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Student Paper

Dispersal patterns and clumping behaviors in the beetle *Trichoton sordidum*

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Abstract

Although a significant number of behavioral studies of desert tenebrionids have been done, almost nothing is recorded of *Trichoton sordidum* (LeConte) (Coleoptera: Tenebrionidae), an inhabitant of the sunny, sparsely vegetated US/Mexican borderlands. For this small, flightless beetle successful predator evasion and adaptation to a desert environment has required development of complicated, quickly utilizable behavioral mechanisms for regulating exposure to extremes of heat, light, humidity, and habitat structure. In this study, *T. sordidum* was exposed to sudden changes in temperature, illumination, and habitat complexity, and some patterns representing its normal aggregation were recorded. Minimum Risk Distribution models (Floater 2001) predict changes in spatial distribution patterns of groups of individuals as they are exposed to environmental change. A successful species must have a large percentage of individuals adhering to changes with a set pattern of behaviors. All groups of *T. sordidum* tested demonstrated both rapid and cohesive dispersal patterns. They normally showed little tendency toward clustering, except clear adhesive aggregation patterns in cases of limited resources in a fragmented environment. Under conditions of extreme heat or light, aggregations in the form of clumping did occur. The formation of clumps from simple two-stacks to groups of up to ten is documented here. The sophistication, consistency of use, and rapid initiation of clumps suggest clumping might well be a highly evolved and successful mechanism for group threat evasion. The morphology of *T. sordidum* shows how clumping is achieved. An examination of the conditions leading to clumping gives clues to why clumps are formed.

Keywords: adhesive and cohesive aggregation, clumping, clustering, decomposer, habitat complexity, minimum risk distribution, photonegativity

Abbreviation:

MRD:	Minimum Risk Distribution: A model of spatial distribution of individuals that results in the minimum number of premature deaths in a population, and leads to maximized population growth (Floater 2001).
C-value:	A statistical measurement used in this study to quantify relative clump sizes for *Trichoton sordidum* rather than total number of individuals in a clump.
Homogeneous environment:	Environment composed only of uniform, similar features with no irregular detail. In this experiment, open areas of sand, cloth, or fine debris were used.
Habitat complexity:	Structural interference in a habitat which leads to spatial variability. The result is predicted to be a change in the spatial distribution of individuals within the habitat. In this study pebbles were added to the homogeneous environment to break up a uniform surface area.

Introduction

Our knowledge of the distribution and behaviors of the tenebrionid genus *Trichoton* is extremely limited due to the lack of research (Marcuzzi 1998). In 1851, the subtropical *T. sordidum* species in southern Arizona was recorded and cursorily described by LeConte as a nondescript species inhabiting the U.S./Mexican borderlands (Hardy 1995). In 1890, Wickham noted *T. sordidum* at around 730 meter elevations around Tucson, Arizona (Wickham 1890). He described the habitat as rocky hills and gravely soil with no turf or grasses. He also located *T. sordidum* in a similar setting in mining areas across the foothills of the Pinal Mountains near Florence, Arizona. Marcuzzi (1998) describes *T. occidentale,* which ranges from Northern Argentina and Chile to southern Bolivia, and *T. comarapensis,* which he discovered in the tropical zones of Bolivia. This paper hopes to contribute to a better knowledge of this genus.

T. sordidum specimens for this study were collected in the foothills of the Catalina Mountains (Pima County, Arizona). This area lies in the northeastern subdivision of the Sonoran Desert. Vegetation here is characterized by scattered low brush that is primarily creosote, mesquite, cacti and sparse grass. Bajada areas with large accumulations of rock are abundant. With an average 305 mm of rain a year, this area has been classified as semiarid thornscrub (Dimmitt 2002). The environment presents a real and constant challenge to the survival of any species. Parmenter et al. (1989) refer to the rapid and severe fluctuations of this environment resulting in sudden and disorganizing changes in food, water, and refuge distributions. He points out that individuals may have only minutes to live if they enter a thermally lethal environment.

Convection heat from the substrate is an extremely important variable determining body temperatures in tenebrionidae. King et al. (1980) noted long-term exposure to temperatures below 15 °C might have detrimental effects on beetles, and optimal temperatures range around 20 °C. Turner and Lombard (1990) note that desert tenebrionidae find relatively high temperatures necessary for optimum feeding and growth. Ferguson (1898) in his study of desert tenebrionidae, noted “spurts of courtship chasing activities late in the afternoon (c17h00) when temperatures were the highs of the day.” *T. sordidum* has an excellent tolerance of high temperatures and shows similar courtship and mating behavior spurts at temperatures around 28 °C.

Spatial distribution is intimately related to species survival. Ahearn (1970) used the term ‘separateness’ as a loose concept to explain distances between individuals. This adaptation may assure each individual adequate resources. Random spreading out in space is a common defense behavior resulting in relatively low abundance of prey over an area, and takes advantage of the tendency of predators to remain for some time in the immediate vicinity of their most recent meal (Tilman and Kareiva 1997).

Floater (2001) describes how spatial complexities of habitats interfere with spatial patterns of dispersal. He noted the following predictions of one current model of spatial distribution called minimum risk distribution (MRD): 1) Once an optimum spatial dispersal pattern is adopted divergence from that pattern by individuals results in greater mortality levels for that species. 2) Spatial distribution patterns will vary with changes in habitat complexity and 3) If the population dynamics are governed by adhesive aggregation, aggregation should increase with habitat complexity. Predictions two and three of MRD are tested here. The dispersal patterns for *T. sordidum* documented provide a baseline description of its spatial distributions and some measure of its individual variability.

Aggregation behaviors of *T. sordidum* are analyzed here to show how these behaviors might allow them to adapt to the sudden changes in temperature, light and environmental complexity that they encounter in their environment. *T. sordidum* behaviors were studied at five different illumination levels covering a range of typical light conditions in the desert and at six different substrate temperatures ranging from 3 ºC to 38 ºC, the range encountered in its environment. Finally, *T. sordidum*’s spatial distribution behaviors in both homogeneous and heterogeneous environments were recorded. Cohesive aggregation traits (beetles attracted to each other regardless of habitat structure), adhesive aggregation traits (attraction to particular features of or resources in the environment), and the degree of divergence from any patterns were noted.

Materials and Methods

Over 60 specimens of T. *sordidum* were collected in January of 2002 in the foothills of the Catalina Mountains (Pima Co.) at about 600 meter elevation. The beetles were found singly in crevices around the foundations of homes and under rocks, and were extremely inactive. They were removed from the crevices and placed into clear plastic boxes containing leaf debris, rocks, and sand from the host locality with no more than ten individuals in any one box. Over the next six months these boxes were kept in a greenhouse area with temperature, humidity, and light conditions matching the outside environment.

Specimens were keyed to species with the help of Mr. Carl Olson of the Department of Entomology at the University of Arizona. Observations were made over 100 days from mid January to early April. Basic behavioral inventories and an activity log were done to estimate when overwintering ended, when and if daytime activity resumed, and general cycles of sleeping, foraging and mating.

Within a week of collection, four groups of ten *T. sordidum* were established with five females and five males in each group. The males and females were randomly selected from the general collection. Each group was then housed in an identical 10 × 24 cm clear plastic enclosure containing a cotton cloth cut to fit inside the base or leaf debris from the host locality. Clear bottoms on these containers allowed for observing roosting individuals without disturbing them. These four enclosures were randomly labeled experimental groups A, B, C, and control group D. The remaining 20 individuals were left in the original collection boxes and not tested in any way. Experimental groups A, B, and C were not randomly assigned to different treatments. Instead, each group of ten individuals was subject to all treatments. This was done because of the need for large numbers of individuals to comprise groups. The experiments were designed to study group patterns as well as individual behaviors.

The control group environment matched all other groups except for the particular test variable being applied to the test groups. Scan samplings of the controls were done throughout the 100 days at all hours of the day and night to monitor activity patterns and any diurnal, seasonal, or other changes in aggregation behaviors.

Containers were cleaned weekly. Once a day a fine mist of rainwater was sprayed over the tops of all containers to keep moisture levels the same for all. To eliminate any aggregation effects of scramble competition for food, a constant and varied supply of food was kept in a designated feeding area away from areas where the beetles preferred to sleep. Airflow was essentially zero. Sex ratios were kept constant in each replicate with equal numbers of males and females. Only three beetles died over the 100 days of observation. Replacements were obtained from the original collection boxes.

The effect of light intensity

Measurement of ambient light was done with a Sekonic X-1 Digipro (model L-518) meter (www.sekonic.com). Average lux was calculated at the base of the test enclosures when exposed to 1) a dark cloth over top of enclosure (4–10 lux), 2) diffuse natural daylight in the greenhouse (40–45 lux), 3) a direct overhead 40 Watt light bulb (1515–1525 lux), 4) a direct overhead 75 Watt light bulb (3700–3728 lux), and 5) a direct overhead 150 Watt light bulb (14900–15000 lux). Lux readings in the host environment showed a good correlation between the test lighting and light conditions regularly encountered in the host environment. 40 lux correlates to crevices in rocks, 1500 lux to shade under low brush, 3700 lux to shade under high canopy, and 15,000 lux to full midday sun with no cover.

To separate the reaction to light from that to heat stimulus in the experimental settings, every effort was made to maintain surface temperatures as close to18 °C as possible at all times. This was the temperature when the beetles were collected, and was the approximate average daytime temperature for January and February in the host locality.

At the beginning of each experiment a test group of beetles was transferred to an empty 10 × 24 cm glass enclosure set over a paper grid of 1 × 1 cm squares. The enclosure was then covered with a dark cloth to reduce light levels inside to 0–4 lux. The beetles were left undisturbed in this enclosure for an hour. The cloth was then removed and the distribution of beetles on the grid background was recorded. The container was then covered again for another five minutes and distribution of beetles again recorded. To see behavior changes at 40 lux levels the test container was uncovered in the greenhouse with natural daylight. To test for changes in behavior at 1500, 3700, and 15,000 lux the 10 × 24 glass test container was placed on a stand directly underneath a lamp. The room was darkened and the 40, 75, or 150 Watt bulb was turned on. The location of all ten individuals was recorded immediately and then again at five minutes (at which time all activity had ceased). Each group was tested at only one lux level on any one day.

No aggregations in the dark and at low intensities of light were predicted, based on pretrial observations. At very high intensities of light an insect may be correlating increased light with lethal temperatures and try to avoid it. If any photonegativity persists it might show most at very high intensities of light. Tests were run for each experimental group on random dates between January and April.

The effect of temperature

T. sordidum's behaviors were recorded at six different substrate temperatures: 2, 10, 18, 28, 35, and 38 ºC. These represent a potential range typical of the host environment. During all tests light levels were held at 0–4 lux.

To test the effect of low temperatures, ten active *T. sordidum* were placed in a 10 × 24 cm glass test enclosure at 18 ºC. The enclosure was then transferred to a refrigerator where it was placed on a back shelf in the dark until temperatures on a thermometer (lying next to the container and touching the glass) read 2 °C. Temperature was maintained at that level for five minutes and then the positions of all beetles relative to the grid below the glass was diagrammed. For temperatures of 10 ºC the test enclosure was set on top of a Blue Ice brand ice pack until the temperature of the glass surface reached 10 ºC.

In testing the effect of higher temperatures the test was started at 18 ºC. The glass test area and thermometer were set on top of a heating pad. The temperature on the bottom of the enclosure (substrate heat) could be gradually increased to each temperature level studied and left at that temperature for at least five minutes. As soon as most activity had ceased the positions of the beetles relative to the grid were diagrammed. Aggregations remained intact for up to ten minutes after each experimental phase had ended.

The temperature tests were done for each test group sequentially. That is, each group was run at 18, 10, and 2 ºC in one session. In another session they would be run through 18, 28, 35, and 38 ºC in one session. This sequential running was not done with light intensity experiments.

Since *T. sordidum* typically show optimal activity at temperatures between 18 ºC and 28 ºC (personal observation), it was predicted that increasing temperatures up to 28 ºC would increase mating clumps of two, but probably have no further impact on aggregation. If clumping aggregations are hypothesized to be a response to threat, 28 ºC should not be a threat, and no clumping should occur. Leather (1993) noted lethal temperatures for many beetles at around 45 ºC, so temperatures of 35–38 ºC could be a threat and clumping may well occur at those temperatures. Ladybird beetles cluster significantly at very low temperatures (Copp 1983). Since *T. sordidum* were overwintering in a very non-aggregated pattern, it was predicted they would not cluster or clump at low temperatures.

The effect of habitat complexity

T. sordidum's host environment is composed of large, open areas with totally homogeneous features, as well as areas of scattered rock, pebbles, and vegetation. To examine the effect of habitat complexity, pebbles from the host environment were added to the test enclosure to see whether, and how, breaking up a featureless space would alter any dispersal patterns. These pebbles were all approximately 1 cm^2 in size. Their color was the same as the predominant very dark gray or very white color of pebbles in the normal host environment. Both colors, white and dark gray, were used initially to test for any color preference by the specimens. For a very short period in January the beetles showed a clear preference for the very dark pebbles. This was not noted after January 20.

Groups of ten individuals were taken from their featureless home enclosure and placed in the center of a 10 × 24 cm clear glass enclosure containing a field of pebbles. In one experiment this field consisted of 14 pebbles, seven black and seven white. In the second experiment there were seven black pebbles. After all ten *T. sordidum* had settled and become inactive, aggregation patterns relative to a paper grid were diagrammed. All tests were done at 18–20 ºC in diffuse daylight (40 lux). MRD predicts a new aggregation pattern for *T. sordidum* would emerge, and aggregation would increase.

Strict guidelines were established for measuring clusters and clumps, so as to distinguish between these two types of aggregations. For the purposes of this experiment a cluster of *T. sordidum* was defined as a grouping of individuals where all were within contact range of each other but there was no overlapping. *T. sordidum* average one cm in length. Since a 3 cm^2 space will hold ten non overlapping individual beetles, and the groups were composed of ten, 3 cm^2 was the standard chosen for a cluster. If any part of an individual *T. sordidum* fell within the 3 cm^2 area, that individual was counted as part of that cluster. Overlapping clusters were not counted as separate clusters, and no individual was ever counted in more than one cluster. Clusters could, but usually did not, include clumps.

A clump was distinguished from a cluster in that the individuals had overlapping elytra. Ten clumped *T. sordidum* can fit into a 2 cm^2 grid. For purposes of quantifying clump size a value was computed for a clump that would better indicate the relative size of this aggregation formation without using only the numbers of individuals in the clump. Because of the uniqueness of the clumping it was hoped this would further differentiate the formation from a simple clustering (Table 1).

Results

Behavioral inventories

Adult activity levels were charted between January and April. Behavioral inventories were done to document interactions within the groups of ten beetles (Table 2). This included general foraging and mating behaviors, catalepsy, dispersal and agonistic displays.

The adults showed strong photonegativity and little activity between mid January and mid February. Subsequently, over a period of about one week (temperatures constant) their behaviors changed significantly. By mid-March they were out foraging and mating in diffuse natural daylight conditions (40 lux). Feeding and mating generally took place on the surface of the soil medium. Inactive periods were spent in narrow crevices away from feeding areas. Whether their daytime activity levels and tolerance of light continues and increases through the remainder of the year remains to be studied.

Mating pairs were a common sight in mid February. As ambient temperatures increased in March mating pairs were always present in each group. By early April mating and foraging activity in the groups could be seen at any hour of the day or night, with anywhere from 20–80% of individuals out at a time. The beetles rested singly and come out to forage singly. They did not collect and store food anywhere. Feeding behaviors appear to be consistent with typical detritus feeding by scavenger beetles (Ward and Seely 1996). No special burrow constructions or designated sleep areas were ever observed. No evidence was seen during the 100 days of any chemical use and it is likely that *T. sordidum* does not have pheromones or defensive chemicals.

Effect of light intensity

The patterns of aggregation for controls were consistent over the 100-day observation period. The only clumping noted with no light at 18 ºC, were the mating pairs. There were seldom more than four individuals clustered at any time. The results for no light in the control group were considered the baseline. The null hypothesis was that differing light intensity, with temperature held constant, would make no difference in aggregation patterns, and thus clustering would always be minimal and clumping behaviors other than mate pairs would not be noted at any lux intensity.

Clustering did not change with differing intensities, so the null hypothesis held true for clustering aggregations. ANOVA analysis

Table 1. Example of calculation of clumping values (C-values). C-value is an assigned value designed to reflect the size of a clump by representing the number of individuals in a clump in a more emphatic way. A single individual that is not in a clump is given a value of one. In a clump of 2 beetles both individuals would be assigned a value of 2, and the entire clump would have a C-value of 4. In a clump of 10 individuals each individual would be given a value of ten. The cumulative C-value for that group of ten would be 10x10 or 100. For purposes of data analysis the average C-value is calculated for each ‘n’, or separate group of ten beetles.

Since standard chi-square analysis will show only the number of aggregates versus individuals, the C-value was assigned to show how large clumps get: Do the beetles tend to form only small clumps, or various sized clumps, or only large clumps?

Assignment of c-values to each individual *T. sordidum* in a group of ten, and the calculation of average group c-values for ten different tests.

	Number of individual Trichoton sordidum clumped per test date									
Individual	**1/28**	**1/28**	**1/28**	**1/28**	**3/10**	**3/13**	**3/15**	**3/18**	**3/19**	**3/28**
1	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1
3	1	1	1	1	1	1	1	1	1	1
4	1	1	1	1	1	1	1	1	1	1
5	1	1	1	1	1	1	2	1	1	1
6	1	1	1	1	1	1	2	1	1	1
7	1	1	1	1	2	1	2	2	1	2
8	1	1	1	1	2	1	2	2	1	2
9	2	1	2	2	2	1	2	2	1	2
10	2	1	2	2	2	1	2	2	1	2
Total C value	12	10	12	12	14	10	16	14	10	14
Group number	1	1	3	4	4	4	4	4	4	4

Average c- values	
Group 1	12
Group 3	10
Group 4	12.9

Table2. *Trichoton sordidum* activity log covering select days in a 100-day period from January 12 to April 21, 2001. Numbers represent the mean number of beetles in motion, mating or foraging per group of 10 in 24 hours. Three groups of 10 beetles were observed at each recording.

	Time of Day												
Experiment Day	**0300**	**0600**	**0700**	**0900**	**1100**	**1400**	**1600**	**1800**	**1900**	**2000**	**2200**	**2300**	**2400**
12	8.3	7.7	0.3						0	1.3	2.3	2	1.7
14		4.7		0	0		0		0	0.6	0		
15		6.7		0.6		0	0.3			3	2.7		1.7
19					0	0	0		0		2.3		
23		3.7		0.6	0		0	0		4.7	4.3		
25	5	3.7		0.3	0		0	1.7	5.7	5.7	4.3		
27		6.7			0	0	0						
30	7.7	4.3		0.3		0	0	4.3		5.7	7.7		
33		6.7	3	0			0	3.7	6.7	6.3	7		
38	6		1.3	0		0		3.3		7.7	8		10
41		5	1	0.6	0	0	0	4.7		5			
45	9.3		5.3		0	0	0.3	1.7	5.3	7.7	7		10
52			2.6		2	0	1	5.3		7		8.7	
55							2.3	5.7	9.3		8		8.3
58	8.7												9.3
69	9.3	8	2.3	0			5.3	5.3		7.3	7.7		
74		9.3	5	3	0.3	1.8	4.8		7.8	5.5	9		7.5
84		4.5	3.3	2.5	2.3		2.5	6	7	7.8	7.3		
89		6.8	2.8		5.75	3.5	5.8	3.8	7.8	7.8	8.3	7.8	
100		7	8	7	7	2.8	6.25	5.5	8.5	8	7.3		9

was not done for clusters.

The null for clumping aggregations was rejected (p value at <0.0001). Analysis of means comparison for all light settings showed the mean size of clumps at lux levels of 0–4 and 40–45 did not significantly differ from each other, but did significantly differ from clump sizes at lux levels of 1500 and 3700. The mean size of clumps at 1500 and 3700 lux did not significantly differ from each other, but did differ significantly from mean clump size at 15,000 lux. Clump size at 15,000 lux differed significantly from all other light settings (Figure 1). It is clear that as direct overhead light intensified from diffuse to intense, overhead, directed light, clumps increased in size (Figure 2).

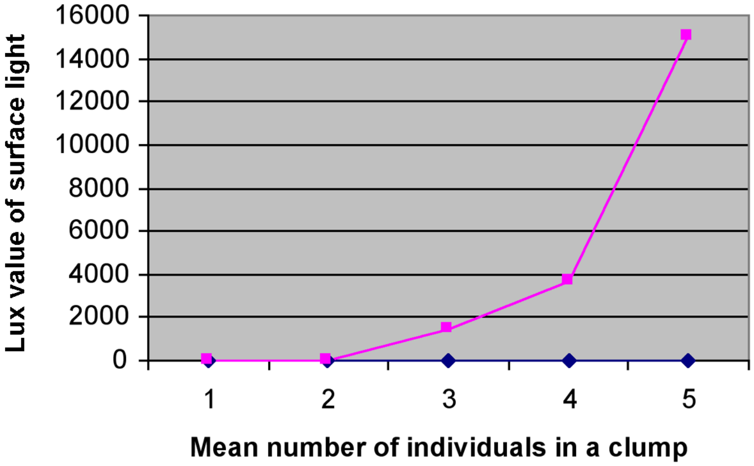


Figure 1. Mean number of individual *Trichoton sordidum* in a clump at five different light intensities and temperature held constant at 20 °C.

Mean differences in aggregation behaviors were examined at the five set light levels. Equality of variances between groups A, B, C, and D assured test assumptions were met and variances were approximating normality. There were no outliers. Data were log-transformed to allow use of a parametric ANOVA analysis. In some cases a group was not run through all light conditions on the same day. Some of the test data thus might not be truly independent because of the time factor involved between tests. In such cases all groups were lumped to get sums of all means and deviations. The amount of independence was somewhat diluted, but given the small standard deviations across groups and the small number of dependent trials it was decided to allow this pooling of means. Because the C-values used for clumps inflated the numerical value of larger clumps, this also inflated the spread of deviations; thus, log-transformation was done to make the big numbers proportionally smaller.

Effect of temperature

Ambient daytime temperatures for all the groups ranged from 18–25 ºC over the 100 day test period. During this period the control group showed no clumping aggregations other than mate pairs and no clustering behaviors except for brief intervals during

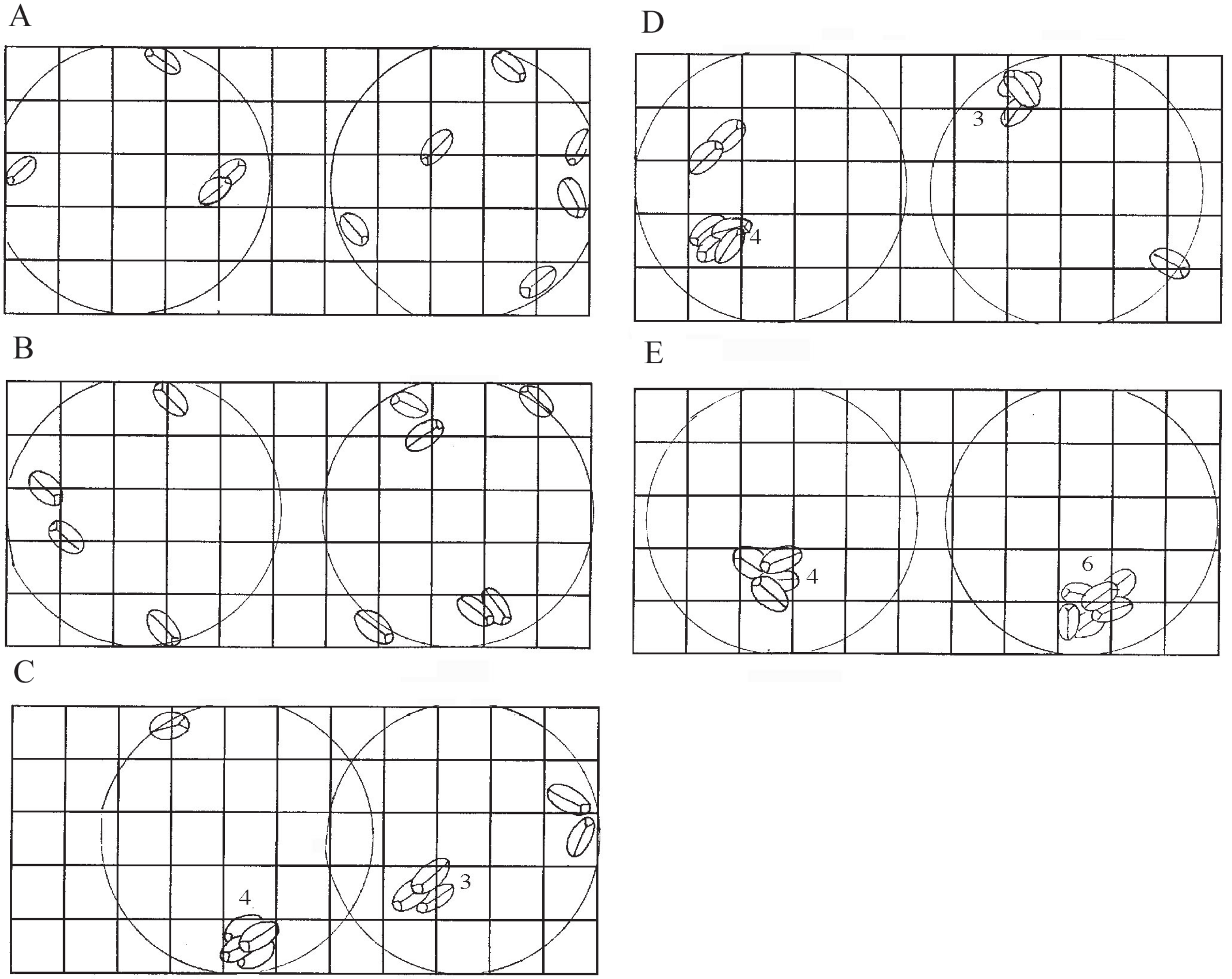


Figure 2. Aggregation patterns of groups of ten *Trichoton sordidum* at 18–20 °C when exposed to surface light at A) 0–4 Lux, B) 40 Lux, C) 1500 Lux, D) 3700 Lux, and E) 15,000 Lux. The circles indicate the radius of a cluster.

foraging. The relatively small size of their enclosures may have made this brief clustering almost inevitable.

The null hypothesis was that there would be no differences in aggregation patterns of clustering or clumping for the temperatures 3, 10, 18, 28, 35, and 38 ºC. In test conditions, T. *sordidum*'s activity became gradually slower as temperatures dropped from 18 ºC to 3 ºC. Almost all of the beetles became totally inactive at 4 ºC. At 3 and 10 ºC, no clumps formed and there were no changes in mean number of clusters. The individual beetles continued to spread out in the same seemingly random pattern of separateness as in the control group. Under test conditions of 18, 28, 35, and 38 ºC, there was still no significant difference in mean numbers of clusters, or mean number of individuals in clusters. There was, however, a dramatic and significant increase in the formation of clumps as surface temperatures rose (Figure 3).

ANOVA for repeated measures was used. An analysis of equality of variance between all groups showed variances were about equal. For histograms, non-transformed data and hand-calculated standard errors were used. Multiple means comparisons showed significant differences between 38 ºC and all other temperatures, and between 35 ºC and all other temperatures. The lowest three temperatures were not significantly different from each other (p value <0.0001). The null was rejected for clump size (Figure 4). ANOVA analysis was not done on clusters as there was clearly no change with temperature. The null hypothesis was not rejected for clustering.

Effect of habitat complexity

When groups of ten *T. sordidum* were removed from the homogeneous environment of their home enclosures and suddenly set down in a field of pebbles in diffuse light their reaction took only minutes to occur. Each beetle circulated through the entire field and around the periphery, and within an average of ten minutes had settled down in a spot where it then remained for a long period of time. The final dispersal of the group represented a totally different aggregation pattern, just as MRD predicts. Individuals did not line the perimeters, nor did they clump on each other. All were drawn to the pebbles and clustered on them, which is an adhesive aggregation trait (Figure 5). In addition, over multiple trials it became obvious that the clustering took on a very randomly distributed pattern, a patchy distribution of clusters, just as was the case when clusters or clumps formed in response to heat and light (Table 3).

Discussion

Four basic questions are explored in these experiments. 1) What aggregation behavior does *T. sordidum* exhibit? 2) Does changing light, temperature, or habitat complexity in the environment alter the aggregation behavior of *T. sordidum*? 3) Does increasing habitat complexity result in behavior that conforms to the predictions of the MRD model? 4) What special adaptation might clumping aggregations represent?

Aggregation behaviors

When collected in January, about 40 individuals were spread out around the perimeter of a 37 meter^2 area (the foundation of a home) with distances of about 1/3 meter between them. An additional 20 individuals were scattered singly around the base of rocks. This pattern of dispersal continued in the test housing with a homogenous environment (Figure 6). Because the 10 × 24 cm experimental enclosures each held ten beetles, some aggregation was being artificially imposed on all groups. The same number of beetles would have occupied approximately five meters^2 in the native locality. Yet, individuals were remarkably consistent in this pattern of seemingly random, well-distributed separateness over the entire 100 days, with only occasional deviations, almost always involving male/female pairing.

T. sordidum was not observed to have adaptations for digging or burrowing. Its preference is to fit itself into very small crevices where tactile stimuli (thigmotaxis) allow it to maximize contact with surfaces all around it. This is often noted as a common cause of aggregation behavior (Leather 1993). Crevice refuges were abundant in *T. sordidum*'s habitat, yet the beetles did not appear to aggregate to any degree in the crevices. When *T. sordidum* were

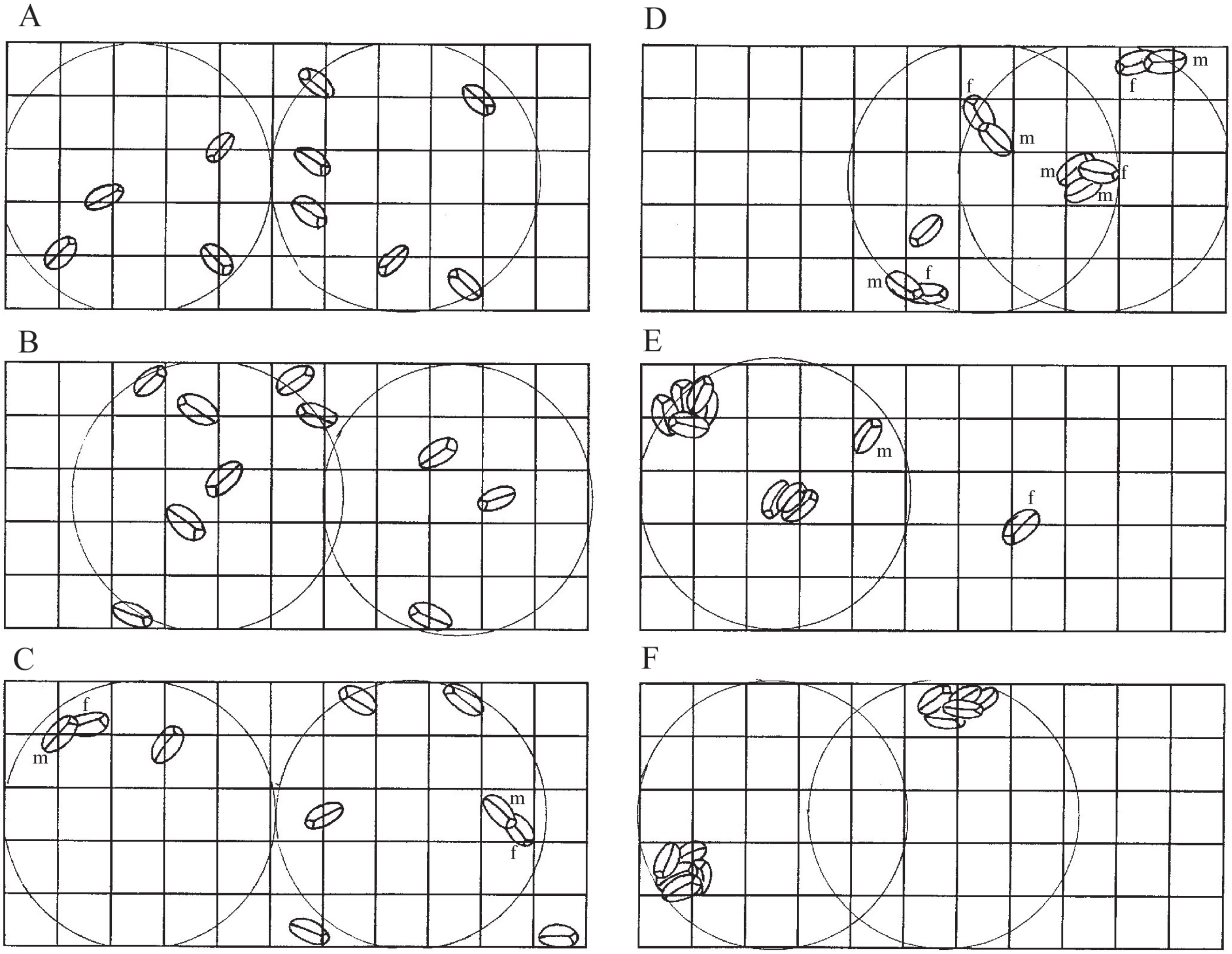


Figure 3. Representative diagrams of clustering and clumping patterns of a group of ten *Trichoton sordidum* at 0–4 Lux and six different temperatures: A) 3 °C, B) 10 °C, C) 18 ºC, D) 28 °C, E) 35 °C, and F) 38 °C. The group of ten was exposed to the six temperatures in sequence on one day.

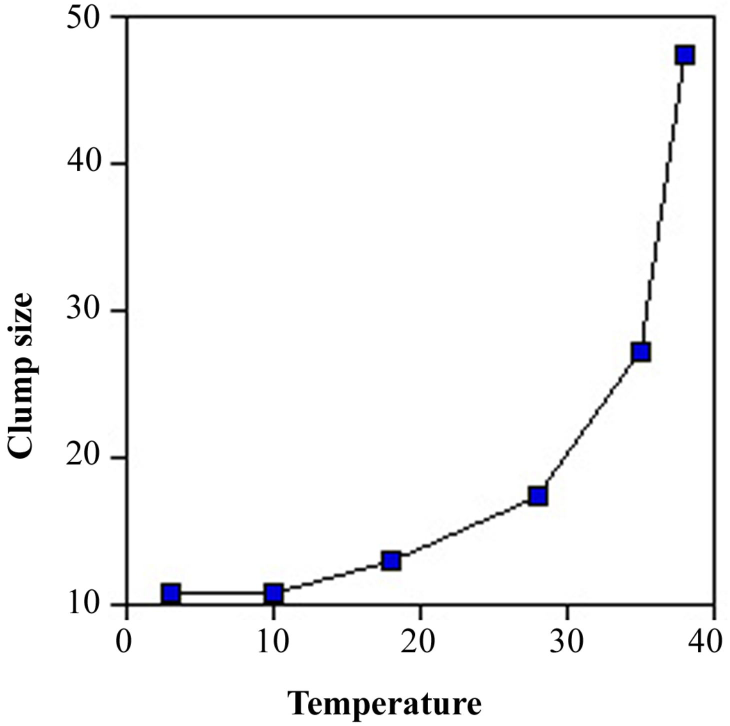


Figure 4. Mean c-values as an indication of clump size of *Trichoton sordidum* at six different temperatures and light held constant at 0–4 Lux.

given a choice of several preferred refuges (a field of 14 pebbles), a group spread itself out into much smaller groups, sometimes even individuals, and utilized as many suitable refuges as possible. Loose aggregations did occur in refuge sites when these sites were in shorter supply (7 pebbles). Thus adhesive aggregation appears to explain much of the clustering behavior that *T. sordidum* did exhibit. Turner et al. (1990) says this is most likely protection from predators. Much of *T. sordidum*'s remaining clustering behavior appeared to be more or less accidental collections.

Suitable surface texture and angles is important for many insects seeking refuge. This certainly appeared to be the case with *T. sordidum.* They showed definite preferences among pebbles presented to them, consistently choosing pebbles with flat, smooth, angular sides (Figure 7). Over wintering when a suitable dark refuge is available, does not appear to be an occasion for clustering. During *T. sordidum*'s photonegative period, roosting aggregations might become sizable if preferred surfaces were in very limited supply.

Light, temperature and habitat complexity variables

T. sordidum was exposed in these experiments to a wide range of light (0 to 15,000 lux) and heat (3 ºC to 38 ºC). Previous experiments with light have indicated that ground activity of beetles is little affected by moonlight intensity (Ahearn 1970) or, in the case of *T. sordidum,* when they are exposed to a black light (personal observation). In these experiments no increased clustering was recorded with the changes in light or heat, but, at the high extremes of both light and heat, unique aggregations in the form of clumping (a cohesive aggregation trait) occurred.

T. sordidum was also exposed in these experiments to sudden shifts from homogeneous to complex habitat features. When habitat complexity was increased by the addition of pebbles individuals did not randomly distribute themselves around the perimeters of their enclosure, nor did they clump on each other. All were drawn to the pebbles and clustered on them, which is an adhesive aggregation trait (Figure 5). In addition, over multiple trials it became obvious that the clustering took on a very randomly distributed pattern, with clusters separated in space. This is very similar to the cluster or clump formations in response to heat and light (Table 3). Seegel and Jackson (1972) noted this predictable patterning of patchy distribution is often seen in predator-prey dynamics. The system works well when predators attack singly, a typical pattern with spiders and scorpions in the *T. sordidum*'s environment.

MRD predictions

MRD predicts low mortality levels for a species which exhibits low divergence from optimum spatial dispersal patterns. *T. sordidum* showed rapid, uniform, and consistent dispersal patterns in both the homogeneous environment and the more complex environment with pebbles.

MRD's predictions of a change in dispersal pattern with changes in habitat complexity were supported, as *T. sordidum* moved from totally random to all clustering behaviors. Spatial analysis testing could be done to look for cluster patterns and randomness.

Table 3. Spatial distributions of *Trichoton sordidum* in habitat-complexity fields of six black pebbles. Shown are mean numbers of beetles in a group of 10 visiting each pebble over 15 trials. Dispersal appeared to be a consistent pattern of random distribution of adhesive aggregation clusters.

	Trial Number															
Pebble #	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**Average**
1	4	1	1	2	3	2	0	2	1	1	2	1	0	0	2	1.5
2	1	3	1	0	0	0	4	3	2	0	2	0	2	2	0	1.3
3	2	3	1	2	1	0	0	3	0	1	2	0	0	1	0	1.1
4	1	3	0	0	0	1	1	1	0	1	2	2	1	1	3	1.1
5	3	1	0	0	3	3	4	1	1	3	0	2	1	1	1	1.6
6	2	2	2	2	0	4	1	2	2	1	4	1	1	0	2	1.7

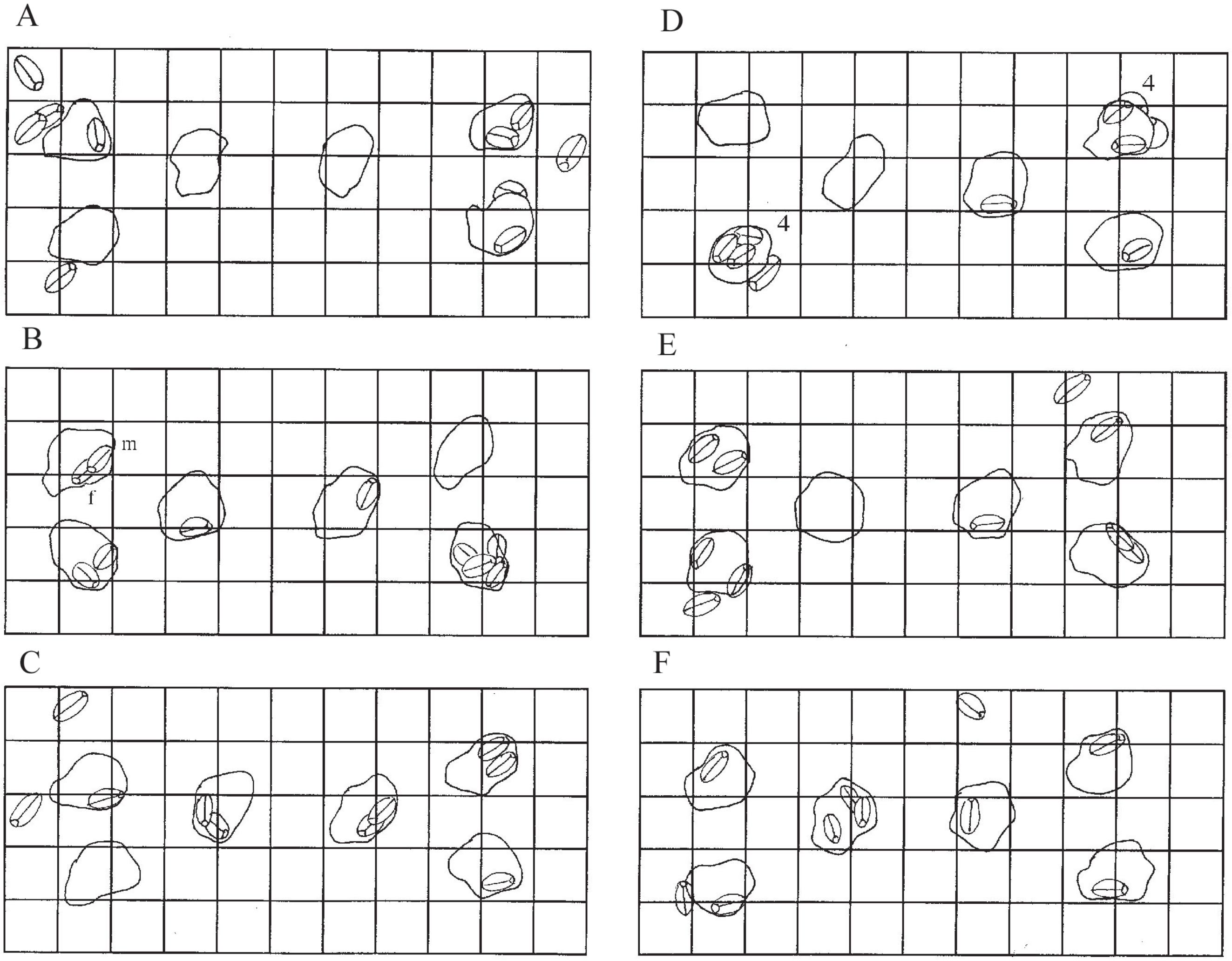


Figure 5. Representative diagrams of dispersal patterns of groups of ten *Trichoton sordidum* in the habitat complexity test with six dark pebbles. Temperature and light were held constant at 18–20 °C 40 Lux.

MRD predicts that if population dynamics are governed by adhesive aggregation, aggregation should increase with habitat complexity. Adhesive aggregation appears to explain much of the clustering behavior of *T. sordidum,* and clustering did increase with habitat complexity in these tests (Floater 2001).

Clumping

Clumps of two individuals were observed in the *T. sordidum* only with mate pairs, where the male was stacked above the female. This was observed in the test enclosures from February through June and through all ambient light levels.

The morphology of *T. sordidum* lends itself to the formation of a stack. The broad base and wide oval shape would give any stacking or clumping more stability. The elytra with many tactile and chemo-mechano-receptor hairs responsive to thigmotaxis would increase contact awareness by all parties. The very hairy body surfaces would add adhesive properties. The ventral abdominal hairs of males function during copulation to help the male maintain a good grip on the female's elytra. For the male to travel about for hours perched atop the female he must have a firm hold. This reduces the odds the female or a competing male could purposefully dislodge him.

T. sordidum's elytra have an extremely close fit along the margins of the sternites all along the lateral edges. This morphological adaptation helps conserve moisture loss from spiracles under the elytral space (Ahearn 1970). It also means the lateral edges are a handy and sturdy shelf to hang on to with tarsal hooks. The long hind legs are flat to fit against the body during catalepsy and crevice crawling. They have widely separated points of articulation, which creates greater stability of motion. Both of these features would provide a flatter ventral surface for packing tightly.

The hook-shaped ends of the front tibias are present on both male and female. These allow *T. sordidum* a perfect fit to hook its front legs over the lateral edges of the pronotum or elytra of

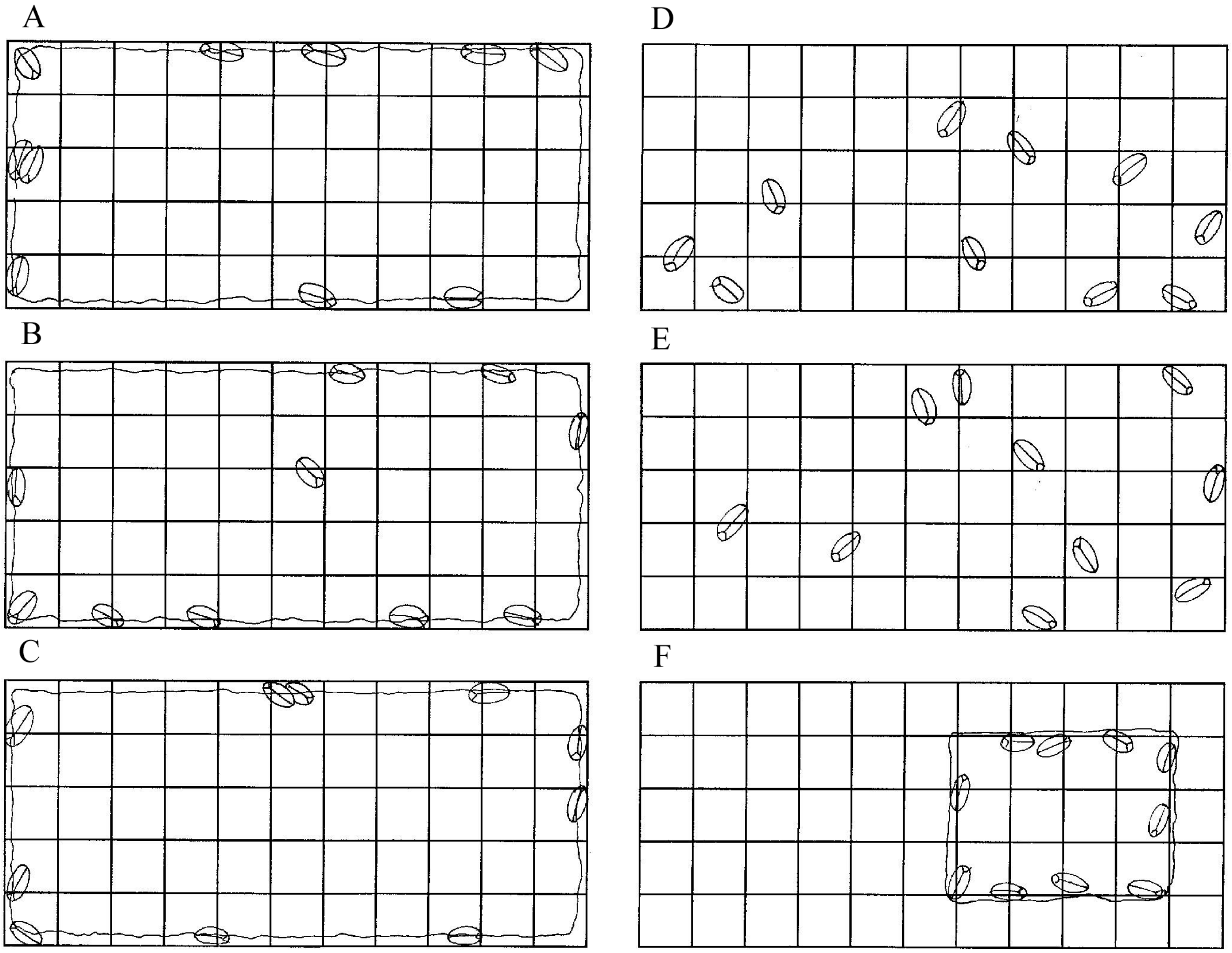


Figure 6. Sleep dispersal patterns of groups of ten *Trichoton sordidum* in a dark, homogeneous habitat at 18–20 °C.

A) Control group: January 16, 1 p.m. All beetles are underneath the cloth covering the bottom of the enclosure. There is one mate pair.
B) Group 2: January 25, 1 p.m. All beetles were underneath the cloth covering the bottom of the enclosure.
C) Group 2: January 16, 10 a.m. All beetles were underneath the cloth covering the bottom of the enclosure. There was one mate pair.
D) Group 1: January 25, 10 a.m. Homogeneous leaf litter environment. No refuge available.
E) Group 2: January 22, 9 a.m. Homogeneous leaf litter environment. No refuge available.
G) Group 1: January 28, 1 p.m. Smaller cloth sheet over bottom of enclosure. All beetles were underneath the cloth.

another male or female *T. sordidum.* This would allow for the use of stacking or clumping behavior beyond purposes of mating. Perhaps the adaptation of larger clump forms (three or more individuals) may have evolved as an extension of the mating pair stack.

A clump of more than two individuals often began formation on a mate pair or a substrate artifact such as a pebble. Male/female pairs often remained paired for over four hours. The female went about her daily routine with the somewhat smaller male firmly ensconced on her back. When a stressful stimulus was introduced, nearby males were frequently the first to climb atop the pair and clump formation began. Climbing atop another *T. sordidum* was almost always started head to head. A male preparing to mate would usually approach and climb over the female's head first, then turn around once on top. Clumps almost always had individuals aligned head over tail. (Figure 8) This may be related to the preferential plane of displacement in the recumbent tactile hairs of the dorsal elytra. SEM photographs of the elytra showed the hairs on the surface of *T. sordidum* to be very directionally oriented. While a clump of three or more individuals very frequently initiated with a mate pair, individuals within the larger clumps never appeared to be involved in any mating behavior. In fact, all individuals in the clump remained rigidly inactive at all times.

Clumps of beetles were so firmly attached to each other that any attempt to pick up one beetle resulted in lifting the entire clump. Adhesion to rocks was also impressive. Lifting an individual attached to a small pebble often resulted in lifting the pebble too. Aggregations remained intact for long periods of time after testing stopped.

Copp (1983) describes clump formations in ladybird beetles as tightly packed groups clinging to each other with the elytra to the outside, which resulted in a reduction in the volume occupied. He noted this phenomenon in ladybird beetles as a nightly roosting phenomenon from August to April. He observed that ladybird beetles form numerous, small, randomly spaced cluster aggregations in Petri dishes. *T. sordidum* clump and cluster aggregations on pebbles formed this same aggregation patterning.

While clumping in *T. sordidum* physically resembles that of ladybird beetles, the stimuli that initiate it appear to be quite different. Ladybird beetles clump in dark conditions during almost all of the year, but *T. sordidum* do not (except at high temperatures). Ladybird beetles tend to remain active at temperatures as low as 0 ºC, and individuals in occasional clumps at that temperature continue to exhibit some movement (Copp 1983). In *T. sordidum* very little movement was noted in individuals in clumps, and below 5 ºC individuals were totally inactive.

Ladybird beetles clump as temperatures fall from 35 to 15 ºC in dark or diffuse light, and they dispersed at temperatures above 35 ºC (Copp 1983). *T. sordidum* show almost no clumping of more than two individuals below 36 ºC under those conditions. No clustering increases occurred in *T. sordidum* over the range of 3 to 38 ºC except in the forms of clumps above 28 ºC. Dense clustering noted in bark beetles (Schmidt et al**.** 1991) and ground beetles (personal observation) takes on an entirely different form.

Why do they clump?

While it might seem clumping could be part of a normal aggregation progression from densely scattered to clustering to clumps, the observations do not appear to support this. At the high extremes of both light and temperature no increased clustering was noted, but clumping was initiated. The aggregation pattern appears to go directly from separateness to clumping.

Clumping of three or more individual *T. sordidum* was observed only under limited conditions: substrate temperatures in the range of 28–38 ºC and ambient illumination in the range of 1500 to 15,000 lux. Under these conditions clumps became a consistent aggregation occurrence. Clumps of three or more initiated very rapidly and persisted at extremes of light and temperature. In contrast, the average number of clusters and average size of clusters prior to clumping simply did not change much across all temperature and light intensities**.** It should be noted that in this study light and temperature variables were separated. It is possible that a combination of less intense ambient light and less intense heat could trigger the same clumping behaviors. It is also interesting to note that lux readings on the ground at midday in the host environment at Tucson registered around 68,000, which is far higher than the 15,000 lux our laboratory light could generate.

Clumping aggregations in *T. sordidum* do appear to be very much a survival mechanism**.** Consider the two major factors here that produced clumps: extreme light and extreme heat. Allee (1931) believes cluster aggregations serve a purpose when shade is limited or not available, allowing light sensitive animals to tolerate longer exposure to high levels of illumination and ultraviolet radiation.

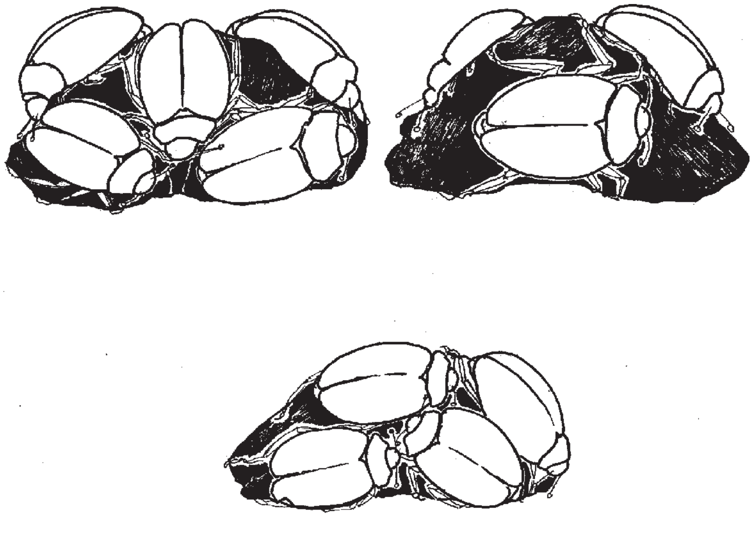


Figure 7. Typical distribution of *Trichoton sordidum* on dark habitat complexity pebbles. The top two diagrams are the front and back of the same pebble. The bottom diagram is a second pebble.

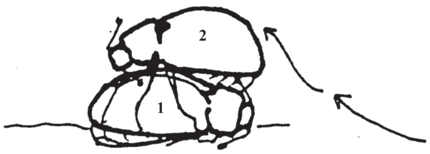
Convection heat is a major variable in the environment of *T. sordidum*, as with all ground beetles. They have an intimate connection with the ground all their lives and are significantly affected by the convection environment (King et al. 1980). Turner and Lombard (1990) note how sudden wind drops can cause surface temperatures in the desert to skyrocket. Tenebrionidae frequently utilize behavioral thermoregulation to control body temperature. Their physiological and behavioral traits are characteristically temperature dependent (Forsman 2000). Any way of raising the body above a hot substrate would be beneficial.

Stilting, the act of raising the body out of a boundary layer of hot air at the soil surface, is a common defense in the tenebrionidae. Ward and Seely (1996) noted that stilting in tenebrionids usually occurs only at temperatures over 35 ºC, and raising the body one cm higher can achieve 4-21% decreases in body temperatures in a desert tenebrionid. No stilting behavior was observed in the *T. sordidum*. The articulation of its long legs allows more for forward and backward movement rather than raising its body up.

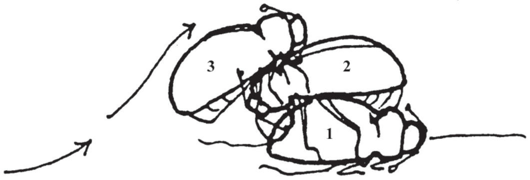
Climbing onto rocks could offer a thermal buffer too, as rocks are not particularly good conductors of heat. *T. sordidum,* however, are generally poor climbers. Even when vegetation was available to climb up off a hot substrate they seldom climbed. Climbing up over another beetle could provide a thermal buffer, making the clump an efficient short-term escape from heat. Although those on the bottom are closest to the surface they are in some shade. So the clumps could in effect be raising a large number of individuals out of the boundary layer of hot air on the surface, making the clumps an example of behavioral thermoregulation.

What of the wind factor? Air temperature has a more

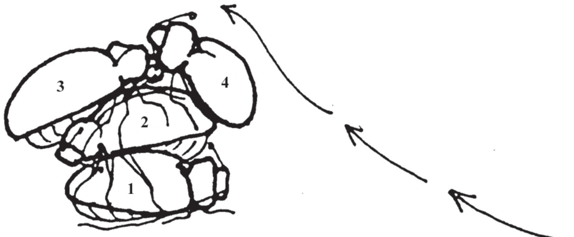
An individul T.sordidum lays down flat on surface and pulls in legs and antennae



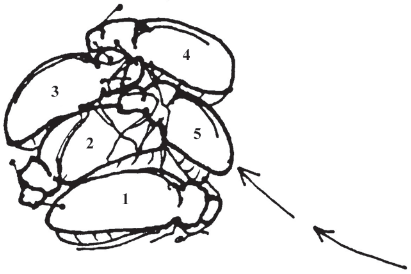
A second beetle approaches from the head end of #1 and climbs up over its head and onto its elytra



3rd beetle approaches #2 head-on and climbs up on top.



4th beetle approaches head of #1, climbs over its head and onto back of #2.



5th beetle climbs over head of #1 and inserts itself into the space between #2 and #4.

Figure 8. The evolution of a "clump" of Trichoton sordidum at 15,000 lux and 20 °C. There was no refuge available in the environment.

significant influence on beetle body temperatures when there is no air movement at the ground (Turner and Lombard 1990). Rising above the ground could become a way of aerating the group.

Ward and Seely (1996) noted that ovipositing in desert tenebrionids is enhanced at higher temperatures, and most female beetles laid their eggs at times of very high summer heat. Forsman (2000) noted darker morphs preferring higher body temperatures in lab thermal-gradient studies, and females typically preferred even higher temperatures. Interestingly, when *T. sordidum* clumps did form, it was most often the female of a mating pair that ended up on the bottom level. The hot surface appears to be a more acceptable or tolerable environment for the female. The males on top are somewhat cooler as they are insulated from the hot surface, and each sex may benefit.

Ward and Seely (1996) believe the consistent adoption by a species of certain body postures may suggest a mechanism for heat gain or loss. Copp (1983), however, found that measurements of cluster temperatures over the range of 14 to –6 ºC shows that clustering had no effect on the temperature of a group of ladybird beetles, or on the rate at which the temperature of the group changed. He concluded that there appeared to be no clear benefit to individual ladybird beetles when tight clusters were formed. Some of the usual benefits of aggregation could apply. For instance, the pile of insects might have a dilution effect on predators: safety in numbers, swamping the consumptive capacity of predators, etc. But the major predators of *T. sordidum* are spiders and scorpions, and they have a fairly small consumptive capacity (Allee 1949). Perhaps the pile itself has a cryptic aspect. It may look more like a pebble than a pile of insects (personal observation), in which case all individuals benefit. Even if a predator did recognize what the clump was, the problem would remain of how to remove an individual beetle.

Could moisture retention be a factor in clumping? Ahearn (1970) notes that for short exposures to heat (12 hours) small individuals lose a greater percentage of their water than do larger individuals. Could clumps aid in trapping more moisture and condensation within the group, particularly for individuals in the center? A reduced surface in relation to increased mass has been shown to have real protective value (Allee 1949). Copp (1983) found that clustered Ladybird beetles died as rapidly, or even more rapidly, than isolated beetles in preliminary experiments designed to test desiccation tolerance. He concluded clustering did not provide protection from desiccation for ladybirds. *T. sordidum* clumps, however, are extremely compact, taking advantage of the beetles' shapes, leg articulations, hairy ventral surfaces, and the close fit margins of the elytra. This might provide more protection from desiccation.

T. sordidum clumps persisted as solid unchanging units for up to 15–20 minutes in these observations. No jockeying for position occurred. This would appear to eliminate selfish herd behavior as a possible source of this behavior. Equal numbers of male and female are likely to make up large clumps, and there was no obvious dominance hierarchy in *T. sordidum*. In any event, regardless of which individuals gain the most, for *T. sordidum* the clump appears to have highly adaptive significance for the individuals involved, although it remains unclear what the advantages are.

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Editor's Note

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