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SIMULTANEOUS OPTIMIZATION OF EGG DISTRIBUTION AND SEX ALLOCATION IN A PATCH-STRUCTURED POPULATION

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Abstract.—The reproductive strategy of a female distributing her eggs over many patches comprises decisions on (1) how many eggs to deposit in a given patch, (2) what sex ratio to produce, and (3) how many patches to visit. In this article simultaneous evolutionarily stable strategy (ESS) solutions are presented for cases in which there is local mate competition and these three decisions interact, a situation that has not been studied previously. Y. Yamaguchi developed a model of optimum sex allocation for foundresses that contribute different numbers of eggs to one patch. Yamaguchi's model is extended here to examine the more general case in which females distribute their eggs over several patches. The key element is that females that visit a larger number of patches (relative to other females) and thus produce smaller clutches in each patch should produce a (relatively) smaller proportion of daughters. These females obtain a higher fitness per egg but invest more time in traveling. A simultaneous ESS is obtained for three variables, that is, clutch size, sex ratio, and number of patches visited, and for two different cases, namely, egg-limited females (no travel costs) and time-limited females (traveling is costly). Analysis shows that sex-allocation strategies can be an important driving force in the distribution of eggs over patches. The predictions of these models are strongly influenced by whether or not the females are able to use information about each other's clutch size. To test the validity of the model predictions, the dispersal behavior of plant-inhabiting predatory mites (Acari: Phytoseiidae) is considered in detail. The females distribute their eggs over many patches even when there is an ample supply of food. The models suggest that dispersal of the predatory mite females is a consequence of the sex-allocation games they play.

Females of many invertebrate species, including hymenopteran parasitoids and predatory mites of the family Phytoseiidae, lay clutches of eggs on a number of different patches, where the larvae mature without parental care. The reproductive strategy of the females has to incorporate decisions on clutch size, sex allocation, and number of patches to visit. If patches can be visited by more than one female, the payoffs from a given ovipositional strategy are likely to depend on the behavior of other females in the same environment. Then a game-theoretical approach is needed to analyze the "oviposition game" in order to find an evolutionarily stable strategy (ESS; Maynard Smith 1982). The game can be subdivided into two main parts: an "egg-distribution game" (Parker and Courtney 1984; Ives 1989; Strand and Godfray 1989) and a "sex-allocation game" (Hamilton 1967; Suzuki and Iwasa 1980; Yamaguchi 1985; Frank 1986). The egg-distribution game

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deals with the problems of clutch size and number of patches to visit. When the issue is optimization over more than one clutch these two decisions of the egg-distribution game are closely interrelated; how should a female distribute her eggs over patches to maximize lifetime fitness? So far this question has been studied mainly in relation to competition among offspring for limited local resources and in relation to the costs for females of traveling between patches in terms of time, resources, or probability of survival. In addition to the egg-distribution game there is the sex-allocation game, provided the females are able to control the sex ratio of their offspring. What sex ratio should a female produce in different patch types? The situation considered here is one in which mating takes place close to the place of birth but inseminated females disperse widely. This mating structure, known as "local mate competition" (Hamilton 1967), favors female-biased sex ratios. The optimum sex ratio depends on the clutch sizes and sex ratios produced by the other females contributing offspring to the local mating group.

In both parts of the oviposition game the optimal strategy in a given patch generally is conditional on the behavior of other females contributing to the same patch. A critical factor in the game is therefore the extent to which females are able to acquire and use information about each other's behavior (Frank 1985; Ives 1989; Stubblefield and Seger 1990). Because in nature information will often be constrained, models have to incorporate assumptions on information use.

Although the egg-distribution game and the sex-allocation game can be interdependent, to date they have mainly been studied separately. Generally, theories about the egg-distribution game do not take sex ratios into account, and sex-allocation theories treat clutch sizes as parameters rather than as variables to be optimized simultaneously with the sex ratios. These two separate approaches have been very productive (Godfray 1987). However, analysis of the oviposition game may require simultaneous models (Waage 1986). Such is the case when the optimum sex ratio depends on clutch size and the optimum clutch size in turn depends on sex ratio (Godfray 1986). Situations in which a simultaneous two-way approach has been shown to be useful can be classified in two main categories. In the first category there are asymmetries between male and female offspring in competition for resources, as analyzed by Godfray (1986). He presented a general model for clutch size and sex allocation with local mate competition, as well as a model for all three decisions without local mate competition. The second category consists of cases with a small number of offspring per clutch. The fact that broods consist of whole numbers of sons and daughters can then no longer be ignored, since this constrains the attainable sex ratios and clutch sizes. Models treating clutch size and sex ratio as continuous quantities are then no longer applicable and a simultaneous approach may be necessary in cases in which sequential separate approaches would suffice in continuous models. One case in which this emerges is when the relation between resource investment and fitness is different for sons and daughters. An example can be derived from the patch-quality effect studied by Charnov et al. (1981) for parasitoids, where small size is less disadvantageous for a male than for a female. A given patch could then, for example, profitably accommodate one female or two male offspring. Another example con-

cerns mammals in which, in contrast, small size is generally more disadvantageous for a male (Williams 1979; Frank 1987a, 1990). A female mammal could, for example, invest her resources in one son or two daughters. In both examples clutch-size and sex-allocation decisions have to be treated simultaneously. Small clutch size is also important when decisions have to be made about clutch size and sex allocation in cases with local mate competition (Waage and Ng 1984; Waage 1986). The possible sex ratios are constrained by clutch size, because, for example, at least one son is necessary to guarantee insemination. Because the payoff from a given clutch size depends on the sex ratio the two decisions are interdependent.

In this article, I identify and analyze a third category in which a simultaneous approach can lead to new insights. This category consists of cases that are characterized by the combination of clutch-size and sex-allocation games that arise between females when they distribute their eggs over a number of patches with local mate competition. The aim is to investigate the evolutionary relation between sex-allocation strategies and egg-distribution behavior. An important simplifying assumption is that offspring in a patch interact only through mating, which implies that within-patch competition between juveniles for resources is not considered.

The models were inspired by observations on predatory mite females of the Phytoseiidae. Some features of the egg-distribution behavior of these predatory mites, especially the high rate of movement of ovipositing females, are difficult to explain in terms of resource exploitation alone. During most of the cycle of exploitation of a prey aggregation by predatory mites there is probably little competition for food between offspring (Janssen and Sabelis 1992), so egg-distribution patterns need to be explained on the basis of factors other than resource acquisition. This contrasts with the subjects of most other studies addressing oviposition strategies, parasitoid wasps. The egg-distribution behavior of parasitoids is generally dominated by the challenges associated with exploitation of limited resources (Waage 1986; Godfray 1987). Explanations for the puzzling above-mentioned aspects of mite oviposition behavior are obtained here by analyzing the interaction of egg-distribution and sex-allocation games between females.

A REVIEW OF SEX-ALLOCATION MODELS

The isolated sex-allocation game with local mate competition was first analyzed by Hamilton (1967), who determined a solution for the optimum value of the local sex ratio (f) for any number (n) of females, each contributing the same number of offspring (a) to a patch. Hamilton assumed that each mating group consists of the offspring born in the same patch and that after mating the females disperse into a large population. To analyze the model, consider a mutant female producing $\tilde{f}$ in a population in which the rest of the females (the "residents") produce f . The fitness ($\tilde{F}$) gained by the mutant female in a patch is then

$$\tilde{F} = \tilde{f}a + (1 - \tilde{f})a \frac{\tilde{f}a + fa(n-1)}{(1 - \tilde{f})a + (1 - f)a(n-1)}, \quad (1)$$

which is the sum of the fitness gained through daughters and the fitness gained through sons. The fitness gained through daughters is $\hat{f}a$, the number of daughters. The fitness gained through sons is the product of $(1 - \hat{f})a$, the number of sons and the number of females expected to be inseminated by one son. The latter quantity is given by the total number of daughters in the patch divided by the total number of sons, because all mating is within the patch and at random.

Hamilton (1967) showed that the ESS (f^*) for the proportion of daughters is given by

$$f^*(n) = \frac{n+1}{2n}. \quad (2a)$$

Substituting the ESS ($\hat{f} = f^*$ and $f = f^*$) in equation (1) and dividing by a gives w^* , the fitness gained per egg under the ESS:

$$w^* = 2f^*. \quad (2b)$$

The notion of "fitness per egg" plays an important role in the approach used in this article. Because females distribute a limited number of eggs over a number of patches, the fitness gain per egg is more closely related to total fitness than is the fitness gain per patch. An implication of equation (2b) is that, in Hamilton's model, where clutch sizes are equal, fitness per egg gained in a patch is proportional to f^* . Combination of equations (2a) and (2b) reveals that under the ESS females have a higher fitness when only a few other females contribute to each patch. In that case each female has a high degree of "local parental control" (the underlying process of local mate competition: Nunney 1985; Nunney and Luck 1988), which means that the sex ratio produced by one female has a relatively large influence on the total sex ratio of a patch. In that case, when clutch sizes are equal, the sex-allocation game results in a high proportion of daughters for each female. This implies that few eggs are "wasted" on males and that fitness per egg is high.

Hamilton (1967) assumed equal clutch sizes. For a group of two females, Suzuki and Iwasa (1980) and Werren (1980) extended the model by allowing for unequal clutch sizes. They showed that the female with the smallest clutch should produce a lower proportion of daughters. Yamaguchi (1985) obtained a solution for any group size and any combination of clutch sizes (versions of this problem are also treated by Herre [1985] and Frank [1985, 1987b]). According to Yamaguchi the total sex ratio in a patch should be the same as the one given by equation (2a), but females are expected to adjust their sex ratio in such a way that in a given patch each produces the same number of sons. In a patch visited by n females the evolutionarily stable (ES) number of sons (s^*) in each clutch should equal

$$s^* = \frac{\sum a_i}{n} \cdot \frac{n-1}{2n}, \quad (3)$$

provided

$$a_i > C(n, a_i).$$

FIG. 1.—Local mate competition with unequal clutch sizes, according to the sex-allocation model of Yamaguchi (1985). Two females contribute offspring to the patch. The curves show the ES proportion of daughters (f_1^*) and fitness per egg (w_1^*) of one of the females as a function of its relative clutch size $a_1/(a_1 + a_2)$, where a_1 and a_2 are the clutch sizes of the female under consideration (female 1) and the other female (female 2), respectively. The Y-axis on the left-hand side shows the proportion of daughters, and the Y-axis on the right-hand side the fitness per egg. The values C_1 and C_2 denote the lower and upper limits of the zone in which both females should produce sons as well as daughters. Below- C_1 female 1 and above- C_2 female 2 should lay male eggs only.

The condition $a_i > C$ means that every female should contribute enough eggs to attain a specified number of sons C . Otherwise females with a very small clutch size should produce sons only, and determination of the ESS becomes more complicated. A consequence of equation (3) is that females with a smaller clutch than that of other females should produce a relatively low proportion of daughters. Reasons for this are the relatively minor influence of a small clutch on the total sex ratio of a patch and the high reproductive success of males in a female-biased mating group. Because of their high proportion of sons and the female bias of the total group, females with a relatively small clutch obtain a higher fitness per egg, although their payoff per clutch is lower. Figure 1 shows the ES proportion of daughters f^* and the resulting fitness per egg w^* as a function of relative clutch size for a group size of two. It is clear from figure 1 that, when clutch sizes are unequal, f^* and w^* of different females are also unequal and depend on their relative clutch sizes.

Yamaguchi's (1985) model assumes complete information on the part of each female with regard to the number and clutch sizes of the other females in the same patch. Stubblefield and Seger (1990) explored the case of more limited information. They found that the predictions of the Yamaguchi model change when "self-knowledge" females—able to respond to their own clutch size but not to each other's—are assumed instead of "complete-knowledge" females. For example, the number of sons was no longer the same for all females irrespective of their clutch size, although the largest clutches remained to be the most female biased.

BASIC MODEL FEATURES

The following assumptions are common to the sex-allocation models cited in the previous section. (1) Eggs are deposited on discrete patches. (2) The total number of available patches is large. (3) Females in a patch have complete information about the number of other females contributing to that patch and about their own and each other's clutch size (complete-knowledge females). (4) Females are able to adjust their sex ratio (proportion of daughters, f) to their assessment of the local situation. (5) There is local mate competition, all matings taking place within the patch of birth and randomly between the offspring of contributing females. (6) All variables, with the exception of the number of visitors to a patch, are treated as continuous and deterministic.

The following assumptions pertain specifically to the models developed in this article. (7) The models are phenotypic and do not take the genetic system into account. (8) Each patch is available for oviposition during a time interval T , after which the patch is no longer available for further oviposition and any offspring present develop to maturity. (9) Each female i has a characteristic clutch size a_i that she deposits on every visited patch. (10) A female visits m_i patches during T . (11) The number (n) of females visiting a given patch follows a Poisson distribution, implying that visits are distributed randomly and independently over patches. (12) Patches are never visited twice by the same female (a consequence of assumption 2). (13) The females maximize their rate of fitness gain over T , with no change in optimum strategy between T 's, meaning that changes in the state of the females or the environment are not taken into account. (14) Traveling between two patches takes a fixed time b . For simplicity, $b < T$, so it is possible for a female to visit at least one patch during T . (15) All patches have the same quality, and competition for resources is not important. Assumption 3 (complete information) will be relaxed in a later section that considers the consequences of more limited information.

Model Structure

The models presented extend the model of Yamaguchi (1985) by allowing the females to decide on clutch size as well as on sex ratio, whereas Yamaguchi sets clutch sizes a priori. Both variables are to be optimized; this is done as follows. The oviposition game is first divided into subgames for each patch that concern sex allocation only and that use the given local distribution of clutch sizes as an input. Then the combined ESS of the two games over all patches is identified by determining the clutch size from which it does not pay to deviate unilaterally. In the subgames the optimum local sex ratios for a given combination of clutch sizes in a patch can be derived from Yamaguchi's model (eq. [3]), without regard to other patches. To evaluate the combined ESS, consider a mutant female whose clutch size differs from the resident clutch size. Two steps are needed to calculate the fitness of the mutant and the residents. First, determine the optimum sex ratios of all females, with the mutant or with the resident clutch size, in all relevant patch types, that is, patches visited by different numbers of females with the resident strategy and with or without one mutant female. If mutant females

are rare, patches with more than one deviant clutch can be ignored. Second, calculate the resulting total fitness of a mutant over all patches visited by her and also the total fitness of resident females in an environment without mutants. The determination of total fitness in this way is made possible by the one-to-one relation between clutch size and number of patches visited, which is a feature of all models used here. Mutant and resident fitnesses are then compared. This approach makes the model tractable, because the optimum local sex ratio can be calculated for each patch type separately, even though clutch size must be optimized over all patches simultaneously.

MODELS WITH AND WITHOUT TRAVEL COSTS

Two variants of the model are considered, one for egg-limited females and one for time-limited females. Egg-limited females do not incur travel costs between patches, whereas time-limited females do. It is assumed that egg-limited females have a fixed number of eggs that are distributed during T and that they always lay all these eggs. This implies that travel time does not reduce total oviposition during T , although traveling between patches takes time b . In contrast, time-limited females are assumed to have a fixed oviposition rate (v) within patches, for example, because they have to forage in the patches for resources necessary to produce eggs. Here, time spent traveling between patches cannot be used for the production of eggs, and, hence, traveling is costly.

Both for egg-limited and time-limited females, dispersal—that is, number of patches visited—and clutch size are negatively related. A large clutch in each patch means that few patches can be visited. This implies that females are confronted with a trade-off when making clutch-size decisions. When females produce small clutches compared with those produced by other females, the sex-allocation game gives them a relatively high fitness per egg (see fig. 1) but they must spend more time on traveling between patches. Alternatively, with a larger clutch size the time spent on traveling is reduced but fitness per egg is also lower. This trade-off is the pivotal factor in the models developed here. Females have to find the best compromise between reducing travel time and increasing the fitness per egg.

Egg-limited Females

If there are no travel costs and the total number of eggs laid per female is fixed, the best strategy is to maximize the fitness per egg. Because the sex-allocation game results in females with the smallest clutch size always having the highest fitness per egg, it always pays to produce a clutch size smaller than the resident clutch size, provided the total number of visited patches can be increased. It is obvious that the outcome of the combined game is an ESS in which everyone produces the smallest possible clutch and visits the maximum number of patches allowed by the travel time between patches. Some results are given in figure 2, in which for convenience total time T is set to one. In figure 2A, B , and C , female density P is on the X -axis. The Y -axes represent the ES number m^* of patches visited (fig. 2A), the number n' of females visiting a patch (fig. 2B), and

FIG. 2.—Female dispersal in a combined clutch-size and sex-allocation model for egg-limited females. The panels show the effect of female density (P) and travel time (b) on ES number of patches visited (m^* ; note that the Y-axis is logarithmic) (A), mean number of visitors to a patch (n'), as experienced by a visiting female (B), and the proportion of daughters (f) and resulting female fitness (W ; presented by the second Y-axis) (C). Panels A, B, and C depict relations for various values of the interpatch travel time b , with female density P on the X-axis. The length T (the time interval during which patches are open for oviposition) is set to one. Panel D is a modification of C in that, instead of P , b is now on the X-axis and the curves are drawn for various values of P (instead of b).

the proportion of daughters f together with the total fitness W (fig. 2C), each for a number of different travel times b . Female density P is relative to patch density and is equal to the total number of females per available patch. Figure 2D presents f and W as a function of travel time b for a number of values of P .

The value of m^* is always at its maximum, which is given by T/b and therefore decreases with b , independent of female density (fig. 2A). The number of visitors (n') is defined as the mean number of visitors averaged over visits ($= 1 + P/b$), which is a better measure of female experience than is the mean number of visitors over patches ($= P/b$). Logically, n' increases with P and decreases with b (fig. 2B). The proportion of daughters is the total over T . Because at the ESS every female produces the same clutch size, the proportion of daughters in each patch follows from equation (2a). Averaging over the Poisson distribution then gives $f = 1/2 + (1/2)\langle 1/n' \rangle = 1/2 + (b/2P)(1 - e^{-P/b})$, where $\langle 1/n' \rangle$ is the average of $1/n'$. Proportion of daughters is negatively related to number of visitors; hence f decreases with density and increases with travel time (fig. 2C). Fitness W is scaled to the total number (vT) of eggs laid per female during T , where scaling factor v serves to facilitate comparison with the time-limited model. For egg-limited females, W is proportional to the fitness per egg, which in its turn is proportional to the proportion of daughters. Therefore, W (fig. 2C, D) decreases with density and increases with travel time in the same way as f .

Time-limited Females

For time-limited females, traveling between patches diminishes the time available for egg production. Producing a smaller clutch size than other females gives rise to a higher fitness per egg, just as for egg-limited females, but it also entails a cost since more time is spent on traveling and thus lost for egg production. Because of these costs a smaller clutch size reduces a female's total number of eggs. Because of this trade-off, the maximum total fitness is (in contrast to egg-limited females) not necessarily achieved by visiting the maximum number of patches.

To solve for the ESS, assume a resident population of females visiting m patches and consider a rare mutant visiting $\bar{m}$ patches. The clutch size a and $\bar{a}$ of residents and mutant can be calculated as

$$a(m) = \frac{T - mb}{m} v$$

(4)

and

$$\bar{a}(\bar{m}) = \frac{T - \bar{m}b}{\bar{m}} v.$$

The optimum proportion of daughters in a patch can then be calculated with Yamaguchi's (1985) model. Because in the first instance the search is for equilibria in which every female produces the same clutch size, we need not be worried that the C threshold from equation (3) is not reached by all females. This C threshold is only important when differences between clutch sizes are large. For example, when $n = 2$, clutch sizes have to differ by a factor larger than seven.

In a large neighborhood of an equilibrium the differences will not be so large. It can therefore be assumed that equation (3) applies. In a patch visited by one mutant and $n - 1$ resident females, s^* is then

$$s^* = \frac{(n-1)a + \bar{a}}{n} \left(\frac{n-1}{2n} \right). \quad (5)$$

Analogous to equation (1) the mutant's fitness $\bar{F}$ gained in this patch is

$$\bar{F} = \bar{d} + s^* \left[\frac{\bar{d} + (n-1)d}{ns^*} \right], \quad (6)$$

where d is the number of daughters.

Using $d = a(m) - s^*$, $\bar{d} = \bar{a}(\bar{m}) - s^*$, and equation (5), we get

$$\bar{F}(\bar{m}, m, n) = \frac{n^2 + 1}{n^2} \bar{a}(\bar{m}) + \frac{n-1}{n^2} a(m). \quad (7)$$

Total n of females in a patch is distributed according to a Poisson distribution $\Psi(n)$ with a mean Pm . The mean is not influenced by mutants since they are assumed to be rare. This yields

$$\Psi(n) = \frac{e^{-Pm}(Pm)^n}{n!}. \quad (8)$$

Let $W(x, y)$ be the total fitness of a female playing x in a population with resident strategy y . Then $\bar{W}(\bar{m}, m)$ is the total fitness of the mutant over T , where, for comparison with the egg-limited model, $\bar{W}$ is scaled relative to vT , the maximum number of eggs that can be produced in T . Total fitness $\bar{W}(\bar{m}, m)$ is determined by averaging $\bar{F}(\bar{m}, m, n)$ over all possible values of n and multiplying by $\bar{m}$. Care has to be taken to allow for the fact that the distribution of visits over patches is more weighted toward patches with a large number of visitors than is the distribution of visitors itself. This gives

$$\bar{W}(\bar{m}, m) = \frac{\bar{m}}{T_v} \frac{\sum_{n=1}^{\infty} \Psi(n) \bar{F}(\bar{m}, m, n) n}{\sum_{n=1}^{\infty} \Psi(n) n}. \quad (9)$$

Substituting equations (4), (7), and (8) into equation (9) gives

$$\bar{W}(\bar{m}, m) = \sum_{n=1}^{\infty} \frac{e^{-Pm}(Pm)^{n-1} \{ \bar{m}[h(n-1) - m(n^2 + n)] + mh(n^2 + 1) \}}{hmn!n}, \quad (10)$$

which is of the form $\bar{m}\Phi(m) + A(m)$, where $\Phi(m)$ and $A(m)$ are independent of $\bar{m}$ and a function of m only.

Parameters T and b appear only as the ratio $h = T/b$, the maximum number of patches that can be visited during T .

Number of patches visited, m^*

FIG. 3.—Time-limited females: the ES values of m^* , the number of patches visited during T , as a function of both female density (P) and the maximum number of patches that can possibly be visited ($h = T/b$).

An evolutionary equilibrium is characterized by the condition that changes in m do not pay, that is,

$$\left. \frac{\partial W(\tilde{m}, m^*)}{\partial \tilde{m}} \right|_{\tilde{m}=m^*} = \Phi(m^*) = 0, \quad (11)$$

where $m^* \geq 1$. The constraint that the value of m^* should be equal to or larger than unity is because every female is assumed to visit at least one patch during T .

Numerical calculations showed that, whenever there was a nontrivial equilibrium, it was stable and hence an ESS, according to the second condition of Parker and Hammerstein (1985, p. 84). This condition implies here that in the equilibrium a rare mutant can “get away” with any strategy but that a mutant will be selected against when it constitutes an appreciable part of the population and the probability that a mutant female meets other mutants in the same patch can no longer be ignored.

In figure 3 the numerical solution of equation (11) for m^* , the ES number of patches visited, is shown as a function of density P and of h , the limit to the number of patches that can be visited. Some sections in figure 3 that are parallel to the P -axis are shown in figure 4A.

The plot of the number of patches visited against the density has a steep “cliff” (figs. 3 and 4A). When female density is very low, dispersal is at its minimum ($m^* = 1$); all females follow a stay-where-you-are strategy. Increasing female density P causes m^* to jump abruptly to a high level and then to decrease gradually. This jump is caused by density-dependent changes in the gains of traveling, which shift the balance between costs and gains. The costs are independent of density, but the gains of traveling are obtained by playing sex-allocation games with the other females visiting the same patches and are therefore density-dependent. When density is low there are too few other females to profit from and it does not pay to incur travel costs. Above a density threshold it becomes profitable for a mutant to increase m considerably and deposit small male-biased

FIG. 4.—Time-limited females: the effect of female density (P) and travel time (b) on ES number of patches visited (m^* ; note that this corresponds to slices through fig. 3) (A), mean number of visitors to a patch (n'), as experienced by a visiting female (B), the proportion of daughters (f) (C), and the resulting female fitness (W) (D). In A–D relations are shown for various values of b , with P on the X-axis and T set to one. Panel E is a modification of D in that b is on the X-axis and the curves are drawn for various values of P .

clutches in other females' patches to take advantage of their large female-biased clutches. Then the ES number of visits m^* rises suddenly and steeply. Thus m^* is dependent on density for time-limited females (figs. 3 and 4A), whereas it is independent of P for egg-limited females (fig. 2A).

Figures 3 and 4A also show the effect of travel time. The density threshold rises with increasing travel time; when traveling becomes more expensive a mutant needs more potential victims before it pays her to abandon the stay-where-

you-are strategy. It is also clear from figures 3 and 4A that above the density threshold the level of m^* is lower when travel costs are high. Thus, m^* decreases with travel time just as in the case of egg-limited females. However, in general, m^* is far lower than with egg-limited females.

Below the density threshold, most patches are not visited at all, implying that the number of patches visited by each female can increase considerably without resulting in many more contacts between females. This is illustrated by the curves of the number of visitors n' (fig. 4B), which above the density threshold initially rises far less steeply than m^* .

Because the ES proportion of daughters f is inversely related to the mean number of visitors, the trend in f largely mirrors the trend in n' (cf. fig. 4B, C). When density increases but m^* remains one, the probability of meeting other females in a patch increases slowly at first and f decreases accordingly. Above the density threshold the mean number of other clutches in a patch increases abruptly, causing the proportion of daughters to drop sharply. When density rises still further the proportion of daughters soon levels off because the sensitivity of the ES sex ratio to changes in the number of visitors is greatest at low n .

Overall fitness W (fig. 4D) is not dependent solely on sex ratio, whereas it is in the case of egg-limited females (fig. 2C). Fitness can now be low despite a high proportion of daughters, since the time lost by traveling is another factor determining fitness.

Plotting overall fitness W against travel time b for a number of different densities (fig. 4E) reveals a counterintuitive result: fitness initially *increases* with travel time. Only after reaching a maximum, which depends on female density, does fitness gradually decrease again. An increase in fitness also occurred with egg-limited females (fig. 2D), but since traveling was cost free it was not as surprising. The result for time-limited females is counterintuitive in that fitness increases when it becomes more costly to travel from patch to patch. This is a consequence of combining sex-allocation and egg-distribution decisions in one game; it can be argued as follows. When travel becomes more costly there is a decrease in the number of patches visited (fig. 3); this results in a lower number of visitors to each patch, a higher proportion of daughters, and a higher fitness per egg. The outcome of a higher fitness per egg, a lower number of traveling events, and a higher cost per event appears to be a higher total fitness. When m^* reaches its lower limit ($m^* = 1$), fitness starts to decrease with travel time.

This argument can be put another way: the increase in fitness with travel time b arises because high costs of traveling can protect females against each other. Females are better off when only a few are in each patch (eqq. [2a] and [2b]), because the sex-allocation game then results in the females producing a high proportion of daughters. However, when traveling is cheap these females are vulnerable (in the combined game) to traveling mutants that produce many small clutches with a high proportion of males. Under these conditions the behavior of the population then settles down at low clutch size, low fitness, and large number of patches visited. In contrast, when traveling is expensive such mutants have no chance.

FIG. 5.—Limited-knowledge females: local mate competition as in fig. 1 for females that can assess their own clutch size and the number—but *not* the clutch sizes—of other females in a patch. Of the two females in a patch, one has the resident strategy of producing clutch size a and one is a mutant with clutch size $\tilde{a}$. The mutant produces a sex ratio optimal for clutch size and environment. The resident sex ratio is the best one when clutch sizes are equal. The X-axis represents the relative clutch size of the mutant female, $\tilde{a}/(\tilde{a} + a)$. The Y-axis on the left-hand side shows the proportion of daughters of either the resident female (f) or the mutant female ($\tilde{f}$). The Y-axis on the right-hand side gives the fitness per egg ($\tilde{w}$) of the mutant female.

FEMALES WITH INCOMPLETE INFORMATION

Thus far it has been assumed that females have complete knowledge about the type of patch they are in. They then know the number and clutch sizes of the other females on the patch and adjust their sex allocation accordingly. When this assumption is relaxed and limits are placed on the females' capacities to respond to local conditions, the outcome can be radically affected and the ESS, if it can be found at all, will generally be different. Consider, for example, females producing a sex ratio that depends on the number of visitors and on their own clutch size but not on the clutch size of others. These can be termed "limited-knowledge" females, analogous to the self-knowledge females of Stubblefield and Seger (1990) but differing from these in that the self-knowledge females know only the expectation of n . A mutant with a deviating clutch size and a sex ratio that is optimal for a rare mutant with that clutch size is then *always* rewarded with a higher fitness per egg, irrespective of the direction of the deviation. Figure 5, which should be compared with figure 1, illustrates this for the case in which a group consists of one mutant female and one with the resident strategy. The consequences differ for the egg-limited and the time-limited females. In the case of egg-limited females a pure ESS is not possible, because every pure ESS can be invaded by any deviant clutch size, as figure 5 shows. It was impossible to establish whether a mixed ESS can exist, because there are too many degrees of freedom in female behavior: at least two clutch sizes and two sex-ratio distributions. The main problem is that sex allocation can no longer be derived from

the local clutch sizes but is an independent parameter. Searching by numerical exploration for examples of a mixed ESS was unsuccessful. The time-limited case is even more complicated, because travel costs play a role as well. It is clear from figure 5 that the gain in fitness per egg w is vanishingly small for a mutant when its clutch size is close to the resident value. This is because, in contrast to the complete-knowledge case, the resident females do not adjust their sex allocation in response to a deviating clutch size. As a result, $\partial w / \partial m$ will be much smaller than in the complete-knowledge case. Because the increase in fitness per egg gained from a somewhat smaller clutch size is then very small for a deviant, it never compensates for the increase in travel costs, whereas it often does in the complete-knowledge case. The result is that a mutant with a small deviation in the direction of a smaller clutch size can never invade. We are confronted with the interesting situation that a mutant needs the informed and self-interested "cooperation" of the other players in the game to be successful. In contrast, deviations with a larger clutch size can always invade; in addition to a small increase in w they give rise to a decrease in travel costs. Thus, when only mutations with a *small* effect on m are permitted, the population will equilibrate at its minimum level of dispersal ($m^* = 1$). This equilibrium, however, is often invadable by mutants with a *large* increase in m because $\Delta w / \Delta m$ can increase with mutation size. No pure ESS is then possible. The nonexistence of ESSs consisting of a mixture of clutch sizes could not be proved for time-limited females either, as the function describing total fitness is even more complicated. Just as in the case of egg-limited females, searching by numerical exploration for examples of a mixed ESS did not unearth any.

DISCUSSION

The models developed here show that analyzing sex allocation and egg distribution as simultaneous rather than separate games leads to new and sometimes counterintuitive results. Sex-allocation decisions not only determine the composition of clutches but can also influence their size and distribution. Most important, the coupling of the two games can instigate dispersal of reproductive females, implying that dispersal can be high even in the absence of the need to find enough food for themselves or for their offspring. The interaction between egg-distribution and sex-allocation games can result in a much wider distribution of eggs than an egg-distribution game in isolation. Another conclusion is that the number of females contributing to a patch, and hence the importance of local mate competition with its associated female-biased population sex ratio, depends not only on female density (Hassell et al. 1983; Comins and Wellings 1985), but also on interpatch travel time and costs. When it is easy to visit a large number of patches during the time that a patch is available, each patch is visited by many females and there will be little local mate competition, just as when female density is high. Local mate competition will increase in importance when travel time between patches is long and especially when traveling is costly. Hence, constraints on the movement of ovipositing females are an important condition for local mate competition to occur. This is in addition to constraints on the move-

ment of juveniles before mating, which have always been recognized as a crucial factor in local mate competition (Hamilton 1967; Waage 1986).

Both for egg-limited and time-limited females the strong influence of travel time on dispersal in the combined game leads to the counterintuitive result that fitness can increase with interpatch travel time. This arises from the fitness-increasing effect of the higher proportion of daughters associated with the lower number of visitors per patch because of the longer travel time.

As in the isolated sex-allocation game (Frank 1985; Stubblefield and Seger 1990), the extent to which females can use information about each other proved to be a critical factor in determining the ESS. Hence, assumptions about use of information are essential if one is studying the combined game. It is shown here that, when females do not know each other's clutch sizes, the models can result in an ESS that is completely different. In many cases no pure ESS exists and mixed ESSs, if they exist, are too complicated to find with the methods used in this article. There may even be cases in which there is no ESS at all, pure or mixed. With regard to theory the limited-information cases therefore remain as an important challenge.

In the models described above there was no resource competition. Because often this assumption will be unrealistic, it is interesting to consider cases in which there is some competition for food between offspring. The general case of females distributing eggs over patches with a varying number of females ovipositing per patch, while taking travel time and competition between offspring into account, is a complex problem that has not been solved even for the isolated egg-distribution game (see, e.g., Ives 1989). Results from the isolated egg-distribution game reported by Ives (1989) suggest that the predictions would depend dramatically on the type of larval competition; it is possible for the ES clutch size to increase or to decrease with the number of females ovipositing per patch. A simplifying approach would be to consider competition as leading to an ideal free distribution of clutches over patches. In that case the result will be a more even distribution of visits over patches. Versions of the models with an even distribution of visits over patches, not presented here, did produce about the same results as versions with a Poisson distribution. This suggests that the main predictions remain unaltered. Another possible consequence of resource competition would be increased female dispersal resulting from a search for unoccupied patches; this would lead to a larger number of visited patches than without resource limitation. Increased juvenile dispersal as a result of food shortage would lead to a larger mating group size, with complex effects on the combined model.

Predatory Mites: A Case Study

Predatory mites of the family Phytoseiidae provide an excellent test case because of their flexible sex allocation and their local population dynamics and spatial distribution. With regard to the first point, it is known that females can control the sex of their offspring precisely and often produce female-biased sex ratios (Sabelis and Nagelkerke 1987; Nagelkerke and Sabelis 1991). The second point, their population characteristics, needs to be considered in more detail. They are plant inhabiting, and often the major prey consists of spider mites, which

FIG. 6.—Scheme of a structured population of predatory mites within an infestation of prey spider mites. Females travel between prey colonies and travel, forage, and deposit eggs within the colonies. The extent of the mating groups is determined by juvenile dispersal. The egg-limited model applies to the case of traveling within colonies, and the time-limited model applies to travel between colonies.

are phytophagous and usually have a strong tendency to form patchy infestations (Sabelis and van der Meer 1986). Each prey infestation is founded by one, or a few, airborne female(s) that by chance finds a suitable host plant. Female offspring disperse (by walking) to form daughter infestations, "colonies," on nearby leaves. As a result, prey infestations are foci consisting of colonies separated by regions devoid of prey. The distance between different infestations is usually much larger than between colonies. Prey infestations can be invaded by female predators that consume prey to produce eggs that they lay in the colonies (see fig. 6). A predator subpopulation develops that overexploits the infestation and wipes out the prey within a few generations. In a discussion of phytoseiid life histories Janssen and Sabelis (1992) asserted that during the greater part of an exploitation cycle there is little competition for prey between different females and between offspring. For example, in experiments, food density generally has to be more than an order of magnitude lower than that of an unexploited prey infestation before any effects on juvenile survival or rate of development can be found. Takafuji and Chant (1976) and Eveleigh and Chant (1980) reported that density of prey spider mite protonymphs needed to be below a (conservative) value of $\pm 0.75/\text{cm}^2$ ($= \pm 2.8 \mu\text{g}/\text{cm}^2$) to diminish survival or rate of development of juvenile *Phytoseiulus persimilis*. When prey eggs were used as food, densities had to be below $1 \text{ egg}/\text{cm}^2$ ($1.2 \mu\text{g}/\text{cm}^2$) for an effect on survival (Takafuji and

Chant 1976). Likewise, Lababidi (1988) found for *Amblyseius bibens* and *Amblyseius longispinosus* a (conservative) density of prey eggs of $\pm 0.6/\text{cm}^2$ as the lowest no-effect level with regard to juvenile rate of development. In spider mite colonies, densities can easily reach 40 or more eggs/ cm^2 (60–120 $\mu\text{g}/\text{cm}^2$) (Sabelis 1981, 1985b). It is therefore reasonable to assume that significant competition among offspring for resources will not occur until near the end of an exploitation cycle. As a consequence, the central assumption about the absence of resource limitation, or heterogeneity in resource quality among patches, affecting offspring fitness will be realistic for phytoseiids during at least part of an exploitation cycle.

Median dispersal distance up to the first mating of offspring is less than 1 cm in *P. persimilis* at high prey density (C. J. Nagelkerke, unpublished data). Therefore, mating will generally be between offspring born in a small neighborhood and produced by only a few females. In this way mating groups are formed, as shown in figure 6, albeit with ill-defined borders. Because, compared with juveniles, the inseminated females have a much higher rate of movement within the infestation, both between and within colonies (Sabelis 1981), it is reasonable to expect that local mate competition occurs.

Dispersal of phytoseiid females may occur on three different spatial scales: within a prey colony on a leaf, between prey colonies on different leaves, and between prey infestations. Clearly, travel costs will increase steeply from the first scale to the last. Hence, one would expect the dispersal rate to decrease in the same order. This is in agreement with available observations on the dispersal behavior of phytoseiid mites. Aerial dispersal from a prey-infested plant tends to occur only after the prey is wiped out (Sabelis and van der Meer 1986). Dispersal on this spatial scale is clearly much less frequent than dispersal between and within prey-infested leaves. The last two types of dispersal occur long before the prey is wiped out (Sabelis 1981; Sabelis and Dicke 1985). In fact, much of the movement within and between prey colonies seems difficult to explain on the basis of foraging considerations alone, since phytoseiid females change position within, and often leave, a prey colony even when the prey supply is still ample.

I hypothesize that the interaction between sex allocation and egg distribution can at least partly explain the frequency of dispersal between and within colonies in a prey infestation. Qualitatively, it explains why the rate of movement between and within colonies is so high and unrelated to food shortage. More precisely, the models predict that the influence of predator density on the movement of gravid females between future mating groups depends on the cost of traveling. It seems reasonable that there are no such costs within prey colonies, since there is little or no loss of foraging opportunities. This means that travel within colonies corresponds to the egg-limited variant of the model, whereby patches are defined by the range of juveniles before mating. Travel costs between colonies are inevitable. The females cannot forage while traveling, and this will lower their mean oviposition rate. A negative effect of travel between colonies on mean oviposition rate was, for example, shown by Eveleigh and Chant (1982b) for *P. persimilis*. Although lifetime fecundity need not be influenced (Sabelis and van der Meer 1986), time is of prime importance for phytoseiids, because they are strongly *r*

TABLE 1
DISPERSAL WITHIN AND BETWEEN PREY COLONIES OF FEMALES OF PREDATORY MITES
IN RELATION TO DENSITY

PREDATOR SPECIES AND NUMBER OF PREDATOR FEMALES IN A PREY COLONY	WITHIN PREY COLONIES		
	Walking Speed (mm/s)	Walking Activity (% of time)	Displacement (mm/s)
<i>Metaseiulus occidentalis</i> :			
1	.20	36	.072
4	.20	38	.076
<i>Phytoseiulus persimilis</i> :			
1	.19	8	.015
4	.20	9	.018
	RATE OF DEPARTURE BETWEEN PREY COLONIES (h ⁻¹)		
<i>Metaseiulus occidentalis</i> :			
1		.020	
2		.032	
3		.096	
4		.133	

NOTE.—Data are from Sabelis (1981, tables 67, 72).

selected (Sabelis and Janssen 1993). Hence, travel between colonies will correspond to the time-limited case. Under these assumptions about travel costs, the models predict that predator density will not have an effect on movement within colonies, whereas it will influence movement between colonies. There is ample evidence of a positive influence of predator density on dispersal of females from colonies within prey infestations (Kuchlein 1966; Fernando and Hassell 1980; Sabelis 1981, 1985a; Eveleigh and Chant 1982a; Bernstein 1984; Ryoo 1986). As an example, table 1 presents data from Sabelis (1981). In contrast, it has been found (Sabelis 1981) that within colonies predator density does not affect walking speed or proportion of time spent walking, as table 1 also shows. The predictions of the models are in agreement with these findings. However, changes in directionality within colonies, possibly affecting effective displacement without changes in walking speed or proportion of time spent walking, have not yet been studied.

Quantitatively, agreement is not perfect. First, it is clear from table 1 that within colonies the proportion of time spent moving is smaller than unity, although the model predicts maximum dispersal. Second, between colonies, the rate of dispersal does not decrease again after reaching a maximum, at least not within the range of densities tested. These deviations could be due to limitations in the models' assumptions. First, like most oviposition models, they do not allow for the fact that clutches consist of a whole number of eggs. This will be most important when clutch sizes are small, as is the case with phytoseiids, who produce only two to six eggs per day. In the egg-limited model the discrete nature of clutches could result in an upper limit to the amount of movement of females,

when the minimum clutch size per patch, one egg, is reached. Second, the models do not incorporate other demands on time, possibly also putting limits on time spent moving. Finally, they do not take into account influences on egg dispersal other than sex-allocation games and costs of traveling. Competition for food could become an extra factor favoring increased dispersal at high predator densities, opposing the decreasing dispersal predicted by the time-limited model.

A crucial factor in the models developed here concerns the extent to which females can use information about each other's clutch size. Phytoseiid females lay their eggs, which are very large compared with their body size, on the surface of the leaves infested by their prey. In doing so they leave the oviposition site open to inspection by other females. Hence, knowledge about each other's clutch size is not *a priori* an unreasonable assumption. Nevertheless, it is an important point that should be investigated.

A simplifying assumption is that oviposition behavior is independent of the state of the female. Models of the isolated egg-distribution game that take female state into account (Iwasa et al. 1984; Godfray 1987; Minkenberg et al. 1992) generally predict that females should spend their eggs more sparingly when the number of eggs left diminishes (i.e., they should become more egg limited). Another factor important in this respect is that maximal oviposition rate of phytoseiids decreases later in life (Sabelis and Janssen 1994). Taken together, these lead to the prediction that clutch size will be smaller, and hence the proportion of daughters lower, for older females. Data about clutch size and sex ratio of females of different ages in mixed-age groups are not available, however.

Population Dynamics

Sex-allocation decisions can influence population dynamics, as demonstrated by Hassell et al. (1983) and Comins and Wellings (1985). They showed that in population-dynamics models a decrease in the proportion of daughters with density, resulting from an increasing number of foundresses per patch, can have a stabilizing influence. The population growth rate decreases with density because of the decrease in the proportion of daughters. In the models presented here there is such a density dependence both for egg- and time-limited females (figs. 2C and 4D). In the time-limited variant there are density intervals in which the effect is very pronounced because the number of visitors increases disproportionally with density, since each female visits an increasing number of patches.

This density dependence is probably not an important stabilizing factor in phytoseiid populations. Locally, their rate of population growth is so large that predator-prey interactions are unstable and prey populations are wiped out (Sabelis and van der Meer 1986). Stability is assumed to be a property of their metapopulations, not of their local populations (Sabelis et al. 1991).

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