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**RESEARCH REVIEW**

# The ecological effects of providing resource subsidies to predators

Thomas M. Newsome[1,2]*, Justin A. Dellinger[3], Chris R. Pavey[4], William J. Ripple[2], Carolyn R. Shores[3], Aaron J. Wirsing[3] and Christopher R. Dickman[1]

[1]Desert Ecology Research Group, School of Biological Sciences, University of Sydney, Sydney, NSW 2006, Australia, [2]Trophic Cascades Program, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA, [3]School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA, [4]CSIRO Land and Water Flagship, PO Box 2111, Alice Springs, NT 0871, Australia

## ABSTRACT

**Aim** Predators often have important roles in structuring ecosystems via their effects on each other and on prey populations. However, these effects may be altered in the presence of anthropogenic food resources, fuelling debate about whether the availability of such resources could alter the ecological role of predators. Here, we review the extent to which human-provided foods are utilised by terrestrial mammalian predators (> 1 kg) across the globe. We also assess whether these resources have a direct impact on the ecology and behaviour of predators and an indirect impact on other co-occurring species.

**Location** Global.

**Methods** Data were derived from searches of the published literature. To summarise the data we grouped studies based on the direct and indirect effects of resource subsidies on predators and co-occurring species. We then compared the types of predators accessing these resources by grouping species taxonomically and into the following categories: (1) domesticated species, (2) mesopredators and (3) top predators.

**Results** Human-provided foods were reported to be utilised by 36 terrestrial predator species in 34 different countries. In the presence of these resources we found that: (1) predator abundance increased, (2) the dietary preferences of predators altered to include the food subsidy, (3) life-history parameters such as survival, reproduction and sociality shifted to the benefit or detriment of the predator, and (4) predators changed their home ranges, activity and movements. In some instances, these modifications indirectly affected co-occurring species via increased predation or competition.

**Main conclusions** The availability of human-provided food to predators often results in behavioural or population-induced changes to predators and trophic cascades. We conclude that there is an urgent need to reduce the access of predators to food subsidies to minimise human–wildlife conflicts and to preserve the integrity of ecosystem functioning in human-influenced landscapes world-wide.

**Keywords**

**Carnivore, conservation, human subsidies, human-wildlife conflict, predator, trophic cascades.**

*Correspondence: Thomas M. Newsome, School of Biological Sciences, University of Sydney, NSW 2006, Australia. E-mail: tnew5216@uni.sydney.edu.au

## INTRODUCTION

Predators structure ecosystems in many parts of the world (Estes *et al.*, 2011). In terrestrial environments, they can exert strong top-down effects on sympatric carnivores and herbivores via interactions such as predation and the generation of fear (Beschta & Ripple, 2009). In many circumstances these impacts help to maintain mammalian, avian, invertebrate and herpetofauna abundance or richness (Ripple *et al.*, 2014), leading to widespread predictions that the existence of complex

top predator communities can mitigate the negative effects of mesopredators on small prey, and that top predators frequently initiate trophic cascades (Ritchie *et al.*, 2012).

A key assumption underlying such predictions is that intraguild feedback loops, in which a top predator both attacks and competes with an intermediate predator (Holt & Huxel, 2007), characterise top predator and mesopredator relationships. An important secondary assumption is that interactions within a food web are controlled primarily by dominant predators or top-down forces. However, bottom-up factors, such as food availability and habitat structure, can also influence predator interactions (Ritchie & Johnson, 2009). For example, resource abundance can temporarily allow prey populations to escape predator regulation and also decouple interactions between predators (Letnic & Dickman, 2010). The relative strength of top-down forces in food webs therefore depends in part on the efficiency with which top predators can suppress mesopredators and exploit their prey (Power, 1992).

Although many factors are likely to affect predator interactions, there is emerging recognition that in human-influenced systems food subsidies may be particularly important (Ripple *et al.*, 2013; Newsome *et al.*, 2014b). The putative influence of such subsidies results primarily from the estimated 1 billion metric tonnes of food produced each year for human consumption that are lost or wasted (The World Bank, 2014). Even in developing regions where food shortages exist, 44% of food produced is lost in production, storage and transport, while consumers also waste large quantities of edible food (The World Bank, 2014). Frequently, this waste food is dumped or discarded so that it is easily accessed by wildlife, particularly in areas where there are high human densities or relaxed environmental policies (Oro *et al.*, 2013). For example, large quantities of human food scraps are often discarded in unfenced rubbish dumps or left to rot around townships (Bino *et al.*, 2010; Newsome *et al.*, 2014a). In Africa and Asia alone, over 10 million tonnes of cattle carcasses are unused and discarded each year (Oro *et al.*, 2013). High livestock mortality rates mean that millions of carcasses are left to decompose in the open (Ripple *et al.*, 2013). Additionally, agricultural cropland has replaced approximately 70, 50 and 45% of the world's grasslands, savannas and temperate deciduous forests, respectively (Oro *et al.*, 2013), resulting in large tracts of modified landscapes where resource subsidies are available as crops. Urban settlements also continue to expand rapidly, adding to the vast expanses of modified landscapes where resource availability is regulated by human activities.

Changes in resource availability and the provision of food subsidies to predators are particularly problematic for conservation efforts because there is little knowledge about how numerically enhanced predator populations interact with populations of other species (Gompper & Vanak, 2008). For example, subsidised predators could drastically reduce prey populations if the subsidies insulate the predators from the effects of prey decline (Gompper & Vanak, 2008). It is also possible that where resource subsidies are available predator densities do not cycle with changes in the density of natural prey, in contrast to expectations derived from many predator–prey models. Indeed, if there is no numerical or functional response of predators to prey availability, hyper-predation could prevent the recovery of prey from low densities (Courchamp *et al.*, 2000) and also dampen prey cycles. Understanding the effects of resource subsidies on predators and co-occurring species is therefore a question of key conservation concern.

In this study we undertook a global review of the extent to which human-provided food resources are utilised by terrestrial mammalian predators. Further, we assessed the potential impact of these anthropogenic resources on the ecology and behaviour of predators and indirectly on other co-occurring species. To derive our results, we reviewed published field studies that describe the effects of resource subsidies on predators and assessed the strength of these effects on the predators and on co-occurring species. We then tested a series of predictions. First, we predicted that access of predators to human-provided foods would directly result in: (1) increased predator abundance, (2) altered predator diets, (3) increased survival, reproduction and altered social behaviour(s) of predators, and (4) shifts in predator home-range size and activity. Second, we predicted that human-provided food resources would indirectly result in: (1) increased competition between co-occurring predators owing to the increased frequency of encounters, and (2) increased density effects (predation pressure) on prey. We use the results to clarify the extent to which three different predator groups (top predators, mesopredators and domestic species) utilise resource subsidies and whether access by predators to resource subsidies has the potential to alter trophic cascades.

## METHODS

### Global review of field studies on resource subsidies and predators

We searched four databases of published literature using relevant search terms with no restrictions applied on year or language (Table 1). Broad search terms such as 'human' were used because very few returns were found when using more specific terms such as 'anthropogenic' (Table 1). Our searches were based on topic areas, and were inclusive of information in abstracts, full text and titles. To provide focus, we considered only terrestrial mammalian predators with a body size greater than 1 kg. Returns were included if studies directly assessed the impacts of human-provided food resources on predators. We also included studies that compared predator ecology and behaviour in urban versus rural settings. Where large numbers of returns were obtained from broad search term combinations, we sorted the results by relevance, an automated feature of each search engine, and checked the first 100 returns. We also cross-checked the reference lists of all relevant papers found during the initial search. Any additional papers found in the reference lists were included in our review.

### Summarising the results

To summarise the data we grouped each study based on the following direct effects on predators: (1) altered abundance, (2)

**Table 1** Search terms used to identify studies on the effects of human-provided food subsidies on terrestrial mammalian predators with a body size of more than 1 kg. Returns were sorted by relevance and the first 100 returns for each search were inspected for each search term combination.

| Database | Search terms | Returns inspected per database |
|---|---|---|
| BIOSIS Previews; Google Scholar; JSTOR; Web of Science | Human AND subsidy AND predator | 30; 100; 100; 36 |
| BIOSIS Previews; Google Scholar; JSTOR; Web of Science | Human AND subsidy AND carnivore | 17; 100; 73; 10 |
| BIOSIS Previews; Google Scholar; JSTOR; Web of Science | Human AND predator AND home range OR diet OR space use OR abundance OR resource selection OR breeding OR recruitment | 658; 700; 700; 663 |
| BIOSIS Previews; Google Scholar; JSTOR; Web of Science | Predator AND carcass OR carrion OR artificial food OR crop OR township OR village OR refuse OR waste OR rubbish OR livestock | 795; 1000; 1000; 758 |
| Total returns inspected | | 6740 |

altered diet, (3) altered life history (e.g. survival and reproduction) and social behaviour (e.g. group size and territoriality), (4) altered use of space (e.g. activity and home range size), (5) multiple impacts, and (6) no impacts. Where possible, we estimated the effect size of the resource subsidy based on the degree of change or percentage use of a predator's resources; for example, 20% of the diet contained human-provided foods. We also grouped the resource subsidies into six main categories: (1) carrion and carcass dumps, (2) artificial food supplementation (e.g. where predators opportunistically use food that humans have provided for other conservation purposes), (3) crops, (4) townships/villages (i.e. where food was available), (5) waste foods (e.g. at rubbish dumps), and (6) domestic animals/livestock (i.e. eaten after predation). We then compared the types of predators accessing these resource subsidies by grouping species taxonomically at the family level and into the following three categories: (1) domesticated species, (2) mesopredators, and (3) top predators. Here, we consider domesticated species as those that have been purposefully changed by genetic selection by humans. We consider mesopredators to be species that suffer from top-down effects, whereas top predators are species that suffer little from top-down effects upon reaching maturity.

To assess the broader ecological effects of providing resource subsidies to predators we searched for evidence of indirect effects on co-occurring species within each published study. Where evidence existed, we grouped the effects into three categories: (1) prey switching, (2) increased predation, and (3) competition (including the direct and indirect effects of interspecific competitive killing, i.e. no consumption of the kill, or intraguild predation, i.e. consumption of the kill). In papers where authors only mentioned the possible indirect effects we state this in our summary. For all comparisons, both direct and indirect, we summed the data according to the number of species that were assessed in each study and the types of resource subsidies present (because some studies had multiple predators and/or multiple resource subsidies present).
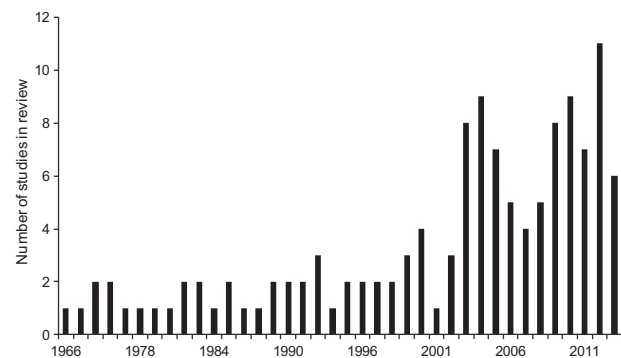


**Figure 1** Number of studies published from 1965–2013 on the direct and indirect impacts of human-provided food subsidies on terrestrial mammalian predators with a body size of over 1 kg.

## RESULTS

### Review of field studies on resource subsidies and predators

We inspected a total of 6740 returns during the literature search (Table 1). After examining the returns and cross-referencing, 129 individual papers were considered relevant and, of these, all but one study found evidence of a direct effect of a resource subsidy on a predator (see Appendix S1 in Supporting Information). The papers we reviewed were considered to be separate, despite some papers coming from the same authors or study locations, because they exposed different effects of human-provided food resources on predators. Seventy per cent of the studies were published after 2000, indicating that access of predators to human-provided food resources is an emerging research topic across the globe (Fig. 1).

The review included 36 different predator species from 34 countries across all continents (Fig. 2). The most prominently featured predators were grey wolves (*Canis lupus*) ($n = 17$), dingoes (*Canis dingo*) ($n = 16$), coyotes (*Canis latrans*) ($n = 14$), red foxes (*Vulpes vulpes*) ($n = 13$), golden jackals (*Canis aureus*)
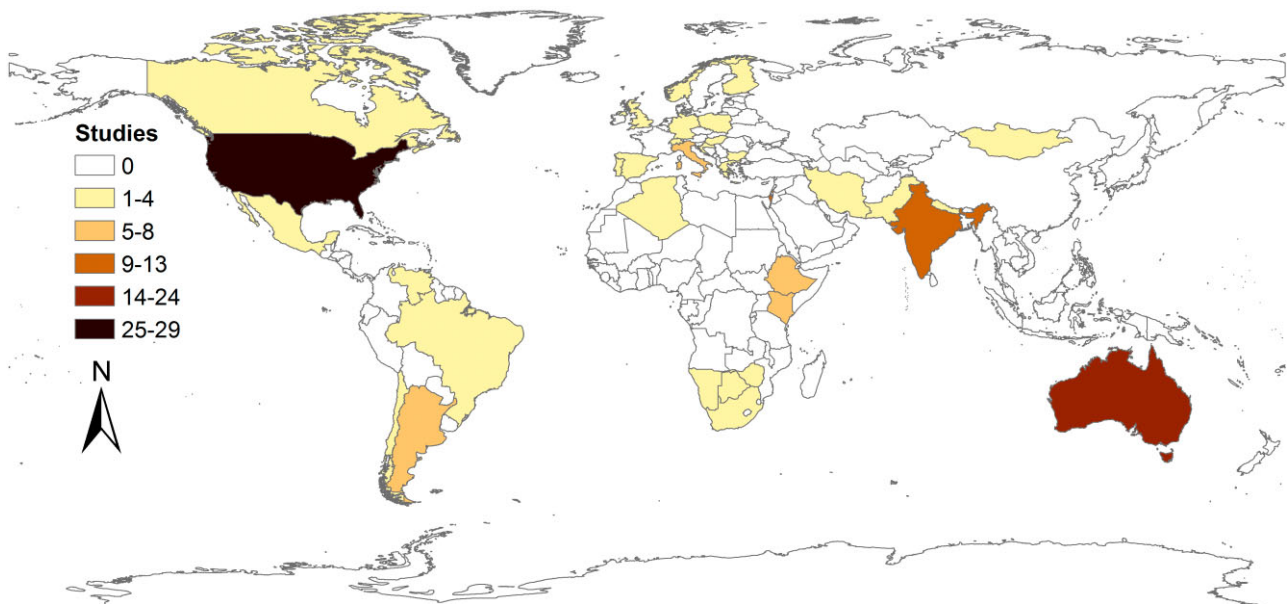
**Figure 2** Geographic distribution and number of studies included in this review on the ecological effects of human-provided food subsidies on terrestrial mammalian predators with a body size of over 1 kg. Note that studies with multiple predators present were summed accordingly.

($n = 10$) and domestic dogs (*Canis familiaris*) ($n = 9$). Over 50% of the studies came from four countries: the United States ($n = 29$), Australia ($n = 24$), India ($n = 13$) and Israel ($n = 9$) (Fig. 2).

Based on family groups, canids featured in the most studies ($n = 94$), followed by felids ($n = 37$) and then ursids ($n = 13$). Top predators featured in 57% of studies, followed by mesopredators (34%) and then domestic animals (9%). The most common resource subsidy exploited was livestock (42% of studies) followed by waste foods (27%) and then carrion/carcasses (21%). Top predators (mostly canids and felids) dominated the use of livestock ($n = 57$), whereas mesopredators (mostly canids) dominated the use of carrion/carcasses ($n = 20$) (Fig. 3). The most prevalent predator group in all studies and subsidies was the family Canidae (17 species) (Fig. 3).

**Direct effects of resource subsidies on predators – abundance**

Of the studies that assessed predator abundance ($n = 23$), all reported an increase in abundance of the study species in the presence of a human-provided food resource (Appendix S1). Most compelling was the work of Fedriani *et al.* (2001), who compared coyote density across a gradient of anthropogenic food availability; in the most developed area, where use of human-provided food by coyotes was greatest, there was an eight-fold increase in coyote density. Similarly large increases were found by Denny *et al.* (2002) and Shapira *et al.* (2008), who reported seven-fold increases in cat (*Felis catus*) and red fox

abundances, respectively. However, effect sizes for abundance were reported in only five studies, and may have been noted largely because they represented extreme results (Appendix S1). Increases in abundance were also most prevalent when predators accessed waste foods (Fig. 4).

**Direct effects of resource subsidies on predators – diet**

Of the studies that assessed patterns of consumption ($n = 107$), all reported that predators included human-provided food resources in their diet to varying degrees (Appendix S1). Some studies reported only minor use of resource subsidies, but most described 10–50% of the predator's diet as being supplemented (Fig. 5a). Of the studies that reported > 90% utilisation of a resource subsidy (Macdonald, 1979; Vos, 2000; Abay *et al.*, 2011; Yirga *et al.*, 2012), all were in peri-urban or agricultural systems where the most readily available prey was the resource subsidy itself (Appendix S1). However, despite livestock being most heavily utilised by top predators and secondly by mesopredators (Fig. 4), when use was quantified, livestock featured least in the diets of these predators in comparison with carcasses and waste foods (Fig. 5a). Moreover, separation of the dietary data by family groups suggests that while the occurrence of livestock in the diet of canids and felids was similar, the occurrence of carcasses and waste foods was higher in the diet of canids in comparison with felids (Fig. 5b). Carcasses and waste foods also featured relatively highly in the diet of ursids, whereas the occurrence of the four main subsidies in the diet of domestic species was similar across the groups (Fig. 5b).
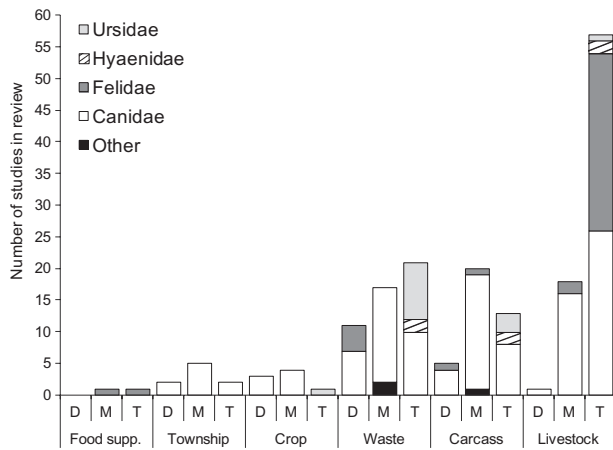
**Figure 3** The types of human-provided food subsidies accessed by terrestrial mammalian predators with a body size of over 1 kg, grouped by family taxonomic level and predator type. Key: Food supp., artificial food supplementation programmes; D, domestic species; M, mesopredator; T, top predator. Domestic species (D) include house cat (*Felis catus*) and dog (*Canis familiaris*). Mesopredators (M) include African wild dog (*Lycaon pictus*), yellow baboon (*Papio cynocephalus*), black-backed jackal (*Canis mesomelas*), bobcat (*Lynx rufus*), chilla fox (*Pseudolopex griseus*), coyote (*Canis latrans*), culpeo fox (*Pseudolopex culpaeus*), dhole (*Cuon alpinus*), common genet (*Genetta genetta*), Geoffroy's cat (*Oncifelis geoffroyii*), golden jackal (*Canis aureus*), Indian fox (*Vulpes bengalensis*), pampas fox (*Pseudolopex gymnocercus*), red fox (*Vulpes vulpes*) and San Joaquin kit fox (*Vulpes macrotis mutica*). Top predators (T) include Arabian wolf (*Canis lupus arabs*), black bear (*Ursus americanus*), brown bear (*Ursus arctos*), cheetah (*Acinonyx jubatus*), dingo (*Canis dingo*), Ethiopian wolf (*Canis simensis*), Eurasian lynx (*Lynx lynx*), grey wolf (*Canis lupus*), Mexican grey wolf (*C.l. baileyi*), Iberian lynx (*Lynx pardinus*), Iberian wolf (*C.l. signatus*), jaguar (*Panthera onca*), leopard (*Panthera pardus*), lion (*Panthera leo*), polar bear (*Ursus maritimus*), puma (*Puma concolor*), snow leopard (*Panthera uncia*), spotted hyena (*Crocuta crocuta*) and tiger (*Panthera tigris*). Note that studies with multiple predators and resource subsidies present were summed accordingly.

### Direct effects of resource subsidies on predators – life history and sociality

Of the studies that assessed the effects of human-provided food resources on life history and sociality ($n = 15$), there were documented changes to fecundity (Beckmann & Lackey, 2008) and territoriality (Newsome *et al.*, 2013a,b), including increased tolerance of conspecifics (Herrero, 1983) and increased group size (Hidalgo-Mihart *et al.*, 2004; Newsome *et al.*, 2013a). There were also documented increases in weight gain (Rogers *et al.*, 1976; Lunn & Stirling, 1985) and survival (Bino *et al.*, 2010) as well as genetic drift and genetic differentiation between rural and urban populations (Wandeler *et al.*, 2003). However, there were also negative effects on predators' life histories when

mortality rates increased due to human–wildlife conflicts (Beckmann & Lackey, 2008) (Appendix S1).

### Direct effects of resource subsidies on predators – space use

Of the studies that assessed the effects of human-provided food resources on the use of space ($n = 39$), there was overwhelming evidence that predators altered their activity and home-range size in response to the subsidy. Of the studies that reported an effect size ($n = 14$), daily activity decreased by up to 36%; one study reported 40% less time spent in feeding and 40% more time spent in resting (Altman & Muruthi, 1988). Home-range size also decreased consistently in the presence of a resource subsidy, and some species doubled their home-range size when resource subsidies were reduced (Bino *et al.*, 2010). However, in some cases, core areas within home ranges contracted most, as opposed to the overall home-range areas (Kolowski & Holekamp, 2007). Support for predator occurrence being influenced by humans was also noted by Randa & Yunger (2006), who found that coyotes were twice as likely to occur in rural than in urban areas. Yet even when predators used a resource subsidy, they often avoided it in the presence of humans (Ciucci *et al.*, 1997; Boydston *et al.*, 2003; Ashenafi *et al.*, 2005; Randa & Yunger, 2006; Gehrt *et al.*, 2009; Valeix *et al.*, 2012) or in disturbed habitats (Atwood *et al.*, 2004).

### Indirect effects of resource subsidies on co-occurring species

Indirect effects were reported or noted 26 times (Fig. 4). The consequences included increased competition between co-occurring predators ($n = 11$), increased predation pressure on native or primary prey ($n = 10$) and prey switching ($n = 5$). Increased predation pressure was linked to lower abundances of prey (Shapira *et al.*, 2008) and altered top-down effects (Wilmers *et al.*, 2003). Increased competition led to constraints on the space use of co-occurring predators (Silva-Rodríguez *et al.*, 2010), outcompeting of other scavengers (Butler & du Toit, 2002) and changes to the distribution of endangered prey (Silva-Rodríguez & Sieving, 2012). The only study that provided evidence against increased competition between co-occurring predators was that by Atickem *et al.* (2010), who found no significant competition between domestic dogs that had access to human-provided resources and the Ethiopian wolf (*Canis simensis*), but in this case the primary diets of the two species did not overlap (Appendix S1). Prey switching was demonstrated in five studies. Among these, Dahle *et al.* (1998) showed that brown bears (*Ursus arctos*) decreased their use of ants, forbs and berries when sheep carcasses were available. Newsome *et al.* (2014b) demonstrated that dingoes selected small mammals over reptiles when waste foods were available, while Yirga *et al.* (2012) demonstrated that spotted hyenas (*Crocuta crocuta*) increased predation on donkeys when waste foods were unavailable.
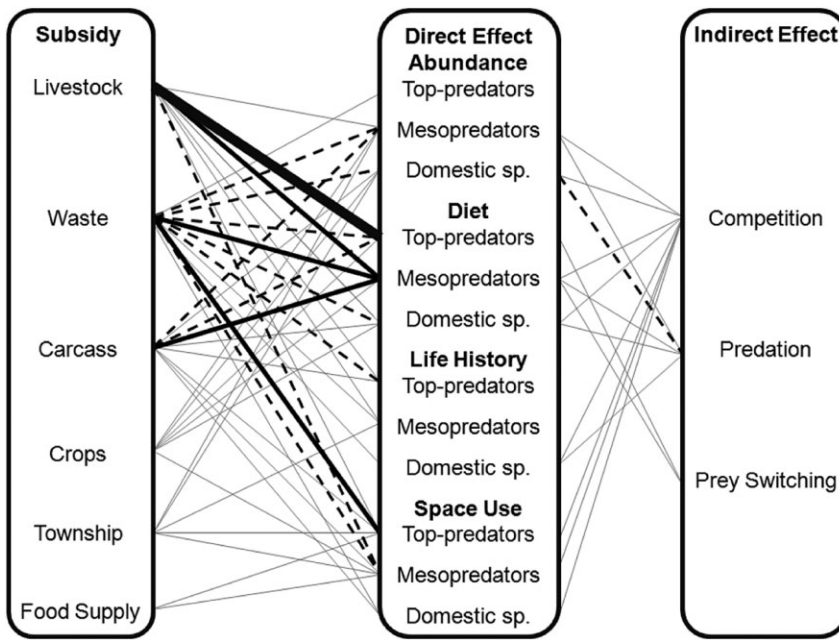
Figure 4 The direct and indirect effects of human-provided food subsidies on terrestrial mammalian predators with a body size of over 1 kg. The type of line reflects the number of published studies (smallest line, < 5 studies; dashed line, 5–10 studies; mid-sized line, > 10 studies; largest line, > 20 studies). Note that studies with multiple predators and resource subsidies present were summed accordingly.

## DISCUSSION

There is growing recognition that human-provided food resources are becoming increasingly available to animals across the globe (Oro *et al.*, 2013). There is also concern that predator interactions are altered in human-influenced systems (Fleming *et al.*, 2012; Newsome *et al.*, 2014b). This work is the first to review the direct and indirect effects of resource subsidies on a large suite of terrestrial predators, and shows that these subsidies are used extensively by all species studied (Fig. 3). Our review of 129 papers therefore provides compelling support for our initial predictions that human-provided food resources would alter the ecology and behaviour of terrestrial mammalian predators with a body size of more than 1 kg. Below, we discuss some of the major direct and indirect effects of resource subsidies and provide a synthetic framework to help guide future research.

We found that top predators primarily utilised livestock, whereas mesopredators took livestock, carcasses and waste foods in equal proportions (Fig. 3). The differential uses of these resource subsidies may reflect predator size and hunting strategies. For example, to meet their high energetic demands (Ripple *et al.*, 2014), large mammalian predators are more likely to consume larger prey (Owen-Smith & Mills, 2008) such as livestock. On the other hand, the equal use of livestock, carcasses and waste foods by mesopredators probably reflects their diverse behaviour and ecology (Roemer *et al.*, 2009) and less restricted diet (Prugh *et al.*, 2009) (Fig. 5a). An additional, related, finding is that felids rarely utilised carcasses or waste foods (Fig. 5b), possibly reflecting their preference for live prey (although further field testing is required to quantify this trend). In contrast, ursids rarely took livestock, but crops, waste foods and carcasses featured highly in their diet (Fig. 5b), suggesting that there are different consumption patterns by the predator groups
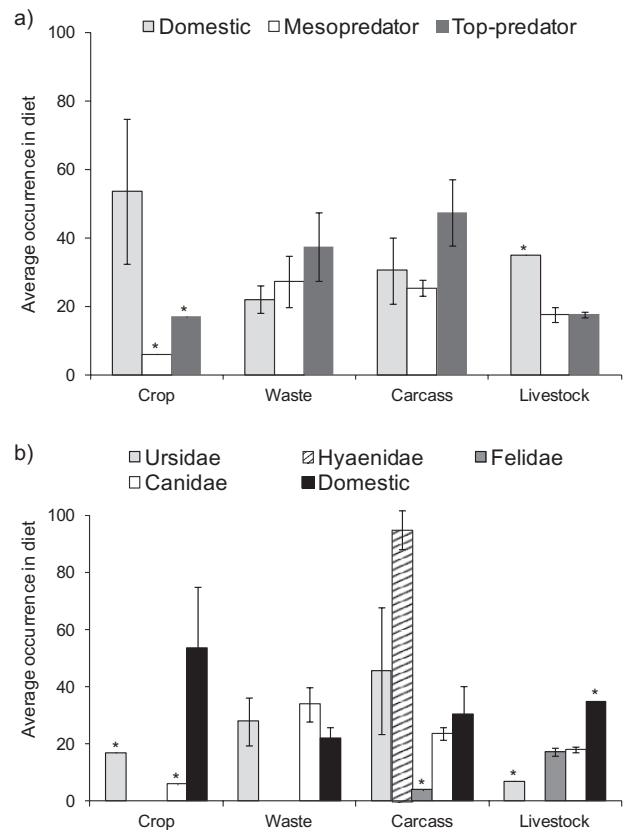


Figure 5 Average occurrence of human-resource subsidies in the diet of a) predator groups and b) family groups, based on data from 83 published studies (± 95% confidence intervals). Frequency of occurrence values were used wherever possible (80% of studies). The asterisk (*) indicates that only one study was available. In b) data from the family Viverridae were excluded because there was only one study available.

assessed in our review. In particular, there was little evidence that the domestic species favoured any particular resource subsidy, whereas there were contrasting differences between the occurrence of different subsidies in the diets of ursids, felids and canids (Fig. 5b). Therefore, the ecological effects of providing resource subsidies to predators may differ depending on the type of resource subsidy and the species present.

We recorded the largest number of effect sizes from dietary studies, providing insight into the extent to which human-provided resources are utilised by the different predator groups. In particular, carcasses and waste foods made up 47 and 37% of the diets of top predators, respectively, with similarly high percentages reported for mesopredators and domestic species (Fig. 5a). There were even extreme cases where human-provided foods made up over 70% of some predators' diets (Appendix S1). However, despite the many studies demonstrating that top predators frequently use livestock, this food source comprised only 17% of their diet on average (Fig. 5a), and there was no significant difference between the occurrence of livestock in the diets of felids and canids (Fig. 5b). These findings are novel and surprising given that livestock is arguably the most widespread resource subsidy available to predators across the globe. It may reflect the high risks associated with taking livestock, such as persecution by humans, with many studies in our review indicating that even when predators use livestock they alter their behaviour to avoid humans. For example, African lions (*Panthera leo*) avoid temporal overlap with humans around cattle-posts, and often travel at high speeds to reduce the time spent in these areas (Valeix *et al.*, 2012). Ethiopian wolves similarly avoid humans in agricultural landscapes and are more active when humans are in close proximity (Ashenafi *et al.*, 2005). Thus, predators may balance the benefits of accessing resource subsidies with the risks associated with coming into contact with people.

Where human-provided foods are readily available, the ecological effects on predators extend well beyond dietary preferences to alter life-history traits and population dynamics. In 17 instances predator abundance increased when animals accessed waste foods. Changes to life history, sociality and space use also were commonly associated with waste foods (Fig. 4). For example, black bears (*Ursus americanus*) experienced higher age-specific fecundity and mortality in urban areas, where they foraged on rubbish, in comparison with wildland populations (Beckmann & Lackey, 2008). They could also exploit highly predictable waste foods by forming social aggregations and tolerating other bears around rubbish dumps (Herrero, 1983). Similar increases in group size or tolerance of conspecifics around rubbish dumps occurred in populations of dingoes (Newsome *et al.*, 2013a), coyotes (Hidalgo-Mihart *et al.*, 2004) and red foxes (Bino *et al.*, 2010), providing compelling evidence that predators alter their behaviours to exploit resource-rich human-provided patches of food. Moreover, in 19 instances predators, including wolves, dingoes, domestic dogs, golden jackals, red foxes, baboons (*Papio cynocephalus*), spotted hyenas, black bears and polar bears (*Ursus maritimus*), altered their home-range size or activity

when they had access to waste foods provided by humans (Appendix S1). Greater recognition of the dispersion and abundance of human-provided foods is therefore required when assessing the impacts of subsidies on predator ecology and behaviour.

In addition to resource subsidies effecting direct changes in predator ecology, our review identified that predator access to human-provided foods can indirectly affect co-occurring species. Indirect effects were noted or quantified 26 times (Fig. 4), with the most commonly reported consequences being increased competition between co-occurring predators and increased predation pressure on prey. For example, Silva-Rodríguez & Sieving (2012) showed that free-roaming domestic dogs in South America, subsidised by humans, are efficient at chasing pudu (*Pudu puda*), a threatened forest ungulate, and that both predation and non-lethal avoidance of dogs shape the distribution of pudu. An influx of free-roaming dogs in human-dominated landscapes in Israel was also the major factor causing decreased recruitment of mountain gazelle (*Gazella gazella gazella*) (Manor & Saltz, 2004). We also found evidence for subsidy-driven prey-switching behaviours (Fig. 4). Most notable was the study by Yirga *et al.* (2012), who demonstrated that spotted hyenas increase predation on donkeys when the availability of urban and rural waste declines during Christian fasting periods.

Taken together, the food web interactions that we have documented lead to the possibility that trophic cascades will alter when predators access human-provided foods. Such a possibility has been raised under circumstances where human harvesting of top predators hinders predators' ability to perform functional ecological roles (Ordiz *et al.*, 2013). Human activity can also alter trophic cascades when predators use human presence as a refuge from predation (Shannon *et al.*, 2014). Here we propose that this possibility be extended to circumstances where top predators focus on human-provided foods, rather than on co-occurring predators and prey, and even more so where human–wildlife conflict leads to high rates of mortality of top predators. Further, mesopredators and domestic species were frequently numerically enhanced because they accessed resource subsidies (Fig. 4). These responses raise the possibility of increased predation on live prey, particularly when food subsidies decline (Yirga *et al.*, 2012) or if there is a depleted prey base and hyper-predation occurs (Courchamp *et al.*, 2000). On the other hand, decreased use of natural foods could be expected when human resource subsidies are available (Dahle *et al.*, 1998), pointing to complex interplays of interactions where the abundance and dispersion of human-provided resources determines food web relationships (Figs 4 & 6).

In addition to altered trophic cascades, access of predators to resource subsidies has the potential to lead to long-term population-level changes in disease transmission (Fig. 6). For example, canids are a major vector for rabies and other infectious diseases that can have significant effects on broader ecological communities and increase human–wildlife conflicts, and they featured in 62% of the studies in our review.
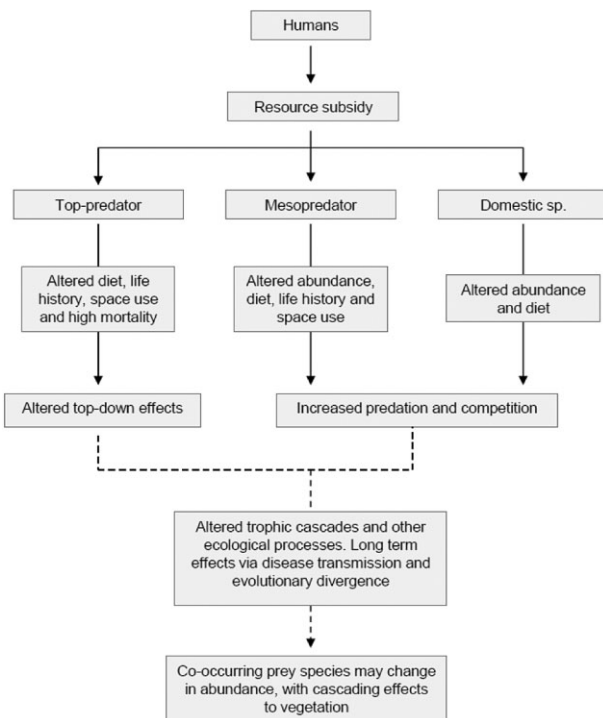
**Figure 6** Conceptual framework depicting behavioural and population-induced changes to trophic cascades when predators access human-provided resource subsidies. Solid lines are direct effects and dotted lines are indirect effects. Subsidies result in changes to space-use, life-history parameters, diet and density of predators. These responses may indirectly affect co-occurring predators and prey.

Increases in the abundance of domestic dogs could therefore create disease reservoirs (Cross *et al.*, 2009) that threaten at-risk species such as African wild dogs (*Lycaon pictus*) and Ethiopian wolves (Alexander & Appel, 1994; Woodroffe *et al.*, 2004; Randall *et al.*, 2006). Resource subsidies may also elicit long-term changes to species' evolutionary trajectories. Under natural conditions genetic differentiation is driven by diet, social structure (Musiani *et al.*, 2007) and selective pressures to disperse into areas where resource bases closely match natal home range areas (Sacks *et al.*, 2005; Carmichael *et al.*, 2007). If predators access human-provided foods, these processes may change such that human-influenced predator populations diverge from those subsisting on more natural foods (Denny *et al.*, 2002; Wandeler *et al.*, 2003). For example, after red foxes colonised the city of Zurich, Switzerland, the population diverged from those in rural areas (Wandeler *et al.*, 2003).

The likelihood that predators alter their behaviour and ecology to access human-provided foods may be influenced by several factors. First, if natural prey is depleted then predators may be more likely to consume human-provided foods. Second, if human-provided foods are easily accessible, and abundant, predators may readily exploit them because they represent an energetically optimal food source. However, in both instances,

accessibility is influenced by the way in which humans manage their waste. In Australia and the United States approximately 3–4 million tonnes of edible food waste is discarded in rubbish dumps annually (Oro *et al.*, 2013). In developing countries, where high human population densities are coupled with relaxed environmental policies (Oro *et al.*, 2013), the opportunities for predators to consume human-provided foods may be higher. Yet the findings documented in our review include many studies conducted in developed regions (Fig. 2) where there are relatively progressive environmental policies. By implication, even technologically advanced countries are addressing inadequately the problems associated with access of predators to resource subsidies.

Assuming that there is an imperative to conserve complex predator communities and maintain natural ecosystem processes (Ripple *et al.*, 2014), our study suggests a need for greater recognition of how human-provided foods shape and drive ecosystem processes. Here we have shown that human-provided foods can alter predator ecology and behaviour, with further effects on co-occurring species. However, there are still many knowledge gaps, due in part to the recent emergence of this topic in the literature (Fig. 1), making detailed insights difficult. For example, relatively few studies in our review assessed the indirect effects of resource subsidies on co-occurring species and some of the effects we identified are based on anecdotal accounts rather than quantitative assessments. Therefore there is broad scope for expanding our synthesis if more detailed studies are conducted on the consumptive and non-consumptive effects of providing resource subsidies to predators. Nevertheless, it is clear that predators frequently utilise human-provided foods, and that the ecological effects appear to be mostly negative. In a world where human activities are continually expanding, it is crucial that humans change the way in which their waste and resources are managed in order to minimise the access of predators to these rich resource subsidies. A key step to achieving this goal is to reduce the amount of edible food that is lost or wasted by humans.

## ACKNOWLEDGEMENTS

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1** The direct and indirect effects of human-provided resources on terrestrial mammalian predators > 1 kg in body size.

### BIOSKETCH

**Thomas Newsome** is a post-doctoral scholar at Oregon State University and Research Fellow at The University of Sydney. Thomas' research focuses on predator ecology and trophic cascades. He is particularly interested in how humans and top predators shape and drive ecosystem processes and is currently the recipient of a Fulbright Scholarship from the Australian-American Fulbright Commission.

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