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Source: Journal of Orthoptera Research, 19(2) : 377-380

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/034.019.0228

Journal of Orthoptera Research 2010,19(2): 377-380

Necrophagy in grasshoppers: Taeniopoda eques feeds on mammal carrion

Submitted September 7, 2010, accepted December 15, 2010

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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 are considered archetypical herbivores that primarily feed on leaves of living plants (Uvarov 1977, Chapman 1990, Chapman & Sword 1997, Muralirangan *et al.* 1997). However, many grasshopper species actually are omnivorous and will consume a wide range of living and dead organic matter. For example, grasshoppers will feed on mushrooms (Jones *et al.* 1988), algae (Ball *et al.* 1942, Bastow *et al.* 2002), moss and lichens (Duke & Crossley 1975, Behmer & Nes 2003), dead plant matter (McKinlay 1981, Raubenheimer & Bernays 1993, Boppré & Fischer 1994, Bright *et al.* 1994), soil (Bright *et al.* 1994), vertebrate feces (Whitman & Orsak 1985, Raubenheimer & Bernays 1993, Bright *et al.* 1994, O'Neill 1994), invertebrate feces (Bright *et al.* 1994, O'Neill *et al.* 1997), paper, wood, fiberglass, linen, silk, and even wool on live sheep (Husain & Mathur 1936, Uvarov 1977, Whitman & Orsak 1985, Boppré & Fischer 1994).

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 arthrophagy: 68% of *Hadrotettix trifasciatus* in Wyoming and 29% of female *Taeniopoda eques* in Arizona contained arthropod exoskeletons in their guts or feces (Lavigne & Pfadt 1964, Whitman & Orsak 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 Huis *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 & Orsak 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 & Orsak 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.

Fig. 1. A carcass of a coyote (*Canis latrans*) being fed upon by adult female *T. eques* grasshoppers in a dried water-impoundment area near Portal, Arizona, USA. For color version, see Plate XV.

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*

Fig. 2. Female *T. eques* consuming dried tissue adhering to the bones of a coyote carcass. For color version, see Plate XV.

Fig. 3. Female *T. eques* consuming dried tissue inside the body cavity of a coyote carcass. For color version, see Plate XV.

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 microsporidia 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.

Acknowledgments

We thank R.F. Mitchell and P.F. Reagel for constructive comments on an earlier draft of the manuscript. This research was supported by NSF grant DBI 0442412.

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