

## EFFECTS OF VECTOR BEHAVIOR AND HOST RESISTANCE ON MISTLETOE AGGREGATION

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**Abstract.** Understanding the factors affecting parasite aggregation in natural host populations is one of the central questions in parasite ecology. While different biological mechanisms giving rise to aggregation have been documented in the literature, the role of established parasites in vector attraction, and its importance in determining clumped parasite distributions has received less attention. In a two-year field study, we evaluated the importance of a bird vector, *Mimus thenca* (Mimidae), on the aggregation dynamics of the holoparasitic mistletoe, *Tristerix aphyllus*, on its cactus host, *Echinopsis chilensis*. Removal of *T. aphyllus* from cacti decreased the number of visits and the time spent by the bird vector, which resulted in a 3.5-fold lower seed deposition of the mistletoe on experimental hosts than on control hosts. Vector preference, however, was not the only factor affecting aggregation in this system. Spine length of the cactus acted as a first line of defense against parasitism, by discouraging bird perching on top of host columns. While heavily parasitized hosts received more seeds than unparasitized hosts, spines counteracted this effect. These results provide field evidence that parasite aggregation results from the balance between vector behavior and host resistance traits.

**Key words:** *Cactaceae*; Chile; host–parasite interaction; *Loranthaceae*; mistletoe; resistance; seed deposition; seed dispersal; tolerance; *Tristerix aphyllus*; vector-borne disease.

### INTRODUCTION

A general characteristic of many host–parasite relationships is the high aggregation of parasites on a small proportion of the host population. This clumped distribution has been the focus of theoretical and empirical research by parasite ecologists (e.g., Crofton 1971, Pennycuik 1971, Anderson and May 1978, Anderson and Gordon 1982, Dietz 1982, Pacala and Dobson 1988, Shaw and Dobson 1995, Poulin 1998, Shaw et al. 1998). Heterogeneity in the susceptibility of hosts to acquiring the infection has been one of the most frequently invoked biological mechanisms to explain clumped parasite distributions. Host susceptibility may occur as a result of several, not mutually exclusive mechanisms. For example, genetic-based susceptibility occurs when some hosts lack parasite resistance and they tend to acquire the infection first, with resistant individuals acquiring the infection later or at a slower rate (Munger et al. 1989, Wassom et al. 1996). Similarly, habitat-based susceptibility occurs if the exposure to infection is patchy in space and time, and some hosts inhabit places where the risk of infection is high in comparison to alternative habitats (e.g., Keymer and Anderson 1979, Anderson and Gordon 1982, Janovy and Kutish 1988). Host behavior-based susceptibility occurs when parasites cause changes in host behavior

that render parasitized hosts more exposed to subsequent infections than unparasitized hosts (e.g., Day and Edman 1983, Dobson 1988, Poulin et al. 1991). Vector behavior-based susceptibility occurs if established parasites render hosts more attractive to the vector species carrying the infectious disease, resulting in an increased infection rate on the previously parasitized hosts. Even though theoretical studies on this last mechanism predict important demographic and evolutionary consequences for host and parasite populations (e.g., Kingsolver 1987, Dye and Williams 1995), empirical evidence for vector-based susceptibility is scarce and entirely confined to arthropod vectors (e.g., Rossignol et al. 1985, Norval et al. 1989, McCall and Lemoh 1997, Kelly and Dye 1997).

Most studies designed to understand the factors involved in parasite aggregation have focused on just one of the mechanisms described above. This simplification, albeit convenient, assumes that mechanisms influence aggregation independently rather than complementarily (reviewed by Combes 2001). This is not necessarily true. The level of parasite aggregation may result from the interplay of diverse mechanisms influencing host susceptibility, and current aggregation patterns may even represent the net result of antagonistic mechanisms. On the one hand, factors increasing host susceptibility will favor reinfection of previously parasitized individuals, therefore increasing aggregation in host populations. On the other hand, factors preventing hosts from becoming parasitized, such as host

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resistance or tolerance to disease (reviewed by Roy and Kirchner 2000, Stowe et al. 2000), will prevent infection or aggregation in host populations. In spite of the simplicity of this idea, evidence for conflicting ecological forces influencing parasite aggregation has not been documented in the literature.

Unlike most host-parasite systems, propagules of parasitic plants represent attractive and often-conspicuous food items, upon which a diverse assemblage of frugivorous birds responsible for seed dispersal converge (Molau 1995, Watson 2001). While several studies have focused on the seed dispersal of parasitic plants (e.g., Godschalk 1983, Davidar 1987, Reid 1989, Sargent 1995), ecologists have only recently begun to study mistletoes in the context of host-parasite relationships (e.g., Martínez del Río et al. 1996, Norton and Carpenter 1998, Medel 2000, 2001, Mutikainen et al. 2000, Aukema and Martínez del Río 2002a, b, c). In this paper, we evaluate the importance of vector behavior and host defensive traits in determining parasite aggregation in a system that consists of the leafless holoparasitic mistletoe *Tristerix aphyllus* (Loranthaceae), its cactus host *Echinopsis chilensis* (Cactaceae), and a bird vector, the Chilean mockingbird *Mimus thenca* (Mimidae) (see Plate 1). Previous work documented that seeds of *T. aphyllus* tend to be deposited on a small proportion of the host population (Martínez del Río et al. 1995). Further correlative and experimental evidence revealed that the spine length of cacti acts as a first line of defense by discouraging the vector *M. thenca* from perching on the top of cactus columns (Medel 2000). Long spine-length *E. chilensis* are less visited by the mockingbird and suffer less seed deposition than short spine-length individuals. For instance, the spine length of cacti unvisited by *M. thenca* is 1.29 cm longer on the average than spines of visited *E. chilensis*. Similarly, individuals that did not receive seeds of *T. aphyllus* have spines 0.84 cm longer on the average than cacti receiving seeds of the mistletoe (Medel 2000). In this paper, we present experimental and correlative information from a two-year field study designed to evaluate the importance of vector behavior and host defensive traits on parasite aggregation. More specifically, we address the following questions: (1) Do parasitized cacti receive higher mistletoe seed deposition than unparasitized hosts? (2) What is the importance of host defensive traits in preventing mistletoe aggregation? (3) Does mistletoe seed deposition on cacti result from a compromise between vector behavior and host defensive traits?

#### METHODS

##### *Study site and natural history*

Field work was conducted during 1994 and 1995 at the Reserva Nacional Las Chinchillas (31°30' S, 71°06' W, IV Región), a 4229-ha Chilean National Reserve located ~300 km northeast of Santiago. The climate is



PLATE 1. A Chilean mockingbird, *Mimus thenca*, perched on *Echinopsis chilensis*. Note the emergence of the mistletoe *Tristerix aphyllus* and seed deposition at the right side of the cactus column. Photo credit: R. Medel.

of a semiarid mediterranean type with most rainfall occurring in the winter season. Long-lasting droughts alternate with unusual years of high precipitation that co-occur with the El Niño Southern Oscillation events. Vegetation is thorny with *Flourensia thurifera*, *Bahia ambrosoides*, and *Porlieria chilensis* as the most common shrub species. Cactus species are columnar *Echinopsis chilensis* and *Eulychnia acida*, and globular *Opuntia berteroniana* and *Eriosyce sandillon*. *Tristerix aphyllus* (Loranthaceae) is a leafless holoparasitic mistletoe endemic to the arid-semiarid region of Chile that parasitizes only species of the family Cactaceae (Kuijt 1988). Its distribution ranges from 27° to 34.5° S (Medel et al. 2002). Fruits are single-seeded pseudoberries. The Chilean mockingbird *M. thenca* swallows whole ripe fruits, and is the only species that disperses the seeds (66.6-h observation). The bird eats 3.16 fruits per bout on the average (1 SD = 3.60,  $N = 120$  observations on *E. chilensis*), and spends most of its time perching on living cacti (45.6%), shrubs (22.9%), and dead cacti (19.2%) (18.3-h observation of *M. thenca*). The sticky seeds of the mistletoe are defecated by the mockingbird, no more than three at a time, and often on perches different from their feeding places (only 10 out of 120 feeding events resulted in defecations in the same cactus). Seeds germinate one day after defecation, then a bright reddish radicle undergoes elongation until reaching the host epidermis. The mistletoe exists as an endophyte for ~17 months before emerging from the cactus tissues as a red inflorescence (Mauseth et al. 1984, 1985, Botto-Mahan et al. 2000). Because more

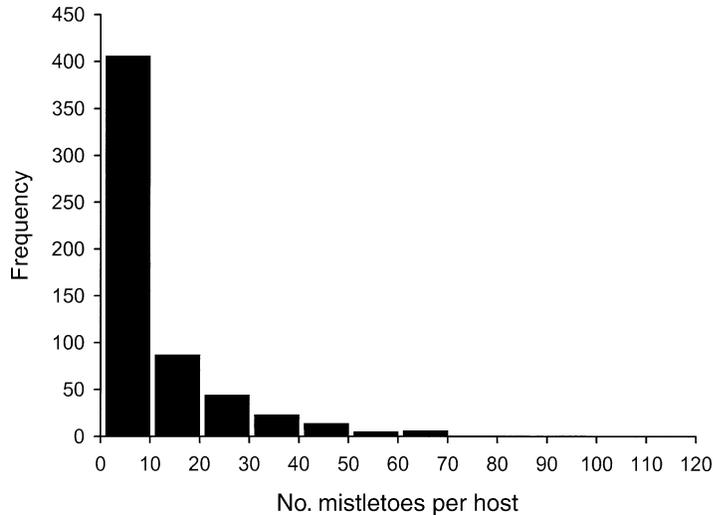


FIG. 1. The distribution of number of hosts of *T. aphyllus* inflorescences on *Echinopsis chilensis*. Total number of hosts = 588. The distribution of the mistletoe on cacti was highly overdispersed relative to a Poisson distribution ( $\chi^2_2 = 172.17$ ,  $P < 0.001$ ), but fit a negative binomial distribution ( $\chi^2_4 = 2.69$ ,  $P = 0.611$ , mean  $\pm 1$  SE =  $0.655 \pm 0.066$ ,  $k \pm 1$  SE =  $0.364 \pm 0.035$ ).

than one mistletoe inflorescence can emerge from a single seed, our measures of aggregation focus on the number of inflorescences rather than on the number of individual mistletoes on cacti.

#### Field and statistical procedures

The degree of parasite aggregation has been primarily described by the negative binomial distribution (NBD hereafter) (Shaw and Dobson 1995). This distribution function has two parameters, the mean ( $\mu$ ), and an inverse measure of aggregation ( $k$ ). If  $k$  approaches infinity, distribution converges to the Poisson, indicating random parasitism over the host population. However, if  $k$  approaches zero, then NBD converges to the logarithmic series. Most estimated  $k$  values in natural host-parasite populations are lower than one, indicating aggregated parasitism (Shaw et al. 1998). We recorded the number of mistletoe inflorescences from parasitized cacti exceeding 1 m height in an area of  $\sim 7$  ha. Data from 588 parasitized cacti were fitted to the Poisson random distribution and then to NBD using maximum likelihood in the  $k$  parameter estimation.

To evaluate the role of established parasites on bird behavior and seed deposition, we focused on a population of  $\sim 3$  ha ( $31^\circ 30' S$ ,  $71^\circ 07' W$ ) with 45.5% mistletoe prevalence on *E. chilensis*. This prevalence is relatively high in comparison to other populations in the Reserve (26% of parasitism on the average,  $N = 10$  populations). We removed the inflorescences of *T. aphyllus* from 45 randomly chosen parasitized individuals of *E. chilensis*, leaving 211 parasitized cacti with intact mistletoes. Parasite removal was performed in May 1994, at the beginning of the seed dispersal season. Experimental and control cacti did not differ either in the number of columns (mean  $\pm 1$  SE, experimental =  $8.09 \pm 0.82$  no. columns; control =  $8.90 \pm 0.43$  no. columns,  $F_{1,254} = 0.786$ ,  $P = 0.376$ ) nor height (mean  $\pm 1$  SE, experimental =  $2.54 \pm 0.11$  m; control =  $2.45$

$\pm 0.05$  m,  $F_{1,254} = 0.570$ ,  $P = 0.451$ ) at the beginning of the experiment. Similarly, experimental and control individuals had a comparable number of inflorescences of *T. aphyllus* prior to parasite removal (mean  $\pm 1$  SE, experimental =  $29.44 \pm 3.60$  no. inflorescences; control =  $33.54 \pm 1.88$  no. inflorescences,  $F_{1,254} = 0.928$ ,  $P = 0.336$ ). Because it was not feasible to remove the portion of the mistletoe that lives within the tissues of the cactus, we restricted our experimental procedure to the external portion of *T. aphyllus*. Experimental and control cacti were tagged with a numbered plate that allowed their identification with binoculars from a 200-m distant observation point. We recorded the foraging behavior of *M. thenca* on *T. aphyllus* during 99 h, from June to November 1994, at 20–25-d intervals. Observations were performed from 0700–1200 hours, and always on sunny days. Besides the observations of foraging birds, we recorded the number of seeds deposited on the cactus surface during 171 days after the start of the experiment, at 20–25-d intervals. Because the seeds of *T. aphyllus* are white translucent when just defecated by the bird, and turn reddish after a week, we focused on white seeds only, probably underestimating the real seed deposition rate but avoiding repeated sampling of seeds. Seed deposition patterns through time were tested by repeated-measures ANOVA for the six posttreatment sampling dates. Cumulative seed deposition was also compared between experimental and control cacti by one-way ANOVA. Data on spine length were the same as used in Medel (2000). We calculated the mean spine length of each cactus by measuring 10 spines from the top of its columns. Every spine was measured from the base of the areole to the tip, with a digital caliper (precision 0.1 mm).

#### RESULTS AND DISCUSSION

There was a low  $k$  value in the negative binomial distribution indicating a high level of aggregation of *T. aphyllus* inflorescences on cacti (Fig. 1). We re-

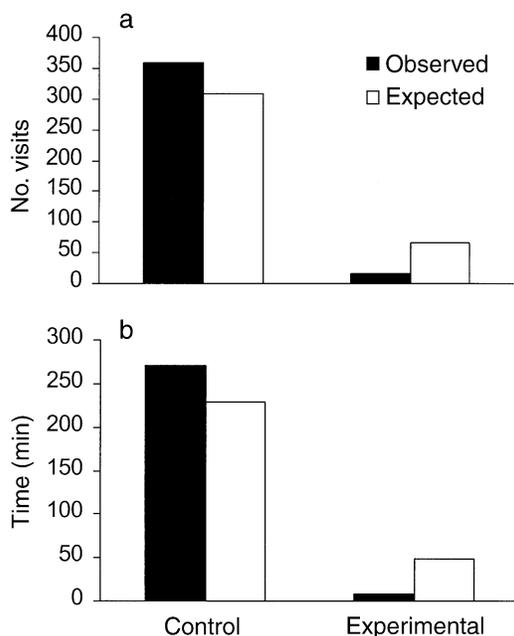


FIG. 2. The observed and expected (a) visits and (b) time spent by *Mimus thenca* on *Echinopsis chilensis* in the presence (control) and absence (experimentally removed) of *Tristerix aphyllus*. Expected values were calculated from the total of visits and time weighted by the relative abundance of cacti.

recorded 375 visits of *M. thenca* to control and experimental cacti after parasite removal. The number of visits to each category differed from a random expectation based on the relative abundance of experimental and control cacti. Individuals with parasite removal were less frequently visited than control cacti (likelihood ratio test,  $G_1 = 27.07$ ,  $P < 0.001$ , Fig. 2a). Similarly, *M. thenca* spent less time on experimental than control cacti (likelihood ratio test,  $G_1 = 1556.5$ ,  $P < 0.001$ , Fig. 2b), which resulted in a lower seed deposition in experimental than control individuals (Fig. 3a). There was a significant effect of time attributable to the seed dispersal phenology of *T. aphyllus*, and the interaction of time and treatment was also significant. Consideration of cumulative seed data revealed a similar pattern. Seed deposition onto experimental cacti was 3.5-fold lower than in control individuals after 171 days (Fig. 3b). This result was confirmed when the number of columns and the height of cacti were included as covariates ( $F_{1,254} = 6.87$ ,  $P = 0.009$ ). These findings indicate that the presence of the mistletoe on *E. chilensis* not only attracted *M. thenca* but increased the chance of parasitized hosts becoming reinfected. However, the presence of the mistletoe on cacti was not the only factor affecting seed deposition. Results from multiple regression analysis revealed that the number of mistletoes and spine length had significant but opposite effects on seed deposition (Fig. 4a,b). While a unit increment in the number of established mistletoes increased seed deposition by 0.196 units, a unit incre-

ment in spine length decreased seed deposition by 0.196 units, suggesting that spines not only prevent *E. chilensis* from becoming parasitized but also compensate for the attractive effect of established mistletoes on seed deposition. This result corroborates previous evidence that spines represent a defensive trait that evolves under parasite-mediated selection (Medel 2000).

Results from this study have at least two consequences for studies of host plant–parasitic plant relationships. First, McElhany et al. (1995) explored the importance of parasite aggregation on the vector behavior and spread of the aphid-transmitted barley yellow dwarf virus. Their results indicate that vector behavior will not limit disease spread at low parasite aggregation. However, when parasites are clumped, the vector preference will contain disease spread. In addition, heterogeneity among host individuals in susceptibility to infection can also reduce the spread of the infectious disease, probably because most infection occurs on a low proportion of the host population (Dwyer et al. 1997, Caraco et al. 2001). Our study

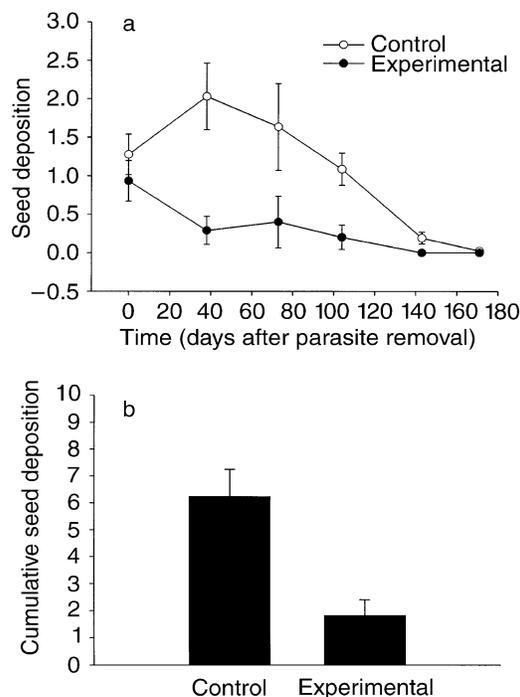


FIG. 3. (a) The pattern of change in the number of seeds of *T. aphyllus* received by experimental and control cacti on a daily basis (mean  $\pm$  1 SE). The first point is the number of seeds deposited on cacti before mistletoe removal. Repeated-measures ANOVA: treatment,  $F_{1,44} = 12.282$ ,  $P < 0.001$ ; time,  $F_{3,220} = 4.246$ ,  $P < 0.001$ ; time and treatment,  $F_{3,220} = 5.853$ ,  $P < 0.001$ . Values on the y-axis are log-transformed (measured in seeds/d). (b) Cumulative seed deposition (mean  $\pm$  1 SE) of *T. aphyllus* on control and experimental cacti 171 days after initiation of the experiment. Experimental mean  $\pm$  1 SE =  $1.82 \pm 0.58$ ; control,  $6.23 \pm 1.01$ ; one-way ANOVA,  $F_{1,254} = 5.416$ ,  $P = 0.021$ .

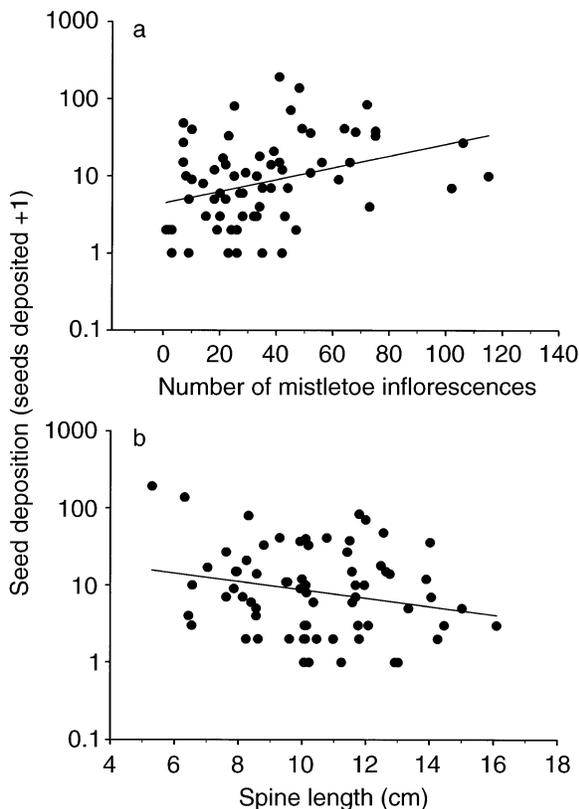


FIG. 4. Effects of (a) number of inflorescences and (b) spine length on seed deposition. Multiple regression model:  $F_{2,106} = 5.35$ ,  $P = 0.006$ ; mistletoe inflorescences (standardized  $\beta$  coefficient  $\pm 1$  SE),  $0.196 \pm 0.094$ ,  $t = 2.07$ ,  $P = 0.040$ ; spines (standardized  $\beta$  coefficient  $\pm 1$  SE),  $-0.196 \pm 0.094$ ,  $t = 2.08$ ,  $P = 0.040$ ; test for homogeneity of slopes,  $t_{214} = 1.987$ ,  $P = 0.048$ . Note that the y-axes are log scales.

indicates that level of parasite aggregation and susceptibility both affect vector behavior and seed deposition. Rather than independent effects, combined effects are expected to determine mistletoe spread in this system, because spine length and number of mistletoe inflorescences have significant but opposite effects on seed deposition. Second, recent evolutionary models predict that the levels of resistance and tolerance in host populations are contingent on the prevalence of parasitism (Roy and Kirchner 2000). While resistance refers to traits that prevent infection or limit its extent, tolerance refers to traits that do not necessarily reduce or eliminate infection, but instead reduce its fitness consequences (Burdon 1987, Fineblum and Rausher 1995). When a host population receives low parasitism, that is, expresses high resistance, parasites may select for increased resistance rather than increased tolerance to an aggregated parasite distribution. On the contrary, when a host population shows high parasite prevalence, that is, expresses low resistance, parasites may select for increased tolerance rather than increased resistance. If spines provide resistance against parasitism, most

seeds will be dispersed to a few short spine-length individuals, therefore leading to the high levels of aggregation found in populations of *E. chilensis*. While unequivocal demonstration of this mechanism is beyond the scope of this paper, it is likely that mistletoe aggregation on *E. chilensis* depends on the prevalence of parasitism and the level of resistance evolved by the host population.

In summary, we conclude that the presence of the mistletoe attracts the bird vector and increases mistletoe aggregation on the plant host species. Aukema and Martínez del Río (2002c) documented a similar pattern for the desert mistletoe *Phoradendron californicum*, *Phainopeplas* (*Phainopepla nitens*), and the velvet mesquite (*Prosopis velutina*). Unlike their study, however, our results show that vector behavior was not the only factor responsible for the aggregated mistletoe distribution. The spine length of cacti compensated for the attractive effect of the mistletoes on seed deposition, therefore suggesting an important role for defensive traits on parasite aggregation dynamics. Our analysis of aggregation was performed in a single population of *E. chilensis*. Our focus upon this relatively small spatial scale reflects our intention of inferring aspects of the seed dispersal dynamics and potential consequences of aggregation for parasite and host populations at the between-host spatial scale. Infection dynamics and host-parasite coevolution, however, can occur across different spatial scales, as documented in several studies (e.g., Real and McElhany 1996, Thrall and Burdon 1997, 1999). For instance, recent geographic mosaic theory of coevolution emphasizes that host and parasite reciprocal responses may be extremely variable across sites (see Thompson 1994, 1999, Lively 1999). Conclusions from this study would benefit from adopting a metapopulation perspective (e.g., Overton 1994, Aukema and Martínez del Río 2002a), especially if seed dispersal occurs between heavily parasitized hosts across distances exceeding local populations.

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