

Habitat Selection in *Nicrophorus investigator* and *defodiens*

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Abstract

We investigated habitat selection in *Nicrophorus investigator*, an obligate carrion breeder. The source-sink hypothesis states that some environments will be resource rich and produce a high amount of offspring while other environments will be resource low and produce a low amount of offspring. Carcasses were put out in pairs with one carcass in the meadow and one in the aspen. *N. investigator* and *N. defodiens* prefer the meadow to the aspen, the size of the *Nicrophorus* beetles was larger in the meadow than the aspen, competition was higher in the aspen than in the meadow, and the only successful broods were in the meadow. All of these support that the meadow and aspen are source and sink environments respectively.

Introduction

Different areas or different habitats inside a species range can be of varying qualities. Some of these areas are of high quality leading to a high production of offspring and increased population. This type of area is called a source. Other areas are lower quality leading to lower production of offspring and a decrease in populations. This type of area is called a sink (Pulliam 1998, Donovan 1995). Even though a sink represents a loss in population they remain populated, escaping the fate that would otherwise meet a declining population. This is because animals tend to disperse from the place they were born causing some emigration from the source areas and immigration into the sink areas (Pulliam 1988). This is not to say that all animals blindly choose where they are going to hunt, forage, breed, as well as anything else they do. The animals, to varying degrees, choose the best habitat that they can to live in. They make these choices considering the resources available, the microclimatic factors, the predators present, and the density of other species occupying a similar same niche or other members of the same species. So an area that has higher quality resources that is already dense may not be as desirable of a place with lower quality resources but which is less dense (Pulliam 1991, Rosenzweig 1981).

Burying beetles (*Nicrophorus investigator* and *N. defodiens*) have to make the same decisions when deciding where to breed. *Nicrophorus investigator* is an obligate carrion breeder which uses small mammals as a food source to rear its young. Because of low density of carrion they compete for carrion both with other scavengers (from flies to foxes), and with other burying beetles. Among burying beetles, usually the largest male and female of a species win (Bartlett 1988, Smith 1998). In the East River valley in Colorado, near the Rocky Mountain Biological Laboratory, *N. investigator* and *N. defodiens* are found to occur in both the aspen forest and the open meadows. However *N. investigator* has been shown to prefer the open meadows for its breeding burying many more carcasses in the open meadows than in the aspen forest (Smith & Heese 1995). On an island in Newfoundland, Canada *N. investigator* was also found to prefer the open meadow while *N. defodiens* was found to prefer forested areas. This is hypothesized to be because in that habitat *N. investigator* is larger than *N. defodiens* (Wilhelm, 2001). One of the reasons that the meadows could be a more desirable habitat than the aspen forests is that the larval development time in the shade is a fair amount longer than in the sun. This could have negative effects on the parents as they are thought to be able to parent a second brood in a summer and the larger development time could lower the parent's chance for a second set of offspring (Smith & Heese 1988). A second reason is that *N. investigator* overwinter as larvae, and pupate and emerge the following year; exclusion is greatly delayed in the shadier Aspen forest habitat (Smith, personal communication). In contrast, *N. defodiens* encloses in the late summer/early fall, and can overwinter in a different site. This would allow for separation of the larval development from the overwintering site. Overall, the difference between the aspen and the meadow habitat, which are in close proximity, follow the source sink dynamics because one will likely produce many fewer offspring than the other.

The source-sink hypothesis explains differences in reproductive success in two habitats, and suggests that organisms in source habitat are better competitors. A test of this hypothesis would lead to the following predictions: Beetles that are large are more likely to "win" intra-

specific competitive encounters (Safryn 2000) and will select and successfully defend carcasses in the sun (meadow) which are a better resource (higher quality habitat) for the beetles. In contrast, adult beetles that are small are less likely to win intra-specific competitive interactions; and thus may reproduce primarily in “sink” habitat- selecting carcasses in the shade (aspen) even though they are of lower resource quality. Thus the beetles in the meadow will be larger than the beetles in the Aspen. There will also be more competition in meadow than in the aspen, with the smaller species (*N. defodiens*) occurring at a higher proportion in the Aspen than meadow. This study will directly test these predictions by observing *Nicrophorus* arrival at carcasses, competitive interactions, body size, and reproductive success in two habitat types.

Methods

Study organism:

Nicrophorus investigator and *N. defodiens*

(Coleoptera: Silphidae) are good study species for this question because the carcasses needed for the beetles reproduction are easy to manipulate and the beetles themselves are easy to manipulate and measure. *Nicrophorus* beetles use mouse carcasses as the food source for rearing their young. They use their sense of smell to find freshly dead carcasses; once there, males will emit pheromones to attract mates. Normally more than one male and one female will find the carcass so the males will fight the males and the females will fight the females (Scott 1998). The winning male and female, normally the largest (Safryn 2000), then proceed to roll the carcass into a ball and bury it in the ground and the female will lay her eggs a little out of the way. After two days the eggs will hatch and the larva will start to feed on the carcass. The larvae will finish feeding on the carcass after about two weeks and dig into the

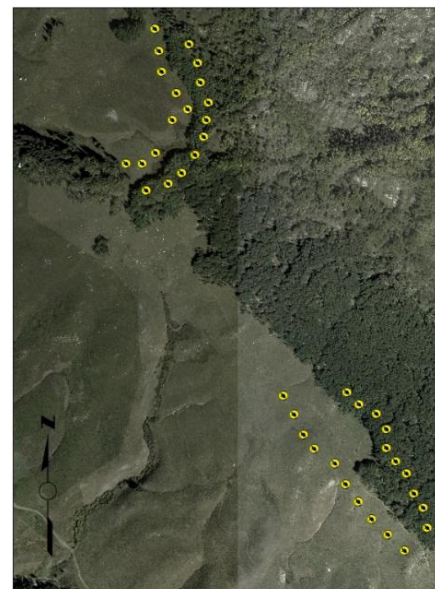


Figure 1. South East of Gothic Colorado In the Upper East River Valley. Yellow dots represent locations of carcasses

surrounding dirt to await the spring. The adult male and female depart the carcass after the young can feed on their own, normally between 6 and 10 days after the larvae hatch (Scott 1998).

Habitat Selection Survey:

This project was conducted in three locations in the Upper East River valley in Gunnison County Colorado. The two sites considered of both Aspen forests and montane meadow interspersed with willow and veratrum swamps. We obtained dead deer mice (*Peromyscus maniculatus*) through trapping in cabins at RMBL. Deer mice weighing from 16.1 to 31.2 grams were used. All mice were trapped and killed the same year as they were set out and frozen shortly after death to prevent decomposition. Each mouse was weighed with a spring balance and tagged. Mice were randomly chosen for use in each survey such that both the environments (aspen and meadow) had mice of similar weights and so that the first two surveys had mice of similar weights and the second two surveys had mice of similar weights.

We conducted four surveys at two different sites. Each survey consisted of three to five days of observations on two rows of either ten or fourteen carcasses, one row in the aspen forest and one row in meadow. We placed out the carcasses at eight in the morning on the first day of the survey. We then checked the carcasses at 14:00 and 17:00 that day. We then checked the carcasses for the next two days at 8:00, 11:00, 14:00, and 17:00. After the first three days the carcasses were checked one or two times per day for the next two days for until the carcasses become unviable. When we checked the carcasses we first put all *Nicrophorus* beetles in a container. Then we identified the species and sex, and then measured and marked each beetle found at each of the carcasses. The mark was made with an insect pin prick into the elytron- a single mark was used to indicate prior capture at a carcass and which environment it was captured in. When returning the beetles to the carcass we first put a can over the carcass and then released the beetles next to a small opening between the can and the ground. Ten days after the carcasses were buried we dug up the carcasses to check on the

progress of the larva. Once the larva had eaten all of the carcass and were about to disperse, the larva, what is left of the carcass, and the surrounding dirt were put into a container to bring back to the laboratory. The larva were then counted and weighted on a pan balance.

Results:

Overall both *N. investigator* and *N.*

defodiens preferred aspen habitat to that of the

meadow (Overall Aspen = 8, Meadow = 78 $X^2=$

65.991, d.f. = 1, $P < 0.001$; *N. investigators* $X^2= 53.8$,

d.f. = 1, $P < 0.001$; *N. defodiens* $X^2= 13.7$, d.f. = 1, $P <$

0.0002). Carcass size did not play a role in the

beetles finding, burying, or the success of the

carcass (Found : $F(1,94) = 0.9251$, $p = .3386$; Buried:

$F(1, 40) = .0561$, $p = 0.8140$; Successful: $F(1,12) = 0.5490$, $p = 0.4730$). Scavenging of the

carcasses did not vary from aspen to meadow (Aspen = 6, Meadow = 4: $X^2 = 0.4027$, d.f. = 1, P

= 0.5257). Only carcasses in the meadow were successful (Aspen = 0, Meadow = 10; $X^2=$

13.86, d.f. = 1, $P = 0.0002$). Competition in the meadow was higher than competition in the

aspen forest (Number of beetles/carcasses discovered: Meadow = 2.6, Aspen: 2.0; $t= 2.960$, df

= 3, $|t| = 0.0595$, Prob > $t = 0.0298$). The average size of *N. investigator* nor *N. defodiens* found

in the meadow was not statistically larger than the average size of the beetles found in the

Aspen ($F(1,58) = 0.2617$, $p = 0.6109$) but overall the size of beetles in the meadow was larger

than the aspen ($t = 20.8$, d.f. = 1, Prob > $|t| = 0.0306$, Prob > $t = 0.0153$). For the first two

surveys the numbers of *N. investigators* and *N. defodiens* were roughly equal (Survey 1: *N.*

investigator = 6 *N. defodiens* = 4; $X^2 = 0.403$, d.f. = 1, $P = 0.526$; Survey 2: *N. investigator* = 13

N. defodiens = 10; $X^2 = .3924$, d.f. = 1, $P = 0.531$) but for the second two surveys and overall

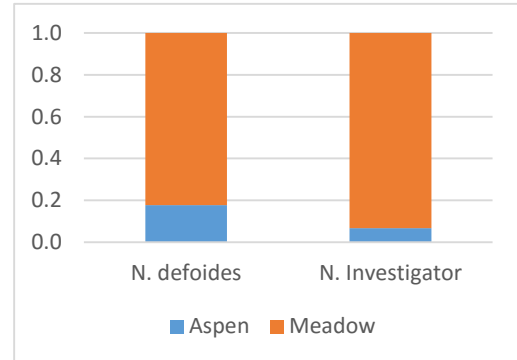


Figure 2. Number of *N. investigator* and *N. defodiens* found in each environment (aspen and meadow) over the four surveys and total *Nicrophorus* found.

Proportional there were more *N. defodiens* in the aspen than *N. investigators*

there were many more *N. investigator* than there were *N. defodiens* (Survey 3: *N. investigator* = 10 *N. defodiens* = 1; $\chi^2 = 8.547$, d.f. = 1, $P = 0.0035$; Survey 4: *N. investigator* = 6, *N. defodiens* = 4; $\chi^2 = 12.560$, d.f. = 1, $P = 0.0004$; Total: *N. investigator* = 56 *N. defodiens* = 22; $\chi^2 = 15.33$, d.f. = 1, $P < 0.001$).

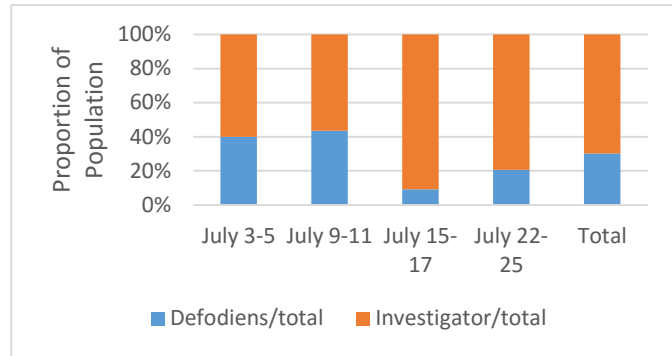


Figure 3.. Number of beetles in each environment in each survey per the number of carcasses that beetles found. The first two surveys showed about the same amount of *N. investigator* and *N. defodiens*. The second two weeks showed a significantly larger proportion of *N. investigator* to *N. defodiens*.

Discussion

The results of this study demonstrate that the meadow and the aspen habitats in the East River valley support the predictions made by the source-sink model of habitat selection for *N. investigator* and *N. defodiens*. A source will have high quality resources and will represent an increase of population. A sink will have low quality resources and will represent a loss of population (Pulliam 1998, Donovan 1995).

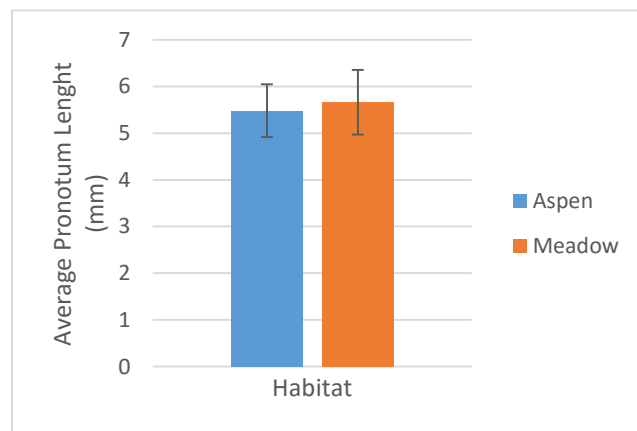


Figure 4.. Average pronotum with (mm) of both *N. investigator* and *N. defodiens* in the meadow and aspen. The beetles in the meadow were larger than the beetles in the aspen. Survey 3 and 4 were omitted because no beetles were found in the aspen forest.

Firstly there is strong preference for the meadow environment for both species. This indicates that the resources in the meadow are better than that of the aspen forest.

There was also higher competition in the meadow, as compared to the aspen. Even though neither *N. investigator* found in the aspen were not on average smaller than the beetles in the meadow. *N. defodiens* nor *N.*

defodiens did not exhibit a size difference between habitats, both species combined were larger in the meadow than in the aspen. The aspen did not produce a single successful brood while

the meadow produced multiple. The aspen and meadow habitats follow what would be expected of a source sink dynamic with the meadow as the source and the aspen as the sink.

It is odd to have two species (*N. investigator* and *N. defodiens*) occupying such a similar niche. In other environments, such as island habitats in Newfoundland Canada, the two species are separated spatially. *N. investigators* living mostly in the meadow and *N. defodiens* living mostly in forested areas (Wilhelm, 2001). This is attributed to the size of two species, *N. investigator* being larger than *N. defodiens* and thus outcompeting them at the carcasses. However there was no size difference between *N. investigator* and *N. defodiens* in this study. In the East River valley the species divide is temporal. *N. defodiens* comes out in higher numbers in the beginning of the summer while *N. investigators* largely comes out later in the summer.

The evidence supports that the source-sink relationship between the meadow and the aspen though the complete mechanism of their aversion for the aspen is unclear. Beetles avoid shade (Smith & Heese). I noticed a variety of different levels of sunlight, moisture of soil, and temperature even within both the aspen and the meadows themselves. It is possible that even though carcasses were in different environments they could be very similar to each other in one or more the previously mentions qualities. To account for that in the future, that sort of data could be taken for each of the positions in which there was a carcass to be able to better asses what the beetles are prefer or do not prefer. This could also be used at a backup in case there remains low numbers of beetles in the aspen forest.

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