

Female biased sex ratios in *Pistacia lentiscus* L. (Anacardiaceae)

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Abstract

Sex ratios of populations of the dioecious shrub *Pistacia lentiscus* L. (Anacardiaceae) were studied. Several hypotheses concerning biased sex ratios were tested. The expected pattern of male preponderance in stressful habitats was not found. The populations located in a microclimatic gradient, such as a slope, did not display a male-biased sex ratio on the stressful middle slope. The populations located in a climatic gradient did not display a male-biased sex ratio in the more xeric habitats. Testing the hypothesis of female preponderance when pollen grain competition exists, we found a significant correlation in the direction opposite to that predicted by this hypothesis. Low density of individuals (an estimate of pollen density) correlates with a high preponderance of females but the sex ratio approaches 1:1 when density increases. This correlation should have an upper threshold in 1:1 because male-biased sex ratios have never been found.

Introduction

Fisher (1930) explained why under natural selection a 1:1 sex ratio should be evolutionarily stable, as there would otherwise be a frequency-dependent advantage to the rarer sex. This theory has been supported by many theoretical contributions (Kolman 1960; Willson & Pianka 1963; Leigh 1970) as well as empirical data (Opler & Bawa 1978; Vasiliauskas & Aarssen 1992; Gibson & Menges 1994). However, when the underlying assumptions of Fisher's argument do not hold, biased sex ratios are to be expected (Hamilton 1967). Many examples of biased sex ratios have been observed in nature, providing new dimensions to Fisher's central theory rather than invalidating it (Frank 1990).

In dioecious plant populations, both male and female biased sex ratios are known (Opler & Bawa 1978; Onyekwelu & Harper 1979; Falinski 1980; Crawford & Balfour 1983). Several mechanisms have been proposed to explain these biased sex ratios:

Sex-differential mortality in stressful habitats. Assuming that reproductive cost is greater for females than for males, female plants may suffer higher mortality in stressful habitats, and therefore these differences can result in spatial segregation of sexes (SSS) or niche partitioning (Cox 1981). So, for *Pistacia vera* L., differences between the sexes in water stress resistance result in male trees to be more frequent in dry habitats and female ones more frequent in moist habitats (Shemeretiev et al., 1980). Competition between sexes has been thought to be the selective force responsible for SSS (Freeman et al. 1976). In contrast, Bierzychudek & Eckhart (1988) state that intersexual competition seems an unlikely ultimate cause for SSS because the effects of this competition are likely to be less severe than those of intrasexual competition. Furthermore, to the extent that increasing the distance between individuals of the opposite sex decreases the probability that pollen grains reach stigma, SSS can reduce the reproductive success of both males and females. Benefits of reduced competition would have to be large enough to compensate for this cost (Bierzychudek & Eckhart 1988). For these

reasons, sex-differential mortality may produce non-adaptive spatial segregation of sexes.

Sex-differential mortality due to herbivory. Differences in palatability between sexes may lead to differential herbivory, and therefore to differential mortality (Danell et al. 1985, 1991; Elmqvist et al. 1988). In most species, males suffer higher rates of herbivory than females (Boecklen & Hoffman 1993).

Pollen grain competition. There is experimental evidence that female-biased sex ratios in several species are due to more frequent fertilization of egg cells by female-determining sperm nuclei than by male-determining nuclei. The reason for female success at high pollen densities could be that female-determining pollen tubes reach the ovules before male-determining pollen tubes either through earlier germination, faster growth, or both (Lloyd 1974, and references therein).

Maximum seed set. Genetic models state that female-biased sex ratios increase the seed set of the population (Kaplan 1972; Lewis 1942; Mulcahy 1967). Maximum seed set could be a consequence of female-biased sex ratios rather than a causal factor and therefore we have not tested this hypothesis.

Sex ratios in populations of *P. lentiscus* vary from 1:1 to being female-biased (Jordano 1988; Hjältén et al. 1993) but the mechanism producing the biases is unknown. It is only known that herbivory does not produce biased sex ratios (Hjältén et al. *op. cit.*). In this paper we examine sex ratios in several populations of *P. lentiscus* to test the other proposed mechanisms producing biased sex ratios. The following questions are addressed:

– If sex-differential mortality in stressful habitats produces sex-bias, then variations in sex ratios across macroenvironmental and microenvironmental gradients are to be expected.

– If pollen grain competition occurs, then variations in sex ratio in populations with different density of *P. lentiscus* individuals would be expected.

Materials and methods

Study species

Pistacia lentiscus L. (*Anacardiaceae*) is a common evergreen, sclerophyllous, dioecious woody shrub liv-

ing in Mediterranean shrublands and old fields (Verdú & García-Fayos 1996a).

Sex determination mechanisms in this species are unknown. The sex of the plant is unrecognisable until it flowers. Reproductive age is reached in no sooner than 5 years. In *Pistacia vera*, Hormaza et al. (1994) using a DNA marker, sexed 94 seedlings and found no differences from a 1:1 sex-ratio.

Flowers are wind pollinated. Flowering dates of males overlap those of females (Jordano 1988; Correia et al. 1992; Verdú, pers.obs.). After pollination, the zygote remains dormant during several weeks (Grundwag 1976). Fruits reach their final size in late summer and then the seeds are dispersed by frugivores, mainly birds (Herrera 1984; Jordano 1989; Verdú & García-Fayos 1994). Rodents and granivorous birds are responsible of post-dispersal seed predation (Verdú & García-Fayos 1996b).

Study sites and methods

Field data were collected during the flowering season of 1994 in Eastern Spain (see Table 1 for description) in several sites in typical Mediterranean maquis that have never been cultivated but have a long history of wild fires and grazing. The main species are *Quercus coccifera* L., *Pistacia lentiscus*, *Chamaerops humilis* L., *Erica multiflora* L., *Brachypodium retusum* (Pers.) Beauv. and *Rosmarinus officinalis* L.

All the males and females of *P. lentiscus* were counted until a minimum number of 150 reproductive individuals was reached in each sampling location. The number of non-reproductive individuals was also counted but they never exceeded 15% of individuals.

Two kinds of stressful habitats were chosen to test sex-differential mortality:

– Microenvironmental gradient: It is well known for temperate ecosystems that water availability varies along hillslope gradients (Burt & Butcher 1985; Kirkby 1985). Water storage capacity of soils decreases from the top of the hillslope to the point of maximum erosion, located at the middle portion of the hillslope. From this point to down the storage capacity increases reaching the maximum at the bottom portion of the hillslope. This pattern is the result of variations in soil depth and texture and also in water circulation along the hillslope (Gerrard 1981; Birkeland 1984). Soil properties related with water storage and direct moisture measures along limestone hillslopes in the study area fitted well with this model (Boix et al. 1995). Freeman et al. (1976) has shown that growing on the valley soils

Table 1. Environmental features of the study sites.

Population	Total annual rainfall	Altitude (m.a.s.l.)	Lithology	Sex ratio males:females
Portacoeli	300	300	Limestones	44:56
Saler	400	0	Sand dunes	39:61
Cabanes	500	200	Limestones	37:63
Dos Aguas	500	400	Limestones	36:64
Altura	500	400	Limestones	39:61
Pego	1000	250	Limestones	45:55

is beneficial for both males and females because plants there are larger than plants on the slope. They have also shown that female function is more limited on the slopes than male function. Thus, we determined whether the slope gradient of limestone hills exerts a significant influence on the proportion of males and females in the subpopulations corresponding to the topslope, the middleslope and the downslope.

– Macroclimatic gradient: Six populations located in a gradient ranging from 300 to 1000 mm of annual rainfall were chosen (see Table 1 for description).

The hypothesis of pollen grain competition was tested in populations with different densities of *P. lentiscus*, ranging from 95 to 278 individuals Ha^{-1} . As population density is highly correlated with male density ($r = 0.99$; $p < 0.001$), we used the former because it reflects the pollen availability per female better. Thus, we assume that the higher the density of individuals, the higher the pollen density.

Regarding data analysis, the null hypothesis was that the expected sex ratio is 1:1. Departures from the unity in the sex ratios of the populations were tested with a *G*-test. The theoretical distribution of this statistic approaches a chi-square when sample size is high. The advantage of the *G*-test over the standard chi-square analysis is its complete additivity, that allows one to split an overall *G*-test into separate *G*-tests representing individual degrees of freedom (Sokal & Rohlf 1981). Thus, deviations from a 1:1 sex ratio in the populations were tested as follows: $G_T = G_P + G_H$, where G_T is the sum of individual *G*-tests for each subpopulation, G_P is the *G*-test for pooled data and G_H is the *G*-test for heterogeneity (intrapopulation differences).

Results

Sex-differential mortality in stressful habitats

Microclimatic gradient

The expected pattern of female mortality was never found because no subpopulation deviated significantly towards a male-biased sex ratio. Sex ratios did not display intrapopulation differences along the microclimatic gradient in two (Dos Aguas and Pego) of the four sites tested (not significant *G*-test for heterogeneity for Dos Aguas and Pego, see Table 2). The other two populations (Cabanes and Portacoeli) displayed intrapopulation differences ($p < 0.001$; *G*-test for heterogeneity for Cabanes and Portacoeli, see Table 2). These intrapopulation differences followed an inverse spatial pattern of sex ratios in both populations: Female preponderance was very high in Cabanes downslope whereas in Portacoeli female preponderance was higher in the topslope.

To test how the different parts of the microenvironmental gradient affected the plants, we measured plant size and density across the slope in two populations, but different patterns in the two populations were found (Figure 1). In contrast to expected differential response to habitat stress between sexes, plant size was not explained by the interaction between slope and sex (Table 3).

Macroclimatic gradient

Sex ratios did not vary with respect to rainfall ($r = 0.5$; $F = 1.34$; $p > 0.5$). All the populations were female-biased and the smallest deviations from 1:1 occurred in those populations receiving the least (Portacoeli) and most precipitation (Pego) (Table 1).

Table 2. Sex ratios and statistical tests of the study sites; G_T is the sum of individual G -tests for each subpopulation, G_P is the G -test for pooled data and G_H is the G -test for heterogeneity (intrapopulation differences)

Population	Subpopulation	Males:females (n)	G -statistics
Cabanes	Topslope	47:53 (173) ^{ns}	$G_P = 37.31^{***}$
	Middleslope	41:59 (208) [*]	$G_H = 29.49^{***}$
	Downslope	20:80 (158) ^{***}	$G_T = 66.76^{***}$
Dos Aguas	Topslope	42:58(161) ^{**}	$G_P = 46.34^{***}$
	Middleslope	35:65 (213) ^{***}	$G_H = 4.21^{ns}$
	Downslope	32:68 (200) ^{***}	$G_T = 50.56^{***}$
Portacoeli	Topslope	30:70 (171) ^{***}	$G_P = 8.35^{**}$
	Middleslope	50:50 (174) ^{ns}	$G_H = 20.39^{***}$
	Downslope	51:49 (162) ^{ns}	$G_T = 28.75^{***}$
Pego	Topslope	39:61(154) ^{**}	$G_P = 4.95^*$
	Middleslope	47:53 (162) ^{ns}	$G_H = 3.34^{ns}$
	Downslope	49:51 (150) ^{ns}	$G_T = 8.29^*$

• $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns not significant.

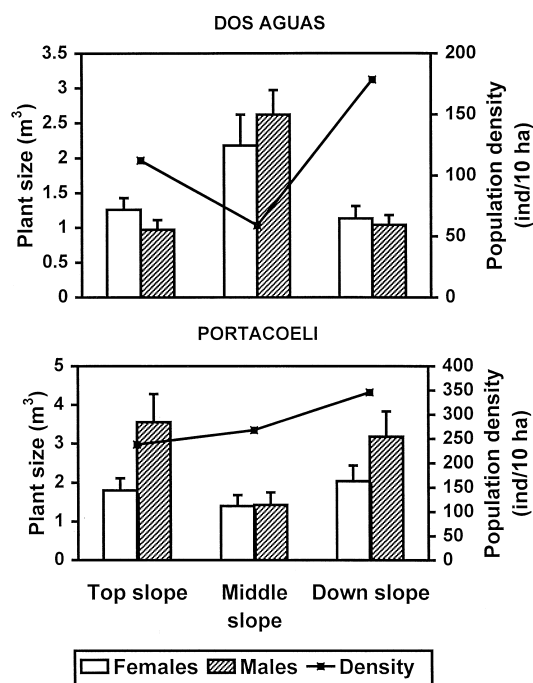


Figure 1. Density and plant size of *Pistacia lentiscus* individuals in the three parts of the slope.

Pollen grain competition

A significant correlation between the population density of *P. lentiscus* individuals and the proportion of females is expected under the hypothesis of pollen grain competition. A significant correlation was found

Table 3. ANOVA of effects of slope and sex on plant size (log transformed) of *Pistacia lentiscus* individuals in (a) Portacoeli and (b) Dos Aguas populations

Source of variation	df	MS	F	P
Portacoeli				
Slope	2	0.221	4.358	0.016
Sex	1	0.212	4.184	0.044
Slope \times Sex	2	0.054	1.071	0.347
Error	83	0.051		
Dos Aguas				
Slope	2	0.359	18.907	0.000
Sex	1	0.000	0.006	0.937
Slope \times Sex	2	0.034	1.772	0.176
Error	84	0.019		

(Figure 2a) but, surprisingly, in the opposite direction of the prediction. Low density of individuals correlates with a high preponderance of females and the sex ratio approaches 1:1 when density increases. The trend of this relationship remains in the same direction, and is marginally significant, when the density of the subpopulations were correlated with the proportion of females (Figure 2b).

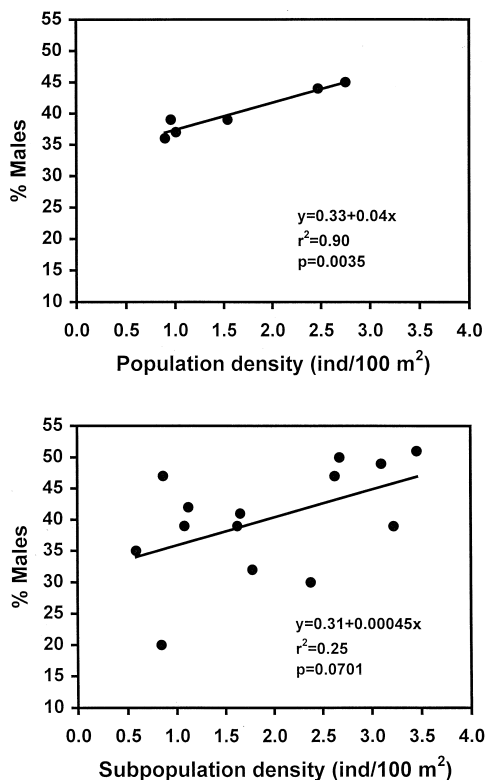


Figure 2. Correlation between *Pistacia lentiscus* density and sex-ratio in (a) populations and (b) subpopulations.

Discussion

Many studies have documented that female allocation to sexual reproduction is higher than that of males and thus, females should have a smaller proportion of energy available for growth and maintenance (Harper & Odgen 1970; Hancock & Bringham 1980; Popp & Reinartz 1988).

Consequently, females should have lower survival rates than males in stressful habitats and therefore the spatial segregation of the sexes should produce a locally biased sex ratio. However, the effect of productivity gradients on the intensity of plant competition is not clear. Some authors state that competition is higher in rich, non-stressful habitats because larger amounts of standing crop in these habitats impose greater demands for resources (Grime 1973; Kadmon 1995). In contrast, other authors have proposed that the limited availability of soil resources in poor habitats may lead to intense competition (Newman 1973). We have measured in *P. lentiscus* two parameters that are probably affected by the intensity of competition

(population density and plant size) along productivity gradients such as hill slopes and we have not found a consistent spatial pattern of variation among populations. Whatever the effects the stressful habitats have in the productivity gradient, the expected pattern of preponderance of males in the stressful habitats did not occur. Populations were never male-biased but they were often female-biased. Similarly, male biased sex ratios were not found across a macroclimatic (rainfall) gradient.

Allocation to reproduction by females depends also on the percentage of flowers producing seeds (Gross & Soule 1981). So, the biomass allocation to flowers in males of *Pistacia terebinthus* is eight times higher than that of females, whereas biomass invested by females when fruit production is included, is 1.5–3 times higher than that of males (Zahoueh et al. 1991). In the same direction, Wallace & Rundel (1979) found that female reproductive effort of *Simmondsia chinensis* was less than that of males unless seed set exceeded 30%. Because females of *P. lentiscus* can adjust, by means of abortion, their reproductive structures to environmental conditions, like pollen and resource availability (Jordano 1988; Verdú 1994), reproductive effort of females in stressful habitats should not be greater than that of males. This adjustment may explain why a differential-sex mortality is not found.

Female-biased sex ratios in the genera *Silene*, *Rumex*, *Cannabis*, and *Humulus* are a result of pollen grain competition (Correns 1928, in Lloyd 1974; Kihara & Hirayosi 1932, in Lloyd 1974). In these genera, the success of female-determining pollen nuclei is greater than that of male-determining nuclei due to earlier germination, faster growth, or both. Alternatively, this hypothesis has been also imputed to a post-parental mortality of male offspring (Carroll & Mulcahy 1993). Although recently, Taylor (1996) supported Corren's hypothesis by demonstrating with PCR technique that female-biased sex ratios in *Silene alba* are produced early in the development and that the sex ratio in the developing seeds and mature seeds were nearly identical to the sex ratios in the adults. However, this mechanism does not occur in *P. lentiscus*, because a positive correlation between overall density of individuals (an estimate of pollen availability) and the proportion of females is not found. Thus, the hypothesis of pollen competition can be rejected because the correlation is significant in the direction opposite to that predicted by the hypothesis. The denser the population, the larger the proportion of males. This correlation should have an upper threshold at the

1:1 sex ratio because a male-biased sex ratio has never been found. In addition to our data, sex ratios of *P. lentiscus* reported in the literature fit the correlation found here. Thus, in southern Spanish populations Hjäältén et al. (1993) found female-biased sex ratios at low densities of *P. lentiscus* individuals whereas Jordano (1988) found 1:1 sex ratios at high densities (Jordano, pers. com.).

In summary, none of the ecological hypotheses addressed can explain the female-biased sex ratio in *P. lentiscus*. Environmental determination of the sex could explain the observed pattern but sex changes have never been documented in *Pistacia* species (Hormaza & Polito 1996).

The ancient use of *P. lentiscus* plants along the Mediterranean Basin by man could help us to explain these deviations. Its use as wood and charcoal, the extraction of resin from shoots, and the extraction of oil from fruits has been widely documented (Liutaghi 1974; Font-Quer 1981; Rouskas 1996). Likewise, farmers living in south and east Spain could favour females living at the border of the orchards because fruiting individuals act as lure for game birds. From these uses, oil and lure for game birds are exclusively linked to females, and these uses could be in conflict with the destructive ones (i.e., wood and charcoal exploitation), preserving females. Intensive human exploitation of *Pistacia* populations could direct the bias on both the population density and the sex-ratio toward female preponderance at a local scale. Populations with big female preponderance due to human use have been cited from Southeast Portugal (García-Novo pers. commun.).

Further investigation on the genetics of sex determination and ecological aspects of the sex ratio are needed to understand the bias of the sex ratio in *Pistacia lentiscus* populations.

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