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## ENVIRONMENTAL SEX DETERMINATION WITH OVERLAPPING GENERATIONS

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Environmental sex determination (ESD), whereby an individual's gender is determined by its current environment, is uncommon yet widespread throughout the animal and plant kingdoms (Charnov and Bull 1977; Charnov et al. 1978; Bull 1980, 1983; Freeman et al. 1980; Charnov 1982; Lloyd and Bawa 1984; Adams et al. 1987; Head et al. 1987). To date, the genetic theory for the evolution of ESD is well developed for the situation of discrete generations (Charnov et al. 1978; Charnov 1979*b*; Bull 1981, 1983; Frank 1987). However, for overlapping generations, ESD theory has not received the same sort of attention. Our purpose here is to extend ESD theory to overlapping generations. In age-structured populations, ESD may take the form of a once-and-for-all gender decision during immature development (e.g., developmental temperature control in some reptiles [Bull 1980, 1983; Head et al. 1987] and nutritional control in mermithid nematodes [Christie 1929; Petersen 1972]) or continuous decisions made during the adult phase (e.g., some plants; Freeman et al. 1980; Dawson and M. Geber, MS).

Natural selection favors ESD when the environment is patchy with respect to opportunities for breeding as a male or female. Some patches are relatively better for female reproduction, some for male. ESD allows an individual to match its sex to the one that performs relatively better in a particular patch (Charnov and Bull 1977; Bull 1981). In this respect, ESD is much like sequential hermaphroditism (sex change), whereby an individual spends the early reproductive years as one sex and then switches to the other sex for the remaining reproductive years (Ghiselin 1969; Warner 1975; Leigh et al. 1976; Charnov 1979*a*). Here, the basis for selection favoring sex change is that age or size, rather than environmental patchiness, benefits one sex relatively more than the other, so that the early years are spent as the sex for which the relative penalty of youth or small size is least (Ghiselin 1969; Warner 1975). Genetic theory for the evolution of sex change is quite well developed (Leigh et al. 1976), and there are many qualitative (and a few quantitative) tests with both fish (Warner et al. 1975) and invertebrates such as pandalid shrimp (Charnov et al. 1978; Charnov 1979*a*, 1982).

In order to complement current sex-change theory, our model allows opportunities for reproduction as a male or as a female to vary with spatial location but *not* with age or size. Thus, spatial patchiness generates all the male-female differ-

ences. Both the fertility and adult-survival components of an individual's fitness are allowed to vary by sex and with patch type. In our model situation, it does not matter whether an individual makes a once-and-for-all gender decision (based on patch type) upon reaching adulthood or whether the adults are assumed to choose their gender anew each year. It is the patch-specific adult sex ratios that are assumed to evolve. The modeling approach consists of using single-locus population genetics to find the evolutionarily stable sex ratios for each of two patch types. (For a general discussion, see Charnov 1982; Maynard Smith 1982. For a much more detailed discussion of the population genetics of sex-allocation problems, see Karlin and Lessard 1986.)

After developing the evolutionarily stable results, we apply the theory to a plant, the arctic willow, *Salix arctica*. This plant shows habitat segregation by sex with the sex ratio biased toward females in wet locations and toward males in dry locations (Dawson and Bliss 1989). The prevalence of ESD in plants is controversial (Freeman et al. 1980; Lloyd and Bawa 1984), and indeed its presence in arctic willow is still uncertain. Habitat segregation by sex may simply result from sex-specific differential mortality in the absence of ESD (Cox 1981). This "non-adaptation" hypothesis is *always* an alternative for the production of biased sex ratios across habitats. Our purpose here is to contrast the predictions made by the ESD (adaptation) and non-adaptation hypotheses about the habitat-specific sex ratios.

#### THE BASIC MODEL

There are two types of patches in the environment (e.g., wet and dry) of contrasting environmental quality. We model the two-patch case for two basic reasons. First, we can handle the math here. Second, our study organism does indeed inhabit two patch types of contrasting environmental quality (discussed further below). Consider a population homozygous (*aa*) at a locus controlling sex choice in the adult phase. The population is censused at yearly intervals. Let  $r_1$  be the proportion of adults in patch-type 1 that are males,  $r_2$  in patch-type 2. If gender is chosen each year by the adults,  $r_i$  also represents the proportion in patch-type  $i$  that elect to reproduce as males. If gender is chosen only once, upon reaching adulthood,  $r_i$  represents the aggregate adult sex ratio resulting from the gender decision *and* the sex-specific mortality rates in a patch. Males have a yearly mortality rate of  $q_{m1}$  and  $q_{m2}$  in patch-types 1 and 2, respectively. Female mortality rates in the two patches are  $q_{f1}$  and  $q_{f2}$ . Let  $n_1$  and  $n_2$  be the yearly recruitment to the adult populations in the two patch types. Finally, let the adult population sizes in the two patches be  $N_1$  and  $N_2$ . We further define  $P = N_1/(N_1 + N_2)$ . If the population is regulated by density-dependent mortality or recruitment, the population sizes in the respective patch types are adjusted such that, in equilibrium, recruitment just balances death, or (for  $i = 1, 2$ ),

$$n_i = N_i[r_i q_{mi} + (1 - r_i) q_{fi}]. \quad (1)$$

Now consider the population dynamics of a rare dominant mutant (*b*) whose bearers alter their sex choice to  $\hat{r}_1$  and  $\hat{r}_2$ . While the dominant mutant is rare, we

need only consider the heterozygote (*ab*) to know if natural selection is acting for or against the altered sex choice. If there are  $\hat{N}_i(T)$  adult mutant individuals in patch-type  $i$  ( $i = 1, 2$ ) at time  $T$ , there will be  $\hat{N}_i(T + 1)$  at  $T + 1$ , or

$$\hat{N}_i(T + 1) \approx n_i \delta(T) + \hat{N}_i(T) [\hat{r}_i(1 - q_{mi}) + (1 - \hat{r}_i)(1 - q_{fi})], \quad (2)$$

where  $\delta(T)$  is the proportion of the  $n_i$  recruits that are *ab* (note that the mutant is too rare to affect the numbers of recruits; its dynamics are to be considered against the background population represented by eq. 1). To develop  $\delta$ , we assume that mating and seed dispersal are at random with respect to patches. Let a female have yearly fertilities (e.g., seed set) of  $b_1$  and  $b_2$  in the two patch types. Let a male in type-2 patches have fertility  $W_m$ , relative to a fertility of one for type-1 males. Note that we measure a male's fertility only relative to other males. Two facts allow us to derive a formula for  $\delta$ . First, while *ab* individuals are rare, virtually all their matings are with wild-type (*aa*) individuals; half of those matings produce *ab* genotypes. Second, half of the genes passed to seeds (here read recruits,  $n_i$ ) come from males and half from females. With these two facts in mind,  $\delta$  is seen to be of the form

$$\delta(T) \approx \frac{1}{2} \left[ \frac{\hat{N}_1(T)(1 - \hat{r}_1)b_1 + \hat{N}_2(T)(1 - \hat{r}_2)b_2}{\hat{N}_1(T)(1 - r_1)b_1 + \hat{N}_2(T)(1 - r_2)b_2} + \frac{\hat{N}_1\hat{r}_1 + \hat{N}_2\hat{r}_2W_m}{\hat{N}_1r_1 + \hat{N}_2r_2W_m} \right]. \quad (3)$$

Combining equations (1) and (3) (for  $n_1, n_2, \delta$ ) with equation (2) (for  $\hat{N}_1(T + 1)$  and  $\hat{N}_2(T + 1)$ ) shows, after a bit of algebra, that the dynamics of  $\hat{N}_1$  and  $\hat{N}_2$  can be written in the following matrix form:

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} \hat{N}_1(T) \\ \hat{N}_2(T) \end{pmatrix} = \begin{pmatrix} \hat{N}_1(T + 1) \\ \hat{N}_2(T + 1) \end{pmatrix}. \quad (4)$$

We will not write down the  $a_{ij}$  terms here. Our interest is in whether the mutant is selected for or against. This information is contained in the dominant eigenvalue ( $\lambda$ ) of the  $a_{ij}$  matrix (eq. 4). If  $\lambda$  is larger than one, the mutant is selected for, since the background population is stable in numbers; and conversely, if  $\lambda$  is smaller than one, the mutant is selected against. The sex ratios  $r_1$  and  $r_2$  are evolutionarily stable (in the sense of Maynard Smith 1982) if no mutant sex ratios ( $\hat{r}_1$  and  $\hat{r}_2$ ) can make  $\lambda$  larger than one. When  $\hat{r}_1 = r_1$  and  $\hat{r}_2 = r_2$ , the mutant is really the wild type, and here  $\lambda = 1$ . From the characteristic equation of the  $a_{ij}$  matrix, we can write the derivatives  $\partial\lambda/\partial\hat{r}_1$  and  $\partial\lambda/\partial\hat{r}_2$ . Since  $\lambda = 1$  whenever  $\hat{r}_1 = r_1$  and  $\hat{r}_2 = r_2$ , we can search for the evolutionarily stable state (ESS) by looking at the derivatives  $\partial\lambda/\partial\hat{r}_1$  and  $\partial\lambda/\partial\hat{r}_2$  when  $\hat{r}_1 = r_1$  and  $\hat{r}_2 = r_2$ . If the derivative  $\partial\lambda/\partial\hat{r}_i$  is positive (and  $r_i$  does not equal one), then  $\hat{r}_i > r_i$  makes  $\lambda > 1$ , and the mutant is selected for. The reverse holds if the derivative is negative. For an evolutionarily stable sex ratio not equal to zero or one,  $\partial\lambda/\partial\hat{r}_i = 0$  when  $\hat{r}_i = r_i$ . If the ESS equals one, the respective condition is  $\partial\lambda/\partial\hat{r}_i > 0$  when  $\hat{r}_i = r_i = 1$ ; for an ESS of zero, we require  $\partial\lambda/\partial\hat{r}_i$  to be less than zero when  $\hat{r}_i = r_i = 0$ . Bulmer and Taylor (1981) showed an alternative method for finding the sign (0, -, +) of the two derivatives. Although we do not discuss their method here, we wish to acknowledge that Taylor's application of it to our problem provided the clue to the explicit evolutionarily stable results for  $r_1$  and  $r_2$  (table 2).

TABLE 1  
EVOLUTIONARILY STABLE SEX RATIOS FOR DISCRETE GENERATIONS

Region	$r_1$	$r_2$
I $P/(1 - P) < W_m$	$r_1 = 1$	$r_2 = \frac{1}{2} - P/2W_m(1 - P)$
II $W_m \leq P/(1 - P) \leq W_f$	$r_1 = 1$	$r_2 = 0$
III $P/(1 - P) > W_f$	$r_1 = \frac{1}{2} + W_f(1 - P)/2P$	$r_2 = 0$

NOTE.— $P/(1 - P) = N_1/N_2$ ; variables defined in the text.

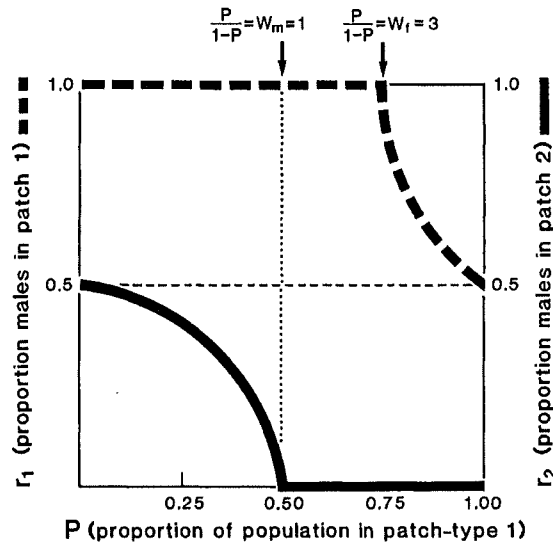


FIG. 1.—Evolutionarily stable sex ratios for discrete generations (from table 1, with  $W_m = 1$ ,  $W_f = 3$ ). The figure illustrates three rules for the sex ratios (recall that  $P = N_1/(N_1 + N_2)$ ). (1) If one patch is very common, its sex ratio is near  $\frac{1}{2}$ . (2) A rare patch has its sex ratio fixed at the sex that does relatively better in that patch ( $r_1 = 1$  or  $r_2 = 0$ ). Patch-type 2 is the “female” patch since  $W_f > W_m$ . (3) At most one patch type can have an intermediate sex ratio; one sex ratio must be at a boundary. Thus, if  $P \approx 0$ ,  $r_1 = 1$  and  $r_2 \approx \frac{1}{2}$ ; if  $P = \frac{1}{2}$ ,  $r_1 = 1$  and  $r_2 = 0$ ; and if  $P \approx 1$ ,  $r_1 \approx \frac{1}{2}$  and  $r_2 = 0$ .

THE ESS ANALYSIS

Discrete Generations

If all the mortality rates are set equal to one, the life history reduces to discrete generations; the results of this case have been known for a decade (Charnov et al. 1978). We review them here to simplify comparison with the situation for overlapping generations. Since patch labels are arbitrary, we call patch-type 2 the type that favors females. Define  $W_f$  to be  $b_2/b_1$ ; patch-type 2 is characterized by  $W_f > W_m$ . For this case, the evolutionarily stable  $r_1$  and  $r_2$  (derivation in Charnov et al. 1978) are given in table 1 and illustrated in figure 1. To summarize the results: (1) patch-type 2 always overproduces females, and type 1 overproduces males ( $r_1 > \frac{1}{2}$ ,  $r_2 < \frac{1}{2}$ , always); (2) when a patch type is very common, it will have nearly

TABLE 2  
EVOLUTIONARILY STABLE SEX RATIOS FOR OVERLAPPING GENERATIONS

REGION	
I	$P/(1 - P) < W_m q_{f2}/q_{m2}$
II	$W_m q_{f2}/q_{m2} < P/(1 - P) < W_f q_{f1}/q_{m1}$
III	$P/(1 - P) > W_f q_{f1}/q_{m1}$
$r_1$ (PROPORTION OF MALES IN PATCH-TYPE 1)	
I	$r_1 = 1$
II	$r_1 = 1$
III	$0 = \frac{1}{r_1} - \frac{1}{W_f(1 - P)/P + (1 - r_1)} + \left[ 1 + \frac{1 - r_1}{W_f(1 - P)/P + (1 - r_1)} \right] \left[ \frac{q_{f1} - q_{m1}}{r_1 q_{m1} + (1 - r_1) q_{f1}} \right]$
$r_2$ (PROPORTION OF FEMALES IN PATCH-TYPE 2)	
I	$0 = \frac{W_m}{P/(1 - P) + r_2 W_m} - \frac{1}{1 - r_2} + \left[ \frac{q_{f2} - q_{m2}}{r_2 q_{m2} + (1 - r_2) q_{f2}} \right] \left[ 1 + \frac{r_2 W_m}{P/(1 - P) + r_2 W_m} \right]$
II	$r_2 = 0$
III	$r_2 = 0$

NOTE.— $P/(1 - P) = N_1/N_2$ ; variables defined in the text.

equal numbers of males and females; when it is more rare, it will contain only the favored sex; and (3) at most one patch type may have a mixed or intermediate sex ratio.

### Overlapping Generations

Again, patch-type 2 favors females because, in that patch type, relative lifetime female fecundity exceeds relative lifetime male fecundity. With discrete generations,  $W_f > W_m$ . With overlapping generations, these fertilities must be corrected for the lengths of life in the two patch types for each sex. The average length of a male's life is  $1/q_{m1}$  and  $1/q_{m2}$  in the two patch types; the relative lifetime of males in type-2 versus type-1 patches is the ratio  $(1/q_{m2})/(1/q_{m1})$ , or  $q_{m1}/q_{m2}$ . Thus, lifetime male fecundity (in type-2 relative to type-1 patches) is written as

$$W_m q_{m1}/q_{m2}.$$

A similar formula obtains for relative lifetime female fecundity. In type-2 patches,

$$W_f q_{f1}/q_{f2} > W_m q_{m1}/q_{m2}. \quad (5)$$

With this definition of type-2 patches, table 2 gives the evolutionarily stable results. As in the discrete-generation case, there are three regions of  $P$  values. At low  $P$  values,  $r_1 = 1$  and  $r_2$  is at an intermediate sex ratio. At intermediate  $P$  values,  $r_1 = 1$  and  $r_2 = 0$ . At high  $P$  values,  $r_2 = 0$  and  $r_1$  is at intermediate values. This table is a generalization of the discrete-generation case (table 1), even though here the intermediate  $r_1$  and  $r_2$  values are given only by implicit formulas. Figure 2 illustrates the table. Notice that as a patch becomes common, its sex ratio ( $r_i$ ) comes to reflect simply its sex-specific mortality rates:  $r_i \rightarrow q_{fi}/(q_{fi} + q_{mi})$ .

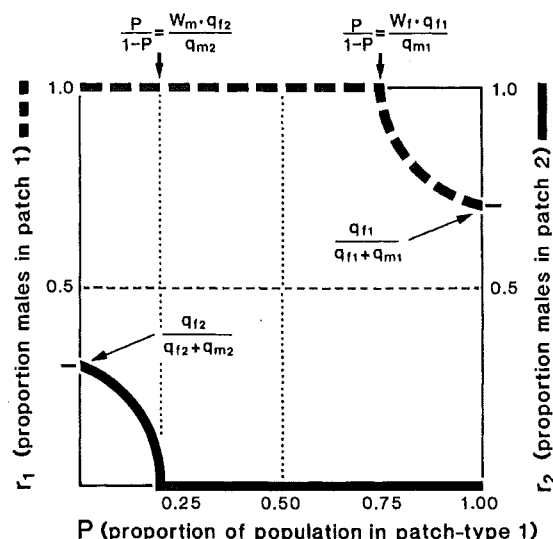


FIG. 2.—Evolutionarily stable sex ratios for overlapping generations (from table 2). Patch-type 2 is designated the female patch since relative lifetime female fecundity exceeds relative lifetime male fecundity in it (see inequality 5). Patch-type 1 is the preferred patch for males. The figure illustrates three rules for the sex ratios, similar to the discrete-generation case of figure 1. (1) A very common patch has its sex ratio near the mortality ratio. (2) When a patch is rare, its sex ratio is fixed at its preferred sex ( $r_1 = 1$ ,  $r_2 = 0$ ). (3) At most one patch type can have an intermediate sex ratio. Thus, if  $P = 0$ ,  $r_1 = 1$  and  $r_2 = q_{f2}/(q_{f2} + q_{m2})$ ; intermediate values for  $P$  lead to  $r_1 = 1$  and  $r_2 = 0$ ; if  $P = 1$ ,  $r_1 = q_{f1}/(q_{f1} + q_{m1})$  when  $r_2 = 0$ . In this figure, females survive better in patch-type 2, males in patch-type 1.

Two special overlapping-generation cases are worth further mention. In figure 3, we assume that females have much better survival than males, independent of patch type. Thus,  $q_{m1} = q_{m2} = q_m$  and  $q_{f1} = q_{f2} = q_f$ ; and  $q_m \gg q_f$ . Both  $r_1$  and  $r_2$ , at their respective boundaries ( $P \rightarrow 0$  or 1), tend to the same sex ratio,  $q_f/(q_f + q_m)$ ; this generates rather asymmetrical relations for  $r_1$  and  $r_2$  versus  $P$ . A second interesting case is one in which the mortalities are habitat-specific but not sex-specific:  $q_{mi} = q_{fi}$ . Inspection of table 2 shows that the evolutionarily stable results reduce to exactly the same form as table 1 whenever  $q_{mi} = q_{fi}$ .

#### ENVIRONMENTAL SEX DETERMINATION IN THE ARCTIC WILLOW

*Salix arctica*, the arctic willow, is a perennial dioecious shrub that inhabits arctic and alpine regions throughout Canada, Alaska, the Soviet Union, and the Rocky Mountain cordillera (Dawson 1987). Its ecophysiology in relation to sex and habitat have been investigated previously, and the methods for determining the sex ratios and plant performance measures in tables 3 and 4 are outlined elsewhere (Dawson and Bliss 1989).

If we look at its sex distribution with respect to water availability (xeric ridges versus mesic meadows), we find more males in the xeric areas and mostly females in the mesic (table 3). In addition, most of the population ( $\approx 70\%$ ;  $P = 0.30$ ) is in the mesic meadow area. If we label the mesic meadow the type-2 patch ( $W_f$  and

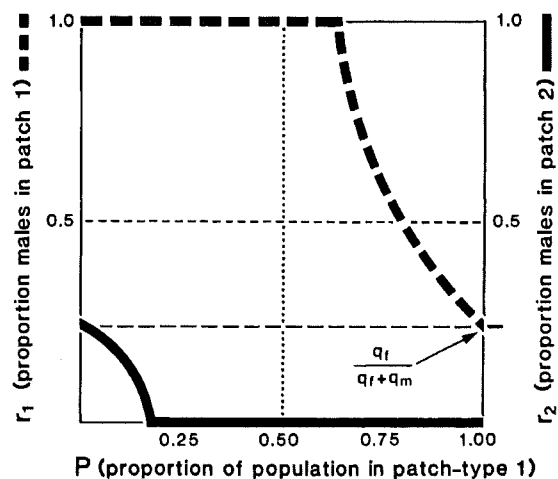


FIG. 3.—Evolutionarily stable sex ratio when adult mortality is sex-specific but not habitat-specific. Here, both boundary ( $P = 1$  or  $0$ ) sex ratios are the same ( $r_1 = r_2 = q_f/(q_f + q_m)$ ); this generates asymmetrical curves of  $r_i$  versus  $P$ .

TABLE 3  
SEX RATIO AS A FUNCTION OF HABITAT TYPE IN *SALIX ARCTICA*

Habitat Type	No. of Males	No. of Females	Sex Ratio (male/female) <sup>a</sup>
Xeric ridge	6366	4244	1.50*
Mesic meadow	1928	11,569	0.17**
Overall	8294	15,813	0.53**

<sup>a</sup> The sex ratio was determined from transects that bisected the different habitat types into areas of equal size. Adapted from Dawson and Bliss 1989. Significance tested by  $\chi^2$  analysis and  $\chi^2$  for heterogeneity.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

TABLE 4  
REPRODUCTIVE EFFORT (% OF DRY WEIGHT), SEED NUMBER, VIABILITY (% STAIN), GERMINABILITY (% GERM.), POLLEN NUMBER, AND POLLEN GERMINABILITY FOR FEMALE AND MALE PLANTS OF *SALIX ARCTICA* INHABITING DIFFERENT HABITAT TYPES WITHIN AN ARCTIC STUDY POPULATION

HABITAT	REPRODUCTIVE EFFORT	SEEDS			POLLEN	
		No. per Catkin	% Stain	% Germ.	No. per Anther	% Germ.
Xeric ridge						
Female	2.48 (0.5)*	518 (79)*	21 (4)	2 (0.4)	—	—
Male	5.45 (0.2)*	—	—	—	473 (104)*	87 (19)*
Mesic meadow						
Female	7.10 (2.3)**	1077 (346)*	42 (9)	8 (1.4)	—	—
Male	1.52 (0.9)**	—	—	—	244 (59)*	53 (19)*

NOTE.—Values are means (standard deviations in parentheses). For reproductive effort,  $n = 15$ ; for seed and pollen parameters,  $n = 50$ . Differences between sexes or between sites within a particular sex tested by Student-Newman-Keuls multiple-range test. Adapted from Dawson and Bliss 1989.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .



$W_m$  are discussed below), then from table 3 we have

$$r_1 = 0.6, \quad r_2 = 0.14, \quad P = 0.30.$$

Table 4 shows plant reproductive performance by sex for the two habitats; the allocation measures strongly suggest that male fertility is absolutely better on the ridge, whereas the reverse is true for female fertility. This may be a conservative estimate for ridge males, who may also gain in pollen-dispersal ability relative to meadow males (as previously suggested in Dawson and Bliss 1989). Using reproductive effort as a rough estimate of  $W_m$  and  $W_f$ ,  $W_f = 7.10/2.48 \approx 3$ ,  $W_m = 1.52/5.45 \approx 0.3$ .

We do not know if this willow exhibits environmental sex determination (ESD), and although direct observation of the presence or absence of ESD is clearly the only conclusive evidence on this point, we think it useful to use present theory to predict just what life-history parameters would be required to account for the observed sex ratios in this willow. We then contrast the ESD adaptation hypothesis with the non-adaptation hypothesis that sex bias by habitat results simply from sex-differential mortality by habitat. Below, we treat  $r_2$  as if it were equal to zero (instead of 0.14); that is, the mesic meadow is treated as all female. After this exercise, we discuss limitations of our present ESD model.

First, let us treat the willow as if the generations were discrete (i.e.,  $q_{mi} = q_{fi} = 1$ ). Using the formulas of table 1, we find that for  $P \approx 0.30$ ,  $W_m$  and  $W_f$  must both be *much less than one* to account for the within-patch sex ratios. In other words, the observed values of  $W_f$  and  $W_m$  near 3 and 0.3 cannot possibly give the correct sex ratios with  $P$  near 0.30. Indeed, this lack of fit for the discrete-generation model led us to look at the situation for overlapping generations.

Before considering overlapping-generation ESD, a comment on just what we mean by the sex ratio is in order. What we count as an individual in table 3 for sex-ratio purposes is a ramet, because there is no simple way to recognize genets. The reproductive performance (table 4) is also on a per-ramet basis. For this reason, adult survival includes clonal propagation as well as individual survival. Thus, it may be that the sexes show different amounts of clonal growth by habitat. Under the "zero population growth" assumption of our model, the yearly mortality ( $q_i$ ) for a ramet includes both its chance of dying and the production of new ramets. In a stable population, individual ramet survival plus new ramet production may be used to calculate an effective mortality rate:  $q_i = 1 - S_i - h_i$ , where  $S_i$  is the probability of a single ramet's surviving and  $h_i$  is the number of new ramets produced per existing ramet, regardless of whether that ramet lives. In a stable population,  $q_i$  is less than one. The ESD model developed here also applies with this somewhat expanded definition of mortality rate; the appropriate sex ratio is now that of the ramets. In the following discussion, this expanded notion of mortality is implied. Of course, this assumption also implies that the unit of sex choice is the ramet.

We use the model to obtain parameter values for the patch mortality rates,  $q_{mi}$  and  $q_{fi}$ , which would account for the observed sex ratios,  $r_1 = 0.6$  and  $r_2 = 0.14$  ( $= 0$ ), given that  $P = 0.30$  and  $W_f$  and  $W_m$  are near 3 and 0.3, respectively. Clearly, we are in region III of table 2. Using the formula here for  $r_1$ , it is

straightforward to show that  $q_{m1} \approx 12q_{f1}$ . Because the mesic meadow is the female patch (type 2), from equation (5),

$$W_f q_{f1}/q_{f2} > W_m q_{m1}/q_{m2}.$$

We have estimates of each of these variables except  $q_{f2}/q_{m2}$ ; thus, we predict that  $q_{m2}$  is larger than  $1.3q_{f2}$ .

Because we do not know if this willow has ESD, it is interesting to contrast the ESD mortality requirement with the non-adaptation hypothesis that the patch-specific sex ratios result simply from differential mortality by sex, combined with the usual primary sex ratio of  $1/2$  (Charnov 1982). The differential mortality could affect immatures or adults. Since females are about six times as numerous as males in the mesic meadow, they must, of course, survive much better there. If all the differential mortality occurs among adults, we would have  $q_{m2} \geq 6q_{f2}$ . To produce an adult sex ratio of  $r_1 = 0.6$  from a primary sex ratio of 0.5 requires that males survive only slightly better than females in the xeric patch. Clearly, the mortality-rate predictions from the ESD model are rather different from these, which may allow a comparison of the two hypotheses. It is not immediately obvious just how plausible the ESD requirement is that  $q_{m1} \approx 12q_{f1}$ , unless  $q_{f1}$  is very near zero. However, even the non-adaptation hypothesis requires rather large mortality differences between the sexes, at least in the mesic meadow ( $q_{m2} \approx 6q_{f2}$ ).

As a final sex-ratio note, Elmqvist et al. (1988) have recently demonstrated that sex-ratio bias in northern willows may arise because specific selection of a particular gender by microtine rodents can occur. Although this may account for the sex ratios in the boreal willow with which they worked, it cannot account for the sex-ratio bias presented here for *S. arctica*. Herbivory on *S. arctica* is minimal in the high-arctic part of its range. It is fed upon only 2%–3% of the time by the lemming *Dicrostonyx groenlandicus* (see Fuller et al. 1977), though this can reach 12.3% in odd years. Muskoxen (*Quibos moschatus*), arctic hare (*Lepus arcticus*), and the arctic woolly-bear caterpillar (*Gynaephora groenlandica*) also may feed on the arctic willow, removing 2%–4% of the early-spring biomass; yet none of these herbivores has been shown to have sex-specific selection (Fuller et al. 1977; Hubert 1977; Smith and Wang 1977; Kukul and Dawson 1989). Finally, recent sex-ratio information gathered from Greenland populations of *S. arctica* corroborate the patterns presented here (R. M. M. Crawford and J. Balfour, pers. comm.).

The present model is probably overly simplified in at least two ways: the assumption of random mating and seed dispersal across patch types; and the lack of a true age structure (i.e., plants are not allowed to get larger in size as they age). Although we originally made these assumptions for mathematical convenience, they may not be too far off the mark for arctic willow. Mesic and xeric sites, although small in individual area, are numerous and show nearly even distribution over a small spatial scale (in meters); thus, wind-dispersed pollen and seed may well see the world as a fine-grained mixture of the two site types. The absence of age structure (= size structure) per se may also be approximately true, since our unit of sex-ratio analysis is the ramet and growth is mostly by the production of new ramets (Dawson 1987).

## SUMMARY

A population-genetics model is developed for environmental sex determination (ESD) in age-structured (overlapping-generation) populations. The model allows opportunities for reproduction by either sex to vary with spatial location (patch type) but not with age. The model is then applied to *Salix arctica*, a dioecious plant that shows habitat segregation by sex and a female-biased sex ratio. To explain the sex-ratio data, the model predicts that male mortality in both patch types is higher than female mortality and that the mortality ratio is much higher (about 12 times) in the dry patches. The sex-ratio data cannot be explained by current (e.g., discrete-generation) ESD theory. The "non-adaptation" hypothesis that the habitat-specific sex ratios are generated by sex-differential mortality is also discussed. The current model may aid in making decisions about whether habitat-specific sex ratios arise from ESD or from differential mortality, be it sex-specific or patch-specific.

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