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HIERARCHICAL LEVELS OF SPATIAL STRUCTURE AND THEIR CONSEQUENCES FOR THE EVOLUTION OF SEX ALLOCATION IN MITES AND OTHER ARTHROPODS

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Abstract.—Evolutionarily stable (ES) sex allocation strategies depend critically on how the population is structured with regard to competition for mates and resources. This structure is determined by spatial heterogeneity, dispersal, and colonization behavior. In mating groups lasting one generation where mating precedes female dispersal, female-biased sex ratios will be favored by "local mate competition," especially when the number of foundresses is small. When groups last several generations before dispersal takes place ("haystack" structure), relatedness among population members develops, and this can favor an extra female bias. However, when groups are permanent, with some dispersal in each generation ("island" structure), relatedness builds up without an effect on sex ratio bias because most competition takes place within groups. Current models of evolution under a haystack structure generally assume unlimited growth for a fixed number of generations (and hence no local density dependence), absence of substructure, and sex ratios that are inflexible over generations. These model limitations warrant scrutiny. Using extended versions of the haystack model, we show that, although local density dependence in the haystack population diminishes the sex ratio bias, strongly female-biased sex ratios are still possible if foundress numbers are low. It is also shown that substructure in the haystack by subdivision into one-generation mating groups promotes the female bias. Finally, it is shown that the ES sex ratio can change radically with generations within haystacks. When population growth is density dependent, the sex ratio of the last generation should be more female biased than in the preceding generations. In the case of haystacks subdivided into local mating groups, the sex ratio in the first generation should be less female biased than in the following generations. It is argued that a haystack structure is frequently found among small arthropods with a colonizing lifestyle and that subdivision into one-generation mating groups may occur, for example, among plant-inhabiting mites. To illustrate these points, predatory mites of the family Phytoseiidae are considered in more detail. Some species are found to exhibit a stronger female bias in their sex ratios than expected from local mating competition alone. This extra bias may well stem from selection in a haystack or subdivided haystack structure. Other phytoseiid species have a lifestyle that leads to more permanent subpopulations that have an island-like structure. As predicted, these species generally show less female-biased sex ratios.

The mating and competition structure of a population plays a decisive role in the evolution of sex allocation (Hamilton 1967; Clark 1978; Bulmer and Taylor

1980; Frank 1986). Group size, group longevity, between-group migration, and local density dependence together determine the extent to which mating and competition take place among relatives, which in turn determines how much the production of sons or daughters will contribute to the fitness of the mother facing a sex allocation decision. One of the most simple population structures consists of one-generation mating groups, where mating takes place locally among the offspring of a few females ("foundresses"), and only the inseminated females disperse into a wider population to found new groups. This population structure induces a selection mechanism, referred to as "local mate competition," that favors a female-biased sex ratio (Hamilton 1967). Local mate competition is held responsible for many cases of skewed sex ratios in arthropods, especially parasitic wasps, but also thrips, aphids, and mites (Hamilton 1967; Charnov 1982; Wrensch and Ebbert 1993).

Perpetuation of groups for longer than one generation can influence the outcome of selection. Taking mice living in haystacks as a caricature, Maynard Smith (1964) considered multigeneration groups, called "haystacks" (fig. 1A). Starting from a few inseminated females, each haystack population expands freely for a fixed number of generations, whereupon dispersal takes place. When only inseminated females disperse, such a haystack structure favors sex ratios with a stronger female bias than a population structure involving one-generation groups of the same size (Bulmer and Taylor 1980; Wilson and Colwell 1981; Frank 1986, 1987; van Tienderen and de Jong 1986).

Although many organisms have a population structure in which subpopulations exploit temporary food sources for more than one generation, the haystack model has remained largely untested; this is surprising in view of the extensive literature on tests of local mate competition. Testing the haystack model is not straightforward, mainly because one of the most obvious animal groups for such tests, small arthropods, shows population structures not covered by current models. For example, plant-inhabiting predatory mites (Acari: Phytoseiidae) form fast-growing populations in patches of spider mites, their phytophagous prey. These populations start from one or a few females, drive local prey populations to extinction, and then disperse. This example and many others can be provided to illustrate the point that the ultimate size of local populations will often be limited by the amount of food available. Therefore, it will often be unrealistic to assume that haystack populations grow without any limit (other than an upper bound on the number of generations). Using Price's covariance equation (Price 1970, 1972) Frank (1986) analyzed the consequences of such a local density dependence, but not in conjunction with another relevant feature of arthropod population structure: substructure in the haystack may violate the assumption of panmixia within the haystack. For example, local populations of plant-inhabiting predatory mites are likely to be further subdivided into one-generation mating groups (Nagelkerke 1993). For these reasons we argue that to test the predictions of haystack models against data from arthropods requires extensions of these models with density dependence and subdivision within haystacks.

Another reason to extend the original haystack models is that they are based on the assumption that the sex ratio in a haystack is fixed and thus cannot be
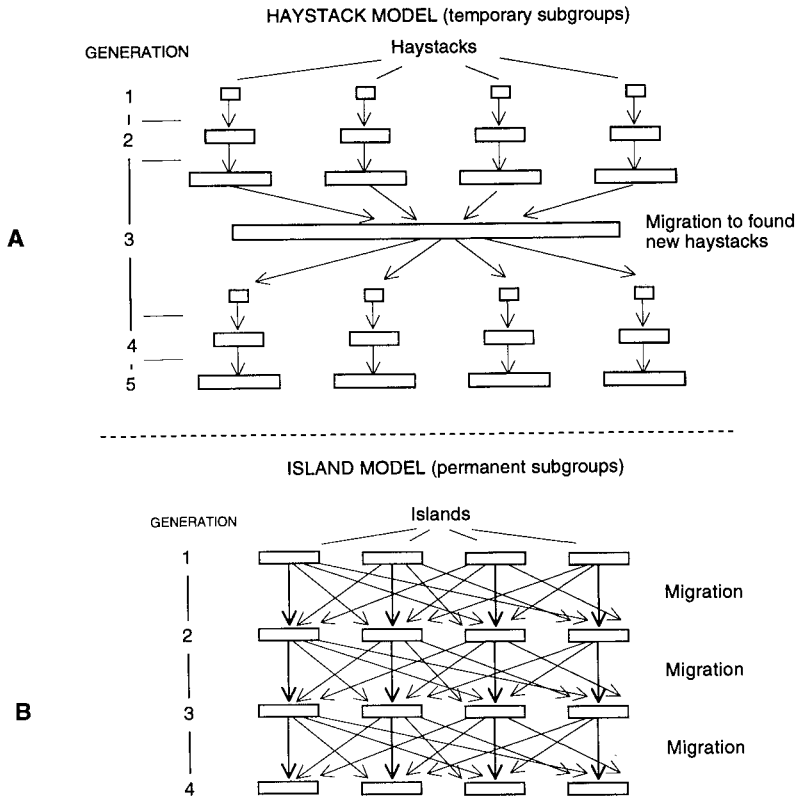
Fig. 1.—Diagram of two multigeneration population structures. *A*, Haystacks (Maynard Smith 1964). These are multigeneration groups founded by a few inseminated females and expanding for a number of generations, after which population-wide dispersal takes place to start a new cycle of haystacks. *B*, Islands (Wright 1945). These are permanent groups with some population-wide intergroup migration in every generation.

adjusted to selection pressures that change from generation to generation. This assumption reduces model generality. Flexible sex allocation is certainly a biologically plausible phenomenon in that animals may have information on conditions in the haystack at their disposal. Frank (1986) determined analytically the optimum of the sex ratio across all generations for the case of inflexible sex allocation but did no more than speculate as to the optimal sex ratio per generation (but see van Tienderen and de Jong 1986, which provided analytical results for the special case of one foundress and two generations per haystack). In this article we explore the consequences of local density dependence, subdivision, and flexibility, both separately and jointly, for the evolution of sex allocation. Flexible sex allocation not only adds realism to the model, but also provides deeper insight into how different selection pressures are distributed over the generations.

As an alternative to the haystack population structure it is relevant to consider yet another multigeneration group structure relevant to many small arthropods.

These are so-called island population structures (Wright 1945; Falconer 1981), in which local populations are permanent and constant in size and in which part of the inseminated females migrate each generation (fig. 1B). Models of this type do not predict the extra female bias obtained in haystack models but rather conform to the predictions of local mate competition models (Bulmer 1986; Taylor 1988).

As a guide to interpreting the results we start with an overview of the selection mechanisms affecting sex allocation in structured populations. Next, results of haystack models with the aforementioned extensions will be presented. Finally, we will identify population structures (island or haystack) among small arthropods, in particular, herbivorous and predatory mites inhabiting plants (Acari: Tetranychidae, Phytoseiidae), and test the predictions of sex allocation for these structures.

SELECTION MECHANISMS OPERATING UNDER VARIOUS POPULATION STRUCTURES

There are two useful ways of viewing selection processes in structured populations. One is to distinguish between "selection within groups" and "selection between groups" (Colwell 1981; Wilson and Colwell 1981; Wade 1985), where the first results from the relative success of a trait within groups and the second, from the differential proliferation of groups. Selection within groups favors an unbiased sex ratio because what counts is the proportional representation in the group; selection between groups favors a bias when it increases the total production of a group relative to other groups. The other way of viewing the selection process is to distinguish between "individual selection" and "group selection" (Grafen 1984; Nunney 1985b). Individual selection concerns the effect of a trait on the number of offspring of the actor, whereas group selection concerns differential production arising because individuals exhibiting the trait are likely to interact with each other. Group selection requires larger genetic variance between groups than expected from random sampling (Frank 1986); otherwise, individual selection is the only selection force. Thus defined, group selection is closely related to kin selection (Nunney 1985b); a high variance between groups is equivalent to high relatedness within groups (Falconer 1981). Contrary to individual selection, group or kin selection can promote the evolution of altruistic behavior (i.e., behavior that reduces the number of offspring of the actor while increasing that of others).

These two views are not equivalent because a trait may spread through individual selection while its relative frequency within the group declines. Such traits are called "benevolent" (Nunney 1985b) because they increase the number of offspring of their bearers while increasing the fitness of the other group members even more. However, in the absence of local density dependence the fitness of other group members does not matter to the actor. The female-biased sex ratio favored under local mate competition is an example of such a benevolent trait. A female bias increases the number of inseminated females produced by the mating group, and an individual producing a female bias thereby increases its absolute genetic representation among the females dispersing from the group

while decreasing its proportional representation. This is a case of individual selection mediated by group structure (Nunney 1985a).

In essence, two factors are necessary for the evolution of biased sex ratios in group-structured populations: (1) variance in genetic composition between groups, relative to within groups, and (2) sex-ratio-dependent differential contribution of groups to a larger population (Wilson and Colwell 1981; Grafen 1984; Nunney 1985a); the latter implies that competition takes place, at least partly, between groups instead of only within groups. Hence, the bias will not develop when local density dependence precludes differential production (cf. Kelly 1994).

If only inseminated females disperse and there is no local density dependence, the evolutionarily stable (ES) proportion of daughters in a diploid population is equal to $1 - 0.5P$ (Hamilton 1979; Frank 1986), where P is Wright's index of panmixia; P is given by the ratio of within-group and population variance. When P is small, the variance between groups is high. In one-generation groups with local mate competition the variance between groups of foundresses results from random sampling, and hence P is $(N - 1)/N$, where N is the number of foundresses. It follows that the ES proportion of daughters is then $(N + 1)/2N$. When groups exist for more than one generation, females become related through interbreeding, and the variance between groups may become higher than through random sampling. Relatedness amplifies the female bias, provided that local density dependence is weak or absent. This extra female bias results from group selection, as a high proportion of daughters (i.e., higher than expected from local mate competition alone) is an altruistic trait. For the more special case of a haystack structure it has been shown that the extent of the female bias depends on factors such as the number of initial foundresses, the number of generations spent in a haystack, the genetic system (haploid, diploid, or haplodiploid), the mode of gene action (degree of dominance), and the mating system (mating before or after dispersal) (Bulmer and Taylor 1980; Wilson and Colwell 1981; Frank 1986, 1987; van Tienderen and de Jong 1986).

In haystack models that have no limits to population growth, the female bias arises because both variance between groups and possibilities for differential expansion can be high. Haystack populations compete with each other in the number of dispersers produced. The genetic variance arises from the settling of foundresses, being a random sample from the total population. When genetic drift within haystacks is ignored, Wright's index of panmixia, P, remains equal over generations. Hence, when only inseminated females disperse, the ES proportion of daughters is $(N_1 + 1)/2N_1$ in every generation (Frank 1986), where N_1 is the number of foundresses of the haystack population. Consequently, in later generations the female bias is stronger than expected from local mate competition alone (i.e., for the same number $[N_g]$ of females as are in the haystack in that generation). The bias will become larger when variance increases—for example, because of a lower number of foundresses, relatedness of haystack foundresses, unequal clutch sizes between females, or genetic drift within haystack populations. The bias will become smaller because of density dependence within the haystack population—for example, when its final size is fixed; then, the importance of between-haystack selection is decreased compared to the importance of

within-haystack selection. Another factor decreasing the female bias is mating after dispersal (Bulmer and Taylor 1980; Wilson and Colwell 1981; van Tienderen and de Jong 1986). Because the dispersing generation then mates randomly in the global population, an unbiased sex ratio in the production of the dispersing generation is selected for reasons similar to those given by Fisher (1930).

In contrast to haystacks, islands do not favor a more female-biased sex ratio than expected under local mate competition. Even when migration is low, the extra bias will not arise despite the development of high local relatedness (Bulmer 1986; Taylor 1988). We suppose that the absence of an extra bias is due to the fact that migration works both ways in an island model (cf. Harpending and Rogers 1987; Kelly 1992). On the one hand, a high level of migration promotes differential proliferation, because groups compete in terms of the production of migrants; on the other hand, migration reduces genetic variance between groups. These effects apparently cancel each other in the case where only inseminated females disperse. The effect of high relatedness between females within an island is counteracted by the competition between related females within islands. Thus, the ES sex ratio is determined only by the amount of local mate competition (the number of breeding females) within an island and is independent of the amount of migration (but see Taylor 1988, which shows that this only applies when migration is finite).

The predictions for optimal sex allocation in haystack and island structures are consistent with the results from models on the evolution of altruism. Whereas altruism is shown to evolve in models with a haystack structure (Maynard Smith 1964; Wilson 1987; Taylor and Wilson 1988), several versions of island models (Harpending and Rogers 1987; Rogers 1990; Taylor 1992) have led to the conclusion that altruism does not develop in the absence of a net benefit to the altruist (thus this type of altruism is in fact benevolence). We therefore conclude that in general, a haystack population structure is conducive to the evolution of an altruistically biased sex allocation, whereas an island structure is not.

HAYSTACK MODELS

A genetic model is used, identical in structure to the haystack models of Bulmer and Taylor (1980) and van Tienderen and de Jong (1986). Haystacks are started by N_1 inseminated females, which multiply for a fixed number G of discrete generations. All mating is within the haystack, and females mate only once. After G breeding generations the inseminated females of the $(G + 1)$th generation disperse, mix within the global population, and start a new cycle of haystacks. There is one locus with two alleles, r and m, corresponding to sex ratios f and $\bar{f}$. The sex ratio of the offspring is determined by the genotype of the mother. The genotype r is the "resident" type in the global population, and m is a rare mutant. The ES sex ratio is determined by searching for an r that will resist invasion by any m. An inseminated female is a composite of her own genotype and that of her mate. A composite is "mutant" when at least one of the two genotypes is mutant. Because m is rare, haystacks having more than one mutant among their foundresses can be ignored. Therefore, there are four different types of haystack:

one resident type and three types with one mutant. The production of the three mutant composites is calculated for each type of haystack (see the appendix). The fate of m can be determined by examining the linearized recurrence relations of the frequencies of the three types of haystack with one mutant. A sex ratio f is an ES strategy (f^*) if $\lambda(f, \hat{f}) < 1$ for all $\hat{f} \neq f$, where $\lambda(f, \hat{f})$ is the dominant characteristic root of the recurrence matrix. An ES strategy can be found numerically by plotting λ in the f-$\hat{f}$ space (Bulmer and Taylor 1980; van Tienderen 1984; van Tienderen and de Jong 1986). An important feature of the haystack model is that a gene that is globally rare can have significant abundance in individual haystacks.

The following assumptions underlying our models may be potentially severe for the outcome and therefore need scrutiny:

1. The number of foundresses is fixed; therefore, the impact of variation remains to be assessed.

2. Settlement of foundresses in a haystack takes place only at its start, whereas in reality invasion will usually be continuous.

3. Generations are discrete, whereas in reality generations may well overlap, implying that many females will be both producers and dispersers and that males from earlier generations will compete with those from later generations. This is a drastic simplification with potentially severe effects on the predictions.

4. Sampling effects within haystacks are ignored, implying that there is no genetic drift and that all variance between haystacks stems from the foundresses. Sampling effects will be small only when fecundity within a haystack is large (Wilson 1987; Taylor and Wilson 1988).

5. The genetic system is biparental and haploid. However, many arthropods with sex ratio control are haplodiploid with uniparental males (Wrensch and Ebbert 1993). Uniparental genetic systems can influence optimal sex allocation in inbreeding systems (Hamilton 1979; Nunney and Luck 1988; Stubblefield and Seger 1990) because of asymmetries in the relatedness between mothers and sons versus between mothers and daughters. The genetic system may therefore influence the predictions of haystack models, especially for the case of mating after dispersal (van Tienderen and de Jong 1986). However, explicit haplodiploid genetics causes the predictions of haystack models to be very dependent on the mode of gene action (van Tienderen and de Jong 1986). We chose to avoid this dependence on detail and used a maximally simple haploid model with the additional advantage that the models are kept tractable enough to cope with complications such as subdivision of haystacks and/or a flexible sex ratio.

The following aspects are varied in our models:

1. Population growth in the haystack is either unlimited or limited such that the dispersing generation is of fixed size (males and females combined). If growth was limited, the generation number at which carrying capacity was first reached was varied as well. In haystacks with a substructure (see 2), density dependence operates at the haystack level (not at the level of the subgroups).

2. The population in a haystack is either completely mixed (single-level haystack) or divided, each generation being split into subgroups of size N_s; within each subgroup there is local mate competition, but the inseminated females mix within the haystacks between generations (two-level haystacks; fig. 2). For sim-
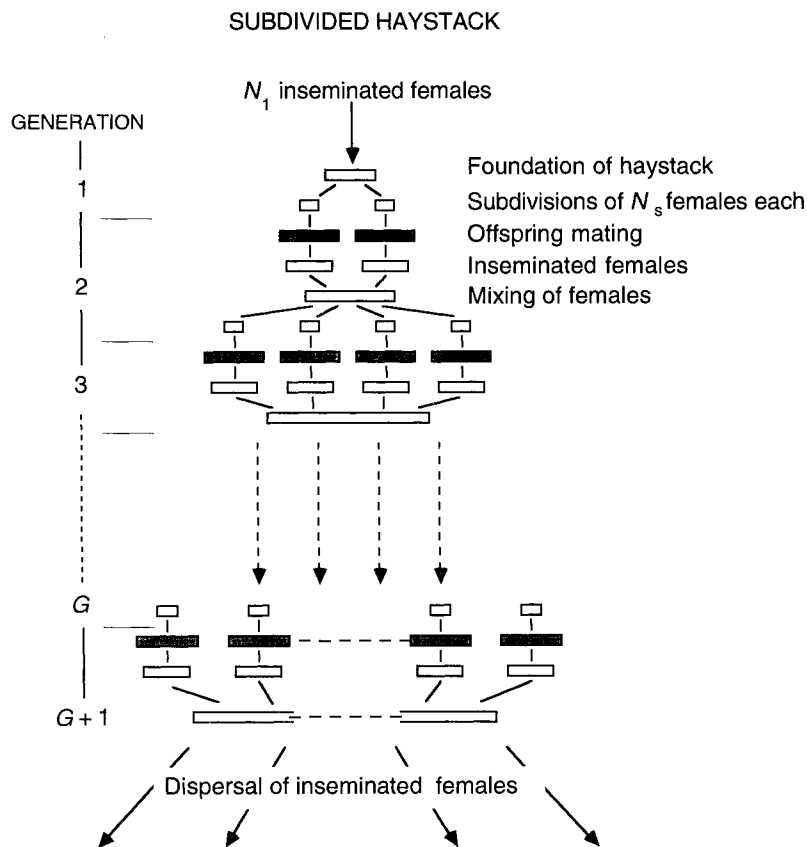
FIG. 2.—Subdivided haystack started by N_1 females and lasting for G breeding generations, after which the inseminated females from the $(G + 1)$th generation disperse. In every generation inseminated females mix first and then found local mating groups of size N_s.

plicity the size of subgroups is limited to two females, meaning there are 10 different types of subgroups. In each generation the total numbers of the four different types of inseminated females that are produced by the subgroups of each type are calculated for each type of haystack. The frequencies of the different types of subgroups in the next generation are then calculated assuming random association of females within haystacks (see the appendix). Sampling effects in the formation of subgroups and in the production of inseminated females in subgroups are ignored.

3. The sex ratio is either fixed over generations or flexible for each separate generation. In the fixed case the ES sex ratio will be a compromise between the optima for different generations. In the flexible case the sex ratio is allowed to evolve to a different level for each generation separately.

Below, the results are discussed first for single-level haystacks and then for two-level haystacks. A convenient first result is that the optimal sex ratio for a

TABLE 1

ES Proportion of Daughters in Single-Level Haystacks with Limits to Population Growth

	INFLEXIBLE SEX ALLOCATION (G)						FLEXIBLE SEX ALLOCATION (g)	
N_1	1	2	3	4	8	16	$1 \cdots G - 1$	G
1	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	Indeterminate	1.0000
2	.7500	.6667	.6250	.6000	.5556	.5294	.5000	.7500
3	.6667	.6000	.5714	.5556	.5294	.5152	.5000	.6667
4	.6250	.5714	.5500	.5385	.5200	.5102	.5000	.6250
6	.5833	.5455	.5313	.5238	.5122	.5062	.5000	.5833
8	.5625	.5333	.5227	.5172	.5088	.5044	.5000	.5625
12	.5417	.5217	.5147	.5111	.5056	.5028	.5000	.5417
16	.5313	.5161	.5109	.5082	.5041	.5021	.5000	.5313
24	.5208	.5106	.5071	.5054	.5027	.5014	.5000	.5208
32	.5156	.5079	.5053	.5040	.5020	.5010	.5000	.5156

Note.—Sex ratios are either inflexible over generations or may have a different value in every generation (flexible sex ratios). For inflexible sex ratios, the ES proportion of daughters (f^*) is calculated for a range of foundress numbers (N_1) and total number of breeding generations spent in the haystack (G). For flexible sex ratios, the ES proportion of daughters from mothers in generation g is calculated for generations 1 to G. The flexible sex ratios appear to be independent of G and to be equal for every $g < G$. The case of population growth without limits is not presented in this table; however, in this case it appears that the value of f^* in every generation g is equal to the value presented in the last column (for the last generation G under limits to growth and flexible sex allocation). It is also equal to that value in the inflexible case.

given generation appeared to be independent of the sex ratio in other generations. This greatly simplified finding the ES strategies for the different generations in the case of flexible sex ratios, as the sex ratios could be determined independently and thus there was no need for simultaneous optimization.

Single-Level Haystacks

Table 1 gives the ES proportion of daughters for the haystack model with limited growth and inflexible sex allocation, f^*, for various combinations of foundress number, N_1, and number of breeding generations per haystack, G. The sex ratio, f^*, decreased with N_1 and with G. When f^* was flexible, the last generation's ES sex ratio was female biased, whereas the ES sex ratios of all previous generations were unbiased (fig. 3A). The female bias of the last generation was then independent of G. The assumption that there are limits to population growth has important implications; when growth was unlimited, sex ratios in all generations were equal and female biased with a value of $(N_1 + 1)/2N_1$, as expected; this corresponds to the ES sex ratio of the last generation predicted for the case of limits to growth (fig. 3A). Comparison of the results for flexible and inflexible sex ratios shows that the inflexible ES sex ratio is a compromise between the optimum for the last generation and that for the earlier generations. The compromise f^* decreased with G because the relative importance of the last generation diminishes with the total number of generations.

Generally, haystack populations compete with each other by means of the number of dispersing females they produce. When growth is unlimited, variation

ES proportion of daughters, f^*,
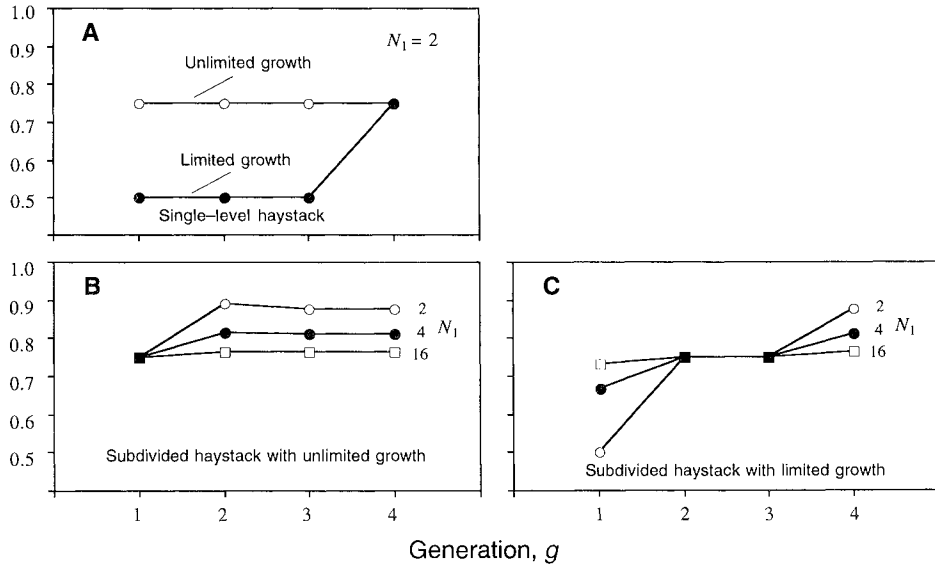per generation

FIG. 3.—Haystack populations with flexible sex ratios that can depend on generation number. The ES sex ratios produced by every generation g are determined independently and are presented for haystacks lasting four generations ($G = 4$). A, Single-level haystacks with and without limits to population growth for the case where the number of foundresses, N_1, is two. B, Subdivided haystacks with unlimited growth for three different N_1's and a subgroup size, N_s, of two. C, Subdivided haystacks ($N_s = 2$) with limited growth for three different N_1's.

in the productivity of haystack populations arises from differences in both the sex ratio and the size of the last generation. The size of the last generation will be determined by the growth rate in the previous generations, and, thus, there will be selection for a female bias in those generations, as this promotes population growth. Haystack populations with limited population growth can compete only by means of the proportion of females in the dispersing generation, because the size of this generation is fixed and independent of the sex ratio in earlier generations. In every generation but the last, competition is then exclusively within haystacks, leading to an unbiased sex ratio. Only in the last generation does competition between haystacks play an additional role, and this favors a female-biased sex ratio. In the last generation, the haystack models with limited and unlimited growth are equivalent. Another way of explaining the results is that individual selection in the earlier generations in haystacks with limits to growth leads to an unbiased sex ratio, because the proportional representation in the last generation is all that counts. Relatedness between females then has no influence, because competition is exclusively within haystacks and hence also between relatives. In the last generation, individual selection favors a biased sex ratio through local mate competition, which tends to be low because the group

TABLE 2

ES Proportion of Daughters in Subdivided Haystacks without Limits to Population Growth

						Flexible Sex Allocation					
	Inflexible Sex Allocation (G)					g(G = 4)				g(G = 2)	
N_1	1	2	4	8	16	1	2	3	4 (= G)	1	2 (= G)
1	1.00	1.0000	1.0000	1.0000	1.0000	1.00	1.0000	1.0000	1.0000	1.00	1.0000
2	.75	.8158	.8476	.8617	.8684	.75	.8926	.8788	.8757	.75	.8889
4	.75	.7821	.7978	.8053	.8089	.75	.8166	.8134	.8127	.75	.8158
8	.75	.7658	.7737	.7775	.7794	.75	.7822	.7815	.7813	.75	.7821
16	.75	.7579	.7618	.7637	.7648	.75	.7659	.7657	.7656	.75	.7658
32	.75	.7539	.7559	.7568	.7573	.75	.7579	.7578	.7578	.75	.7579

Note.—Sex ratios are either inflexible over generations or may have a different value in every generation (flexible sex ratios). For inflexible sex ratios, the f^* (ES proportion of daughters) is presented for a range of foundress numbers (N_1) and total number of breeding generations spent in the haystack (G). For flexible sex ratios, the f^*s are presented for every generation (g) and for two values of G (four and two). The size (N_s) of the subgroups where local mate competition takes place is taken to be two.

size is as large as the number of females in the last breeding generation. However, because females in the last generation are related, kin selection is responsible for increasing the female bias. It is irrelevant in which generation the carrying capacity is reached first, because the limited size of the dispersing generation ensures that only within-haystack competition exists in the earlier generations, independent of whether the haystack population is still growing or not.

Two related predictions concerning haystacks with limited population growth stand out, because these are in conflict with predictions of Frank (1986, 1987). When the sex ratio is inflexible, the generation number where the carrying capacity is reached first has no influence on the compromise in the ES sex ratio, whereas Frank (1986) predicted the reverse for reasons not made explicit. Second, when the sex ratio is flexible, the ES sex ratio in every generation but the last is unbiased, independent of the generation number at which carrying capacity was reached first. This is in agreement with Frank's 1986 speculation but seems contrary to the one made in a later discussion of the same model (Frank 1987), where he predicted that an unbiased sex ratio is only favored after the carrying capacity is reached.

Two-Level Haystacks

The results from models of haystacks with unlimited growth are presented in table 2 for various values of G and for the case of inflexible and flexible sex ratios, whereas figure 3B serves as an illustration of the latter. When inflexible, the sex ratio, f^*, decreased with the number of foundresses, N_1, just as in the single-level haystacks. Contrary to that in single-level haystacks, f^* now increased with the number of generations, G, instead of staying the same. The haystack level and the local mate competition level reinforced each other in their influence on the female bias in sex ratio. This can be concluded because the

TABLE 3

ES Proportion of Daughters in Subdivided Haystacks with Limits to Population Growth

	Inflexible Sex Allocation (all G)	Flexible Sex Allocation					
		$g(G = 4)$				$g(G = 2)$	
N_1		1	2	3	4	1	2
1	1.00	Indeterminate	Indeterminate	Indeterminate	1.0000	Indeterminate	1.0000
2	.75	.5000	.75	.75	.8757	.5000	.8889
4	.75	.6667	.75	.75	.8127	.6667	.8158
8	.75	.7143	.75	.75	.7813	.7143	.7821
16	.75	.7333	.75	.75	.7656	.7333	.7658
32	.75	.7419	.75	.75	.7578	.7419	.7579

Note.—Sex ratios are either inflexible over generations or may have a different value in every generation (flexible sex ratios). For inflexible sex ratios, the f^*s (ES proportion of daughters) are presented for a range of foundress numbers (N_1); they appear to be independent of the number of generations spent in the haystack (G). For flexible sex ratios, the f^*s are presented for every generation (g) and for two values of G (four and two). The size (N_s) of the subgroups where local mate competition takes place is taken to be two.

inflexible f^* was always higher than in equivalent single-level haystacks (cf. table 2 with the last column of table 1) and was also consistently higher than 0.75 (which follows from $N_s = 2$ under local mate competition in the absence of a superimposed haystack structure).

Studying the case of flexible sex ratios helps to explain the above results. When growth is unlimited, all generations contribute to between-haystack competition. In the first generation the ES sex ratio was equal to the value expected from local mate competition with group size N_s. Because first-generation females are unrelated and there is no density dependence, individual selection results in a proportion of daughters of 0.75. In later generations, local mate competition (with a group size of two) will still operate, but the ES proportion of daughters increases because by now the females have become related to each other. This explains the stronger female bias compared to local mate competition without an additional haystack level. The stronger bias compared to a single-level haystack arises from the smaller size of the local mate competition groups in two-level haystacks. It also explains why the inflexible f^* increased with G, because the first generation becomes relatively less important when the number of generations increases. The compromise between the low value in the first generation and the higher values in later generations leads to an increasing f^* with G. Inspection of figure $3B$ shows that there was a slight decrease in f^* in the generations following the second one; this is probably because the frequency distribution of different types of composites over subgroups was initially not yet in equilibrium.

Results for the case of limited growth, assuming either inflexible or flexible sex ratios, are presented in table 3. Figure $3C$ serves as an illustration of the case with flexible allocation. When inflexible, the ES sex ratio was 0.75 for every G and for $N_1 > 1$. This may result from the choice of the relative sizes of the subgroups, N_s, and the number of foundresses, N_1. When $N_s < N_1$, at least one

complete subgroup will be present in the first generation; in that case the overall sex allocation depends only on N_s and is the same as under local mate competition with group size N_s. Thus, the haystack superstructure apparently has no influence on sex allocation; only the substructure is important, which suggests that local mate competition is the major selective process. When $N_s > N_1$, the subgroup will be incomplete in the first generation; in that case the superstructure gives rise to selection that increases the proportion of daughters.

For the case of flexible sex ratios, the ES sex ratios in the last generation of haystack populations with unlimited growth were equal to those in the last generations of haystacks with limited growth (cf. tables 2 and 3). This makes sense, because mating structure, competition structure, and relatedness did not differ in the last generation. The preceding generations, however, differed in their ES sex ratio levels. When there were limits to population growth, the ES sex ratio in the first generation was equal to the value expected from local mate competition with a finite number of groups (see Taylor and Bulmer 1980). The sex ratio was less biased than for the standard case of an infinite number of subgroups, because the behavior of females was no longer fully benevolent with respect to members of their subgroup. As a consequence of density dependence in the haystack, the fitness of a subgroup member was influenced by the fitness of the other females in the subgroup. Individual selection resulted in a proportion of daughters intermediate between the value promoted under local mate competition and the 0.5 promoted by selection under haystack-wide mating. In generations 2 to $G - 1$ the proportion of daughters became 0.75. There was then local mate competition (again with a finite number of subgroups), but relatedness developed between females within their own subgroup and with those in other subgroups. Contrary to expectation, this resulted in an ES sex ratio equal to the value obtained under local mate competition; one would expect a lower proportion of daughters than under local mate competition because competition was also with relatives and the size of the haystack was limited. It is striking, but difficult to understand, that when the sex ratio is inflexible the effects of the first and the last generation cancel each other out.

A dependence of sex allocation on the number of the generation can have an important bearing on the mean sex ratio of a metapopulation, because generally the last generation will dominate numerically. For example, when growth is limited, the compromise in the sex ratio under inflexible allocation lowers the proportion of daughters in the last generation and increases it in the preceding generations. The net result for the population at large will be a less strong female bias than under flexible allocation. Thus, for the case of flexible sex ratios and limited growth, superposition of a haystack structure will increase the mean sex ratio in addition to when $N_s < N_1$ but not when sex ratios are inflexible (table 3).

Thus, when only mated females disperse, haystacks with limits to population growth can also lead to a stronger female bias than expected under local mate competition. The reason is that haystack populations can compete via the sex ratio of the last generation. Such a strong female bias can be considered altruistic and is unique compared to other altruistic traits, since these cannot be promoted by selection when the size of the last generation is fixed (Wilson 1987). Another

TABLE 4

Summary of the Results of Different Versions of the Haystack Model and the Island Model

	Unlimited Growth	Limited Growth
Haystacks (transient groups):		
Inflexible sex allocation:		
Single-level haystacks	$(N_1 + 1)/2N_1$ (decreases with N_1); independent of G	Decreases with G; decreases with N_1; independent of the generation number where the carrying capacity is first reached
Two-level (subdivided) haystacks	Increases with G; decreases with N_1	$(N_s + 1)/2N_s$; independent of G; independent of N_1
Flexible sex allocation over generations:		
Single-level haystacks	$(N_1 + 1)/2N_1$ for all g (decreases with N_1)	$(N_1 + 1)/2N_1$ in the Gth, .5 in all earlier generations
Two-level (subdivided) haystacks	$(N_s + 1)/2N_s$ in the first generation, higher in the later generations	$(N_s + 1)/2N_s$ in the middle generations, lower in the first and higher in the Gth generation
Islands (permanent groups)		$(N_g + 1)/2N_g$*

Note.—In several cases the numerical solutions of the ES sex ratios (proportion of daughters) exactly correspond to a formula, which is then used to summarize the model results. The term N_1 is the number of haystack foundresses, N_s is subgroup size, g is the generation number, G is the total number of breeding generations spent in the haystack, and N_g is the number of females at generation g. In the case of limited growth the size of the last generation (males plus females) is fixed. Frank (1987) and Avilés (1993) analyzed various extensions of the haystack model that take the peculiarities of the population structure of social spiders into account. The model of Avilés (1993) also includes between-colony migration in every generation, as in island models.

* Bulmer 1986; Taylor 1988.

major conclusion is that subdivision of haystacks into groups with local mate competition leads to a stronger female bias than expected under a single-level haystack structure. However, the reverse is not always true; the superposition of haystacks on groups with local mate competition does not necessarily increase the female bias. A third major conclusion is that when sex allocation is flexible over generations, predicted ES sex ratios may differ dramatically between generations. Table 4 gives a summary of the results.

BIOLOGICAL RELEVANCE OF HAYSTACK AND ISLAND MODELS

It is well established that many small arthropods have a metapopulation structure. However, they may differ in whether the local populations are permanent or transient, whether there is local density dependence, and whether there is substructure in local populations. These differences need an assessment before testing the predictions of the various haystack and island models. In the following discussion, we will first consider the population structure of plant-inhabiting mites in more detail and then test predictions on sex allocation emerging from our

models. Finally, we will briefly review the evidence on population structure and sex allocation in other small arthropods.

Relevance to Plant-Inhabiting Mites

Population structure.—Spider mites (Acari: Tetranychidae) are a good example of herbivorous arthropods with low mobility and fast rates of population growth, likely to form multigeneration groups. Their subpopulations will often crash because of predation, infectious diseases, or local food exhaustion. They form locally dense infestations on their food plants, subdivided into colonies on different leaves. These haystack-like structures are probably subdivided because females deposit their eggs close together and juveniles disperse very little before mating (McEnroe 1969; Mitchell 1973). Thus, the haystacks will contain local mating groups. Of particular interest is that local spider mite populations can resemble either haystacks with limited growth or haystacks with unlimited growth. The former type occurs when the food plants become overexploited, whereas the latter may occur when predators and pathogens cause the population crash.

Predatory mites (Acari: Phytoseiidae) differ widely in their population biology, depending on characteristics of the prey species and other food items included in their diet (Sabelis and Janssen 1993). Generalist species roam around in search for widely dispersed food items, including pollen and fungi. They are consequently more evenly distributed. As a result of the relatively tame dynamics of their food, their local populations do not undergo large fluctuations and may even be relatively constant in size (McMurtry 1992).

At the other extreme there are specialist species of predatory mites, which forage in locally dense populations of spider mites; a typical example is the predatory mite *Phytoseiulus persimilis,* foraging for spider mites in the genus *Tetranychus.* These spider mite infestations are initially colonized by one or a few inseminated female predators; they are the foundresses of a predator subpopulation that expands rapidly for a number of generations until the prey population is wiped out. The female predators then disperse to search for new infestations (Sabelis and van der Meer 1986). Thus, these predators have local, multigeneration subpopulations that are ephemeral, and the final size of these populations will be determined by the amount of prey available. In fact, the colonization-dispersal cycles of specialist predatory mites are much like those of their prey.

A female of *P. persimilis* typically distributes her eggs over a number of prey colonies, where the high prey density ensures a high rate of oviposition and low mobility of the predator; hence, the eggs of each mother have a clumped distribution within a colony. Juvenile predators tend not to leave a prey colony (Sabelis 1981; Wheatly and Boethel 1992), whereas mated females disperse throughout the infested plant area (e.g., Sabelis 1981; Nagelkerke 1994). Under conditions of high prey density, juvenile dispersal *within* a prey colony is also very restricted; juvenile predators typically move no farther than 1 cm from their natal site (C. J. Nagelkerke, unpublished data). Taken together, these characteristics lead to the supposition that mating takes place on a scale much smaller than the area infested by spider mites. Hence, there will be local mate competition on a spatial scale that is smaller than that of the prey-infested plant area and thus also of the local predator population inhabiting this area. Therefore, for this specialist it

seems most realistic to describe their population structure by a two-level haystack model incorporating limits to population growth.

The studies on *P. persimilis* provide a picture of one of the most extreme specialists among predatory mites in the family Phytoseiidae. In fact, there is a continuum of species ranging from generalist to specialist lifestyles. An earlier article (Sabelis and Janssen 1994) presented evidence for gradual differences in egg production rates and argued that these reflect the constraints imposed by the local densities of their preferred prey species. Thus, specialists forage for high-density prey species and have high egg production rates, whereas generalists forage for low-density prey species and have low egg production rates.

We propose that the population structures in phytoseiid mites show a haystack-island gradation across species that corresponds to the generalist-specialist continuum. At one extreme, there are haystack species with subpopulations subject to an invasion-exploitation-dispersal cycle, where the first female to invade a prey patch gives rise to fast population growth and is therefore able to dominate the population of her haystack in a genetic respect. When the prey population crashes, the inseminated females disperse and face a risky future. Intermediate between haystack types and island types, there are species with a lower rate of local population growth, where the first female is less able to dominate the population (and possibly the invasion rate is higher, because of the resulting metapopulation dynamics; cf. van Baalen and Sabelis 1995). The lower the growth rate, the longer subpopulations persist, implying that more generations are spent in a patch. This results in less violent fluctuations in the interaction with the food source and consequently more steady and less abrupt dispersal. At the other extreme, there are island types with more or less constant local populations and continuous migration between populations.

Sex ratios in spider mites.—Sex ratios in tetranychid mites are generally female biased (Sabelis 1991), but whether they are more skewed than expected from local mate competition theory is hard to tell, because information on the exact size of the local mating group is lacking.

However, spider mites stand out as one of the best examples supporting a haystack-like population structure, as some species, such as *Oligonychus pratensis* (Banks) and *Tetranychus urticae* Koch, exhibit an extra female bias when forced to reside on damaged leaves (Wrensch and Young 1978, 1983; Kondo and Takafuji 1982; Young et al. 1986; Stiefel and Margolies 1992). This suggests that spider mites produce a stronger female bias in the last generation before overexploitation of the host plant. This is exactly what is predicted for the case of flexible sex allocation by our models of single-level and two-level haystacks with limited growth. However, the prediction from the substructured haystack model hinges on the assumption that subgroup size does not undergo major changes. This assumption needs scrutiny, as subgroup size may change when the host plant nears exhaustion as a food source and spider mite density peaks.

It would be interesting to investigate sex allocation in local populations of spider mites that differ in whether they overexploit their host plant or are overexploited by natural enemies, as the overall female bias in the latter case should be more pronounced.

Sex ratios of predatory mites.—As in the spider mites, sex ratios of phytoseiid

mites are generally female biased. A particularly well-investigated species is *P. persimilis*. Like females of most other specialists among the Phytoseiidae, females of *P. persimilis* produce strongly female-biased sex ratios under conditions of high prey density. They lower the proportion of daughters when predator density increases (Nagelkerke 1993; Sabelis and Nagelkerke 1993). The female bias and the sex ratio response to predator density are qualitatively in agreement with predictions from local mate competition theory.

However, quantitatively, local mate competition alone does not seem sufficient to explain the extent of the female bias in *P. persimilis*. In experiments with four females on a 1.25-cm leaf disk, the proportion of daughters was 0.72–0.78 (Nagelkerke 1993), while local mate competition theory (Hamilton 1979; Taylor and Bulmer 1980) predicts a sex ratio of 0.65 for haplodiploids with a group size of four. This difference between observations and predictions should be taken very seriously, because realistic, complicating factors, such as secondary matings, ambulatory dispersal of males between mating groups, and movement of females between oviposition sites would lead to an even larger discrepancy between observations and predictions.

As an alternative to hypotheses based on local mate competition alone, we suggest that selection for a stronger female bias results from the existence of a haystack structure above the level where local mate competition prevails. This hypothesis is detail independent, because a strongly female-biased sex ratio can be favored in all versions of the haystack model considered in this article. The strongest female bias is favored when growth is unlimited and the haystacks are subdivided, but even when there are limits to growth and the haystacks have no substructure, very skewed sex ratios—that is, more skewed than expected for single-generation groups subject to local mate competition—can be favored. However, this requires that the effective number of haystack foundresses be sufficiently low. This may be so because invasions will take place in a sequential manner and exponential population growth will enable the first invader to dominate the genetic composition of the haystack populations.

Models of single-level and two-level haystacks with limited growth and flexible sex allocation predict that the proportion of daughters should be highest in the last generation. If, for example, the decreasing prey density and increasing predator density in the last phase of population growth serve as a cue indicating the last generation, then—under our model assumptions—an increase in the proportion of daughters is predicted. However, female predatory mites respond to increasing predator density and decreasing prey density by producing less female-biased sex ratios (Nagelkerke and Sabelis 1991; Nagelkerke 1993; Sabelis and Nagelkerke 1993). This is in conflict with the predictions. Reasons for the deviating prediction may be that the size of local mating groups is not fixed but increases because decreasing prey density and increasing predator density will promote within-haystack mobility of the predatory mites (Sabelis and Nagelkerke 1993; Nagelkerke 1994).

We conclude that a haystack structure could in principle explain strongly skewed sex ratios in *P. persimilis,* but to enable more critical tests we need to know whether the effective number of foundresses is sufficiently low, and we

need more information on the haystack substructure and the degree to which females are able to use information about the growth phase of the haystack population.

Although a haystack structure may explain female-biased sex ratios of phytoseiid mites, does it help to explain differences between species? We found a positive correlation between the rate of oviposition and the proportion of daughters across species and proposed an explanation based on local mate competition alone (Sabelis and Nagelkerke 1988, 1993). Species with a low ovipositional rate produce small broods and are assumed to forage for low-density prey; therefore, to obtain food they have to disperse over longer distances. Consequently, there will be mixing of ovipositing females and of juveniles, resulting in mixing of broods. Hence, species with low ovipositional rates are expected to produce less female-biased sex ratios, because the number of foundresses will be high (Nagelkerke 1993; Sabelis and Nagelkerke 1993) and the broods will be small, which favors a diminished bias because of the discrete nature of offspring (Nagelkerke 1993, 1996). This remains a viable proposition, in agreement with what is known about diets (Sabelis and Nagelkerke 1993).

Here, we propose an alternative hypothesis by invoking the haystack-island gradation between specialist and generalist species. This prediction is broadly in agreement with the available evidence; phytoseiid species that are specialized on high-density prey types have a high egg production rate and a strong female bias in their sex ratio, whereas phytoseiid species that use low-density prey types have a low egg production rate and a lower female bias (Sabelis and Nagelkerke 1993). It would be interesting to check whether these population structures also affect other "altruistic" traits, such as cannibalism; interestingly, there is some evidence that specialists are less cannibalistic (Croft et al. 1992).

The haystack-island hypothesis is not incompatible with the local mate competition hypothesis. In fact, the two hypotheses relate to different levels of population structure and can reinforce each other. Both hypotheses predict female-biased sex ratios for phytoseiid species feeding on high-density prey types; they differ only in the degree of skewness associated with a given amount of local mate competition. It is too early to assess the relative importance of the two hypotheses, as there is a lack of information on the mating structure of phytoseiid populations.

Potential Relevance to Other Small Arthropods

Haystack-like population structures seem to be widespread among small arthropods, as illustrated in table 5. Evidence for the existence of local populations that are temporary, but last for several generations, is available for various carnivorous, phytophagous, fungivorous, and parasitic mites, aphids, thrips, and social spiders. What these organisms have in common is that while they are in the haystack, long-range dispersal is suppressed behaviorally and sometimes even morphologically (absence of wings, as, e.g., in aphids). Dispersal is delayed until after the resources are overexploited, except in the case of social spiders, where dispersal starts above a threshold group size and then continues over a longer period (Avilés 1986). In many of these organisms the sex ratio seems too female

TABLE 5

REVIEW OF FEATURES RELEVANT TO THE EXISTENCE OF HAYSTACK-LIKE POPULATION STRUCTURES
IN SMALL ARTHROPODS OTHER THAN PHYTOSEIID AND TETRANYCHID MITES

Taxon	Population Structure	Sex Allocation	References
Parasitic wasps	Local mate competition with females dispersing every generation; haystack structures may well be present in, e.g., parasitoids of scale insects	Female biased	Werren and Simbolotti 1989; Ikawa et al. 1993; Godfray 1994
Syringophilidae (feather mites)	Two-generation haystacks, started by one or a few females, in the shaft of a bird feather; mated females disperse	Very female biased	Kethley 1971; Charnov 1982
Tarsonemid mites	Exploit both transient and continuous food sources; haystack-like structures with more than one generation exist; mated females disperse	Species exploiting transient food sources have a more strongly female bias	White and Sinha 1981; Lindquist 1986; Bruce and Wrensch 1990; Kaliszewski and Wrensch 1993
Hummingbird flower mites	Haystack-like structure	Female bias	Wilson and Colwell 1981
Water mites	Unknown	Often an enigmatic female bias	Gledhill 1969; Proctor 1989
Thrips	Both island-like (fungivores) and haystack-like (gall formers) situations	Often a strong female bias in gall formers	Crespi 1993; Taylor and Crespi 1994
Bark and ambrosia beetles	Local mate competition; sometimes more generations are spent in one patch	Often a strong female bias	Kirkendall 1993
Aphids with wingless males	Parthenogenetic haystacks producing locally mating sexuals	Lack of data on investment ratios	Moran 1993
Social spiders	Colonies founded by one or more females from parent colony; after reaching a threshold size, colonies send out dispersers; mating takes place within colony	Strong female bias	Lubin and Crozier 1985; Avilés 1986; Vollrath 1986; Elgar and Godfray 1987; Lubin 1991

NOTE.—The taxa referred to in the table indicate broad groups containing at least some species that may have a haystack-like population structure.

biased to be explained by local mate competition alone. This strong skew may arise as a consequence of selection in a population with a haystack structure under at least one of the following conditions: there is no limit to population growth, haystacks are subdivided into local mating groups, and the initial number of foundresses is low. Generally, limits to population growth will lead to a decrease in female bias, but when the initial number of foundresses is small enough, a strong female bias is possible. When population growth is subject to a limit and the sex ratio is flexible over generations, an exceptionally strong female bias is expected in the last generation. As argued earlier, spider mites may provide an example, because they produce a relatively higher proportion of daughters when food sources become depleted. Haystack-like group selection may play a much larger role in sex allocation than formerly thought. Many of the examples relating to small arthropods that have been discussed warrant further study. It is encouraging to observe that sex allocation research nowadays covers a larger range of arthropods than hymenopterans alone (e.g., Wrensch and Ebbert 1993).

APPENDIX
HAYSTACK MODELS
SINGLE-LEVEL HAYSTACKS

Let the numbers of the four different mated female composites in a given haystack at generation g be $C_{r.r}$, $C_{r.m}$, $C_{m.m}$, and $C_{m.r}$, where the two subscripts refer to the genotype of the female and her mate, respectively; r refers to a resident and m to a mutant. In the first generation ($g = 1$) C represents the foundresses. These composites produce total numbers D and S of unmated female and male offspring, respectively, which are given by

$$D_r = af(C_{r.r} + 0.5C_{r.m}) + 0.5a\tilde{f}C_{m.r},$$

$$D_m = 0.5afC_{r.m} + a\tilde{f}(0.5C_{m.r} + C_{m.m}),$$

$$S_r = a(1 - f)(C_{r.r} + 0.5C_{r.m}) + 0.5a(1 - \tilde{f})C_{m.r},$$

and

$$S_m = 0.5a(1 - f)C_{r.m} + a(1 - \tilde{f})(0.5C_{m.r} + C_{m.m}),$$

where a is fecundity, f is the resident sex allocation, and $\tilde{f}$ is the mutant sex allocation. Assuming random mating within a haystack, the numbers of mated composites in $g + 1$ are then given by

$$C_{r.r} = D_r\frac{S_r}{S_r + S_m}; \quad C_{r.m} = D_r\frac{S_m}{S_r + S_m};$$

$$C_{m.m} = D_m\frac{S_m}{S_r + S_m}; \quad C_{m.r} = D_m\frac{S_r}{S_r + S_m}.$$

This is done for all G breeding generations. In the dispersing $(G + 1)$ generation the numbers of the three mutant composites produced by the three corresponding mutant haystacks are then divided by the per-foundress production by a haystack population without mutants. These ratios are used in the recurrence matrix.

SUBDIVIDED HAYSTACKS

In each generation the composites in a haystack are randomly distributed over 10 different types of local mating subgroups of two composites each. The total number, M_g, of subgroups in a given generation is given by $(C_{r.r} + C_{r.m} + C_{m.m} + C_{m.r})/2$. Let the relative frequencies of the composites in the haystack be $q_{r.r}$, $q_{r.m}$, $q_{m.m}$, and $q_{m.r}$. The frequencies of the subgroups can be straightforwardly calculated from the relative frequencies of the composites in the haystack. For example, the number of subgroups of composition $\{r.m, m.r\}$ is given by $2q_{r.m}q_{m.r}D_g$ (again, r.m denotes a resident female mated by a mutant male). Calculation of the production of new composites by each type of subgroup is analogous to calculation of the production from a single-level haystack. The new composites are then pooled to form the next generation of subgroups. In the first generation the calculation has to be done differently because there is only one mutant composite, and hence only one mutant subgroup, in each mutant haystack. In later generations such effects of discreteness are ignored.

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