Parapatry and Encounter Competition between Chipmunk (Tamias) Species and the Hypothesized Role of Parasitism

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ABSTRACT.—Two parapatric species of chipmunks occur in the Front Range of Colorado: *Tamias quadrivittatus* only below 2130 m in lower montane life zones and *Tamias umbrinus* from 2130 m upward in upper montane life zones. The smaller and ecologically distinct *Tamias minimus* occurs sympatrically in nearly all life zones at elevations above 1750 m. Of the three species, which all display intra- and interspecific territoriality, *T. umbrinus* is the most aggressive. Populations of *T. umbrinus* at the lower-elevation margin of its distribution in the Front Range and of *T. quadrivittatus* can suffer heavy infestations by larval cuterebrid bot flies (*Cuterebra fontinella*), whereas *T. minimus* is virtually resistant to bot myiasis. Since bot flies are virtually limited to elevations below 2200 m, I propose that parapatry between the two common host species results from a balance between aggressive dominance by *T. umbrinus* above 2130 m and increased sensitivity to the adverse effects of bot parasitism by the dominant host species below this elevation. *Tamias quadrivittatus* shares more biogeographical similarities with the warmer climate-adapted parasite than does *T. umbrinus* and so has had greater evolutionary opportunity to become coadapted as a host. There is a vital need in community ecology for hypotheses concerning the interaction of parasitism and competition and its effect on species distributions to be developed and tested.

INTRODUCTION

Parapatry and distributional gaps between similar vertebrate species have not been well-explained in cases lacking a striking habitat discontinuity. Most explanations of parapatry have invoked a changing balance of resource consumptive superiority along an environmental gradient (*e.g.*, Andrews and Petney, 1981; Odendaal and Bull, 1980). If the limiting factor inherent in that gradient is a resource, this would imply fixed differences in habitat preferences between the contiguous species (as in, *e.g.*, States, 1976). Among the 20 or so species of chipmunks (*Tamias*) found in western North America (Levenson *et al.*, 1985), there are numerous cases of parapatry (Hall, 1981; Hoffmann, 1974), which may or may not correspond to sharp environmental gradients. Although differences in microhabitat preferences have been found for species pairs that are sympatric (Bergstrom, 1986; Larrison, 1947; Brown, 1971; Smith, 1977; Sharples, 1983), active encounter competition (*sensu* Schoener, 1983) has often been invoked to explain parapatry between species of chipmunks, which are typically solitary and display territorial aggression (Bergstrom, 1986; Heller, 1971; Meredith, 1977; Chappell, 1978).

Effects of parasitism on a host's population dynamics or ecology have received some theoretical attention (Holmes, 1982; May and Anderson, 1978, 1983) but little empirical investigation (Munger and Karasov, 1989). A few studies demonstrate dramatic effects on distribution and abundance when a parasite has differential impact on host populations (Park, 1948; Anderson, 1972; Nelson and Smith, 1976). Distribution and population density of moose (*Alces alces*) in much of North America are thought to be limited by dense

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populations of white-tailed deer (*Odocoileus virginianus*), which carry the brainworm *Parelaphostrongylus tenuis,* pathogenic in moose but not normally so in deer (Anderson, 1972; Gilbert, 1974, and references therein). The lesser susceptibility of *Peromyscus maniculatus* to *Yersinia pestis* (agent of sylvatic plague), as compared to the alternate host *Neotoma cinerea,* allows it to occupy certain cave habitats in sympatry with *Neotoma* (Nelson and Smith, 1976). Similarly the stomach nematode *Graphidium strigosum* was implicated in the invasion of hare habitat by rabbits in Europe (Broekhuizen and Kemmers, 1976). Elevational restrictions of host ranges are evidenced by the postinvasion avifauna of the Hawaiian Islands, where endemic species surviving the diseases of exotic arthropod-borne microbes exist only in mountaintop refuges where mosquito vectors cannot survive (Warner, 1968).

Although no study has yet dealt with parasitism as a determinant of parapatry, Cornell (1974) invoked differential coadaptation with parasites to explain certain distributional gaps between related allopatric hosts. Barbehenn (1969) proposed the general hypothesis that competitive exclusion of species A by species B may be prevented by a parasite to which A is better adapted than is B. A similar hypothesis may be formulated to address parapatry *per se.* Any environmental factor(s) that limited the distribution of a parasite and caused it to co-occur more extensively with host species A than with related host species B may result in the A pair being more coevolved than the B pair, resulting in more deleterious effects on populations of B that are exposed to the parasite than on populations of A. If B were the superior competitor in the absence of the parasite, A, in the parasite's presence, may be able to exclude B from a portion of what should otherwise be B's range. Price's (1980) conclusion about distributional gaps was that they involved at least a pair of infectious parasites which themselves (or whose vectors) traveled beyond the range boundaries of the ecologically similar hosts, each of which is better adapted to one of the parasites. Parapatry, on the other hand, suggests a single parasite (not necessarily infectious) having differential impacts on hosts A and B.

Two species of western chipmunks, *Tamias quadrivittatus* and *T. umbrinus,* are parapatric at a remarkably consistent elevation (2130 m) in the Front Range of northern Colorado (Bergstrom and Hoffmann, 1991). Their habitat and food preferences are similar, however, and changes in resource composition with elevation are gradual (Marr, 1961; Bergstrom and Hoffmann, 1991). In fact, each species shows dramatic "niche shifts" (Diamond, 1978) where it occurs far removed from the parapatric zone (Armstrong, 1972). A third species, *T. minimus,* is ecologically distinct and is widely sympatric with each of the two larger chipmunks. I propose the hypothesis that parapatry between these chipmunks is determined by active encounter (interference) competition, and that the location of the parapatric boundary represents a balance between degree of aggressiveness and susceptibility to the sublethal effects of an abundant parasite. According to the hypothesis, the aggressive superiority of the upper-elevation host (*T. umbrinus*) is negated at lower elevations as a result of subcutaneous infestation by larvae of the bot fly, *Cuterebra fontinella,* which generally occurs only below 2200 m elevation.

METHODS

Sixty-eight study sites ranging in elevation from 1700 to 2900 m (parapatry occurs at 2130 m) were chosen for live trapping, which was conducted during 4 consecutive summers, 1981–1984. Most of these sites were located within the Roosevelt National Forest in Boulder and Larimer counties, Colorado. They were located in ecosystems ranging from grassland-lower montane woodland/shrub ecotone to upper montane forest-subalpine forest ecotone (Marr, 1961). Each trapping site was sampled for at least a 2-wk period. Smaller trapping grids varied from 24–36 stations, with a trap spacing of from 25–35 m; one Sherman live

trap (3.5 × 3.5 × 23.0 cm) was placed at each station, baited with cracked grain and sunflower seeds, and provided with cotton nesting material. The three largest study sites, at ca. 2000, 2100 and 2700 m and ranging in area from 8–35 ha each, were monitored over a longer time than the others, and accounted for most of the behavioral observations (bot flies occurred only in the lower two). Further details of trapping procedures, study sites and habitats are given in Bergstrom and Hoffmann (1991).

All captured animals were examined for subcutaneous myiasis caused by larval bot flies and for open or healing warble pores, which persist for up to 2 wk after larval emergence (Catts, 1982). First-instar larvae could not be detected by palpation, but a random sample of chipmunks of the three species was sacrificed, mostly during 1981, providing some data on early infestation. Several mature third-instar larvae were extracted from chipmunk hosts. Diapause was induced by planting the prepuparia in soil and allowing them to overwinter (Catts, 1964); adult flies were captured upon hatching in spring to determine species identity.

Live-trapped animals were ear-tagged and marked with individual patterns using Nyanzol B dye. Behavioral data were collected by observation of both dye-marked and radiotracked animals (Bergstrom, 1986) and by observation of encounters at feeding stations. Beginning in 1982 and after observing the phenomenon the previous 2 field seasons, I recorded whether trapped chipmunks vocalized and if so to what degree (slight: 1–2 chips; moderate: 3–10 chips or a bout of <10 sec; extreme: a bout of >10 sec); this determination was made blind, before opening the trap. Trapping and radiotelemetry at the three long-term study sites allowed mapping of home ranges and defended territories of chipmunks of the three species. A territory was defined as that portion of the home range that contained a concentration of captures, telemetry locations, or incidental observations (below) along with at least one of the following: (1) a known burrow, larder, or tree nest in use by the animal; (2) observation of scatter-hoarding and/or scent-marking in the area; and (3) observation of at least two vocalization bouts in the area (discounting incidents when there was evidence of a predator nearby). The mapped territory was a convex polygon whose vertices were the outermost grid stations nearest to which any of the above three conditions were met and including all stations at which an animal was captured three or more times or nearest to which a radiotelemetered animal was observed more than 10% of its total time (range 30–120 h) under observation or an untelemetered animal was observed three or more times on different days.

Feeding stations consisting of piles of sunflower seeds placed on rocks or stumps were then established in the three larger study sites and moved frequently so as to lie in or near known individuals' territories. An encounter consisted of an approach of 0.5 m or less involving two or more chipmunks and lasted as long as the activity displayed at the onset of the encounter was continuous, that is, was not interrupted by a qualitative change in activity or by one or both animals leaving the area of the station (or the initial site of encounter). Encounters were then classified as no interaction, cohesive interaction, mutual agonism, or asymmetric agonism. In the latter case, I attempted to determine which animal was the territory "owner" and which was the "invader." Since feeding stations were deployed mainly in late summer and early autumn (mid July–early October), after most adults in the area were marked, I determined site "ownership" of participants in asymmetric contests as follows. If the feeding station was positioned in the normal home range and in or near the territory of animal A, but clearly not of B, A was the owner; in the same situation, if B was a newly observed animal, A was the owner. When the station was placed in an area of home range overlap between A and B, A was the owner only if both territories could be mapped and A's territory was at most half the distance from the station as B's. In all other cases, ownership was not determined.
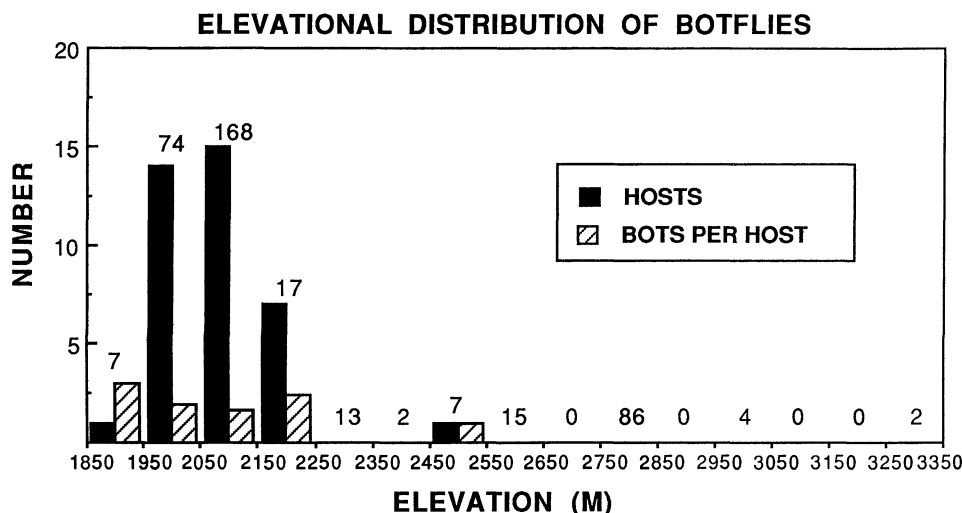
ELEVATIONAL DISTRIBUTION OF BOTFLIES

FIG. 1.—Elevational distribution of bot fly (*Cuterebra fontinella*) larvae in chipmunk (*Tamias*) hosts in the northern Front Range of Colorado, showing number of infested hosts and average number of bot larvae per host. Number above each bar or elevation interval indicates number of different chipmunks examined within the active larval development season, 20 July to 1 October, during the years 1981–1984

RESULTS AND DISCUSSION

Cuterebrid infestation.—During 1981, chipmunks collected from lower-elevation sites were infested with bot larvae; infested animals held in captivity seemed lethargic and suffered either stress-related or nutrition-related mortality more readily than uninfested captive animals (pers. observ.). Other small mammals, especially *Peromyscus maniculatus, P. difficilis* and *Neotoma mexicana,* were also infested with bot larvae at elevations of 2200 m and below (pers. observ.). This altitudinal restriction of bots was also seen in chipmunk hosts (Fig. 1); one *Tamias umbrinus* was found to be infested with a single second-instar larva at 2500 m, but no other bot larvae were found in any mammal host above 2200 m. This elevational restriction seems to be the case in general across the Front Range (R. B. McLean; G. O. Maupin, pers. comm.) and in central and southern Colorado (J. H. Honacki, pers. comm.).

Bot fly larvae were found in chipmunk hosts from early August (rarely late July) through late September. Trapping did not extend past the first few days of October in any year, so it is possible that the infestation extended into October, but the peak period was mid-August. Out of 101 *Tamias minimus* captured during this season at or below 2200 m, only one animal was infested (that with one second-instar larva, and at a locality where 60% of *T. umbrinus* captured were infested at the time). In contrast, substantial proportions of both *T. quadrivittatus* and *T. umbrinus* were infested in all four years (Table 1). Four adult flies were successfully reared from different hosts (two from each of the two host species) and determined to be *Cuterebra fontinella,* the same species that infests *Peromyscus* in the Front Range (R. B. Finley, pers. comm.; Catts, 1982, and references therein).

There was no difference between the two chipmunk species in distributions of number of bot larvae per infested host in this study (Kolmogorov-Smirnov two-sample test, $P >$ 0.1). Overall, infestation rates in *Tamias umbrinus* were similar to those in *T. quadrivittatus* (Table 1; sample sizes of infested hosts were too small to allow meaningful significance

TABLE 1.—Incidence of bot fly larvae (*Cuterebra fontinella*) infestation in two chipmunk hosts (Q = *Tamias quadrivittatus*; U = *Tamias umbrinus*) at or below 2200 m elevation in four successive seasons (20 July–5 October)

	1981		1982		1983[1]		1984		Combined[2]	
	Q	U	Q	U	Q	U	Q	U	Q	U
Chipmunks caught	26	28	15	16	11	9	12	9	64	62
									53	*53*
No. infested	5	10	4	6	6	1	3	2	18	19
									12	*18*
% infested	19.2	35.7	26.7	37.5	54.5	11.1	25.0	22.2	28.1	30.6
									22.6	*34.0*
Avg. no. bots/host	1.6	2.1	1.8	1.2	2.3	2.0	1.7	1.5	2.00	1.74
									1.83	*1.72*
Max. no. bots/host	3	5	4	2	5	2	2	2	5	5
									5	*5*

[1] Sample was unreplicated (all 11 Q from one locality, all 9 U from another)
[2] Numbers in italics are totals without 1983 data

testing). It was difficult to get an unbiased sampling of host populations, as my trapping schedules (designed for other aspects of the research) were not uniform from year to year in the geographic extent of coverage during the active bot season. Because proportion of host population infested varied considerably from one locality to another, the unreplicated data from 1983 (Table 1) are clearly uninformative with regard to species differences in infestation rates. The season in which sampling was least biased by pseudoreplication (Hurlbert, 1984; *i.e.*, most replicates of different infested populations) was that of 1981 (n = 10), in which *T. umbrinus* showed nearly twice the infestation rate of *T. quadrivittatus*.

The ratio of immature (young-of-year) to adult hosts was low (26% for *Tamias umbrinus*, 5% for *T. quadrivittatus*) both absolutely and compared to the immature/adult ratio of all animals caught between 1 August and 1 October in all years (49%, 17% for the two host species). However, young-of-year are not always reliably separated from adults, especially after August, as their size and weight reach adult dimensions by then. This is especially true of the low-elevation *T. quadrivittatus*, whose young emerge from their natal burrows (at which time they are roughly three-fourths grown) up to 2–3 wk earlier than the lowest-elevation *T. umbrinus* (Bergstrom, 1986).

Although most species of *Cuterebra* are fairly host-specific, *Cuterebra fontinella* appears to have a wider range of host acceptance than most (Catts, 1982); this is the first detailed report of the species infesting *Tamias* (Sabrosky, 1986 cites a few scattered reports of *C. fontinella* infesting *T. umbrinus* and *T. amoenus*). It is important to emphasize that, based on all four criteria defined by Catts (1982), *T. umbrinus* and *T. quadrivittatus* behaved as "normal" hosts for *C. fontinella* in the Front Range. The sex ratio of infested hosts (43% male) was similar to the sex ratio of all captures (45% male). Fifty-four percent of all bot warbles occurred inguinally, 18% occurred anteroventrally (including the throat), and 28% occurred dorsolaterally. Preference for the inguinal development site agrees with other studies of *C. fontinella* (Dunaway *et al.* 1967; Catts, 1982) and of other *Tamias* bot flies (Bennett, 1955; Timm and Lee, 1982).

Aggressive interactions in chipmunks.—All three species of *Tamias* showed evidence of intra- and interspecific territorial behavior (Bergstrom, 1986), including three instances of

TABLE 2.—Classification of outcomes of interindividual encounters between chipmunks at feeding stations (M = *Tamias minimus*, Q = *T. quadrivittatus*, U = *T. umbrinus*)

Species pair	No. diff. pairs ob-served	No. diff. encoun-ters ob-served[1]	Percent of total encounters					
						Asymmetric agonism: territorial status of winner		
			No inter-action[2]	Cohe-sive inter-action	Mutual agonism	A. Territory owner	B. Invader	C. Coequal (or undetermined status)
M-M	23	39	48.7	25.6	0	10.3	0	15.4
Q-Q	7	21	52.4	19.0	0	14.3	0	14.3
U-U	40	151	25.2	8.6	2.6	39.7	8.6	14.6
M-Q	7	10	60.0	10.0	0	10.0 (M)	0	20.0 (both Q)
M-U	10	23	47.8	0	4.3	21.7 (all U)	0	30.4 (all U)
Q-U	5	20	10.0	0	5.0	15.0 (2Q, 1U)	0	70.0 (all U)

[1] Each bout of mutual activity between two animals at or near a feeding station, whether agonistic, cohesive, or noninteractive, was counted as one encounter for as long as that activity was continuously displayed, *i.e.*, was not interrupted by a different type of activity or by one or both animals leaving the station or the field of view

[2] Two animals must have come within 0.5 m of one another with no apparent response by either to the other's presence

dominance reversals resulting from shifting the location of the feeding station [what Maynard Smith (1976) termed the "Bourgeois Strategy"]. *Tamias umbrinus* displayed a higher rate of agonistic interactions than either of its congeners both intra- and interspecifically (Table 2), and its greatest likelihood of aggressive interaction was with *T. quadrivittatus*. Asymmetric encounters between *T. quadrivittatus* and *T. umbrinus* were virtually always won by territory owners, or, in those cases where ownership was undetermined or not a factor, by *T. umbrinus* (binomial goodness-of-fit test, $\chi^2 = 14.0$, P < 0.001); the 14 "coequal status" encounters won by *T. umbrinus* (Table 2) represented four different dyads, including four different *T. umbrinus*, and took place on separate days in 1983 and 1984 at two feeding stations separated by more than 600 m; data include repeated assessments of two dyads that were separated by at least 24 h).

Data were insufficient to compare aggressive dominance between infested and uninfested individuals, but one effect was noticed during live trapping in 1980–1981 and monitored in 1982–1984: chipmunks had a tendency to vocalize in the traps as I approached to check them. First, in this partial sample (Table 3), the proportion of infested *Tamias quadrivittatus* was significantly greater than that of *T. umbrinus*, but this is an artifact, because the sample included localities up to 2500 m, where *T. umbrinus* occurs and bot flies are rare or absent. *Tamias umbrinus* vocalized significantly more frequently than *T. quadrivittatus*. Both species vocalized less frequently, though not significantly (Table 3B), when they were infested with bot larvae. Infestation appeared to diminish the level of vocalizing; I recorded 18 cases where trapped chipmunks vocalized to an "extreme" degree (a bout lasting longer than 10 sec), and these were all uninfested animals (binomial goodness-of-fit test, $\chi^2 = 18.0$, P < 0.001). In other words, degree of aggressive energy as reflected by calling was significantly lower in the sample of infested animals.

Given that *Tamias quadrivittatus* has habitat and diet preferences very similar to *T. umbrinus*, especially when compared to *T. minimus* (Bergstrom, 1986), and that *T. quad-*

TABLE 3A.—Contingency table to test differences between host species [*Tamias quadrivittatus* (Q) and *Tamias umbrinus* (U)] in vocalization while in live traps and effect of bot fly larval infestation on vocalization; captures sampled from 20 July to 1 October 1982–1984. Data indicate number of captures (number of individuals in parentheses)

Host species	Vocalized?	Uninfested	Infested
Q	No	84 (46)	23 (11)
	Yes	10[1] (6)	1 (1)
U	No	104 (43)	6 (6)
	Yes	165[1] (65)	3 (3)

TABLE 3B.—Results of log-linear analysis of dependency of data in Table 3A, including two-way interaction terms from the model

Interaction	Chi-square	Probability
Species × vocalize	15.15	0.0001
Species × infest	6.37	0.012
Infest × vocalize[1]	2.80	0.094

[1] 35% of uninfested *T. umbrinus* that vocalized did so at "extreme" level, whereas 10% of uninfested *T. quadrivittatus* that vocalized did so at "extreme" level. No infested chipmunks of either species vocalized at "extreme" level. *See* text for further explanation

rivittatus appears capable of occupying upper-elevation habitats elsewhere in the absence of *T. umbrinus* (Armstrong, 1972), I postulate that aggresive exclusion of *T. quadrivittatus* by *T. umbrinus* prevents the former from occupying upper-elevation habitats in the Front Range of Colorado. Brown (1971) concluded that aggressive dominance by *T. dorsalis* excluded *T. umbrinus* from certain microhabitats (although in that case, distinct differences in habitat preferences allowed sympatry). Chappell (1978) concluded that an interspecific dominance hierarchy among *T. speciosus, T. amoenus* and *T. minimus* accounted for the nonoverlapping distribution of these species along a steep escarpment. *Tamias minimus,* owing to its ability to use different habitats and food sources, its lesser degree of arboreality, and its smaller body size (Bergstrom, 1986), partly escapes the territorially aggressive energies of *T. umbrinus* (Table 2) and is able to occur sympatrically with both of its larger congeners (Bergstrom and Hoffmann, 1991).

What then prevents *Tamias umbrinus* from excluding *T. quadrivittatus* completely from the Front Range and occupying areas below 2130 m? For example, *T. umbrinus* is found as low as 1600 m in open, xeric piñon pine (*Pinus edulis*)-juniper (*Juniperus* sp.) habitats in Rio Blanco Co. (pers. observ.). A plausible hypothesis is that *T. umbrinus* in the Front Range loses its aggressive advantage at lower elevations because of the negative effects of bot parasitism. The virtual lack of cuterebrid infestation in *T. minimus* suggests that there may be a difference in susceptibility between the other two *Tamias* species. Also, one would expect the density of bot flies and their eggs (oviposited on the substrate, often near host burrows—Catts, 1982) gradually to attenuate as the parasite species approaches the upper-elevation limit of its distribution (Brown, 1984), especially since the limitation may be a temperature-related physiological tolerance (E. P. Catts, pers. comm.). If that is the case, then *T. umbrinus* suffers a rate of infestation comparable with *T. quadrivittatus* even though it experiences a lower rate of random encounter of viable bot eggs. To confirm this distri-

butional pattern in the bot fly, however, one would have to examine a single host species that is uniformly distributed across the entire elevational range of the parasite. Both Front Range species of *Peromyscus* are infested with *Cuterebra fontinella*—*P. difficilis* is common up to 2200 m and *P. maniculatus* is common at all elevations.

A mechanism accounting for a difference in host susceptibility might take one of the following three forms: (1) A physiological response, *i.e.*, difference in the level of immunity (Gingrich and Barrett, 1976; Baird, 1979). (2) A difference in host behavioral responses or abilities to recognize infective larvae. There is no *a priori* reason to believe that there are important differences in grooming behavior among species of chipmunks (it is not clear whether infective larvae more often enter through the nasal mucosa *unless* they are groomed, most likely from the mustachial vibrissae, or enter through the oral cavity *when* they are groomed; Catts, 1982). (3) Specificity of fly-oviposition behavior mediated by differences in host habitat/burrow selection—this appears a plausible mechanism, as female flies often display very specific search images for host burrow sites (Beamer, 1950; Catts, 1967; R. B. Finley, pers. comm.). Although data are scant for *Tamias quadrivittatus* burrows, *T. umbrinus* is probably the most restricted of the three Front Range species to rocky microhabitats and burrow sites, while *T. minimus* is least dependent on rocky sites (Bergstrom, 1986). Another ecological difference distinguishing the species is the degree of arboreality, *T. umbrinus* displaying the highest, *T. minimus* the lowest (Bergstrom, 1986). Thus, there are ecological differences among the three potential host species that could possibly account for a different rate of exposure to substrates containing bot eggs or newly hatched, infective larvae.

However, a difference in susceptibility between hosts is not vital to the hypothesis. Alternatively, the fact that *Tamias quadrivittatus* is exposed to bot parasitism throughout its distribution in the Front Range, whereas *T. umbrinus* is exposed only at the lower margin of its distribution, would argue that *T. quadrivittatus* has had more opportunity for coevolution with the parasite and would, therefore, be less negatively affected by it (*see below*). Moreover, the ranges of the two unrelated species (Levenson *et al.*, 1985) probably expanded eventually coming into contact, *T. quadrivittatus* from the S and a fauna with more Chihuahuan affinities (and more bot flies, because they would extend into higher elevations), and *T. umbrinus* from a northern, more boreal fauna (Armstrong, 1972). Therefore, the codistributional argument can be extended by analogy to include coevolutionary time as well. A better adapted host might have the same rate of infection but show lesser lethal and sublethal effects (Holmes, 1982), a hypothesis for which Smith (1977) provided some experimental support.

Although Boonstra *et al.*, (1980) documented significant negative effects of bot myiasis on survival and reproduction in *Microtus townsendii*, other laboratory and field studies of cuterebrid parasitism in normal hosts concluded that there was little negative effect except in cases of large multiple infestations (Getz, 1970; Timm and Cook, 1979). However, studies have suggested increased vulnerability to predation (Smith, 1978b) and marked declines in activity levels of the host as a result of infestation (Bennett, 1973; Smith, 1978a). Since vocalizations are very important in chipmunk territorial behavior (Dunford, 1970), any diminished capacity for vocalization (Table 3), aggressive posturing, or other behaviors related to territorial defense would be critical, especially considering that bot infestations occur at the time of year when chipmunks are most likely to aggressively defend territories related to the provisioning of hibernacula (Bergstrom, 1986). In red grouse, birds unable to establish territories were more burdened with intestinal parasites than territorial birds (Jenkins *et al.*, 1963).

Tamias umbrinus either may be more susceptible to bot parasitism and its effects on activity levels or (the more parsimonious hypothesis) may adopt interspecific territorial aggression
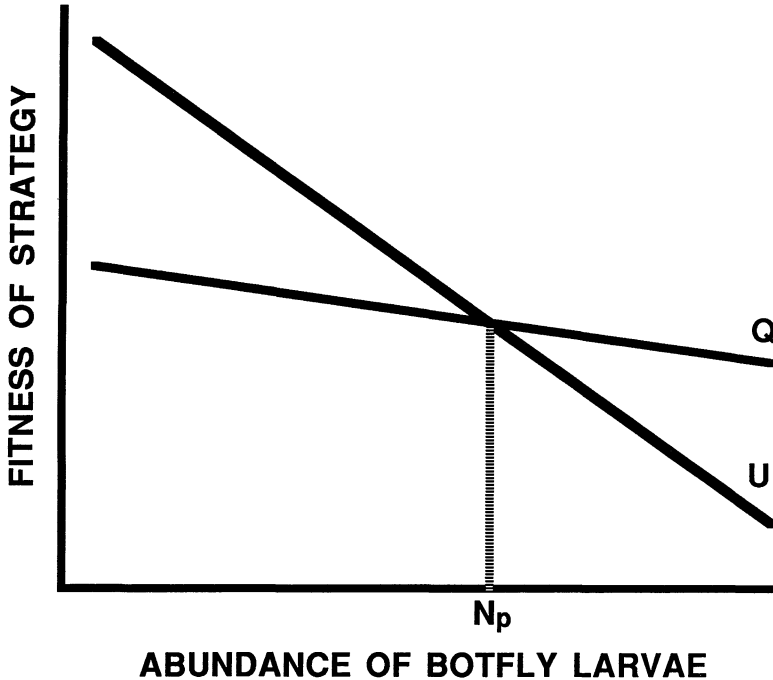
ABUNDANCE OF BOTFLY LARVAE

FIG. 2.—A graphical model of parapatry as a manifestation of varying relative fitnesses of behavioral (competitive) strategies of host species *Tamias quadrivittatus* (Q) and *Tamias umbrinus* (U) in relation to abundance of the bot fly parasite. An assumption of the model is that both hosts suffer equal infestation given equal exposure to the parasite. However, *T. umbrinus'* more aggressive strategy becomes relatively maladaptive at high densities of the parasite, because infested animals can no longer afford such metabolically wasteful behavior. A threshold occurs at N_p, the parasite density at which competitive advantage shifts to the less aggressive *T. quadrivittatus*. Presumably botfly density increases with decreasing elevation such that N_p occurs at 2130 m, the elevation of parapatry between the two host species

to a greater degree than *T. quadrivittatus*. Eroding this territorial aggression yields competitive advantage to its congener. The otherwise successful aggressive strategy of *T. umbrinus* may become relatively maladaptive in the presence of the bot fly (Fig. 2)—infested hosts may waste energy by excessive vocalization, posturing, or chases, further depleting metabolic resources already made scarce by the parasite.

More data are needed on several aspects of the hosts' and parasites' biologies in order to conclusively establish causation between the hypothesized interaction and the relative distributions of chipmunk species. Among other things, following the long term fates of free-ranging infested and uninfested chipmunk hosts would be desirable but very difficult. But failing any evidence of significant habitat and diet segregation between *Tamias quadrivittatus* and *T. umbrinus* (Bergstrom, 1986), and given the niche shifts displayed by the two species (Armstrong, 1972) and the consistency of the elevation of parapatry (Bergstrom and Hoffmann, 1991), a model involving this elevationally restricted parasite seems the most plausible explanation for the occurrence of parapatry at 2130 m elevation.

The idea that species' ecologies and geographic distributions are constrained more by a

combination of different community interactions that by competition alone has long-standing precedent (*e.g.*, Park, 1948; Paine, 1974) but overall has received rather little attention. The effects of parasitism, and especially its more subtle sublethal effects, on species coexistence and community structure have received practically no attention (Barbehenn, 1969), but certainly warrant further theoretical and empirical investigation.

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