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The consequences of predators without prey

Mitchell A Parsons¹, Thomas M Newsome², and Julie K Young^{1*}

Rapid and ongoing environmental change is leading to scenarios where marine and terrestrial predators are persisting without prey, either by scavenging or using anthropogenic foods. Despite investigations into the effects of predator presence or absence on prey behavior and ecology, little research has assessed the effect of prey absence on predators. Here, we synthesize research on scavenging and the use of anthropogenic resources by marine and terrestrial predators; hypothesize how the use of these resources may change predator behavior with respect to their social structure, space use, life history, and individual behavioral traits; and illustrate how these changes are likely to have cascading effects through ecosystems. The prevalence of predators persisting without prey will almost certainly change in the future due to altered availability of anthropogenic foods, scavenging opportunities, and natural prey. We discuss areas of needed research and the relevance of our findings to both the conservation and ecology of predators and management of human–wildlife conflict.

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Predator–prey interactions have long held the fascination of ecologists and non-scientists alike. Research has investigated the extent of top-down and bottom-up forces, trophic cascades, fear effects, and the role predators play in shaping communities and modifying prey behavior (Ripple *et al.* 2014). Motivated by global declines of apex predators, extensive research has examined how ecosystems operate in their absence (Terborgh and Estes 2010).

In trying to understand the role of predators, researchers have addressed – but only to a limited degree – how predators are affected by the absence of live prey. Prey depletion

threatens carnivores globally (Ripple *et al.* 2014) and although predators persisting without prey may seem unrealistic, many predators can switch strategies when populations of primary prey decline, relying on alternative prey or adopting a new foraging tactic, such as scavenging (Figure 1; Périquet *et al.* 2015). The latter often occurs when anthropogenic food is abundant and accessible (Newsome *et al.* 2015). Understanding the ecological and management implications of predators persisting without prey has implications in diverse fields, including carnivore ecology, animal behavior, disease ecology, and human–wildlife conflict (Newsome and van Eeden 2017).

Environmental change is occurring globally via urbanization, climate change, habitat fragmentation, and resource extraction. Such changes alter the distribution of wildlife and negatively influence biodiversity, with species at higher trophic levels usually affected to a greater degree due to their space and resource needs (Ripple *et al.* 2014). Along with predator losses, there has been a growing understanding of predators' ability to exist in human-altered environments (Beckmann and Berger 2003). Predators inhabiting modified landscapes are often facilitated by diverse food resources, including carcasses, livestock, rubbish, and anthropogenic foods (Figure 2; Abay *et al.* 2011; Ciucci *et al.* 2020).

Although the ecological roles of scavenging and anthropogenic foods have been reviewed separately (Wilson and Wolkovich 2011; Newsome *et al.* 2015), these factors have not been unified despite the implications for predator–prey relationships in the absence of hunting. We propose that the loss of prey from food webs could influence predator behavior, health, and demographics, and decouple trophic relationships, leading to behavioral changes at top trophic levels and ecosystem-wide changes at lower trophic levels (Figure 1). To develop this idea, we discuss predator traits likely to change when prey is lost, ecological impacts of predators switching to different foraging strategies, and factors that might alter predation rates (Table 1). We define predators as terrestrial, aquatic, and aerial animals that pursue and hunt live prey, and although we highlight

In a nutshell:

- Many predators subsist without hunting live prey by consuming carrion, human-provided foods, and other non-prey resources
- Predator foraging patterns have cascading effects on prey and ecosystems but the consequences of non-hunting predators are poorly understood
- Non-hunting predators may instigate human–wildlife conflict, spread disease, or cause cascading effects that degrade ecosystems
- While addressing human-provided food waste and the provisioning of wildlife, management and policy changes will affect the prevalence and ecological influence of non-hunting predators
- Research should evaluate how hunting live prey influences predator behavior, and how predator conservation and human–wildlife conflict may be affected by non-hunting predators

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Figure 1. (a1) Diagram of a three-level trophic cascade. Ecologists frequently ask (a2) how the presence or absence of predators influences other trophic levels, but rarely assess (a3) how the presence or absence of live prey affects systems. (b) In the absence of live prey, predators may die off, switch to alternative prey, or shift to scavenging or non-prey resources. Shifting away from live prey may have ecosystem-level impacts comparable to trophic cascades (Whitehead and Reeves 2005; Ciucci *et al.* 2020). + indicates positive effects; – indicates negative effects.

examples from mostly large-bodied vertebrates, the same lessons can be applied to other taxonomic groups. We include omnivores (eg bears), but acknowledge that changes stemming from the loss of prey may vary alongside variation in dietary needs from omnivores to obligate carnivores. We use the term “non-prey resources” to refer to food resources other than live prey.

■ Predators without prey: do they already exist?

To evaluate the extent of predators without prey, we conducted a literature search in Scopus and PubMed in November 2019. We searched for articles with titles, abstracts, and keywords that included anthropogenic food, carnivore, carrion, facilitation, facultative scavenger, foraging behavior,

human subsidies, hunting, prey switching, and scavenger. This search returned 238 articles. We reviewed these articles and removed those that were irrelevant to our objective, resulting in a final count of 173 articles. We supplemented this search using the same search terms in Google Scholar and via conversations with colleagues, through which we found an additional 157 articles.

Our review of these studies revealed that many predators take advantage of landfills, refuse, and provisioned food in urban and rural areas, and that some predators persist completely without live prey. For example, although spotted hyenas (*Crocuta crocuta*) typically hunt for prey, in urban areas of Ethiopia they consume carcasses, waste from butcher shops, and provisioned food (Abay *et al.* 2011). Some groups of banded mongoose (*Mungos mungo*) also rely on garbage dumps instead of hunting prey (Gilchrist and Otali 2002). The most common predators that lack live prey exist in captive facilities, such as zoos and research facilities. Although artificial, these systems offer opportunities to learn about different behavioral traits that may emerge in predators without prey. Use of non-prey resources is not limited to artificial or urban systems, as evidenced by case studies on blacktip reef sharks (*Carcharhinus melanopterus*; Mourier *et al.* 2021), dingoes (*Canis dingo*; Newsome *et al.* 2019), gray wolves (*Canis lupus*; Ciucci *et al.* 2020), and grizzly bears (*Ursus arctos horribilis*; Peirce and Van Daele 2006). Many predators also scavenge and utilize non-prey food items more than previously thought, including white sharks (*Carcharodon carcharias*; Fallows *et al.* 2013), and dingoes (Newsome *et al.* 2019). For other species, such as polar bears (*Ursus maritimus*), continuing global changes may result in a higher prevalence of scavenging (Laidre *et al.*

2018). These examples of predators consuming food without hunting live prey represent diverse predators and food resources (Panel 1).

■ Traits altered with the loss of hunting

Social structure

Changes in predator social structures due to the loss of live prey likely depend on the distribution and richness of food resources. At highly concentrated food sites, conspecific tolerance can increase, leading to increased group size and breakdown of territorial behavior as illustrated by bears (Peirce and Van Daele 2006), coyotes (*Canis latrans*;

Hidalgo-Mihart *et al.* 2004), and bottlenose dolphins (*Tursiops truncatus*; Chilvers and Corkeron 2001). Carcasses of large vertebrates also provide concentrated food resources and facilitate conspecific tolerance (Fallows *et al.* 2013). Less extreme cases of non-prey resources also influence social structures. Coyotes that consume large ungulates tend to be found in larger groups than coyotes that hunt small mammals (Bowen 1981). Increased group size helps defend carcasses from other predators and benefits all individuals (Bowen 1981; Périquet *et al.* 2015).

Exploiting non-prey resources may also influence dominance hierarchies and social relationships. Dominance hierarchies determine feeding order in spotted hyenas in the Namib Desert, while hyenas in more productive environments of East Africa display scramble competition at large carcasses (Tilson and Hamilton 1984). Similar changes in social structure occur in bottlenose dolphins, which typically hunt with preferred feeding associates (although less so around aquaculture sites or near fishing vessels; Díaz López and Shirai 2008).

Loss of hunting live prey may also impact interspecific social interactions and local enhancement when an individual uses other feeding animals as a cue for available food. Multiple predator species will share large carcasses suggesting increased interspecific tolerance (Lewis and Lafferty 2014). Local enhancement occurs during both hunting and scavenging, but is particularly beneficial when resources are difficult to locate (Kane and Kendall 2017). Additional scavengers on the landscape therefore could lead to increased probability of local enhancement.

Despite increased tolerance by predators around non-prey resources, antagonism still occurs. Animals that congregate at landfill sites still display agonistic behavior (Peirce and Van Daele 2006). Agonistic behavior, and even cannibalism, may increase with access to anthropogenic food (Newsome *et al.* 2019), although separating the effects of anthropogenic food from increased likelihood of intraspecific interaction is difficult.

Movement and space use

The distribution of predators may shift with changing foraging strategies. Provisioning of sharks by tourism operations appears to decrease core-use areas and increase shark residency times in feeding areas (Mourier *et al.* 2021), but does not affect migration patterns (Hammerschlag *et al.* 2012). Terrestrial predators with access to landfill sites have smaller home ranges than individuals away from these sites (Hidalgo-Mihart *et al.* 2004; Newsome *et al.* 2013). In contrast, predators that rely on scavenging of natural carcasses are often adapted for efficient travel over long distances (Kane *et al.* 2017). Smaller amounts of non-prey food can also influence space use (Young *et al.* 2008). Pacific sleeper sharks (*Somniosus*

Figure 2. A polar bear (*Ursus maritimus*) and gulls scavenging at a whale bonepile in Alaska. Reductions in sea ice may lead to increased frequency of scavenging by polar bears in the future.

pacificus) enter into shallow habitats to take advantage of whale carcasses (Barrett-Lennard *et al.* 2011), while tiger sharks (*Galeocerdo cuvier*) spend more time at the surface, where they are likely to encounter green sea turtle (*Chelonia mydas*) carcasses (Hammerschlag *et al.* 2016). The effects of using non-prey resources on space use seemingly depends on the distribution and richness of resources and whether carrion is natural prey or anthropogenic food (Hidalgo-Mihart *et al.* 2004; Newsome *et al.* 2013).

Many anthropogenic food sources have consistent locations to which animals repeatedly return (Chilvers and Corkeron 2001; Bino *et al.* 2010), thereby limiting the amount of time predators spend searching for food (Beckmann and Berger 2003). Sharks and rays that have been provisioned arrive at provisioning sites sooner and return during typical feeding times whether or not provisioning has occurred (Gallagher *et al.* 2015). Carcasses of large animals provide abundant food that permits predators to spend less time in motion and searching for prey (Gese *et al.* 1996), possibly reducing energetic demands and resource needs. However, whitetip reef sharks (*Triaenodon obesus*) increased metabolic rates on days of provisioning because sharks remained active during the day, when they would normally rest (Barnett *et al.* 2016). Food available only outside of typical activity periods therefore alters diel activity patterns and energy expenditure.

Individual behavior

Boldness, exploration, and innovation likely facilitate the persistence of predators without prey. Bold and exploratory individuals are more willing to approach and explore novel environments that may provide new food resources (Breck *et al.* 2019). Innovative predators may solve novel problems to access new resources (Whitehead and Reeves 2005). However, bold behavior has negative consequences. Bold predators are more likely to cause human–wildlife conflict,

Table 1. Observed and hypothesized behavioral consequences of predators switching from live prey to non-prey resources

Foraging strategy	Sociality	Territoriality	Individual traits	Life history
Predators with prey	Group size based on needs for hunting, reproduction, and territory defense ¹ ; strong dominance hierarchies and social structures ² ; strong feeding partnerships ³	Larger territories ⁴ ; well defended	More cooperative individuals ⁵	Migration and seasonal behavior related to prey availability; reproductive strategies based on prey availability and offspring learning to hunt ⁶
Predators without prey	Larger groups when food is predictable and available ⁷ ; break down of social hierarchies ² ; reduced social bonds ³	Smaller territories ⁸ ; break down of territorial boundaries at concentrated food sources ⁹	Bolder and more innovative ¹⁰ ; individuals display domestic-like traits ¹¹	Reduced activity levels and energy demands ¹² ; shorter hibernation ¹³ ; reduced migration activity ¹⁴ ; migration based on carrion availability ⁹

Sources: ¹MacNulty *et al.* (2012); ²Tilson and Hamilton (1984); ³Díaz López and Shirai (2008); ⁴Hidalgo-Mihart *et al.* (2004); ⁵Marshall-Pescini *et al.* (2017); ⁶Bekoff *et al.* (1984); ⁷Newsome *et al.* (2013); ⁸Young *et al.* (2008); ⁹Fallows *et al.* (2013); ¹⁰Newsome *et al.* (2013); ¹¹Breck *et al.* (2019); ¹²Hare *et al.* (2012); ¹³Gese *et al.* (1996); ¹⁴Beckmann and Berger (2003); ¹⁵Cozzi *et al.* (2016).

with potentially lethal consequences (Breck *et al.* 2019). The benefits of boldness will therefore be context dependent based on availability of novel food sources and the degree of persecution by humans. Bold and innovative individuals may benefit conspecifics through social learning or sharing information at communal resting places (eg Harel *et al.* 2017). Bold individuals identify and use new food resources, while other members of the group learn to use these resources (Whitehead and Reeves 2005). Social learning has been documented in multiple carnivores when accessing non-prey resources (Young *et al.* 2019). However, dominant individuals may limit access to food by subordinate individuals.

Health and life-history traits

Bold and innovative behaviors may be influenced by gut microbiome. Changes in individual diet linked to the loss of hunting could alter gut microbiome in ways to reinforce or change certain behaviors (Cryan and O'Mahony 2011). Gut microbiome has been linked to age and social status of spotted hyenas (Heitlinger *et al.* 2017) and differs between active and hibernation seasons in Chinese alligators (*Alligator sinensis*; Tang *et al.* 2019). How these linkages shape behavior are still being explored.

Use of anthropogenic resources may alter predator and ecosystem health. Non-prey food may lack sufficient nutrients (Le Bot *et al.* 2019), and a reduced nutritional state could lead to increased risk-taking behavior by predators to access resources (Heithaus *et al.* 2007), further increasing reliance on non-prey resources (Murray *et al.* 2015). Consuming rotting food is also potentially dangerous to predators (Kane *et al.* 2017) because it increases risk of disease and exposure to pathogens with zoonotic potential. Conversely, scavenging removes carrion that could spread disease. Furthermore, because many parasites move from intermediate to definitive hosts via predation, decreased predation can reduce parasite loads in predator populations (Hegglin *et al.* 2007).

Non-prey resources also influence predator life history. Bears undergo shorter hibernation periods and alter migration in areas with abundant anthropogenic food (Beckmann and Berger 2003; Cozzi *et al.* 2016). These changes are more

frequent when large quantities of concentrated food are available.

Non-prey food also influences reproduction and offspring care. Access to landfills affects reproduction in multiple avian species (Tortosa *et al.* 2002; Steigerwald *et al.* 2015), and although direct evidence of food subsidies on mammal reproduction is limited (Beckmann and Lackey 2008), increased abundance in populations with access to anthropogenic food supports a hypothesis of enhanced reproduction (Newsome *et al.* 2015). Bekoff *et al.* (1984), in a review of carnivore diet and reproductive traits, concluded that increased food reliability leads to longer lactation periods in omnivores and longer time until independence in carnivores, possibly because of the need to train offspring to capture prey. Extending these hypotheses, non-prey foods, particularly predictable anthropogenic foods, can provide reliable food sources, thereby reducing the risks of extended lactation, and do not require honed hunting skills, which could lead to reduced time until independence.

Ecological consequences

Predator–prey dynamics and cascading effects

Predators shifting from predation of live prey to non-prey resources could reduce overall predation pressure, resulting in the release of prey species and ecosystem impacts that mirror the loss of apex predators (Ripple *et al.* 2014; Gallagher *et al.* 2015). The availability of non-prey resources affects predation rates in both marine (Fallows *et al.* 2013) and terrestrial systems (Yirga *et al.* 2012). However, abundant non-prey resources also could potentially increase predation on live prey through hyperpredation (Gallagher *et al.* 2015; Newsome *et al.* 2015). If non-prey resources are inconsistently available, predator populations may increase during times of high availability, and subsequent declines in subsidies could increase predation pressure (Yirga *et al.* 2012), akin to patterns observed via apparent competition (Grendelmeier *et al.* 2018). Increased use of anthropogenic foods could also increase niche overlap among carnivores (Manlick and Pauli 2020), resulting in increased competition,

Panel 1. Hunting behavior

Hunting typically consists of six phases: search, approach, watch, attack group, attack individual, and capture (MacNulty *et al.* 2007). In the absence of hunting, some phases remain (search) whereas others are absent (attack). Whether the loss of these phases affects carnivore ecology or behavior is unknown. One reason to expect changes in carnivore behavior is the relationships between hunting and social structure in carnivores. Individuals accept different roles during hunting and feeding; dominant individuals typically lead the hunt, while subordinates may or may not participate (MacNulty *et al.*

2012). Some species form preferred feeding partnerships, which can break down when scavenging (Díaz López and Shirai 2008). Because hunting and feeding roles are often associated with social status, social carnivores that do not hunt may exhibit different social structures. The absence of hunting also removes the most energetically demanding and dangerous phases of predation. By reducing the dangers associated with food acquisition, different individual behavioral traits, such as boldness or exploration, may be favored in the absence of hunting.

interspecific killing, and other changes to carnivore communities.

Other ecological consequences

Reduced predation of live prey could result in decreased fear effects on prey species; however, research in this area is lacking. Alternatively, non-consumptive effects could increase locally if predators aggregate at non-prey resource sites. Gerbils (*Gerbillus* spp) reduced foraging activity in areas with where red foxes (*Vulpes vulpes*) were abundant due to agricultural development (Shapira *et al.* 2008). Predators altering their space use to access alternative resources influences where and when prey are exposed to predators (Cozzi *et al.* 2016), changing consumptive and non-consumptive effects. In addition, aggregations of predators could create reservoirs of disease that spread to other species (Newsome *et al.* 2015).

Finally, predators without prey have the potential to create distinct ecotypes because the use of non-prey resources facilitates distinct behaviors and life histories within predator populations (Chilvers and Corkeron 2001; Cozzi *et al.* 2016). Chilvers and Corkeron (2001) documented trawler-foraging and non-trawler-foraging bottlenose dolphin communities with overlapping ranges and found that only three of 463 sightings consisted of individuals from both communities, suggesting minimal interactions and the potential for distinct ecotypes to emerge.

Whether predators consume carrion of natural prey or non-prey items may influence how a shift in foraging strategy affects behavior and ecology. Increased consumption of natural prey carrion would be an extension of natural behavior for most predators (Wilson and Wolkovich 2011), whereas shifting strategies to consume anthropogenic carrion or non-carrion resources may have greater effects. One aspect likely to be changed by carrion type is energetics. Natural prey carrion is sparsely distributed on the landscape, requiring extensive energy expenditure searching for carrion (Kane *et al.* 2017). Alternatively, non-prey carrion is often concentrated, requiring less energy to exploit (Young *et al.* 2008; but see Barnett *et al.* 2016). Subtle differences may also occur; for instance,

scavenging on livestock can increase exposure to pharmaceuticals (Blanco *et al.* 2017) that may affect behavior and reproduction.

■ Prevalence of scavenging versus predation

The net benefits of using non-prey food resources likely depend on both food availability and strategies used by other predators. Larger predators, including humans, may facilitate scavenging by providing a consistent supply of carrion (Whitehead and Reeves 2005). In other situations, competition and kleptoparasitism may enhance scavenging rates; for example, spotted hyenas increase large-prey scavenging when lion (*Panthera leo*) abundance increases, possibly due to an escalated prevalence of kleptoparasitism of medium-sized prey or greater availability of large carrion (Périquet *et al.* 2015). Further research on the conditions under which species shift from predation to scavenging and vice-versa would improve our understanding of these mechanisms.

■ Predators with versus without prey in the future

Predicting changes in the prevalence of non-prey foods is complex. Anthropogenic food availability increases alongside the human population (Newsome and van Eeden 2017). Yet many cities, countries, and food-transport systems are improving waste-management processes (Newsome *et al.* 2019). There is a global push to reduce food waste (Gordon *et al.* 2016), such as ongoing efforts to reduce fishery discards in marine systems (Le Bot *et al.* 2019). At a smaller scale, provisioning of wildlife for tourism is a common practice. Although there are concerns over the effects of provisioning, it is recognized that the associated revenue could enhance species conservation (Gallagher *et al.* 2015).

Multiple factors influence carrion availability for predators. Baleen whales provide the largest opportunities for marine scavengers, and interactions between the cessation of industrial whaling, long-term global declines in whale populations, and recent recovery of whales in some areas creates uncertainty around the availability of such resources (Whitehead and Reeves 2005; Laidre *et al.* 2018). In both

marine and terrestrial systems, mass mortality events (MMEs) provide large pulses of carrion (Fey *et al.* 2015). MMEs occur naturally and as a result of anthropogenic activities, with increasing frequency and magnitude (Fey *et al.* 2015). However, if MMEs lead to the decline of prey species, then availability of carcasses will also decrease and will not sustain predators over the long term (Wilson and Wolkovich 2011). Predator declines could also affect carcass availability, as dominant predators facilitate scavenging by providing consistent supplies of carrion (Périquet *et al.* 2015). Conversely, the global reduction in apex predators (Ripple *et al.* 2014) could result in increased prey populations and carcasses of prey dying from other causes (Wilson and Wolkovich 2011; Fey *et al.* 2015). Human hunters also provide carrion to scavengers, and the global increase in hunting and abundance of game species could increase hunter-provided carrion (Mateo-Tomás *et al.* 2015). While predicting how the availability of carrion will change under the presence of an apex predator is challenging, the presence of predators, including humans, likely promotes consistent carrion availability, facilitating the emergence of other predators without live prey.

In contrast, live prey availability and predation rates may increase for some predators, counteracting changes from the availability of non-prey foods. The removal of apex predators in association with the prevalence of agricultural lands and artificial water points have provided favorable conditions to some herbivores, such as white-tailed deer (*Odocoileus virginianus*; VerCauteren 2003) and kangaroos (*Macropus* spp; Letnic *et al.* 2009). In step with these shifts, mesopredators can take advantage of ungulate prey. Berger *et al.* (2020) outlined that coyote predation on pronghorn (*Antilocapra americana*) fawns is highest when gray wolf densities are low, and that predation rates by coyotes on ungulates and domestic species are influenced by the loss of alternative prey, such as rabbits and hares. This exemplifies how mesopredator release alters predator-prey dynamics, with higher predation rates by mesopredators in some cases. Nonnative prey species and trophic downgrading can also enhance prey availability (Estes *et al.* 2011; Cerri *et al.* 2017). In areas with increasing prey, predators may not shift to non-prey resources, and facultative scavengers may predate on live prey more frequently (Prugh 2005). Some predators may increase predation rates in developed areas; for example, Smith *et al.* (2015) documented a positive relationship between human housing density and kill rate by female cougars (*Puma concolor*).

For predators, reductions in non-prey food could not only lead to lower survival and altered interactions but also facilitate a return to natural conditions. The closure of dumps at Yellowstone National Park in Wyoming led to rapid dispersal, increased home-range size, and reduced reproduction and population size in grizzly bears (Craighead and Craighead 1971). Similarly, the implementation of sanitation procedures for poultry farms in Israel resulted in high mortality of urban red foxes and increased home-range sizes for surviving individuals (Bino *et al.* 2010). Newsome *et al.* (2019) observed reduced cannibalism by dingoes and increased predation of feral domestic cats (*Felis catus*) after a dumpsite was closed, indicating changes to intra- and interspecific interactions. Such closures may increase human-wildlife conflict as predators seek out other food sources (Craighead and Craighead

Figure 3. Conceptual diagram of hypothesized behaviors of predators with and without prey. Specific examples and references for hypothesized changes are presented in Table 1. Dashed lines indicate examples presented in the text and dotted lines indicate hypothesized ecological impacts of predators without prey. Modified from Newsome and van Eeden (2017). Original images are courtesy of the Integration and Application Network, University of Maryland.

1971); alternatively, the removal of attractants near human settlements may reduce overlap and conflict with humans (Wilson *et al.* 2005). In marine systems, it is hypothesized that fishery discards, such as the disposal of bycatch, support millions of birds globally, and therefore reducing discards could have population-level consequences for seabirds and other marine predators (Le Bot *et al.* 2019). These examples illustrate how foraging strategies affect diverse aspects of predator behavior. Assessing these impacts through controlled experiments and additional observational studies will improve our understanding of predators without live prey (Figure 3).

■ Conclusions and future directions

The presence of predators without live prey is a novel scenario in the Anthropocene. Predators in both marine and terrestrial environments are increasingly relying on non-prey resources. Understanding the effects of this pattern on predator behavior, fitness, sociality, and space use, prey behavior and demographics, and ecosystems will provide a more complete understanding of predator–prey relationships and ecosystem function. The pursuit of live prey likely influences predator behavior, life history, and evolution in myriad and unexpected ways. Although our synthesis speculates about these changes, research designed to address these questions is necessary. Captive facilities breeding endangered animals for reintroduction programs often use prey models as enrichment and hunter training prior to release. Expansion of such projects to evaluate behavioral changes of individuals exposed to hunting, including behavioral budgets, interactions with conspecifics, and reproductive behavior, could provide insights into the effects of hunting on predator behavior. Observations of wild carnivores are also necessary because they display a wide variety of feeding strategies even within species. Observational studies of wild carnivores with and without access to non-prey food can evaluate how hunting may influence social structure, reproduction, and territoriality. Furthermore, manipulative studies that present wild carnivores with novel objects, puzzle boxes, or unknown stimuli can evaluate behavioral traits of hunting and non-hunting predators (Breck *et al.* 2019). As human alterations to the environment continue, the prevalence of predators without live prey will likely increase, and research on the nature of these relationships will benefit predator conservation and management.

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■ References

- Abay GY, Bauer H, Gebrihiwot K, and Deckers J. 2011. Peri-urban spotted hyena (*Crocuta crocuta*) in northern Ethiopia: diet, economic impact, and abundance. *Eur J Wildlife Res* **57**: 759–65.
- Barnett A, Payne NL, Semmens JM, and Fitzpatrick R. 2016. Ecotourism increases the field metabolic rate of whitetip reef sharks. *Biol Conserv* **199**: 132–36.
- Barrett-Lennard LG, Matkin CO, Durban JW, *et al.* 2011. Predation on gray whales and prolonged feeding on submerged carcasses by transient killer whales at Unimak Island, Alaska. *Mar Ecol-Prog Ser* **421**: 229–41.
- Beckmann JP and Berger J. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *J Zool* **261**: 207–12.
- Beckmann JP and Lackey CW. 2008. Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. *Human-Wildlife Conflicts* **2**: 168–74.
- Bekoff M, Daniels TJ, and Gittleman JL. 1984. Life history patterns and the comparative social ecology of carnivores. *Annu Rev Ecol Syst* **15**: 191–232.
- Berger J, Wangchuk T, Briceno C, *et al.* 2020. Disassembled food webs and messy projections: modern ungulate communities in the face of unabating human population growth. *Front Ecol Evol* **8**: 1–23.
- Bino G, Dolev A, Yosha D, *et al.* 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *J Appl Ecol* **47**: 1262–71.
- Blanco G, Junza A, and Barrón D. 2017. Occurrence of veterinary pharmaceuticals in golden eagle nestlings: unnoticed scavenging on livestock carcasses and other potential exposure routes. *Sci Total Environ* **586**: 355–61.
- Bowen WD. 1981. Variation in coyote social organization: the influence of prey size. *Can J Zool* **59**: 639–52.
- Breck SW, Poessel SA, Mahoney P, and Young JK. 2019. The intrepid urban coyote: a comparison of bold and exploratory behavior in coyotes from urban and rural environments. *Sci Rep-UK* **9**: 1–11.
- Cerri J, Ferretti M, and Bertolino S. 2017. Rabbits killing hares: an invasive mammal modifies native predator–prey dynamics. *Anim Conserv* **20**: 511–19.
- Chilvers BL and Corkeron PJ. 2001. Trawling and bottlenose dolphins' social structure. *P Roy Soc B-Biol Sci* **268**: 1901–05.
- Ciucci P, Mancinelli S, Boitani L, *et al.* 2020. Anthropogenic food subsidies hinder the ecological role of wolves: insights for conservation of apex predators in human-modified landscapes. *Global Ecol Conserv* **21**: e00841.
- Cozzi G, Chynoweth M, Kusak J, *et al.* 2016. Anthropogenic food resources foster the coexistence of distinct life history strategies: year-round sedentary and migratory brown bears. *J Zool* **300**: 142–50.
- Craighead JJ and Craighead FC. 1971. Grizzly bear–man relationships in Yellowstone National Park. *BioScience* **21**: 845–57.

- Cryan JF and O'Mahony SM. 2011. The microbiome–gut–brain axis: from bowel to behavior. *Neurogastroenterol Motil* **23**: 187–92.
- Díaz López B and Shirai JAB. 2008. Marine aquaculture and bottlenose dolphins' (*Tursiops truncatus*) social structure. *Behav Ecol Sociobiol* **62**: 887–94.
- Estes JA, Terborgh J, Brashares JS, *et al.* 2011. Trophic downgrading of planet Earth. *Science* **333**: 301–06.
- Fallows C, Gallagher AJ, and Hammerschlag N. 2013. White sharks (*Carcharodon carcharias*) scavenging on whales and its potential role in further shaping the ecology of an apex predator. *PLoS ONE* **8**: e60797.
- Fey SB, Siepielski AM, Nusslé S, *et al.* 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *P Natl Acad Sci USA* **112**: 1083–88.
- Gallagher AJ, Vianna GMS, Papastamatiou YP, *et al.* 2015. Biological effects, conservation potential, and research priorities of shark diving tourism. *Biol Conserv* **184**: 365–79.
- Gese EM, Ruff RL, and Crabtree RL. 1996. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. *Can J Zool* **74**: 769–83.
- Gilchrist JS and Otali E. 2002. The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. *Can J Zool* **80**: 1795–802.
- Gordon IJ, Altwegg R, Evans DM, *et al.* 2016. Reducing agricultural loss and food waste: how will nature fare? *Anim Conserv* **19**: 305–08.
- Grendelmeier A, Arlettaz R, and Pasinelli G. 2018. Numerical response of mammalian carnivores to rodents affects bird reproduction in temperate forests: a case of apparent competition? *Ecol Evol* **8**: 11596–608.
- Hammerschlag N, Bell I, Fitzpatrick R, *et al.* 2016. Behavioral evidence suggests facultative scavenging by a marine apex predator during a food pulse. *Behav Ecol Sociobiol* **70**: 1777–88.
- Hammerschlag N, Gallagher AJ, Wester J, *et al.* 2012. Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Funct Ecol* **26**: 567–76.
- Hare B, Wobber V, and Wrangham R. 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Anim Behav* **83**: 573–85.
- Harel R, Spiegel O, Getz WM, and Nathan R. 2017. Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. *P Roy Soc B-Biol Sci* **284**: 20162654.
- Hegglin D, Bontadina F, Contesse P, *et al.* 2007. Plasticity of predation behaviour as a putative driving force for parasite life-cycle dynamics: the case of urban foxes and *Echinococcus multilocularis* tapeworm. *Funct Ecol* **21**: 552–60.
- Heithaus MR, Frid A, Wirsing AJ, *et al.* 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *J Anim Ecol* **76**: 837–44.
- Heitlinger E, Ferreira SCM, Thierer D, *et al.* 2017. The intestinal eukaryotic and bacterial biome of spotted hyenas: the impact of social status and age on diversity and composition. *Front Cell Infect Mi* **7**: 262.
- Hidalgo-Mihart MG, Cantú-Salazar L, López-González CA, *et al.* 2004. Effect of a landfill on the home range and group size of coyotes (*Canis latrans*) in a tropical deciduous forest. *J Zool* **263**: 55–63.
- Kane A and Kendall CJ. 2017. Understanding how mammalian scavengers use information from avian scavengers: cue from above. *J Anim Ecol* **86**: 837–46.
- Kane A, Healy K, Guillerme T, *et al.* 2017. A recipe for scavenging in vertebrates – the natural history of a behaviour. *Ecography* **40**: 324–34.
- Laidre KL, Stirling I, Estes JA, *et al.* 2018. Historical and potential future importance of large whales as food for polar bears. *Front Ecol Environ* **16**: 515–24.
- Le Bot T, Lescroël A, Fort J, *et al.* 2019. Fishery discards do not compensate natural prey shortage in northern gannets from the English Channel. *Biol Conserv* **236**: 375–84.
- Letnic M, Koch F, Gordon C, *et al.* 2009. Keystone effects of an alien top-predator stem extinctions of native mammals. *P Roy Soc B-Biol Sci* **276**: 3249–56.
- Lewis TM and Lafferty DJR. 2014. Brown bears and wolves scavenge humpback whale carcass in Alaska. *Ursus* **25**: 8–13.
- MacNulty DR, Mech LD, and Smith DW. 2007. A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *J Mammal* **88**: 595–605.
- MacNulty DR, Smith DW, Mech LD, *et al.* 2012. Nonlinear effects of group size on the success of wolves hunting elk. *Behav Ecol* **23**: 75–82.
- Manlick PJ and Pauli JN. 2020. Human disturbance increases niche overlap in terrestrial carnivore communities. *P Natl Acad Sci USA* **117**: 26842–48.
- Marshall-Pescini S, Schwarz JFL, Kostelnik I, *et al.* 2017. Importance of a species' socioecology: wolves outperform dogs in a conspecific cooperation task. *P Natl Acad Sci USA* **114**: 11793–78.
- Mateo-Tomás P, Olea PP, Moleón M, *et al.* 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Divers Distrib* **21**: 913–24.
- Mourier J, Claudet J, and Planes S. 2021. Human-induced shifts in habitat use and behaviour of a marine predator: the effects of bait provisioning in the blacktip reef shark. *Anim Conserv* **24**: 230–38.
- Murray M, Edwards MA, Abercrombie B, and St Clair CC. 2015. Poor health is associated with use of anthropogenic resources in an urban carnivore. *P Roy Soc B-Biol Sci* **282**: 20150009.
- Newsome TM and van Eeden LM. 2017. The effects of food waste on wildlife and humans. *Sustainability* **9**: 1269.
- Newsome TM, Ballard GA, Dickman CR, *et al.* 2013. Home range, activity and sociality of a top predator, the dingo: a test of the resource dispersion hypothesis. *Ecography* **36**: 914–25.
- Newsome TM, Dellinger JA, Pavey CR, *et al.* 2015. The ecological effects of providing resource subsidies to predators. *Global Ecol Biogeogr* **24**: 1–11.
- Newsome TM, Howden C, and Wirsing AJ. 2019. Restriction of anthropogenic foods alters a top predator's diet and intraspecific interactions. *J Mammal* **100**: 1522–32.
- Peirce KN and Van Daele LJ. 2006. Use of garbage dump by brown bears in Dillingham, Alaska. *Ursus* **17**: 165–77.
- Péruquet S, Valeix M, Claypole J, *et al.* 2015. Spotted hyaenas switch their foraging strategy as a response to changes in intraguild interactions with lions. *J Zool* **297**: 245–54.
- Prugh LR. 2005. Coyote prey selection and community stability during a decline in food supply. *Oikos* **110**: 253–64.

- Ripple WJ, Estes JA, Beschta RL, *et al.* 2014. Status and ecological effects of the world's largest carnivores. *Science* **343**: 1241484.
- Shapira I, Sultan H, and Shanas U. 2008. Agricultural farming alters predator–prey interactions in nearby natural habitats. *Anim Conserv* **11**: 1–8.
- Smith JA, Wang Y, and Wilmers CC. 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. *P Roy Soc B-Biol Sci* **282**: 20142711.
- Steigerwald EC, Igual JM, Payo-Payo A, and Tavecchia G. 2015. Effects of decreased anthropogenic food availability on an opportunistic gull: evidence for a size-mediated response in breeding females. *Ibis* **157**: 439–48.
- Tang KY, Wang ZW, Wan QH, and Fang SG. 2019. Metagenomics reveals seasonal functional adaptation of the gut microbiome to host feeding and fasting in the Chinese alligator. *Front Microbiol* **10**: 1–17.
- Terborgh J and Estes JA (Eds). 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Washington, DC: Island Press.
- Tilson RL and Hamilton WJ. 1984. Social dominance and feeding patterns of spotted hyaenas. *Anim Behav* **32**: 715–24.
- Tortosa FS, Caballero JM, and Reyes-Lopez J. 2002. Effect of rubbish dumps on breeding success in the white stork in southern Spain. *Waterbirds* **25**: 39–43.
- VerCauteren K. 2003. The deer boom: discussions on population growth and range expansion of the white-tailed deer. In: Hisey G and Hisey K (Eds). Bowhunting records of North American white-tailed deer. Chatfield, MN: The Pope and Young Club.
- Whitehead H and Reeves R. 2005. Killer whales and whaling: the scavenging hypothesis. *Biol Lett-UK* **1**: 415–18.
- Wilson EE and Wolkovich EM. 2011. Scavenging: how carnivores and carrion structure communities. *Trends Ecol Evol* **26**: 129–35.
- Wilson SM, Madel MJ, Mattson DJ, *et al.* 2005. Natural landscape features, human-related attractants, and conflict hotspots: a spatial analysis of human–grizzly bear conflicts. *Ursus* **16**: 117–29.
- Yirga G, De longh HH, Leirs H, *et al.* 2012. Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia. *J Anim Ecol* **81**: 1052–55.
- Young JK, Glasscock SN, and Shivik JA. 2008. Does spatial structure persist despite resource and population changes? Effects of experimental manipulations on coyotes. *J Mammal* **89**: 1094–104.
- Young JK, Touzot L, and Brummer SP. 2019. Persistence and conspecific observations improve problem-solving abilities of coyotes. *PLoS ONE* **14**: e0218778.