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## SEX-RATIO AND REPRODUCTIVE VARIATION IN THE MISTLETOE PHORADENDRON JUNIPERINUM (VISCACEAE)<sup>1</sup>

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### ABSTRACT

Despite the fact that many parasitic and hemiparasitic plant species such as mistletoes are dioecious and occur in both the new and the old world, few data exist on variation in the sex ratio and allocation to reproduction in these taxa. We investigated 1) the sex-ratio of the xylem-tapping mistletoe *Phoradendron juniperinum* in relation to its age and position within the canopy of its host tree *Juniperus osteosperma*, and 2) reproductive effort in relation to the gender and age of mistletoe plants. Our surveys showed that *P. juniperinum* has a male-biased sex ratio. Despite this predominance of male individuals, females lived longer and had a greater reproductive effort than did males. A statistical analysis of the age distribution data indicated that the peak in the frequency of reproductively mature individuals was later in females than in males. These gender-specific distributions may have resulted 1) from sequential hermaphroditism (age-specific sex switching), or 2) because the average age of peak reproduction is later in female individuals. Because sex is genetically determined in a closely related genus of mistletoe and because we have no data to indicate sex switching in this species, we feel that our data support the interpretation that female individuals, on average, show a peak in reproductive vigor at an older age relative to males. While delayed reproduction in females may be favored because reproductive effort and success appear to be age-dependent in females of this species, both sexes can become reproductively mature relatively early in life. Further, because 1) allocation to reproduction as a function of age increases more rapidly for females of this species relative to males, and 2) because there may be a higher resource cost associated with reproduction in females, we hypothesized that female individuals would be more abundant in the best quality locations within the host tree so as to maximize the opportunity to meet those costs. In spite of the association between gender and some host characteristics, there was no indication that female plants were located in sites most favorable to either their carbon or water balance. We discuss reasons why this may be the case.

THE SEX RATIO of many dioecious plants often deviates significantly from 1:1 with a tendency towards a male bias (Willson, 1983). In some, but not all instances, biased sex ratios have been linked with an intrinsic biological characteristic of the plant (i.e., physiological condition—Dawson and Bliss, 1989; age or size—Lloyd and Bawa, 1984) or extrinsic ecological

factors (i.e., habitat quality—Freeman, Klickoff, and Harper, 1976). A number of studies have shown that female individuals of dioecious species tend to be older or larger and to occur in habitats with more resources (e.g., water, nutrients, light) compared to males (Lloyd and Bawa, 1984). One thought is that the resource costs of reproduction are greater in females than in males and that older or larger plants in a high resource environment would be relatively better able to pay these costs (Law, 1979; Bierzychudek, 1984). Deviation in the sex ratio could arise by several mechanisms, including differential growth or mortality of each gender by age, size, or habitat, and environmental sex determination (Charnov, 1982; Bierzychudek and Eckhart, 1988; Charnov and Dawson, 1989).

Nearly all reports of biased sex ratios come from terrestrially rooted plants. By contrast, few reports of sex ratio biases exist from parasitic or hemiparasitic species, such as mistletoes, which include a great number of dioecious

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species from both the new and the old world (Calder, 1983). Because they are dependent upon their hosts for not only a substrate on which to grow but also resources critical to that growth, mistletoes may provide a model study system for the study of environmental influences on sex ratio bias; terrestrially rooted dioecious plants grow under a much broader range of conditions and span a tremendous number of life forms; hence, the task of uncovering patterns of sex ratio biases is made much more difficult. Here, we report on variation in the sex ratio and in reproductive effort in a parasitic higher plant, the xylem-tapping mistletoe *Phoradendron juniperinum*, and on the relationship of sex ratio variation to age and habitat. In mistletoes, the habitat is defined by the host tree; its size and particular aspects of its canopy where mistletoe individuals may occur. Previous studies have shown that mistletoes of the genus *Phoradendron* depend on their hosts for water and inorganic nutrients (Ehleringer et al., 1985), but not carbon (Hull and Leonard, 1964). Since mistletoes are autotrophic, individuals must also be located in favorable light environments within a host tree. Factors such as host size and locations within the host tree as well as the number of infections within an individual host tree may therefore affect mistletoe growth and reproduction through their influences on carbon, nutrient, and water balance of the mistletoe. We surveyed the distribution of mistletoes to address the following questions: 1) what is the sex ratio in this population of *P. juniperinum*; 2) do males and females allocate biomass equally to reproduction; 3) do the sexes exhibit similar age distribution patterns; 4) are the sexes evenly distributed across the same locations on the host; and 5) do female mistletoes predominate in locations expected to be most favorable to their carbon balance?

**MATERIALS AND METHODS**—The study site is located in the southwestern corner of Utah, adjacent to the Coral Pink Sand Dunes State Reserve (37°3'N, 112°45'W, elev. 1,855 m). It is located in a pinyon-juniper woodland (Cronquist et al., 1972) on deep, poorly developed sandy soils. Infected host trees within a single population of *Juniperus osteosperma* (Torr.) Little, the Utah juniper, were surveyed for the number, age, gender, and position of all mistletoes (*Phoradendron juniperinum* Gray). For each mistletoe individual, gender (nonreproductive, male, female), age, host tree size class, and the height and compass aspect within the host tree were recorded. The survey was conducted in August 1988 while the mistletoes

were at or near peak anthesis and gender could be easily ascertained. Age of the mistletoe plants was determined using the branch structure, a morphological feature shown to be highly correlated to age determined by anatomical methods (Dawson, King, and Ehleringer, 1990). Host trees that were sampled were randomly chosen from three broadly separated size classes based on the circumference of the main trunk at its base. The size classes were 45–60 cm, 75–90 cm, and >105 cm; ten trees were surveyed per size class. Eighty-six percent of all the host trees in the sample population fell within these size classes. Size class divisions based on tree diameter at breast height were inappropriate for *J. osteosperma* because many trees had more than one trunk at their base. A mistletoe's height in the trees was estimated to the nearest meter from the ground. Compass aspect of each mistletoe was assigned to one of four sectors: NE to SE (between 45° and 135°), SE to SW (135°–225°), SW to NW (225°–315°), and NW to NE (315°–45°). These compass aspects will be referred to as east, south, west, and north, respectively.

To substantiate the claim that female individuals of *P. juniperinum* had greater reproductive effort than males, 25 plants of each gender were harvested during peak anthesis. An additional 46 female plants were sampled during peak fruit set. Reproductive effort (RE) was calculated as the percent reproductive biomass divided by the current year's vegetative biomass (after Schulze and Ehleringer, 1984). This estimate of RE avoids having to adjust for differences in total plant mass among the samples (Samson and Werk, 1986).

A multiway contingency analysis (Feinberg, 1970) was used to determine whether any association existed between mistletoe gender and its age, host tree size class, height in the tree, or compass aspect. Analyses of the gender association with host characteristics were not changed by removing nonreproductive individuals. The data for each host tree size class were pooled for the analysis after finding no significant sex ratio differences (chi square of heterogeneity) among individual trees within a particular size class. The analysis is based on a log likelihood ratio chi-square statistic ( $G$  value). In the analysis, the interaction of gender with any one or more of the other variables is tested by comparing the goodness of fit between observed and expected cell values, with expected values calculated both from models including and excluding the interaction of interest. Vepsäläinen, Savolainen, and Penttinen (1988) provide a review of this analysis and its use with ecological data.

TABLE 1. Overall number of male, female and nonreproductive individuals and the sex ratio of *Phoradendron juniperinum* ( $N = 660$ ) in 30 host trees. The sex ratio (male:female) deviated significantly from 1:1 at  $P = 0.001$  (log likelihood ratio chi-square statistic; see Methods)

Male	Female	Nonreproductive	Sex ratio (male:female)
271	195	194	1.39

RESULTS—The overall sex ratio in *P. juniperinum* was significantly male-biased (Table 1). The age specific distribution of each mistletoe gender showed that 1) nonreproductive individuals (probably prereproductive) were most abundant in the 3-year-old age class, 2) male plants had a peak abundance in the 5-year-old age class, and 3) female plants had the broadest age distribution and tended to be best represented in the 7- to 9-year-old age classes (Fig. 1). The log-linear analysis indicated a significant gender by age interaction ( $G = 410.3$ ,  $P = 0.0001$ ) across all pairwise comparisons, indicating that the distributions in Fig. 1 were different from each other.

There was no significant interaction of mistletoe sex with host tree size class or height. In all tree size classes and height categories males were more numerous than females (Table 2), but the sex ratio was significantly male-biased only when mistletoe sample sizes were large (i.e., on large trees at intermediate heights; Table 2).

There was a significant sex by compass aspect interaction ( $G = 286.7$ ,  $P = 0.0001$ ). As previously shown (Table 1), the overall sex ratio was male-biased, but the bias was only significant on the east and south sides of host trees (Table 2). On the north side of trees there was a tendency for more male plants than female plants, but not significantly so, while on the west side of trees the sex ratio was essentially 1:1 (Table 2).

There was a highly significant correlation between the age of an individual and reproductive effort in both sexes (Fig. 2). In addition, as plants aged, females allocated a consistently higher proportion of their biomass to reproduction than did males (Fig. 2).

DISCUSSION—To date, the limited number of sex ratio surveys conducted on parasitic mistletoes have reported a female-bias (Showler, 1974; Barlow and Wiens, 1976; Wiens and Barlow, 1979; Nixon and Todzia, 1985). Our findings of a strong male-bias in *P. juniperinum*, while clearly different from these earlier mistletoe studies, parallel the more common

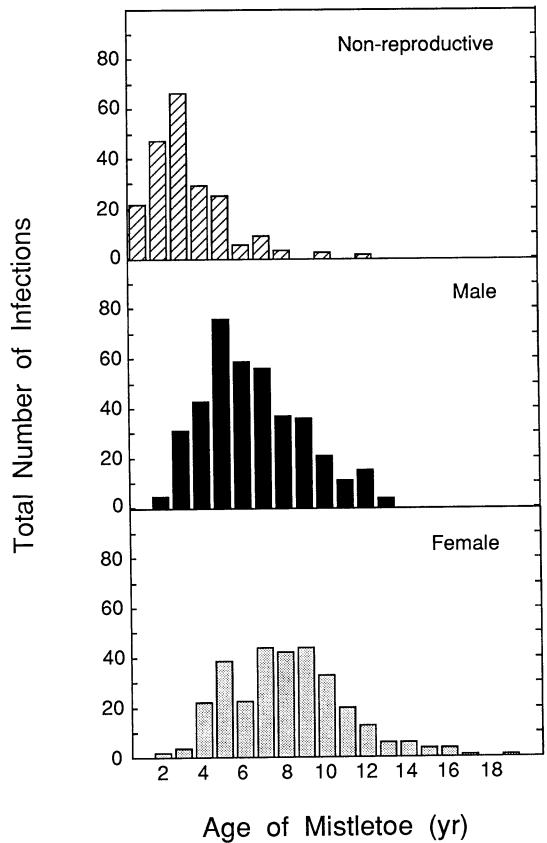


Fig. 1. Frequency histogram of the total number of mistletoe (*Phoradendron juniperinum*) infections as a function of plant age on 30 trees of *Juniperus osteosperma* in nonreproductive (top), male (middle), and female (bottom) plants. Based on a log-linear analysis, significant differences among the three frequency distributions occurred as a function of age (log likelihood ratio chi-square statistic;  $P = 0.0001$ ).

pattern of male-biased sex ratios in dioecious plants as a whole (Willson, 1983). For the mistletoe *P. tomentosum*, Nixon and Todzia (1985) suggested that biased sex ratios might have been generated through a variety of mechanisms, ranging from translocation heterozygosity to differential growth or mortality, but with their data they could not distinguish among these possibilities. Theoretical models indicate that, in species with environmental sex determination (ESD) or sex switching, male-biased sex ratios are expected when fertility and/or fecundity increases relatively more with age, size, or across habitats in females than in males (Charnov, 1982; Charnov and Bull, 1989). The basis of sex-determination (genetic or environmental) and the mechanism generating sex ratio biases (e.g., differential growth or mortality of the sexes, sex switching) in *P. juniperinum* are not known. However, Barlow and

TABLE 2. Number of male, female, and nonreproductive individuals, and the total number of individuals of *Phoradendron juniperinum* in relation to the size class of the host tree (circumference at base of main trunk), height (m) within the tree it was found parasitizing, and compass aspect on the tree at which the plants were growing<sup>a</sup>

	Male	Female	Non-reproductive	Total
Tree size class (cm)				
45-60	43	33	30	106
75-90	69*	45*	46	160
>105	159*	117*	118	394
Height within tree (m)				
0-1	5	3	14	22
1-2	33	23	20	76
2-3	59	49	42	150
3-4	79*	50*	53	182
4-5	56	44	28	128
5-6	22	14	19	55
>6	17	12	18	4
Compass aspect				
North	69	54	54	177
South	95**	57**	59	211
East	52*	30*	40	122
West	55	54	41	150

<sup>a</sup> Significant deviations in the sex ratio from 1:1 are noted with a single (\*  $P = 0.05$ ) or double (\*\*  $P = 0.01$ ) asterisk (log likelihood ratio chi-square statistic).

Wiens (1975, 1976), Wiens and Barlow (1979), and most recently, Schink and Mechelke (1989) have shown that sex is genetically determined in the mistletoe genus *Viscum*, which is linked with a chromosomal complex translocation heterozygosity. Thus, we do not believe that the findings for *P. juniperinum* we report here and discuss further below provide support for ESD theory.

In this study we found that the degree of sex ratio bias varied across age classes of the mistletoe and across habitat (location) on the host plant. However, when sex ratio was regressed on the number of infections per host tree size class, we found no correlation ( $y = 6.119 + 0.103x$ ,  $r^2 = 0.07$ ,  $P = 0.112$ ), a result that differs from that of Nixon and Todzia (1985) who reported, for *P. tomentosum*, an increasingly more female-biased sex ratio as the total number of mistletoes per tree increased. Ours is the first study to document, for a parasitic species, age-specific gender and habitat associations with sex ratio bias. We found that the male-biased sex ratio in *P. juniperinum* differed significantly from 1:1 as the host size and the total number of reproductive individuals per tree increased (Table 2), but that the male-bias did not become increasingly more significant (e.g., the ratio of number of male in-

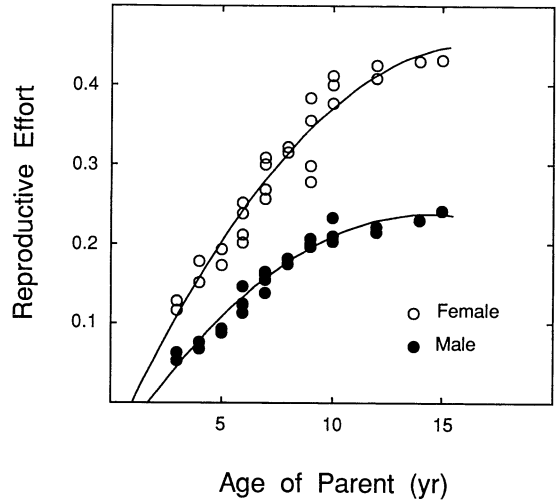


Fig. 2. Reproductive effort for male (closed symbols) and female (open symbols) individuals of *Phoradendron juniperinum* as a function of age. The regression equations are for females,  $y = -5.923e^{-2} + 6.104e^{-2}x - 1.823e^{-3}x^2$ ;  $r^2 = 0.931$  and for males,  $y = -6.971e^{-2} + 4.249e^{-2}x - 1.471e^{-3}x^2$ ;  $r^2 = 0.963$ . Lines differed significantly at  $P = 0.01$ .

dividuals to total number of reproductive individuals). We also found that nonreproductive plants were most common in the youngest age classes, suggesting that these were simply juvenile plants.

Females, on average, demonstrated a peak in reproductive activity later than males. This suggests that either the average age of peak reproduction is later in females than in males, or that *P. juniperinum* is sequentially hermaphroditic, functioning first as a male at a younger age and then switching to female at older ages (see Policansky, 1981; Charnov, 1982; Bierzychudek, 1984, for discussions of sequential hermaphroditism in plants). As previously mentioned, sex in all mistletoes studied to date is genetically determined, and we have no evidence in *P. juniperinum* of sex-switching. Thus, we feel that the data presented here support the interpretation that male and female plants have clear differences in peak reproductive activity leading to the age-distributions we found. Further, females lived longer than males and allocated a greater proportion of their biomass to reproduction as they aged. Delayed reproduction in females or switching to female function later in life would be favored if success as a female was strongly age-dependent (Charnov, 1982; Bierzychudek, 1984). Our data as well as those gathered previously by Schulze and Ehleringer (1984) suggest that in *P. juniperinum* this in fact occurs. Further sup-

port for this conclusion comes from information gathered on the seed and seedling biology in this and other mistletoe species. Seedling growth rate of *P. juniperinum* is strongly correlated with seed size in the pre-establishment stage (Dawson and Ehleringer, unpublished data). In species with high seed and seedling mortality rates, such as mistletoes (Kuijt, 1969; Lamont, 1983; Sallé, 1983), growth rate may be crucial to a seedling's ability to establish at suitable sites on the host plant. These observations and our data suggest that reproductive output and perhaps success in females increase with age, because older females of *P. juniperinum* are more likely to produce surviving seedlings than younger females (see also Charlesworth, 1980, and Lacey, 1986). Although one might expect that plant size rather than age may be the more important determinant of reproductive success, these two parameters are correlated in this species (Schulze and Ehleringer, 1984).

Do female mistletoes occur in sites most favorable to their energy or water balance? In many plant communities of the southwestern United States, northern exposures are the least favorable locations from the standpoint of energy balance (Whittaker and Niering, 1965), because they receive the lowest light levels. Southern and western exposures, on the other hand, are often considered the most stressful from a water-balance standpoint, because high solar radiation levels, air temperatures, and low humidities combine to produce the highest leaf temperatures and greatest water deficits. As a result, the lowest leaf water potentials are recorded in both the host and mistletoe on southerly and western exposures (Schulze and Ehleringer, 1984). Therefore, overall, the eastern sides of trees should be most favorable for mistletoes if carbon and water relations are important parameters influencing the micro-distributions of the sexes. Our data show that sex ratios were most male-biased on the eastern side (most favorable locations), while females were relatively more common on the western and northern sides (less favorable locations) of host trees. Thus, we cannot conclude that females occurred in the most favorable locations. Recent work on aspects of the carbon economy in this mistletoe (Marshall and Ehleringer, unpublished data) indicate that this parasite may derive a significant proportion of its carbon via xylem sap. If carbon, in addition to water and nutrients, is obtained in this manner, there is no necessary reason to expect that these partially heterotrophic plants, be they female or male, must occur in locations most favorable to their energy balance. This finding could ex-

plain why we did not see females restricted to locations in the host tree canopy most favorable to their energy or water balances.

Our data demonstrate that female individuals *P. juniperinum* live longer than males. Despite this fact, the sex-ratio of this species is male-biased. Given these observations, we would predict that either 1) female plants must have a lower cost associated with reproduction, 2) a lower reproductive effort, and/or 3) occur in locations within the host tree canopy most favorable to acquiring resources necessary to meet the higher costs associated with female reproduction. It is very unlikely that the costs of reproduction are lower in females relative to males given that they not only produce flowers and floral structures, but also nitrogen and carbohydrate-rich fruit and seed which males do not (Schulze and Ehleringer, 1984). Further, we found that females had higher reproductive effort than males and did not occur in the most favorable host canopy locations. Past research with dioecious plants has shown that if segregation of the sexes occurs between sites of different quality, then females commonly occur in the better quality sites (reviewed in Bierzychudek and Eckhart, 1988). For the heterotrophy reasons discussed above, there is no necessary reason to find support for this pattern in *P. juniperinum*. We believe that the key to understanding the patterns of sex-ratio bias and allocation to reproduction in this species will come with studies of both the demographic and population dynamics of these unusual hemiparasites combined with a more detailed understanding of physiological processes unique to male and female individuals of this species. These investigations are currently in progress.

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