HABITAT USE AND POPULATION SPATIAL STRUCTURE OF THE FORKED FUNGUS BEETLE, *Bolitotherus cornutus* PANZER.

by

Sonja Teichert
B.Sc. (Hon), University of Western Ontario, 1995

Thesis
submitted in partial fulfillment of the requirements for
the Degree of Masters of Science (Biology)

Acadia University
Fall Convocation 1999

Table of Contents

Chapter 1: A multi-scale examination of habitat use and population spatial structure of the forked fungus beetle (*Bolitotherus cornutus* Panzer) in continuous forest of Nova Scotia.

Table of Contents (cont'd)

Chapter 2: The influence of sporophore decay on habitat use by the forked fungus beetle, *Bolitotherus cornutus* Panzer: A field experiment.

List of Tables

List of Tables (Cont'd)

List of Figures

List of Figures (Cont'd)

List of Figures (Cont'd)

List of Appendices

List of Appendices (cont'd)

Abstract

In this study I use an exploratory approach for examining habitat use at multiple scales by modeling two responses of adult forked fungus beetles: the incidence of beetles and the number of individuals counted in units of habitat. Characteristics of the sporophores (size and decay) were important for the beetles at all scales examined, however, the ability to describe patterns of habitat use increased with scale. Examining the spatial structure of the incidence of the forked fungus beetle in its natural environment supports these observations and also suggest that the dynamics of individual beetle populations occur at even larger scales. These results demonstrate the importance of the scale at which ecological questions are posed and the influence of space across scales. In this system, factors other than sporophore attributes that are acting at broader scales, result in the distribution and abundance of the forked fungus beetle.

I also used an experimental approach to more closely examine the influence of sporophore decay on the oviposition behaviour and nightly activity of the forked fungus beetle. In a field experiment, I presented pairs of adult beetles housed in enclosures sporophore combinations of varying decay levels. The number of eggs laid decreased with increasing decay of the sporophore, and egg laying was delayed by beetles presented with more decayed sporophore combinations. In another field experiment I presented adult beetles, housed in arenas, with 3 sporophores that differed in their level of decay and were attached to logs. I counted their positions during the night and observed that both males and females congregate in areas near live and intact sporophores. Beetles were found most often on the bark near these sporophores suggesting that their activities during this time consist mainly of behaviours (mating, aggression) other than feeding. These findings demonstrate the importance of examining small scale habitat attributes (*i.e.* resource composition) for determining a species habitat requirements.

Acknowledgments

I thank my supervisor, Søren Bondrup-Nielsen for his enthusiasm during our first long-distance correspondence, for portraying the forked fungus beetle as a really interesting beast and not 'just a bug'. Throughout my masters experience, he has been invaluable for offering new insight and alternative ways for thinking about things, forcing me to focus and find my own path. Doing so has been a tremendous learning experience, allowing me to recognize some of the abilities I never before thought I possessed. I also thank him for making time for me at the stage when I really needed his guidance the most.

I thank my committee members Tom Herman and Phil Taylor. Tom and I enjoyed interesting and insightful chats about the biology of the critter, which helped me a lot. I am especially grateful to Phil Taylor, who acted as my supervisor while Søren was on sabbatical. He has inspired and challenged me and provided me with the guidance and support to face those challenges. His confidence in my abilities has been truly encouraging. My research and education have benefited immeasurably from his generosity and friendship.

Thanks are extended to Patrick Farrell of the Statistical Consulting Centre, Department of Mathematics and Statistics, Acadia University.

Special thanks are extended to Ian Jonsen and Nicole Humble for their assistance, advice, and friendship. I thank my field assistant Tricia Lundrigan for two great seasons, and Nicole Humble and Tina Moore for their invaluable help in the field as well. Tina taught me to drive a standard car, and volunteered a number of hours in the field. Her light-heartedness and humor made her a real treat to tromp around the woods with. Thanks to Paul Chamberland for being a great buddy from both near and afar, and for all those very effective pep-talks. For providing avenues of release from my studies, thanks guys for the beers, pot-lucks, pool, and pin-ball.

I am indebted to all the people who are part of the biology department (fellow grads, undergrads, staff and faculty), for they have created an incredibly dynamic community which I have cherished being a part of.

I extend my sincerest thanks to two of my special friends and colleagues, Samara Eaton and Jamie Gibson. Both were there to listen, commiserate and comfort. They have given me excellent advice and provided me with really simulating conversation. My progression has benefited incalculably with their support and friendship. I am extremely grateful to Jamie for his invaluable comments on this thesis. Also, thank you to Tracy Horsman, friend and fellow gardener. The cards and the camaraderie have helped keep me sane.

I thank my family for their love and support. My mother was an excellent role model for me. She completed an Hon.B.A. although it took approximately 10 years because she was raising my sister and I. My sister also completed her B.A.. I'm proud of them both.

Finally, I thank my husband Mark Johnston. He has volunteered numerous hours in the field and in the workshop helping me build my enclosures. More importantly, he has been my best friend for almost half my life, sometimes knows me better than I do myself, and loves me unconditionally. Without his unwavering belief in me and dedication through those 'hard times', this thesis would not have been. I love you. Also, that he's an excellent cook and doesn't mind housework, has helped this thesis tremendously.

General Introduction

A main goal in population ecology is to understand the distribution and abundance of organisms. To understand fully the relationships between populations and their landscapes it is necessary to determine how the individuals that comprise those populations behave, and how they use the habitat present within those landscapes. An individual's behaviour is assumed to reflect responses to its environment that are molded by natural selection.

Increasingly, the landscapes of organisms are being thought of in terms of mosaics (Dunning *et al.* 1992; Wiens 1989; Wiens *et al.* 1993). As described by Wiens (1995), spatial variation was first built into the theory of heterogeneous landscapes in the form of patches. Originally, patches were assumed to be internally homogeneous and similar to one another, and embedded in a matrix which was homogeneous and of poor quality. Following this, the spatial configuration of patch and matrix was taken into account, and the pattern of this spatial variation was viewed in terms of a mosaic of patches. This mosaic approach, coupled with examining differences in patch attributes (*e.g.* size, shape and quality) and matrix attributes (*e.g.* movement corridors), results in viewing the entire space in which an organism is found, as a landscape mosaic.

Wiens (1995, 1997) suggested that elements in a landscape mosaic should be viewed in terms of costs and benefits, where heterogeneity in patch quality arises due to differences in the physiological stress experienced by an organism, food availability, predation risk, mating probability *etc.*, among elements. Different areas in a mosaic may

have different cost-benefit values to an organism and the mosaic as a whole can be viewed in terms of spatial cost-benefit contours (Wiens *et al.* 1993).

Three aspects of patches that likely influence their cost-benefit values are: 1) size; the area of resource (*e.g.* food, mates, or shelter) available, 2) composition; the type of habitat within a patch (*e.g.* quality of food, shelter, or microclimate), and 3) configuration; the position of a patch in space relative to other patches of different size and composition (Dunning *et al.* 1992). Differences in the cost-benefit values of patches due to these three aspects will likely influence reproduction and the movement behaviour of individuals within a landscape, and hence play a role in their distribution and abundance. For example, a larger patch will have a higher probability of being encountered by colonizers, and will also be able to support larger populations than a smaller area of the same quality (Hanski 1991). Smaller populations may be subject to a higher risk of stochastic extinction (Gilpin 1987). The composition of a patch can also influence the size of population that can inhabit it; patches composed of higher quality habitat can support larger populations than lower quality patches.

There has been increasing recognition of the importance of including the spatial configuration of patches in the study of ecological systems (Legendre and Fortin 1989; Turner 1989; Wiens 1989; Kareiva 1990; Kotliar and Wiens 1990; Gilpin and Hanski 1991; Dunning *et al.* 1992; Hanski and Gilpin 1997), which has largely been prompted by conservation issues (Diamond 1975; Wilcox and Murphy 1985; Lord and Norton 1989; Murphy 1989). Consideration of the role of space has arisen through the need to understand how the patterns arising from human activity influence the patterns and

processes of organisms and systems affected. An increasingly prevalent pattern created through humans' use of nature is habitat fragmentation (Saunders *et al.* 1991; Doak *et al.* 1992; Fahrig and Merriam 1994; Davies and Margules 1998; Thomas *et al.* 1998). Fragmentation is the spatial subdivision of once continuous habitat, as well as a reduction in the total amount of useable habitat. The spatial configuration of patches becomes an issue because isolation of remnant habitat is one of the primary consequences of habitat fragmentation (Saunders *et al.* 1991). Isolation can lower the recolonization rate of empty habitat and may also increase the probability of patch extinction (Brown and Kodric-Brown 1977).

When examining systems in a natural context, scale is an important aspect of spatial structuring to take into account. Organisms respond to characteristics of their habitat across a range of spatial scales (Wiens 1989; Roland and Taylor 1997; Wiens *et al.* 1997), and those responses depend on the behaviour being carried out (*e.g.* migration vs. daily feeding). Since the responses at a given spatial scale may be affected by processes acting at broader scales, determining the relative importance of scale-specific habitat attributes and processes to organisms and their systems is fundamental to our understanding of their ecology (Turner *et al.* 1989). Therefore, we must recognize the range of spatial scales across which an organism views its landscape as heterogeneous. In many situations, the set of relevant scales can only be determined by first examining the dynamics of a system at a number of scales. Thus, a multi-scale approach enables researchers to determine what the relevant scales are for a particular organism or process.

In studying the ecology of any organism, it is important to consider space, because in nature organisms are not usually distributed randomly or uniformly. Rather, they tend to aggregate in patches, to be distributed along gradients, or exhibit some other spatial structure. This is also true for the organism's physical environment, because elements of an ecosystem that are close to one another in space or time are more likely to be influenced by the same generating processes (Legendre and Legendre 1998). Often the result is that data collected from natural systems tend to be autocorrelated (Sokal and Oden 1978; Cliff and Ord 1981; Legendre and Fortin 1989; Rossi *et al.* 1992; Legendre 1993; Legendre and Legendre 1998; Sokal *et al.* 1998). Spatial autocorrelation occurs when pairs of sampling units at certain distances apart are either more or less similar for a measured feature than expected for randomly associated pairs of observations. Hence, sampling units are not independent, violating a fundamental assumption of most classical statistical analyses. Positive spatial autocorrelation results in a greater chance of concluding that there is some relationship when there actually is none. Spatial structuring or autocorrelation is a major source of false correlations *i.e.* those that do not represent a causal relationship (Legendre and Legendre 1998). This is the case when we observe a relationship between a response and an explanatory variable, which is really only a consequence of some other process causing them to have similar spatial patterns.

Holling (1998) proposed that there are two cultures of ecology which represent distinct approaches to the way organisms are studied. One is represented by advances in molecular biology and genetic engineering, which is an analytical stream of biology that is essentially experimental and reductionist in character. The other culture is integrative,

and is represented by evolutionary biology and systems approaches that include the analysis of populations, ecosystems, landscape structures and dynamics of organisms. Holling (1998) describes some of the attributes associated with each culture. With the analytical approach, methods are primarily experimental, and the philosophy is to answer questions which are narrow and targeted, and to parsimoniously find disproof through experiment. This approach usually examines one scale where causation is found to be single and separable, with the goal of eliminating uncertainty by examining single hypotheses. Standard statistics are usually employed and the major concern is the potential for Type I error.

The integrative culture in ecology, however, is broad and exploratory, and there may be multiple lines of converging evidence. Studies may incorporate multiple scales of examination, where causation of observed patterns may be due to multiple factors that are only partially separable. This approach incorporates uncertainty, and studies often use non-standard statistics where the concern is the potential for Type II error. Holling (1998) summarizes the danger of the two cultures: the analytical approach often finds exactly the right answer for the wrong question, whereas the integrative approach finds exactly the right question but a useless answer. To balance these dangers, both cultures are essential for understanding the individuals and systems that they are a part of (Holling 1998).

In this thesis I use both approaches to explore habitat use at different scales by the forked fungus beetle, *Bolitotherus cornutus* Panzer, to gain insight into how patch attributes influence patterns of their distribution and abundance. This beetle is an

especially good species for examining the importance of space and scale because it lives in a patchy environment that is spatially heterogeneous at a number of easily defined scales. The forked fungus beetle is fungivorous, most commonly inhabiting the fruiting bodies of fungus in the genera *Fomes* and *Ganoderma* that grow on dead trees. Natural scales for the beetle include a single sporophore, a log supporting sporophores, and a forest or woodlot.

Most studies have focused at the scale of deadwood supporting sporophores (Heatwole and Heatwole 1968; Conner 1988, 1989; Whitlock 1992). At this scale, a population of forked fungus beetles was defined as beetles inhabiting a single patch, where a patch consisted of a series of logs with sporophores, such that a beetle could walk from any sporophore to another without leaving the log(s) (Whitlock 1992). Individuals spent the majority of their lives in a single patch, within which their movement was quite extensive (Heatwole and Heatwole 1968). Relatively little inter-patch movement by this beetle was observed (Pace 1967; Heatwole and Heatwole 1968; Whitlock 1992). Whitlock (1992, 1994) described and treated the forked fungus beetle as a metapopulation because of the patchy nature of its habitat, and its limited ability for long-distance dispersal. Supporting this idea, he estimated that during their life-time, 30% of individuals make only a single inter-patch movement (Whitlock 1992).

In a recent Honors study at Acadia University, Lundrigan (1997) explicitly examined the beetle's movement behaviour, and found they had much more inter-patch movement than had previously been observed. Also, an increase in the isolation of a forest fragment decreased the incidence of beetles there (Kehler and Bondrup-Nielsen

1999). This relationship suggests that movement by the beetle occurs at the scale of kilometers, presumably by flight. Another Honors study at Acadia University was the first to attempt to relate the forked fungus beetle's demography to characteristics of its habitat (Barlow 1996). The study was unique since much of the literature that has focused on population dynamics and movement of the beetle has addressed neither the characteristics of their habitat, nor how or why these distributions and movement events had arisen (Pace 1967; Heatwole and Heatwole 1968; Conner 1988; Whitlock 1992, 1994).

Besides the presence or absence of its host fungus, several other aspects of the environment may be important to this beetle: their microclimate which could be influenced by the position of the wood upon which the sporophores are growing, properties of the wood which influence growth of the sporophores such as the tree species, and the amount and decomposition of the wood. Also, there may be properties of the wood which are directly important to the beetle's use of habitat, *e.g.* the number of hiding places it provides. Characteristics of the fungus likely play a primary role in the forked fungus beetle's use of habitat such as the amount of fungus and inherent properties of sporophores (*e.g.* species, state (alive or dead), and level of decay). For example, Kehler and Bondrup-Nielsen (1999) reported that at the scale of a single sporophore, the state (live or dead) influenced the presence/absence of the forked fungus beetle, and at the scale of the sporophore and a group of logs supporting sporophores, its incidence increased with patch size.

The objectives of this study were to examine habitat use by the forked fungus beetle at three scales using an exploratory model building approach, to determine the influence of the size, composition and configuration of habitat on their distribution and abundance. Also, in examining habitat configuration, the spatial structure of the beetle's incidence and relative numbers were quantified to determine how they arrange themselves within their landscape. Lastly, using an experimental approach, a specific component of their habitat's composition, the decay of the sporophore, was more closely examined to determine its influence on both the oviposition and the nightly activities of adult beetles.

Details of the Study System

The forked fungus beetle is a North American tenebrionid beetle which is dark brown to black in colour, and approximately 9 to 12 mm in length. Adults are cryptic, and their dorsal surface is textured and rigid. Male beetles possess horns originating at the pronotum, females do not. Although they have well developed metathoracic wings (Graves 1960), their flight has only been observed in a laboratory setting (Teichert 1999), and so their propensity for flight is as yet unknown.

The forked fungus beetle carries out most of its life cycle on a single patch of fungi (Liles 1956). The primary host in Nova Scotia is *Fomes fomentarius* (Fr.) Kickx, but *Ganoderma applanatum* (Pers. ex Wall.) Pat. and *Fomitopsis pinicola* (Fr.) Kar. are also used. The beetles are most active at night and have peaks in activity from 2000 to 0400 hr. (Liles 1956), as well as from 2400 to 0700 hr. (Conner 1989). Beetles may be found during the day feeding on the underside of sporophores, within crevices of bark, or

mating on the sporophores or the bark of the trees. Adult beetles can live at least five years in nature (Brown and Rockwood 1986).

Their mating behaviour is complex and is initiated when males mount females in such a way that the ventral surface of his abdomen rests on the dorsal surface of her thorax. The male then rubs his abdomen across the two tubercles which project from the female's thorax. This reverse position can last up to three hours (Conner 1989). For copulation, the male reverses position, and for the transfer of the spermatophore to be successful, the female must open the plate at the tip of her abdomen. After successful transfer, the male guards the female for two to five hours (Conner 1988). A male's courtship frequency is determined at least in part by male competition, since males often aggressively chase each other away from sporophores occupied by females (Conner 1988). Horn-size is related to mating success; long-horned males have a distinct advantage during fights over females, and in prying males off females during courtship (Conner 1989). Horn-size plays little role in intersexual selection since it is not related to a female's choice of mate (Brown *et al.* 1985).

Mating and egg laying occur throughout the spring and summer, and the eggs are laid singly on the surface of the sporophores and covered with feces (Liles 1956). Individual females may lay only 1 or 2 eggs per day and up to 12 eggs over the course of a season (Liles 1956). After the eggs hatch, the larvae burrow into the sporophore where they feed, and may either pupate and overwinter as adults, or overwinter in the larval stage (Liles 1956). In the spring, the new overwintered adults emerge and the larvae resume development and then emerge as adults later during the season (Liles 1956).

Adults overwinter either within the sporophore, under the bark, or within the dead wood on which the fungi grows (Pace 1967).

The sporophores of the bracket fungi can survive for several years (Graves 1960). These perennial fruiting bodies allow several generations of the beetles to inhabit the same patch (Whitlock 1992). Since both the adult beetles and the larvae feed on the tissue of the sporophore causing extensive tunneling, the sporophores are eventually killed by the beetles (Brown and Bartalon 1986). Matthewman and Pielou (1971) surveyed a number of *Fomes* in Gatineau Park, Quebec, and found that the forked fungus beetle killed more sporophores than any other beetle.

General Methods

Generalized Linear Models

All of the models presented in this study were generated using the generalized linear modeling (GLM) framework (McCullagh and Nedler 1989) in S-PLUS (MathSoft 1998). This exploratory approach was used not for explicit hypothesis testing, but to examine patterns in the data, and the effects of multiple factors (McCullagh and Nedler 1989). This approach allows additional and more specific questions to be derived (Nicholls 1989). Significance of variables was determined by the likelihood-ratio test, or G-test. This tests the reduction in the model deviance resulting from the addition of a variable, as a Chi-squared statistic. Comparisons were made at the 0.05 α-level. Coefficients for logistic regression models represent the log of the odds ratio of success (for incidence in this case, success = beetle presence). For regressions of counts of individuals modeled with Poisson errors, coefficients for continuous variables represent

the natural logarithm of the slope defining the relationship between the relative abundance of the beetles and the explanatory habitat variables, whereas for nominal variables (unordered factors), the coefficient represents the natural logarithm of the mean response for each level of the factor. In both the logistic and the Poisson case, for each variable that is a factor with k levels, $k - 1$ coefficients are supplied; subsequent levels are compared to the first level of the factor. For GLMs an R^2-like measure can be calculated by (Agresti 1990, Myers and Montgomery 1997):

$$1 - (\text{residual deviance} / \text{null deviance})$$

and standardized by:

$$1 - ((\text{residual deviance} / \text{residual df}) / (\text{null deviance} / \text{null df}))$$

The fit of all the models was assessed by examining influence plots, plots of the deviance residuals versus the fitted values (to check for random scatter in the points), and quantile plots of the Pearson's residuals. The parameter estimates and their standard errors were also examined for unusually large values, and the t-value for each coefficient was checked for significance. Since the results of t-tests are only asymptotically correct, and there is no theory on the probability for the significance test (Crawley 1993), the likelihood ratio-tests were chosen over the t-test when a discrepancy arose. Also, the dispersion parameter ($\emptyset$), was calculated for each model as the ratio of the Pearson's χ^2 statistic to the residual degrees of freedom (Chambers and Hastie 1992). This was done to check for deviations from the assumption that the variance to mean ratio of the response was equal to one. The Pearson's product moment correlations presented are significant at the 0.05 α-level, unless otherwise stated.

Mantel Tests

Mantel tests are based on similarity or distances between pairs of observations and are used to determine whether the variation in the similarities of one factor is correlated to the variation in similarities of another factor (Mantel 1967). The sum of the cross-products of two similarity matrices are calculated, and the value returned is standardized into a coefficient ranging between -1 and 1 (Mantel r-statistic; r_M), which is similar to the Pearson correlation coefficient. This value is tested by permutation where the values in one of the matrices are randomly assigned new positions, and a new correlation is calculated. This is done many times to produce a distribution of values which represents the probability of a random association between the two similarity matrices. The actual value is compared to this distribution to determine the probability for the correlation between the two matrices.

For Mantel correlograms, instead of comparing similarity in incidence or counts of individuals to the Euclidean distance, similarity in patterns between pairs of units that are a certain distance apart are linked together using a model matrix of 1 and 0; *e.g.* for distance class 1, neighbouring station pairs (that belong to the first class of geographic distances) are linked by 1's, while the remainder of the matrix contains zeros. A Mantel statistic is calculated for this distance class. The process is repeated for each distance class, building a new model matrix and computing a new statistic. Each value is tested by permutation, correcting the α-level using the progressive Bonferroni correction to account for multiple tests on the same data.

References

Agresti, A. 1990. Categorical data analysis. John Wiley and Sons, Toronto.

Barlow, J. 1996. Populations attributes, habitat characteristics, and spatial dynamics of the forked fungus beetle, *Bolitotherus cornutus* (Panzer). B.Sc. Honors Thesis. Acadia University, Nova Scotia.

Brown, J.H. and A. Kodric-Brown 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

Brown, L. and J. Bartalon 1986. Behavioral correlates of male morphology in a horned beetle. The American Naturalist 127: 565-570.

Brown, L., J. MacDonell and V.J. Fitzgerald 1985. Courtship and female choice in the horned beetle, *Bolitotherus cornutus* (Panzer) (Coleoptera: Tenebrionidae). Annals of the Entomological Society of America 78: 423-427.

Brown, L. and L.L. Rockwood 1986. On the dilemma of horns. Natural History 7: 55-61.

Chambers, J.M. and T.J. Hastie 1992. Statistical models in S. Wadsworth and Brooks/Cole, Pacific Grove, California.

Cliff, A.D. and J.K. Ord 1981. Spatial processes: models and applications. Pion, London.

Conner, J. 1988. Field measurements of the natural and sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 42: 736-749.

Conner, J. 1989. Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 43: 1378-1386.

Crawley, M.J. 1993. GLIM for ecologists. Blackwell Scientific, Boston.

Davies, K.F. and C.R. Margules 1998. Effects of habitat fragmentation on carabid beetles: experimental evidence. Journal of Animal Ecology 67: 460-471.

Diamond, J.M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7: 129-146.

Doak, D.F., Marino, P.C. and P.M. Kareiva 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theoretical Population Biology 41: 315-336.

Dunning, J.B., Danielson, B.J. and H.R. Pulliam 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169-175.

Fahrig, L. and G. Merriam 1994. Conservation of fragmented populations. Conservation Biology 8: 50-59.

Gilpin, M. 1987. Spatial structure and population vulnerability. In: Soulé, M.E. (ed.), Viable populations for conservation. Cambridge Press, Cambridge.

Gilpin, M. and I. Hanski (eds.) 1991. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Graves, R.C. 1960. Ecological observations on the insects and other inhabitants of woody shelf fungi (Basidiomycetes: Polyporaceae) in the Chicago area. Annals of the Entomological Society of America 53: 61-78.

Hanski, I. 1991. Single-species metapopulation dynamics: Concepts, models and observations. Biological Journal of the Linnean Society 42: 17-38.

Hanski, I. and M. Gilpin (eds.) 1997. Metapopulation biology: ecology, genetics and evolution. Academic Press, London.

Heatwole, H. and A. Heatwole 1968. Movements, host-fungus preferences, and longevity of Bolitotherus cornutus. Annals of the Entomological Society of America 61: 18-23.

Holling, C.S. 1998. Two cultures of ecology. Conservation Ecology [online] 2(2): 4. http://www.consecol.org/vol2/iss2/art4.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London, B-Biological Series 330: 175-190.

Kehler, D. and S. Bondrup-Nielsen 1999. Effects of isolation on the occurrence of a fungivorous forest beetle (Bolitotherus cornutus Panzer) at different spatial scales in fragmented and continuous forests. Oikos 84: 35-43.

Kotliar, N.B. and J.A. Wiens 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659-1673.

Legendre, P. and M. Fortin 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107-138.

Legendre, P. and L. Legendre 1998. Numerical ecology. 2nd ed. Elsevier, New York.

Liles, M.P. 1956. A study of the life history of the forked fungus beetle, *Bolitotherus cornutus* (Panzer). The Ohio Journal of Science 56: 329-337.

Lord, J.M. and D.A. Norton 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4: 197-202.

Lundrigan, T.A. 1997. Movement rates as an indicator of dispersal potential in the forked fungus beetle, *Bolitotherus cornutus*. Hon.B.Sc. thesis, Acadia University, Wolfville, Nova Scotia.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209-220.

MathSoft 1998. S-PLUS 4 Guide to statistics. Data Analysis Products Division, MathSoft, Seattle.

Matthewman, W.G. and D.P. Pielou 1971. Arthropods inhabiting the sporophores of *Fomes fomentarius* (Polyporaceae) in Gatineau Park, Quebec. The Canadian Entomologist 103: 775-847.

McCullagh, P. and J.A. Nedler 1989. Generalized linear models. 2nd ed. Chapman and Hall, London.

Murphy, D.D. 1989. Conservation and confusion. wrong species, wrong scale, wrong conclusions. Conservation Biology 3: 82-84.

Myers, R.H. and D.C. Montgomery 1997. A tutorial on generalized linear-models. Journal of Quality Technology 29: 274-291.

Nicholls, A.O. 1989. How to make biological surveys go further with generalised linear models. Biological Conservation 50: 51-75.

Pace, A.E. 1967. Life history and behavior of a fungus beetle, *Bolitotherus cornutus* (Tenebrionidae). Occasional Papers of the Museum of Zoology, University of Michigan 653: 1-15.

Roland, J. and P.D. Taylor 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386: 710-713.

Rossi, R.E., Mulla, D.J., Journel, A.G. and E.H. Franz 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62: 277-314.

Saunders, D.A., Hobbs, R.J. and C.R. Margules 1991. Biological consequences of fragmentation: a review. Conservation Biology 5: 18-32.

Sokal, R.R. and N.L. Oden 1978. Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. Biological Journal of the Linnean Society 10: 229-249.

Sokal, R.R., Oden, N.L. and B.A. Thomson. 1998. Local spatial autocorrelation in biological variables. Biological Journal of the Linnean Society 65: 41-62.

Teichert, S. 1999. First reported flight of *Bolitotherus cornutus* (Panzer) (Coleoptera: Tenebrionidae). The Coleopterists Bulletin 53: *in press*.

Thomas, C.D., Hill, J.K. and O.T. Lewis 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. Journal of Animal Ecology 67: 485-497.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecological Systematics 20: 171-197.

Turner, M.G., Dale, V.H. and R.H. Gardner 1989. Predicting across scales: theory development and testing. Landscape Ecology 3: 245-252.

Whitlock, M.C. 1992. Nonequilibrium population structure in forked fungus beetles: extinction, colonization, and the genetic variance among populations. The American Naturalist 139: 952-970.

Whitlock, M.C. 1994. Fission and the genetic variance among populations: the changing demography of forked fungus beetle populations. The American Naturalist 143: 820-829.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

Wiens, J.A. 1995. Landscape mosaics and ecological theory. In: Hannson, L., Fahrig, L. and G. Merriam (eds.). Mosaic landscapes and ecological processes. Chapman and Hall, New York.

Wiens, J.A. 1997. Metapopulation dynamics and landscape ecology. In: Hanski, I. and M. Gilpin (eds.), Metapopulation biology: ecology, genetics and evolution. Academic Press, London.

Wiens, J.A., Stenseth, N.C., Van Horne, B. and R.A. Ims 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

Wiens, J.A., Schooley, R.L. and R.D. Weeks 1997. Patchy landscapes and animal movements - do beetles percolate? Oikos 78: 257-264.

Wilcox, B.A. and D.D. Murphy 1985. Conservation strategy: the effects of fragmentation on extinction. The American Naturalist 125: 879-888.

Chapter 1. Multi-scale habitat use and population spatial structure of the forked fungus beetle (*Bolitotherus cornutus* Panzer) in continuous forest of Nova Scotia.

Introduction

An organism's habitat is comprised of the conditions and resources that it needs to survive and reproduce. Fundamental to understanding any organism's ecology is recognizing what it perceives as suitable and preferred habitat. An individual's choice of a particular habitat patch is assumed to reflect responses that are molded by natural selection.

The patterns of distribution and abundance of an organism are partly a function of habitat size, composition and configuration. A larger area of habitat will have a higher probability of being encountered by colonizers, and will also be able to support larger populations than a smaller area (Hanski 1994). The suitability of habitat patches can vary through differences in their composition (*e.g.* quality of food, shelter, or microclimate). Habitat composition can influence a population's growth rate and the habitat's carrying capacity; higher quality patches may support larger populations than lower quality ones. The configuration or spatial pattern of habitat can influence organisms' patterns, since moving individuals are more likely to encounter less isolated patches. Hence, investigating these habitat characteristics may provide insight into the patterns of distribution and abundance created by moving, breeding individuals.

When examining systems in a natural context, the scale at which questions are addressed is a vital consideration because organisms respond to characteristics of their habitat across a range of spatial scales. The scales of these responses depend on the

behaviour (*e.g.* migration versus daily feeding) being carried out (Addicot *et al.* 1987; Wiens 1989; Kotliar and Wiens 1990; Wiens *et al.* 1993), and so the range of spatial scales across which an organism views its landscape as heterogeneous must be recognized. In many situations, the set of relevant scales can only be determined by first examining the dynamics of a system at a number of scales. Such an approach enables researchers to determine which scales are relevant for a particular organism or process.

Another consideration is that in nature, organisms are not usually distributed randomly or uniformly. Rather, they tend to aggregate in patches, distribute along gradients, or form some other spatial structures because reproduction and movement do not occur randomly in space. As a result, in many ecological studies of natural systems, the data collected tend to be spatially autocorrelated (Sokal and Oden 1978; Cliff and Ord 1981; Legendre and Fortin 1989; Rossi *et al.* 1992; Legendre 1993; Legendre and Legendre 1998; Sokal *et al.* 1998). In examining the importance of habitat, the spatial arrangement of an organism must be addressed because with the use of classical statistics, autocorrelation will often result in concluding some relationship exists when in reality it does not (Legendre and Fortin 1989). Also, exploring systems for patterns of autocorrelation can give insight into the scales that are important to the organism and its behaviours (Wiens 1989).

The forked fungus beetle (*Bolitotherus cornutus* Panzer) is an excellent candidate for examining the importance of space and scale on patterns of distribution and abundance. This beetle carries out its complete life cycle on the sporophores of fruiting shelf fungi that grow on dead trees (Pace 1967), allowing habitat patches to be discretely

defined at several spatial scales. Also, the patchy nature of the fungus and the high incidence of both the beetle and fungus allow intensive monitoring of the activity of the beetle, and detailed quantification of its habitat.

This beetle-fungus system has clearly defined habitat units at nested scales of resolution. A sporophore, which can be considered the grain size for the beetle (Kotliar and Wiens 1990), is the smallest unit of habitat, and is internally homogeneous and discrete. At a larger scale, a piece of dead wood supporting the fungus, although not internally homogeneous because of differences in the state of the sporophores it supports, is also relatively discrete. However, pieces of dead wood may be spatially arranged so that there is some cohesion between units, where the beetle may respond similarly to groups of logs close to one another. At the next level, the unit of habitat may appear to be either continuous or discrete; uninterrupted tracts of forest, or woodlots and forest fragments, respectively.

Both the fungus and beetle are common throughout North America. The incidence in forests of dead trees supporting fungus is high, and sporophores occur in densities that make it feasible to intensively study beetle patterns and their landscape at multiple scales. Habitat can therefore be censused, providing an actual picture of the beetle's spatial patterning. Hence, sampling the beetle within its actual landscape will provide greater information about the system compared to that obtained merely by sampling the habitat there.

Except for work by Kehler and Bondrup-Nielsen (1999), and Honours studies by Barlow (1996) and Lundrigan (1997), at Acadia University, there has been relatively

little study regarding how this beetle uses its habitat. These works have led to questions about the role that space plays in the dynamics of habitat use by the beetle. What is the nature of spatial structuring by individuals in an area? What interactions exist between this patterning and the spatial structure of the habitat they require? Relating to both of these points, the question of scale arises: At what scale is this beetle responding to its habitat?

Within this study I attempt to answer these questions by examining the beetle's habitat use and spatial structuring at multiple scales in their natural environment. The specific objectives are to: 1) use pattern-seeking models to examine and compare habitat use of the beetle at three scales, to discover how the size, composition and configuration of habitat may be related to their distribution and abundance 2) use these models to predict incidence and number of individual beetles from novel data thereby testing the adequacy of the models, and 3) examine the spatial pattern of the forked fungus beetle's incidence and numbers of individuals at three scales to determine whether there is spatial autocorrelation, and at what scales and distances it is occurring.

Methods

Study Organisms

The primary host of the forked fungus beetle in Nova Scotia is *Fomes fomentarius*, although *Ganoderma applanatum* and *Fomitopsis pinicola* are also used (pers. obs.). Mating and oviposition occur throughout the spring and summer, during which time the adult beetles are most active at night. Females lay eggs singly on the

surface of the sporophores, from which larvae hatch and burrow into the sporophore (Liles 1956, Matthewman and Pielou 1971), where they feed and develop, usually emerging as adults the following year (Pace 1967). Both the larvae and adults can overwinter within the sporophore (Liles 1956; Pace 1967). Adults use both the sporophore and the wood of the tree supporting the fungus, for overwintering and temporary refuge (Conner 1989, pers. obs). The forked fungus beetle has well-developed wings (Graves 1960), but its flight has only been observed in the laboratory (Teichert 1999). Adult beetles can live up to five years in nature (Brown and Rockwood 1986).

The sporophores can last for 10 years or more (Schwarze 1994), and so are a potential resource for several generations of beetles. The primary host trees in Nova Scotia, Canada include white birch (*Betula papyrifera*), yellow birch (*Betula lutea*), American beech (*Fagus grandifolia*), and large-toothed aspen (*Populus grandidentata*). Tunneling of sporophores by larvae and adult forked fungus beetles is a primary cause of the sporophores death and decay (Matthewman and Pielou 1971).

Study Areas

In 1995 several forested areas near the town of Wolfville, Nova Scotia were surveyed for the presence of fungi infested by the forked fungus beetle. Two sites in mixed continuous forest were chosen for the study: the Reservoir site, located approximately 6 km south-east of town on Gaspereau Mountain, and the 101 site, located approximately 20 km south-west of town skirting highway 101. Through casual observation it appeared that the dominant tree species at the Reservoir site included:

eastern hemlock (*Tsuga canadensis*), paper birch, sugar maple (*Acer saccharum*), red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), and yellow birch, and at the 101 site included: American beech, paper birch, eastern hemlock; and large-toothed aspen, red maple (*Acer rubrum*) and red spruce were also present.

At both sites, snags or logs supporting *Fomes*, *Ganoderma*, or *Fomitopsis* were given a unique number. Dead wood without sporophores were not included in the study because they lack the fungus that the beetle requires for survival and reproduction. The spatial location of the ends of each log and the base of each snag were mapped using a compass and measuring tape. The Reservoir site was 0.8 hectares and had 39 and 61 trees supporting sporophores in 1996 and 1997, respectively, and the 101 site was 1.24 hectares and had 74 and 87 infected trees in 1996 and 1997, respectively (Table 1-3b).

Beetle Monitoring

The activity of adult beetles was monitored to determine the incidence of habitat use during the 1996 and 1997 breeding seasons, and the relative number of individuals using habitat during those periods. Sites were monitored between 5 June and 7 August during 1996, and between 1 June and 8 August during 1997. Sites were monitored in the morning between 0800 and 1200 hr., and checked every second or third day. All fungus infected trees at each site were checked for the presence of beetles. A mirror and flashlight were used to assist in looking for the beetles under the logs, sporophores, and in places difficult to be observed directly. When a individual was found that had not been observed before, it was uniquely marked with up to 5 dots of Testor's non-metallic paint

on the pronotum and the four quadrants of the elytra in different combinations. Each new

beetle's sex, body length, and horn size (if male) were recorded. Hand-held calipers were

used to measure body length and horn size to the nearest 0.1 mm. The paint marks lasted

for the duration of the study period. During 1997, some of the paint marks, although

legible, were re-applied because some wear was evident.

During each visit, the following information was recorded for recaptured beetles:

date, site, patch number, sporophore number (all sporophores in the sites were labeled

with numbered thumb tacks), sex, location (*i.e.* on or off a sporophore), mating (yes or

no), partner (if applicable), and pair's orientation to one another if applicable (*i.e.* head to

head or head to abdomen).

Habitat Measurements

The following data on the sporophores were collected at both sites during the

period between 25 July and 7 August, 1996: level of decay (live, dead but intact, dead

and partially decayed or dead and very decayed), hemispherical circumference‡, height†

of sporophore (length contacting tree), location along the central axis of the tree

(longitudinal axis on log = top surface, longitudinal axis on snag = surface in arbitrarily

chosen direction), distance and orientation from the central axis, and whether emergence

holes were present. Emergence holes are produced when beetles chew through the

surface of the sporophore after their development from larvae to adult is complete.

Sporophores were described as live by their white to off-white colour and by their

production of sporophores, and dead sporophores were described by their grey colour and

lack of sporulation. A dead sporophore was intact if a very dense sound was produced by rapping ones knuckles on its surface. Intact sporophores appeared as solid as a newly cut piece of wood. Partially decayed sporophores lacked emergence holes but had a slightly spongy texture when squeezed. Very decayed sporophores usually had one or more emergence holes indicating that some portion of their context was hollowed through use by the beetle, or lacking emergence holes, was degraded by the weather or through infection by other fungi or molds. The hemispherical circumference and height were measured using a flexible centimeter tape measure to approximate the volume of each sporophore. The volume was calculated using the average of two volumes using the formulas for a half of the cap of a sphere, and half of a cone:

$$\text{Volume} = \frac{([\pi\, h^2\, (r-h/3)]/2) \;+\; ([\pi\, h^2\, (h/3)]/2)}{2}$$

where h = height†
     r = radius

radius = circumference / 2 (π)
circumference = 2 (hemispherical circumference‡)

The following data were collected by visually assessing each fungus infected tree between 5 July and 7 August, 1996: tree species, tree state (snag or log), level of wood's decomposition (not very decomposed, partially decomposed or very decomposed), percent of wood covered by bark, bark complexity (smooth, partially ridged with few crevices, complex-very ridged with many crevices), percent of wood covered with vegetation (*e.g.* mosses and lichens), complexity of the vegetation on the wood surface

(smooth (*e.g.* crustose lichens), moderately complex (*e.g.* simple mosses), and complex (*e.g.* leafy lichens and bushy mosses)), average diameter to the nearest 1 cm (logs), diameter at breast height to the nearest 1 cm (snags), and length of both snags and logs to the nearest 0.1 m. The diameter and length were measured to determine the volume and surface area of the wood. During the 1997 field season, the above habitat variables were measured for any newly discovered logs supporting sporophores, or for logs from 1996 that contained new sporophores not observed during 1996.

Data Analysis

<u>Spatial Scales</u>

In this study three relatively discrete spatial scales were defined: a single sporophore ('sporophore scale'), a single log or snag supporting sporophores ('log scale'), and a log or group of logs supporting sporophores separated by less than 1 meter ('patch scale'). The polar co-ordinates obtained for the ends of the logs and for the snags using compass and measuring tape, were transformed into Cartesian (x,y), co-ordinates. The mid-point of each log was used as co-ordinates at the log scale and the average of the mid-points of the logs was used as the co-ordinates for the patch scale.

At the sporophore scale, an x,y co-ordinate was calculated for each sporophore based on its location on the tree. All the sporophores which were located on a particular snag were assigned the same co-ordinate (that of the position of the snag within the site), since a third dimension could not be created by including a z axis for height (information about the elevation of the snags was not collected). For sporophores on logs, however, a

unique co-ordinate was calculated for each based on its distance along the log's central axis ('along'), and its distance right or left of the central axis ('from').

The nearest neighbour distances for the log and patch scale units were calculated using their x,y co-ordinates. This was also done for the sporophores on logs, however, since the sporophores on a snag all had the same co-ordinates, calculations were done separately for each snag using measurements 'from' and 'along' the central axis of the tree.

Habitat Use Models

Models for both incidence and the count of individuals were constructed for each site, year, and scale, using the marked beetle data and habitat data (variables listed in Table 1-1), resulting in 24 models (12 of incidence and 12 of beetle counts). As well, incidence data was pooled to create a single model for each scale which included a site and year term (3 models). This was not possible for the count of individuals because there was so much variation between sites and years. All habitat use models were generated using the generalized linear modeling framework (McCullagh and Nedler 1989) in S-PLUS (MathSoft 1998).

Responses: A unit at any scale was occupied if at least one beetle was observed on it during the breeding season, and beetle counts were calculated as the number of unique individuals observed. For the logistic regression models created for incidence data, units at all scales that were composed solely of red-belted sporophores (*F. pinicola*) were removed from the analyses, since there were only two observations of beetles using them

during the two-year study. It appears that the forked fungus beetle uses these sporophores differently than *Ganoderma* or *Fomes*. For the models of the count of individuals, only the units where beetles were present were included in the analyses, eliminating all zero counts. Since there were relatively few non-zero counts it appeared that leaving the zeros in the analyses was identical to modeling a logistic process rather than a true Poisson process.

Sporophore Scale: There were only three terms tested for each of the sporophore scale data sets for beetle incidence and counts of individuals: DECAY, VOLUME and NND (Table 1-1). A univariate model was built with each of these variables and terms were included in the order of how much each reduced the deviance (*i.e.* the term that reduced the deviance the most was included in the model first, *etc.*). At this scale, all possible two-way interactions were also tested.

Log and Patch Scale: At the log and the patch scales, for both incidence and counts, the first habitat terms that were tested for each model related to fungus volume, since the sporophores are fundamental to this beetle's survival and reproduction. Three models for each site and year were created; one testing TOTVOL only (general), one testing DVOL and LVOL only (moderately specific), and a model where all four decay levels: LVOL, D1VOL, D2VOL and D3VOL, were tested (very specific).

For each of these three models, a forward step-wise procedure was used to test the terms which related to other attributes of the sporophores (proportion of total fungus represented by each decay level: PLVOL, PD1VOL, PD2VOL, and PD3VOL; average size of sporophores in each decay level: TOTAVEVOL, DAVEVOL, LAVEVOL, D1AVEVOL,

D2AVEVOL, and D3AVEVOL. After this, another forward step-wise procedure was used to test the significance of the variables describing dead wood. Only main effects were examined at the log and patch scale. The best of the three models (general, moderately specific, very specific), was chosen based on its fit (see 'Model Diagnostics') and by the amount of variation in the response that it explained.

Pooled Incidence Models: The pooled logistic regression models for each scale (all data for that scale regardless of site or year) were built similar to the individual models. In each, however, the influence of site and year on beetle incidence was tested, as well as their interactions with the habitat variables. Interactions between pairs of habitat variables were tested in these pooled models as well.

Model Diagnostics: The fit of all the models was assessed by examining influence plots, plots of the deviance residuals vs. fitted values (checked for random scatter in the points), and quantile plots of the Pearson's residuals. The parameter estimates and their standard deviations were also examined for unusually large values, and the t-values were checked for significance. The likelihood ratio-test was chosen over the t-test when a discrepancy arose. Also, the dispersion parameter ($\varnothing$) was calculated for each model to determine whether the response followed the assumption that the variance to mean ratio equaled 1. The likelihood ratio tests and Pearson's product moment correlations presented are significant at the 0.05 α-level, unless otherwise stated.

<u>Habitat Use Predictions</u>

The adequacy of the models that were built for the Reservoir site, for each scale, and year was tested by attempting to predict both beetle incidence and the count of individuals in the 101 site. The 101 site was chosen as the site for which beetle patterns would be predicted because it had more habitat units at each scale than at the Reservoir site. Also, the Reservoir site models were used as predictors because the ranges of the values for the habitat variables were greater than in the 101 site and hence, fewer units for which the response was to be predicted were excluded from the analyses (*i.e.* more habitat units for which to predict incidence and beetle counts). The models tested were those that best described the data in the Reservoir ('best' models) models that only included the term TOTVOL, and models that only included the term log (TOTVOL). The last two types of models were tested to examine how very general models performed in predicting beetle patterns. As well, for incidence at the sporophore scale, these three types of models were also built and tested using only sporophores on logs that were occupied ('Sporophore (B)' scale). These predictions were compared to the models that were created using all of the sporophores.

<u>Beetle Spatial Structure</u>

Responses: Both incidence and count of individuals were examined for patterns of spatial autocorrelation. A unit at any scale was occupied if at least one beetle was observed on it during the breeding season, and the count of beetles was calculated as the number of unique individuals observed on occupied habitat units. As with incidence in

the habitat use models, units at all scales that were composed solely of red-belted sporophores were removed from the analyses.

Simple Mantel Tests: Mantel tests (Mantel 1967) were performed for log and patch scales, and compared the pattern of similarity in incidence and the pattern of Euclidean or geographic distances between pairs of logs and patches in each site during each year (*e.g.* Reservoir, 1996, log scale; 8 data sets total). This method was not used for the sporophore scale data because sporophores on snags all had the same co-ordinates, and the distance between these pairs were all zero. This would significantly bias the results. Instead, a Mantel test was performed separately for each tree that was occupied by beetles. Using the co-ordinates mapped 'from' and 'along' the tree's central axis the test determined the presence of spatial autocorrelation among the sporophores on a given tree. This method was used for both incidence and the count of individuals, and only logs with more than 9 sporophores and which had at least 4 occupied sporophores were used. This cut-off was used to ensure a large enough sample size of both occupied and unoccupied sporophores so that results would not be biased. Also, a Bonferroni correction (Nams *pers. comm.*) was used since the same test was being done successively a number of times.

Similarity Measures: The similarity measure for incidence at the log and patch scale was calculated two ways: the difference of all pairs observation and the sum of all pairs of observations. Taking the difference of pairs of observations resulted in a matrix of 0 and 1; 0 representing patches that were similar in their incidence (both are occupied, or both are unoccupied), and 1 representing patches that were dissimilar in their incidence. This

measure was used for the tests. Calculating the sum of pairs of observations resulted in a matrix of 0, 1, and 2; 0 representing patches that were similarly unoccupied, 2, patches that were similarly occupied and 1, patches that were dissimilar in their beetle incidence. This measure was used to illustrate graphically how each type of pair differed in their distances. For beetle counts only logs and patches with beetles present were included in the analyses. The similarity in beetle counts was calculated as the difference in the number of unique individuals observed during the year, and was tested against the Euclidean distance between these pairs. For all Mantel tests, the α - level was 0.025 because they were two-tailed, and p-values were calculated using 10 000 permutations.

Mantel Correlograms: Using Mantel correlograms, beetle incidence at the log and patch scale were more closely examined to determine at what distances autocorrelation was present. Correlograms could not be constructed for the counts of beetles, or for the sporophore scale incidence and beetle counts, because there were too few sampling units. The α-level for r_M at each distance class (0.025 because the tests are two-tailed) was corrected using the progressive Bonferroni correction (Legendre and Legendre 1998) to account for multiple tests on the same data. Since a simple Mantel test had already been performed for each data set, the α-level for the first distance class was set to 0.0125, the second to 0.0083, *etc.*.

Results

Beetle Monitoring

More individuals were captured in both years at the 101 site than at the Reservoir site, but on average individuals were caught more often at the Reservoir site (Table 1-2). For both sites, the number of individuals as well as the number of times individuals were observed was lower in 1996 than 1997. At all scales, a greater proportion of habitat was used at the Reservoir site than at the 101 site, although individuals tended to be more clumped at the Reservoir site (Table 1-3).

Habitat Use Models

Beetle Incidence

The models built for each scale using the data pooled across both sites and years are similar in the amount of variation in beetle incidence that they explain, although the R^2 values for the log and patch scale are slightly higher (sporophore scale $R^2 = 0.20$, log scale $R^2 = 0.26$, patch scale $R^2 = 0.26$). The volume of sporophores at each scale explained a large portion of the variation in beetle incidence (Table 1-4), although at the patch scale, it was the volume of sporophores at certain decay levels which explained the incidence data best (Table 1-4c). The volumes of both live and dead intact sporophores were highly correlated with total volume ($r = 0.81$ and $r = 0.89$, respectively).

Unlike the models at the other two scales, site and year terms are significant at the sporophore scale; beetle incidence was higher on sporophores in 1996 than 1997, and higher at the Reservoir than at the 101 site (Table 1-4a; Figure 1-1). Also, there are some

significant interactions in the sporophore scale model; while both the decay level of a sporophore and its volume significantly explained the probability of being occupied, the importance of each decay level was different between years and sites. Unlike at the 101 site where beetle incidence was lower the more decayed the sporophore, at the Reservoir the occurrence of beetles on dead and very decomposed sporophores (D3) was second only to live sporophores (L) (Figure 1-2). A similar pattern is evident between years; very decomposed sporophores were more often occupied than dead and partially decomposed sporophores in 1996, but in 1997 incidence decreased with increasing sporophore decay (Figure 1-3). The influence of volume on beetle incidence differed between sporophores of different decay levels. Increasing sporophore size increased the probability of beetle occurrence the most on live sporophores, less so on dead and intact sporophores, and very little on partially and very decomposed sporophores (Figure 1-4).

Models for the log and patch scale are similar in the sporophore terms used to describe beetle incidence (Table 1-4b and 1-4c). Since both live and dead/intact volume were correlated with total sporophore volume (log scale: LVOL r = 0.84, D1VOL r = 0.90 and patch scale: LVOL r = 0.81, D1VOL r = 0.89), both models include information about the overall amount of fungus at a patch. The importance of live and dead/intact fungus is expressed in terms of total amounts at the patch scale, whereas at the log scale it is expressed as the proportion of live volume and the average size of dead/intact sporophores. Some properties of the wood that the fungus infected were important for describing the incidence of beetles' use. At the log scale, wood that was more decayed tended to have a higher beetle incidence (Figure 1-5), while at the patch scale, snags were

more often occupied than logs, and wood supporting more complex vegetation had higher incidence as well (Figure 1-6).

Although there is variation, some general trends are apparent in the individual models of incidence built for each year, site and scale, which concur with the pooled models. As with the pooled models, the size and decay of the sporophore is important to beetle incidence at the sporophore scale. Generally, incidence increased with the size of the sporophore and decreased with the decay of sporophores (Table 1-5). At the log and patch scales, the probability of use by the forked fungus beetle increases with the total amount of fungus, and the amount of live and dead, intact fungus (Table 1-5). As well, the decay and complexity of the vegetation on the tree influenced their use by the beetle in some of the individual models of the log and patch scale. In others, however, trees with less bark and more vegetation had higher incidence. Coefficients, deviance values, and p-values are presented for each individual model in Appendices 1-1 to 1-3. Plots showing the fit of each model are given in Appendices 1-4 to 1-6.

Beetle Counts

No pooled models were created for beetle counts because there was too much variation in the data. This is apparent in the variety of habitat variables that were included in the individual models (Table 1-6). Attempts at pooling these data across sites and years resulted in models with upwards of 16 terms (one third were interactions), that had dispersion parameters between 5 and 9. Even for the individual models describing

the number of beetles in occupied patches, some data were overdispersed with their $\emptyset$-values ranging between 0.9358 and 1.9873 (mean = 1.2587).

Individual models show some interesting trends despite the variation in them. The variation explained by the sporophore scale models was low (Reservoir 1996 R^2 = 0.17, 101 1996 R^2 = 0.22, 101 1997 R^2 = 0.25), although they are quite consistent in their significant terms. As with incidence, in all the individual beetle count models, the number of individuals observed increased with increasing sporophore size. The relationship between beetle numbers and decay was also similar to incidence; fewer individuals used decayed sporophores except for very decayed sporophores which were used almost as much as live sporophores.

The log scale models explain almost all of the variation in beetle counts (Reservoir 1996 R^2 = 0.96, Reservoir 1997 R^2 = 0.93, 101 1996 R^2 = 0.96, 101 1997 R^2 = 0.81). While generally logs with more fungus were used by more individuals, the importance of the decay of the sporophores varied (Table 1-6). Logs with more live, dead and partially decayed, and dead and very decayed sporophores were used by more individuals. In these cases, however, the amount of dead fungus was correlated with the total amount (D2VOL r = 0.84, D3NUM r = 0.52). Although there is much variation between models, the same attributes of the wood that were important for incidence, also appear to be important for describing the number of individuals using a log. In one of the data sets, however, counts decreased when the distance to the next nearest neighbour increased. At the 101 site, a log was removed from the analysis because it was the only

one that had many individuals but relatively small sporophores. The model with this term included was highly overdispersed ($\emptyset = 4.3$).

Patch scale models of the number of individuals are relatively similar to the log scale models in their trends, and in the amount of variation they explain (Reservoir 1996 $R^2 = 0.98$, Reservoir 1997 $R^2 = 0.78$, 101 1996 $R^2 = 0.95$, 101 1997 $R^2 = 0.83$). More individuals visited patches that contained more fungus, and those with more live and partially decayed sporophores (Table 1-6). The amount of partially decayed sporophores is highly correlated with the total volume of fungus (101 1996 $r = 0.83$, 1997 $r = 0.79$). As well, the characteristics of the wood important to the number of individuals were similar to those important for both incidence and beetle counts at the log scale. Outliers were removed for 2 of the patch scale models. At the Reservoir site a log supporting approximately 8000 cm^3 of fungus was removed because its high fungus volume (compared to the mean = 1229.0 cm^3) was driving the relationships in the model. At the 101 site, the same log that was removed at the log scale, was removed from the patch scale analysis because in this case, it had many individuals but only a single live sporophore. Coefficients, deviance values, and p-values are presented for each individual model in Appendices 1-7 to 1-9. Plots showing the fit of these models are given in Appendices 1-10 to 1-12.

Habitat Use Predictions

<u>Beetle Incidence</u>

Values between 0 and 1 were returned for the predictions from incidence models, representing the probability of a unit being occupied. To determine how well the models predicted beetle incidence, these probabilities were transformed to either present or absent, where probabilities greater than 0.5 became 1 (present), and values less than 0.5 became 0 (absent). From these data, the proportion of correctly predicted units was calculated. Results focus on the proportion of occupied patches correctly predicted, because the ratio of occupied to unoccupied patches is different for each scale. Especially at the sporophore scale, there are a large number of unoccupied units. Since an occupied sporophore is such a rare event, the models had a difficult time predicting them. The 95% confidence interval was calculated for the proportion of occupied units correctly predicted as well as the mean probability predicted for occupied units.

Generally, although at all scales occupied patches were predicted better in 1996 than in 1997, the ability to predict beetle presence increased with scale (except for the sporophore scale 'best' model predictions for 1996) (Table 1-7). Also, when only one term, log (TOTVOL), was used to describe beetle incidence, predictions on average were better than those from the models with more complexity ('best'), and those with less complexity ('TOTVOL only'). At the sporophore scale, beetle presence was better predicted when logs that were unoccupied were removed from the model.

Beetle Counts

For these models, the predicted values that were returned were continuous. To determine how well these values coincided with the observed values, the slope of the line of best fit through the origin was calculated (*i.e.* the best model relating the predicted values to those observed), its 95% confidence interval, and the coefficient of non-determination ($1 - R^2$). The slopes were compared to the model of perfect prediction (a line with a slope of 1 and an intercept of 0), and so the smaller the difference between the best fitting line and a slope of 1, the better the model predicted. However, the confidence interval was taken into account since there is 95% confidence that the actual slope lay at any point within those bounds. As well as examining the slope of the line of best fit, the $1 - R^2$ value was examined to get an indication of the amount of 'spread' in the data. The greater the spread, the less related the predictions are to the observed values.

All of the models built to describe beetle counts at the Reservoir site predicted the 101 site data poorly (Figures 1-7 to 1-9, Appendix 1-13). In the log and patch scale predictions, there was an obvious outlier and so for all scales and years, the observations which were predicted most poorly by the models were removed (Appendix 1-13b). For those data, in all but two cases (1996 patch scale 'best' model and 1997 log scale 'best' model), the slope of the line of best fit was closer to 1 than with the worst prediction left in. Although the confidence intervals were not as tight around each slope as for the slopes without the worst predictions removed, the variation of the data around the slopes was less. There was little improvement in the slope of the best fitting line for the data at the sporophore scale (Figures 1-7 to 1-9 (a and b), Appendix 1-13b). At the log and the

patch scale, however, a consistent pattern emerges: improvement in the difference of the slope's line to that of one (perfect prediction) is least for the 'best' models (Figure 1-7), and highest for the models which only included the term log (TOTVOL) (Figure 1-9). For the log (TOTVOL) models, the average deviation of the slope of the line of best fit was 0.25 (compared to 'best' models: 0.49, and 'TOTVOL' models: 0.45) (Appendix 1-13b). Despite the improvements in the log (TOTVOL) predictions with the worst prediction removed, they are still quite poor; on average predictions are off by approximately 6 beetles, and in the worst case, off by an average of 15 beetles (patch scale in 1996). The log and patch scales predicted similarly poorly while the sporophore scale did substantially worse.

Beetle Spatial Structure

In total, 26 of the 58 occupied logs were tested for the presence of spatial autocorrelation among their sporophores. Of these, only 3 logs showed autocorrelation in beetle incidence. At the 101 site in 1996, results from 2 logs suggested that pairs of sporophores that were similar in whether or not they were used during the season (both used, or both not used), were closer to one another than dissimilar pairs ($r_M = 0.211$, p-value = 0.0038; $r_M = 0.213$, p-value = 0.0071). Contrary to this, in 1997 at the 101 site results from a different log suggest the opposite; pairs of sporophores dissimilar in their incidence were closer to each other ($r_M = -0.097$, p-value = 0.0091). When the Bonferroni correction ($\alpha = 0.001$) was applied to the p-values of the results for these 3 logs, autocorrelation among their sporophores was not significant.

Simple Mantel tests for the incidence of the forked fungus beetle reveal the presence of spatial autocorrelation in 2 of the 8 log and patch scale data sets. In both cases there was positive spatial autocorrelation at the log scale (Table 1-8). Boxplots indicate that logs that were similarly occupied were closer to one another than expected for randomly associated pairs; pairs of patches that were unoccupied were closer than pairs that were both occupied, and pairs of logs that were dissimilar in beetle incidence were farthest apart. This trend is stronger for the 1996 Reservoir data (Figure 1-10a), than the 1997 101 data (Figure 1-10b).

For beetle counts at the sporophore scale only 2 of the 26 occupied logs that were tested showed spatial autocorrelation. Both were at the 101 site (one in 1996 and a different one in 1997), and their results are contradictory. Results from the log showing significant autocorrelation in 1996 suggested that pairs of sporophores that were more similar in the number of individuals which used them, were closer to one another ($r_M = 0.239$, p-value = 0.0100), while results from the log in 1997 suggested that pairs that were more different were closer ($r_M = -0.150$, p-value = 0.0088). When the Bonferroni correction ($\alpha = 0.001$) was applied to the p-values of the results for these 2 logs, autocorrelation among their sporophores was not significant.

Simple Mantel tests for the count of individuals reveal the presence of spatial autocorrelation in only one data set. At the patch scale at the Reservoir site in 1997, occupied patches that were most similar in beetle counts were farther apart than expected at random (pairs = 68, $r_M = -0.16$, p = 0.0116). There were 12 patches tested, one of which had a very large count (69 individuals), compared to the other patches (mean = 6.2

individuals). The correlation was not significant after testing the data with this observation removed (pairs = 66, r_M = -0.15, p = 0.0627). The Mantel test may be sensitive to outliers at such a small sample size, and to conclude the presence of spatial autocorrelation on the basis of one observation would be dubious.

Mantel correlograms for incidence were created for each of the 8 data sets at the log and patch scale (Figures 1-13, and 1-14). Distance classes were chosen by examining plots of the relative locations of occupied and unoccupied patches (Figures 1-11 and 1-12). Especially at the Reservoir site, it appears that there are two clumps of patches, separated by approximately 100 meters (Figure 1-12a). The majority of patches in one clump consist of occupied patches while the other is mostly unoccupied patches. The clumps appear to be approximately 50-60 meters in diameter. Therefore, I chose 50 meter distances classes which enabled patterns of spatial autocorrelation to become evident while maximizing the number of pairs tested in each distance class. The clumping in the plot of patch locations was revealed in the Mantel correlograms. At the log scale at the Reservoir in 1996 (Figure 1-13a), logs within the 50 m distance class show highly significant spatial autocorrelation (p < 0.0001). Beyond 50 meters, although not significant, the correlation is negative, and beyond 100 meters there is significant negative autocorrelation between logs separated by up to 200 meters (p = 0.0038 and p = 0.0047, respectively). This pattern is evident in all the data sets regardless of scale, site or year; pairs of patches within approximately 50 meters of one another are more positively autocorrelated in their beetle incidence (either both occupied or both unoccupied), past which they are less similar than expected for randomly associated pairs

(Figures 1-13 and 1-14). A summary of the correlogram results, including the number of pairs used for each distance class is presented in Appendix 1-14.

Discussion

At all three scales, the size (volume of sporophores), and composition (sporophore decay) of habitat were important to its use by the beetle. At the log and patch scales, attributes of the dead wood were also important for beetle use. The incidence of the forked fungus beetle at these scales was autocorrelated, although its influence on the models of habitat use appear negligible since predictions of incidence between the two forests was adequate. This may be due to a common pattern of autocorrelation in both forests where positive autocorrelation was detected at 50 m, beyond which incidence was negatively autocorrelated. From predictions of habitat use models, it appears that the beetle responds to habitat attributes at the scale of a group of logs within a meter, although the analysis of the spatial structure of beetle incidence suggests that the scale of this response is larger *i.e.* a group of logs supporting fungus within a 50 meter area.

At all scales, both the incidence and the number of beetles using a habitat unit increased with the volume of the sporophore(s). In a study of the effect of isolation on the incidence of the forked fungus beetle, Kehler and Bondrup-Nielsen (1999) found that the size of a sporophore and the size of a cluster of sporophores were both positively related to its use by the beetle. Use was measured as the presence of eggs, beetles, or emergence holes, and therefore provided a historical view of the beetle's incidence. Another tenebrionid beetle, *Bolitophagus reticulatus*, also lives primarily on *Fomes*

sporophores in Scandinavia, and its life cycle is very similar to that of the forked fungus beetle (Nilsson 1997a; Rukke and Midtgaard 1998). Removal and dissection of dead sporophores from birch trees revealed that at three scales presence of *B. reticulatus* increased with the size of the sporophore, the amount of fungus in an infected tree, and the m^2 area of a forest island containing infected trees (Rukke and Midtgaard 1998). Also, presence of the beetle increased with the amount of fungus on an infected tree and their occurrence was most common near large sporophores (Nilsson 1997a).

Higher incidence at the log and patch scale on larger units (more fungus) may be due to a higher colonization rate of them by the forked fungus beetle because they are more easily found (Hanski 1994). This may also reduce their probability of stochastic extinction due to the rescue-effect (Brown and Kodric-Brown 1977), or because logs and patches supporting more fungus were used by more individuals. Larger demographic units are less at risk of becoming extinct due to random population fluctuations than smaller populations (Gilpin 1987; Schaffer 1987; Schoener and Spiller 1987). Hanski and Thomas (1994) also found that the incidence of butterflies increased with habitat size and Kindvall and Ahlén (1992) found that the population size of bush crickets increased with patch area.

Although factors such as colonization rate and stochastic extinction may contribute to the patterns of incidence observed at these scales, in light of the results observed in the spatial analysis of the distribution of beetles, they are likely more important at higher scales that were not directly examined here. If the grouping of the forked fungus beetle in patches within a 50 m area represents a unique demographic unit,

then the processes described above are likely to act most strongly at this scale. Stochastic processes may not be as important on logs and patches within this 50 m area since there is considerable movement between them (pers. obs.).

At all scales the level of sporophore decay in a habitat unit was important to its use by the forked fungus beetle. At the sporophore scale, there generally was a decrease in use with the decay of the sporophore. In a field experiment (Chapter 2), egg-laying by females and the presence of adults during the night decreased with the decay of the sporophores.

In contrast, in some of the models of habitat use in the present study, both the incidence and number of individuals found on very decayed sporophores were almost as great as on live sporophores. This contradiction has also been observed with *B. reticulatus*. In a study that examined the incidence of beetles caught in pitfall traps situated near sporophores, presence appeared higher for live sporophores than dead ones (Nilsson 1997a). Midtgaard *et al.* (1996), however, examined dissected *Fomes* sporophores for the presence of the beetle at any of its stages of development, and found incidence higher in dead than live sporophores. Incidence also decreased with increasing decay, although the latest stage of decay was dominated by adults (Midtgaard *et al.* 1996). This may reflect two different ways that a sporophore is used by the beetle. While live sporophores likely represent a good source of food, they provide little in the way of daily refuge from the weather and potential predators. On the other hand, while very decayed sporophores provide good refuge, they may have little nutritional value. The relationship between very decayed sporophores and the number of individuals counted was stronger

than for incidence. This might reflect the activity of the beetles at the time of sampling; during the day beetles are not as active (Conner 1989).

Forked fungus beetles preferred larger sporophores that were alive or dead and intact, but they did not prefer larger sporophores that were dead and decayed. In light of their apparent preference for laying eggs on less decayed sporophores (Chapter 2), this interaction would fit with oviposition behaviour of females. Larger live or dead, intact sporophores would provide a more long-term resource for their offspring. The size of decayed sporophores would not reflect their duration as a food source since much of their mass would already be reduced to some degree through decay and previous use by the beetle. It would also not reflect the amount of space hollowed out inside them (since that was not directly measured), which might be the most important factor for their use as resting spots.

At the log and patch scale, the amount of sporophores at certain decay levels was also important to their use by the beetles. For both the incidence and the count of beetles, results concur with the patterns of use observed at the sporophore scale. Nilsson (1997a) found that *B. reticulatus* incidence was better modeled at the scale of the infected tree by including both the amount of live and dead fungus as terms in the model, instead of only including a term for the total volume of sporophores.

Pooled models suggest that the incidence of use by the forked fungus beetle was influenced by level of a tree's decay at the log scale, and by the predominant state of the tree, and vegetation complexity at the patch scale. Logs that were more decayed had a higher incidence of use than less decayed trees. This may reflect the level of infection by

the fungus and hence the number of sporophores it can support; the number of sporophores on a dead tree may be correlated with its level of decay. For beetle counts, in general, partially decayed trees had the greatest number of individuals visit them, followed by very decayed trees. Perhaps trees that were extremely decayed were spent in their ability to nourish the fungus; new sporophores could not be supported and existing ones may have been exhausted as a food resource.

Patches that contained snags had higher beetle incidence than logs. This might be due to their differences in micro-climate; sporophores on a snag may be warmer and/or drier because they are farther from the ground. Midtgaard *et al.* (1996) found a higher incidence of *B. reticulatus* in dissected sporophore specimens that were drier. At the tree scale, Rukke and Midtgaard (1998) suggested that a microclimate of low moisture content and with high temperature improves the habitat quality for the beetle since lower forest height, more open forest type and lower basal area around an infected tree coincided with increased beetle incidence. During overwintering, *B. reticulatus* were observed to be freeze-tolerant in moister sporophores and freeze-avoidant in drier sporophores, and their survival was always lower in moister sporophores (Gehrken *et al.* 1991). Similarly, Nilsson (1997a) found that the presence of the beetle was positively related to the proportion of a log not touching the ground; snags had 10 times the odds of being occupied.

The complexity of the vegetation structure on the wood's surface may directly influence use of a patch by the forked fungus beetle. Wood in patches with more complex structure had higher beetle incidence. The forked fungus beetle has been

observed on wood supporting sporophores, especially in crevices and under the bark (Conner 1989; Pace 1967; pers. obs.). As an extension of this substrate, vegetation which is large and leafy may provide hiding places from predators or may be used for resting, and hence patches with such structure may be preferred by the beetle. Although this has not been explored for *B. reticulatus*, the importance of shelter for a number of animals has been demonstrated (*e.g.* territoriality in European robins (Cuadrado 1997); butterfly distributions (Dover 1996); influence on home range size of fox (Lucherini *et al.* 1995); habitat use kiwis (Taborsky and Taborsky 1995)).

No effect of the relative isolation of habitat units was detected for beetle incidence at any of the scales examined. The measure for isolation was calculated as the distance to the nearest neighbouring habitat unit (NND). Kehler and Bondrup-Nielsen (1999) found that isolation influenced beetle incidence (present and historical) at the scale of a single sporophore, a cluster of sporophores, and the forest fragment, and that from ten different measurements of isolation, an adequate measure was the distance of the nearest neighbour. The effects of isolation were also found for the incidence of *B. reticulatus* individuals (Nilsson 1997b), and for those dissected from sporophores (Rukke and Midtgaard 1998; Sverdrup-Thygeson and Midtgaard 1998). In these studies, increasing isolation decreased the presence of the beetle at the scale of an individual infected tree.

The number of individuals using a log or patch at the Reservoir site during 1997 decreased with greater distance to the nearest habitat unit after accounting for the size of units. According to the analysis of the spatial structure of the beetles, the probability that the nearest neighbour of an occupied unit also has beetles is greater than would be

expected if they were randomly associated. Beetles moving between logs and patches likely have a greater chance of encountering units that are nearby, and hence less isolated logs would receive more of these individuals.

A potential problem when using incidence as a measure of habitat use at the sporophore scale is that the frequency and timing of sampling for beetles during a season may be insufficient to detect usage. Sites were visited only every other day and not during the period when the beetles were most active. However, some relatively clear patterns did emerge in the models of beetle incidence, suggesting it was not a major source of error. For beetle counts, however, patterns were less clear, possibly due to limited data. For example, data were inadequate to model beetle counts for the Reservoir site in 1997.

For the log and the patch scale, the measure of the number of individuals raised another concern as well. The measure used here does not take into account differences in the capture probabilities of individuals at different units. For example, some logs touched the ground completely while others were slightly elevated from the forest floor, providing fewer hiding places for the beetles that our flashlights and mirrors could not reach. Consequently, the results from this study may simply reflect our ability to find individuals rather than the beetles' use of habitat. Although it is likely that there was some influence of variation in capture probabilities between units (since some models were overdispersed), had differences in capture probabilities predominated the data, few general patterns across sites and years would have been observed. Also, models would

likely consist mostly of terms relating to the host tree, *i.e.* terms relating to our ability to observe beetles. This pattern was not observed.

Overdispersion can occur if one or more of the factors that is important for describing the variation in the response have not been measured (Agresti 1990), or when the underlying distribution of the response is not Poisson (McCullagh and Nedler 1989). Overdispersion may also be due to inter-subject variability, where the response for a given individual (or log or patch) might be a Poisson process, but together, a group of these individuals may exhibit some other distribution (McCullagh and Nedler 1989). This is a feature that is common in count data, and results in a model which may fit the data more poorly since the standard error of the parameters is calculated using the dispersion parameter (Crawley 1993; McCullagh and Nedler 1989; Myers and Montgomery 1997; Agresti 1990). McCullagh and Nedler (1989) present a model of accidents in ships, where they suggested that the $\varnothing = 1.69$ in the final model was due to inter-ship variability, and hence used caution in drawing firm conclusions from the results. In this study, it appeared that the raw count data followed a binomial instead of a Poisson distribution. The problem of overdispersion due to the distribution was partially corrected by removing 0 counts.

The ultimate test of any model is its ability to predict given a new set of explanatory variables. With two study sites, I was able to test the adequacy of the exploratory models of the forked fungus beetle's habitat use. For both incidence and beetle counts the amount of variation in the response explained by the sporophore scale models (R^2) was lower than those of the log and patch scale (more so for count data

models). The R^2 values for the log and patch scale are fairly similar to one another for both beetle incidence and counts, yet in both cases it is slightly higher at the log scale. For incidence though, predictions using novel data were the best at the patch scale. This pattern may have arisen because logs that were within a meter of one another were considered independent when they actually were not. At the patch scale, although there was still positive autocorrelation within a 50 m area, the autocorrelation due to logs close to one another (within a meter), was accounted for since they were treated as the same unit.

For the count data models, the R^2 values were suprisingly large for the higher scales. On average, models at the log scale explained 91% of count of individuals (patch scale = 88%). Considering this supposedly high explanatory power, the actual predictions of the 'best' models from one site to another are extremely poor. This reflects the variability observed in the data of beetle counts within and across data sets, and likely some of the factors influencing the number of beetles using a habitat are missing from the models. Information about the conspecifics in habitat units (e.g. the number of individuals, sex ratio, male horn sizes) would likely influence the number of individuals visiting the area, but not be as important for the choice of whether or not a beetle uses a particular habitat unit.

Results of predictions for the models of incidence raise some important points in light of the results obtained in the spatial analysis. With the presence of spatial autocorrelation at the log and patch scale, theory states that the relationships observed for the models might be an artifact of the units not being independent of each other. Since a

similar pattern of autocorrelation occurred in both sites and years, this artifact may not have been detected by the predictions. The extremely small p-values for some of the models' terms, however, may be a sign that because of autocorrelation, the variation explained by each may have been overestimated.

Predictions of the habitat use models demonstrate the importance of scale. Although similar habitat attributes were important across scales (size and decay of sporophore(s)), habitat use by the forked fungus beetle was described most accurately at higher scales. The sporophore scale incidence and count models predicted much more poorly than the log or patch scales, which had fairly similar predictive ability. Interestingly, though, there was some improvement for sporophore scale models when information about a higher scale was included in the model (whether or not the log the sporophore occurred on was occupied). This suggests that whether or not a beetle uses a particular habitat unit, is more than just a function of the attributes of the particular sporophore there.

Incidence of habitat use by the forked fungus beetle was best predicted on the patch scale and predictions were fairly accurate, supporting the conclusion that beetles tend to aggregate within a 50 m area. Habitat choice is occurring on at least the scale of the patch, suggesting that the boundaries for dynamics of individual populations is not substantially larger. Therefore, future studies will likely find clearer answers to questions about the dynamics of this system if focused at a larger scale than that of a patch (*e.g.* forest/site).

Spatial analysis of the incidence and counts of the forked fungus beetle provide some interesting insight into their population spatial structure. No autocorrelation was detected among sporophores on occupied logs. For the log and patch scale though, while no autocorrelation was detected for beetle counts, there was a distinct pattern of autocorrelation observed for beetle incidence. That a common pattern was observed for both sites and during both years, when the layout of the fungus infected trees appeared quite varied through time and space, suggests that this pattern does not reflect the beetle's response to a similar habitat configuration. Instead, it seems that the pattern is generated by the behaviour of the beetle. Perhaps 50 m marks the boundaries of the size of a beetle population, within which exists a continuum for the dynamics of reproduction and movement.

In a recent study, Bondrup-Nielsen (*unpubl. data*) collected samples of forked fungus beetle larvae from forest fragments and continuous forests. He found that the genetics of larvae were more different among the sites within a continuous forest than they were among larvae taken from isolated forest fragments. The increased variation in the genetics of the beetles within continuous forest suggests that walking may be the main means of movement there, perhaps resulting in aggregations of beetles within 50 m areas.

Whitlock (1992, 1994) describes and treats the forked fungus beetle as a metapopulation because of the patchy nature of its habitat, and its limited long-distance dispersal. In past studies, there was relatively little inter-patch movement observed by the forked fungus beetle (Heatwole and Heatwole 1968; Pace 1967; Whitlock 1992), and Whitlock (1992) estimated that during their life-time, 30% of individuals move from one

patch to another only once. He defined a population of forked fungus beetles as individuals inhabiting a single patch, where a patch is a series of logs with sporophores such that a beetle could walk from any sporophore to another without leaving the log(s). The results of the present study indicate that unique populations occur on a larger scale, since beetle incidence on patches within a 50 m area were more likely to be similarly occupied. Also, recent Honours studies at Acadia University (Lundrigan 1997; Barlow 1996), found there was much more movement between fungus infected logs than had been previously observed. Moreover, flight by the beetle has been confirmed (Teichert 1999), and Kehler and Bondrup-Nielsen (1999) found a relationship between incidence and the isolation of forest fragments (km scale). These findings suggest that this beetle moves quite extensively, and so likely does not represent a metapopulation at the scale of the patch.

The data collected here suggest a number of further avenues of investigation. The two analyses of this study (habitat use and population spatial structure) could potentially be more connected through the use of partial Mantel tests which would incorporate the beetle's spatial structure in the examination of habitat use. This would give a clearer picture of the relative contribution of habitat and space to the patterns observed in the forked fungus beetle's distribution and abundance. Examining these components separately may have resulted in false correlations for the habitat use analysis presented here. For example, both the spatial pattern of decayed sporophores and the spatial pattern of beetle incidence may be due to a common influence acting similarly on them *e.g.* microclimate.

In this study I explored habitat use at multiple scales by examining two responses of adult forked fungus beetles: the incidence of beetles and the number of individuals counted in units of habitat. Characteristics of the sporophores (size and decay), were important for the beetles at all scales examined; however, the ability to describe patterns of habitat use increased with scale. The spatial structure of the incidence of the forked fungus beetle in its natural environment supports these observations and also suggests that the dynamics of individual beetle populations occur at even larger scales. These results demonstrate the importance of the scale at which ecological questions are posed and the influence of space across scales. In this system, factors other than sporophore attributes that are acting at broader scales result in the distribution and abundance of the forked fungus beetle.

Table 1-1. Habitat variables for each scale (pooled over both sites and years), used in analyses of the incidence and count of *B. cornutus* individuals.

VARIABLE		RANGE	MEAN ±SD
Sporophore Scale (n = 2393)			
DECAY	factor (L = live, D1 = dead/intact, D2 = dead/partially decayed, D3 = dead/very decayed)		
TOTVOL	volume of sporophore (cm³)	0.1 - 927.5	46.6 ± 70.2
NND	distance to the nearest sporophore (m)	0.0 - 14.0	0.23 ± 0.65
Log Scale (n = 261)			
TOTVOL	total volume of sporophores (cm³)	3.9 - 8776.7	438.4 ± 889.1
LVOL	volume of live sporophores (cm³)	0.0 - 4322.3	122.1 ± 427.9
DVOL	volume of dead sporophores (cm³)	0.0 - 4454.4	316.2 ± 424.7
D1VOL	volume of dead/intact sporophores (cm³)	0.0 - 1889.7	151.9 ± 295.1
D2VOL	volume of dead/partially decayed sporophores (cm³)	0.0 - 1395.8	50.2 ± 140.6
D3VOL	volume of dead/very decayed sporophores (cm³)		
TOTNUM	total number of sporophores	1 - 26	10.3 ± 14.8
LNUM	number of live sporophores	0 - 89	3.1 ± 9.4
DNUM	number of dead sporophores	0 - 52	7.2 ± 10.1
D1NUM	number of dead/intact sporophores	0 - 39	2.7 ± 5.9
D2NUM	number of dead/partially decayed sporophores	0 - 30	3.4 ± 5.7
D3NUM	number of dead/very decayed sporophores	0 - 11	2.2 ± 1.1
PLVOL	proportion live sporophore volume	0 - 1	0.29 ± 0.42
PD1VOL	proportion dead/intact sporophore volume	0 - 1	0.19 ± 0.30
PD2VOL	proportion dead/partially decayed sporophore volume	0 - 1	0.36 ± 0.38
PD3VOL	proportion dead/very decay sporophore volume	0 - 1	0.16 ± 0.30
TOTAVEVOL	average volume of all sporophores (cm³)	2.5 - 603.2	53.2 ± 89.9
LAVEVOL	average volume of live sporophores (cm³)	0.0 - 603.2	27.9 ± 87.4
DAVEVOL	average volume of dead sporophores (cm³)	0.0 - 516.6	36.5 ± 57.5
D1AVEVOL	average volume of dead/intact sporophores (cm³)	0.0 - 516.6	20.7 ± 53.2
D2AVEVOL	average volume of dead/partially decay sporophores (cm³)	0.0 - 251.0	27.8 ± 37.9
D3AVEVOL	average volume of dead/very decayed sporophores (cm³)	0.0 - 465.3	14.8 ± 39.8
TRSTATE†	tree state; factor (1 = snag, 2 = log)		
TRDECAY*	tree decay; factor (1 = firm, 2 = slightly decayed, 3 = well decayed)		
TRSA	tree surface area (m²)	0.9 - 21.2	2.9 ± 3.3
PERBARK*	percent of tree covered with bark	0.0 - 100.0	85.9 ± 21.0
PERVEG*	percent of tree covered with vegetation	0.0 - 90.0	19.6 ± 25.6
COMBARK*	bark complexity; factor (1 = smooth, 2 = partially curled/ragged, 3 = very curled, many crevices/holes)		
COMVEG*	vegetation complexity; factor (1 = not complex, small surface area, e.g. crustose lichen, 2 = moderately complex, e.g. simple mosses, 3 = complex, e.g. leafy lichens, bushy mosses)		
NND	nearest neighbor distance; measured from either the centre or ends of each log to either the centre or ends of the nearest log (m)	0.0 - 43.9	3.6 ± 6.0

Patch Scale (n = 167)

SAME VARIABLES AS FOR THE LOG SCALE. Values for terms are the sums across the logs within a patch unless otherwise indicated (below).

* the mean of the values for each piece of dead wood was calculated for the patch scale

† where there were both logs and snags, the patch was assigned the state of those pieces of dead wood that supported the largest proportion of sporophore volume

Table 1-2. Summary of monitoring marked *B. cornutus* individuals: the sampling frequency, the number of unique individuals caught, and the total captures for each site and year.

Site	Year	Number of Visits	Number of Individuals	Number of Captures
Reservoir	1996	20	122	345
	1997	18	81	167
101	1996	20	125	292
	1997	19	119	225
Total			786	1933

Table 1-3. Summary of habitat use by *B. cornutus* at each year, site and scale.

a) Sporophore Scale

Site	Year	Number of Sporophores	Sporophores with Eggs	Sporophores with Beetles	Number of Individual Beetles maximum	mean ± SD
Reservoir	1996	364	186	100	20	2.4 ± 2.4
	1997	507	174	71	8	1.8 ± 1.5
101	1996	710	135	76	17	2.6 ± 2.9
	1997	812	153	53	13	2.3 ± 2.3

b) Log Scale

Site	Year	Number of Logs	Logs with Eggs	Logs with Beetles	Number of Individual Beetles maximum	mean ± SD
Reservoir	1996	39	12	11	100	23.7 ± 33.3
	1997	61	19	15	69	9.6 ± 17.5
101	1996	74	20	16	84	14.6 ± 21.9
	1997	87	28	20	57	8.5 ± 12.1

c) Patch Scale

Site	Year	Number of Patches	Patches with Eggs	Patches with Beetles	Number of Indidvidual Beetles maximum	mean ± SD
Reservoir	1996	25	10	9	100	31.2 ± 37.2
	1997	40	15	13	69	11.0 ± 18.5
101	1996	47	16	15	84	15.9 ± 22.2
	1997	55	22	17	58	10.4 ± 13.0

Table 1-4. Analysis of deviance in the incidence of *B. cornutus* at each scale pooled across both sites and years (models were fit in the generalized linear modeling framework using a binomial error distribution and a logit link function).

a) Sporophore Scale

Term	Df	Deviance	Pr (Chi)
Null	2306	1786.93	
YEAR	1	9.98	0.0016
SITE	1	44.46	0.0000
DECAY	3	137.51	0.0000
TOTVOL	1	115.40	0.0000
DECAY:VOLUME	3	27.22	0.0000
SITE:DECAY	3	19.01	0.0003
YEAR:DECAY	3	19.15	0.0002
Residual	2291	1414.20	

b) Log Scale

Term	Df	Deviance	Pr (Chi)
Null	236	266.00	
log (TOTVOL)	1	38.32	0.0000
PLVOL	1	22.92	0.0000
DIAVEVOL	1	4.38	0.0363
TRDECAY	2	9.14	0.0104
Residual	231	191.23	

c) Patch Scale

Term	Df	Deviance	Pr (Chi)
Null	144	189.26	
DIVOL	1	27.04	0.0000
LVOL	1	10.06	0.0015
TRSTATE	1	8.61	0.0033
COMVEG	3	8.78	0.0324
Residual	139	134.78	

Table 1-5. The terms included in the individual models for each year, site and scale that significantly contributed to describing the incidence of *B. cornutus* (models were fit in the generalized linear modeling framework using a binomial error distribution and a logit link function).

| Term | 1996 | | | | | | 1997 | | | | | |
| | Reservoir | | | 101 | | | Reservoir | | | 101 | | |
	Sporophore	Log	Patch	Sporophore	Log	Patch	Sporophore	Log	Patch	Sporophore	Log	Patch
TOTVOL		•				•				•		
log (TOTVOL)	•			•			•	•				
LVOL or LNUM											•	•
DVOL or DNUM			•						•			
DIVOL					•						•	•
DECAY	•			•			•			•		
PD2VOL									•			
PERBARK	•	•										
PERVEG											•	
TRDECAY					•	•						
COMVEG												•
log (TOTVOL):DECAY				•								

59

Table 1-6. The terms included in the individual models for each year, site and scale that significantly contributed to describing the count of *B. cornutus* individuals in occupied habitat units (models were fit in the generalized linear modeling framework using a Poisson error distribution and a log link function).

Term	1996 Reservoir Sporophore	Log	Patch	1996 101 Sporophore	Log	Patch	1997 Reservoir Sporophore	Log	Patch	1997 101 Sporophore	Log	Patch
TOTNUM									•			
log (TOTVOL or TOTNUM)	•	•	•	•				•		•		
LVOL or LNUM					•	•						•
D2VOL					•	•						•
D3NUM											•	
DECAY	•			•						•		
PLVOL			•									
PD2VOL		•										
TOTAVEVOL					•							
DAVEVOL		•										
D2AVEVOL	•	•				•						
PERBARK					•							
PERVEG					•							
TRDECAY					•	•			•		•	•
COMVEG								•				
TRSTATE									•			•
TRSA											•	
NND								•	•			

69

Table 1-7. Predicting beetle incidence at one site using models built from data of a different site. The proportion of correct predictions of *B. cornutus* incidence in all habitat units ('all'), the proportion of occupied units correctly predicted ('occupied'), the upper and lower 95% confidence interval for the proportion occupied units correctly predicted, and the mean probability predicted for occupied units at the 101 site. Models were built using data of the Reservoir site for each year and scale. For the sporophore scale, as well as building a model with all the sporophores in the site (A), models were built for only those sporophores situated on occupied logs (B). The types of models that were used to predict incidence include: Best models: the models which best describe the variation in beetle incidence, log (TOTVOL): models that contain only a term for the log of the total volume of sporophores, TOTVOL: models that contain only a term for the total volume of sporophores.

Year	Scale	Best models					TOTVOL models					log (TOTVOL) models				
		all	occupied	95% C.I. lower	upper	mean prob.	all	occupied	95% C.I. lower	upper	mean prob.	all	occupied	95% C.I. lower	upper	mean prob.
1996	Sporophore (A)	0.89	0.16	0.08	0.27	0.59	0.89	0.16	0.09	0.27	0.66	0.88	0.26	0.16	0.38	0.57
	Sporophore (B)	0.86	0.43	0.10	0.81	0.57	0.95	0.14	0.00	0.58	0.64	0.86	0.43	0.10	0.81	0.57
	Log	0.70	0.38	0.15	0.65	0.79	0.79	0.56	0.30	0.80	0.80	0.70	0.75	0.48	0.93	0.66
	Patch	0.59	0.60	0.32	0.84	0.71	0.59	0.60	0.32	0.84	0.71	0.54	0.73	0.45	0.92	0.64
1997	Sporophore (A)	0.92	0.08	0.03	0.17	0.58	0.91	0.04	0.01	0.12	0.64	0.91	0.00	NA	0.05	NA
	Sporophore (B)	0.76	0.08	0.03	0.17	0.57	0.76	0.04	0.01	0.12	0.59	0.75	0.00	NA	0.05	NA
	Log	0.76	0.45	0.23	0.68	0.62	0.77	0.35	0.15	0.59	0.75	0.72	0.45	0.23	0.68	0.61
	Patch	0.60	0.41	0.18	0.67	0.73	0.60	0.41	0.18	0.67	0.73	0.54	0.53	0.28	0.77	0.65

Table 1-8. Results of the simple Mantel tests to detect the presence of spatial autocorrelation in the incidence of *B. cornutus* at each scale, site and year. The matrices used were the difference in pairs as the similarity measure for incidence, and the geographic distance between pairs. Bolded p-values are significant.

Year	Site	Scale	Number of Pairs	Distance Range (m)	Mantel r-statistic	P-value ($\alpha = 0.025$)
1996	Reservoir	Log	435	0.6 - 216.4	0.36	**0.0011**
		Patch	120	4.4 - 210.6	0.18	0.0635
	101	Log	2485	0.3 - 228.3	0.11	0.0339
		Patch	946	1.7 - 228.3	0.0	0.4061
1997	Reservoir	Log	1378	0.2 - 211.4	0.15	0.0290
		Patch	528	3.8 - 210.6	0.15	0.0257
	101	Log	3486	0.3 - 228.3	0.16	**0.0042**
		Patch	1326	1.7 - 228.3	0.05	0.0810
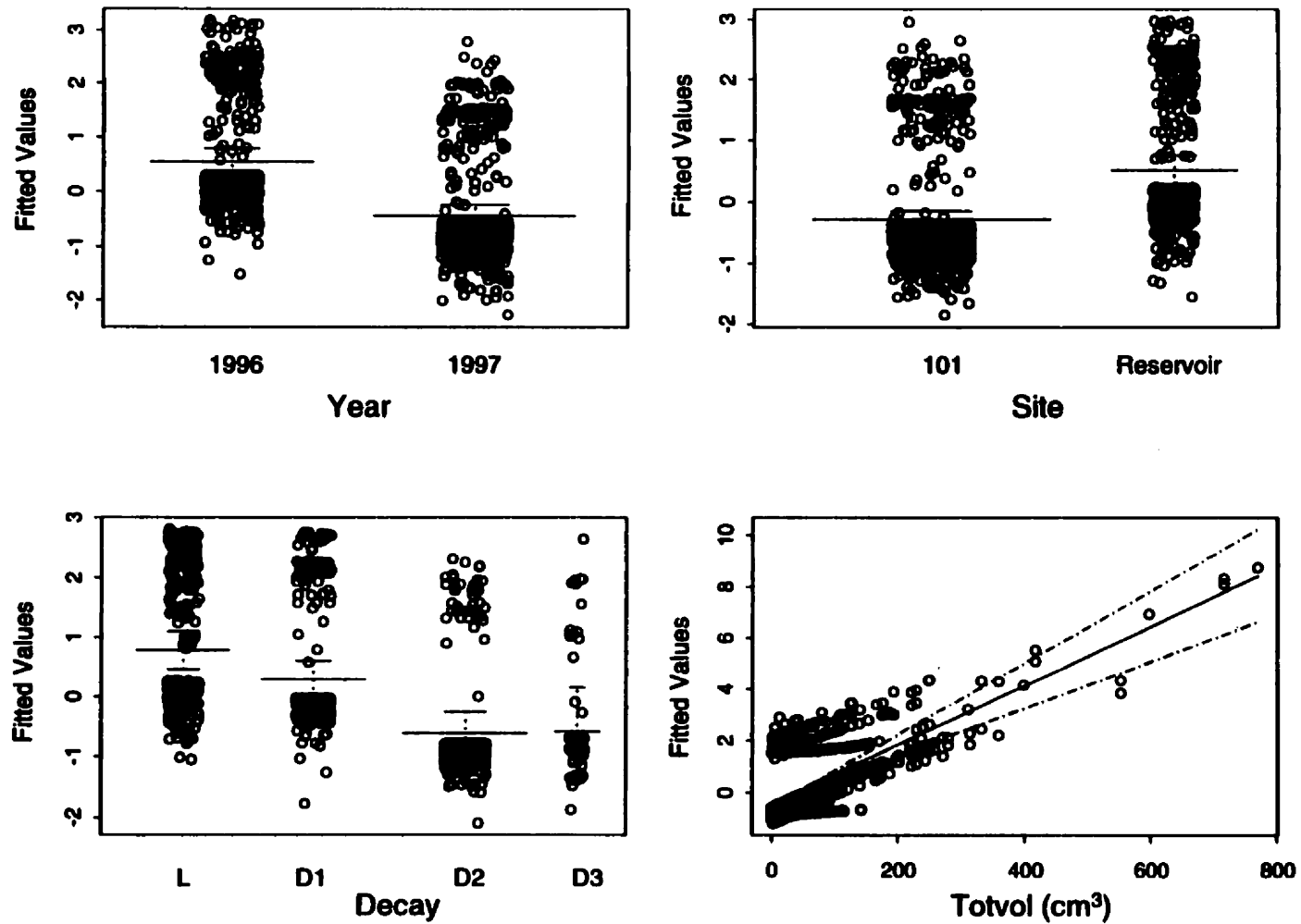
Figure 1-1. Plots of the contribution of each variable to the model describing the incidence of *B. cornutus* for all sites and years at the sporophore scale (dashed lines = approximate 95% pointwise confidence intervals, open circles = partial residuals). Lateral variation in plots of factors reflects the number of observations in each category.
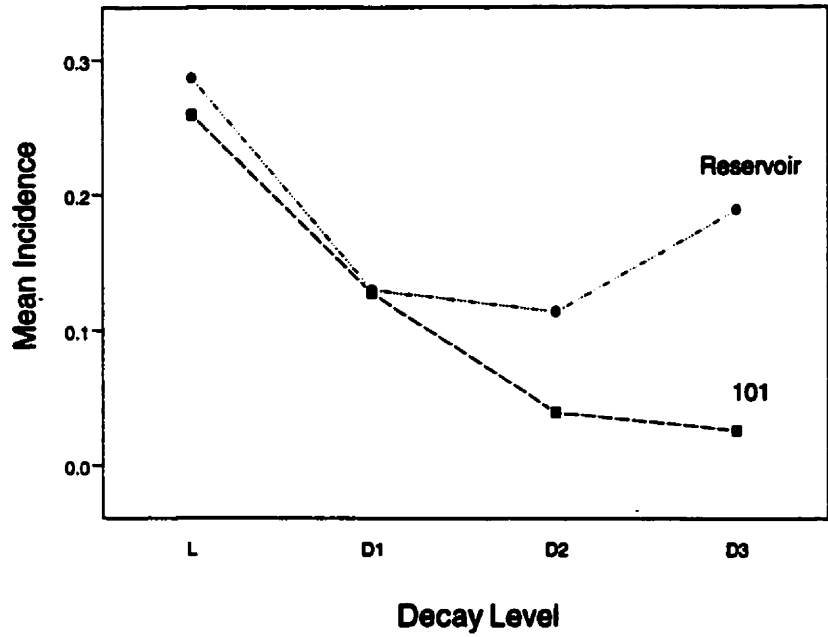
Figure 1-2. Interaction plot showing how the incidence of *B. cornutus* on sporophores at different decay levels varied between sites.
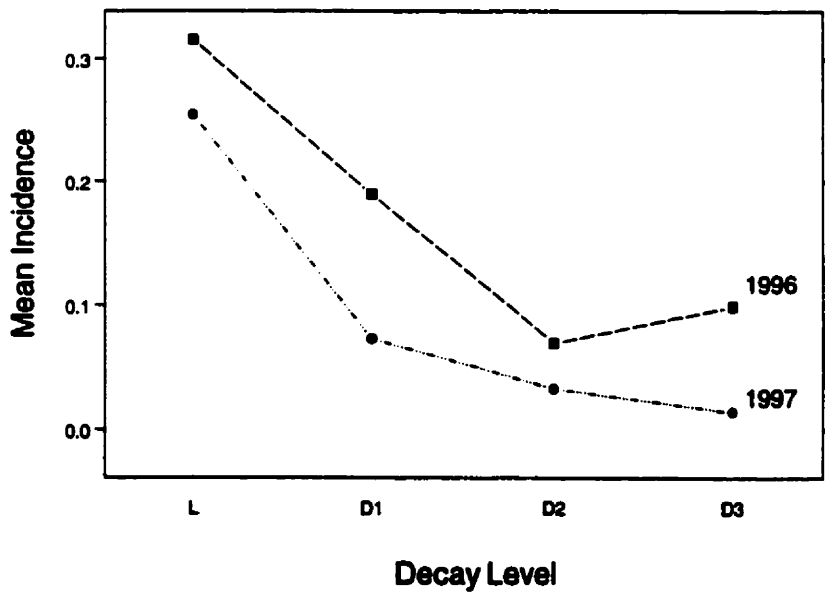
Figure 1-3. Interaction plot showing how the incidence of *B.cornutus* on sporophores of different decay levels varied between years.
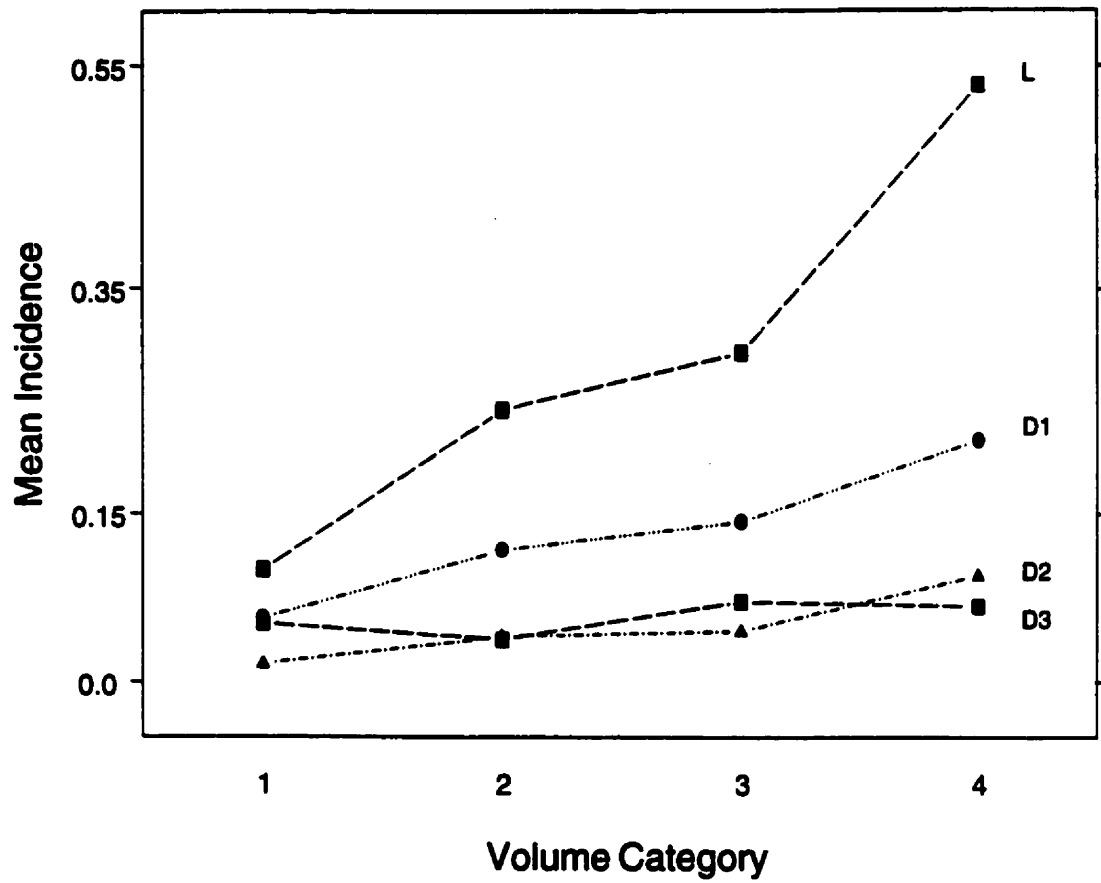
Figure 1-4. Interaction plot showing how the influence of volume (1<2<3<4) on the incidence of *B. cornutus* differed between sporophores of different decay levels.
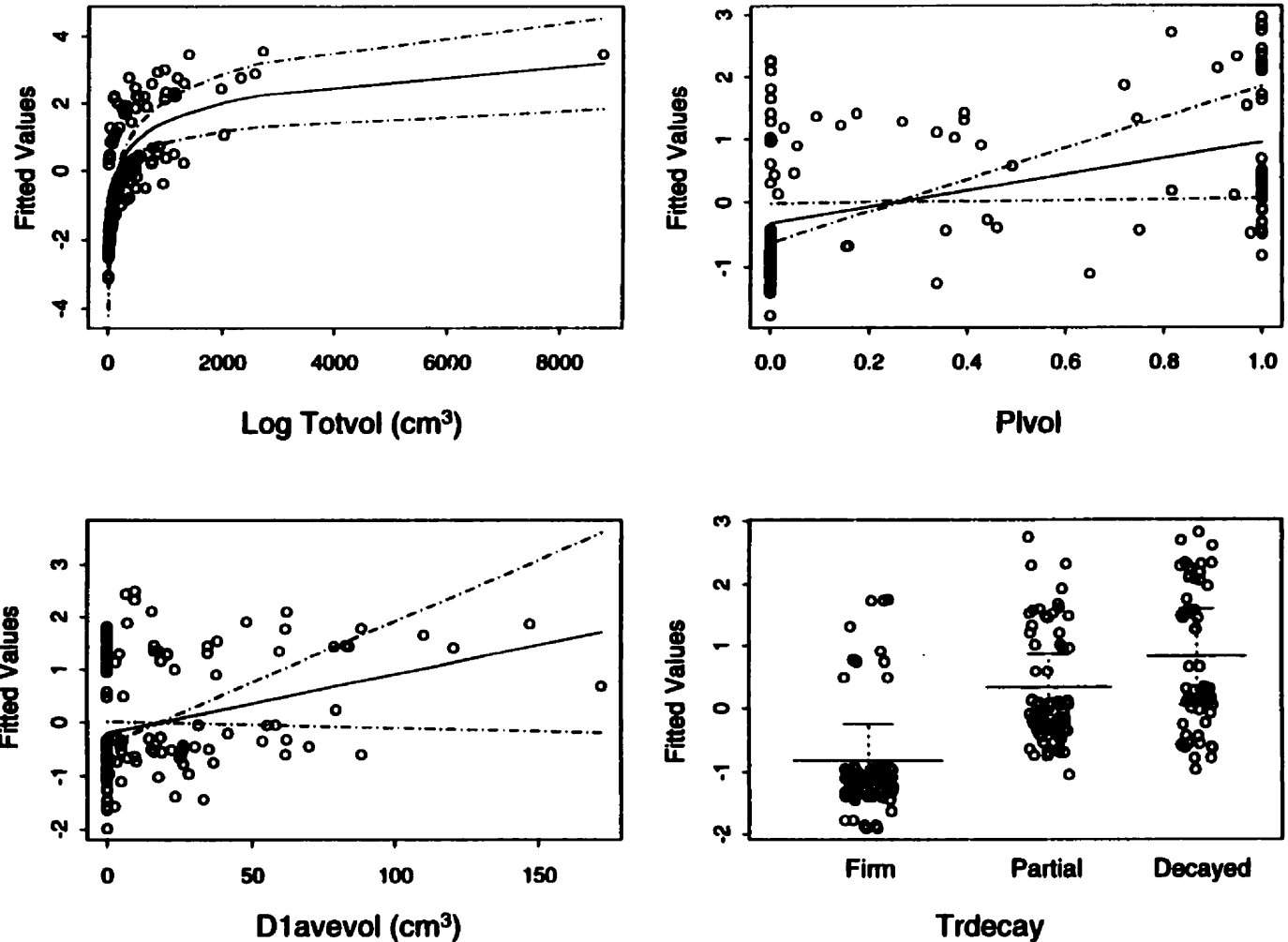
Figure 1-5. Plots of the contribution of each variable to the model describing the incidence of *B. cornutus* for all sites and years at the log scale (dashed lines = approximate 95% pointwise confidence intervals, open circles = partial residuals). Lateral variation in plots of factors reflects the number of observations in each category.
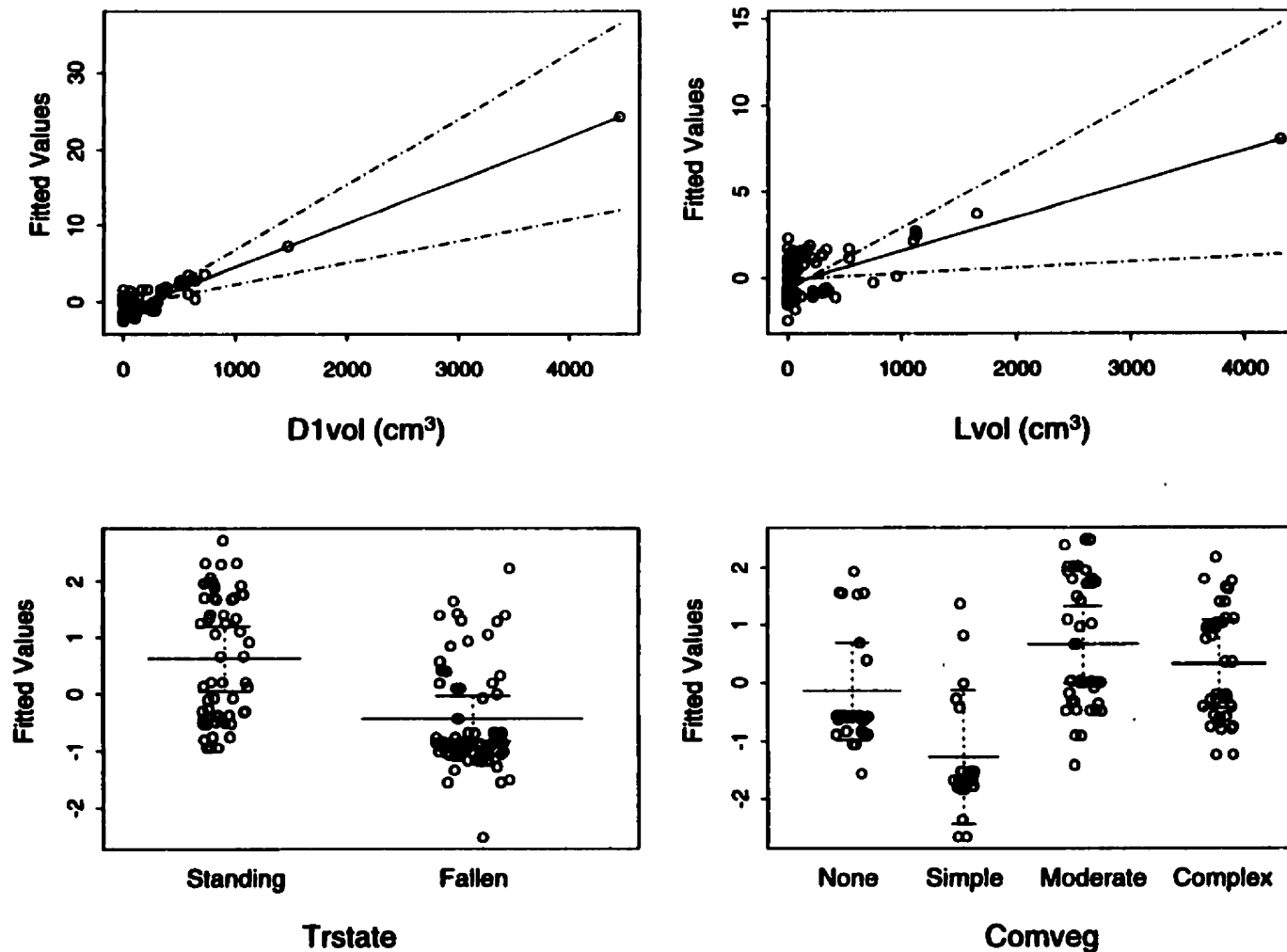
Figure 1-6. Plots of the contribution of each variable to the model describing the incidence of *B. cornutus* for all sites and years at the patch scale (dashed lines = approximate 95% pointwise confidence intervals, open circles = partial residuals). Lateral variation in plots of factors reflects the number of observations in each category.
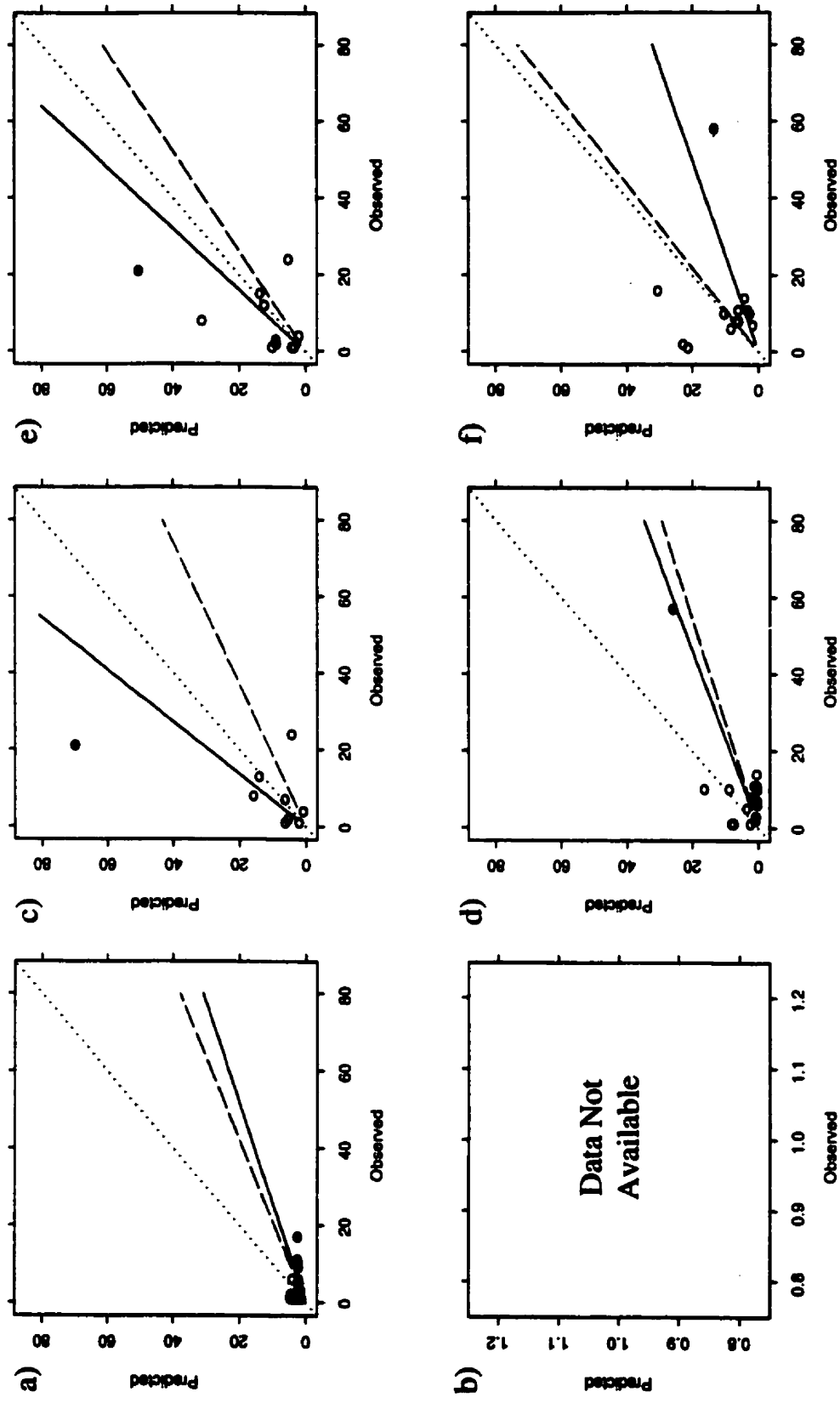
Figure 1-7. Plots of the predicted and observed count of *B. cornutus* individuals for the sporophore scale: a)1996 and b) 1997 (no model), log scale: c)1996 and d) 1997, and patch scale: e) 1996 and f) 1997. Models that best describe the counts in the Reservoir site were used to predict data at the 101 site. Dotted line = perfect prediction, solid line = best fit, dashed line = best fit with outlier (filled circle) removed.
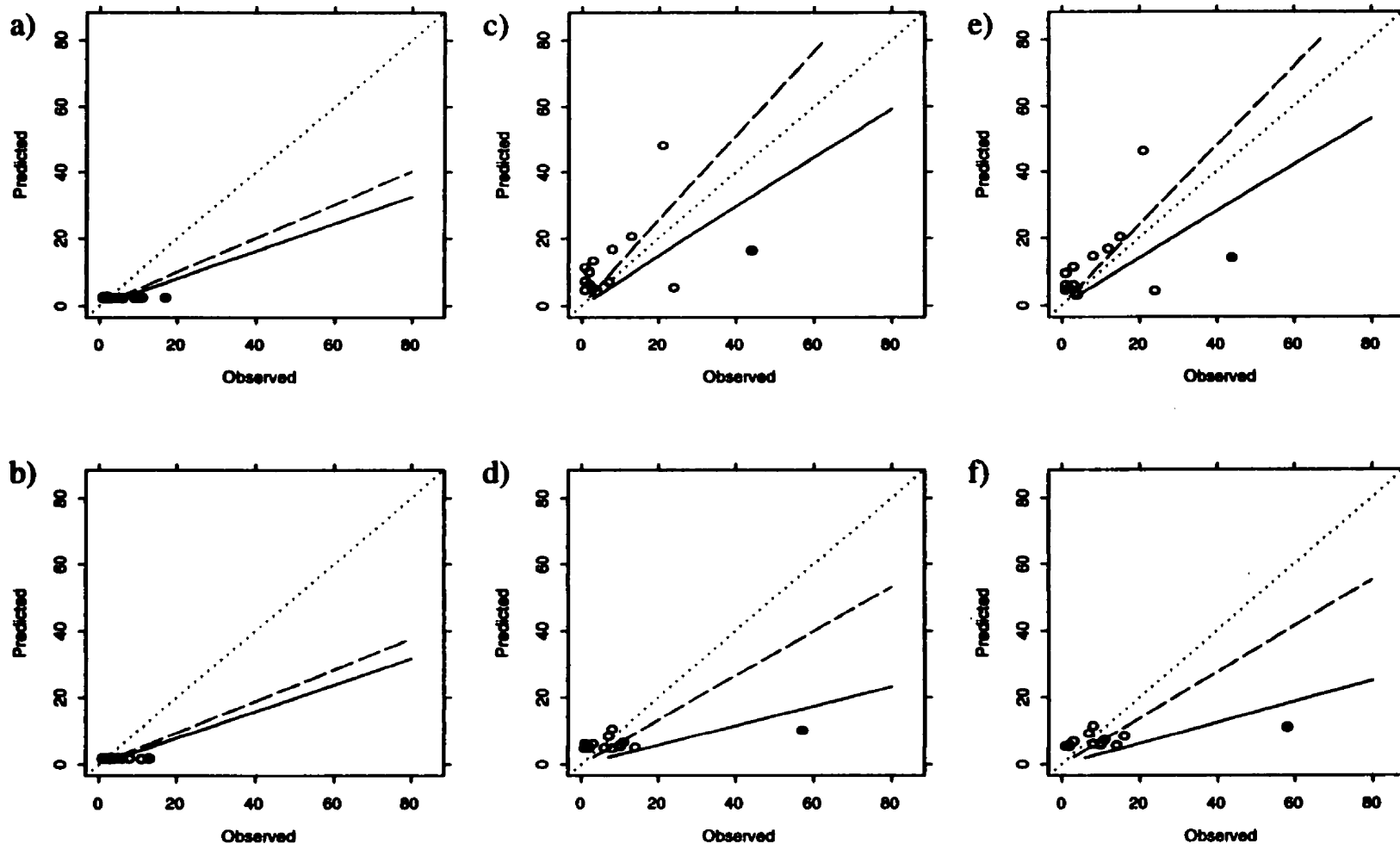
Figur 1-8. Plots of the predicted and observed count of *B. cornutus* individuals for the sporophore scale: a)1996 and b) 1997, log scale: c)1996 and d) 1997, and patch scale: e) 1996 and f) 1997. Models built for the Reservoir site that only include the term TOTVOL were used to predict data at the 101 site. Dotted line = perfect prediction, solid line = best fit, dashed line = best fit with outlier (filled circle) removed.
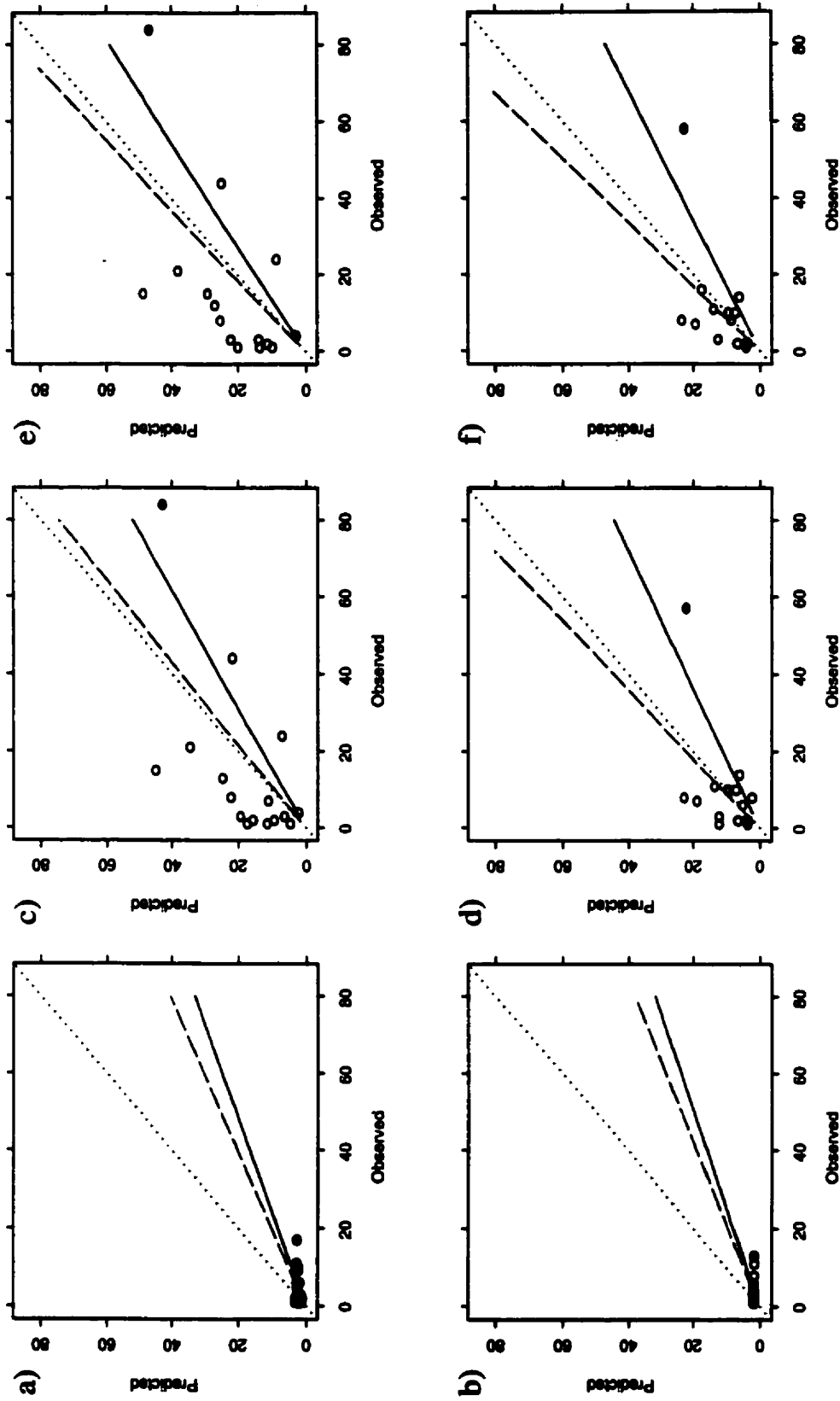
Figure 1-9. Plots of the predicted and observed counts of *B. cornutus* individuals for the sporophore scale: a)1996 and b) 1997, log scale: c)1996 and d) 1997, and patch scale: e) 1996 and f) 1997. Models built for the Reservoir site that only include the term log (TOTVOL) were used to predict data at the 101 site. Dotted line = perfect prediction, solid line = best fit, dashed line = best fit with outlier (filled circle) removed.
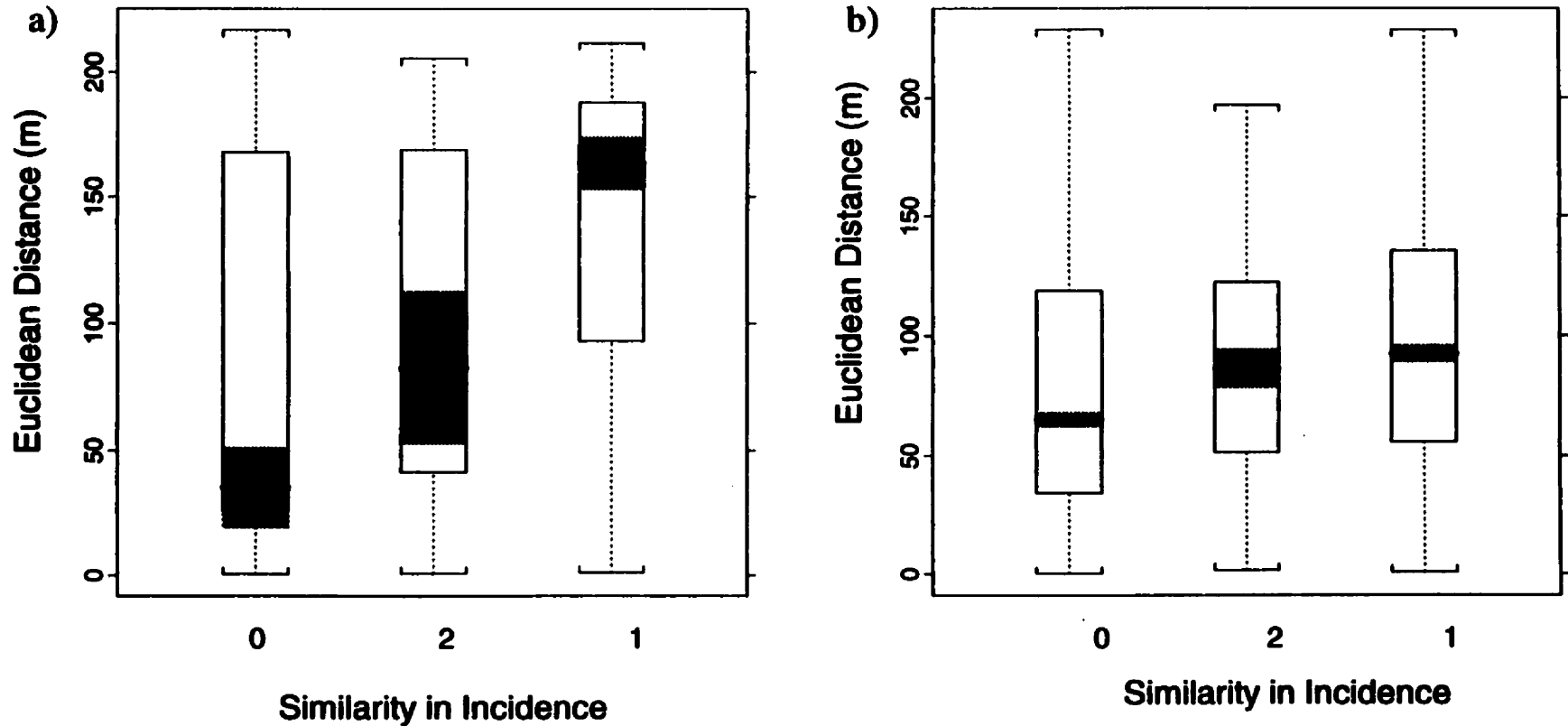
Figure 1-10. Boxplots showing the medians (black bar), 95% confidence intervals (shaded), inter-quartile ranges (box), ranges (whiskers), and outliers (bars) of the distance between pairs of habitat units in each category of similarity in *B. cornutus* incidence at the log scale a) Reservoir site in 1996, and b) the 101 site in 1997 (0 = both unoccupied, 2 = both occupied, 1 = one occupied the other not).
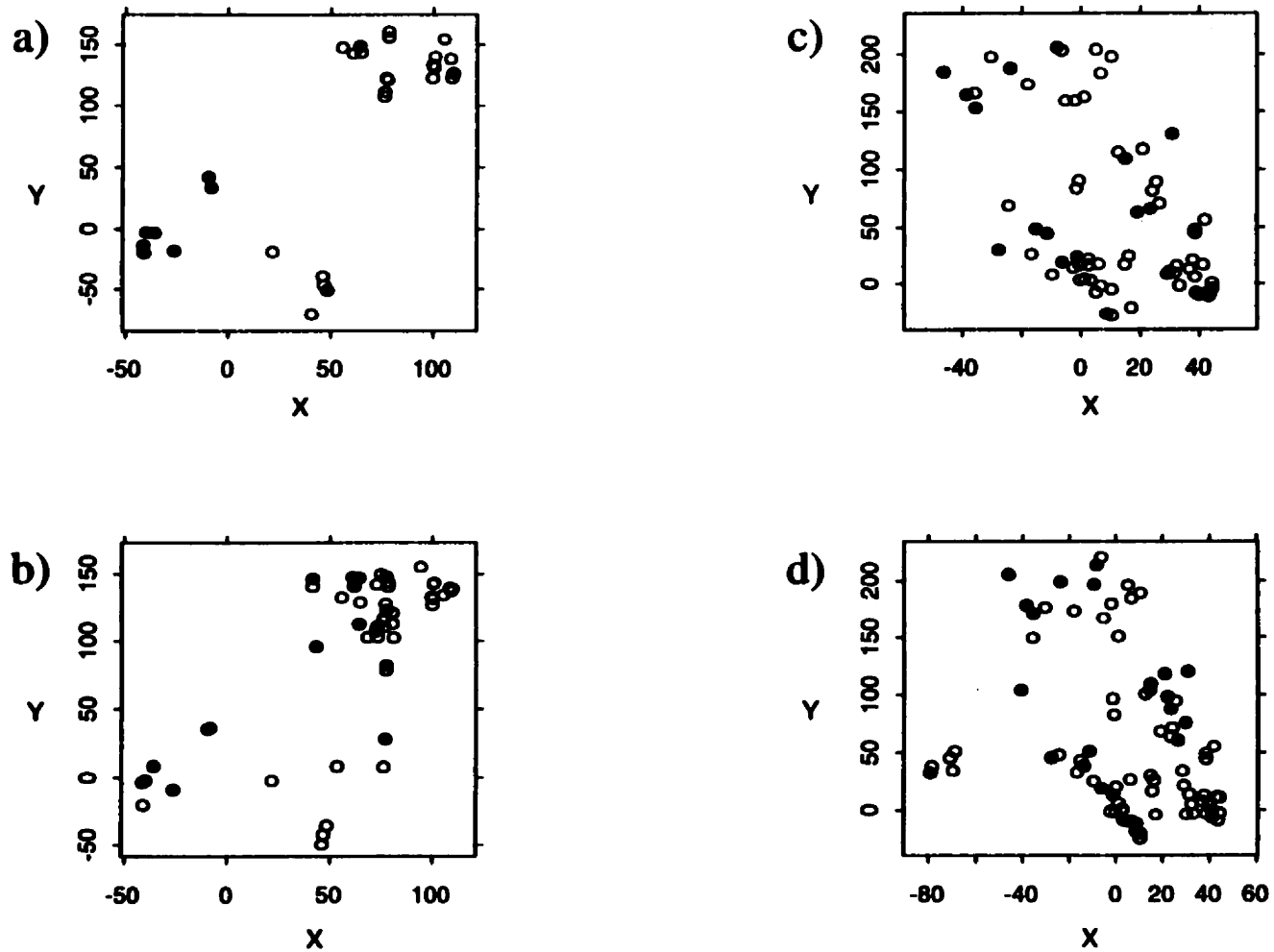
Figure 1-11. Plots of habitat locations at the log scale for the Reservoir site a) 1996, b) 1997, and the 101 site c) 1996, d) 1997 (open circles = unoccupied habitat, closed circles = occupied habitat). Points are jittered for broad patterns to be apparent. Consequently, the same habitat unit may appear to be in a different location each year.
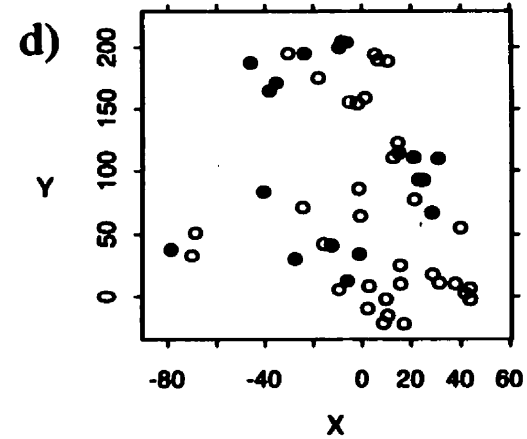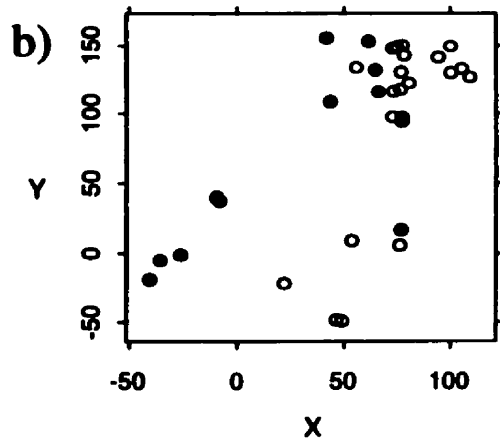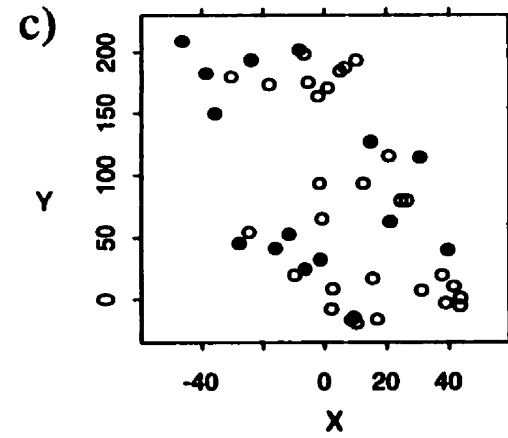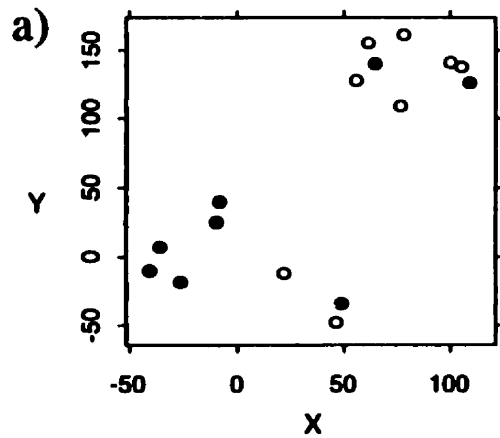
Figure 1-12. Plots of habitat locations at the patch scale for the Reservoir site a) 1996, b) 1997, and the 101 site c) 1996, d) 1997 (open circles = unoccupied habitat, closed circles = occupied habitat). Points are jittered for broad patterns to be apparent. Consequently, the same habitat may appear to be in a different location each year.
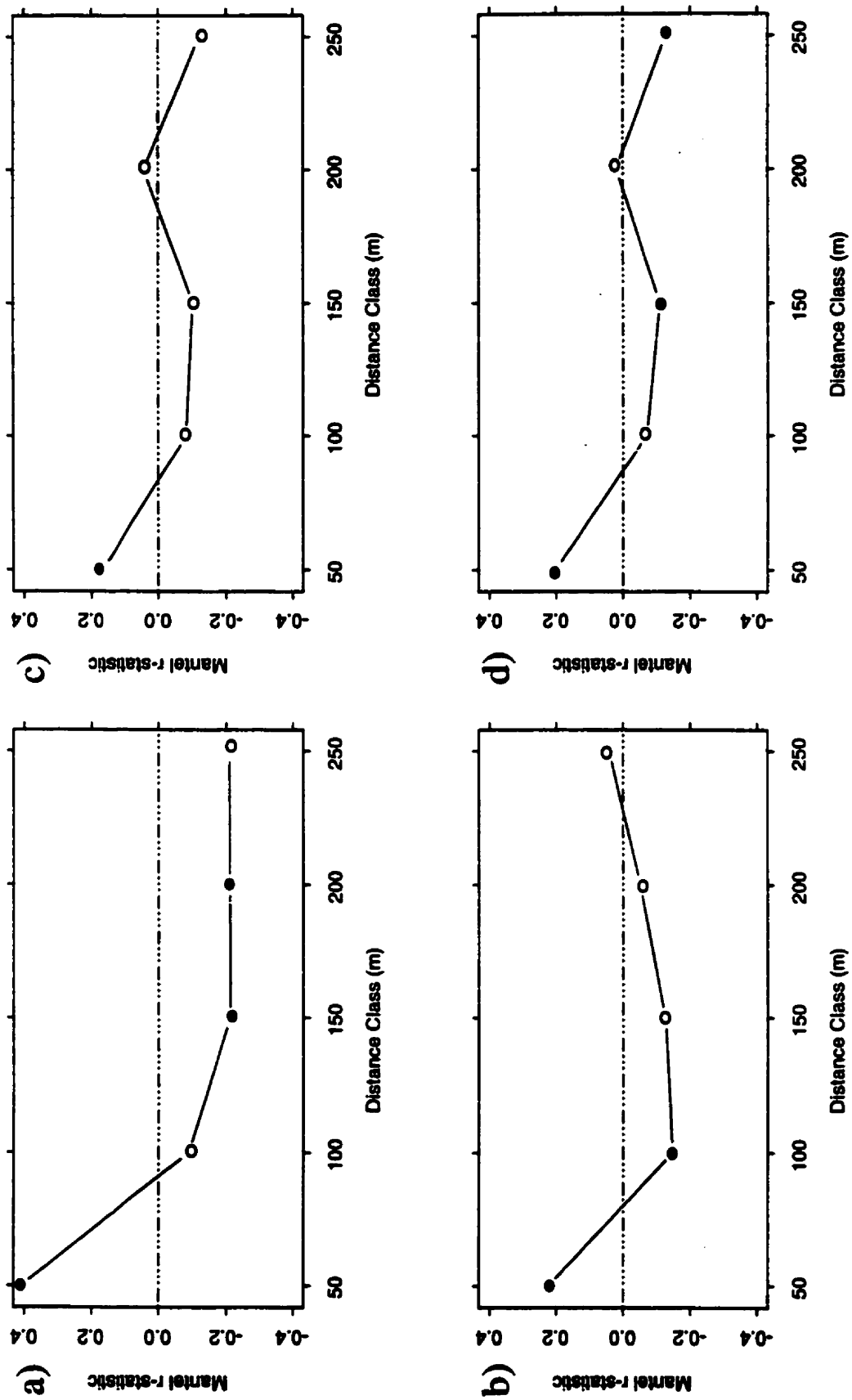
Figure 1-13. Mantel correlograms for of the incidence of *B. cornutus* at the log scale for the Reservoir site a) 1996, b) 1997, and 101 site c) 1996, d) 1997 (closed circles = significant at the progressive Bonferonni corrected alpha level).
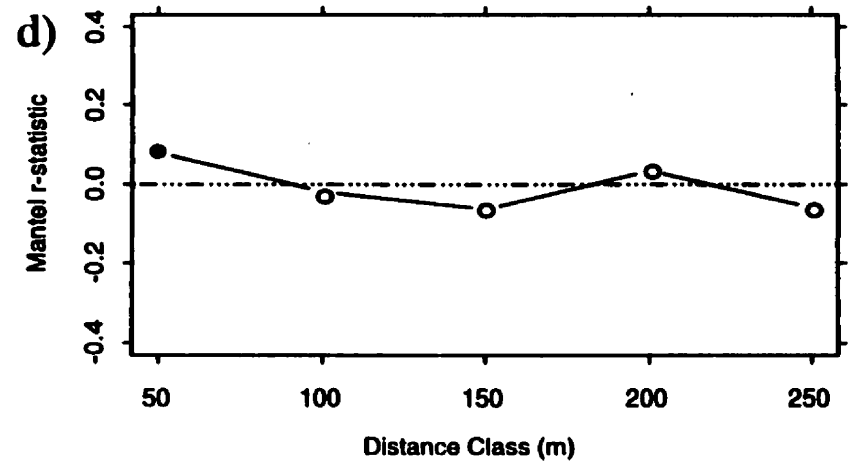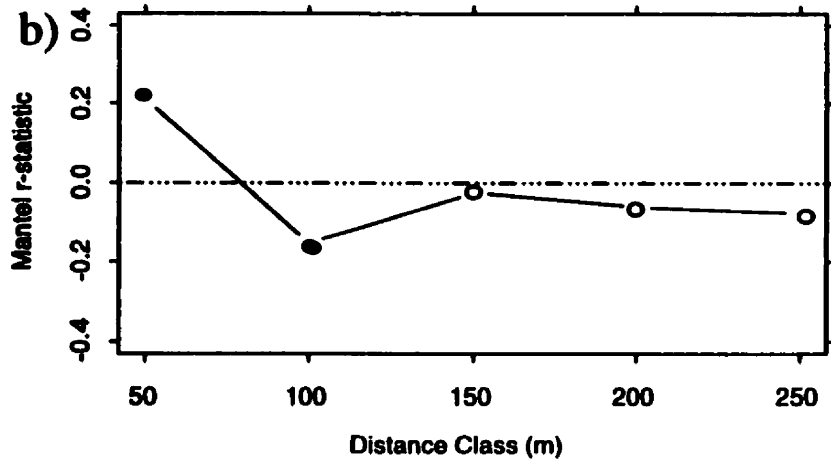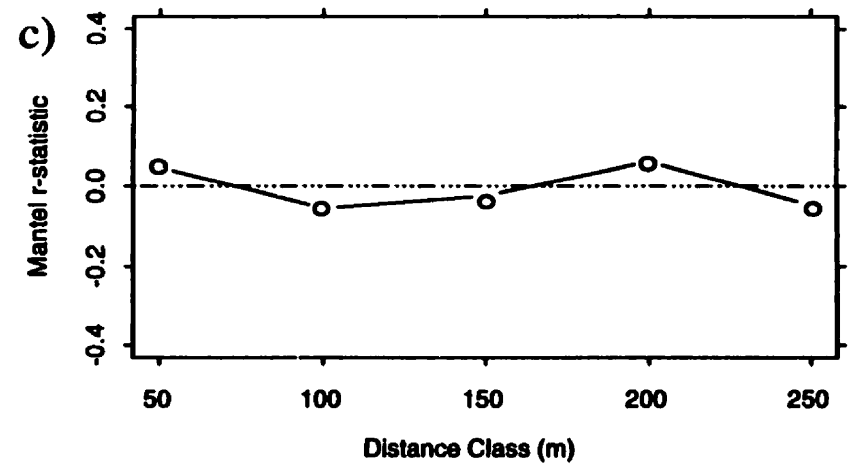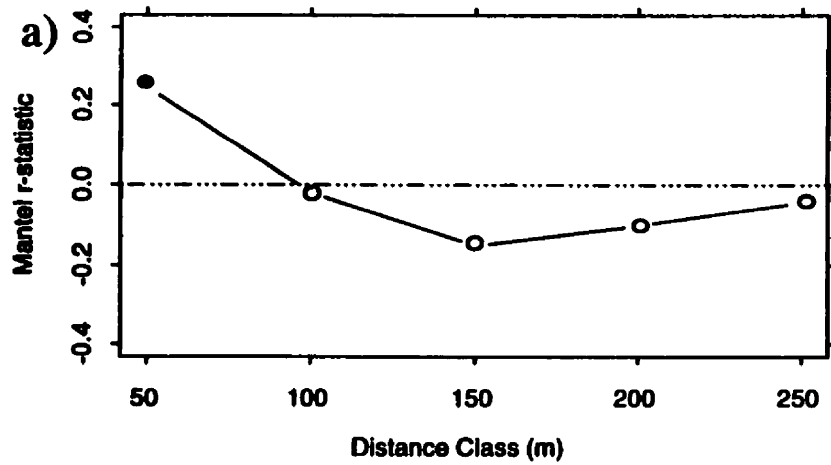
Figure 1-14. Mantel correlograms of the incidence of *B. cornutus* at the patch scale for the Reservoir site a) 1996, b) 1997, and 101 site c) 1996, d) 1997 (closed circles = significant at the progressive Bonferonni corrected alpha level).

References

Addicott, J.F., Aho J.M., Antolin M.F., Padilla D.K., Richardson J.S. and D.A. Soluk 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49: 340-346.

Agresti, A. 1990. Categorical data analysis. John Wiley and Sons, Toronto.

Barlow, J. 1996. Populations attributes, habitat characteristics, and spatial dynamics of the forked fungus beetle, *Bolitotherus cornutus* (Panzer). Hon.B.Sc. Thesis. Acadia University, Nova Scotia.

Brown, J.H. and A. Kodric-Brown 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

Brown, L. and L.L. Rockwood 1986. On the dilemma of horns. Natural History 7: 55-61.

Cliff, A.D. and J.K. Ord 1981. Spatial Processes: models and applications. Pion, London.

Conner, J. 1989. Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 43: 1378-1386.

Crawley, M.J. 1993. GLIM for ecologists. Blackwell Scientific, Boston.

Cuadrado, M. 1997. Why are migrant robins (*Erithacus rubecula*) territorial in winter? The importance of the anti-predatory behaviour. Ethology Ecology and Evolution 9: 77-88.

Dover, J. W. 1996. Factors affecting the distribution of satyrid butterflies on arable farmland. Journal of Applied Ecology 33: 723-734.

Gehrken, U., Strømme, A., Lundheim, R. and K.E. Zachariassen 1991. Inoculative freezing in overwintering tenebrionid beetle, *Bolitophagus reticulatus* Panz. Journal of Insect Physiology 37: 683-687.

Gilpin, M. 1987. Spatial structure and population vulnerability. In: Soulé, M.E. (ed.), Viable populations for conservation. Cambridge Press, Cambridge.

Graves, R.C. 1960. Ecological observations on the insects and other inhabitants of woody shelf fungi (Basidiomycetes: Polyporaceae) in the Chicago area. Annals of the Entomological Society of America 53: 61-78.

Hanski, I. 1994. Spatial scale, patchiness and population dynamics on land. Philosophical Transactions of the Royal Society of London B-Biological Sciences 43: 19-25.

Hanski, I. and C.D. Thomas 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biological Conservation 68: 167-180.

Heatwole, H. and A. Heatwole 1968. Movements, host-fungus preferences, and longevity of *Bolitotherus cornutus*. Annals of the Entomological Society of America 61: 18-23.

Kehler, D. and S. Bondrup-Nielsen 1999. Effects of isolation on the occurrence of a fungivorous forest beetle (*Bolitotherus cornutus* Panzer) at different spatial scales in fragmented and continuous forests. Oikos 84: 35-43.

Kindvall, O. and I. Ahlén 1992. Geometrical factors and metapopulation dynamics of the bush cricket, *Metrioptera bicolor* Philippi (Orthoptera: Tettigoniidae). Conservation Biology 6: 520-529.

Kotliar, N.B. and J.A. Wiens 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Legendre, P. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology 74: 1659-1673.

Legendre, P. and M. Fortin 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107-138.

Legendre, P. and L. Legendre 1998. Numerical ecology. 2nd ed. Elsevier, New York.

Liles, M.P. 1956. A study of the life history of the forked fungus beetle, *Bolitotherus cornutus* (Panzer). The Ohio Journal of Science 56: 329-337.

Lucherini, M., S. Lovari and G. Crema 1995. Habitat use and ranging behavior of the red fox (*Vulpes vulpes*) in a Mediterranean rural area: Is shelter availability a key factor? Journal of Zoology 237: 577-591.

Lundrigan, T.A. 1997. Movement rates as an indicator of dispersal potential in the forked fungus beetle, *Bolitotherus cornutus*. Hon.B.Sc. thesis, Acadia University, Wolfville, Nova Scotia.

Matthewman, W.G. and D.P. Pielou 1971. Arthropods inhabiting the sporophores of *Fomes fomentarius* (Polyporaceae) in Gatineau Park, Quebec. The Canadian Entomologist 103: 775-847.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209-220.

MathSoft 1998. S-PLUS 4 Guide to statistics. Data Analysis Products Division, MathSoft, Seattle.

McCullagh, P. and J.A. Nedler 1989. Generalized linear models. 2nd ed. Chapman and Hall, London.

Midtgaard, F., Rukke, B.A. and A. Sverdrup-Thygeson 1996. Habitat selection of *Bolitophagus reticulatus* (L.) (Coleoptera, Tenebrionidae) inhabiting tinder fungus (*Fomes fomentarius*) in three boreal forest areas. In: Midtgaard, F. (ed.) The significance of fragmentation of boreal forest for the occurrence of selected Coleoptera. Ph.D. thesis. University of Oslo, Norway.

Myers, R.H. and D.C. Montgomery 1997. A tutorial on generalized linear-models. Journal of Quality Technology 29: 274-291.

Nilsson, T. 1997a. Survival and habitat preferences of *Bolitophagus reticulatus*. Ecological Entomology 22: 82-89.

Nilsson, T. 1997b. Metapopulation dynamics in the black tinder fungus beetle, *Bolitophagus reticulatus*. In: Nilsson, T. Spatial population dynamics of the black tinder fungus beetle, *Bolitophagus reticulatus*. Ph.D. thesis. Uppsala University, Sweden.

Pace, A.E. 1967. Life history and behavior of a fungus beetle, *Bolitotherus cornutus* (Tenebrionidae). Occasional Papers of the Museum of Zoology, University of Michigan 653: 1-15.

Rossi, R.E., Mulla, D.J., Journel, A.G. and E.H. Franz 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62: 277-314.

Rukke, B.A. and F. Midtgaard 1998. The importance of scale and spatial variables for the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae) in a fragmented forest. Ecography 21: 561-572.

Schaffer, M.L. 1987. Minimum viable populations: coping with uncertainty. In: Soulé, M.E. (ed.) Viable populations for conservation. Cambridge University Press, Cambridge.

Schoener, T.W. and D.A. Spiller 1987. High population persistence in a system with high turnover. Nature 330: 474-477.

Schwarze, F. 1994. Wood-rotting fungi: *Fomes fomentarius* (L.:Fr)Fr. Mycologist 8: 32-34.

Sokal, R.R. and N.L. Oden 1978. Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. Biological Journal of the Linnean Society 10: 229-249.

Sokal, R.R., Oden, N.L. and B.A. Thomson 1998. Local spatial autocorrelation in biological variables. Biological Journal of the Linnean Society 65: 41-62.

Sverdrup-Thygeson, A. and F. Midtgaard 1998. Fungus-infected trees as islands in boreal forest: spatial distribution of the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae). Ecoscience 5: 486-493.

Taborsky, B. and M. Taborsky 1995. Habitat use and selectivity by the brown kiwi (*Apteryx australis mantelli*) in a patchy environment. Auk 112: 680-689.

Teichert, S. 1999. First reported flight of *Bolitotherus cornutus* (Panzer) (Coleoptera: Tenebrionidae). The Coleopterists Bulletin 53: *in press*.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

Wiens, J.A., Stenseth, N.C, Van Horne, B. and R.A. Ims 1993. Ecological mechanisms and landscape ecology. Oikos 66(3): 369-380.

Whitlock, M.C. 1992. Nonequilibrium population structure in forked fungus beetles: extinction, colonization, and the genetic variance among populations. The American Naturalist 139: 952-970.

Whitlock, M.C. 1994. Fission and the genetic variance among populations: the changing demography of forked fungus beetle populations. The American Naturalist 143: 820-829.

Chapter 2. The influence of sporophore decay on habitat use by the forked fungus beetle, *Bolitotherus cornutus* Panzer: A field experiment.

Introduction

Fundamental to understanding any organism's ecology is recognizing what it perceives as suitable or preferred habitat. The suitability of habitat patches can vary because they differ in their composition (*e.g.* quality of food, shelter, or microclimate). Differences in habitat composition can be viewed in terms of costs and benefits, where heterogeneity arises due to differences in physiological stress, food availability, predation risk, mating probability *etc.*, among elements (Wiens 1995; Wiens *et al.* 1993). Their choice of a particular habitat patch is assumed to reflect responses that are molded by natural selection. Therefore, a patch that is optimal maximizes an individual's fitness relative to the costs of that individual living and breeding there.

There are a variety of methods for measuring habitat suitability. For example, the frequency of individuals in a particular habitat (independent of the proportion of that habitat available) can indicate that it contains some preferred attribute (Haila *et al.* 1996). For insects that lay their eggs and subsequently provide no parental care for their offspring, the location and number of eggs laid by a female should reflect that there are attributes of that habitat which make it favourable for the development and survival of her offspring (Carr *et al.* 1998). The forked fungus beetle (*Bolitotherus cornutus* Panzer) is such an insect. Individuals complete their entire life cycle on the perennial fruiting bodies of fungi in the genera *Fomes* and *Ganoderma*. They use this resource for feeding, mating, egg-laying and to develop from larva to adult (Liles 1956; Pace 1967; Conner

1988, 1989). As well as the presence or absence of its host fungus, several other aspects of the environment may be important to this beetle. Their microclimate could be influenced by the position of the wood that the sporophores are growing on, properties of the wood which influence growth of the sporophores may be important such as the tree species, amount or decomposition of wood. There are properties of the wood which may also be directly important to the beetle such as the number of hiding places it provides.

In a study of the forked fungus beetle in its natural habitat, characteristics of the fungus appeared to play a primary role in the incidence and the relative numbers of individuals observed at patches (Chapter 1). Specifically, beetle use decreased with the decay of the sporophores. Live and dead but intact sporophores had a higher incidence of use, and were used by more individuals than decayed sporophores. Kehler and Bondrup-Nielsen (1999) also found that the beetle's use of their habitat was related to the state (living or dead) of a sporophore.

Sporophore decay may affect the nutritional value of sporophores (Heatwole and Heatwole 1968) for both adults and larvae, or reflect future duration as a food resource. Females would be expected to lay eggs on sporophores where the chance for survival of their offspring is the highest. Decay level of the sporophore may also influence use by adults since poor nutrition could constrain investment in reproduction and hence decrease fitness. Live sporophores might be preferred if they have higher nutritional value than dead sporophores. They may also be preferred for oviposition since they are still actively growing, and hence could provide a more long-term food resource for larvae.

Using an experimental approach, this study more closely examines the influence of sporophore decay on beetle's habitat use. In a field experiment I presented pairs of adult forked fungus beetles sporophore combinations of varying decay levels. I monitored the location and number of eggs laid to determine if and how sporophore decay was related to its quality. In another field experiment, I presented adult beetles with 3 sporophores that differed in their level of decay, and that were attached to logs. To determine how sporophore decay might be related to its quality for adult beetles, I counted the number and location of males and females during the night.

Methods

Study Organism

In Nova Scotia, the primary source of food for the forked fungus beetle is *Fomes fomentarius*, but *Ganoderma applanatum* and *Fomitopsis pinicola* are also used (pers. obs.). These beetles are most active at night, but may be found in the day feeding on the underside of sporophores, within crevices of bark, or mating on the sporophores or the bark of the trees. Mating and egg-laying occur throughout the summer; eggs are laid singly on the surface of the sporophores and covered with feces (Liles 1956), and young feed and develop within the sporophore. Both larvae and adults overwinter within the sporophore, but some adults overwinter under the bark of the trees (Pace 1967).

The host fungi invade decaying and primarily deciduous trees (Schwarze 1994), and their sporophores can survive for more than 10 years (Graves 1960). Since both the

beetle and the larvae feed on the tissue of the sporophore and cause extensive tunneling, the sporophores are eventually killed by the beetles (Matthewman and Pielou 1971).

Field Collections

Forked fungus beetles were collected from three areas in the Gaspereau Valley, Nova Scotia (45°5'N, 64°25'W), between 11 June and 26 June, 1997. Each beetle was uniquely marked with up to five dots of Testor's non-metallic paint, sexed, and had its body length and horn size (males only), measured to the nearest 0.1 mm using hand-held calipers. Approximately 200 collected beetles were housed in a glass terrarium measuring 50 x 25 x 36 cm, which was stored indoors and exposed to natural daylight. The lid of the terrarium was made of two thirds Plexiglas and one third window screening. The habitat provided to the beetles consisted of moss, a small birch log, and approximately 15 sporophores of *F. fomentarius* that varied in size, state (dead or alive) and level of decomposition (intact to very decomposed). The contents were kept moist by spraying them with a fine mist of water when necessary. Living conditions were much more crowded than in their natural environment.

During the same time period, logs of paper birch (*Betula papyrifera*) supporting sporophores were cut into smaller sections. The sections were of similar length (approximately 40 cm), diameter (approximately 20 cm) and decay level, and each section was cut so that there was a single sporophore attached to it. These sections were also chosen so that each supported a similar sized sporophore. In some cases, it was not always possible to cut sections of log with similar diameter, so to standardize the volume

of wood to a given section, those with greater girth were cut shorter than those with the average diameter, and sections with smaller girth were cut longer. In total, 63 sections of logs were cut: 21 supporting a sporophore which was alive (L), 21 supporting a dead and intact sporophore (DI) and 21 supporting a dead and decomposed sporophore (DD). Sporophores were classified as alive if they were white to off-white in colour and/or if they were producing sporophores. Sporophores were classified as dead if they were grey in colour and were not producing sporophores. A dead sporophore was intact if a very dense sound was produced by rapping ones knuckles on its surface. Intact sporophores appeared as solid as a newly cut piece of wood. Decayed sporophores usually had one or more emergence holes indicating that some portion of their context was hollowed through use by the beetle, or lacking emergence holes, was degraded by the weather or through infection by other fungi or molds. Collected beetles and logs were used for the oviposition and nightly activity experiments described below.

Oviposition Experiment

Twenty-one enclosures were constructed measuring 45.7 x 45.7 x 30.5 cm and covered with window screening, such that logs with sporophores and beetles could be put in, but beetles could not escape. The enclosures were placed on the ground in the forest under a large hemlock tree (*Tsuga canadensis*), and arranged so that they were separated by about a meter, and were all within the shade of the tree as much as possible. Two beetles (male and female), two logs and a handful of moss were placed within each

enclosure. Seven had both a L and a DI log, 7 had a L and DD log, and 7 had a DI and a DD log.

The experiment was set up on the afternoon of 8 July 1997, and enclosures were monitored daily for evidence of egg-laying until 8 August 1997. When a newly laid egg was found on a sporophore, a dot of permanent black marker was placed beside it so that it would not be confused with eggs laid in the future. The date, the type of sporophore an egg was laid on, and the enclosure that the beetle was in, were recorded.

Nightly Activity Experiment

Seven triangular arenas measuring 123 x 123 x 123 x 65 cm were built under the forest canopy such that beetles could not escape, using wooden stakes, heavy translucent polyethylene film for the sides, and window screening for the top. The arenas were spaced approximately 5 m from one another. Three logs (a L log, a DI log and a DD log), 10 beetles (5 males and 5 females) and a handful of moss were placed in each arena. The experiment was set up in the early evening of 21 July 1997, by placing the logs near each of the three corners of the arena, the moss in the centre and the beetles on top of the moss. Also, before the beetles were put into the arenas, each was marked with fluorescent powder on the distal end of their elytra. Males were powdered blue, and females were powdered pink.

Monitoring began that night by recording the number of males and females on each log in each arena. The beetles were located using a hand-held, long-wave ultraviolet lamp (VWR Scientific Inc., San Gabriel, CA). The arenas were checked four times at

approximately 2100 hr., 0100 hr., 0500 hr. and 0900 hr., for the next three days. Not all of the 10 beetles in each arena used the logs, and since beetles were readily found when they were on a log, the remainder of the beetles was assumed to be on the ground or in the moss. Also, the position of the beetles was noted; whether they were on the bark or the sporophore of the log.

Data Analysis

Oviposition Experiment

To determine which sporophore type the beetles chose for oviposition, the difference in the number of eggs laid between pairs in each sporophore combination was summed over the 7 enclosures. A sign test was performed on these differences to determine whether there was significantly more positive values than negative ones throughout the course of the experiment. Since the difference in the number of eggs was calculated daily, time effects such as weather were controlled for. This analysis was performed for each sporophore combination.

To determine whether egg-laying on the sporophore types differed through time, the vector of differences for each combination of pairs of sporophores was regressed against time. For example, a significant positive slope for the L-DI combination would indicate that the beetles oviposited first on the L sporophores and then later on the DI sporophores. A slope of 0, would indicate no change in egg-laying preference with time.

To determine whether the forked fungus beetle's egg-laying behaviour was influenced by the habitat they were in, the second step in the analysis compared the

number and laying time of eggs among each sporophore combination (*i.e.* L-DI vs. L-DD vs. DI-DD). The total number of eggs laid for each combination of pairs during each of four time periods was summed (12 July-18 July, 19 July-25 July, 26 July-1 August, 1 August-8 August). Using this information a log-linear regression model was built using the count of eggs laid as the response variable, and (sporophore) combination, beetles nested in combination, and time as the explanatory variables. The model was built to determine whether time or habitat (sporophore combination) influenced the number of eggs laid, and whether the timing of egg-laying was different among combinations (interaction). The nested variable 'beetles' was included in the model to control for variation due only to the behaviour of beetle pairs within the seven enclosures of each combination. Once this variation was taken into account, the influence of time and sporophore combination on egg laying was assessed. The fit of the model was assessed by examining plots of the deviance residuals vs. fitted values (checking for random scatter of the points), and quantile plots of the Pearson's residuals. The parameter estimates and their standard deviations were also examined for unusually large values, and the t-value for each coefficient was checked for significance. The likelihood ratio-test was chosen over the t-test when a discrepancy arose. Also, the dispersion parameter ($\varnothing$), was calculated for each model to determine whether the response followed the assumption that the variance to mean ratio equaled 1.

Nightly Activity Experiment

Nightly activity was analyzed with the goal of determining how sporophore state and decay influenced beetle use (any of the following: feeding, mating, egg-laying or resting), whether use differed between the sexes, and whether sporophore types were used differently throughout the beetle's active period. Also, since observations included information about the beetles' positions on logs (sporophore or bark), the term position was included in the analysis to determine whether there were differences in beetles' locations between sexes, among the log types and through time. A log-linear regression model was built for these data using counts of the males and females on each log type, in each position, during each time period summed across the three nights, as the response. Arena, sex, position, log type and time were used as the explanatory variables. The arena term was used to account for the variation in log use due to underlying differences between the seven replicate arenas (or the beetle assemblages within). Once this variation was accounted for, the influence of log type, sex, position and time on the count of beetles was assessed. The fit of the model was assessed in the same manner as described for the model of oviposition preference.

Results

Oviposition Experiment

A total of 71 eggs was laid by only 16 of the 21 beetles during their month in the enclosures. All of the females in the 7 L-DI combinations, 5 of the females in 7 L-DD combinations and only 4 of the females in the 7 DI-DD combinations laid at least one egg

during the experiment. The number of eggs laid on the live sporophores was significantly higher than on both the DI and DD for the L-DI and L-DD combinations (Table 2-1). In the DI-DD combinations 9 eggs were laid on the dead/intact sporophores while none were laid on the dead/decayed sporophores. There was no relationship between the difference in eggs laid and time (the slope of this relationship is not significantly different from 0), indicating that the timing of egg-laying did not differ between sporophore types in any of the three types of sporophore combinations (Figure 2-1).

However, combining all the enclosures, the number of eggs laid decreased through time (Table 2-2, Figure 2-2). Also, the number of eggs laid in the three sporophore combinations differed significantly (Table 2-2), and there was a significant interaction indicating the number of eggs laid was different for each combination through time (Figure 2-3). The number of eggs laid during the first two time periods on L-DD combinations is lower than on the L-DIs. For the L-DI combinations the number of eggs laid was similarly high during the first two time periods, after which egg-laying decreased. Oviposition on the L-DD combinations increased in time period two, and then decreased in the third and fourth periods. The number of eggs laid in the first two periods was lowest on the DI-DD combinations, although unlike the other two enclosure types, the numbers laid increased slightly over the first three periods.

Nightly Activity Experiment

There was a significant effect of log type on location of beetles (Table 2-3). Males and females chose the same log types (Figure 2-4a), and all of the three log types

were used similarly through the night (Figure 2-4b). Logs supporting live sporophores were used most often, and logs supporting decayed sporophores were used least often.

Beetles were found significantly more often on the bark of the log compared to the sporophore (Table 2-3, Figure 2-5a). Although both the sexes were found more often on the bark, males used the sporophores more than females (Table 2-3, Figure 2-5b). There was a significant interaction between position and log type (Table 2-3). Although beetles were found most often on the bark of all log types, once on the sporophore, the use of live sporophores was the highest and beetles used dead/intact less than dead/decayed sporophores (Figure 2-5a).

There was a significant interaction between time and in which position on the log the beetles were found (Table 2-3), and this pattern seemed to be different for males than females since the three-way interaction of sex:time:position is close to significance. Generally, both sexes used the sporophores much less than the bark (Figure 2-6), and the most notable difference in this pattern is that at 0500 hr. when approximately the same number of males was found on the sporophore as on the bark (Figure 2-6b). The count of males on sporophores at 0500 hr. is much higher than at any other time.

Discussion

Sixteen of the 21 females oviposited, and 56% of the eggs were laid by only 6 of those females. Four of these 6 females were presented with the L-DI combination, the fifth was presented with L-DD, and the last female was presented with a DI-DD combination. Four of these females laid the maximum of 7 eggs (3 presented with the L-DI sporophore combination and the other with the L-DD combination). The reasons for

such variation in the data of this study may lie in the effect of the beetle's confinement, or be a result of the limited amount of resource they were provided with compared to what they would experience under natural conditions. Also, some of the male/female pairs simply may not have been compatible, which could explain why some females did not lay any eggs at all.

Females preferred to lay their eggs on live rather than dead and intact sporophores. As well, females preferred both live and dead/intact sporophores for egg-laying to decayed ones. That females rarely laid eggs on decayed sporophores is not surprising because they can provide little in the way of food for the larva that would develop therein. Initially, it was expected that females would lay their eggs on live sporophores since it is a resource which is still growing, and hence the food source that it provides would be more long-term than a dead sporophore.

One study seems to support the results observed here (Matthewman and Pielou 1971). Of 464 *Fomes fomentarius* collected and housed in the laboratory, adults emerged from 5 live sporophores while larvae (dissected from the sporophores) were found in 17 live sporophores. That adult beetles emerged from sporophores that were still alive at the time (Matthewman and Pielou 1971) is interesting considering observations from the field (Chapter 1). A log supporting predominantly live and dead, intact fungus had approximately 128 eggs laid on its sporophores. The following year, less than a dozen emergence holes were counted among them. This was observed for a number of live sporophores on other logs during the study, suggesting that although females are laying

their eggs on these sporophores, many of them do not successfully develop into adult beetles the year following hatching.

There are at least two scenarios which might explain these observations. Perhaps the forked fungus beetle sacrifices some potential offspring to colonize a patch of live and intact sporophores. Although some of their offspring may not survive, newly hatched larvae may contribute to death and decay of the fungus allowing it to be used later by both adults and future offspring. Mortality of the larvae may be due to defense mechanisms of the fungus. Considering adult beetles may breed for up to five years, the initial cost of a few eggs may be outweighed by the benefits of successful development of future young.

The second scenario is that there is conditional delayed development by the larvae of the forked fungus beetle. Pace (1967) observed that of 35 eggs laid on a *Ganoderma applanatum* sporophore, 15 larvae were found in it on 1 Nov. 1965. Of these, 2 larvae, were found to be alive and still in their fourth-instar in Oct. 1966. She suggested that although most overwintering larvae mature before fall, some may overwinter a second time either as larvae or adults before reproducing; larvae from eggs laid in early summer possibly do not mature until the following summer. Prolonged diapause is not uncommon in insects that use temporary unpredictable resources (see Hanski 1988 for a review). An oligophagous fungivore could solve the problem of year-to-year variability in resource availability by delaying the emergence of some of its offspring by one or more years (Hanski 1989). The forked fungus beetle larvae might delay stages of molting or pupation until conditions of the sporophore become more favourable (the sporophore is dead) for them to complete their development. This second scenario seems less likely

since first instar larvae have often been found dead near the egg cavity (Bondrup-Nielsen *pers. comm.*).

The number of eggs laid among the 3 sporophore combinations supports the results of egg-laying activity between pairs of sporophores differing in their decay. The enclosures that contained the least decayed sporophore combinations (L-DI), generally had the greatest number of eggs laid in them. As well, the timing of laying differed between sporophore combinations. Generally, the more decayed the sporophore combination was, the later the peak of egg-laying occurred. This might reflect females' preference; those provided with the most suitable sporophore combinations wasted no time and began laying right away (L-DI), whereas given less suitable combinations, the females waited longer (L-DD) and longer (DI-DD) before laying many of their eggs. Hence, females in the enclosures with the less suitable sporophores may have been waiting for better habitat to become available before investing their reproductive energies.

That females preferred to lay their eggs on live sporophores suggests that doing so increases their fitness. This may be due to an increase in reproductive success (*i.e.* enhanced survival of offspring, increasing the probability of passing on their genes to future generations), or it may be due to enhanced survival; their cost is a few eggs, and their reward is an optimal sporophore state (dead but intact) for future attempts at reproduction. Future studies should examine larval performance on sporophores at all levels of decay to determine what the ultimate benefits may be for females' choice of live sporophores for oviposition. As yet, there is no indication (even through casual

observation) of the relative success of eggs laid on dead and decayed sporophores compared to live ones.

Beetles in the nightly activity study spent the majority of their time on logs supporting live sporophores, less time on those with dead/intact, and the least amount of time on those with dead/decayed carps. This may be reflect the preference by females for live or intact dead sporophores for oviposition, or it may represent a food preference of the adults. In a related study of beetles in continuous forest, the incidence of the forked fungus beetle, decreased with the decay of the sporophores (Chapter 1). In Scandinavia, studies of *Bolitophagus reticulatus*, which has a similar life history to the forked fungus beetle, found higher incidence of trapped beetles at live sporophores (Nilsson 1997). In dissected specimens of *Fomes*, *B. reticulatus* was found more often in dead sporophores, although more individuals were counted in less decayed dead sporophores (Midtgaard *et al.* 1996).

More beetles were found on the bark of the logs than on the sporocarps. Although only information on mating was recorded, this suggests that they did not spend much of their active period feeding. Mating, traveling, or resting are possible activities that could be carried out on the bark of the log. Intensive field observations for studies of sexual selection by the forked fungus beetle have found that their level of activity during the night is high (Conner 1988, 1989), much of which was invested in mating activities. Mating can last 10 minutes to several hours (Conner 1988). It is likely then, that beetles in this experiment were traveling or at some stage of mating.

Males used sporophores slightly more than females during the night, and for both sexes their positions on the logs differed through the night. This difference is mostly due to the males' behaviour during the very early morning. At the 0500 hr. check of the arenas, similar numbers of males were found on both the bark and sporophore of the log. Based on nightly observations in the field, Pace (1967) suggested that males might be territorial, since a number of individuals were found repeatedly on the same sporophores in aggressive behaviours towards other males. Conner (1989), however, discounted this notion because he observed that both males and females roamed widely among fungi on a single tree. It is possible, however, that all sporophores might represent focal areas where males and females meet and aggressive behaviour ensues for access to the females. In this case, individual males might not stake out particular sporophores to defend, but roam among them searching for access to females. This patrolling behaviour has been described as an alternative to resource defense when hosts are easily found by both sexes and provide enough biomass in one clump to create concentrations of individuals (Lederhouse 1982). This situation is common for groups of forked fungus beetles on dead wood supporting sporophores. Patrolling behaviour has been observed for species of butterfly (Scott 1975; Hidaka and Yasmashita 1975).

This study experimentally examined the influence of the decay level of sporophores on the oviposition and nightly activity of the forked fungus beetle. Females exhibited a preference for laying their eggs on live sporophores, suggesting this attribute is important for describing the quality of habitat for their offspring. It is unclear, however, what benefits there may be for individuals arising from eggs laid on live

sporophores, or the ultimate benefit it may have on the fitness of a female that lays her eggs on live sporophores. The experiment of nightly activity indicated that adult beetles congregate near live and intact sporophores, suggesting they may represent higher quality habitat for beetles than dead and decayed sporophores. More research is needed to determine why this is a preferred feature, and what the long-term benefits might be for adults that associate with live sporophores.

This study has provided some insights into the small scale habitat features that are important for use by the forked fungus beetle. These results might form the basis for more detailed examinations of the direct influence of habitat quality on beetle fitness, or they may be incorporated into more large scales studies of beetle demography and of colonization and extinction dynamics for this system.

Table 2-1. The total and the mean (± SD) number of eggs laid by *B. cornutus* on each sporophore type in each sporophore combination, and the sign test p-values for the difference in eggs laid per day.

Enclosure Type	Sporophore Combination	Total Eggs	Mean Eggs (per day)	Standard Deviation	Sign Test P - value
type 1	L	31	1.12	1.67	0.02
	DI	7	0.25	0.58	
type 2	L	21	0.75	1.38	0.04
	DD	3	0.12	0.31	
type 3	DI	9	0.32	0.61	0.02
	DD	0	0.00	0.00	

Table 2-2. Analysis of deviance in the count of the eggs laid by *B. cornutus* on each sporophore combination (models were fit in the generalized linear modeling framework using a Poisson error distribution and a log link function).

Term	Df	Deviance	Residual Df	Residual Deviance	Pr(Chi)
NULL			83	135.33	
combination	2	19.26	81	116.08	0.0001
beetles	18	41.80	63	74.29	0.0012
time	3	19.21	60	55.08	0.0002
combination:time	6	14.80	54	40.30	0.0221

Table 2-3. Analysis of deviance in the count of *B. cornutus* observed in arenas summed across three days (models were fit in the generalized linear modeling framework using a Poisson error distribution and a log link function).

Term	Df	Deviance	Residual Df	Residual Deviance	Pr(Chi)
NULL			335	800.31	
arena	6	28.51	329	771.80	0.0001
time	3	6.04	326	765.76	0.1095
log type	2	131.18	324	634.58	0.0000
position	1	174.44	323	460.14	0.0000
sex	1	0.20	322	459.94	0.6515
arena:log type	12	110.24	310	349.69	0.0000
arena:position	6	36.15	304	313.54	0.0000
time:position	3	14.79	301	298.75	0.0020
time:sex	3	0.66	298	298.08	0.8815
log type:position	2	13.40	296	284.68	0.0012
sex:position	1	12.09	295	271.42	0.0003
arena:log type:position	12	47.66	283	223.76	0.0000
time:position:sex	3	6.78	280	216.98	0.0791
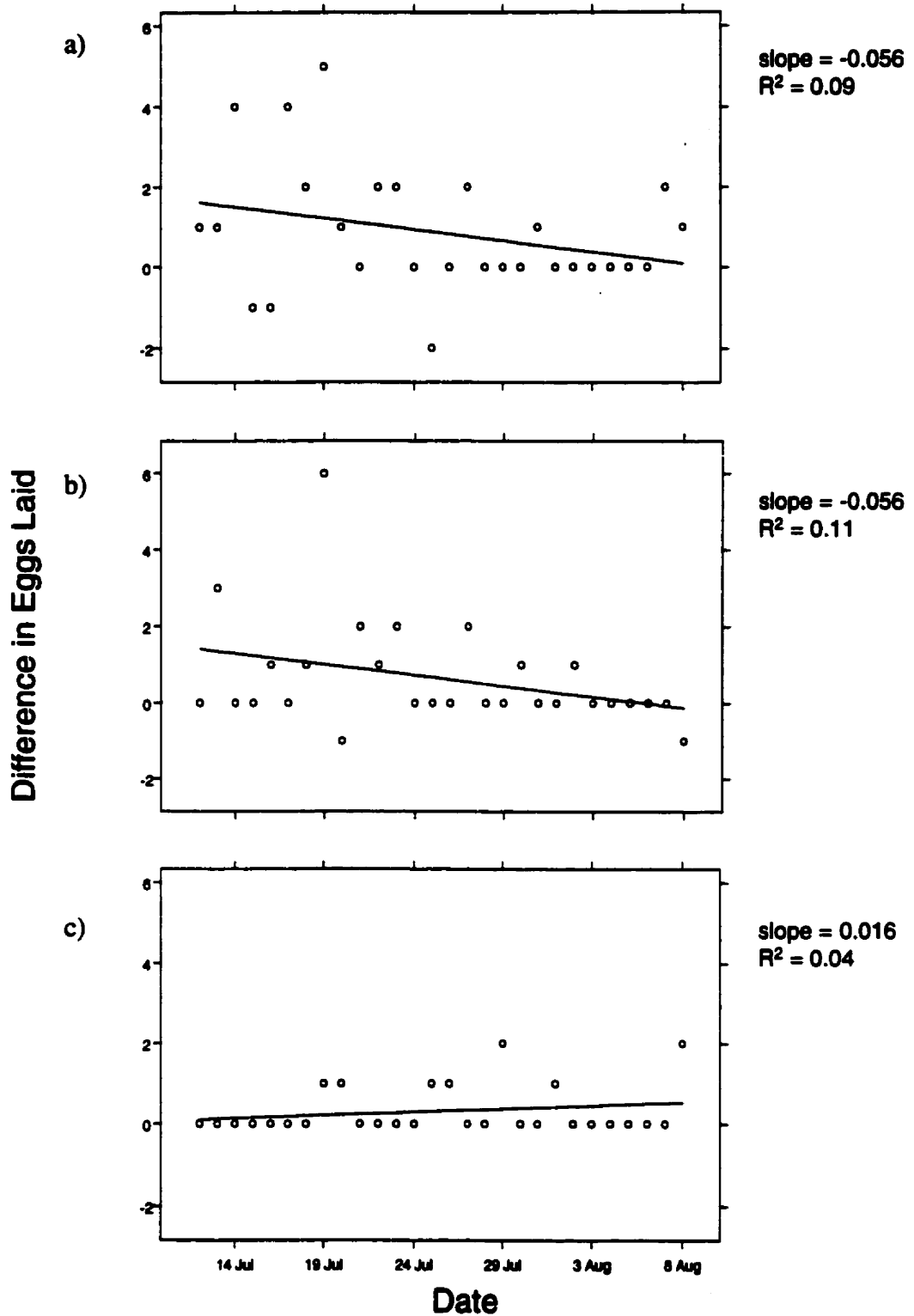
Figure 2-1. Plots of the differences in the sum of eggs laid by *B. cornutus* on each sporophore type, each day for the a)L-DI, b)L-DD and c)DI-DD combinations. Adjacent to each is the value of the slope (none are significant),and the coefficient of determination (R^2).
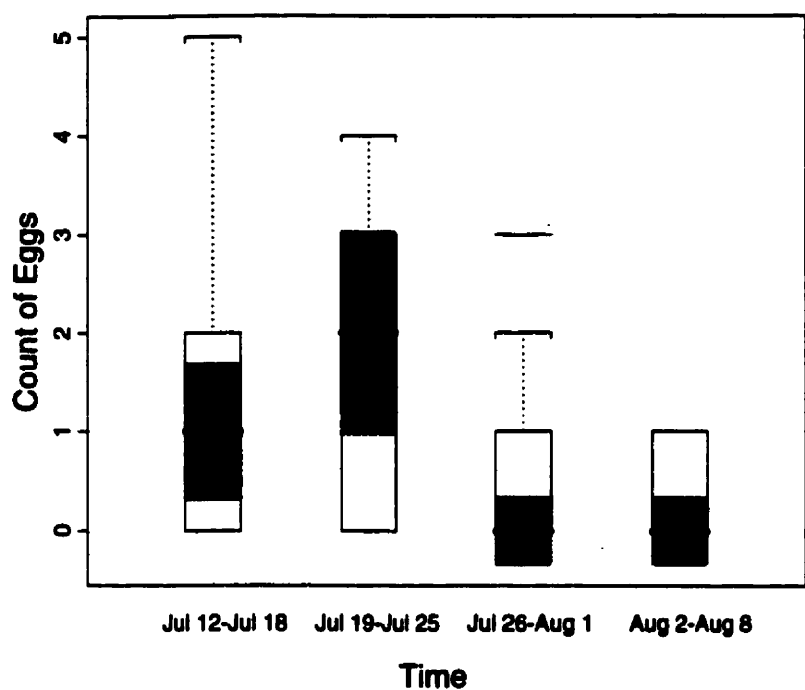
Figure 2-2. Boxplot showing the medians (black bar), 95% confidence intervals (shaded), inter-quartile ranges (box), ranges (whiskers), and outliers (bars), of the count of eggs laid by *B. cornutus* during the four time periods of the experiment.
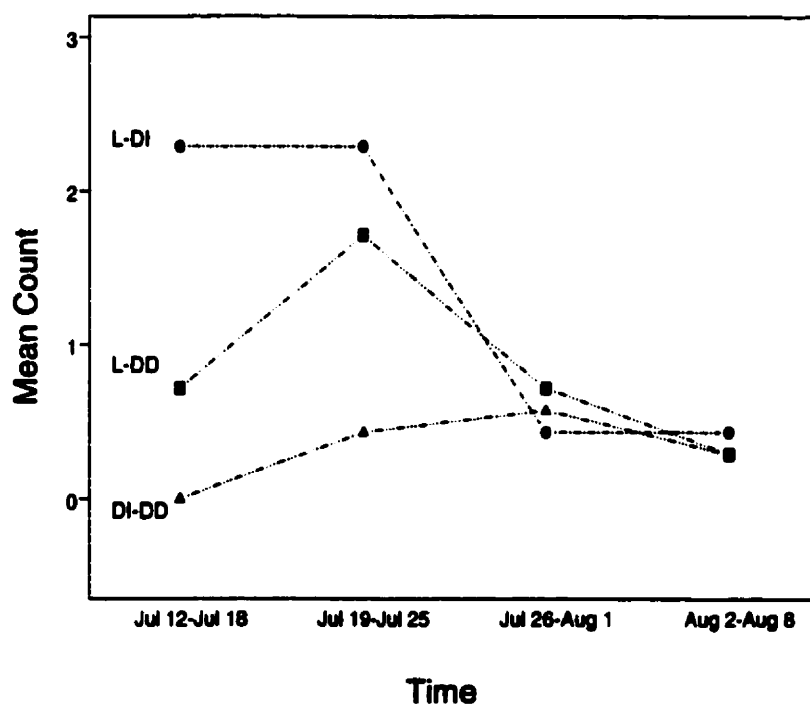
Figure 2-3. Interaction plot showing how the number of eggs laid by *B. cornutus* in the L-DI, L-DD and the DI-DD combinations, changed through time.
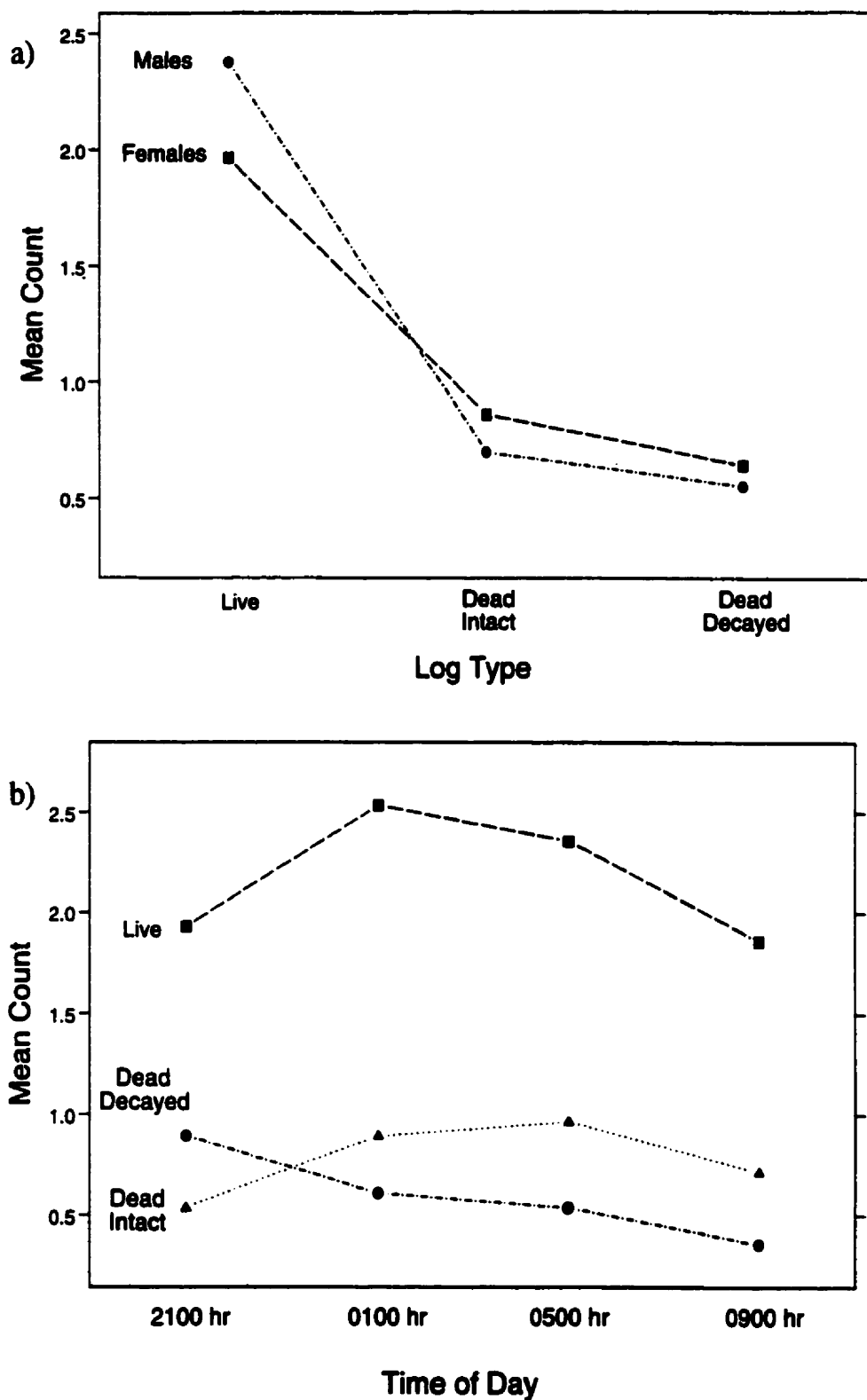
Figure 2-4. Interaction plots showing how the number of *B. cornutus* observed on the A, DI and the DD log types, a) was similar between males and females and b) how the number of beetles observed through time was similar among log types.
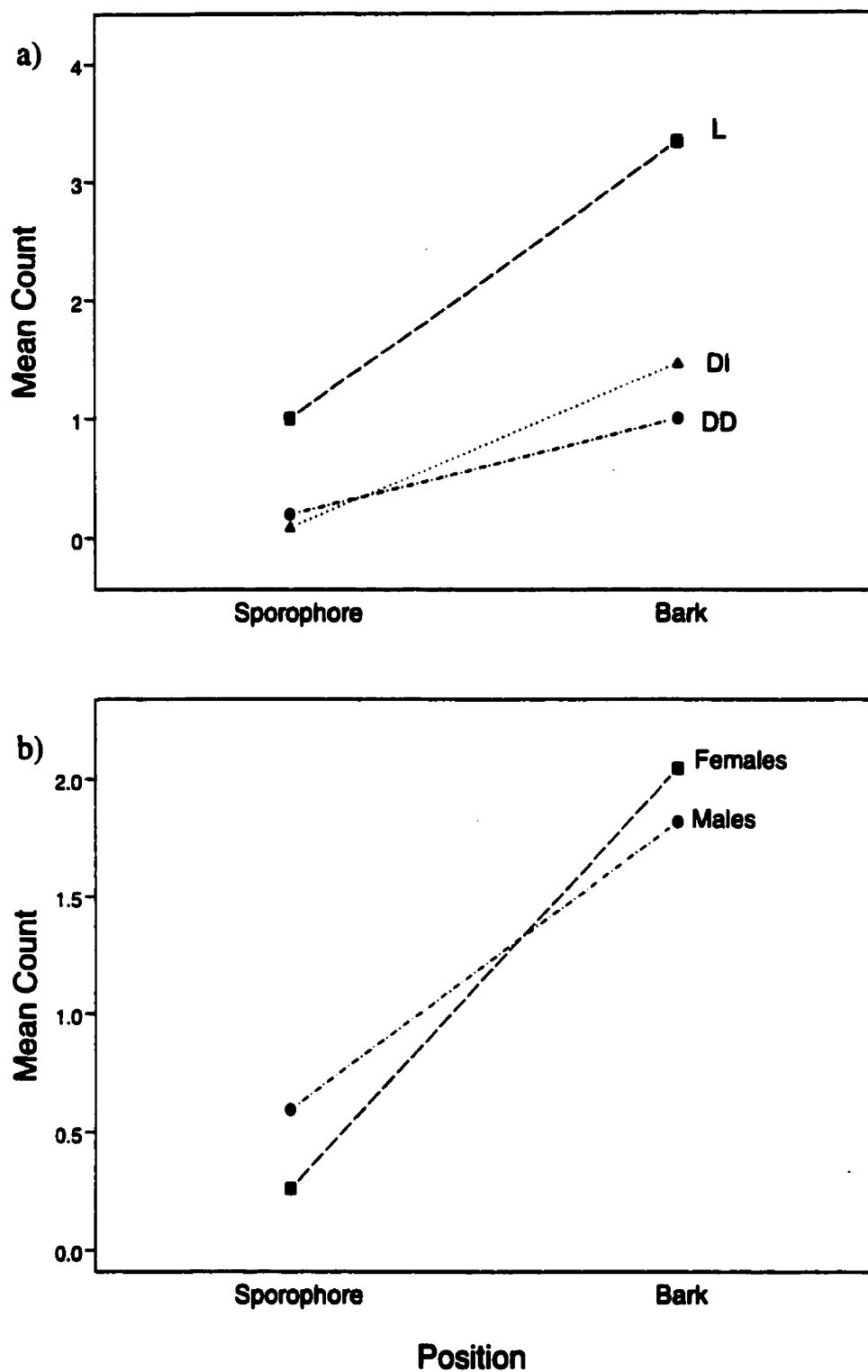
Figure 2-5. Interaction plots showing how the number of *B. cornutus* observed on the sporophore and the bark of the logs, a) differed among log types b) differed between the sexes.
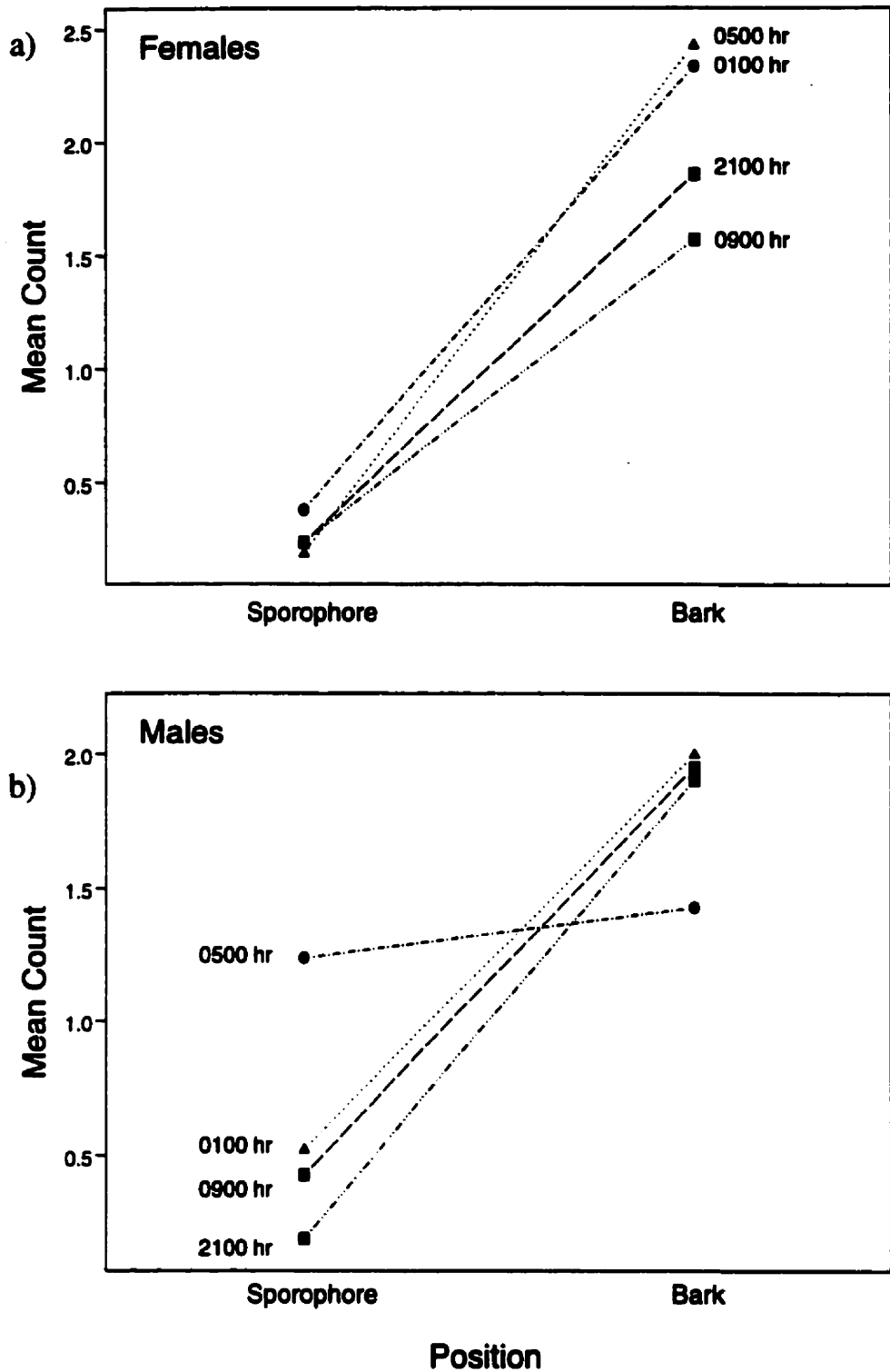
Figure 2-6. Interaction plots showing the number of *B. cornutus* observed on the sporophore and the bark of the logs at each time period for a) females, and b) males.

References

Carr, T.C., Roinnen, H., and P.W. Price. 1998. Oviposition preference and larval performance of *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in relation to host plant vigor. Environmental Entomology 27(3): 615-625.

Conner, J. 1988. Field measurements of the natural and sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 42(4): 736-749.

Conner, J. 1989. Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 43(7): 1378-1386.

Graves, R.C. 1960. Ecological observations on the insects and other inhabitants of woody shelf fungi (Basidiomycetes: Polyporaceae) in the Chicago area. Annals of the Entomological Society of America 53: 61-78.

Haila, Y., Nicholls, A.O., Hanski, I.K. and S. Raivio. 1996. Stochasticity in bird habitat selection: year-to-year changes in territory locations in a boreal forest bird assemblage. Oikos 76: 536-552.

Hanski, I. 1988. Four kinds of extra long diapause in insects: a review of theory and observations. Annals Zoologici Fennici 25: 37-53.

Hanski, I. 1989. Fungivory: fungi, insects and ecology. In: Insect-fungus interactions. 14th Symposium of the Royal Entomological Society of London, London.

Heatwole, H. and A. Heatwole 1968. Movements, host-fungus preferences, and longevity of *Bolitotherus cornutus*. Annals of the Entomological Society of America 61: 18-23.

Hidaka, T. and K. Yamashita 1975. Wing color pattern as the releaser of mating behaviour in the swallowtail butterfly, *Papilio xuthus* L. (Lepidoptera: Papilionidae). Applied Entomological Zoology 10: 263-367.

Kehler, D. and S. Bondrup-Nielsen 1999. Effects of isolation on the occurrence of a fungivorous forest beetle (*Bolitotherus cornutus* Panzer) at different spatial scales in fragmented and continuous forests. Oikos 84(1): 35-43.

Lederhouse, R.C. 1982. Territorial defense and lek behaviour of the black swallowtail butterfly *Papilio polyxenes*. Behavioral Ecology and Sociobiology 10: 109-118.

Liles, M.P. 1956. A study of the life history of the forked fungus beetle, *Bolitotherus cornutus* (Panzer). The Ohio Journal of Science 56(6): 329-337.

Matthewman, W.G. and D.P. Pielou 1971. Arthropods inhabiting the sporophores of *Fomes fomentarius* (Polyporaceae) in Gatineau Park, Quebec. The Canadian Entomologist 103(6): 775-847.

Midtgaard, F., Rukke, B.A. and A. Sverdrup-Thygeson 1996. Habitat selection of *Bolitophagus reticulatus* (L.) (Coleoptera, Tenebrionidae) inhabiting tinder fungus (*Fomes fomentarius*) in three boreal forest areas. In: Midtgaard, F. (ed.) The significance of fragmentation of boreal forest for the occurrence of selected Coleoptera. Ph.D. thesis. University of Oslo, Norway.

Nilsson, T. 1997. Survival and habitat preferences of *Bolitophagus reticulatus*. Ecological Entomology 22: 82-89.

Pace, A.E. 1967. Life history and behavior of a fungus beetle, *Bolitotherus cornutus* (Tenebrionidae). Occasional Papers of the Museum of Zoology, University of Michigan 653: 1-15.

Schwarze, F. 1994. Wood-rotting fungi: *Fomes fomentarius* (L.:Fr)Fr. Mycologist 8: 32-34.

Scott, J.A. 1975. Mate-locating behaviour of western North American butterflies. The Journal of Research on the Lepidoptera 14: 1-40.

Wiens, J.A. 1995. Landscape mosaics and ecological theory. In: Hannson, L., Fahrig, L. and G. Merriam (eds.). Mosaic landscapes and ecological processes. Chapman and Hall, New York.

Wiens, J.A., Stenseth, N.C., Van Horne, B. and R.A. Ims 1993. Ecological mechanisms and landscape ecology. Oikos 66(3): 369-380.

General Discussion

Consideration of spatial scale brought a greater understanding of how the forked fungus beetle uses its habitat. The importance of small scale habitat attributes translated to the broader scales examined, where sporophores (grain size *sensu* Kotlair and Wiens 1990) that are larger and less decayed were used more by the beetle across all scales. At the scale of a log or group of logs supporting sporophores within a meter of one another, beetles most often used units that consisted of a large amount of fungus, and specifically fungus consisting of live and intact sporophores. Wiens *et al.* (1993) suggested that the organism can generally be regarded as the basic unit in ecology, regardless of its position in a given hierarchy. The forked fungus beetle, which is highly specialized in its use of perennial sporophores, requires this resource for all aspects of its life-history. It is not surprising then, that the importance of sporophore attributes translated across the scales examined in this study. Likely, these small scale attributes also constrain processes at higher scales than those studied here.

Conversely, it appears that the smaller scale process of a beetle using a suitable sporophore, is constrained by larger scale phenomena. Although sporophore characteristics were important across scales, the ability to predict patterns of use increased with scale suggesting that there are factors other than the properties of the fungus that are important for defining suitable habitat. At the log and patch scales, characteristics of the wood upon which sporophores were growing were also important for describing habitat use. Some of these characteristics may be indirectly related through their influence on the growth of sporophores (*e.g.* tree decay), or on the microclimate

which the beetle experiences (*e.g.* standing versus fallen trees). Other factors, however, may directly influence the suitability of the habitat; the amount and structural complexity of the vegetation on the tree may be important to the beetle as a source of daily shelter. Not examined in this study, but which is expected to be an extremely important aspect of habitat use, is the presence or absence of conspecifics. The forked fungus beetle may use habitat units according to the sex ratios of the individuals within them, to maximize mating success. Also, male horn size is directly related to mating success (Conner 1988, 1989), and so males may choose habitats to maximize their success at copulating by avoiding long-horned males that might dominate in aggressive encounters.

Consideration of the spatial structuring in the distribution of the forked fungus beetle at multiple scales revealed that individuals are likely responding to their habitat at broader scales than those examined in this study. Positive spatial autocorrelation in the incidence of beetle was detected among both logs and patches within a 50 meter area. This pattern was observed in two continuous forest sites during two of their breeding seasons. On casual observation, the forest sites appeared quite different in the configuration of their logs and patches, and during the second year of the study colonization of newly formed habitat units and extinctions occurred at both sites. This pattern therefore likely arose through behaviours of the beetle, suggesting that their congregation in 50 meter areas of habitat marks the boundaries for individual local populations. Hence, studies of population dynamics of the forked fungus beetle should occur at this scale or higher.

Habitat use was examined using an exploratory approach: models were created in the generalized linear modeling framework, where although explicit hypotheses were not tested, patterns in the data, and the effects of multiple factors were examined (McCullagh and Nedler 1989). This approach has allowed additional and more specific questions to be derived (Nicholls 1989). How do space and particular habitat features interact to produce patterns in beetle habitat use? How do habitat features at various scales influence movement behaviour by the forked fungus beetle? What scales provide the best proximate cues for movement between habitat units? How are the spatial patterns of beetle patch occupancy influenced by movement? What are the dynamics of colonization and extinction of populations across larger scales and over longer time periods than those studied here?

The importance of small scale habitat attributes on resource use by the forked fungus beetle was also examined using field experiments. Using this approach, some of the confounding factors which may have influenced patterns observed using the exploratory approach were controlled for. Since sporophores are such a fundamental requirement for the this beetle's life cycle, the influence of their state and level of decay on female oviposition and adult nightly activity was explored.

In the oviposition experiment, females were given a choice of between two sporophores of approximately equal size, that differed in their level of decay. Three combinations of two different sporophores were presented to a pair of adult beetles housed in enclosures under the forest canopy. By monitoring the location and number of eggs laid between sporophores, I observed that females preferred live sporophores for

oviposition, and their use of dead sporophores decreased with the decay of the sporophore. These results are supported by comparisons between the three combinations because less eggs were laid in the enclosures containing the most decayed sporophore combination. Also, the timing of egg-laying on these combinations was delayed compared to the less decayed combinations. Females that lay their eggs on live sporophores may increase their fitness by directly enhancing the survival and fitness of their young. Alternatively, the benefits of this behaviour may not be translated to the female until after her initial investment of some larvae which help to kill the live sporophores, hence providing optimal habitat for the survival of eggs laid there afterward.

For the second experiment, adult beetles housed in arenas under the forest canopy were presented with 3 sporophores that differed in their level of decay and that were attached to logs. Beetle positions during the night were monitored; both males and females congregated in areas near live and intact sporophores. Beetles were found most often on the bark near these sporophores suggesting that their activities during this time consist mainly of behaviours (mating, aggression) other than feeding. This may reflect patrolling behaviour by males since hosts are easily found by both sexes and provide enough biomass in one clump to create concentrations of individuals (Lederhouse 1982).

These field experiments raise questions about how small scale habitat features are important for use by the forked fungus beetles, and also provide additional support for the patterns observed in the exploratory analysis of habitat use. These results might form the basis for more detailed examinations of the direct influence of habitat quality on beetle

fitness, or they may be incorporated into larger scale studies of beetle demography and of

colonization and extinction dynamics in this system.

References

Conner, J. 1988. Field measurements of the natural and sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 42: 736-749.

Conner, J. 1989. Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. Evolution 43: 1378-1386.

Kotliar, N.B. and J.A. Wiens 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Lederhouse, R.C. 1982. Territorial defense and lek behaviour of the black swallowtail butterfly *Papilio polyxenes*. Behavioral Ecology and Sociobiology 10: 109-118.

McCullagh, P. and J.A. Nedler 1989. Generalized linear models. 2nd ed. Chapman and Hall, London.

Nicholls, A.O. 1989. How to make biological surveys go further with generalised linear models. Biological Conservation 50: 51-75.

Wiens, J.A., Stenseth, N.C., Van Horne, B. and R.A. Ims 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

Appendix 1-1. Analysis of deviance in the incidence of *B. cornutus* at the sporophore scale in each site during 1996 and 1997 (models were fit in the generalized linear modeling framework using a binomial error distribution and a logit link function).

a) Reservoir Site

Term	1996				1997			
	Coefficient	Df	Deviance	Pr (Chi)	Coefficient	Df	Deviance	Pr (Chi)
Null		330	381.32			473	393.37	
log (TOTVOL)	0.7291	1	49.67	0.0000	0.6261	1	29.92	0.0000
DECAY		3	13.70	0.0033		3	34.38	0.0000
(L)	0.6370				1.4390			
(D1)	-0.4107				-0.0518			
(D2)	-0.4715				-0.4409			
(D3)	0.2451				-0.9464			
Residual		326	317.95			469	329.07	

b) 101 Site

Term	1996				1997			
	Coefficient	Df	Deviance	Pr (Chi)	Coefficient	Df	Deviance	Pr (Chi)
Null		699	468.16			801	484.44	
log (TOTVOL)	0.5757	1	38.63	0.0000				
TOTVOL					0.0106	1	21.36	0.0000
DECAY		3	37.96	0.0000		3	92.90	0.0000
(L)	-2.2762				2.2683			
(D1)	1.0531				0.2244			
(D2)	-1.0493				-0.7073			
(D3)	2.2724				-1.7854			
log (TOTVOL):DECAY		3	14.61	0.0022				
(L)	0.8985							
(D1)	0.0005							
(D2)	0.0999							
(D3)	-0.9990							
Residual		692	376.96			797	370.17	

Appendix 1-2. Analysis of deviance in the incidence of *B. cornutus* at the log scale in each site during 1996 and 1997 (models were fit in the generalized linear modeling framework using a binomial error distribution and a logit link function).

a) Reservoir Site

Term	Coefficient	Df	1996 Deviance	Pr (Chi)	Coefficient	Df	1997 Deviance	Pr (Chi)
Null		28	37.36			52	59.05	
TOTVOL	0.0026	1	12.54	0.0004				
log (TOTVOL)					0.8164	1	11.37	0.0007
PERBARK	-0.1148	1	6.74	0.0094				
Residual		26	18.08			51	47.68	

b) 101 Site

Term		Coefficient	Df	1996 Deviance	Pr (Chi)	Coefficient	Df	1997 Deviance	Pr (Chi)
Null			70	75.77			83	92.21	
LVOL						0.0046	1	12.14	0.0012
D1VOL		0.0132	1	24.99	0.0000	0.0046	1	10.47	0.0012
PERVEG						0.0304	1	6.50	0.0107
TRDECAY			2	9.47	0.0088				
	(1)	-1.5283							
	(2)	-0.0210							
	(3)	1.5493							
Residual			67	41.31			80	63.09	

Appendix 1-3. Analysis of deviance in the incidence of *B. cornutus* at the patch scale in each site during 1996 and 1997 (models were fit in the generalized linear modeling framework using a binomial error distribution and a logit link function).

a) Reservoir Site

Term	1996				1997			
	Coefficient	Df	Deviance	Pr (Chi)	Coefficient	Df	Deviance	Pr (Chi)
Null		15	22.18			32	43.26	
DVOL	0.0018	1	5.61	0.0178				
DNUM					0.1632	1	7.45	0.0063
PD2VOL					-4.2385	1	4.24	0.0394
PERBARK	-0.1018	1	3.88	0.0489				
Residual		13	12.69			30	31.56	

b) 101 Site

Term		1996				1997			
		Coefficient	Df	Deviance	Pr (Chi)	Coefficient	Df	Deviance	Pr (Chi)
Null			43	56.46			51	65.72	
TOTVOL		0.0016	1	5.04	0.0247				
LNUM						0.1429	1	9.82	0.0017
DIVOL						0.0037	1	7.10	0.0077
TRDECAY			2	7.35	0.0253				
	(1)	-1.4916							
	(2)	0.6828							
	(3)	0.8088							
COMVEG							3	9.78	0.0205
	(0)					-1.2523			
	(1)					-1.2542			
	(2)					0.8794			
	(3)					1.6271			
Residual			40	44.07			46	39.01	
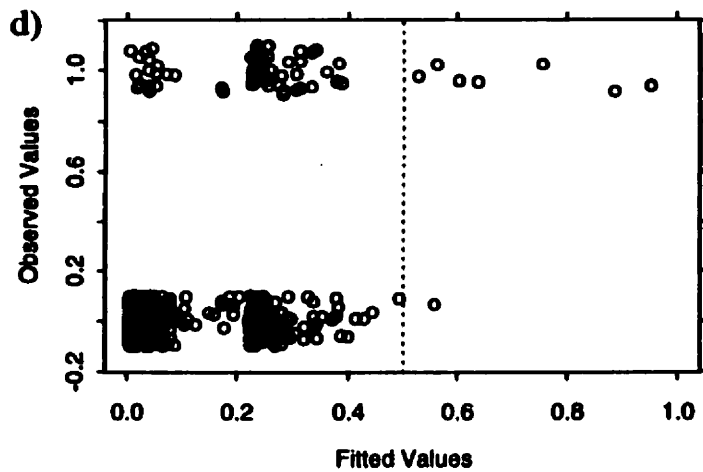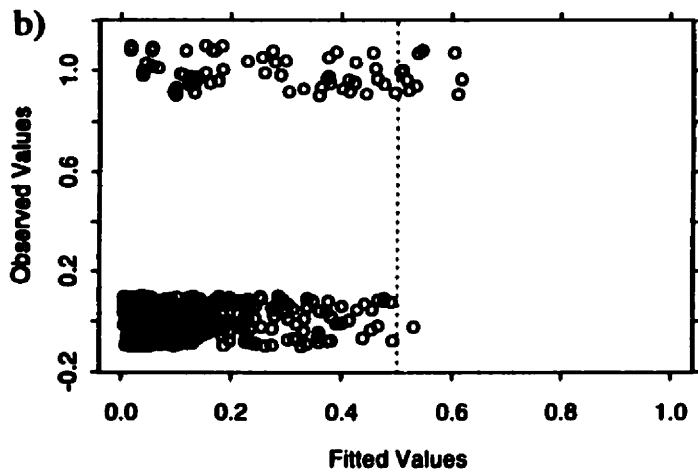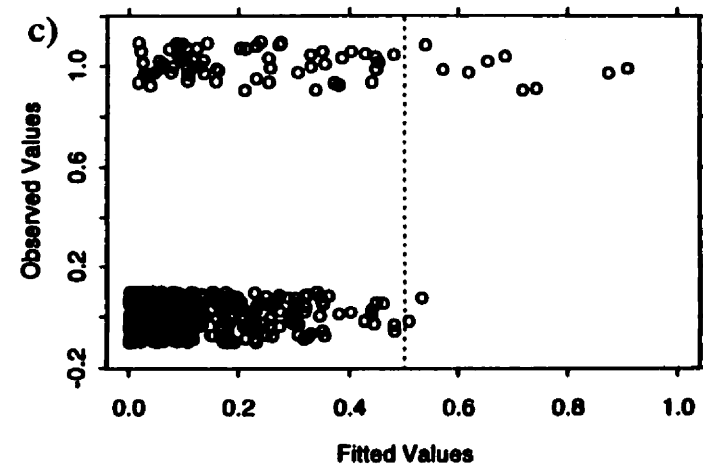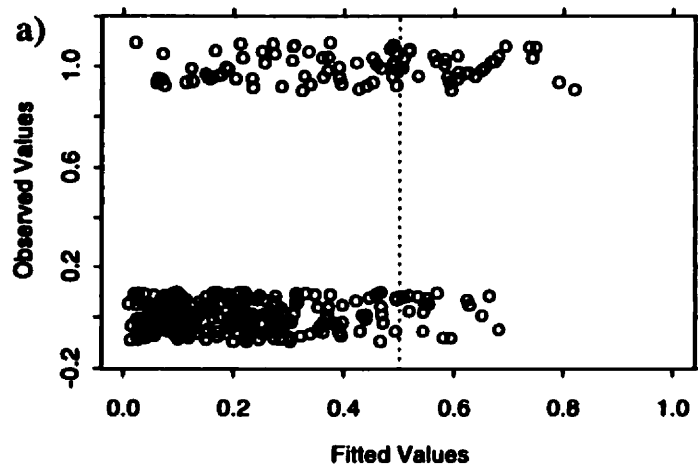
Appendix 1-4. Observed and fitted values for models of the incidence of *B. cornutus* at the sporophore scale at the Reservoir site a) 1996, b) 1997 and 101 site c) 1996, d) 1997 (observed values are jittered to enhance patterns).

Appendix 1-5. Observed and fitted values for models of the incidence of *B. cornutus* at the log scale at the Reservoir site a) 1996, b) 1997 and 101 site c) 1996, d) 1997 (observed values are jittered to enhance patterns).
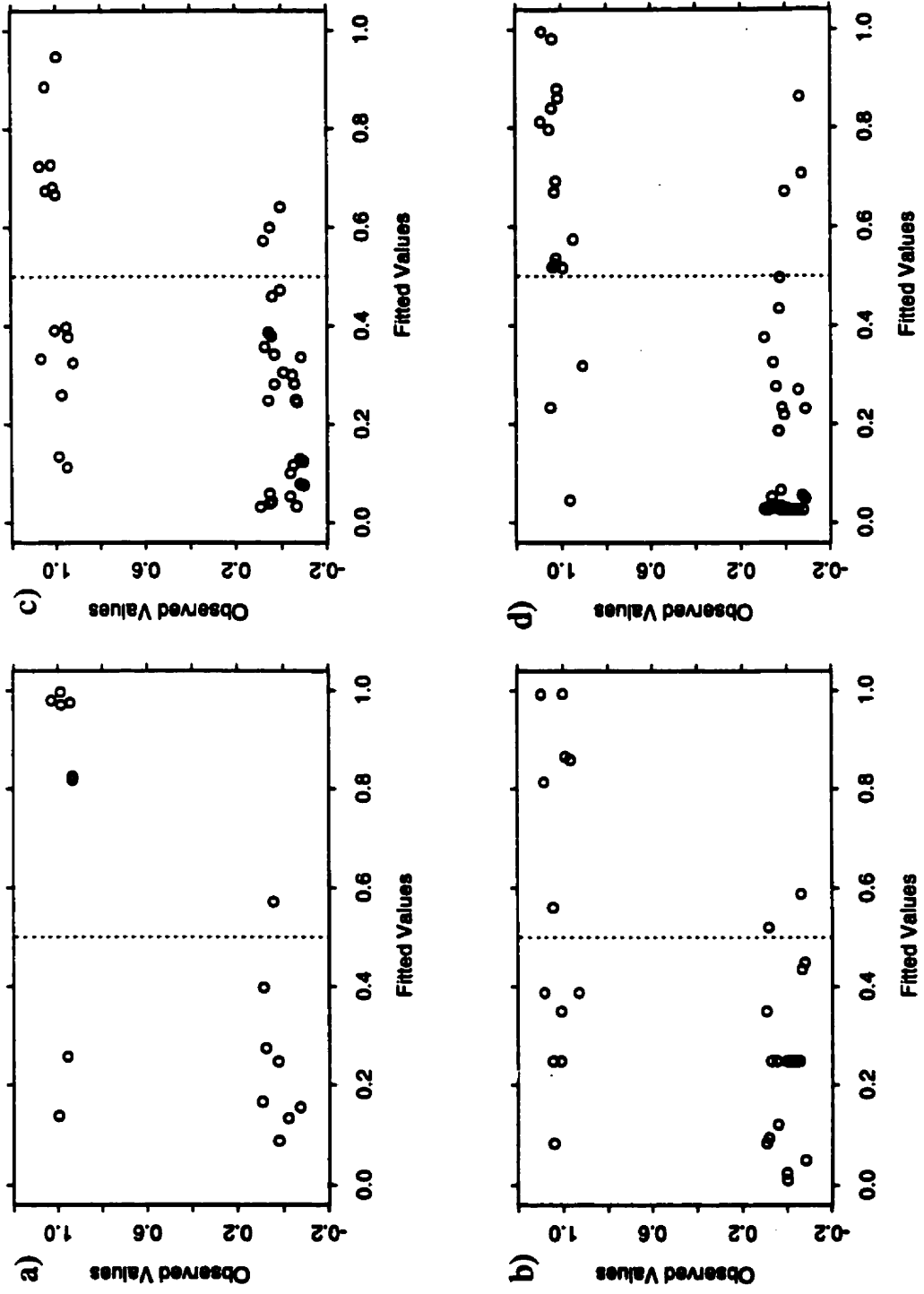
Appendix 1-6. Observed and fitted values for models of the incidence of *B. cornutus* at the patch scale at the Reservoir site a) 1996, b) 1997 and 101 site c) 1996, d) 1997 (observed values are jittered to enhance patterns).

Appendix 1-7. Analysis of deviance the number of *B. cornutus* individuals observed at the **sporophore scale** in each site during 1996 and 1997 (models were fit in the generalized linear modeling framework using a Poisson error distribution and a log link function).
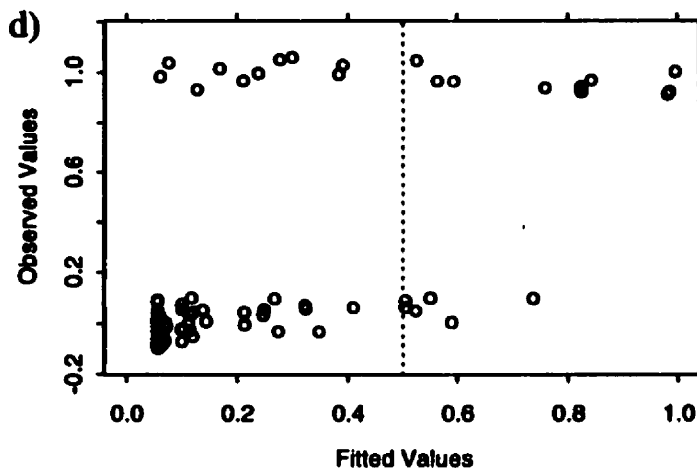
a) Reservoir Site

Term	1996				1997			
	Coefficient	Df	Deviance	Pr (Chi)	Coefficient	Df	Deviance	Pr (Chi)
Null		88	125.76					
log (TOTVOL)	0.1094	1	5.85	0.0155				
DECAY		3	20.45	0.0001				
(L)	-0.0863							
(D1)	-0.1967							
(D2)	-0.3677							
(D3)	0.6507							
Residual		84	99.46					

b) 101 Site

Term	1996				1997			
	Coefficient	Df	Deviance	Pr (Chi)	Coefficient	Df	Deviance	Pr (Chi)
Null		72	152.30			71	111.30	
log (TOTVOL)	0.1202	1	3.80	0.0514	0.2703	1	13.97	0.0002
DECAY		3	35.75	0.0000		3	18.61	0.0003
(L)	0.5569				0.3024			
(D1)	-0.2225				0.0025			
(D2)	-0.4567				-0.9419			
(D3)	0.1222				0.6370			
Residual		68	112.76			67	78.72	

Appendix 1-8. Analysis of deviance in the number of *B. cornutus* individuals observed at the **log scale** in each site during 1996 and 1997 (models were fit in the generalized linear modeling framework using a Poisson error distribution and a log link function).
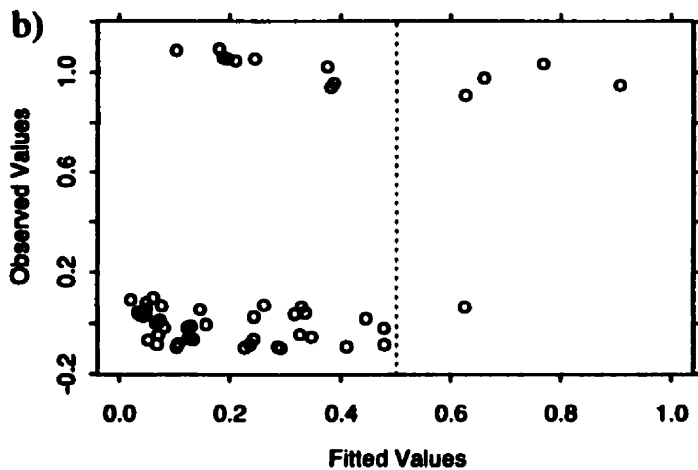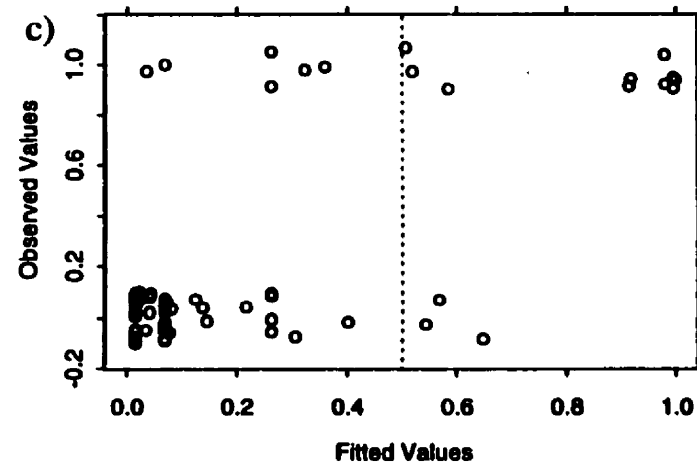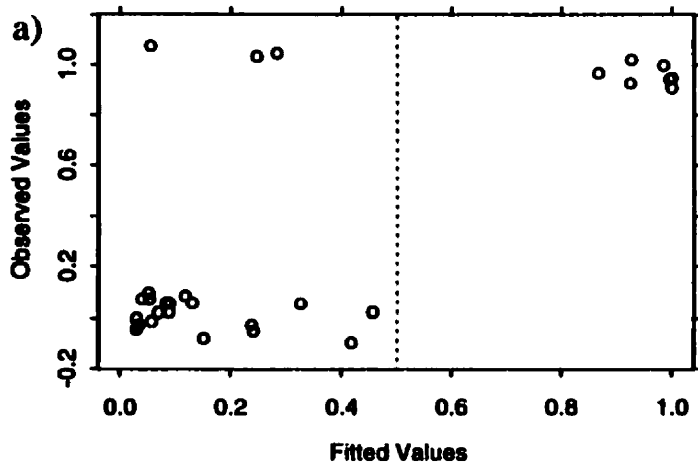
a) Reservoir Site

Term	1996				1997			
	Coefficient	Df	Deviance	Pr (Chi)	Coefficient	Df	Deviance	Pr (Chi)
Null		10	404.96			14	266.66	
log (TOTNUM)					0.8058	1	196.50	0.0000
log (TOTVOL)	1.0630	1	333.63	0.0000				
DAVEVOL	-0.0025	1	9.76	0.0018				
D2AVEVOL	0.0260	1	48.04	0.0000				
PD2VOL	-1.4822	1	4.42	0.0355				
NND					-0.0534	1	5.54	0.0186
COMVEG						3	53.03	0.0000
(0)					0.9019			
(1)					-1.1372			
(2)					1.4914			
(3)					-1.2561			
Residual		6	9.12			9	11.59	

b) 101 Site

| Term	1996				1997			
	Coefficient	Df	Deviance	Pr (Chi)	Coefficient	Df	Deviance	Pr (Chi)
Null		14	342.39			19	197.13	
LVOL	0.0010	1	106.95	0.0000				
D2VCL	0.0014	1	78.30	0.0000				
D3NUM					0.5873	1	41.55	0.0000
TOTAVEVOL	0.0297	1	75.39	0.0000				
PERVEG	-0.0204	1	21.13	0.0000				
TRSA					0.0000	1	24.21	0.0000
TRDECAY		2	53.04	0.0000		2	102.46	0.0000
(1)	-0.8795				-0.8610			
(2)	-0.1020				0.8475			
(3)	0.9816				0.0135			
Residual		8	7.58			15	28.91	

Appendix 1-9. Analysis of deviance in the number of *B. cornutus* individuals observed at the patch scale in each site during 1996 and 1997 (models were fit in the generalized linear modeling framework using a Poisson error distribution and a log link function).

a) Reservoir Site

Term	1996 Coefficient	Df	Deviance	Pr (Chi)	1997 Coefficient	Df	Deviance	Pr (Chi)
Null		8	369.96			11	69.92	
TOTNUM					0.0372	1	13.40	0.0002
log (TOTVOL)	0.9873	1	298.04	0.0000				
D2AVEVOL	0.0278	1	53.47	0.0000				
PLVOL	1.7808	1	14.24	0.0002				
NND					-0.1219	1	25.45	0.0000
TRSTATE						1	11.38	0.0007
(1)					-0.4601			
(2)					0.4601			
TRDECAY						1	9.77	0.0018
(1)					NA			
(2)					-0.4224			
(3)					0.4224			
Residual		5	4.22			7	9.91	

b) 101 Site

Term	1996 Coefficient	Df	Deviance	Pr (Chi)	1997 Coefficient	Df	Deviance	Pr (Chi)
Null		13	320.57			16	165.31	
LVOL	0.0010	1	91.12	0.0000	0.0008	1	62.66	0.0000
D2VOL	0.0028	1	75.65	0.0000	0.0010	1	39.30	0.0000
D2AVEVOL	0.0118	1	50.02	0.0000				
PERBARK	0.0476	1	5.12	0.0236				
TRSTATE						1	4.15	0.0416
(1)					0.2371		.	
(2)					-0.2371			
TRDECAY		2	89.98	0.0000		2	40.29	0.0000
(1)	-1.6933				-0.9966			
(2)	0.5199				0.9171			
(3)	1.1734				0.07947			
Residual		7	8.67			11	18.90	
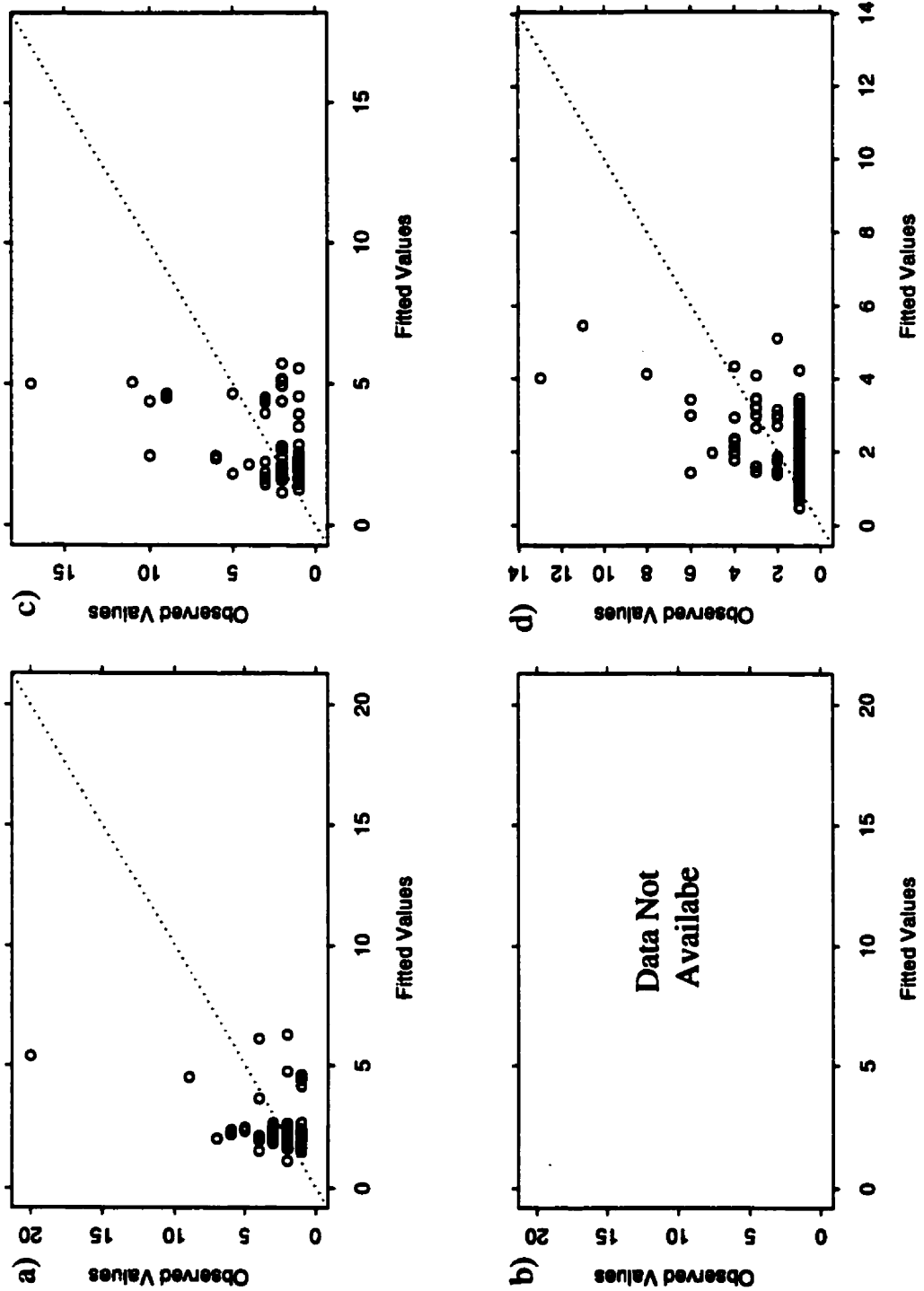
Appendix 1-10. Observed and fitted values for models of the count of individual *B. cornutus* at the sporophore scale at the Reservoir site a) 1996, b) 1997 (no model), and 101 site c) 1996, d) 1997.
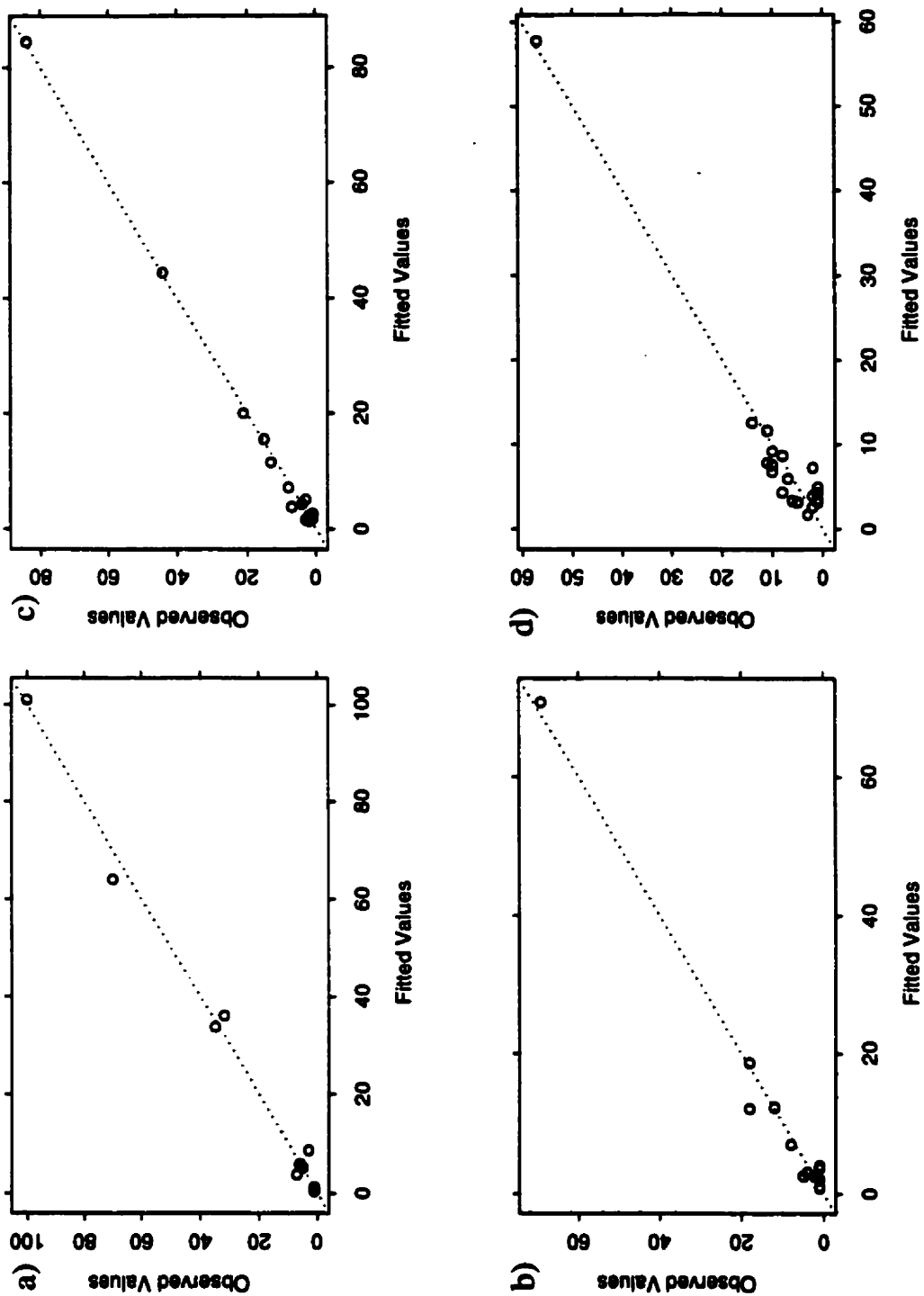
Appendix 1-11. Observed and fitted values for models of the count of individual *B. cornutus* at the log scale at the Reservoir site a) 1996, b) 1997 and 101 site c) 1996, d) 1997.
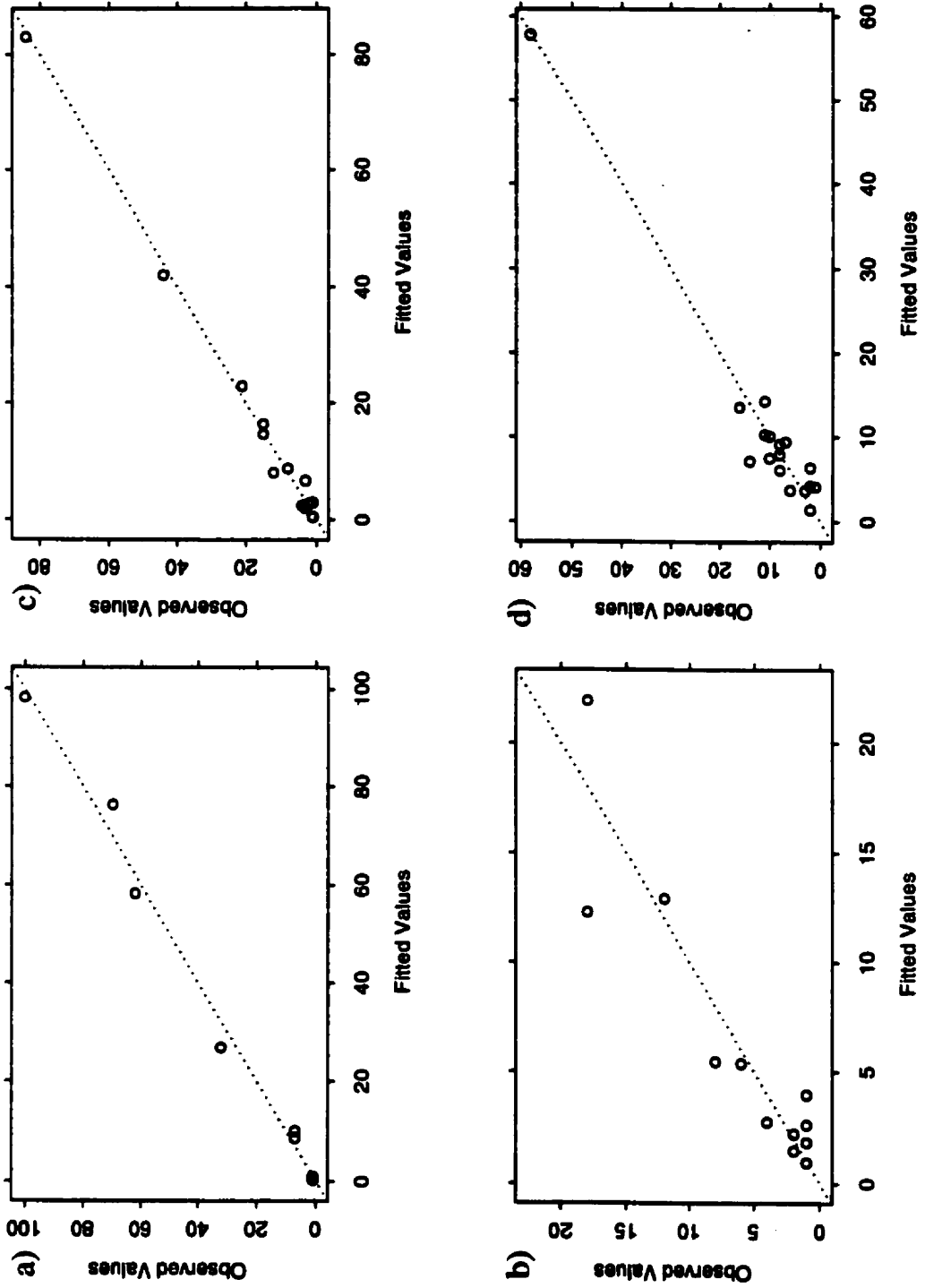
Appendix 1-12. Observed and fitted values for models of the count of individual *B. cornutus* at the patch scale at the Reservoir site a) 1996, b) 1997 and 101 site c) 1996, d) 1997.

Appendix 1-13. The slope (intercept = 0), coefficient of non-determination and 95% confidence interval of the best fitting line relating the number of *B. cornutus* individuals predicted for the 101 site (using the models created with the Reservoir site data), to those actually observed for each scale and year. Best models: the models that best described relative abundance at the Reservoir site, TOTVOL models: models including only the term for the total volume of sporophores, and log (TOTVOL) models: models including only the term for the log of the total volume of sporophores.

a) With worst prediction

Year	Scale	Best Models				TOTVOL Models				log (TOTVOL) Models			
		Df	Slope	$1-R^2$	95 % C.I.	Df	Slope	$1-R^2$	95 % C.I.	Df	Slope	$1-R^2$	95 % C.I.
1996	Sporophore	71	0.39	0.54	0.10	71	0.41	0.55	0.11	72	0.41	0.53	0.10
	Log	8	1.47	0.48	1.15	13	0.74	0.54	0.49	15	0.65	0.44	0.32
	Patch	10	1.25	0.44	0.78	12	0.70	0.53	0.47	14	0.74	0.44	0.37
1997	Sporophore	na	na	na	na	68	0.40	0.49	0.09	68	0.40	0.49	0.10
	Log	18	0.43	0.32	0.15	16	0.29	0.50	0.15	16	0.56	0.46	0.27
	Patch	12	0.40	0.70	0.39	14	0.31	0.47	0.17	14	0.59	0.41	0.28

b) Without worst prediction

Year	Scale	Best Models				TOTVOL Models				log (TOTVOL) Models			
		Df	Slope	$1-R^2$	95 % C.I.	Df	Slope	$1-R^2$	95 % C.I.	Df	Slope	$1-R^2$	95 % C.I.
1996	Sporophore	70	0.47	0.48	0.11	70	0.50	0.49	0.12	71	0.51	0.48	0.11
	Log	7	0.54	0.55	0.53	12	1.28	0.40	0.66	14	0.93	0.50	0.54
	Patch	9	0.77	0.62	0.74	11	1.20	0.37	0.61	13	1.09	0.47	0.62
1997	Sporophore	na	na	na	na	67	0.47	0.43	0.10	67	0.47	0.44	0.10
	Log	17	0.37	0.74	0.31	15	0.66	0.28	0.23	15	1.11	0.37	0.47
	Patch	11	0.92	0.59	0.72	13	0.69	0.25	0.24	13	1.19	0.27	0.43

Appendix 1-14. The correlations, p-values and number of pairs used for simple Mantel tests of the incidence of *B. cornutus* for both sites and years. Bold p-values are those significant at the progressive Bonferroni corrected α - level.

a) Log Scale

	1996						1997						Bonferroni
	Reservoir			101			Reservoir			101			
distance	pairs	r_M	p-value	pairs	r_M	p-value	pairs	r_M	p-value	pairs	r_M	p-value	α - level
0-50	171	0.41	**0.0000**	963	0.16	**0.0020**	667	0.22	**0.0060**	1137	0.20	**0.0000**	0.0125
50-100	44	-0.09	0.0541	626	-0.08	0.0550	188	-0.15	**0.0070**	1011	-0.07	0.0260	0.0083
100-150	39	-0.21	**0.0038**	318	-0.10	0.0190	206	-0.13	0.0390	652	-0.11	**0.0060**	0.0063
150-200	145	-0.21	**0.0047**	454	0.04	0.1820	288	-0.05	0.1730	539	0.02	0.3300	0.0050
200-250	36	-0.21	0.0049	124	-0.12	0.0120	29	0.04	0.2070	147	-0.13	**0.0020**	0.0042

b) Patch Scale

	1996						1997						Bonferroni
	Reservoir			101			Reservoir			101			
distance	pairs	r_M	p-value	pairs	r_M	p-value	pairs	r_M	p-value	pairs	r_M	p-value	α - level
0-50	37	0.24	**0.0128**	272	0.05	0.0920	201	0.21	**0.0020**	341	0.08	**0.0167**	0.0125
50-100	18	-0.02	0.3320	262	-0.05	0.1050	101	-0.15	**0.0050**	391	-0.02	0.3060	0.0083
100-150	15	-0.15	0.0360	173	-0.02	0.1910	114	-0.02	0.2350	300	-0.06	0.0350	0.0063
150-200	47	-0.10	0.1140	181	0.06	0.0550	106	-0.06	0.1030	230	0.03	0.1650	0.0050
200-250	3	-0.04	0.3120	58	-0.05	0.0920	6	-0.08	0.0730	64	-0.06	0.0320	0.0042