The Effects of Roads on Arthropod Dispersal Ability

by

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Literature Review

Roads present dispersal problems for several reasons. Firstly, the microclimatic conditions surrounding roads are often different than those of a forest. More light reaches the edge of a road because of the break in tree cover, and the area is therefore often warmer and drier. The area may also be windier because of the opening in the trees. These conditions may be repellant to species which, for example, avoid open spaces where they are more vulnerable to predators, or avoid dry, sunny areas to prevent dehydration. Roadside conditions may also be more hospitable to a different flora than is present in a forest, creating a habitat some species may not find appealing or where they may be excluded by species more adapted to that habitat. Collectively, these conditions result in the rapid transition from forest conditions to altered conditions, the effects of which are known as edge effects. Finally, noise from traffic on the road may be a deterrent, as well as the possibility of animals getting killed while crossing the road.

The effects of roads on different animal species have been investigated in numerous studies. Baur and Baur (1989) investigated the effects of roads on the dispersal of the land snail *Arianta arbustorum*. They examined the movements of snails across paved and unpaved roads, and found that the snails primarily followed the vegetation belts at the sides of the roads. Despite travelling great distances, only one of the snails recaptured was found to have crossed the paved road, and only two were found to have crossed the unpaved road. They concluded that high-traffic roads present barriers to snail dispersal and may isolate snail populations.

Fahrig et al. (1994) studied the effect of traffic density on frogs and toads in Ottawa, Canada. They counted the number of dead and live frogs and estimated population sizes using chorus intensities in similar habitats but with roads with varying levels of traffic intensity. They found that the number of dead and live anurans found per km decreased with increasing traffic intensity. The proportion of dead anurans increased with increasing traffic intensity, and the anuran density, as determined by chorus intensity decreased with increased traffic. They conclude that traffic mortality is significantly detrimental to anuran density and that the decline in their populations worldwide may be in part a result of increased traffic volume.

Oxley et al. (1973) studied the effects of roads on small mammals by trapping and marking, assessing roadkill, and direct observation. They concluded that roads inhibit the movements of small mammals due to varying factors such as traffic, road surface, and clearance. Increased traffic volume was found to increase mortality. Road surface was not found to be a deterrent to animals' road-crossing, but because asphalt allows for greater traffic volume and speed, mortality on these roads did increase. Road clearance, or the openness of the area around the road, was the most important factor inhibiting the movements of small mammals. Light intensity was suggested as one possible repellant stimuli for forest-dwelling species, and wider roads were crossed almost exclusively by larger mammals. The authors suggest that less frequent roadside mowing and planting shrubs along roadsides could increase road-crossing by animals. This begs the question, however, of whether increased mortality in road-crossing would be better or worse for animal populations than the fragmentation of gene pools by uncrossable roads. Their observations also suggest that a four-lane divided highway may be as effective a barrier to dispersal than a body of fresh water twice as wide.

Didham (1997) attempted to tease apart the influence of edge effects and forest fragmentation in leaf litter invertebrates. Edge effects refer to the sudden habitat change that occurs at the edges of sections of forests or other habitats that are fragmented. They include the physical differences in habitat that occur at the transition between two matrices, and the change in species type, abundance, and interaction at these transitions, such as the invasion of edge species, often generalists, which competitively exclude forest-dwelling species. Forest fragmentation refers the division of habitat by any barrier, such as a road, an agricultural field, a body of water, etc. Some studies have shown that invertebrate abundance is greatest in small fragments and in the presence of edge effects. In a patch of habitat, the amount of original habitat decreases in relation to increasing edge area, a phenomenon which may be particularly significant for small patches. Didham concludes that the increased abundance observed in small patches is attributable to edge effects rather than area effects.

The ability of a species' to transverse a linear barrier such as a road is dependent on its vagility, or dispersal ability. The significance of dispersal is that is serves to replenish old or found new populations of a species, thereby maintaining or extending that species range. Den Boer (1990) investigated the survival value of dispersal in terrestrial arthropods using pitfall traps and discusses the selective advantages and disadvantages faced by dispersing individuals. He states that dispersing individuals of some species show higher egg production than non-dispersing individuals, but that weak dispersers will suffer high mortality because they will only reach suitable habitat by chance. Therefore, for some species, selection will favor individuals that do not disperse from the parent population, especially if it is isolated and stable. As the number of new colonies being founded decreases, dispersal ability of a species will also diminish, perhaps to the point at which flight is lost altogether. This is what is thought to have occurred in some wingless carabid species. However, selection for dispersal may occur if new suitable and unexploited habitats become available. Natural selection can therefore act in one of two ways. It can either increase the chance of successful colonization by increasing the fitness of dispersers, or it can decrease the dispersal abilities of individuals if they live in a fairly stable habitat.

Vermeulen (1994) looked at the dispersal of several species of ground beetles along a road verge serving as a corridor between open areas of drift sand, which is the normal habitat of these species. Corridors are often suggested in reserve design to connect two areas of suitable habitat that are surrounded by unsuitable habitat, presumably so that the intended species will move through the corridor and have access to both the resources of the habitat and to other individuals in the habitat. The three species used in the experiment were able to make use of the corridor in different ways. One species was found all along the road verge and was able to make full use of the road verge as a corridor. Numbers of the second species decreased along the road verge as the distance from the drift area increased. The road verge acted as a sink habitat for this species. The third species was rarely found within the road verge and then only very close to the drift, and it was therefore concluded that this species would also be unable to utilize this area as a corridor to reach new habitats. Although these three species have similar dispersal methods (two are brachypterous or flightless and one flies only rarely and for short distances), they clearly had different abilities or tendencies in dispersal that would affect the founding and replenishing of populations that were isolated.

When a road or other barrier is an effective deterrent to dispersal, species may be isolated from other habitats and other populations. This isolation can have deleterious effects on the stability of local populations by fragmenting the gene pool, prohibiting individuals from accessing new food or nesting resources and founding new populations, and prohibiting individuals from replenishing dwindling populations through migration. Several attributes characteristic of certain insect populations such as fluctuating population densities, poor dispersal abilities, and patchy distributions, make them especially susceptible to local extinction in fragmented habitats (Panzer, 1988). Klein (1989) studied the effects of forest fragmentation on dung and carrion beetles in forest fragments of varying sizes and varying levels of fragmentation. He found that beetles rarely moved from forested areas into areas that had been clear-cut and that all but one species was found more frequently in forested areas. The beetles captured in the forest fragments represented fewer species, had sparser populations, and smaller individuals than beetles captured in the contiguous forest.

The environment is becoming increasingly fragmented as the result of human activities and the effects this fragmentation on individual species is largely unknown. Most habitat fragmentation initially occurs when an intact patch of habitat is subdivided because a linear barrier such as a road is built through it. Because they play such a large role in habitat fragmentation, knowing the biotic responses to the presence of roads is important.

Barriers such as roads can have a potentially great effect on arthropod populations and the persistence of many arthropod populations is contingent upon those species' dispersal abilities. If roads are effective barriers to dispersal, they will essentially divide populations of arthropod species whose individuals are unable to transverse these roads.

My study investigates the specific effects of roads on the distribution and dispersal of three species of carrion beetles of varying vagilities.

ABSTRACT

Fragmentation isolates populations. This increases local extinction rates, decreases local diversity, and possibly decreases ecosystem functioning. We tested whether arthropod distribution and dispersal were affected by the presence of minimally traveled, single-lane, dirt roads and whether these effects differ based on species' vagility. Three sites of varying levels of fragmentation were chosen in a mixed hardwood forest. Mark-and-recapture data was gathered for three species of Silphid beetles, Necrophila americana, Nicrophorous orbicollis, *and* Nicrophorous tomentosus *over an eight week period. Numbers caught per trap, distances traveled, and mean travel distance for each species were calculated. Vagility tests were done to assess each species' tendency to fly. Our results indicate that* Ni. orbicollis *and* Ni. tomentosus *are more vagile and are more likely to cross roads than* Ne. americana *and that* Ne. americana *was the only species significantly affected by the presence of roads. We conclude that even minimally invasive roads affect the movement and home range sizes of these beetles and that this effect is greatest on less vagile species. Therefore, less vagile species are most prone to fragmented populations and likely to be affected by relatively insignificant linear barriers.*

INTRODUCTION

The persistence of many arthropod populations is contingent upon their dispersal abilities. Important habitat variation occurs on the scale of meters for ground-dwelling arthropods, but the critical distance between patches depends on the organisms' dispersal ability (Niemela, 1997). The biological significance of dispersal is maintenance and extension of a species presence by founding, replenishing, and refounding populations. Factors that influence dispersal are therefore critical in reserve design (den Boer, 1990). Small populations that are isolated and therefore without replacement dispersers are likely to become extinct, while weak dispersers isolated by unfavorable areas will be unable to make it to suitable territory to start new populations.

Barriers such as roads can have a potentially great effect on arthropod populations. If roads are effective barriers to dispersal, they will essentially divide populations of arthropod species whose individuals are unable to transverse these roads. Many studies have shown fragmentation and patchiness to be detrimental to arthropod populations. Barriers such as roads may result in the destruction or reduction of habitat and therefore reduction in population size, increased egde effects, corridors for foreign species, invasion of ecotonal species, increased mortality due to traffic, and fragmentation of populations (Goosem, 1997). Additional studies suggest that populations of other animal species such as snails, amphibians, and certain vertebrates are adversely affected by the presence of roads (Baur & Baur, 1989; Fahrig et al., 1994; Goosem, 1997). Isolation of populations will also increase the likelihood of local extinction due to decreased genetic diversity.

There are several other factors that predispose arthropod populations to higher extinction rates that may be exacerbated by the presence of roads. Panzer (1988) states that small, isolated insect populations on small sites are very likely to go extinct due to demographic instability, genetic deterioration, and natural catastrophes, and several attributes such as fluctuating population densities, poor dispersal abilities, and patchy distributions (colonies), increase the likelihood of extinction.

Danoff-Burg & Dunn (submitted) determined that roads are barriers to the dispersal of the three species of beetles. Because the repellent stimuli associated with roads vary throughout the day and year and because species respond to stimuli differently, species may be affected differently by the presence of roads according to individual species' characteristics such as vagility.

The three hypotheses tested in this study were that firstly, roads will affect beetle distribution and beetles will be present in greater abundance in unfragmented areas. We expect that the presence of roads will affect species differently in that the distributions of more vagile species will be less affected by fragmentation. We defined vagility as likeliness to fly. Secondly, roads are barriers to beetle dispersal and beetles will be unlikely to cross them. The presence of roads will affect species differently in that more vagile species will be more likely to cross roads. Lastly, less vagile species will be more likely to be recaptured because they will remain in the study area, while more vagile species will be more likely to disperse out.

METHODS

Species

Three species of carrion beetles were used in this experiment: *Nicrophorus orbicollis, Ni. tomentosus*, and *Necrophila americana*, all belonging to the family Silphidae. Individuals of all three species are scavengers of vertebrate carcasses. The beetles bury the carcasses for use as a food source and also lay their eggs in them. Individuals live from two to four months and travel by walking and flight (Anderson & Peck, 1985), but different species prefer different methods of travel (Danoff-Burg & Dunn, submitted). *Ne. americana* prefers to walk, while *Ni. orbicollis* and *Ni. tomentosus* tend to prefer flight.

Vagility tests

Sixty beetles of each species were placed individually in flat planter trays 5 cm high from which they were unable to escape except by flight. The time at which each individual took flight was recorded. If the individual did not take flight after ten minutes, they were recorded as such and released.

Site Description

The field site was in Black Rock Forest in Cornwall, New York, a mixed hardwood forest with annual rainfall of approximately 125 cm/yr. Three sites of similar age were selected within a quarter mile by quarter mile area. The unfragmented site contained 18 pitfall traps and was located at the top of a hill approximately 1400 ft. above sea level. The moderately fragmented site contained 18 pitfall traps and was broken by one road. The fragmented site contained 36 pitfall traps arranged about the intersection of two roads (site layout, Figure 1).

Each pitfall trap was assigned a unique series of three colors with which the captured beetles would be marked using paint markers. Local topography prevented the pitfall traps from being exactly equal distances from each other, but they were arranged in columns approximately 7 m. apart and rows approximately 15 m. apart.

Pitfall Trap Design

Baited pitfall traps were used to capture all individuals used in this experiment. Chicken wire held in place by large rocks was placed over the mouth of each trap to exclude small animals. Flat pieces of wood were balanced on the rocks above the mouth of the trap to prevent rainfall from pooling in the trap. Small holes were also punched in the bottom of the bottle for drainage.

Mark & Release Procedure

Marking and releasing was repeated weekly between 19 June and 4 August 1998. Each trap was baited with a piece of chicken gizzard or heart weighing approximately 10 g. and left for four days. In one instance, the traps were left for five days. On the fifth day, the traps would be emptied, the beetles caught would be tallied, marked on the left elytra with the colors of the trap in which they were caught, and released near the trap in which they were caught. The traps were then left empty for four days before being reset to allow beetles to disperse and to decrease the chances of beetles returning directly to the same trap or to adjacent traps. Recaptured beetles were marked on the right elytra with the colors of the trap in which they were recaptured. Beetles captured a third time were marked on the pronotum, and the few beetles that were captured a fourth time were marked with a purple dot below the third set of colors on the pronotum. No beetles were recaptured more than four times. Each recaptured beetle's pathway was traced on a map of the study area and the distances traveled between captures was calculated. Chi square analysis was used to compare the distributions of species in different conditions, the likelihood of road-crossing for each of the species, and the percent recaptured of each species.

RESULTS

Vagility Test Results

The results of the vagility test suggested that *Ni. tomentosus* is the quickest to take flight, followed by *Ni. orbicollis* and then *Ne. americana.* (Figure 2.)

Mark & Release Results

The percentage caught per site for each species suggests that distributions of all three species are significantly skewed (*Ni. orbicollis* $p<0.025$, *Ne. americana* $p<0.0001$, *Ni. tomentosus* $p<0.005$). *Ni. orbicollis* and *Ni. tomentosus* were caught more frequently in the most fragmented site, while *Ne. americana* was found more frequently in the unfragmented site. (Figure 3.)

The most fragmented site contained 36 pitfall traps which was twice as many as the moderately fragmented and unfagmented sites. Therefore, it is possible that a larger number of beetles were caught there simply because there were more traps and in a larger area. In order to account for this, the per trap capture rates were determined by dividing the total number of individuals of each species caught per site by the number of traps in that site. Per trap, *Ne. americana* was caught in significantly greater numbers in the unfragmented condition ($p<0.05$), while *Ni. tomentosus* and *Ni. orbicollis* did not show a significant site preference. (Figure 4.)

The percent recaptured per total captured was 5.2% for *Ni. orbicollis* and 7.0% for *Ni. tomentosus*. The percent recaptured per total captured for *Ne. americana* was 19.7%, which is significantly greater ($p<0.05$) than the percent recaptured for the other two species. (Figure 5.)

Of the 12 *Ni. tomentosus* recapture events, 20% involved road-crossing. Of the 13 recapture events for *Ni. orbicollis*, 23% involved road crossing. Of the 43 *N.americana* recapture events, only 14% involved road-crossing, and. Chi square tests indicate that only *N.americana* was significantly unlikely to cross roads (*Ne. americana* $p<0.001$, *Ni. Orbicollis* $p<0.9$, *N. tomentosus* $p<0.9$). This along with the percent of recaptures requiring road-crossing suggest that *N.americana,* the least vagile species, is the least likely to cross roads. (Figure 6.)

DISCUSSION

Vagility tests suggest that *Ne. americana* is the least vagile, in accordance with Danoff-Burg & Dunn's data (unpublished). *Ni. orbicollis* and *Ni. tomentosus* did not significantly differ from each other in their vagilities.

The percentage of individuals caught per site suggest that beetle distribution for all three species is affected by the presence of roads. *Ni. tomentosus* and *Ni. orbicollis* were present in highest numbers in the most fragmented site, while *Ne. americana* was present in highest numbers in the unfragmented site.

Based on per trap capture rates per species, *Ne. americana*, the least vagile species, was the only species whose distribution was significantly negatively affected by fragmentation. This supports the hypothesis that roads affect species differently because the least vagile species showed uneven distribution and was most abundant in unfragmented areas, where road-crossing is not necessary. The other two more vagile species did not have a significantly skewed distribution, and therefore appear to be less affected by the presence of roads.

Only *Ne. americana* crossed roads significantly less frequently than traveling within unfragmented areas. There was not a significant difference between road-crossing and non-road-crossing events for the other two species. However, there were very few recaptures for these two species, and it is possible that with adequate data these species would also show road avoidance. The percentage of recaptures that required road-crossing was also higher for the two more vagile species, *Ni. tomentosus* and *Ni. orbicollis,* than for the less vagile *Ne. americana.* These data suggest that of the three species, only *Ne. americana* selectively avoids roads. Therefore, this data suggests that the presence of roads inhibits beetle movement and less vagile species are more susceptible to their presence.

Finally, the percentage of individuals that were recaptured per total number captured of each species was significantly higher for *Ne. americana.* This suggests that *Ne. americana* individuals were not moving out of the testing area and that roads affect less vagile species because have smaller home range sizes and are less likely to cross roads. The other two more vagile species may not have been recaptured as frequently because the geographic scale of our project was much less than the cruising range of these individuals.

These results are in accordance with other studies examining fragmentation and roads as barriers to dispersal. Baur & Baur (1989) found that paved roads and unpaved tracks prevented snail dispersal, while overgrown paths did not, and suggest that snail populations separated by high-traffic, paved roads may be isolated from each other. Fahrig et al. (1994) concluded that amphibian population density was inversely related to traffic density. Among rainforest vertebrates, arboreal and understory species are most likely to be effected by environmental discontinuity. The effect of linear barriers on these species depends on their mobility and behavioral characteristics, especially relating to open-space avoidance, but species likely to cross roads may experience greater mortality rates due to traffic or predation. As the width of a barrier increases, road-crossing attempts of many species decrease, and differences in habitat around roads create areas unsuitable for certain species (Goosem, 1997).

Our study demonstrates that even populations of relatively vagile organisms such as carrion beetles can be negatively affected by the presence of barriers such as roads. By fragmenting or isolating populations and therefore increasing local extinction rates, linear barriers such as roads also have implications on biodiversity, perhaps affecting other levels of the ecosystem and even altering ecosystem functions such as decomposition.

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FIGURE LEGENDS

Figure 1. Vagility test results. Bars represent the total number of individuals that flew within ten minutes out of 60 replicates for each species. *Ne. americana* flew significantly less frequently than the other two species and was therefore concluded to be least vagile.

Figure 2. Percent Captured per Species. Pie sections represent number of individuals of each each species caught per total number of that species in each site. *Ni. tomentosus* ($p<0.005$) and *Ni. orbicollis* ($p<0.025$) were captured significantly more frequently in the most fragmented site, while *Ne. americana* ($p< 0.0001$) was captured significantly more frequently in the unfragmented site.

Figure 3. Per Trap Recapture Rates for each species in each site. *Ne. americana*, the least vagile species, was found in significantly greater numbers ($p< 0.05$) in the unfragmented site than in the other two sites. The other two more vagile species, *Ni. tomentosus* and *Ni. orbicollis*, did not show a significant site preference.

Figure 4. The Percent Recaptured per Species. *Ne. americana* showed a significantly higher percent recapture than the other two more vagile species, *Ni. tomentosus* and *Ni. orbicollis*.

Figure 5. Recapture Events Involving Road-Crossing for each species. Ne. americana, the least vagile species, had significantly fewer ($p< 0.001$) road-crossing recaptures than non-road-crossing recaptures. The other two more vagile species, *Ni. tomentosus* and *Ni. orbicollis*, did not show significant road avoidance.

Figure 1.

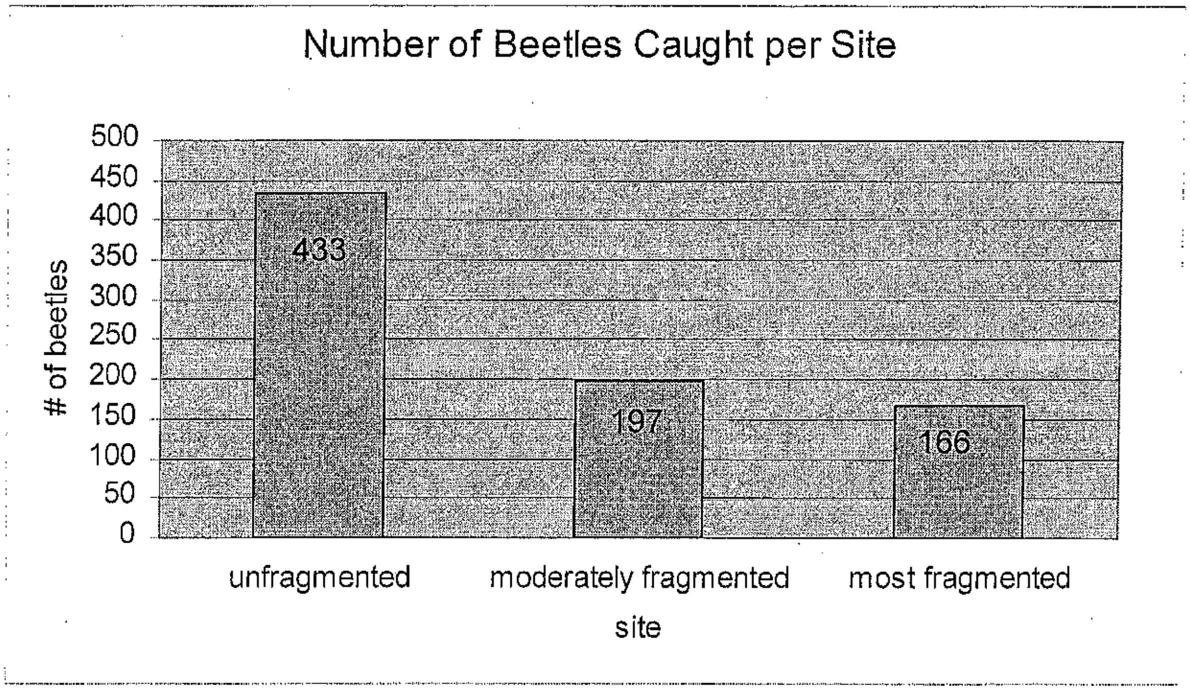
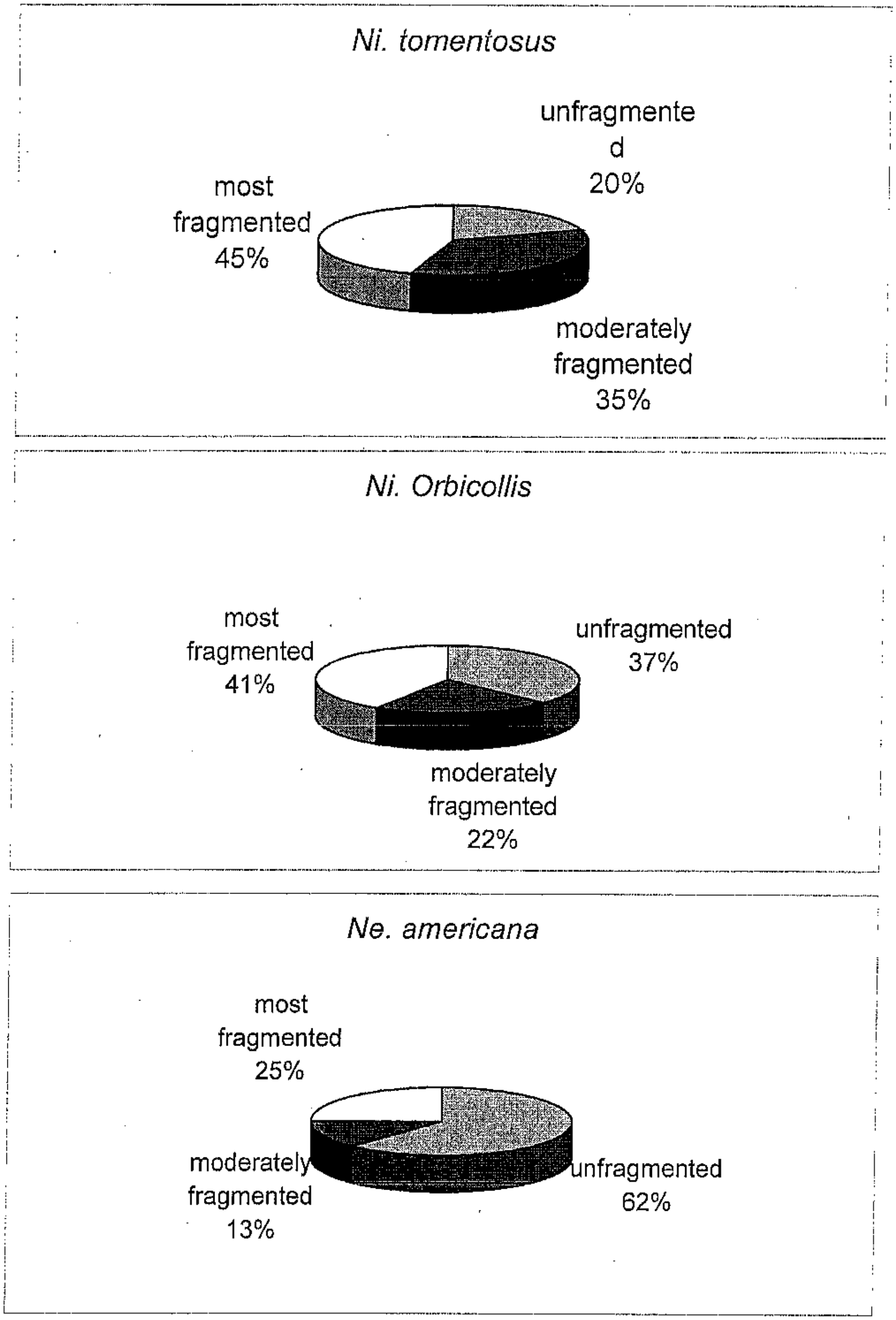

Number of Beetles Caught per Site
500
450
400
350
300
250
200
150
100
50
0
# of beetles
433
197
166
unfragmented
moderately fragmented
most fragmented
site

Figure 2.



Ni. tomentosus
unfragmented 20%
most fragmented 45%
moderately fragmented 35%
Ni. Orbicollis
most fragmented 41%
unfragmented 37%
moderately fragmented 22%
Ne. americana
most fragmented 25%
moderately fragmented 13%
unfragmented 62%

Figure 3.

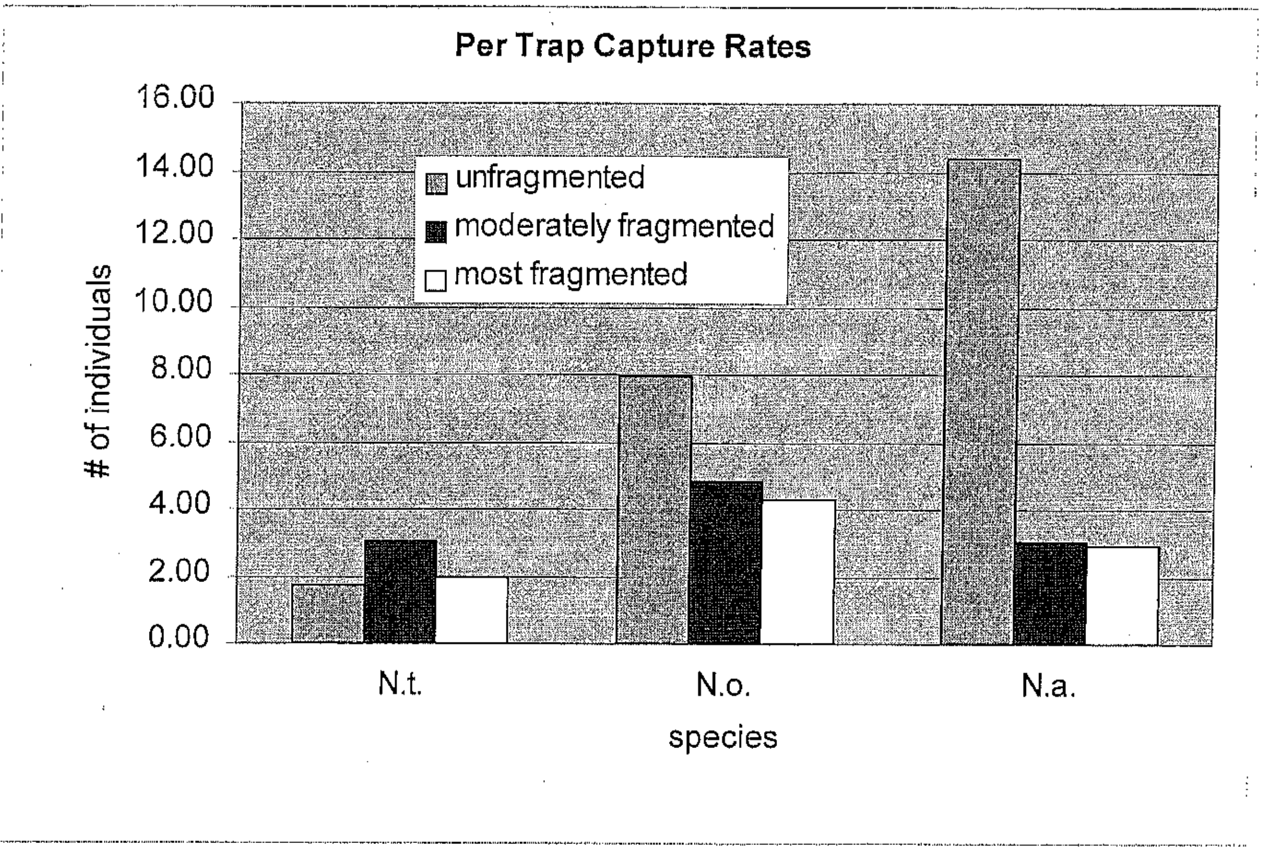

Per Trap Capture Rates
unfragmented
moderately fragmented
most fragmented
16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
# of individuals
N.t.
N.o.
N.a.
species

Figure 4.

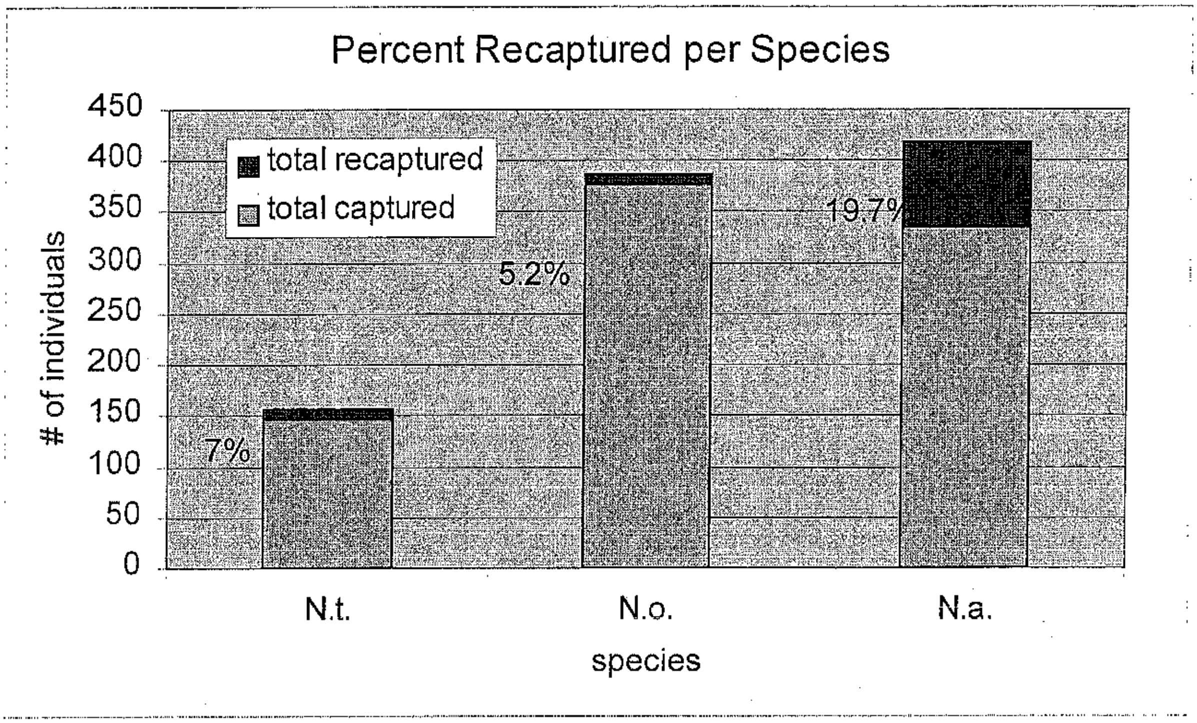
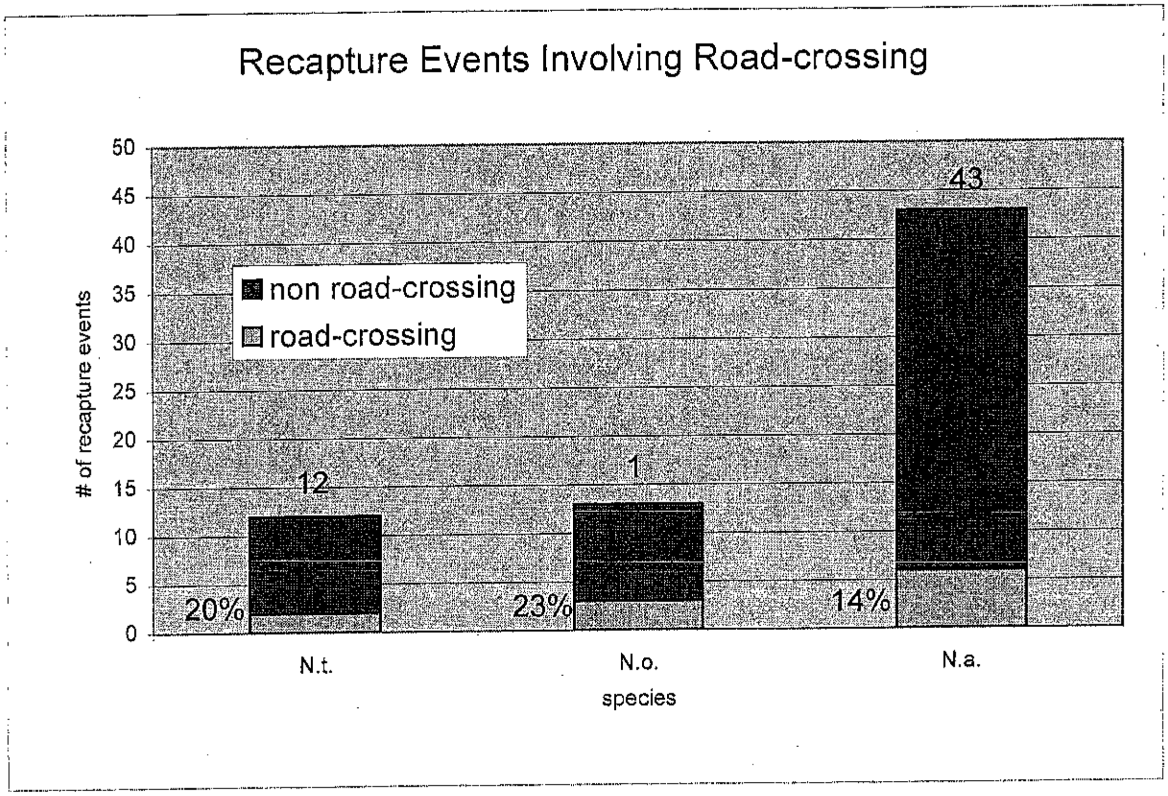

Percent Recaptured per Species
total recaptured
total captured
# of individuals
450
400
350
300
250
200
150
100
50
0
7%
5.2%
19.7%
N.t.
N.o.
N.a.
species

Figure 5.


Recapture Events Involving Road-crossing
50
45
40
35
30
25
20
15
10
5
0
# of recapture events
▩ non road-crossing
▨ road-crossing
12
1
43
20%
23%
14%
N.t.
N.o.
N.a.
species