.50	1.00	0.50	1.00
Raccoon (*Procyon lotor*)	5.2	Omnivore	42	26	0.52	0.68	0.73	0.36	0.73
Grey wolf (*Canis lupus*)	39.6	Carnivore	4	10	1.00	0.75	0.30	0.75	0.30
ORDER RODENTIA									
Doulas squirrel (*Tamiasciurus douglasii*)	0.2	Herbivore	5	0	0.60	0.33	---	0.20	---
ALL SPECIES - Bwindi	---	---	**661**	**---**	**0.72**	**0.86**	**---**	**0.62**	**---**
ALL SPECIES - Clayoquot	---	---	**131**	**190**	**0.58**	**0.66**	**0.75**	**0.38**	**0.75**

1. Body mass and functional group information were taken from del Hoyo et al. 1997; Nagorsen 2002; Hatler et al. 2008; Kingdon et al. 2013; Shackleton 2013
2. The *proportion triggered* metric only applies to Mark 1 ABR systems, in which the camera trap and the speaker are triggered by separate motion sensors.

4.4.2 Measuring ABR System Success

4.4.2.1 Success Metrics

We defined a trial of the ABR system as any video of an animal, and calculated three metrics of success for ABR trials. As described above, when using the Mark 1 system, there is the possibility that an animal will trigger the camera trap, but will not trigger the motion sensor for the speaker. We calculated *proportion triggered* as the proportion of total trials in which the speaker triggered, broadcasting a playback. Note that this metric is applicable to all trials in Bwindi (where we used exclusively the Mark 1 system), but only to the subset of Clayoquot trials in which the Mark 1 system was used; with the Mark 2 system, the camera itself triggers the speaker, precluding the possibility of a video without a playback (see above). As with any camera trap study, the field of view of our cameras limited the amount of time an animal was visible if that animal was moving perpendicular to the camera. Thus for any trial in which the playback was triggered, it was possible for the animal to move out of the camera's field of view before the animal's response to the playback was recorded. We calculated *proportion observable* as the proportion of trials in which the animal's response to the playback was observable (i.e., recorded by the camera) out of only those trials in which the playback was triggered. This metric is applicable to all trials, whether the Mark 1 or Mark 2 system was used. Finally, we calculated an *overall success rate*, incorporating both of the above metrics. *Overall success rate* was measured as the proportion of all trials in which both the playback triggered and the animal's response was observable. Note that, for trials using the Mark 2 system, *proportion observable* and *overall success rate* are necessarily equivalent.

4.4.2.2 Factors Affecting ABR System Success

At both Bwindi and Clayoquot, the ABR systems were successful in quantifying the behavioural responses of a remarkably diverse array of species, which varied in body size across four orders of magnitude, and occupied various ecological roles (Table 4.1). We tested the effect of both these factors on the likelihood of obtaining successful trials. We identified the average body mass (kg) of each species from the published literature (del Hoyo et al. 997; Nagorsen 2005; Hatler et al. 2008; Kingdon et al. 2013; Shackleton

2013), and also assigned each species to one of three "functional groups" (carnivore, herbivore or omnivore) based on dietary and feeding habit information from the literature (del Hoyo et al. 1997, Nagorsen 2002, Hatler et al. 2008, Kingdon et al. 2013, Shackleton 2013). At Bwindi, we recorded several videos of small rodents (rats and mice, family Muridae) that could not be identified to species. We therefore included all "unidentified small rodents" as a single data point in all analyses presented below, using the mean body mass of 11 Murid species found in this region (Table 4.1). As noted above, all ABR systems were baited during field tests in Bwindi. Just as with camera trap studies *per se* (Rowcliffe et al. 2011; Hamel et al. 2013; Burton et al. 2015), an animal actively investigating or eating the bait may increase ABR system success by increasing the amount of time the animal spends within the detection range of the system. To determine the effect of baiting on ABR system success, a single researcher (BM) scored videos of all Bwindi trials, noting each animal's pre-playback behaviour. Pre-playback behaviour was grouped into two categories: "foraging" (includes active feeding, olfactory investigation, and processing/ingesting food) and "non-foraging" (includes vigilance behaviour and moving/transiting). Behaviours scored as "foraging" were assumed to be associated with the animal investigating or eating the bait. Finally, we tested for the effects of ABR system design by comparing the success of trials conducted in Clayoquot using Mark 1 and Mark 2 systems.

4.4.3 Statistical Analyses

We obtained trials from multiple mammal species at both Bwindi and Clayoquot (Table 4.1), and a single species of bird at Bwindi (handsome francolin [*Pternistis nobilis*]). To avoid possible confounds from including a single non-mammal in our data set, all analyses were restricted to mammals. To determine whether location, body size and functional group affected the likelihood of obtaining a successful trial, we first calculated each of the three success metrics (defined above) for each species at both locations (Bwindi and Clayoquot, Table 4.1). These analyses used data from Mark 1 trials only to facilitate comparison between the two locations (all Bwindi trials used the Mark 1 system). We then conducted ANCOVAs separately for each success metric, testing for the main effects of body mass (kg, log base 10-transformed in all analyses), functional group, and location (Bwindi and Clayoquot), as well as all two- and three-way interactions between these variables (Table 4.2). These analyses were initially conducted using the numbers of successful and unsuccessful trials for each species as a binary response variable for each success metric, and fitting generalized linear models (GLM) with a binomial distribution and logit link function. However, model-checking routines revealed very poor model fit for all three success metrics due to overdispersion that could not be adequately addressed using quasi-binomial models (Zuur et al. 2009). We therefore refit all models with the Gaussian distribution, using the proportion of successful trials for each species as the response variable. All models included the number of trials as a weighting term to account for large differences between species in the number of trials obtained. If ANCOVAs revealed a significant interaction (at $\alpha = 0.05$) between body mass and location, we then tested for an effect of body mass on ABR system success within each location using separate linear regression models. Non-significant interactions and main effects were sequentially dropped from the analysis and models were refit to obtain accurate P-values for remaining terms (Zuur et al. 2009). We confirmed the adequate fit of all models by testing for normality (Shapiro-Wilks Test) and homogeneity (Flinger-Killeen Test) of residuals and visually inspecting residual vs. fitted value plots and quantile-quantile plots (Zuur et al. 2009).

To assess whether baiting increased the likelihood of obtaining successful trials, we tested the effect of pre-playback behaviour on each of the three success metrics, using data from Bwindi only. Preliminary analyses revealed substantial interspecific variation in system success, which could mask overall patterns in the relationship between pre-playback behaviour and success. We therefore calculated the number of successful and unsuccessful trials following “foraging” and “non-foraging” behaviours for each species, and included species identity as a random effect in our analyses. These binary response data were analyzed using generalized linear mixed effects models (GLMM) with a binomial distribution and logit link function. We tested for a main effect of pre-playback behaviour (“foraging” or “non-foraging”). We also included species body mass and functional group (and their two-way interactions with pre-playback behaviour) in all models (Table 4.3). As above, non-significant interactions and main effects were sequentially dropped from the models. We tested the significance of main effects and interactions using Type II Wald’s χ^2 test (Bolker et al. 2009). If we detected a significant effect of functional group on a particular success metric, we performed Tukey's Post Hoc Tests to determine which of the three functional group categories differed.

As noted above, we conducted trials using both Mark 1 and Mark 2 ABR systems in Clayoquot. We tested for the effects of system design on ABR success by comparing *proportion observable* and *overall success rate* between Mark 1 and Mark 2 trials (note that *proportion triggered* is necessarily 1 with the Mark 2 design [see above] and as such, we did not compare this success metric between system design types). We calculated the number of successful and unsuccessful trials for each species separately for trials using Mark 1 and Mark 2 systems, and analyzed these binary response data using Generalized Linear Models with a binomial distribution and the logit link function. We tested for the main effects of system design type (Mark 1 or Mark 2) and body mass, and the interaction between the two (Table 4.4). We did not include functional group in these analyses, as there were too few herbivores in the Clayoquot dataset to adequately estimate their effects. We tested the significance of main effects and interactions using Likelihood Ratio Tests (Zuur et al. 2009) and confirmed model fit as described above. All analyses were performed in R (Version 3.2.2; R Core Team 2015).

4.5 Results

We obtained successful trials of the ABR system from 17 identifiable species across six vertebrate orders in Bwindi and 9 species across three vertebrate orders in Clayoquot (Table 4.1). When comparing Mark 1 trials between the two locations, ABR system success was higher in Bwindi than in Clayoquot for both *proportion triggered* (72% [Bwindi] vs. 58% [Clayoquot]; ANCOVA, $F_{1,19} = 7.61$, $P = 0.013$) and *proportion observable* (86% vs. 66%; $F_{1,19} = 11.61$, $P = 0.003$), resulting in significantly higher *overall success rate* at Bwindi (62%) as compared to Clayoquot (38%) ($F_{1,21} = 15.53$, $P = 0.001$; Table 4.2).

Table 4.2. Results from ANCOVA models testing the effects of species body mass (log base 10-transformed), field test location and functional group on ABR system success at both Bwindi and Clayoquot. P-values shown in bold are significant at α = 0.05.

	Proportion Triggered (n = 25)				**Proportion Observable (n = 23)**				**Overall Success Rate (n = 25)**			
	Sum of Squares	**DF**	**F-Value**	**P-Value**	**Sum of Squares**	**DF**	**F-Value**	**P-Value**	**Sum of Squares**	**DF**	**F-Value**	**P-Value**
Body Mass	1.061	1	3.699	0.070	0.793	1	1.544	0.229	3.710	1	8.807	**0.007**
Location	2.181	1	7.607	**0.013**	5.963	1	11.610	**0.003**	6.543	1	15.534	**0.001**
Functional Group	1.580	2	2.756	0.089	0.865	2	0.602	0.565	0.684	2	0.635	0.545
Body Mass x Location	2.662	1	9.283	**0.007**	1.099	1	2.139	0.160	2.209	1	5.243	**0.032**
Body Mass x Functional Group	0.314	2	0.459	0.642	0.314	2	0.218	0.807	0.329	2	0.305	0.742
Location x Functional Group	0.230	2	0.337	0.720	0.031	2	0.022	0.979	0.073	2	0.068	0.935
Body Mass x Location x Functional Group	0.255	2	0.372	0.696	0.511	2	0.356	0.709	0.791	2	0.734	0.499
Body Mass (log) - BWINDI ONLY	1.603	1	4.576	**0.049**	---	---	---	---	2.400	1	4.983	**0.041**
Body Mass (log) - CLAYOQUOT ONLY	10.431	1	7.737	**0.032**	---	---	---	---	3.519	1	13.023	**0.011**

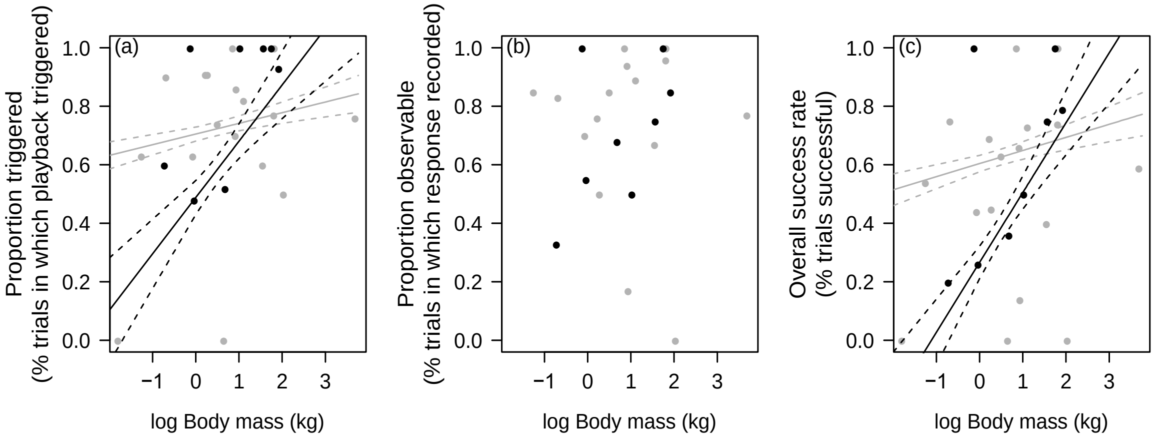

Figure 4.2. The effect of focal animal body mass (log base 10-transformed) on ABR system success at Bwindi (gray symbols) and Clayoquot (black symbols). ABR system success was measured as (a) *proportion triggered*, (b) *proportion observable*, and (c) *overall success rate* (see text for success metric definitions). Each data point represents the proportion of successful trials for a single mammal species. Solid lines represent a significant, positive relationship between focal animal body mass and ABR system success within a given site, as estimated by weighted linear regression. Dashed lines represent ± 1 SE of model estimates.

We obtained trials from species representing an enormous spectrum of body sizes (Table 4.1), ranging from forest elephants (average body mass = 5250 kg) to ground squirrels (*Funisciurus carruthersi*, 0.2 kg) in Bwindi, and black bears (89.5 kg) to Douglas squirrels (*Tamiasciurus douglasii,* 0.2 kg) in Clayoquot. Species body mass had a significant, positive effect on system success when considering Mark 1 trials at both locations (*overall success rate;* ANCOVA $F_{1,21}$ = 8.81, P = 0.007). However the influence of body mass was stronger at Clayoquot, leading to a significant interaction between body mass and location for *proportion triggered* ($F_{1,19}$ = 9.28, P = 0.007; Fig. 4.2A), and *overall success rate* ($F_{1,21}$ = 5.23, P = 0.032; Fig. 4.2C). Location-specific linear regressions showed that both *proportion triggered* (Slope = 0.19, R^2 = 0.56, P = 0.032) and *overall success rate* (Slope = 0.24, R^2 = 0.68, P = 0.011) increased more quickly with increasing body mass for trials run at Clayoquot as compared to Bwindi, where body mass had a significant, but weaker effect (*proportion triggered*: Slope = 0.04, R^2 = 0.23, P = 0.049; *overall success rate*: Slope = 0.04, R^2 = 0.25, P = 0.041; Fig.

4.2A,C). *Proportion observable* was not affected by the interaction between body mass and location (Table 4.2, Fig. 4.2B).

At Bwindi, *proportion observable* was significantly higher (Walds $\chi^2_1 = 5.72$, $P = 0.017$; Fig. 4.3A) and *overall success rate* was marginally higher (Walds $\chi^2_1 = 3.68$, $P = 0.055$; Fig. 4.3B) when animals were engaged in "foraging" behaviour, relative to "non-foraging" behaviour, immediately prior to the playback (Table 4.3). *Proportion triggered* was unaffected by pre-playback behaviour (Walds $\chi^2_1 = 0.79$, $P = 0.374$). As expected, this GLMM analysis of Bwindi data again showed a significant effect of species body mass on *overall success rate* (Walds $\chi^2_1 = 14.51$, $P < 0.001$), but there was no interaction between body mass and pre-playback behaviour (Table 4.3).

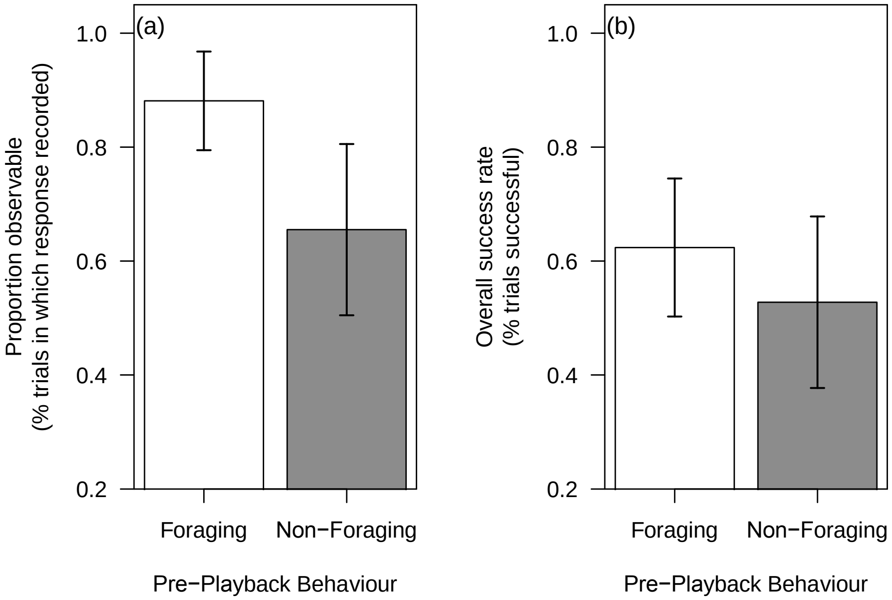

Figure 4.3. The effect of pre-playback behaviour on ABR system success, measured as (a) *proportion observable* ($P = 0.017$) and (b) *overall success rate* ($P = 0.055$) (see text for success metric definitions). Animals engaged in "Foraging" behaviours were assumed to be investigating and/or eating the bait, while animals engaged in "Non-Foraging" behaviours were not. Height of the bars represents the proportion of successful trials across all mammal species at Bwindi and error bars represent proportional standard error.

Table 4.3. Results from Generalized Linear Mixed Effects Models testing the effects of pre-playback behaviour, species body mass, and functional group on ABR system success at Bwindi Impenetrable National Park. P-values shown in bold are significant at α = 0.05.

	Proportion Triggered (n = 27)			**Proportion Observable (n = 24)**			**Overall Success Rate (n = 27)**		
	Walds χ^2	**DF**	**P-Value**	**Walds χ^2**	**DF**	**P-Value**	**Walds χ^2**	**DF**	**P-Value**
Pre-Playback Behaviour	0.789	1	0.374	5.719	1	**0.017**	3.676	1	0.055
Body Mass (log)	0.937	1	0.333	0.245	1	0.621	14.507	1	**<0.001**
Functional Group	14.232	2	**0.001**	1.285	2	0.526	2.159	2	0.340
Behavoiur x Body Mass (log)	0.364	1	0.547	0.258	1	0.611	0.002	1	0.964
Behaviour x Functional Group	0.457	2	0.796	0.315	2	0.854	0.254	2	0.881

Table 4.4. Results from Generalized Linear Mixed Effects Models testing the effects of ABR system design (Mark 1 or Mark 2) and species body mass on system success at Clayoquot. P-values shown in bold are significant at α = 0.05.

	Proportion Observable (n = 15)			**Overall Success Rate (n = 15)**		
	LRT[1] χ^2	**DF**	**P-Value**	**LRT χ^2**	**DF**	**P-Value**
System Design	1.359	1	0.244	5.540	1	**0.019**
Body Mass (log)	38.195	1	**< 0.001**	49.815	1	**< 0.001**
System Design x Body Mass (log)	1.734	1	0.188	0.342	1	0.559

1. Likelihood Ratio Test

When considering data from both locations (i.e., ANCOVAs including all species' body mass and functional group), we found no significant effect of species functional group on any of the success metrics, though *proportion triggered* showed a marginal difference between functional groups ($F_{1,19} = 2.76$, $P = 0.089$) (Table 4.2). When considering only data from Bwindi (i.e., GLMM analyses including pre-playback behaviour, body mass and functional group), we found a significant effect of species functional group on *proportion triggered* (Walds $\chi^2_2 = 14.23$, $P = 0.001$; Fig. 4.4, Table 4.3). Both functional carnivores (which do not include all members of order Carnivora, Table 4.1) and herbivores were more likely than omnivores to trigger the playback (Tukey's Post Hoc Test; Carnivore-Omnivore: $P = 0.028$, Herbivore-Omnivore: $P = 0.004$), while carnivores and herbivores did not differ ($P = 0.952$).

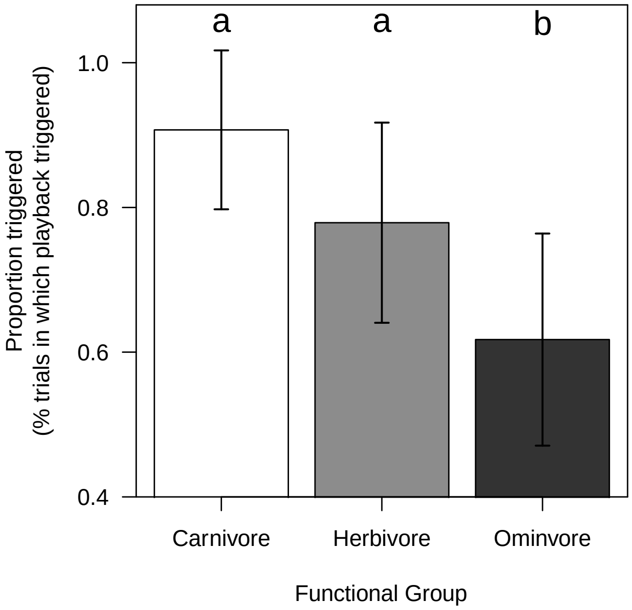

Figure 4.4. The effect of species functional group on the *proportion triggered* for all species at Bwindi. Height of the bars represents the proportion of successful trials across all mammal species of a given functional group and error bars represent proportional standard error. Different letters above bars denote significant differences between functional groups, as determined by Generalized Linear Mixed Effects Models and Tukey's Post Hoc test.

The Mark 2 system provided a substantial improvement over the Mark 1 system. When comparing Mark 1 and Mark 2 trials in Clayoquot, we found a significant 49.3% increase in *overall success rate* (Binomial GLM: Likelihood Ratio Test [LRT] $\chi^2_1 = 5.54$, $P = 0.019$), from 38% with the Mark 1 system to 75% with Mark 2 system (Tables 4.1 and 4.4). This was due largely to the substantial increase in *proportion triggered* (which is necessarily 1 with the Mark 2 system), as *proportion observable* did not differ significantly between system design types (LRT $\chi^2_1 = 1.36$, $P = 0.244$; Table 4.4). Species body mass was positively related to both *proportion observable* (LRT $\chi^2_1 = 38.20$, $P < 0.001$) and *overall success rate* (LRT $\chi^2_1 = 49.82$, $P < 0.001$) for trials run at Clayoquot, but there was no interaction between body mass and system design for either success metric (Table 4.4).

By using the Mark 2 system and applying lessons learned regarding experimental set-up from both the Bwindi and Clayoquot field tests, we succeeded in achieving a 100% *overall success rate* in field trials on cougars in Santa Cruz (see Discussion).

4.6 Discussion

Camera traps provide the capacity to collect observational data on a wide array of species, remotely and at relatively low cost, and as such have become increasingly popular in conservation biology and wildlife ecology research (O’Connell et al. 2011). However, given the often course-scale, correlational nature of standard camera trap data, aspects of study design (Hamel et al. 2013) and animal detectability (Rowcliffe et al. 2013, Burton et al. 2015) may complicate inference by introducing bias or failing to exclude alternative hypotheses. We developed and tested an Automated Behavioural Response system that directly addresses these issues by combining camera traps with playback experiments, allowing researchers to rigorously test hypotheses regarding wildlife behavioural responses, while using experimental controls to avoid bias, remove confounds, and address concerns related to weak inference in camera trap studies (O’Connell et al. 2011; Burton et al. 2015). ABR system success in field tests was influenced by several factors that affect camera trap studies in general, including animal body size and movement, camera set-up (i.e., detection ability) and the use of attractants (Rowcliffe et al. 2008, 2011; Hamel et al. 2013; Burton et al. 2015). Rowcliffe et al.

(2011) note that these factors are major sources of bias in non-experimental studies aimed at estimating animal density. In the context of the ABR system, which permits the incorporation of experimental controls, these factors will simply reduce the efficiency of experimental data collection, and, as our field test results demonstrate, can be partially or completely overcome by optimizing experimental set-up.

The success of the ABR system was strongly positively associated with species body size, a common issue in many camera trap studies, as smaller species are simply less likely to trigger detection devices (Kelly and Holub 2008, Tobler et al. 2008, Rowcliffe et al. 2011). However, body size was a much stronger predictor of whether an animal triggered the playback (and thus *overall success rate*) at Clayoquot than at Bwindi (Fig. 4.2), likely due at least in part to aspects of experimental set-up. In Bwindi, systems were set along well-used game trails and all animals passed within a few meters of the camera and speaker motion sensors, resulting in comparable triggering rates for both relatively small- and large-bodied species (Table 4.1). The positioning of systems along shorelines in Clayoquot meant that, at lower tide levels (when mammals were most likely to be present and foraging in the intertidal), animals could pass anywhere from immediately in front of the camera to several tens of meters out into the intertidal, which may account for low triggering rates for smaller species such as mink and raccoon. To maximize system performance, researchers interested in the behaviour of small-to-medium sized species should therefore attempt to deploy ABR units in proximity to habitat features that concentrate animal activity (i.e. natural attractants such as trails, logs, den sites, etc.; Datta et al. 2008; O’Brien and Kinnaird 2011).

Performance of the ABR system can also be significantly improved through the use of baits and lures. Such attractants are commonly used to draw animals in to camera trap locations (Brook et al. 2012; Lazenby and Dickman 2013, Burton et al. 2015), but may also serve to increase the amount of time animals spend within the detection zone, thus reducing interspecific variability in movement speed (Rowcliffe et al. 2011), and increasing the quantity and resolution of behavioural data. In trials run at Bwindi (where all ABR systems were baited), whether or not an animal investigated/consumed the bait had no effect on the probability of its triggering the playback (i.e., no effect of pre-playback behaviour on *proportion triggered*; Table 4.3), but strongly affected the likelihood of the animal’s response to the playback being recorded (i.e., *proportion observable*), which in turn had a marginal effect on the *overall success rate* of trials (Fig. 4.3). By slowing animals down as they passed through the ABR detection zone, baiting increased our ability to obtain detailed behavioural data. However, the increase in *proportion observable* provided by this reduction in movement speed may have come at a slight cost to triggering rate for some species. Omnivores were highly attracted to the bait in Bwindi trials (97% of omnivore trials were classified as ‘foraging’), which may have contributed to their being significantly less likely than carnivores or herbivores to trigger the playback (Fig. 4.4). PIR motion sensors, such as those used to trigger the ABR speaker in the Mark 1 design, require a minimum amount of lateral movement to activate, and the propensity of omnivores to stop and feed at our bait stations may have in some cases reduced their movement speed below this threshold. However, increasing the fully adjustable sensitivity of the Mark 1 speaker motion sensor (see below) could be used to compensate for the reduction in animal movement speed induced by baiting.

Finally, the design of the ABR system itself significantly affected the success of our field trials; by integrating the camera and speaker motion sensors (and thus precluding the possibility of the playback failing to trigger if the camera triggered), the Mark 2 system led to a 49.3% increase over the Mark 1 in *overall success rate* for trials run at Clayoquot. This suggests that, by combining the Mark 2 system design with an optimized experimental set-up (i.e., baited trials in which animals move in close proximity to the camera), system success could approach 100%, which we’ve shown to be the case in field tests with cougars in Santa Cruz (see below). Nonetheless, the Mark 1 design may be desirable for some applications, such as those in which researchers wish to target large-bodied species while minimizing the chance that smaller, non-target species will trigger the playback (potentially exposing individuals of the target species in the vicinity to the treatment). In Clayoquot, the largest body size species consistently triggered the Mark 1 system (black bears: 93% of trials, grey wolves: 100%; see Table 4.1), and Mark 1 system parameters can be further refined to increase selectivity for large-bodied species. The motion detector modules used to trigger the speakers in the Mark 1 system have built-in, continuous sensitivity adjustments, while the motion sensitivity of most commercial camera traps (including the 2014 model Moultrie M-990i, used here) is either not or only coarsely adjustable. The Mark 1 system can therefore be programmed to be insensitive to small-bodied, non-target species and only trigger to larger animals. Some environmental factors, such as strong winds causing vegetation to move, may also necessitate reduced motion sensitivity to minimize unwanted broadcasts of playbacks.

Even with the *overall success rate* of trials in both Bwindi and Clayoquot being less than 100% (Table 4.1), we were able to successfully experimentally test our hypotheses regarding the responses of tropical species to cues associated with illegal hunting (Bwindi) and the responses of mammalian carnivores to their large carnivore predators/competitors (Clayoquot). The unique capacity of the ABR system to remotely collect experimental behavioural data from a range of cryptic species permitted us to detect significant differences in response to our playback treatments in both field tests.

Using the lessons learned from field tests in Bwindi and Clayoquot, and the increased system performance provided by the Mark 2 design, we achieved a 100% success rate in preliminary trials on cougars in Santa Cruz. We used an optimized experimental set-up, including a powerful attractant (the cougar's own deer kill, secured in place in front of the camera) and the placement of equipment in close proximity (3 m) to the animal's area of movement, and further increased our likelihood of observing the cougars' behavioural responses to the playback by deploying a second camera trap to obtain 360° visual coverage of the area around each kill site. These refinements of the experimental set-up allowed us to take advantage of the ABR system's delay setting to obtain pre-playback behaviour for all trials, and in some cases (two out of five cougar kill sites) record responses by the same individual to both treatment and control sounds, permitting a powerful repeated measures analysis that further accounts for within-individual behavioural variation by comparing pre- and post-playback behaviour. Following the recommendations described here should allow other researchers to obtain similarly high success rates with the ABR system.

By incorporating the non-invasive features of camera trapping with the experimental rigor of playback studies, the ABR system has the potential to greatly expand the range of research questions addressed by wildlife ecologists and conservation biologists. Human disturbance of wildlife is an issue of major conservation concern (Griffiths and Van

Schaik 1993; Frid and Dill 2002; Valeix et al. 2012; Cristescu et al. 2013; Wilmers et al. 2013; Ordiz et al. 2014; Oriol-Cotterill et al. 2015b; Smith et al. 2015), with human-induced changes in animal behaviour suggested to affect the condition and fitness of wildlife populations (Ciuti et al. 2012; Bryan et al. 2015; Smith, Wang and Wilmers 2015). The sources of human disturbance and the categories of behaviour they affect (e.g., movement, feeding, reproductive) may be difficult to assess in free-living populations (Wilmers et al. 2013) using observational techniques alone. Use of the ABR system will allow researchers to directly test hypotheses regarding the impact of specific human disturbance types (e.g., hunting, recreation, development) on wildlife behaviour, helping to clarify conservation and management objectives. The intensity of wildlife responses to sounds associated with humans may also correlate with the level of threat posed by human activity, and can be directly quantified with the ABR system. Moreover, use of this system will allow camera trap studies of animal behaviour to go beyond broad patterns of habitat use and temporal activity (Bridges and Noss 2011; Brooks et al. 2012; Steinmetz et al. 2013; Dorresteijn et al. 2015), facilitating the collection of fine-scale data on animal responses to predators, competitors and conspecifics – cryptic behaviours that may be unlikely to be observed in traditional camera trap studies.

Chapter 5 – Discussion

Understanding the mechanisms through which apex predators structure communities and ecosystems is critical to mitigating the negative effects of human-driven apex predator declines (Estes et al. 2011). Large carnivores and other apex predators are known to elicit fear-based behavioural changes in their prey (Basille et al. 2015, Burkholder et al. 2013) that affect where and how their prey feed (Laundré et al. 2001, Wirsing et al. 2007, Creel et al. 2008, Fortin and Fortin 2009), but the degree to which these fear effects cascade to shape abundance and community structure at lower trophic levels remains the subject of intense debate (Kauffman et al. 2010, Dobson 2014). In this dissertation, I provide experimental evidence that the fear of large carnivores can indeed affect multiple lower trophic levels by altering mesopredator foraging behaviour. In the absence of their native large carnivore predators, mesopredator raccoons in the Gulf Islands dramatically impact prey communities both on land and in the sea (Figs 2.2 to 2.6). Comparing the shoreline activity of raccoons between habitats with and without large carnivores indicated that raccoon behavioural changes in the absence of their predators (i.e., unrestricted foraging in the absence of predator-induced fear) at least partially account for these impacts, and subsequent experimental investigation revealed that this was indeed the case. Experimentally restoring just the fear of large carnivores resulted in a reversal of raccoon impacts on their intertidal and shallow subtidal prey (Figs 3.3 to 3.6).

Mammalian mesopredators on islands are known to impact terrestrial vertebrate communities, and have been repeatedly implicated in extinctions of island birds and mammals (Burbidge and Manly 2002; Blackburn et al. 2004, 2005; Banks et al. 2008; Galetti et al. 2009). Curiously however, examples of their effect on the surrounding marine community are scarce. This may be due to an implicit assumption that the ocean provides an effectively limitless resource for terrestrial species. Indeed, numerous studies highlight the importance of marine resources in subsidizing terrestrial communities (Polis and Hurd 1996, Rose and Polis1998, Carlton and Hodder 2003, Stapp and Polis 2003, Field and Reynolds 2011), but consideration of the reciprocal interaction, i.e., terrestrial consumers affecting marine communities, appears to be rare (Ellis et al.

2007). Our results indicate that, for mammalian mesopredators on islands, this interaction can be strong; surveys of marine species abundance across multiple Gulf Islands showed significant impacts of raccoon foraging on intertidal and shallow subtidal crabs and fish (Chapter 2), and likely represent a conservative estimate of the total mesopredator impact, as raccoons almost certainly prey on species that we did not survey. The strength of this cross-ecosystem interaction is perhaps best exemplified by raccoon impacts on red rock crabs, a species that occurs in large subtidal populations along the coast of British Columbia (Robles et al. 1989). Raccoons kill sufficient numbers of red rock crabs during low tides in the Gulf Islands (up to 16 individual crabs km^{-1} of shoreline during a single low tide; Chapter 2) to alter the abundance (Fig. 2.5) and size distribution (Fig. 2.6) of this subtidal population, which likely has further cascading effects on intertidal community structure by affecting red rock crab interactions with their competitors and prey (Fig. 3.6). Impacts of unrestricted foraging by mesopredators on nearshore marine communities may be a pervasive, but understudied consequence of mesopredator release – most mesopredator release studies of terrestrial predators focus solely on the impacts to terrestrial prey (Prugh et al. 2009, Ritchie and Johnson 2009, Brashares et al. 2010; but see Barton and Roth 2008). Thus, understanding how the loss of apex predators from coastal communities affects both terrestrial and marine ecosystems is an important area for future research.

In Chapter 3, I present what is to my knowledge the first direct experimental demonstration of a trophic cascade caused by the fear of large carnivores. As discussed in Chapter 1, previous studies have linked large carnivore-induced behavioural changes in ungulates (Ripple and Beschta 2004, Ford et al. 2014) and mesopredators (Brook et al. 2012) to changes in species abundance and/or community composition at lower trophic levels, and similar behaviourally mediated trophic cascades (BMTC) have been described in other large predator systems (e.g., tiger sharks *Galeocerdo cuvier* – dugongs *Dugong dugon* – multiple seagrass species; Burkholder et al. 2013). However, examples of BMTC initiated by large carnivores remain controversial (Dobson 2014, Peterson et al. 2014, Ford and Goheen 2015), and attempts to replicate the findings of large carnivore BMTC studies often yield conflicting results (Kauffman et al. 2010; Winnie 2012, 2014). Approaches to studying the cascading effects of the fear of large carnivores have frequently relied on indirect estimates of predation risk, quantifying gradients in environmental features thought to increase prey susceptibility to predation (e.g., impediments to movement and/or vision, such as fallen logs; Ripple and Beschta 2004, 2012; Halofsky and Ripple 2008; Winnie 2012, 2014) or comparing habitat types associated with high and low prey mortality (Kauffman et al. 2010, Ford et al. 2014). These risk proxies are then correlated with differences in prey behaviour and changes in the growth, abundance or community composition of the prey's resource. However, this approach does not allow researchers to isolate the effects of large carnivores from those of other environmental factors that may co-vary with assumed risk (Ford and Goheen 2015), and these confounds may contribute to the inconsistent results obtained from studies using very similar methodologies (Ripple and Beschta 2004, 2012; Halofsky and Ripple 2008; Kauffman et al. 2010; Winnie 2012, 2014). In the work presented here, we manipulated fear itself using playbacks of large carnivore vocalizations, allowing us to isolate the effects of fear from those of actual predation (Zanette et al. 2011), and our experimental design, in which all sites received both the large carnivore and non-predator playback treatments, allowed us to control for the effects of environmental variables on mesopredator behaviour and the abundance of intertidal prey. We were thereby able to unambiguously experimentally demonstrate that the fear of large carnivores can cause a BMTC. The use of large carnivore cues to directly manipulate fear could help to resolve the uncertainty regarding the role of large carnivores in other ecosystems, most notably in Yellowstone National Park, where perhaps the greatest controversy exists (Ripple and Beschta 2012, Mech 2012, Dobson 2014)

The ambiguity regarding large carnivore-mediated trophic cascades is not restricted solely to the cascading effects of fear. The strength and ecological importance of large carnivore-induced trophic cascades in general, whether mediated by changes in prey behaviour, reductions in prey density, or both, have been repeatedly challenged, leading to scepticism among some authors regarding the suggested ecological role of large carnivores in regulating biodiversity and promoting ecosystem function (e.g., Mech 2012; Allen et al. 2013, 2015). Studies of the cascading effects of large carnivores have typically exploited the decline (Ripple and Beschta 2006), reintroduction (Ripple and Beschta 2012) or recolonization (Hebblewhite et al. 2005, Peterson et al. 2014) of a single large carnivore species, unreplicated events that require researchers to rely on correlations between large carnivore presence and the abundance of lower trophic level species. Such methods are subject to criticism because changes in species abundance attributed to, e.g., large carnivore reintroduction often coincide with other sources of environmental change (Vucetich et al. 2005, Mech 2012, Allen et al. 2013). This lack of strong inference in the study of large carnivore-mediated trophic cascades stands in contrast to work in systems with small-bodied predators and prey (e.g., terrestrial invertebrate systems, freshwater mesocosms) where trophic cascade studies typically employ the replicated removal or addition of whole trophic levels to test the strength of direct and indirect interactions among species (Schmitz et al. 2000, Shurin et al. 2002, Priesser et al. 2005). This is often achieved by experimentally constructing one-, two-, and three-trophic level food chains, and estimating the response (e.g., abundance, biomass, growth rate) of the lowest trophic level in each (Schmitz 2010). I note that the work presented here has largely followed this approach, and may indeed be the first test of a large-carnivore mediated trophic cascade to do so. We experimentally created replicate two-trophic level (mesopredator – mesopredator’s prey) and three-trophic level (large carnivore - mesopredator – mesopredator’s prey) food chains in a free-living wildlife system by using predator and non-predator playbacks to simulate the presence or absence of large carnivores, and conclusively demonstrated an indirect effect of large carnivores on the lowest trophic level (intertidal crabs and fish; Fig. 3.4) mediated by changes in mesopredator behaviour (Fig. 3.3). By comparing our experimental results to those presented in Chapter 2, in which we quantified intertidal prey abundance on multiple islands with and without raccoons (i.e., replicate two- and one-level food chains) we are further able to show that, by suppressing mesopredator foraging behaviour, just the fear of large carnivores largely counteracts the full impact of the mesopredator on its prey (see Chapter 3)

Ford and Goheen (2015) have recently called for tests of large carnivore-mediated trophic cascades to employ this “gold standard” approach used by classic trophic cascade studies with small-bodied species, deconstructing the cascade into it’s constituent interactions and quantifying the response of the lowest trophic level. They highlight the perceived difficulty of conducting replicated experiments with large carnivores, and indeed the replicated removal or addition of entire trophic levels may be infeasible in many wildlife systems with large-bodied predators and prey. However, our approach, using playback manipulations to simulate the presence or absence of large carnivores, may be readily adapted to other wildlife systems. For instance, in habitats without large carnivores, the use of replicated exclosures to estimate the effects of large herbivores on plants (Winnie 2012, Ford et al. 2014), in combination with controlled playback experiments to manipulate the perceived presence or absence of large carnivores, could achieve the proposed deconstruction of the large carnivore-mediated trophic cascade into its constituent parts. Conducting such experiments in habitats adjacent to areas of large carnivore reintroduction or recolonization would permit comparison of these experimental results with the total effect (i.e., fear plus actual predation) of large carnivores on their prey.

There is ongoing debate regarding the strength and importance of trophic cascades in terrestrial relative to aquatic ecosystems (Strong 1992; Schmitz et al. 2000; Shurin et al. 2002, 2006), with several authors arguing that consistent differences between ecosystem types in, e.g., predator-prey size structure (Shurin and Seabloom 2005) and growth rate of primary producers (Shurin et al. 2006), will cause the top-down effects of predators to be more influential in aquatic than terrestrial systems (Polis and Strong 1996). Meta-analysis of manipulative experiments would appear to confirm these assertions (Shurin et al. 2002), yet several compelling examples exist of fundamental changes in the primary producer community following the loss or reintroduction of apex predators to terrestrial ecosystems (Terborgh et al. 2001, Estes et al. 2011). Most experimental tests of terrestrial tri-trophic cascades (predator – herbivore – plant) to date have involved invertebrate predators and prey in grassland or agricultural systems (Shurin et al. 2002, Mooney et al. 2010) and may therefore be less likely to detect the types of community-level changes associated with the removal or addition of large-bodied apex predators. A crucial step towards clarifying the ambiguity regarding cascade strength in terrestrial ecosystems will be to conduct direct, experimental tests of terrestrial trophic cascades involving large-bodied vertebrate predators and prey. The results presented in Chapter 3 conclusively demonstrate that fear of terrestrial vertebrate predators (large carnivores) can indeed cascade through food webs, initiating a mesopredator cascade (apex predator

– mesopredator – mesopredator’s prey) in an intertidal ecosystem. Importantly, though, this work also demonstrates the feasibility of testing for cascading effects of large carnivores in free-living wildlife systems using playback manipulations. Similar manipulative studies should be conducted in the continental grassland and woodland ecosystems that are the primary focus of studies on large carnivore-mediated trophic cascades (Ripple et al. 2014), using the methods outlined above to experimentally quantify the indirect effect of large carnivores on terrestrial primary productivity.

Human presence dominates much of the globe (Foley et al. 2005), meaning that in many terrestrial and marine food webs, humans are the true apex predators (Myers et al. 2007, Darimont et al. 2015, Oriol-Cotterill 2015b). However, very little research has been devoted to understanding the role of humans in trophic cascades (Hebblewhite et al. 2005, Dorresteijn et al. 2015) and virtually none has explored the cascading effects of human-induced fear. Human activity can drastically alter the ecological role of large carnivores through extirpations (Estes et al. 2011), but even where large carnivores persist, human impacts on large carnivore behaviour may have community-level consequences. Many large carnivore populations experience high levels of human-caused mortality (Wilmers et al. 2013, Darimont et al. 2015, Oriol-Cotterill et al. 2015b), and individuals may therefore be expected to be highly sensitive to humans. Indeed fear of humans in large carnivores appears to be widespread, as several studies have shown that large carnivores alter their behaviour and habitat use in response to human disturbance (Valeix et al. 2012; Cristescu et al. 2013; Wilmers et al. 2013; Oriol-Cotterill et al. 2015a,b; Smith et al. 2015). Such human-induced fear could affect the interaction between large carnivores and their prey by inducing changes in large carnivore hunting effort (Smith et al. 2015), or creating spatial refuge for prey through changes in large carnivore habitat use (i.e., the human shield effect, Berger 2007), with potential cascading effects on lower trophic levels. Work described in Chapter 4 has begun to address the effect of human cues on large carnivore behaviour. However, the cascading effects of human-induced fear in large carnivores and other species remain largely unknown and present an important area for future research. The novel experimental capabilities provided by the Automated Behavioural Response system (Chapter 4) will hopefully help to stimulate this new research direction.

Our results strongly support the contention that top-down control by large carnivores is an important mechanism of biodiversity regulation in terrestrial ecosystems (Letnic et al. 2012, Ritchie et al. 2012, Ripple et al. 2014), and further suggest that, in coastal habitats, the ecological role of large carnivores extends to the surrounding marine community. The "landscape of fear" engendered by the mere presence of large carnivores is likely a critical component of this role and as such should be a conservation target in itself. Indeed management strategies that do not account for predator fear, such as hunting or removal programs to manage outbreaks of large herbivores and mesocarnivores, are frequently unsuccessful (Prugh et al. 2009, Conner and Morris 2015), potentially because these management efforts cannot replicate the behavioural suppression of herbivores and mesopredators provided by the actual presence of large carnivores. After centuries of extirpation, large carnivore populations are recovering throughout much of Europe (Chapron et al. 2014) and, to a lesser extent, North America (Hebblewhite et al. 2005, Oakleaf et al. 2006, Ripple and Beschta 2006, Newsome and Ripple 2015). Protecting these populations and promoting further large carnivore recovery may serve multiple conservation objectives (Ritchie et al. 2012) by restoring fear to terrestrial food webs.

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