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Necrophagy in grasshoppers: Taeniopoda eques feeds on mammal carrion

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Abstract

Grasshoppers are thought to be herbivores that primarily feed on plant leaves. But, many grasshopper species actually are omnivorous and will consume a wide range of living and dead organic matter. We documented the feeding behavior of the Western Lubber grasshopper, Taeniopoda eques, on a coyote, Canis latrans, carcass in Arizona, USA. The number of adult T. eques on the carcass ranged from 1 to 8 during each of six visits to the site and were predominantly female. Nymphs were not observed on or immediately adjacent to the carcass, although they were present in low numbers in the surrounding population. We observed females attempt to consume hair, dried hide, and especially dried tissue adhering to the bones. Our observation that most of the individuals feeding on the carcass were female, suggests that egg production requires nutrients that may make vertebrate carrion a complement to a herbivorous diet. T. eques lives in a desert habitat with a short and highly variable growing season, so carnivory/necrophagy may be adaptive by providing essential nutrients, thereby speeding oocyte maturation and increasing the likelihood that females will be able to develop and lay eggs before the onset of winter.

Key words

necrophagy, carnivory, Western Lubber, Acrididae, Romaleidae, Taeniopoda, carrion

Introduction


Grasshoppers also can be surprisingly carnivorous/necrophagous, consuming a wide range of animal matter (Whitman et al. 1994). Gut analysis of wild grasshoppers often reveals high levels of arthropathy: 68% of Hadrotreulus triscicatus in Wyoming and 29% of female Taeniopoda eques in Arizona contained arthropod exoskeletons in their guts or feces (Lavigne & Pfadt 1964, Whitman & Orsk 1985). Grasshoppers often attack and eat weak, wounded, or molting conspecifics in the laboratory and field, especially during periods of food or water deficiency (Ashall & Ellis 1962, Rizvi 1967, Whitman et al. 1994, Bazazi et al. 2008, van Huys et al. 2008, Richardson et al. 2010). For example, nymphs of Schistocerca gregaria consumed molting and newly hatched conspecifics during a drought (Ashall & Ellis 1962). Carnivorous grasshoppers can be very aggressive: Lavigne (1963) watched a Melanoplus foedus repeatedly challenge a large robber fly, Stenopogon coyote, for possession of a dead Amphitornus grasshopper impaled on the fly’s proboscis. The large and powerful plains lubber grasshopper, Brachystola magna, will pursue, capture, and consume living arthropods (Chapman 1992, Bright et al. 1994). In Arizona we observed four adult female Western Lubber grasshoppers, T. eques, fight over a single dead sibling, each female pulling the carcass with her mandibles while simultaneously pushing away her competitors with the front or middle legs. Of course, the propensity for carnivory varies with phylogeny and ontogeny, and some grasshopper stages and species exhibit little or no carnivory/necrophagy (Lavigne & Pfadt 1964, Lockwood 1989).

In this paper, we report necrophagy on a coyote carcass by the grasshopper T. eques in the field. T. eques is primarily phytophagous, but opportunistically consumes a wide range of animal materials, including living and dead arthropods, spider silk, and vertebrate and invertebrate feces (Whitman & Orsk 1985, Raubenheimer & Bernays 1993).

Methods

T. eques is a large, flightless, and chemically defended species that is native to the deserts of northern Mexico and the southwestern United States (Whitman & Orsk 1985, Whitman & Vincent 2008). While conducting field studies in southeast Arizona, USA on 7 September 1983, we discovered the dried carcass of a coyote (Canis latrans) being fed upon by adult T. eques. The site was ~5 km east of Portal, Arizona, at ~1,300 m elevation in a cattle-grazed Chihuahuan Desert community containing some elements of the Sonoran Desert. The carcass lay in a water-impoundment area that was ~25 m in diameter. The impoundment was sometimes filled with runoff to a 50-cm depth, but on this date had completely dried and the silty soil had cracked (Fig. 1). The coyote lay near the center of the impoundment and the nearest low, annual vegetation was ~2 m distant. Lush honey mesquite (Prosopis juliflora) bushes 2-3 m tall lined the perimeter of the impoundment and the nearest bush was ~5 m from the carcass. Over 11 d we visited the site a total of six times between 08:00 and 15:30 h in order to observe the feeding behavior of grasshoppers and to note their age and sex.
Results

We observed 1 to 8 adult *T. eques* on the carcass during each of six visits to the site (Fig. 1). Although the area exhibited high grasshopper diversity, we did not observe other species of grasshopper on the carcass. Nymphs of *T. eques* were not observed on or immediately adjacent to the carcass, although 15% of the grasshoppers in the surrounding population were nymphs at the beginning of the study. The total number of females (20) on the carcass across all dates, outnumbered males (2), despite an abundance of males in nearby vegetation. Most individuals on the carcass were actively feeding, based on observing or hearing their mandibles scraping various body parts. We observed females attempt to consume hair, dried hide, and especially dried tissue adhering to the bones (Fig. 2). Some females entered and fed inside the body cavity of the carcass (Fig. 3).

Discussion

*T. eques* primarily feeds on plants (Whitman & Orsak 1985, Raubenheimer & Bernays 1993). However, we found individuals feeding on a mammal carcass despite an abundance of green vegetation within and around the study area. In fact, the grasshoppers had to leave the vegetation and travel 5 to 15 m over dry and relatively barren soil to reach the carcass, suggesting an attraction to this food resource. Grasshoppers can orient to odors from plants (Helms et al. 1998).
al. 2003) and odors emanating from insect carcasses, especially fatty acids (Bomar 1993). T. eques may have used similar chemical cues to locate this mammal carcass.

Why is T. eques necrophagous? Plant tissue, the primary diet of these insects, generally contains low titers of proteins, lipids, and certain minerals that are essential for all insects (Mattson & Scriber 1987, Slansky 1993, Whitman et al. 1994) and strict herbivory may not promote optimal growth, development, and fecundity. Nitrogen can be especially limiting for insect herbivores (Mattson 1980). Grasshoppers will self-select diets high in protein when offered a choice between high and low protein diets (Behmer & Joern 1993). Adopting a broader diet may provide a herbivore with better nutrition and improve fitness. For example, grasshoppers that feed on plants or artificial diets with high nitrogen, or include meat, amino acids, or complex protein in their diet, have increased growth, developmental rate, survival, oocyte development, and fecundity (Ashall & Ellis 1962, Rizvi 1967, MacFarlane & Thorsteinson 1980, Whitman et al. 1994, Chapman & Sword 1997, Joern & Behmer 1997, Danner & Joern 2004).

Interestingly, we observed that nearly all the T. eques feeding on the carcass were adult females. Behmer and Joern (1994) noted that adult female grasshoppers and not males, preferred diets high in the amino acid proline. These observations suggest that adult females, in particular, may have an elevated need for protein and other nutrients that are more abundant in animal tissue to produce eggs. Dietary protein and lipids and rapid oocyte production may be especially important for T. eques because it lives in a desert habitat with an extremely short growing (rainy) season (Stauffer et al. 2011). This environmental constraint is compounded by the fact that T. eques deposits a relatively large egg pod of 37-79 eggs, weighing ~3 g, which accounts for approximately one-third of the mass of a gravid adult female (Whitman 1986, Stauffer & Whitman 2007). Therefore, carnivory/necrophagy may be adaptive for this desert species because these foods may speed maturation time and increase the likelihood that females can develop and lay their eggs before the onset of winter (Whitman 1987, 1988).

Necrophagy also has potentially negative effects. Carnivory/necrophagy can reduce fitness of grasshoppers and other insects if the prey is diseased (Whitman et al. 1994, Richardson et al. 2010). Grasshoppers are attacked by a vast array of pathogens (Streett & McGuire 1990) that may be acquired by feeding on diseased, dead, or dying animals and their excrement (Lockwood & Ewen 1990, Lange et al. 2009). For instance, the microsporidian Encephalitozoon romalea is endemic to populations of the omnivorous Eastern Lubber Grasshopper, Romalea microptera, a close relative of T. eques. This pathogen is acquired via consumption of contaminated feces, and may quickly kill infected R. microptera (Lange et al. 2009). Interestingly, this genus of microsporida generally is restricted to vertebrates, and, in fact, many primary pathogens of humans belong to this genus (Johny et al. 2009, Lange et al. 2009).

The discovery that grasshoppers and vertebrates share this group of pathogens suggests the possibility of a previous host-jump from vertebrates to invertebrates or vice versa (Johny et al. 2009). R. microptera may have fed on infected vertebrate carcasses or feces, thereby becoming infected with E. romalea and becoming a reservoir or alternative host for E. romalea (Johny et al. 2009). Likewise, vertebrate predators might become infected by feeding on R. microptera. Field observations and circumstantial evidence indicate that interphyla transmission of grasshopper pathogens is possible (Nunamaker et al. 2003), but no research to date has demonstrated this phenomenon in lubber grasshoppers.

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References

