Geographic patterns in the flight ability of a monophagous beetle

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etraopes

Summary. The migratory ability of a monophagous insect, *T. tetraophthalmus* (Coleoptera: Cerambycidae), was measured in ten populations in each of two regional types. In the first region, a river valley, populations were abundant and close together; in the second regional type, mountainous and peripheral areas, populations were uncommon and far apart. The data revealed that regional variation in migratory behavior occurred along two dimensions. Regions differed not only in the mean migratory ability of individuals (1st dimension) but in the amount of variation between populations (2nd dimension). Whereas river valley populations were found to be uniformly sedentary, mountainous and peripheral populations were found to be heterogeneous, some being very vagile, others being very sedentary. In the mountainous and peripheral areas, small and sparse populations were more vagile than large dense populations. The site to site variation in the mountainous and peripheral areas was due exclusively to females. In these areas, the mean migratory ability of females in a population was positively correlated with mean body size of the females, and inversely correlated with populations density. The data are consistent with the FLY hypothesis for this species (long distance migraters = Females, Large, and Young). Taken together, the geographical patterns support the "founding hypothesis" of migration. According to this theory, the inevitable selection against migration within populations is balanced by periodic extinctions of the populations and the founding of new populations by migrating individuals.

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Animals inhabiting islands are notoriously sedentary (Darwin 1859; Darlington 1943). Presumably, islands are originally colonized by individuals with great powers of migration, however once established, the populations gradually become more sedentary as migratory individuals leave the island and effectively remove themselves from the island's gene pool.

For herbivorous insects, patches of host plants may function as islands in an otherwise inhospitable landscape (Janzen 1968). Habitat islands, however, generally persist for far shorter periods of time than do oceanic islands. Whereas selection in an oceanic archipelago continually favors sedentary individuals, selection in a terrestrial archipelago periodically favors migrants, since habitats occasionally disappear. In the terrestrial system, migration may be maintained in a region because populations are periodically re-

founded by migrants, compensating for the selection against migration which inevitably occurs within populations (den Boer 1971; Van Valen 1971). The "founding hypothesis" of migration (den Boer 1971) suggests that biogeographic patterns in migratory behavior among herbivorous insects may be more complex than those of true island species. For example, considerable inter-site variation in migratory ability would be expected to occur in regions that contain populations of different ages (Fig. 1).

Davis (1981a) predicted that detailed regional surveys of migratory behavior might reveal that biogeographic patterns of migration have two dimensions. The first dimension would involve regional differences in the mean migratory ability of individuals. The second dimension would involve regional differences in the amount of variation in migratory ability between populations. Previous studies have documented the existence of biogeographic trends along the first dimension (Darwin 1859; Darlington 1943; Dingle 1978). The purpose of the study described here was to determine whether or not geographic trends in migratory behavior exist along this second dimension.

The species and its host plant

The subject of this study, the red milkweed beetle, *Tetraopes tetraophthalmus* Forster (Cerambycidae) is a common, univoltine, and monophagous beetle which feeds on common milkweed, *Asclepias syriaca* L. (Asclepiadaceae). The large (1 cm) and robust adult beetles feed on the flowers and leaves of their host plant, an herbaceous and rhizomatous perennial which grows in fields, floodplains, and roadsides throughout northcentral and northeastern United States. Mating occurs on the host plant and eggs are laid in hollow stems of grasses and dead milkweed plants (Gardiner 1961). The larvae, which drop to the ground after they hatch, burrow into the soil where they feed on milkweed roots and overwinter as prepupae.

Thus, scattered throughout an otherwise inhospitable countryside, milkweed patches provide the beetles with everything they need to survive and reproduce. The habitat islands in this archipelago are not permanent, however, and beetles persist in a region because some individuals successfully migrate from one patch to another, thereby periodically founding new populations. Beetles are monomorphic with respect to wing length, and all beetles can fly. However, beetles have been reported to be weak fliers (Chemsak 1963), and laboratory tests indicate that few beetles are
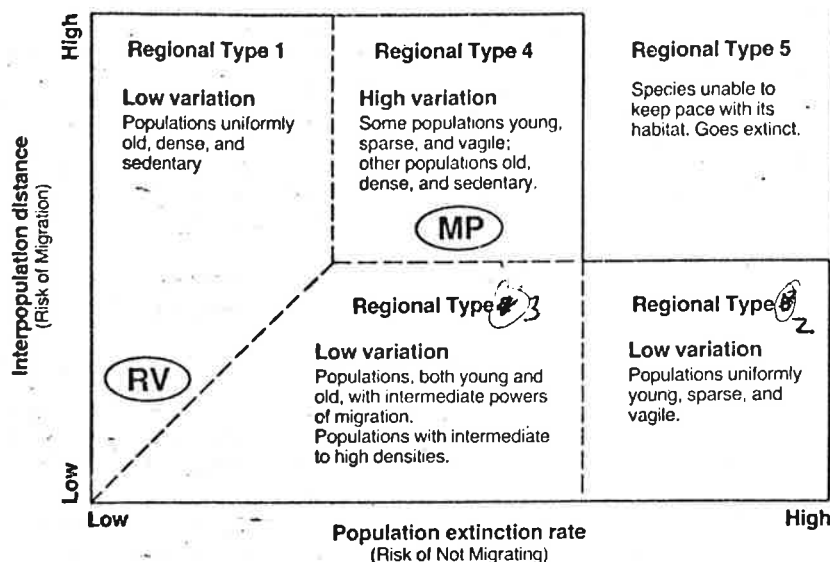
Fig. 1. The predicted amount of interpopulation variation in migratory ability shown as a function of interpopulation distance and population extinction rate. (Diagram developed from den Boer's (1971, 1977) description of his "founding hypothesis" of migration and from a computer simulation of migration (Davis 1981a)). According to this model, populations that are homogeneous with respect to mean migratory ability of their inhabitants could arise in three different regional types: *1* where most populations are very old (very low extinction rate), in which case the populations should be uniformly dense and sedentary; *2* where most populations are very young (very high extinction rates), in which case they should be uniformly sparse and vagile; and *3* where young and old populations are both common, but the difference in vagility between the two is very small. Number three should occur in regions with an intermediate rate of population extinction and low migration risk. Due to the risk of migration in this region, colonizers will include both highly and moderately vagile individuals.

Moreover, populations will continue to receive large numbers of emigrants, and as a result the level of vagility will decline only slightly following the founding of the population. Populations differing significantly with respect to the mean migratory ability of their inhabitants could arise in only one regional type: *4* where both young and old populations are common and where the difference in vagility between the two is great. These conditions should occur in regions where the risk of migration is high (resulting in a pronounced founder effect) and where extinction rates are intermediate. In such a region, both young (sparse and vagile) and old (dense and sedentary) populations would exist. In some regions, e.g., Regional Type *5*, the combined effect of high extinction rates and high risks of migration will result in populations going extinct faster than new ones are founded. At this point, the species will disappear from the region even though suitable habitat is available. The relative positions of the river valley (*RV*) and mountainous, and peripheral (*MP*) regions sampled in this study are shown

capable of flying more than a few hundred m (Davis 1984). Electrophoretic studies have substantiated the sedentary nature of most beetles, documenting genetic divergence among populations only a few hundred meters apart (Eanes et al. 1977). Significant individual variation in flight ability exists among *Tetraopes* beetles and these differences are intrinsic, meaning that the flight capacity exhibited by a young adult, whether great or small, generally persists throughout life (Davis 1980). On average, males take off more readily than females (Davis 1984), and move around more than females within milkweed patches (Lathrop 1981; McCauley et al. 1981). Extensive laboratory testing of flight ability (Davis 1984) indicates that females, on average, possess greater long distance flight ability than males. This and limited field evidence (Davis 1981b) demonstrates that some females, including fecund females, are capable of undertaking long distance and colonizing flight of isolated milkweed patches.

Methods

Beetles were collected from roadside patches of milkweed located in New Hampshire, Vermont, and Long Island, NY. Ten of these patches were growing in the Connecticut River Valley of Vermont and New Hampshire. In the river valley, *A. syriaca* is ubiquitous, growing in old fields, flood-

plains, and along roadsides. Patches inhabited by beetles are very common in this region. A census of 101 km of road in the river valley revealed that milkweed was found along 6.9% of the roadside. Large patches, (>30 m long) occurred every 1.3 km, on the average. Of the remaining ten patches, eight were growing in the lower elevation sites of either the Green Mountains in Vermont or the White Mountains of New Hampshire. *A. syriaca* becomes progressively scarcer, and eventually drops out completely as elevation increases in this part of its range and thus these patches were more isolated than in the river valley. In the mountainous areas, milkweed was found along only 4.0% of the roadside and large patches occurred only every 2.5 km (63 km of road were sampled). The remaining two patches were located at the eastern periphery of its range in Suffolk County in Long Island, NY. Here, milkweed was very scarce and although roadside densities were not measured, they were without a doubt the lowest of all. In the mountainous and peripheral regions, not only were patches less common, fewer of them contained beetles. In addition, most populations were small.

Thus, beetles were collected in two regional types – a river valley where patches of its habitat were abundant, and mountainous and peripheral areas where patches of its host plant were uncommon to scarce. Assuming risks of migration are associated with inter-patch distances, bee-

Table 1. Mean flight durations of males and females (separate and together) for the ten central and ten marginal populations, along with the density indexes for the populations. Standard Deviations are presented

River Valley Populations					Mountainous and Peripheral Populations				
Population	Density Index	Mean Flight Durations (Min.)			Population	Density Index	Mean Flight Durations (Min.)		
		♀ (n=8)	♀ & ♂ (n=16)	♂ (n=8)			♀ (n=8)	♀ & ♂ (n=16)	♂ (n=8)
1	8	4.88 ± 5.23	3.56 ± 4.69	2.23 ± 3.97	1	0	9.04 ± 3.97	7.13 ± 4.26	5.21 ± 3.83
2	10	2.71 ± 2.20	4.26 ± 5.29	5.81 ± 7.04	2	1	6.54 ± 2.85	5.10 ± 4.68	3.65 ± 5.84
3	10	3.13 ± 4.23	2.45 ± 3.45	1.76 ± 2.56	3	2	10.73 ± 3.70	7.05 ± 5.49	3.37 ± 4.46
4	16	2.42 ± 4.47	2.59 ± 4.25	2.76 ± 4.33	4	2	2.54 ± 3.66	3.47 ± 4.57	4.39 ± 3.45
5	22	5.04 ± 4.96	4.17 ± 4.26	3.29 ± 3.53	5	5	7.63 ± 6.09	5.32 ± 5.19	3.00 ± 2.88
6	41	1.37 ± 2.40	3.16 ± 6.25	4.94 ± 8.40	6	15	3.15 ± 5.00	2.45 ± 4.06	1.74 ± 3.05
7	42	6.33 ± 8.58	4.12 ± 7.10	1.91 ± 4.81	7	15	5.38 ± 2.37	5.53 ± 4.02	5.68 ± 5.38
8	43	2.80 ± 4.84	1.81 ± 3.51	0.82 ± 4.84	8	22	6.63 ± 3.15	4.89 ± 3.18	3.14 ± 2.21
9	50	4.31 ± 6.54	3.50 ± 5.18	2.68 ± 3.63	9	60	3.47 ± 4.25	2.58 ± 3.61	1.69 ± 2.83
10	101	0.75 ± 1.10	1.80 ± 3.88	2.84 ± 3.34	10	112	1.02 ± 1.67	1.37 ± 1.93	1.71 ± 2.21

tles in the mountainous and peripheral areas faced a higher migration risk than those in the river valley.

When an inhabited patch was found, in either region, the first 9 males and the first 9 females that were encountered were collected. (Beetles are slow moving and easily collected by hand.) Beetles were placed individually into small plastic vials, along with pieces of a milkweed leaf for food, and taken back to the lab for testing. All populations were sampled during the second and third weeks of July.

Within 24 h of collection, the flight capacity of beetles was tested using a still air tethering technique (Davis 1980a). Beetles were tested for 30 min and the cumulative time spent in tethered flight was used as an index of flight ability. (The tethered flight performances of insects in the laboratory have been found to be correlated with their flight performances in the field: Dingle et al. 1980; Rankin and Rankin 1980; Davis 1981 b.) Following each flight test, the body width, at the anterior edge of the elytra, was measured using a hand held micrometer. Body width is strongly correlated with body mass ($r = 0.93$; Davis 1984) and thus is a good measure of overall body size. I obtained an index of beetle abundance by recording the number of beetles I observed during five min of searching, after I had collected the initial eighteen beetles.

A multiple analysis of variance was used to compare flight capacities and body sizes between regions and between populations within regions. Flight times, but not body widths, were log transformed before analysis to ensure homoscedasticity. Due to occasional deaths or injuries to beetles prior to flight testing, 16 beetles (8 males, 8 females) from each population were used in the analysis. In the subsequent presentation of data standard deviations are presented along with mean values.

Results

Flight ability

Beetles from the mountainous and peripheral (MP) areas possessed greater migration ability than did beetles from the river valley (RV) populations (MP = 4.61 ± 4.66 min; RV = 3.11 ± 5.04 min; $F = 6.53$, $P < 0.025$). This regional difference was due exclusively to females, however (MP = 5.68 ± 4.64 min; RV = $3.38 + 4.92$ min; $F = 6.34$, $P < 0.025$). Males in the two regions did not differ in their migration ability (MP = 3.38 ± 4.02 min; RV = $2.88 + 4.80$ min; $F = 2.48$, $P > 0.1$). Overall, females (4.53 ± 4.74 min) possessed greater flight capacity than males (3.13 ± 4.40 min; $F = 8.74$, $P < 0.01$).

Populations in the Connecticut River Valley were found to be homogeneous with respect to mean migration power of beetles ($F = 0.85$, $P > 0.5$). This was not the case in the mountainous and peripheral locations, where significant variation existed between populations ($F = 5.20$, $P < 0.001$), and where the heterogeneity was found to be significantly greater than in the river valley ($F = 4.22$, $P < 0.025$). The mountainous and peripheral regions contained the most sedentary and most vagile populations of all those sampled (Table 1). The heterogeneity in migration ability in these regions was due to the significant geographic variation in the flight capacity of females ($F = 7.48$, $P < 0.001$). The flight capacity of MP males did not vary between populations ($F = 1.28$, $P > 0.25$). Overall, there was no significant correlation between the mean flight capacity of females in mountainous and peripheral populations and the mean flight capacity of males from the same population ($r = 0.43$, $P > 0.2$).

In the mountainous and peripheral regions, populations 9 and 10 (Table 1) were large and dense while populations 1–5 were small and very sparse. The mean flight capacity of beetles in the small sparse populations (5.43 ± 4.87 min) was significantly greater than that of beetles in the two large populations (1.97 ± 2.91 min; S = 4.36, $P < 0.05$; Scheffe test). Again, this difference was due to differences among females (7.30 ± 4.86 min, small populations; 2.24 ± 3.37 min, large populations; S = 5.43, $P < 0.0025$). As indicated above, flight capacity of males did not differ among populations.

An examination of the data revealed that vagile populations did not contain individuals with unusually great powers of migration. In fact, the sedentary populations usually contained one or two individuals with a flight ability comparable to the long fliers in the vagile populations. The
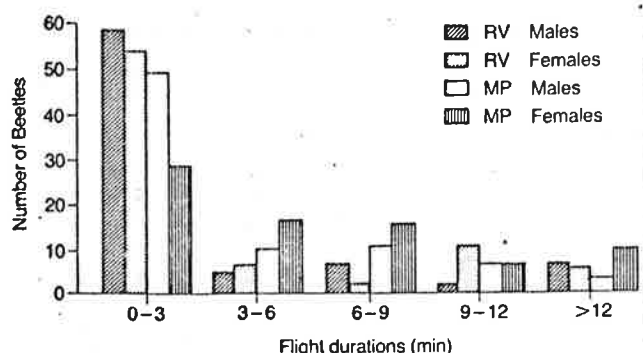
Fig. 2. Flight distributions for males and females in river valley (RV) and mountainous and peripheral (MP) regions. Nine beetles flew longer than 15 min, two flew longer than 20 min, none flew longer than 25 min. The distributions are significantly different from one another, $X^2 = 40.80$, $P < 0.001$, however most of the difference is due to MP females. Without the distribution of MP females, the remaining 3 distributions are just barely significantly different from one another, $X^2 = 15.71$, $P = 0.046$

difference was that vagile populations contained more long fliers. Figure 2 shows that the distributions of flight durations of RV and MP males and RV females are very similar. The distribution of MP females is unique, containing proportionately more long fliers than the other groups.

Size

There was no significant difference in the sizes of the beetles from the two regions (RV = 4.04 ± 0.43 mm; MP = 4.13 ± 0.50 mm; $F = 1.20$, $P > 0.25$).

Populations in the Connecticut River Valley were found to be homogeneous with respect to mean size of beetles ($F = 1.59$, $P > 0.1$), however mountainous and peripheral populations were found to be heterogeneous ($F = 4.91$, $P < 0.001$). When both males and females were considered, mountainous and peripheral populations were not significantly more heterogeneous (with respect to beetle size) than river valley populations ($F = 2.88$, $P > 0.05$). However, MP populations were more heterogeneous when only females

were considered ($F = 4.36$, $P < 0.025$). As was the case with migratory ability, the geographic variation in size that existed among MP populations was due to inter-site variation among females ($F = 4.36$, $P < 0.001$). The mean size of MP males did not vary among populations ($F = 1.01$, $P > 0.4$).

Average male size in a MP population was correlated with average female size ($r = 0.85$, $P < 0.005$). However, the magnitude of the size difference between males and females was also correlated with female size ($r = 0.90$, $P < 0.001$), meaning that the magnitude of the sexual dimorphism varied considerably between populations.

Correlation between size and migration ability

A significant positive correlation existed between the mean size of female beetles in MP populations and the mean flight ability of those females ($r = 0.67$, $P < 0.05$, Tables 1 and 2).

Discussion

The findings confirmed the existence of a second dimension in the geography of migration. Whereas river valley populations were found to be uniformly sedentary, mountainous and peripheral populations were found to represent a mosaic, some being very vagile, others being very sedentary. This rather complex geographic pattern of migratory behavior can be accounted for by the "founding hypothesis" of migration (den Boer 1971). This hypothesis emphasizes a fundamental relationship between the age structure of populations and the geographic patterns of density and migratory behavior in a region (Fig. 1). Specifically, the hypothesis holds that populations usually become more dense and more sedentary as they age (den Boer 1971, 1977).

An important prediction of the founding hypothesis is that regions containing mostly dense populations should be inhabited by a greater proportion of sedentary individuals than regions containing a significant number of sparse populations (den Boer 1977). The lack of sparse populations is taken as evidence that founding of new populations seldom occurs, and thus that selection against migration within populations is only infrequently countered by selec-

Table 2. Mean body widths of males and females (separate and together) for the ten central and ten marginal populations, along with the density indexes for the populations. Standard deviations are presented

River Valley Populations					Mountainous and Peripheral Populations				
Population	Density Index	Mean Body Width (mm)			Population	Density Index	Mean Body Width (mm)		
		♀ ($n=8$)	♀ & ♂ ($n=16$)	♂ ($n=8$)			♀ ($n=8$)	♀ & ♂ ($n=16$)	♂ ($n=8$)
1	8	4.01 ± 0.560	3.98 ± 0.436	3.95 ± 0.306	1	0	4.63 ± 0.292	4.33 ± 0.434	4.03 ± 0.333
2	10	4.34 ± 0.619	4.20 ± 0.533	4.06 ± 0.426	2	1	4.10 ± 0.449	3.93 ± 0.500	3.76 ± 0.511
3	10	4.21 ± 0.493	4.09 ± 0.464	3.97 ± 0.433	3	2	4.97 ± 0.368	4.57 ± 0.547	4.16 ± 0.374
4	16	4.17 ± 0.406	4.09 ± 0.401	4.00 ± 0.403	4	2	3.93 ± 0.495	3.84 ± 0.494	3.75 ± 0.511
5	22	4.08 ± 0.571	3.75 ± 0.577	3.42 ± 0.374	5	5	4.42 ± 0.357	4.23 ± 0.427	4.04 ± 0.426
6	41	4.34 ± 0.325	4.08 ± 0.458	3.82 ± 0.430	6	15	4.38 ± 0.419	4.18 ± 0.471	3.97 ± 0.454
7	42	4.00 ± 0.260	3.95 ± 0.270	3.90 ± 0.290	7	15	4.25 ± 0.188	4.13 ± 0.260	4.01 ± 0.277
8	43	4.22 ± 0.275	4.15 ± 0.345	4.07 ± 0.410	8	22	4.08 ± 0.413	3.90 ± 0.441	3.71 ± 0.407
9	50	4.16 ± 0.300	4.12 ± 0.297	4.07 ± 0.312	9	60	4.42 ± 0.473	4.13 ± 0.579	3.84 ± 0.550
10	101	4.10 ± 0.327	4.01 ± 0.341	3.91 ± 0.351	10	112	4.19 ± 0.499	4.05 ± 0.410	3.91 ± 0.255

tion for migraters (den Boer 1977). Data from this study support den Boer's prediction. On average, RV populations were both more dense and more sedentary than MP populations.

As predicted by the founding hypothesis, these regional differences are related to differences in the age structures of the populations in the two regions. River valley populations experienced low extinction rates. (Of ten *Tetraopes* populations sampled in 1977, all were present four years later.) Thus, the river valley could be described as regional type 1, with uniformly old populations (Fig. 1). The predicted regional patterns of flight abilities for this type of region are low to moderate mean levels of abilities within populations and low variation between populations (Fig. 1), both of which were recorded in this study. Inter-patch distances were greater in the mountainous and peripheral regions, and thus presumably beetles faces a higher risk of migration. In addition, the fact that few dense populations were found and that uninhabited milkweed patches were common suggests that the extinction rates of beetle populations were higher than in the riber valley, where sparse populations and uninhabited patches occurred less frequently. Given the increased risks of migration and assuming higher extinction racls, the mountainous and peripheral area could be described as regional type 4, with both young and old populations present (Fig. 1). The predicted geographical pattern of flight ability for this type of region, and the pattern observed in this study, is a mosaic, with some populations being very vagile and sparse and others being very sedentary and dense (Fig. 1).

To summarize, migrating individuals in the river valley probably seldom found new populations, because most sites are already inhabited. Thus, sparse and vagile (i.e., young) populations are rare and the river valley contains mostly dense and sedentary populations (i.e., old). On the other hand, migrating individuals in the mountainous and peripheral areas probably found new populations frequently, since empty sites are abundant. Thus, in this region, sparse and vagile populations are present as well as dense and sedentary ones.

The individual size and flight data provide independent support of a previous study of *T. tetraophthalmus* (Davis 1984). In that study, females exhibited greater flight capacity than males. In addition, size and flight capacity were found to be positively correlated in females, but not in males. These, and other data (Davis 1980), suggested that the individuals best equipped to migrate are young, large females. Although it was impossible to know the ages of the beetles collected in the current study, the data presented here are consistent with the FLY hypothesis (Migraters = Females, Large, and Young). Females possessed greater migration ability than males and vagile populations contained larger and more vagile females than sedentary populations. Moreover, the migration ability of males showed no geographic variation at all, despite the fact that the risk of migration varied between regions. Presumably changes in the proximity of populations should affect the flight capabilities only of those individuals that regularly migrate.

An unexpected finding was that in small and vagile populations, the difference in size between males and females was much greater than in large and sedentary populations. Although he did not test for flight ability, McCauley (1979) also found that the mean size of females, but not males, varied geographically. Price and Willson (1976) hypothe-

sized that the relative size of male and female beetles might influence copulation efficiency. If this were true, then copulation efficiency would be expected to be reduced in small populations due to a pronounced sexual dimorphism in these populations. However, data obtained by McCauley (1982) indicated that relative size of two mating individuals did not affect copulation efficiency. Very large females still could be at a disadvantage, however, since in some populations large females were found to mate less frequently than females of intermediate sizes (Mason 1964; Scheiring 1977; McCauley 1979). Since migrating females tend to be large, they might experience reduced mating success if they migrated as virgins and if the new population happened to contain smaller beetles. However, this problem could be avoided if the females mated prior to migrating. This possibility is supported by other data showing that flight capacity is not reduced by mating (Davis 1984), and by the fact that fecund females have been captured migrating between populations (Davis 1984).

The migratory ecology of *T. tetraophthalmus* (Davis 1984; this study) resembles that described for many species of ground beetles (Carabidae) (Meijer 1974; den Boer 1977, 1979, 1981, 1985), but differs in two important ways from the migration ecology described for a great many other insect species (Johnson 1969; Dingle 1972). First, the "oogenesis-flight syndrome" (Johnson 1969) is exhibited by neither *T. tetraophthalmus* (Davis 1984) nor the majority of Carabid species that have been studied (den Boer et al. 1980). Second, migration in *Tetraopes* and the Carabid species occurs regularly in all populations, young and old, sparse and dense, and does not represent an escape from a deteriorating (or soon to be deteriorating) habitat (Johnson 1969), nor a kind of overflow from a high density population (Dempster 1975).

T. tetraophthalmus and most of the Carabid species differ from the majority of other species studied in being distinctly sedentary. This is evidence that the migratory ecology of sedentary insect species differs in several fundamental ways from that of more vagile species.

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