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SEED DISPERSERS AS DISEASE VECTORS: BIRD TRANSMISSION OF MISTLETOE SEEDS TO PLANT HOSTS[1]

C. MARTÍNEZ DEL RIO
Department of Zoology and Physiology, University of Wyoming, P.O. Box 3166, Laramie, Wyoming 82071-3166 USA

A. SILVA
Centro de Ecología, UNAM, Apartado Postal 70-75, Coyoacán 04510, México

R. MEDEL
Departamento de Ciencias Ecologicas, Universidad de Chile, Casilla 633, Santiago, Chile

M. HOURDEQUIN
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08540-1003 USA

Abstract. The relationship between mistletoes and birds has been studied from the perspectives of mutualism and seed dispersal. Here, we emphasize the role that avian dispersers play as agents of mistletoe seed transmission to plant hosts. We describe the patterns of transmission of the seeds of *Tristerix aphyllus,* an endophytic Chilean mistletoe, on two of its columnar cacti hosts (*Eulychnia acida* and *Echinopsis skottsbergii*) by the Chilean Mockingbird *Mimus thenca.* In north-central Chile, these cacti grow in relatively discrete subpopulations on north-facing slopes. We measured variation in seed transmission within 10 subpopulations varying in species composition, host density, parasite density, parasite prevalence (defined as the percentage of hosts infested in a given population), and disperser abundance. Seed transmission was independent of species, but was strongly dependent on prior parasitism. Parasitized individuals received seeds much more frequently than expected from their relative abundance. We found no correlation between the density of hosts and seed transmission. We found strong positive correlations, however, between parasite prevalence and seed transmission to both parasitized and nonparasitized hosts. Seed transmission of *T. aphyllus* seeds by *M. thenca* appeared to be frequency- rather than density-dependent. Seed transmission was also tightly and positively correlated with the abundance of seed-dispersing birds at each site. Because bird abundance and parasite prevalence were correlated, we conducted path analysis to disentangle their relative effect on seed transmission. A model including only the direct effect of bird abundance and the indirect effect of parasite prevalence through bird abundance explained roughly the same variance as a full model including both the direct and indirect effects of bird abundance and prevalence on seed transmission. Apparently, variation in bird abundance was the main determinant of variation in transmission. We suggest that mistletoes, host plants, and the birds that disperse mistletoe seeds are systems well suited for studies of the ecological and evolutionary dynamics of disease transmission.

Key words: cacti hosts; disease transmission; Echinopsis skottsbergii; Eulychnia acida; Mimus thenca; *mistletoes; parasitism; seed dispersal;* Tristerix aphyllus.

INTRODUCTION

The ecological and evolutionary dynamics of diseases are molded by the processes by which parasites and pathogens are transmitted (Ewald 1993). Disease transmission can be passive, as in water- and air-borne diseases, it can be direct when one host infects another by contact, or it can be mediated by vectors (Southwood 1987). When disease transmission is the result of random encounters between diseased and healthy individuals, the probability of healthy individuals becoming infected depends on the absolute density of infected individuals (Anderson and May 1979). Density dependence of disease transmission has been well studied, and is the form most commonly assumed in mathematical models of parasite–host populations (Anderson and May 1991).

When transmission occurs through active search of host individuals by vectors, or as a result of sexual encounters between a diseased and a healthy individual, the probability of healthy individuals becoming infected can depend on the fraction of diseased individuals in the population rather than on their absolute density (Anderson 1988, Antonovics 1993). This mode of parasite transmission has been called "frequency-dependent." Although frequency-dependent transmission is probably ubiquitous and its occurrence can have

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strong consequences on the outcome of host–parasite interactions, it has been relatively unstudied (Thrall et al. 1993). Getz and Pickering (1983) argued that frequency-dependent transmission can lead to very unstable population dynamics. Ewald (1993) linked frequency-dependent transmission with the evolution of increased parasite virulence. Antonovics et al. (1993) suggested that frequency-dependent transmission will occur when disease vectors are capable of adjusting the distance moved among hosts as spacing varies with host population densities. Thus, frequency-dependent transmission seems to be prevalent in sexually transmitted plant diseases in which spore deposition is mediated by the host plant's pollinators (Antonovics and Alexander 1992). Here, we report a possible case of bird-mediated frequency-dependent transmission of mistletoe seeds.

Unlike many pathogenic fungi that use the pollinators of their hosts as vehicles for spore transmission (Roy 1994), mistletoes maintain a mutualistic relationship with their vectors. The reliance of mistletoes on bird mutualists for seed transmission makes the epidemiology of mistletoe infestations distinctive. For example, it is likely that mistletoe seed dispersers respond behaviorally by varying visitation rates to individual plants and habitats when the abundance of fruit-producing parasites changes, rather than when the abundance of hosts per se changes. In contrast, many blood-sucking arthropod vectors aggregate in response to the abundance of vertebrate hosts, but show no behavioral response to the frequency of parasites in these hosts (Rogers and Randolph 1985). The effect of mistletoe infection intensity and prevalence (the percentage of hosts infested in a given population) on bird behavior and numbers, and hence on seed transmission, is largely unknown.

Overton (1994) used a metapopulation approach to study seed dispersal and distribution of mistletoes to host plants. He assumed that the mistletoes inhabiting a host plant constituted a subpopulation in the subdivided habitat constituted by habitable patches (host trees) and uninhabitable patches (non-host trees). Here, we adopted a different perspective. We viewed local cactus groves as subpopulations of hosts (Jennersten et al. 1983), and investigated the influence of local factors such as host density, mistletoe prevalence (the percent of hosts infested in a given population), and abundance of disease vectors (birds) on mistletoe seed transmission among hosts. We could do this because, in north-central Chile, columnar cacti grow in discrete, isolated subpopulations on north-facing slopes (see Nobel 1988).

Many mistletoe species are bird-transmitted parasites that can have severe effects on their plant hosts (Hawksworth 1983). Although the relationship between birds and mistletoes has been relatively well studied from the point of view of bird–plant coevolution (Reid 1991), the role of birds as vectors of mistletoe transmission has received little attention (Rahman et al. 1993). The main objective of this study was to describe the patterns of disease transmission produced by the behavior of fruit-eating birds, a group of disease vectors that has been largely ignored by parasitologists.

Materials and Methods

Tristerix aphyllus*: natural history and seed dispersal*

We studied seed dispersal of *Tristerix aphyllus* (Loranthaceae), a leafless, endophytic mistletoe that infects several species of cacti in Chile (Follman and Mahú 1964, Kuijt 1988). The fruits of *T. aphyllus* are pseudoberries containing a single seed, and are presented on reddish branches protruding from the spine areoles of parasitized cacti. Seeds are dispersed exclusively by Chilean Mockingbirds (*Mimus thenca,* Mimidae), which swallow fruits whole and defecate the seeds intact (Martínez del Rio et al. 1995). The naked seeds are coated with a sticky viscin layer that adheres to the cuticle and spines of cacti hosts. Seeds germinate within a day of being defecated and grow for up to 8 wk or until their radicle encounters the epidermis of a cactus (Martínez del Rio et al. 1995). Once the tip of the radicle makes contact with the epidermis of a host, it swells and forms a haustorium producing several one-cell-wide filaments that penetrate into cactus tissues through stomatal openings. After successful infection, the seed and radicle dry out and fall (Mauseth et al. 1984, 1985). In its endophytic phase, *T. aphyllus* is one of the most highly reduced seed plants known (Mauseth 1990); the inflorescence is the only plant part to emerge from the host; the rest of the plant exists as an endophytic haustorial system without roots, leaves, or vegetative stems. Mauseth et al. (1984, 1985) described in detail the morphology of the vegetative body of *T. aphyllus,* its mechanisms of host infection, and how the endophyte produces inflorescences.

Study sites and methods

All work was conducted at Parque Nacional Fray Jorge (30°38′ S, 71°40′ W), which is located at the northern limit of the Mediterranean ecosystem of Chile. Fray Jorge has a semiarid Mediterranean climate with variable winter precipitation (mean annual rainfall = 84 mm; Gutiérrez et al. 1993) and warm, dry summers (di Castri and Hajek 1976). At Fray Jorge, *T. aphyllus* parasitizes the arborescent cacti *Echinopsis skottsbergii* and *Eulychnia acida.* These cacti grow together in isolated subpopulations located on the north-facing slopes of hills and ravines. The sudy sites all had sandy soils and similar vegetation, characterized by sparse shrubby cover (*Adesmia bedwelli, Flourensia thurifera,* and *Haplopappus* sp.) and a scant lower herbaceous layer that included the annuals *Erodium cicutarium, E. malacoides,* and *Plantago hispidula* (Muñoz and Pisano 1947).

TABLE 1. Characteristics of 10 north-facing subpopulations of *Echinopisis skottsbergii* and *Eulychnia acida* at Parque Nacional Fray Jorge, Chile.

Site no.	Density (no. individuals/ha)* Total cacti	Density (no. individuals/ha)* Parasitized cacti	Prevalence (%) of *Tristerix aphyllus*†	Relative species compositon (%) *Echinopsis skottsbergii*	Relative species compositon (%) *Eulychnia acida*
1	707.7	87.8	13	71	29
2	720.6	53.2	7	77	23
3	252.9	71.0	28	67	33
4	40.0	3.6	9	100	0
5	843.0	229.6	27	46	54
6	122.3	21.0	18	78	22
7	348.7	64.4	19	35	65
8	353.0	10.6	3	68	32
9	491.8	65.3	13	54	46
10	832.0	99.8	12	54	46

* Estimated from nearest neighbor distances based on Krebs (1989:95).

† Percent of individual cacti infected by *Tristerix*.

We selected 10 subpopulations located on north-facing slopes as study sites. The area occupied by each subpopulation ranged from 5 to 15 ha. In each subpopulation, we randomly selected 100 cacti and recorded their species, whether or not they were parasitized, height, distance to nearest neighbor, and the number of *T. aphyllus* seeds deposited by birds on each of them. Because the life-span of seeds is shorter than a few months (M. Hourdequin and C. Martínez del Rio, *unpublished data*), the number of seeds found represents only seeds deposited by birds during the fruiting season of 1993. At each subpopulation, we also estimated the abundance of *Mimus thenca* by conducting three replicated 0.8–1.5-km transect counts (Conner and Dickson 1980). Bird counts were done between 0800 and 1000. We express relative abundance of *M. thenca* among sites as individuals detected per kilometre (Ryder 1986). All observations and measurements were done during August 1993 at the peak of the fruiting season of *T. aphyllus*.

RESULTS

Differences among subpopulations

The prevalence of *T. aphyllus* (defined as the percent of infected cacti individuals) varied 10-fold among subpopulations (Table 1). Although the subpopulations differed considerably in cactus species composition (percentage *E. skottsbergii*), cactus density, and cactus height (Table 1, Fig. 1), none of these variables was significantly correlated with prevalence. For species composition, $r = -0.38$, $P > 0.1$; for cactus density, $r = -0.01$, $P > 0.5$; for cactus height, $r = -0.07$, $P > 0.5$. Cactus height differed significantly among subpopulations ($F_{8,982} = 7.5$, $P < 0.001$) and between species ($F_{1,982} = 7.5$, $P < 0.001$; two-way ANOVA). There was a highly significant interaction between species and subpopulation on cactus height ($F_{8,982} = 3.4$, $P < 0.001$; two-way ANOVA). *Eulychnia acida* was significantly taller than *Echinopsis skottsbergii* in most subpopulations (Tukey's test, $P < 0.05$; Fig. 1). At subpopulations 3 and 8, however, there were no significant differences in height between species (Fig. 1).

Because parasite prevalence and transmission among hosts can be influenced by host age and behavior of the transmission vector (Crofton 1971, Pacala and Dobson 1988), we examined the relationship between presence of infection and cactus size. For *E. acida,* a two-way ANOVA using subpopulation and parasitism as factors revealed significant differences in height among subpopulations ($F_{8,332} = 37.5$, $P < 0.001$) and between parasitized and nonparasitized individuals ($F_{1,332} = 29.9$, $P < 0.001$), but no significant interaction between subpopulation and parasitism ($F_{9,332} = 1.1$, $P > 0.3$). Thus, parasitized *E. acida* individuals were significantly taller than nonparasitized individuals, and this height difference was consistent across subpopulations. Although our analysis revealed significant differences in the height of *E. skottsbergii* among subpopulations ($F_{9,651} = 37.5$, $P < 0.001$) and between parasitized and nonparasitized individuals ($F_{1,651} = 37.5$, $P < 0.001$), it also revealed a significant interaction ($F_{9,651} = 37.5$, $P < 0.001$). Parasitized *E. skottsbergii* individuals were taller than nonparasitized ones in all subpopulations (Tukey's test, $P < 0.05$), except subpopulations 1, 3, and 4, in which there were no significant differences in height between parasitized and nonparasitized cacti (Tukey's test, $P > 0.05$, Fig. 1).

Seed deposition: effects of parasitism and subpopulation prevalence

The prevalence of *T. aphyllus* on *E. skottsbergii* and *E. acida* was not significantly different from that ex-

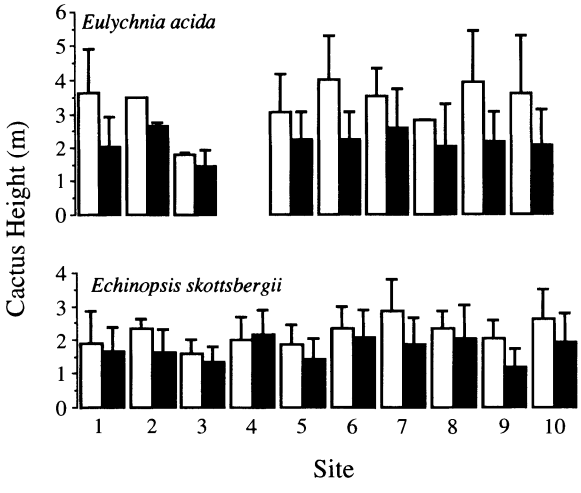

FIG. 1. Mean cactus height in 10 different subpopulations (sites) at Parque Nacional Fray Jorge. Open bars, parasitized cacti; closed bars, nonparasitized cacti. Errors are standard deviations. Sample sizes per species are given in Table 1.

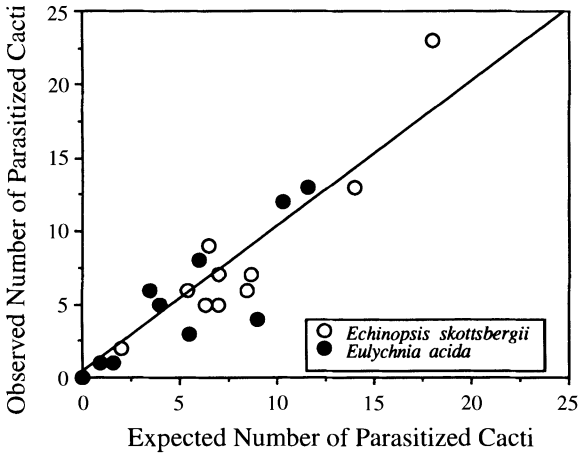

FIG. 2. Observed vs. expected number of *E. skottsbergii* and *E. acida* parasitized by *T. aphyllus* in 10 subpopulations. The frequency of seed deposition on cacti was independent of species at all sites. The number of parasitized cacti of each species was not significantly different from that expected based on the specific relative abundances at each subpopulation.

pected from the relative abundances of these species in each subpopulation (G^2 tests, $P > 0.05$; Fig. 2). In addition, the frequency of individuals receiving seeds was independent of species for parasitized and nonparasitized individuals in all subpopulations ($P > 0.05$; G^2 tests or Fisher's exact tests for conditional association given parasitism/nonparasitism; Wickens 1989). Infection levels and seed deposition appeared to be distributed between both host species with equal relative frequency.

The frequency of seed deposition on cacti was independent of species but was highly dependent on parasitism. The frequency of parasitized individuals receiving seeds was much higher than that expected from their relative abundance in all subpopulations (G^2 or Fisher's exact tests, $P < 0.0001$; Fig. 3). When all the subpopulations were pooled, only 2.8% of nonparasitized cacti received at least one seed, whereas 57.0% of the parasitized individuals were seed recipients. Because seed deposition appeared to be independent of species, we used seed deposition in both species to estimate the magnitude of transmission in each subpopulation.

We used the percentage of cacti receiving seeds and the mean number of seeds received per cactus as estimators of seed transmission. Seed deposition on nonparasitized cacti estimates new infections, whereas seed deposition on parasitized cacti estimates reinfections. In order to distinguish between these two processes, we analyzed seed rain on parasitized and nonparasitized cacti separately. The percentage of nonparasitized cacti receiving seeds increased significantly with *T. aphyllus* prevalence ($r = 0.75$, $P < 0.03$; Fig. 4c). Surprisingly, we found no significant correlation between the percentage of nonparasitized cacti receiving seeds and parasitized cactus density or total cactus density ($r = 0.31$, $P > 0.3$; and $r = -0.09$, $P > 0.5$, respectively). The pattern of transmission from parasitized to parasitized cacti followed a similar pattern: The percentage of parasitized individuals receiving seeds increased significantly with increasing *T. aphyllus* prevalence ($r = 0.58$, $P > 0.05$; Fig. 4b) but was not significantly correlated with parasitized cactus density or total cactus density ($r = -0.41$, $P > 0.5$; $r = -0.01$, $P > 0.1$, respectively). The mean number of seeds received by parasitized and nonparasitized cacti followed trends similar to those for the percentage of cacti receiving seeds. The mean number of seeds received by parasitized and nonparasitized cacti increased significantly with *T. aphyllus* prevalence ($r = 0.59$ and $r = 0.81$, $P < 0.05$, respectively). The mean

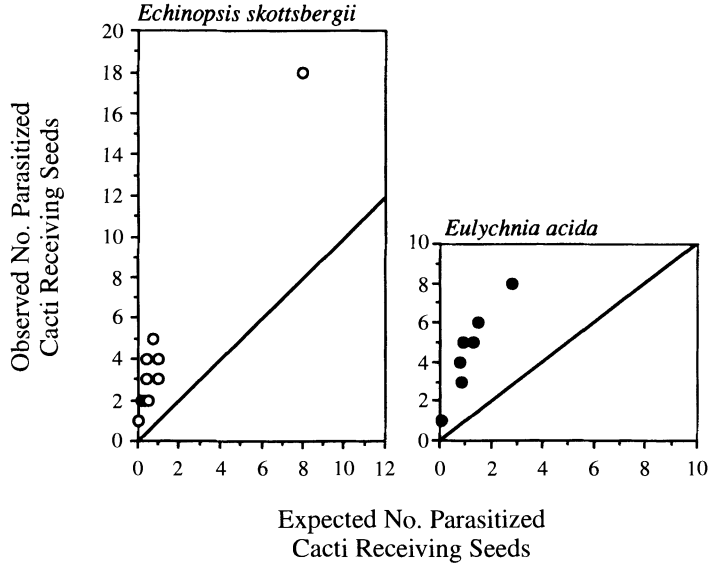

FIG. 3. Observed vs. expected number of parasitized cacti receiving seeds of *T. aphyllus*. In all subpopulations, the number of seeds deposited on parasitized *E. skottsbergii* and *E. acida* individuals was significantly higher than that expected from their relative abundance at each subpopulation.

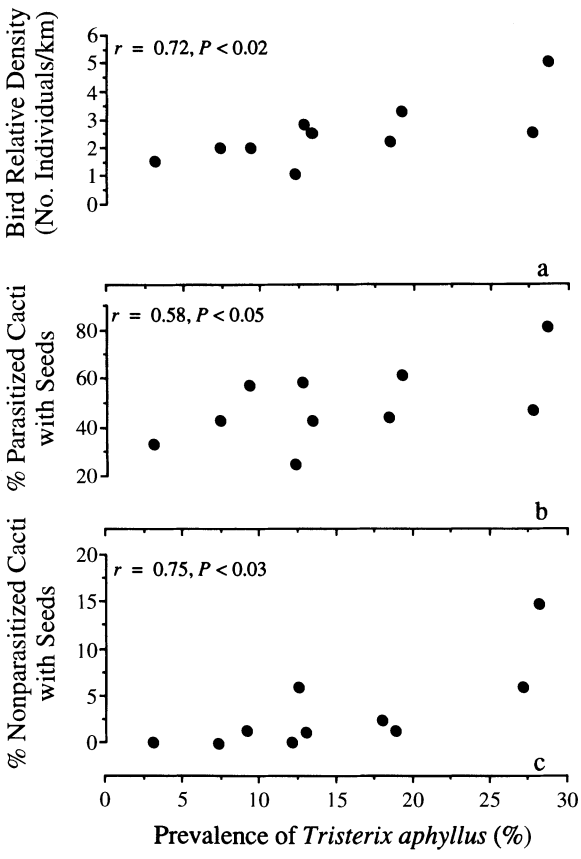

FIG. 4. (a) Density of Chilean Mockingbirds, *M. thenca,* and seed deposition frequency of *T. aphyllus* on (b) parasitized and (c) nonparasitized cacti, as a function of *T. aphyllus* prevalence (percent of 100 cacti individuals infected).

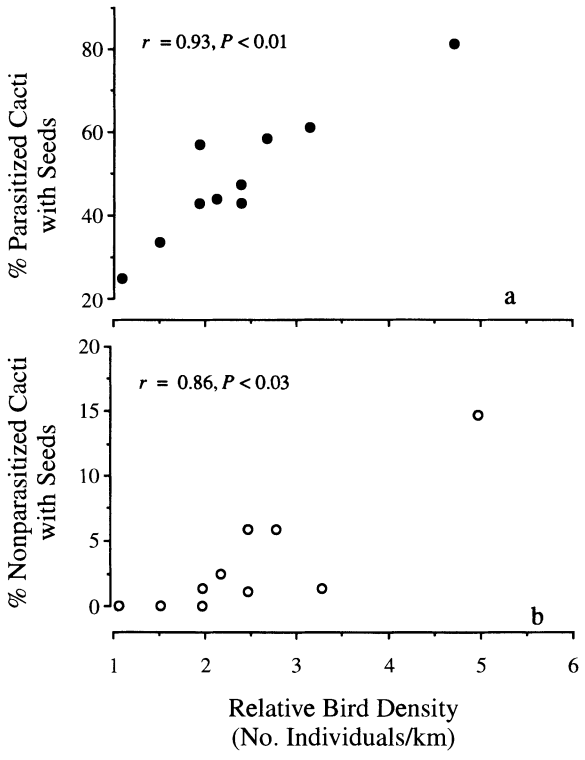

FIG. 5. Seed deposition frequency on parasitized (a) and nonparasitized cacti (b) as a function of *M. thenca* density at each subpopulation. Note that the correlation between deposition frequency and bird density is higher than that between deposition frequency and prevalence of *T. aphyllus* (see Fig. 4).

number of seeds received per cactus was not significantly correlated with parasitized cactus density (r = 0.06 and r = 0.43, $P > 0.05$, for parasitized and nonparasitized cacti, respectively) or with total cactus density ($r = -0.45$, $r = -0.02$, $P > 0.05$ for parasitized and nonparasitized cacti, respectively). At Fray Jorge, the transmission of *T. aphyllus* seeds among cacti appeared to be frequency dependent and to be largely independent of the density of hosts or the density of parasitized hosts.

Prevalence, bird abundance, and seed transmission

The number of birds (*M. thenca*) counted per transect increased significantly with increased *T. aphyllus* prevalence (r = 0.72, $P < 0.02$; Fig. 4a). Bird abundance, however, was not significantly correlated with total cactus density or with the density of parasitized cacti ($r = -0.27$, $P > 0.5$; r = 0.12, $P > 0.1$, respectively). All the estimates of seed transmission were highly correlated with bird abundance (Figs. 5 and 7). In all cases, the correlations between seed transmission and bird abundance were higher than those found between *T. aphyllus* prevalence and seed transmission (Figs. 5 and 7).

DISCUSSION

Birds that maintain mutualistic associations with plants often respond to variation in the abundance of the rewards that plants offer. At the individual plant level, bird visitation and, hence, fruit removal are positively correlated with fruit crop size (Murray 1987, Sallabanks 1993, Willson and Whelan 1993). At the habitat level, bird abundance can also be positively correlated with fruit abundances and can result in increased rates of fruit removal (Sargent 1990). The variable most often measured to assess the effect of bird abundance on bird–plant interactions is fruit removal (Willson and Whelan 1993). Our observations suggest that, for birds associated with mistletoes, the response of birds to fruit abundance can also result in variation in the transmission of disease. Specifically, the mutualistic interaction between birds and mistletoes seems to result in a positive correlation between parasitism level and seed transmission.

We documented this positive association between parasitism and seed transmission at two scales. Within a subpopulation, parasitized hosts were more likely to

receive seeds than were nonparasitized individuals. Among subpopulations, individual hosts in subpopulations with higher *T. aphyllus* prevalences were more likely to receive seeds, and received more seeds, than individuals in subpopulations with low prevalence. We will discuss in turn these two scales of association between parasitism and seed transmission.

Causes and consequences of increased seed deposition on parasitized cacti

Why do birds deposit more seeds on parasitized than on nonparasitized cacti? The simple answer provided by behavioral observations of *M. thenca* individuals is that these birds perch and defecate frequently on parasitized cacti, which provide fruit and accessible perching spots, but avoid perching on nonparasitized cacti (Martínez del Rio et al. 1995). Birds perch on the protruding branches of *T. aphyllus* while feeding, and often use dead cactus branches as perches. These dead branches frequently lack spines and are more common in parasitized than in nonparasitized cacti, as a result of the effects of *T. aphyllus* infection, which causes drying and withering of the spongy parenchyma. Because nonparasitized cacti are covered with long, very sharp spines and do not provide fruit, birds avoid perching on them (Martínez del Rio et al. 1995).

Although not in itself surprising, the fact that more seeds are deposited by birds on parasitized than on nonparasitized individuals can have strong evolutionary consequences. A bias in the transmission of propagules favoring parasitized hosts can lead to the presence of several parasites in a single cactus host ("superparasitism") and to competition among them. Several theoretical analyses have concluded that superinfection and competition among parasite strains leads to the evolution of higher levels of parasite virulence (Bremermann and Pickering 1983, Nowak and May 1994). Infection by *T. aphyllus* significantly decreases cactus flower and fruit production (Silva and Martínez del Rio 1995) and often leads to branch death. We hypothesize that the high virulence observed in *T. aphyllus* is an evolutionary consequence of preferential seed deposition by birds on parasitized individuals.

Causes and consequences of increased seed transmission in subpopulations with high T. aphyllus *prevalence*

The transmission of *T. aphyllus* seeds to cactus hosts was positively correlated with infection prevalence, but was not significantly correlated with the density of parasitized cacti. Furthermore, the abundance of *M. thenca* was positively correlated with *T. aphyllus* prevalence, but was independent of the density of infected cacti. Thus, our results suggest that transmission of *T. aphyllus* seeds is frequency dependent, and indicate that this frequency dependence is mediated by the response of birds to the frequency of infection at each subpopulation. The hypothesis that the abundance of birds increases with the frequency, rather than the density, of parasites at each subpopulation is puzzling. Although, in the following path analyses, we explore an alternative hypothesis, namely that increased *T. aphyllus* prevalence is a consequence rather than a cause of bird abundance, here we suggest two possible reasons why bird abundence may increase as a result of mistletoe prevalence. (1) Birds presumably can adjust their flight distances to compensate for changes in the spacing of parasitized cacti (Schmitt 1983); consequently, the absolute density of parasitized cacti may not be a good estimator of habitat quality (see Antonovics and Alexander 1992). (2) The average number of parasites per host is often positively correlated with *T. aphyllus* prevalence (Anderson 1982). In mistletoes, increasing the number of mistletoe individuals per cactus also increases the number of fruits available for dispersers. Thus, high *T. aphyllus* prevalence may mean high fruit abundance. These hypotheses remain to be tested.

Because transmission was significantly correlated with both bird abundance and parasite prevalence, and these two variables were significantly correlated, it is difficult to unravel the contribution of each to seed transmission. It is conceivable that both bird abundance and parasite prevalence contribute to the variation in transmission among subpopulations. Prevalence presumably increases the availability of seeds, and bird abundance increases the number of agents available to disperse these seeds. We used path analysis to explore the relative contribution of bird abundance and parasite prevalence on seed transmission (Sokal and Rohlf 1981). We analyzed the two alternative structural hypotheses depicted in Fig. 6. We emphasize that we use path analysis as a tool to explore the plausibility of one hypothesis over the other, not to "test" whether or not one hypothesis is better than the other as a descriptor of causal relationships. The inferences from our analyses should be construed as hypotheses to be examined with more data and/or with experimental manipulations.

Hypothesis (A) assumes that both bird abundance and parasite prevalence have a direct effect on transmission. Thus, the coefficient of correlation (r) of a full model that incorporates both transmission (t) and bird density (b) includes terms for direct (p_{bt} and p_{pt}) and indirect effects (Fig. 6; Sokal and Rohlf 1981). Hypothesis (B), in contrast, assumes that the direct effect of parasite prevalence on transmission is nil, and that the variation in transmission is uniquely attributable to bird abundance (Mitchell 1993). The direct effect is estimated by the path coefficient (p_{bt}) from bird abundance to transmission (which, in this case, is the same as the correlation between bird abundance and transmission). Path coefficients are simply partial regression coefficients obtained through multiple regression of standardized variables (Sokal and Rohlf 1981). The indirect effect is estimated by the product of the path coefficient from prevalence to transmission (p_{pt})

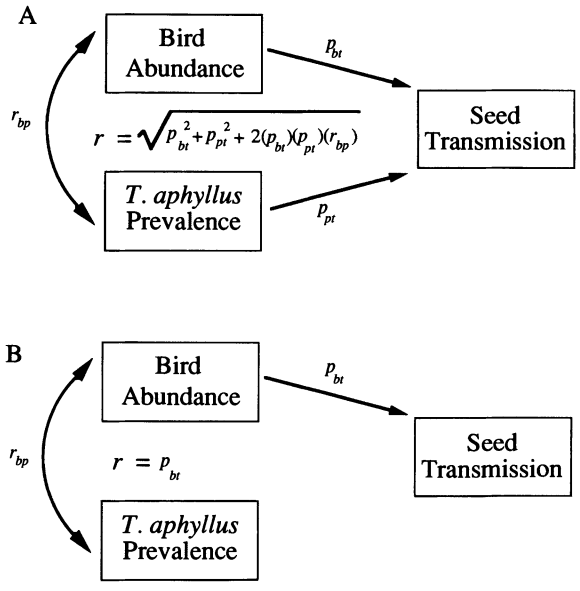

FIG. 6. Two alternative structural models illustrating the possible causal relationships between seed transmission and seed disperser abundance and mistletoe prevalence. In model (A), both bird abundance and *T. aphyllus* prevalence have direct and indirect effects on transmission. Thus, the coefficient of correlation (r) for model (A) includes terms for both direct and indirect effects. In model (B), only bird abundance has a direct effect on seed transmission; mistletoe prevalence influences transmission only indirectly through its effect on bird abundance. Thus, the coefficient of correlation (r_{bt}) for model (B) includes only the direct effect of bird abundance (p_{bt}).

and the correlation coefficient between bird abundance and prevalence (r_{bp}).

Fig. 7 shows the path coefficients between bird abundance and *T. aphyllus* prevalence and our two estimators of seed transmission to parasitized and nonparasitized individuals. It also shows the coefficients of correlation for hypotheses (A) and (B). These coefficients can be used to calculate coefficients of determination (r^2 and r_{bp}^2) that estimate the percentage of variation accounted for by each hypothesis. With one exception (panel IV in Fig. 7), hypotheses (A) and (B) explain roughly the same percentage of variation. These results suggest that variation in bird abundance is the main direct effect on seed transmission. Infection prevalence seems to affect transmission primarily through its influence on bird abundance. The only exception to this pattern was found in the mean number of seeds received by nonparasitized cacti. In this case, hypothesis (A) explained 18% more variation than did hypothesis (B), suggesting an important direct prevalence component to the intensity of transmission to nonparasitized cacti, measured by the mean number of seeds received.

The positive and highly significant correlation between parasite prevalence and bird abundance seems to support the notion that birds aggregate and increase the seed transmission in areas with high parasite prevalence. The results from path analysis, however, suggest an alternative hypothesis. It is possible that prevalence is increased in areas of high bird density by increased transmission without a major direct effect of local prevalence. Variation in the abundance of adequate perches, water, or other factors not considered in this study may lead to variation in bird densities and transmission rates and, hence, to variable parasite prevalences among subpopulations.

Thus, the positive correlation between prevalence and bird abundance could be the result of two different (albeit nonexclusive) processes: a numerical response by birds to prevalence, and increased prevalence resulting from higher bird abundances resulting from other factors. Distinguishing the relative importance of these two alternatives has relevance for the dynamics of mistletoe infection. A direct causal chain between prevalence, bird abundance, and seed transmission would lead to a positive feedback in infection, and, thus, to unstable host–parasite dynamics (Getz and Pickering 1983). If, in contrast, bird density is relatively independent of prevalence but leads to higher seed transmission, then the factors that influence the abundance of *M. thenca* also determine intersite variation in parasitism. Without stronger evidence supporting a causal relationship between prevalence and bird abundance, the positive relationship between prevalence and transmission of *T. aphyllus* seeds supports the hypothesis of frequency-dependent transmission only weakly. Experimental manipulation of parasite prevalence can help to unravel the role of prevalence, and other factors influencing bird density, on seed transmission. If birds aggregate in areas of high prevalence, mistletoe removal should have a strong effect on their abundance and, hence, on seed transmission.

Mistletoe seed dispersers as disease vectors

Seed dispersal studies are often hindered by the "almost hopeless" tasks of monitoring the fate of seeds, identifying the responsible dispersers, and recognizing suitable germination sites (Wheelwright and Orians 1982). Mistletoes and the birds that disperse their seeds offer an ideal opportunity to overcome these problems. Suitable dispersal sites are evident, seeds are dispersed by organisms that are easy to observe, and the fate of the seeds on hosts can be followed. Not surprisingly, mistletoe seed dispersal has been relatively well studied and the patterns of mistletoe seed deposition by birds have been relatively well documented (Davidar 1983, Reid 1989, Overton 1994).

To date, most studies on mistletoe seed dispersal have highlighted the role of birds in disseminating seeds to safe germination sites, and thus have emphasized the mutualistic aspects of mistletoe–host–bird systems (Sargent 1995). With few exceptions (see Rahman et al. 1993), seed dispersal studies of mistletoes

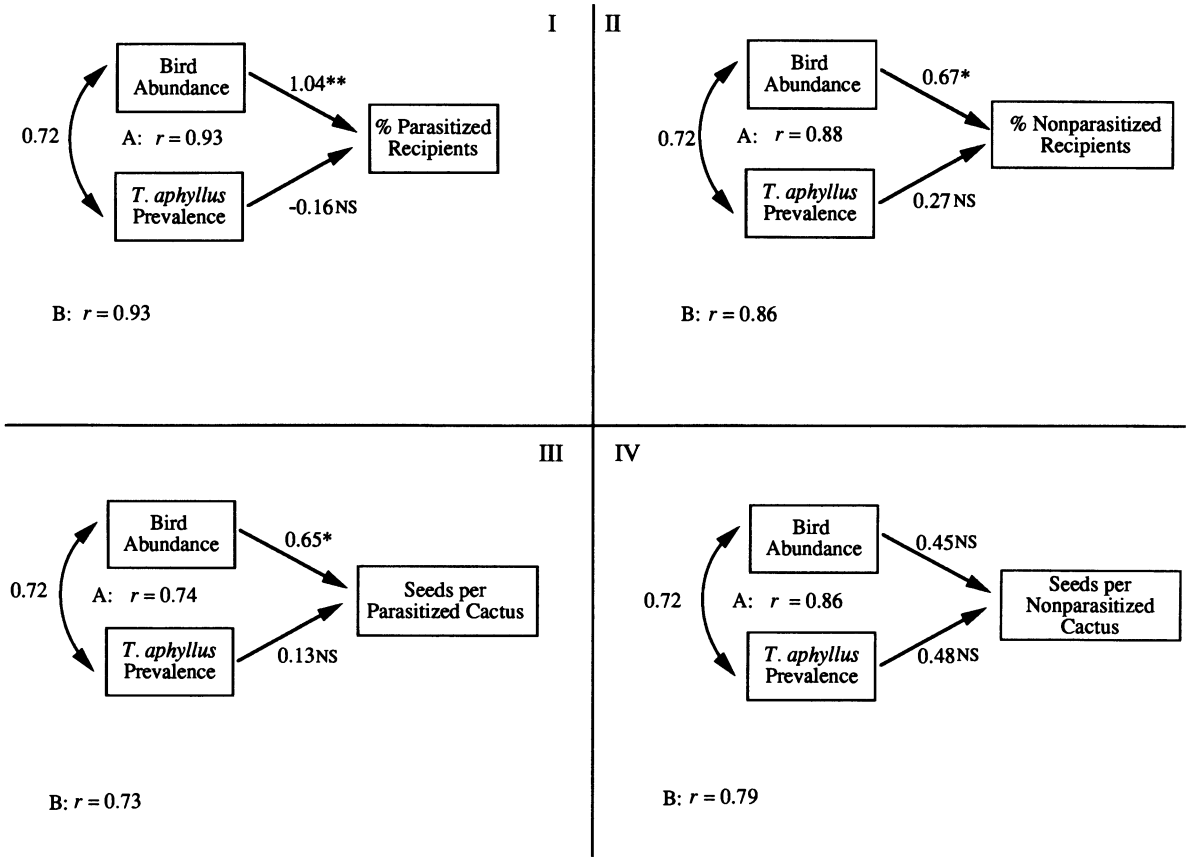

FIG. 7. Comparison of the performance of two structural models relating bird abundance and *T. aphyllus* prevalence with several estimators of seed transmission to parasitized and nonparasitized cacti. In each panel, the values contiguous to straight arrows connecting the independent variables (bird abundance and *T. aphyllus* prevalence) with the dependent variable (seed transmission) are path coefficients. The value contiguous to the curved arrow connecting the two independent variables is the correlation coefficient between them. Each panel contains the coefficient of correlation (r) for model (A), which includes the direct and indirect effects of both independent variables on seed transmission (see Fig. 6). Each panel also includes the correlation coefficient (r) for model (B). Significance levels of each path coefficient are indicated with asterisks (*, $P < 0.05$; **, $P < 0.005$; NS, not significantly different from 0).

have ignored the fact that successful dispersal and germination of a mistletoe seed signifies successful transmission of a parasite into a host. Ignoring the role of birds as parasite vectors has obscured the existence of a system that appears well suited to study disease transmission. The same features that make mistletoes useful for studying seed dispersal make them suitable for studying disease transmission.

Although mode of transmission can have important consequences for the ecological and evolutionary dynamics of host–parasite systems, its quantification can be extremely difficult (Real et al. 1992). Several recent studies have quantified spore transmission in pollinator-borne plant diseases (Roy 1994). Transmission can be studied with relative ease in these systems because both pollinator movements and spore deposition can be monitored (Jennersten 1983, Elmquist et al. 1993). Mistletoe–plant–bird systems share many of the features that facilitate the study of disease transmission in sexually transmitted plant diseases, and may provide useful systems for epidemiologists.

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