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Molting inhibits feeding in a grasshopper

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Abstract

In the laboratory, we measured the nonfeeding periods that precede and follow molting and hatching in the lubber grasshopper, *Romalea microptera*. New hatchlings first fed ~ 16 h after egg eclosion. A similar ~ 12-h nonfeeding period was observed after each molt. In contrast, the premolt nonfeeding period increased from 25 h for the 1st molt, to 64 h for the adult molt. In total, hatch- and molt-related nonfeeding periods comprised ~ 272 h, or 21% of the total 54-d nymphal development period. Scientists need to be aware of molt-related nonfeeding periods in arthropods, because they could influence nutrition, growth, physiology, feeding ecology, predator exposure, and life history. They may also hamper pest control, because short-lived poison baits or ingestion-dependent insecticides will not harm individuals that are not feeding. In this study, grasshoppers tended to molt near the beginning of the photophase. Early morning molting might have nutritional, thermal, humidity, or antipredator benefits for grasshoppers in the field.

Key words

Romaleidae, Acrididae, *Romalea microptera*, molting, feeding, feeding rhythm, molting rhythm, circadian rhythm, hatching, grasshopper

Introduction

Scientists are generally aware of the seasonal and daily feeding rhythms of insects. For example, insects usually do not feed during winter diapause or summer estivation (Masaki 1980, Slansky & Scriber 1985). Likewise, diurnal, nocturnal, or crepuscular species usually feed only during those specific times (Gangwere 1958, Beck 1980). Within periods of normal activity, feeding may be periodic or nearly constant (Slansky & Scriber 1985). Less well known, however, are the nonfeeding periods associated with hatching or molting (Bernays & Simpson 1982, Sehnal 1985, Slansky 1985); these fasting periods can be substantial, lasting, in some cases, several days. For scientists studying nutrition, physiology, growth, development, or feeding ecology, it is important to be aware of such nonfeeding periods. In this paper, we document the lengths of the posthatch, premolt, and postmolt nonfeeding periods in the Eastern Lubber grasshopper, *Romalea microptera* (Beauvois) (Romaleidae), in the laboratory.

Materials and Methods

Insects.—Our animals derived from a laboratory colony of *Romalea microptera* (Beauvois) established at Illinois State University from insects collected in 2004 near Shark Valley, Everglades National

Park, Florida, and thereafter maintained as per Matuszek and Whitman (2001).

Experimental design.—We examined the relationship of feeding to molting at seven points in the life cycle of lubber grasshoppers: before the 1st, 4th, and 5th molts, after hatch, and after the 1st, 3rd, and adult molts. Insects were kept individually in 1-L clear plastic containers with nylon netting as a molting substrate. Hatchlings (first instars) were maintained in environmental chambers at 13:11 LD photoperiod, constant 32°C, and > 85% RH, with lights-on at 8 AM and lights-off at 9 pm local time. Subsequent stages were maintained in a similar manner, except we used a 32:24°C thermoperiod, because we believed that cooler scotophase temperatures would more closely mimic nature. We examined containers every half hour from ~15 min prior to lights-on, to ~ 45 min after lights-off, and noted any molting or feeding. We placed a fresh piece of Romaine lettuce in the bottom of each cup at the beginning and end of the day, whenever the lettuce started to wilt (~ every 4 h), and whenever feeding occurred. The amount of lettuce varied with the instar: hatchlings received ~ a 4-cm² piece, and adults received ~ 40 cm² of lettuce. The lettuce was cut with straight edges, which allowed easy detection of any feeding.

Results

Virtually all feeding occurred during the photophase: in the evening, prior to lights-off, the insects generally ascended to the top of the containers, where they remained throughout the cooler scotophase. Table 1 shows that the grasshoppers failed to feed after hatching and both before and after molting. The lengths of the postmolt nonfeeding periods were related to the time of day of hatch or molt. Lubbers that molted or hatched early in the day (i.e., before noon) generally began feeding that same day, whereas those that hatched or molted late in the day (after 2 PM) generally did not feed until lights-on the next day. Females exhibited a non-significant trend for longer nonfeeding periods than males (Table 2). The longest nonfeeding period was observed in one 5th instar female that did not feed for 91.5 h prior to molting to the adult, and 8 h after molting (total time = 99.5 h). In contrast, the shortest total nonfeeding time for the adult molt was 28.5 h for a male. Fig. 1 illustrates the estimated mean lengths of the nonfeeding periods for all molts. Note that lengths of the premolting nonfeeding periods increase with instar. Finally, Fig. 2 is a plot of the time of day of molting for 4th and 5th instars combined, and suggests that most molting occurs in the morning, or even prior to lights-on.

Table 1. Lengths of various pre- and postmolt nonfeeding periods in *Romalea microptera* grasshoppers. "Before 1st molt" refers to the molt from 1st to 2nd instar, "Before 5th molt" refers to the molt to adult, "same day" refers to individuals that begin feeding during the same day (photophase) that they molted, and "next day" refers to individuals that began feeding the day after they molted (after an intervening scotophase).

Mean length of nonfeeding period (h)		
Stage	n	$\bar{x} \pm s_{\bar{x}}$ (h)
After hatch (same day)	9	8.7±2.3
After hatch (next day)	20	19.8±2.7
After hatch (all animals)	29	16.3±5.8
Before 1 st molt	16	25.2±4.0
After 1 st molt (same day)	6	7.8±2.0
After 1 st molt (next day)	4	19.5±1.8
After 1 st molt (all animals)	10	12.5±6.3
After 3 rd molt (same day)	7	8.4±3.0
After 3 rd molt (next day)	4	17.5±2.8
After 3 rd molt (all animals)	11	11.7±2.8
Before 4 th molt	16	40.4±8.4
Before 5 th molt	29	63.7±22.5
After adult (same day)	17	9.8±2.7
After adult (next day)	7	19.0±4.3
After adult (all animals)	24	12.5±5.3

Discussion

Our results show that lubber grasshoppers do not feed immediately before or after molting. The nonfeeding period for the adult molt alone (including both pre- and postmolt), can be as long as 99.5 h (= 4.1 d). These findings corroborate previous studies of hatching and molting *vs* feeding in grasshoppers (Valova 1924, Goodhue 1962, Blaney *et al.* 1973, Uvarov 1977, Chapman & Beerling 1990). For example, newly hatched *Locusta migratoria* do not feed for the first 12 to 18 h (Nikol'skii 1925).

For lubbergrasshoppers, the sum of all hatching- and molt-related nonfeeding periods is estimated to be ~ 272 h or 11.3 d. (Fig. 1) out of a 54-d nymphal development period (at 32:24°C thermo-period) (Matuszek & Whitman 2001). Hence lubber grasshoppers are unable to feed for ~ 21% of their nymphal development period. This compares with total molt-related nonfeeding periods of ~ 10% for the grasshopper *Schistocerca gregaria*, and ~ 25% for *Stauroderus scalaris* (Valova 1924, Husain *et al.* 1946, Goodhue 1962). These fasting periods could influence nutrition, growth, physiology, feeding ecology, and life history. For example, up to 33% of accumulated lipid and 73% of accumulated carbohydrate can be metabolized during a single molt in some insects (Hiratsuka 1920, Woodring *et al.* 1977). Thus, these nonfeeding periods may be stressful, because they coincide with the most metabolically demanding moments of nymphal development. Finally, these fasting periods may impede pest control, because short-lived poison baits or ingestion-dependent insecticides will not harm individuals that are molting and thus, not feeding. Scientists working in these areas need to be cognizant of these relationships.

The physiology underlying these nonfeeding periods is unknown, but probably relates to apolysis prior to molting, and cuticular hardening after molting. During apolysis, the old cuticle (including that

Table 2. Comparison of the lengths of the premolt nonfeeding periods for male *vs* female *Romalea microptera* grasshoppers for the 4th and 5th molts. Males and females did not differ significantly in variances ($p > 0.05$, F-tests) or means ($p > 0.05$, t-tests).

Mean length of nonfeeding period (h)			
Stage	Sex	n	$\bar{x} \pm s_{\bar{x}}$ (h)
Before 4th molt	Males	6	37.1±5.6
	Females	10	42.4±9.5
Before 5th molt	Males	16	60.5±23.8
	Females	13	67.8±21.1

of mouthparts, foregut, and hind gut) digests away and separates from the underlying epidermis (Chapman 1998, Nation 2001). Presumably, the mandibles and gut cannot be used for feeding at this time. Likewise, after molting, the cuticle is soft, untanned, and nonfunctional in regard to feeding. Insects may also need to partially empty their gut prior to molting, not only to facilitate the shedding of the cuticular linings of the fore and hind guts, but to reduce internal mass and size in order to facilitate the sliding of the insect body through the old cuticle during ecdysis. A full gut, and resulting large mass, might also deform soft, untanned exoskeleton. In addition, before ecdysis the gut is filled with air and remains that way for some time after (Uvarov 1966, Chapman 1998).

In our studies, there were strong trends for the premolt fasting period to increase with instar (Table 1) and for females to exhibit longer nonfeeding periods than males (Table 2). Similar trends have been observed in *S. gregaria* and *S. scalaris* (Valova 1924, Husain *et al.* 1946, Goodhue 1962). For example, the nonfeeding period in *S. gregaria* averaged 28 h for the 1st molt, but 53 h for the adult molt (Husain *et al.* 1946). This may be related to thicker cuticle in older and larger instars and females, which may require more time to prepare for molting and more time to tan after molting.

During our experiments, the posthatch or postmolt nonfeeding periods for individuals ranged from 5 to 29 h, and depended on the time of day the insect hatched or molted. Individuals that hatched or molted before dawn or early in the day, generally fed before nocturnal roosting, whereas those that hatched or molted in the afternoon did not feed until the next day (next photophase) (Table 1). In nature, lubbers roost at the tops of plants at night and generally do not feed during this period (Whitman & Orsak 1985, Whitman 1987). Hence the instinct to roost at night appears to override the need to feed after molting.

Delays in feeding could be harmful for insects, because growth and development rates are related to feeding. In nature, insects are often in a race against time to complete development and reproduce prior to death; early maturation and reproduction can increase fitness (Stearns 1992). Other factors being equal, we would expect selective pressure for early morning hatching and molting in grasshoppers, which would allow them to feed that same day.

Daily hatching and molting times are unknown for *R. microptera* in the field. However, in this laboratory experiment with a 13:11 L:D photoperiod, lights-out at 8 AM, and L:D temperatures of 32:24°C, nearly 70% of 4th and 5th instar grasshoppers molted in the 8-h period between 4 AM and noon, suggesting that lubbers have evolved to molt early in the day.

Insects often display circadian periodicity in hatching or molting (Beck 1980), and some grasshopper species tend to hatch in

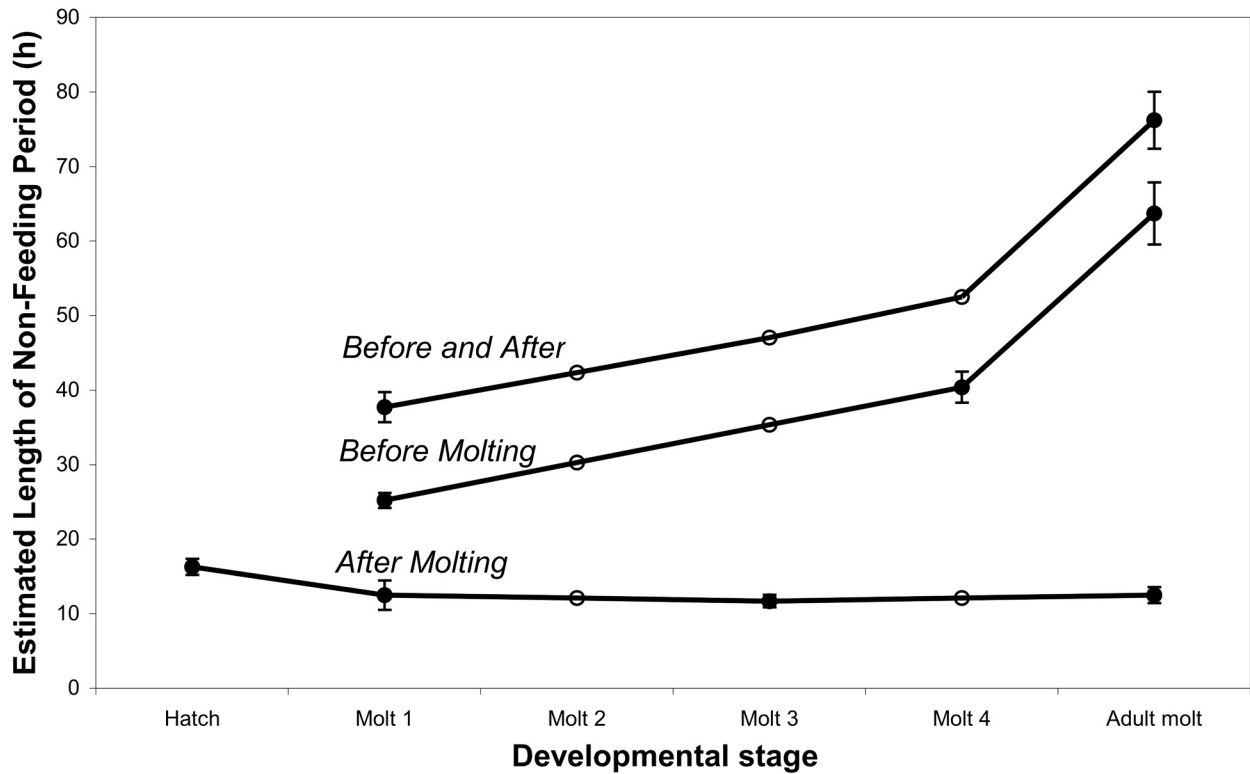


Fig. 1. Estimated nonfeeding times associated with hatching and molting for the grasshopper *Romalea microptera*, based on empirical data (solid circles with SE bars) derived from Table 1. Empty points that lack SE bars represent estimates, based on empirical data.

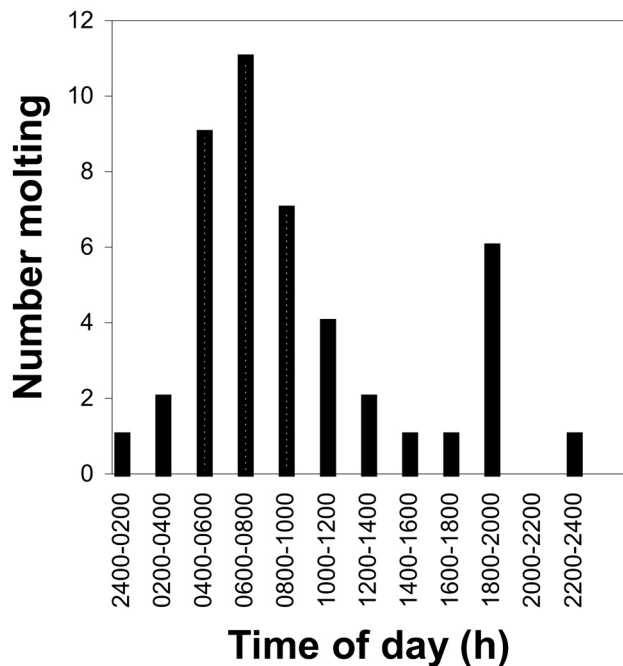


Fig. 2. Time of day of molting for 4th and 5th stadium (combined) *R. microptera* grasshoppers held in environmental chambers at 32: 24°C thermoperiod and 13:11 L:D photoperiod, with lights on at 8:00 am. Note that most animals molt in the morning.

the morning (Wardhaugh *et al.* 1969, Farrow 1975). In *S. gregaria*, in the field, hatching occurred over a short period each day, from just before dawn to 4 h after sunrise (Ellis & Ashall 1957). In desert-dwelling *Taeniopoda eques*, a close relative of *R. microptera* (Rehn & Grant 1961, Stauffer & Whitman, forthcoming), molting is controlled primarily by temperature; insects are physiologically unable to complete molting at body temperatures below 22°C or above 40°C (Whitman & Orsak 1985). In the field, molting begins once air temperatures rise above 26°C. Thus on hot days, when dawn temperatures are above 26°C, molting begins at or before sunrise, and most molting occurs before 1 PM. On cool days, when 26°C is not reached until near noon, most molting occurs in the afternoon. On cold, cloudy days (<21°C) there is no molting, whereas on warm evenings (>26°C), molting continues into the night (Whitman & Orsak 1985). However, attempting to link molting with air temperature in the field is problematic, because grasshoppers solar-bask and when sunlight is available, can raise their body temperatures as much as 18°C above air temperatures (Chappell & Whitman 1990). For *R. microptera* and other hot-climate grasshoppers, early morning or predawn hatching and molting may have thermal, humidity, and antipredator benefits.

Finally, we point out that the lengths of these nonfeeding periods are undoubtedly determined by an interplay between innate and environmental factors, including time of day of hatching or molting. Innate physiological response would best be observed under constant light and constant favorable temperature. However, in our experiment, we tested animals under variable conditions that mimicked the environment. Consequently, our results were influenced by nocturnal roosting, which greatly lengthened the postmolting nonfeeding periods for some individuals. The use of different temperatures, thermoperiods, and photoperiods, or us-

ing only animals that had molted at a specific time of day, would probably have produced different results. Despite these sources of variation, we conclude that grasshoppers, and probably other molting animals, spend a significant proportion of their development period unable to feed.

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