



Promoting the Science of Ecology

Mechanisms of Competitive Exclusion Between Two Species of Chipmunks

Author(s): James H. Brown

Source: *Ecology*, Vol. 52, No. 2 (Mar., 1971), pp. 305-311

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1934589>

Accessed: 20/06/2011 15:16

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=esa>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

MECHANISMS OF COMPETITIVE EXCLUSION BETWEEN TWO SPECIES OF CHIPMUNKS¹

JAMES H. BROWN

Department of Zoology, University of California, Los Angeles 90024

Abstract. Two species of chipmunks, *Eutamias dorsalis* and *E. umbrinus* exclude each other from certain elevations on isolated mountain ranges in the central Great Basin. Competitive success is determined by habitat; *dorsalis* excludes *umbrinus* from the sparse piñon-juniper forests at lower elevations and *umbrinus* excludes *dorsalis* from the denser forests at higher altitudes. The two species occur together only in a very narrow strip of intermediate habitat. Observation of the behavior and interactions of the two species within this overlap zone resulted in the following explanation for the mutual exclusion. *E. dorsalis*, the more aggressive and more terrestrial species, chases *umbrinus* from those areas where the trees are so widely spaced that *umbrinus* must flee on the ground. The competitive advantage immediately shifts to the more social and arboreal *umbrinus* when the trees are sufficiently large and dense that their branches interlock. In these habitats *umbrinus* readily escapes *dorsalis* by fleeing through the trees over routes that the more aggressive species cannot follow. In such situations the aggressive nature of *dorsalis* actually becomes competitively disadvantageous because the more social *umbrinus* is so numerous that *dorsalis* wastes a great deal of time and energy on fruitless chases. The differences between the two species in aggressive behavior apparently represent adaptations to the density of cover and food resources in their habitats. The main mechanisms of the competitive interaction between these two chipmunks (interspecific aggression, the ability of the subordinate species to utilize some feature of the habitat to escape from the dominant species, and aggressive neglect on the part of the dominant species) may frequently be important in cases of competitive exclusion between highly mobile animals.

Competitive exclusion has been documented both in the laboratory (Gause 1934, Park 1962, and others) and in the field (Connell 1961, Beauchamp and Ulyyott 1932, Hairston 1951, Tanner 1952, Istock 1967, and others). However most of the cases of competitive exclusion in nature are based upon circumstantial, distributional evidence, and only Connell (1961) has done extensive experimental work in the field and described mechanisms by which exclusion is effected. In his study of the interactions between two species of sessile, intertidal barnacles, Connell showed that the distribution of one species was limited to the uppermost region of the intertidal zone because below that region it was physically crowded out of the limited available space by a second species. This is of particular interest because many of the observed cases of competitive exclusion in nature occur between species of highly mobile vertebrates where the mechanisms of exclusion must be very different.

The present paper describes the interactions between two species of chipmunks (*Eutamias dorsalis* and *E. umbrinus*) which exclude each other from certain altitudinal ranges on numerous isolated mountain peaks in the central Great Basin. Hall (1946) provided excellent distributional evidence indicating that competitive exclusion occurred between the two species. The present study was designed to answer the question: How do the species utilize their habitats and interact so as to exclude each other from all areas but a narrow zone of overlap?

METHODS

This study occupied most of two summers, 1968 and 1969. The first summer was spent visiting many of the mountain ranges in central and eastern Nevada where one or both species of chipmunk were known to occur, in order to confirm Hall's (1946) distributional data and become familiar with the general distribution and ecology of the species. Three weeks (August 5 to 26) of 1968 and most of the summer (July 2 to August 7 and August 21 to September 9) of 1969 were spent in the Snake Range where a study area was established on Baker Creek, elevation 2,300 m, 7 miles west of Baker, White Pine County, Nevada. At this study area the microdistribution, habitat utilization, and interspecific interactions of the chipmunks were investigated in detail as described below.

Microdistribution.—An area of approximately 1 mile² (2.6 km²) which included portions inhabited by each species was censused regularly both summers. All parts of the area were covered at least twice each summer and those places where the ranges of the two species abutted or overlapped were observed much more intensively. Censuses were made by slowly walking through selected areas in the early morning and plotting on a map the location and species of each chipmunk observed.

Interspecific aggression.—Although both species were abundant in the study area both summers, individuals were sufficiently mobile and dispersed that it was impossible to observe a significant number of interspecific interactions among animals in com-

¹ Received June 1, 1970; accepted August 5, 1970.

pletely natural circumstances. It was found that an artificial feeding station, baited with crushed peanuts, attracted individuals of both species when it was placed in an area where their altitudinal and habitat ranges overlapped. The feeding station made it possible to observe numerous interspecific and intraspecific interactions between chipmunks and to compare the behavior of the two species in identical surroundings. The feeding station was maintained from August 9 to 20, 1968, and from July 4 to August 7 and August 23 to September 1, 1969. During these periods observations were made 6 days per week from sunrise, when the chipmunks first became active, until about 0930 hr, when activity began to wane. Occasionally observations were also made in the late afternoon, but activity was much less than in the morning and they were not very profitable. The chipmunks rapidly habituated to the presence of the observer, who recorded each visit and aggressive encounter. In 1969 the individuals visiting the station were trapped, marked with colored plastic discs riveted through each ear, and released. With the chipmunks individually marked it was possible to determine the total number of individuals visiting the station, the frequency of visits by each individual, and the fate of individuals involved in aggressive interactions.

Habitat utilization.—It was obvious that the two species differed in the extent to which they were arboreal or terrestrial. Two methods were used to quantify the nature of this difference. First, on four different days the frequency with which individuals of each species used the various routes by which the chipmunks approached the feeding station were recorded. Secondly, the amount of time spent in trees or on the ground by individuals of each species was recorded on 8 different mornings. These latter observations were made on undisturbed chipmunks at least 300 m from the feeding station.

RESULTS AND DISCUSSION

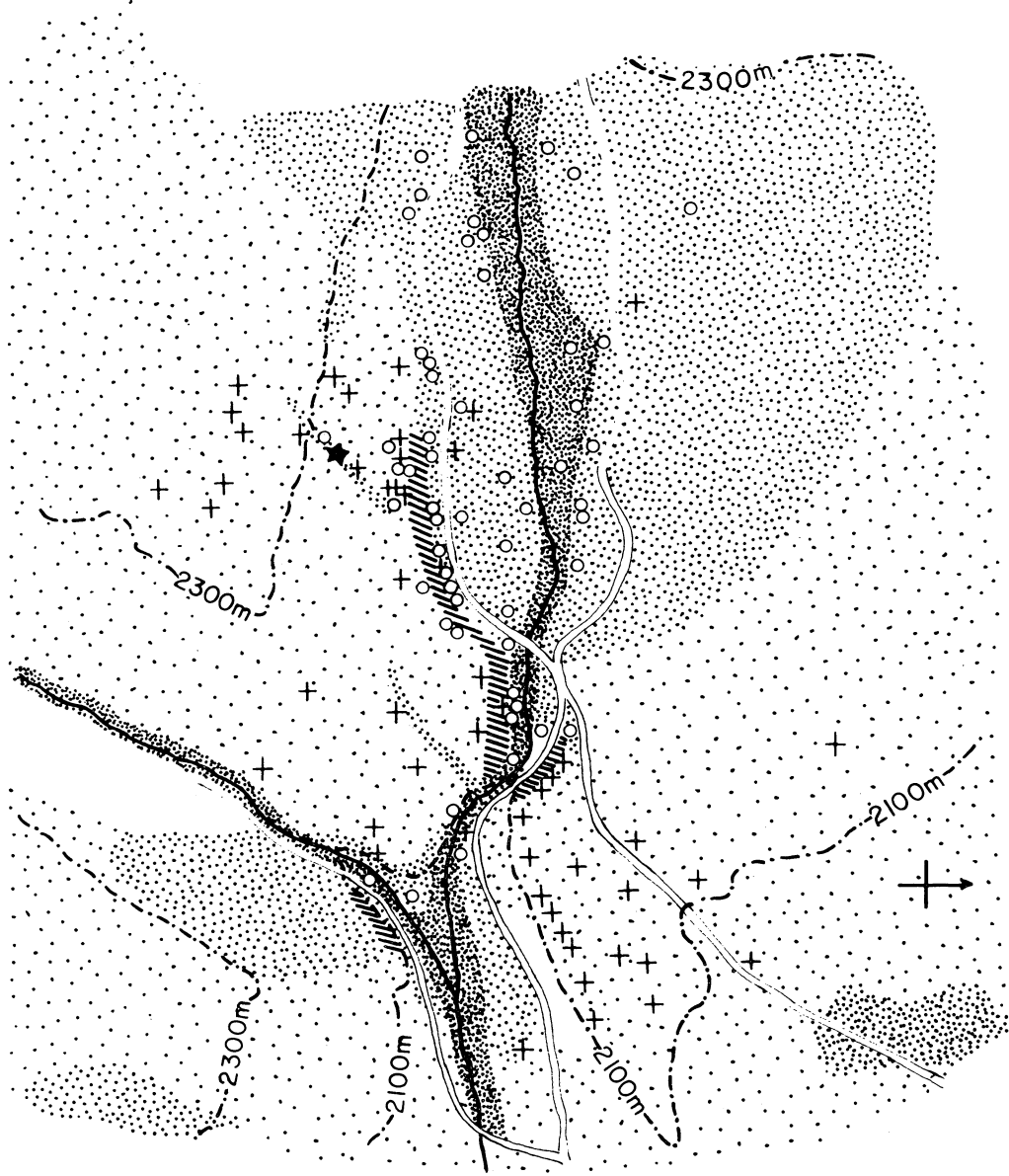
General ecology and distribution.—*Eutamias dorsalis* and *E. umbrinus* are similar in size (body weights are 55–68 and 51–80 g respectively) and general body proportions. As chipmunks go, they are quite different in coloration (*dorsalis* is pale, *umbrinus* brightly striped) so that they can be distinguished at a distance by an experienced observer. Both species feed mainly on the seeds and fruits of a variety of plants including piñon (*Pinus monophylla*), juniper (*Juniperus osteosperma*), mountain mahogany (*Cercocarpus montanus*), wild rose (*Rosa* sp.), prickly pear (*Opuntia* sp.), and several grasses and forbs. In addition, *umbrinus* were observed feeding on fungi and the seeds and fruit of chokecherry (*Prunus virginiana*) while *dorsalis* were seen feeding on the seeds of cliff rose (*Cowania mexicana*). Both species pre-

fer somewhat open, rocky habitats. Both live in burrows which they dig among rocks or at the base of trees.

Both *umbrinus* and *dorsalis* are widely distributed in the forested areas of the southwestern United States in general and on the isolated mountain ranges of the central Great Basin in particular. On most of the mountains of eastern and central Nevada (see Hall 1946 for details) both species are present and the forested habitats are partitioned altitudinally between them. *E. dorsalis* is restricted to the sparse piñon-juniper associations on the lower slopes. At higher elevations it is replaced by *umbrinus* which ranges up to treeline.

There are two mountain ranges where only one of the two species occurs. *E. dorsalis* inhabits the Pilot Range and *umbrinus* is found in the Ruby Mountains. Both of these mountain ranges are found at the northern edge of the geographical distributions of both species and the absence of one may be attributed to historical accident. Each of these mountain ranges has large areas of habitat that is apparently suitable for the missing species, but in its absence the other species has expanded its altitudinal range to include all forested habitats from the lowest pinons and junipers to treeline (Hall 1946; confirmed in the present study). This observation that each species occupies a wider range of habitats in the absence of the other than it does where both species occur together is excellent circumstantial evidence that their distributions are limited by competitive exclusion when both species inhabit the same mountain.

No direct attempt was made to determine the resource for which the chipmunks are ultimately competing, but two observations suggest that it is food. First, the animals dig their own burrows and suitable sites appear to be so numerous that it is hard to imagine that shelter could be a limiting resource. Secondly, individuals of both species engage in rigorous contests to obtain access to local concentrations of food. This is particularly obvious in summer and early fall when seeds and fruits are ripening and the chipmunks are storing them away for the winter. The bait put out at the feeding station not only attracted numbers of both species to feed, but it also apparently induced several *umbrinus* to establish permanent residence in the immediate vicinity. It should be noted that similar concentrations and interactions of chipmunks occur at natural concentrations of food as well as at the artificial feeding station. I have observed up to five *umbrinus* and two *dorsalis* (on different occasions) feeding in and under a single piñon with an exceptionally heavy crop of cones. The preceding observation counters the possible objection that the behavioral interactions of chipmunks at the feeding station reported here were the aberrant results of totally unnatural concentrations of individuals.



KEY:

- *E. umbrinus* + *E. dorsalis* [grid pattern] Dense thickets of aspen, chokecherry, rose [stippled pattern] Piñons and junipers, branches frequently interlocking
- [widely spaced stippled pattern] Piñons and junipers widely spaced [empty square] No trees or shrubs (meadows or bare ground) [diagonal lines] Rocky cliffs
- [wavy line] Dirt roads [solid line] Streams [dashed line] Contour lines ★ Feeding station [scale bar] 20 km

FIG. 1. The microdistributions of the two species of chipmunks on the study area during July and August 1969.

Microdistribution.—The location of sightings of individual chipmunks on the study area in the Snake Range during 1969 are shown in Figure 1. In 1968 the pattern was essentially identical, and it is possible to tell from field notes and specimens in the Museum

of Vertebrate Zoology (University of California, Berkeley) that the distributions of the two species have not changed significantly since field parties visited the Baker Creek area 40 years ago. The distributions of the species are largely nonoverlapping.

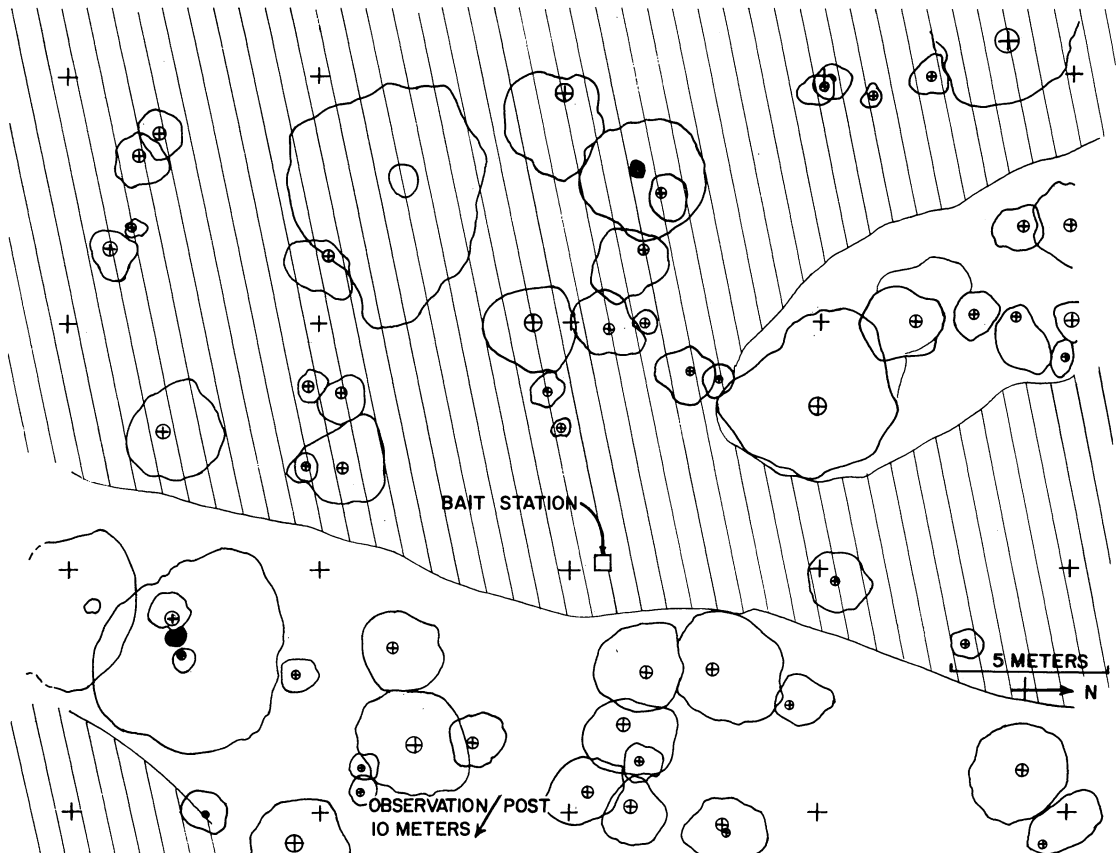


FIG. 2. Detail of the habitat in the vicinity of the feeding station where both species of chipmunks occur. Hatched areas indicate bare, rocky ground; unhatched areas, soil and litter substrate. Large irregular outlines indicate the canopy spread of the following trees: piñon, circle with cross; juniper, unshaded circle; mountain mahogany, shaded circle.

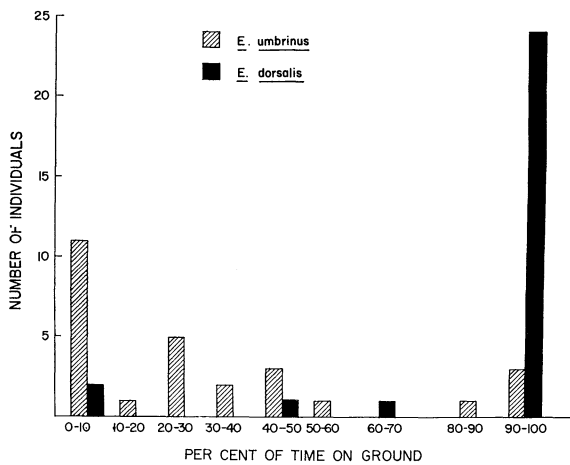


FIG. 3. Frequency distribution of the amount of time spent on the ground, as opposed to in trees, by each species. The difference between species is highly significant ($P < 0.001$).

Only in a narrow zone, varying in width from a few meters to about 200 m, can both species be found. Since these chipmunks frequently have home ranges

measuring more than 100 m in greatest dimension, the zone of overlap is narrow relative to the movements of the chipmunks themselves.

The small degree of distributional overlap and its temporal stability suggests that the shift in competitive advantage from one species to the other must be dependent upon some relatively permanent feature of their environment. It is apparent from Figure 1 that the distributions are conspicuously correlated with the density and size of trees. The transition from one species to the other does not correspond to an ecotone between plant communities, but occurs within the piñon-juniper association.

E. dorsalis is restricted to the stands of piñon-juniper where the trees are small and spaced so that there is considerable open ground between them. When the piñons and junipers become sufficiently dense that some of their branches interlock, *dorsalis* is replaced by *umbrinus*. An area of intermediate habitat, where both species occur, is mapped in detail in Figure 2. It consists of interdigitating areas of open, rocky ground and stands of piñon and juniper with interlocking branches. *E. umbrinus* also inhabits

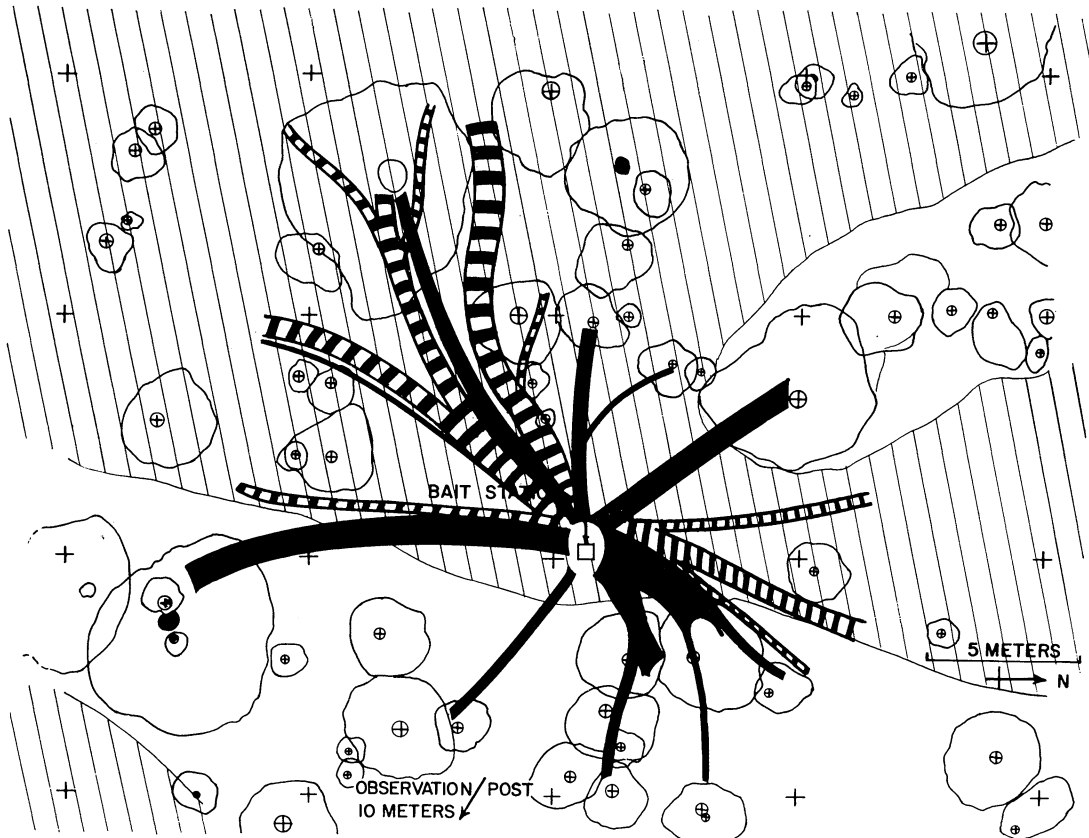


FIG. 4. Paths utilized by each species as it approached the bait station. Paths of *umbrinus* are indicated by complete shading, those of *dorsalis* by cross banding. Other symbols are explained in Figure 2.

other dense stands of trees including aspen groves, chokecherry thickets, and, at higher elevations, forests of mixed conifers.

Several other pairs of vertebrate species have strikingly similar distributions on the mountains of the Great Basin, and this may reflect a similar effect of vegetation structure and competitive interaction on these species. They include desert and bushy-tailed woodrats (*Neotoma lepida* and *N. cinerea*), Scrub and Steller's Jays (*Alphelcoma coerulescens* and *Cyanositta stelleri*), and Plain Titmouse and Mountain Chickadee (*Parus inornatus* and *P. gambelli*). The microdistributions of the last-mentioned pair correspond almost exactly to the local distributions of *E. dorsalis* and *E. umbrinus* respectively. This correspondence is maintained despite the much greater mobility of the birds and I have watched flocks of titmice fly over or around vegetation of inappropriate density without stopping to forage. Effects of vegetation structure on interspecific interactions are apparently of quite general occurrence, at least in vertebrates.

Rosenzweig and Winakur (1969) have recently found habitat structure to have an important effect on the microdistribution of desert rodents and Cody

(1968) has analyzed its influence on the competitive relationships between species of birds in grasslands.

Habitat utilization.—Despite the fact that both species harvest much of their food in trees, *umbrinus* is much more arboreal than *dorsalis*. It spends a greater proportion of its time in trees than *dorsalis* (Fig. 3) and when approaching the feeding station it tended to dash out from a nearby clump of trees whereas *dorsalis* usually approached on open, rocky ground (Fig. 4). This very significant difference in the ability of the two species to utilize trees is also apparent from the following qualitative observations. When approached by man, or a predator, *dorsalis* usually runs away on the ground until out of sight, and when disturbed it will often descend from a tree and flee in this manner. On the other hand, *umbrinus* usually climbs the nearest good-sized tree and "freezes" when it is disturbed. In interspecific aggressive encounters an *umbrinus* frequently escaped from a pursuing *dorsalis* by climbing a tree and either running out to the tip of a long, thin branch or crossing to another tree through the branches and the *dorsalis* failed to follow.

Interspecific aggression.—The feeding stations were highly successful at attracting members of both species and a large number of interspecific and intra-

TABLE 1. Visits and aggressive interactions at the feeding station in 1969

	Visits			Aggressive encounters		
	<i>umb</i>	<i>dor</i>	<i>umb</i> > <i>umb</i>	<i>umb</i> > <i>dor</i> ^a	<i>dor</i> > <i>umb</i> ^a	<i>dor</i> > <i>dor</i>
Total number.....	1,162	946	143	83	310	166
Observed frequency ^b551	.449	.203		.560	.237
Expected frequency ^b	—	—	.304		.495	.201
Number of individuals.....	18	11	13		21	9

^aThe winner is the species on the left of the > symbol, the loser is the species on the right.

^bThe expected frequencies of aggressive encounters are those expected if encounters among individuals were random with respect to species identity, and are calculated from the observed frequency of visits by binomial expansion. The difference between observed and expected frequencies of encounters is highly significant ($\chi^2 = 33.2$; $P < .005$).

specific behavioral interactions were observed. The results of the observations at the feeding station during 1969 are summarized in Table 1. As soon as the chipmunks were coming to the station regularly, an interspecific dominance hierarchy was rapidly established; higher ranking individuals chased away and defended the feeding area against subordinate animals. *E. dorsalis* was significantly more aggressive than *umbrinus*. Individuals of *dorsalis* occupied the four highest positions in the dominance hierarchy, won four-fifths of all interspecific encounters, and engaged in more interspecific and intraspecific interactions than predicted on the basis of the number of visits of each species. Qualitatively it was apparent that individuals of *dorsalis* invariably approached the feeding station alone whereas those of *umbrinus* frequently traveled in pairs made up of varying combinations of ages, sexes, and individuals.

The aggressive nature of *dorsalis* is apparently an adaptation to its sparsely vegetated habitat, where selection favors those chipmunks that are sufficiently aggressive to defend the scarce, widely distributed food sources against conspecific and heterospecific competitors. Where the local distributions of the two species overlap, *umbrinus* is more numerous and more tolerant of other chipmunks than *dorsalis*. This probably reflects not only reduced selection for the aggressive defense of a large area, but also selection for some sort of loose social association because of the advantage of having additional animals nearby to detect and give warning of concealed predators. Certainly the opportunities for a predator to approach unobserved are much greater in the densely vegetated habitats.

Between July 4 and August 7, 1969, the longest period that the feeding station was in continuous operation, there were interesting changes in the number of individuals of each species that were using the bait (Fig. 5). Although *dorsalis* began to visit the bait first, new individuals of *umbrinus* were attracted until they were twice as numerous as *dorsalis*. Additional *umbrinus* were recruited to the station despite repeated aggressive encounters (which they usually lost) with *dorsalis*. These encounters seldom resulted

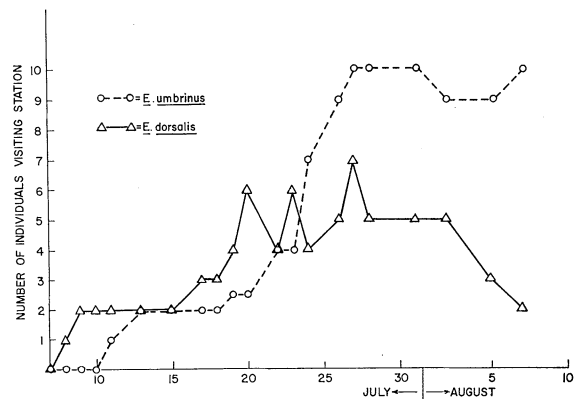


FIG. 5. Numbers of individual chipmunks of each species visiting the feeding station during a 5-week period in 1969.

in injury to the *umbrinus* because they immediately fled to nearby trees and evaded the pursuing *dorsalis* as described in the previous section.

The data presented in Figure 5 suggest that the continued utilization of the bait by large numbers of *umbrinus* led to the abandonment of the station by several *dorsalis*. Certainly the number of *dorsalis* visiting the station declined and this decline was not owing to mortality because two marked *dorsalis* frequently were seen in the general area, but many yards from the station, after their last visit. The following sequence of interspecific interactions, frequently observed once more than five or six *umbrinus* were visiting the bait, probably accounts for the decline in the number of *dorsalis* in the immediate vicinity of the station. A *dorsalis* would chase an *umbrinus* from the bait into a nearby tree and return to the station only to find it occupied by another *umbrinus* busily feeding or filling its cheek pouches. The *dorsalis* would banish the second *umbrinus* to a tree, but meanwhile the first *umbrinus* would have slipped in again to feed, and so the process would continue. Often the *dorsalis* would eventually leave the station without having fed. In such cases the aggressive nature of *dorsalis* obviously worked to its disadvantage. Similar inefficient and competitively disadvantageous

effects of interspecific aggression have been described in several species of birds (Ripley 1961) and termed aggressive neglect.

CONCLUSIONS

I conclude that mutual competitive exclusion between the two species of chipmunks is effected in the following manner. *E. dorsalis* is more aggressive than *E. umbrinus* and is better at moving over open ground. When trees are sufficiently widely spaced that its competitor must flee significant distances on the ground, *dorsalis* efficiently defends localized resources and excludes *umbrinus* by means of interspecific aggressive encounters. The aggression rapidly becomes ineffective when the trees become so closely spaced that the more arboreal *umbrinus* can readily escape. In fact, once the density of trees reaches a critical level, *umbrinus* (which is more numerous and more tolerant of other chipmunks than *dorsalis*) is able to exclude *dorsalis* because the latter wastes excessive time and energy on fruitless chases.

The interacting behavioral mechanisms of exclusion between these chipmunks are very different from the simple physical destruction by crowding that occurs in barnacles (Connell 1961). In fact the particular combination of behavioral patterns in each species of chipmunk and the way that these interact in interspecific encounters seems highly specialized for this particular situation and hardly likely to be a general feature of competitive interactions, even in very similar, highly mobile vertebrates. In this regard it is interesting to compare the results of the present study with the unpublished results of a study by D. H. Sheppard (reported in Miller 1967) of competition between two other species of chipmunks (*Eutamias minimus* and *E. amoenus*) in western Alberta, Canada. Some aspects of that interaction appear similar to those between *E. dorsalis* and *E. umbrinus*, as the competitors divide the habitat on the basis of density of vegetation and interspecific aggression plays an important role in exclusion. Others, however, are quite different; the distribution of only one of the species is limited by competitive exclusion, and it is the forest-dwelling species that is more aggressive. From the fragmentary data available, it also appears that most of the important components of the interactions between *dorsalis* and *umbrinus* have been implicated in cases of exclusion between other species of both vertebrates and invertebrates. Interspecific aggression plays an important role in competitive interactions between rats, mice, blackbirds, titmice, hummingbirds, and ants (many sources reviewed by

Miller 1967). The inefficient, self-defeating effects of interspecific aggression in some circumstances have been observed in several bird species (Ripley 1961). Differences in ability to locomote and take refuge in certain portions of the habitat such as trees or tall buildings, in addition to differences in aggressiveness, are an important part of the interaction between Norway and roof rats (Ecke 1954). It certainly seems that interspecific aggression which seldom results in mortality or even injury is a common element in many cases of competitive exclusion between highly mobile animals. The effect of the aggression is counterbalanced by the ability of the subordinate species to take refuge in some portion of the habitat from which the dominant species cannot displace it.

ACKNOWLEDGMENTS

My wife, Astrid, provided invaluable assistance with all phases of the project. G. A. Bartholomew and M. L. Cody have kindly read and criticized an earlier draft of the manuscript. The cooperation of the personnel of the U. S. Forest Service in Baker and Ely, Nevada, did much to make the field work pleasant.

LITERATURE CITED

- Beauchamp, R. S. A., and P. Ulyyott. 1932. Competitive relationships between certain species of freshwater triclads. *J. Ecol.* **20**: 200-208.
- Cody, M. L. 1968. On methods of resource division in grassland bird communities. *Amer. Naturalist* **102**: 107-147.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**: 710-723.
- Ecke, D. H. 1954. An invasion of Norway rats in southwest Georgia. *J. Mammal.* **35**: 521-525.
- Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore.
- Hairston, N. G. 1951. Interspecies competition and its probable influence on the vertical distribution of Appalachian salamanders of the genus *Plethodon*. *Ecology* **32**: 266-274.
- Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley and Los Angeles.
- Istock, C. A. 1967. Transient competitive displacement in natural populations of whirligig beetles. *Ecology* **48**: 929-937.
- Miller, R. S. 1967. Pattern and process in competition. *Adv. Ecol. Res.* **4**: 1-74.
- Park, T. 1962. Beetles, competition and populations. *Science* **138**: 1369-1375.
- Ripley, S. D. 1961. Aggressive neglect as a factor in interspecific competition in birds. *Auk* **78**: 366-371.
- Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* **50**: 558-572.
- Tanner, J. T. 1952. Black-capped and Carolina Chickadees in the southern Appalachian Mountains. *Auk* **69**: 407-424.