WHERE DOES A FRUIT-EATING BIRD DEPOSIT MISTLETOE SEEDS? SEED DEPOSITION PATTERNS AND AN EXPERIMENT

JULIANN E. AUKEMA[1,3] AND CARLOS MARTÍNEZ DEL RIO[2]

[1]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA*
[2]*Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071-3166 USA*

Abstract. The distribution of desert mistletoes (*Phoradendron californicum*) among mesquite (*Prosopis velutina*) hosts is significantly aggregated. We hypothesized that the aggregation of mistletoes among hosts is produced by the pattern of seed rain generated by seed dispersers. We tested whether frugivorous Phainopeplas (*Phainopepla nitens*) foraged preferentially, and hence deposited mistletoe seeds disproportionately, in already parasitized mesquites. We found that Phainopeplas favored parasitized tall trees as perching and feeding sites and deposited mistletoe seeds disproportionately on trees with these characteristics. To assess experimentally the effect of the presence of mistletoes on seed deposition, we removed mistletoes from host trees. Before mistletoe removal, seed deposition was equivalent and temporally correlated in pairs of control and removal trees. After removal, deposition was lower into removal trees than into unmanipulated trees. Although mistletoe removal resulted in lower seed deposition, it did not eliminate it. We inferred that seed deposition into parasitized hosts can result from deposition of seeds originating from within a host and from other infected hosts. We conclude that the response of seed-dispersing birds to mistletoes leads to disproportionate seed deposition into already parasitized trees and that the heterogeneous distribution of seeds among hosts created by birds contributes to the clumped distribution of mistletoes among hosts.

Key words: aggregated spatial distributions; desert mistletoes; directed dispersal; foraging; frugivory; habitat use; parasitism; Phainopepla nitens; Phoradendron californicum; Prosopis velutina; *seed dispersal; velvet mesquites.*

INTRODUCTION

The association between mistletoes and birds has been chronicled since ancient times by Aristotle, Pliny, and Virgil. The Roman proverb ''Turdus sibi malum cacat'' (the thrush defecates its own misfortune) vividly highlights the irony of capturing thrushes with the sticky mucilage produced by mistletoes that are dispersed by the same thrushes (Browne 1646). Today, it is well known that most mistletoe seeds are dispersed by birds, many of which are highly specialized for consumption of their berries (Kuijt 1969, Reid et al. 1995). Mistletoes are one of the classic examples of directed dispersal because their potentially coevolved (Reid 1991) avian dispersers disproportionately deposit their seeds in narrowly defined (host species, branch diameter) safe sites (Reid 1989, Sargent 1995, Wenny 2001). Although this relationship is well known, its effect on the distribution of these parasitic plants has not been quantified.

The distribution of mistletoes, like that of many other macroparasites, is aggregated among hosts (Overton 1993, Donohue 1995, Aukema and Martínez del Rio 2002*a*), and seed deposition is higher in trees that are

already parasitized by mistletoes (Martínez del Rio et al. 1996, Aukema and Martínez del Rio 2002*a*, *b*). In many species of mistletoes, infection and seed deposition rates are greater in taller or larger trees (Donohue 1995, Martínez del Rio et al. 1996, Reid and Stafford Smith 2000, Aukema and Martínez del Rio 2002*a*, *b*). In macroparasites other than mistletoes, aggregation within hosts has been ascribed to differences in host susceptibility and/or to variation in infection rates among different host age classes (Anderson and Gordon 1982, Pacala and Dobson 1988). Although these two processes may also lead to aggregation in mistletoe populations, we postulate a third non-exclusive hypothesis. Because mistletoes are mutualists of their avian vectors, the fruit produced by mistletoes may attract fruit-eating birds to already parasitized host trees, causing the observed disproportionate mistletoe seed rain into these hosts and consequent reinfection of these hosts (Martínez del Rio et al. 1996). The deposition of mistletoe seeds into already infected hosts may be an example of directed dispersal (Wenny 2001). The system in which we examined this hypothesis is the desert mistletoe (*Phoradendron californicum*).

The desert mistletoe is a dominant feature of the Sonoran desert, where it parasitizes legume trees. Because it is one of the few berries abundant during the winter, the desert mistletoe is an important resource for many birds (Cowles 1936). However, this parasitic

plant is most closely associated with Phainopeplas (*Phainopepla nitens*, silky flycatcher family), which are its most effective dispersers (Larson 1996). These birds are found in the desert only during the winter, when mistletoes are fruiting (Chu and Walsberg 1999). Like many birds that specialize on mistletoes (Reid et al. 1995), Phainopeplas have specialized digestive systems that allow them to process hundreds of mistletoe berries in a day (Walsberg 1975, Chu and Walsberg 1999). Male and female Phainopeplas defend separate territories prior to courtship and nesting, and use conspicuous perching as a territorial display throughout the season (Walsberg 1977, Chu 1999). This behavior led us to predict that Phainopeplas would perch preferentially on tall, and hence more visible, host trees.

We examined patterns of mistletoe infection and seed deposition and documented the movement of Phainopeplas among host trees in a study plot in which all trees were mapped. Because we had detailed information about the height and the number of mistletoes in each tree, we were able to investigate the factors that determine the use of different hosts by Phainopeplas. We found that Phainopeplas visited infected tall trees preferentially. To investigate whether the presence of mistletoes leads to differential seed deposition, we removed mistletoes from host trees and compared seed deposition into these manipulated trees with that into neighboring unmanipulated trees.

METHODS

We studied mistletoes, mesquites, and Phainopelas at the Santa Rita Experimental Range in southern Arizona, USA (31°53′ N, 110°54′ W). The range is in semidesert grassland scrub at the foothills of the Santa Rita Mountains (Burgess 1995). Our study site was located in a grassy savanna with large stands of velvet mesquite (*Prosopis velutina*) that have apparently invaded the area over the last 100 yr (Martin and Turner 1977, Medina 1996). During the winter and spring of 2000, we observed Phainopepla movements on a 4-ha plot in which all of the trees were tagged and mapped, and in which the height, number of mistletoes, and number of deposited seeds had been recorded (details can be found in Aukema and Kunzmann 2000). Seeds per tree were recorded once, at roughly the middle of the mistletoe fruiting season (2–9 February 2000). We located Phainopeplas by sight or sound and recorded the identity of the tree in which they perched. We actively looked for Phainopeplas throughout the plot to ensure coverage of the entire area, and we observed both males and females. We followed individual birds for observation bouts that lasted from 2 to 75 min. We followed them until we lost them, until they left the plot's boundary, or until they were repeatedly returning to the same trees. In these bouts, we recorded the identity of, and the time spent in, each of the trees in which they perched or fed on mistletoes. Because all host trees in the plot were mapped, we were able to calculate

Phainopepla flight distances among trees and to determine the characteristics (such as height and number of mistletoes) of the trees in which they were observed perching and feeding.

On 19 and 20 October 1999, we chose eight pairs of mistletoe-infected mesquite trees. Pairs were in the same upland neighborhood, within 30 m of each other, and were matched by height (we chose tall trees, 4.2 ± 0.35 m, mean ± 1 SD, $N = 16$) and parasite load (we chose trees with a heavy parasite load, 21.1 ± 5.7 mistletoes per tree, $N = 16$). We chose 10 branches on each tree. Because seed rain within a tree is not uniform, we selected branches that had received seeds before the beginning of the experiment. We counted and removed the seeds on each of these branches approximately weekly for six weeks. On 28 December 1999, all of the mistletoes were removed from one randomly selected tree of each pair (the ''removal'' tree). We removed mistletoes by pulling down mistletoe foliage by hand or with clippers. Mistletoe branches snap off very easily at the place where they make contact with their host, leaving only the haustorial connection. While we removed mistletoes from a removal tree, another group of volunteers disturbed the control tree by climbing, shaking, and shouting insults at it. After mistletoe removal, we returned to count and remove seeds on the marked branches of both the removal and control trees approximately once per week (seven times) until the end of February. We then did a final count on 11 April. There was very little growth of the removed mistletoes during the treatment period and any mistletoe foliage observed on manipulated trees was immediately removed.

Seed deposition data were not normally distributed, so they were natural-log-transformed. Log-transformed data were normally distributed and had homogeneous variances. We used profile analysis to examine post-removal repeated-measures seed deposition data (SAS procedure GLM, REPEATED; SAS Institute 1989). Profile analysis is a method of using multivariate ANOVA to analyze repeated-measures data. It allows one to address hypotheses about the shapes, levels, and slopes of response curves after a manipulation (von Ende 1993). We also compared seed deposition between removal and control trees at each date, using one-tailed paired *t* tests adjusted with a Bonferroni correction (Ramsey and Schafer 1997).

RESULTS

Patterns of distribution of mistletoes and mistletoe seeds

We counted and marked 887 potential host trees in the plot. Although the vast majority of these trees were velvet mesquites (826), the plot included a few cat's claw acacias (*Acacia greggii*, 49 individuals), and palo verdes (*Cercidium* spp., 12 individuals). The analyses presented here were conducted on mesquites exclu-

sively. About 28% of all mesquites (232 individuals) were infected by mistletoes. The spatial distribution of mistletoes among hosts is discussed in more detail in Aukema (2001). Mesquites had, on average, 1.8 ± 4.7 mistletoes per host (all data are expressed as mean $\pm$ 1 SD) and the maximal number of mistletoes found in a tree was 54. The distribution of mistletoes per host was very strongly aggregated (Fig. 1). Mistletoes had an aggregated distribution even among large (>3 m tall) individuals (Fig. 1).

Both the number of mistletoes per tree and the probability that a host tree was infected increased with the height of the host tree (Fig. 2). Likewise, both the probability that a host tree would receive seeds (Fig. 3) and the number of seeds received per tree increased with host height ($r_S = 0.8$, $N = 760$). Fig. 3 illustrates the probability of receiving seeds as a function of both host tree height and the number of mistletoes present on the host. A logistic regression analysis indicated that both height and mistletoe number had a significant positive effect on the probability of seed deposition ($\chi^2_{height} = 51.1$ and $\chi^2_{mistletoes} = 26.1$, $P < 0.001$). In addition to the direct effects of host height and mistletoe load, we also found a small, but statistically significant, negative effect of their interaction on the probability of seed deposition ($\chi^2_{interaction} = 28.0$, $P < 0.001$; Fig. 3). Because seed number increased with both height and mistletoe number, the distribution of seeds among trees was very aggregated (Fig. 1). More than half of all trees did not receive seeds, but 10 individuals received more than 1000 seeds (Fig. 1).

Seed disperser perching patterns and flight distances

Phainopeplas perched primarily in *Prosopis velutina*, the dominant host species of *Phoradendron californicum* (256 observations). We observed them perching in *Acacia greggii* only three times, and occasionally in hackberry bushes (*Celtis pallida*, 45 observations). Although seeds were often deposited in hackberry bushes, we have never observed mistletoe infections in them. Phainopeplas perched in a nonrandom subset (114 individuals) of the 826 mesquite trees available. The probability that a tree would be visited in the plot increased with both the height of the tree and with its mistletoe load (logit(p) = -4.48 + 0.75[height] + 0.11[number of mistletoes]; $\chi^2_{height} = 65.2$, $\chi^2_{mistletoes} = 25.8$, $r^2 = 0.3$, $P < 0.001$). Consequently, the trees used by Phainopeplas as perches and feeding sites were taller (4.2 ± 1.5 m) and had a higher number of mistletoes (6.4 ± 7.1 mistletoes per tree) than those not used (mean height 2.3 ± 1.2 m, mean mistletoe number 1.4 ± 3.7; $t > 12.5$, $P < 0.001$). Although only 28% of the trees on the plot were parasitized, 79% of the trees used by Phainopeplas were parasitized.

Phainopepla flight distances had a right-skewed distribution ($g_1 = 1.1$, $P < 0.001$, $N = 144$). Although most flights were fairly short (half of the flights were <25 m), a few flights were long (>120 m; Fig. 4).
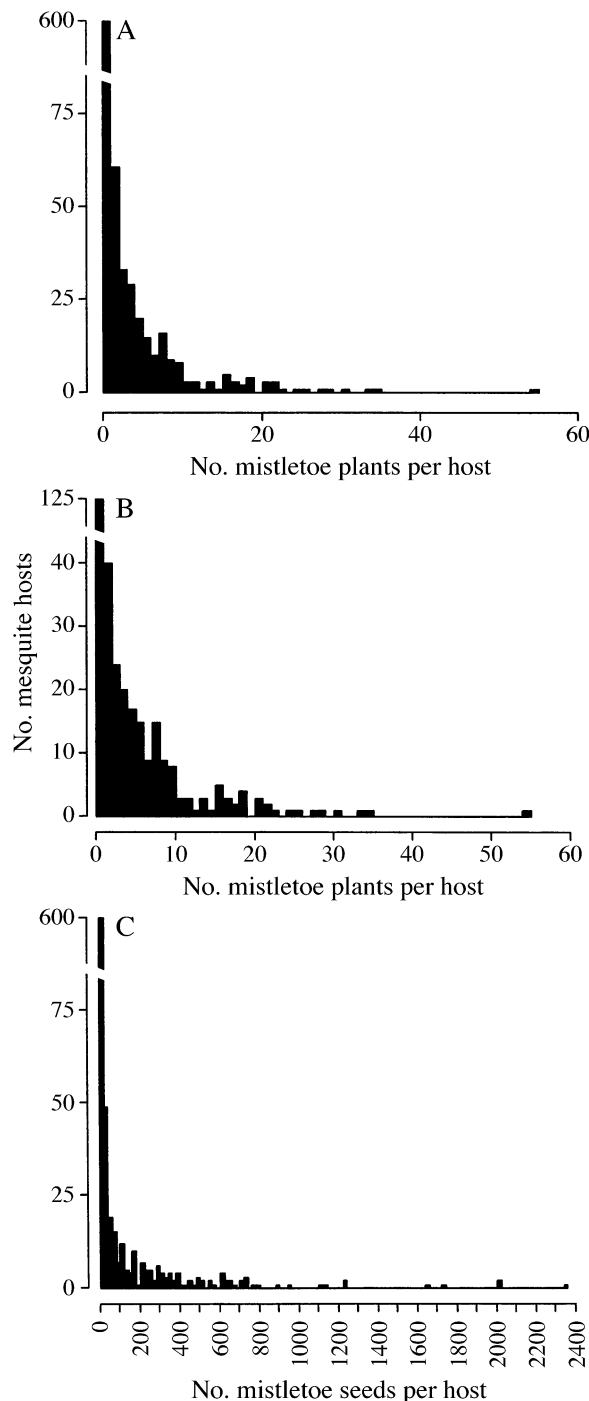

Fig. 1. (A) The distribution of desert mistletoes (*Phoradendron californicum*) among velvet mesquite (*Prosopis velutina*) hosts, showing that plants and seeds are highly aggregated; variance/mean = 12.3, negative binomial's $k = 0.2$, $N = 816$. (B) Because small trees are never infected and may bias our estimation of aggregation, we investigated aggregation in tall mesquites (>3 m) which are frequently infected. Mistletoes show an aggregated distribution among this restricted subsample as well (variance/mean = 10.3, negative binomial's $k = 0.5$, $N = 303$). (C) The distribution of seeds deposited by birds on mesquites also is highly aggregated; variance/mean = 685.5, negative binomial's $k = 0.1$, $N = 762$.

However, because long-distance flights were more difficult to follow, long flights were probably undersampled. Visits to trees were usually brief (2.6 ± 2.9 min, $N = 116$), but one bird spent 13 min in a tree (Fig. 4).

Effect of mistletoe removal on seed deposition

There was no significant difference in the height of removal and control trees (paired $t_7 = 0.1$, $P = 0.899$) or in the initial number of mistletoe infections (paired $t_7 = 0.5$, $P = 0.616$). Seed deposition before mistletoe removal did not differ between treatments ($t_7 = 1.4$, $P = 0.196$). After mistletoe removal, however, removal trees received fewer seeds than control trees ($F_{1,14} = 25.8$, $P = 0.0002$; Fig. 5). Seed deposition varied over time ($F_{7,8} = 4.8$, $P = 0.0001$; Figs. 5 and 6) and there was a time by treatment interaction ($F_{7,98} = 2.3$, $P = 0.035$). Seed deposition into removal trees was significantly greater in the first week after removal than in the following week (paired $t_7 = -3.00$, $P = 0.01$; Fig. 5). Before mistletoe removal, the number of seeds deposited per branch per week was highly temporally correlated between removal and control trees. The correlation coefficient (mean ± 1 SD) in seed deposition for the eight pairs of trees was significantly positive ($\bar{r} = 0.8 \pm 0.2$, $t = 11.6$, $P < 0.001$, $N = 8$ tree pairs and 6 wk/pair). Fig. 6 shows the temporal correlation in seed rain for only one pair of trees. After mistletoe removal, this correlation broke down as a result of the sharp decrease in seed deposition into trees from which mistletoes had been removed. Indeed, the mean correlation in seed rain between pairs was not significantly different from 0 ($\bar{r} = 0.2 \pm 0.3$, $t = 2.0$, $P > 0.1$, $N = 8$ tree pairs and 8 wk/pair; Fig. 6). Although seed deposition decreased after mistletoes were removed, all manipulated trees continued to receive seeds for the duration of the experiment. Manipulated trees received an average of 0.9 seeds deposited per branch per tree per week after mistletoes were removed, but they received 3.0 seeds per branch per tree in the week immediately after the removal (Fig. 5).

DISCUSSION

Our results strongly supported our hypothesis that mistletoe infection and host tree height serve as perching and feeding cues for Phainopeplas. Seed deposition was higher in infected than in non-infected trees. Seed deposition increased with the number of mistletoes per host tree and with the height of host trees. This pattern appears to be a direct consequence of the perching preferences of the seed-dispersing birds. Phainopeplas perched more frequently in parasitized trees than in unparasitized trees. In addition, the trees in which Phainopeplas perched were taller than the average of those trees available. Interestingly, we did find a slight negative interaction between tree height and number of mistletoes on seed deposition. In addition, few uninfected 4–5 m trees received seeds (Fig. 3) and a small percentage of 4–6 m trees were infected (Fig. 2). We
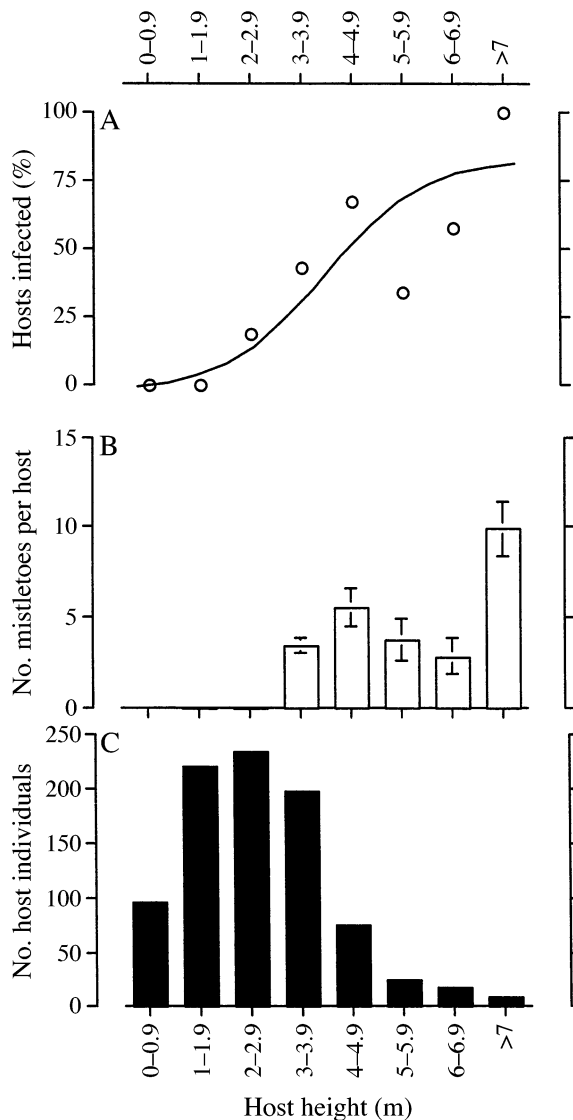

FIG. 2. (A) A logistic regression model indicating that the probability that a velvet mesquite (*P. velutina*) tree would be parasitized by desert mistletoes (*P. californicum*) increases significantly with host tree height ($\chi^2 = 165.2$, $P < 0.001$, $N = 814$). For clarity, host tree heights are pooled in 1-m intervals in all panels. The curve in (A) is the fitted logistic relationship (logit(p) = $-4.72 + 1.34$[height], $r^2 = 0.3$). (B) The number of mistletoes per host also increases with host height ($r_S = 0.6$, $P < 0.001$, $N = 814$). Of the 236 trees in the third height class (2–2.9 m), 19% were parasitized, but there were only 0.05 ± 0.1 mistletoes per tree (mean ± 1 SE) because of the large number of trees that were not infected. Panel (C) shows the height distribution of velvet mesquites at our study site.

do not have an adequate explanation for these perplexing patterns. The results of our mistletoe removal experiment provided additional support for the observation that seed dispersers perched more frequently in parasitized trees. They also provided clear evidence in favor of the idea that the presence of mistletoes dictates
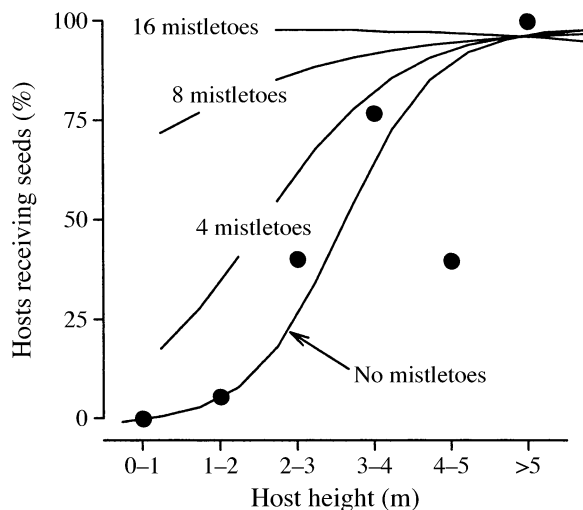
FIG. 3. The percentage of hosts receiving mistletoe seeds, shown as increasing with both host height and the number of mistletoes. The curves are logistic regression estimates of the probability of receiving seeds for hosts, with the number of mistletoes indicated. Points are shown only for hosts with no mistletoes. Curves were constructed with the following equation: $\text{logit}(p) = -4.75 + 1.66[\text{height}] + 1.65[\text{no. mistletoes}] - 0.24[\text{height}][\text{no. mistletoes}]$; $r^2 = 0.5$.

the magnitude of the deposition of mistletoe seeds on tree hosts. Mistletoe removal greatly decreased seed deposition.

Although removal had a strong effect on seed rain, birds showed a significant lag in their response to mistletoe removal (Fig. 5). Rates of seed deposition onto manipulated trees were slightly higher a week after the experiment than they were later, and there was no difference in deposition between removal and control trees in the first week after removal. It is possible that Phainopeplas not only use mistletoe plants as cues in their perching and foraging decisions, but also rely on the memory of expected food availability in local trees. Because there were no seed sources in manipulated trees, the observation of seed deposition on them indicates that inter-host dispersal of mistletoe seeds was common (Fig. 5). The disproportionate presence of seeds in already infected hosts has been interpreted as the result of intra-host infections (Overton 1994). However, the amount of time that Phainopeplas spent in a tree (mean 2.6 min; Fig. 4B) was shorter than the 12–45 min that it takes for an ingested seed to pass through the digestive tract (Walsberg 1975). The short time spent in each host tree suggests that most intra-host dispersal occurs when Phainopeplas return to a host tree from forays into other trees. Our results suggest that intra-host dispersal is not the only source of seeds into an infected host. Inter-host dispersal probably plays an important role as well, but given the short flight distances that we observed (Fig. 4A), most inter-host dispersal probably takes place among neighboring trees. Only genetic analyses of mistletoes and deposited

seeds can clarify the relative contribution to total seed deposition of seeds produced by mistletoes within a host vs. those from other hosts (Ouborg et al. 1999, Cain et al. 2000).

Because tree pairs were within close proximity of each other, the temporal correlation in seed deposition between pairs of tree hosts before mistletoe removal indicates that neighborhood characteristics are important in determining seed deposition. Habitat selection by birds has been described as a hierarchical spatial
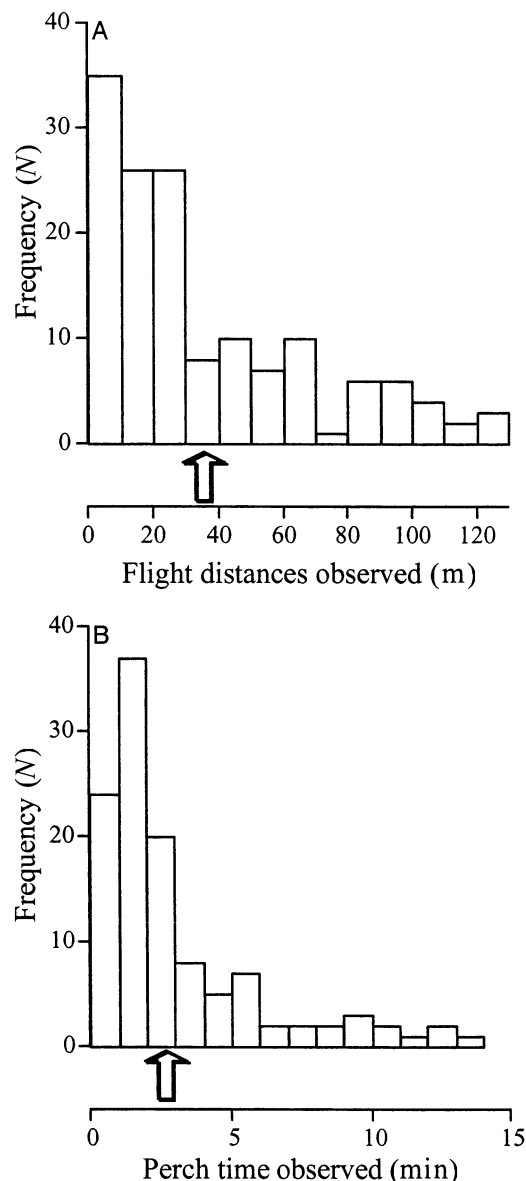

FIG. 4. The frequency distribution of Phainopepla flight distances and perching duration. (A) Phainopeplas made mostly short flights among host trees and (B) spent a relatively small time in each host. The time spent in each host was nearly always shorter than the 12–45 min that it takes for an ingested seed to pass through the digestive tract (Walsberg 1975). Arrows indicate means.
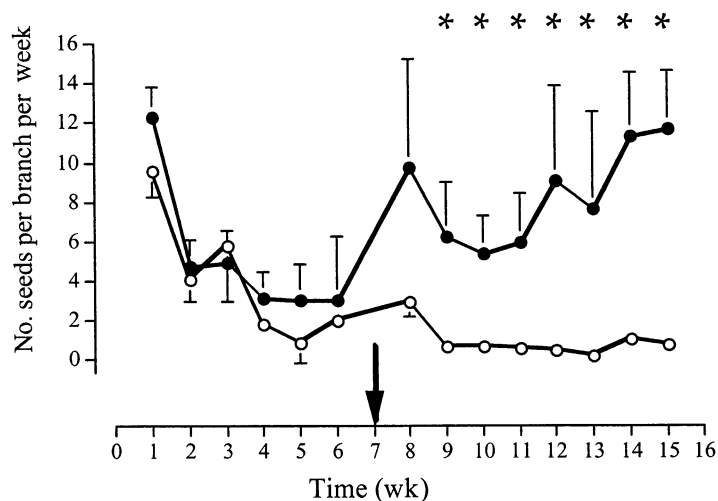
FIG. 5. Density of mistletoe seeds on hosts over time. Seed deposition (mean $\pm$ 1 SE, $N =$ 8 trees) decreased significantly after mistletoes were removed from host trees (open circles) relative to that in trees from which mistletoes were not removed (solid circles). Mistletoes were removed from experimental trees in week 7 (indicated by the arrow). Asterisks indicate those weeks for which there were significant differences (Bonferroni-corrected one-tailed paired t tests, $P < 0.05$) between seed deposition into removal and control trees. Note that there was no difference in seed deposition in the week immediately following removal.

process that ranges from choice of food items in a patch to choice of home range in a landscape (Johnson 1980). Different environmental cues may be responsible for decisions at different scales (Johnson 1980, Rolstad et al. 2000). One can envision a Phainopepla making selections of home range based on overall abundance of mistletoes in an area. These home ranges or territories may be the cause of the correlation in seed deposition between paired trees prior to mistletoe removal. At another scale, a Phainopepla might select feeding sites based on the presence of mistletoes in a given tree. This mechanism is probably responsible for the reduction of seed deposition after mistletoes are removed.

In summary, our results support the idea that the foraging and perching behavior of seed-dispersing birds generates an aggregated distribution of seeds among host trees. Tall, already parasitized trees receive a disproportionate fraction of the total seed rain. Similar patterns have been found in other mistletoes as well: larger trees and previously infected trees receive more seeds (Martínez del Rio et al. 1996). The response of seed-dispersing birds to the presence of mistletoes in host trees may be one of the mechanisms through which these birds perform directed dispersal (Wenny and Levey 1998). If germination success is assumed to be equal in all hosts, then it follows that already parasitized trees will be reinfected more often than nonparasitized trees are infected. Thus mistletoe individuals will accumulate in already infected trees, leading to aggregation (Donohue 1995, Reid and Stafford Smith 2000, Aukema and Martínez del Rio 2002*a*). Although this scenario is plausible and it is tempting to attribute the aggregation of mistletoes solely to this positive feedback, it is probably premature to blame the birds exclusively. The spatial distribution of plants is the result of both dispersal and establishment success (Herrera et al. 1994, Schupp 1995, Nathan and Muller-Landau 2000). We do not have data on the relative
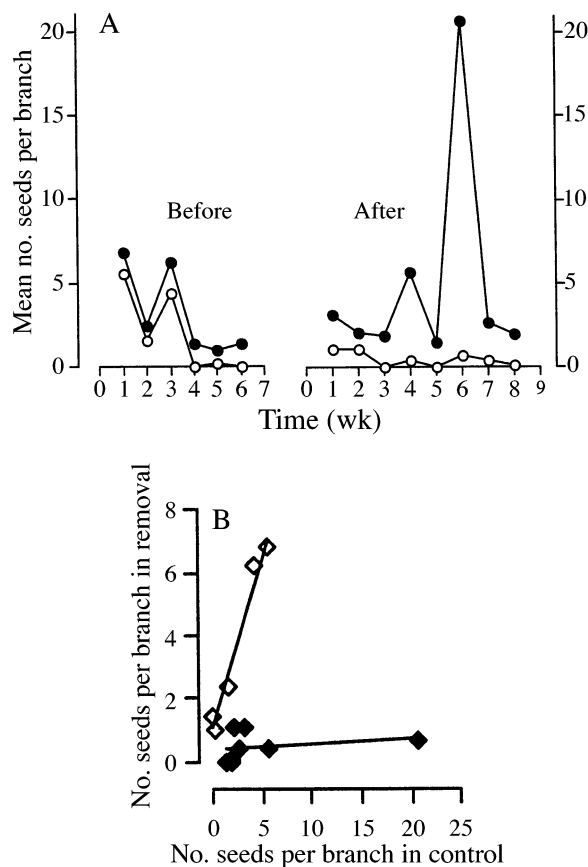

FIG. 6. Density of mistletoe seeds on one pair of hosts over time before and after removal. Seed deposition was temporally correlated between removal and control trees before removal (left of panel A and open diamonds in panel B; $r =$ 0.98, $P < 0.05$ for the example illustrated). After removal, however, this correlation disappeared (right of panel A and solid diamonds in panel B; $r = 0.24$, $P > 0.1$).

success with which mistletoes become established and persist among different host individuals.

Differences in susceptibility among plant hosts produce differences in performance and local abundance among herbivorous insects; see Cobb et al. (1997) and references therein. Thus, differences in susceptibility can lead to the aggregation of natural enemies among host plants. In some mistletoe–host systems, variation in susceptibility of host plants to mistletoe infection has been documented (Sallé et al. 1993, Snyder et al. 1996), and it may be that both susceptibility and seed dispersal play a role in creating aggregation. Although the relative roles of these two processes are unknown, if there are differences in susceptibility among hosts, these differences probably act together with, and indeed are reinforced by, differential seed dispersal to produce aggregation. If susceptible individuals are those that host the largest numbers of mistletoes, they also will be the ones receiving the most mistletoe seeds, strengthening the contagious distribution.

Our results suggest that birds shape the distribution of the resources that they will use in the future. Rather than sowing their own misfortune, we propose the following contemporary rendition of the Roman proverb to more ecologically portray the interaction between birds and mistletoes: ''Phainopepla sibi segetem futuram cacat'' (the Phainopepla defecates its own future harvest). Indeed, the birds that disperse mistletoe seeds defecate their own future bounty.

Literature Cited

Anderson, R. M., and D. M. Gordon. 1982. Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. Parasitology **85**:373–398.

Aukema, J. E. 2001. Dispersal and spatial distribution of the desert mistletoe, *Phoradendron californicum*, at multiple scales: patterns, processes and mechanisms. Dissertation. University of Arizona, Tucson, Arizona, USA.

Aukema, J. E., and M. R. Kunzmann. 2000. The use of GPS and GIS tools to help document the spread of desert mistletoe (*Phoradendron californicum*), a plant parasite in Arizona. 20th Annual ESRI User Conference Proceedings: 521. [Online, URL: ⟨http://gis.esri.com/library/userconf/proc00/professional/papers/PAP521/p521.htm⟩.]

Aukema, J. E., and C. Martínez del Rio. 2002*a*. Mistletoes as parasites and seed-dispersing birds as disease vectors: current understanding, challenges, and opportunities. Pages 99–110 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed dispersal and frugivory: ecology, evolution and conservation. CAB International Press, Oxfordshire, UK.

Aukema, J. E., and C. Martínez del Rio. 2002*b*. Variation in mistletoe seed deposition: effects of intra- and interspecific host characteristics. Ecography **25**:139–144.

Browne, Sir Thomas. 1646. Pseudodoxia epidemica, or, Enquiries into very many received tenents and commonly presumed truths. Printed by T. H. for Edward Dod, London, UK.

Burgess, T. L. 1995. Desert grassland, mixed shrub savanna, shrub steppe, or semidesert scrub? The dilemma of coexisting growth forms. Pages 31–65 *in* M. P. McClaran and T. R. Van Devender, editors. The desert grassland. University of Arizona Press, Tucson, Arizona, USA.

Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany **87**:1217–1227.

Chu, M. C. 1999. Ecology and breeding biology of Phainopeplas (*Phainopepla nitens*) in the desert and coastal woodlands of southern California. Dissertation. University of California, Berkeley, California, USA.

Chu, M., and G. E. Walsberg. 1999. Phainopepla (*Phainopepla nitens*). Number 415 *in* A. Poole and F. B. Gill, editors. The birds of North America. The Birds of North America, Philadelphia, Pennsylvania, USA.

Cobb, N. S., S. Mopper, C. A. Gehring, M. Coulette, K. M. Christensen, and T. G. Whitham. 1997. Increased moth herbivory associated with environmental stress of pinyon pine at local and regional scales. Oecologia **109**:389–397.

Cowles, R. B. 1936. The relation of birds to seed dispersal of the desert mistletoe. Madroño **3**:352–356.

Donohue, K. 1995. The spatial demography of mistletoe parasitism on a Yemeni acacia. International Journal of Plant Science **156**:816–823.

Herrera, C. M., P. Jordano, L. López-Soria, and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs **64**:315–344.

Johnson, D. H. 1980. The comparison of usage and availability measurements for valuating resource preference. Ecology **61**:65–71.

Kuijt, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley, California, USA.

Larson, D. 1996. Seed dispersal by specialist versus generalist foragers: the plant's perspective. Oikos **76**:113–120.

Martin, S. C., and R. M. Turner. 1977. Vegetation change in the Sonoran Desert Region, Arizona and Sonora. Journal of the Arizona Academy of Science **12**:59–69.

Martínez del Rio, C., A. Silva, R. Medel, and M. Hourdequin. 1996. Seed dispersers as disease vectors: bird transmission of mistletoe seeds to plant hosts. Ecology **77**:912–921.

Medina, A. L. 1996. The Santa Rita experimental range: history and annotated bibliography (1903–1988). Rocky Mountain Forest and Range Experiment Station, USDA Forest Service General Technical Report **RM-GTR-276**.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution **15**:278–285.

Ouborg, N. J., Y. Piquot, and J. M. Van Groenendael. 1999. Population genetics, molecular markers and the study of dispersal in plants. Journal of Ecology **87**:551–568.

Overton, J. M. 1993. Dispersal in mistletoes and models. Dissertation. University of California, Los Angeles, California, USA.

Overton, J. M. 1994. Dispersal and infection in mistletoe metapopulations. Journal of Ecology **82**:711–723.

Pacala, S. W., and A. P. Dobson. 1988. The relation between the number of parasites/host and host age: population dynamic causes and maximum likelihood estimation. Parasitology **96**:197–210.

Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth. Duxbury Press, Albany, New York, USA.

Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. Ecology **70**:137–145.

Reid, N. 1991. Coevolution of mistletoes and frugivorous birds. Australian Journal of Ecology **16**:457–469.

Reid, N., and N. M. Stafford Smith. 2000. Population dynamics of an arid zone mistletoe (*Amyema preissii*, Loranthaceae) and its host *Acacia victoriae* (Mimosaceae). Australian Journal of Botany **48**:45–58.

Reid, N., N. M. Stafford Smith, and Z. Yan. 1995. Ecology and population biology of mistletoes. Pages 285–310 *in* M. D. Lowman and N. M. Nadkarni, editors. Forest canopies. Academic Press, San Diego, California, USA.

Rolstad, J., B. Løken, and E. Rolstad. 2000. Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. Oecologia **124**: 116–129.

Sallé, G., E. B. Hariri, and C. Andary. 1993. Structural and biochemical bases of the resistance to mistletoe in the genus *Populus*. Acta Botanica Gallica **140**:633–648.

Sargent, S. 1995. Seed fate in a tropical mistletoe: the importance of host twig size. Functional Ecology **9**:97–204.

SAS Institute. 1989. SAS/STAT user's guide, version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

Schupp, E. W. 1995. Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany **82**:399–409.

Snyder, M. A., B. Fineschi, Y. B. Linhart, and R. H. Smith. 1996. Multivariate discrimination of host use by dwarf mistletoe *Arceuthobium vaginatum* subsp *cryptopodum*: inter- and intraspecific comparisons. Journal of Chemical Ecology **22**:295–305.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113–137 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.

Walsberg, G. E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. Condor **77**:169–174.

Walsberg, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilogonatidae). University of California Publications in Zoology **108**: 1–63.

Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evolutionary Ecology Research **3**:51–74.

Wenny, D. G., and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences (USA) **95**:6204–6207.