Orientation and Dispersal Patterns of the Eastern Tent Caterpillar, *Malacosoma americanum* F. (*Lepidoptera: Lasiocampidae*)

L. K. Rieske[1,2] and L. H. Townsend[1]

Larvae of the eastern tent caterpillar, Malacosoma americanum, *undergo density-dependent dispersal in response to depleted resources. Because these caterpillars have recently been implicated in abortions of pregnant mares (equine Mare Reproductive Loss Syndrome, or MRLS), there is increased interest in managing caterpillar populations, potentially through manipulation of caterpillar dispersal behavior. Consequently, we investigated dispersal patterns of food-deprived eastern tent caterpillars in artificial arenas with respect to distance, direction, and response to visual stimuli. Distance traveled is influenced by time of day, and is strongly correlated with time elapsed. Movement is non-random, and correlates closely with the position of the sun. The pattern is more pronounced with foraging third instars than with penultimate fifth instars. Visual cues appear important in caterpillar orientation, and caterpillars are responsive to vertically oriented, black objects.*

INTRODUCTION

Density-dependent dispersal of phytophagous insects is a behavioral adaptation that alleviates the negative impacts of overcrowding, and enhances resource partitioning within a local population. Density-dependent

[1]Department of Entomology, University of Kentucky, Lexington, Kentucky.
[2]To whom correspondence should be addressed at University of Kentucky Department of Entomology, S-225 Ag. Science North, Lexington, Kentucky. E-mail: lrieske@uky.edu.

dispersal is well documented among tree-feeding lepidopterans in both deciduous (Doane and McManus, 1981) and coniferous systems (Morris, 1963), and is commonplace among folivores. The majority of examples involve dispersal of winged adults (Morris, 1963; Rainey, 1976) or neonate larvae by ballooning (Barbosa *et al.*, 1989), but of necessity, older larvae are often forced to move considerable distances to locate suitable resources.

The eastern tent caterpillar, *Malacosoma americanun* (Fabricius) (Lepidoptera: Lasiocampidae), is a native tree-feeding folivore. Caterpillars are gregarious, and are central-place foragers (sensu Fitzgerald, 1995) that construct conspicuous silken tents that increase in size as the caterpillars mature (Stehr and Cook, 1968; Dethier, 1980; Drooz, 1985). Eastern tent caterpillars prefer foliage of wild cherry, *Prunus serotina* Ehrh. (Drooz, 1985), which grows abundantly along forest edges and roadsides. At endemic levels, caterpillars forage only as far as necessary to feed (Fitzgerald and Willer, 1983; Fitzgerald *et al.*, 1988), and may remain in their natal tree throughout development (Fitzgerald, 1995). But as populations increase to outbreak levels and preferred hosts are defoliated, host plant requirements become less stringent (Tietz, 1972; Rieske, 2004). Caterpillar foraging is highly dependent on the production of and response to trail pheromones, whose effectiveness is enhanced by the production of silken filaments. Eastern tent caterpillar dispersal behavior has been studied extensively in the context of diurnal feeding patterns (Fitzgerald and Willer, 1983; Fitzgerald *et al.*, 1988), trail pheromone production (Fitzgerald, 1993), and recruitment behavior (Fitzgerald and Peterson, 1983), but little is known about inter-tree dispersal and dispersal patterns from depleted food sources.

Because eastern tent caterpillars have recently been implicated in equine Mare Reproductive Loss Syndrome (MRLS) (Kane and Kirby, 2001), there is increased awareness of and interest in managing caterpillar populations. Eliminating exposure of pregnant mares to caterpillar cuticle is critical for reducing foal losses associated with MRLS (McDowell and Webb, 2003), but grazing restrictions and environmental concerns make widespread insecticide applications for tent caterpillar control impractical on horse farms. Highly mobile, dispersing caterpillars, and use of alternate host plants by feeding caterpillars (Rieske, 2004), make efforts at focused control difficult (Townsend, 2002a,b), but also raises the possibility that dispersal behavior might be manipulated to manage local caterpillar populations.

We investigated the orientation and dispersal patterns of food-deprived eastern tent caterpillars from a point source in artificial arenas. Our specific objectives were to assess age-specific and diurnal dispersal

patterns with respect to (1) distance, (2) direction, and (3) response to visual stimuli.

MATERIALS AND METHODS

Experiments were conducted in the spring of 2002 using field-collected eastern tent caterpillars that were obtained by clipping intact tents from wild cherry trees in and around Lexington, Kentucky (Fayette County). As caterpillars matured and local sources were depleted, additional caterpillars were obtained from south-central Wisconsin (Dane and Sauk Counties) and northern Michigan (Houghton County). Caterpillars were held in the laboratory in growth chambers (23°C, 15:9 L:D), and fed fresh field-collected wild cherry foliage as needed. All caterpillars were sorted and aged (Fitzgerald, 1995), and only those that appeared healthy were used in experiments. All caterpillars were deprived of food for 12 h before use, and released en masse from the centers of the test arenas. Immediately before release, caterpillars were powdered with a fluorescent dye (DayGlo Color Corp., Cleveland, OH) to facilitate tracking.

Distance traveled by dispersing caterpillars was measured using a measuring tape or measuring wheel, and bearings from the release point were assessed with a compass. Our experiments were conducted in a roughly rectangular, ~1.5 ha, recently paved asphalt parking area on the campus of the University of Kentucky. In the first dispersal experiment (Time interval dispersal), we utilized the entire 1.5 ha area, whereas in the second and third experiments (Fixed distance and Visual stimuli, respectively), the study site was divided into 16 circular arenas arranged in four blocks.

Time Interval Dispersal

Food-deprived, foraging caterpillars (third instars, $N = 75$) were released from the center point of the 1.5 ha study area at 0600 h (EDST) and 1800 h (EDST), coinciding with times of natural foraging activity, on three consecutive days (15–17 May 2002). Distance and bearing were monitored at intervals of 30, 60, 90, 120, and 360 min for those released at 0600 h, and at intervals of 30, 60, 90, and 120 min for those released at 1800 h. Evening releases could only be tracked for 120 min because of impending darkness. There were three replicates of the 0600 h release, but due to inclement weather there were only two completed replicates of the 1800 h release ($N = 75$ caterpillars per release). The mean air temperature at 0600 h was 12.3°C, with an average of 15.2°C over the 120 min morning assay ($N = 3$). At 1800 h, the mean air temperature was 17.1°C, averaging 17.9°C over the

corresponding 120 min ($N = 2$) (UK Ag. Weather Data, 2002). Sky conditions during relevant time intervals (0600–1200 h and 1800–2000 h) during 15–17 May were classified as 'cloudy,' containing 100% opaque cloud coverage, with the exception of a single 1-h interval (0800–0900) on 16 May, when coverage was 'partly sunny,' containing 38–63% cloud coverage (UK Ag. Weather Data, 2002). Wind direction was highly variable, and wind speed averaged 12.2 km/h (range: 0–19 km/h). Although surface temperature measurements were not consistently taken over the course of the study, temperatures obtained from a mercury thermometer placed on the surface at 0600 and 1800 h were 19.5 and 27°C, respectively, each averaged over two measurements.

Fixed Distance Dispersal

To assess dispersal direction independent of distance, and to evaluate age-specific differences in dispersal behavior, a second set of experiments were developed where caterpillars were released from the center of circular arenas drawn in chalk on the surface of the 1.5 ha study site. There were four blocks of four circular arenas, for a total of 16 arenas. Arenas for replicates involving foraging third instar caterpillars were 10 m in diameter, and arenas for replicates using penultimate fifth instars were 20 m in diameter. In both cases there was a minimum distance of 10 m between arenas. Food-deprived caterpillars ($N = 25$) were released from the center of each arena, and dispersal direction was monitored for 120 min. When caterpillars reached the edge of the arena, their bearing was noted and they were removed from the study. Measurements were made of the final bearing from the release point for all caterpillars, including those that did not leave their arenas.

Visual Stimuli

Response to visual cues was assessed by measuring caterpillar movement toward vertically oriented objects, designed to simulate tree-trunk images. Each arena included vertically oriented objects consisting of two adjacent 122-cm tall sections of 25-cm diameter pvc pipes, one of which was painted flat black (ColorCast, C& M Coatings, Wheeling, IN, #165965), and the other of which was painted flat white (#165964), placed at the edge of the 20-m diameter arena in one of eight randomly assigned compass directions (N, NE, E, SE, S, SW, W, NW). The reflectance spectrum of both colors was measured using a Labsphere RSA-HP-84 integrating sphere (Labsphere, North Sutton, NH) attached to a Hewlett-Packard HP 8452A

Diode Array spectrophotometer. Caterpillars ($N = 25$ fourth instars) were then released in the arena center ($N = 16$), and orientation and movement was monitored for 60 min. Caterpillar response was scored as positive if caterpillar movement was arrested within 2.5 cm of a vertically oriented black or white PVC pipe. Again, when caterpillars reached the edge of the arena, their bearing from the release point was noted and they were removed from the study. Secondly, to evaluate the importance of visual cues in orientation, caterpillar stemmata were blocked with acrylic fabric paint (Duncan Enterprises, Fresno, CA), effectively eliminating visual stimuli. The visually altered caterpillars ($N = 25$ fourth instars) were then released in the center of each arena ($N = 16$) as described above, and dispersal direction was monitored for 60 min.

Data Analysis

Linear regression analysis was used to assess the relationship between distance traveled and time elapsed following release. Analysis of variance was used to determine if distance traveled by released caterpillars differed between time increments. After analyzing across all releases, we performed a separate analysis for morning and evening releases. We compared dispersal distance at each time increment (up to 120 min) for morning and evening releases using a t-test. To assess the extent to which caterpillar dispersal direction was random, we performed a chi-square analysis across all releases, as well as individually for time of day (morning vs. evening releases), and for time elapsed (120 min vs. 360 min post-release). A separate chi-square analysis was conducted to compare dispersal direction of foraging third instars to penultimate fifth instar caterpillars in the circular arenas. We calculated the empirical mean vector (Batschelet, 1981) across all releases in the Fixed distance dispersal experiments, and for individual releases based on time of day, time elapsed, and caterpillar age. Because dispersal in the morning occurred slowly, we calculated the empirical mean vector using only those caterpillars that had dispersed greater than 5 m at 120 min. We conducted a logistic regression analysis (CATMOD, SAS, 1997) to generate a predictive model of caterpillar dispersal based on time of day (morning vs. evening) and time elapsed (up to 120 min), using eight compass directions (N, NE, E, SE, S, SW, W, NW) and two measures of distance (greater than and less than 5 m from the release point). We used a chi-square analysis to measure the randomness of orientation, and calculated an empirical mean vector, of caterpillars with blocked stemmata to assess the reliance of dispersing caterpillars on visual stimuli. Lastly, a paired t-test was performed to assess differences in sighted caterpillar response to black and white vertically oriented objects.

RESULTS

Time Interval Dispersal

The proportion of caterpillars dispersing in the evening ($\bar{x} = 82\%$) was greater than the proportion dispersing in the morning ($\bar{x} = 73\%$), but this difference was not significant ($|t| = 1.4$, $P = 0.39$). Across all replicates the distance traveled by released third instar caterpillars increased significantly over time ($F = 23.7$, $P < 0.001$). The relationship between distance traveled and time elapsed was significant in both morning ($F = 13.4$, $P = 0.003$) and evening ($F = 11.1$, $P = 0.001$) releases. The distance traveled by caterpillars released in the evening was significantly greater than that traveled by caterpillars released in the morning at each time interval (Fig. 1). Caterpillars released in the morning (3 releases of 75 caterpillars each) traveled at a relatively slow and steady rate of ~2.5 cm/min, and covered an average distance of ~3 m in 120 min. The distance traveled at 30 min differed from the distance traveled at 90 min ($P = 0.02$) and 120 min ($P = 0.003$), and the distance traveled at 60 min differed from that at 120 min ($P = 0.03$) (Fig. 1). However, there was no difference in distance traveled between the 30 and 60 min time increments, between the 60 and 90 min increments, and between 90 and 120 min increments. In contrast, the distance traveled by caterpillars released in the evening ($N = 2$ releases of 75 caterpillars each) increased steadily, but was similar across intervals. Caterpillars released in
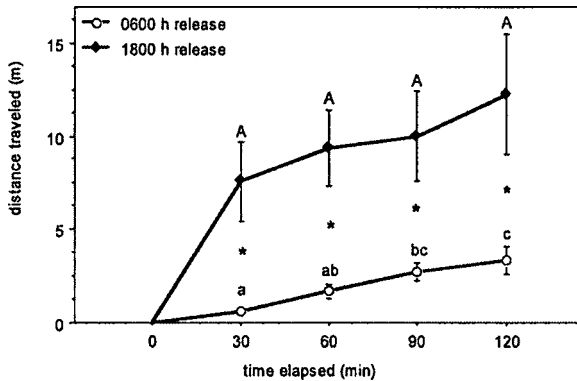
Fig. 1. Distance traveled (m) over time (min) by eastern tent caterpillars released in a 1.5 ha arena from a central release point. Within a release, means followed by the same letter are not significantly different; ∗ indicates significant differences between morning and evening releases at specified time intervals.

the evening traveled at a relatively rapid average rate of 17 cm/min, and covered an average distance of 12.5 m in 120 min, over four times the distance of those released in the morning (Fig. 1).

Third instar eastern tent caterpillar dispersal direction across all releases was non-random ($\chi^2 = 47.1$, $P < 0.0001$), with an empirical mean vector of 351.4° (due north: 0°or 360°). The non-random dispersal pattern was most apparent in the morning (Table IA), when dispersing caterpillars (those that moved >5 m) showed greatest movement in the northerly directions (north, northeast, and northwest). Over 53% of the caterpillars tracked in the morning were concentrated in the northeast compass quadrant (Fig. 2A), with a mean vector of 57.1° (Fig. 2A). In Lexington, Kentucky in mid-May, the sun rises at approximately 65° (ENE) at 0528 h (U.S. Naval Observatory, 2003), which differs from the direction of dispersing caterpillars by only 8°. This directional pattern was evident 2 h postrelease, and persisted for 6 h following the morning releases (Table IB), after which the caterpillars were no longer tracked. In the evening, caterpillar movement was only marginally non-random, but again, appeared biased away from the south (Table IA and Fig. 2B). Nevertheless, 47% of the tracked caterpillars moved in a west-northwesterly direction (Fig. 2B), with a mean vector of 301.7°. Sunset occurred at 295° (WNW) at approximately 1942 h (U.S. Naval Observatory, 2003), a difference of less than 7°. The directional difference at this time and location between sunrise and sunset was 130°, and the directional difference between morning and evening dispersing caterpillars was similar, at 115°.

Logistic regression analysis generated a predictive model for the position of a dispersing third instar caterpillar using time of day (morning vs. evening) and time elapsed from the initiation of dispersal (up to 120 min). The analysis determined the likelihood of finding a dispersing caterpillar in

Table I. Dispersal Direction (% response) of Foraging Eastern Tent Caterpillars Released from the Center of a 1.5 ha Study Site

	Magnetic compass direction									
	N	NE	E	SE	S	SW	W	NW	χ^2/P	Mean vector[b]
A. Release time[a]										
0600 h ($N = 3$)	20	19	14	7	6	7	12	16	43.7/<0.001	57.1°
1800 h ($N = 2$)	19	11	12	10	12	9	17	11	12.2/0.09	301.7°
B. Time elapsed[c]										
2 h post-release	19	13	13	9	9	9	15	14	19.7/0.006	29.2°
6 h post-release	21	22	13	6	6	6	11	13	32.9/0.001	21.3°

[a]assessed: 2 h post-release.
[b]for caterpillars dispersing >5 m.
[c]for morning releases only.
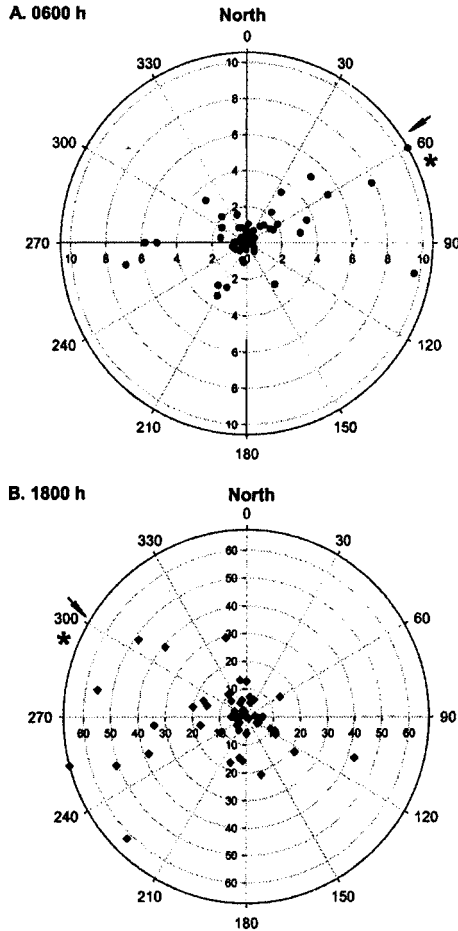
A. 0600 h

B. 1800 h

Fig. 2. Representative dispersal patterns of eastern tent caterpillars released in a 1.5 ha study site at A. 0600 h, and B. 1800 h. → denotes empirical mean vector across all releases within each time period, and * denotes position of sunrise (A) and sunset (B), respectively. Note the difference in distance traveled (m) between morning and evening releases.

one of eight compass directions (N, NE, E, SE, S, SW, W, NW), at either greater than or less than 5 m from a dispersing point (Table II). The model corroborates the previous assay analysis demonstrating that caterpillars disperse more slowly in the morning, since all predicted likelihoods greater

Table II. Predicted Probability (%) of Finding a Dispersing Eastern Tent Caterpillar in One of Eight Compass Directions (N, NE, E, SE, S SW, S, and NW) and Greater Than or Less Than 5 m from the Dispersal Point, Based on Time of Day and Time Elapsed. Only Those Outcomes Generating >10% Predicted Probabilities Are Included

Release time	Time elapsed (min)	Compass direction	Distance (m)	Predicted probability
0600 h	30	N	≤ 5	25.7
		NW	≤ 5	23.2
		S	≤ 5	17.6
	60	E	≤ 5	10.4
		N	≤ 5	16.2
		NE	≤ 5	13.1
		NW	≤ 5	17.9
		W	≤ 5	10.7
	90	N	≤ 5	14.0
		NE	≤ 5	14.1
		NW	≤ 5	13.9
		SW	≤ 5	11.4
	120	N	≤ 5	13.1
		NE	≤ 5	18.2
		NW	≤ 5	13.0
1800 h	30	N	≤ 5	18.0
		S	≤ 5	12.6
		SE	< 5	10.5
		E	≤ 5	12.2
	60	—	—	—
	90	N	> 5	13.2
		SW	≤ 5	10.3
		W	> 5	23.1
	120	N	> 5	11.1
		S	> 5	12.5
		W	> 5	17.3

than 10% in the morning releases occurred <5 m from the point of dispersal. The logistic regression model proved more robust in predicting patterns of caterpillar dispersal in the morning than in the evening. The model's greatest predictive potential occurred at 30 min post-dispersal for morning-dispersing caterpillars, when it generated a 25.7% likelihood of finding a caterpillar within 5 m and in a northerly direction from the point of dispersal, and a 23.2% likelihood of finding a caterpillar <5 m in a northwesterly direction. For evening-dispersing caterpillars, the greatest predictive potential occurred 90 min post-release, when the model predicted a 23.1% likelihood of finding a caterpillar >5 m west of the dispersing point.

Fixed Distance Dispersal

Caterpillars demonstrated directional movement in the circular arenas that was strongly non-random across both age groups ($\chi^2 = 42.2$,

Table III. Dispersal Direction (% response) of Food-Deprived Eastern Tent Caterpillars Released from the Center of Circular Arenas ($N = 16$)

| | Magnetic compass direction | | |
	N	NE	E	SE	S	SW	W	NW	χ^2/P	Mean vector
A. Caterpillar age[a]										
Foraging	18	11	11	3	4	6	19	28	302.4/ $\ll$ 0.0001	23.9
Penultimate	16	15	14	10	10	9	11	16	11.6/0.11	348.2
B. Visual status[b]										
Sighted	20	16	13	8	8	8	14	14	42.27/0.001	348.0
Altered	12	14	16	13	14	13	11	7	26.8/0.004	46.12

[a]'foraging' are third instar caterpillars; 'penultimate' are fifth instars.
[b]'sighted' are caterpillars with full vision; 'altered' are caterpillars with stemmata obstructed.

$P < 0.001$), with a mean vector of 32.6°. Third instar, foraging caterpillars' directional movement was non-random, again biased away from the south and with a mean vector of 23.9° (Table III.A). In contrast, dispersal direction of fifth instars was random, with a mean vector 348.2°, and differed significantly from directional patterns of the younger foraging caterpillars ($\chi^2 = 47.3$, $P < 0.0001$).

Visual Stimuli

When caterpillar stemmata were blocked, effectively eliminating visual stimuli, the bias in caterpillar orientation shifted significantly ($\chi^2 = 131.9$, $P \ll 0.0001$), but the non-random orientation persisted. Dispersal of caterpillars with blocked stemmata was more even across directions, with the lowest response to the northwest (Table IIIB).

Sighted caterpillars responded to the vertically oriented objects in 80% of the releases. The proportion of caterpillars responding to black was significantly greater than those responding to white (83% vs. 22%; $|t|_{1,37} = 5.31$, $P < 0.0001$), and the relative reflectance of the black objects was lower than the white at every wavelength measured (Fig. 3).

DISCUSSION

Eastern tent caterpillars released in the evening traveled at over four times the rate of those released in the morning. Since both release times coincided with periods of active tent caterpillar foraging and feeding (Fitzgerald *et al.*, 1988), the differences in dispersal rates are most likely due to external factors such as temperature and light. Caterpillar dispersal rate is temperature dependent, and is a function of body length and
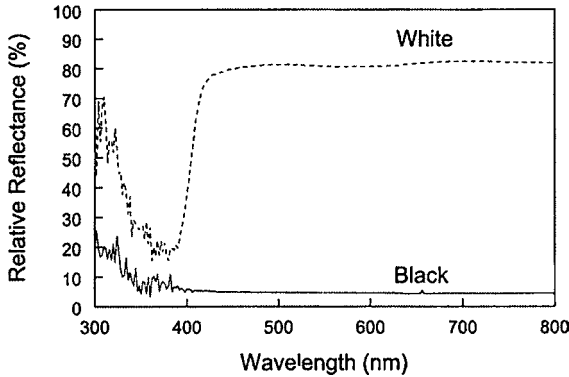
Fig. 3. Reflectance spectra of vertically oriented objects painted with flat black and flat white (generated by B.L. Strom, U.S. Forest Service). Each spectrum is its reflectance relative to a white standard.

body temperature (Joos, 1992). Skies remained cloudy over the duration of our study, but the air temperature averaged 2.7°C higher at 1800 h than at 0600 h, and perhaps more importantly, there was a 7.5°C difference in surface temperature between the two release times. Clearly, elevated evening air and surface temperatures will influence dispersal rate. Ambient light intensity undoubtedly varies between 0600 h and 1800 h, but other than noting nearly 100% opaque cloud coverage during our study (UK Ag. Weather Data, 2002), light intensity was not quantified.

The patterns of orientation of morning-released and evening-released foraging caterpillars strongly suggests that caterpillar dispersal is influenced by the position of the sun. Foraging third instar eastern tent caterpillars did not disperse randomly in artificial arenas, but showed a distinct pattern and bias away from southerly movement, with net movement to the north northeast. This non-random dispersal persisted for at least several hours; the mean vector of dispersing caterpillars tracked for 2 h and those tracked for 6 h differed by less than 8°. The direction of caterpillar dispersal in the morning differed from the direction of sunrise by only 8°, and the difference between evening dispersal direction and sunset was less than 7°.

Given that eastern tent caterpillars have a well-developed system of trail pheromone production, it's possible that the observed dispersal patterns could be influenced by exploratory trail pheromones produced by the early dispersing caterpillars within a release, but we did not observe processional behavior and the consistency of caterpillar orientation to the sun's position suggest this is unlikely. Eastern tent caterpillars seeking food deposit exploratory foraging pheromone trails, composed of a diketone

(5β-cholestane-3,24-dione) on silken fibers (Crump *et al.*, 1987). Upon location of a suitable food source, recruitment pheromone trails are laid repeatedly on top of the silken trails, which elicit elevated response by colony-mates, thereby recruiting additional caterpillars to a food find. Each passing caterpillar reinforces the trail, and caterpillars choose stronger trails over weaker trails (Fitzgerald and Peterson, 1983). These steroidal trail pheromones have relatively low volatility (Crump *et al.*, 1987); caterpillars are not attracted from great distances, and show little lateral displacement when following trails (Roessingh *et al.*, 1988). The considerable variability in dispersal direction that we observed within each release would not have occurred had response to trail pheromone been the primary orientation mechanism.

In contrast to the younger caterpillars, the penultimate fifth instar caterpillars in our study were nearly random in their orientation and movement. As tent caterpillars develop, they become less responsive to environmental stimuli. Older caterpillars may have been undergoing physiologically-based migratory behavior characterized by reduced response to environmental stimuli and more direct movements, presumably in preparation for pupation, whereas the foraging caterpillars appear to demonstrate nonmigratory, 'trivial' movements (sensu Dingle, 1972) associated with feeding.

Dependence of eastern tent caterpillar on sunlight for orientation is further supported by the observed shift of nearly 58° in caterpillar orientation when stemmata were obstructed. If caterpillar movement were primarily olfactory-based, a shift due to stemmata obstruction would be unlikely. The observational data of Wellington *et al.* (1951) suggest that caterpillars utilize polarized light detected through stemmata for orientation. They demonstrated that several caterpillar species are sensitive to the plane of polarization, and that by rotating the plane of polarized light a specific amount with polarizing filters, forest tent caterpillar, *M. disstria*, movement can be shifted by a similar amount. Caterpillar stemmata can also detect visible light and are allegedly capable of crude image formation (Chapman, 1998). Larvae swing their heads back and forth, scanning their surroundings, and can detect object shape and orientation (Dethier, 1942, 1943). Studies of other tree-feeding lepidopterans have demonstrated caterpillar orientation toward objects (Hundertmark, 1937), and a limited ability to discern an objects' size and relative distance (Roden *et al.*, 1992). Our results corroborate earlier findings that suggest that eastern tent caterpillars are capable of discriminating between objects with differing light reflectance, appear able to detect the contrast between black and white, and may be capable of discerning the relative position of vertical objects (Fitzgerald, 1995). Response to vertically oriented black objects resembling

tree trunks would be an adaptive advantage to caterpillars seeking food after their natal hosts were depleted.

As with many lepidopterans, density-dependent dispersal of older larvae is most likely triggered by depletion in resource quantity or quality, or increased contact between larvae (Horn, 1988). However, genetic variability within a local population cannot be completely discounted, nor can behavioral differences between geographically distinct populations. Wellington *et al.* (1975) suggest that populations of the closely related western tent caterpillar contain active (Type I) morphs that disperse outward and establish new infestations, and inactive (Type II) morphs that remain local. However, Edgerly and Fitzgerald (1982) question the existence of active and inactive larval types in *M. americanum*, and minimize the importance of behavioral polymorphism in this species. They suggest that the activity level of a given caterpillar, and its relative aggressiveness related to construction of exploratory trails and feeding bouts, and is simply a function of hunger. All caterpillars utilized in our study were equally food-deprived, however, suggesting that observed differences in dispersal may be more complex than a simple hunger reflex. Regardless of the driving mechanism, it is clear that the aggregated spatial distributions of eastern tent caterpillars becomes less pronounced as larvae mature and exhaust optimal resources, prompting caterpillar dispersal.

Knowledge of the processes influencing the spatial dynamics of a population is key to understanding temporal and spatial fluctuations in caterpillar density. Eliminating exposure of pregnant mares to eastern tent caterpillars appears critical for reducing equine foal losses to MRLS. The ability to anticipate the direction and distance of dispersing caterpillars from infested fence rows relative to grazing mares is a key step in minimizing exposure. Increasing our knowledge of caterpillar dispersal may permit eventual manipulation of caterpillar behavior to allow suppression of populations through very focused control efforts and/or pasture management.

ACKNOWLEDGMENTS

REFERENCES

Barbosa, P., Krischik, V., and Lance, D. (1989). Life history traits of forest-inhabiting flightless Lepidoptera. *Am. Midl. Nat.* **122:** 262–274.

Batschelet, E. (1981). *Circular Statistics in Biology*, Academic Press, New York.

Chapman, R. F. (1998). *The Insects: Structure and Function, 4th ed,* Cambridge University Press, Cambridge.

Crump, D., Silverstein, R. M., Williams, H. J., and Fitzgerald, T. D. (1987). Identification of trail pheromone of larva of eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *J. Chem. Ecol.* **13:** 397–402.

Dethier, V. G. (1942). The dioptric apparatus of lateral ocelli. I. The corneal lens. *J. Cell. Comp. Physiol.* **19:** 301–313.

Dethier, V. G. (1943). The dioptric apparatus of lateral ocelli. II. Visual capacities of the ocellus. *J. Cell. Comp. Physiol.* **22:** 115–126.

Dethier, V. G. (1980). *The World of the Tent-Makers: A Natural History of the Eastern Tent Caterpillar,* University of Massachusetts Press, Amherst.

Dingle, H. (1972). Migration strategies of insets. *Science* **15:** 1327–1335.

Doane, C. C., and McManus, M. L. (1981). The gypsy moth: Research toward integrated pest management. USDA For. Serv. Tech. Bull. 1584. Washington, DC.

Drooz, A. T. (1985). Insects of eastern forests. USDA For. Serv. Misc. Publ. 1426. Washington, DC.

Edgerly, J. S., and Fitzgerald, T. D. (1982). An investigation of behavioral variability within colonies of the eastern tent caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *J. Kansas Entomol. Soc.* **55:** 145–155.

Fitzgerald, T. D. (1993). Trail following and recruitment: Response of eastern tent caterpillar, *Malacosoma americanum*, to 5β-cholestane-3,24-dione and 5β-cholestane-3-one. *J. Chem. Ecol.* **19:** 449–457.

Fitzgerald, T. D. (1995). *The Tent Caterpillars,* Comstock Publishing, Ithaca, New York.

Fitzgerald, T. D., Casey, T., and Joos, B. (1988). Daily foraging schedule of field colonies of the eastern tent caterpillar, *Malacosoma americanum*. *Oecologia* **76:** 547–578.

Fitzgerald, T. D., and Peterson, S. C. (1983). Elective recruitment communication by the eastern tent caterpillar (*Malacosoma americanum*). *Anim. Behav.* **31:** 417–423.

Fitzgerald, T. D., and Willer, D. E. (1983). Tent-building behavior of the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *J. Kans. Entomol. Soc.* **56:** 20–31.

Horn, D. J. (1988). *Ecological Approach to Pest Management*, Guilford Press, New York.

Hundertmark, A. (1937). Das Formunterscheidungsvermogen der Eiraupen der Nonne (*Lymantria monacha*). *Z. Verg. Physiol.* **24:** 563–582.

Joos, B. (1992). Adaptations for locomotion at low body temperatures in eastern tent caterpillars, *Malacosoma americanum*. *Physiol. Zool.* **65:** 1148–1161.

Kane, E., and Kirby, E. (2001). Death in the bluegrass. *Equus* **287:** 60–68.

McDowell, K., and Webb, B. (2003). Deductive Investigation of the Causes of Mare Reproductive Loss Syndrome: Experiment 4. http://www.uky.edu/Agriculture/VetScience/mrls/Deductive%20Investigation060603.html.

Morris, R. F., (ed.) (1963). The dynamics of epidemic spruce budworm populations. *Mem. Entomol. Soc. Can.* **31:** 1–332.

Rainey, R. C., (ed.) (1976). Insect Flight. Symp. R. Entmol. Soc. London 7, Royal Entomological Society of London.

Rieske, L. K. (2004). Age-specific host utilization in the eastern tent caterpillar, *Malacosoma americanum* Fabricius (Lepidoptera: Lasiocampidae). *J. Entomol. Sci.* **39:** 94–100.

Roden, D. B., Miller, J. R., and Simmons, G. A. (1992). Visual stimuli influencing orientation by the larval gypsy moth, *Lymantria dispar* (L.). *Can. Entomol.* **124:** 287–304.

Roessingh, P., Peterson, S. C., and Fitzgerald, T. D. (1988). The sensory basis of trail following in some lepidopterous larvae: Contact chemoreception. *Physiol. Entomol.* **13:** 219–224.

SAS Institute. (1997). *SAS/STAT Software: Changes and Enhancements Through Release 6.12*, Cary, North Carolina.

Stehr, F. W., and Cook, E. F. (1968). A revision of the genus Malacosoma Hubner in North America (Lepidoptera: Lasiocampidae): Systematics, biology, immatures, and parasites. US Natl. Mus. Bull. 276. Washington, DC.

Tietz, H. M. (1972). *Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of the Continental United States and Canada, Vol. 1,* Allyn Museum of Entomology, Sarasota, Florida.

Townsend, L. H. (2002a). *Control of Eastern Tent Caterpillars*, http://www.uky.edu/Agriculture/VetScience/mrls/ETC502.html.

Townsend, L. H. (2002b). *Farm Contingency Plan for MRLS Risk Reduction for Kentucky Horse Farms; Eastern Tent Caterpillar Recommendations – 2002*, http://www.uky.edu/Agriculture/Entomology/bugalert/bugalert15.htm.

UK Ag. Weather Data (2002). University of Kentucky Agricultural Weather. http://wwwagwx.ca.uky.edu/.

U.S. Naval Observatory. (2003). *Astronomical Applications*. http://aa.usno.navy.mil/data/docs/.

Wellington, W. G., Sullivan, C. R., and Green, G. W. (1951). Polarized light and body temperature level as orientation factors in the light reactions of some hymenopterous and lepidopterous larvae. *Can. J. Zool.* **29:** 339–351.

Wellington, W. G., Cameron, P. J., Thompson, W. A., Vertinsky, I. E., and Landsberg, A. S. (1975). A stochastic model for assessing the effects of external and internal heterogeneity of an insect population. *Res. Popul. Ecol.* **17:** 1–28.