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REVIEW AND SYNTHESIS

Predator interactions, mesopredator release and biodiversity conservation

Euan G. Ritchie* and Christopher N. Johnson
School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia
**Correspondence:*
E-mail: euan.ritchie@jcu.edu.au.

Abstract

There is growing recognition of the important roles played by predators in regulating ecosystems and sustaining biodiversity. Much attention has focused on the consequences of predator-regulation of herbivore populations, and associated trophic cascades. However apex predators may also control smaller 'mesopredators' through intraguild interactions. Removal of apex predators can result in changes to intraguild interactions and outbreaks of mesopredators ('mesopredator release'), leading in turn to increased predation on smaller prey. Here we provide a review and synthesis of studies of predator interactions, mesopredator release and their impacts on biodiversity. Mesopredator suppression by apex predators is widespread geographically and taxonomically. Apex predators suppress mesopredators both by killing them, or instilling fear, which motivates changes in behaviour and habitat use that limit mesopredator distribution and abundance. Changes in the abundance of apex predators may have disproportionate (up to fourfold) effects on mesopredator abundance. Outcomes of interactions between predators may however vary with resource availability, habitat complexity and the complexity of predator communities. There is potential for the restoration of apex predators to have benefits for biodiversity conservation through moderation of the impacts of mesopredators on their prey, but this requires a whole-ecosystem view to avoid unforeseen negative effects.

'*Nothing has changed since I began.*
My eye has permitted no change.
I am going to keep things like this.'
From 'Hawk Roosting', by Ted Hughes.

Keywords

Carnivore, competition, distribution and abundance, extinction, foraging behaviour, interspecific killing, landscape of fear, predation, risk effects, trophic cascade.

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INTRODUCTION

Recent studies have drawn attention to the importance of apex predators in suppressing populations of smaller predators (mesopredators) and thereby moderating the impact of predation on smaller prey species (Crooks & Soulé 1999; Johnson *et al.* 2007; Berger *et al.* 2008). When populations of apex predators are reduced or go extinct, previously suppressed mesopredator populations may erupt in a phenomenon known as 'mesopredator release' (Soulé *et al.* 1988; Courchamp *et al.* 1999; Crooks & Soulé 1999). We define apex predators as species which occupy the top trophic position in a community; these are often large-bodied and specialized hunters. Mesopredators occupy trophic positions below apex predators. The definitions of apex predators and mesopredators are, therefore, relative and to an extent context-dependent. For instance, in some systems the coyote (*Canis latrans*) may be considered an apex predator (Crooks & Soulé 1999) but in others a mesopredator (Berger & Conner 2008), depending on whether it co-occurs with the larger wolf (*C. lupus*).

Apex predators have suffered major declines worldwide, due to habitat loss and fragmentation, overexploitation, and direct persecution by humans. Terrestrial large mammalian carnivores have declined by 95–99% in many regions of the world (Berger *et al.* 2001) and similarly, large fish and elasmobranchs have declined by more than 90% from some marine environments (Myers & Worm 2003; Heithaus *et al.* 2008). Such declines may have large consequences for trophic dynamics and community organization. The disappearance of apex predators may facilitate invasion by alien mesopredators as well as population outbreaks of native mesopredators, creating secondary pest problems for commercial industries such as fisheries (Baum & Worm 2009) and threatening vulnerable prey species (Polis & Holt 1992). Mesopredator outbreaks have the potential to lead to extinction of some prey, especially those that are susceptible because they have low population growth rates or live in situations that leave them exposed to attack by mesopredators (Courchamp *et al.* 1999). Mesopredator release is therefore important not only for our understanding of how complex food webs are regulated, but also has applications in conservation of biodiversity and habitat restoration (Glen & Dickman 2005; Sergio *et al.* 2008).

The structure, function and stability of ecosystems have traditionally been considered to be under the control of either top-down processes imposed by predators, or bottom-up processes due to nutrients and productivity (Pace *et al.* 1999). In many cases both processes are probably important (Boyce & Anderson 1999; Wilmers *et al.* 2006; Elmhagen & Rushton 2007). Apex predators often have strong effects on the trophic dynamics and diversity of the systems in which they occur (Estes *et al.* 1998; Palomares & Caro 1999; Terborgh *et al.* 2001; Heithaus *et al.* 2008; Sergio & Hiraldo 2008). Despite this, their functional roles cannot be fully appreciated in isolation from bottom-up effects, including anthropogenic habitat change (Litvaitis & Villafuerte 1996; Estes *et al.* 1998; Elmhagen & Rushton 2007). Habitat loss and modification inevitably result in changes to resource availability (e.g. increased food resources in urban landscapes), which in turn may alter the dynamics of competitive and predatory interactions. We need a better understanding of the complexity of species interactions in multi-predator communities, how these may be influenced by bottom-up processes, and how they contribute to the maintenance of species diversity.

Here we first review studies of interactions between apex predators and mesopredators and assess the strength of these interactions. We then describe how and why apex predators suppress mesopredators and why the effects of apex predators on mesopredators may often be disproportionately large. We briefly review the possibilities of restoring apex predators as a biodiversity conservation tool. Next we explore in more detail how predator interactions may be influenced by bottom-up effects. We highlight the conservation implications of understanding predator interactions with emphasis on systems containing exotic mesopredator species.

We do not consider the roles of apex predators as flagship species and/or biodiversity surrogates for conservation, because these issues are covered extensively elsewhere (Glen & Dickman 2005; Sergio *et al.* 2006, 2008; Cabeza *et al.* 2008). Our review focuses on vertebrate apex predators in both terrestrial and marine ecosystems, although many of the processes we describe are also important among invertebrates (Schoener & Spiller 1987; Harley & Lopez 2003).

REVIEW OF FIELD STUDIES

A search of the literature using Web of Science (keywords used: apex predator, carnivore, interspecific killing, mesopredator, mesopredator release, predator interaction, trophic cascade) between the years of 1972 and 2009, as well as cross-citations and in press manuscripts from colleagues yielded an initial total of 94 studies of the effects of vertebrate apex predators on mesopredators and prey communities in terrestrial and marine ecosystems. These studies represent a variety of approaches, including phenomenological studies of mesopredator abundance comparing places or times with different abundance of apex predators, experimental removals of apex predators, or field studies of behavioural effects of apex predators on mesopredators. Of these, 73 (78%) reported primary data, all from the years of 1988–2009. These studies are divided between and summarized in Tables 1 and 2. Of all studies, 38% were of aquatic systems (all marine except one freshwater study) and 62% of terrestrial systems. Studies were geographically biased to North America and taxonomically biased towards mammals, especially canids (wolves, coyotes and foxes), but reports of systems in which apex predators affect mesopredator populations came from all continents (with the apparent exception of South America).

Table 1 summarizes 61 studies that reported on interactions between apex- and mesopredators. More than 95% of studies found evidence consistent with mesopredator release and/or the suppression of mesopredators by apex predators. Two studies found no evidence of mesopredator control by apex predators (studies 45 and 50, Table 1). These exceptions help to identify conditions under which the intensity of competitive and antagonistic interactions between predators is reduced. These include mesopredators having specialized defences, such as the repellent chemicals sprayed by skunks (*Mephitis mephitis*) that are effective against large attackers (study 50, Table 1). In other cases, resource availability appears to have been very high so that

Table 1 Empirical studies (1989–2009) of interactions between apex- and mesopredators, and mesopredator release

Study	Number	Region	System	Apex predator(s)	Mesopredator(s)	Summary research results
Creel & Creel 1996; Creel 2001	1, 2	Africa	T	Hyena, lion	Wild dog	Wild dogs may be kept at low densities or driven to extinction by lions and hyenas, especially in open habitats.
Durant 1998, 2000	3, 4	Africa	T	Hyena, lion	Cheetah	Cheetahs survive with larger predators by seeking areas with low predator densities.
Ainley *et al.* 2006	5	Antarctica	T, M	Adelie penguin, minke and killer whales	Antarctic silverfish, krill	High seasonal increased abundance of apex predators led to a decrease in silverfish and krill.
Blanchard *et al.* 2003; Daan *et al.* 2005	6, 7	Atlantic Ocean	M	Large fish	Small fish	Large fish overexploited, lead to increase in smaller size-classed fish.
Carscadden *et al.* 2001	8	Atlantic Ocean	M	Cod, benthic fishes, harp seals	Capelin	Exploitation of apex predators resulted in increased capelin biomass.
Estes *et al.* 1998; Springer *et al.* 2003	9, 10	Atlantic Ocean	M	Killer whale	Sea otter	Killer whale predation of otters resulted in release of urchins and substantial overgrazing of kelp.
Fogarty & Murawski 1998; Shackell & Frank 2007	11, 12	Atlantic Ocean	M	Cod and groundfish	Silver hake, redfish, yellow tail and winter flounder	Exploitation of cod and groundfish resulted in release of mesoconsumers.
Frank *et al.* 2006	13	Atlantic Ocean	M	Cod, benthic fishes	Small pelagic fish	Exploitation of cod and benthic fish led to increases in small pelagic fish, but only in northern regions; southern regions were under apparent bottom-up control.
Myers *et al.* 2007	14	Atlantic Ocean	M	Large elasmobranchs	Medium-sized elasmobranchs	As large shark abundance fell over 35 years, their prey species (elasombranch mesopredators) increased four to 10-fold.
Shepherd & Myers 2005	15	Atlantic Ocean	M	Large elasmobranchs	Smaller elasmobranchs	Exploitation of large elasmobranchs lead to increased deepwater small elasmobranchs.
Burrows *et al.* 2003	16	Australia	T	Dingo	Domestic cat	An index of cat abundance doubled following dingo removal.
Johnson & VanDerWal in press	17	Australia	T	Dingo	Red fox	When dingoes are abundant foxes are rare. Dingoes set an upper limit to fox abundance.
Heithaus & Dill 2002, 2006	18, 19	Australia	M	Tiger shark	Bottlenose dolphin	Dolphin foraging indicated a trade-off between predation risk and food availability
Mitchell & Banks 2005	20	Australia	T	Dingo/wild dogs	Red fox	Evidence of dietary competition and fine-scale exclusion of foxes by larger canids, but no support for landscape-scale exclusion.
Moreno *et al.* 2006	21	Central America	T	Jaguar	Puma and ocelot	Evidence of competitive release for puma and ocelot, following the decline of jaguars.
Boveng *et al.* 1998	22	Europe	M	Leopard seal	Antarctic fur seal	Leopard seals limit fur seal population growth.

Table 1 *continued*

Study	Number	Region	System	Apex predator(s)	Mesopredator(s)	Summary research results
Elmhagen & Rushton 2007	23	Europe	T	Wolf, Eurasian lynx	Red fox	Red fox increase most rapid where decline in top predators most rapid. However, productivity had greater impact (~10 times) than mesopredator release on population growth.
Fedriani *et al.* 1999	24	Europe	T	Iberian lynx, Eurasian badger	Red fox	Foxes avoided habitats frequented by lynxes. The particular foraging mode of badgers may aid their coexistence with other carnivores.
Helldin *et al.* 2006	25	Europe	T	Eurasian lynx	Red fox	Annual number of fox litters declined after lynx re-established.
McDonald *et al.* 2007	26	Europe	T	Eurasian otter	American mink	Between 1991 and 2002, where found, mink signs decreased by 60% and otter signs increased by 62%, providing evidence of the reversal of mesopredator release
O'Gorman *et al.* 2008	27	Europe	M	Benthic fish	Small fish	Increased top predator diversity coincided with increased secondary production. Manipulating top predators suppressed mesopredator density, releasing benthic invertebrates from heavy predation. Without top predators a cascade occurred.
Palomares *et al.* 1996	28	Europe	T	Iberian lynx, European badger	Common genet, Egyptian Mongoose, Red fox	Mongooses and genets avoided areas used by lynx but not badgers. The relationship between foxes and lynx is unclear.
Salo *et al.* 2008	29	Europe	T, M	White-tailed sea eagle	American mink	Mink modified behaviour according to predation risk, which may lower population growth and have cascading effects on lower trophic levels.
Scheinin *et al.* 2006	30	Europe	T	Golden jackal	Red fox	Experiments show that foxes fear jackals.
Trewby *et al.* 2008	31	Europe	T	European badger	Red fox	Culling badgers was associated with an increase in red fox densities of > 40% per km^2.
Mukherjee *et al.* 2009	32	Middle East	T	Striped hyena	Red fox	Foxes are more active when hyena activity is low.
Tompkins & Veltman 2006	33	New Zealand	T	Stoat, brushtail possum	House mouse, Ship rat	Reduction in either rat and stoat numbers or rats only released mice. Reduction in stoats led to increases in rats. Possums can regulate rats. Complex negative indirect effects can occur during pest control.
Barr & Babbitt 2007	34	North America	F	Brook trout	Two-lined salamanders	Salamander density and daytime activity decreased following trout addition to streams.
Barton & Roth 2008	35	North America	T, M	Raccoon	Ghost crab	Predation by raccoons limits ghost crabs.
Berger & Conner 2008; Berger *et al.* 2008	36, 37	North America	T	Wolf	Coyote	Wolves limit coyote habitat use and density. In particular, transient rather than resident coyotes are most vulnerable to wolf attack.

Table 1 *continued*

Study	Number	Region	System	Apex predator(s)	Mesopredator(s)	Summary research results
Burkepile & Hay 2007	38	North America	M	Predatory fish, invertebrates	Gastropod	Eight times more coral damage by gastropods where predators excluded
Crooks & Soulé 1999	39	North America	T	Coyote	Domestic cat, gray fox, opossum, raccoon, skunk	Coyotes suppressed cats and other mesopredators.
Ellis *et al.* 2007	40	North America	M	Herring and black-backed gulls	Crab	Gulls reduced abundance of one dominant crab, increasing the abundance of two other predators (a gastropod and another crab).
Fedriani *et al.* 2000	41	North America	T	Coyote	Gray fox, bobcat	Coyotes kill both gray fox and bobcats, but exert greater pressure on foxes.
Frid *et al.* 2008	42	North America	M	Pacific sleeper shark	Harbour seal	Reduced fear of sharks by seals allowed change to habitat use and foraging.
Harrison *et al.* 1989	43	North America	T	Coyote	Red fox	Coyotes presence appears to limit red fox habitat use
Henke & Bryant 1999	44	North America	T	Coyote	American badger, bobcat, gray fox	Following coyote removal mesopredator abundance increased.
Gehrt & Prange 2007	45	North America	T	Coyote	Raccoon	No evidence that coyotes reduce or limit raccoon abundance.
Kamler *et al.* 2003	46	North America	T	Coyote	Swift fox	Coyotes suppress swift foxes and reducing coyotes can assist increases in swift fox populations.
Karki *et al.* 2007	47	North America	T	Coyote	Swift fox	Swift fox density similar between areas with varying coyote abundance. Despite coyote predation being additive for juvenile foxes, it appeared compensatory with dispersal.
Mezquida *et al.* 2006	48	North America	T	Coyote	American badger, common raven, red fox	Control of coyotes may cause mesopredator release and decrease the survival of sage grouse.
Moehrenschlager *et al.* 2007	49	North America	T	Coyote, golden eagle	Mexican kit fox	Fox survival regionally dependent on prey availability and predator (coyote) abundance.
Prange & Gehrt 2007	50	North America	T	Coyote	Skunk	No evidence that coyotes adversely affect skunks.
Ralls & White 1995	51	North America	T	Coyote, red fox	Kit fox	Large canids caused 78% of all verified fox deaths.
Switalski 2003	52	North America	T	Wolf	Coyote	There is an apparent trade-off, where wolf kills provide a low-energy cost food source to coyotes; but, coyotes must increase vigilance, decrease rest, and may be killed when co-occurring with wolves
Thompson & Gese 2007	53	North America	T	Coyote	Swift fox	Fox density negatively related to coyote abundance. Fox exposure to predation moderated by shrub density.
Dulvy *et al.* 2004	54	Pacific Ocean	M	Predatory fish	Starfish	Predatory fish declined by 61% due to fishing, starfish densities increased three orders of magnitude.

Table 1 *continued*

Study	Number	Region	System	Apex predator(s)	Mesopredator(s)	Summary research results
Essington 2006	55	Pacific Ocean	M	Sperm whales, swordfish, blue shark	Large squid	When apex predators were reduced through exploitation, squid became the dominant predator guild.
Kitchell *et al.* 2006	56	Pacific Ocean	M	Billfish, sharks and yellowfin tuna	Mahi-mahi, smaller tuna and other pelagic fishes	Decrease in large predatory fish resulted in release of mesopredators. Following cessation of exploitation of large pelagic fishes, marlin increased eightfold, and tuna and sharks two- to four-fold, with a subsequent decline in some pelagic (mesoconsumers) fishes.
Oguz & Gilbert 2007; Daskalov *et al.* 2007; Daskalov 2002	57, 58, 59	Pacific Ocean	M	Bonito, mackerel, bluefish	Horse mackerel, sprat, anchovy, jellyfish	When large pelagic fishes decreased, there was an increase in smaller fish species and a jellyfish invasion.
Parrish 2009	60	Pacific Ocean	M	Hawaiian monk seal	Subphotic fishes	Changes in fish biomass density correlated with spatial variation in distance to seal colonies and their size.
Ward & Myers 2005	61	Pacific Ocean	M	Tunas, billfishes, elasmobranchs	Various mesoconsumers	Ten fold declines in large pelagic predators coincided with 10–100-fold increases in small-bodied mesoconsumers.

competitive interactions between predators were reduced (studies 45 and 50, Table 1), or mesopredators used very different structural niches from apex predators, such as by being arboreal and thus avoiding ground-dwelling apex predators (study 45, Table 1). One study (study 40, Table 1) found that the presence of apex predators (gulls) facilitated higher abundance of some mesopredators (a crab and gastropod), by reducing the abundance of a dominant member of the mesopredator guild (another crab).

These exceptions notwithstanding, and allowing for the strong possibility of publication bias in favour of findings of mesopredator suppression/release, it seems that the control of community organization through effects of apex predators on mesopredators may be common and widespread in both marine and terrestrial ecosystems. In some cases predators may even be involved in complex trophic linkages across ecosystems. Estes *et al.* (1998) showed how changes to predator - prey relationships in oceanic environments (caused by declines in fish and seals) had a direct impact on the functioning of near-shore coastal environments, through killer whale (*Orcinus orca*) prey switching from Stellar sea lions and harbour seals (*Eumetopias jubat* and *Phoca vituline*) to sea otters (*Enhydra lutris*).

STRENGTH OF EFFECT OF APEX PREDATORS ON MESOPREDATORS

Of the studies listed in Table 1, seven provided quantitative measurements of the change in mesopredator abundance associated with a measured change in abundance of an apex predator. These seven studies (studies 16, 24, 26, 28, 37, 44 Table 1 and study 4, Table 2) contained information on 14 pairwise interactions between an apex predator (represented by the families Canidae, Felidae and Mustelidae) and mesopredator (Canidae, Felidae, Herpestidae, Mephitidae, Mustelidae and Viverridae). In 12 of 14 (86%) cases, the abundances of apex predators and mesopredators were negatively related (Fig. 1). Typically, a change in abundance of an apex predator was associated with a larger change in mesopredator abundance. On average, a 2.84 (±SE 1.88) unit change of apex predator abundance was associated with a 11.00 (±SE 5.46) unit change in mesopredator abundance in the opposite direction. Hence on average, an increase in the abundance of an apex predator is likely to have a disproportionate (approximately fourfold) negative effect on mesopredator abundance.

The studies listed in Table 1 reveal two distinct mechanisms by which apex predators affect the abundance of mesopredators: (1) through direct lethal encounters, and (2) through adjustments in behaviour and distribution made by mesopredators to avoid direct encounters with apex predators, and motivated by fear of apex predators.

Table 2 Empirical studies (1988–2009) examining whether apex predators indirectly benefit prey species through the control of mesopredator populations, or alternatively, when apex predator populations collapse does mesopredator release result in decreased prey populations and/or diversity?

Study	Number	Region	Apex predator(s)	Mesopredator(s)	Summary research results
Lloyd 2007	1	Africa	Large carnivores	Mongoose species	No evidence that removing apex predators reduces bird nesting success through mesopredator release.
Myers *et al.* 2007	2 (14)	Atlantic Ocean	Large elasmobranchs	Medium-sized elasmobranchs	Overexploitation of large elasmobranchs led to increases in cownose rays (eightfold) and a crash in bay scallops.
Johnson *et al.* 2007	3	Australia	Dingo	Domestic cat, red fox	Mammal persistence strongly positively associated with persistence of dingoes. Dingoes are thought to suppress cat and fox populations.
Letnic *et al.* in press	4	Australia	Dingo	Domestic cat, red fox	Abundance of a threatened rodent species was positively associated with dingo activity
Lundie-Jenkins *et al.* 1993	5	Australia	Dingo	Red fox	A solitary red fox may have caused the extinction of the last remaining mainland rufous hare-wallaby population, following dingo removal.
Wallach *et al.* 2009	6	Australia	Dingo	Domestic cat, red fox	Positive association found between the occurrence of dingoes and two threatened species (rock wallaby and malleefowl).
Palomares *et al.* 1995	7	Europe	Iberian lynx	Egyptian mongoose	4.8–9.5 times more rabbits eaten by mesopredators when lynx absent. Rabbit population growth 12–22% lower when lynx absent. Rabbit densities in areas used by lynx were two to four times higher than in areas not used by lynx.
Sergio *et al.* 2007	8	Europe	Eagle owl	Tawny owl	Tawny owl avoidance of eagle owls allows increased diversity and abundance of other owls.
Rayner *et al.* 2007	9	New Zealand	Domestic cat	Pacific rat	Breeding success of Cooks Petrel with cats and rats was ~3.5 times higher than with rats only.
Barton & Roth 2008	10 (35)	North America	Raccoon	Ghost crab	Mesopredator release of ghost crabs can increase sea turtle egg mortality.
Berger & Conner 2008; Berger *et al.* 2008	11 (36), 12 (37)	North America	Wolf	Coyote	Pronghorn fawn mortality 34% lower in presence of wolves, which suppress coyote populations and habitat use.
Crooks & Soulé 1999	13 (39)	North America	Coyote	Domestic cat, gray fox, opossum, raccoon, skunk	Coyotes protect songbirds through mesopredator suppression.
Ellis *et al.* 2007	14 (40)	North America	Herring and black-backed gulls	Crab	Reduced abundance of one mesopredator led to an increase in the abundance of two other mesopredators.
Frid *et al.* 2008	15 (42)	North America	Pacific sleeper shark	Harbour seal	Change in habitat use by seals put pressure on fish prey.
Henke & Bryant 1999	16 (44)	North America	Coyote	American badger, bobcat, gray fox	Mesopredator increases after coyote removal led to reduced rodent diversity and increased dominance of one species.
Rogers & Caro 1998	17	North America	Coyote	Raccoon	Lower nest success of song sparrows when coyote absent due to probable raccoon predation.

Table 2 *continued*

Study	Number	Region	Apex predator(s)	Mesopredator(s)	Summary research results
Soulé *et al.* 1988	18	North America	Coyote	Gray fox, domestic cat	Evidence that coyotes suppress foxes and cats and may benefit bird populations.
Sovada *et al.* 1995	19	North America	Coyote	Red fox	Duck nest success 88% higher where coyotes were most abundant than where red foxes were most abundant, due to presumed negative relationship between coyotes and foxes.
Dulvy *et al.* 2004	20 (54)	Pacific Ocean	Predatory fish	Starfish	Starfish release from predatory fish resulted in subsequent coral and coralline algae decreases of 35% and were replaced by non-reef building taxa.

Numbers in parentheses are the reference number for those references also in Table 1.

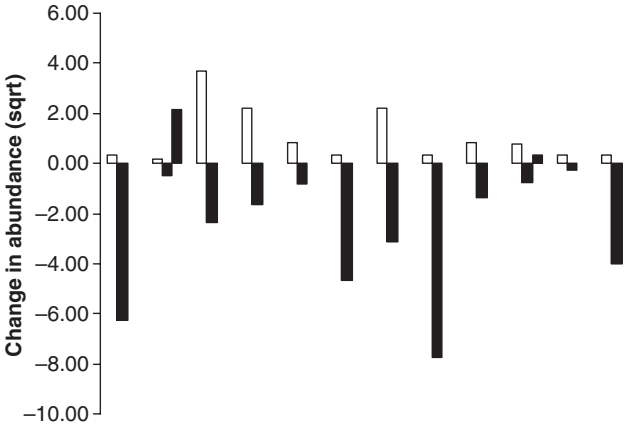

Figure 1 Differences in indices of abundance of apex predators (white bars), compared with associated changes in abundance of mesopredator(s) (black bars). Where more than one mesopredator was included in the same study, they are clustered together on the diagram. In each study, abundances of apex and meso- predators were measured in the same units, but units of measurement differ between studies. Original values were square root transformed to reduce differences in scale among studies.

Direct lethal encounters

Killing of mesopredators by apex predators is widespread, especially among mammals. Killing can be divided into two types: predation, where the victim is killed and eaten; and interspecific killing, where the victim is killed for reasons other than for food (Minta *et al.* 1992; Gese *et al.* 1996; Palomares & Caro 1999; Helldin *et al.* 2006). Lethal interactions between predator species often have a simple basis in body size: larger species kill smaller ones (Donadio & Buskirk 2006; Sergio & Hiraldo 2008). An apex predator might have two motivations for killing a smaller one: for food, and to eliminate an ecological competitor. This implies that 'intraguild predation' may often be, primarily, an intense form of pre-emptive interference competition, with the food reward an incidental benefit. This view is supported by the observation that interspecific killing is common between predator species in the same family, and of not-dissimilar body mass, both factors which imply significant ecological overlap.

Donadio & Buskirk (2006) argued that interspecific killing between predators is most prevalent in cases where (1) the smaller predator is close enough in size to the larger that it could use some of the same prey species and be a significant ecological competitor, but (2) not so close in size that to launch an attack would incur a high risk of injury for the larger animal. They suggested that this range is represented by a body-mass ratio of apex to mesopredators of between 2 (less than this and attack is too dangerous) and 5.4 (greater than this, and the killing provides too little ecological benefit

to justify the energy cost). The sub-sample of cases represented by Fig. 1 consisted of species-pairs in which the apex predator was on average quite large, and the mesopredator was significantly smaller, but not extremely so. The mean mass of all apex predators was 12.9 kg (± SE 1.9 kg) and 6.1 kg (± SE 0.9 kg) for mesopredators. On average the mass of the mesopredator in these interactions was 45% (± SE 5%) of the apex predator's mass. The mean ratio of the apex predator's weights divided by the mesopredator's weights was 2.5 (±SE 0.2).

Rates of killing of mesopredators by apex predators can be high enough to have large demographic effects on mesopredator populations (Caro 1987; Palomares & Caro 1999; Sergio & Hiraldo 2008). Berger & Gese (2007) attributed 83% of predation-related mortality of coyotes to wolves, with 17% being attributed to mountain lions (*Puma concolor*). Predation-related mortality of coyotes accounts for 30% of total mortality, with human-related deaths accounting for 45%, other causes (10%), disease (5%) and 10% is unaccounted for. Helldin *et al.* (2006) found that 50% of deaths in a population of red foxes (*Vulpes vulpes*) were due to attacks by the larger Eurasian lynx (*Lynx lynx*). This death rate was sufficient to explain an observed rate of decline of red foxes in Sweden of 10% per year. Overall, mortality rates in carnivore populations due to attacks by other predators may be in the range of 40–80% (Ralls & White 1995; Palomares & Caro 1999; Helldin *et al.* 2006).

Interspecific killing is especially common among felids, canids and mustelids (Palomares & Caro 1999). In predator-rich systems, the pressure of interspecific killing may be very great. In intact predator communities in Africa a carnivore may be at risk of attack from as many as 14.7 species of other carnivores (Caro & Stoner 2003). Sergio & Hiraldo (2008) also found interspecific killing to be common among raptors; it is likely to occur between some species of marine mammals, sharks and fishes (Baum & Worm 2009). However, our understanding of the extent and effects of interspecific killing among vertebrate predators is heavily biased towards canids in the northern hemisphere and terrestrial ecosystems more broadly.

In assessing the impact of one predator on another, it is important to ascertain whether mortality caused by interspecific killing is additive or compensatory. If the killing of mesopredators by apex predators simply reduces the negative effects of other factors such as intraspecific competition, then this mortality may have a stabilizing effect by dampening effects of intraspecific competition on population fluctuations. However, if mesopredator mortality caused by apex predators is not biased towards weaker individuals and/or can be shown to be as important as or more important than other sources of mortality, it has the capacity to be additive and cause significant population decline (Ralls & White 1995). To our knowledge no studies of predator interactions have examined this in detail. Perhaps the best study to date is by Karki *et al.* (2007), who found that although swift fox (*Vulpes velox*) survival increased in areas where coyotes were removed, the density of swift foxes was similar between treatments due to compensatory dispersal rates among juveniles, suggesting that populations were already saturated. They concluded that although coyote predation appeared additive for juveniles, it was compensatory with dispersal. In the majority of studies the evidence of direct killing of mesopredators by apex predators is circumstantial and actual mortality rates remain largely unquantified.

Fear and loathing

How and why do apex predators suppress mesopredators and why are the effects of apex predators on mesopredators often disproportionately large? We propose the answers to these questions are related to fear and loathing. (1) Loathing: top predators do more than prey on mesopredators, they actively persecute them, and may kill without eating carcasses (2) Fear: because of this, mesopredators are very strongly motivated to avoid interacting with top predators, and restrict habitat use accordingly. This is especially so considering that, among mammals, many terrestrial mesopredators are not as fast or well-adapted for escape as are the prey species that apex predators typically hunt. At the same time, they are typically less well-armed than apex predators. For many mesopredators, this means that to come within range of an apex predator is to place oneself at very high risk. Therefore, selection for avoidance of apex predators could in some circumstances be even stronger for mesopredators than for the typical prey of top predators. The mesopredator's 'landscape of fear' (Laundre *et al.* 2001) may be an especially steep and treacherous terrain, with few patches of safety. The resulting restriction of habitat use by mesopredators to places where they can most readily avoid direct encounters with apex predators may contribute greatly to reducing their overall population size (Sergio & Hiraldo 2008).

Mesopredators could reduce encounters with apex predators in two ways, by: (1) changing habitat use in favour of habitats that offer refuge from apex predators (Palomares *et al.* 1996; Durant 2000; Heithaus & Dill 2002; Mitchell & Banks 2005; Salo *et al.* 2008; Sergio & Hiraldo 2008); and (2) altering foraging behaviour and activity (Griffen & Byers 2006; Heithaus & Dill 2006; Griffen & Williamson 2008; Sergio & Hiraldo 2008). There is a growing appreciation that such restrictions on habitat use and activity can have large effects on growth, reproduction and survival of species that are subject to them (Creel & Christianson 2008), because they effectively reduce the availability of space and prey resources for mesopredator

populations. These may translate to larger impacts on demography of mesopredator populations than are produced by direct kills, which may be rare events, and can explain why some mesopredator species show strong declines in abundance in the presence of an apex predator even when interspecific killing appears to be rare. Sergio *et al.* (2007) found that tawny owls (*Strix aluco*) changed their behaviour and habitat use in relation to the nesting location of their intraguild predator, the eagle owl (*Bubo bubo*). When predation risk was low (no or few eagle owls and/or high availability of refuges) tawny owls were indifferent to the distance from eagle owls, however where there was an intermediate level of perceived predation risk they switched to distance-sensitive avoidance. Where predation risk was high (because of high abundance of eagle owls together with low availability of refuges) tawny owls avoided eagle owl habitat altogether. Despite actual kill rates being low, tawny owl breeding output declined with proximity to eagle owl nests. Habitat loss mediated by predation risk resulted in negative population effects for tawny owls and a negative association between the densities of the two owl species. Furthermore, spatial gaps in the distribution of tawny owls caused by eagle owls facilitated habitat use by other owl species, thereby increasing local owl diversity. Because effects other than interspecific killing are often harder to observe, it is highly likely that their significance in predator interactions has been underestimated.

One of the best examples of how threats from apex predators combine to suppress a mesopredator's distribution and abundance is the interaction of African wild dogs (*Lycaon pictus*) with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Gorman *et al.* 1998; Creel 2001). African wild dogs and hyenas have extensive dietary overlap and where hyenas are common in open habitats, stealing of their kills by hyenas may impose large energetic costs on wild dogs. Where such kleptoparasitism occurs wild dogs are forced to increase their hunting effort from an average of 3.5 h per day to 12 h a day, at high energetic cost (Gorman *et al.* 1998). This, combined with regular direct killing by lions and occasionally by hyenas, holds wild dogs at low population densities over large parts of their distribution (Creel & Creel 1996). A similar effect is seen in cheetahs (*Acinonyx jubatus*) (Durant 1998, 2000). The effect of fear on foraging behavior of predators has also been examined experimentally. Scheinin *et al.* (2006) found that red foxes gave up food when confronted by live golden jackals (*C. aureus*), but not when confronted only by jackal scent or a model jackal, implying that foxes may vary their foraging behaviour according to variation in perceived risk levels.

Fear also affects habitat use and foraging decisions by marine predators. Heithaus & Dill (2002, 2006) show that bottlenosed dolphins (*Tursiops aduncus*), themselves apex- or meso-predators depending on habitat, trade off food acquisition against safety. Dolphins often prefer deeper waters over resource-rich shallow waters because of the higher risk of predation by tiger sharks (*Galeocerdo cuvier*) in the latter habitats. Both predation risk and prey availability influence dolphin habitat use, but intrinsic risk associated with habitat type rather than simple encounter rates with predators is critical in influencing dolphin foraging (Heithaus & Dill 2006). Dolphins not only come under direct threat of predation from apex predators (sharks), but they are also in competition for resources with many of these predators (Heithaus 2001).

Interestingly, when foraging predators face a risk of being attacked themselves, differences in the size and boldness of individual predators seem to influence their own risk-taking behaviour and can indirectly affect the predation risk to their prey. The result of this is a form of behaviourally mediated trophic cascade. Ioannou *et al.* (2008) found that differences in the boldness of pairs of three-spined sticklebacks led to differential predation risk for their prey (Chironomidae larvae). Pairs of large-bodied individual sticklebacks started foraging more readily and ate more prey in less time than smaller-bodied pairs that were less bold. A tradeoff was detected where fish were more likely to leave refuge (increased risk) in the presence of more prey (higher foraging reward).

EFFECTS ON PREY BIODIVERSITY: RESTORATION OF APEX PREDATORS AS A CONSERVATION TOOL?

In addition to table one, we review another 20 studies that tested whether mesopredator suppression by apex predators resulted in increased abundance and diversity of the prey of mesopredators, or whether prey populations declined following mesopredator release from apex predator suppression (Table 2). Studies that demonstrated such effects covered both aquatic and terrestrial ecosystems across a wide geographical range. However, most were from terrestrial systems in Australia and North America under the apparent top-down control of large canid species. They typically involved moderately simple predator communities, in which one apex predator interacted strongly with one or two mesopredators. Only two studies showed no such benefit of mesopredator suppression. In one case, complex interactions in diverse predator communities may mean that the suppression of one mesopredator by an apex predator was cancelled by the indirect benefit this provided to another mesopredator (Ellis *et al.* 2007). Lloyd's (2007) study further suggests that in some cases the release of mesopredators from suppression by apex predators may not always impact negatively on prey populations. The control of apex predators did not reduce bird nesting success (as would be predicted), perhaps due to complex interactions among predators of bird's nests. It is possible that

mammalian mesopredators released from top down control may themselves limit other mesopredators (snakes).

Just as the intense aggression often directed by apex predators to mesopredators can mean that small changes in abundance of apex predators translate to disproportionate demographic effects on mesopredators, there is an allometric argument which suggests that the presence of apex predators may have large beneficial effects for a wide range of small prey species. Among mammalian predators, mass-related energetic requirements mean that specialization on killing of large prey increases with body size. This leads to 'hypercarnivory' – obligate hunting of large prey – above a predator body mass of about 20 kg (Carbone *et al.* 1999). Hypercarnivory at large body mass requires large foraging ranges (Carbone *et al.* 2005), and therefore low population densities, especially in species that defend territories. Because of their low densities and inclination to pursue large prey, apex predators exert low predation pressure on small prey species. However, active patrolling of their large territories is likely to result in apex predators exerting substantial effects on mesopredators, through aggressive encounters which may be fatal for mesopredators or by fear-induced changes to mesopredator activity and distribution, as described above. Mesopredators are more likely than apex predators to be versatile generalist hunters, with a capacity to reach high population densities and have large impacts on a wide range of prey species. Controls on the numbers and behaviour of mesopredators by relatively sparse populations of apex predators may therefore have significant effects in moderating the intensity of predation on many species of small prey.

It follows from the above that restoration of apex predators could be a powerful tool for regulating the impacts of predation on prey species at lower trophic levels. In North America, coyote populations have declined where gray wolves have been re-established, although the strength of this effect varies, from modest in some areas (Grand Teton National Park) to high (Yellowstone National Park) or extreme (Isle Royale) in others (Krefting 1969; Smith *et al.* 2003; Berger & Conner 2008). Berger *et al.* (2008) showed that wolf-driven declines in coyotes led to a four-fold increase in survival of juvenile pronghorn antelope (*Antilocapra americana*) in wolf restoration areas in the Greater Yellowstone Ecosystem. In Europe, restored lynx and wolf populations suppress red foxes (Elmhagen & Rushton 2007). In an interesting variation, van Dijk *et al.* (2008) show how the re-establishment of wolves on the Scandinavian peninsula may have benefited a facultative scavenger, the wolverine (*Gulo gulo*), by increasing the availability of large carcasses (e.g. moose *Alces alces*). This resulted in a diet switch of wolverines away from reindeer and smaller prey such as rodents (consumed in higher amounts by wolverines when wolves are absent) to increased feeding on moose carcasses in sympatry with wolves. In some cases, the recolonization of native predators may not only limit native mesopredator populations, but reduce the impact of exotic mesopredators. Salo *et al.* (2008) provide evidence that female American mink (*Mustela vison*) in Europe modify their movement patterns to reduce their exposure to re-colonizing white-tailed sea eagles (*Haliaeetus albicilla*), and that this in turn may benefit species eaten by mink.

Perhaps the most dramatic illustration of the biodiversity effects of mesopredator suppression by an apex predator comes from the interaction of the dingo, red fox, feral cat, and native small mammals in Australia. Australia is unusual among the continents in having few apex mammalian predators. This is largely due to the Late Quaternary extinction of marsupial lions *Thylacoleo* and the mainland forms of the thylacine (*Thylacinus cynocephalus*) and 'Tasmanian devil' *Sarcophilus* (Johnson 2006). This diverse community of large carnivores was replaced on the mainland by a single species, the dingo, about 4000 years ago. Dingoes in their turn have been heavily persecuted since the arrival of Europeans, who also introduced two mesopredators, the red fox and domestic house cat. Australian mammals have suffered an exceptionally high rate of extinction over the last 200 years: at least 29 species have disappeared from mainland Australia, and at least 19 of these are totally extinct (Sattler & Creighton 2002; Johnson 2006). The majority of these extinctions are attributable to predation by the red fox and domestic cat (Johnson 2006).

They are also indirectly related to the decline of the dingo. Across the whole continental fauna, species with distributions that overlap the current range of the dingo have persisted better than species from areas were dingoes have been eliminated (Johnson *et al.* 2007; Smith & Quinn 1996). More detailed studies of particular threatened species such as the bilby (*Macrotis lagotis*) and dusky hopping mouse (*Notomys fuscus*) show that surviving populations occur where dingoes are most abundant (Southgate *et al.* 2007; Letnic *et al.* in press). There is also evidence from a range of environments that the abundances of red foxes and domestic cats are negatively related to abundance of dingoes (see Table 1). In some cases the link between persistence of dingoes and threatened mammal species has been made painfully clear. For example, one of the last two remaining populations of the rufous hare-wallaby (*Lagorchestes hirsutus*) on mainland Australia went extinct after the local dingo population was eliminated by poisoning, an event that was quickly followed by a fox invasion (Lundie-Jenkins *et al.* 1993). Probably, the coexistence of dingoes and small prey species such as bilbies and hare-wallabies is due to the fact that dingoes typically have large ranges, low population densities and low reproductive rates, whereas foxes and cats can occur at much higher densities, have higher population growth rates, and also preferentially prey on small-medium

sized mammals (Johnson 2006). Further, in many parts of Australia populations of foxes especially are maintained at high densities by the introduced European rabbit (*Oryctolagus cuniculus*), and this increases the rate of opportunistic predation by foxes on native species that are not only less common than rabbits but have lower population growth rates. Restoration of dingoes in parts of Australia is now being advocated as a necessary condition for the large-scale re-establishment of declined mammal species (Dickman *et al.* 2009).

An obstacle for many conservation initiatives will be the need for long-term monitoring of apex predator and mesopredator populations, to account for their dynamic nature. Studies are required which investigate interactions between species across resource, geographical and temporal scales (Estes *et al.* 1998; Prange & Gehrt 2007). Estes *et al.* (1998) showed how the collapse of otter populations (a keystone predator) was due to increased predation by killer whales, brought about by the depletion of seals as a result of lower fish stocks. This in turn resulted in a spike in sea urchin numbers and profound habitat change. Adding to this, we will have to account for how the effects of climate change will impact interactions (Wilmers *et al.* 2006; Carroll 2007), particularly through effects on bottom-up processes. Mathematical modelling of current predator community interactions and their relationship(s) with prey species, as well as those following hypothetical management decisions, may offer a useful, and powerful first step to predicting likely outcomes (see Courchamp *et al.* 1999; Blackwell *et al.* 2001; Fan *et al.* 2005; Caut *et al.* 2007; Vance-Chalcraft *et al.* 2007). However, models will always be oversimplifications of natural systems and should not be used in isolation from detailed field studies (Linnell & Strand 2000).

MESOPREDATOR RELEASE AND BOTTOM-UP EFFECTS

Habitat complexity and productivity may have large effects on competitive and predatory interactions between species (Muller & Brodeur 2002; Thompson & Gese 2007). Because primary productivity potentially affects abundance of populations at all trophic levels and can vary both temporally and spatially, it may serve either to attenuate or to exacerbate the nature, strength and direction of interactions between predators (Linnell & Strand 2000; Meserve *et al.* 2003; Holmgren *et al.* 2006; Elmhagen & Rushton 2007). Studies which do not simultaneously consider top-down and bottom-up processes may fail to fully identify the major drivers of ecosystem function and patterns in biodiversity. Litvaitis & Villafuerte (1996) argue that anthropogenic habitat change may be as important as the loss of apex predators in explaining increased abundance of mesopredators. The studies of Lariviere (2004) and Prange & Gehrt (2004) provide evidence that the expansion in range of the raccoon (*Procyon lotor*) in parts of North America is probably attributable to urbanization and increased food availability rather than decline of apex predators.

There are at least two major ways in which bottom-up effects may shape the strength and direction of interactions among predators: through the availability of food resources and the influence of variation in habitat structure. Food web and community structure depend on productivity (Arim & Jaksic 2005), but how is variation in resource availability likely to affect mesopredator abundance? Where prey, or some prey, of mesopredators are highly abundant, are mesopredators less affected by apex predators? There is evidence that predator coexistence may be facilitated in lower-productivity environments because apex predators may not reach sufficient densities to suppress mesopredators (Linnell & Strand 2000; Creel 2001; Hunter *et al.* 2007). For example, wild dogs declined to extinction in the Serengeti National Park when predator (lions and hyenas) and prey densities were high, but remain most abundant where prey densities are low and other predators are uncommon (Creel & Creel 1998). This situation arose because although prey species were abundant, they were large, dangerous and energetically costly to hunt. Because larger predators were able to dominate wild dogs at kills, they preferred to steal kills from wild dogs rather than actively pursuing prey, leading to an 'uncoupling of interference and exploitation competition' (Creel 2001).

There are contrary examples, such as wolves appearing to be more tolerant of coyotes where the abundance of a shared prey (elk, *Cervus elaphus*) was higher (Berger *et al.* 2008). In one of the most comprehensive studies examining the interplay between bottom-up effects and mesopredator release, Elmhagen & Rushton (2007) found in Sweden that the productivity of ecosystems set the upper limits on mesopredator populations once they were released from control by apex predators. It is likely in this case that restoration of apex predators would be more effective in controlling mesopredators in productive than in unproductive ecosystems.

Habitat structure and complexity, which may be linked with productivity, could also have a large bearing on the strength of interactions between predators. Structural complexity of habitats (e.g. rainforests and coral reefs) may reduce the likelihood of negative interactions between predators (Petren & Case 1998; Finke & Denno 2006; McGee *et al.* 2006) by providing refuges that allow mesopredators to avoid direct encounters with apex predators. Conversely, less complex environments could sometimes intensify these interactions, possibly driving mesopredators to extinction (Creel 2001). Potentially, habitat structure and complexity, and food availability,

may combine in a number of different ways, which in turn may influence the outcomes of interactions between predators. At present, these effects are poorly understood.

INTERACTIONS IN COMPLEX PREDATOR COMMUNITIES AND THEIR CONSERVATION AND MANAGEMENT IMPLICATIONS

The suppression of mesopredators by apex predators can indirectly benefit prey species by reducing mesopredator predation intensity (see meta-analysis by Vance-Chalcraft *et al.* 2007). Prey that are killed primarily by mesopredators, and shared prey, may both benefit from the presence of apex predators because of the lower densities of apex predators relative to prey populations, as explained earlier. In this section we highlight case studies from New Zealand to illustrate how predators influence each other and prey species within relatively complex and simple predator communities. We also illustrate the role of introduced prey species and the ways in which they further influence predator interactions (e.g. Courchamp *et al.* 1999; Norbury 2001; Pope *et al.* 2008). New Zealand provides excellent opportunities to explore these interactions, as many of the predator and prey species are recently introduced (≤ 200 years). Therefore, these species have not coevolved with native species, and are unlikely to have reached stable equilibria with them through such processes as niche differentiation.

New Zealand has a uniquely diverse set of introduced mammalian predators, including northern hemisphere mustelids and rodents, the hedgehog (*Erinaceus europaeus*) and the domestic cat, and a southern hemisphere marsupial, the common brushtail possum (*Trichosurus vulpecula*, a herbivore in Australia which often behaves as a predator in New Zealand, robbing birds' nests and killing and eating chicks Clout & Ericksen 2000). Pest management in the face of such complexity is difficult: control of one species because it is the most obvious or apparently worst pest, may do more harm than good, e.g. increased predation by stoats (*Mustela erminea*) on birds when rats are removed (Murphy & Bradfield 1992). Indirect effects of control operations may thwart management goals, and there may be thresholds in control effort at which such effects result in conservation costs rather than benefits (Tompkins & Veltman 2006). Another feature of New Zealand ecosystems, particularly the forests, is the pulsing of resources associated with masting events, which are significant in shaping the nature of predator interactions and effects on prey (Ostfeld & Keesing 2000).

Several studies have examined the implications of complex interactions among invasive predators in New Zealand's *Nothofagus* forests. Tompkins & Veltman (2006) found that reducing numbers of both rats (*Rattus rattus*) and stoats, or rats only, led to an increase in numbers of mice (*Mus musculus*), and reducing stoat numbers led to higher rat numbers. Presence of the larger brushtail possum, often the target of control operations, may help in regulating rat numbers through competition for food resources (see Fig. 2). White & King (2006) show how the nature of predator-prey interactions may vary geographically. In the Holarctic, mustelid predation of birds is often linked to rodent population cycles, such that birds may be depredated less when rodents are abundant and mustelids prey-switch from birds to rodents. In New Zealand this effect usually fails, because peak house mouse densities are typically much lower than in the northern hemisphere. The exception is when large masting events temporarily boost rodent numbers. Blackwell *et al.* (2003) found that stoats may slow but not prevent outbreaks of house mouse and ship rat populations, and therefore that resource pulses have more influence on the dynamics of this system than top-down pressures. Finally, Rayner *et al.* (2007) provided evidence of how interactions among predators may be mediated not only by resource availability but also by its distribution. They demonstrated that a reduction in numbers of domestic cats allowed rat populations to increase, which in turn caused a population crash in Cook's petrel (*Pterodroma cookii*). Petrels subsequently recovered after rat removal. However, the predation of seabirds by rats was also habitat dependent, being higher at increased elevation. Their results suggest that altitudinal variation in food resources has a large effect on the risk to petrels of predation following mesopredator release.

Our case studies above highlight that a better understanding of predator interactions and functional roles within a whole of ecosystem context are crucial before wildlife management is applied, to avoid unforseen deleterious effects (see Norbury 2001; Courchamp *et al.* 2003; Caut *et al.* 2007; Hoare *et al.* 2007). Failure to do so may result in unexpected negative conservation outcomes which may also be extremely costly to fix (see, Bergstrom *et al.* 2009).

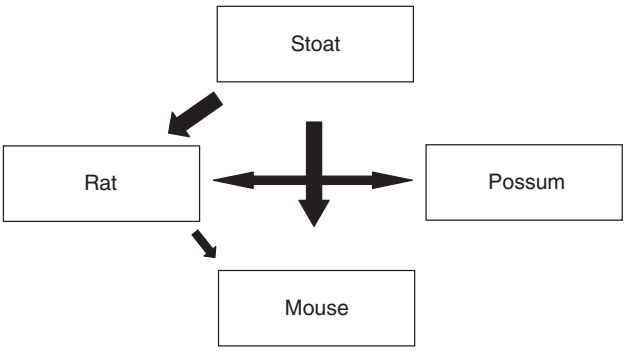

Figure 2 Relationships between predators in New Zealand's *Nothofagus* forests (modified from Tompkins & Veltman (2006)). Arrow thickness indicates strength and direction of population reduction effects.

CONCLUSION

It is clear that apex predators can have significant influences on ecosystem function and community organization through their effects on mesopredator populations. However, the complexity of these interactions, and how in turn these may be affected by bottom-up processes, is far from being understood in sufficient detail for the majority of the world's ecosystems and taxonomic groups. This information is vital before management of predators as a biodiversity conservation tool is employed. We can identify at least two prominent shortfalls in research of predator community interactions and their associated effects on prey species. First, relative to area and species diversity, the marine environment appears severely underrepresented in comparison to terrestrial environments. We therefore do not know whether marine systems are likely to be controlled by apex predators in the same way that terrestrial systems are. Baum & Worm's (2009) review provides an excellent starting point to addressing this problem. Secondly, we believe a key consideration which is poorly understood in the majority of studies, is the genetics of predator populations and its connection with social structure and behaviour. For the conservation of predators and their associated potential ecosystem benefits to be realized, we will need to accept that ecological function is more than simply a case of mere numbers (Chapron *et al.* 2008), but inevitably will also depend on the genetic integrity and social structure of populations.

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REFERENCES

Ainley, D.G., Ballard, G. & Dugger, K.M. (2006). Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology*, 87, 2080–2093.

Arim, M. & Jaksic, F.M. (2005). Productivity and food web structure: association between productivity and link richness among top predators. *J. Anim. Ecol.*, 74, 31–40.

Barr, G.E. & Babbitt, K.J. (2007). Trout affect the density, activity and feeding of a larval plethodontid salamander. *Freshw. Biol.*, 52, 1239–1248.

Barton, B.T. & Roth, J.D. (2008). Implications of intraguild predation for sea turtle nest protection. *Biol. Conserv.*, 141, 2139–2145.

Baum, J.K. & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.*, 78, 699–714.

Berger, K.M. & Conner, M.M. (2008). Recolonizing wolves and mesopredator suppression of coyotes: impacts on pronghorn population dynamics. *Ecol. Appl.*, 18, 599–612.

Berger, K.M. & Gese, E.M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *J. Anim. Ecol.*, 76, 1075–1085.

Berger, J., Stacey, P.B., Bellis, L. & Johnson, M.P. (2001). A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecol. Appl.*, 11, 947–960.

Berger, K.M., Gese, E.M. & Berger, J. (2008). Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology*, 89, 818–828.

Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K. *et al.* (2009). Indirect effects of invasive species removal devastate World Heritage Island. *J. Appl. Ecol.*, 46, 73–81.

Blackwell, G.L., Potter, M.A. & Minot, E.O. (2001). Rodent and predator population dynamics in an eruptive system. *Ecol. Modell.*, 142, 227–245.

Blackwell, G.L., Potter, M.A., McLennan, J.A. & Minot, E.O. (2003). The role of predators in ship rat and house mouse population eruptions: drivers or passengers? *Oikos*, 100, 601–613.

Blanchard, J.L., Dulvy, N.K., Jennings, S., Ellis, J.E., Pinnegar, J.K., Tidd, A. *et al.* (2003). Ecological and environmental factors influence size-based metrics of Celtic Sea fish communities. *ICES J. Mar. Sci.*, 62, 405–411.

Boveng, P.L., Hiruki, L.M., Schwartz, M.K. & Bengtson, J.L. (1998). Population growth of Antarctic fur seals: limitation by a top predator, the leopard seal? *Ecology*, 79, 2863–2877.

Boyce, M.S. & Anderson, E.M. (1999). Evaluating the role of carnivores in the Greater Yellowstone Ecosystem. In: '*Carnivores in Ecosystems: The Yellowstone Experience*'.(Eds. Clark, T.W., Curlee, A.P., Minta, S.C. & Kareiva, P.M.). Yale University Press, New Haven, pp. 265–283.

Burkepile, D.E. & Hay, M.E. (2007). Predator release of the gastropod *Cyphoma gibbosum* increases predation on gorgonian corals. *Oecologia*, 154, 167–173.

Burrows, N.D., Algar, D., Robinson, A.D., Sinagra, J., Ward, B. & Liddelow, G. (2003). Controlling introduced predators in the Gibson Desert of Western Australia. *J. Arid Environ.*, 55, 691–713.

Cabeza, M., Arponen, A. & Van Teeffelen, A. (2008). Top predators: hot or not? A call for systematic assessment of biodiversity surrogates *J. Appl. Ecol.*, 45, 976–980.

Carbone, C., Mace, G.M., Roberts, S.C. & Macdonald, D.W. (1999). Energetic constraints on the diet of terrestrial carnivores. *Nature*, 402, 286–288.

Carbone, C., Cowlishaw, G., Isaac, N.J.B. & Rowcliffe, J.M. (2005). How far do animals go? Determinants of day range in mammals *Am. Nat.*, 165, 290–297.

Caro, T.M. (1987). Cheetah mothers vigilance – looking out for prey or for predators. *Behav. Ecol. Sociobiol.*, 20, 351–361.

Caro, T.M. & Stoner, C. (2003). The potential for interspecific competition among African carnivores. *Biol. Conserv.*, 110, 67–75.

Carroll, C. (2007). Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: Marten and Lynx in the northern Appalachians. *Conserv. Biol.*, 21, 1092–1104.

Carscadden, J.E., Frank, K.T. & Leggett, W.C. (2001). Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. *Can. J. Fish. Aquat. Sci.*, 58, 73–85.

Caut, S., Casanovas, J.G., Virgos, E., Lozano, J., Witmer, G.W. & Courchamp, F. (2007). Rats dying for mice: modelling the competitor release effect. *Austral Ecol.*, 32, 858–868.

Chapron, G., Andren, H. & Liberg, O. (2008). Conserving top predators in ecosystems. *Science*, 320, 47.

Clout, M.N. & Ericksen, K. (2000). Anatomy of a disastrous success: the brushtail possum as an invasive species. In: *The Brushtail Possum: Biology, Impact and Management of an Introduced Marsupial* (ed Montague, T.). Landcare Research Lincoln, New Zealand, pp. 1–9.

Courchamp, F., Langlais, M. & Sugihara, G. (1999). Cats protecting birds: modelling the mesopredator release effect. *J. Anim. Ecol.*, 68, 282–292.

Courchamp, F., Chapuis, J.L. & Pascal, M. (2003). Mammal invaders on islands: impact, control and control impact. *Biol. Rev.*, 78, 347–383.

Creel, S. (2001). Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conserv. Biol.*, 15, 271–274.

Creel, S. & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends Ecol. Evol.*, 23, 194–201.

Creel, S. & Creel, N.M. (1996). Limitation of African wild dogs by competition with larger carnivores. *Conserv. Biol.*, 10, 526–538.

Creel, S. & Creel, N.M. (1998). Six ecological factors that may limit African wild dogs. *Anim. Conserv.*, 1, 1–9.

Crooks, K.R. & Soulé, M.E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, 400, 563–566.

Daan, N., Gislason, H., Pope, J.G. & Rice, J.C. (2005). Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES J. Mar. Sci.*, 62, 177–188.

Daskalov, G.M. (2002). Overfishing drives atrophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.*, 225, 53–63.

Daskalov, G.M., Grishin, A.N., Rodionov, S. & Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc. Natl Acad. Sci. USA*, 104, 10518–10523.

Dickman, C.R., Glen, A.S. & Letnic, M. (2009). Reintroducing the dingo: can Australia's conservation wastelands be restored? In: *Reintroduction of Top-Order Predators* (eds Hayward, M.W. & Somers, M.J.). Wiley-Blackwell, Oxford, pp. 238–269.

van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H. *et al.* (2008). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *J. Anim. Ecol.*, 77, 1183–1190.

Donadio, E. & Buskirk, S.W. (2006). Diet, morphology, and interspecific killing in carnivora. *Am. Nat.*, 167, 524–536.

Dulvy, N.K., Freckleton, R.P. & Polunin, N.V.C. (2004). Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecol. Lett.*, 7, 410–416.

Durant, S.M. (1998). Competition refuges and coexistence: an example from Serengeti carnivores. *J. Anim. Ecol.*, 67, 370–386.

Durant, S.M. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behav. Ecol.*, 11, 624–632.

Ellis, J.C., Shulman, M.J., Wood, M., Witman, J.D. & Lozyniak, S. (2007). Regulation of intertidal food webs by avian predators on New England rocky shores. *Ecology*, 88, 853–863.

Elmhagen, B. & Rushton, S.P. (2007). Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecol. Lett.*, 10, 197–206.

Essington, T.E. (2006). Pelagic ecosystem response to a century of commercial fishing and whaling. In: *Whales, Whaling and Ocean Ecosystems* (eds Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M. & Brownell, R.L.). University of California Press, Berkeley, CA, pp. 38–49.

Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, 282, 473–476.

Fan, M., Kuang, Y. & Feng, Z.L. (2005). Cats protecting birds revisited. *Bull. Math. Biol.*, 67, 1081–1106.

Fedriani, J.M., Palomares, F. & Delibes, M. (1999). Niche relations among three sympatric Mediterranean carnivores. *Oecologia*, 121, 138–148.

Fedriani, J.M., Fuller, T.K., Sauvajot, R.M. & York, E.C. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia*, 125, 258–270.

Finke, D.L. & Denno, R.F. (2006). Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia*, 149, 265–275.

Fogarty, M.J. & Murawski, S.A. (1998). Large-scale disturbance and the structure of marine system: fishery impacts on Georges Bank. *Ecol. Appl.*, 8, S6–S22.

Frank, K.T., Petrie, B., Shackell, N.L. & Choi, J.S. (2006). Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecol. Lett.*, 9, 1096–1105.

Frid, A., Baker, G.G. & Dill, L.M. (2008). Do shark declines create fear-released systems? *Oikos*, 117, 191–201.

Gehrt, S.D. & Prange, S. (2007). Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. *Behav. Ecol.*, 18, 204–214.

Gese, E.M., Stotts, T.E. & Grothe, S. (1996). Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. *J. Mammal.*, 77, 377–382.

Glen, A.S. & Dickman, C.R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biol. Rev.*, 80, 387–401.

Gorman, M.L., Mills, M.G., Raath, J.P. & Speakman, J.R. (1998). High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyenas. *Nature*, 391, 479–481.

Griffen, B.D. & Byers, J.E. (2006). Intraguild predation reduces redundancy of predator species in multiple predator assemblage. *J. Anim. Ecol.*, 75, 959–966.

Griffen, B.D. & Williamson, T. (2008). Influence of predator density on nonindependent effects of multiple predator species. *Oecologia*, 155, 151–159.

Harley, C.D.G. & Lopez, J.P. (2003). The natural history, thermal physiology, and ecological impacts of intertidal mesopredators, Oedoparena spp. (Diptera: Dryomyzidae). *Invertebr. Biol.*, 122, 61–73.

Harrison, D.J., Bissonette, J.A. & Sherburne, J.A. (1989). Spatial relationships between Coyotes and Red Foxes in Eastern Maine. *J. Wildl. Manage.*, 53, 181–185.

Heithaus, M.R. (2001). Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *J. Zool.*, 253, 53–68.

Heithaus, M.R. & Dill, L.M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83, 480–491.

Heithaus, M.R. & Dill, L.M. (2006). Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos*, 114, 257–264.

Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.*, 23, 202–210.

Helldin, J.O., Liberg, O. & Gloersen, G. (2006). Lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*) in boreal Sweden – frequency and population effects. *J. Zool.*, 270, 657–663.

Henke, S.E. & Bryant, F.C. (1999). Effects of coyote removal on the faunal community in western Texas. *J. Wildl. Manage.*, 63, 1066–1081.

Hoare, J.M., Adams, L.K., Bull, L.S. & Towns, D.R. (2007). Attempting to manage complex predator-prey interactions fails to avert imminent extinction of a threatened New Zealand skink population. *J. Wildl. Manage.*, 71, 1576–1584.

Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutierrez, J.R. *et al.* (2006). Extreme climatic events shape arid and semiarid ecosystems. *Front. Ecol. Environ.*, 4, 87–95.

Hunter, J.S., Durant, S.M. & Caro, T.M. (2007). To flee or not to flee: predator avoidance by cheetahs at kills. *Behav. Ecol. Sociobiol.*, 61, 1033–1042.

Ioannou, C.C., Payne, M. & Krause, J. (2008). Ecological consequences of the bold-shy continuum: the effect of predator boldness on prey risk. *Oecologia*, 157, 177–182.

Johnson, C.N. (2006). *Australia*'s Mammal Extinctions: A 50 000 Year History. Cambridge University Press, Cambridge.

Johnson, C.N. & VanDerWal, J. (in press). Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests. *J. Appl. Ecol.*, 46, 641–646.

Johnson, C.N., Isaac, J.L. & Fisher, D.O. (2007). Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proc. R. Soc. B Biol. Sci.*, 274, 341–346.

Kamler, J.F., Ballard, W.B., Gilliland, R.L., Lemons, P.R. & Mote, K. (2003). Impacts of coyotes on swift foxes in northwestern Texas. *J. Wildl. Manage.*, 67, 317–323.

Karki, S.M., Gese, E.M. & Klavetter, M.L. (2007). Effects of coyote population reduction on swift fox demographics in southeastern Colorado. *J. Wildl. Manage.*, 71, 2707–2718.

Kitchell, J.F., Martell, S.J.D., Walters, C.J., Jensen, O.P., Kaplan, I.C., Watters, J. *et al.* (2006). Billfishes in an ecosystem context. *Bull. Mar. Sci.*, 79, 669–682.

Krefting, L.W. (1969). The rise and fall of the coyote on Isle Royale. *Naturalist*, 20, 24–31.

Lariviere, S. (2004). Range expansion of raccoons in the Canadian prairies: review of hypotheses. *Wildl. Soc. Bull.*, 32, 955–963.

Laundre, J.W., Hernandez, L. & Altendorf, K.B. (2001). Wolves, elk, and bison: re-establishing the 'landscape of fear' in Yellowstone National Park, USA. *Can. J. Zool. Rev. Can. Zool.*, 79, 1401–1409.

Letnic, M., Crowther, M. & Koch, F. (in press). Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Anim. Conserv.* DOI: 10.1111/j.1469-1795.2009.00250.x.

Linnell, J.D.C. & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Divers. Distrib.*, 6, 169–176.

Litvaitis, J.A. & Villafuerte, R. (1996). Intraguild predation, mesopredator release, and prey stability. *Conserv. Biol.*, 10, 676–677.

Lloyd, P. (2007). Predator control, mesopredator release, and impacts on bird nesting success: a field test. *Afr. Zool.*, 42, 180–186.

Lundie-Jenkins, G., Corbett, L.K. & Phillips, C.M. (1993). Ecology of the Rufous Hare-Wallaby, *Lagorchestes hirsutus* Gould (Marsupialia, Macropodidae), in the Tanami Desert, Northern-Territory .3. Interactions with Introduced Mammal Species. *Wildl. Res.*, 20, 495–511.

McDonald, R.A., O'Hara, K. & Morrish, D.J. (2007). Decline of invasive alien mink (*Mustela vison*) is concurrent with recovery of native otters (*Lutra lutra*). *Divers. Distrib.*, 13, 92–98.

McGee, B.K., Ballard, W.B., Nicholson, K.L., Cypher, B.L., Lemons, P.R. & Kamler, J.F. (2006). Effects of artificial escape dens on swift fox populations in northwest Texas. *Wildl. Soc. Bull.*, 34, 821–827.

Meserve, P.L., Kelt, D.A., Milstead, W.B. & Gutierrez, J.R. (2003). Thirteen years of shifting top-down and bottom-up control. *Bioscience*, 53, 633–646.

Mezquida, E.T., Slater, S.J. & Benkman, C.W. (2006). Sage-Grouse and indirect interactions: potential implications of coyote control on Sage-Grouse populations. *Condor*, 108, 747–759.

Minta, S.C., Minta, K.A. & Lott, D.F. (1992). Hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). *J. Mammal.*, 73, 814–820.

Mitchell, B.D. & Banks, P.B. (2005). Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps *Austral Ecol.*, 30, 581–591.

Moehrenschlager, A., List, R. & Macdonald, D.W. (2007). Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. *J. Mammal.*, 88, 1029–1039.

Moreno, R.S., Kays, R.W. & Samudio, R. (2006). Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *J. Mammal.*, 87, 808–816.

Mukherjee, S., Zelcer, M. & Kotler, B.M. (2009). Patch use in time and space for a meso-predator in a risky world. *Oecologia*, 159, 661–668.

Muller, C.B. & Brodeur, J. (2002). Intraguild predation in biological control and conservation biology. *Biol. Control*, 25, 216–223.

Murphy, E. & Bradfield, P. (1992). Change in diet of stoats following poisoning of rats in a New Zealand forest. *N. Z. J. Ecol.*, 16, 137–140.

Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280–283.

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P. & Peterson, C.H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, 315, 1846–1850.

Norbury, G. (2001). Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. *J. Appl. Ecol.*, 38, 1350–1361.

O'Gorman, E., Enright, R. & Emmerson, M. (2008). Predator diversity enhances secondary production and decreases the likelihood of trophic cascades. *Oecologia*, 158, 557–567.

Oguz, T. & Gilbert, D. (2007). Abrupt transitions of the top-down controlled Black Sea pelagic ecosystem during 1960–2000: evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. *Deep Sea Res. Part I Oceanogr. Res. Pap.*, 54, 220–242.

Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.*, 15, 232–237.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, 14, 483–488.

Palomares, F. & Caro, T.M. (1999). Interspecific killing among mammalian carnivores. *Am. Nat.*, 153, 492–508.

Palomares, F., Gaona, P., Ferreras, P. & Delibes, M. (1995). Positive effects on game species of top predators by controlling smaller predator populations – an example with lynx, mongooses, and rabbits. *Conserv. Biol.*, 9, 295–305.

Palomares, F., Ferreras, P., Fedriani, J.M. & Delibes, M. (1996). Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. *J. Appl. Ecol.*, 33, 5–13.

Parrish, F.A. (2009). Do monk seals exert top-down pressure in subphotic ecosystems? *Mar. Mamm. Sci.*, 25, 91–106.

Petren, K. & Case, T.J. (1998). Habitat structure determines competition intensity and invasion success in gecko lizards. *Proc. Natl Acad. Sci. U.S.A.*, 95, 11739–11744.

Polis, G.A. & Holt, R.D. (1992). Intraguild predation – the dynamics of complex trophic interactions. *Trends Ecol. Evol.*, 7, 151–154.

Pope, K.L., Garwood, J.M., Welsh, H.H. & Lawler, S.P. (2008). Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator. *Biol. Conserv.*, 141, 1321–1331.

Prange, S. & Gehrt, S.D. (2004). Changes in mesopredator-community structure in response to urbanization. *Can. J. Zool. Revue Canadienne De Zoologie*, 82, 1804–1817.

Prange, S. & Gehrt, S.D. (2007). Response of skunks to a simulated increase in coyote activity. *J. Mammal.*, 88, 1040–1049.

Ralls, K. & White, P.J. (1995). Predation on San-Joaquin kit foxes by larger canids. *J. Mammal.*, 76, 723–729.

Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K. & Clout, M.N. (2007). Spatial heterogeneity of mesopredator release within an oceanic island system. *Proc. Natl Acad. Sci. U.S.A.*, 104, 20862–20865.

Rogers, C.M. & Caro, M.J. (1998). Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. *Oecologia*, 116, 227–233.

Salo, P., Nordström, M., Thomson, R.L. & Korpimäki, E. (2008). Risk induced by a native top predator reduces alien mink movements. *J. Anim. Ecol.*, 77, 1092–1098.

Sattler, P. & Creighton, C. (2002). Australian terrestrial biodiversity assessment. National Land and Water Resources Audit, Canberra.

Scheinin, S., Yom-Tov, Y., Motro, U. & Geffen, E. (2006). Behavioural responses of red foxes to an increase in the presence of golden jackals: a field experiment. *Anim. Behav.*, 71, 577–584.

Schoener, T.W. & Spiller, D.A. (1987). Effect of lizards on spider populations – manipulative reconstruction of a natural experiment. *Science*, 236, 949–952.

Sergio, F. & Hiraldo, F. (2008). Intraguild predation in raptor assemblages: a review. *Ibis*, 150, 132–145.

Sergio, F., Newton, I., Marchesi, L. & Pedrini, P. (2006). Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *J. Appl. Ecol.*, 43, 1049–1055.

Sergio, F., Marchesi, L., Pedrini, P. & Penteriani, V. (2007). Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? *Anim. Behav.*, 74, 1607–1616.

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J. *et al.* (2008). Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Ann. Rev. Ecol. Evol. Syst.*, 39, 1–19.

Shackell, N.L. & Frank, K.T. (2007). Compensation in exploited marine fish communities on the Scotian Shelf, Canada. *Mar. Ecol. Prog. Ser.*, 336, 235–247.

Shepherd, T.D. & Myers, R.A. (2005). Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecol. Lett.*, 8, 1095–1104.

Smith, A.P. & Quin, D.G. (1996). Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation*, 77, 243–267.

Smith, D.W., Peterson, R.O. & Houston, D.B. (2003). Yellowstone after wolves. *Bioscience*, 53, 331–340.

Soulé, M.E., Bolger, D.T., Alberts, A.C., Sauvajot, R., Wright, J., Sorice, M. *et al.* (1988). Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.*, 2, 75–92.

Southgate, R., Paltridge, R., Masters, P. & Carthew, S. (2007). Bilby distribution and fire: a test of alternative models of habitat suitability in the Tanami Desert, Australia. *Ecography*, 30, 759–776.

Sovada, M.A., Sargeant, A.B. & Grier, J.W. (1995). Differential effects of coyotes and red foxes on duck nest success. *J. Wildl. Manage.*, 59, 1–9.

Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M. *et al.* (2003). Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proc. Natl Acad. Sci. U.S.A.*, 100, 12223–12228.

Switalski, T.A. (2003). Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. *Can. J. Zool. Revue Canadienne De Zoologie*, 81, 985–993.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G. *et al.* (2001). Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923–1926.

Thompson, C.M. & Gese, E.M. (2007). Food webs and intraguild predation: community interactions of a native mesocarnivore. *Ecology*, 88, 334–346.

Tompkins, D.M. & Veltman, C.J. (2006). Unexpected consequences of vertebrate pest control: predictions from a four-species community model. *Ecol. Appl.*, 16, 1050–1061.

Trewby, L.D., Wilson, G.J., Delahay, R.J., Walker, N., Young, R., Davison, J. *et al.* (2008). Experimental evidence of competitive release in sympatric carnivores. *Biol. Lett.*, 4, 170–172.

Vance-Chalcraft, H.D., Rosenheim, J.A., Vonesh, J.R., Osenberg, C.W. & Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology*, 88, 2689–2696.

Wallach, A.D., Murray, B.R. & O' Neill, A.J. (2009). Can threatened species survive where the top predator is absent? *Biol. Conserv.*, 142, 43–52.

Ward, P. & Myers, R.A. (2005). Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology*, 86, 835–847.

White, P.C.L. & King, C.M. (2006). Predation on native birds in New Zealand beech forests: the role of functional relationships between Stoats *Mustela erminea* and rodents. *Ibis*, 148, 765–771.

Wilmers, C.C., Post, E., Peterson, R.O. & Vucetich, J.A. (2006). Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecol. Lett.*, 9, 383–389.

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