

Cannibalism of Pupae by Caterpillars of the Ranchman's Tiger Moth, *Arctia Virginalis*, (Lepidoptera: Erebidae)

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Notes and Discussion Piece

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ABSTRACT.—While once dismissed as an artifact of unnatural laboratory conditions, cannibalism is now widely accepted as a common behavior exhibited by multiple insect taxa, including primarily herbivorous species. In some cases cannibalism provides a means of acquiring nutrients and defensive compounds, reducing competition, and decreasing population density. For plants, inducing insect cannibalism is a defense mechanism to decrease damage by pests. Despite the growing awareness of cannibalism, its causes, and its ecological importance, few model systems exist, largely because observations of cannibalism are not reported. Here, we investigated the cannibalism of pupae by caterpillars of the ranchman's tiger moth, *Arctia virginalis*, [Lepidoptera: Erebiidae] based on an observation of a late instar caterpillar attacking the pupa of a conspecific in our laboratory. We conducted separate laboratory and field experiments to confirm this observation and determine the propensity for cannibalism under more natural conditions. We confirmed our observation of cannibalism in the laboratory experiment but failed to detect evidence of this behavior in the field. Consequently, the frequency of cannibalism, the conditions under which it occurs, and its impact on the population dynamics of *A. virginalis* are still unknown.

INTRODUCTION

Intraspecific predation, more generally known as cannibalism, is a common behavior exhibited by numerous insect taxa (Fox, 1975; Polis, 1981). While once considered an incidental phenomenon attributed to laboratory conditions, it is now known as an important means of acquiring nutrients (Polis, 1981; Mayntz and Toft, 2006) and defensive compounds (Bogner and Eisner, 1992; Bogner, 1996), reducing competition (Wise, 2006), and decreasing parasitism in future generations by consuming infected hosts (Reed *et al.*, 1996). Earlier work focused on the causes and consequences of cannibalism in carnivorous insects, but a recent review found cannibalism is also common in herbivorous insects (Richardson *et al.*, 2010).

Richardson *et al.* (2010) found both density-dependent and -independent factors, such as temperature and humidity, increased the propensity of insect herbivores to attack and consume conspecifics. In both laboratory and field studies, the major predictor of cannibalism was food limitation (Kakimoto *et al.*, 2003; Vijendravarma *et al.*, 2013) or low food quality (van Huis *et al.*, 2008). This was especially true for populations that exhibit developmental asynchrony. For example, in Lepidoptera, the cannibalizing of eggs and early instars by larger caterpillars was common across multiple families when food was limiting (Richardson *et al.*, 2010; appendix Table 1). Recent work by Orrock *et al.* (2017) found low quality food induced cannibalistic behavior in a common pest, the beet armyworm (*Spodoptera exigua*); caterpillars that were fed leaves sprayed with methyl jasmonate, a known elicitor of plant defenses, were more likely to attack conspecifics compared to those that were fed control leaves.

Even with this recent attention, the prevalence of intraspecific predation in herbivorous insects and its drivers and consequences are understudied. This is in part due to the challenges of observing cannibalism, especially in the field, and the lack of reporting such observations once made. Here we report our observations of cannibalism in an eretid caterpillar, *Arctia virginalis*. While rearing field-collected caterpillars in our laboratory, we opportunistically observed indirect evidence of cannibalism (partially consumed pupae in a cage with conspecific caterpillars) and one direct observation of a caterpillar attacking a pupa. While cannibalism of *A. virginalis* eggs by neonate caterpillars was observed previously (per obs), intraspecific predation of pupae has never been documented. Pupal cannibalism is relatively rare in herbivorous Lepidoptera (Richardson *et al.*, 2010 but see appendix Table1). We conducted separate laboratory and field experiments to confirm our initial observation of cannibalism and to determine if this behavior occurs under more natural conditions.

METHODS

STUDY SYSTEM

The Field experiment was conducted within the Bodega Marine Reserve (BMR), Sonoma County, California (38.3184°N, 123.0718°W). The coastal scrub community within BMR is dominated by two shrubs, coyote bush (*Baccharis pilularis*) and bush lupine (*Lupinus arboreus*), with *L. arboreus* serving as primary host plant at our study site. Caterpillars are gregarious feeders but leave food plants to pupate singularly on surrounding vegetation in late spring (Grof-Tisza *et al.*, 2015). Adults emerge in June–August and engage in hilltopping behavior (Grof-Tisza *et al.*, 2016, 2017). Eggs are laid on the underside of low-lying vegetation, including nonhost plants, and hatch within 2 wk. Early-instars are cryptic and over-summer in leaf litter until favorable conditions return during the wet cool winter, typical of Mediterranean climates (Karban *et al.*, 2015). Caterpillars are attacked by multiple parasitoids, including two wasps (Ichneumonid spp. and Braconid spp.) that never reach high densities, and a fly (*Theleaira americana*) that becomes abundant in some years (Karban & de Valpine, 2010).

LABORATORY AND FIELD STUDIES

To confirm our observation that pupal predation occurred under laboratory conditions, and to determine if this behavior occurred in the field, we conducted a laboratory and a field study in the summer (June–July) of 2017. In both experiments we used late-instar field collected caterpillars found at BMR.

In the first experiment, approximately 25 caterpillars were transported to our laboratory in Davis, CA and placed into a 75 × 45 × 45 cm flight cage with a bouquet of *L. arboreus* flowers. The mean (\pm SD) temperature within the flight cage was 22 (\pm 1) C. Caterpillars were misted daily to prevent desiccation, but humidity was not recorded. After 2 wk, six late-instar caterpillars and six recently (within the last 7 d) pupated individuals were removed from the flight cage and haphazardly assigned to plastic containers (163 ml, Dart Industries, Mason, Michigan). Each lidded container received one active caterpillar and one pupa. No food was added. The experiment was terminated when all caterpillars pupated or died. We recorded the number of pupae that were partially or fully consumed.

To determine the propensity of cannibalism under field conditions, we conducted a second experiment at BMR. Ten caterpillars were placed into 20 × 50 × 60 cm polyfiber sleeve cages (Kleen Test Products, Port Washington, Wisconsin) on 15 *L. arboreus* plants. The resulting density was chosen a priori to simulate the density of conspecific caterpillars experienced in our flight cage, where we originally observed cannibalistic behavior (caterpillars/m³; field experiment 166.7, laboratory experiment 164.6). The mean daily summer temperature at our field site in 2017 was 13.3 C. The experiment was terminated upon pupation of all the caterpillars.

RESULTS

In the laboratory container experiment, four out of five pupae were either partially or fully consumed by the active caterpillar. All caterpillars that exhibited cannibalism pupated and eclosed successfully. The only caterpillar that did not attack its associated pupa died prior to pupation. In the field experiment, we found no evidence of intraspecific predation; all pupae were accounted for and intact.

DISCUSSION

Arctia virginalis exhibited intraspecific pupal predation under laboratory conditions, a relatively uncommon behavior that has been documented in a few other herbivorous lepidopterans (Richardson *et al.*, 2010), including two other erebid species (Banerjee and Mahapatra, 1987; Bogner and Eisner, 1992). Our field experiment suggests cannibalism may be less common under natural conditions; more than 100 pupae were found intact (*i.e.*, no evidence of attack) despite being caged with a high density of active late instar caterpillars. Similar to what others have reported, the observed cannibalism was likely attributable to low food abundance or quality, nonoptimal rearing conditions (*e.g.*, temperature and humidity), or some other factors that contributed to stress (Fox, 1975; Richardson *et al.*, 2010; Vijendravarma *et al.*, 2013). Because we only tested one conspecific density (\sim 165 caterpillars/m³) with one level of food (*i.e.*, laboratory experiment, no food; field experiment, ad libitum) in separate

experiments with different rearing conditions, we cannot determine which factor or suite of factors drove the observed intraspecific predation. Below we discuss the likely importance of factors found to be predictive in increasing the propensity of cannibalism in other systems and propose additional experiments to help elucidate underlying drivers of pupal cannibalism in *A. virginalis*.

High conspecific density is often reported as an explanation for cannibalistic behavior in herbivorous insects (Richardson *et al.*, 2010). Only observing cannibalism in the laboratory despite caterpillars being exposed to similar rearing densities in both experiments, suggests that density may be less important than other factors such as food availability, although we acknowledge that density and food availability are often correlated.

Food limitation and low food quality (Kakimoto *et al.*, 2003; van Huis *et al.*, 2008) can cause species that are generally not considered carnivores to exhibit cannibalism, especially for species that have overlapping life stages (Polis, 1981). Our observations agreed with this general finding; during all observations of cannibalism, caterpillars were either starved (no food; container experiment) or only had access to low quality food (e.g., *L. arboreus* bouquet; flight cage). In contrast caterpillars in the field, which were not found to exhibit cannibalistic behavior, were less food limited.

Due to our study design, we were unable to tease apart food limitation from alkaloid deficiency. *Utetheisa ornatrix* caterpillars cannibalize eggs and pupae not out of hunger but to increase stores of pyrrolizidine alkaloids (PAs), a class of toxic compounds produced by plants. *U. ornatrix* sequesters PAs for protection and mate attraction (Bogner and Eisner, 1992; Bogner, 1996). *Lupinus arboreus* contains a similar defensive compound, quinolizidine alkaloids (QAs; Adler and Kittelson, 2004), but it is unclear if *A. virginalis* co-opt them. Karban *et al.* (2010) demonstrated caterpillars did not sequester QAs in their tissues, but QA levels in other life stages have not been tested.

Many Lepidoptera cannibalize pupae and other caterpillars that are parasitized or diseased (Reed *et al.*, 1996). Because we used field-collected individuals in this study, their infection status was unknown; therefore, we cannot rule it out as a causal mechanism of cannibalism. However, because we collected caterpillars from the same locations and randomly assigned them to either the laboratory or field experiments, we would expect that infection rates, and consequently proportion of cannibalized individuals, should be similar in both experiments if caterpillars preferentially attack infected pupae. In contrast to this expectation, we found the proportion of observed cannibalism in the laboratory and field experiment were 80% and zero, respectively. Moreover, the rate of parasitism in 2017 was 5% (unpubl. data), substantially lower than the proportion of cannibalized pupae in the laboratory.

To better assess the drivers of cannibalism in *A. virginalis*, a factorial experiment could be conducted in the field, where different levels of conspecific density and food are imposed on laboratory reared caterpillars (*i.e.*, unparasitized). *A. virginalis* moths readily mate and lay eggs in captivity. This design could be expanded to include different levels of temperature and humidity using insect rearing chambers in the laboratory. To test the defensive compound deficiency hypotheses, caterpillars, and pupae (reared from caterpillars) can be fed on diets with and without QA alkaloid addition.

While *A. virginalis* caterpillars feed gregariously, prepupating caterpillars leave host plants and pupate singly on nonfood plants (Grof-Tisza *et al.*, 2015). Locating pupation sites away from conspecifics likely decreases the risk of cannibalism. The two other erebid species, whose larvae were found to cannibalize pupae, also move to reduce cannibalism risk: *Argina cribraria* caterpillars exhibited cannibalism in a laboratory study, but late instars are generally solitary under natural conditions (Banerjee and Mahapatra, 1987); despite studies of the cannibalistic behavior, *U. ornatrix*, caterpillars leave host plants and pupate in leaf litter and cannibalism in the field has been reported only rarely (Bogner and Eisner, 1992). To assess the importance of pupation site limitation on cannibalism, which is rarely if ever, distinguished from other forms of density-dependence mesocosm experiments could be conducted, in which the number of pupation sites and the presence of pupa are manipulated. Such studies, especially those under more natural conditions, are needed to determine if cannibalism is as frequent and important for population dynamics and to better understand its role in ecological processes.

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