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Author(s): Kathleen Donohue
Reviewed work(s):
Source: *International Journal of Plant Sciences*, Vol. 156, No. 6 (Nov., 1995), pp. 816-823
Published by: The University of Chicago Press
Stable URL: http://www.jstor.org/stable/2475113
Accessed: 12/04/2012 13:21

Int. J. Plant Sci. 156(6):816–823. 1995.

1058-5893/95/5606-0008$02.00

THE SPATIAL DEMOGRAPHY OF MISTLETOE PARASITISM ON A YEMENI ACACIA

KATHLEEN DONOHUE[1]

American Institute for Yemeni Studies, P.O. Box 2658, Sana'a, Yemen

The frequency of parasitism of a mistletoe, *Plicosephalus curviflorus,* on *Acacia tortilis* as a function of host density and host size was investigated. The influence of host size and parasite frequency on flowering success of the parasite was also investigated. Parasitism was contagiously distributed but occurred most intensely in low-density *Acacia* stands. The distribution of *Acacia* size classes showed spatial autocorrelation, with smaller, more shrublike trees occurring in high-density clusters. Parasitism frequency and intensity were highest on larger trees, indicating that the spatial patterns of parasite distribution could be explained in part by the spatial patterns of the host size classes. Flowering success of mistletoes was not influenced by tree size but was negatively correlated with the number of mistletoes on the host. The late onset of parasitic attack with respect to the age or size of the host and the negative conspecific density effects on flowering success by the parasite could reduce adverse fitness effects on the host and thereby increase the probability of stable coexistence of *A. tortilis* and *P. curviflorus.* The size structure of the host population, by influencing the distribution of parasites among the hosts, may influence the population dynamics of the parasite and the stability of the host-parasite association.

Introduction

The population dynamics of parasites and their hosts influence each other (Anderson and May 1978; May and Anderson 1978; Renaud and De Meeus 1991). Identifying factors that influence parasite population dynamics, both independently and in conjunction with host population processes, therefore contributes to an understanding of the conditions for stability of parasite populations and host-parasite associations.

Availability of the host is a prerequisite for most parasite populations. Host population size, therefore, can directly influence parasite population size and has been a key parameter in theoretical models of host-parasite population dynamics (Anderson and May 1978; May and Anderson 1978). However, total host population size is unlikely to be the most important demographic factor by which the host influences parasite populations, since all individuals of the host may not be equal in their suitability for parasites. Even if resistance to the parasite were constant among all individuals of the host population, the spatial distribution of the host as well as the age or size structure of the host population could be equally or more important to the parasite than the total host population size.

Not only may the demography of the host population influence parasite population dynamics but parasite populations may also be internally regulated. For example, the spatial distribution of parasites among hosts and density-dependent reproduction of the parasite within a host influence both parasite population dynamics and the stability of host-parasite associations (Anderson and May 1978; Bremermann 1983; Bremermann and Pickering 1983).

In this study, I investigated how demographic factors of a host and a parasite can influence parasite population dynamics. *Acacia tortilis* (Forsk.) Hayne (Mimosaceae) has a parasitic association with the mistletoe *Plicosephalus curviflorus* Van Teigh. (Loranthaceae) in Wadi Hadramaut in southern Yemen. Unlike most host-parasite systems, in which the host is of primary economic or cultural importance, both species within this association have local economic significance. Minimizing the parasite population, therefore, is not necessarily a desired objective, and parasite population dynamics have relevance independent from their effects on the *Acacia* population. To investigate the extent to which a *P. curviflorus* population was influenced by its own demographic structure and by that of the host, I addressed the following questions: (1) What is the spatial distribution of mistletoes among the host *Acacias?* (2) What factors influence the spatial distribution of mistletoes among hosts? In particular, does host density or host size class distribution influence mistletoe distributions? (3) What factors influence the reproductive success of the mistletoes? In particular, does host size or mistletoe distribution among hosts influence the reproductive success of mistletoes, as estimated by flowering success?

Material and methods

Acacia tortilis (*sillum* in Arabic) is a tree of great economic use in Wadi Hadramaut. Its timber is used for firewood, its nectar provides honey, and its leaves are used for fodder for goats and sheep. It is one of the most common species in the dry valleys and spate flood paths of the wadi system, capable of growing in very rocky lime and dry alluvial soils in intense heat. *Acacia tortilis* flowers from March through May and sets

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[1] Address for correspondence and reprints: Harvard Forest, P.O. Box 68, Petersham, Massachusetts 01366.

Manuscript received December 1994; revised manuscript received May 1995.

fruit through August. *Acacia tortilis* trees are less than 10 m tall in this habitat and often have multiple branches ("basal branches") emerging from ground level. Younger trees sometimes have a shrublike habit. *Acacia tortilis* is abundant in a scattered distribution throughout this habitat, and is the only abundant tree species present except for *Acacia ehrenbergiana* Hayne (*sumr* in Arabic), which was not observed to have a parasitic association with any mistletoe.

Plicosephalus curviflorus (*'anma* in Arabic) is a mistletoe capable of photosynthesis that grafts itself onto the branches of *A. tortilis* and shares its xylem sap. *Plicosephalus curviflorus* flowers in December and January and has perfect, red-orange zygomorphic flowers that are pollinated by Palestine sunbirds (*Nectarinia osea*) and possibly by Abyssinian sunbirds (*Nectarinia habessinica*) and white-breasted white-eyes (*Zosterops abyssinica*), although the latter two birds were not seen on the site but are known to occur in the region. Flowers have nectar but are not strongly scented. Self-compatibility is not uncommon in related mistletoes, but its occurrence remains unknown for this species. According to local inhabitants, its seeds are dispersed by the Palestine sunbird from March through the summer. People grind the stems and leaves of *P. curviflorus* and use them to cure animal hides.

The study site was located outside of the town of Taribah in Wadi Hadramaut in southern Yemen. The site is within Wadi Taribah, not far from agricultural fields and within lands used for grazing of goats and sheep. The terrain consists of white lime rocks and gravel with some alluvial soil beneath. The habitat is very dry, with intense sun throughout the year, but occasional rain and flooding occur infrequently during the rainy season (Kennenni 1991).

A 500-m transect was established along a trail. A complex network of trails exists throughout the narrow wadi, and much of the wadi is easily accessible from these trails. The transect extended 15 m on either side of the trail and was divided into segments of 50 m in length. All *A. tortilis* trees within the transect were measured and tagged, and the number of *P. curviflorus* parasites on each tree was recorded. Measurements of *A. tortilis* included height, the number of basal branches, the average diameter of the basal branches, and the number of "secondary" branches. The number of secondary branches was obtained by counting the number of branches that grew directly from each basal branch, while defining the continuation of the basal branch to be the larger branch at each bifurcation. In addition to trees within the transect, pairs of infected trees and the nearest noninfected tree were also measured within the area approximately 30 m from the trail to compare sizes of infected and noninfected trees. All available pairs were measured. On all infected trees, both within the transect and those within 30 m of the trail, the most heavily infected accessible secondary branch on a tree was used as a focal branch, and the following measurements were taken: length of branch, diameter, number of branches, number of *P. curviflorus* infections, and number of *P. curviflorus* flowers. The number of branches was obtained by counting the number of branches growing directly from the focal branch, while defining the continuation of the focal branch to be the larger branch at each bifurcation. Choosing the most heavily infected branch assured a large range of infection intensity and established a strong regression relationship.

For the analysis, I investigated the spatial distribution of parasitism among the hosts and along the transect. The hypothesis of a random distribution of *P. curviflorus* attack along the transect was tested with a Wald-Wolfowitz runs test, with infection or noninfection being the random binomial variable and distance along the transect as ordering the sequence of observations. Spatial autocorrelation of the number of parasites on each tree was calculated. These analyses used only those trees within the transect.

I also investigated how density and size class of *Acacia* influence the distribution of mistletoes among hosts. Density was calculated as the number of *A. tortilis* trees within each 50-m section of the transect. The effect of *A. tortilis* density on the proportion of trees infected within each 50-m section was tested using simple regression. The variance of the proportion of infected trees for each section of the transect depends on the number of trees within that section, so it was expected that the regression should be weighted by the variance of each estimate to control for unequal variances. However, the simple regression did not differ qualitatively from the weighted regression, and there was no evidence of heteroscedasticity in the simple model, so the simpler, more conservative model is presented. The effect of *A. tortilis* density on infection intensity of trees within each 50-m section was estimated with simple regression. Measures of infection intensity included the average number of infections on trees and the average number of flowers on the most heavily infected branch of the tree. If the tree had no infections, it had a value of zero mistletoe flowers.

To investigate how *A. tortilis* size and morphology influenced the presence or intensity of parasitism, variables of tree size and infection were natural log transformed to normality. Only the total number of infections per tree could not be transformed to normality. Tree traits were highly intercorrelated, so principal components analysis was conducted using the transformed,

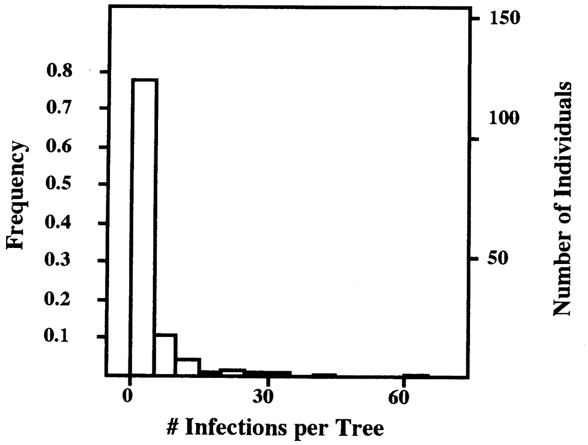

Fig. 1 Frequency distribution of parasitic attack among infected hosts. Forty-eight percent of the trees within the transect had at least one mistletoe infection. The frequency distribution is negative binomial, with $x = 3.667$ (SD = 0.634) and $k = 0.223$ (SD = 0.036); χ^2 for goodness of fit = 4.95, df = 3, $P = 0.30$. Cells with expected values of less than 4 were pooled. Parameter estimates and expected values were calculated after Bliss and Fisher (1953).

normally distributed data. The first two components were used for subsequent analysis. Spatial autocorrelation analysis was performed on the principle components to compare the autocorrelation of tree traits to that of parasitism. To determine whether tree traits influenced the probability of infection, tree traits were compared between all infected and noninfected trees using an independent samples t-test. To determine whether tree traits influenced the intensity of infection on infected trees only, multiple regression of tree traits on the number of infections was performed and verified with nonparametric Spearman rank correlations. Multiple regression also tested for an effect of tree traits on the number of mistletoe flowers on the focal branches of infected trees.

Finally, I investigated factors that influenced mistletoe flowering success. Tree traits and total number of infections on the tree were used as independent variables in a multiple regression to determine their effect on the average number of flowers on the mistletoes on the focal branch. In a second regression, natural log transformed traits of the focal branch, as opposed to those of the tree, and the number of mistletoe infections on the focal branch were included in a multiple regression to determine whether branch traits influence the average number of flowers on the mistletoes on the focal branch.

Results

The distribution of parasitic attack among hosts approximated a negative binomial, with a few individuals having a very large number of infections and most individuals having very few infections (fig. 1), indicating a contagious distribution. Results of the Wald-Wolfowitz runs analysis indicated that the distribution of infected trees was more clumped than expected by random distribution, such that an infected tree was more likely to have an infected neighbor than would be expected by chance alone ($n = 159$, expected runs = 75, observed runs = 58, $Z = -3.551$, $P < 0.001$). Spatial autocorrelation was significant for the total number of parasites per tree between adjacent trees (Spearman's $r = 0.32$, $P < 0.001$, $n = 159$) but not between trees at any greater scale of separation, indicating that contagion, if present, is highly localized.

Higher *Acacia tortilis* density was associated with a lower proportion of infected trees (table 1; figs. 2, 3). Density was not associated with the number of parasites on a tree nor with the total number of parasite flowers on the most heavily infected branch. There is no evidence, therefore, of a significant association between density and intensity of parasitic infection. In this analysis, calculation of infection intensity included trees that were not infected. If only infected trees were used in the analyses, the association with density would be even weaker, since the proportion of infected trees and the intensity of infection would be more highly correlated when noninfected trees are part of the sample.

The first two principal components of tree traits

Table 1

SIMPLE REGRESSION TESTING FOR EFFECTS OF HOST (*Acacia tortilis*) DENSITY ON DIFFERENT MEASURES OF INFECTION

Dependent variable	R^2	Regression coefficient	SE	t-ratio	n
Proportion of trees infected...	0.49	−0.02	0.01	−2.77**	10
Average infections per tree ...	0.17	−0.13	0.10	−1.27	10
Average mistletoe flowers	0.21	−0.63	0.43	−1.47	10

Note. "Average mistletoe flowers" is the number of mistletoe flowers on the focal branch. Trees without infection have zero mistletoe flowers.
** $P < 0.01$.

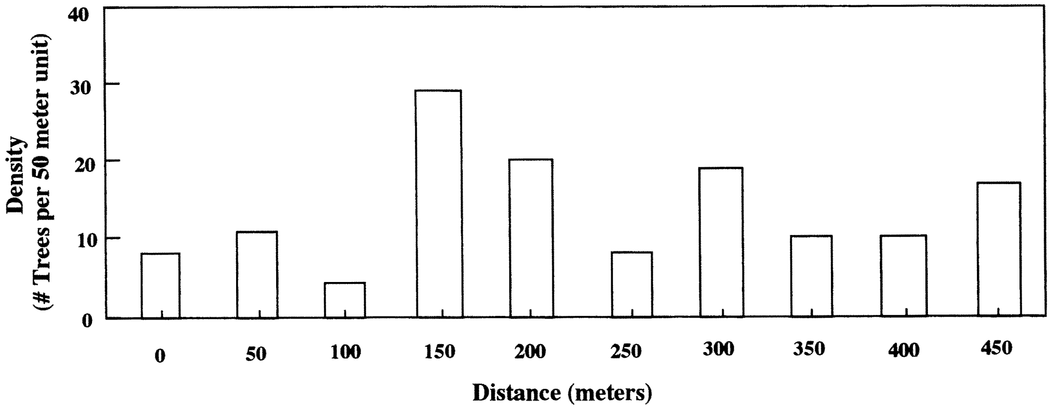

Fig. 2 Density as a function of distance along transect. The total number of *Acacia tortilis* trees within each 50-m section of the transect is shown at 50-m intervals along the transect.

explained over 90% of the variance (table 2). The first component (PC1) had positive loadings for all tree traits and can be interpreted as a measure of tree size. The second component (PC2) distinguished between tall trees with few but large branches and shorter trees with many small branches, and it can be interpreted as a measure of the degree to which the tree is shrublike.

Smaller individuals tended to occur in high-density stands (Pearson's r for PC1 and density $= -0.71, P = 0.02, n = 10$), and a nonsignificant trend was apparent for more shrublike individuals to be in high-density stands (Pearson's r for PC2 and density $= -0.57, P = 0.08, n = 10$; fig. 4). The first principal component had significant spatial autocorrelation along the transect, with the highest autocorrelation between adjacent trees (Pearson's $r = 0.41, P < 0.001, n = 128$), and some significant positive autocorrelation between trees separated by up to 11 trees. After a separation of 40 trees, the correlations became negative, but not significantly so, and then approached and remained very close to zero. A very similar pattern was observed for the second principal component, although the correlations were generally weaker (Pearson's $r = 0.29, P < 0.001, n = 128$, for adjacent trees). These results reflect the easily observable pattern that smaller, more shrublike individuals tended to occur more in clusters than at random. Tree traits and parasitism both, therefore, are spatially autocorrelated at small spatial scales.

Infected trees were larger and less shrublike than noninfected trees (fig. 5). The number of parasites on infected trees depended on tree traits (table 3), although tree traits did not influence the total number of flowers on focal branches. Therefore, tree traits appear to influence both the probability of parasitism and the intensity of parasitism, as measured by number of parasites, but not the flowering success of the groups of parasites that inhabit individual trees.

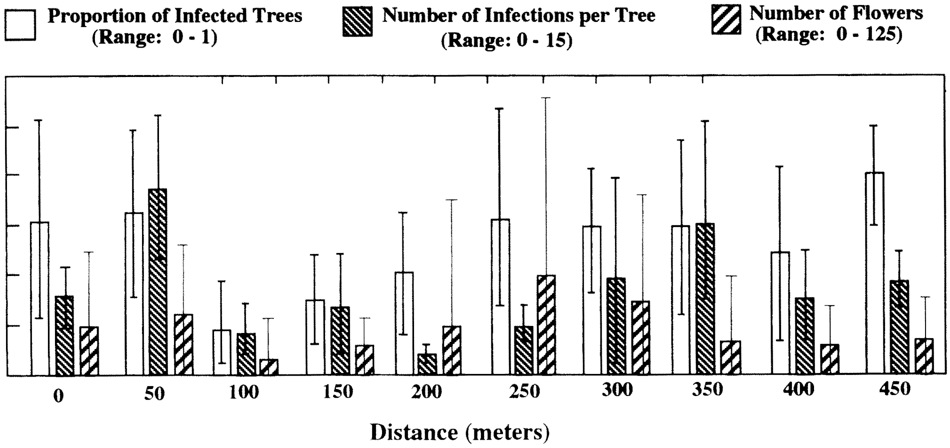

Fig. 3 Infection intensity as a function of distance along transect. The proportion of infected *Acacia tortilis* trees, the average number of infections, and the number of mistletoe flowers on the most heavily infected branch of each tree within 50-m sections of the transect are shown at 50-m intervals along the transect. Bars show standard deviations.

Table 2

PRINCIPAL COMPONENT ANALYSIS OF TREE VARIABLES

Variable	Component loadings PC1	Component loadings PC2
ln height	0.91	0.21
ln number of basal branches	0.74	−0.60
ln diameter	0.61	0.74
ln number of secondary branches	0.93	−0.23
% total variance explained	65.06	25.05

Tree traits did not influence mean flowering success of individual *Plicosephalus curviflorus* plants, but the number of infections on the tree was significantly negatively correlated with the average number of flowers on a mistletoe (table 4). There is no evidence that branch traits influence flowering success of mistletoes, although the number of infections on the focal branch (which is highly correlated with the total number of infections on the tree) was strongly negatively correlated with the average number of flowers on an individual (table 4). These results indicate that although tree traits influence how many parasites will occur on a tree, they do not influence the flowering success of parasites directly. Rather, their effect on flowering success is indirect, through their effects on parasite load, which in turn influences flowering success.

Discussion

I found that the mistletoes were contagiously distributed among trees and that they were more prevalent in low-density stands than in high-density stands. I also observed that parasitism was most intense on larger, less shrublike *Acacias*, and that smaller, shrublike *Acacias* tended to occur in higher-density clusters. The spatial distribution of mistletoes, therefore, could be explained in part by the spatial distribution of tree size classes. Because density and tree size are correlated, it is not possible to determine conclusively which factor is more important in determining the distributional patterns of the mistletoe. However, given the counterintuitive observation that parasitism is more prevalent in low-density host stands, tree size appears to be the factor that is more likely to influence parasite abundance directly.

The observation that larger trees have a higher frequency of parasitic attack and more intense infection than smaller trees is not uncommon (Overton 1994; Vergara and George-Nascimento 1994). Smaller *Acacia* trees are likely to be younger (Prins and Van der Jeugd 1993) and may not have parasitic infections because they have not had time to become infected (Mathiasen et al. 1990*a*), because they have a smaller crown area, or because smaller trees do not attract the bird dispersers of *Plicosephalus curviflorus*. Very small trees were never seen with parasites; nor were any dead small trees with parasites observed. Because smaller trees tend not to be infected, it is unlikely that *P. curviflorus* parasitism causes mortality at an early life stage of the host, as some mistletoes have been shown to do (Thompson et al. 1984; Mathiasen et al. 1990*b;* Reid et al. 1992). Moreover, mortality of larger trees resulting from heavy mistletoe infection was not observed anywhere in the wadi, so there is no evidence that the mistletoe currently causes host mortality in this system.

Low host density is associated more strongly with the presence of parasitism on a tree than with the intensity of parasitism on a tree. This trend could be explained by the behavior of the

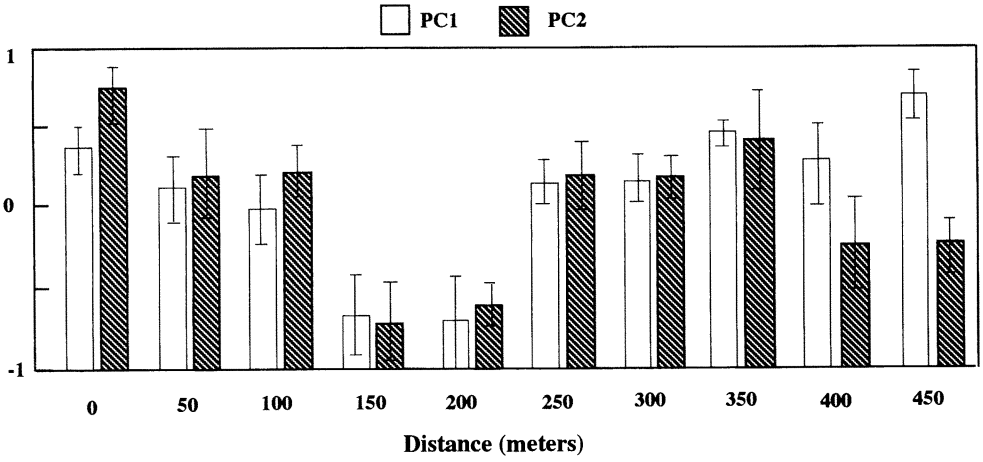

Fig. 4 Tree traits as a function of distance along the transect. The average value of the two principal components of *Acacia tortilis* trees within each 50-m section of the transect are shown at 50-m intervals along the transect. Bars show standard deviations.

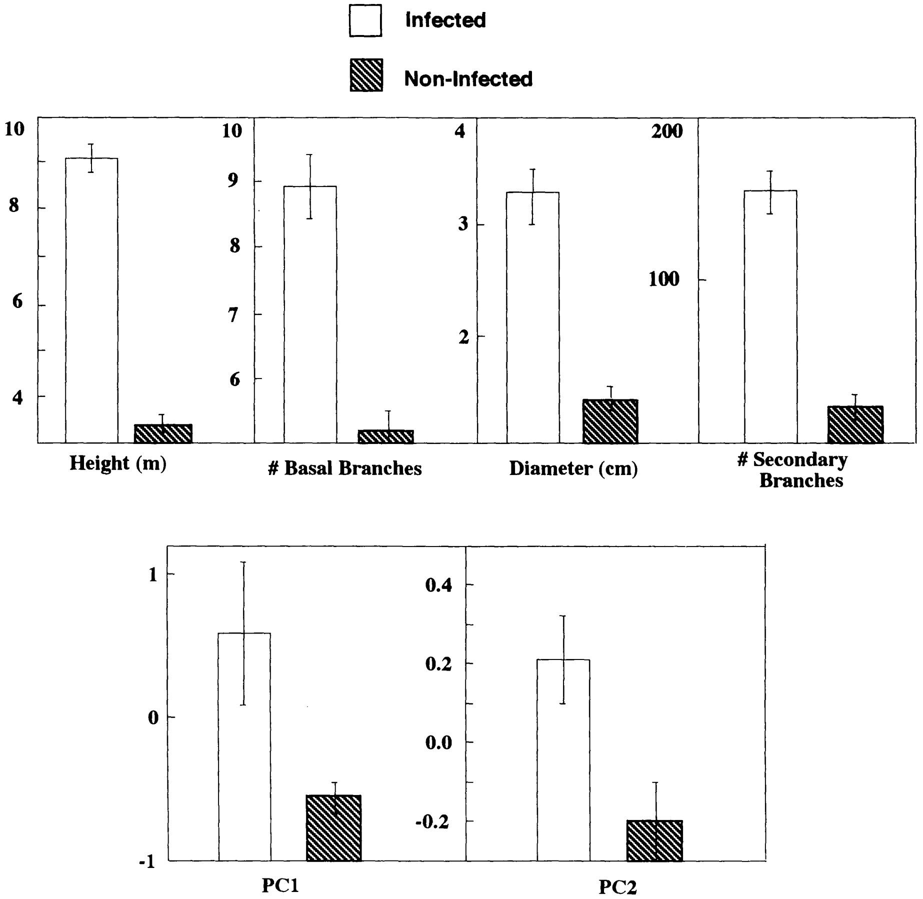

Fig. 5 Tree traits of infected and noninfected trees. Mean values of tree traits and principal components derived from these traits are shown for infected and noninfected trees. Means and 95% confidence intervals of the original tree traits were calculated from natural log transformed values and were then transformed back into the units in which the variables were measured. As shown by comparing the means of the principal components, infected trees were significantly larger than noninfected trees ($t = 9.27$, $P < 0.001$, $n = 177$) and infected trees were significantly less shrublike than noninfected trees ($t = 2.78$, $P = 0.006$, $n = 177$).

avian dispersing agents that may be attracted to mature, sparsely placed trees, regardless of size variation among mature trees, whereas intensity of infection could be more a function of individual tree size. Reid (1989) observed that specific measurements of tree size, such as the number or diameter of branches, influenced dispersal and establishment of another *Acacia* mistletoe species, *Amyema preissii.* In this case, tree traits influenced the duration of time that bird dispersers spent within a tree and consequently influenced the number of seeds eaten and deposited within a tree. Information on how the dispersing behavior of the Palestine sunbird is influenced by *Acacia* size and spatial distribution, and by the distribution and fruiting success of the mistletoe, could explain the spatial distribution of the mistletoes in this system more completely.

Intraspecific density-dependent flowering success was observed such that fewer flowers were produced by individuals in more heavily infected trees. Such intraspecific density-dependent flowering success could inhibit fluctuations in parasite population size or limit parasite population size, if flowering success is indicative of reproductive success. Density-dependent reproduction by the parasite has been shown theoretically to limit adverse fitness consequences of parasitism of the host, by limiting the growth rate of the parasite group within the host (Anderson and May 1978; May and Anderson 1978). The exact effect of parasite load and parasite reproduction on host fitness would have to be acquired empirically, however; it could be that a smaller parasite load with greater reproductive activity could be as detrimental to the host as a larger load with little reproduction. Dispersal among the hosts would also influence this relationship, since increased reproduction of individuals on a particular host will not necessarily cause increased seedling recruitment on that host if dispersal is efficient.

The distribution of *Acacia tortilis* size classes may influence parasite population dynamics by directing, in part, the spatial distribution of mistletoes among hosts and consequently influencing the intensity of density-dependent limitation of

Table 3

MULTIPLE REGRESSION OF TREE TRAITS AGAINST DIFFERENT MEASURES OF INFECTION INTENSITY

	ln (total infections)			ln (number of mistletoe flowers)		
Source	Coefficient	SE	*t*-ratio	Coefficient	SE	*t*-ratio
PC1 ..	1.12	0.23	4.91***	−0.37	0.27	−1.36
PC2 ..	0.57	0.11	4.97***	0.17	0.13	1.30
	$R^2 = 0.31$	$n = 86$		$R^2 = 0.07$	$n = 74$	

Note. Total number of infections per tree was not normally distributed, so probabilities shown in the table are only approximate. The nonparametric Spearman rank correlation between PC1 and total number of infections was significant ($r = 0.38$, $P < 0.001$), as was that between PC2 and total number of infections ($r = 0.34$, $P = 0.001$). "Number of mistletoe flowers" is the total number of mistletoe flowers on the focal branch. Only infected trees were used for this analysis.

*** $P < 0.001$.

reproduction by the mistletoe. The number of mature trees in the area may influence mistletoe populations more than would the total number of trees. If, in addition to the spatial autocorrelation of parasitism resulting from the *Acacia* size class distribution, true contagion occurs at a small spatial scale among mature trees even in low-density stands, it seems possible that contagion could occur at greater spatial scales if mature trees were more densely or continuously distributed. This study shows the importance of examining host age or size structure when investigating patterns of parasitism and stability of host-parasite associations.

Table 4

MULTIPLE REGRESSION OF FLOWERING SUCCESS AGAINST INFECTION FREQUENCY AND SIZE TRAITS

Variable	Regression coefficient	SE	*t*
Constant	3.82	0.27	14.20***
PC1	−0.21	0.36	−0.58
PC2	0.09	0.16	0.57
ln (total infections)..............	−0.40	0.14	−2.83**
$n = 57$, $R^2 = 0.19$			
Constant	2.62	1.39	1.83
ln (length of focal branch)	0.61	0.49	1.24
ln (diameter of focal branch)	−0.34	0.28	−1.23
ln (branches on focal branch).....	0.06	0.40	0.15
ln (infections on focal branch)....	−0.81	0.21	−3.90**
$n = 57$, $R^2 = 0.29$			

Note. The dependent variable for both regression models is the average number of flowers per mistletoe plant growing on the focal branch. The upper part of the table tests for effects of tree traits and infection of the entire tree on the flowering success of mistletoes located on the focal branch. The lower part of the table tests for effects of branch traits and the number of infections on a single branch on flowering success of mistletoes located on that branch. Only infected trees were used for this analysis. In the first regression, although the number of infections per tree was not normally distributed, the residuals of the regression were normally distributed, and a nonparametric Spearman rank correlation between number of infections and average number of flowers per infection was significant (Spearman's $r = -0.38$, $P = 0.004$). For the second regression, the number of infections on the focal branch were not normally distributed, but the residuals of the regression were normally distributed and the nonparametric Spearman rank correlation between the number of infections on the focal branch and the average number of flowers per infection was significant (Spearman's $r = -0.47$, $P = 0.003$).

** $P < 0.01$.

*** $P < 0.001$.

Another extremely important component to this system is the human population. It is probable that the *A. tortilis* size distribution in this study area was influenced by human activity. Both timber collection and periodic grazing of seedlings could lead to patchy distributions of tree size classes, and such practices could easily alter tree morphology by causing sprouting and increased branching, which results in bushier trees. Humans and their domestic animals are important components of the ecology of the wadi, and they have been present there for thousands of years. Because some of the human population does not live in permanent settlements, human activity is dispersed widely throughout the wadi in addition to being clustered around town centers. Both sorts of activity would influence the ecology of many plant species, but probably in different ways. In particular, *A. tortilis* size and shape could be influenced by these different activities. This study indicates that changes in the size structure of one economically important species could influence the population biology of another.

Acknowledgments

I am grateful to Engseng Ho for field assistance. I thank the Kathiri in Taribah for allowing me to work on their property and Dr. Abdul Rahman Dubaie for his sponsorship. Steven Brewer, David Griffin, Jake Overton, Tatayana Rand, Ellen Simms, Daniel Varisco, Jon Whitman, and an anonymous reviewer gave many useful comments on the manuscript. I thank Richard Lent for discussions concerning the analysis. This research was funded by the American Institute for Yemeni Studies.

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