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Dispersal and spatial distribution of the desert mistletoe, *Phoradendron californicum*,  
at multiple scales: patterns, processes and mechanisms

by

Juliann Eve Aukema

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A Dissertation Submitted to the Faculty of the  
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY  
In Partial Fulfillment of the Requirements  
For the Degree of  
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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Juliann Eve Aukema entitled Dispersal and spatial distribution of the desert mistletoe, Phoradendron californicum, at multiple scales: patterns, processes and mechanisms

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy

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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

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A handwritten signature in cursive script, appearing to read "Julian Ruppel", is written over a horizontal line.

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**DEDICATION**

In memory of Sasha.

## TABLE OF CONTENTS

ABSTRACT.....	7
CHAPTER 1: INTRODUCTION.....	9
Mistletoes.....	11
Mistletoes as Plant Pathogens.....	12
Metapopulation, Landscape Ecology and Hierarchical Patchiness.....	13
Host Distributions.....	16
Explanation of Dissertation Format.....	17
CHAPTER 2: PRESENT STUDY.....	20
I. Summary of Papers.....	20
II. Interpretation.....	23
REFERENCES.....	30
APPENDIX A: MISTLETOES AS PARASITES AND SEED-DISPERSING BIRDS AS DISEASE VECTORS: CURRENT UNDERSTANDING, CHALLENGES, AND OPPORTUNITIES.....	36
APPENDIX B: WHY DO MISTLETOES SHOW A CLUMPED DISTRIBUTION? THE ROLE OF SEED-DISPERSING BIRDS IN CREATING HETEROGENEOUS SEED RAIN AMONG HOSTS.....	82
APPENDIX C: QUANTIFYING SPATIAL PATTERNS OF MISTLETOE SEED DEPOSITION BY A FRUGIVOROUS AVIAN DISPERSER.....	106
APPENDIX D: THE IMPORTANCE OF SCALE IN THE STUDY OF DESERT MISTLETOE DISTRIBUTIONS.....	128
APPENDIX E: VARIATION IN MISTLETOE SEED DEPOSITION: EFFECTS OF INTRA- AND INTERSPECIFIC HOST CHARACTERISTICS.....	161

## ABSTRACT

Describing processes that lead to the distribution of parasites in space is important for understanding disease transmission and spread. Similarly, describing plant distribution patterns is important to understanding ecological processes. Indeed, distinguishing between dispersal and establishment limitation is central in plant ecology. Mistletoes allow doing both because they are plant parasites with clearly defined spatial distributions among hosts. Most mistletoes are dispersed by birds that consume mistletoe berries and defecate seeds onto host trees in a mutualistic relationship.

I studied desert mistletoes, *Phoradendron californicum* (Viscaceae), which in the Sonoran desert, parasitize legume trees and are dispersed by *Phainopepla nitens* (phainopeplas). I examined patterns of spatial distribution and dispersal of *P. californicum* and the processes and mechanisms underlying these patterns at multiple scales. By counting mistletoes and deposited mistletoe-seeds, and watching phainopepla behavior, I found that mistletoes were aggregated within host trees, and that seed deposition was highest in tall and infected hosts. Likewise, phainopeplas perched preferentially in these trees, creating a positive feedback in which highly infected trees received many seeds and were likely to become reinfected. However, phainopeplas spent less time in trees than it takes for a seed to pass through their guts, which suggested inter-host seed dispersal. I conducted a mistletoe removal experiment that confirmed a high degree of inter-host seed dispersal.

These observations suggested that mistletoes would be aggregated at scales larger than individual trees. By mapping mistletoes and defecated seeds within a 4-hectare plot,

I found that mistletoes were spatially correlated to at least 145 meters. Sampling at larger scales indicated that mistletoe prevalence was spatially correlated to approximately 1500 m, and at scales larger than 4000 m. I also found that seed deposition increased with mistletoe prevalence in local neighborhoods.

In conclusion, mistletoes are dispersal limited plants and are spatially correlated at several scales. Desert mistletoes are aggregated within hosts and their prevalence is spatially correlated at  $< 1500$  m and  $> 4000$  m. At the individual and local scales, their distribution is shaped by where birds defecate, which is influenced by host and neighborhood characteristics. At larger scales, their distribution may be primarily influenced by abiotic effects.

## **CHAPTER 1**

### **INTRODUCTION**

Space has been described as the "final frontier" in ecology (Kareiva 1994). The past decade has seen a growing awareness of the need for increased attention to spatial processes if we are to understand the distribution, dynamics, and interactions of organisms in natural or human-altered environments. A critical feature of spatially explicit studies is scale. Pattern and scale are inextricably intertwined (Turner 1989, Levin 1992, Gardner 1998). Spatial variation in nature can take place over a wide range of spatial scales, because the processes underlying the patterns of variation operate and interact at different levels (Oliver and Webster 1986). The scale of landscape patterns depends on the organisms and ecological processes being investigated (Kotliar and Wiens 1990). Patterns and processes at one scale are constrained by processes at smaller and larger scales,, and for this reason, the scale of a study can have a significant impact on the patterns observed (O'Neill et al. 1986, Wiens 1989, Wu and Louks 1995). The ability to detect ecological patterns is a function of the extent (the overall area or upper limit) and grain (the units of observation or lower limit) of the study (Wiens, 1989). Examining ecological processes at an appropriate scale can uncover important patterns, whereas if the scale is too large or too small, interesting patterns may be obscured or artifacts of scale may be identified as patterns (Carlile et al., 1989; Wiens, 1989).

Because patches at different scales often form nested hierarchies (Kotliar and Wiens 1990), studies conducted at several scales provide better resolution of patterns and the interrelationships of scales (Wiens, 1989). Because organisms differ in their response to the environment, and their ecological neighborhoods differ in size, appropriate scaling is particularly important in studies of interactions among species (Wiens 1989). Once patterns have been detected and described, the processes and mechanisms that generate and maintain them may be identified and understood, enabling predictions to be made and tested (Turner 1989, Levin 1992).

This dissertation investigates how the spatial distribution of a plant parasite, *Phoradendron californicum*, is shaped by seed dispersal patterns and activities of its avian seed dispersers, *Phainopepla nitens*. I examine this problem from multiple spatial scales and integrate pattern, process, and mechanism. *Phoradendron californicum*, the desert mistletoe, plays a dual role in biological communities of the Sonoran desert; it is both a parasite of its hosts (members of Fabaceae, especially *Prosopis*, *Olneya*, *Cercidium* and *Acacia* spp.) and a mutualist of the birds that disperse its seeds. Likewise, phainopeplas are both seed dispersers for mistletoes and disease vectors for the mistletoe host plants. The foraging patterns of these seed dispersing birds create seed shadows that, with time, develop into mistletoe spatial distributions. The response of these birds to mistletoe abundance can create a positive feedback: high local abundances of mistletoes can lead to higher seed deposition. Furthermore, because both seeds and seed-dispersing birds are visible and relatively easy to track, this system offers a good opportunity to examine the mechanisms that shape disease transmission in space and time. Additionally,

the role of mistletoes as both parasites and mutualists places their study at the convergence of epidemiology and seed dispersal and will provide a better understanding of processes of pathogen transmission and seed dispersal. Here I link mechanisms of phainopepla behavior to the processes of seed dispersal that create patterns of mistletoe infections in the landscape at multiple scales ranging from single host trees to several kilometers. This study helps to elucidate processes of pathogen transmission at several scales, as well as the ways in which phainopeplas, and potentially other seed dispersing birds, shape their landscape.

### ***Mistletoes***

Mistletoes are aerial hemiparasites in the plant families Loranthaceae, Viscaceae, Misodendraceae, Eremolepidaceae, and Santalaceae that infect a variety of plants, from pines in Pakistan to eucalypt in Australia to columnar cacti in Chile (Hawksworth, 1983). With a few notable exceptions, such as the explosively dispersed *Arceuthobium*, most mistletoe seeds are dispersed by birds, many of which are highly specialized to consume mistletoe berries (Reid et al., 1995). Seeds are deposited onto host plants by defecation, regurgitation, or bill wiping (Reid et al., 1995). After being deposited onto an appropriate host, a seed germinates and forms a haustorium, tapping into the xylem, and in some cases, the phloem of the host plant to absorb water and minerals (Calder, 1983).

The desert mistletoe, *Phoradendron californicum* (Viscaceae), is found from Southern Utah through Northern Mexico (Kearney and Peebles, 1960). In the Sonoran desert, *P. californicum* infects *Prosopis* spp. (mesquite), *Cercidium* spp. (palo verde),

*Olneya tesota* (ironwood) and *Acacia* spp. (acacia), all in the plant family Fabaceae. The seeds of *P. californicum* are dispersed primarily by *Phainopepla nitens*, whose breeding season in the desert coincides with the fruiting of mistletoes in the winter (Walsberg, 1977; Chu and Walsberg, 1999). In the desert, both males and females defend all-purpose feeding and nesting territories, but following courtship, they defend only one territory together (Walsberg 1977, Chu 1999). Inter-nest distances are approximately 50 - 170 meters (Chu 1999, pers. comm.). They frequently use conspicuous perching as a form of territorial display (Walsberg 1977). Phainopeplas have highly specialized digestive tracts enabling them to rapidly process large numbers of mistletoe berries (Walsberg, 1975; Chu and Walsberg, 1999), and they are the most effective dispersers of mistletoe seeds (Larson, 1996). Desert mistletoe berries are also an important resource for mockingbirds, thrashers, and quail because they are one of the few berries abundant during the winter (Cowles, 1936).

### ***Mistletoes as Plant Pathogens***

Plant pathogens have not been well studied in natural settings or in a spatial context (Alexander, 1989). Despite the historical lack of communication among scientists in the disciplines of epidemiology, parasitology, plant pathology and plant ecology, all of these fields have made interesting advances that can contribute to each other (May, 1990; Alexander, 1990; Harper, 1990). For example, Anderson and May (1979) differentiate between microparasites and macroparasites as a way of distinguishing the life histories of pathogens such as viruses, bacteria, and protozoans

from parasitic helminths and arthropods. Their definition of macroparasites as having a relatively long generation time and causing persistent infections with continual reinfection of hosts also describes mistletoes and other parasitic angiosperms. Many pathogens are transmitted by vectors and this type of transmission has implications for disease spread, requiring the interaction of the host, pathogen and vector with their environment (Irwin and Kampmeier, 1989; Kitron, 1998).

Parasites have been studied in a spatial context, and aggregated patterns of parasite numbers per host are commonly observed in parasite-host systems (Anderson and Gordon, 1982; Pacala and Dobson, 1988). Overton (1996) found evidence of aggregation within trees, and I found that the numbers of *P. californicum* per host was leptokurtic and right skewed (Appendix A). The spatial pattern of mechanisms of pathogen dispersal affect the spatial properties of a spreading pathogen, and understanding dispersal is important for making predictions about the spread of disease (Minogue, 1989). Density of hosts and spatial heterogeneity have also been shown to be important in disease spread (Alexander, 1984). In addition, genetic differences in susceptibility of hosts and the spatial distribution of these hosts affects the spread of disease (Thrall and Jarosz, 1994).

### ***Metapopulation, Landscape Ecology and Hierarchical Patchiness Approach***

To better understand the spatial relationships of parasites, their hosts and vectors in a heterogeneous environment, an approach that combines hierarchical, metapopulation and landscape ecology perspectives may shed be useful. Hierarchy theory predicts that

patches nested hierarchically are prevalent in nature. Furthermore, this theory predicts that hierarchical levels can be distinguished by different rates of processes and that hierarchical levels are explicitly linked (O'Neill et al. 1986). However, hierarchical distributions of plants have rarely been demonstrated empirically (Kotliar 1996, van Collier 2000). The theories of hierarchical patch dynamics, metapopulation dynamics, landscape ecology and hierarchical habitat selection are explicitly spatial and share a recognition of the importance of scale, and the interaction between pattern and process. Thus it is useful to consider these theories and their overlap in a study of spatial pattern, process and scale.

Several important insights in metapopulation theory were first made in epidemiology. For instance, eradication thresholds and optimal programs of eradication have long been understood in a disease context (Kermack and McKendrick, 1927; May, 1990), and the knowledge that a disease can be successfully eradicated even with remaining habitat patches (susceptible hosts) is critical for vaccination programs worldwide (Nee et al. 1997). The best developed metapopulation theory is also in the area of epidemiology, in which each host individual represents a clear patch and the dynamics of colonization and extinction are clearly those of metapopulations (Lawton et al. 1994; Nee et al. 1997). Although few empirical metapopulation studies have explicitly considered scale, it is important in metapopulation dynamics because some species conform to different categories of population structure at different scales (Thomas and Kunin 1999, Menendez and Thomas 2000).

Like other parasites, mistletoes can be thought of as spatially structured populations in which each host tree is a patch. Overton (1994, 1996) used a metapopulation approach to study the distribution of *P. californicum* but did not find evidence of over-dispersion of mistletoes on a local level. His Levins (1970) type metapopulation model predicted that occupancy of trees by mistletoes should increase with tree age. Donohue (1995) found that the mistletoe *Plicosephalus curviflorus* was contagiously distributed on *Acacia tortilis*, but occurred most intensely on larger trees in low density *Acacia* stands.

As with metapopulations, movement of individuals is a vital element of landscape ecology (Hanson 1991, Taylor et al. 1993, Ims 1995, Wiens 1997). The connectivity of a landscape is the degree to which organisms move between landscape elements. This connectivity depends upon the scale of observation and the organisms of interest (Taylor et al. 1993, Ims 1995). Many plants are dependent on an animal vector to disperse their propagules, and their fitness is dependent on not only the quantity of seeds dispersed, but on the probability of seeds being deposited in a suitable site (Schupp 1993, Wenny and Levey 1998). The dispersers, then, are critical in determining the spatial distribution of the plants. Suitable habitat patches are likely to be different for a plant and its animal disperser, but the plant has to sample its landscape through the habitat preferences of its disperser. Habitat selection by birds has been described as a hierarchical spatial process that ranges from choice of food items in a patch to choice of home range in a landscape (Johnson 1980). The connectivity of the landscape for the plant is entirely dependent on the ability of its animal disperser to move through space.

From the point of view of the phainopepla, many hectares of upland Sonoran desert vegetation may constitute a single patch. Within this patch there may be areas of high and low quality. However from the perspective of the mistletoe, each host tree is a patch and the only way to get propagules to a patch is, literally, through the phainopepla. For a mistletoe, the exact location within the phainopepla's patch where it defecates is critical. Furthermore, phainopeplas, as dispersers, are creating patches of mistletoe and actually altering the landscape while, simultaneously, they are responding to the patches of mistletoes. This type of positive feedback is likely to have consequences for the distribution and spread of the parasite. Studying this type of interaction in the landscape requires simultaneous awareness of the scales, heterogeneity, and patches that are important for a plant and for its animal disperser. The synthesis of the metapopulation approach with landscape ecology is a potentially powerful way of understanding the dynamics, distribution, genetics and processes affecting species in a spatial context (Husband and Barrett 1996, Wiens 1997).

### ***Host distributions***

Although a parasite species can be described as a generalist, and be able to infect a number of species, this does not necessarily mean that it will infect all of these species in a heterogeneous environment. Frequently, parasites do not use the host species that they are capable of parasitizing in proportion to their abundance (*Cuscuta*, Kelly et al. 1988; *Tristerix aphyllus*, Martínez del Rio et al. 1995) or they use different species in different parts of their range (*Phoradendron*, Schneck 1884). One aspect of the interaction

between host and pathogen is host specialization. Host races are populations of parasites that specialize on a subset of the potential host species and may be an example of incipient speciation (Norton and Carpenter 1998). Host specialization may be advantageous if there are genetically based trade-offs in performance on different hosts; however, the benefits of specializing depend on relative host abundance (Jaenike 1990, Norton and Carpenter 1998). Host races have been reported for several species of mistletoes, including *P. californicum* (Clay et al. 1985, Glazner et al. 1988, Overton 1997, Norton and Carpenter 1998). May (1971) found differences in both infectivity of *P. tomentosum* from different locations and resistance of *Prosopis* from different locations.

### ***Explanation of Dissertation Format***

The chapters in this dissertation are included as five appendices. Appendices A and E represent work that I did in collaboration with Dr. Carlos Martínez del Río and he is coauthor of these papers. A shortened version of Appendix A is a chapter in *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* edited by D. J. Levey, W. R. Silva, and M. Galetti. Appendix E has been accepted for publication in the journal *Ecography*. I collaborated with Dr. David Smith on the analysis presented in Appendix C and he is a co-author on this paper.

Appendix A presents a review of mistletoe biology and seed dispersal. In addition, we present data from two desert mistletoes (*Tristerix aphyllus* and *Phoradendron californicum*) on distribution of mistletoes and seed deposition at the scale of individual hosts and at sites with varying mistletoe prevalences. We suggest that

mistletoe distributions may be spatially aggregated at larger spatial scales. We also use our data to test predictions of a metapopulation model, and we extend that model to include conspecific attraction.

In Appendix B, I present the results of direct observations of phainopepla behavior on a 4-hectare plot in the Santa Rita Experimental Range, southeast of Tucson, Arizona, USA in which all host trees (almost entirely *Prosopis velutina*) had been tagged, and characteristics such as height, number of mistletoes, and number of seeds were known. I also present the results of an experiment in which mistletoes were removed from host trees and seed deposition was compared with control trees before and after removal. I relate the mechanism of phainopepla foraging behavior to the process of seed deposition and discuss how they may shape spatial distributions of mistletoes.

Using the same 4-hectare plot, Appendix C uses geostatistics to examine the patterns of mistletoe distribution at the scale of several hectares and uses mathematical models to examine the process of seed deposition at this scale. We relate our findings to bird foraging and territorial behavior and aspects of mistletoe life history beyond seed dispersal.

Scaling up to several kilometers, Appendix D examines mistletoe distributions and seed rain patterns across the Santa Rita Experimental Range. Abiotic factors, physiological tolerances of mistletoes and hosts, and behavior of populations of phainopeplas are discussed as potential explanations of large scale patterns in mistletoe distributions.

Finally, increasing complexity in the system is examined in Appendix E. Mistletoe distributions and seed deposition are examined in the Silverbell Mountains, Northwest of Tucson, Arizona, USA, a site with greater host species diversity than SRER. We examined differences in infection and seed deposition rates among different host species. Seed-disperser preferences, establishment and host races are postulated as explanations of the patterns found. We return to the idea of considering mistletoes as plant metapopulations.

## CHAPTER 2

### PRESENT STUDY

#### *I. Summary of papers*

The methods, results, and conclusions of this study are presented in the papers appended to this thesis. The following is a summary of the most important findings in these papers.

In Appendix A, we review the literature on mistletoes and their interactions with seed-dispersing birds. We then use data from two desert mistletoes (*Tristerix aphyllus* and *Phoradendron californicum*) to demonstrate that previous parasitism of a host leads to increased seed deposition and, presumably, to increased re-infection. At a larger spatial scale, in both species, seed deposition (both to infected and uninfected hosts) increases as the local mistletoe prevalence increases. This result suggests that mistletoe infections may show significant spatial aggregation at large spatial scales. A simple metapopulation model that assumes that hosts are patches inhabited by mistletoes predicts, under general conditions, that patch occupancy (host infection frequency) increases with host age (Overton 1994). Our data uphold this prediction. We identify the ingredients needed to analyze spatial patterns of mistletoe infection and to construct models of the spatial and temporal dynamics of mistletoe infections. We propose that the characteristics of mistletoes place their ecology at the convergence of metapopulation ecology, the biology of seed dispersal, and plant physiology.

Appendix B examines the ways in which birds, specifically *Phainopepla nitens*, can shape mistletoe distribution through their foraging behavior. I used direct observation of phainopepla behavior and experimental removal of mistletoes from host trees to examine patterns of seed deposition onto host trees. I found that phainopeplas moved preferentially among parasitized trees. Before mistletoe removal, seed deposition was equivalent and temporally correlated in pairs of control and removal trees. After removal, deposition into removal trees was significantly lower than into unmanipulated trees. Bird behavior and the mistletoe removal experiment suggest that inter-host dispersal contributes significantly to seed deposition. The average time birds perched in hosts was much lower than the time for ingested seeds to pass through their gut. Although mistletoe removal resulted in lower seed deposition, it did not abolish it. The response of birds to mistletoes leads to disproportionate seed deposition into parasitized trees and probably causes the clumped distribution of mistletoes. Thus, in desert mistletoes, dispersal limitations shape spatial distribution.

Appendix C uses mathematical models and geostatistics to analyze patterns of distribution and seed dispersal of *Phoradendron californicum* on a 4-hectare mapped plot on the Santa Rita Experimental Range in Arizona. We found spatial correlation in the number of mistletoes per host, host tree height, and number of seeds deposited on trees. To investigate the process that generated the seed distribution patterns, we used mathematical models to predict the seed deposition patterns as a function of the number of mistletoes, the tree height, and the proximity to other infected trees. The model indicated that number of mistletoes and the height of hosts were the most important

predictors of the number of seeds that would be deposited on a tree. These patterns are likely to be due to the foraging and perching behavior of seed-dispersing birds.

In Appendix D, I examined the pattern and scales of the spatial distribution of infection on host plants by *Phoradendron californicum* in a landscape spanning several square kilometers. I also studied the relationship between mistletoe infection and seed dispersal. I used a combination of nested analysis of variance and variograms to examine spatial structure. I found that seed rain is higher in areas with a high prevalence of mistletoes and that a higher proportion of trees receive seeds than are infected. This suggests that mistletoes will be aggregated in space. I found that mistletoe prevalence was spatially correlated at scales up to 1500 meters, and at scales greater than 4000 meters. However correlation at the largest scales was due to the effect of elevation. Sites at higher elevations showed reduced mistletoe infection compared to sites at lower elevations. I propose that at small scales, mistletoe distributions are due to aggregation of seed dispersing birds, that the elevational effect reflects the limits of the mistletoes' physiological tolerance to freezing-induced cavitation and that this pattern should also be evident latitudinally.

In Appendix E, we looked at patterns of infection by *Phoradendron californicum* at a site with a high diversity of host species. We investigated differences in host infection and examined one of the processes that contributes to these differences: variation in seed deposition among host individuals and species. At a site in the Silverbell Mountains in Arizona, frequency of infection did not reflect host relative abundance. *Olneya tesota* was parasitized at a higher frequency than that expected from its

abundance and maintained the highest mistletoe loads per individual host. In contrast, *P. velutina* was infected less frequently than expected. Infection frequency increased with host tree height. Mistletoe seed deposition by avian dispersers differed among host species and was disproportionately high in *O. tesota* and *P. velutina*. Seed deposition was higher in infected than in non-infected host trees, and increased with tree height in *O. tesota* but not in *C. microphyllum*. We hypothesize that seed deposition depends on host height and crown architecture. Seed deposition increases with height in *O. tesota* because seed-dispersing birds generally prefer higher perches. Some host tree species, such as *C. microphyllum* and *A. constricta*, probably receive fewer mistletoe seeds because birds avoid hosts with dense and spiny crowns. It may be useful to consider mistletoe populations as plant metapopulations in which the frequency of infection in each host species/patch type is the result of interspecific differences in the balance between seed deposition, mistletoe establishment and extinction. From this perspective, our study of host use and seed dispersal can be conceived as a metapopulation study of patch occupancy and propagule distribution among available patch types.

## ***II. Interpretation***

I will attempt here to synthesize my findings from each of the different aspects of the study and place them in the context of current ecological theory.

This study draws on a number of related subdisciplines including metapopulation dynamics, landscape ecology, hierarchy theory and hierarchical habitat selection.

Because the desert mistletoe is dispersed by birds, it is impossible to examine the spatial

population structure of these plants without considering the effect of their distribution on their seed dispersers and the consequences of the behavior of these dispersers for the mistletoes. The desert mistletoe is distributed patchily at several scales (Appendix D). These patches are nested hierarchically and different processes operate at different scales. Furthermore, phainopeplas seem to exhibit hierarchical habitat selection (Appendix B).

Hierarchical plant distributions have rarely been demonstrated empirically (Kotliar 1996, van Collier 2000). Desert mistletoes were patchily distributed at three scales. They were aggregated within *P. velutina* trees (Appendix A) and this aggregation is the product of a positive feedback in which more seeds are deposited in infected trees than in uninfected trees, leading to greater numbers of mistletoes within these infected trees (Appendix A, B).

This positive feedback is repeated at larger scales as well. In sites with a high prevalence of mistletoe infections (a large proportion of infected trees), the probability that a tree, especially an uninfected tree, will receive seeds, is greater than in areas with a low prevalence of mistletoe infections (Appendix A, D). This creates mistletoe aggregations at scales of 145 m - 1500 m (Appendix C, D). This is also likely to be due to phainopepla behavior, specifically phainopeplas establishing territories near other birds (Chu 1999, pers. comm.), perhaps to facilitate mate selection, and such an aggregation of birds could create this intermediate pattern of mistletoe distributions.

Mistletoe prevalence was also spatially correlated at scales greater than 4000 m (Appendix D). This large scale effect was due to changes in elevation. Mistletoes were more abundant at low elevations than at high elevations and at the highest elevations

sampled, mistletoes were nearly non-existent. This large scale pattern of mistletoe distributions may be due to abiotic factors such as winter temperatures.

Phainopeplas show evidence of hierarchical habitat selection in a positive feedback that creates hierarchical patches of mistletoe infections at two levels. Evidence of positive feedbacks in ecological systems is extensive and it can be an important factor in the formation of system structure (O'Neill et al. 1986). Examples of positive feedbacks, such as desertification and glaciation, are particularly abundant at large spatiotemporal scales (Maruyama 1963, O'Neill et al. 1986, De Angelis et al. 1986). The interaction between desert mistletoe infection of host trees and phainopepla behavior is an example of positive feedback creating hierarchical structure in an ecological system at a small spatiotemporal scale.

The response of phainopeplas to mistletoe plants in individual host trees (Appendix B), is probably due to immediate foraging decisions. Phainopeplas also appear to respond to the abundance of mistletoes in larger neighborhoods comprising many host trees. This level of habitat selection is probably the result of two complementary processes: phainopeplas are more abundant at sites with higher mistletoe infections, and they spend more time in them. Phainopeplas probably exhibit a larger density of breeding territories in more heavily infected areas, and non-breeding floaters are likely to visit these resource-rich areas more frequently. The consequence of the hierarchical foraging decisions of phainopeplas at these larger spatial scales is that trees in neighborhoods with a high prevalence of mistletoe infections are more likely to have seeds deposited on them than trees in neighborhoods with a low prevalence of mistletoes (Appendix A, D). At

intermediate scales phainopeplas produce aggregations of infected trees: some areas are heavily infected whereas others are free of mistletoes.

The behavior of phainopeplas at these two scales of habitat selection appears to be the process responsible for the small and intermediate scale patterns of mistletoe distribution. Phainopeplas are likely to show higher level habitat selection as well. In the Sonoran desert, these birds are rarely found in areas lacking abundant mistletoe resources. At the Santa Rita Experimental Range there are hundreds of hectares with dense mesquite populations, very few or no mistletoe infections, and almost no phainopeplas. Abiotic factors are probably responsible for the larger scale patterns of mistletoe distribution and this, in turn, affects phainopepla distributions. Because the foraging patterns of phainopeplas actually creates patches to which they later respond, the interaction between phainopeplas and mistletoes is somewhat different from those in which hierarchical patches of prey lead to a hierarchical distribution of predators tracking those prey (Fauchald et al. 2000). The mutualistic interaction between seed dispersing birds and mistletoes defines many of the processes that mold the spatial infection patterns that we observe. Further studies of phainopepla spatial distributions and their response to large-scale mistletoe manipulations will further elucidate the connections between patterns and processes in this interaction

Mistletoes can be thought of as having a metapopulation structure because host trees represent discrete habitat patches (Overton 1994, Appendix A, E). Indeed, mistletoe infections can be profitably modeled using classical metapopulation models. However, some species fit different categories of population structure, such as metapopulations and

patchy populations, at different scales and differences between size, isolation and quality of patches at different scales blur the distinction between the categories (Thomas and Kunin 1999, Menendez and Thomas, 2000). The desert mistletoe is probably another species for which different categories of population structure are useful ways of describing the species at different scales, only genetic studies that assess the degree of inter- and intra-patch (host) dispersal can clarify whether the mistletoes within a host represent a supopulation and whether the collection of infected hosts is a metapopulation in the strict definition of the term (Hanski and Simberloff 1997).

Within the landscape, mistletoes can also be thought of as having a patchy population structure. Colonization of isolated trees or uninfected neighborhoods is probably a rare event. Desert mistletoes may exhibit a phenomenon that is analogous to an Allee effect. An infection can only spread in relatively uninfected areas after a threshold density of mistletoes is reached. I suspect that the isolated instances of infection that can be found in otherwise uninfected areas are frequently due to birds other than phainopeplas, such as mockingbirds or thrashers. Frequently, when I found a single mistletoe infection in an area far from other infections, it was on a small tree (pers. obs.), unlike those that are favored by phainopeplas (Appendix B). Pollination limitation is another possible impediment to the establishment of an infection front by a single or a few individuals. *Phoradendron californicum* is dioecious and may experience an Allee effect in pollination, and hence fruit production, if pollinators have difficulty locating isolated individuals.

In a heterogeneous landscape - one with many host species - the interaction between dispersers, hosts and mistletoes is more complex, leading to different spatial patterns. Mistletoe distributions depend on seed deposition, seedling establishment, mistletoe growth and mortality. I found that host species were not always infected in proportion to their abundance (Appendix E). Seed deposition was higher than expected, based on species abundance, in *O. tesota* and *P. velutina* which have very open canopies. Seed deposition was lower than expected in *C. microphyllum* and *Acacia* spp. which have closed canopies (*C. microphyllum*) and grabbing thorns (*Acacia*). Seed rain is mediated by phainopepla perching preferences (Appendix B). In this case, tree architecture may be important in phainopepla preferences, leading to the observed patterns of seed deposition. There were also differences in establishment success between hosts. Nearly all of the *P. velutina* at the Silverbells site received seeds, but only one *P. velutina* at the site was observed with a mistletoe infection. This is probably due to an inability of the parasite to establish on this host at this site and is in striking contrast to the high rates of infection of *P. velutina* observed at the Santa Rita site only 50 miles away. I suspect that *P. californicum* is specializing on the most abundant hosts at these two sites, and this may even be an example of two host races. This could be further resolved with transplant experiments. At the regional scale, the difference in infection patterns between the Silverbell and Santa Rita sites (Appendix A, E) suggests a high degree of isolation. At this scale these areas probably represent nearly closed populations. Again genetic studies can clarify the degree of isolation between populations in different ranges.

In conclusion, desert mistletoes are an excellent system in which to study spatial ecology. Their spatial patterns are relatively clear, and their mode of dispersal allows establishing clear connections between the spatial patterns found in a landscape and the processes and mechanisms that create them. At the smallest scale, that of individual trees, my experiments and observations of birds and seeds provided the clues to explain the patterns at the intermediate or neighborhood level. These, in turn, provided hypotheses for the patterns that I could find in the landscape and the region.

## REFERENCES

- Alexander, H.M. 1984. Spatial patterns of disease induced by *Fusarium moniliforme* var. *subglutinans* in a population of *Plantago lanceolata*. *Oecologia* 62:141-143.
- Alexander, H.M. 1989. Spatial heterogeneity and disease in natural populations. Pages 144-164 *In* M. Jeger, editor. *Spatial Components of Plant Disease Epidemics*. Prentice-Hall Inc., Englewood Cliffs, New Jersey, USA.
- Alexander, H.M. 1990. Dynamics of plant-pathogen interactions in natural plant communities. Pages 31-45 *In* J.J. Burdon and S.R. Leather, editors. *Pests, Pathogens and Plant Communities*. Blackwell Scientific Publications, Boston, Massachusetts, USA.
- Anderson, R.M. and D.M. Gordon. 1982. Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology* 85: 373-398.
- Anderson, R.M. and R.M. May. 1979. Population biology of infectious diseases: Part I. *Nature* 280: 361-367.
- Calder, D.M. 1983. Mistletoes in focus: an introduction. Pages 1-18 *In*: Calder, M. and P. Bernhardt, editors. *The Biology of Mistletoes*. Academic Press, San Diego, California, USA.
- Carlile, D. W., J. R. Skalski, J. E. Barker, J. M. Thomas and V. I. Cullinam. 1989. Determination of ecological scale. *Landscape Ecology* 2: 203-213.
- Chu, M.C. 1999. Ecology and Breeding of Phainopeplas (*Phainopepla nitens*) in the Desert and Coastal Woodlands of Southern California. Ph.D. Dissertation. University of California at Berkeley. Berkeley, California, USA.
- Chu, M. and G. Walsberg. 1999. Phainopepla (*Phainopepla nitens*). No. 415 *In*: A. Poole and F. Gill, editors. *The Birds of North America*. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Clay, K., D. Dement, and M. Rejmanek. 1985. Experimental evidence for host races in mistletoe (*Phoradendron tomentosum*). *American Journal of Botany* 72: 1225-1231.
- Cowles, R.B. 1936. The relation of birds to seed dispersal of the desert mistletoe. *Madroño* 3: 352-356.

- DeAngelis, D. L., W. M. Post and C.C. Travis. 1986. Positive Feedback in Natural Systems. Springer-Verlag, New York, New York, USA.
- Donohue, K. 1995. The spatial demography of mistletoe parasitism on a Yemeni Acacia. *International Journal of Plant Science* 156: 816-823.
- Fauchald P., K. E. Erikstad and H. Skarsfjord. 2000. Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. *Ecology* 81: 773-783.
- Gardner, R. H. 1998. Pattern, process and the analysis of spatial scales. Pages 17-34 *In* D. L. Peterson and V. T. Parker, editors. *Ecological Scale*. Columbia University Press, New York, New York, USA.
- Glazner, J. T., B. Devlin and N. Ellstrand. 1988. Biochemical and morphological evidence for host race evolution in desert mistletoe, *Phoradendron californicum* (*Viscaceae*). *Plant Systematics and Evolution* 161: 13-21.
- Hanski, I. A. and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5 - 26 *In* I. A. Hanski and M. Gilpin, editors. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California, USA.
- Hanson, L. 1991. Dispersal and connectivity in metapopulations. Pages 89-103 *In* M. Gilpin and I. Hanski, editors. *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, San Diego, California, USA.
- Harper, J.L. 1990. Pests, pathogens and plant communities: an introduction. Pages 3-14 *In* J.J. Burdon and S.R. Leather, editors. *Pests, Pathogens and Plant Communities* Blackwell Scientific Publications, Boston, Massachusetts, USA.
- Hawksworth, F.G. 1983. Mistletoes as forest parasites. Pages 317-333 *In* Calder, M. and P. Bernhardt, editors. *The Biology of Mistletoes*. Academic Press, San Diego, California, USA.
- Husband, B. C. and S.C.H. Barrett. 1996. A metapopulation perspective in plant population biology. *Journal of Ecology* 84: 461-489.
- Ims, Rolf A. 1995. Movement patterns related to spatial structures. Pages 85-109 *In* L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic Landscapes and Ecological Processes*. Chapman and Hall, London, UK.

- Irwin, M. E. and G. E. Kampmeier. 1989. Vector behavior, environmental stimuli, and the dynamics of plant virus epidemics. Pages 14-39 *In* M. Jeger, editor. *Spatial Components of Plant Disease Epidemics*. Prentice-Hall Inc., Englewood Cliffs, New Jersey, USA.
- Jaenike, J. 1990. Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics* 21: 243-73.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for valuating resource preference. *Ecology* 61: 65-71.
- Kareiva, P. 1994. Space: the final frontier for ecological theory. *Ecology* 75: 1.
- Kearney, T. and R. Peebles. 1969. *Arizona Flora*. University of California Press, Los Angeles, California, USA.
- Kelly, C., D. L. Venable, and K. Zimmer. 1988. Host specialization in *Cuscuta costaricensis*: an assessment of host use relative to host availability. *Oikos* 53: 315-320.
- Kermack, W.O. and A.G. McKendrick. 1927. A contribution to the mathematical theory of epidemics. *Proceedings of the Royal Society of London A* 115: 700-721.
- Kitron, U. 1998. Landscape ecology and epidemiology of vector-borne diseases: tools for spatial analysis. *Journal of Medical Entomology* 35: 435-445.
- Kotliar, N. B. 1996. Scale dependency and the expression of hierarchical structure in *Delphinium* patches. *Vegetatio* 127: 117-128.
- 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.
- Larson, D. 1996. Seed dispersal by specialist versus generalist foragers: the plant's perspective. *Oikos* 76:113-120.
- Lawton, J. H., S. Nee, A. J. Letcher, and P. H. Harvey. 1994. Animal distributions: patterns and processes. Pages 41-58 *In* P.J. Edwards, R.M. May, and N. R. Webb, editors. *Large-Scale Ecology and Conservation Biology*. Blackwell Scientific Publications, Boston, Massachusetts, USA.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.

- Levins, R. 1970. Extinction. Pages 77-107 *In* M. Gestenhaber, editor. *Some Mathematical Problems in Biology*. American Mathematical Society, Providence, Rhode Island, USA.
- Martínez del Rio, C., M. Hourdequin, A. Silva, and R. Medel. 1995. The influence of cactus size and previous infection on bird deposition of mistletoe seeds. *Australian Journal of Ecology* 20: 571-576.
- Maruyama, M. 1963. The second cybernetics: deviation-amplifying mutual causal processes. *American Scientist* 51: 164-179.
- May, D. 1971. The role of populational differentiation in experimental infection of *Prosopis* by *Phoradendron*. *American Journal of Botany* 58: 921-931.
- May, R.M. 1990. Population biology and population genetics of plant-pathogen associations. Pages 309-326 *In* J.J. Burdon and S.R. Leather, editors. *Pests, Pathogens and Plant Communities*. Blackwell Scientific Publications, Boston, Massachusetts, USA.
- Menendez, R. and Thomas, C. D. 2000. Metapopulation structure depends on spatial scale in the host-specific moth *Wheeleria spilodactylus*(Lepidoptera: pterophoridae). *Journal of Animal Ecology* 69: 935-951.
- Minogue, K.P. 1989. Diffusion and spatial probability models for disease spread. Pages 127-143 *In* M. Jeger, editor. *Spatial Components of Plant Disease Epidemics*. Prentice-Hall Inc., Englewood Cliffs, New Jersey, USA.
- Nee, S., R. May, and M. Hassell. 1997. Two-species metapopulation models. Pages 123-147 *In* I. A. Hanski and M. E. Gilpin, editors. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California, USA.
- Norton, D. A., and M. A. Carpenter. 1998. Mistletoes as parasites: host specificity and speciation. *Trends in Ecology and Evolution* 13: 101-5.
- Oliver, M A. and R. Webster. 1986. Combined nested and linear sampling for determining the scale and form of spatial variation of regionalized variables. *Geographical Analysis* 18: 227-242.
- O'Neill, R. V. D. L. DeAngelis, J. B. Waide and T.F. H. Allen. 1986. *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Overton, J.M. 1994. Dispersal and infection in mistletoe metapopulations. *Journal of Ecology* 82: 1-13.

- Overton, J. M. 1996. Spatial autocorrelation and dispersal in mistletoes: field and simulation results. *Vegetatio* 125: 83-98.
- Overton, J.M. 1997. Host specialization and partial reproductive isolation in desert mistletoe (*Phoradendron californicum*). *Southwest Naturalist* 42: 201-209
- Pacala, S. W. and A. P. Dobson. 1988. The relation between the number of parasites/host and host age: population dynamic causes and maximum likelihood estimation. *Parasitology* 96: 197-210.
- Reid, N., N.M. Smith and Z. Yan. 1995. Ecology and population biology of mistletoes. Pages 285-310 *In* Lowman, M.D. and N.M. Nadkarni, editors. *Forest Canopies*. Academic Press, San Diego, California, USA.
- Schneck, J. 1884. Notes on *Phoradendron flavescens*, Nutt II. *Botanical Gazette* 9: 101-103.
- Schupp, E. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107: 15-29.
- Taylor, P. D., L. Fahrig, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68: 571-573.
- Thomas, C. D and Kunin, W. E.. 1999. The spatial structure of populations. *Journal of Animal Ecology* 68: 647-657.
- Thrall, P. H. and A. M. Jarosz. 1994. Host-pathogen dynamics in experimental populations of *Silene alba* and *Ustilago violacea*. I. Ecological and genetic determinants of disease spread. *Journal of Ecology* 82: 549-559.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171-197.
- van Coller, A. L., K. H. Rogers and G. L. Heritage. 2000. Riparian vegetation-environment relationships: complimentarity of gradients versus patch hierarchy approaches. *Journal of Vegetation Science* 11: 337-350.
- Walsberg, G. E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. *Condor* 77:169-174.
- Walsberg, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilonotidae). University of California Publications in Zoology 108:1-63.

- Wenny, D. G. and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Science, USA* 95: 6204-6207.
- Wiens, J..A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wiens, John A. 1997. Metapopulation dynamics and landscape ecology. Pages 43-62 *In* I. A. Hanski and M. E. Gilpin, editors. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California, USA.
- Wu, J. and O. L. Louks. 1995. From balance of nature to hierarchical patch dynamics: paradigm shift in ecology. *Quarterly Review of Biology* 70: 439-466.

## APPENDIX A

MISTLETOES AS PARASITES AND SEED-DISPERSING BIRDS AS DISEASE  
VECTORS: CURRENT UNDERSTANDING, CHALLENGES, AND  
OPPORTUNITIES.

Mistletoes as parasites and seed-dispersing birds as disease vectors: current understanding, challenges, and opportunities.

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**Key words:** Mistletoes, seed-dispersers, metapopulation models, parasitism.

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**ABSTRACT**

Mistletoes play a dual role in biological communities: they are parasites of host plants and mutualists of the birds that disperse their seeds. These birds, therefore, are seed dispersers and disease vectors at the same time. Like many foraging animals, mistletoe seed-dispersers react to the abundance of resources by varying their density and activity in response to mistletoe abundance. These responses can create a positive feedback – high local abundances of mistletoes can lead to higher seed deposition. Data from two desert mistletoes (*Tristerix aphyllus* and *Phoradendron californicum*) demonstrate that previous parasitism in a host leads to increased seed deposition and presumably to increased re-infection. At a larger spatial scale, both species show that transmission (both new and reinfections) increases as the local mistletoe prevalence increases. This result suggests that mistletoe infections may show significant spatial aggregation at large spatial scales. A simple patch-occupancy metapopulation model that assumes that hosts are patches inhabited by mistletoes predicts under general conditions that host infection frequency increases with host age. Our data uphold this prediction. We identify the ingredients needed to analyze spatial patterns of mistletoe infection and to construct models of the spatial and temporal dynamics of mistletoe infections. We propose that the characteristics of mistletoes place their ecology at the convergence of metapopulation ecology, the biology of seed dispersal, and plant physiology.

## Introduction

Mistletoes are plant parasites in the families Loranthaceae, Viscaceae, Misodendraceae, Eremolepidaceae, and Santalaceae. They are found on almost every continent and in a diverse range of habitats. They infect a wide variety of host species ranging from eucalypt trees and shrubs in Australian rainforests to columnar cacti in Chilean deserts (Hawksworth, 1983). Most mistletoes are vector-borne parasites, in which the vectors are seed-dispersing birds (Martínez del Rio *et al.*, 1996). In most vector-borne parasites and diseases, the vector maintains a parasitic or, at best, a commensal relationship with the parasite (Price, 1980). Mistletoes are unique among vector-borne parasites because they maintain a mutualistic interaction with their vectors (Martínez del Rio *et al.*, 1996, Fig. 1). Birds obtain nutrients, energy and, in the desert, water from mistletoes (Walsberg, 1975; Reid, 1991). In turn, mistletoes benefit from directed movement of their propagules into safe germination sites (Reid, 1991).

Most mistletoes share a common life history: Typically, when a seed germinates on an appropriate host, the radicle elongates until it contacts the host; it then forms a haustorium, consisting of a holdfast and specialized penetration cells that grow into the host's branch (Calder, 1983). The mistletoe's haustorium establishes contact with the host's xylem, allowing the mistletoe to absorb water, minerals and, in some cases, sugars and amino acids (Calder, 1983). Mistletoes grow to reproductive age, their flowers are pollinated, often by animals, and flowers become seed-containing fruits. The seeds of most mistletoe species are dispersed by birds, many of which are highly specialized to consume and process mistletoe berries (Reid, 1991). The seeds are either defecated,

regurgitated or wiped onto host branches where they adhere by means of their viscous endocarp (Reid *et al.*, 1995). A very small fraction of seeds ends up on branches of suitable size in appropriate hosts (Sargent, 1994), and the cycle starts again.

Because of the apparently specialized nature of the interaction between mistletoes and birds, the dispersal of mistletoes has received considerable attention (Cowles, 1936; Reid, 1991; Larson, 1996; Overton, 1994; Sargent, 1995; Martínez del Río *et al.*, 1995). Here we will attempt to place the interaction between birds, mistletoes, and host plants in a broad context. We will argue that mistletoes present unique opportunities to integrate seed dispersal ecology with several other, seemingly disparate, areas of biology such as plant physiology, parasitology, and metapopulation ecology. We will also contend that the biology of mistletoes makes them well suited to elaborate and test models about the role played by seed dispersal in shaping the spatial and temporal dynamics of plant populations.

First we describe the natural history of two species of desert mistletoes:

*Phoradendron californicum* (*Viscaceae*) and *Tristerix aphyllus* (*Loranthaceae*).

Throughout, we use parasitology terminology such as “prevalence” and “intensity” of infection. Prevalence is infection frequency; intensity is the number of parasites per host (Price, 1980).

### **The natural history of two desert mistletoes**

The two arid land mistletoes, *Phoradendron californicum* and *Tristerix aphyllus*, for which we will present data share many characteristics, but differ in others.

*Phoradendron californicum* is found in northwestern Mexico and the southwestern United States where it infects a variety of woody trees and shrubs (Kuijt, 1994). *Tristerix aphyllus* inhabits the arid and semiarid regions of central and northern Chile where it infects columnar cacti (Follman and Mahu, 1964; Martínez del Rio *et al.*, 1995). Whereas *P. californicum* is a typical hemiparasitic aerial mistletoe, *T. aphyllus* is a largely non-photosynthetic holoparasite (Kraus *et al.*, 1995) that produces an extensive internal endophyte that invades the succulent tissues of its hosts (Mauseth, 1990). *Tristerix aphyllus* exhibits an external phase only when it blooms and produces fruit (Mauseth *et al.*, 1983).

Both mistletoes are animal pollinated. *Tristerix aphyllus* produces hermaphroditic, showy, red flowers that are visited by hummingbirds (Martínez del Rio, 1995). *Phoradendron californicum* is dioecious and produces tiny insect-pollinated flowers. The seeds of both *T. aphyllus* and *P. californicum* are dispersed primarily by a single species of avian frugivore. The fruits of *T. aphyllus* are consumed by endemic Chilean mockingbirds (*Mimus thenca*, Mimidae; Martínez del Rio *et al.*, 1995) and the fruits of *P. californicum* are consumed by phainopeplas (*Phainopepla nitens*, Ptilogonatidae; Cowles, 1936). Although other bird species consume the fruits of these two mistletoes (Larson, 1996), in both cases a single frugivore is responsible for the vast majority of the fruits consumed and of the seeds dispersed.

### **Mistletoes and scales: patterns and mechanisms**

The web of interactions in which mistletoes are involved can be investigated at many spatial, temporal, and conceptual scales (Carlile *et al.*, 1989; Kotliar and Wiens, 1990). Even a cursory visit to a geographical area where mistletoes occur reveals clear patterns at a variety of spatial scales. At a given site, and for a single host species, some individuals are more intensely infected than others. Like many other parasites, it is common to find that the distribution of mistletoes among individual hosts is heavily clumped (Fig. 2 and Overton, 1996). Why are some individual hosts more intensely parasitized than others? If the site contains several potential host species, it is sometimes the case that the frequency of parasitism differs among host species (Lamont, 1982; Appendix E). Why does the prevalence of mistletoes differ among host species?

At a larger spatial scale, the overall prevalence and intensity of infection may vary among sites (Overton, 1996). Why are mistletoes more abundant in some sites than in others? Providing mechanistic answers to these questions requires consideration of all the steps in the life history of mistletoes: seed rain, seedling establishment, mistletoe growth and survival, and mistletoe reproductive success.

**Seed rain.**- The actions of seed dispersers can lead to differential deposition of seeds among hosts or sites. Birds may choose to perch on individual hosts and may move preferentially among sites with predictable characteristics. Birds may prefer hosts with specific heights, canopy architectures, and resource abundances. For example, Medel (2000) found that the time spent by Chilean Mockingbirds on individual cacti and the rate

at which they deposited *T. aphyllus* seeds on them declined with the length of the cacti's protective spines. In Arizona, we have found that territorial phainopeplas significantly prefer to perch in the tallest trees (Appendix B). Their preference for taller trees leads to increased seed deposition with increased height (Fig. 3). Differences in site characteristics, such as abundance of critical resources and cover, may lead to variation in seed disperser abundance among sites (Sallabanks, 1993 and references therein) and/or in the frequency and time spent by dispersers at different sites (Sallabanks, 1993; Martínez del Rio *et al.*, 1995). These differences can translate into differences in seed rain among sites.

**Seedling establishment.**- After differential seed rain among hosts, seedling establishment is the next step that can lead to variation in mistletoe prevalence and intensity among hosts and sites. Once a seed is deposited onto a host and germinates, the probability that the seedling will become established is dependent on the match between the characteristics of the host and those of the mistletoe. Hosts may show a variety of "incompatibility" mechanisms and responses that prevent mistletoes from establishing (reviewed in detail by Reid *et al.*, 1995). A potential host that is "resistant" may remain relatively free of infection even if it receives large numbers of mistletoe seeds. We use quotation marks in the words "incompatibility" and "resistant" to denote lack of certainty about the evolutionary mechanisms that lead to interspecific differences in susceptibility to infection. Barlow (1981) has suggested that mistletoes may show local adaptation to the most abundant local host species and that these adaptations may reduce the mistletoe's

effectiveness at infecting other host species. Research on the factors that lead to local adaptation of mistletoes to different hosts is an area that requires attention and that is likely to yield interesting results (Norton and Carpenter, 1998). The frequent reports of host races in mistletoes suggest dynamic evolutionary interactions between mistletoes and their hosts (Norton and Carpenter, 1998; Overton, 1997 and references therein).

**Host quality, mistletoe persistence and reproductive success.**- After germination, successful mistletoe seeds establish an intimate haustorial connection with their hosts (Yan, 1993 and references therein). The growth, survival, and reproductive output of mistletoes depend to a large extent on their success at using this connection to tap their host's resources. Although many of the details of the physiological interaction between mistletoes and their hosts have been elucidated in detail (Press, 1995; Ehleringer and Marshall, 1995), the consequences of this interaction for the population biology of mistletoes and hosts is to a large extent unknown.

Mistletoes obtain water, carbon in the form of organic solutes, nitrogen, and minerals from their hosts. The availability of all these resources in hosts can limit their growth, reproduction, and survival. Mistletoes procure carbon photosynthetically from the atmosphere and/or heterotrophically from their hosts. Some species, such as dwarf mistletoes (*Arceuthobium spp.*) and *T. aphyllus*, tap both the xylem and phloem of the host and are considered primarily heterotrophic (Press, 1995). Other species tap only the xylem stream and have traditionally been considered autotrophic (Raven, 1983). This

view has been challenged by the discovery of substantial heterotrophic carbon transfer from hosts to several species of "xylem-tapping" mistletoes (reviewed by Press, 1995).

Because, unlike carbon, nitrogen and water are obtained exclusively from hosts, these nutrients can be regarded as limiting to mistletoes. Schulze and Ehleringer (1984) demonstrated faster growth of mistletoes infecting nitrogen-fixing than non-nitrogen fixing hosts. Because mistletoe size appears to determine fruit production and fruit size (Dawson and Ehleringer, 1991), nitrogen availability may be a key determinant of host quality.

For desert mistletoes, host water status is a primary influence on growth and reproduction. Gregg (1991) and Ehleringer (1989) observed that mistletoes were found more commonly on hosts with relatively low water stress than on those experiencing severe water stress. Presumably, increased water stress can induce cavitation in the parasite's xylem and lead to death (Ehleringer and Marshall, 1995). Lei (1999) found that host trees (*Acacia greggii*) were significantly more water stressed in upland terrace sites than in washes in the Mojave Desert. The intensity of parasitism, size of parasite individuals, and fruit crops of *P. californicum* were all greater on host trees found in washes than on those found in upland terraces (Lei, 1999). In arid Australia, roadside mulga trees (*Acacia aneura*) were more intensely parasitized by mistletoes (*Amyema maidenii* and *Lysianna spp.*) than trees away from roads (Norton and Stafford Smith, 1999). Roads slow overland water flow and increase runoff increasing local infiltration and hence the water supply for mistletoe hosts. As these last two examples indicate, even

subtle differences in the hydrology and geomorphology of the microsites inhabited by mistletoe hosts can influence the quality of these hosts as mistletoe habitats.

### **Mistletoes, parasitism, and metapopulations.**

The natural history of mistletoes reveals potential mechanisms that can lead to differences in mistletoe prevalence and intensity among hosts and sites. Here we attempt to incorporate these mechanisms into an integrative, potentially predictive framework that emerges directly from recognizing that mistletoes are parasites with a metapopulation structure. This section poses several predictions that spring from this view and uses data on *P. californicum* and *T. aphyllus* to evaluate these predictions.

What are the consequences of the mutualism between mistletoes and birds for the population biology of mistletoes? Like other consumers, mistletoe-feeding birds tend to concentrate their activity at sites with relatively high resource densities (Martin, 1985; Sargent, 1990). The response of birds to mistletoes is likely to take place at two scales: birds should perch in fruit-bearing parasitized trees more frequently than in non-parasitized trees (Martínez del Rio *et al.*, 1995), and birds should be more abundant and spend more time at sites with higher mistletoe prevalences (Martínez del Rio *et al.*, 1996). Furthermore, prevalence and intensity of infection are often correlated in host-parasite systems (Fig. 4, for example). Fruit abundance at a site is a multiplicative function of the number of fruits per parasite, infection intensity, and prevalence. Thus, fruit abundance should increase in an accelerating fashion with prevalence.

The mutualism between birds and mistletoes leads to two simple predictions: (1) Because birds should preferentially visit hosts that are infected by mistletoes, already parasitized hosts should receive seeds more frequently than non-parasitized hosts. (2) Because birds should show higher densities and/or spend more time at sites with higher mistletoe infection frequencies, seed deposition by birds should increase with mistletoe prevalence.

Several studies have provided support for the first prediction (see Figs. 3 and 5). In general, seed rain is higher on parasitized than on non-parasitized hosts (Martínez del Rio *et al.*, 1996), and experimental removal of mistletoes from hosts leads to reduced seed deposition (Appendix B). Unless infection by mistletoes induces host resistance (Hoffmann *et al.*, 1986), increased seed deposition onto already infected hosts should lead to re-infection and increased parasite loads. The extremely clumped distribution of mistletoes among host individuals seen in many mistletoe populations (Fig. 2) is probably a result of the disproportionate number of seeds deposited by birds onto already parasitized hosts (Overton, 1996). Preferential seed dispersal onto already parasitized hosts is a special case of “conspecific attraction” (i.e., preferential dispersal to occupied patches over suitable empty ones, Smith and Peacock, 1990), a phenomenon that can lead to a lower frequency of occupied patches and hence to lower mistletoe prevalences (Ray *et al.*, 1991, and see section **Overton’s model**).

The response of birds to mistletoe-infected hosts can lead to increased seed rain into already infected trees. Can the response of birds to mistletoes be extended to a larger spatial scale? Do sites with higher prevalences also receive more seeds? Both *T. aphyllus*

and *P. californicum* show a positive, accelerating relationship between seed deposition onto non-infected hosts and prevalence (Fig. 5; Martínez del Río *et al.*, 1996). This relationship could lead to a positive correlation between the rate at which new hosts are infected at a site and prevalence. Thus, the response of birds would lead to a positive feedback in infection that could lead to spatial aggregation of parasitism in a landscape and to a positive autocorrelation in prevalence across it (Martínez del Río *et al.*, 1996). The spatial scale at which this aggregation can be detected, however, depends on the scale at which individual birds and bird populations respond to the density of mistletoes and generate spatial patterns of seed deposition.

Overton (1996) found significant clumping of *P. californicum* and *Psittacanthus sonorae* mistletoes at the level of individual hosts, although he did not find autocorrelation at a larger spatial scale. The relatively small area he studied ( $\approx 1.5$  ha.) may not be large enough to reveal variation in the spatial pattern of mistletoe infections. Determining the spatial scale at which mistletoe seed dispersal mechanisms generate spatial infection patterns is a significant challenge (Levin, 1992). However, it is a challenge that must be tackled in order to understand the effect of disperser behavior and ecology on the spatial dynamics of mistletoe populations.

**Mistletoes and metapopulations.**- Overton (1994) treated mistletoes as patch-occupancy metapopulations. Hosts can be identified as “patches,” infection and loss of infection can be characterized as patch occupancy and patch extinction, respectively, and seed dispersal and establishment can be equated with patch colonization. Mistletoe hosts

can be viewed as living patches (hosts) inhabited by mistletoe subpopulations. Strictly, a subpopulation is a set of individuals that interacts with each other with high probability (Hanski and Simberloff, 1997). Many mistletoes have animal pollinators that can travel, and hence can move genes in the form of pollen among patches, one consequence of which is to homogenize the spatial structure of mistletoe subpopulations (Reid *et al.*, 1995).

Mistletoes form discrete groups that inhabit distinct patches separated by unsuitable habitat. Populations in these patches can become extinct, either when all mistletoes in a patch die or when the host dies. Patches/hosts can be colonized only when propagules from other patches immigrate into them. Mistletoe subpopulations rarely inhabit all patches/hosts available, and hosts show turnover, both because mistletoe populations go extinct and because hosts die. Patch turnover is a key element of the colonization-extinction dynamics that characterize metapopulations (Hanski and Simberloff, 1997).

**Overton's model.-** A variety of host traits can influence the fraction of each host/patch that is occupied and the number of mistletoes inhabiting a host/patch. Here we present the simplest possible metapopulation model that explores one of these factors. Overton (1996) modified Levins' (1969, 1970) classical metapopulation model to explore the role of host age on host occupancy. Patch turnover confers an age structure to the patch population, and thus Overton's (1996) model can be used to predict the relationship between host/patch occupancy and age. Overton's model depicts an array of

hosts/patches that are either occupied or unoccupied at any point in time. Empty patches are equally likely to receive seeds and occupied hosts are equally likely to produce them. Changes in patch occupancy ( $x$ , where  $0 \leq x \leq 1$ ) are then described by:

$$dx/dt = mx(1-x) - (e_h + e_d)x, \quad \text{equation (1)}$$

where each occupied host contributes colonists to other hosts at a rate  $m$ . Infected hosts become vacant at a rate  $e = e_h + e_d$ , where  $e_d$  is the rate at which mistletoe subpopulations go extinct ( $e_d$  is the rate of “demographic extinction” in mistletoe subpopulations) and  $e_h$  is the intrinsic rate at which hosts are lost and replaced (the host population is assumed to be in equilibrium). Solving for the equilibrium fraction of hosts occupied (i.e.  $dx/dt = 0$ ) gives:

$$x^* = (m - (e_h + e_d))/m. \quad \text{equation (2)}$$

This equilibrium is positive and less than 1 only if mistletoes can invade when their frequency is low (i.e.,  $m > (e_h + e_d)$ ) and if the turnover of mistletoes in patches is positive (i.e.,  $(e_h + e_d) > 0$ ).

Let  $x_c(a)$  be the fraction of a cohort of age  $a$  that is infected/occupied. Assuming that the probability that a host dies is independent of mistletoe infection, then the loss rate of infection is due only to mistletoe demographic extinction (measured by  $e_d$ ). At equilibrium, the overall rate at which hosts become infected is:

$$dx_c(a)/da = mx^*(1-x_c) - e_d x_c, \quad \text{equation (3)}$$

which can be solved to yield

$$x_c(a) = (x^*m/(m-e_h))(1-\exp(-(m-e_h)a)).$$

equation (4)

Equation 4 yields two predictions: (1) Occupancy should increase as a function of host age that tends asymptotically to  $x^*_c = x^*m/(m-e_h)$ , and (2) occupancy should increase with host age at an increasing rate at sites with higher among-host/patch dispersal rates (i.e., if  $m$  is large, the relationship between  $x_c$  and  $a$  is steeper).

A positive relationship between host age/size and infection prevalence is commonly found in mistletoe populations (Figs. 6, 7; Appendix C, E; Donohue, 1995; Overton, 1996; Kelly, 1998; Lei, 1999). Thus, prediction 1 appears to hold true, assuming that size is a good proxy for age. However, the positive relationship between infection prevalence and host age that is commonly found in mistletoes can be attributed to two non-exclusive hypotheses: (1) accumulation of mistletoes with age (as implied in equations 3 and 4), or (2) the preference of avian seed-dispersers for taller, and likely older, host individuals. Explanations based on larger hosts receiving more seeds should result in a strongly positive size-intensity relationship. Although many mistletoes exhibit a significant and positive host size-infection intensity relationship (Overton, 1996), these

relationships are often weak (Fig. 6). Two factors may account for the weakness of this relationship: (1) not only are already parasitized hosts more likely to receive seeds, and hence become reinfected, but (2) older/taller trees are also more likely to receive seeds (Fig. 3). Age/size-specific differences in seed deposition onto hosts may exacerbate the age-occupancy relationship, but they are not required to generate it (Overton, 1996).

According to Overton's (1996) model, occupancy should increase with host age at an increasing rate at sites with higher among host/patch dispersal. For *P. californicum* infecting velvet mesquites (*Prosopis velutina*) at 10 sites in Arizona, we found positive relationships between host-size and occupancy (Fig. 8a) but no relationship between the steepness of these relationships (as measured by the slope of the log odds function; Ramsey and Schafer, 1997) and seed dispersal into non-parasitized hosts (Fig. 8b).

Because many of the assumptions of Overton's (1996) model are not met by most mistletoe systems, we propose a modification to the model that would incorporate new or modified assumptions. Overton's model assumes that seed dispersal is random. If  $mx$  describes the rate of successful dispersal from occupied patches, only  $(1-x)$  of these propagules disperse to unoccupied patches. Most of the available data suggests that, in mistletoes, dispersal is not random. Because a disproportionate number of seeds fall onto already infected hosts, mistletoes are a good example of organisms exhibiting conspecific attraction (Stamps, 1991). Ray *et al.* (1991) modified Levins' model to incorporate conspecific attraction by assuming that a fraction  $A$  of all propagules is deposited in already occupied patches. Altering Overton's (1996) model to incorporate conspecific attraction makes mistletoe invasion more difficult (the criterion for invasion is  $m(1-A) >$

$(e_h + e_d)$ ) and yields a lower occupancy equilibrium ( $x^* = (m(1-A) - (e_h + e_d)) / (m(1-a))$ ), but leaves all other qualitative predictions unchanged. Occupancy still increases as a function of host age, although at a reduced rate and with a lowered maximal occupancy ( $x_c^* = mx^*(1-A) / (m(1-A) - e_h)$ ). Conspecific attraction does not explain the lack of a significant positive relationship between the steepness of the occupancy vs. age curve and dispersal efficiency.

**Beyond Overton's model: structured and spatially explicit models.-** Although conspecific attraction does not change the predictions of Overton's model qualitatively, it is likely to have a significant effect on more realistic, and hence more complex models. Exploration of the effects of host age and parasite status on infection intensity may be facilitated by construction of structured mistletoe metapopulation models. The goal of these models is to determine how different processes produce a distribution of local population sizes (Gyllenberg *et al.*, 1997 and references therein).

So far, all the models that we have described for mistletoe populations are spatially implicit. They ignore the spatial location of hosts/patches and hence assume that all subpopulations are equally connected (Hanski and Simberloff, 1997). Although we believe that a large number of questions can be explored with these models, other questions require explicit consideration of space. For example, we have argued that the positive, accelerating relationship between seed deposition onto non-infected hosts and prevalence (Fig. 5) may lead to spatial aggregation of parasitism in a landscape and to a positive autocorrelation in prevalence across it (Martínez del Río *et al.*, 1996). Testing

the logical merit of this hypothesis requires a spatially explicit model. Overton (1996) and Lavorel *et al.* (1999) offer two elegant examples of spatially structured models for mistletoes. Mechanistic models of seed dispersion patterns can be constructed directly from the characteristics of mistletoes and hosts (density, size, and distribution) and from the behavior of the birds that disperse their seeds (Overton, 1996, Lavorell *et al.*, 1999). Spatial patterns of seed dispersal are key to understanding plant population dynamics in a spatial context (Nathan and Muller-Landau, 2000). Mistletoes offer an unparalleled opportunity to document the consequences of seed dispersal by animals on the spatial dynamics of plant populations.

### **Future directions**

In this paper we have emphasized the consequences of the interaction between seed-dispersers and mistletoes for the metapopulation ecology of these plant parasites. We have placed less emphasis on the fact that the patches occupied by mistletoes are exploited living organisms, and we have ignored the roles they play in their biotic communities. We believe that a more complete understanding of mistletoe population ecology must recognize the intricacies of their interactions with hosts and their roles in biotic communities.

**Hosts and mistletoes.-** The biological characteristics of hosts and the physical environment they occupy can determine their quality as patches for mistletoe occupancy. In a previous section we reviewed some of the physiological characteristics that can

determine a host's quality. We provided examples that suggest that the survival, growth, and reproduction of mistletoes can depend on the host's water and nitrogen status. In mistletoes, knowledge about the physiology of hosts/patches can allow one to predict which patches are sources that contribute mistletoe colonists to other patches, and which are sinks, where mistletoe subpopulations would go extinct in the absence of immigration (Pulliam, 1988; Hanski and Simberloff, 1997). Several studies have documented differences in mistletoe performance among host types (i.e., hosts of different species and/or hosts with contrasting physiological status). To our knowledge, no study has investigated whether these differences lead to characterization of some host types as sources and others as sinks. Because at least some mistletoes can be accurately aged (Dawson *et al.*, 1990), the effect of the host's physiology on the demography of subpopulations can be studied. Mistletoes and their hosts offer a unique opportunity to integrate the physiological details of a plant-plant interaction with their demographic and even metapopulation consequences.

Mistletoes are not only influenced by the physiological status of their hosts, but have important impacts on it. Mistletoes probably degrade the quality of the patches that they occupy, and increase their turnover by killing their hosts. Using Burdon's (1991) colorful classification, mistletoes can be castrators, debilitators, or killers. Because some mistletoes can infect and damage economically important plants, there is some information on their effects on host growth, reproduction, and survival (reviewed by Reid *et al.*, 1995). Little is known, however, about their effects on host populations (Silva and Martínez del Rio, 1996; Medel, 2000). Most models that explore mistletoe population

and metapopulation dynamics assume that mistletoe infection has no effect on host survival and reproduction, and that host populations are at equilibrium. Addressing how mistletoes affect host populations and how this interaction affects the temporal and spatial dynamics of mistletoes requires that we obtain better empirical data on the effects of mistletoes on hosts and that we incorporate these effects into models of mistletoe-host interactions.

Several important insights in metapopulation theory were first made in epidemiology where the effects of parasites/pathogens on hosts cannot be ignored. For instance, eradication thresholds and optimal programs of eradication have long been understood in a disease context (Kermack and McKendrick, 1927; May, 1990) and the knowledge that a disease can be successfully eradicated even with remaining habitat patches (susceptible hosts) is critical for vaccination programs worldwide (Nee *et al.*, 1997). The most well-developed metapopulation theory is also in epidemiology, where each host individual represents a clear patch and the dynamics of colonization and extinction are clearly those of metapopulations (Lawton *et al.*, 1994; Nee *et al.*, 1997). These insights have begun to make their way into conservation biology with the goal, not of eradicating species, but of preserving them (Lawton *et al.*, 1994; Nee, 1994). Models of the interaction between mistletoes, hosts, and birds can be used to control mistletoe populations when needed (Lavorel *et al.*, 1999), and to conserve mistletoes when imperiled (Marvier and Smith, 1997; Robertson *et al.*, 1998). As many epidemiological studies exemplify, construction of these models must pay attention to, and incorporate, the details of the association between hosts and parasites.

**Mistletoes as community members.-** Mistletoes are intriguing elements of biotic communities because they play the dual role of host scourges and bird mutualist benefactors (Martínez del Rio, 1995; Fig. 1). In addition to the direct effects that mistletoes can have on the fecundity and viability of their hosts and mutualists, they may indirectly affect the host's competitors, herbivores, pollinators, and seed dispersers. Although community-level effects of plant pathogens have received significant attention (Dobson and Crawley, 1994 and references therein), we know little about the contribution of mistletoes to community composition and function.

Mistletoes can have significant effects on bird communities (Bennets *et al.*, 1996, Turner, 1991). Because many mistletoes are pollinated and dispersed by birds, their direct influence on birds is through the abundance of nectar and fruit. For example, *T. aphyllus* and *P. californicum* bloom and produce abundant fruit during the winter, when food resources are scarce. Areas heavily infected by these species are hot spots of activity for nectar- and fruit-eating animals (Martínez del Rio *et al.*, 1995, J. Aukema and C. Martínez del Rio unpubl data). Mistletoes can also have significant indirect effects on bird communities. For example, prevalence of the dwarf mistletoe *Arceuthobium vaginatum* was positively correlated with bird abundance and species richness (Bennets *et al.*, 1996). Because the fruit of dwarf mistletoes are not extensively used by birds, Bennets *et al.* (1996) concluded that mistletoe infections increase bird abundances by enhancing insects that feed on and pollinate mistletoes or that take advantage of the weakened condition of tree hosts.

Dwarf mistletoes promote bird diversity because they create a mosaic of habitat structures within a forest stand through their effect on tree growth and mortality. They also increase nesting habitat. Several forest bird species use the dense clumps (“witches’ brooms”) that are formed by branches of the host tree for roosts and nest sites (Bennets, 1991 and references therein). Mistletoes are often considered insidious forest pests that reduce the economic value of timber stands (Wicker, 1984). As such, mistletoe removal is practiced in managed forests with the objective of increasing timber production (Hawksworth and Wiens, 1995; Kelly *et al.*, 1997). In areas where management goals are not strictly focused on timber production, the value of mistletoes for biodiversity may make their control unjustified, impractical, or undesirable (Bennets *et al.*, 1996).

Although it is likely that mistletoes play a role in modulating the interaction of their hosts with competitors and mutualists, these effects have not been studied. Pennings and Callaway (1996) and Gibson and Watkinson (1992) have documented strong effects of the hemiparasites *Cuscuta salina* (*Convolvulaceae*) and *Rhinanthus minor* (*Scrophulariaceae*) on the communities that they inhabit. In both cases, the parasites increased local plant diversity by suppressing their primary hosts. It is unknown if mistletoes can also mediate the interaction between hosts and their competitors. Gehring and Whitham (1992) reported an intriguing interaction between a mistletoe (*Phoradendron juniperum*), its host tree *Juniperus monosperma*, and the host’s mycorrhizal mutualists. Mycorrhizal levels were negatively correlated with mistletoe infection. Gehring and Whitham (1992) pose two alternative hypotheses for this correlation: mistletoe infection may suppress mycorrhizae or mycorrhizae may protect

trees from mistletoe infection (Dehne, 1982). Although Gehring and Whitham's (1992) study does not allow distinguishing these two hypotheses, it highlights the potential complexity of the role of mistletoes in biological interactions and communities.

**Conclusions: a few relatively solid patterns and much work ahead**

The main messages of this paper can be summarized in the following sentence:

*“Mistletoes are parasitic plants that exhibit a metapopulation structure, and whose seeds are dispersed by mutualistic avian seed-dispersers”*

The elements highlighted in this sentence are responsible for several patterns that may characterize many, if not most, mistletoe populations. In this final section, we list these patterns and reiterate the mechanisms that probably shape them. Because the patterns listed here have been well documented in just a few mistletoe-host systems, and primarily in desert mistletoes, their generality is uncertain. These patterns should be viewed as testable hypotheses rather than general and firmly established results.

Mutualistic avian seed dispersers seem to respond to the abundance of mistletoes at two scales: individual hosts and sites. The consequence of this response is that seed dispersal is not random among hosts and across landscapes. We hypothesize that:

- 1) Seeds fall disproportionately more frequently on already parasitized than on non-parasitized hosts, and
- 2) seed rain increases with mistletoe prevalence across sites.

Hypotheses 1 and 2 yield two ancillary hypotheses:

1a) Disproportionate seed deposition onto already parasitized hosts leads to superinfection and to a highly aggregated distribution of parasite numbers among hosts, and

2a) Disproportionate seed deposition at sites with higher prevalence leads to spatial autocorrelation in parasitism prevalence across a landscape.

Mistletoe populations can be perceived as metapopulations in which hosts are patches. Under fairly general conditions, a simple metapopulation model suggests that:

3) The frequency of occupied hosts/patches increases with host age.

The logical and empirical validity of hypotheses 1a and 2a, and the generality of hypothesis 3 must be tested by the complementary use of structured (1a and 3) and spatially explicit (2a and 3) metapopulation models and, of course, by field research.

Mistletoes provide theoreticians and empiricists with unique opportunities and peculiar challenges. Many of the processes that are difficult to investigate in other species are relatively straightforward to study in mistletoes because they are sessile and hence relatively easy to count. Because in some cases they can be aged (Dawson *et al.*, 1990), their demography can be studied. Their seeds are large and visible and are dispersed by birds whose movements are relatively easy to follow (e.g., relative to vectors such as mosquitoes and tsetse flies; Kitron, 1998). Wheelwright and Orians (1982) have characterized the task of distinguishing safe germination sites as nearly impossible, but this task is relatively straightforward in mistletoes because seeds only establish on suitable hosts (Sargent, 1995). Mistletoes are ideal systems to integrate the ecology of

seed-dispersal into the larger framework of the temporal and spatial dynamics of plant metapopulations. Because the fine points of the interaction between hosts and mistletoes probably have significant consequences for the population biology of mistletoes, these plants provide a unique opportunity to determine the ecological penetrance of physiological processes. Finally, because data can be generated relatively rapidly in mistletoe systems, they provide an ideal arena for the testing and refinement of plant metapopulation models. We hope that the themes developed here will stimulate empiricists to explore other mistletoe systems and challenge theoreticians to model them.

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### Literature Cited

- Barlow, B. A. (1981) The loranthaceous mistletoes of Australia. In: Keast, A. (ed.) *Ecological biogeography of Australia*. Dr. W. Junk, Publ., The Hague, Netherlands. pp. 34-45.
- Bennets, R. E. (1991) The influence of dwarf mistletoe infestation on bird communities in Colorado ponderosa pine forests. Ph D thesis, Colorado State University, Fort Collins, Colorado, USA.
- Bennets, R. E., White, G. C., Hawksworth, F. G., and Severs, S. E. (1996) The influence of dwarf mistletoe on bird communities in Colorado ponderosa pine forests. *Ecological Applications* 6, 899-909.
- Burdon, J. J. (1991). Fungal pathogens as selective forces in plant populations and communities. *Australian Journal of Ecology* 16, 423-432.
- Calder, D. M. (1983) Mistletoes in focus: an introduction. In: Calder, M. and Bernhardt, P. (eds.) *The biology of mistletoes*. Academic Press, San Diego, California, USA. pp. 1-18.
- Carlile, D.W., Skalski, J. R., Barker, J. E., Thomas, J. M. and Cullinam, V. I. (1989) Determination of ecological scale. *Landscape Ecology* 2, 203-213.
- Cowles, R. B. (1936) The relation of birds to seed dispersal of the desert mistletoe. *Madroño* 3, 352-356.
- Dawson, T. E. and Ehleringer, J. R. (1991) Ecological correlates of seed mass variation in *Phoradendron juniperinum*, a xylem-tapping mistletoe. *Oecologia* 85, 332-342.

- Dawson, T., King, E. and Ehleringer, J. (1990) Age structure of *Phoradendron juniperinum* (Viscaceae), a xylem-tapping mistletoe: inferences from a non-destructive morphological index of age. *American Journal of Botany* 77, 573-583.
- Dehne, H. W. (1982) Interactions between vesicular-arbuscular mycorrhizal fungus and plant pathogens. *Phytopathology* 70, 293-296.
- Dobson, A. and Crawley, M. (1994) Pathogens and the structure of plant communities. *Trends in Ecology and Evolution* 9, 393-398.
- Donohue, K. (1995) The spatial demography of mistletoe parasitism on a Yemeni Acacia. *International Journal of Plant Science* 156, 816-823.
- Ehleringer, J. R. (1989) Carbon isotope ratios and physiological processes in arid land plants. In: Rundel, P. W., Ehleringer, J. R. and Nagy, K. A. (eds.). *Stable Isotopes in Ecological Research* Springer Verlag, New York, New York, USA. pp. 41-54.
- Ehleringer, J. R. and Marshall, J. D. (1995) Water relations. In: Press M. C. and Graves J. D. (eds.) *Parasitic Plants*. Chapman and Hall, New York, New York, USA. pp. 125-140.
- Follman, G. and Mahú, M. (1964) Las plantas huespedes de *Phrygilanthus aphyllus* (Miers) Eichl. *Boletín de la Universidad de Chile, Ciencias* 7, 39-41.
- Gehring, C. A. and Whitham T. G. (1992) Reduced mycorrhizae on *Juniperus monosperma* with mistletoe: the influence of environmental stress and tree gender on a plant parasite and a plant-fungal mutualism. *Oecologia* 89, 298-303.

- Gibson, C. C. and Watkinson, A. R. (1992) The role of the hemiparasitic annual *Rhinanthus minor* in determining grassland community structure. *Oecologia* 89, 62-68.
- Gregg J. W. (1991) The differential occurrence of the mistletoe *Phoradendron juniperum*, on its host *Juniperus osteosperma* in the Western United States. MS thesis, The University of Utah, Salt Lake City, Utah, USA.
- Gyllenberg, M., Hanski, I., and Hastings, A. (1997) Structured metapopulation models. In: Hanski, I.A., and Gilpin, M.E. (eds.) *Metapopulation biology: ecology genetics and evolution*. Academic Press, New York. New York, USA. pp. 93-122.
- Hanski, I. A. and Simberloff, D. (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. In Hanski, I. A., and Gilpin, M. E. (eds.). *Metapopulation biology: ecology genetics and evolution*. Academic Press, New York, New York, USA. pp. 5-26.
- Hawksworth, F. G. (1983) Mistletoes as forest parasites. In: Calder, M. and Bernhardt, P. (eds.) *The biology of mistletoes*. Academic Press, San Diego, California, USA. pp. 317-333.
- Hawksworth, F. G. and Wiens, D. (1995) *Dwarf mistletoes: biology, pathology, and systematics*. USDA Forest Service Agriculture Handbook Number 450, Washington D. C., USA.
- Hoffmann, A. J., Fuentes, E. R., Cortes, I., Liberona, F. and Costa, V. (1986) *Tristerix tetrandrus* (Loranthaceae) and its host-plants in the Chilean matorral: Patterns and mechanisms. *Oecologia* 69, 202-206.

- Kelly, D. (1998) Spatial clumping of *Tupeia antarctica* at Wainui. *Canterbury Botanical Society Journal* 32, 62-65.
- Kelly, P., Reid, N. and Davies, I. (1997) Effects of experimental burning, defoliation, and pruning on survival and vegetative resprouting in mistletoes (*Amyema miquelii* and *Amyema pendula*). *International Journal of Plant Science* 158, 856-861.
- Kermack, W. O. and A. G. McKendrick. (1927) A contribution to the mathematical theory of epidemics. *Proceedings of the Royal Society of London, Series A.* 115, 700-721.
- Kitron, U. (1998) Landscape ecology and epidemiology of vector-borne diseases: tools for spatial analysis. *Journal of Medical Entomology* 35, 435-445.
- Kotliar, N. B. and Wiens, J. A.. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59, 253-260.
- Kraus, R., Trimborn, P. and Ziegler, H. (1995) *Tristerix aphyllus*, a holoparasitic Loranthaceae. *Naturwissenschaften* 82, 150-151.
- Kuijt, J. (1994) Typification of New World mistletoe taxa (Loranthaceae and Viscaceae) described by Martius and Eichler. *Taxon* 43, 187-199.
- Lamont, B. (1982) Host range and germination requirements of some South African mistletoes. *South African Journal of Science* 78, 41-42.
- Larson, D. (1996) Seed dispersal by specialist versus generalist foragers: the plant's perspective. *Oikos* 76, 113-120.
- Lavorel, S., Stafford Smith, M. and Reid, N. (1999) Spread of mistletoes (*Amyema preisii*) in fragmented Australian woodlands. *Landscape Ecology* 14, 147-160.

- Lawton, J. H., Nee, S., Letcher, A. J. and Harvey, P. H. (1994) Animal distributions: patterns and processes. In: Edwards, P. J., May, R. M. and Webb, N. R. (eds.) *Large-Scale Ecology and Conservation Biology*. Blackwell Scientific Publications, Boston, USA. pp.41-58.
- Lei, S. (1999) Age, size and water status of *Acacia greggii* influencing the infection and reproductive success of *Phoradendron californicum*. *American Midland Naturalist* 141, 358-365.
- Levin, S. A. (1992) The problem of pattern and scale in ecology. *Ecology* 73, 1943-1967.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15, 237-240.
- Levins, R. (1970) Extinction. In: Gestenhaber, M. (ed.) *Some Mathematical Problems in Biology*. American Mathematical Society, Providence, Rhode Island, USA. pp. 77-107.
- Martin, T. E. (1985) Resource selection by tropical frugivorous birds: integrating multiple interactions. *Oecologia* 66, 563-573.
- Martínez del Rio, C. (1995) Murder by Mistletoe. *Natural History* 105, 64-70.
- Martínez del Rio, C., Hourdequin, M. Silva, A. and Medel, R. (1995) The influence of cactus size and previous infection on bird deposition of mistletoe seeds. *Australian Journal of Ecology* 20, 571-576.

- Martínez del Rio, C., Silva, A., Medel, R. and Hourdequin, M. (1996) Seed dispersers as disease vectors: bird transmission of mistletoe seeds to plant hosts. *Ecology* 77, 912-921.
- Marvier, M. A. and Smith, D. L. (1997) Conservation implications of host use for rare parasitic plants. *Conservation Biology* 11, 839-848.
- Mauseth, J. D. (1990) Morphogenesis in a highly reduced plant: the endophyte of *Tristerix aphyllus* (Loranthaceae). *Botanical Gazette* 151, 348-353.
- Mauseth, J. D., Montenegro, G. and Walckowiak, A.M. (1983) Host infection and flower formation by the parasite *Tristerix aphyllus* (Loranthaceae). *Canadian Journal of Botany* 63, 567-581.
- May, R. M. (1990) Population biology and population genetics of plant-pathogen associations. In: Burdon, J. J. and Leather, S. R. (eds.) *Pests, Pathogens and Plant Communities* Blackwell Scientific Publications, Boston, USA. pp.309-326.
- Medel, R. (2000) Assessment of parasite-mediated selection in a host-parasite system in plants. *Ecology* 81, 1554-1564.
- Nathan, R. and Muller-Landau, H. C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15, 278-285.
- Nee, S. (1994) How Populations persist. *Nature* 367, 123-124.
- Nee, S., May, R. and Hassell M. (1997) Two-species metapopulation models. In: Hanski, I. A. and Gilpin, M. E. (eds.) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California, USA. pp. 123-147.

- Norton, D. A., and Carpenter, M. A. (1998) Mistletoes as parasites: host specificity and speciation. *Trends in Ecology and Evolution* 13, 101-5.
- Norton, D. A. and Stafford-Smith, M. (1999) Why might roadside mulgas be better mistletoe hosts? *Australian Journal of Ecology* 24, 193-198.
- Overton, J. M. (1994) Dispersal and infection in mistletoe metapopulations. *Journal of Ecology* 82, 711-723.
- Overton, J. M. (1996) Spatial autocorrelation and dispersal in mistletoes: field and simulation results. *Vegetatio* 125, 83-98.
- Overton, J. M. (1997). Host specialization and partial reproductive isolation in desert mistletoe (*Phoradendron californicum*). *The Southwestern Naturalist* 42, 201-209.
- Pennings, S. C., and Callaway, R. M. (1996) Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. *Ecology* 77, 1410-1419.
- Press, M. C. (1995) Carbon and nitrogen relations. In: Press, M. C. and Graves, J. D. (eds.) *Parasitic Plants*. Chapman and Hall, New York, New York, USA. pp. 103-124.
- Price, P. W. (1980). *The evolutionary biology of parasites*. Princeton University Press, Princeton, New Jersey, USA.
- Pulliam, R. H. (1988) Sources, sinks, and population regulation. *The American Naturalist* 132, 652-661.
- Raven, J. A. (1983). Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Advances in Ecological Research* 13, 135-234.

- Ramsey, F. L. and Schafer, D. W. (1997) *The Statistical Sleuth: A Course in Methods of Data Analysis*. Duxbury Press, Boston, USA.
- Ray, C., Gilpin, M. and Smith A.T. (1991) The effect of conspecific attraction on metapopulation dynamics. In: Gilpin, M. and Hanski, I. (eds.) *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, New York, New York, USA. pp. 123-134.
- Reid, N. (1991) Coevolution of mistletoes and frugivorous birds. *Australian Journal of Ecology* 16, 457-469.
- Reid, N., Smith, N. M. and Yan, Z. (1995) Ecology and population biology of mistletoes. In: Lowman, M. D. and Nadkarni, N. M. (eds.) *Forest Canopies*. Academic Press, San Diego, California, USA. pp. 285-310.
- Robertson, A. W. Kelly, D. Ladley J.J. and Sparrow, A.D. (1998) Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). *Conservation Biology* 13, 499-508.
- Sallabanks, R. (1993) Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74, 1326-1336.
- Sargent, S. (1990) Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology* 71, 1289-1298.
- Sargent, S. (1994) Seed dispersal of mistletoes by birds in Monteverde, Costa Rica. PhD dissertation. Cornell University, Ithaca, New York, USA.
- Sargent, S. (1995) Seed fate in a tropical mistletoe: the importance of host twig size. *Functional Ecology* 9, 197-204.

- Schulze, E. D. and Ehleringer, J. R. (1984) The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes. *Planta* 162, 268-275.
- Silva, A. and Martínez del Rio, C. (1996) Effects of mistletoe parasitism on the reproduction of cacti hosts. *Oikos* 75, 437-442.
- Smith, A. T. and Peacock, M. M. (1990) Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology* 4, 320-323.
- Stamps, J. A. (1991) The effects of conspecifics on habitat selection in territorial species. *Behavioral Ecology and Sociobiology* 28, 29-36.
- Turner, R.J. (1991) Mistletoe in eucalypt forests –a resource for birds. *Australian Forestry* 54, 226-235.
- Walsberg, G. E. (1975) Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. *Condor* 77, 169-174.
- Wheelwright, N. T. and Orians, G. H. (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *The American Naturalist* 119, 402-413.
- Wicker, E. F. (1984) Dwarf mistletoe insidious pest of North American conifers. In: Hawksworth F.G. and Scharpf (eds.) *Biology of the dwarf mistletoes; proceedings of the symposium* USDA Forest Service General Technical Report, RM 111. p. 1.
- Yan, Z. (1993) Resistance to haustorial development of two mistletoes, *Amyema preissi* (Miq.) and *Lysiana exocarpi* (Behr) Tieghem spp. Exocarpi (Loranthaceae) on host and non-host species. *International Journal of Plant Science* 154, 386-394.

## Figure Legends

Fig. 1.- Relationships between mistletoes (parasites), their hosts, and the birds (vectors) that disperse mistletoe seeds. Solid arrows indicate the direction of interaction between two participants of the mistletoe system, and the signs above the arrows indicate whether the interaction is beneficial (+), detrimental (-), or has no effect (0) on the participant at the arrow's head. The mistletoe is both a parasite of its host plant and a mutualist of the birds that feed on its berries and disperse its seeds. These birds act both as seed dispersers and as disease vectors. Dashed arrows indicate interactions in which most other parasites differ from mistletoes. In many parasitic systems, the parasite has a negative or neutral (-/0) effect on its vector. Also, the mistletoe dispersers do not have a direct negative effect on the host, as do many vectors that are themselves parasites, such as mosquitoes or ticks.

Fig. 2. - The distribution of *Phoradendron californicum* infections among *Prosopis velutina* hosts was significantly aggregated (variance:mean ratio = 10.9, N = 137) at a site in Southern Arizona (the Santa Rita Experimental Range). Most individuals had very few mistletoe infections while a few hosts harboured most of the mistletoes.

Fig. 3.- Relationship of seed deposition to host height and previous infection. The probability that a *P. velutina* tree host received seeds of the parasite *P. californicum* increased significantly with both height and previous infection (logistic regression  $p < 0.001$ ; open circles are infected hosts and closed circles are uninfected hosts,). Points are average values for size classes (bars are standard errors). Data were divided into size classes for visual clarity. Curves were fitted using a logistic regression procedure (logit  $(\pi) = -2.56 + 0.66(\text{height}) + 1.46(\text{infection status})$ ).

Fig. 4.- Correlation between prevalence and intensity of infection. At 10 sites in the Santa Rita Experimental Range (Arizona, United States), mean infection intensity (mistletoes per host) of *P. velutina* increased significantly with the prevalence of infection

(frequency of infected hosts) by *P. californicum* at each site ( $r^2 = 0.77$ ,  $p = .0018$ ;  $intensity = -0.584 + 7.93 (prevalence)$ ).

Fig. 5.- Relationship between seed deposition and neighborhood infection prevalence. At 10 sites in the Santa Rita Experimental Range (Arizona, United States), the probability of receiving *P. californicum* seeds increased with infection prevalence in uninfected *P. velutina* hosts (closed circles). The relationship between the fraction of infected hosts receiving seeds and prevalence, however, was non-linear. For descriptive purposes, we fitted a second degree polynomial to the data. The quadratic coefficient for this polynomial was significantly positive ( $p < 0.03$  indicating an accelerating relationship,  $y = 0.05 - 0.91x + 5.10x^2$ ,  $r^2 = 0.81$ ,  $p < 0.007$ ). For already infected hosts (open circles), there was no significant relationship between the fraction of hosts receiving seeds and prevalence at the site ( $r = 0.06$ ,  $p = 0.62$ ).

Fig. 6. Relationship between host height and infection by *P. californicum*. The number of *P. californicum* individuals increased with host (*Prosopis velutina*) height ( $r = 0.07$ ,  $p < 0.0001$ ,  $N = 115$ ), but very little variation was explained by the regression line ( $r^2 = 0.269$ ). Although host height is a good predictor of infection frequency, it is a poor predictor of infection intensity.

Fig. 7.- Relationship between host height and infection by *T. aphyllus*. At the Reserva Nacional Las Chinchillas, Chile, the frequency with which hosts were infected by *T. aphyllus* increased with height for both *Echinopsis chilensis* (open circles;  $\text{logit}(\pi) = -1.779 + 0.5632(\text{height})$ ,  $p < 0.01$ ,  $N = 122$ ) and *Eulychnia acida* hosts (closed circles,  $\text{logit}(\pi) = -6.244 + 1.7039(\text{height})$ ,  $p < .00063$ ,  $N = 52$ ). This positive relationship is in accord to that predicted by Overton's (1996) model of mistletoe metapopulations.

Fig. 8.- Test of model predictions. The first prediction of Overton's (1996) model was met by *P. californicum* infecting *P. velutina* at 10 sites in the Santa Rita Experimental Range (Arizona, United States). Frequency of infection increased with height at all sites ( $p < 0.05$ , after logistic regression). Curves in the upper panel are relationships between frequency of infection and height at each site constructed using logistic regression. However, the second prediction of Overton's model (1996), namely that the steepness of the relationship between infection frequency and host age/height would increase with the probability of unparasitized trees receiving seeds (dispersal efficiency) was not met ( $r = 0.015$ ,  $p = 0.772$ , lower panel).

Figure 1

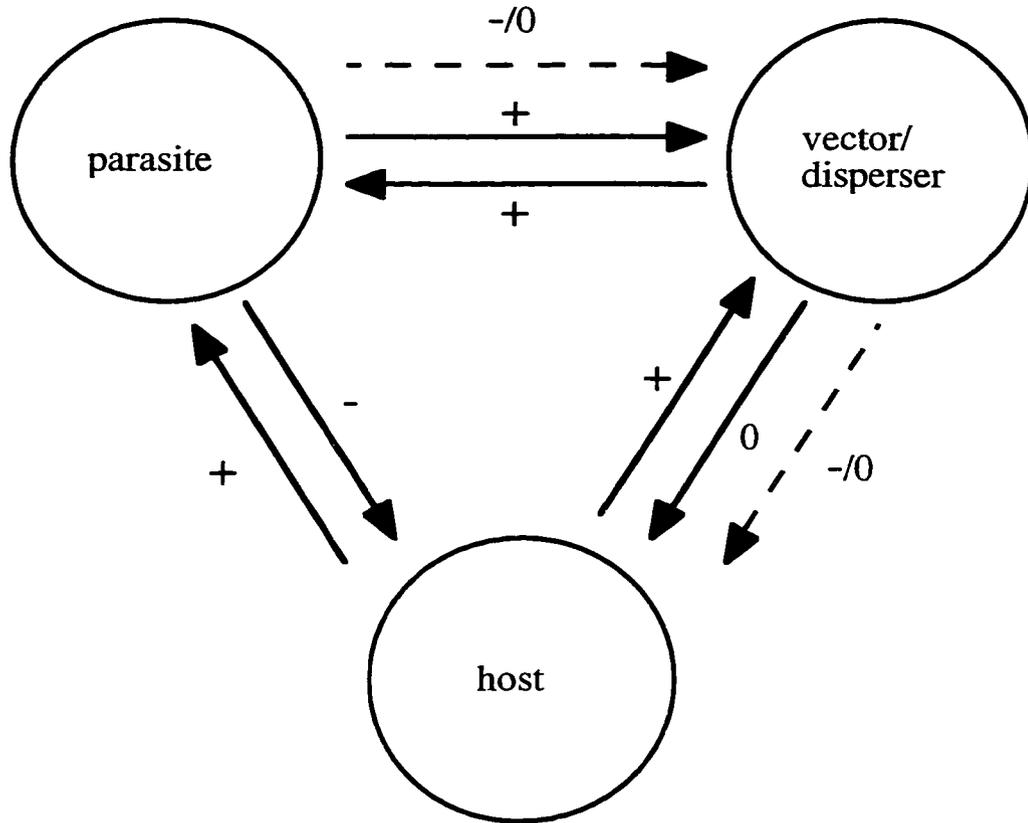


Figure 2.

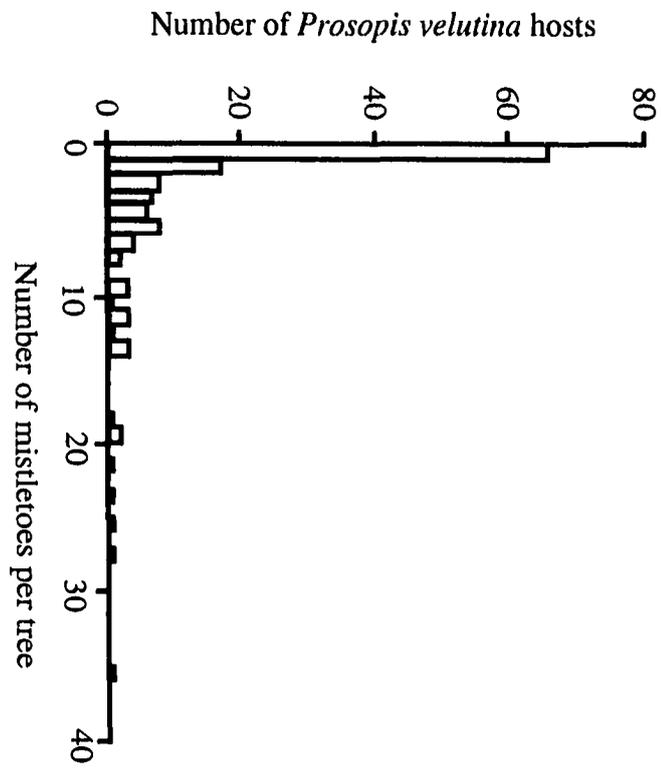


Figure 3.

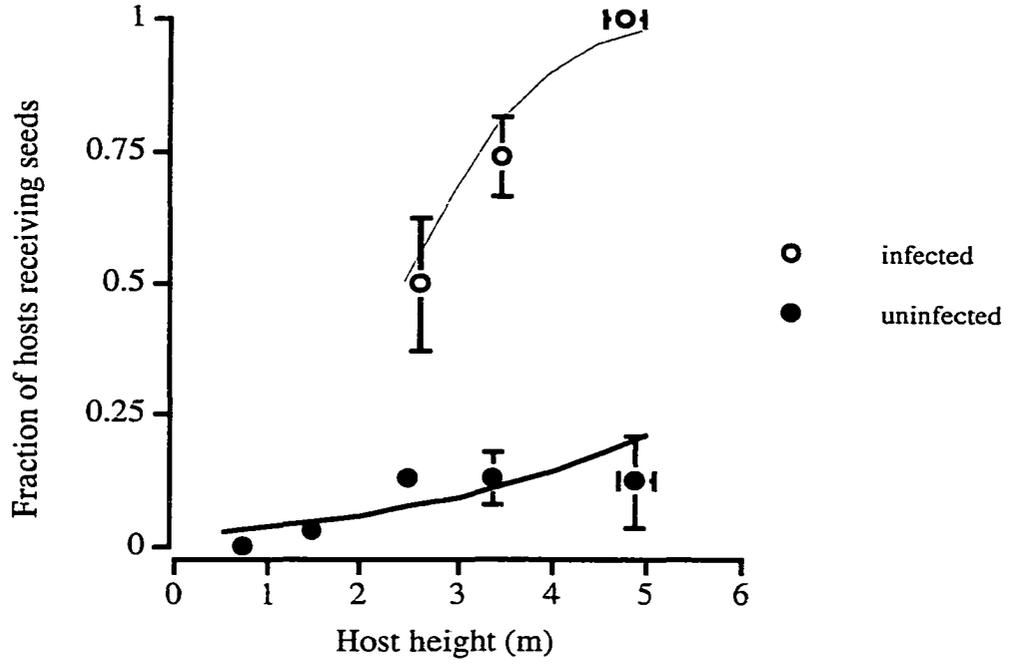


Figure 4.

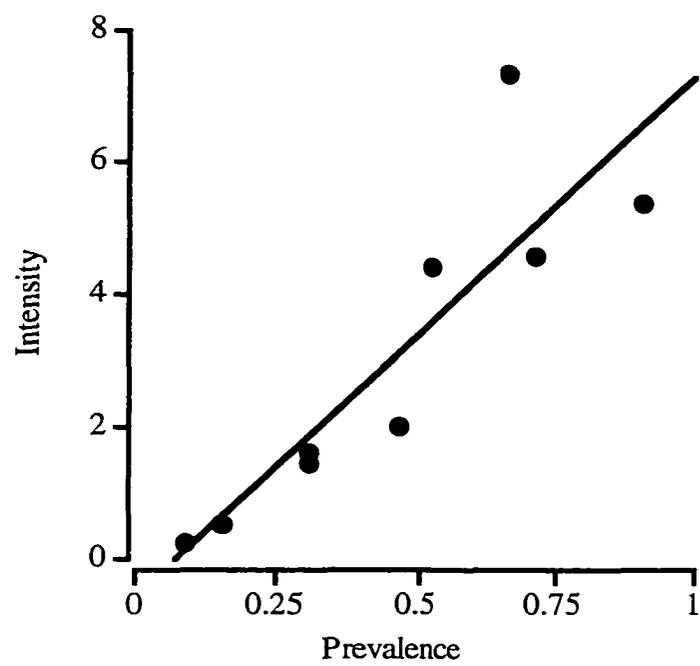


Figure 5

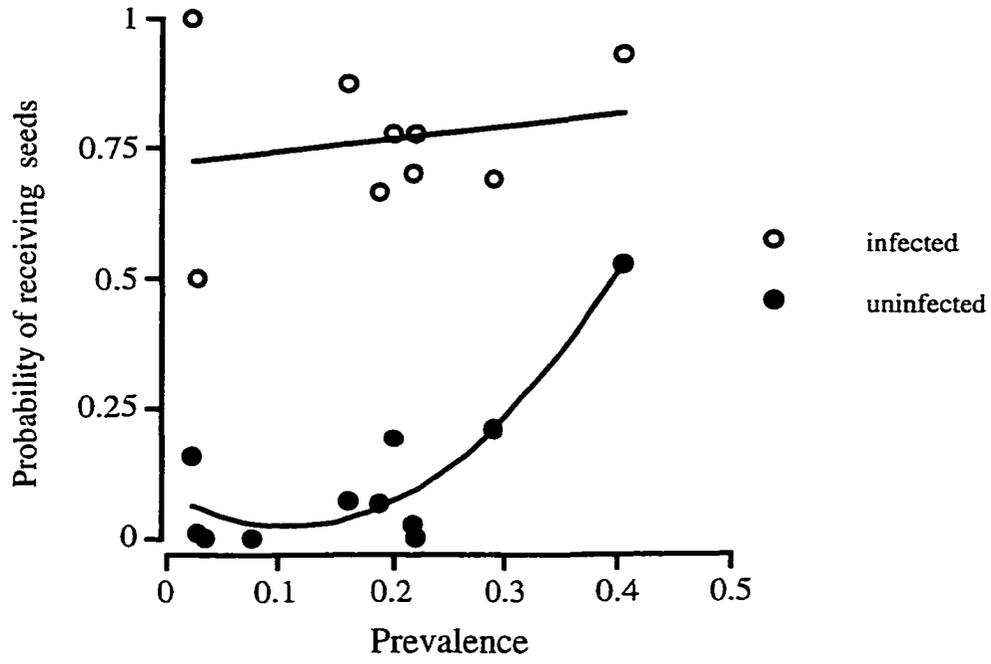


Figure 6.

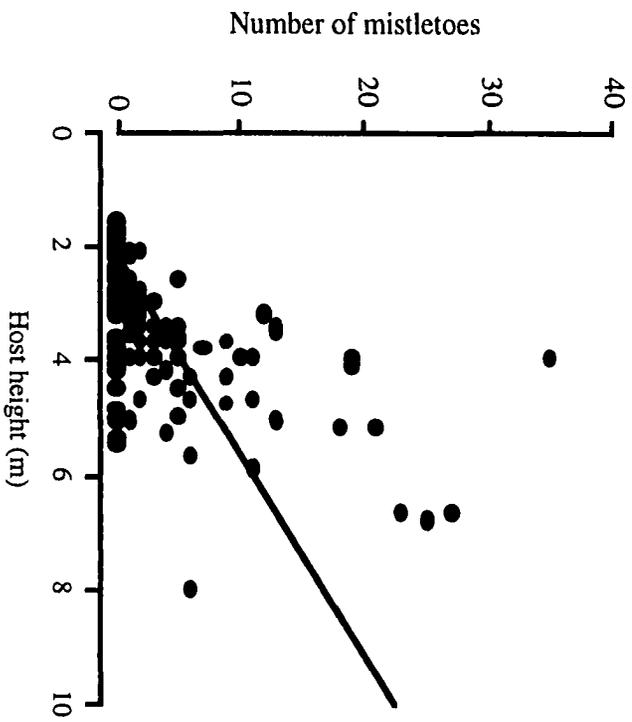


Figure 7.

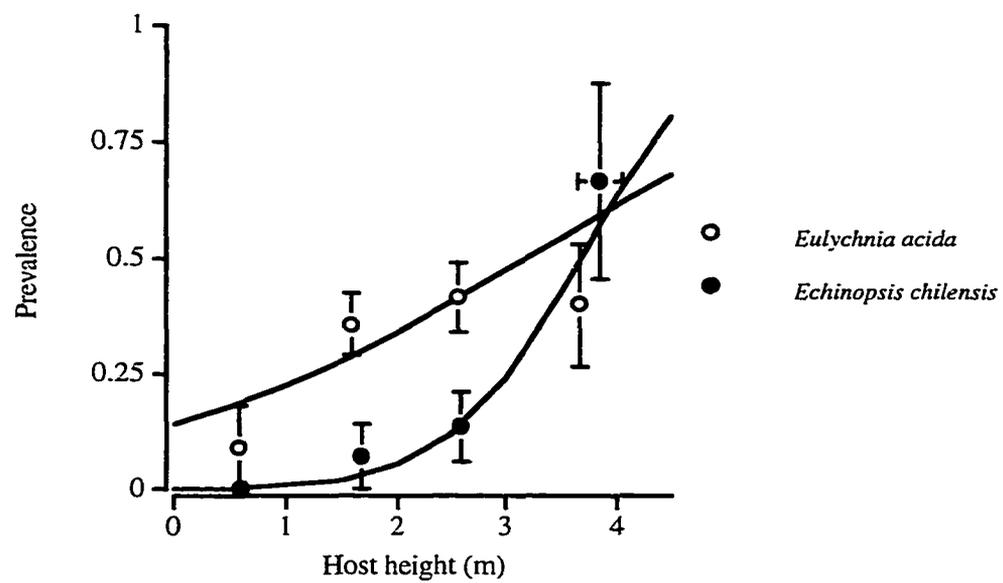
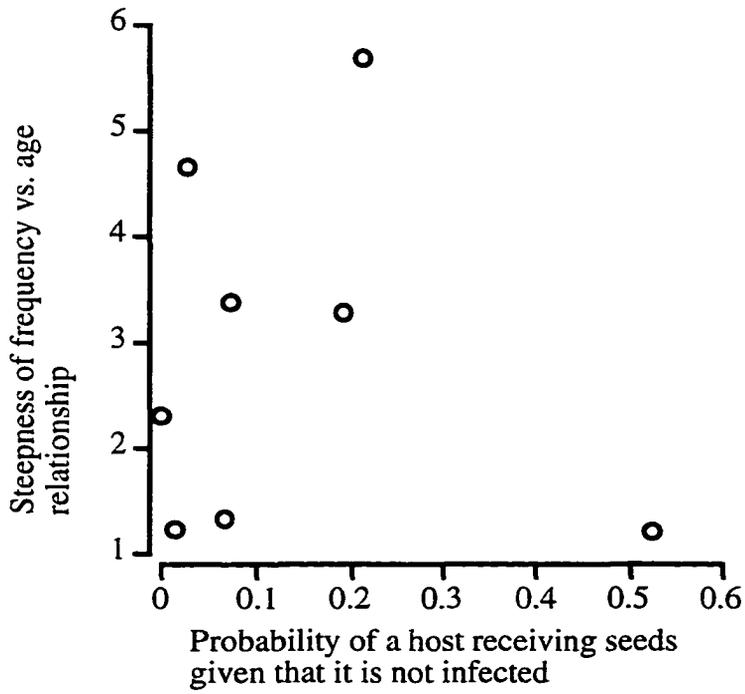
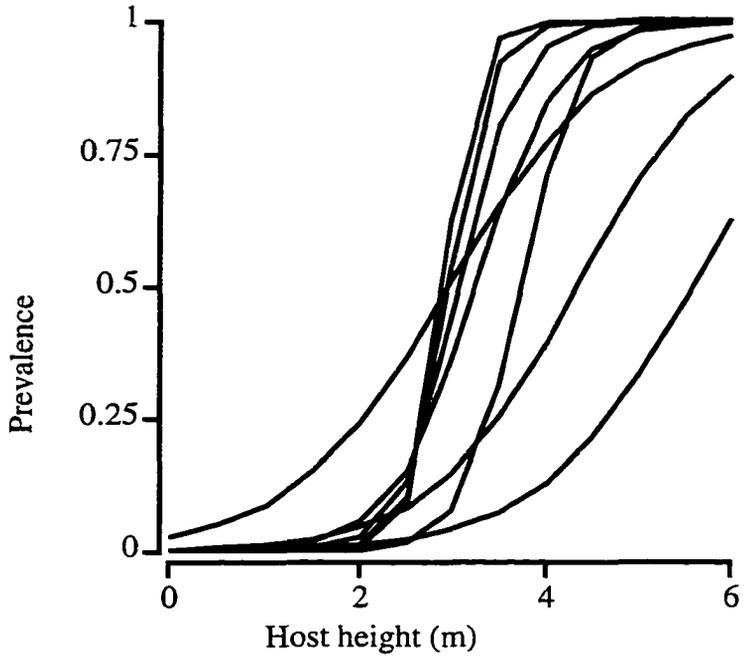


Figure 8.



**APPENDIX B**

**WHY DO MISTLETOES SHOW A CLUMPED DISTRIBUTION? THE ROLE OF  
SEED-DISPERSING BIRDS IN CREATING HETEROGENEOUS SEED RAIN  
AMONG HOSTS.**

Why do mistletoes show a clumped distribution? The role of seed-dispersing birds in creating heterogeneous seed rain among hosts.

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## ABSTRACT

Most mistletoes are dispersed by frugivorous birds. Because foraging movements determine where seeds are deposited, birds both respond to and can shape mistletoe distribution. Desert mistletoes (*Phoradendron californicum*) are extremely clumped among hosts. I hypothesized that this distribution resulted from disproportionate seed deposition onto parasitized hosts by phainopeplas (*Phainopepla nitens*), the primary mistletoe dispersers. To determine the phainopeplas' role in the distribution of mistletoe seeds among host trees (*Prosopis velutina*), I counted the number of mistletoe infections and seeds deposited on hosts, and monitored bird behavior on a mapped plot in which host tree characteristics were known. Because phainopeplas moved preferentially among parasitized tall trees, mistletoe seeds were deposited preferentially on them. To test the prediction that the preference of phainopeplas leads to higher seed deposition onto parasitized trees, I removed mistletoes from host trees and examined seed deposition before and after removal. Before mistletoe removal, seed deposition was equivalent and temporally correlated in pairs of control and removal trees. After removal, deposition into removal trees was significantly lower than into unmanipulated trees. Although mistletoe removal resulted in lower seed deposition, it did not abolish it. Seed deposition into parasitized hosts can result from deposition of seeds originating within a host (intra-host dispersal) or from other infected hosts (inter-host dispersal). Bird behavior and the mistletoe removal experiment suggest that inter-host dispersal contributes significantly to seed deposition. The average time birds perched in hosts was much lower than the time

for ingested seeds to pass through their gut. The response of birds to mistletoes leads to disproportionate seed deposition into parasitized trees and probably causes the clumped distribution of mistletoes.

## INTRODUCTION

Mistletoes are parasitic plants that often infect woody trees and shrubs (Kuijt 1969). The association between mistletoes and birds has been chronicled since ancient times. References are found in the work of Aristotle, Pliny and Virgil and, vividly, in the Roman proverb "*Turdus sibi malum cacat*" (the thrush defecates its own misfortune). This proverb highlights the irony of capturing thrushes with birdlime made from mistletoes that are dispersed by the same thrushes (Browne 1646). Today, it is well known that most mistletoe seeds are dispersed by birds, many of which are highly specialized for consumption of their berries (Kuijt 1969, Reid et al. 1995). Although this relationship is well-known, the implications of the interaction for the distribution of these parasitic plants have not been quantified.

Desert mistletoes (*Phoradendron californicum*) are a dominant feature of the Sonoran desert where they parasitize legume trees such as *Prosopis* spp., *Cercidium* spp., *Acacia* spp., and *Olneya tesota*. Because they are one of the few berries abundant during the winter in the North American desert southwest, the desert mistletoe is an important resource for many birds, including mockingbirds, thrashers, and quail (Cowles 1936). However, this parasitic plant is most closely associated with phainopeplas (*Phainopepla*

*phainopepla*), which are its most effective dispersers (Larson 1996). These birds are only found in the desert during the winter, coinciding with the fruiting of mistletoes, which they depend on for food (Chu and Walsberg 1999). Male and female phainopeplas defend separate territories prior to courtship and nesting, and use conspicuous perching as a territorial display (Walsberg 1977, Chu 1999). Like many birds that specialize on mistletoes (Reid *et al.* 1995), phainopeplas have specialized digestive systems that allow them to process hundreds of mistletoe berries in a single day (Walsberg 1975, Chu and Walsberg 1999).

The distribution of *P. californicum* is determined not only by the distribution of its hosts, but also by the behavior of its seed dispersers. Previous studies have found that mistletoe seed deposition is higher in trees that are already parasitized by mistletoes (Appendix A) and that there is a clumped distribution of mistletoes within trees (Overton 1993, Appendix A). This clumped distribution of parasites within hosts is found in many macroparasites and has been ascribed to differences in host susceptibility or infection rates (Anderson and Gordon 1982, Pacala and Dobson 1988).

Two possible and non-exclusive mechanisms can account for the aggregation of mistletoes within a few host trees. 1) Seeds deposited in infected trees may originate from mistletoes in the same trees (intra-host infection, Overton 1994). 2) If phainopeplas move primarily among infected trees, infected trees may receive a disproportionate amount of seeds from other infected trees (inter-host infection). In this study, I examined patterns of mistletoe infection and seed deposition and documented the movement of phainopeplas among host trees in a study plot in which all trees were mapped. Because I had detailed

information about the height and the number of mistletoes in each tree, I was able to investigate the factors that determine the use of different hosts by phainopeplas. I found that phainopeplas visited infected tall trees preferentially. To investigate whether the presence of mistletoes leads to differential seed deposition, I removed mistletoes from host trees and compared seed deposition into these manipulated trees with that into neighboring unmanipulated trees.

## METHODS

***Patterns of distribution and bird observations.*** This study was conducted at the Santa Rita Experimental Range, in southern Arizona, USA (31° 53' N, 110° 54' W). The range is at the foothills of the Santa Rita mountains and in semidesert grassland scrub habitat (Burgess 1995). My study site was located in a grassy savanna with large stands of velvet mesquite (*Prosopis velutina*) that have apparently invaded over the last 100 years (Martin and Turner 1977, Medina 1996). During the winter and spring of 2000, I observed phainopepla movements on a four hectare plot in which all of the trees were tagged, mapped, and height, number of mistletoes and number of deposited seeds had been recorded (details can be found in Aukema and Kunzmann 2000). I located phainopeplas by sight or sound, identified their gender and recorded the identity of the tree in which they perched. I followed individual birds for observation bouts that lasted from 2 to 75 minutes. I followed them until I lost them, until they left the plot's boundary, or until they were repeatedly returning to the same trees. In these bouts, I recorded the identity of, and the time spent in, each of the trees in which they perched or fed on mistletoes. Because

all host trees in the plot were mapped, I was able to calculate phainopepla flight distances and determine the characteristics (such as height and number of mistletoes) of the trees in which they were observed perching and feeding. I hypothesized that they would spend the majority of their time in tall trees and in infected trees because tall trees would provide more conspicuous perches for territorial displays and mistletoes represent a food resource to which I expected them to respond.

***Mistletoe removal experiment.*** On October 19 and 20, 1999, I chose 10 pairs of mistletoe-infected mesquite trees (*Prosopis velutina*). Pairs were in the same upland neighborhood, within 30 meters of each other and were matched by height (I chose tall trees, mean  $\pm$  SD =  $4.2 \pm 0.34$  m,  $N = 20$ ) and parasite load (I chose trees with a heavy parasite load, mean  $\pm$  SD =  $21.4 \pm 5.8$  mistletoes,  $N = 20$ ). I chose ten branches on each tree. Because seed rain within a tree is not uniform (pers. obs.), I selected branches that had received seeds naturally prior to the beginning of the experiment. I counted and removed the seeds on each of these branches approximately weekly for six weeks. On December 28, 1999, all of the mistletoes were removed from one randomly selected tree of each pair (the “removal” tree). Mistletoes were removed by climbing trees and pulling down mistletoe foliage by hand or with clippers. Mistletoe branches snap off very easily at the place where they make contact with their host, leaving only the haustorial connection. Simultaneously, the control tree was disturbed, by climbing and shaking the tree, for an equivalent amount of time. After mistletoe removal, I returned to count and remove seeds on the marked branches approximately once per week (seven times) until

the end of February. There was very little growth of the removed mistletoes during this time and any mistletoe foliage observed on manipulated trees was immediately removed.

The residuals of seed deposition data were not normally distributed, so they were natural log transformed. The residuals of log transformed data were normally distributed and had homogeneous variances. I used profile analysis to examine post-removal repeated-measures seed deposition data (SAS procedure GLM, REPEATED; SAS Institute 1989). Profile analysis is a method of using multivariate analysis of variance to analyze repeated-measures data. It allows addressing hypotheses about the shapes, levels, and slopes of response curves after a manipulation (von Ende 1993).

## RESULTS

**Patterns of distribution.** Both the probability that a host tree was infected ( $r^2 = 0.30$ ,  $\chi^2 = 318$ ,  $P < 0.0001$ ,  $N = 874$ ) and the number of mistletoes infecting a tree ( $r^2 = 0.17$ ,  $F = 173.5$ ,  $P < 0.0001$ ,  $N = 74$ ) increased with the height of the host tree. Likewise, both the probability that a host tree received seeds ( $r^2 = 0.45$ ,  $\chi^2 = 504$ ,  $P < 0.0001$ ,  $N = 810$ ) and the number of seeds received per tree ( $r^2 = 0.15$ ,  $F = 141$ ,  $P < 0.0001$ ,  $N = 810$ ) increased with host height. The probability of receiving seeds was a function of both host tree height and the number of mistletoes present on the host (Logistic regression:  $\text{logit}(\text{probability of receiving seeds}) = -3.57 + 1.18 (\text{height}) + 1.07(\text{number of mistletoes}) - 0.25(\text{height}-2.66)(\text{number of mistletoes} - 1.79)$ ,  $r^2 = 0.51$ ,  $\chi^2 = 568.7$ ,  $P < 0.0001$ ,  $N = 809$ , Fig. 1).

**Bird observations.** Phainopeplas were observed in *Prosopis velutina* (the dominant host species), once in *Acacia greggii*, and occasionally in hackberry bushes (*Celtis pallida*), a non-host species. Seeds were often deposited in hackberries, but these trees do not become infected. Therefore, they were not considered hosts and are not considered in the following analysis. The subset of trees phainopeplas used were significantly taller than the trees available on the plot ( $P < 0.0001$ ,  $t = -13.59$ ,  $df = 873$ , Table 1); and the number of mistletoes on the trees that they used (mean  $\pm$  SD =  $6.3 \pm 7.1$ ) was significantly greater than the number of mistletoes on unused trees (mean  $\pm$  SD =  $1.7 \pm 4.6$ ;  $P < 0.0001$ ,  $t = -12.81$ ,  $df = 874$ ). Although only 28% of the trees on the plot were parasitized, 79% of the trees used by phainopeplas were parasitized (Table 1), and 89% of the trees used more than once were parasitized. The trees in which phainopeplas were observed perching more than once were significantly taller (mean  $\pm$  SD =  $4.59 \pm 1.3$ m,  $N = 64$ ) and had higher numbers of mistletoes (mean  $\pm$  SD =  $8.1 \pm 7.2$ ,  $N = 64$ ) than other trees in the plot (height:  $t = -12.47$ ,  $P < 0.0001$ ,  $df = 873$ ; mistletoes:  $t = -12.47$ ,  $P < 0.0001$ ,  $df = 874$ ) and than trees that were visited only once (height:  $t = -3.94$ ,  $P = 0.0001$ ; mistletoes:  $t = -2.99$ ,  $P = 0.0034$ ,  $df = 115$ ). I found that the distribution of flight distances was right skewed ( $g_1 = 1.08$ ,  $P < 0.0001$ ,  $N = 144$ ). Half of the flights were shorter than 25 m (mean  $\pm$  SD =  $36 \pm 32.2$ m,  $N = 144$ ), but a few flights exceeded 120 m (Fig. 2). However, long flights were probably undersampled because long distance flights were more difficult to follow. Visits to trees were usually brief (mean  $\pm$  SD =  $2.63 \pm 2.9$  minutes,  $N = 116$ ), but one bird spent 13 minutes in a tree (Fig. 2).

***Mistletoe removal experiment.*** Two pairs of trees were removed from the analysis because of methodological inconsistencies (a pack rat repeatedly removed the branch labels from pair 6 and I changed sampling methods after counting seeds on pair 1; in addition, there was a greater discrepancy in height between the members of these pairs than the other pairs). This left 8 pairs, or 16 trees in the analysis. There was no significant difference in the height of these trees (two-tailed paired t-test,  $t_7 = 0.131$ ,  $P = 0.899$ ) or in the initial number of mistletoe infections (two-tailed paired t-test,  $t_7 = 0.524$ ,  $P = 0.616$ ). Total seed deposition prior to the removal did not differ between treatments (paired t-test,  $t_7 = 1.43$ ,  $P = 0.196$ ). Trees whose mistletoes had been removed received fewer seeds than control trees ( $F_1 = 25.78$ ,  $P = .0002$ , Fig. 3). Seed deposition varied over time ( $F_7 = 5.28$ ,  $P = 0.016$ , Wilks' Lambda test; Rao 1973, Figs. 3, 4), but there was no time by treatment interaction ( $F_7 = 2.53$ ,  $P = 0.109$ , Wilks' Lambda test; Rao 1973). Before mistletoe removal, the number of seeds deposited per branch per week was highly temporally correlated between experimental and control trees (mean  $r \pm SD = 0.79 \pm 0.19$ ,  $t = 11.63$ ,  $P < 0.001$ ,  $N = 8$  tree pairs and 6 weeks per pair, Fig. 4) although it was not synchronous for all of the trees. After removal, this correlation broke down as a result of the sharp decrease in seed deposition into trees from which mistletoes had been removed (mean  $r \pm SD = 0.19 \pm 0.27$ ,  $t = 2.0$ ,  $P > 0.1$ , Fig. 4). Although seed deposition decreased after mistletoes were removed all manipulated trees continued to receive seeds for the duration of the experiment. Manipulated trees received an average of 0.9 seeds deposited per branch per tree per week post removal, but they received three seeds per branch per tree

in the week immediately after the removal (Fig. 3). Two different trees received no seeds during a single week and one tree received no seeds during two weeks.

## DISCUSSION

In desert mistletoes the spatial distribution of dispersed seeds, is a simple consequence of the perching patterns of bird seed dispersers. Seed deposition increased with the height of host trees and with the number of mistletoes in the trees. This pattern seems to be a direct consequence of the perching preferences of the seed-dispersing birds. *Phainopepla* perched more frequently in parasitized trees than in unparasitized trees, and the trees that they perched in were taller than the average of those available in the study area.

The results of the removal experiment provided additional support for the observation that seed dispersers perched more frequently in parasitized trees. They also provided clear evidence in favor of the notion that the presence of mistletoes in a host is an important -perhaps the most important- factor predicting the magnitude of mistletoe seed deposition. Birds seemed to show a lag in their response to mistletoe removal (Fig. 3). Rates of seed deposition onto manipulated trees were slightly higher a week after the experiment than they were later. It is possible that these birds not only use the mistletoe plants themselves as cues in their perching and foraging decisions, but also rely on a memory of expected food availability in local trees. Because there were no seed sources in these manipulated trees, this observation indicates that inter-host dispersal of mistletoe seeds was common (Fig. 3).

The importance of inter-host seed dispersal is highlighted by the persistent deposition of some seeds onto trees from which mistletoes were removed. The disproportionate presence of seeds in already infected hosts has often been interpreted as the result of intra-host infections (Overton 1994). These results suggest that intra-host dispersal is not the only source of seeds into an infected host. Inter-host dispersal plays an important role as well. The amount of time that phainopeplas spent in a tree was shorter (about 3 minutes) than the 12-45 minutes that it takes for an ingested seed to pass through the digestive tract (Walsberg 1975). The short time spent in each host tree suggests that most intra-host dispersal occurs when phainopeplas return to a host tree from forays into other trees. Genetic analyses of mistletoes and deposited seeds can clarify the relative contribution of seeds produced by mistletoes within a host and in other hosts to total seed deposition (Ouborg et al. 1999, Cain et al. 2000).

My results suggest that seed dispersers shape the spatial distribution of mistletoes among hosts. Seed dispersers probably also shape the spatial distribution of genes in mistletoe populations. Birds moved frequently among trees and most flights were among neighboring trees, suggesting that birds create small genetic neighborhoods among the seeds dispersed each season (Loveless and Hamrick 1984, Eguiarte et al. 1993). However, I observed occasional long distance flights. These long flights may be important in that they provide the opportunity for long distance movement of mistletoe genotypes (Cain et al., 2000). Because individual birds were not marked, territorial individuals could not be identified. Thus, it is possible that some of the phainopeplas observed flying long distances were non-territorial birds that were passing through the

study area. The social structure of seed dispersing birds may have significant consequences for plant populations.

Because trees pairs were within close proximity of each other, the temporal correlation in seed deposition between pairs of tree hosts before mistletoe removal indicates that neighborhood characteristics are important in determining seed deposition. Habitat selection by birds has been described as a hierarchical spatial process that ranges from choice of food items in a patch to choice of home range in a landscape (Johnson 1980). Different environmental cues may be responsible for decisions at different scales (Johnson 1980, Rolstad et al. 2000). One can envision a phainopepla making selections of home range based on overall abundance of mistletoe resources in an area. These home ranges or territories may be the cause for the correlation in seed deposition between paired trees prior to mistletoe removal. At another scale, a phainopepla might make feeding site selections based on the presence of mistletoes in a given tree. This mechanism is probably responsible for the reduction of seed deposition after mistletoes are removed.

The role that seed dispersal plays in the spatial distribution of plants is the result of both dispersal and establishment success (Herrera et al. 1994, Schupp 1995, Nathan and Muller-Landau 2000). Because the fate of seeds is difficult to follow, and because safe germination sites are not easy to identify (Wheelwright and Orians 1982), the relative importance of these two processes remains contentious (Herrera et al. 1994, Schupp and Fuentes 1995). This study provides an example of a group of plants in which dispersal limitations shape spatial distribution. Seed dispersers used and deposited seeds

preferentially in already infected trees. When mistletoes were removed, seed deposition was dramatically reduced. Thus, the response of birds to mistletoes seems to be responsible for the highly clumped distribution of mistletoes among host populations.

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## LITERATURE CITED

- Anderson, R. M., and D. M. Gordon. 1982. Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology* **85**: 373-398.
- Aukema, J. E., and M. R. Kunzmann. 2000. The Use of GPS & GIS tools to help document the spread of desert mistletoe (*Phoradendron californicum*), a plant parasite in Arizona. 20th Annual ESRI User Conference Proceedings, p 521.  
<http://www.esri.com/library/userconf/proc00/professional/papers/PAP521/p521>.
- Browne, Sir Thomas. 1646. *Pseudodoxia epidemica, or, Enquiries into very many received tenents and commonly presumed truths*. Printed by T. H. for Edward Dod, London.
- Burgess, T. L. 1995. Desert grassland, mixed shrub savanna, shrub steppe, or semidesert scrub? The dilemma of coexisting growth forms. Pages 31-65 in M.P. McClaran and T.R. Van Devender, editors. *The Desert Grassland*. University of Arizona Press, Tucson, Arizona, USA.
- Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* **87**: 1217-1227.
- Cowles, R. B. 1936. The relation of birds to seed dispersal of the desert mistletoe. *Madroño* **3**: 352-356.

- Chu, M. C. 1999. Ecology and Breeding Biology of Phainopeplas (*Phainopepla nitens*) in the Desert and Coastal Woodlands of Southern California, PhD dissertation. University of California, Berkeley, California, USA.
- Chu, M. and Walsberg, G. H.. 1999. Phainopepla (*Phainopepla nitens*). No. 415 in Poole A. and Gill F, editors. The Birds of North America. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Eguiarte, L. E., A. Burquez, J. Rodriguez, M. Martinez-Ramos, J. Sarukhan and D. Pinero. 1993. Direct and indirect estimates of neighborhood and effective population size in a tropical palm, *Astrocaryum mexicanum*. *Evolution* **47**: 75-87.
- Herrera, C. M., P. Jordano, L. López-Soria, and J. A. Amat. 1994. Recruitment of a mast-fruited, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* **64**: 315-344.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for valuating resource preference. *Ecology* **61**:65–71.
- Kuijt, J. 1969. The Biology of Parasitic Flowering Plants. University of California Press, Berkeley, California, USA.
- Larson, D. 1996. Seed dispersal by specialist versus generalist foragers: the plant's perspective. *Oikos* **76**:113-120.
- Loveless, M. D. and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics* **15**: 65-95.
- Martin, S. C., and R. M. Turner. 1977. Vegetation change in the Sonoran Desert Region, Arizona and Sonora. *Journal of the Arizona Academy of Science* **12**: 59-69.

- Medina, A. L. 1996. The Santa Rita Experimental Range: history and Annotated bibliography (1903-1988). General Technical Report RM-GTR-276. Rocky Mountain Forest and Range Experiment Station. Forest Service, U.S. Department of Agriculture.
- Nathan, R., and Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* **15**: 278-285.
- Ouborg, N. J., Y. Piquot, and J. M. Van Groenendael. 1999. Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology* **87**: 551-568.
- Overton, J. M. 1993. Dispersal in Mistletoes and Models. Ph. D. dissertation. University of California, Los Angeles, California, USA.
- Overton, J. M. 1994. Dispersal and infection in mistletoe metapopulations. *Journal of Ecology* **82**: 711-723.
- Pacala, S. W. and A. P. Dobson. 1988. The relation between the number of parasites/host and host age: population dynamic causes and maximum likelihood estimation. *Parasitology* **96**:197-210.
- Rao, C. R. 1973. *Linear Statistical Inference and Its Applications*, 2d Edition. John Wiley & Sons, Inc. New York, New York, USA.
- Reid, N., N. M. Smith and Z. Yan. 1995. Ecology and population biology of mistletoes. Pages 285-310 *in* M.D. Lowman and N. M. Nadkarni, editors. *Forest Canopies*. Academic Press, San Diego, California, USA.

- Rolstad, J., B. Løken, and E. Rolstad. 2000. Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. *Oecologia* **124**:116-129.
- SAS Institute. 1989. SAS/STAT user's guide, version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.
- Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany* **82**: 399-409.
- Schupp, E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**: 267-275.
- von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113-137 in S. M. Scheiner and J. Gurevitch, editors. *Design and Analysis of Ecological Experiments*. Chapman and Hall, New York, New York, USA.
- Walsberg, G. E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. *Condor* **77**:169-174.
- Wheelwright, N. T. and Orians, G. H. 1982 Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *The American Naturalist* **119**: 402-413.

Table 1. Phainopeplas visited parasitized trees more frequently (79% of all trees visited) than expected from their frequency in the plot (28%,  $\chi^2 = 177$ ,  $P < 0.0001$ ). Both parasitized and non-parasitized trees that were visited by phainopeplas were taller than trees that were not used of the same infection status. Numbers are observed numbers in each category, and in parentheses, mean height  $\pm$  S.D. in meters.

	Visited (height)	Not Visited (height)	Total (height)
Parasitized (height)	96 (4.3 $\pm$ 1.5)	164 (3.6 $\pm$ 1.0)	260 (3.9 $\pm$ 1.3)
Not Parasitized (height)	21 (3.2 $\pm$ 0.9)	595 (2.1 $\pm$ 1.1)	616 (2.1 $\pm$ 1.1)
Total (height)	117 (4.1 $\pm$ 1.5)	759 (2.4 $\pm$ 1.3)	876 (2.6 $\pm$ 1.4)

## FIGURE LEGENDS

Fig. 1. Relationship of height to the probability that infected or uninfected hosts received seeds. The probability of receiving seeds increased with height for both parasitized (filled circles) and unparasitized (open circles) hosts. Previously infected hosts of all heights had a higher probability of receiving seeds than uninfected hosts. Trees have been divided into height classes for visual clarity. Bars are standard errors.

Fig. 2 - The frequency of flight distances observed (A) and flight times observed (B). Arrows indicate means. The distribution of flight distances was right skewed. Most flights were short distances, but a few long distance flights were observed. The mean perch time observed was 2.6 minutes. Even the maximum recorded perch time of 13 minutes is less than the time it takes for a seed to pass through a phainopepla's digestive system (Walsberg, 1975).

Fig. 3.- Seed deposition before and after mistletoe removal experiment. Seed deposition in host trees from which mistletoes were removed (open circles) declined relative to that in trees from which mistletoes were not removed (closed circles). Mistletoes were removed from experimental trees in week 7 (indicated by an arrow). Points are means and bars are standard errors (N = 8 trees).

Fig. 4.- (A) Time course of seed deposition in one pair of control (closed circles) and removal (open circles) trees. (B) Seeds deposited in removal tree plotted against seeds deposited in control tree. The average number of seeds deposited per branch per week was significantly correlated between control and experimental trees before mistletoe removal (open diamonds,  $r = 0.98$ ,  $p < 0.05$  for the example illustrated). After mistletoe removal this correlation decreased (closed diamonds,  $r = 0.24$ ,  $p > 0.1$ ).

Figure 1

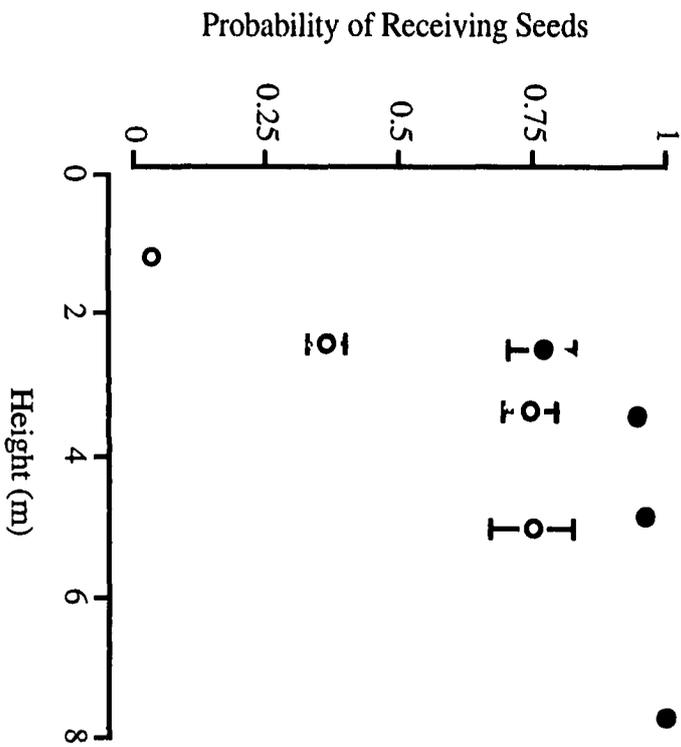


Figure 2.

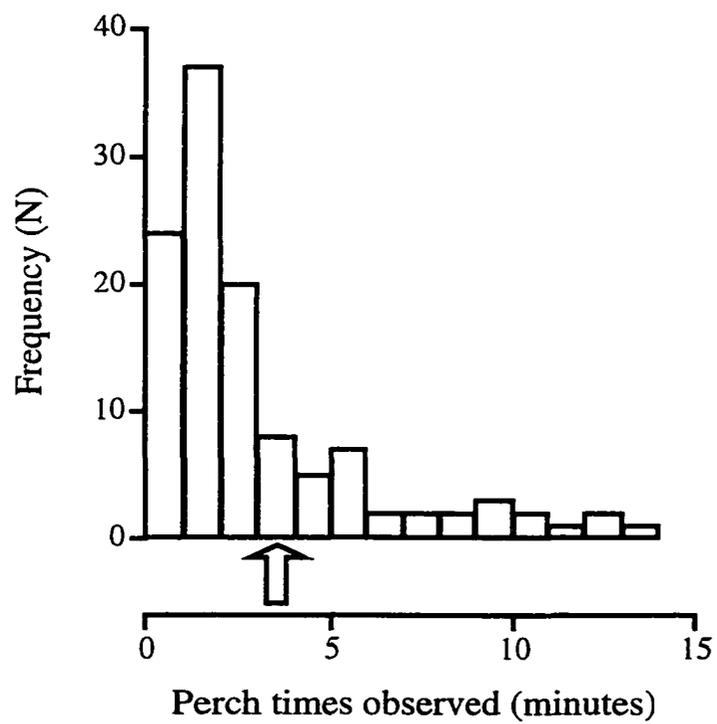
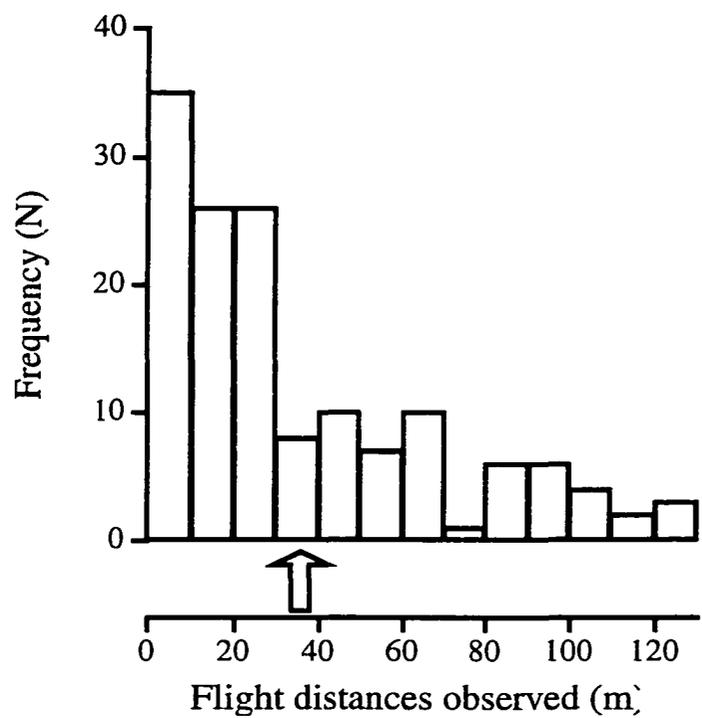


Figure 3.

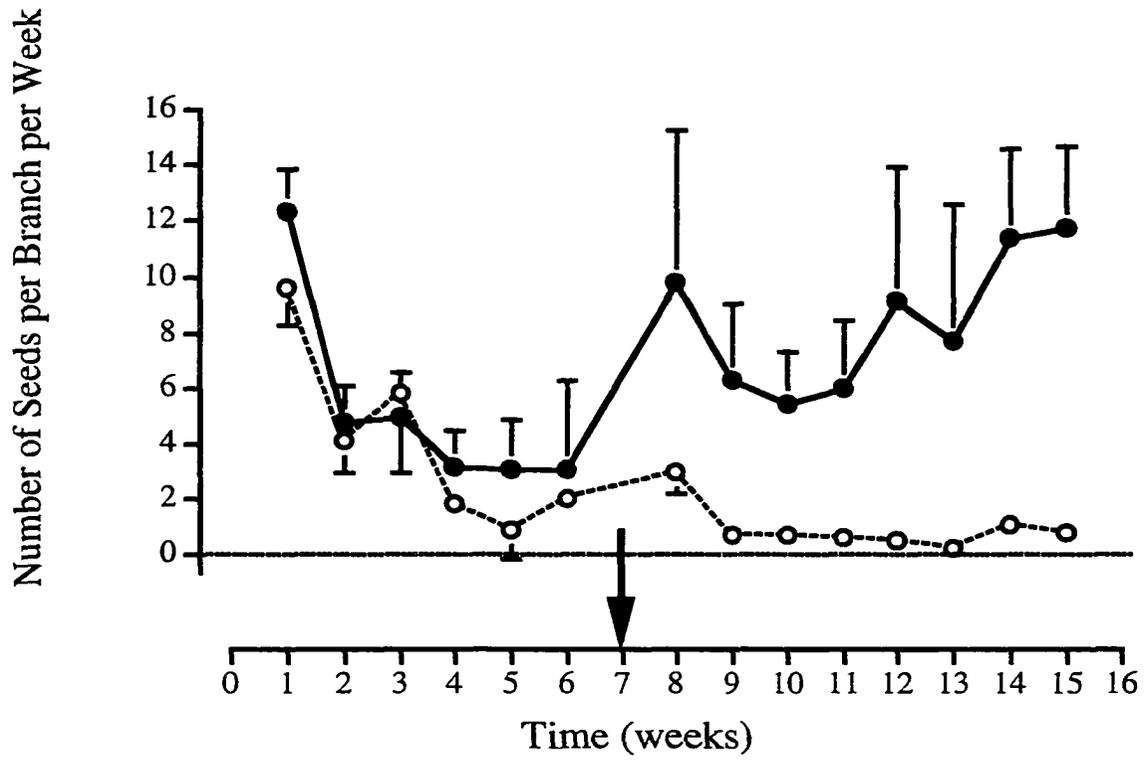
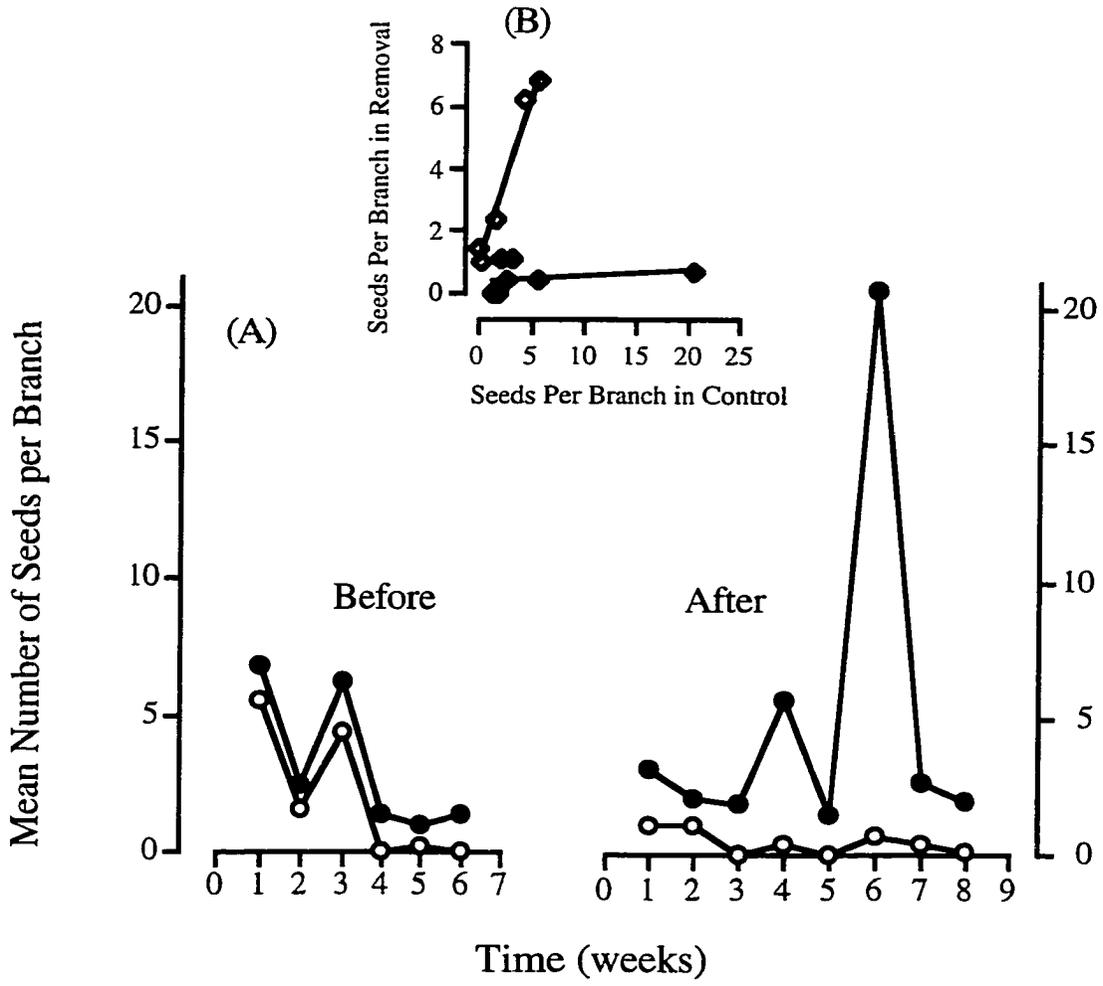


Figure 4.



## APPENDIX C

QUANTIFYING SPATIAL PATTERNS OF MISTLETOE SEED DEPOSITION BY A  
FRUGIVOROUS AVIAN DISPERSER

Quantifying spatial patterns of mistletoe seed deposition by a frugivorous avian disperser

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## ABSTRACT

Mistletoes are large-seeded, obligate parasitic plants dispersed by frugivorous birds. Safe sites are easily identifiable, and patterns of seed dispersal are related to bird perching and foraging behavior. These characteristics make mistletoes one of the most tractable plants to investigate seed dispersal and its consequences for the spatial distribution of plant populations. We examined the patterns of distribution and seed dispersal of the desert mistletoe, *Phoradendron californicum*, on a 4-hectare mapped plot in the Sonoran desert. Using geostatistics, we found spatial patterns in the distribution of mistletoes, tree height, and seed counts. To investigate the processes that generated the seed distribution patterns, we used mathematical models to predict the seed deposition patterns as a function of mistletoe number, tree height, and proximity to other infected trees. The model indicated that number of mistletoes and the height of hosts were the most important predictors of the number of seeds that would be deposited on a tree. The spatial patterns of seed dispersal are likely due to the foraging and perching behavior of seed-dispersing birds, specifically, their preference for tall, parasitized trees.

## INTRODUCTION

Identifying safe germination sites for seeds of plants is notoriously difficult (Wheelwright and Orians 1982). Likewise, identifying sources and destinations of disease propagules is complicated. Studying mistletoes provides a unique opportunity to accomplish both of these tasks. Mistletoes are parasitic plants, most of which are dispersed by birds that consume their fruits and deposit their seeds on host plants. These birds play a dual role in ecological communities: they are both mutualistic seed dispersers and disease vectors (Appendix A).

Seed dispersal is the first step in generating the distribution of plants that one sees in a landscape. Seed rain varies with distance from maternal (seed) parents, frequently exhibiting a leptokurtic distribution with a peak very close to the parent and a decrease in seed density further from the parent (Hoppes 1988, Willson 1993, Schupp and Fuentes 1995). Seed shadows generated by frugivores can be idiosyncratic (Jordano and Schupp 2000). They may depend on bird movement patterns, gut passage times, preferences of frugivores for certain microhabitats, and landscape distribution of these microhabitats (Alcanatará et al. 2000; Jordano and Schupp 2000; Wescott and Graham 2000). The behavior of frugivores is important in generating spatial patterns of seeds and adult plants, but our knowledge of the factors that determine the spatial variation in seed deposition remains incomplete.

Mistletoes offer a relatively simple system in which to examine spatial patterns in seed deposition and the processes that lead to them. Because mistletoes are parasitic plants, the sites in which they can potentially be found are limited to the locations of host

trees and shrubs. Likewise, safe sites for dispersed seeds are easily identified. We used the desert mistletoe, *Phoradendron californicum*, to examine patterns and processes of dispersal. *Phoradendron californicum* parasitizes primarily legume trees (*Acacia* spp., *Prosopis* spp., *Cercidium* spp. and *Olneya tesota*) in the North American desert southwest, and is dispersed predominantly by phainopeplas (*Phainopepla nitens*). These birds breed in the desert during the winter and depend on mistletoe berries for food (Chu and Walsberg 1999). Phainopeplas usually arrive in the desert in October and leave for higher elevations in late May. This roughly corresponds to the time when mistletoe fruits are available. Male and female phainopeplas are territorial during their desert breeding season and use conspicuous perching as a form of territorial display (Walsberg 1977). They have been observed to spend more than 85% of their time perching (Chu and Walsberg, 1999). Because frugivores dispersing mistletoe seeds are likely to respond to both mistletoes and their hosts, it is instructive to also consider the behavior of these seed dispersers as disease vectors. The behavior of vectors in response to infected or uninfected hosts can have a strong influence on the spatial distribution of a pathogen (McElhany et al. 1995) and their behavior influences the rate and extent of pathogen spread (Berger and Ferriss 1989). *Phoradendron californicum*, like many parasites, has a clumped, overdispersed, distribution among hosts (Overton 1994; Appendix A). A negative binomial distribution is frequently fitted to this type of data although the underlying processes generating it are poorly understood (Crofton 1971; Overton 1994). Because mistletoes represent a food resource for its vectors, mistletoe dispersing birds are likely to prefer infected hosts and this may account for the clumping within trees. Seed

deposition decreases greatly on trees from which mistletoes have been removed (Appendix B).

We attempted to understand the patterns found in mistletoe populations at scales larger than individual trees and the processes that generate and maintain these patterns. Different sites have varying prevalences of mistletoes with different patterns of seed rain (Appendix A). However, Overton (1996) did not find spatial aggregation of mistletoes at scales larger than individual trees. By mapping the locations of potential host trees, mistletoes, and dispersed seeds on a 4-hectare plot, we hoped to better understand the distribution of mistletoes and the processes that generate and maintain these patterns. Specifically, we investigated whether the patterns of seed deposition are related to properties of the host, such as the height of the trees, or the spatial distribution of mistletoes. To investigate these questions, we coupled geostatistical analysis with mathematical modeling and model-fitting using maximum likelihood estimation.

## METHODS

### *Field methods*

This study was conducted on the Santa Rita Experimental Range (31° 53' N, 110° 54' W), 35 miles south of Tucson, Arizona. Host species in this area are primarily *Prosopis velutina*, as well as some *Acacia greggii* and a few *Cercidium microphyllum*. Between June 1999 and April 2000, we tagged each tree in a 4 ha plot with a unique identification code, recorded its species, height, canopy radius, number of mistletoes and number of seeds deposited on the tree. We counted mistletoe seeds deposited onto trees

between 1 and 10 February, 2000. We climbed tall trees and searched all branches, or used binoculars to examine branches we could not reach, to obtain complete counts for each tree. We obtained UTM coordinates for 774 trees using differential GPS (details can be found in Aukema and Kunzmann 2000).

### ***Analysis***

Geostatistical Analysis - We used geostatistical methods to detect spatial patterns in seed deposition, mistletoe distribution, and host tree height. Geostatistics compare the value of a variable of interest at one location with its value at another location to determine whether they are more similar if they are closer together in space (Rossi et al. 1992). A variogram is a plot of the difference between all possible pairings of data that are separated by a lag distance  $h$  (Isaaks and Srivastava 1989). Typically, variograms tend asymptotically to the *sill*; the distance at which this occurs, the *range*, is the average distance within which samples are spatially dependent. Lower variogram values indicate greater similarity between samples than higher variogram values. We constructed variograms and fitted models using Variowin (Pannatier 1996).

Statistical Models - We developed a set of statistical models to understand the underlying processes that generated the observed patterns of seed deposition. We assumed that seeds are dispersed to individual trees at a constant rate that is determined by bird perching and feeding preferences. Under this assumption, the seed counts have a compound Poisson distribution. A compound Poisson distribution may assume a variety of forms, depending on the distribution of the rate parameter. In one special case, a

compound Poisson is precisely a negative binomial distribution if the rate parameter has a Gamma distribution (Evans et al. 2000). To compute the expected number of seeds, we considered three factors that reflect our understanding of bird behavior and mistletoe seed dispersal: tree height, the number of mistletoes that infect a tree, and proximity to infected trees. We developed 11 specific models that considered these factors, and we fit them to the data using maximum likelihood. Our methods are similar to methods for computing the dispersal kernels of forest trees developed by Ribbens et al. (1994).

The 11 models that we considered ranged from the very simple to the very complex. In the simplest model, the expected number of seeds deposited was high if the tree was infected with mistletoes, and low if it was not. We modified the model by considering the effects of constant, linear, and saturating functions of height and mistletoes on expected distributions of seeds. Combinations of these functions account for the first nine models. In the tenth model, the expected number of seeds for infected trees was a saturating function of a linear combination of height and mistletoes, but the number of expected seeds for a tree without mistletoes was a saturating function of height. The eleventh model was a modification of the tenth model that allowed trees to have a higher or lower number of expected seeds depending upon proximity to infected trees. In this model, we used a general probability distribution function described by Ribbens et al. (1994). The full set of models and the specific mathematical formulations are found in Table 1.

To fit these models to the data, we used a numerical method that combines a random hill-climbing algorithm with a bisection method that is guaranteed to find local

maxima (Press et al. 1988). To rank the models, we used Akaike's Information Criterion (AIC). AIC compares non-nested models with different model complexity.

Conceptually, AIC is a measure of the information lost from the data, and the model with the lowest AIC is the one that loses the least information (Burnham and Anderson 1998).

In practice, AIC is a simple function of the log likelihood:  $-2 * L(\text{Data} | \text{model}) + 2K$  where  $K$  is the number of parameters in the model. Information is lost because the model fits poorly, or because adding one new parameter decreases the support in the data for all the parameters. Thus, AIC is implicitly a criterion for parsimony (Burnham and Anderson, 1998), balancing model complexity with model fit. AIC ranks models relative to one another, but does not provide any measure of the overall goodness of fit. To generate a measure of the goodness of fit, we used the maximum likelihood estimated parameters to compute the expected number of seeds. We used the expected number of seeds to compute  $\chi^2$ .

## RESULTS

We found spatial correlation in number of mistletoes, height of host trees, and number of seeds deposited on trees (Fig. 1). The variogram of number of mistletoes on a tree was best fit by a power model. This is a continuously increasing function for which a sill was not reached within the distance for which the variograms could be calculated. The number of mistletoes was spatially correlated to at least 145 meters. Height of trees reached a sill at approximately 40 meters. That is, that trees within 40 meters of each

other were more similar in height than they were to trees farther away. The variogram of number of seeds on a tree showed spatial correlation to approximately 70 meters (Fig. 1).

The number of mistletoes per tree was the strongest predictor of mistletoe seed deposition, followed by tree height and by proximity to an infected tree. The full ranking of models are found in Table 1. The best fit parameters for model 10 were: expected number of seeds =  $-100.6 + 806(M + 0.23H + 0.05HM) / (11.1 + M + 0.23H + 0.05HM)$  +  $(-34 + 228.8H / (10.7 + H))$  where M is number of mistletoes, and H is height. The expected number of seeds increased with the number of mistletoes, but the relationship saturated at high mistletoe densities (Fig. 2a). Taller trees had a higher number of expected seeds than did shorter trees at all levels of mistletoe infection (Fig. 2b). At light mistletoe infection, the expected number of seeds did not increase with height until the height exceeded a threshold.

Proximity to an infected tree led to an expectation of a decreased rate of seed deposition. This result was the opposite of what we expected. Although the maximum likelihood estimation and model selection preferred this model, we are inclined to regard it with skepticism. Proximity had no effect beyond three meters, a distance that is smaller than the canopy size of large trees. Because the effect of proximity only operated at very close distances, only eighteen trees were affected by proximity, and all of these were heavily infected. We are more inclined to interpret this result as strong evidence that there was no increased seed deposition near heavily infected trees.

The best model was significantly different from the data ( $\chi^2 = 106403.8$ ,  $P < 0.0001$ ,  $df = 759$ ). The model had a tendency to overestimate the number of seeds

deposited on trees on which we actually found 0 or few seeds and to underestimate seeds deposited on trees on which we actually found a very large number of seeds (Fig. 3).

## DISCUSSION

The maximum likelihood analysis suggests that proximity to infected trees does not increase the expected deposition of mistletoe seeds at small spatial scales. According to the model, heavily mistletoe-laden trees received more seeds than less parasitized trees. Furthermore, tall trees tend to receive more seeds. This is consistent with observations that phainopeplas perch preferentially in parasitized and tall trees (Appendix B). Observations of phainopepla behavior and the results of a mistletoe removal experiment also indicate that inter-host seed deposition is frequent (Appendix B), in contrast to the suggestion that intra-host seed deposition is the most important component of seed deposition (Overton 1994). Unfortunately, the model can not distinguish the source of deposited seeds and thus, we are unable to separate the relative contributions of inter- and intra-host seed dispersal.

We suggest that perching and feeding behavior of territorial, frugivorous birds need not generate a seed rain that declines with distance. For example, birds might spend all of their time within a small territory, but distribute their time evenly over the territory. In this case, our observed patterns are consistent with observations that tall trees with many mistletoes are preferred to all other trees, and that the distribution of mistletoes and height explain the distribution of seeds. This distinction between intra- and inter-host

seed deposition is important from the perspective of gene flow, metapopulation dynamics, and the evolution of parasite life-history traits.

Although we can not distinguish inter- and intra- host seed dispersal with these methods, it is clear that host tree characteristics are important in determining the quantity of seeds deposited on them. Host trees can be thought of as resource patches, or alternatively as territory markers, whose quality depends on the quantity of mistletoe fruits available. Foraging birds can be expected to respond to mistletoes, learn which patches are of the highest quality, and spend more time in high quality patches than in low quality patches. However, because mistletoe fruits ripen progressively throughout a six-month fruiting season, birds may need to return to patches frequently to sample fruit availability. The model indicated that the presence of mistletoes in a tree was the best predictor of seed rain to the tree. If a tree had at least one mistletoe, it was much more likely to receive seeds than if it had none. Observations of phainopeplas indicate that they prefer infected trees over uninfected trees (Appendix B). In addition, the number of seeds a tree was expected to receive increased with the number of mistletoes on the tree, but this function saturated. This may be due to a type II functional response (Gotelli 1998) in which resources on heavily infected trees are not depleted either because birds become satiated, feeding rate is constrained by handling time, or birds need to be present in other areas of their territories.

In addition to the number of mistletoes on a tree, the height of a tree was an important predictor of the number of seeds deposited on it. Very short trees did not receive seeds. The negative intercept of the height function indicates a threshold at which

increased height began to increase the probability that a tree received seeds. However, this function was also saturating. That is, once a tree is tall, birds appear no longer to respond to differences in height. Tall trees have a very high probability of receiving seeds even if they are not infected. This corresponds to observations of phainopepla behavior and observations of seed deposition in other sites. Very short trees virtually never receive seeds and phainopeplas are not observed perching in them, whereas tall trees are preferentially used as perches (Appendix B). However, there is an interaction between height and number of mistletoes, in which tall, heavily infected trees receive the most seeds. The preference for tall trees is likely to be related to the conspicuous perching of phainopepla territorial displays.

The difference between observed and predicted seed deposition may be due to tree characteristics that we did not measure. Certain trees may be highly preferred perches due to their architecture, location within a bird's territory, or use as a nesting tree. The difference is probably also due, in part, to the Poisson distribution, which is an assumption of the model. Given a Poisson distribution with a rate parameter  $\lambda$ , the probability of zero seeds is  $\exp(-\lambda)$ . Even if  $\lambda$  is 1, the probability of 0 is only 40%. Thus, many trees on which zero seeds were observed were predicted to receive one or more seeds according to the model.

Using geostatistics, we have found spatial correlation of mistletoes up to at least 145 meters, and spatial correlation of seed deposition to approximately 70 meters, but the processes of seed dispersal that we modeled do not explain the pattern. There appears to be a positive feedback in which infected trees receive seeds and become reinfected

(Appendix A). We have only examined patterns of seed rain, and plant distributions are determined not only by seed rain but also by establishment, persistence, and mortality (Jordano and Herrera 1995, Schupp 1995). The patterns of seed dispersal observed here are likely to be due, in large part, to the foraging and perching behavior of phainopeplas and other mistletoe seed dispersing birds. Inter-nest distances of phainopeplas at SRER are 50 -100 m (Chu pers. comm.). Thus the 70 meter spatial correlation in seed deposition could be a reflection of phainopepla territory sizes. Phainopepla territories may not be evident in adult mistletoe distributions because these plants are long-lived and changes in the birds' territory boundaries from year to year could dilute any effects of territory size on the spatial distribution of adult mistletoe plants. Further examination of other aspects of mistletoe life history are necessary to fully understand the processes that generate local patterns of mistletoe distribution.

## LITERATURE CITED

- Alcantará, J. M., P.J. Rey, F. Valera, and A. M. Sánchez-Lafuente. 2000. Factors shaping seedfall pattern of a bird-dispersed plant. *Ecology* 81: 1937-1951.
- Aukema, J. E. and M. R. Kunzman. 2000. The Use of GPS & GIS tools to help document the spread of desert mistletoe (*Phoradendron californicum*), a plant parasite in Arizona. 20th Annual ESRI User Conference Proceedings, p 521.  
<http://www.esri.com/library/userconf/proc00/professional/papers/PAP521/p521>.
- Berger, P. H. and R. S. Ferriss, 1989. Mechanisms of arthropod transmission of plant viruses: implications for the spread of disease. In "Spatial Components of Plant Disease Epidemics" (Michael Jeger, ed.), pp. 40-84. Prentice-Hall Inc., Englewood Cliffs, New Jersey, USA.
- Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference, a Practical Information Theoretic Approach. Springer-Verlag, New York, New York, USA.
- Chu, M. and G. Walsberg. 1999. Phainopepla (*Phainopepla nitens*). In: A. Poole and F. Gill, editors. The Birds of North America, No. 415. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Crofton, H. D. 1971. A quantitative approach to parasitism. *Parasitology* 62: 179-193.
- Evans, M., N. Hastings and J. B. Peacock. 2000. Statistical Distributions, 3rd ed. John Wiley & Sons, Inc.
- Gotelli, N. J. 1998. A Primer of Ecology, 2<sup>nd</sup> edition. Sinaur Associates, Inc. Sunderland, Massachusetts, USA.

- Hoppes, W. G. 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69: 320-329.
- Isaaks, E. H. and R. M. Srivastava. 1989. *Applied Geostatistics*. Oxford University Press, New York, New York, USA.
- Jordano, P. and C. M. Herrera. 1995. Shuffling the offspring: Uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal
- Jordano, P. and E. W. Schupp. 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70: 591-615.
- McElhany, P., L. Real, and A. Power. 1995. Vector preference and disease dynamics: a study of barley yellow dwarf virus. *Ecology* 76: 444-457.
- Overton, J. M. 1994. Dispersal and infection in mistletoe metapopulations. *Journal of Ecology* 82: 711-723.
- Overton, J. M. 1996. Spatial autocorrelation and dispersal in mistletoes: field and simulation results. *Vegetatio* 125:83-98.
- Pannatier, Y. 1996. *VARIOWIN: Software for spatial data analysis in 2D*. Springer-Verlag, New York, New York, USA.
- Press, W. H., S. A. Teukolsky, W. T. Vetterling and B. P. Flannery. 1988. *A Numerical Recipes in C*. Cambridge University Press. New York, New York, USA.
- Ribbens E., Silander Jr. J. A. and S. W. Pacala. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75:1794-1806.

- Rossi, R. E., D.J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* 62: 277-314.
- Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany* 82:399-409.
- Schupp, E. W. and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2: 267-275.
- Walsberg, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilonotidae). University of California Publications in Zoology 108: 1-63.
- Wescott, D. A. and D. L. Graham. 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*: 122:249-257
- Wheelwright, N. T. and Orians, G. H. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *The American Naturalist* 119, 402-413.
- Willson, M. F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108: 261-280.

Table 1. The models tested, delta AIC values and model rankings. Models have been partitioned into number of mistletoes and height of target trees. In the first nine models, seed deposition is constant (C) (uncorrelated with height (H) or mistletoes (M)), increases linearly (L) with H or M, or is an increasing, but saturating (S) function of H or M. In the tenth model, we include an interaction term for trees that are both tall and heavily laden with mistletoes (LxH). The eleventh model is a more complicated form of the tenth model; we modify the expected number of seeds by computing its proximity to infected trees (SxP). The constant models have one parameter,  $\alpha$  or  $\beta$ . Linear models have two parameters, an intercept ( $\alpha$  or  $\beta$ ) and a slope ( $\gamma$  or  $\sigma$ ). Saturating models have three parameters, an intercept ( $\alpha$  or  $\beta$ ), the slope at zero ( $\gamma$  or  $\sigma$ ) and an asymptote relative to the intercept ( $\lambda$  or  $\eta$ ). In the tenth model, the expected number of seeds is a saturating function of number of mistletoes and height;  $\alpha$  is the intercept,  $\sigma$  is the asymptote relative to  $\alpha$ ,  $\kappa$  scales the units of H relative to M and  $\rho$  measures the interaction between M and H. In the eleventh model,  $\theta$  and  $m$  determine the shape of the probability distribution function of seeds with respect to the source, while  $s$  measures the fecundity of the source tree and  $D$  is the Euclidean distance between the source and target trees (Ribbens et al. 1994). A negative total expected number of seeds for height or mistletoes implies a threshold.

Model #	Expected Seeds				$\Delta$ AIC	Rank
	Number of Mistletoes		Height of Target			
	model	type	model	type		
1	$\alpha$	C	$\beta$	C	34565	11
2	$\alpha + \sigma M$	L	$\beta$	C	14565	8
3	$\alpha + \sigma M / (\lambda + M)$	S	$\beta$	C	9682	7
4	$\alpha$	C	$\beta + \gamma H$	L	25273	10
5	$\alpha + \sigma M$	L	$\beta + \gamma H$	L	5771	6
6	$\alpha + \sigma M / (\lambda + M)$	S	$\beta + \gamma H$	L	1207	4
7	$\alpha$	C	$\beta + \gamma H / (\eta + H)$	S	25059	9
8	$\alpha + \sigma M$	L	$\beta + \gamma H / (\eta + H)$	S	5559	5
9	$\alpha + \sigma M / (\lambda + M)$	S	$\beta + \gamma H / (\eta + H)$	S	984	3
10	$\alpha + \sigma (M + \kappa H + \rho H M) / (\lambda + M + \kappa H + \rho H M)$	LxH	$\beta + \gamma H / (\eta + H)$	S	477	2
11	$\alpha + \sigma (M + \kappa H + \rho H M) / (\lambda + M + \kappa H + \rho H M)$	LxH	$\beta + \gamma H / (\eta + H) + \sum_i s M_i \exp(-D m_{i,j}^{\theta}) / N(D, \theta)$	SxP	0	1

## FIGURE LEGENDS

Figure 1. Variograms of (A) number of mistletoes per tree (B) height of host trees and (C) number of seeds deposited per tree. The number of mistletoes variogram (A) was best fit by a power model ( $\gamma(h) = 13.4 + 0.25 h^{0.68}$ ), indicating spatial correlation in the number of mistletoes to at least 145 meters. The height of host trees (B) reached a sill at 38 meters ( $\gamma(h) = 1.14 + 0.88 * \{ 1.5(h/38.4) - 0.5(h/38.4)^3 \text{ if } h \leq 38.4; 1 \text{ otherwise} \}$ ). The number of seeds deposited onto trees (C) reached a sill at approximately 70 meters ( $19200 + 21200 (1 - \exp(-3h/68.8))$ ). Points are experimental variogram values, lines are the model variograms.

Figure 2. The fitted parameters for model 10 A) holding number of mistletoes constant and B) holding height constant. The expected number of seeds increases with height of trees for all numbers of mistletoes. A) For some trees, the predicted number of seeds deposited would be negative. In our model, these seeds were expected to receive no seeds. This reflects a threshold in the model; trees with 0 or 1 mistletoe must exceed a minimum height before they are expected to receive any seeds. B) The model also predicts that the number of seeds increases in a decelerating fashion with the number of mistletoes on a host tree for all sizes of trees.

Figure 3. The relationship between the expected and observed number of seeds per host tree. The  $y = x$  line indicates an exact correspondence between observed and expected numbers of seeds. Points above the line are trees for which the model overestimated seed deposition and points below the line are trees for which the model underestimated seed deposition. The model had a tendency to overestimate a) the number of seeds deposited on trees which actually received zero or few seeds and b) to underestimate the number of seeds deposited on trees which received many seeds.

Figure 1

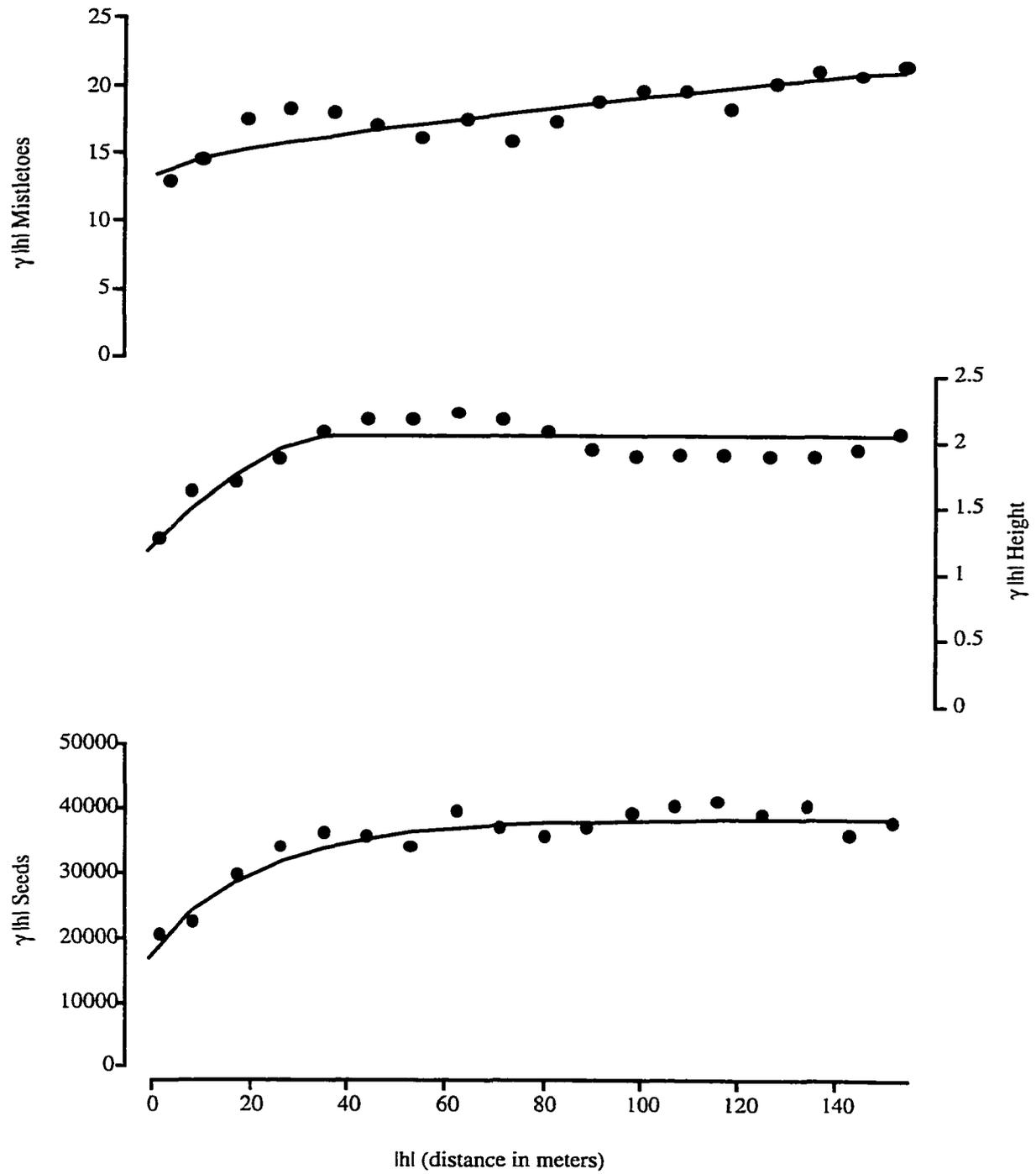


Figure 2

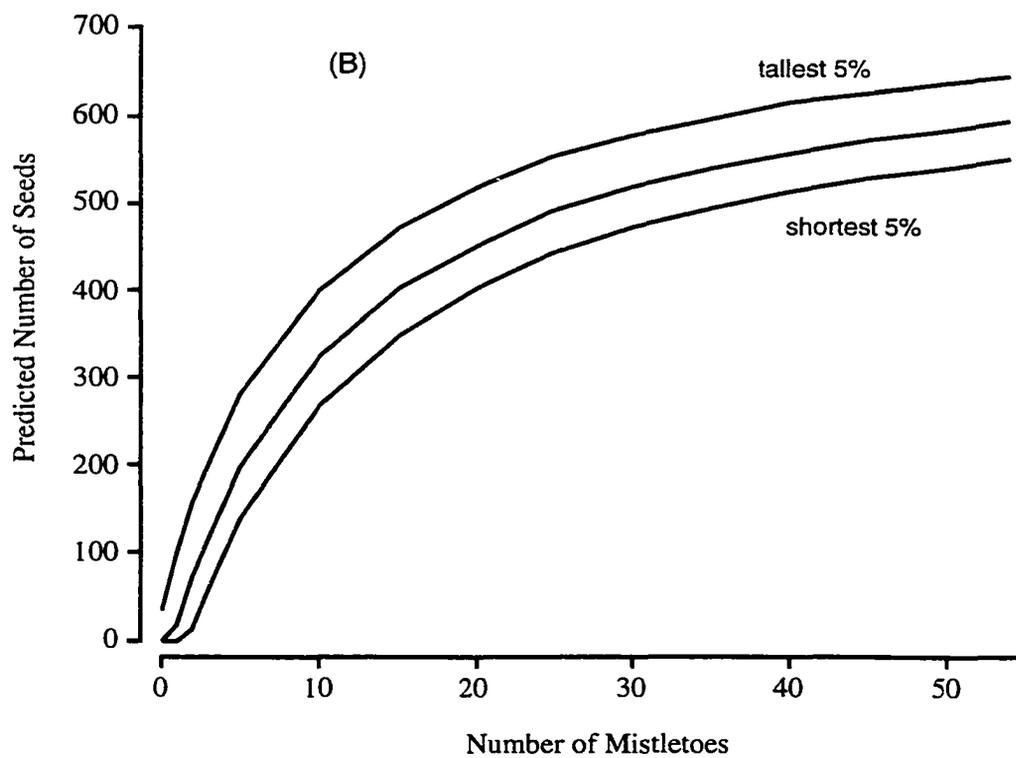
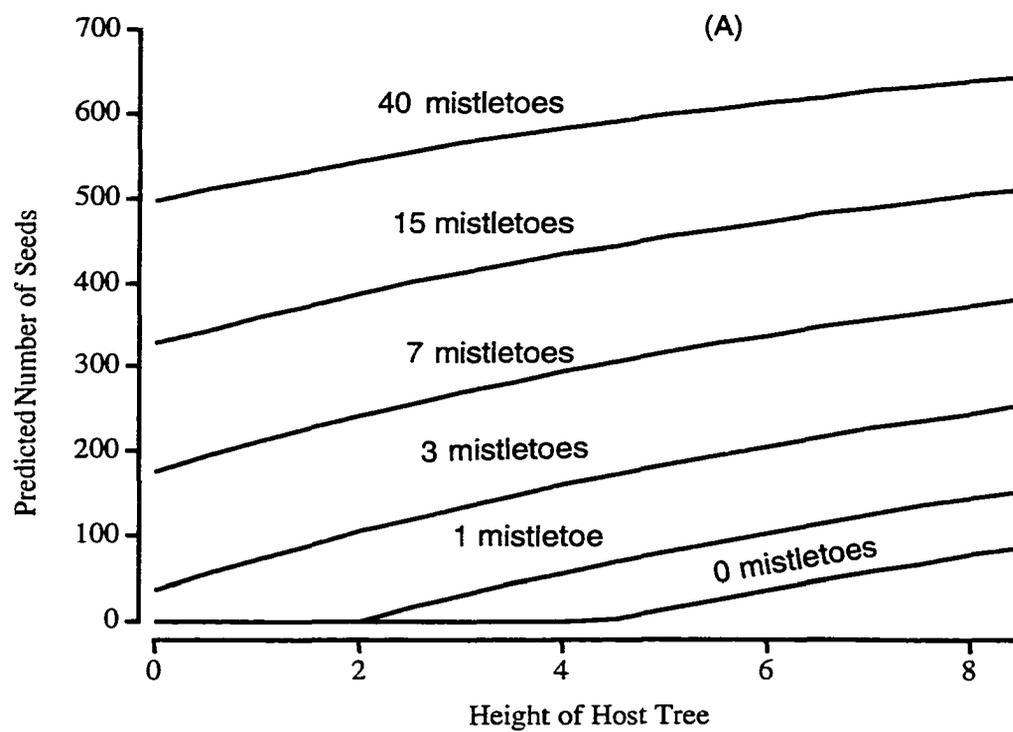
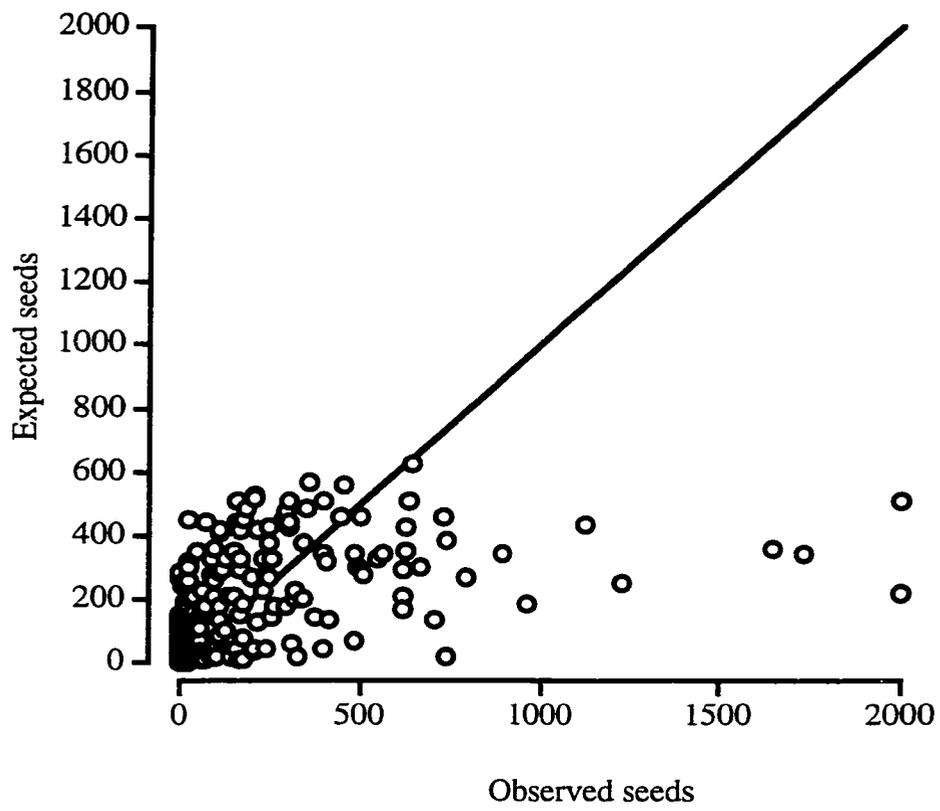


Figure 3



**APPENDIX D****THE IMPORTANCE OF SCALE IN THE STUDY OF DESERT MISTLETOE  
DISTRIBUTIONS**

The importance of scale in the study of desert mistletoe distributions

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## ABSTRACT

Spatial patterns are important to many ecological processes, and scale is a critical component of these patterns and processes. I examined the pattern and scale of the spatial distribution of infection on host plants by the desert mistletoe, *Phoradendron californicum*, in a landscape that spans several square kilometers. I also studied the relationship between mistletoe infection and seed dispersal. I found elevated seed rain in areas with a high prevalence of mistletoes and I found that a greater proportion of trees receive seeds than are infected, suggesting that mistletoes will be aggregated in space. Using nested analysis of variance and variograms, I found that mistletoe infections were distributed in hierarchical patches. Mistletoe prevalence was correlated at scales of 1500 meters, and at scales greater than 4000 meters. Correlation at the largest scales was due to the effect of elevation: sites at higher elevations showed reduced mistletoe infection compared to those at lower elevations. I propose that at small scales, mistletoe distributions are primarily the result of aggregation of seed-dispersing birds, and that the elevational effect reflects the limits of the mistletoes' physiological tolerance to freezing-induced cavitation. I predict that this pattern should also be evident latitudinally.

## INTRODUCTION

Recent years have seen a growing awareness of the need for increased attention to spatial processes and patterns in order to understand the factors that shape distribution, dynamics, and interactions of organisms (Kareiva 1994). There is a great deal to be

learned about how spatial patterns are generated and maintained and about the interaction between patterns at different scales. Pattern and scale are inextricably intertwined. The description of spatial distribution patterns and of their variation in time depend on identifying the scales at which patterns occur (Turner 1989, Levin 1992). The hierarchical patch dynamics paradigm provides a conceptual framework for examining pattern-process-scale interactions in the landscape (Wu and Louks 1995). Under this paradigm, patches are functional units that are scale and organism dependent (Wiens 1976, O'Neill et al. 1986, Kotliar and Wiens 1990). Patches at different scales form nested hierarchies (Kotliar and Wiens 1990) in which the scales are explicitly linked (O'Neill et al. 1986) and the dynamics of ecological systems are a composite of the dynamics and interactions of these nested patches (Wu and Louks 1995). Hierarchical patch dynamics is a useful framework because it emphasizes the multiscale properties of pattern and process in ecological systems and recognizes the potential for emergent properties from interactions between scales (Wu and Louks 1995). In this study, I describe spatial variation in the distribution and seed dispersal of *Phoradendron californicum* (desert mistletoe) and the scales at which this variation occurs. My purposes are to describe mistletoe distributions and seed dispersal patterns at the scale of several kilometers, to generate hypotheses about the processes that lead to these patterns, and to identify the scales at which future studies should focus to better understand processes affecting mistletoe distribution and dispersal. I consider the processes that may be acting to create spatial mistletoe aggregations at different scales and I use the ideas of

hierarchical patch dynamics to try to understand how these processes and patterns are linked across scales.

*Phoradendron californicum* (Viscaceae) is a parasite of legume trees in the North American arid southwest. Its seeds are dispersed primarily by *Phainopepla nitens* (phainopeplas), although the berries are consumed by many other birds as well (Larson 1996). During their winter breeding season, both male and female phainopeplas defend all-purpose nesting and feeding territories (Walsberg 1977). This breeding season coincides with the fruiting of mistletoes. Phainopepla breeding failures have been linked to the absence of mistletoe-berries due to drought (Chu 1999) and freezing (Larson 1991). Phainopeplas consume mistletoe berries and defecate the seeds onto host branches. The seeds germinate, penetrate the branch and tap into the host's xylem to absorb water, minerals and nutrients (Calder, 1983). Phainopeplas respond to the distribution of mistletoes in their foraging, and by distributing mistletoes seeds differentially among hosts, they create mistletoe patches in the landscape (Herrera 1985). Phainopeplas both respond to, and contribute to shaping the spatial distribution of the mistletoes whose fruits they feed on and whose seeds they disperse.

The spatial variation in abundance of *P. californicum* depends on the distribution of its host trees, on the behavior of seed dispersers, and on its own physiological tolerance to abiotic factors. Previous studies have shown that mistletoes have a clumped distribution within trees (Overton 1994; Appendix A) and that parasitized trees receive more seeds than unparasitized trees (Appendix A, E). Overton (1994) found that mistletoes were not spatially autocorrelated at small scales, but Aukema and Smith

(Appendix C) found spatial correlation of *P. californicum* infections to more than 145 meters. In a previous report, I documented a positive correlation between prevalence of mistletoes in a neighborhood and seed deposition into unparasitized trees (Appendix A). This result suggests that mistletoes will be spatially aggregated, but the scale at which they are aggregated in the landscape is unclear.

Spatial variation in nature can take place over a wide range of spatial scales (Oliver and Webster 1986). For example, at the scale of a few meters, *P. californicum* is aggregated within host trees (Overton 1994; Appendix A); and at the scale of many kilometers, host trees in one mountain range may be heavily infected whereas those in another range may be uninfected (pers. obs.). Scales of landscape pattern vary depending on the organisms and ecological processes being investigated (Kotliar and Wiens 1990). An important component of ecological hierarchy theory is that processes at one scale may generate patterns at other scales (O'Neill et al. 1986, Wu and Louks 1995). For this reason, the scale at which a study is conducted can have significant impacts on the patterns found and on inferences about the processes that create these patterns (Wiens 1989). Because organisms differ in their response to the environment, and because their ecological neighborhoods differ in size, appropriate scaling is particularly important in studies of interactions between and among species (Wiens 1989).

Geologists, miners, and geographers have long been aware of the frequently hierarchical nature of patchiness in nature. They have been detecting, quantifying and predicting spatial patterns of qualities such as soil types and ores (Oliver and Webster 1986). This is of interest to ecologists, not only because the distribution of these

phenomena is often directly responsible for the distribution of organisms, but also because ecologists are just beginning to take advantage of the techniques created by geographers and geologists to describe spatial pattern (Rossi et al. 1992, Orum et al. 1997). I used a combination of techniques to examine the spatial distribution of desert mistletoes. First, I conducted an exploratory analysis to detect patterns that could suggest hypotheses about the spatial distribution of mistletoes and mistletoe seeds. Next, I used spatially explicit statistical methods to conduct a formal spatial analysis..

#### METHODS

This study was conducted at the Santa Rita Experimental Range (SRER , 31°53' N, 110° 54' W), south of Tucson, Arizona, USA. The Santa Rita Experimental Range consists of 53,159 acres of semidesert grassland scrub habitat (Burgess 1995) at the base of the Santa Rita Mountains. Over the last 100 years, velvet mesquite (*Prosopis velutina*) has become dominant on as much as 30,000 acres that were previously dominated by grassland (Martin and Turner 1977, Medina 1996). SRER ranges in elevation from less than 900 meters in the northwestern corner to about 1300 meters in the southeast (Fig. 1). Average annual rainfall increases with elevation, ranging from 250 to nearly 500 millimeters (Martin and Turner 1977). The main hosts of *P. californicum* at SRER are *Prosopis velutina* (velvet mesquite) as well as *Acacia greggii* (cat-claw acacia) and *Cercidium microphyllum* (yellow palo verde), although the latter two hosts are less abundant.

I used a balanced hierarchical sampling scheme in a nested survey (Oliver and Webster, 1986) of mistletoe infection, seed deposition, and host attributes. Samples were gathered throughout SRER in a nested design with four levels. I selected four widely spaced primary sample areas. Within each of these areas, I sampled at 16 points, nested as follow. Within each primary area, I chose points 2000 meters apart (level 1); from each of these points, I chose a second point 1000 meters distant (level 2); from each of these points, I chose pairs 500 meters apart (level 3) and from each of these, I chose points 250 meters apart (level 4). I did this by obtaining a sample at an arbitrary point at least 50 meters from a road. I then chose a random direction with the second hand of a watch and a compass and walked 250 meters, measured with a pedometer, for another sample. I then walked in a semi-random direction (constrained to 180° so that I would not return to my original point) 500 meters for a sample. Next, I walked 250 meters for a sample. Then I sampled at 1000 meters, 250 meters, 500 meters and 250 m. I then returned to my starting point and drove 2 kilometers to repeat the sampling scheme. All samples were taken in upland areas, if the random point took me to a point near an arroyo (dry stream), I selected the closest upland point for the sample. Likewise, roads were avoided to keep the vegetation as physiognomically homogeneous as possible (Norton and Smith 1999). At each sample point I recorded the location in UTM coordinates using a Garmin II Plus handheld GPS receiver (selective availability was active at this time).

Samples at each point consisted of all of the *P. velutina*, *C. microphyllum*, and *Acacia* spp. trees within a 20 m radius circle, determined with a laser range finder. For each tree, I recorded tree species, height, number of mistletoes, and number of deposited

mistletoe seeds. I measured height with a measuring pole and counted mistletoes and seeds by thoroughly inspecting each of the trees. For each sample point, I calculated mistletoe infection prevalence and intensity, seed infection prevalence and intensity, mean host height, host tree density, and host species composition. I use the parasitological term prevalence to imply the fraction of hosts with a given attribute (in this case, infected with one or more mistletoes or receiving one or more seeds). Similarly, I use intensity to denote the mean number of parasites or seeds present per tree in my samples.

*Analysis:* I began with an exploratory analysis of patterns and correlations in the data (Rossi et al. 1992). Then I used two types of analysis to examine spatial correlation of mistletoe infections and mistletoe seed deposition. The hierarchical sampling protocol was designed to facilitate both nested analysis of variance and geostatistics. Both of these methods were first used to examine geological spatial patterns (Youden and Mehlich 1937, Isaaks and Srivastava 1989, Webster and Oliver 1990, Bellehumeur and Legendre 1998). Combining both methods provided corroboration of the results and extended the range of distances that I could examine.

I analyzed infection prevalence and seed prevalence with nested analysis of variance in which distances were nested random effects (PROC NESTED, SAS Institute 1989). Infection and seed prevalences were logit transformed. This sampling design leads to a nested analysis of variance in which distance effects are assumed to be random (Model II, Marcuse 1949). From this analysis, the components of variance contributed by

each distance can be estimated and relative contributions to the total variance can be calculated as a percentage (Webster and Boag 1992). High variance components indicate stages with greater spatial dependence (Webster and Oliver 1990). The cumulative components of variance can be plotted as a function of distance to produce a variogram (Miesch 1975, Webster and Oliver 1990). Variograms are a central feature of geostatistics. Thus, the nested analysis of variance approach is closely related to geostatistics.

Geostatistical methods allow quantification of the relationship between the value of a variable at one location and its value at another location, with the expectation that samples close together will have more similar values than those farther apart (Rossi et al. 1992, Liebhold et al. 1993). One of the best-known tools of geostatistics, the variogram or semi-variogram, summarizes the difference in the value of the variable of interest between all possible pairings of data that are a lag distance,  $\mathbf{h}$ , apart (Isaaks and Srivastava 1989, Liebhold et al. 1993). The semi-variance,  $\gamma(\mathbf{h})$ , for lag distance  $\mathbf{h}$  is equal to half the average squared difference between the paired values:

$$\gamma(\mathbf{h}) = 1/2N(\mathbf{h}) \sum (z_i - z_j)^2 \quad (1)$$

where  $N(\mathbf{h})$  is the number of pairs of points separated by  $\mathbf{h}$ ,  $z_i$  is the value of a variable at location  $i$ , and  $z_j$  is the value of the same variable at location  $j$ , a distance  $\mathbf{h}$  from the first point.  $\gamma(\mathbf{h})$  is calculated for different values of  $\mathbf{h}$  and is plotted as a function of  $\mathbf{h}$ . Lower  $\gamma(\mathbf{h})$  values indicate greater similarity in the variable of interest at that distance than higher  $\gamma(\mathbf{h})$  values. Typically, the variogram tends asymptotically with distance to the *sill*, which is usually equal to the sample variance; the distance at which this occurs, the

*range*, is the average distance within which the samples are spatially dependent. From equation 1,  $\gamma(\mathbf{h}) = 0$  when  $\mathbf{h} = 0$ . However, when values are extrapolated to lag 0 in practice, the intercept is often  $> 0$ . This error is termed the *nugget* and is due to experimental error and to spatial variability at a scale smaller than the minimum lag distance (Liebhold et al. 1993, Bellehumeur and Legendre 1998). I used all of the points from the hierarchical sampling survey plus an additional two points (selected in the same way as the original points, 2000 m apart) for a total of 66 points. I constructed variograms using all pairwise comparisons of points and fitted models using Geoeas (Englund and Sparks 1991) and Variowin (Pannatier 1996) software packages. Variograms can be reasonably constructed for lag distances including at least 30-50 pair comparisons. The standard rule is to construct a variogram not more than half the maximum distance between points (Liebhold et al. 1993). Therefore I was able to examine the variogram at lag distances greater than the maximum 2000 meter sampling distance that I could examine using the nested ANOVA method. Although the smallest lag distance I used was 1000 m (due to the number of pairwise comparisons at the smallest lag distances), the nested analysis of variance provided a picture of smaller lag distances than I could calculate accurately using geostatistics.

## RESULTS

***Exploratory data analysis.*** In the area of the study, elevation ranged from 880 -1190 meters. Host tree density ranged from 48 to 756 trees per hectare, while average height ranged from 1.4 to 3.5 meters. Mistletoe infection prevalence (proportion of trees

infected) ranged from 0 to 75% and intensity (mean number of mistletoes per tree) ranged from 0 to 10.5. Seed deposition prevalence ranged from 0 to 88% of trees receiving one or more seeds, and mean seed deposition intensity ranged from 0 to 92 seeds per tree.

Mistletoe infection prevalence and intensity were strongly positively correlated ( $r^2 = 0.965$ ,  $P < 0.0001$ ,  $N = 66$ ). Thus, in the analyses that follow, I will only consider prevalence. Prevalence of seed rain was positively correlated with infection prevalence ( $r^2 = 0.92$ ,  $P < 0.0001$ ,  $N = 66$ ), but the slope of a regression fitted through the origin ( $1.19 \pm 0.04$ ) was significantly greater than 1 ( $t = 4.42$ ,  $P < 0.005$ ; Fig. 2a), indicating that nearly at any level of prevalence, 20% more trees receive seeds than are infected. By separating infected and uninfected trees, I found that, although seed rain was higher in infected trees than in uninfected trees, prevalence of seed rain increased with overall infection prevalence in the neighborhood for both uninfected (Spearman's  $\rho = 0.59$ ,  $P < 0.0001$ ) and infected (Spearman's  $\rho = 0.40$ ,  $P = 0.0077$ ) trees (Fig. 2b). Hence, at higher infection prevalences, more uninfected trees received seeds than at lower prevalences, indicating a positive feedback at two scales. At the scale of individual trees, parasitized trees receive more seeds than uninfected trees, leading to an aggregated distribution of mistletoes per tree (Appendix A). At a local scale, neighborhoods with a high prevalence of mistletoe infections have a higher rate of seed deposition into uninfected trees, and hence more new infections occur at higher than at lower prevalence neighborhoods. The seed deposition patterns suggested that mistletoes will be aggregated in space and motivated the following spatial analysis.

***Spatial analysis.*** Nested analysis of variance indicated spatial variation in the prevalence of both mistletoe infections and seed deposition. For both infection and seed prevalences, nearly half of the variation occurred at the largest distance of 2000 m, whereas the components of variance for the three lowest levels account for another 40% of the variation. There was considerable residual variation (more than 10%), representing variation occurring over distances of less than 250 meters, random variation, and variation due to measurement error. Because the largest distance level accounted for the majority of the variation, there is the possibility of additional spatial structure at larger scales.

Because the greatest distance between points was 12,635 meters and because the number of pairwise comparisons was high, I could reasonably construct variograms to approximately 6300 meters. The variogram for both infection prevalence and seed prevalence (Fig. 3) leveled off between 1000 and 4000 meters, reaching a sill at a range of about 3300 meters (indicative goodness of fit: 0.00804). However, starting at about 4000 meters, the variogram began to rise sharply, indicating that even at these large scales, points closer together (4000 m apart) were more similar than points farther apart (6000 m apart). The small nugget of the variograms corroborated the nested ANOVA result that there was not a great deal of spatial structure at smaller scales than were examined with the variogram.

I suspected that the large-scale (greater than 4000 m) effects were due to elevation, because SRER is at the base of the Santa Rita Mountains and elevation increases in a southeasterly direction (Fig. 1). In fact, infection prevalence was

significantly negatively correlated with elevation (Spearman's  $\rho = -0.73$ ,  $P < 0.0001$ ; Fig. 1, 4) and with host tree density Spearman's  $\rho = -0.42$ ,  $P = 0.0005$ ; Fig. 4). Because host tree density increased linearly with elevation ( $r^2 = 0.69$ ,  $P < 0.0001$ ; Fig 4), it was difficult to disentangle the relative effect of each factor on infection prevalence. To separate the contributions of density and elevation, I examined the correlation between the residuals of the relationships between prevalence and elevation and that between density and elevation. However, I found no correlation between them ( $r^2 = 0.02$ ;  $P = 0.32$ ). Hence, it is impossible to separate these two effects.

The biology of mistletoes suggests that elevation is likely to be an important factor due to physiological effects related to temperature and precipitation changes correlated with elevation (see Discussion). Therefore, I repeated the spatial analyses on the residuals of prevalence and elevation (the analyses using the residuals of prevalence versus density were qualitatively identical). Using these residuals, the variograms of infection prevalence and seed prevalence reached a sill at approximately 1500 meters (Fig. 5). Performing the analysis on the residuals effectively removed the effect of elevation. Therefore, this analysis reflects the spatial effect of prevalence independent of elevation.

Because the spatial analysis of mistletoe seed prevalence so closely matched that of mistletoe infection prevalence (Table 1, Figs. 3, 5), I suspected that seed prevalence was reflecting infection prevalence. Therefore, I examined the residuals of seed prevalence vs. infection prevalence and found a pure nugget variogram (Fig. 6). A pure nugget variogram is a horizontal line and indicates no spatial correlation for the values. In

this case the best fit nugget model was equivalent to the overall covariance, indicating no signal in seed prevalence that is independent of that in infection prevalence.

## DISCUSSION

Hierarchy theory predicts that hierarchical patchiness is prevalent in nature and it has provided a valuable conceptual framework for descriptions of vegetation patterns and studies of heterogeneity (O'Neill et al. 1986, van Coller 2000). However hierarchical patchy distributions have rarely been demonstrated empirically in plant populations (Kotliar 1996, van Coller 2000). By explicitly addressing the scales at which mistletoe infections vary, I discovered that mistletoe distributions are patchy and their patchiness is nested hierarchically across scales. Examining a wide range of scales allowed me to identify patterns of mistletoe spatial variation and processes that might be important in creating patterns at those scales.

Mistletoe infection prevalence was highly variable across the landscape, with infection rates ranging from zero to three-quarters of all trees infected within a 1257 square meter circle (Fig. 1). Patterns of seed deposition changed with infection prevalence. Nearly 20% more trees received seeds than were infected at each sample plot, and uninfected trees in areas of high mistletoe prevalence received more seeds than those in areas of low mistletoe prevalence. This suggested the existence of a positive feedback in which high mistletoe prevalence in an area leads to increased seed deposition in uninfected trees, more new infections, and higher mistletoe prevalences. The positive feedback is also seen at the level of individual trees (Appendix B) and is due to

phainopeplas preferentially using infected trees and depositing seeds in them and it leads to an aggregated distribution of mistletoes within host trees. This neighborhood level positive feedback is probably also due to greater phainopepla activity in areas with high mistletoe prevalence than in areas with low prevalence. This process should lead to a patchy distribution of mistletoes in the landscape. Indeed, the spatial analysis indicated that the spatial correlation in mistletoe infections was distance dependent. However, at scales larger than the individual samples, seed prevalence did not show spatial correlation independent of infection prevalence, but was simply a reflection of it. This result suggests that increased spread of the parasite occurs at small scales (but see Appendix C).

I found spatial correlation in mistletoe prevalence at small scales of approximately 250 m - 1500 m and at much larger scales greater than 4000 m. The scale of spatial correlation can also be thought of as the size of a patch. The relatively small-scale patterns of 250 -1500 meters are greater than typical inter-nest distances (136 +/- 68 m in the Colorado Desert; Chu 1999, but 50 -100 m at SRER, Chu pers. comm.). I suspect that this is because phainopeplas aggregate when they establish territories. Both males and females defend territories in the early fall prior to the beginning of courtship. Once pairs are formed, territories are either combined, if they are adjacent, or one territory is abandoned (Walsberg 1977). Phainopeplas are likely to establish territories near other birds in order to facilitate mate selection, and such an aggregation of territorial birds could be responsible for small scale patterns of mistletoe distributions. In addition, because mistletoes are long-lived, changes in phainopepla territory boundaries from year to year could dilute effects of territory size on the spatial distribution of mistletoes.

The analysis of the residuals of elevation indicated that elevation likely was responsible for the larger-scale patterns of infection prevalence (Fig. 1). There are several testable explanations for the low mistletoe prevalence at high elevations. 1) It is possible that for phainopeplas to breed successful, temperatures must remain above a particular temperature and that at the higher desert elevations, winter temperatures drop below this threshold and therefore these birds avoid the higher elevations. 2) The relatively dense stands of *P. velutina* hosts at high elevations may represent recent colonizations in the invasion of mesquites in this area (Martin and Turner 1977) Thus, it is possible that mistletoes simply have not spread to the mesquite trees at higher elevations yet. My results suggested that mistletoe spread occurs locally, so a larger scale spread of mistletoes could take many years. Also, phainopeplas may prefer less dense stands of mesquites, which could contribute to the slow spread of mistletoes at the higher elevations. 3) Alternatively, low mistletoe prevalence at high elevations could be due to an inability of the plant to colonize this area. Because this hypothesis is consistent with current knowledge about the physiology of mistletoes and their hosts trees, it is the one that I suspect is accurate. In following paragraphs, I will elaborate in some detail the effect of elevation on infection prevalence may be due to the physiological tolerance of either the mistletoe or its hosts to freezing. Mistletoes are entirely dependent on their hosts for water and minerals, which they obtain through xylem-to-xylem contact via the haustorium, the morphological and physiological bridge between the parasite and its host (Kuijt, 1969). Xylem cavitation is caused by bubbles forming in the xylem conduits under low xylem pressure and is frequently caused by freezing or drought. The resulting

embolized conduit no longer contributes to water transport and cannot refill unless xylem pressure increases substantially (Pockman and Sperry 1997). In many temperate woody plants, cavitation and refilling are seasonal events. *Prosopis velutina* is resistant to drought-induced cavitation (Pockman and Sperry 2000), but is susceptible to freezing-induced embolism, with nearly 100% embolism in freezing temperatures (Pockman and Sperry 1997). Susceptibility to drought- and freezing-induced cavitation can define the limits of a plant's range (Pockman and Sperry 1997, 2000). For example, the range of *Larrea tridentata*, an evergreen desert plant, closely follows the temperature at which it experiences freezing embolism (Pockman and Sperry 1997).

Ehleringer and Marshall (1995) speculated that cavitation should be fatal in obligate parasitic plants. Two species of *Phoradendron* differentially parasitize hosts that are less water-stressed, and therefore less likely to induce cavitation in the parasite, than neighboring unparasitized hosts (Ehleringer and Marshall 1995 and references therein). I postulate that *P. californicum* is either susceptible to freezing-induced cavitation itself or that it experiences cavitation due to freezing-induced embolism of its host, and thus, its distribution is limited by winter temperatures. I predict that the geographical range of *P. californicum*, both latitudinally and elevationally, reflect its physiological tolerance to freezing-induced cavitation.

In conclusion, mistletoe infections were patchily distributed. Mistletoe infections were correlated at scales of more than 4000 meters. Nested within these large patches were patches of mistletoe infections of approximately 1500 meters. And within these intermediate patches, mistletoes are patchily distributed within individual host trees

(Appendix A, B). Because patterns and processes at one scale are constrained by processes at smaller and larger scales (O'Neill et al. 1986, Wu and Louks 1995), recognizing the hierarchical nature of the distribution of mistletoes is important for understanding the processes generating the patterns. To further elucidate the processes of seed dispersal and transmission of desert mistletoes, future studies of the spatial distribution of this plant parasite should focus on scales of approximately 1500 meters and on scales of more than 4000 meters. Future studies of the spatial distribution of phainopeplas and the physiological tolerances of mistletoes should illuminate the processes underlying the patterns I have observed.

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## LITERATURE CITED

- Bellehumeur, C. and P. Legendre. 1998. Multiscale sources of variation in ecological variables: modeling spatial dispersion, elaborating sampling designs. *Landscape Ecology* **13**: 15-25.
- Burgess, T. L. 1995. Desert grassland, mixed shrub savanna, shrub steppe, or semidesert scrub? The dilemma of coexisting growth forms. Pages 31-65 *in* M. P. McClaran and T. R. Van Devender, editors. *The Desert Grassland*. University of Arizona Press, Tucson, Arizona, USA.
- Calder, D. M. 1983. Mistletoes in focus: an introduction. Pages 1-18 *In* Calder, M. and P. Bernhardt, editors. *The Biology of Mistletoes*. Academic Press, San Diego, California, USA.
- Chu, M. C. 1999. Ecology and Breeding of *Phainopepla nitens* in the Desert and Coastal Woodlands of Southern California. Ph. D. Dissertation. University of California at Berkeley. Berkeley, California, USA.
- Ehleringer, J. R. and J. D. Marshall. 1995. Water relations. Pages 125-140 *In* M. C. Press and J. D. Graves, editors. *Parasitic Plants*. Chapman and Hall, New York, New York, USA.
- Englund, E. and A. Sparks. 1991. Geo-Eas 1.2.1 Geostatistical Environmental Assessment Software User's Guide. United States Environmental Protection Agency. Las Vegas, Nevada, USA.

- Herrera C. M. 1985. Habitat-consumer interactions in frugivorous birds. Pages 341-365  
In M. L. Cody, editor. *Habitat Selection in Birds*. Academic Press, Inc. San  
Diego, California, USA.
- Isaaks, E.H. and R.M. Srivastava. 1989. *Applied Geostatistics*. Oxford University Press,  
New York, New York, USA.
- Kareiva, P. 1994. Space: the final frontier for ecological theory. *Ecology* **75**: 1.
- Kotliar, N. B. 1996. Scale dependency and the expression of hierarchical structure in  
*Delphinium* patches. *Vegetatio* **127**: 117-128.
- 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.
- Kuijt, J. 1969. *The Biology of Parasitic Flowering Plants*. University of California Press,  
Berkeley, California, USA.
- Larson, D. 1991. Ecology of desert mistletoe seed dispersal. Ph.D. Dissertation.  
University of Illinois. Chicago, Illinois, USA.
- Larson, D. 1996. Seed dispersal by specialist versus generalist foragers: the plant's  
perspective. *Oikos* **76**:113-120.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**: 1943-1967.
- Liebhold, A. M., R.E. Rossi, and W.P. Kemp, 1993. Geostatistics and geographic  
information systems in applied insect ecology. *Annual Review of Entomology* **38**:  
303-327.
- Marcuse, S. 1949. Optimum allocation and variance components in mixed sampling with  
application to chemical analysis. *Biometrics* **5**: 189-206.

- Martin, S. C and R. M. Turner. 1977. Vegetation change in the Sonoran Desert Region, Arizona and Sonora. *Journal of the Arizona Academy of Science*. **12**: 59-69.
- Miesch, A. T. 1975. Variograms and variance components in geochemistry and ore evaluation. *Geological Society of America Memoir* **142**: 333-340.
- Norton, D. A. and M. S. Smith. 1999. Why might roadside mulgas be better mistletoe hosts? *Australian Journal of Ecology* **24**: 193-198.
- Oliver, M. A. and R. Webster. 1986. Combined nested and linear sampling for determining the scale and form of spatial variation of regionalized variables. *Geographical Analysis* **18**: 227-242.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide and T. F. H. Allen. 1986. *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Orum, T. V., D. M. Bigelow, M. R. Nelson, D. R. Howell and P. J. Cotty. 1997. Spatial and temporal patterns of *Aspergillus flavus* strain composition and propagule density in Yuma county, Arizona, soils. *Plant Disease* **81**: 911-916.
- Overton, J. M. 1994. Dispersal and infection in mistletoe metapopulations. *Journal of Ecology* **82**: 711-723.
- Pannatier, Y. 1996. *VARIOWIN: Software for spatial data analysis in 2D*. Springer-Verlag, New York, New York, USA.
- Pockman, W. T. and J. S. Sperry. 1997. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* **109**:19-27.

- Pockman, W. T. and J. S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany* **87**: 1287-1299.
- Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* **62**: 277-314.
- SAS Institute Inc. 1989. SAS/STAT User's Guide. Version 6, fourth edition. Volume 2. SAS Institute, Cary, North Carolina, USA.
- Silva, A., and C. Martinez del Rio. 1996. Effects of the mistletoe *Tristerix aphyllus* (Loranthaceae) on the reproduction of its cactus host *Echinopsis chilensis*. *Oikos* **75**: 437-442.
- Turner, M.G. 1989. Landscape Ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* **20**: 171-197.
- van Coller, A. L., K. H. Rogers and G. L. Heritage. 2000. Riparian vegetation-environment relationships: complementarity of gradients versus patch hierarchy approaches. *Journal of Vegetation Science* **11**: 337-350.
- Walsberg, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilonotidae). University of California Publications in Zoology **108**:1-63.
- Webster, R. and B. Boag. 1992. Geostatistical analysis of cyst nematodes in soil. *Journal of Soil Science* **43**: 583-595.

- Webster, R. and M. A. Oliver. 1990. *Statistical Methods in Soil and Land Resource Survey*. Oxford University Press. New York, New York, USA.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385-397.
- Wu, J. and O. L. Louks. 1995. From balance of nature to hierarchical patch dynamics: paradigm shift in ecology. *Quarterly Review of Biology* **70**: 439-466.
- Youden, W. J. and A. Mehlich. 1937. Selection of efficient methods for soil sampling. *Contributions from the Boyce Thompson Institute* **9**: 59-70.

Table 1. Nested analysis of variance results. Logit transformed mistletoe prevalence and seed prevalence were dependent variables and sources of variation were distances, which were nested random effects. The greatest component of variation was at the 2000 m scale.

Source	DF	Variance component		Percent of total	
		<u>mistletoes</u>	<u>seeds</u>	<u>mistletoes</u>	<u>seeds</u>
2000 m	3	1.314727	1.618807	49.9574	45.7671
1000 m	4	0.251261	0.281546	9.5475	7.9599
500 m	8	0.423055	0.737210	16.0754	20.8425
250 m	16	0.372093	0.416814	14.1389	11.7842
20 m (error)	32	0.270558	0.482679	10.2808	13.6463
Total	63	2.631693	3.537056	100	100

## FIGURE LEGENDS

Figure 1. Outline of the Santa Rita Experimental Range (SRER) with contour lines at 30 meter intervals. Circles represent sample locations. The shaded portion of each circle is the proportion of trees infected with *P. californicum*.

Figure 2. Relationship between mistletoe infection prevalence and seed rain prevalence. Prevalence of seed rain increased with mistletoe prevalence for (a) both infected (filled circles) and uninfected (open circles) trees, although infected trees had a higher probability of receiving seeds than uninfected trees. Seed rain also increased with prevalence for all trees combined (b), but the slope was 19% greater than that of a one-to-one relationship (dashed line).

Figure 3. Variogram of mistletoe prevalence (solid line) and seed prevalence (dashed line). For both mistletoe and seed prevalence, a sill was reached between 1000 and 4000 meters, but semivariance began to rise again sharply at 4000 meters and continued to rise thereafter.

Figure 4. Relationship between mistletoe prevalence, elevation and host tree density. Mistletoe prevalence decreased with (a) elevation (infection prevalence =  $\text{Exp}(-0.0194(\text{elevation} - 880)) / (1.216 + (\text{Exp}(-0.0194(\text{elevation} - 880))))$ ) and with (b) density (infection prevalence =  $\text{Exp}(-0.0194(\text{density} - 47.8)) / (0.925 + (\text{Exp}(-0.0194(\text{density} -$

47.8))))), whereas (c) density and elevation were positively correlated (density =  $-945 + 1.19 * \text{elevation}$ ,  $r^2 = 0.49$ ). For descriptive purposes, the relationship between mistletoe prevalence and elevation (A) and tree density (B) was fitted using sigmoidal functions.

Figure 5. Variogram of the residuals of mistletoe prevalence vs. elevation (solid line) and of seed prevalence vs. elevation (dashed line). For both mistletoe and seed prevalence, semivariance reached a sill at approximately 1500 meters.

Figure 6. Variogram of the residuals of seed prevalence vs. mistletoe prevalence. The variogram was best fit by a pure nugget model equivalent to the overall covariance (dashed line). This indicates that there is no spatial correlation between these variables.

Figure 1.

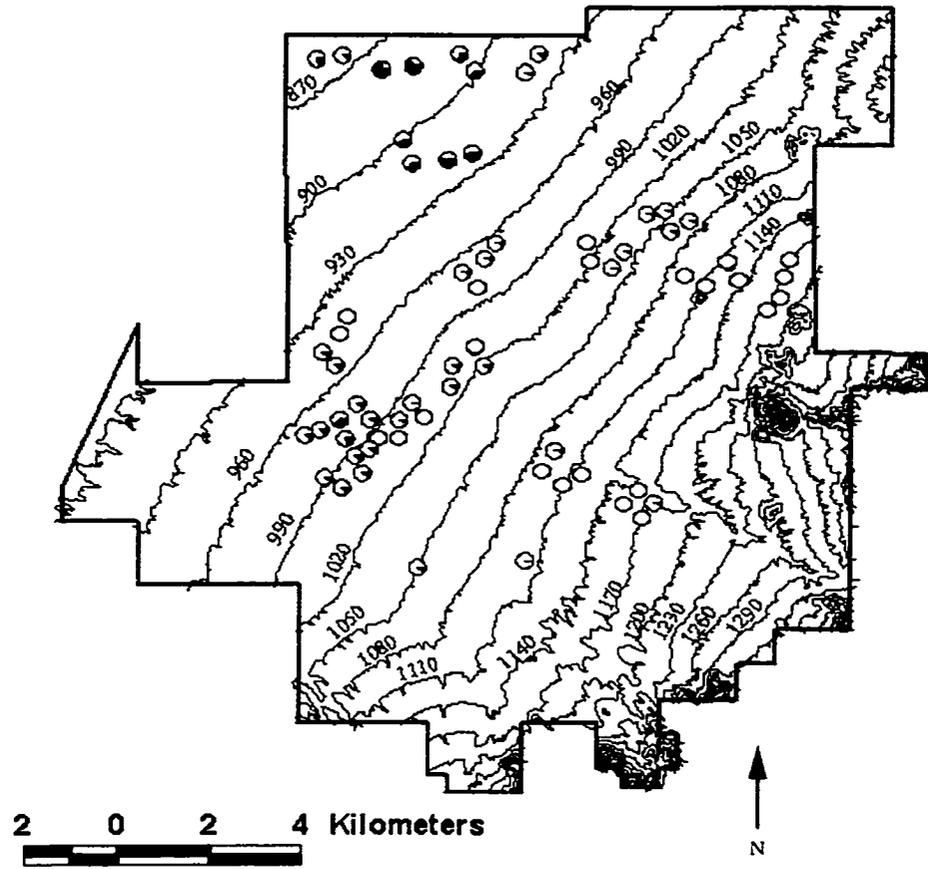


Figure 2

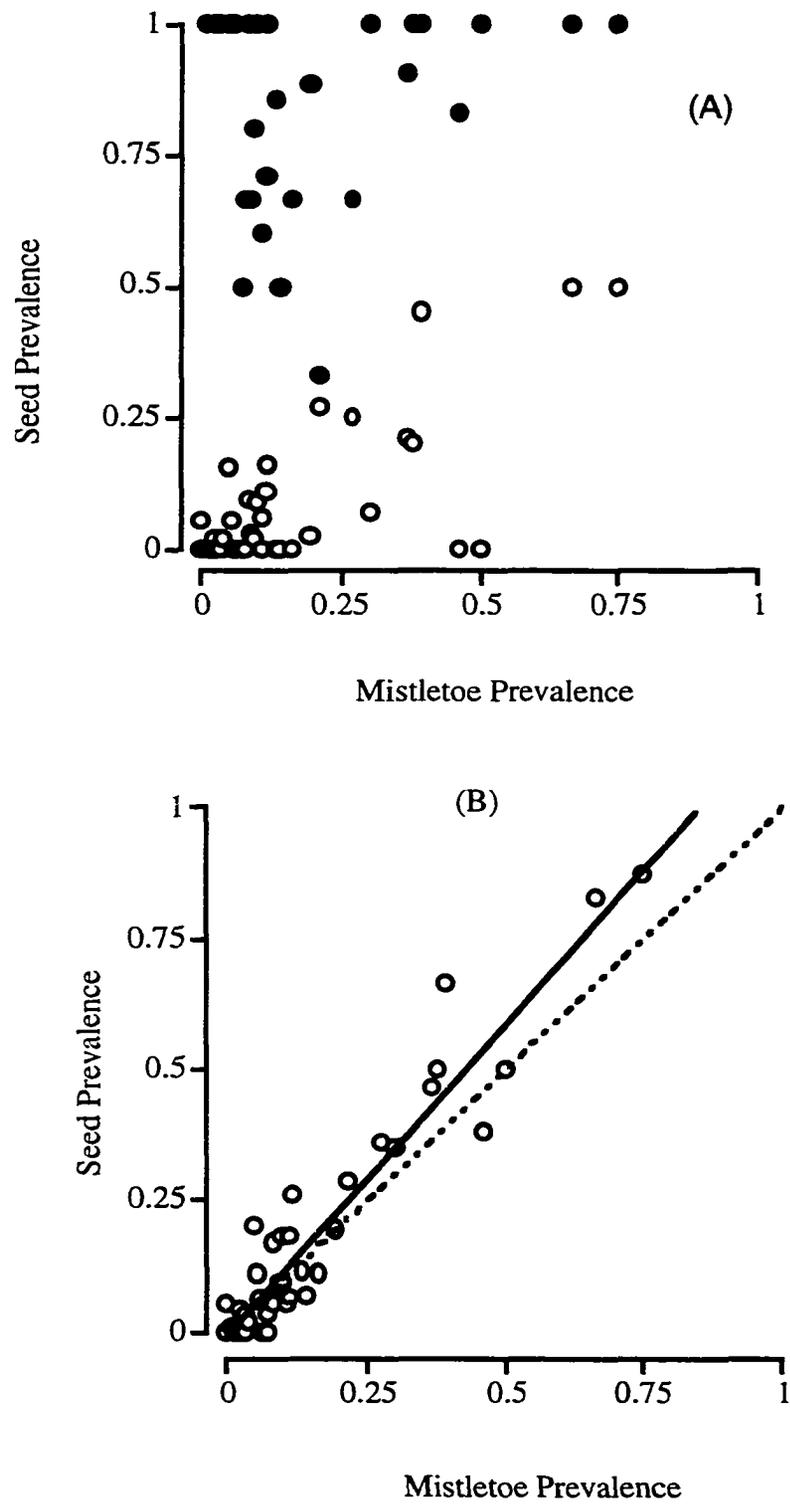


Figure 3.

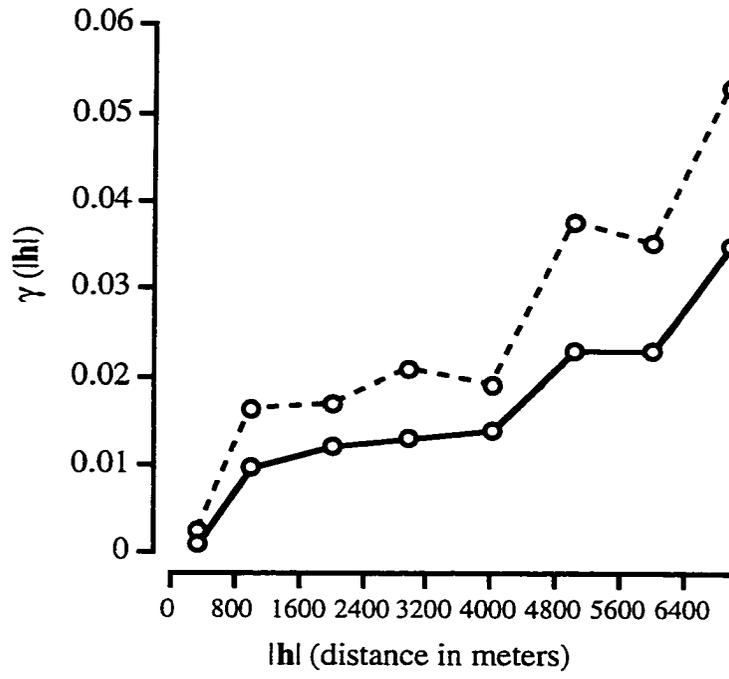


Figure 4.

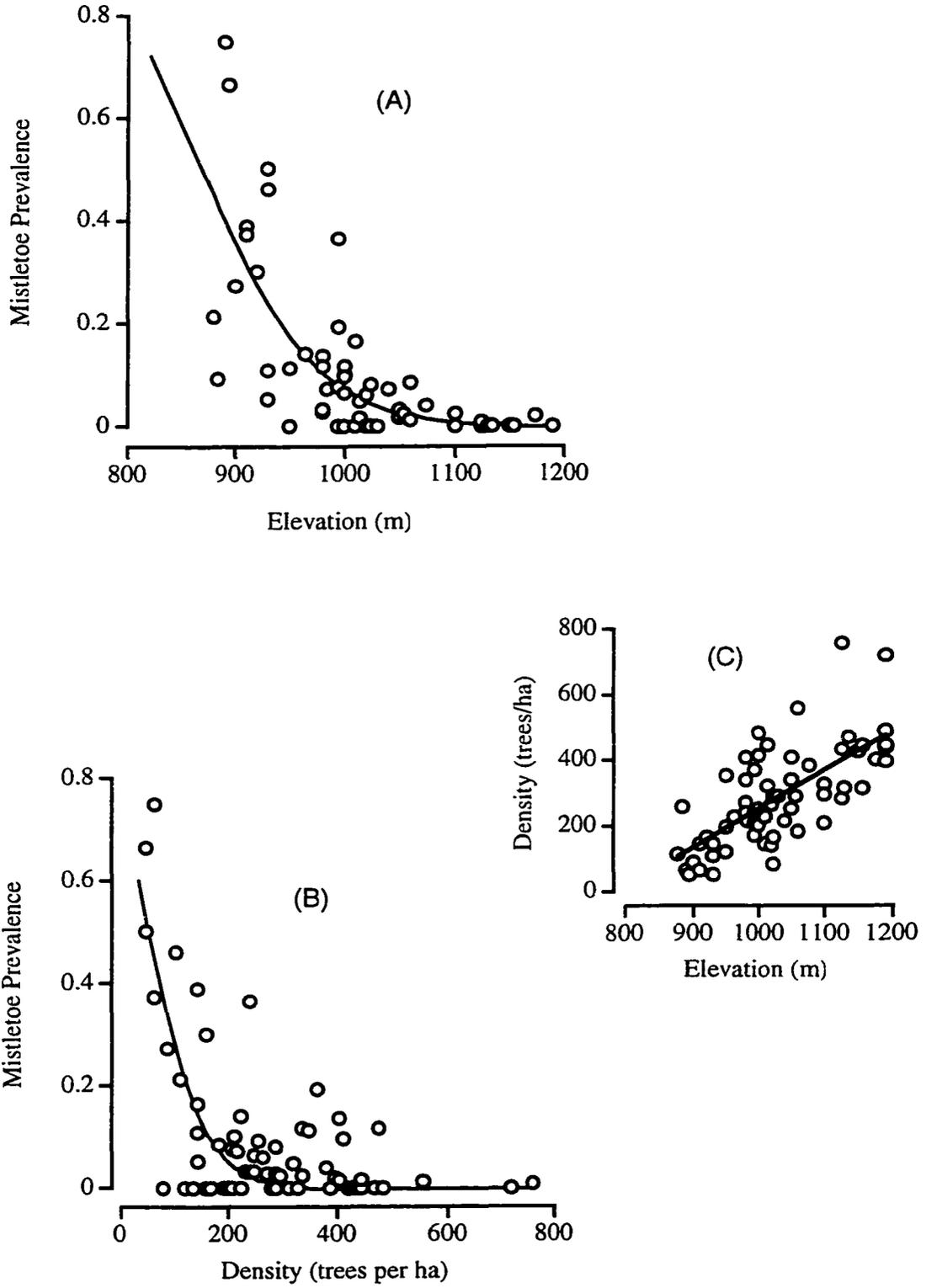


Figure 5.

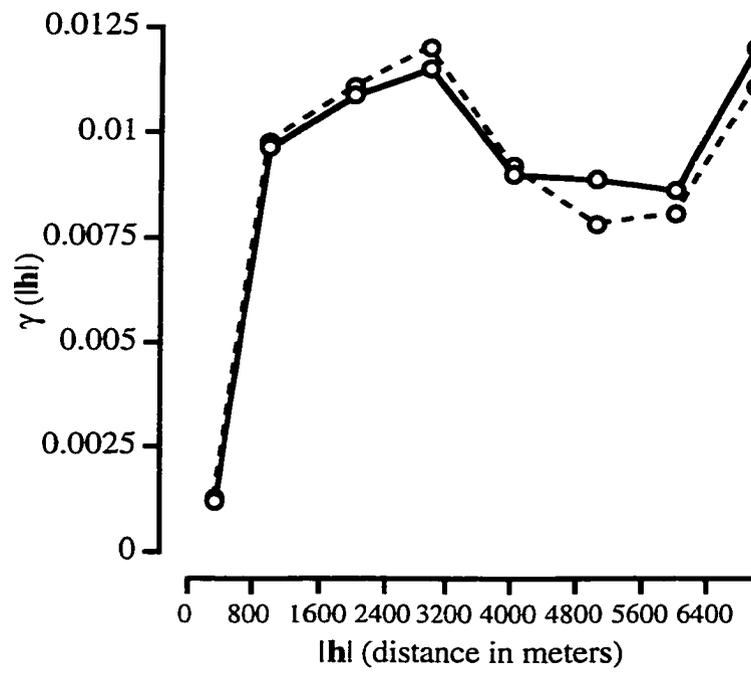
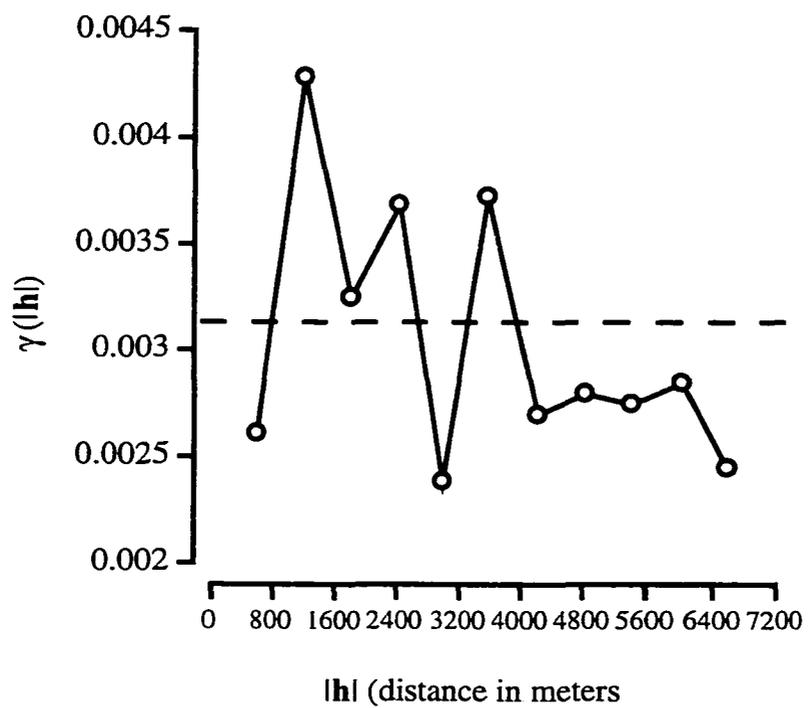


Figure 6.



**APPENDIX E**

**VARIATION IN MISTLETOE SEED DEPOSITION: EFFECTS OF INTRA- AND  
INTERSPECIFIC HOST CHARACTERISTICS.**

**Variation in mistletoe seed deposition:  
effects of intra- and interspecific host characteristics.**

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We investigated differences in host infection by a desert mistletoe, Phoradendron californicum, and examined one of the processes that contributes to these differences: variation in seed deposition among host individuals and species. In the Sonoran Desert, P. californicum parasitizes the sympatric leguminous trees Olneya tesota, Cercidium microphyllum, Prosopis velutina, Acacia constricta, and Acacia greggii. We hypothesized that seed deposition depends on host height and crown architecture. At a site in Arizona, frequency of infection did not reflect host relative abundance. Olneya tesota was parasitized at a higher frequency than expected from its abundance and maintained the highest mistletoe loads per individual host. In contrast, P. velutina was infected less frequently than expected. Infection frequency increased with host tree height for all hosts. Mistletoe seed deposition by avian dispersers differed among host species and was disproportionately high in O. tesota and P. velutina. Seed deposition was higher in infected than in non-infected host trees, and increased with tree height in O. tesota but not in C. microphyllum. We suspect that increased seed deposition with height in O. tesota may be due to the preference of seed-dispersing birds for higher perches. Some host tree species, such as C. microphyllum and A. constricta, probably received fewer mistletoe seeds because birds avoid hosts with dense and spiny crowns. Mistletoe populations are plant metapopulations in which host trees are patches and the frequency of infection in each host species/patch type is the result of interspecific differences in the balance between mistletoe colonization and extinction. From this perspective, our study of host use and seed dispersal is a metapopulation study of patch occupancy and propagule distribution among available patch types. Our seed-dispersal study demonstrates that the

mechanisms that create pattern in patchy plant populations can be investigated in mistletoe systems.

Mistletoes are common aerial stem-parasites that infect vascular plants ranging from pines to cacti (Hawksworth 1983, Martínez del Rio et al. 1996). With a few notable exceptions, such as the explosively dispersed Arceuthobium spp., mistletoe seeds are dispersed by fruit-eating birds, many of which are highly specialized to consume their berries (Reid et al. 1995). After being deposited by a bird onto an appropriate host, a seed germinates and forms a haustorium that taps into the xylem of the host plant to absorb water, minerals and, in some cases, sugars and amino acids (Calder 1983, Marshall and Ehleringer 1990).

Mistletoes range from extremely host specific (e.g. Arceuthobium apachecum) to host generalist (e.g. Dendrophthoe falcata) (Reid et al. 1995, Norton and Carpenter 1999). Often, the prevalence and intensity of mistletoe infections differ among host species (Yan 1993). The differential use of hosts by mistletoes within a site has been explained by three processes. First, because birds may perch and defecate mistletoe seeds more frequently on some hosts than on others, seed rain may differ among hosts (Reid 1989). Second, mistletoe seedlings may become established more successfully on some host species than others (Reid et al. 1995). Third, adult mistletoes may differ in persistence among host species (Hoffmann et al. 1986).

Phoradendron californicum, the desert mistletoe, is found from southern Utah to northern Mexico (Kearney and Peebles 1960). In the Sonoran desert, it infects Prosopis spp. (mesquite), Cercidium spp. (palo verde), Olneya tesota (ironwood) and Acacia spp. (acacia). Here we describe patterns of host use in P. californicum in the Sonoran Desert at a site in which it infects several species of trees. We also describe variation, both between and among hosts, in one of the processes that can produce differences in host use: the seed rain generated by seed-dispersing birds. In addition to exploring interspecific differences in infection and seed rain, we also investigate some of the factors that can lead to intraspecific variation in infection and seed rain. Specifically, we investigated whether host tree height was correlated with the probability or intensity of parasitism and whether tree height or current parasite load affected the probability of a tree receiving mistletoe seeds. Because host trees continue growing throughout their lives, height can be used as a rough approximation of the relative age of trees. We expected taller, and therefore older, trees to have a higher incidence of parasitism (Overton 1994, Martínez del Rio et al. 1995, Lei 1999), both because they would have more time to accumulate mistletoes and because phainopeplas (Phainopepla nitens), the avian dispersers of P. californicum seeds, use conspicuous perching as a form of territorial display (Walsberg 1977). Because mistletoes represent a food resource to which phainopeplas can be expected to respond, we hypothesized that previously infected trees were more likely to receive seeds, and therefore would be more likely to become reinfected (Martínez del Rio et al., 1995).

Mistletoe populations can be envisioned as assemblages of plants inhabiting different patch types represented by host species. The frequency of infection in each patch type/host species is the result of differences in the balance between colonization and extinction (Overton 1994). Overton (1994) suggested that mistletoe populations can be studied using a metapopulation perspective (but see Hanski and Gilpin 1991). From this perspective, our study of host use and seed dispersal can be conceived as a study of propagule distribution, which is one of the determinants of colonization among available patches (Hansson 1991).

### **Study sites and Methods**

We conducted this study in the Silverbell Mountains west of Marana, Arizona, USA (32° 27' N, 111° 27' W) in January and February 1998. The vegetation of this area is characterized as upland Sonoran Desert scrub (Turner and Brown, 1994) with a relatively high diversity of mistletoe host trees. We used two data sets for this study. First, we determined the relative abundance of each host tree species at the site by following twenty-three 50-meter strip transects radiating from an arbitrarily selected central location. We used these data (dataset 1, Table 1, Fig. 1) only for analyses that depended on relative abundance of host species. Each transect comprised a sample area of 400 m<sup>2</sup>; all individuals of each host species (Acacia constricta, Acacia greggii, Cercidium microphyllum, Olneya tesota, and Prosopis velutina) were counted within 4 m of each side of the transect line. For each individual, we recorded species, tree height, the number of mistletoe plants in the tree and the number of mistletoe seeds defecated onto each tree.

Because the seeds are large and light-colored, in contrast to the bark of hosts, they are easy to count by visually inspecting branches. Once deposited on a tree, the sticky viscin surrounding the seed adheres it to the branch, making it difficult to dislodge. Seeds from previous years are easily distinguished by their bleached color and crumbly texture. To increase our sample size of the two most frequently parasitized hosts, we recorded the same variables for all trees in a straight line, from the same origin, until we reached 100 individuals of both C. microphyllum and O. tesota. We used the combined, larger, data set (dataset 2) for the majority of analyses, especially for intraspecific analyses and interspecific analyses that did not depend on relative abundance.

## Results

### Inter-specific patterns of infection

Cercidium microphyllum (mean height  $\pm$  SE = 3.3  $\pm$  0.2 m, N = 101) was the most abundant host, followed by A. constricta (mean height  $\pm$  SE = 2.0  $\pm$  0.1 m, N = 62), O. tesota (mean height  $\pm$  SE = 4.5  $\pm$  0.1, N = 103), and P. velutina (mean height  $\pm$  SE = 3.6  $\pm$  0.2, N = 24). Acacia greggii was the least common host species (data set 1, Table 1, Fig. 1). Frequency of infection differed significantly among species (one way ANOVA,  $F_{4,168} = 10.04$ ,  $p < 0.001$ ) and did not reflect relative host species abundance ( $\chi^2_{4,168} = 24.86$ ,  $p < 0.001$ ; Table 1, Fig. 1). Olneya tesota was infected at a much higher frequency than expected from its abundance: this species accounted for 36.6% of all parasitized trees but made up only 12.5% of all host trees sampled. At the other extreme, no P. velutina individuals were infected in the first set of transects but this species represented

8.3% of all trees surveyed (Table 1, Fig. 1). We consider P. velutina and A. greggii hosts of P. californicum at our site because outside of our transects we encountered infected individuals and because at other sites these species are frequently infected.

The number of mistletoes per host individual differed significantly among species ( $F_{2,259} = 14.5$ ,  $p < 0.0001$ ). Olneya tesota had the highest number of mistletoes per individual (mean parasite load  $\pm$  SE =  $2.8 \pm 0.5$ ,  $N = 96$ ). Cercidium microphyllum and A. constricta individuals had much lower parasite loads ( $0.6 \pm 0.21$ ,  $N = 101$  and  $0.3 \pm 0.14$ ,  $N = 62$ , respectively). The difference in parasite loads among these three species was, in part, due to the higher mistletoe prevalence (proportion of trees infected) in O. tesota. However, when only parasitized individuals were analyzed, the same pattern emerged. There were significant species differences in parasite loads among infected individuals ( $F_{2,71} = 5.1$ ,  $p < 0.0084$ ) and infected O. tesota individuals had higher parasite loads ( $6.5 \pm 0.9$ ,  $N = 41$ ) than infected C. microphyllum ( $2.8 \pm 0.8$ ,  $N = 23$ ) and A. constricta ( $2.9 \pm 0.9$ ,  $N = 7$ ) individuals.

The frequency with which different species received seeds in our sample differed significantly among species (one way ANOVA,  $F_{4,296} = 24.8$ ,  $p < 0.0001$ ) and the frequency of seed reception did not reflect relative host species abundance ( $\chi^2_{4,168} = 31.12$ ,  $p < 0.001$ ; Table 1, Fig. 1). Olneya tesota and P. velutina received seeds more frequently than expected from their relative abundances (Fig. 1) and C. microphyllum and both species of Acacia received seeds less frequently than expected.

### **Intra-specific patterns**

The frequency of parasitized hosts increased significantly with tree height in O. tesota, C. microphyllum and A. constricta (logistic regression,  $p < 0.001$ , Fig. 2). The number of mistletoes per host increased significantly with height in O. tesota ( $r_s = 0.57$ ,  $N = 21$ ,  $p = 0.0065$ ) and C. microphyllum ( $r_s = 0.32$ ,  $N = 91$ ,  $p = 0.0021$ ).

Parasitized C. microphyllum trees were significantly more likely to receive seeds than were unparasitized trees (logistic regression,  $\beta_{\text{parasitism}}$ ,  $\chi^2 = 21.18$ ,  $p < 0.0001$ ,  $N = 101$ ). However, tree height had no effect on the frequency of seed deposition in this species (logistic regression, infected  $\chi^2 = 0.96$ ,  $p = 0.327$ ,  $N = 23$ ; uninfected  $\chi^2 = 0.184$ ,  $p = 0.668$ ,  $N = 78$ ; Fig. 3). In contrast, in O. tesota, presence of seeds increased with both height and infection (logistic regression, height  $\chi^2 = 9.47$ ,  $p = 0.0021$ ; infection  $\chi^2 = 20.15$ ,  $p < 0.0001$ ,  $N = 102$ ; Fig. 3).

In A. constricta, C. microphyllum, and O. tesota, the number of seeds deposited on a tree was significantly correlated with the number of mistletoes found on the tree (A. constricta:  $r_s = 0.50$ ,  $N = 59$ ,  $p < 0.0001$ ; C. microphyllum:  $r_s = 0.48$ ,  $N = 101$ ,  $p < 0.0001$ ; O. tesota:  $r_s = 0.72$ ,  $N = 96$ ,  $p < 0.0001$ ). Tree height had no influence on the number of seeds received by A. constricta or C. microphyllum. However, in O. tesota, height was also positively correlated with number of seeds deposited ( $r_s = 0.42$ ,  $N = 102$ ,  $p < 0.0001$ ).

## Discussion

Interspecific differences in mistletoe prevalence are likely the result of several non-exclusive processes. First, they may result from differential seed deposition resulting from the perching preferences of the mistletoe's avian dispersers. Second, we speculate that they may result from differential susceptibility of hosts to parasites or differential persistence of mistletoes on different host species. Our study emphasized the first of these processes, differential seed deposition. This discussion is organized in three sections. First, we identify the interacting factors that lead to inter- and intra-specific variation in seed rain. We submit that host height, previous infection, and host architecture are the main factors that shape seed deposition. The second section identifies seedling establishment as another factor that shapes infection prevalence. A third section frames our study in the broader context of structured plant populations. We claim that mistletoes are suitable systems to scrutinize the patterns created by seed-dispersal in plant metapopulations.

### Height, previous infection, tree architecture and seed deposition

Among the most frequently infected hosts, 61% of O. tesota hosts received seeds, whereas only 22% of C. microphyllum, and only 14 % of A. constricta received seeds. The difference in seed reception among these species can probably be attributed to the preference of phainopeplas for O. tesota over C. microphyllum and A. constricta as perch trees. The possible preference of phainopeplas for O. tesota over C. microphyllum and A. constricta can be detected in both infected and non infected trees. Most (91%) of the

infected O. tesota individuals received seeds, whereas only 61% and 50% of the infected C. microphyllum and A. constricta trees received seeds. Furthermore, a large fraction (35%) of uninfected O. tesota trees received seeds, whereas relatively few uninfected C. microphyllum (10%) and A. constricta (9%) trees received seeds.

Phainopeplas may perch preferentially, and hence deposit seeds disproportionately, on O. tesota because it is, on average, the tallest host tree. It is also the host with the highest parasite loads, and hence the highest mistletoe fruit availability. In O. tesota, both infected and uninfected trees were more likely to receive seeds if they were taller. However, height was not the only factor determining seed rain. Although C. microphyllum and P. velutina were very similar in height, a higher fraction of P. velutina trees (83%) received seeds. Recall that the frequency of parasitism in P. velutina is very low (Table 1, Fig. 1). Hence the high seed rain in this species cannot be attributed to a response of birds to high parasite infection.

Following Overton (1993), we hypothesize that, in addition to height, the architecture of trees may influence their attractiveness as perches. Prosopis velutina and O. tesota tend to have open canopies that allow easy perching, whereas C. microphyllum individuals tend to have a dense canopy that bristles with flexible thorn-like branchlets. Acacia constricta individuals have dense canopies and branches armed with sharp grabbing thorns. Larson (1991) found that birds spent relatively more time perching in P. velutina individuals than in C. microphyllum, and Acacia spp. Overton (1993) found that, in communities with varying proportions of host species, phainopeplas preferred

Prosopis and avoided Cercidium as perches. This ranking in the perching preference of birds is similar to our observations of seed deposition.

Within a host species, previously infected trees were significantly more likely to receive seeds than uninfected trees. Furthermore, the number of seeds that a tree received correlated positively with the number of mistletoes infecting it. As observed by Larson (1991, 1996), phainopeplas spend more time in trees with many mistletoes, and may use mistletoes as a cue for visiting a tree and for perching on it. The preference of mistletoe seed dispersers for already parasitized trees seems to be a general pattern in mistletoe-host-disperser systems (see Martínez del Río et al. 1995). This process has been labeled "conspecific attraction" by Stamp (1988) and can lead to two important consequences: 1) it may facilitate the reinfection of already parasitized trees and thus lead to strong aggregation of mistletoes in hosts (Appendix A) and 2) it may lower the fraction of occupied hosts/patches accessible to the mistletoe metapopulation (Ray et al. 1991).

### **Variation in establishment**

Elucidating differential seed deposition is a necessary step in the search for the causes of variation in mistletoe infection among host individuals and species. Because the presence and intensity of a mistletoe infection depends also on establishment and persistence, this step alone is not sufficient. Due to physiological or morphological differences between hosts, establishment and persistence of mistletoes may differ among species (Hoffmann et al. 1986, Yan 1993). Prosopis velutina exemplifies the significance of establishment as a determinant of prevalence. This species had the highest rate of seed reception, with

83.3% of individuals receiving seeds. Curiously, P. velutina showed very low infection prevalence, a characteristic that cannot be explained by low seed deposition and hence may be attributed to low establishment success. In contrast, at a site in another nearby mountain range (the Santa Rita Mountains) P. velutina is heavily parasitized by P. californicum, with rates of infection as high as 75% (Appendix D). Although Cercidium spp. and Acacia spp. are present at the Santa Rita site, P. velutina is the numerically dominant host and the most frequently infected one. Previous studies have provided preliminary evidence for the existence of geographically isolated host races in the genus Phoradendron (Clay et al. 1985, Glazner et al. 1988, Overton 1997). We hypothesize that P. californicum in the Silverbell mountains of Arizona has reduced ability to infect P. velutina.

### **Conclusion: mistletoes and plant metapopulations**

The population of P. californicum at the Silverbell Mountains can be viewed as an assemblage of mistletoe groups inhabiting discrete patch types represented by host species. The frequency of infection in each host results from interspecific differences in the balance between mistletoe colonization and extinction (Overton 1994). The process of colonization of a patch depends on seed deposition and establishment. Hence, differences in seed rain among host species should be important determinants of interspecific differences in infection. Indeed, excluding P. velutina, which seems to be relatively unaffected by mistletoe infection at our site, the most frequently infected species (O. tesota) was also the one that received the highest number of seeds.

Although it is tempting to attribute the interspecific differences in mistletoe prevalence reported here to variation in seed rain, other factors may also play an important role. *Olneya tesota* is a slow-growing and extraordinarily long-lived species (Nabhan and Carr 1994). Individuals that are several hundred years old are not uncommon at our site (Suzán 1994). In contrast, *C. microphyllum* and *A. constricta* grow relatively quickly, and probably have higher population turnover (Turner 1963). Thus, *O. tesota* individuals have had a longer time period to accumulate mistletoes than *C. microphyllum* and *A. constricta* individuals of equal height. In addition to differences in growth rate and age, it is likely that mistletoes have contrasting success at establishing among different hosts (Thomson and Mahall 1983), and that established mistletoes have dissimilar mortalities among host species (J. Aukema unpubl. data). *Olneya tesota*, *C. microphyllum* and *A. constricta* differ in morphological and physiological characteristics that are likely to influence the growth and survival of the mistletoes that infect them (Yan 1993 and references therein). Understanding interspecific differences in mistletoe infection requires thorough comprehension of the biological differences in the interaction between several hosts and their parasite.

Although our study touched upon only a single factor that impinges on parasitism frequency, it highlighted a significant aspect of the interaction between mistletoes, hosts, and avian-seed dispersers. As Overton (1994) suggested, mistletoe populations may be profitably viewed as structured metapopulations. We have demonstrated that the factors that govern differential seed rain, and hence patch colonization, can be recognized and that their relative importance can be disentangled. Other determinants of patch

occupancy, such as success in seedling establishment, patch longevity, and the comparative demography of mistletoes within hosts can be studied with a combination of experimental approaches and long-term observations. Husband and Barrett (1996) lamented the paucity of metapopulation studies in plants and identified the difficulties that plant populations can pose for metapopulation perspectives. The biology of mistletoes permits overcoming many of these difficulties. Mistletoes show much promise as model systems to investigate the mechanisms and processes that create pattern in spatially structured plant populations.

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## References

- Calder, D. M. 1983. Mistletoes in focus: an introduction. -In: Calder, M. and Bernhardt, P. (eds.), The biology of mistletoes. Academic Press, San Diego. pp. 1-18.
- Clay, K., Demet, D. and Rejmanek, M. 1985. Experimental evidence for host races in mistletoe Phoradendron tomentosum (Viscaceae). -American Journal of Botany 72: 1225-1231.
- Glazner, J. T., B. Devlin, and N. Ellstrand. 1988. Biochemical and morphological evidence for host race evolution in desert mistletoe, Phoradendron californicum (Viscaceae). -Plant Systematics and Evolution 161: 13-21.
- Hanski, I. and Gilpin, M. 1991. Metapopulation dynamics: concepts, models, and observations. -In: Gilpin, M. and Hanski, I (eds.), Metapopulation dynamics: empirical and theoretical investigations. Academic Press, New York, pp. 3-16.
- Hansson L. 1991. Dispersal and connectivity in metapopulations. -In. Gilpin, M. and Hanski, I (eds.), Metapopulation dynamics: empirical and theoretical investigations. Academic Press, New York, pp. 89-103.
- Hawksworth, F. G. 1983. Mistletoes as forest parasites. -In: Calder, M. and Bernhardt, P. (eds.), The biology of mistletoes. Academic Press, San Diego. pp. 317-333.
- Hoffmann, A. J. et al. 1986. Tristerix tetrandus (Loranthaceae) and its host plants in the chilean matorral: patterns and mechanisms. -Oecologia 6: 202-206.
- Husband, B. C. and Barrett, S. C. H. 1996. A metapopulation perspective in plant population biology. -Journal of Ecology 84: 461-469.

- Kearney, T. H. and Peebles, R. H. 1960. Arizona Flora. University of Arizona Press, Berkeley.
- Larson, D. 1991. Ecology of desert mistletoe seed dispersal. Unpublished Ph.D. dissertation. University of Illinois. Chicago, Ill.
- Larson, D. 1996. Seed dispersal by specialist versus generalist foragers: the plant's perspective. -Oikos 76: 113-120.
- Lei, S. 1999. Age, size and water status of Acacia greggii influencing the infection and reproductive success of Phoradendron californicum. -American Midland Naturalist 141:358-365.
- Marshall, J. D. and Ehleringer, J. R. 1990. Are xylem-tapping mistletoes partially heterotrophic? -Oecologia 84: 244-248.
- Martínez del Rio, C. et al. 1995. The influence of cactus size and previous infection on bird deposition of mistletoe seeds. -Australian Journal of Ecology 20: 571-576.
- Martínez del Rio, C., et al. 1996. Seed dispersers as disease vectors: bird transmission of mistletoe seeds to host plants. -Ecology 77: 912-921.
- Nabhan G. P. and Carr J. L. 1994. Ironwood: an ecological and cultural keystone of the Sonoran Desert. -Occasional Papers in Conservation Biology, 1: 9-27.
- Norton, D. A., and M. A. Carpenter. 1998. Mistletoes as parasites: host specificity and speciation. -Trends in Ecology and Evolution 13: 101-5.
- Overton, J. M. 1993. Dispersal in Mistletoes and Models. Unpublished Ph.D. dissertation. University of California, Los Angeles.

- Overton, J. M. 1994. Dispersal and infection in mistletoe metapopulations. -*Journal of Ecology* 82: 711-723.
- Overton, J. M. 1997. Host specialization and partial reproductive isolation in desert mistletoe (*Phoradendron californicum*). -*The Southwestern Naturalist* 42: 201-209.
- Ray, C., M. Gilpin, and A. T. Smith. 1991. The effect of conspecific attraction on metapopulation dynamics. In: Gilpin M. and Hanski I (eds.), *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, New York, pp. 123-134.
- Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. -*Ecology* 70: 137-145.
- Reid, N., N. M. Smith and Z. Yan. 1995. Ecology and population biology of mistletoes. In: Lowman, M. D. and Nadkarni, N. M. (eds.), *Forest Canopies*. Academic Press, San Diego. pp. 285-310.
- Suzán, H. 1994. Ecological effects of exploitation of *Olneya tesota* Gray and associated species in the Sonoran Desert. Unpublished Ph. D. Dissertation, Arizona State University, Tempe, Arizona.
- Thomson, V. E. and Mahall, E. 1983. Host specificity by a mistletoe, *Phoradendron villosum* (Nutt.) Nutt. subsp. *villosum*, on three oak species in California. - *Botanical Gazette* 144: 124-131.
- Turner, R. M. 1963. Growth in four species of Sonoran Desert trees. -*Ecology* 44: 760-765.

- Turner, R. M. and D. E. Brown. 1994. Sonoran Desertscrub. -In: D. E. Brown (ed.),  
Biotic Communities: southwestern United States and northwestern Mexico.  
University of Utah Press, Salt Lake City. pp. 181-222.
- Walsberg, G. E. 1977. Ecology and energetics of contrasting social systems in  
Phainopepla nitens (Aves: Ptilonotidae). University of California Publications  
in Zoology 108: 1-63.
- Yan, Z. 1993. Resistance to haustorial development of two mistletoes, Amyema preissi  
(Miq.) and Lysiana exocarpi (Behr) Tieghem spp. exocarpi (Loranthaceae) on  
host and non-host species. -International Journal of Plant Science 154: 386-394.

Table 1.- Relative abundance, number infected, and number of individuals receiving seeds among the hosts of P. californicum. Data are based on 23, 50X8 m transects that included 168 host trees (dataset 1). Values in parentheses are expected values, assuming that numbers of individuals that were parasitized and that received seeds were independent of species. The overall frequency of parasitism was 24.4% and the overall frequency of individuals that received seeds was 32.7%. See also Fig. 1.

Species	Number of Individuals	Parasitized	Receiving Seeds
<u>Cercidium microphyllum</u>	93	21 (22.7)	21 (30.4)
<u>Acacia constricta</u>	37	5 (9.0)	6 (12.1)
<u>Olneya tesota</u>	21	15 (5.1)	16 (6.8)
<u>Prosopis velutina</u>	14	0 (3.4)	12 (4.6)
<u>Acacia greggii</u>	3	0 (0.7)	0 (1)
Total	168	41	55

### Figure legends

Fig. 1. Relationship of relative host abundance (RHA) to relative infection (filled circles) and seed deposition (open circles) of each host. RHA is the proportion of each host species out of all host trees available. Relative host infection is the number of infected trees of each species out of all infected trees, presented as a percent. Relative seed deposition is the number of trees of each species receiving seeds out of all trees receiving seeds, presented as a percent. Each species is labeled above its RHA. Ag. = *Acacia greggii*, A.c. = *Acacia constricta*, C.m. = *Cercidium microphyllum*, O.t. = *Olneya tesota*, P.v. = *Prosopis velutina*. The  $y = x$  line is the expected relationship if species are infected and receiving seeds in proportion to their abundance. Values below the  $y = x$  line mean that fewer trees of this species were infected or received seeds than expected based on its abundance. Values above the line indicate that the species had more than expected. Note that in *Prosopis*, infections fell below and seeds above the  $y = x$  line. See also Table 2.

Fig. 2. The fraction of infected hosts increased with tree height in *C. microphyllum*, *O. tesota* and *A. constricta*. Curves were fitted using logistic regression (*O. tesota*:  $\text{logit}(p) = -2.91 + 0.61(\text{height})$ ,  $\chi^2 = 12.5$ ,  $p = 0.0004$ ,  $N = 102$ , *C. microphyllum*:  $\text{logit}(p) = -4.44 + 0.91(\text{height})$ ,  $\chi^2 = 10.1$ ,  $p = 0.0015$ ,  $N = 101$  and *A. constricta*:  $\text{logit}(p) = -5.96 + 1.82(\text{height})$ ,  $\chi^2 = 8.4$ ,  $p = 0.0038$ ,  $N = 62$ ). Trees were divided into height classes for visual clarity in the figure: points are means and bars are standard errors.

Fig. 3. The fraction of hosts receiving seeds increased with height in *Olneya tesota* (lower panel). Previously infected hosts (open circles) had a higher probability of receiving seeds than uninfected hosts (filled circles). Logistic regression:  $\text{logit}(p) = -2.825 + 0.857(\text{height}) + 1.414(\text{infection})$  (intercept  $\chi^2 = 5.57$ ,  $p = 0.018$ ; height  $\chi^2 = 9.48$ ,  $p = 0.002$ ; infect  $\chi^2 = 20.15$ ,  $p < 0.0001$ ;  $N = 102$ ). In contrast, in *C. microphyllum* (upper panel) there was no significant effect of host height (the logistic regression coefficients for height were non-significant for infected and non-infected trees  $\chi^2 < 1$ ,  $p > 0.1$ ,  $N = 101$ ). However there was a highly significant effect of previous infection on the fraction of hosts receiving seeds (logistic regression coefficient for infection status,  $\chi^2 = 21.18$ ,  $p < 0.001$ ,  $N = 101$ ). Trees have been divided into size classes for visual clarity. Bars are standard errors. Curves were fitted using the logistic equation shown above.

Figure 1.

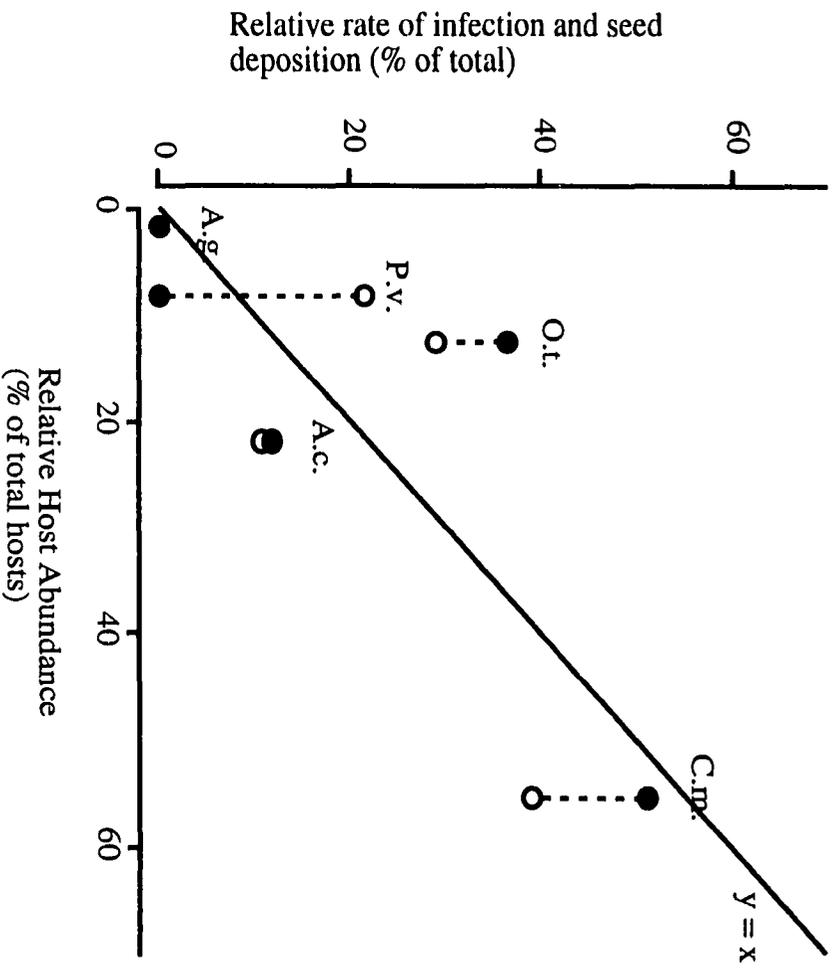


Figure 2.

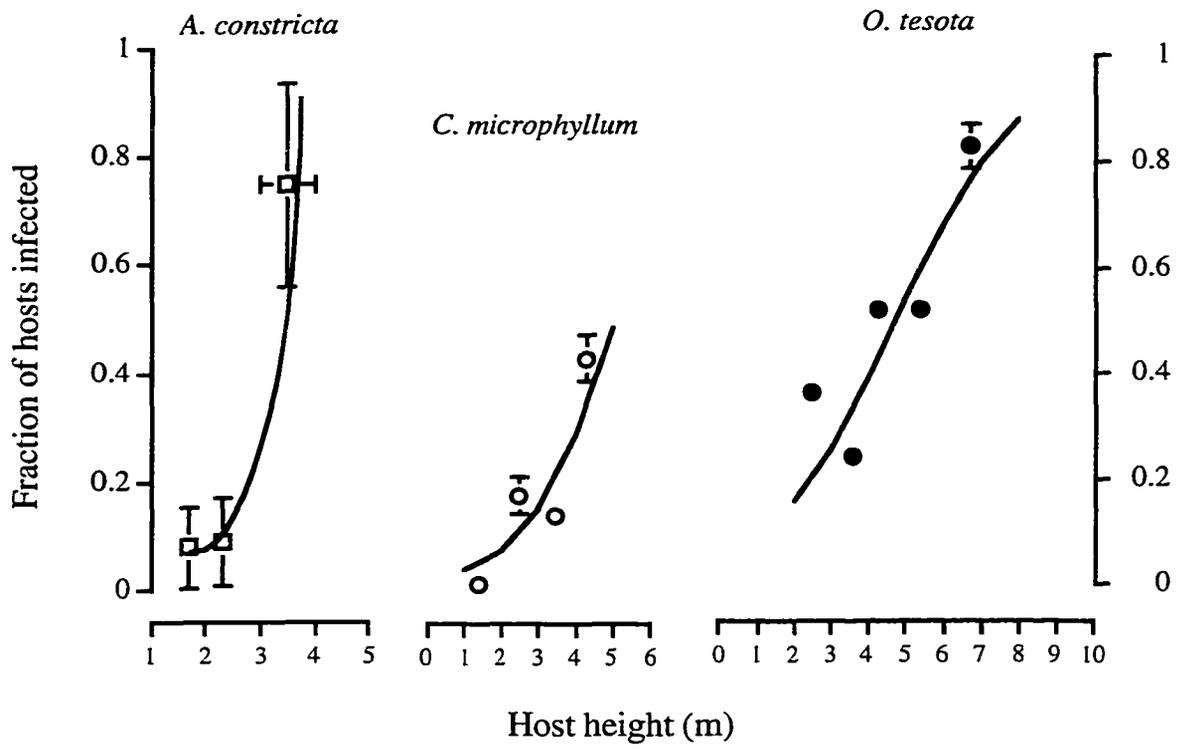


Figure 3.

