Population Size, Microgeographic Distribution and Habitat Separation in Some Tenebrionid Beetles (Coleoptera)[1]

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ABSTRACT

Mark-recapture analyses of 6 species of geophilous tenebrionid beetles in montane Arizona during July and August indicate that local populations vary from several hundred to less than 25 individuals, depending on the species. Adults of some species are long lived, surviving at least one winter, while those of other species are ephemeral, dying after a few weeks. Significant differences in vagility among the 6 species are broadly correlated with patterns of distribution, the most sessile species being the most underdispersed. Species with the most contagious distributions are those with the smallest populations.

All 6 species were strictly nocturnal and all were using the same food resources as adults. However, differential occurrence of the various species on different substrates suggests partial spatial and ecological separation of most. Separation is greatest between species with very large and very small population sizes. Species with small populations are more restricted to one or a few types of habitats than are the more abundant species. Available evidence suggests that physical and topographic characteristics of the substrate are of general importance in the ecology of tenebrionid beetles.

Beetles of the family Tenebrionidae are a conspicuous element of most arid and semi-arid environments. In North America over 1000 species are known, many occupying extensive geographic ranges or becoming extremely abundant locally or seasonally. Adults of most species are flightless, ambulatory organisms. They are typically active nocturnally or during the early morning or evening, but diurnal activity may occur when temperatures are suitable (Kramm and Kramm 1972). Larvae of most arid land species mature in the soil, feeding on plant roots or decaying organic material. Some species of *Eleodes* and *Embaphion* are occasionally economic pests, especially in grasslands or grain fields, and most ecological information for North American tenebrionds consists of life history descriptions for these species (Wade 1921; Wade and St. George 1923; McColloch 1918, 1919). The temperature and water regulatory characteristics of a few species have been described in detail (Ahearn and Hadley 1969; Ahearn 1970; Hadley 1970) and population size estimates are available for a few others (Rickhard and Haverfield 1965; Turner 1962). Kramm and Kramm (1972) analyzed seasonal and daily activity patterns of 2 species of *Eleodes* in terms of temperature and insolation. The most comprehensive account of characteristics of distribution and vagility is the study of Calkins and Kirk (1973), comparing 5 economically important species of *Eleodes*. Approximate estimates of seasonality and habitat preference are available for a variety of species through the pitfall sampling studies of Tanner and Packham (1965) and Rickhard (1971a, b).

The intent of this paper is to examine the interrelationships of the tenebrionid fauna at one locality. The parameters intensively investigated were microgeographic distribution, substrate preference and population size, but observations were also made on activity patterns and their correlation with climatic factors, feeding habits, diurnal sheltering preferences and longevity.

THE STUDY SITE

All investigations were made at an elevation of 2680 m in oak-conifer woodland in the Chiricahua Mountains, Cochise County, Arizona. The study site occupied a northeast facing slope near Turkey Park, located east of the road connecting Rustlers' Park Public Camp with Onion Saddle. The upper story vegetation at this elevation and exposure is dominated by *Pseudotsuga menzesii* (Mirb.) Franco, with significant admixture of *Pinus ponderosa* Douglas and *Quercus gambelii* Nuttall. *Juniperus deppeana* Steudel and *Pinus flexilis* James also occurred within the study plot, but in very low incidence. The understory consisted primarily of *Muhlenbergia longigula* Hitch, *Odontotrichium decompositum* (A. Gray) Rydb., *Solidago altissima* L., and *Monarda austromontana* Epling. However, the vegetation in the region is extremely mosaic, and species of *Quercus* dominated a west facing slope less than 200 m to the southwest. The study site was located in an opening in the forest, with dense stands of young douglas fir bordering the western and southern margins. The large number of fallen logs of approximately the same age suggested that the opening had been created by a severe storm, perhaps 20 years previous, producing a temporary meadow. The results discussed below show the importance of such clearings in determining beetle population densities.

Observations were made during July and August of 2 successive years. In 1971, beetles were marked and released nightly, except during rainstorms, when they remained concealed. In 1972, no beetles were marked, but counts of individuals were made several times. Local weather conditions were very different

during these 2 years, which obviously altered plant growth and composition. In 1971, a very dry year, the study plot was relatively open, with sparse vegetative growth reaching only about 30–45 cm in height. In 1971, *Muhlenbergia* showed no annual growth or bloom. In 1972, with moderate rainfall, the study plot was extensively covered with a dense understory of herbs, making nighttime observations very difficult. The effects of these climatic differences on the beetle populations are unknown.

METHODS

Most observations were made within a 40×40 m plot subdivided into 100 quadrats each 4 m on a side. The boundaries of the plot and subdivisions were marked by strings held a few inches above the ground by stakes. Use of a simple coordinate system allowed the position of each beetle to be recorded as it was observed and marked. The use of coordinates also simplified calculations of movements of individuals.

The beetles were marked with dots of aluminum, laquer base paint, using a coding system allowing identification of up to 999 individuals. To insure retention of the painted dots, the cuticle was abraded with fine sand-paper disks glued onto the ends of small dowels. Under laboratory conditions, beetles marked in this manner retained their painted spots for over 18 months, with no noticeable effect on their activity and with practically no mortality. Nevertheless, partly obscured spots on beetles observed under natural conditions indicate that the paint may occasionally fail to adhere to the cuticle.

Nightly searching was conducted using gasoline and carbide lanterns. Two persons searched for beetles, while 2 others recorded observations. Sampling was conducted by searching quadrats in alternate rows. The starting point was varied each night to eliminate the effect of time on differences in beetle density. Sampling was initiated at dusk, when the beetles became active. Since the aluminum paint could possibly bias searching success in favor of marked beetles, day time counts were made, which also revealed diurnal shelter site preference and distribution.

During 1971, temperatures and relative humidity were recorded with a Frieze hygrothermograph sup-

ported in a standard weather box 4 in. above ground level. Precipitation was measured with a raingage situated 6 in. above ground level. Climatic variables were not monitored in 1972.

RESULTS

At least 8 species of tenebrionid beetles occurred within the boundaries of the sampling plot, but 2 of these, *Iphthinus lewisi* (Horn) and *Coniontis* sp., were so uncommon or difficult to observe that they are not considered below. Of the other 6 species, *Asidopsis quadricollis* (Horn) (tribe Asidini), is short lived as an adult and seasonally restricted to the summer months. Four species, *Eleodes beameri* Blaisdell, *Eleodes extricata* (Say), *Eleodes arcuata* Casey and *Neobaphion planipennis* Blaisdel, are members of the tribe Eleodini, whose members are widespread and abundant in western North America. Species of the Eleodini are typically long-lived, strongly geophilous, ambulatory organisms. One species, *Coelocnemis magna* LeConte (Coelometopini), shows a strong preference for a substrate of standing dead wood, which the adults use as daytime shelters and in which the larvae develop (Doyen 1973). The other species shelter opportunistically beneath fallen trunks, limbs, bark, or occasionally stones.

All the tenbrionid species at Turkey Park were strictly nocturnal. Beetles were never observed until well after sunset, even on overcast days when temperatures fell within the nightly range where activity occurred. Possible reasons for strict nocturnality, which does not seem to be typical of tenebrionids, are discussed subsequently.

Numbers of active beetles varied greatly among nightly observations. Practically no activity occurred on nights with measurable precipitation, but a great deal of additional variation was unexplainable in terms of rainfall, and also showed no significant correlation with temperature, relative humidity, cloud cover, moon phase or soil moisture when analyzed by stepwise multiple regression.

All species were observed feeding on a variety of vegetable materials. No quantitative data are available except number of times each food source was being used (Table 1). G-tests for independence were insignificant, indicating that all the species were util-

Table 1.—Food utilization by tenebrionid species at Turkey Park. Numbers of observations are shown on the left in each cell. Percentages over all resources for each species are shown on the right.

Resources:	Staminate cones	Living herbaceous vegetation	Dry herbaceous vegetation	Living & dry grass (except *Muhlenbergia*)	Other	Total %
Eleodes beameri	27 (47)	4 (7)	18 (32)	7 (12)	1[a] (2)	57
E. extricata	6 (40)	1 (7)	7 (47)	—	1[b] (7)	15
E. arcuata	7 (50)	3 (21)	3 (21)	1 (7)	—	14
Neobaphion	3 (75)	—	—	—	1[c] (25)	4
Coelocnemis	3 (100)	—	—	—	—	3
Asidopsis	5 (71)	—	2 (29)	—	—	7
Total	51 (51)	8 (8)	30 (30)	8 (8)	3 (3)	100

[a] Dead wood; [b] Agaricales; [c] mistletoe.

izing these resources in the same proportions. All the resources were extremely abundant, and it would seem evident that direct competition for food is unimportant in interactions between the beetles. However, when suitable habitats have a patchy occurrence, even rare species may compete with one another, at least theoretically (Levins and Culver 1971). The distributions of several of the species considered here are decidedly patchy, so that competition for resources cannot be ruled out. For the more generally distributed species, such as *E. beameri,* competition is probably not an important factor.

POPULATION SIZE

The beetle populations at Turkey Park were not restricted to the sampling plot—that is, movement occurred into and out of the sampling area. Moreover, it is likely that there were births and deaths during the period of the study. For these reasons, deterministic methods of population estimation were not used. Daily recaptures were too few for the calculations required by the stochastic method of Manly and Parr (1968). Therefore, Jolly's (1965) multiple recapture method was used for population estimates.

Recaptures were too few to allow separate estimates for males and females of any species but *E. beameri,* and too few to allow any estimate for *Neobaphion,* for which the Lincoln Index was used. Analysis of vagility and activity patterns (discussed subsequently) indicate that intermixing of marked and unmarked beetles occurs slowly especially for the less vagile species. Furthermore, daytime shelter sites examined at night frequently contained beetles, sometimes in large numbers, suggesting that not all individuals may be active every night. Thus, all mark-recapture methods are somewhat inappropriate. In addition, wide fluctuations occurred in daily sample sizes and population estimates, and standard errors were quite large. Roff (1973a, b) showed that mark-recapture estimators are generally inaccurate and that it is usually impossible to set reliable confidence intervals for population estimates. Because of these difficulties, an average of daily values for each species is probably the best estimate of size, at least for relatively stabile populations. Averages and standard errors are reported here.

Table 2.—Sampling statistics for tenebrionid beetles at Turkey Park. Values were compiled from 21 mark-recapture sessions over a 5-week period.

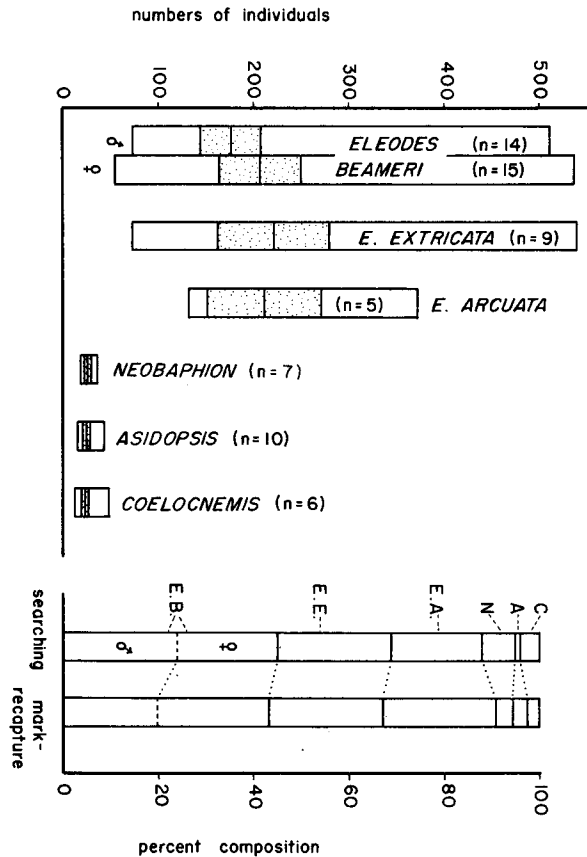| | Average | | Total no. marked |
	% marked individuals	% population sampled/day	
Eleodes beameri	37	10	492
E. arcuata	16	6	167
E. extricata	22	6	136
Asidopsis	61	20	52
Coelocnemis	38	10	25
Neobaphion	—	—	26
Total			898

numbers of individuals

FIG. 1.—Composition of tenebrionid beetle population at Turkey Park in 1971. Histogram on left shows numbers of individuals of each species, as estimated from mark-recapture data. Limits of each vertical bar represent the range of population estimates. Shaded portions of each bar represent one standard error around the mean. The central line in each shaded portion represents the mean of daily estimates for each species, and n the number of estimates. Histogram on right compares percentage composition of the population as estimated by mark-recapture procedures and by hand searching the sampling plot. Population figures for *Neobaphion* are based on Lincoln Index estimates. Values for other species are derived from Jolly's multiple recapture method.

Eleodes beameri was the most abundant species (Fig. 1), constituting about 43% of the total beetle population on the average, and together with *E. extricata* and *E. arcuata,* nearly 92%. *Coelocnemis* and *Asidopsis* were present in small numbers, but both are relatively sedentary so that a comparatively large proportion of the total population was marked and sampled each day (Table 2). Consequently, population size estimates are probably more reliable for these species than are those for the species of *Eleodes.* It must be emphasized that the areas effectively sampled varied among the species. For *Asidopsis,* which is quite sedentary, the estimated population probably occupied an area only slightly larger than the sampling plot. For *E. beameri,* which is relatively vagile, the sampled population must have occupied an area

several times larger than the plot. On the other hand, the populations were somewhat circumscribed by the clearing in which the plot was centered. The paucity of shelter sites and presence of dense thickets of young conifers or solid stands of *Muhlenbergia* in surrounding areas greatly decreased the density of beetles. Thus, even for *E. beameri,* the sampled population was probably spread over an area no greater than 4 to 5 times that of the plot.

Since marked beetles could have been unintentionally captured more frequently than unmarked ones, the plot and an area 440 meters in all directions around it were searched by day, after the mark-recapture study had been concluded. Among 47 beetles recovered from the plot, 20 were marked (42.5%). During the last 4 nights of sampling, 54 of 136 (39.7%) of the beetles were marked, indicating that no bias was introduced by marking. Estimates of species composition of the population were also similar for the 2 methods (Fig. 1).

In 1972, no marking was done, but day and night captures of 192 beetles included 3 marked individuals of *E. beameri* (4.4%) and 6 of *E. arcuata* (8.8%). Since both these species are relatively vagile and because the paint marks probably were lost from some individuals, the actual proportion of beetles surviving the winter must have been considerably higher than indicated by these figures. No marked individuals of *Coelocnemis* or *Neobaphion* were found, probably because relatively few were captured in 1972. *Eleodes extricata* requires a different explanation, since the numbers of marked and recaptured beetles were considerable. Possibly this species is annual, although in the laboratory survival through the winter occurs with little mortality.

DISTRIBUTION AND VAGILITY

The size of the sampling plot limited measurable distances to 68.5 m (except for the few marked individuals recovered outside of the plot). This limitation would cause underestimates of vagility, especially for the most mobile species and for movements which were measured after a lapse of more than one day. For this reason, movements occurring during a single period of activity are probably the best estimates of mobility. By this measure the species at Turkey Park show distinct differences in vagility (Fig. 2), and these differences are correlated to some extent with differences in distribution. *Asidopsis,* the least vagile species, also showed the most contagious distribution (Table 3). Marked individuals were usually encountered repeatedly in the same or adjacent quadrats, with infrequent longer movements. Total distance moved is very significantly correlated with the interval between observations for this species ($r = 0.72$) indicating that the recorded distances are an accurate estimate of actual vagility. For the other species, the relationship of total distance to time interval is curvilinear, probably because of underestimation due to the restricted size of the sampling area. Alternatively, a curvilinear relationship might result from differences in turning rates among species.

Eleodes beameri is the most vagile species by all methods of comparison, showing highly significant differences from the least vagile species. *Neobaphion* and *Coelocnemis* were encountered so infrequently that averages for single day movements could not be computed. By other measures *Neobaphion* is nearly as mobile as *E. beameri*. *Coelocnemis* is noteworthy in that the average of all observed distances is relatively large, while the average distance travelled per day is small. *Coelocnemis* occurred predominantly around dead wood, particularly standing tree snags, and the same individuals were often encountered repeatedly in restricted areas of the sampling plot. Occasional long distance movements away from these concentrations of dead wood caused the increase in the average of all observed movements.

No effort was specifically made to estimate dispersal, but some indication of dispersal ability is provided by the numbers of marked beetles recovered outside the plot after marking was terminated. Among a total of 144 beetles collected within a strip 20 m wide around the plot, 10.3% were marked; among 37 beetles collected between 20–40 m, 10% were marked.
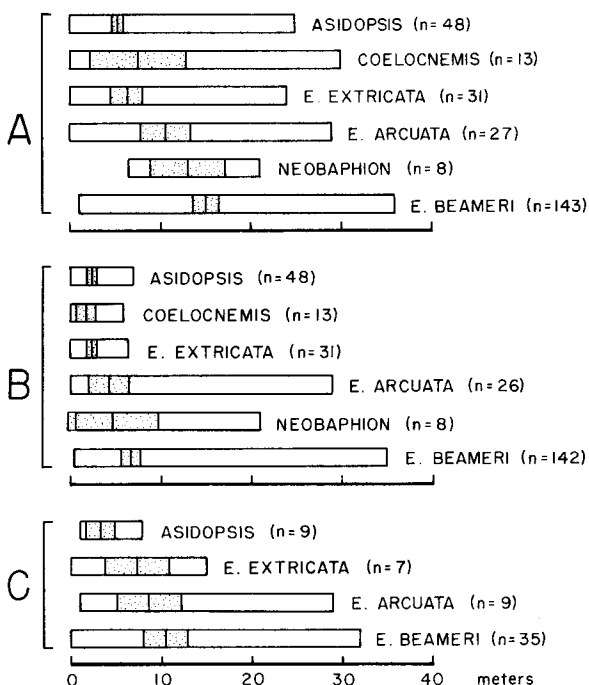

FIG. 2.—Vagility characteristics of tenebrionid beetles at Turkey Park. Limits of each horizontal bar indicate range. Shaded portions of bars indicate limits of 1.96 S.E. Means are indicated by lines in centers of shaded portions. Sample sizes are shown in parentheses. A, all observed movements; B, velocities (distances moved/time interval between observations); C, movements over single day intervals. Note that the observed range of velocities for *Neobaphion* falls within the limits of 1.96 S.E.

Table 3.—Indices of dispersion (I.D. $= [s^2/X]$) estimated from analyses based on 100 quadrats (16 m^2) and 400 quadrats (4 m^2). Most species are significantly aggregated, even for the smaller sampling unit.

	4m^2			16m^2		
	X	s^2	ID	X	s^2	ID
Eleodes beameri	1.24	2.22	1.79*	5.02	15.04	3.00*
E. arcuata	0.48	0.62	1.27*	1.94	4.26	2.19*
E. extricata	0.40	0.65	1.63*	1.68	3.58	2.13*
Neobaphion	0.11	0.10	0.94	0.25	0.56	2.23*
Coelocnemis	0.17	0.98	1.72*	0.91	0.39	2.34*
Asidopsis	0.29	1.14	3.99**	1.00	6.10	6.10**

* $p<.05$; ** $p<.01$.

Since the areas of these 2 surrounding strips are 3 times and 5 times that of the plot, expected percentages of marked beetles within each strip would be ca. 20% and 12%. These estimates are based on the unlikely assumptions that all the marked beetles which disappeared from the plot area (60%) diffused equally throughout the larger areas, that no births or deaths occurred during the study period, and that there were no differences in dispersal characteristics among the species. It is puzzling that more marked beetles were not recovered close to the plot, especially since large concentrations of dead wood occurred there, particularly along the western boundary. The western margin of the plot supported relatively dense populations of the 3 most abundant species, and it was expected that they would use the dead wood as shelters. In any case it is evident that considerable movement by the most vagile species must occur over distances of a few hundred meters. Movements over equal or larger distances have been demonstrated for species of *Eleodes* (Calkins and Kirk 1973).

At least one beetle was observed in every quadrat of the plot during the course of the study, but some areas obviously supported denser populations than others. For descriptions of distributional patterns, coefficients of dispersion were calculated for each species using the total numbers of beetles observed in each subarea during the entire study. Thus, the coefficients are measures of spatial dispersion of active beetles. During the day, while the beetles are congregated beneath dead wood, their distributions would be much more contagious. The index of dispersion (Southwood 1966: 36) was used because of simplicity of calculation (I.D. $= [S^2/X]$). Since this index is influenced by the size of the sampling unit, indices were calculated for 4m^2 and 16m^2 units. The larger sampling unit indicated significant aggregation for all species and the smaller sampling unit showed significant aggregation for all but *Neobaphion* (Table 3). The dimensions of the smaller unit (2m × 2m) are approximately equal to the average daily distances moved by the less vagile species. For the most vagile species, the larger sampling unit is probably more appropriate.

The most aggregated species, *A. quadricollis*, was also the least vagile, occurring primarily in barren areas or in regions with a sparse vegetative cover

(Fig. 3), but even within these restricted regions the distribution was highly contagious, with 22 occurrences in a single 16m^2 quadrat. The reason for these local aggregations was unclear, and the daytime hiding places of this species are unknown. *Coelocnemis* was closely associated with accumulations of dead wood, and the adults were frequently encountered on logs or more than a meter high on snags. *Coelocnemis* is distinguished by a relatively large proportion of occurrences under tree canopies, which were less frequented by other species. *Eleodes arcuata, E. extricata* and *Neobaphion* occur predominantly in the vicinity of dead wood, beneath which they shelter. *Eleodes beameri*, although relatively mobile, shows significant aggregation, even for the smaller sampling unit, whose dimensions are less than one-fifth the daily average distance moved by this species. The reasons for the aggregation are not entirely clear, since *E. beameri* occurred in significant numbers on all types of substrates except bare ground and beneath tree canopies (Fig. 3). However, it was most abundant along the southwest border of the plot, where a dense accumulation of dead wood provided shelter sites.

The contagious distributions and differences in substrate preferences suggest that some of the species may be positively or negatively associated with others. Associations between each species pair were examined using the χ^2 test for independence. Results indicated only 3 significant relationships (Table 4). However, this method of analysis, which is based only on occurrence in a sampling unit, does not take into account differences in numbers of individuals in different samples. If 2 species occur in most samples no association will be indicated, even though most samples contain few individuals. If 2 species are rare (absent from most samples) too many positive associations will be indicated. Since 3 of the species investigated here (*E. beameri, E. extricata,* and *E. arcuata*) occurred in most quadrats, while the other species were relatively rare, the associations indicated by the tests for independence are probably not very reliable. In these circumstances a coefficient based on numbers of individuals occurring together is more appropriate. One such coefficient was used by Whittaker and Fairbanks (1958) to compare communities on the basis of shared species, and, in the

Table 4.—Coefficients of association between tenebrionid species, based on total numbers of individuals occurring together in samples as a percentage of total numbers. Eb = *Eleodes beameri;* Ea = *E. arcuata;* Ee = *E. extricata;* Np = *Neobaphion planipennis;* Cm = *Coelocnemis magna;* Aq = *Asidopsis quadricollis.* Significance values are based on analysis of 2×2 contingency tables, which consider only mutual occurrence of species in a sample, not numbers of individuals occurring together. For this reason some coefficients of high value appear to be insignificant.

	Eb	Ea	Ee	Np	Cm	Aq
E. beameri						
E. arcuata	0.62					
E. extricata	.51	0.59**				
Neobaphion	—.34	—.18	—.30			
Coelocnemis	—.45	—.08	—.39**	0.23		
Asidopsis	.01	.10	.17**	—.36	—.57	

** p<.01.

form suggested by Southwood (1966), can be used to measure association between species. The index is computed as:

$$K = \left(\frac{Ji}{A + B} - 0.5 \right)^2$$

where Ji = number of individuals of A and B in samples where both are present and A,B = total numbers of individuals of A, B in all samples. Results are shown in Table 4. This index will be misleading when samples contain large numbers of one species and small numbers of the other, since the abundant species will largely determine the value of Ji. An extreme example would involve 2 species which both occur in all samples. In half the samples A is 10 times as abundant as B; in the other half B is 10 times as abundant as A. Intuitively A and B are negatively associated, but a contingency test
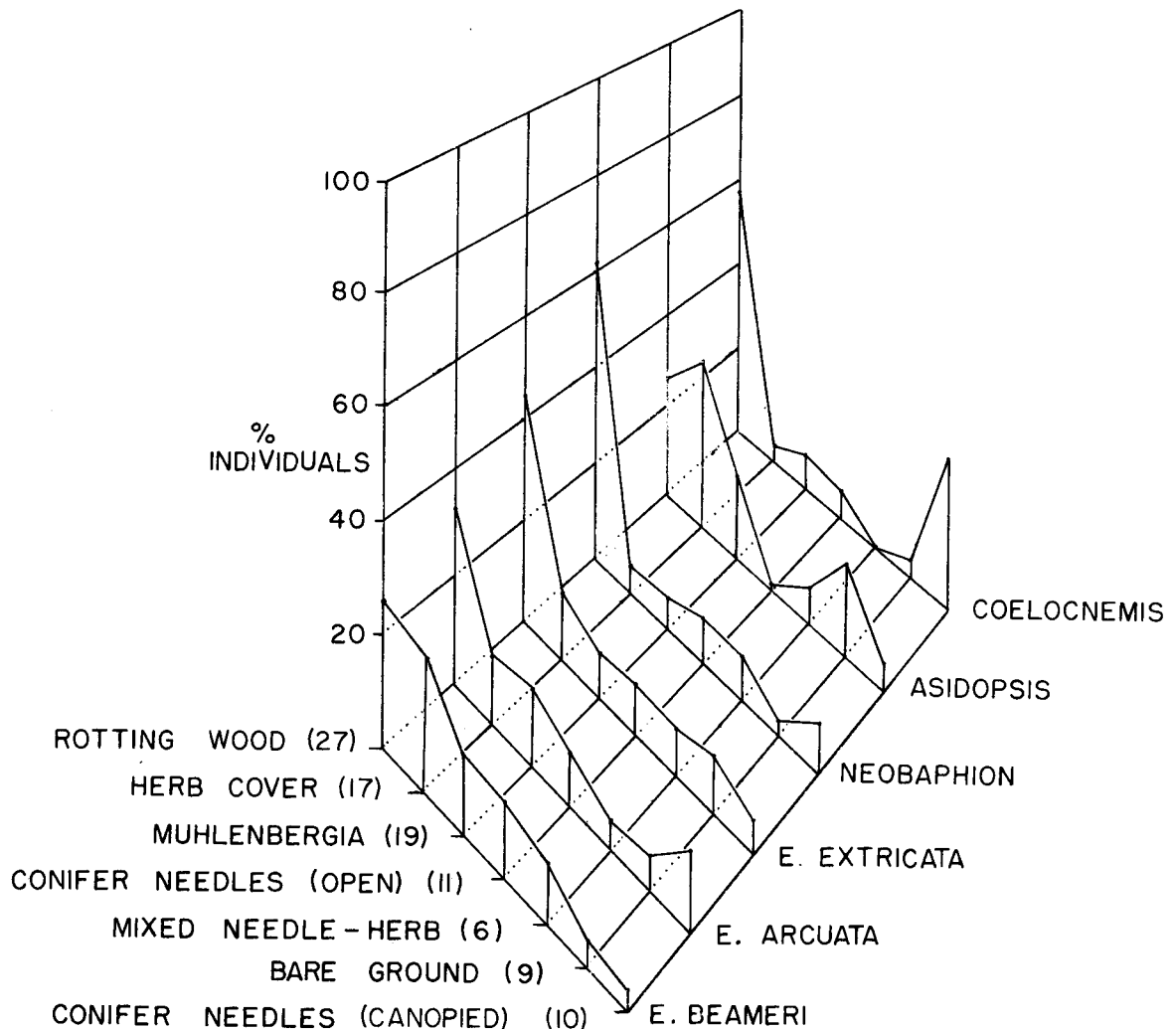

FIG. 3.—Occurrence of tenebrionid species on different substrates. Values for each species have been converted to percentages to make them comparable. The percentage of the sampling area covered by each substrate is shown in parentheses beside the substrate designation.

Table 5.—Results of G-tests of independence for occurrence of tenebrionid species on different substrates. G-values appear in each cell. Degrees of freedom = 6 for each case. Significant G-values indicate that distributions differ over the substrates indicated in Fig. 3. Abbreviations as in Table 4.

	Eb	Ea	Ee	Np	Cm	Aq
E. beameri						
E. arcuata	49.97***					
E. extricata	34.31***	19.41**				
Neobaphion	24.65***	7.20	6.75			
Coelocnemis	56.77***	14.19*	17.58**	8.62		
Asidopsis	14.60*	35.03***	26.66***	29.94***	113.8***	

* .05≥p≥.10; ** .01≥p≥.005; *** .005≥p.

would indicate no association, while Whittaker and Fairbanks' index would indicate absolute positive association. The results for *E. beameri, E. arcuata* and *E. extricata* (Table 4) represent inconsistencies of this sort. All 3 species occurred in most quadrats, and contingency tests indicated no association, while Whittaker and Fairbanks' coefficients suggest positive association.

Another method of analyzing association is to categorize each species according to type of habitat and compare the numbers in the various habitats by goodness of fit tests for each species pair. For the tenebrionids at Turkey Park, substrate characteristics seemed to be the most important habitat differences. On this basis, 7 substrate types were recognized (Fig. 3). Areas dominated by rotting wood, bark, and fallen limbs or trunks occupied the largest proportion of the sampling plot. Bare ground and areas with a mixed cover of conifer needles and sparse herb cover occupied the smallest proportions. Herb cover, mixed needle-herb and bare ground intergraded imperceptibly with one another and categorization was somewhat arbitrary. In intermediate situations half the observations were tallied in both categories. The other substrates were clearly differentiated, and there was little difficulty in assigning each observation to one of them.

In general, the grouping of species on the substrates agrees with the Whittaker and Fairbanks association coefficients. The 3 species of *Eleodes* form one group, characterized by moderate occurrence around rotting wood and low but significant occurrence on the other substrate types. Within this group, *E. extricata* and *E. arcuata* are extremely similar in substrate preference, with a high proportion of occurrences on rotting wood. *E. beameri* is more evenly distributed across all substrates. *Neobaphion* and *Coelocnemis* form another group, differentiated by extremely high incidence on decaying wood and relatively high occurrence beneath tree canopies. *Asidopsis* is distinguished from all other species by relatively high incidence on bare ground and herb-dominated areas, and low incidence around dead wood.

The results of goodness of fit tests for associations between different species pairs are significant in almost every case (Table 5), indicating that differences in distribution are dependent on substrate. Even species pairs which seem to occupy very similar substrates by inspection of Fig. 3 shows significant differences (for example, *E. extricata* and *E. arcuata*). However, G-values are much higher for obviously different species such as *Asidopsis quadricollis* and *Coelocnemis magna*. Goodness of fit tests would undoubtedly show significant differences in spatial distribution for most species pairs, but would be very laborious to compute due to the large number of samples.

These distributions according to substrate type represent partitions of time spent during periods of activity. Differences also exist in sheltering sites chosen (Fig. 4). All species except *A. quadricollis* (day-time shelters unknown) used dead wood of various sorts as primary day-time hiding places. *E. beameri*, however, made greater use of fallen trunks and limbs, while the other species appeared more often under slabs of bark lying about stumps or prostrate trunks. *E. arcuata* was further distinguished by the relatively high proportion of individuals found under bark still adhering to trunks.

The paucity of tenebrionids sheltering beneath stones is noteworthy, since stones provide an important hiding place for many species, particularly in arid regions. Suitable stones (those with space underneath) were less common than fallen wood at Turkey Park, but were still present in appreciable numbers. Possibly the beetles avoided them because of the relatively high rainfall at this elevation, which kept the ground relatively moist. In contrast, piles of dehisced bark are relatively friable and dry out more quickly.

DISCUSSION

In certain ecological characteristics, tenebrionid beetles are not greatly different from small nocturnal vertebrates. Like vertebrates, and unlike most insects, they are relatively long lived' as adults, appreciable numbers of individuals surviving at least one year. Adult lifespans of a year or more have been reported for other species under both natural conditions (Pace 1967) and in the laboratory (King and McMullen 1953; Kramm and Kramm 1972; Doyen 1973). Larval lifespans are also relatively long, usually about one year. During periods when they are not active, adults remain concealed in relatively protected shelters, where they are probably safe from predators as well as adverse weather. Mortality among adults is probably relatively low, since they are protected from most invertebrate predators by their hard cuticle and from vertebrates by quinonoid defensive secretions. What factors might
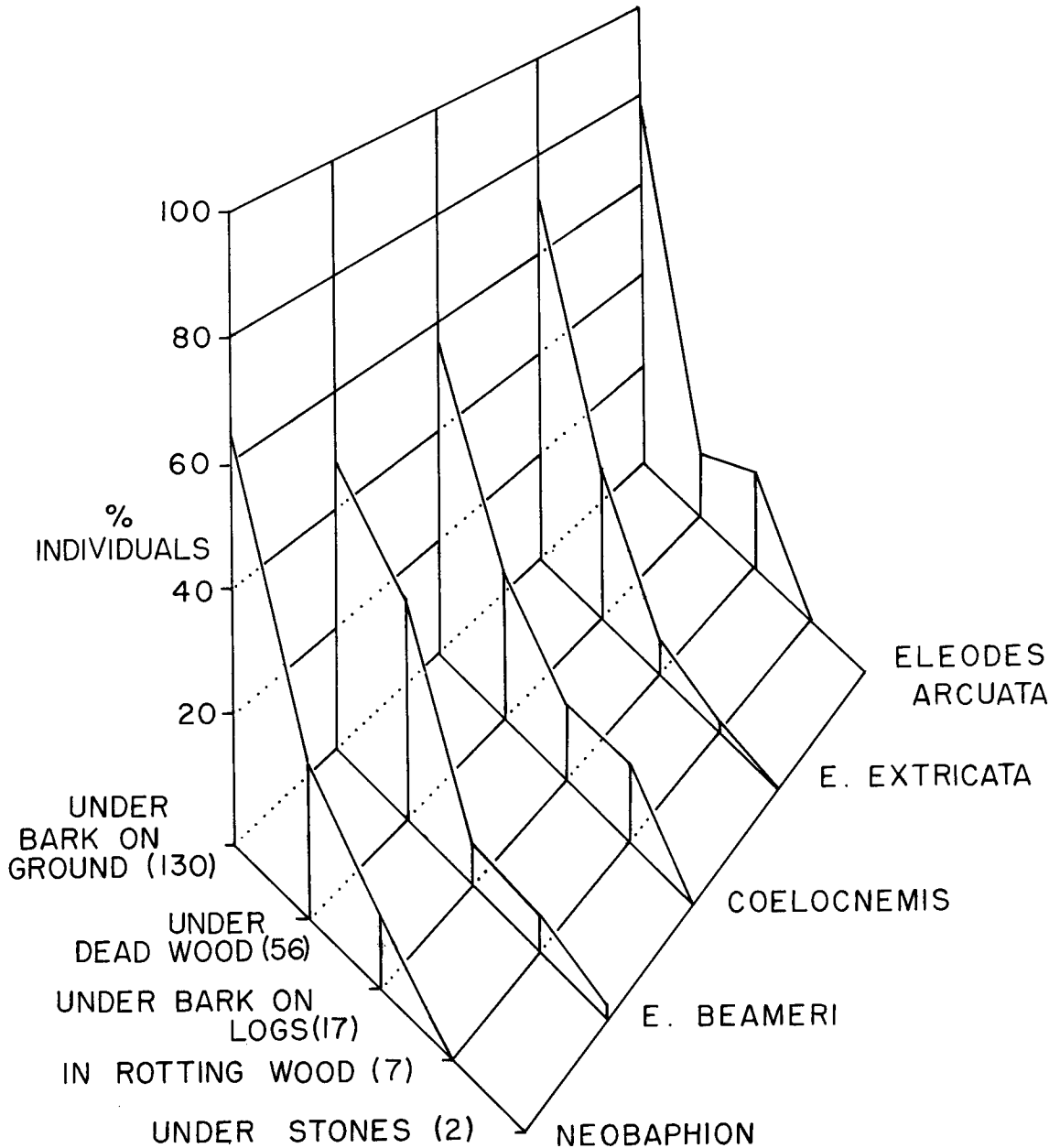
FIG. 4.—Shelter sites. Values for each species are converted to percentages. Numbers of all species combined in each shelter type appear in parentheses after substrate designations.

operate to limit population sizes of these beetles are not clear. Food could be a limiting resource for some species, but probably not for all. Daytime shelters might restrict population size, but many apparently suitable shelters were unoccupied, and others could have harbored many more beetles than were present. Adult tenebrionids, including many species of *Eleodes,* are attacked by parasitoid flies (Tachinidae) and wasps (Braconidae) but no parasites emerged from

over 200 laboratory-maintained individuals of the species at Turkey Park. Possibly larvae are extensively parasitized or predated, but this has not been recorded and seems unlikely, since they occur in the soil where they would be relatively immune to attack. In general, the evidence, though fragmentary, seems to indicate that, relative to most insects, many tenebrionids probably operate under a K-mode of selection (Gadgil and Solbrig 1972), but detailed evidence

regarding reproductive potentials and the relative amount of energy devoted to reproduction is unavailable.

The results suggest that substrate characteristics are very important to tenebrionids. Obviously, geophilic organisms will adapt to differences in the physical qualities of their environment. Medvedev (1965) illustrated some of the major ways that tenebrionid leg structure corresponds to soil characteristics. For example, species occurring on hard substrates generally have relatively long legs specialized for ambulation. Such species shelter opportunistically in animal burrows or under stones or other objects. Contrastingly, species occurring on unconsolidated sand usually have the legs specialized for burrowing and shelter in the substrate. Correlations of substrate features with species composition or abundance are also revealed by sampling studies (Rickhard and Haverfield 1965; Tanner and Packham 1965; Quezel 1950; Rickhard 1971a; Calkins and Kirk 1973).

The tenebrionids discussed here would all belong to Medvedev's ambulatory group, but, nevertheless, show distinct differences in substrate preference. Some species (*C. magna, N. planipennis*) occur almost exclusively around decaying wood. Other species (*E. beameri, E. extricata, E. arcuata*), although using the same wood as daytime shelter sites, wander widely over diverse substrates. Still other species (*A. quadricollis*) occur predominantly in localized areas with sparse vegetation or bare ground. Corresponding differences may exist in larval distribution since adults probably oviposit predominantly in the areas where they spend most of their time. This idea is substantiated to some extent by other evidence. For instance, *Coelocnemis* larvae occur largely in rotting wood, while *Eleodes* larvae are soil dwellers. In any case, it seems apparent that the species at Turkey Park have partitioned the habitat by type of substrate. This is particularly true of the less vagile species, such as *Coelocnemis* and *Asidopsis*, which might be termed "specialists" in terms of substrate requirements. Others species, such as *E. beameri*, range widely over many types of substrates, and might be called "generalists."

It is interesting that adults of the species considered here spend so much time exposed on the soil surface. Paris (1965) considered this question with regard to the terrestrial isopod *Armadillidium*, concluding that surface activity was largely a respsonse to the necessity to feed, but other workers have contradicted this idea since the food of isopods is generalized and widespread in the litter habitats where they shelter during the day. This also appears to be the situation with the beetles. Certainly feeding requirements could be met by short forays from the daytime shelters, and this seems to occur in the more sessile species. Paris speculated that part of the activity of *Armadillidium* must be spent in searching for new shelters. This is undoubtedly true of the beetles as well, but cannot account for the great differences in vagility between species. Greater vagility might increase contacts between males and females,

particularly for underdispersed species. At Turkey Park, the most uniformly distributed species (*E. beameri*) was also the most vagile. The most sedentary species (*Coelocnemis, Asidopsis*) were strongly aggregated on specific substrates, so that sexual contacts would not require increased vagility.

It is curious that the beetles at Turkey Park were so strictly nocturnal. Facultative patterns of daily activity have been reported for a variety of tenebrionids, particularly those inhabiting arid regions (Kramm and Kramm 1972; Cloudsley-Thompson 1956, 1963; Hafeez and Makky 1959). In general, these species are active at dusk and dawn, but may show diurnal activity during the cool months of the year, or may shift to nocturnal activity during the hottest months. Even during the hottest months, diurnal activity may occur during temporary periods of cool, overcast weather (Doyen, unpublished data for *Eusattus muricatus* LeC.). For several species, these adjustable activity patterns have been interpreted as a response to temperature, which is highly variable and unpredictable in many desert habitats. Under such conditions, where favorable temperatures may occur for only short periods, it may be important for the beetles to quickly adjust to fluctuations. An alternative explanation is that the more rigorous conditions of xeric habitats favor increased periods of activity. For example, high rates of water loss might necessitate longer feeding times whenever possible. In this context it is interesting that one of the species at Turkey Park (*E. extricata*), which also occurs on the desert about 1400m lower, became active diurnally during overcast periods at the lower elevation. In this case activity continued into nocturnal hours. In contrast, at the higher elevation where temperatures were uniformly lower and the soil was almost constantly moist beneath the debris where the beetles sheltered, diurnal activity was never observed, even when temperatures fell within the nightly range where activity occured.

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