

## EVOLUTIONARILY STABLE STRATEGY SEX RATIOS WHEN CORRELATES OF RELATEDNESS CAN BE ASSESSED

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**Abstract.**—In a structured population, with partial dispersal of offspring, there will be competition among related offspring for reproductive resources, or local resource competition (LRC), and, when the strength of this competition differs between the sexes, this will generate a sex ratio bias in favor of the sex with the least LRC. Standard models assume that the parent, in choosing the sex ratio, responds to the average level of LRC in the population. However, there will always be variation in the relatedness of the parent to her breeding neighbors, and this will affect the strength of the LRC experienced by her offspring. If she can assess this relatedness variation, or correlates thereof, it might be adaptive for her to respond by shifting the sex ratio bias of her offspring appropriately. We examine this question with an inclusive fitness model in a patch-structured population with partial dispersal of mated offspring. The analysis is complicated, but an overall conclusion is that, for moderate dispersal rates, natives should employ a more female-biased sex ratio than immigrants. We find that these results fit sex ratio data in a thrips *Hoplothrips pedicularius* population.

Suppose you are a female trying to choose the best offspring sex ratio. A general evolutionarily stable strategy (ESS) argument says that, at equilibrium, your marginal fitness through extra sons and extra daughters must be the same. If your offspring, in their efforts to grow and reproduce, interact with other individuals who are related to you, then, in calculating those marginal fitnesses, you must take these interactions into account. The results of inclusive fitness theory give us a powerful way to do this accounting. If the existence of an extra offspring causes a change in fitness of a relative, then this change, multiplied by the relatedness of the relative to you, must be included in your marginal fitness. These interactions may be of a variety of different kinds, competitive or cooperative, and intra- or intersexual. Such interactions are generally described as local competition (or cooperation) for reproductive resources.

Hamilton (1967) was the first to do a calculation of this type, and since that time a number of articles have appeared that calculate ESS sex ratios,  $s$ , in situations in which offspring must interact with relatives; most often these have involved competition among males for mates or among females for reproductive resources. In these models, a population structure is postulated, average relatednesses between interactants of different types are calculated, and then these relatednesses are assumed to be the ones that apply to the mother.

However, there will surely be considerable variation in the actual relatedness of the mother to a fixed class of interactants, and there is increasing evidence that females are able to perceive such differences in relatedness (or differences that correlate with relatedness) and respond to them. For example, C. Roeder, R. Harmsen, and S. Mouldey (unpublished manuscript) showed that, in populations of the two-spotted spider mite *Tetranychus urticae*, females are able to distinguish between patch mates that are sibs and nonsibs and between outbred sibs and inbred sibs. In such cases, one must ask how the ESS sex ratio should be altered in response to these perceived differences. As we shall see, this question turns out to be rather complicated, and our intuition can be tested by even the qualitative form of the answer.

In this article, we examine this question for Hamilton's (1967) local mate competition (LMC) model, with mating before dispersal, except that, as in other articles (Bulmer 1986; Frank 1986; Taylor 1988), we extend the model to allow only partial dispersal. Thus, we have local competition between males for mates and between females for reproductive resources (the home patch). It is important to note that we assume a fixed patch size (number of colonists). The question of response to relatedness in a population with variable patch size is more complicated and is not discussed here.

In this model there are a large number of patches, each colonized by  $N$  mated females, who each produce a large number of offspring. The offspring mate at random on the patch, and then the mated females either stay at home or disperse. In the latter case, they will, with some probability, establish themselves as immigrants on a random patch. After the dispersal phase, the remaining natives and new immigrants on each patch compete to occupy  $N$  breeding spots, and the cycle starts again. It is assumed that immigrants on any patch are unrelated to all other breeding females on that patch.

On the assumption that all females use the same sex ratio, the ESS sex ratio for this model depends, in general, on  $N$  and on the immigration rate,  $u$ , which is the average probability that a breeding female is an immigrant. The ESS sex ratio also depends on the genetic system. In a diploid population the sex ratio (proportion of males) is given by

$$s = \frac{N - 1}{2N} \quad (1)$$

and is independent of  $u$ . For the case,  $u = 1$ , of complete dispersal, this ratio was obtained by Hamilton (1967, 1979) and Taylor and Bulmer (1980). For arbitrary dispersal rates, this ratio was obtained by Bulmer (1986) and Frank (1986). Bulmer's computer calculations show a slight dependence on  $u$  when gene action is nonadditive. In a haplodiploid population, for the case,  $u = 1$ , of complete dispersal, the sex ratio is given by

$$s = \frac{(N - 1)(2N - 1)}{N(4N - 1)}, \quad (2)$$

obtained by Hamilton (1979) and Taylor and Bulmer (1980). For arbitrary dispersal rates, there is a slight dependence on  $u$ , as discussed by Bulmer (1986)

and Taylor (1988). They show that, as  $u$  approaches zero (isolated patches), the limiting value of the sex ratio is given by

$$s = \frac{(N-1)(3N-1)}{N(6N)}. \quad (3)$$

Sample values are calculated in table 1 for  $N = 4$  and  $N = 10$ .

These results assume that females all use the same sex ratio. But suppose they can recognize fellow natives or have some, even rudimentary, mechanism for estimating their relatedness to patch mates. In this case, how should the sex ratio respond to these perceptions?

We will formulate a general inclusive fitness condition for sex ratio equilibrium, which will show that this problem is mathematically complex. We will analyze this condition under two simple assumptions about what females are able to perceive. As in the standard models discussed above, females "know" (in an evolutionary sense) the average immigration rate, but, in each model below, we assume females have some additional information.

*Model 1.*—A female knows whether she is native or immigrant to her breeding patch.

*Model 2.*—A female can recognize fellow natives. Thus, she knows whether she is an immigrant, and, if she is a native, she knows how many natives and immigrants there are on the patch.

In these models, a female is not supposed to recognize kinship per se, as much as to perceive familiarity—in model 1, she recognizes her familiar colony, and, in model 2, she recognizes fellow natives. If dispersal typically occurs over a great distance, these perceptions should correlate with kin recognition, with model 2 offering a greater ability to distinguish levels of average relatedness.

We will then test for the presence and form of a sex ratio response to variation in correlates of relatedness, using data from the colonial thrips *Hoplothrips pedicularius* (Insecta: Thysanoptera). The data support the hypothesis that immigrant females of *H. pedicularius* produce a less female-biased sex ratio than do natives because they are breeding among nonrelatives.

#### THE THEORETICAL MODEL

##### *Summary of the Results*

In model 1, a female knows whether she is native or immigrant to her breeding patch but cannot tell the number of natives or immigrants on the patch. Thus, there are two sex ratios used in the population; natives use  $s$  and immigrants use  $t$ . In model 2, an immigrant knows she is an immigrant, and a native knows how many natives there are on her breeding patch. In this case there are  $N + 1$  sex ratios in use in the population, a native on a patch with a total of  $n$  natives uses sex ratio  $s_n$  ( $1 \leq n \leq N$ ), and all immigrants use sex ratio  $t$ .

Note that, in both models, on any particular patch, there are two types of individuals, natives and immigrants, and each type uses a common ratio. Note also that, in model 2,  $s_1$  may differ from  $t$ . On a patch with exactly one native,

TABLE 1

SAMPLE SEX RATIOS FOR THE STANDARD CASE IN WHICH CORRELATES OF RELATEDNESS CANNOT BE ASSESSED, FOLLOWING EQUATIONS (1)–(3)

|                   | $N = 4$ | $N = 10$ |
|-------------------|---------|----------|
| Diploid:          |         |          |
| All $u$ (eq. [1]) | .375    | .450     |
| Haplodiploid:     |         |          |
| $u = 1$ (eq. [2]) | .350    | .438     |
| $u = 0$ (eq. [3]) | .344    | .435     |

all females perceive the same (zero) relatedness to their patch mates, but the native has more information than the immigrants, because she knows what type of patch she is on. The immigrant ratio is always a compromise value over all patch types that an immigrant may be on.

The sex ratio condition (6) derived below is, in general, analytically intractable, and the results of computer calculation are presented in tables 2 (model 1) and 3 (model 2). We make a number of general observations.

*Average sex ratio.*—The average sex ratio over the entire population does not vary greatly with immigration rate and is close to the standard (no relatedness response) value given by equation (1) for diploidy and equations (2) ( $u$  large) and (3) ( $u$  small) for haplodiploidy (table 1).

*High immigration rates.*—For  $u$  close to 1, there is substantial agreement between natives and immigrants on a moderately female-biased ratio, close to that given by formulas (1) and (2), with natives exhibiting slightly more female bias. Thus, in model 1 (table 2)  $s$  and  $t$  are close, with  $s$  slightly more female biased, and in model 2 (table 3) the same is true of  $s_1$  and  $t$ . In model 2, when natives find themselves on a patch with an unusually large number of other natives ( $s_n$  for  $n$  large), they respond with an increased female bias. For small patch sizes ( $N = 4$ ) these conclusions hold for moderate immigration rates as well ( $u \geq 0.3$ ).

*Intermediate immigration rates.*—For  $0.1 \leq u \leq 0.9$  it is generally true, for both models, that the native sex ratio is more female biased than the immigrant ratio. This is, biologically, the most significant result, and it is supported by our experimental results.

*Low immigration rates.*—This is the case of patches that are mostly isolated and rely, for their continued genetic variance, on the occasional invasion by an immigrant. Here there are some interesting variations; there is a difference between the results of the two models and a striking difference between the diploid and haplodiploid systems.

In model 1 (table 2) the natives exhibit a modest female bias, in line with equations (1) and (3) (table 1), but the immigrants employ a strong male bias under diploidy and a larger female bias under haplodiploidy. The analysis below will show that the immigrant is doing what she can to move the average patch ratio toward  $1/2$  under diploidy and toward  $1/3$  under haplodiploidy. In model 2 (table 3), an all native patch shows a modest female bias, and in a mixed patch there is close agreement between natives and immigrants on a sex ratio near  $1/2$

TABLE 2

MODEL 1: AVERAGE INBREEDING COEFFICIENT  $F$  AND SEX RATIOS  $s$  FOR NATIVE FEMALES AND  $t$  FOR IMMIGRANT FEMALES IN DIPLOID AND HAPLODIPLOID POPULATIONS, FOR DIFFERENT IMMIGRATION RATES,  $u$ , AND  $N = 4$  AND  $N = 10$  MATED FEMALES ON A PATCH

| $u$           | $F$  | $s$  | $t$  | Population<br>Average<br>Sex Ratio |
|---------------|------|------|------|------------------------------------|
| $N = 4$ :     |      |      |      |                                    |
| Diploid:      |      |      |      |                                    |
| .001          | .976 | .372 | .623 | .372                               |
| .01           | .805 | .370 | .617 | .373                               |
| .1            | .296 | .356 | .563 | .377                               |
| .3            | .136 | .335 | .478 | .378                               |
| .5            | .098 | .329 | .424 | .377                               |
| .7            | .083 | .337 | .392 | .375                               |
| .9            | .078 | .358 | .377 | .375                               |
| .99           | .077 | .373 | .375 | .375                               |
| Haplodiploid: |      |      |      |                                    |
| .001          | .981 | .345 | .324 | .344                               |
| .01           | .836 | .345 | .338 | .345                               |
| .1            | .339 | .338 | .406 | .345                               |
| .3            | .150 | .322 | .408 | .348                               |
| .5            | .103 | .317 | .382 | .350                               |
| .7            | .085 | .322 | .362 | .350                               |
| .9            | .078 | .338 | .351 | .350                               |
| .99           | .077 | .349 | .350 | .350                               |
| $N = 10$ :    |      |      |      |                                    |
| Diploid:      |      |      |      |                                    |
| .001          | .933 | .455 | .677 | .456                               |
| .01           | .582 | .453 | .672 | .456                               |
| .1            | .125 | .436 | .630 | .455                               |
| .3            | .050 | .410 | .555 | .454                               |
| .5            | .035 | .400 | .503 | .452                               |
| .7            | .029 | .407 | .469 | .450                               |
| .9            | .027 | .430 | .452 | .450                               |
| .99           | .027 | .448 | .450 | .450                               |
| Haplodiploid: |      |      |      |                                    |
| .001          | .941 | .432 | .000 | .431                               |
| .01           | .624 | .434 | .075 | .431                               |
| .1            | .150 | .438 | .421 | .436                               |
| .3            | .058 | .414 | .493 | .438                               |
| .5            | .038 | .403 | .474 | .439                               |
| .7            | .030 | .406 | .452 | .439                               |
| .9            | .027 | .424 | .440 | .438                               |
| .99           | .027 | .437 | .438 | .438                               |

for diploidy and 1/3 for haplodiploidy. In both cases, the difference in the two genetic systems is accounted for by the asymmetry in reproductive value of the two sexes that is found in haplodiploidy but not in diploidy.

It is interesting that the sex ratio conflict between natives and immigrants that appears in model 1 is resolved in model 2. Some conflict is expected in model 1: natives are unaware of the presence of immigrants and choose their sex ratio to respond to the common case of an all-native patch. In model 2, natives know when there is an immigrant on the patch, but it is not at all clear that this should

TABLE 3

MODEL 2: SEX RATIO  $s_n$  ( $n \geq 1$ ) FOR NATIVE FEMALES ON A PATCH WITH A TOTAL OF  $n$  NATIVES, AND  $t$  FOR IMMIGRANT FEMALES ON ALL PATCH TYPES, IN DIPLOID AND HAPLODIPLOID POPULATIONS, FOR DIFFERENT IMMIGRATION RATES,  $u$ , AND  $N = 4$  AND  $N = 10$  MATED FEMALES ON A PATCH

| $u$           | $s_4$ | $s_3$ | $s_2$ | $s_1$ | $t$  | Population Average Sex Ratio |
|---------------|-------|-------|-------|-------|------|------------------------------|
| $N = 4$ :     |       |       |       |       |      |                              |
| Diploid:      |       |       |       |       |      |                              |
| .001          | .346  | .498  | .499  | .498  | .501 | .347                         |
| .01           | .345  | .484  | .490  | .485  | .509 | .350                         |
| .1            | .333  | .404  | .423  | .414  | .523 | .370                         |
| .3            | .311  | .346  | .367  | .385  | .466 | .377                         |
| .5            | .296  | .323  | .347  | .381  | .418 | .377                         |
| .7            | .286  | .311  | .337  | .378  | .389 | .376                         |
| .9            | .282  | .306  | .332  | .375  | .376 | .375                         |
| .99           | .281  | .305  | .332  | .375  | .375 | .375                         |
| Haplodiploid: |       |       |       |       |      |                              |
| .001          | .346  | .334  | .334  | .324  | .334 | .346                         |
| .01           | .345  | .342  | .341  | .342  | .341 | .345                         |
| .1            | .331  | .353  | .360  | .357  | .392 | .343                         |
| .3            | .309  | .328  | .341  | .353  | .401 | .348                         |
| .5            | .295  | .312  | .329  | .353  | .378 | .350                         |
| .7            | .286  | .303  | .322  | .352  | .360 | .350                         |
| .9            | .282  | .298  | .318  | .350  | .351 | .350                         |
| .99           | .281  | .298  | .318  | .350  | .350 | .350                         |
| $N = 10$ :    |       |       |       |       |      |                              |
| Diploid:      |       |       |       |       |      |                              |
| .001          | .445  | .498  | .489  | .472  | .507 | .446                         |
| .01           | .444  | .484  | .405  | .276  | .555 | .449                         |
| .1            | .438  | .437  | .160  | .000  | .640 | .456                         |
| .3            | .424  | .419  | .214  | .040  | .577 | .454                         |
| .5            | .415  | .412  | .323  | .250  | .513 | .452                         |
| .7            | .408  | .409  | .399  | .389  | .470 | .450                         |
| .9            | .405  | .407  | .431  | .445  | .452 | .450                         |
| .99           | .405  | .407  | .433  | .450  | .450 | .450                         |
| Haplodiploid: |       |       |       |       |      |                              |
| .001          | .445  | .340  | .358  | .391  | .322 | .444                         |
| .01           | .445  | .384  | .507  | .708  | .267 | .438                         |
| .1            | .437  | .437  | .461  | .485  | .420 | .436                         |
| .3            | .422  | .419  | .304  | .208  | .507 | .438                         |
| .5            | .413  | .412  | .348  | .297  | .481 | .439                         |
| .7            | .408  | .408  | .400  | .393  | .453 | .439                         |
| .9            | .405  | .406  | .424  | .435  | .440 | .439                         |
| .99           | .405  | .406  | .426  | .438  | .438 | .438                         |

NOTE.—For  $N = 10$ , the intermediate values of  $s_n$  are omitted but can be qualitatively interpolated.

lead to sex ratio agreement—after all, natives and immigrants typically have vastly different average relatedness to patch offspring. However, it turns out that these relatedness differences are the same for both male and female, and natives and immigrants should agree on the patch sex ratio.

The reader who wishes to omit the details of the model can skip to the Discussion.

### *The Inclusive Fitness Argument*

We define  $r_i$  to be the relatedness of a mother to her own offspring of sex  $i$ ,  $R_i$  to be the average relatedness of a mother to a random offspring of sex  $i$  on her patch,  $F$  to be the inbreeding coefficient,  $S$  to be the average patch sex ratio (proportion of males), and  $v$  to be the reproductive value of a female relative to that of a male. Under diploidy,  $v = 1$ , but, under haplodiploidy,  $v = 2$  (Price 1970; Hamilton 1972).

We calculate the inclusive fitness of a mother through extra male and female offspring. The fitness of a male is the product of mating success,  $(1 - S)/S$ , and average female breeding success, which we normalize at unity. An extra male has relatedness  $r_m$ , but each successful mating replaces an existing male with average relatedness  $R_m$ . Thus, the marginal inclusive fitness ( $W$ ) through a male is

$$W_m = (r_m - R_m) \frac{1 - S}{S}. \quad (4)$$

An extra female has relatedness  $r_f$  and acquires a mate with average relatedness  $R_m$ . Given that she is successful, she breeds on a random patch with probability  $u$  and breeds at home with probability  $1 - u$  and in this case displaces a fellow native with probability  $1 - u$ . The marginal inclusive fitness through a female is then

$$\begin{aligned} W_f &= (1 - u)[(vr_f + R_m) - (1 - u)(vR_f + R_m)] + u[vr_f + R_m] \\ &= vr_f - (1 - u)^2 vR_f + u(2 - u)R_m. \end{aligned} \quad (5)$$

*The equilibrium condition.*—The condition for sex ratio equilibrium is

$$W_m = W_f$$

and

$$(r_m - R_m) \frac{1 - S}{S} = vr_f - (1 - u)^2 vR_f + u(2 - u)R_m. \quad (6)$$

There are two qualifications here. One is that the only control a female has over the  $W_i$  is through her own sex ratio, and this affects  $S$  and  $R_i$  only in a limited fashion. Even by using an extreme sex ratio (0 or 1) a female may be unable to achieve equal fitness through sons and daughters, and in this case she should act to make  $W_m$  and  $W_f$  as close as possible. The second qualification is that a female will not generally have enough information to know the  $R_i$  and  $S$  values of the patch she is on; the best she can do is to choose her sex ratio so that  $W_m$  and  $W_f$  are equal on the average, where the average is taken over all possible situations that correspond to the information that she has.

Thus, making use of whatever cues are available to her, a female must estimate the average patch sex ratio and her average relatednesses to random patch off-

spring, and both these estimates can be complicated. First of all, the average patch ratio is determined by the sex ratios used by her patch mates, and this depends on what set of relatednesses *they* perceive. In addition, the average relatednesses,  $R_i$ , also depend on the various sex ratios used by her different patch mates. For example, if those more closely related to her make mostly females and those more distantly related make mostly males, this will cause  $R_f$  to be higher and  $R_m$  to be lower than she might otherwise estimate from her average relatedness to her patch mates. In mathematical terms, this dependence of  $R_i$  on the sex ratios used by other mated females on the patch typically makes the problem analytically intractable.

*Stability of the equilibrium.*—Condition (6) always gives a stable equilibrium point. For example, if a mutant female increased her production of males, this would affect three of the parameters in equations (4) and (5):  $S$  and  $R_m$  would both increase, and  $R_f$  would decrease. The first two cause  $W_m$  to decrease, and the last two cause  $W_f$  to increase. Thus,  $W_m$  becomes lower than  $W_f$ , and the female could increase her inclusive fitness by decreasing her male production.

*The effect of relatedness on sex ratio.*—Equation (6) can be used to display the different routes through which relatedness to patch mates can affect a female's sex ratio. It is useful to think in terms of a four-way classification of the effects of a female's offspring on the fitness of the other offspring with which they interact (Taylor 1981): sons on males, sons on females, daughters on males, and daughters on females. Condition (6) exhibits three of these four possibilities.

i) The negative effect of sons on males: the  $R_m$  term in  $W_m$ . This is commonly called local mate competition: an extra son competes with random male patch offspring requiring the  $r_m$  relatedness to be discounted by the average relatedness  $R_m$  of these male offspring.

ii) The negative effect of daughters on females: the  $R_f$  term in  $W_f$ . This is commonly called local resource competition (LRC), in this case, competition among related females for breeding space. An extra daughter competes with random female patch offspring requiring the  $r_f$  relatedness to be discounted by the average relatedness  $R_f$  of these female offspring. This effect is greatest at low immigration rates and vanishes with complete dispersal ( $u = 1$ ).

iii) The positive effect of daughters on males: the  $R_m$  term in  $W_f$ . Essentially, extra females provide extra breeding opportunities for males. This effect is greatest at high immigration rates and vanishes with zero dispersal ( $u = 0$ ); in this case, a fixed number of female offspring will win breeding spots on the patch, so an extra female offspring cannot increase male reproductive success on the patch.

According to equation (6), increased relatedness to patch mates should select for greater female bias through i and iii and for greater male bias through ii. The question of whether high relatedness within a patch should cause a male or a female bias in the sex ratio can be answered only by assessing the relative strength of these opposing factors.

### *Numerical and Analytical Results*

The equations to calculate the relatedness coefficients are developed in Appendix A, and the results of computer calculations of the equilibrium condition (6) are presented in tables 2 and 3.



*Intermediate immigration rates.*—The numerical results in tables 2 and 3 generally show a native sex ratio  $s$  or  $s_n$ , which is somewhat more female biased than the immigrant sex ratio, for both models 1 and 2 and both genetic systems. As discussed below, this situation appears to correspond to the parameter values found in *Hoplothrips pedicularius*.

An analytic analysis is available for the two extreme cases of high and low immigration rates.

*High immigration rates* ( $u \approx 1$ ).—This case is not hard to understand. If we set  $u = 1$  in the equilibrium equation (6) and solve for  $S$ , we get

$$S = \frac{r_m - R_m}{r_m + vr_f}. \quad (7)$$

When  $u \approx 1$ , most patches will have  $N$  immigrants or  $N - 1$  immigrants and one native, and, on such patches (if the sex ratio is uniform), all individuals will experience the same average value of  $R_m$ , and so, from equation (7) (which will approximately hold), there will be no disagreement over the value of  $S$ . Thus, on such patches we expect a uniform sex ratio: in model 1, we expect  $s \approx t$ , and in model 2, we expect  $s_1 \approx t$ , and these should all be close to the values given by equations (1) and (2). This is observed by comparing tables 2 and 3 with table 1. In model 2, on patches with more than one native (which happens rarely), the natives experience higher  $R_m$  values, causing them to want a lower patch ratio, and thus we expect a somewhat greater female bias in  $s_n$  for  $n > 1$ . This is understood in terms of the above discussion of the effect of relatedness on sex ratio. Since  $u$  is close to 1, the local resource competition factor (ii) is small, leaving us with only factors i (local mate competition) and iii (females as a resource for males), both of which promote a female bias with increasing relatedness.

*Low immigration rates* ( $u \approx 0$ ).—If we set  $u$  equal to zero in the equilibrium equation (6), we get

$$(r_m - R_m) \frac{1 - S}{S} = v(r_f - R_f). \quad (8)$$

We discuss the two models separately.

*Model 1, natives.*—Most natives are on an all-native patch, which makes  $r_i = R_i = 1$  (to zeroth order in  $u$ ), and equation (8) reads  $0 = 0$  and gives no information. The analysis in this case requires us to look at the first-order terms (in  $u$ ) of equation (6). Since most individuals in the population are native, we expect the results of this analysis to be very close to those of the standard model in which relatedness cannot be assessed. A comparison of tables 1 and 2, for small  $u$ , shows this to be the case.

*Model 1, immigrants.*—Recall that the results here are unexpected and completely different for the two genetic systems, with a male bias under diploidy and a substantial female bias under haplodiploidy. An immigrant is most likely to be on a patch with  $N - 1$  natives, and, with the approximation  $r_i = 1$ , her relatednesses to random male and female offspring on the patch (which must take account of the fact that she may use a different sex ratio from the natives) will be given by  $R_m = t/NS$  and  $R_f = (1 - t)/N(1 - S)$ . If we put these into equation (8) we get

$$\text{Immigrant: } \left( \frac{S}{1-S} \right)^2 = \frac{1}{v} \left( \frac{s}{1-s} \right). \quad (9)$$

This is an approximation to the equilibrium equation for an immigrant, when  $u$  is small. It is noteworthy that it involves the average patch sex ratio and the native sex ratio, and we know that the latter is approximately given by equations (1) and (3). Since the immigrant has no control over  $s$ , she can only hope to satisfy the equation through her effect on  $S$ . We look at the two genetic systems separately.

Under diploidy,  $v = 1$ , and, if  $s$  were equal to  $1/2$ , equation (9) would hold with an average patch sex ratio of  $1/2$ . But in this case,  $s$  is less than  $1/2$  (eq. [1]), and this requires  $S$ , and hence  $t$ , to be greater than  $s$ . Indeed, since most often an immigrant will be on a patch with  $N - 1$  natives, the average patch sex ratio is fairly insensitive to changes in  $t$ , especially when  $N$  is large, and she may have to use a substantial male bias to make equation (9) hold. This is seen to be the case in table 2, for  $u \leq 0.1$ : the immigrant ratio shows a substantial male bias, which actually increases with patch size  $N$ . Under haplodiploidy,  $v = 2$ , and the very same argument gives  $S = 1/3$  as the target value for an immigrant. In this case, the native ratio is less female biased than  $1/3$ , and the immigrants must actually employ a ratio  $t$  more female biased than  $s$  (table 2,  $N = 4$ ,  $u \leq 0.01$  and  $N = 10$ ,  $u \leq 0.1$ ).

In summary, in model 1, when immigration is rare, there is a sex ratio conflict between natives and immigrants. Natives employ a modest female bias, and immigrants use a male bias under diploidy and a more extreme female bias under haplodiploidy.

*Model 2, all-native patch.*—In this case, the natives know what type of patch they are on. On an all-native patch, as above,  $r_i = R_i = 1$  to zeroth order in  $u$ , and equation (8) reads  $0 = 0$ . An analytic treatment, which looks at the first-order terms in  $u$  (App. B), gives the result

$$s_N = \frac{1}{2} \frac{(N-1)^2}{(N-1)^2 + N} \quad (10)$$

for both diploid and haplodiploid populations. For  $N = 4$ , this formula gives  $s_N = 0.346$  and for  $N = 10$ , we get  $s_N = 0.445$ , and the data of table 3 for  $u = 0.001$  match these values exactly. Here, it is mathematically interesting that the two genetic systems give the same result, unlike the case of high immigration ( $u \approx 1$ ) for which equations (1) and (2) give different, though similar, results.

*Model 2, mixed patch.*—If there are  $n$  natives and  $N - n$  immigrants on a patch, an argument similar to that which leads to equation (9) gives the equilibrium conditions

$$\text{Native: } \left( \frac{S}{1-S} \right)^2 = \frac{1}{v} \left( \frac{t}{1-t} \right) \quad (11)$$

and

$$\text{Immigrant: } \left( \frac{S}{1-S} \right)^2 = \frac{1}{v} \left( \frac{s_n}{1-s_n} \right). \quad (12)$$

Note that the equation for a native to be at equilibrium involves the immigrant ratio, and the immigrant equation involves the native ratio. As before, the only way each party can achieve equilibrium is through its effect on the average ratio  $S$ . Equations (11) and (12) have the simultaneous solution

$$s_n = t = \frac{1}{1 + v}. \quad (13)$$

This is a striking result. On a mixed patch, there is no conflict over sex ratio between natives and immigrants; they should have a common ratio, independent of patch size  $N$  but dependent upon the genetic system, being  $1/2$  for diploidy and  $1/3$  for haplodiploidy. This result, which is observed in table 3, for small values of  $u$  is at first surprising, because natives perceive much higher values of average relatedness than do immigrants. However, it turns out that male and female offspring are affected in the same way, and the ratio of  $r_m - R_m$  to  $r_f - R_f$  is the same for both natives and immigrants; hence in equation (8) they equilibrate at the same average patch ratio.

*Pathologies.*—Over some ranges of  $u$  there are behaviors, such as the variation in immigrant sex ratio with intermediate values of  $u$  in table 3,  $N = 10$ , haplodiploid, that are difficult to analyze. However, certain unexpected intermediate results can be explained as belonging to individuals who find themselves in rare situations. As an example, consider the extreme result  $s_1 = 0$  in table 3,  $N = 10$ , diploid,  $u = 0.1$ . To explain this, note that, with this value of  $u$ , an immigrant typically finds herself on a patch with a large number of natives, and her ratio is chosen to respond to this. These natives use a slightly female-biased ratio, and the immigrant responds with a male-biased ratio of  $t = 0.64$ . Thus, a native who finds herself on a patch with nine immigrants (a very rare event) will expect a male-biased ratio from her patch mates and responds by making all females. The effect is caused by an information asymmetry—she knows more than the immigrants, who are unlucky to find themselves on a patch with only one native, and takes advantage of them. Patches that have only two or three natives on them are also rare, but here the natives do make some males, though not many ( $s_2 = 0.16$  and  $s_3 = 0.28$ ). This analysis offers an explanation for the otherwise curious result of an increase in  $s_n$  with  $n$ , that is, a decrease in female bias among natives with increasing relatedness. This pattern is observed for  $N = 10$  for  $0.1 \leq u \leq 0.7$  (table 3).

*Mating after dispersal.*—An alternative model has females mating before dispersal, and negligible male dispersal, and this behavior might provide a better fit to the thrips population described below. The equations for this model are quite similar. In fact, for  $u \approx 0$ , the equilibrium equation is identical to equation (8), and the sex ratio results will be the same as those described above. For  $u \approx 1$ , the results are qualitatively similar to those described above. The equilibrium equation, the analogue of equation (7), is

$$S = (1 - \bar{S}) \frac{r_m - R_m}{vr_f}, \quad (14)$$

where  $\bar{J}$  is the population-wide average sex ratio. With no relatedness response, the ESS sex ratio turns out to be

$$s = \frac{N - 1}{2N - 1} \quad (15)$$

for both diploid and haplodiploid populations—this is the analogue of equations (1) and (2)—and, as above, this is expected to be the ratio used by immigrant females. Rare natives, on the other hand, will experience increased relatedness to random male offspring on the patch and will use a more female-biased ratio, just as discussed above.

#### A TEST OF SEX RATIO RESPONSE TO RELATEDNESS VARIATION

The theory described above predicts that, under a wide range of conditions as regards relatedness and immigration rates, females should produce different sex ratios in accordance with their perception of whether they are breeding with relatives of varying degree or with nonrelatives. As described below, *Hoplothrips pedicularius* provides a useful test of the theory because it lives in subdivided populations (such that within-group relatedness is sometimes quite high), and female immigration into established colonies appears to be reasonably frequent (such that relatedness perception and actuality should often vary between natives and immigrants). The data collected to test the theory and its assumptions were threefold.

Field data were collected to measure the natural number and sexes of adults and wing morphs of pupae and to determine the relationship, among colonies, between birth sex ratio and immigration rate, with immigration rates estimated as proportion of breeding females in a colony that were dealate (formerly winged females, which are putative immigrants) rather than wingless. These data were designed to detect differences in offspring sex ratio between natives and immigrants.

Allozyme analyses were performed on these same field populations to estimate relatedness and immigration presence and rates. These data provide estimates of the important model parameters.

Laboratory experiments were conducted, with field-collected females, to determine (a) whether females adjust offspring sex ratio in response to relatedness to colony mates, and (b) whether wingless females and dealate females produce different offspring sex ratios. These data provide information on perception of relatedness and its correlates.

#### *The Life History of Hoplothrips pedicularius*

In southern England, the thrips *Hoplothrips pedicularius* lives in colonies of from several to hundreds of individuals under the bark of trees infested with *Stereum* fungus and feeds on mycelium (Crespi 1986). This species provides a useful test of the sex ratio modeling for three main reasons. First, *H. pedicularius* lives in semi-isolated demes whose resident adult populations remain fairly constant over multiple generations because a large fraction of newly eclosed adults

disperse. As a result, the equilibrium colony size assumption of the model may be approximately met. Second, this species is wing polymorphic in both sexes, such that wingless (brachypterous) adults are recognizable as being native to their home colonies, while winged adults, which in this species shed their wings upon initiation of breeding and are referred to as dealate, may be either natives or immigrants. If females or males immigrate to established colonies of nonrelatives, then within-colony relatedness is expected to vary substantially among colonies, which may select for a sex ratio response. Third, because this species is haplo-diploid (Crespi 1993), females can facultatively determine the sex of their offspring, which allows a response to sex ratio selection. In *H. pedicularius*, winged females probably mate before dispersal, but, if some females immigrate into established colonies, they probably mate after dispersal as well.

### *Collections and Experimental Methods*

To analyze the relation between the theory developed above and the life history of *H. pedicularius*, it is necessary to (1) measure genetic relatedness, to determine whether or not colonies are made up of relatives, (2) establish whether dispersing females sometimes immigrate into other established colonies, and (3) measure sex allocation ratios. During the spring and summer of 1990, colonies of *H. pedicularius* were collected from dead logs in woodlots in Oxfordshire (Wytham Wood, Bagley Wood, Shotover Wood, and Wychwood Forest) and Kent (Badger's Mount and Silwood Park). The adults were removed from the colonies, their wingedness status was recorded as either wingless (brachypterous) or dealate, and they were frozen at  $-80^{\circ}\text{C}$ . If colonies contained pupae, they were allowed to become adult and their sex and wingedness status were recorded (wingless or winged). If colonies contained eggs, they were allowed to hatch in  $50 \times 9$ -mm tight-sealing petri dishes and the sex of a sample of the first-instar larvae was determined by counting the number of setae on their ninth abdominal segment (in the family Phlaeothripidae, female first-instar larvae have two pairs of setae on this segment and males have three pairs) (Crespi 1993).

Horizontal starch-gel electrophoresis of adults from the Wytham Wood and Bagley Wood populations confirmed male haploidy and revealed two useful allozyme polymorphisms, for glucose-phosphate isomerase (GPI) and the peptidase for glycine-leucine (PEP). Both loci were analyzed for eight to 17 females from 16 colonies (183 individuals in all), and GPI was analyzed for two to 10 males from 21 colonies (163 individuals in all). The method of Queller and Goodnight (1989) was used to estimate average relatedness and  $F$  statistics. Because the woodlots were genetically differentiated ( $F_{st}$  of 0.128 for females and 0.092 for males), relatedness was calculated taking account of population subdivision, and, because colonies varied in number of adults, colonies rather than individuals were weighted equally.

The possibility of a direct sex ratio response to relatedness variation was tested experimentally by allowing field-collected wingless females to breed on mycelium-infested wood in  $50 \times 9$ -mm petri dishes containing either females from the same colony (presumed related) or females from a different colony (presumed less related than the same-colony treatment). Females were allowed to breed

either in pairs or in groups of four with one treatment comprising all four from the same-source colony and the other treatment comprising two females from each of two different colonies (from the same woodlot). The females were allowed to breed for 21 d, and the first-instar larvae from their eggs were sexed soon after hatching. If females adjust sex ratio in response to relatedness, then we might expect the birth sex ratio to differ between the treatment with females from the same-source colony and the treatment with females from different-source colonies.

To assess whether females immigrate into established colonies, we compared the distributions of GPI genotypes between wingless and dealate females from the same colony, for the 14 colonies containing females of each wing morph (data from the PEP locus were insufficient for this test). Because expected values in some cells of the  $2 \times 3$  tables were sufficiently low to invalidate a  $\chi^2$  test or a  $G$  test, we used an exact test for multiway tables. Tables in which individuals of one genotype were absent were collapsed to  $2 \times 2$  and analyzed with Fisher's exact test. If winged females immigrate into established colonies of nonrelatives, then the genotype distributions of natives and immigrants should differ in some colonies.

We measured the birth sex ratios produced by wingless females and by dealate females in the laboratory to determine whether they differ. The females were collected in the field from two large colonies and allowed to breed individually in  $50 \times 9$ -mm petri dishes containing mycelium-infested wood. After 21 d of breeding, their eggs were allowed to hatch and the first-instar larvae were sexed. Only data from females that had laid 20 or more eggs were retained for the analysis.

All data that ranged between zero and one were arcsine transformed prior to analysis, to better satisfy the assumptions of parametric tests.

#### *Relatedness and Correlates of the Birth Sex Ratio*

*Field data.*—A total of 98 colonies were collected, which contained a total of 1,153 wingless (brachypterous) males, six dealate males (mean 12.0 total males per colony,  $SD = 0.96$ , range 0–36), 2,395 wingless females, and 368 dealate females (mean 28.2 total females per colony,  $SD = 2.14$ , range 1–99). Pupae were found in 21 colonies, and they comprised 85 wingless males, 17 winged males, 127 wingless females, and 72 winged females. Samples of newly hatched larvae were sexed in 61 colonies; these sex ratios estimate colony-specific sex allocation ratios but cannot be used to estimate the population-wide sex allocation ratio because not all larvae were sexed.

Among field colonies, the birth sex ratio (percentage of males) was significantly positively correlated with the percentage of females that were dealate in colonies ( $r = 0.28$ ,  $P < .05$ ,  $N = 61$ ), and this relationship was due primarily to a lack of colonies with a high percentage of females dealate and a female-biased sex ratio (fig. 1). These data suggest that the sex allocation ratio is less female biased in colonies with a higher proportion of females dealate.

*Allozyme analysis.*—For adult females, average relatedness was significantly above zero, 0.49 with a jackknifed standard error of 0.12, and  $F$  values were

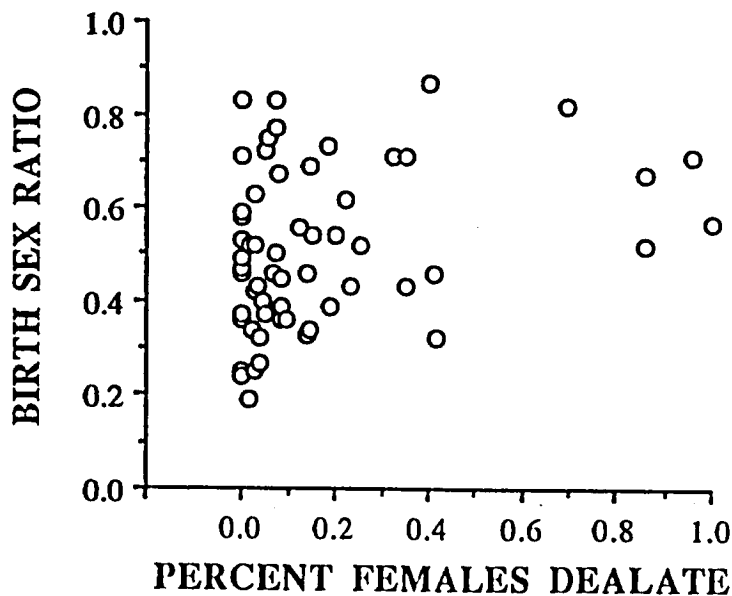


FIG. 1.—Among field-collected colonies of *Hoplothrips pedicularius*, the percentage of females dealate (that had wings and shed them rather than being wingless at eclosion) is positively correlated with the birth sex ratio.

consistent with substantial population subdivision and inbreeding ( $F_{st} = 0.086$ ,  $F_{it} = 0.259$ ,  $F_{is} = 0.189$ ). For males, average relatedness was 0.40 (jackknife SE = 0.134), and  $F_{st}$  was 0.093, similar to the value in females. Dealate females and wingless females differed significantly in genotype frequency in three of 14 colonies, and overall by Fisher's combining test ( $\chi^2 = 46.1$ ,  $df = 28$ ,  $P < .025$ ). These differences suggest that at least some dealate females had immigrated to the colonies in which they were found.

*Laboratory experiments.*—Wingless females breeding in the laboratory with other females from the same source colony (and presumably related to them) produced birth sex ratios not significantly different from females breeding with other females from a different source colony (and presumably unrelated). (Two females: same colony, 0.364 males, SD = 0.100,  $N = 17$ ; different colonies, 0.352 male, SD = 0.131,  $N = 10$ ,  $t = 0.23$ ,  $P > .50$ . Four females: same colony, 0.322 male, SD = 0.116,  $N = 11$ ; different colonies, 0.407 male, SD = 0.162,  $N = 4$ ,  $t = 1.12$ ,  $P > .25$ .) However, the experiment testing for a birth sex ratio difference between wingless females and dealate females showed that dealate females produced a significantly less female-biased sex ratio (mean, 0.386 male, SD = 0.143,  $N = 15$ ) than did wingless ones (mean, 0.288 male, SD = 0.084,  $N = 17$ ;  $t = 2.4$ ,  $P < .025$ ). This mean sex ratio difference, between wingless and dealate females, was found within each of the two colonies from which females for this experiment were taken (mean differences of 0.07 and 0.13).

## DISCUSSION

*Conditional Sex Ratio Response*

There has been considerable work on conditional sex ratio response to varying levels of information. A good example is found in a patch-structured population, such as the one we are considering here, in which there is variation in the number of hosts on a patch, and therefore in the strength of local competition among patch offspring. Hamilton (1967) was the first to pose the problem of how a female who was sensitive to host number should alter her sex ratio; Werren (1980, 1983) extended the theory and provided some excellent data, and Frank (1985) added an array of models in the context of fig wasps. More recently Stubblefield and Seger (1990) considered a collection of patch-structured models, both population-genetic and inclusive-fitness, in which a female may have information about her own fecundity and/or that of the other females breeding on the patch. In all such models, the question of what information is available to whom is crucial, because the fitness of any sex ratio strategy will depend on the strategies of the other females, so that a female's assessment of local conditions must also include a judgement of the assessment capabilities of the other females on her patch.

In this article we began with the question of finding the ESS sex ratio in a simple patch-structured population, with partial dispersal of mated females between patches, when females can assess, to some extent, their level of relatedness to patch mates. In this case, in estimating her patch mates' perception of their relatedness to one another, a female must take an average over all situations that correspond to her own relatedness perception, and, when  $N$  is large, the number of possibilities for different relatedness relationships are unwieldy. As a simplification, we have assumed that individuals can perceive not relatedness, but familiarity—of the native colony (model 1) or of fellow natives (model 2). Even with this assumption, the sex ratio equations cannot be analytically solved except in the extreme cases of high or low immigration rates.

The numerical results of the theoretical model are summarized for  $N = 4$  and  $N = 10$  in tables 2 (model 1) and 3 (model 2). For intermediate immigration rates, which appear to apply to the thrips population studied here, the sex ratios are generally female biased, with the native ratios showing a greater bias than the immigrant ratios. In these models, there is local competition for reproductive resources among both male and female offspring, but the female bias suggests that the intermale competition is more intense. Among natives, whose offspring may be related to other patch offspring, the local competition among both sexes is more intense, and this tends to have the effect of increasing the female bias. For large immigration rates ( $u \approx 1$ ) this effect is small and there is little difference between native and immigrant sex ratios. For low immigration rates ( $u \approx 0$ ) the results do not fit this pattern, and there is a striking difference between the diploid and haplodiploid results. For example, in model 1, natives always show a female bias and immigrants show a male bias under diploidy and a stronger female bias under haplodiploidy.



*Relatedness, Sex Ratio, and Immigration in Hoplothrips pedicularius*

The finding, from the allozyme analysis, of significant and substantial average relatedness in males and females of *Hoplothrips pedicularius* indicates that LMC and LRC effects are likely to be strong, with males competing for ovipositing females (Crespi 1986) and females competing for breeding space in colonies where the number of offspring produced each generation can greatly exceed the number of breeding adults that the colony can support. The differences in genotype frequencies between dealate and wingless females in some colonies supports the hypothesis that some dispersing females immigrate into established colonies to breed therein, presumably with nonrelatives. The percentage of breeding females that are dealate, 368 of 2,763 (13%), represents an approximate upper limit to the immigration rate. The finding that, in the field, a larger percentage, 35%, of females collected as pupae developed wings suggests that some females disperse and attempt to initiate new colonies, some disperse and join existing colonies (as suggested by the genetic data), and others, perhaps, remain in their natal colony to breed.

The lack of a difference, in the laboratory experiments, in offspring sex ratio between females breeding with colony mates and with females from other colonies suggests that females do not assess local relatedness variation directly. Such a lack of kin recognition per se is consistent with findings from other animals, in which kin recognition normally occurs through responses to correlates of relatedness such as nest-mate status (Grafen 1990).

An obvious cue, correlated with relatedness, that females of *H. pedicularius* might use to adjust offspring sex ratio is immigration status. Thus, a simple explanation for the two main results: (1) the difference in offspring sex ratio between wingless and dealate females found in the experiment and (2) the positive correlation in the field between percentage of females dealate and colony birth sex ratio is that immigrants perceive that they are breeding with nonrelatives and produce a less female-biased sex ratio than do the natives. Moreover, immigrants have an obvious cue as to their local relatedness situation: they have dispersed and joined another colony. The lack of a kin recognition effect in the laboratory experiments suggests that natives do not perceive and react to the presence of immigrants by adjusting their offspring sex ratio. Thus, model 1 may fit the situation in *H. pedicularius* better than does model 2. However, the two models do predict similar differences in offspring sex ratio between natives and immigrants over much of the space of the parameters (tables 2 and 3). Two sources of evidence, the correlation in the field between birth sex ratio and percentage of females dealate, and the difference in the laboratory between the sex ratios produced by wingless and dealate females, are therefore consistent with the predictions of both models.

Is there a quantitative fit of the data to predictions of model 1 or model 2? The magnitude of the offspring sex ratio difference, in the laboratory experiments, between dealate females (0.386 male) and wingless females (0.288 male) of *H. pedicularius*, and the values of the sex ratios themselves, are close to those found for

the theoretical cases of  $u = 0.1-0.5$  for  $N = 4$  and  $u = 0.3$  for  $N = 10$  under model 1, and, for model 2,  $u = 0.1-0.3$  for  $N = 4$  and  $u = 0.3-0.5$  for  $N = 10$  (tables 2 and 3). In addition, for both the  $N = 4$  and  $N = 10$  cases in model 1, the observed  $F$  value for females (0.086) is within the expected range for  $u$  between 0.1 and 0.5 (0.058–0.339). The estimated maximum immigration rate in field colonies, 0.13, is included by some of the values for  $u$  above but is quite close to their lower limit, and, although many colonies are in the range of  $N = 4$  to  $N = 10$ , many others are much larger.

These comparisons between observed and predicted parameters suggest that either model 1 or model 2 may realistically apply to *H. pedicularius* sex ratios and that females do indeed adjust offspring sex ratio in response to variation in correlates of relatedness. More precise testing of the models requires field or laboratory experiments in which female immigrant and native status are controlled, more detailed knowledge of the genetic structure of field populations, and experiments designed to determine whether native females can detect the presence of immigrants.

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#### APPENDIX A

##### CALCULATION OF RELATEDNESS COEFFICIENTS

A patch with  $n$  natives and  $N - n$  immigrants ( $0 \leq n \leq N$ ) is said to be of type  $n$ . On the assumption that offspring disperse independently of one another, patch type  $n$  has frequency,  $q_n$ , given by

$$q_n = \binom{N}{n} (1-u)^n u^{N-n}.$$

We extend the notation of the main text as follows:  $s_{ni}$  is the proportion of sex  $i$  offspring of a native female on patch type  $n$ , and  $S_{ni}$  is the average proportion of sex  $i$  offspring on patch type  $n$  ( $1 \leq n \leq N$ ). Also,  $t_i$  is the proportion of sex  $i$  offspring of an immigrant female, and  $k_{ni} = ns_{ni}/NS_{ni}$  is the probability that a random sex  $i$  offspring on a type  $n$  patch has native parents.

The coefficient of consanguinity between two individuals  $y$  and  $x$  is defined as the probability that random alleles from  $y$  and  $x$  are identical by descent (Crow and Kimura 1970, p. 68). We define the following coefficients of consanguinity:  $r_{ij}$ , between sibs of sex  $i$  and sex  $j$ ;  $b_{ij}$ , between offspring of sex  $i$  and sex  $j$  born of different native parents on the same patch;  $g_{ij}$ , the average coefficient over all patch types between offspring of sex  $i$  and sex  $j$  born on the same patch;  $F = g_{mf}$ , the average inbreeding coefficient;  $r_i$ , between a mother and her offspring of sex  $i$ ;  $R_i$ , between a mother and a random offspring of sex  $i$  on her breeding patch. The last coefficient will depend on the patch type and on whether the mother is native or immigrant.

The  $g_{ij}$  are found by solving the recursive formulae:

$$g_{ij} = \sum_{n=0}^N q_n \left[ k_{ni} k_{nj} \left( \frac{1}{n} r_{ij} + \frac{n-1}{n} b_{ij} \right) + (1 - k_{ni})(1 - k_{nj}) \frac{1}{N-n} r_{ij} \right],$$

where the coefficients of consanguinity are found in terms of the  $g_{ij}$  as follows:

Diploid:

$$r_i = r_{ij} = (1 + 3F)/4$$

and

$$b_{ij} = (g_{mm} + 2g_{mf} + g_{ff})/4.$$

Haplodiploid:

$$r_m = r_{mm} = (1 + F)/2,$$

$$r_f = r_{mf} = (1 + 3F)/4,$$

$$r_{ff} = (3 + 5F)/8,$$

$$b_{mm} = g_{ff},$$

$$b_{mf} = (g_{mf} + g_{ff})/2,$$

and

$$b_{ff} = (g_{mm} + 2g_{mf} + g_{ff})/4.$$

For both diploidy and haplodiploidy, on patch type  $n$ ,

$$\text{Native mother: } R_i = s_{ni}[r_i + (n-1)b_{mi}]/NS_{ni} \quad (n \geq 1)$$

and

$$\text{Immigrant mother: } R_i = t_i[r_i]/NS_{ni} \quad (n < N).$$

Here we note that, in both cases (diploid and haplodiploid),  $b_{mi}$  serves as the coefficient between a native mother and a random sex  $i$  offspring from another native mother.

We point out that the coefficients  $r_i$  and  $R_i$  here refer to consanguinity but in the main text these represent relatedness coefficients. In fact, the relatedness of the actor  $x$  to the recipient  $y$  is defined as

$$R_{x \rightarrow y} = \frac{f_{yx}}{f_{xx}},$$

where  $f_{yx}$  is the coefficient of consanguinity between  $y$  and  $x$ . In our sex ratio model,  $x$  is always a mated female, and the denominator is always the same, and, in this case, relatedness coefficients can be replaced by the numerators  $f_{yx}$ .

## APPENDIX B

### DERIVATION OF $s_N$

We derive equation (10) for the sex ratio  $s_N$  on an all-native patch for a model 2 diploid population when the immigration rate is small.

The inbreeding coefficient, to first order in  $u$ , is

$$F = 1 - 8(N-1)u,$$

found as the solution to the recursion

$$F = \frac{1}{N} \left[ \frac{1+3F}{4} \right] + \frac{N-1}{N} (1-u)^2 F.$$

The logic of this equation is that two offspring born on the same patch are either sibs (probability  $1/N$ ) or nonsibs. In the second case, if they both have native parents (probability  $(1 - u)^2$ ), the coefficient is  $F$  (of the previous generation).

By a similar argument, on an all-native patch, the coefficient between a mother and a random patch offspring is

$$R = \frac{1}{N} \left[ \frac{1 + 3F}{4} \right] + \frac{N-1}{N} F = F + \frac{1-F}{4N}.$$

The inclusive fitnesses, from equations (4) and (5), are

$$W_m = (r - R) \frac{1 - S}{S}$$

and

$$W_f = r - R + 2u(R + R) = r - R + 4u,$$

ignoring  $u^2$ , where  $r = (1 + 3F)/4$ . If this is put into the equilibrium equation (6), equation (10) emerges. Equation (10) also applies to a haplodiploid population, but the derivation of the coefficients of consanguinity is more complicated (Taylor 1988).

#### LITERATURE CITED

- Bulmer, M. G. 1986. Sex ratio theory in geographically structured populations. *Heredity* 56:69-73.
- Crespi, B. J. 1986. Territoriality and fighting in a colonial thrips, *Hoplothrips pedicularius*, and sexual dimorphism in Thysanoptera. *Ecological Entomology* 11:119-130.
- . 1993. Sex ratio selection in Thysanoptera. Pages 214-234 in D. L. Wrensch and M. Ebbert, eds. *Evolution and diversity of sex ratio in insects and mites*. Chapman & Hall, New York.
- Crow, J. F., and M. Kimura. 1970. *An introduction to population genetics theory*. Harper & Row, New York.
- Frank, S. A. 1985. Hierarchical selection theory and sex ratios. II. On applying the theory, and a test with fig wasps. *Evolution* 39:949-964.
- . 1986. The genetic value of sons and daughters. *Heredity* 56:351-354.
- Grafen, A. 1990. Do animals really recognize kin? *Animal Behaviour* 39:42-54.
- Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* (Washington, D.C.) 156:477-488.
- . 1972. Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics* 3:192-232.
- . 1979. Wingless and fighting males in fig wasps and other insects. Pages 167-220 in M. S. Blum and N. A. Blum, eds. *Sexual selection and reproductive competition in insects*. Academic Press, New York.
- Price, G. R. 1970. Selection and covariance. *Nature* (London) 227:520-521.
- Stubblefield, J. W., and J. Seger. 1990. Local mate competition with variable fecundity: dependence of offspring sex ratios on information utilization and mode of male production. *Behavioural Ecology* 1:68-80.
- Taylor, P. D. 1981. Intra-sex and inter-sex sibling interactions as sex ratio determinants. *Nature* (London) 291:64-66.
- . 1988. Inclusive fitness models with two sexes. *Theoretical Population Biology* 34:145-168.
- Taylor, P. D., and M. G. Bulmer. 1980. Local mate competition and the sex ratio. *Journal of Theoretical Biology* 86:409-419.
- Werren, J. H. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. *Science* (Washington, D.C.) 208:1157-1159.
- . 1983. Sex ratio evolution under local mate competition in a parasitic wasp. *Evolution* 37:116-124.

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