

RESEARCH ARTICLE

Intrapopulation size and mate availability influence reproductive success of a parasitic plant

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Abstract

1. Aggregated distributions of parasite individuals across host individuals are nearly ubiquitous among parasitic taxa. The size and sex ratio of the population of one parasite species infecting a single host (hereafter “intrapopulation”) can influence parasite fitness through intraspecific competition, mate availability and the ability to attract vectors for transmission of parasite propagules. Competition for resources and for pollen and seed vector services may limit reproductive success (pollen receipt, fruit production and seed dispersal) in large intrapopulations of parasitic plants, while mate limitation or reduced ability to attract vectors may limit this success in small intrapopulations.
2. Using a dioecious parasitic plant, desert mistletoe *Phoradendron californicum*, we experimentally removed reproductive tissue from male parasites in whole intrapopulations to test for independent effects of intrapopulation size and within-host mate availability on female fitness. As desert mistletoe requires both pollen and seed vectors for successful reproduction, the species provides the opportunity to test how intrapopulation characteristics affect multiple components of parasite fitness.
3. We found that insect-mediated pollen receipt decreased for parasites on treated hosts, consistent with within-host mate limitation. Additionally, the relationship between mate availability and fruit production per flower ranged from neutral to positive depending on year of the experiment.
4. As expected if competition for host resources limits reproductive success more than mate availability in larger intrapopulations, the greater pollen receipt to females in large intrapopulations did not generally translate into increased mistletoe fruit production. Relationships between mistletoe fruit production per flower and intrapopulation size ranged from negative to neutral.
5. Both pollen receipt and pollinator visitation increased with intrapopulation size, indicating that larger populations can be more attractive to pollen vectors independent of mate availability. However, we found no relationship between intrapopulation size and fruit removal by dispersers and, thus, no evidence that attraction of seed dispersal vectors increases with intrapopulation size.
6. *Synthesis.* These results highlight the interactive roles of within-host processes (resource competition, mate availability and vector attraction) in determining the fitness of biotically transmitted parasite individuals.

KEYWORDS

mate limitation, mistletoe, *Phoradendron californicum*, pollination, seed dispersal, vector transmission, Viscaceae, within-host aggregation

1 | INTRODUCTION

Aggregation of parasites within infrapopulations, that is, groups of conspecific parasites infecting single host individuals, has attracted extensive attention due to its hypothesized consequences for the ecology and evolution of host–parasite interactions (Anderson & May, 1978; Jaenike, 1996; Morrill, Dargent, & Forbes, 2017; Poulin, 2006). Negative binomial distributions of parasites across hosts, in which most potential hosts are uninfected or harbour few parasites and a small number of hosts carry the majority of the parasite population, are present across diverse parasite taxa (Poulin, 2013; Shaw & Dobson, 1995). This distribution can result from reproduction within hosts, intrinsic differences in the susceptibility of hosts to parasites and/or differences in host exposure to parasite propagules (Poulin, 2006). Hence, fewer parasites occupy intermediate-sized infrapopulations than occupy small or large ones. Here, we investigate the effects of infrapopulation size and composition on fitness in a dioecious parasitic plant, desert mistletoe *Phoradendron californicum*.

While parasites are phylogenetically diverse, most studies examining infrapopulation characteristics and their consequences have focused on a very narrow range of taxa: trophically or directly transmitted parasites of animals, especially parasitic helminths (Poulin, 2006; Shaw & Dobson, 1995). Parasitic plants have been relatively poorly studied (Press & Phoenix, 2005; Watson, 2009), even though they are diverse, ecologically important, and show largely the same epidemiological patterns as other parasites (García, Rodríguez-Cabal, & Amico, 2009; Okubamichael, Griffiths, & Ward, 2016; Overton, 1994; Robinson & Geils, 2006). Yet, these systems offer many advantages for studying infrapopulation characteristics, such as size and sex ratio, as well as their consequences. They are large and amenable to experimental manipulations. Their vectors (pollinators and seed dispersers) are well studied and easily observed, allowing us to adopt both tools and general knowledge from pollination and seed dispersal biology to study transmission dynamics.

While being infected with a large infrapopulation is nearly always expected to have negative fitness consequences for an individual host (Jaenike, 1996), the effects of infrapopulation size on individual parasite fitness are not well understood. Infrapopulation size is hypothesized to relate to parasite fitness either positively or negatively through a variety of mechanisms that are rarely investigated simultaneously (Heins, Baker, & Martin, 2002; Johnson, Lafferty, van Oosterhout, & Cable, 2011). For example, competition for resources obtained from the host can influence parasite success and result in the negative relationships between infrapopulation size and reproduction that are present across a diversity of parasites (Dobson, 1986; Heins et al., 2002; Poulin, 2006). Small initial differences in size or order of arrival will be exaggerated by competition for resources

gained from the host when parasites do not have determinate growth, as is the case in parasitic plants, thereby increasing variance in reproductive success among parasites (Dobson, 1986). However, parasite reproduction is not always limited by host resources, especially when parasites are small relative to hosts (Hughes et al., 2004; Weinersmith et al., 2014). It has been hypothesized that high levels of parasitic plant aggregation within hosts should have detrimental effects on fitness (Watson & Rawsthorne, 2013), but competition within hosts has largely been untested in these systems (but see Queijeiro-Bolaños, González, Martorell, & Cano-Santana, 2017).

It is known that the relationship between infrapopulation size and fitness can be further complicated for animal parasites that reproduce sexually in or on a host individual (Galvani, Coleman, & Ferguson, 2003). Mate limitation can cause within-host Allee effects, that is, positive relationships between infrapopulation size and individual fitness, and local mate limitation can cause strong selection on parasite sex ratios (Drapeau & Werren, 1999). Researchers have found that biased sex ratios can reduce reproductive success of dioecious free-living plants (Karst, Antos, & Allen, 2008; Lin, Nol, & Dorken, 2015; Oster & Eriksson, 2007), but such work has not been conducted in parasitic plants, which show a higher frequency of dioecy (Bellot & Renner, 2013). If individuals of each sex accumulate on hosts at random, larger infrapopulations will have less biased sex ratios and mate limitation will disproportionately affect parasites in small infrapopulations (Poulin, 2006). Experimental approaches that can independently assess how mate availability and infrapopulation size alter parasitic plant fitness are needed to disentangle the relative effects of each process on within-host interactions.

Just as density or patch size of free-living plants can influence pollinator and seed disperser behaviour (Essenberg, 2012; Ghazoul, 2005; Saracco, Collazo, & Groom, 2004; Saracco, Collazo, Groom, & Carlo, 2005), vectors may visit parasitic plants at different rates depending on the characteristics of the infrapopulation they inhabit. The attraction of bird dispersers to parasitic plant fruit crops is a well-studied example of the effect of parasite presence on vector attraction (Aukema & Martinez del Rio, 2002b; Carlo & Aukema, 2005; Martinez del Rio, Silva, Medel, & Hourdequin, 1996; Medel, Vergara, Silva, & Kalin-Arroyo, 2004; Mellado & Zamora, 2016), but whether dispersal service scales with the size of the infrapopulation are not known. If few parasites can be as attractive as many, these parasites will compete within an infrapopulation for vector services, resulting in decreasing propagule transmission per parasite individual with increasing infrapopulation size. Studies are needed that evaluate how these relationships with vectors interact with within-host mate limitation and competition for host resources.

We investigate the effects of within-host mate availability and overall infrapopulation size on parasitic plant fitness, using a common

and widespread dioecious parasitic plant, desert mistletoe *P. californicum*. In order to reproduce and be transmitted between susceptible hosts, this species requires both pollination by generalist insects and seed dispersal by a specialist bird. By experimentally removing the reproductive tissue of male parasites on treated hosts, we evaluate the impact of within-host mate availability independent of natural variation in infrapopulation size. (1) If female parasites experience mate limitation, females on treated hosts should receive less pollen. (2) If competition for resources gained from hosts rather than mate availability limits female reproductive success, pollen receipt will not predict offspring production (fruit set); rather, females in large infrapopulations should produce proportionally fewer offspring than those in small infrapopulations. (3) If the presence of parasites is important for attracting pollen and seed vectors, visitation by vectors will be higher in larger infrapopulations, as will the likelihood that a parasite's propagules are transmitted to and from that host (movement of pollen and fruit). Alternatively, (4) if females compete within infrapopulations for vector services, vectors will visit parasite individuals in large infrapopulations less frequently and disperse fewer parasite propagules per female from larger infrapopulations.

2 | MATERIALS AND METHODS

2.1 | Study system

Mistletoes are aerial parasitic plants. They include over 1,500 species in five families in the order Santalales (Nickrent, 2011; Norton & Carpenter, 1998). One of these families, Viscaceae (syn. Santalaceae-Visceae), is comprised of about 550 species, including 230 *Phoradendron* species (Nickrent, 2002). Desert mistletoe *P. californicum* is a dioecious, non-apomictic, hemiparasite that primarily infects trees and shrubs of the Fabaceae family, especially *Prosopis* spp., *Senegalia* spp. and *Parkinsonia* spp. throughout the Sonoran and Mojave deserts of the United States and Mexico. These xylem-tapping parasites are capable of photosynthesis, but gain much of their carbon, in addition to all of their water and other nutrition, from the host individual (Hull & Leonard, 1964; Marshall & Ehleringer, 1990). The extraction of host resources is likely to have negative consequences for host growth and fecundity, as has been noted for other mistletoe species (Henríquez-Velásquez, Henríquez, & Aravena, 2012; Silva & Martínez Del Río, 1996), although desert mistletoe has only been implicated in host mortality under drought conditions (Spurrier & Smith, 2007). Desert mistletoe infrapopulations can include more than 30 individuals, and negative fitness effects on hosts should be most severe at these large infrapopulation sizes. A previous study of infrapopulations of 816 hosts found that desert mistletoes are highly aggregated across hosts (variance to mean ratio = 12.3, negative binomial's $k = 0.2$) and that deposited mistletoe seeds show an even more skewed distribution (variance to mean ratio = 685.5, negative binomial's $k = 0.1$) (Aukema & Martínez del Río, 2002a).

Desert mistletoe flowers are visited by a diverse assemblage of generalist pollinating insects, primarily small bees (especially

Lasioglossum spp.) and flies (especially Syrphidae and Calliphoridae). Flowers of both sexes produce nectar (Wiesenborn, 2016), but males have larger flowers that produce greater quantities (Yule & Bronstein, 2018b). In addition to nectar, many of the floral visitors collect pollen (Wiesenborn, 2016). Each successfully pollinated flower may initiate a fruit, but these remain undeveloped through spring and summer. Throughout the following October–March, these fruits mature, such that females bear ripe fruits intermixed with the following year's flowers. Infructescences contain 2–25 ripe fruits, each c. 5 mm in diameter, translucent, white to red in colour, and single-seeded. When a consumer removes a fruit, the c. 2 mm crater remains visible until the infructescence abscises, which occurs either when all fruits have been removed or the season has ended. Infructescences with fruit remaining in summer are either abscised or remain on the plant in a desiccated state. Other sources of fruit loss or abortion are rare and can be readily distinguished from fruit removal. Flowers that do not produce fruits also remain visible, as the flowers' perianths remain on the infructescences.

Like many mistletoes, desert mistletoe requires frugivores to disperse seeds to suitable establishment sites. Generalist birds and mammals consume desert mistletoe berries, but one specialist bird, the phainopepla *Phainopepla nitens*, disperses a much larger proportion of seeds than other fruit consumers and, unlike most other consumers, does not destroy the seeds during digestion due to its specialized crop (Larson, 1996; Walsberg, 1975). Phainopepla populations depend on desert mistletoe fruit crops, and these fruit comprise the majority of the phainopepla diet during the fruiting season (Walsberg, 1978). Positive feedbacks between mistletoe density and seed disperser activity are hypothesized to lead to high levels of within-host aggregation in mistletoes in general (Watson & Rawsthorne, 2013). In desert mistletoe specifically, seed dispersal, especially by specialists, is indeed directed towards previously infected hosts (Aukema & Martínez del Río, 2002a). Fewer desert mistletoe seeds are dispersed to host individuals following experimental removal of adult desert mistletoe plants, indicating that seed vectors are attracted to parasites and the resources they provide (Aukema & Martínez del Río, 2002a). In addition, these seed dispersers have innate preferences for larger, likely older, host trees due to their conspicuous perching behaviours related to territoriality (Aukema & Martínez del Río, 2002b; Walsberg, 1978). If these mechanisms, rather than intrinsic differences in host susceptibility, are primarily responsible for desert mistletoe aggregation, then mistletoe infrapopulations are likely to increase in size throughout an infected host's life. Indeed, older trees consistently have higher infection rates and harbour larger infrapopulation sizes than younger trees (Aukema & Martínez del Río, 2002a, 2002b).

2.2 | Natural infrapopulation characteristics

To understand the relationship between infrapopulation size and within-host mate availability, desert mistletoe infrapopulations on

catclaw acacia *Senegalia greggii*; hereafter acacia, and velvet mesquite *Prosopis velutina*, hereafter mesquite, trees were characterized at Organ Pipe Cactus National Monument (OP, about 200 km west of Tucson, AZ, USA), the Santa Rita Experimental Range (SR, about 65 km south of Tucson) and Tonto National Forest (TF, about 240 km northeast of Tucson). The total number of adult male and female desert mistletoes was counted within each infrapopulation (OP: $n = 20$ acacia, $n = 23$ mesquite; SR: $n = 67$ acacia, $n = 108$ mesquite; TF: $n = 27$ acacia, $n = 15$ mesquite infrapopulations).

2.3 | Focal observations of pollinator visitation

In 2015, we surveyed insect visitors to individual desert mistletoe plants at SR infecting 19 mesquite and 11 acacia hosts growing in sympatry across a range of infrapopulation sizes (1–20 mistletoes/host individual). We made 20-min focal plant observations on 27 (10 female and 17 male) desert mistletoes on acacia and 39 (20 female and 19 male) desert mistletoes on mesquite. In order to capture the peak-flowering season of each population, data were recorded on three dates (24 January 2015, 7 February 2015 and 14 February 2015) for acacia-infesting mistletoes and on four dates (1 March 2015, 8 March 2015, 14 March 2015 and 22 March 2015) for mesquite-infesting mistletoes. We observed a single plant across multiple survey dates when flowering duration permitted, for a total of 108 20-min observations. During each observation, we recorded the number of visits by putative pollinator taxa (*Lasioglossum* spp., syrphid flies and other Brachycera, *Apis mellifera* and other dipterans under 2 mm in length). These taxa were chosen because they are known to carry desert mistletoe pollen grains (K. Yule, unpubl. data; Wiesenborn, 2016).

2.4 | Male removal experiment

Host trees infected with desert mistletoe at SR were randomly assigned to male removal treatment and unmanipulated control groups (control: $n = 27$ hosts, male removal treatment: $n = 38$ hosts). All inflorescences from all male desert mistletoe plants in the infrapopulation on hosts in the treatment group were removed prior to flower opening (for a picture of a male desert mistletoe with inflorescences removed see Figure S1). Treatments were applied to mesquite hosts in January 2013 and to acacia and velvet mesquite hosts in December 2015. This treatment allows us to independently assess the role of natural infrapopulation size and the effective adult sex ratio. While prediction 2, that competition for resources obtained from host trees limits reproduction, would best be tested by a pollen addition experiment across varying infrapopulation sizes, the reproductive structures of desert mistletoe preclude this type of manipulation: each adult female desert mistletoe can produce thousands of minute (c. 1 mm diameter) flowers over a period of several months in winter and spring (January–April on acacia hosts; February–May on mesquite hosts) (Yule & Bronstein, 2018b). In the absence of a pollen addition experiment, integrating the observational and experimental work, we present here allows us to test prediction 2 by connecting

pollinator visitation, pollen receipt and offspring production for plants that differ in their potential number of competitors.

On both male removal treatment and unmanipulated control trees, focal female desert mistletoes (1–7 per host) were tagged (control: $n = 60$ desert mistletoes, male removal treatment: $n = 96$ mistletoes). In 2016, 10 open flowers were collected from each focal female individual on 14 February 2016 on acacia and 15 March 2016 on mesquite. The flower collection dates on each host were chosen based on the approximate dates of the maximum proportion of plants flowering and pollen receipt in observational data (Yule & Bronstein, 2018b). The stigmas of each flower were swabbed with fuchsin-dyed glycerin gel to remove stained, deposited pollen grains, which were then counted using a light microscope (100 \times). After fruit ripening initiated, an c. 10 cm long section of branch was collected from each focal female desert mistletoe in February 2014 and November 2016. Fruit set, defined as the proportion of flowers successfully converted to fruit, was assessed by counting failed fruits (c. 0.5 mm craters containing senesced perianths) and successfully pollinated fruits (ripe, unripe or removed fruit).

The proportion of fruits removed was estimated from the number of craters present on the infructescences collected in 2016. Although most seeds from removed fruit will not establish and some are lost to consumption, proportion of fruit removed provides an upper bound for per-fruit probability of being dispersed and establishing. Collections late in the fruiting season (2014) were not used for estimates of fruit removal, as earlier infructescence abscission when all fruits have been removed causes biases that lead to underestimation of fruit removal.

2.5 | Statistical analyses

A non-constant variance score test was used to test if variance in parasite sex ratio, measured as the proportion female (number of females/total number of adult desert mistletoes in the infrapopulation), changes with infrapopulation size. Divergence from 0.5 in the proportion of female desert mistletoes of each site and host species was tested using chi-square tests. To understand the effects of infrapopulation size and mate availability on female fitness, generalized linear mixed effects models were used to analyse all response variables from the male removal experiment and visitation data. Pollen receipt (number of grains present on stigmas) was modelled as a negative binomial response; fruit set (ripe, unripe or removed fruit vs. failed flowers) and fruit removal (removed fruit vs. ripe fruit) were modelled as binomial responses; and pollinator visitation (number of visits in a 20-min observation period) was modelled as a zero-inflated negative binomial response. Models included the random effects of host individual and, for the analysis of pollen receipt, desert mistletoe individual nested within host individual. Host species (by year, when appropriate), treatment (except for with observational visitation data), infrapopulation size (total number adult desert mistletoes infecting host individual), mistletoe sex (for observational visitation data) and interactions between these factors were considered fixed effects in models.

Female desert mistletoes from hosts lacking male parasites were analysed together with those from treated hosts, as they did not differ statistically for any response variable. Host species was included as a fixed effect because desert mistletoes infesting mesquite and acacia are known to form genetically distinct host races (Yule, Koop, Alexandre, Johnston, & Whiteman, 2016) with different reproductive ecologies (Yule & Bronstein, 2018b) that may influence the relationship between intrapopulation characteristics and fitness. Stepwise backwards model selection, comparing nested models by likelihood ratio test, was performed for all response variables (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Sample sizes in the experiment, model selection procedures and best-fitting model results are presented in the electronic supplement (Tables S1–S9). Adjusted McFadden's pseudo- R^2 -values were calculated from the log likelihoods of the selected model and a null, intercept-only model. Analyses were conducted using the lme4 and glmmTMB (for observational visitation data) packages in R version 3.2. (Bates, Maechler, Bolker, & Walker, 2015; Brooks et al., 2017; R Development Core Team, 2014).

3 | RESULTS

3.1 | Sex ratios within natural intrapopulations

Across all hosts and sites, intrapopulations were comprised of 1–43 ($M = 6.95$, variance = 60.55) adult desert mistletoes. The proportion of female individuals within intrapopulations ranged from 0 to 1 ($M \pm SE = 0.46 \pm 0.02$). 871 of the 1,806 (48.22%) desert mistletoes encountered across all intrapopulations were female. The proportion female was notably variable within small intrapopulations (Figure 1a). In larger intrapopulations, the proportion female approached 0.5, as expected if individuals of each sex accumulate at random as intrapopulation sizes increase. This higher variance in proportion female at smaller intrapopulation sizes was evident by significant heteroscedasticity in the relationship between variance in sex ratio and intrapopulation size (non-constant variance test: $\chi^2 = 40.33$, $df = 1$, $p < .001$). Although fewer females than males were present in 4/6 host by site combinations, the proportion of desert mistletoes that were female did not differ significantly from 0.5 (OP: on acacia = 0.44, on mesquite = 0.50; SR: on acacia = 0.54, on mesquite = 0.44; TF: on mesquite = 0.49), except on acacia at TF (0.36; $\chi^2 = 8.33$, $p = .004$; Figure 1b).

3.2 | Pollinator visitation to natural intrapopulations

The number of pollinator visitors during 20-min focal plant individuals varied from 0 to 9 ($M \pm SE = 1.64 \pm 0.19$). Consistent with prediction 3, that vectors may be attracted to large intrapopulations, the number of visits increased with intrapopulation size ($z = 2.40$, $p = .016$). Additionally, pollinator visitation was greater for males ($z = 2.27$, $p = .023$, Figure 2). Although the interaction was not significant, visitation to males increased less than visitation to females as intrapopulation increased (Table S3; Figure 2). Host species did not significantly

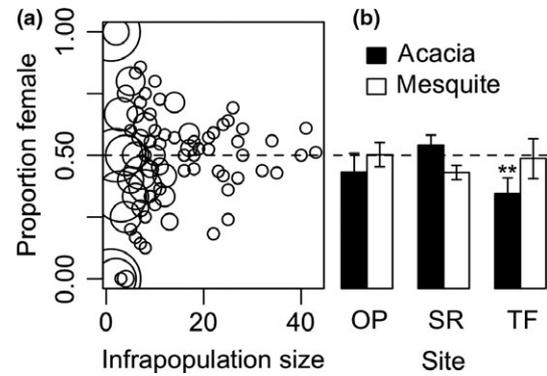


FIGURE 1 The size and proportion female of naturally occurring desert mistletoe intrapopulations. (a) Small intrapopulations vary in proportion female while large intrapopulations approach an even sex ratio. The size of the circle indicates the number of overlapping data points at its center. (b) The proportion female ($M \pm SE$) at a site rarely departs from 0.5. The star indicates a significant difference from 0.5 in the overall proportion female at a site on a given host species (chi-squared test, $p < .01$). The dotted lines represent a proportion female of 0.5. All data are from mesquite and acacia hosts at three sites, abbreviated as follows: OP = Organ Pipe Cactus National Monument; SR = Santa Rita Experimental Range; TF = Tonto National Forest

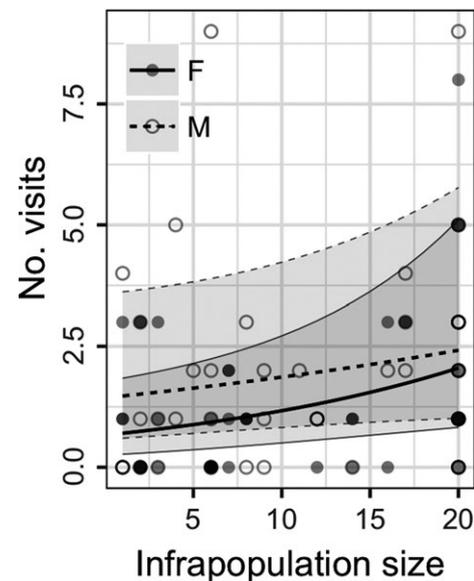


FIGURE 2 The effect of intrapopulation size and plant sex on pollinator visitation to desert mistletoe (*Phoradendron californicum*) individuals. Visitation is measured as the number of visits by putative pollinator taxa during the 20-min focal observation period. Gray areas outlined with gray lines represent the 95% confidence intervals around the predicted relationships, shown with black lines from the Poisson general mixed effect model

affect overall visitation rate (Table S2). The model including the random effect of host individual and the fixed effects of intrapopulation size, mistletoe sex and the interaction between sex and intrapopulation size best explains the variation in pollinator visitation (adjusted pseudo- $R^2 = .11$; Table S2).

3.3 | Relationships among mate availability, infrapopulation size and pollen receipt

Flowers on female desert mistletoes had each received $0\text{--}72$ ($M \pm SE = 3.54 \pm 0.21$) conspecific pollen grains at the time of census. Consistent with prediction 1, that mate availability can limit female success, the presence of reproductive males had a significant positive effect on pollen receipt among females: female flowers on treated hosts received less pollen on average (treatment, $z = -3.071$, $p = .002$; Figure 3a). Consistent with prediction 3, females in larger infrapopulations also received more pollen grains on average per flower than those in smaller infrapopulations (infrapopulation size, $z = 2.999$, $p = .003$; Figure 4a). The model including the fixed effects of treatment and infrapopulation size best explains the variation in pollen receipt/flower (adjusted pseudo- $R^2 = .09$). Host species and interactions between fixed effects did not significantly improve the fit of the model (Table S4).

3.4 | Relationships among mate availability, infrapopulation size and fruit set

Fruit set generally was not positively correlated with pollen receipt. Estimated fruit set varied from 0.19 to 1.00 ($M \pm SE = 0.68 \pm 0.01$). Consistent with prediction 1, the presence of reproductive males had a significant positive effect on fruit set only for desert mistletoes on mesquite in 2014 (treatment \times population effect, $z = -4.092$, $p < .001$; Figure 3b). However, increasing infrapopulation size had a negative effect on fruit set for individuals on mesquite in 2014 (infrapopulation size \times population, $z = -2.807$, $p = .005$; Figure 4b), consistent with prediction 2 that competition for resources obtained from hosts can limit reproductive success. In contrast to the results for pollen receipt, neither male removal treatment nor infrapopulation size were significantly related to fruit set of parasites on either host in 2016 (Figure 3, Figure S2), consistent with prediction 2. Treatment, host species and infrapopulation size did not significantly affect relative fruit set across both years of the experiment

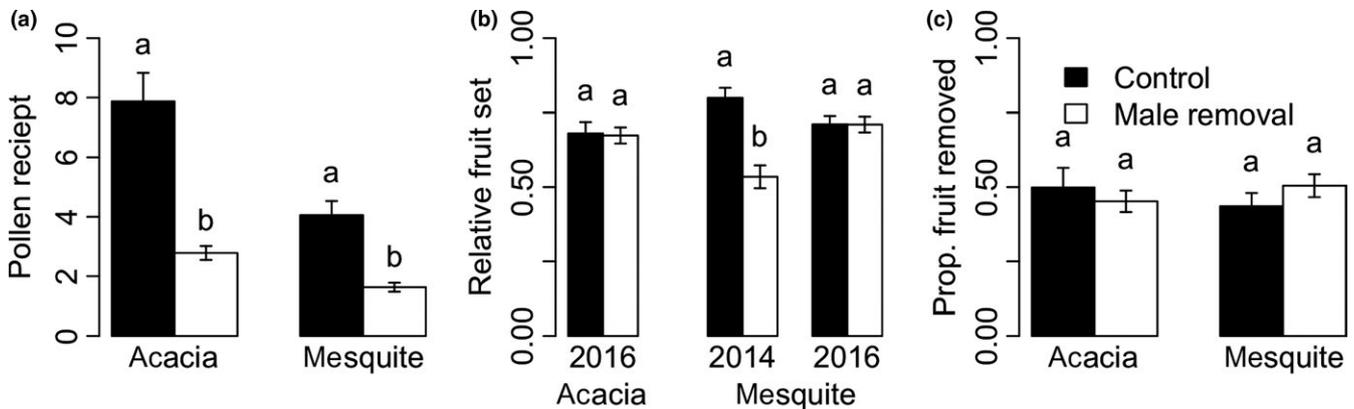


FIGURE 3 The effect of treatment to remove all reproductive tissue from co-infecting males on female reproductive success. (a) Pollen receipt ($M \pm SE$ grains) per flower is lower for females on treated hosts in 2016. (b) Fruit set ($M \pm SE$ proportion of flowers converted to fruit) is lower for females on treated hosts only for those on mesquites in 2014. (c) The proportion of fruit removed ($M \pm SE$) is not affected by treatment in 2016. Lowercase letters indicate significant differences between groups ($p < .05$) from generalized linear mixed models

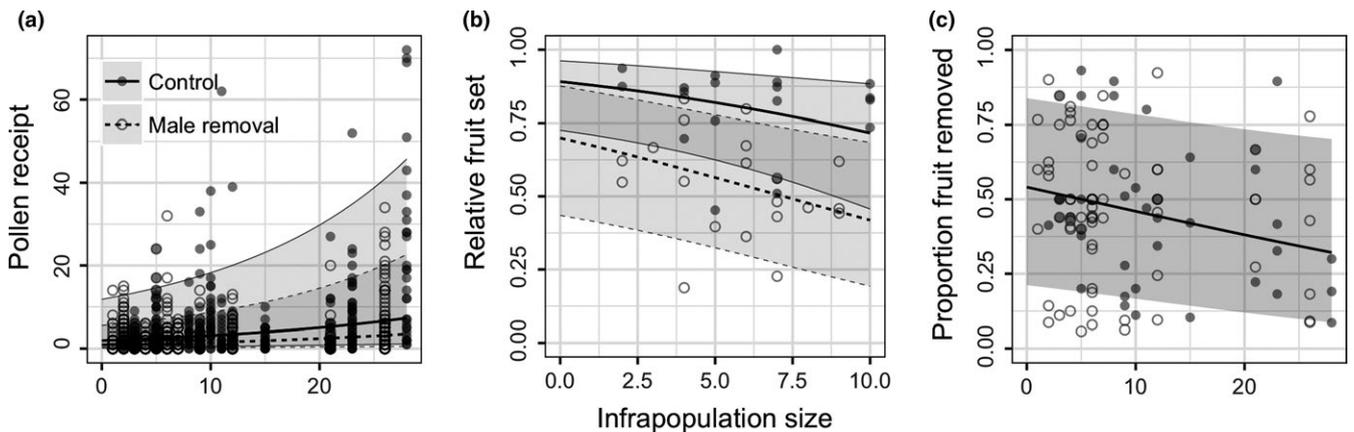


FIGURE 4 The effect of infrapopulation size on female reproductive success. (a) More pollen grains are received by flowers on female mistletoes within larger infrapopulations on both acacia and mesquite hosts in 2016. (b) Fruit set (proportion of flowers converted to fruit) is lower for females within larger infrapopulations on mesquites in 2014. (c) The proportion of fruit removed shows a marginal negative relationship with infrapopulation size on both acacia and mesquite hosts in 2016. Gray areas outlined with gray lines represent the 95% confidence intervals around the predicted relationships, shown with black lines, from the best-fitting generalized linear mixed effect models

combined (Table S6). The model that included fixed effects of treatment, scaled infrapopulation size, species by year combination, the interaction between treatment and species by year combination and the interaction between scaled infrapopulation size and species by year combination best explains variation in relative fruit set (adjusted pseudo- $R^2 = .30$).

3.5 | Relationships among mate availability, infrapopulation size and proportion fruit removal

Estimates of the proportion of fruits removed from female desert mistletoes varied from 0.06 to 0.93 ($M \pm SE = 0.47 \pm 0.02$). There was no significant effect of treatment or host species on fruit removal in 2016 (Figure 2c; Table S8). The proportion of fruit removed showed a non-significant negative trend with infrapopulation size ($z = -1.828$, $p = .0675$; Figure 4c). However, the model that included only the random intercepts by host individual best explained variation in fruit removal (adjusted pseudo- $R^2 = .14$; Table S9). These results provide no support for prediction 3 or 4 that individuals compete within infrapopulations to attract seed dispersers.

4 | DISCUSSION

Infrapopulation size and composition have complex effects on parasites whose fitness depends on the availability of mates and resources as well as upon vector behaviour. Parasitic plants provide a convenient, yet underutilized system for studying the ecological and evolutionary consequences of parasite aggregation. These systems offer three major advantages: parasites can be directly observed, they can be non-destructively manipulated, and their survival and reproductive success can be estimated. We experimentally tested four predictions relating infrapopulation size of female desert mistletoes to vectored transmission of their reproductive propagules. We found that females receive fewer pollen grains when mate availability was experimentally reduced (prediction 1). Yet, mating frequency did not predict offspring production within large infrapopulation sizes, indicating the potential for competition for resources gained from hosts (prediction 2). Larger infrapopulation sizes also had positive effects on per capita transmission of pollen, supporting the prediction that larger infrapopulations can increase attraction of pollen vectors (prediction 3). However, we found no significant effect of infrapopulation size on per capita transmission of seeds by dispersers. Below, we review these findings and highlight gaps in our current understanding of how infrapopulation characteristics influence parasite transmission. We then describe how competition for host resources may influence fitness of parasitic plants. Finally, we hypothesize how interactions among mate availability, vector attraction and competition should influence selection on parasites across different infrapopulations.

Within-host mate availability can influence reproductive success of parasites that mate with the members of their infrapopulation. In our study, the negative effect of male removal on the number

of pollen grains received by flowers on female plants is consistent with within-host mate limitation for parasites on treated hosts. For this species, mating may frequently occur among individuals inhabiting the same infrapopulation, as the pollinators are small insects with short-foraging distances (Herrera, 1987; Waddington, 1979; Wiesenborn, 2016; Yule & Bronstein, 2018b). Indeed, genetic relatedness among desert mistletoes within an infrapopulation can exceed that of nearby conspecifics on different host individuals (Yule et al., 2016). Alternatively, a similar response to male removal could result if males are particularly important for the attraction of vectors to the infrapopulation, such that females within infrapopulations lacking males are visited less frequently. Perhaps because they produce more flowers, larger flowers, more nectar per flower as well as pollen that can attract pollen-consuming insects, male desert mistletoe plants receive more frequent and longer visits from pollinators than do females (Yule & Bronstein, 2018b). While sex-based differences in attractiveness to vectors have not been widely investigated across parasites, sex-based differences in pollinator attraction by dioecious plants are well-documented (Delph, Galloway, & Stanton, 1996; Vaughton & Ramsey, 1998; Waelti, Page, Widmer, & Schiestl, 2009). Released from the need to provision fruit, males may invest more resources in attracting pollinators to the host tree which, once foraging within the infrapopulation, may also visit female plants incidentally. Future work connecting pollen transfer with individual visits by pollinators could determine the relative importance of mate limitation and male-biased vector attraction.

Independent of the composition of the infrapopulation, infrapopulation size can influence parasite fitness through its effect on interactions with vectors. The relationship between vector attraction and desert mistletoe infrapopulation size is complex, as indicated by positive effects at pollen receipt and the potential for negative effects at fruit removal of increasing infrapopulation size. In free-living plants, plant density can have positive or negative effects on pollination (reviewed in Ghazoul, 2005) and seed dispersal (Carlo & Morales, 2008; Saracco et al., 2005; Sargent, 1990). In our study, increasing infrapopulation size, analogous to increasing plant density, had a positive effect on both visitation rate by pollinators and pollen receipt, independent of the presence of reproductive males. This pattern may be due to pollinators visiting proportionally more flowers in a larger patch, as predicted by optimal foraging theory and seen in a variety of free-living plant systems (Cheptou & Avendaño, 2006; Cresswell & Osborne, 2004; Essenberg, 2012). In contrast, the proportion of fruit removed decreased marginally with infrapopulation size. Although the relationship between infrapopulation size and the proportion of fruit removed by dispersers was not statistically significant, a qualitatively similar but statistically significant relationship was found in a previous study of the same mistletoe species (Larson, 1996). In that study, dispersers spent more time on host trees with more female desert mistletoes, but per capita fruit removal decreased with infrapopulation size. Therefore, while female mistletoes within an infrapopulation may facilitate each other in the attraction of pollinators, and mistletoe infection is positively related to disperser activity on hosts (Aukema & Martinez del Rio,

2002b; Carlo & Aukema, 2005; Martinez del Rio et al., 1996; Medel et al., 2004; Mellado & Zamora, 2016), female individuals apparently compete within hosts for the attention of seed dispersers. It should be noted that in other mistletoe systems, other factors, such as the fruiting phenology of hosts or the presence of other food sources, can be the primary drivers of mistletoe disperser activity (Caraballo-Ortiz, Gonzalez-Castro, Yang, dePamphilis, & Carlo, 2017; Ladley & Kelly, 1996).

Our study highlights the interaction between intrapopulation size and transmission, a poorly studied component of our understanding of the fitness consequences of parasite aggregation. Although a number of studies have studied these relationships in parasites transmitted either trophically (Dianne, Bollache, Lagrue, Franceschi, & Rigaud, 2012; Franceschi, Bauer, Bollache, & Rigaud, 2008; Lafferty & Morris, 1996; Leung, Keeney, & Poulin, 2010) or socially (Johnson et al., 2011), the response of biotic vectors to differing intrapopulations has received little attention. In our system, parasites in larger intrapopulations gain more from increased vector attraction than they lose to competition for vector services. Parasite or pathogen presence itself has been seen to increase vector visitation to hosts in insect-vectored plant bacteria and viruses (Casteel & Falk, 2016; Mann et al., 2012; Mauck, De Moraes, & Mescher, 2010; Orlovskis & Hogenhout, 2016) and malaria (Kelly et al., 2015; Lacroix, Mukabana, Gouagna, & Koella, 2005). However, we do not yet know whether larger intrapopulations of other parasites are generally better able to attract vectors than small intrapopulations and, if so, to attract enough vector attention to override competition for services.

Increases in visitation by vectors do not necessarily translate into fitness benefits when parasite reproduction is limited more by resources gained from hosts than by transmission of propagules. While pollen receipt and pollinator visitation increased with the presence of males and larger intrapopulation sizes, female desert mistletoes in 2016 could not translate these benefits into higher fruit set. In contrast, in 2014, female desert mistletoes produced proportionately more fruit in the presence of reproductive males, but a decreasing proportion of fruit as intrapopulation size increased. These results, analogous to pollen addition studies that fail to find pollen limitation, provide evidence that parasites in large intrapopulations are limited by resources rather than mating opportunities (Ashman et al., 2004). As the fitness estimates here are measured per flower, the negative effect on fruit set of sharing a host will be magnified when competition for resources also limits flower production or plant growth rate, as has been demonstrated in other mistletoes (Queijeiro-Bolaños et al., 2017). However, more mating opportunities (greater pollen receipt) may represent a fitness benefit to females even in the absence of greater offspring production when females can selectively provision offspring (Marshall & Folsom, 1991; Sakai, 2007). Just as outcrossing rates can increase with free-living population density (Karron, Thumser, Tucker, & Hessebauer, 1995), the presence of more male partners within the host could decrease inbreeding depression (Nadler, 1995). In this case, co-occurring in an intrapopulation with females will also positively influence male fitness through siring success, even if those females

are able to produce fewer fruit per capita. However, alternative explanations for decreasing fruit set with increasing intrapopulation size, such as declines in host quality or increased inbreeding between co-infecting relatives with increasing intrapopulation size, cannot be discarded and merit future investigation.

Desert mistletoes benefit from sharing a host with some members of the opposite sex, although resource competition among parasites in large intrapopulations apparently reduces their reproductive success. Relatively small intrapopulations, but not so small as to prevent mating, are adaptive for many other parasite species as well, even if they are not generally common in nature (Shaw & Dobson, 1995). For long-lived desert mistletoes, intrapopulation size and mate availability are dynamic. Over time, desert mistletoes, especially those that colonize a host early in its infection, will share a host with an increasingly large intrapopulation of progressively more even sex ratio. Much research has focused on the ability of some animal parasites to influence characteristics of their offspring based on intrapopulations they are likely to inhabit, such as by adjusting their sex ratios or investment in male and female reproductive structures based on intrapopulation characteristics (Ryder & Griffin, 2003; Shuker, Pen, Duncan, Reece, & West, 2005; Trouve et al., 1999; Warren, 1980). Systems such as mistletoe, in which parents have little control over the type of intrapopulation that their offspring will inhabit, may be more common in nature, especially when vector transmission is required. For such systems, future studies should investigate plasticity in response to intrapopulation characteristics. Desert mistletoes that arrive first to a host may experience strong mate limitation even if they invest heavily in reproductive tissues; yet, these individuals will suffer little from resource competition before other individuals arrive. Selection should therefore be expected to increase allocation to growth in early arriving individuals, such that their increased size will afford them a reproductive advantage as more members of the intrapopulation accumulate through time. A prior study of desert mistletoe found no relationship between number of parasites per host and fruit production per volume of fruiting desert mistletoe (Larson, 1996). That result is consistent with our study, which showed decreased flower to fruit conversion in larger intrapopulations, only if mistletoes in larger intrapopulations produce more flowers per unit plant volume. Similarly, studies of another *Phoradendron* mistletoe have found increasing allocation to reproduction, including carbon and nitrogen to seed production, with age (Dawson & Ehleringer, 1990, 1991). Together, these results indicate the potential for mistletoes to increase resource allocation to reproduction relative to growth as intrapopulation size increases. Future work should investigate the evolutionary and plastic responses of parasites to interactions among competition, mate limitation and vector attraction within intrapopulations.

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AUTHORS' CONTRIBUTIONS

K.M.Y. designed and conducted the study and analysed the data; K.M.Y. and J.L.B. wrote the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.m2763r3> (Yule & Bronstein, 2018a).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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