Social implications of human food subsidies on wildlife populations

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Abstract

Human activities—intentionally or not—generate a variety of novel food sources that wild animals exploit. On land and in water, human food sources can profoundly alter intraspecific interactions with cascading effects on population dynamics and ecosystem functioning. Yet, despite their growing ecological relevance, the role of human food subsidies in shaping intraspecific interactions remains underexplored. We propose a novel framework that highlights how key characteristics of human food—such as high abundance, predictability, increased proximity to humans, and dietary composition—shape social interactions. Specifically, we discuss how individual-level changes in fitness, time allocation, movement, and social choices can shape group size and composition, the quantity and quality of social interactions, as well as the social structure, with implications for social transmission (of stress, information, or diseases), selection, and development. Collectively, these alterations highlight the broad social implications that intentional and unintentional human food subsidies can have for ecological and evolutionary processes in wildlife populations.

Keywords: anthropogenic environmental change, food provisioning, human-wildlife interactions, foraging, social behaviour, social structure, wildlife feeding, intraspecific interactions, human food subsidies

Introduction

The Anthropocene is marked by rapid human-driven changes that are reshaping terrestrial and aquatic ecosystems (1–4) with profound implications for wildlife behaviour, including intraspecific interactions (5–8). Social interactions, in particular, are fundamental to animal life and form the basis of a population's social structure, shaping population dynamics (9,10). The positioning of individuals within the social structure can influence survival (11,12) and reproductive success (13,14), both of which are critical determinants of fitness. At the group and population levels, social structure influences key processes such as the transmission of diseases (15,16) and information (15), dispersal (17,18), mating systems (19,20), and the direction and intensity of selection (21,22). Hence, understanding how human-induced environmental changes impact social structure is crucial to anticipate the consequences for future population functioning and viability.

Animal social structure emerges from several factors, including the number of individuals within a given area (population size and density, (23,24)), the composition of phenotypes within the population (25,26), and, at the individual level, the extent and patterns of social interactions (i.e., who interacts with whom and how frequently, (9,27)). Increasing evidence shows that human activities—such as pollution, direct human presence, and climate change—impact these factors, with profound consequences for social interactions and the emerging population-level social structure (7,28–30). However, a so far often-overlooked human activity with considerable consequences for intraspecific interactions are human food subsidies.

Human modifications to food availability date back to the time of nomadic hunter-gatherer societies, which unintentionally provided scavenging species with food remains such as carcasses (31–33). For example, synanthropic behaviour in small carnivores such as red and Arctic foxes (*Vulpes vulpes* and *V. lagopus*) emerged as early as 42,000 years ago (33). As such, food subsidies may be one of the earliest forms of human-induced environmental change, with lasting effects on animal behaviour and ecosystems that persist until today. In the present, human-generated food sources are ubiquitous and exploited by many animal species (Box 1; Figure 1). These subsidies include all food made available through human activities (see (34)), whether intentional—such as feeding stations, religious offerings, or wildlife feeding by tourists—or unintentional, arising from agriculture (e.g., crops, livestock), food waste (e.g., landfills, trash bins, restaurants), and hunting or fishery discards (Box 1).

Importantly, human food sources differ markedly from natural food sources in various ways. Human food sources are often highly abundant, predictable in space and time, distinct in nutritional composition, and exposes animals to novel stimuli such as traffic, noise, and direct human presence in modified landscapes (34). These features can strongly influence individuals by altering fitness, movement decisions, time allocation across behaviours, and social choices (i.e., with whom and how to interact). Such individual-level changes can then cascade to shape key determinants of social structure, including population density, encounter rates, time budgets for social behaviour, and the necessity or intensity of social interactions. For example, human food subsidies can directly concentrate conspecifics through altered individual movement and time allocations or indirectly increase population size through changes in fitness (34), leading to more inter-individual encounters and denser social structures. Yet, despite recognition of the widespread ecological impacts of human food subsidies (34), the social implications of food subsidies on wildlife populations remain poorly known.

Here, we outline the diverse pathways through which human food subsidies can affect wildlife populations by altering intraspecific interactions. We begin by examining how central features of human-generated food—its abundance, predictability, proximity to humans, and dietary composition—shape individual-level traits (e.g., survival, movement), and how these changes cascade into altered social interactions and population social structures. We then discuss how these changes in social dynamics can impact population-level processes such as the transmission of diseases or the direction and intensity of selection. While human food sources also impact intraspecific interactions in invertebrates, we here focus on vertebrates. By providing a conceptual framework (Figure 2), we aim to stimulate future research and deepen our understanding of the diverse impacts of human activities on wildlife populations.

Box 1. Intentional and unintentional human food subsidies.

Humans provide a vast range of food sources to wildlife (Figure 1). For example, it is estimated that 30–40% of all food is wasted globally (34), with landfills accumulating waste at rates outpacing urbanization (35). Landfills are often highly abundant and predictable in both space and time, thus constituting a highly profitable food source that is exploited by various species, including mammals, birds, amphibians, and reptiles (36). Similarly, waste bins and food leftovers at restaurants are an attractive food source to many terrestrial animals (37). Fishery and hunting discards, as well as middens, are another globally abundant human-derived food source. Approximately 8% of caught fish is discarded (34,38) and up to 10^5 tonnes of carcasses are left in the field by game hunters in the US each year (34). Additionally, agricultural land covers about 36% of the world's land area (http://data.worldbank.org/), and provides crop and residues that can be used as a food source by wildlife (34,39).

Humans also intentionally provide food to animals for various reasons. Feeding stations for birds and game, for example, are common practices. In the UK, 50% of households with garden access provide supplementary food for birds (40), and supplemental feeding of game during winter is often used for wildlife management and hunting purposes (41). Feeding of wild animals has also become a popular tourist activity. For instance, managed tourism programs frequently provide food to dolphins and sharks to facilitate close encounters (42,43). Finally, feeding animals plays a significant role in some religious practices. In the Indian culture, people commonly feed animals across all taxa, either routinely or during festive occasions, often at sites of religious significance such as temples (44).

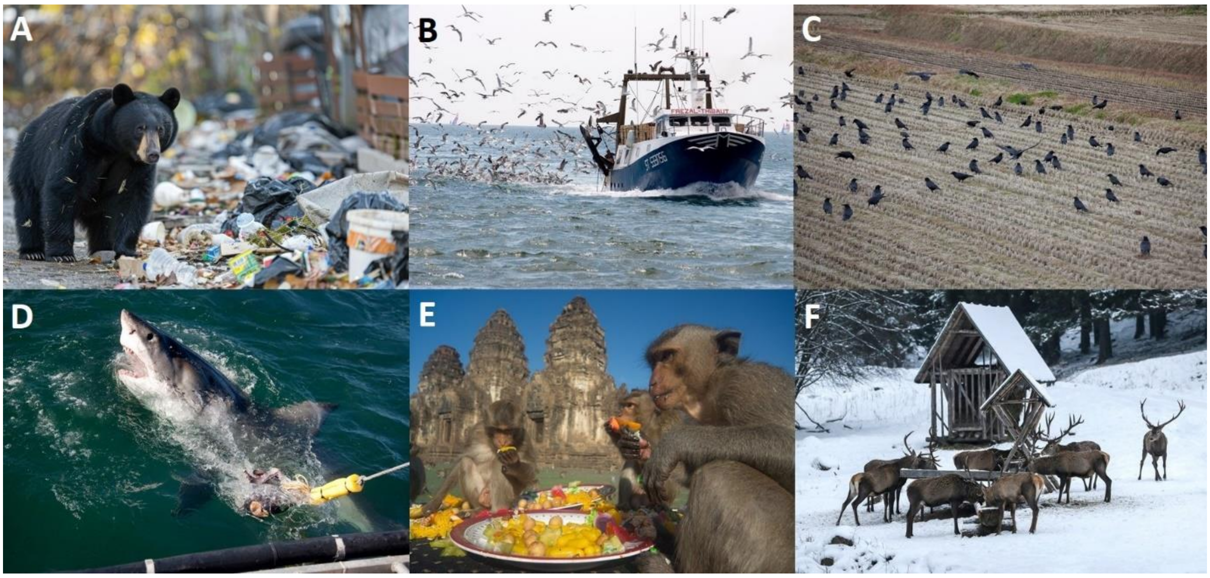

Figure 1: Examples of intentional and unintentional human food subsidies. A: Bear scavenging from waste. **B**: Seabirds following fishing trawlers to feed on discarded fish. **C**: Crows foraging in a crop field. **D**: Shark attracted with meat during cage-diving. **E**: Macaques consuming food offerings at a temple. **F**: Supplemental feeding of deer during winter. Photo credits [start top left, clockwise: Serhii/Adobe Stock, Simon Ebel/Adobe Stock, Paylessimages/Adobe Stock, Conchi Martinez/Adobe Stock, topten22photo/Adobe Stock, Michal/Adobe Stock].

Social implications of human food subsidies

Survival and reproduction

Fitness is fundamentally shaped by access to food resources, which sustain daily survival and provide the energy necessary for raising offspring. The high abundance and predictability of human food subsidies can significantly alter individual fitness (34). Supplemental food has been shown to positively affect survival during food shortages (45,46) and increase reproductive success (47–49). However, supplemental feeding can also have no or negative effects on survival and reproduction if the supplemental food is of poorer quality than natural food (50), if immunity is compromised (51), or if disease transmission is facilitated (52). Alterations in individual fitness have consequences for the current and future population size and density – a key component for many social dynamics (Figure 2). For example, higher population densities can increase group size (53–55) and social encounter rates (56) while also influencing various measures of social structure such as network centrality, fragmentation, the density of social connections, and the strength of social relationships (57,58,23).

Moreover, by altering individual fitness, human food subsidies can modify both the phenotypic and demographic composition of populations. For example, human food can influence survival and reproduction in distinct ways. In winter, adult tit species (*Paridae*) generally have higher survival than yearlings, likely due to greater foraging experience and dominance (59). Increased adult survival through human-provided food would result in an older age structure, maintaining more experienced individuals within the population. In contrast, human food subsidies can also enhance reproductive success and juvenile survival, thereby offsetting natural mortality biases and shifting population age structure toward younger individuals (59). Younger animals often maintain more and broader social connections compared to older, more selective conspecifics (60). Therefore, the demographic consequences of human food subsidies—whether promoting adult survival or juvenile recruitment—can differentially shape social networks, potentially leading to either more stable, age-structured systems or denser, highly interconnected social structures.

In addition, individuals often differ in their use of human food sources, which can further impact the phenotypic composition of groups and populations. For example, sex- and age-biased foraging is increasingly reported. In primates, males are more frequently associating with humans and the food provided (e.g., chimpanzees *Pan troglodytes* (61), moor macaques *Macaca maura* (62), Cape Chacma Baboons *Papio ursinus* (63)); and younger individuals tend to use human food subsidies more often in bearded vultures *Gypaetus barbatus* (64), while older individuals do so in white storks *Ciconia ciconia* (65). Such non-random use of human food by particular phenotypes can shape the future composition of populations as well as current social dynamics. For example, individuals with similar responses to human subsidies may encounter and interact more frequently, leading to the formation of phenotypically structured groups. Social community membership in toothed whales (e.g., orcas *Orcinus orca*, sperm whales *Physeter macrocephalus*, bottlenose dolphins *Tursiops* spp.) is commonly linked to foraging responses (e.g., depredation, scavenging, cooperation, and begging) to a diverse range of fishing activities (e.g., long-lining, trawling, net-casting, recreational fishing; (66). Individuals that forage in association with humans are then more likely to associate with one another (67) and are part of the same social community (68,69), whereas the removal of the human food source (e.g., prawn trawler discards) reverses changes in (dolphin) community membership (70).

Time allocation

Successfully surviving and reproducing in human-modified landscapes requires individuals to efficiently allocate their time across daily activities. As such, individuals need to balance time spent forming and maintaining social relationships with other activities, such as foraging (71,72). The high abundance and predictability of human food subsidies can ease this trade-off by reducing the energetic and temporal costs of foraging (73), thereby allowing individuals to allocate more time to other behaviours—such as social interactions (Figure 2). For instance, food-supplemented vervet monkeys (*Chlorocebus pygerythrus*) showed increased time spent resting and socializing, as well as more frequent grooming of conspecifics, compared to periods before or after supplementation (74). Similarly, individual Trinidadian guppies (*Poecilia reticulata*) exposed to a highly predictable food source spent more time associating with conspecifics (75). Moreover, the presence of humans close to food subsidies can serve as 'shields' against competitors and predators ('human shield effect'; (76)) allowing animals to allocate more time to other behaviours (77). Highly urbanized fox squirrels (*Sciurus niger*), for instance, exhibit reduced vigilance and diminished responses to predator vocalization compared to less urbanized squirrels (78), potentially freeing up time to increased engagement in other activities. Similarly, in Scandinavian brown bears (*Ursus arctos*), females with prolonged maternal care are found to utilize habitats in closer proximity to human settlements, while males occupy more distant areas. This suggests that the females' use of human-adjacent habitats during the mating season is a tactic to mitigate adverse interactions with males that could result in the premature weaning of offspring (79).

Human food subsidies can also increase time constraints, particularly if humans are perceived as threats or when accessing human-derived food, and navigating human-modified environment requires more time. For instance, animals may need to travel long distances to reach provisioned sites or spend time monitoring human activity before approaching (63,80). In two macaque species (*Macaca mulatta; M. radiata*), individuals that frequently interact with humans spent significantly less time resting and groomed fewer group members (81,82); and food-provisioned female bottlenose dolphins spent less time socializing (83). Such patterns may occur because provisioned individuals must invest time in an atypical foraging strategy—waiting for the right opportunity to approach food near humans, or handling difficult-to-access resources such as opening rubbish bins. Determining whether human food subsidies ultimately free up time or create time constraints—and how these outcomes influence social interactions—remains an important avenue for future research.

Finally, many human food sources follow distinct patterns of availability with consequences for animals' daily activity patterns. While some resources, such as landfills, might be constant, others are more fleeting and available only at specific times. Food provisioning associated with tourism is often limited to certain, recurrent times of day (e.g., lunchtime) or specific seasons (e.g., holidays). For example, in Shark Bay, Australia, bottlenose dolphins are fed with fish for a maximum of three times daily between 7:30 and 13:00 (43). Similarly, several bird species, including pigeons and gulls, have been observed gathering around noon at sites where people regularly eat lunch (84,85), sulphur-crested cockatoos (*Cacatua galerita*) visited balconies (to receive food) before and after working hours when residents were most likely to be home (86), and in southern stingrays (*Dasyatis americana*), individuals shifted from nocturnal to diurnal activity patterns in response to ecotourism feeding schedules (87). Human food subsidies can thus crucially alter the diel activity patterns of individuals, for example, by shifting the time of day that individuals engage in foraging activities, with consequences for social interactions. Particularly when human subsidies take the form of resource pulses—highly predictable but short-lived food sources—they can draw large numbers of individuals into the same area, increasing local population density, intensifying social encounters, and potentially heightening competition and aggression. For instance, supplemental feeding of chimpanzees in Gombe National Park significantly increased aggression, as profitable food was available only briefly during a short time (88).

Movement

Movement is an important driver of social interactions as it affects the number of conspecifics an individual may encounter (89). Increasing evidence shows that individuals across various taxa reduce their movements in response to human food subsidies (90–92). This may be due to the predictable and abundant nature of human-provided food, reducing the need to range widely in search of resources, which can concentrate many individuals in limited areas (e.g., landfills). In Yellowstone National Park, grizzly bears (*Ursus arctos horribilis*) fed almost exclusively from waste disposal sites; once these were not available anymore, bear densities declined rapidly and individuals massively enlarged their spatial range (93). Similarly, African stripe mouse (*Rhabdomys pumilio*) females reduced their home ranges by 43% when being supplemented with food (94). In addition, migrating species that utilize human food are increasingly reported to cease migrating altogether, forming stationary populations (95,96) or shorten their migration routes (97). Human food subsidies can thus impact both short- and long-distance movements with consequences for social interactions (Figure 2). At local scales, food subsidies and the associated reduction in space use can increase local population densities, heightening the frequency of social encounters (98,99). Conversely, at broader spatial scales, human subsidies may reduce social interactions, as limited space use may constrain the range of intraspecific encounters, potentially fragmenting social communities and populations. Thus, the effects of altered animal movement on intraspecific interactions may vary depending on spatial scale and requires future research.

Social choices

Social behaviour is often highly plastic, and individuals can flexibly adjust group size or even shift between solitary living and group formation, depending on ecological conditions. For example, in many species, social foraging arises as an adaptive strategy, offering benefits such as increased efficiency in locating food in unpredictable environments (100,101). The high abundance and predictability of human food sources can reduce the benefits of, and thus the need for, social foraging. Consequently, individuals may opt to forage in smaller, cohesive subgroups of preferred associates or even solitarily. This shift can lead to more fragmented population social structures with smaller and more modular groups. For example, in chacma baboons (*Papio ursinus*), groups were more spread out and less cohesive while foraging in urban environment, likely caused by lower predation risk and a large number of available food sources (80). Similarly, in bottlenose dolphins, individuals that frequently begged food from humans were less socially connected, probably because human-provided prey can be acquired individually rather than in groups, isolating these individuals from conspecifics that forage on natural prey (102). Rich and predictable human-derived food landscapes may however also reduce conflict among group members, thereby facilitating group cohesion (103).

Moreover, human food sources often differ markedly from natural diets in nutrient composition, with implications for social behaviour, particularly aggression. Food rich in sugars and fats is typically perceived as a high-value resource, intensifying competition and increasing the likelihood of aggressive interactions (104). Such diets may further directly affect aggression through physiological mechanisms. Although links between diet composition and aggression are well established in humans (105), corresponding research in non-human animals remains limited. For example, dogs on high-protein diets were significantly more likely to show aggressive behaviours toward both their owners and other dogs (106), and high-fat diets increased aggression levels in captive male rats and mice (107). Finally, human food can be heavily contaminated with pollutants such as heavy metals (108), impacting the ability to socially interact (30). However, studies examining these patterns in wild animals—and the underlying physiological mechanisms—are notably scarce.

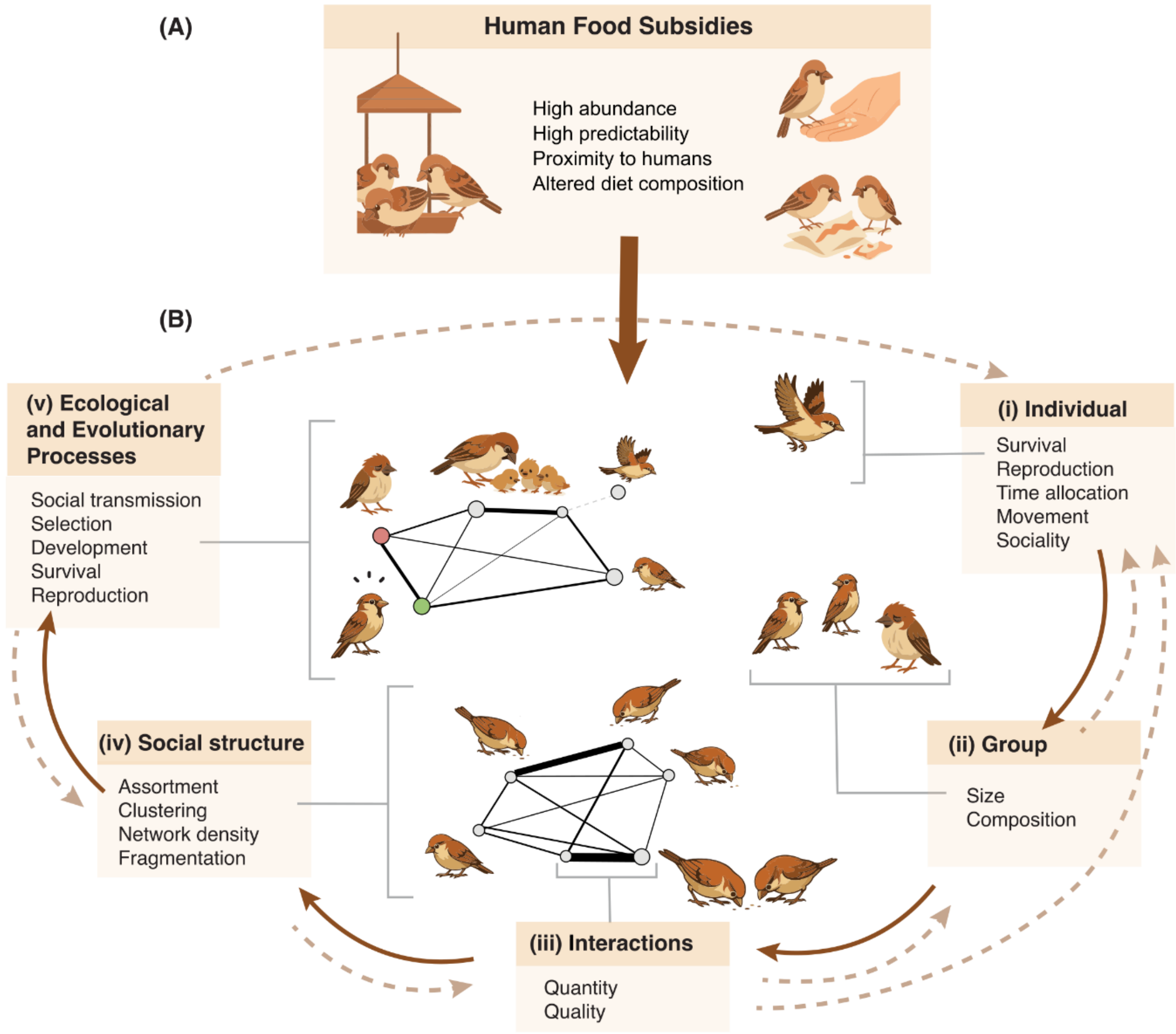

Figure 2. Human food subsidies can impact animal social structure through a range of pathways and have implications for a range of ecological and evolutionary processes. Human food subsidies are characterized by an increased abundance, predictability, proximity to humans, and altered diet composition, which can affect individual behaviours (i) such as movement decisions with consequences for the size and composition of animal groups and aggregations (ii). This impacts the quantity and quality of social connections (iii), scaling up to features of social structure such as assortment and social fragmentation (iv). Changes in social connections can influence ecological and evolutionary processes such as social transmission of information, diseases, and stress (v). Note that

there are feedback loops (dashed arrows) from processes to social structure, as well as at the group and individual level (10), which are not elaborated on in this review.

Ecological and evolutionary consequences

Numerous studies have documented the effects of human food subsidies on population processes such as disease prevalence, animal migration, and natural selection (34). However, the underlying mechanisms through which human food subsidies cause ecological and evolutionary change often remain unclear. We now turn the attention to the implications of human food subsidies through their impact on intraspecific interactions (Figure 2). We synthesise empirical evidence to argue that examining the link between human food subsidies and social behaviour can provide new insights into social transmission, the spatiotemporal distribution of animals, development, as well as selection and the evolution of cognitive traits. Developing a deeper understanding of the social implications of human food subsidies, along with their ecological and evolutionary consequences, will offer valuable information to predict the consequences of future environmental changes, such as the removal of subsidies (e.g., landfill closures) or increased food availability due to tourism.

Social transmission

Disease transmission

Human food subsidies are frequently linked to increased disease transmission. This is largely because human subsidies increase exposure to pathogens and facilitate spread through increased social encounters (109). For instance, wild birds show a higher prevalence of infectious diseases among individuals foraging at supplemented forest sites compared to those at unsupplemented sites (110), and experimentally increased feeder density led to a higher pathogen transmission in captive house finches (*Haemorhous mexicanus*) (111). Human food subsidies can also increase disease transmission by directly altering the type of social interactions. For example, banded mongooses (*Mungos mungo*) exhibited higher levels of aggression when foraging from garbage compared to natural habitats, leading to more injuries and a higher likelihood of infection with a form of tuberculosis (112). Although many studies point to changes in intraspecific interactions as the mechanism driving increased disease prevalence at supplemented sites, few explore the detailed social connections between individuals.

Mapping animal social networks often shows that greater clustering (well-connected sub-groups) and stronger connections facilitate disease spread, while high modularity (i.e., social fragmentation) hinders transmission (113,114). Studies examining disease transmission in the context of human subsidies typically focus on small spatial scales (e.g., one local population), but it would be valuable to gather detailed information on the use of human food sources, intraspecific interactions, and disease transmission at larger spatial scales (i.e., across local populations). This broader perspective is important because human food subsidies may increase social encounter rates locally while simultaneously reducing encounters at larger spatial scales. Such shifts in movement and contact patterns can fragment social communities, reduce interactions between populations, and potentially decrease the wider spread of pathogens. For instance, migration is often assumed to facilitate the geographical spread of pathogens, as animals are exposed to diverse parasites while moving annually between breeding and wintering grounds (115,116). However, species that utilise human food sources are increasingly reported to cease migrating altogether, forming stationary populations (95,96), while others shorten their migration routes (97). By reducing long-distance movements—coupled with findings of decreased movement in human-modified environments (117)—human food provisioning may thus limit disease spread on a broader scale. Therefore, how food subsidies influence disease outcomes may be a question of scale, with patterns observed locally not necessarily aligning with those at broader scales, warranting future research to determine whether these relationships hold.

Furthermore, studies including experimental approaches on animals' responses to the addition and removal of human subsidies are crucial for managing disease spread more effectively. During disease outbreaks, wildlife authorities often recommend halting the feeding of wildlife to reduce transmission. However, animals frequently respond to the loss of a key resource by expanding their range (93,118). Therefore, while the removal of key resources may reduce social contact locally, the resulting increase in space use may lead to more social interactions across a broader area, potentially facilitating disease spread between otherwise isolated social groups or populations.

Stress transmission

There is growing awareness that not only pathogens but also physiological states can be transmitted among animals. Of particular importance is stress as it impacts how animals interface with their environment (e.g. responding to stimuli) and can shape social behaviours (119). Individuals that interact with conspecifics exposed to stress—whether from an acute or chronic source—can exhibit similar physiological responses (e.g., elevated circulating stress hormones) and behavioural changes (e.g., altered movement patterns) that correspond to transmission of stress (120). Stress transmission can greatly amplify the impact of human food subsidies by affecting not only direct recipients but also individuals beyond subsidy sites. In principle, food subsidies could reduce stress transmission by increasing food abundance and predictability, both of which have been shown to lower physiological stress (121), especially during challenging periods like reproduction (122,123). In practice, however, competition, intensified social interactions, and greater exposure to threats (e.g., predators, humans) at subsidy sites may elevate stress levels instead. Either way, stress transmission is likely to play an important ecological role for species accessing human food subsidies through the combined physiological effects of accessing supplemental food and impacts on social connections.

Information transmission

The structure of social networks also influences the spread of information and novel behaviours across populations (15,10). Social contacts are a key source of information for individuals, and thus who, how often, and how many individuals come into contact will impact how information spreads. Similar to disease transmission, human-induced changes in social networks can affect how information circulates within a population. If human subsidies increase social encounter rates among individuals, novel behaviours (e.g., on how to access a food resource (124)) may spread more rapidly through the population, while transmission can be reduced in more modular social structures (114).

By providing abundant and predictable resources, human food subsidies can also directly diminish the value of social information. Foragers are believed to rely more on social information when resources are scarce and unpredictable, as this increases their chances of locating food. In contrast, individual foraging and individual learning become more advantageous in environments where resources are abundant and predictable, as this can help avoid competition (101,125). For instance, bat species that feed on unpredictable prey are more likely to forage near conspecifics and emit echolocation calls indicating prey capture, whereas this behaviour is less common among species that target predictable food sources (126). Human subsidies may thus simultaneously accelerate the spread of certain behaviours (e.g., through increased social connections) while reducing the overall reliance on social information, ultimately reshaping the cultural dynamics of animal populations.

Socio-cognitive traits

The evolution of cognition is hypothesised to be driven by the demands of group living (the social intelligence hypothesis) and ecological challenges, such as finding and accessing food (127). Successfully meeting these challenges directly affects individual fitness, thereby influencing the evolution of cognitive traits. On the one hand, subsidies can reduce cognitive requirements if such food sources become predictable and abundant, prompting individuals to invest more in competitive ability. On the other hand, human food subsidies can introduce new challenges that require cognitive skills, such as interpreting human behavioural cues to locate food (128,129) or remembering the exact timing of food availability (84–86). In both cases—by easing foraging challenges or by introducing novel ones—human food subsidies set the stage for changes in social interactions and the cognitive demands of group living.

By changing the time available for social interactions (see '*Time allocation*'), human food sources can reshape the social environment (and its associated challenges), ultimately altering the development of (socio-) cognitive skills. Previous research has identified various cognitive traits linked to group living, including social learning, individual recognition, and third-party relationships (130–132). In addition, increased local population densities can drive increased group sizes. Larger groups should—mathematically—exhibit better problem-solving abilities and more frequent behavioural innovations (133). However, being in a larger group can also increase innovation rates (133). One explanation for this phenomenon is the 'pool of competence' effect, which suggests that larger groups contain individuals with diverse skills, increasing the likelihood of problem-solving (134). Additionally, increased competition in larger groups may drive improved problem-solving and behavioural innovation, a concept known as the 'skill pool effect' (135). For example, in vervet monkeys, individuals facing higher feeding competition learned a new and more efficient foraging skill faster (136), and in three-spine sticklebacks (*Gasterosteus aculeatus*), high intraspecific competition led to greater diversity in food resources used (137). Finally, forming groups can allow individuals to more effectively distribute themselves across resources—i.e. express the ideal free distribution—than what individuals are capable of doing alone (138). Therefore, human food subsidies may enhance problem-solving performance and behavioural innovation through increases in group size. Gaining deeper insights into the behavioural innovations associated with human food provisioning and their ultimate impact on individual fitness will enhance our understanding of how human food subsidies shape specific cognitive abilities through changes in the social environment.

<u>Development</u>

Human food can affect not only the individuals directly receiving the subsidy but also their offspring, with downstream developmental effects on sociality. Having more food is then likely to have impacts on the growth and traits of the offspring. Red kite (*Milvus milvus*) chicks that received food supplementation (via their parents) developed distinctly different social and spatial preferences to those that did not (139). For example, the youngest (and least competitive) chick in the nest typically avoids conspecifics after hatching and during dispersal. However, in nests where parents received food supplements, the youngest chick instead became the most social after fledging (139). These effects are likely tied to physiological conditions experienced during development (140), which are very likely to be altered by food supplementation. Such effects could be direct (e.g. via the amount of food that young animals receive during development (141)) or indirect (e.g. via stress experienced by their parents, see also '*Stress transmission*'). The links between food supplementation, development, and future social behaviour are poorly understood and require urgent study.

<u>Selection</u>

While it is recognised that human activities, including food subsidies, influence selection pressures and drive evolutionary changes in natural populations (142,143), the contribution of changes in intraspecific interactions caused by food supplementation to population and evolutionary dynamics has remained largely overlooked. Simply, being part of a group has fitness consequences, such as the benefits of social foraging or the costs of increased competition. Human-provided food can modify these effects by influencing group size, elevating competition and disease prevalence, enabling rapid transmission of stress, and potentially reducing the fitness benefits of social foraging when food is abundant.

Fitness and selection consequences also depend on the phenotypic traits of social associates. In animals that exhibit social behaviour, selection can be mediated by the interaction between an individual's phenotype and those of its associates—a concept known as social selection (144). For instance, if a certain trait, such as body size, increases the chances for copulation, the individual's reproductive success may be influenced by the average expression of this trait among its associates. The resultant effects on phenotypic selection emerge at the population level when social selection gradients are experienced nonrandomly among individuals (i.e. positive or negative phenotypic assortment; (145,146)). Thus, when populations become phenotypically structured, local differences in the social environment that individuals experience can influence the strength and direction of selection (22). Because human food sources can cause positive phenotypic assortment, such as if individuals of similar phenotypes preferably associate, it is expected that food supplementation impacts selection.

Individuals can also adjust their phenotype in response to the conspecifics they associate with (i.e. social plasticity (147,148)). For example, individuals might exhibit higher levels of aggression in the presence of more aggressive conspecifics compared to the presence of more passive ones (149). Consequently, indirect genetic effects (i.e., when one individual's genes affect another individual's phenotype (150)) can alter selection by either decreasing or increasing genetic variance, affecting evolutionary trajectories. Human food subsidies may play a role here if they attract individuals with particular traits—for example, more aggressive individuals—leading to changes in phenotypic variation in the population and selection strength. The effect of social plasticity on evolutionary outcomes further depends on the pattern of social interactions within a population. For example, the contribution of indirect genetic effects to phenotypic variance can be highest at intermediate social network densities and decreases at higher densities (22). This is because at high social network densities individuals tend to interact with most group members, homogenising the social environment across individuals (22). By increasing population densities, human subsidies may thus reduce the impact of indirect genetic effects.

Community structure

Although we primarily focus on intraspecific interactions, many of the social implications of human food subsidies extend to interspecific interactions, with potential consequences for community structure and ecosystem processes (34,151). For example, changes in population size and density resulting from food supplementation can alter interactions within and across trophic levels of supplemented and unsupplemented species (152,153). For example, human food subsidies attract pigeons into urban areas, where they constitute one of the primary food sources for raptors such as peregrine falcons (*Falco peregrinus*). During the COVID-19 pandemic and resulting lockdowns, however, falcons substantially shifted their diets, consuming far fewer pigeons—likely because pigeons abandoned city centres and foraged in the countryside in response to the absence of human-provided food (154).

Human food subsidies also strongly shape interactions between humans and wildlife. While feeding wildlife can provide psychological and cultural benefits, contributing to human well-being (155,156), it is also a major driver of human–wildlife conflict. Food subsidies can lead to habituation and reduced wariness in wildlife, while crop and property damage often heighten aggression on both sides (157). Moreover, food-induced increases in wildlife population size can intensify human–animal encounters, and associated shifts in phenotypic composition may further accelerate conflict. For instance, in brown bears, females and young individuals are more frequently observed near human settlements (158). If food subsidies enhance the survival of young bears, this may increase the number of young individuals living close to humans, thereby raising the potential for conflict. Such patterns could be further reinforced through cultural transmission if young bears learn from their mothers and other conspecifics to exploit human food subsidies. The complex interplay between food subsidies and wildlife social dynamics underscores the importance of future research to better understand these interactions and develop strategies that mitigate conflict while promoting coexistence.

Conclusion

Human food subsidies are more than ecological inputs; they are transformative forces reshaping the social dynamics of wildlife populations. By altering the abundance, predictability, proximity to humans, and nutritional composition of resources, subsidies influence fitness, how animals allocate time, where they move, and with whom they interact. These direct and indirect effects on intraspecific interactions can cascade from individuals to groups, restructuring social systems with profound ecological and evolutionary consequences – shaping social transmission, development, selection, and even broader community structure. Crucially, the outcomes are not uniform. They vary with the ecology of the species, the type of food source, and animals' perceptions of humans. The same subsidy may suppress social opportunities in one context while amplifying them in another, with impacts ranging from heightened local disease risks to reduced connectivity across populations. Recognizing food subsidies as both ecological and social drivers offers a new perspective on anthropogenic change. The central challenge now is to move beyond documenting effects toward developing predictive principles: under what conditions do human food subsidies destabilize animal societies, and when might they instead foster novel cooperation, competition, or transmission pathways? Addressing these questions will be essential for understanding how human-provided subsidies are shaping the future of animal societies in the Anthropocene.

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