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Grasshopper consumption by grey wolves and implications for ecosystems

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The eradication and subsequent reintroduction of grey wolves (*Canis lupus*) in the western United States has provided unique insights into the role these predators play in regulating ecosystem functioning and dynamics. Although the importance of wolves in ecosystems has been recognized for nearly a century, recent work has reported ecological interactions that reach beyond their direct effects on ungulates and indirect effects on plants (Beschta and Ripple 2019). This point was unexpectedly demonstrated to us during a detour on our way to the 2017 Ecological Society of America conference, when we spent a few days backpacking in Idaho, USA. While walking along a ridgeline that overlooked the Hells Canyon Wilderness, we saw fresh tracks from a wolf. We continued down the trail with our heads down, following the tracks while dodging seemingly endless numbers of grasshoppers that jumped in and out of our path. Apparently, we were not the only ones that had taken notice of the abundant grasshoppers, as we soon stumbled upon evidence that wolves were taking advantage of this plentiful food source.

Remains of grasshoppers were noticeable even before picking up the scat (Fig. 1). Closer examination revealed that it was chock full of undigested grasshopper parts, with legs, wings, and other parts of the exoskeleton clearly visible. We collected this scat, along with several others in the immediate area, to examine the contents more closely in the lab. To estimate the number of grasshoppers within each sample, we first rehydrated it in water then counted the number of grasshopper forewings present, and then divided by two, as each grasshopper has two forewings (Appendix S1). Only one scat sample contained grasshopper parts, but the presence of 362 forewings revealed that this wolf had consumed at least 181 grasshoppers in a short amount of time (i.e., quickly enough to be deposited as a single scat). The abdominal remains of some grasshoppers remained intact, allowing us to dissect their reproductive organs (Appendix S1) and identify them as Payette's short-winged grasshopper (*Melanoplus payettei*). Although consumption of individual grasshoppers has been previously documented in grey wolves (Stebler 1944) as well as other canids (De Arruda Bueno and Motta-Junior 2004), insectivory of this magnitude by wolves has not been documented.

The observation immediately stimulated several questions. First, how does a wolf catch so many grasshoppers? Wolves are agile, but anyone that has spent time behind a sweep net knows that catching grasshoppers is challenging. Part of the answer may lie in the activity patterns of both species. We placed a camera trap over the trail that had contained the scat, producing photos of wolves between 22:56 and 04:29 for six consecutive nights (Fig. 2A). Grasshoppers are largely known for their hopping behavior, but at night they are less active, roosting on plants or sluggishly feeding in the cool night temperatures (Barton and Schmitz 2018). Given the density and conspicuousness of inactive grasshoppers (Fig. 2B), we suspect that a wolf could easily catch and consume hundreds of grasshoppers in a night.

Wolves are well-known for their ability to initiate trophic cascades. Interestingly, work on the behaviorally mediated indirect effects of wolves in western North America was largely inspired by earlier work on grasshoppers and their spider predators (W. J. Ripple, *personal communication*). Indeed, invertebrates can be useful as model systems to test and develop ideas that cannot as easily be studied with vertebrates (Schmitz 2005). However, considering the large body of literature on trophic cascades in insect systems that has amassed, it has been

FIG. 1. Photograph of wolf scat collected on 5 August 2017 in Adams county, Idaho. The scat contained remains of at least 181 Payette's short-winged grasshoppers (*Melanoplus payettei*). Labels highlight a subset of the visible grasshopper structures, including femur, pronotum, abdomen, and forewing.

argued that carnivore research would be well-served if wildlife biologists learned more from arthropod systems (Meadows et al. 2017). Unfortunately, this view recapitulates the fallacy that vertebrate and invertebrate food webs are separate entities, which they clearly are not (e.g., Grinath 2018). Our observation of nearly 200 partially digested grasshoppers within the scat of North America's iconic large carnivore graphically illustrates that nature does not heed to the taxonomic boundaries imposed by ecologists. Although it is great for ecologists to be read broadly, moving beyond inspiration and toward integration of species from different taxonomic groups will be essential to appreciate ecosystem functioning fully.

Beyond the philosophical implications for a more integrated ecology, what are the ecological implications of wolves eating grasshoppers? One possibility is that wolves affect grasshoppers in the same way that spiders do, by limiting their abundances and inducing antipredator phenotypes that indirectly influence plant communities (Fig. 3A). However, this seems unlikely. The sheer number of grasshoppers dwarfs the potential density effects of consumption by the comparatively few wolves, and our finding of grasshopper remains in only one sample suggests that this dietary choice is not ubiquitous. Although we cannot rule out the possibility that wolves induce a defensive phenotype in grasshoppers that subsequently affects lower trophic levels, we remain skeptical. However, the hypothesis could be easily tested by examining grasshopper behavior, morphology, and other traits when exposed to wolf cues, such as commercially available wolf urine or wolf sounds.

The camera survey captured 14 wolf images in the 3 weeks following the discovery of the scat. Images were usually at night (12 of 14 images) and never contained multiple wolves. Additionally, the photographed individuals were superficially similar, suggesting that the scats and images were from a lone wolf. Although wolf packs generally prey on ungulates, lone wolves are less likely to take down large animals and instead rely on alternative prey (Mech and Ciucci 2003) until they can establish or join a new pack (Fig. 3B). However, evaluating the nutritional significance of grasshoppers for wolves is difficult. Published estimates of the daily caloric needs of wolves range from as low as 1,300 kCal in captive studies (Lindsey and Hopkins 2009) to estimates of nearly 6,000 kCal for wild animals (Mech and Ciucci 2003). Based on published data for *Melanoplus* grasshoppers and estimated 400 mg wet weight, 181 grasshoppers could provide 35 g of protein and 160 kCal. Although not enough to sustain a wolf indefinitely, this level of insectivory could represent as much as 10% of daily nutritional demand. Alternative prey such as grasshoppers could help lone wolves persist until they can join or establish a new pack (Fig. 3B). As wolves spread across the American west, our understanding of wolf diet is being reshaped (Collins et al. 2019), but the importance of

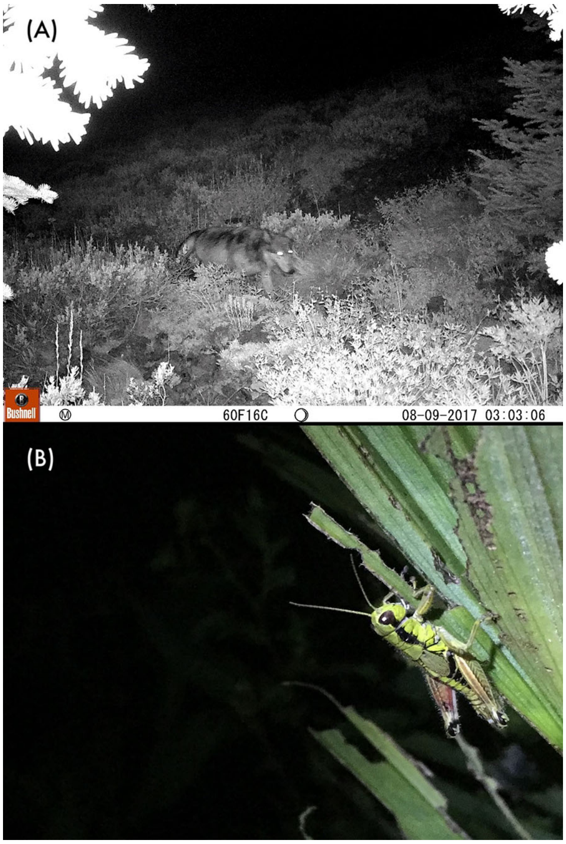

FIG. 2. Photographs demonstrating that wolf activity corresponds with grasshopper inactivity, making grasshoppers easy targets for wolves. (A) A wolf on the trail from which scat samples were collected. (B) Images of a wolf were captured on six consecutive nights following the collection of scat samples. Grasshoppers (unidentified species) were abundant at night and did not flee when approached, suggesting they may be easy prey for wolves and other predators.

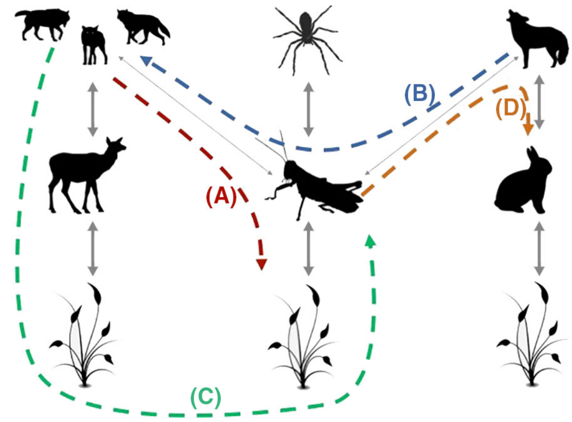

FIG. 3. Diagram of four possible connections mediated by interactions between wolves and grasshoppers. (A) Although unlikely, wolves may affect grasshopper density or induce defensive phenotypes, thereby having indirect effects on plants consumed by grasshoppers. (B) Grasshoppers may be an alternative food source for lone wolves, providing some nourishment until they are able to join or establish a new pack. (C) Despite evidence of eating grasshoppers, wolves may ultimately benefit grasshoppers by reducing competition with elk and other ungulates for plants. (D) Abundant grasshoppers may indirectly affect other species by altering wolf abundance or behavior.

alternative small prey has been largely overlooked as an important factor (Newsome et al. 2016). Indeed, published data on wolf diet is biased towards large ungulates, because most studies in the contiguous United States focus on large ungulate kill sites. Surprisingly few published studies have assessed the occurrence of other smaller prey items in wolf diets through analysis of scats or stomach contents (Newsome et al. 2016), which are needed to provide a comprehensive view of wolf diet and their role as a predator.

Although our observation demonstrates a direct interaction between wolves and grasshoppers, it is also worth highlighting the potential for other indirect interactions between these species and the broader ecosystem. For example, elk (*Cervus canadensis*) densities are significantly lower now than before the reintroduction of wolves into Yellowstone National Park (Painter et al. 2018). Concurrent with decreased elk densities, elk have changed behavior and shifted some of their habitat use from grasslands (where grasshoppers are most common) to forests. The decreased browsing and subsequent increase in vegetation biomass in some areas (Beschta and Ripple 2019) may provide increased food-web support for a variety of species, including grasshoppers and their predators (Fig. 3C). Grasshoppers may also generate bottom-up indirect effects that cascade through the ecosystem if they influence the abundance or behavior of wolves (Fig. 3D). For example, capitalizing on these resource pulses may uncouple the numerical response of wolf populations with changes in the abundance of their preferred prey that is seen in other canids (e.g., White et al. 1996), allowing them to maintain high densities despite fluctuations in mammalian prey abundance. Alternatively, attraction of wolves and other predators to insect outbreaks may affect other prey species through mechanisms such as apparent competition (Fig. 3D).

Our observation contributes to a growing appreciation for the complexity of ecosystems, especially those species and interactions that are overlooked yet may be essential for ecosystem processes (McCann et al. 1998). Grasshoppers are not often considered in discussions about wolves, but theory predicts that stronger trophic cascades arise when top-trophic levels are subsidized by allochthonous resources (Leroux and Loreau 2008). Although such subsidies are usually conceptualized as the flow of resources from one geographically distinct system to another (e.g., terrestrial to aquatic), the in situ flow of energy from invertebrate food webs to vertebrate food webs may have similar impacts. Thus, it begs the question, "how do insects like grasshoppers influence the interactions of vertebrate predators that shape ecosystems?" Such questions are unlikely to arise entirely from theoretical endeavors, but instead rely on natural history observations that are the product of dirty boots. Here, we have speculated on the potential impacts of grasshopper subsidies to wolves. Some of these ideas could be wrong, and others could be right. We encourage our colleagues—the wildlife biologists and the entomologists, the empiricists, and the theoreticians—to reach across discipline boundaries and work together to sort out which is which.

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