

# When should a female avoid adding eggs to the clutch of another female? A simultaneous oviposition and sex allocation game

CORNELIS J. NAGELKERKE<sup>1\*</sup>, MINUS VAN BAALEN<sup>2</sup> and MAURICE W. SABELIS<sup>3</sup>

<sup>1</sup>*Imperial College at Silwood Park, Department of Biology, Ascot, Berkshire SL5 7EN, UK*

<sup>2</sup>*Department of Biological Sciences, Ecosystems Analysis and Management Group, University of Warwick, Coventry CV4 7AL, UK*

<sup>3</sup>*Department of Pure and Applied Ecology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands*

## Summary

Avoidance of double oviposition (ADO) is the strategy not to oviposit on food patches where another female has oviposited before. If two females oviposit on the same patch, competitive and mating interactions within and between broods may lead to both a clutch size game and a sex allocation game between the two visitors. Though the two games interact, they are usually considered separately. Here, the ESS conditions for ADO are investigated in an analysis that combines the two games into one. The analysis strengthens the notion that it is really ADO that needs to be explained, because role-dependent net pay-off from an additional egg is most likely to favour double oviposition (DO). To a first female, the net pay-off includes the effect on the eggs already present, whereas to a second female only the egg's gross pay-off matters. ADO is the evolutionary stable strategy (ESS) if there are enough patches still without eggs and either (1) the fitness of an additional egg is so low that the first female would not lay it even in the absence of detrimental effects on earlier offspring, so neither would a second female, or (2) differences in either the survival probability of the offspring or their reproductive success are sufficient to counterbalance the differential interest in the eggs already present. The first condition requires that eggs are relatively large, because then the decrease in pay-off between two successive eggs can be large. The second condition may be met when there is a time interval between ovipositions of subsequent females. The resulting developmental lag of the second clutch will (1) diminish its ability to compete for food and (2) lower its reproductive success when there is local mate competition and sons are too late to mate with daughters of the first female. If sons of first and second females compete on equal terms, however, ADO is unlikely. Male migration between patches reduces the influence of sex allocation strategies on clutch size decisions; the same holds for small clutch sizes. To illustrate the importance of considering sex allocation and clutch size decisions in an integrated way, oviposition strategies of plant-inhabiting predatory mites (Acari: Phytoseiidae) are discussed.

**Keywords:** oviposition; avoidance of double oviposition; sex allocation; local mate competition; Phytoseiidae

## Introduction

Females of many invertebrate species search for oviposition sites ('patches') with food for their offspring. When a female encounters a patch that has already been oviposited on she may either

\* Address all correspondence to Cornelis J. Nagelkerke, Department of Pure and Applied Ecology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands.

add a clutch or refrain from oviposition (Waage, 1986). In the early literature (cf. Howard, 1897; Fiske, 1910) the former (called 'double oviposition' or, in the case of parasitoids, 'super-parasitism') was viewed as a *faux pas* of an imperfect female. Recently, however, the adaptive value of this behaviour has become better understood (Parker and Courtney, 1984; Strand and Godfray, 1989; van Alphen and Visser, 1990). When it is no longer rewarding for a first visitor to continue ovipositing on a patch, it may still be profitable for a subsequent visitor to deposit additional eggs. As pointed out by Ives (1989), a first female's decision to leave is influenced by the extra competition an additional egg would imply for the offspring already in place. However, a second female will not consider the fitness effects on eggs that are not hers and, hence, it is not the occurrence of double oviposition (DO), but rather the avoidance of double oviposition (ADO), that needs to be explained.

In this article we will perform an analysis of the oviposition game and investigate under what circumstances ADO is expected to occur. The general analysis applies to a broad range of organisms, but the more detailed models we consider are inspired by observations on the oviposition behaviour of predatory mites.

### **Predatory mites**

Predatory mites of the family Phytoseiidae prey upon spider mites, which have a very patchy distribution over the plants they infest. The relatively mobile female predatory mites search for prey 'colonies' to feed and oviposit in (Sabelis, 1985; Sabelis and van der Meer, 1986). Juvenile predatory mites disperse little; this may lead to local competition for food and to 'local mate competition' (Hamilton, 1967; Nagelkerke and Sabelis, 1991; Nagelkerke, 1993; Sabelis and Nagelkerke, 1993). Both kinds of interactions will affect the optimal clutch size and sex allocation decisions. It is known that when female predatory mites find patches that have received a clutch before, they may refrain from oviposition (Hislop and Prokopy, 1981; Sabelis, 1981). In addition, they are able to adjust the sex ratio of their offspring in response to the presence of other females (Nagelkerke and Sabelis, 1991; Nagelkerke, 1993).

The oviposition behaviour of predatory mites is probably influenced by the following characteristics. First, the offspring depend upon the same food source as is used by the females to produce eggs. Consequently, adding eggs diminishes the amount of food left and competition among the juveniles becomes more intense. In addition, food depletion will imply that patches differ in the time it takes a female to produce an additional egg. Second, eggs of phytoseiids are relatively large and a female produces only up to six eggs per day, which means that we should take the constraints inherent to small integer-sized clutches into account. Third, a time interval between the arrivals of successive females can lead to asynchronous mating among the offspring in the two clutches. Fourth, when all females in a prey colony are mated, the males may leave in search of other females.

### **Oviposition as a game**

In determining how many eggs to deposit on a given patch a female should take into account to what extent competition will affect the developing juveniles. The pay-offs from the oviposition strategy of a female therefore depend on the oviposition strategy of other visitors to the patch. Such mutual dependency means that a game-theoretical approach is required to analyse the 'clutch size game'. In order to understand why sometimes DO and sometimes ADO is the outcome of the clutch size game, it has to be determined under what conditions ADO is an evolutionarily stable strategy (ESS).

Strand and Godfray (1989) showed that ADO will be an ESS if the first clutch has a sufficiently large competitive advantage, for example because of its developmental headstart. In this article we analyse the conditions that may favour ADO in more detail. In the first section we develop a general model of the clutch size game and present a graphical analysis to capture the underlying mechanisms. We derive explicit general conditions for the evolutionary stability of ADO, based on the marginal effects of depositing extra eggs. We then formulate models to investigate how the ESS depends on such factors as competitive asymmetry and search time.

In the second section we include sex allocation strategies in the oviposition game, in addition to clutch size decisions. Under local mate competition (Hamilton, 1967) the optimal sex ratio depends on a female's own clutch size and on the clutch sizes and sex ratios produced by the other females ovipositing on a patch. Therefore, if sex determination is under maternal control, sex allocation decisions will be an important part of the oviposition game (Waage, 1986). When there is no DO, females should produce strongly female-biased sex ratios, with just enough sons in a clutch to inseminate all daughters. For a subsequent female, producing a much smaller clutch, it is then advantageous to produce a male-biased sex ratio, to capitalize on the high reproductive success of males in a female-biased mating group (Suzuki and Iwasa, 1980; Werren, 1980).

Until now both parts of the oviposition game – the clutch size game and the sex allocation game – have been studied in isolation and not simultaneously. Usually, in analyses of the sex allocation game, the number of clutches on a patch and their sizes are regarded as parameters. In turn, clutch size is analysed typically without taking sex allocation into account. However, by influencing the pay-offs from ovipositing, sex allocation strategies may interact with the clutch size game. Therefore, we investigate the interaction between the two games. In particular we address the question of whether the inclusion of sex allocation strategies will make ADO more or less likely to be an ESS.

We studied three scenarios with local mate competition, differing in the amount of asynchrony in reproduction between the two clutches and in the importance of male migration between patches.

- (1) The classical case with no asynchrony in reproduction and no male migration.
- (2) A scenario where, due to a time difference between the laying of the two clutches, the daughters of the first female only mate with their brothers. Sons from both clutches compete for matings with daughters of the second female.
- (3) A scenario where after the females have been mated, the males leave their natal patch to search for mates in other patches.

The clutch size and sex ratio are generally treated as continuous quantities (but see Waage and Ng, 1984). However, when clutch sizes are small, as is the case for predatory mites and many other organisms, the constraints on the clutch size and sex ratio caused by the discreteness of eggs can no longer be ignored. We therefore investigate both continuous and discrete models to show that the discrete nature of eggs can be a crucial factor in determining when ADO will be an ESS.

### **The clutch size game**

If ADO is the resident strategy, there will be two types of patches: 'occupied' patches with a single clutch of eggs and empty patches. ADO is evolutionarily stable if a mutant female that oviposits on occupied patches does less well than a female that leaves immediately to search for better alternatives (i.e. empty patches).

For simplicity, assume that at most two females can oviposit on one patch. Then females can be first or second on a patch and their strategy should specify a clutch size  $n$  for each of the two roles (assuming that females can adequately assess whether a patch is occupied or not). A resident female's strategy will be denoted as  $S^* = (n_1^*, n_2^*)$ , which means that a resident female deposits  $n_1^*$  eggs in an empty patch and  $n_2^*$  eggs in an occupied patch. Assuming that the females are time limited, their overall fitness will be proportional to the mean production of offspring per unit time (Parker and Courtney, 1984; Strand and Godfray, 1989). Thus, the overall fitness will depend on the yields (surviving offspring) and costs (oviposition time) associated with visiting occupied and unoccupied patches and on the rates of encounter with both patch types.

Consider a mutant female with strategy  $S = (n_1, n_2)$  that has arrived on an occupied patch. She will have an expected number of  $Y_2(n_1^*, n_2)$  surviving offspring from the patch. The time needed to produce the  $n_2$  eggs is given by  $T_2(n_1^*, n_2)$ ; note that the oviposition time of the second female may be influenced by the size of the first clutch ( $n_1$ ), for example because food is removed from the patch. Similarly, when the mutant is the first visitor on a patch, she will have an expected number of  $Y_1(n_1, n_2^*)$  surviving offspring, at a time cost of  $T_2(n_1)$ .

If  $\lambda_1$  and  $\lambda_2$  represent the encounter rates with, respectively, unoccupied and occupied patches, the expected fitness of the mutant is

$$W(S, S^*) = \frac{\lambda_1 Y_1(n_1, n_2^*) + \lambda_2 Y_2(n_1^*, n_2)}{1 + \lambda_1 T_2(n_1) + \lambda_2 T_2(n_1^*, n_2)} \quad (1)$$

which is a 'gain rate function', by analogy to the theory of optimal foraging (Charnov, 1976; Charnov and Skinner, 1984; Stephens and Krebs, 1986). (Notice that  $Y_1$  will depend on the probability of a second visit, but we will assume that this probability is constant.)

ADO implies a strategy  $S^* = (n_1^*, 0)$ . The (local) ESS condition therefore leads to

$$\left. \frac{\partial W}{\partial n_1} \right|_{(n_1, n_2) = (n_1^*, 0)} = 0 \quad (2a)$$

and

$$\left. \frac{\partial W}{\partial n_2} \right|_{(n_1, n_2) = (n_1^*, 0)} < 0 \quad (2b)$$

The first of these conditions implies that 'first' females should deposit the clutch size that is optimal in the absence of DO. We will call this clutch size the 'single-clutch optimum' and denote it by  $n^s$ . The second condition means that fitness should be maximal for  $n_2$  equal to zero. These two conditions combined imply that ADO is an ESS if it is not profitable for a second female to oviposit on a patch where another female has laid the single-clutch optimum already. (Remark: the second order derivatives of  $W$  with respect to  $n_1$  should be negative, but this holds for all cases considered here. Moreover, unless the yield and cost functions have very special shapes, the solutions of Equation 2a and Inequality 2b will be global optima.) Applying conditions 2a and 2b to the fitness function, Equation 1, yields

$$\frac{\partial Y_1 / \partial n_1}{\partial T_1 / \partial n_1} = W(S^*, S^*) \quad (3a)$$

and

$$\frac{\partial Y_2 / \partial n_2}{\partial T_2 / \partial n_2} < W(S^*, S^*) \quad (3b)$$

evaluated at  $S = S^* = (n^s, 0)$ . The left-hand sides of these conditions express the marginal profitability of adding eggs, whereas the right-hand sides represent the mean gain rate (surviving offspring per unit time) associated with ADO. This is equal to the fitness of a female laying the single-clutch optimum, in a population avoiding DO, namely

$$W(S^*, S^*) = \frac{\lambda_1 Y_1(n^s, 0)}{1 + \lambda_1 T_1(n^s)} \quad (3c)$$

These results have a simple interpretation. First, the single-clutch optimum is reached when the net profitability of an additional egg decreases below the mean gain rate given by Equation 3c. Second, only if the profitability of an additional egg laid by a subsequent female is also below the mean gain rate, is ADO evolutionarily stable.

We will first discuss why for the most simple assumptions the second condition is unlikely to hold and then discuss a number of 'real world' mechanisms that may result in ADO nonetheless being the ESS.

#### *Role-dependent net pay-off*

An optimal clutch size exists if competition among the juveniles decreases their survival probabilities. Competition might also lead to a reduction in size or negatively affect other fitness components, but we will assume these factors are all incorporated in the survival  $s$ . The larger the clutch already present, the lower the survival chances of an additional egg. However, an extra egg will also mean that the eggs already in place face a bleaker future. Therefore, we have to make a distinction between the gross pay-off of an additional egg (its survival probability) and the net pay-off to its mother (incorporating its effect on other eggs). The survival probability of an additional egg (as long as no others follow) is termed the marginal gross pay-off and the net fitness gain to its mother the marginal net pay-off. As Ives (1989) pointed out, even if the marginal gross pay-off is the same, there is a disparity (we call this a 'role dependency') between females in the marginal net pay-off, because the first female has an interest in the eggs already present, whereas a second female has not. We use role dependency to indicate any difference in the pay-off of an egg of a given sequence number for the patch as a whole that is due to whether it is laid by the first or by the second female.

Consider a graphical representation of the simple case in which oviposition time per egg,  $t$ , is constant. Figure 1a shows the marginal effects of adding eggs, as a function of invested time. First there is the marginal gross pay-off,  $e$  and, second, there is the detrimental effect,  $d$ , the reduction in the number of eggs already present that survive. Thus, for a first female, the net marginal yield (= marginal net pay-off) will be given by

$$y_1 = e(n_1) - d(n_1) \quad (4)$$

By calculating the cumulative net yield  $Y_1$  and using the standard graphical technique of gain rate maximization (Charnov, 1976), one can easily determine the single-clutch optimum  $n^s$  given an

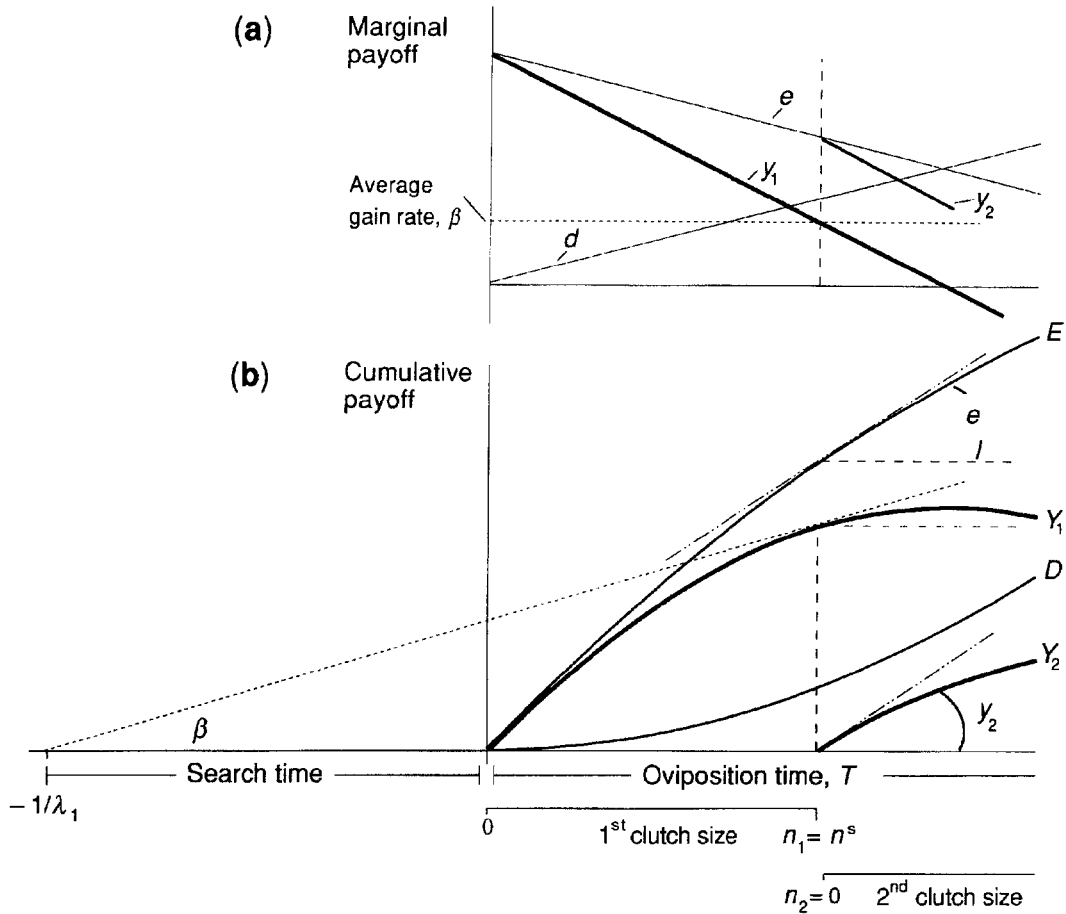


Figure 1. Example of a graphical solution of the single-clutch optimum, for a continuous model with constant oviposition time per egg and no role dependency in the gross pay-off. The graphs show, for subsequent eggs deposited on a patch, (a) the marginal gross pay-off,  $e$ , detrimental effect,  $d$  and net marginal pay-offs  $y_1$  and  $y_2$  to the first and second females, respectively and (b) the cumulative gross pay-off,  $E$ , cumulative detrimental effect,  $D$  and net pay-offs  $Y_1$  and  $Y_2$ . Note that constant oviposition time per egg implies that clutch size is proportional to invested time. Because the marginal net pay-off to the second female is larger than  $\beta$  (the mean gain rate in the absence of DO) it pays to produce a second clutch and, consequently, ADO is not an ESS. The search time for unoccupied patches is  $1/\lambda_1$ .

encounter rate with unoccupied patches  $\lambda_1$  (Fig. 1b). Now let a second female enter the patch. She should not be concerned about detrimental effects on eggs that are not her own, so if the egg survival probability does not change, her cumulative net yield curve  $Y_2$  will initially have slope

$$y_2 = e(n^s) \tag{5}$$

which is larger than the mean gain rate given by  $y_1(n^s)$  (Fig. 1a and b). Hence, ADO will not be an ESS unless  $d = 0$ . The female's differential interest in the eggs already present constitutes an

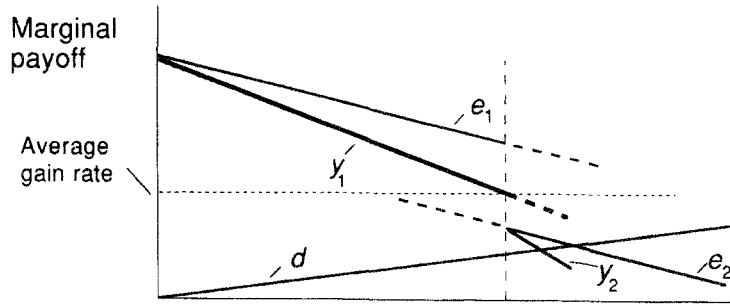


Figure 2. For the strategy ADO to be an ESS a discontinuity in  $e$  is required at  $n^s$ . In a continuous model this can arise if the marginal gross pay-off of additional eggs is role dependent. For subsequent eggs deposited on a patch, the marginal gross pay-off to first and second females,  $e_1$  and  $e_2$ , detrimental effects,  $d$  and the net marginal pay-offs  $y_1$  and  $y_2$  are shown. Note that role dependency implies  $e_1 \neq e_2$ . The oviposition time per egg is assumed to be constant.

elementary mechanism disfavouring ADO. ADO thus requires additional factors that counterbalance this role dependence of the marginal net pay-off. We will now discuss two basic mechanisms that produce such a counterbalance.

*Small eggs: role dependencies*

If clutches are represented by continuous variables, ADO is the ESS if the marginal net pay-off to a second female  $y_2 = e_2(n^s)$  is less than the mean gain rate  $y_1 = e_1(n^s) - d_1(n^s)$  (see Fig. 2). Thus, there must be a role dependency in  $e$ :

$$e_2(n^s) < e_1(n^s) - d_1(n^s) \tag{6}$$

so an additional egg must have a lower survival probability when laid by a second female than it would have had when laid by the first. (The only exception is when  $d_1(n^s) = 0$ , implying that newly laid eggs do not affect the survival of eggs that were laid previously.) This could happen if the time interval between visits is sufficiently large, giving the offspring of the first female a developmental headstart and making them superior competitors.

*Large eggs: stepwise drop in survival probability*

A role difference in the gross pay-off is not a necessary condition for ADO when the eggs are relatively large. Then clutches should no longer be represented by continuous variables. Figure 3 shows the essentials of an analysis for integer-sized clutches. The single-clutch optimum is given by

$$e(n^s + 1) - d(n^s + 1) < W^* \tag{7}$$

but note that the last egg of the single-clutch optimum will still be sufficiently profitable:

$$e(n^s) - d(n^s) \geq W^* \tag{8}$$

Combining Inequality 8 and the ESS condition

$$e(n^s + 1) < W^* \tag{9}$$

shows that survival of subsequent eggs should decrease in large steps,

$$e(n^s + 1) < e(n^s) - d(n^s) \tag{10}$$

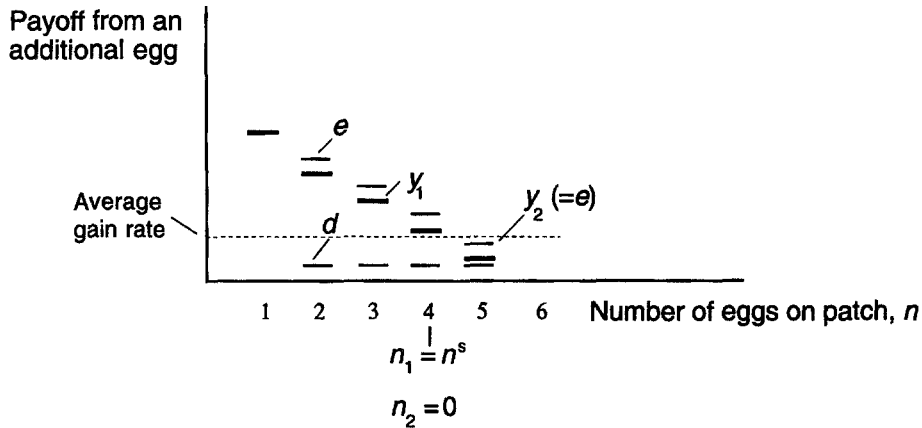


Figure 3. In a discrete model ADO can be the ESS without a role dependent marginal gross pay-off, provided the eggs are large enough. The symbols are the same as in Figs 1(a) and 2. Note that  $y_1$  and  $y_2$  drop below the mean gain rate at the same egg number.

Then, an additional egg will be unprofitable in both roles, even in the absence of role dependencies. This is most likely to occur when eggs are large compared to the carrying capacity of the patch, resulting in small clutches. It is, however, dependent on details of the way competition takes place. For example, when only one egg survives on a patch, the marginal net pay-off is zero for the first female for any egg following the first. DO will occur when the second egg has a sufficient probability of being the survivor (cf. Ives, 1989).

*ADO and the discontinuity in survival*

The necessary condition for ADO to be the ESS can be captured in a single phrase: the survival probability of the first egg of a second clutch should be lower, by a sufficient amount, than that of the last egg of the first clutch. If there is no such discontinuity, ADO will not be an ESS. Role dependencies (the survival of an additional egg depends on which female has laid it) and large eggs (resulting in a stepwise decrease of survival chances of subsequent eggs) can lead to such discontinuities.

*Variable oviposition times*

The profitability of an additional egg may diminish not only because of decreased survival, but also because food depletion may increase the time needed to collect enough food to produce an egg (cf. conditions 3a and 3b). However, analogous to the effect of survival on the marginal profitability, ADO will be promoted only when there is a discontinuity in food availability, caused by large egg size or by the first brood having begun to consume food.

*Mean survival*

To elucidate the ESS condition for ADO, we framed the analysis in terms of the marginal pay-off (fitness of additional eggs) but in many cases only the mean survival probability in a clutch will be known. In the remainder of this paper, we will mainly refer to clutch means. If  $s_i$  denotes the mean survival probability of the  $i$ th clutch and a patch is visited a second time with probability  $q$ , then  $Y_1(n_1, n_2^*) = (qs_1(n_1, n_2^*) + (1 - q)s_1(n_1, 0))n_1$  and  $Y_2(n_1^*, n_2) = s_2(n_1^*, n_2)n_2$ . Assuming constant per egg oviposition times, the ESS condition becomes



$$\frac{s_1(n^s, 0) + n^s \frac{\partial s_1}{\partial n_1}(n^s, 0)}{t} = W(S^*, S^*) \tag{11a}$$

and

$$\frac{s_2(n^s, 0)}{t} < W(S^*, S^*) \tag{11b}$$

Thus, ADO is an ESS if

$$s_2(n^s, 0) < s_1(n^s, 0) + n^s \frac{\partial s_1}{\partial n_1}(n^s, 0) \tag{12}$$

Notice that the probability  $q$  of a second visit is irrelevant. Under ADO it pays to produce the single optimum both when the patch will be visited a second time and when it will not; to a second visitor nothing changes. When there are no survival differences within clutches the terms in Inequality 12 are identical to  $e_2$ ,  $e_1$  and  $-d_1$  in Inequality 6. However, if eggs that are deposited later have lower survival probabilities, the meanings of the terms in the right-hand side of the inequality differ.

An expression for the optimum single clutch is obtained after substitution of the mean gain rate, Equation 3c, into Equation 11a and rearranging:

$$n^s = \left[ \frac{tn^s}{\frac{1}{\lambda_1} + tn^s} - 1 \right] \frac{s_1(n^s, 0)}{\frac{\partial s_1}{\partial n_1}(n^s, 0)} \tag{13}$$

When the survival probability function  $s_1(n_1, 0)$  is known this equation can be used to solve for  $n^s$ . Substitution into the ESS condition, Inequality 12, yields

$$\frac{s_2(n^s, 0)}{s_1(n^s, 0)} < \frac{tn^s}{\frac{1}{\lambda_1} + tn^s} \tag{14}$$

This is the ‘non-equivalence condition’ of Strand and Godfray (1989). ADO is only an ESS if the relative survival probability of a second clutch is less than the critical value specified by the right-hand side of Inequality 14. As the right-hand side of this equation will be less than unity, survival of the second clutch has to be comparatively low. Note that to obtain this condition clutch sizes are assumed to be continuous variables; it is possible to derive a similar condition for discrete clutch sizes.

Though the ESS condition framed in terms of the mean survival (Inequality 14) and the ESS condition based on marginal survival (Inequality 6) can be translated into each other, Inequality 14 is more easy to work with in practice, because mean survival is easier to measure. Yet the condition based on the marginal survival gives more insight into the basic factors underlying DO and ADO, because it is explicitly based on differences in the pay-offs to the first and second visitors from adding extra eggs.

*Predictions*

It should be stressed that survival asymmetries within or between clutches are neither necessary nor sufficient for ADO. Survival differences are not sufficient because if survival decreases with

egg number, differences in the mean survival,  $s$ , will result, but will not be sufficiently large for ADO if there are no role dependencies in the marginal gross pay-off,  $e$  (cf. Fig. 1). Survival differences are not necessary because in a discrete model ADO can be the ESS without any asymmetries within or between clutches, as long as the second clutch (when both clutches are present) has a lower survival than a single first clutch. This condition can be met when the eggs are sufficiently large.

Notice that only the encounter rate with unoccupied patches  $\lambda_1$  appears in the ESS condition; the abundance of occupied patches is of no concern. The decision whether or not to add eggs to occupied patches thus only depends on the abundance of better alternatives (i.e. unoccupied patches). Furthermore, when the search time,  $1/\lambda_1$ , increases, the critical difference in survival (Inequality 14) becomes larger and ADO becomes less likely. This stems from the fact that the single-clutch optimum,  $n^s$ , also tends to increase with the search time (Fig. 1b). Detrimental effects, responsible for the role dependencies in the marginal net pay-off, disappear when clutch sizes decrease (see Fig. 1a). Therefore, it is likely that under conditions favouring a small single clutch, the ESS condition for ADO is more likely to hold, which may be a counter-intuitive result. Indeed, the critical relative mean fitness is close to unity for short search times.

If the search time for unoccupied patches,  $1/\lambda_1$ , is large, the optimum size of a single clutch approaches the 'Lack' clutch size (Parker and Courtney, 1984), which maximizes the total number of surviving offspring from a patch. Then there is an exact balance between the fitness of an additional egg and its detrimental effect on earlier eggs. The role dependence in the marginal pay-off is large, and ADO is unlikely.

In summary, we conclude that ADO is most likely to be an ESS if the search time for unoccupied patches is low. Moreover, the survival of a single first clutch must be higher than for a small second clutch and/or the oviposition time per egg must be larger for the second clutch. In the realistic case where increasing the number of eggs has a detrimental effect on the fitness of eggs already present, there has to be a large enough discontinuity in the marginal gross pay-off between the last egg of the first clutch and the first egg of the second clutch. This implies that there should exist a role dependency in the fitness of an additional egg or that clutches are small.

### Sex allocation and the oviposition game

When mating groups are small, there will be local mate competition. By manipulating the sex ratio of their clutches, individual females can then influence the sex ratio of a mating group and, hence, the reproductive success of their offspring (local parental control; Nunney, 1985; Nunney and Luck, 1988). Here, we combine the sex allocation game and clutch size game into one single oviposition game, to investigate the consequences of sex allocation for the conditions under which ADO is an ESS.

As in the previous section, we will formulate the game for the case of two visitors and then investigate the conditions for ADO. An oviposition strategy must specify the clutch size and sex ratio for the two types of patches, i.e.  $S = (n_1, f_1, n_2, f_2)$ . To include sex allocation, the fitness is measured in terms of the production of grandoffspring per unit time; our approach is to multiply the number of surviving offspring by their mean reproductive success  $F_1(\bullet)$  and  $F_2(\bullet)$ . The 'yield' functions of a mutant female can then be rewritten as

$$Y_1(S, S^*) = F_1(\bullet) s_1(n_1, n_2^*)n_1 \quad (15a)$$

$$Y_2(S, S^*) = F_2(\bullet) s_2(n_1^*, n_2)n_2 \quad (15b)$$

The functions  $F_1(\bullet)$  and  $F_2(\bullet)$  depend on the structure of the mating group. First we investigate simple cases where mating is exclusively between offspring born in the same patch. This includes

a variant in which developmental asynchrony of the two clutches prevents sons of the second female from mating with daughters of the first female. Second, we will investigate the effect of male migration between patches. This implies that the sex allocation game involves more females than the patch foundresses only.

*Synchronous development*

Assume that the two clutches complete their development synchronously; all male offspring compete on equal terms for matings with all females. Then, the expected mating success  $R$  of a son is proportional to the patch sex ratio

$$R = \frac{f_1 N_1 + f_2 N_2}{(1 - f_1)N_1 + (1 - f_2)N_2} \tag{16}$$

where  $N_1$  and  $N_2$  represent the number of surviving offspring at the time of mating. Mortality is assumed to be sex-independent and therefore  $N_1 = s_1(n_1, n_2)n_1$  and  $N_2 = s_2(n_1, n_2)n_2$ . The mean reproductive success of the two clutches can be written as

$$F_1(n_1, f_1, n_2, f_2) = f_1 + (1 - f_1) R \tag{17a}$$

$$F_2(n_1, f_1, n_2, f_2) = f_2 + (1 - f_2) R \tag{17b}$$

The two terms in these expressions represent the relative genetic contributions to grandoffspring through daughters and through sons. Note that the patch sex ratio will be influenced not only by the sex allocation strategies, but also by differential mortality of the two clutches.

As before, ADO requires an ESS with  $n_2^* = 0$ . This means that we will obtain a set of conditions similar in structure to Equation 2a and Inequality 2b, one set that specifies the single-clutch optimum and another that states that DO is unprofitable on a patch containing the single-clutch optimum already. However, now the single-clutch optimum is a combination of clutch size  $n^s$  and sex ratio  $f^s$  and, hence,

$$\left. \frac{\partial W}{\partial n_2} \right|_{S = S^*} < 0 \tag{18}$$

should hold for any  $f_2$  in the range  $[0, 1]$ .

The single-clutch optimum is given by a set of conditions

$$\left. \frac{\partial W}{\partial n_1} \right|_{S = S^*} = 0 \tag{19a}$$

specifying the optimal clutch size and

$$\left. \frac{\partial W}{\partial f_1} \right|_{S = S^*} = 0 \tag{19b}$$

(or an appropriate boundary condition) for the optimal sex ratio. The gain rate function (Equation 1) now expresses the mean production of grandoffspring per unit time. The first condition gives rise to equations similar in structure to those studied in the previous section and, hence, a single-clutch optimum  $n^s$  will exist.

The question is how the inclusion of sex allocation strategies affects the decision of a subsequent female whether or not to add eggs. The mutant under consideration will encounter

patches with the sex ratio  $f^s$ . Whether or not her fitness increases with oviposition on such patches depends on the partial derivative of  $W$  with respect to  $n_2$ . As before

$$\frac{\partial W}{\partial n_2} = \frac{\partial Y_2 / \partial n_2}{\partial T_2 / \partial n_2} \quad (20)$$

where for  $n_2$  close to zero

$$\frac{\partial Y_2}{\partial n_2} = F_2(n^s, f^s, n_2, f_2) s_2(n^s, n_2) \quad (21)$$

which implies that the offspring fitness is now measured as survival probability multiplied by reproductive success. By a derivation similar to the derivation of Inequality 14, the ESS condition becomes

$$\frac{F_2(n^s, f^s, n_2, f_2)}{F_1(n^s, f^s, 0, \bullet)} \frac{s_2(n^s, n_2)}{s_1(n^s, 0)} < \frac{tn^s}{\frac{1}{\lambda_1} + tn^s} \quad (n_2 \rightarrow 0, \text{ any } f_2) \quad (22)$$

where, again,  $t$  denotes the oviposition time per egg and  $\lambda_1$  denotes the encounter rate with unoccupied patches. Thus, in determining whether ADO is an ESS, the ratio of reproductive successes,  $F_2/F_1$ , is as important as the ratio of survival probabilities,  $s_2/s_1$ . If  $F_2/F_1 > 1$ , ADO will be less likely to evolve, whereas if  $F_2/F_1 < 1$  ADO is promoted. Although, in general, the single-clutch optimum  $n^s$  depends on sex allocation (i.e. on details of the function  $F_1$ ), we will ignore its (subtle) effect and focus on the ratio  $F_2/F_1$ . Note, however, that  $F_2/F_1$  still depends on survival (see Equations 17a and 17b).

The value of  $F_2/F_1$  depends on  $f_1$  and  $f_2$ ;  $f_1$  is equal to the optimal proportion of daughters,  $f^s$ , for the first female in the absence of DO, whereas  $f_2$  is optimized given  $f_1$ . Therefore,  $f^s$  has to be determined first. As the oviposition time does not depend on the sex allocation, a first female maximizes her fitness by maximizing the yield  $Y_1$  and this, in turn, means choosing an  $f_1$  that maximizes the mean reproductive success  $F_1$ . Because in the absence of juvenile migration ADO implies that all matings occur between the offspring of the first female, survival cancels out in Equation 17a and the mating success of sons is entirely determined by  $f_1$ . The mean reproductive success of the first female becomes

$$F_1(n_1, f_1, 0, \bullet) = f_1 + (1 - f_1) \frac{f_1}{1 - f_1} = 2f_1 \quad (23)$$

It is easy to see that  $F_1$  is maximal for  $f_1 = 1$ . This means that it pays to produce as high a proportion of daughters as is possible, given the need to produce sons for insemination of the daughters.

Now consider the optimal sex allocation strategy of a second female. Under the assumption of developmental synchrony, a small second clutch may have a much larger per capita reproductive success than the first one. For a small second clutch (i.e.  $n_2 \ll n^s$ ), Equation 17b is approximated by

$$F_2(n^s, f^s, n_2, f_2) = f_2 + (1 - f_2) \frac{f^s}{1 - f^s} \quad (24)$$

Since both  $F_2$  and  $F_1$  no longer depend on survival, the influence of survival differences and sex allocation strategies can be studied separately.

Because the proportion of daughters in the first clutch,  $f^s$ , is large, the female to male ratio  $f^s/(1 - f^s)$  will be larger than unity (the fitness equivalent of a daughter) and thus the expected reproductive success of a second clutch would be largest if it were completely male ( $f_2 = 0$ ). In that case the ratio

$$\frac{F_2}{F_1} = \frac{f^s}{1 - f^s} / 2f^s = \frac{1}{2} \frac{1}{1 - f^s} \quad (25)$$

will exceed unity. In other words, because the sex ratio of the patch is female biased and dominated by the first clutch, it is very profitable for a second female to add at least a small male-biased clutch. As a consequence, ADO is less likely to be an ESS than it is in the absence of local mate competition.

Note that if  $f^s$  approaches unity, the ratio  $F_2/F_1$  goes to infinity, which is unrealistic. However, because at least one son, representing  $1/n^s$  of the clutch, is necessary to guarantee fertilization,  $F_2/F_1$  is bounded. We explore the consequences of this constraint in the section on discrete eggs.

#### *Asynchronous development*

The second visitor to the patch may have arrived so late that her male offspring do not have access to the daughters of the first. Then the mean reproductive success of a small second clutch is given by

$$F_2(n^s, f^s, n_2, f_2) = f_2 + (1 - f_2) \frac{f_2 N_2}{(1 - f^s)n^s + (1 - f_2)N_2} \quad (26)$$

which in the case of a single-egg approximation becomes either zero (a single son would have a fitness of zero) or unity (the value of a single daughter, inseminated by a son of the first female). The best option open to a second female is to produce a daughter, if she is to add an egg at all. However, even this option is not very profitable. The ratio of reproductive success would become

$$\frac{F_2}{F_1} = \frac{1}{2f^s} \quad (27)$$

which shows that to the first female the mean value of a surviving offspring can be up to twice as high. If the critical fitness ratio given by the right-hand side of Inequality 22 is larger than approximately one-half, ADO would be the ESS, even in the case where the survival probabilities of both clutches are equal. Thus, developmental asynchrony promotes ADO.

#### *Discrete eggs*

The discrete character of eggs not only constrains the attainable values of the clutch size, but also those of the sex ratio. In particular when clutch sizes are small, these sex allocation constraints may have a crucial effect on the evolutionary stability of ADO. This is demonstrated most clearly when it is assumed that mortality is zero, as then the fitness effects of sex allocation decisions can be analysed in isolation.

If one male can inseminate all the daughters, under ADO the first female should produce one son and  $n_1 - 1$  daughters. Suppose she starts by laying a son. Figure 4 shows the fitness effects of subsequent male or female eggs. Because an extra daughter improves the mating chances of

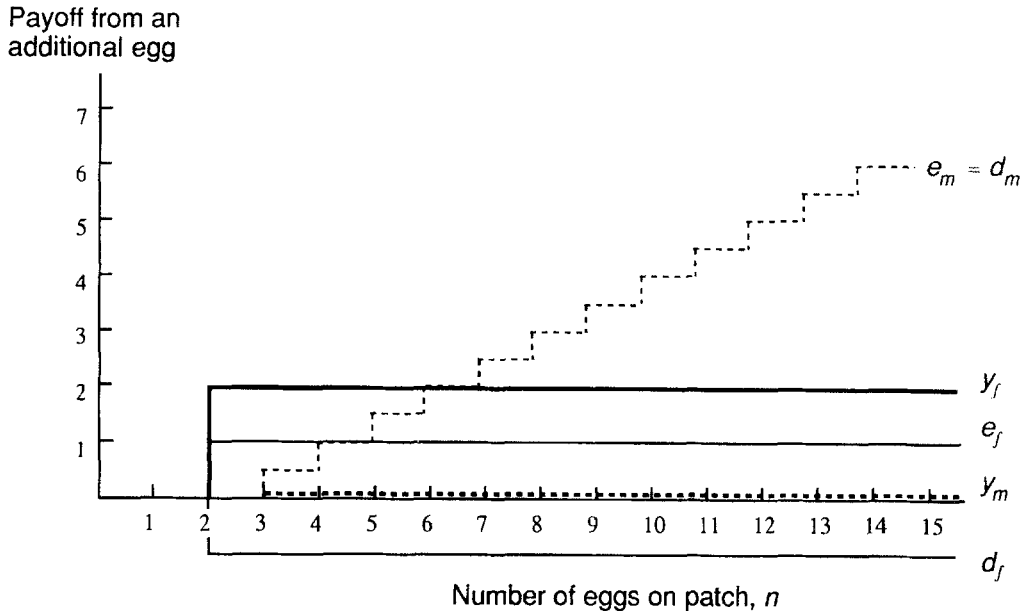


Figure 4. In a discrete model with local mate competition, the fitness effects of an additional egg depend on its sex. (The symbols are as in Fig. 3, but differentiated with respect to sex.) Pay-offs are shown for the first female. No juvenile mortality occurs and the oviposition time per egg is constant. Note that, in contrast to the clutch size only model,  $d$ , the 'detrimental effect' to earlier eggs, can be negative, i.e. when daughters are added. An extra daughter has a constant fitness  $e_f$  and increases the combined pay-off from earlier males by the same amount. An extra son will have a high fitness  $e_m$  when  $n$  is large. However, the extra male harms the mating chances of previous males and  $d_m$  will exactly offset  $e_m$ . Thus, after a single visitor has laid a male egg, she should add female eggs only. To a second visitor it pays to add a son only if  $n_1$  is sufficiently large. See the text for more explanation.

earlier males, the 'detrimental effect' of a female egg ( $d_f$ ) is negative and, hence, the marginal net pay-off,  $y_f$ , becomes larger than the marginal gross pay-off,  $e_f$ . An extra male, however, does not affect total pay-off from a patch ( $d_m = e_m$  and therefore  $y_m = 0$ ; see Fig. 4). The available females now just have to be divided between more males. This illustrates why the first visitor, after she has produced a son, should lay daughters only.

If a second visitor is to produce the additional egg, the situation is different. Whether it should be male or female depends on the net pay-offs,  $e_f$  and  $e_m$ , only. To her  $d_f$  and  $d_m$ , whether positive or negative, are of no concern. Figure 4 shows that if  $n_1 > 3$  the second visitor's egg should be male, but it should be female if  $n_1 < 3$  (if  $n_1 = 3$  the pay-offs are equal). Thus, for the sex allocation decisions of the second visitor the discreteness of eggs may be important. When the first clutch is small and, hence, a son has few mating chances, the balance is tipped in favour of a daughter.

Not only may the optimal sex be affected by the discreteness of the eggs, but also the decision whether or not to add an egg at all. Elementary algebra shows that for a second visitor adding a single son to a clutch of  $n_1$  eggs, one of which is male, the ratio of mean pay-offs is

$$\frac{F_2}{F_1} = 0.25 n_1 \quad (28)$$

which implies that a second visitor can only obtain a higher mean pay-off than the first if  $n_1 > 4$ . This means that the inclusion of sex allocation strategies makes ADO less likely to be an ESS (as in the continuous model) when  $n_1 > 4$  whereas when  $n_1 < 4$ , it makes it more likely. Hence, the continuous model goes awry if the first clutch is not sufficiently large. This is because the mating success of an extra male is low when the first clutch is small. There are fewer females to begin with and an extra male will cause a significant reduction in the number of matings per male. This decrease in male mating success attenuates the effect of sex allocation strategies on the clutch size game and may even invert predictions with respect to the evolution of ADO.

That asynchrony promotes ADO remains valid when clutch sizes are small, because a second female always has zero pay-off from a son and gains less than a first female from a daughter. However, a small clutch size diminishes  $f^s$  (and, hence,  $F_1$ ) and thereby keeps  $F_2/F_1$  closer to unity. Therefore, the effect of sex allocation strategies on the ratio of fitness pay-offs will be less pronounced. As in the synchronous case this results from reduced male mating success.

The analysis presented above illustrates, firstly, how the inclusion of sex allocation strategies changes the gains and losses associated with the laying of additional eggs. There are important additional role dependencies in the marginal net pay-off and, as a result, the optimal sex of additional eggs may become role dependent. Secondly, it shows once more that the discrete nature of eggs can be of crucial importance in determining whether ADO is an ESS.

### *Migrating males*

Unless development is asynchronous, a strong female bias in the clutch of a first female will undermine the evolutionary stability of ADO. Factors that decrease the optimum proportion of daughters (e.g. small clutch size) in a single clutch are therefore expected to promote ADO. Migration of males between mating groups could be such a factor because it diminishes the intensity of local mate competition. In the previous models we assumed that the mating arena and the arena in which competition for food between offspring takes place were identical. Here we will investigate a model in which, after the locally hatched females are mated, male offspring disperse in search of other patches to compete for matings with the local males. This implies that males will also face competition at their natal patch by older males from other patches. Thus even in absence of DO there is a sex allocation game between females.

We base our analysis on a model of Nunney and Luck (1988) to calculate the optimal sex ratio under male dispersal and then we will investigate its consequences for the evolution of DO. If sons visit  $M$  clutches later in life, Nunney and Luck's (1988) model predicts an evolutionarily stable proportion of daughters for a single clutch

$$f^s = \frac{M + 1}{2M + 1} \quad (29)$$

(their Equation 16). Note that  $f^s$  is 1 when  $M = 0$  (local mate competition only) but approaches 0.5 when  $M \rightarrow \infty$  (random mating). Thus, the more patches a male is able to visit, the less female biased the sex ratios in a single clutch will be.

Whether it pays to add a second clutch will depend on the degree of synchrony. Let the probability that sons of the second female will mature fast enough to be able to mate with the daughters of the first be represented by  $p$ . Then, relative reproductive success of the second clutch is given by

$$\frac{F_2}{F_1} = \frac{M + p}{M + 1} \frac{2M + 1}{2M} \quad (30)$$

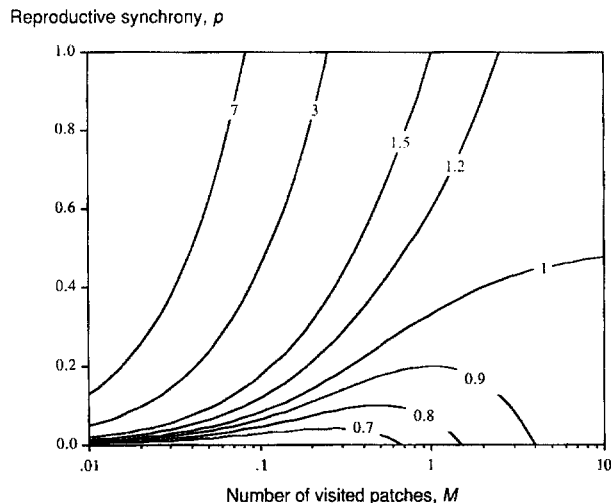


Figure 5. Contours of the ratio of reproductive success of the second and first clutch ( $F_2/F_1$ ), as a function of male migration ( $M$ , number of patches visited by a migrant male) and the degree of reproductive synchrony ( $p$ , the probability for a son of a second female to be in time to mate with daughters of the first). If this ratio is less than unity, ADO is more likely to be favoured by natural selection.

(see the Appendix for a derivation). Figure 5 shows that  $F_2/F_1$  increases with  $p$ ; as expected, the likelihood that ADO is an ESS decreases when the mating opportunities for a second female's sons increase. In the synchronous case ( $p = 1$ ), the value of  $F_2/F_1$  decreases with  $M$ , the amount of migration. As a consequence, ADO becomes more likely to be the ESS. Increased male migration favours a lower proportion of daughters in the first clutch and this reduces the reproductive success of additional males (and, hence, it reduces  $F_2$ ). In contrast, under complete asynchrony ( $p = 0$ ), the value of  $F_2/F_1$  increases with  $M$  and migration will make ADO less likely to be the ESS. This is because increased male migration causes a reduction in  $F_1$  whereas  $F_2$  is less affected. Generally, increasing  $M$  results in the convergence of  $F_2/F_1$  to unity (albeit not always monotonically). We therefore conclude that the main effect of male migration is that the mating structure tends to become more random and, hence, the evolutionary stability of ADO becomes less dependent on sex allocation strategies. Depending on the degree of synchrony, male migration can result in an increase or in a decrease of the profitability of DO.

#### *Migration and discrete eggs*

We investigated the role of integer clutch size under male migration with a semi-discrete model. The number of eggs laid in a patch was taken to be discrete, as was the distribution of their sex, whereas the number of visiting migrants and the number of patches visited by migrants were represented by continuous variables for reasons of simplicity.

The optimal sex allocation strategy of the first female necessarily consists either of an integer number of sons or of a mixture of different numbers produced with given probabilities. It appeared that the numbers of sons in the ESS are only recruited from the two integers that flank the ESS value from the continuous model. The optimal mixture of these two numbers of sons was calculated. This mixture can both be a mixed strategy or a mixture of pure strategies, provided the total population produces the optimal mixture.

In Fig. 6 the discrete model is compared with the continuous model. Figure 6a gives the ES sex ratio  $f^s$  in relation to the amount of migration,  $M$ , for an example where the clutch size is seven



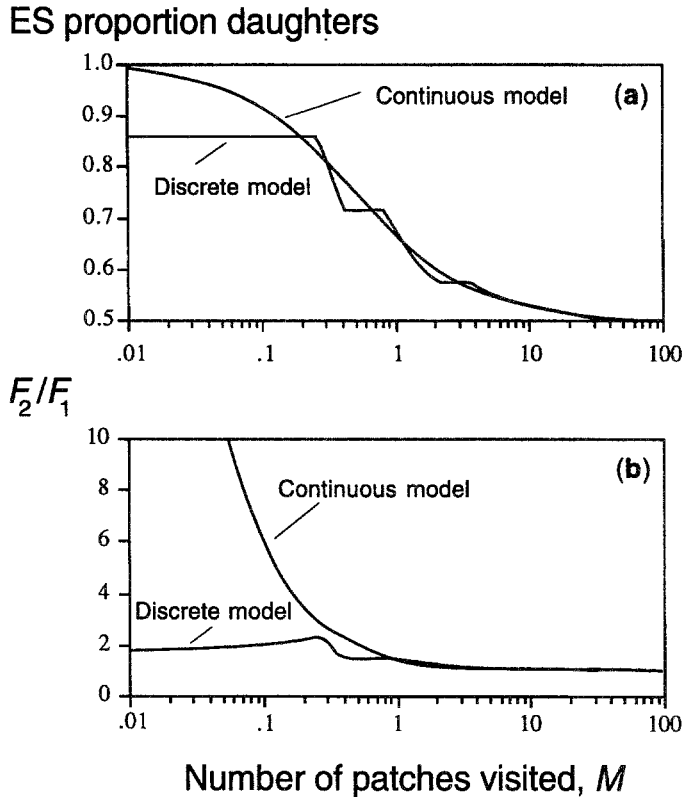


Figure 6. The consequences of male migration in a discrete model and in a continuous model. There is reproductive synchrony between the first and second clutch ( $p = 1$ ) and the first female has a clutch size  $n_1$  of seven eggs in the discrete model. The following optimization results are shown as a function of the number of patches visited by migrating males: (a) optimal (mean) proportion daughters for a single clutch  $f^s$  and (b) ratio of reproductive successes of second and first clutches ( $F_2/F_1$ ), given that the second female produces a son.

eggs. The staircase-like curve of the ES proportion of daughters is caused by two effects: (1) the number of sons cannot be lower than unity and (2) the sex ratio tends to ‘stick’ to or near the values corresponding to an integer mean number of sons. The result is a curve that meanders around the continuous curve for higher values of  $M$  and stays below it when  $M$  is low.

For low migration  $F_2/F_1$  is much lower than the unrealistically high values in the continuous model (Fig. 6b). This is because the constrained proportion of daughters of the first female diminishes the mating success of sons. Just as in the continuous model, increasing migration diminishes the effect of sex allocation strategies: when  $M$  increases,  $F_2/F_1$  converges to unity. Results not presented here show that lower clutch sizes bring  $F_2/F_1$  closer to unity. Hence, just as in the case without migration, a small clutch size diminishes the effect of sex allocation strategies. Increasing  $p$  again always promotes DO, as expected (results not shown).

**Discussion**

DO will occur whenever adding an extra egg to a patch is not profitable for the first visiting female but is profitable for the next visitor. DO will be avoided only when adding an extra egg

Table 1. Factors influencing whether ADO or DO is an ESS

| <i>Favouring ADO</i>                              | <i>Favouring DO</i>                              | <i>Interactions between effects</i>  |
|---|--|--|
| Short search times for unoccupied patches         | Long search times for unoccupied patches         | Small clutch sizes (large eggs) moderate the effect of sex allocation strategies     |
| Lower survival of second clutch                   | Equal survival of both clutches                  | Migration of males between patches moderates the effect of sex allocation strategies |
| Longer oviposition time per egg for second clutch | Equal oviposition time per egg for both clutches |  |
| Small clutches (large eggs)                       | Large clutches (small eggs)                      |  |
| Asynchronous mating of first and second clutch    | Synchronous mating of first and second clutch    |  |

is unprofitable in both roles. A basic factor favouring DO is that, in contrast to a first visitor, a second visitor will not be concerned about the detrimental effect an extra egg may have on the survival of the eggs already in place. When local mate competition favours female-biased sex ratios, DO may become even more profitable.

In this article we have studied a number of mechanisms that may nevertheless promote ADO. For time-limited females, ADO is the ESS if the gain rate within a patch for a second female starting to oviposit is lower than the overall gain rate in the absence of DO (Inequality 3b). This occurs whenever (1) there are enough empty patches and (2) the gross profitability per egg of a second clutch is sufficiently low compared to that of a first clutch. Table 1 summarizes the factors favouring either ADO or DO.

We stress that for ADO to evolve there must be either a sufficiently large drop in fitness between the last egg from a first clutch and the first egg of a second clutch or a large increase in their oviposition times. This discontinuity is the factor preventing DO and not any resulting difference in the mean profitability per egg between the two clutches. Such a discontinuity may result from the discrete nature of eggs or from a role dependency in the marginal gross pay-off due to a competitive or oviposition time disadvantage of the second clutch. A time interval between the laying of both clutches may cause such role dependency.

#### *Combined analysis of clutch size and sex allocation decisions*

Sex allocation is not only an important part of the oviposition game in its own right, but it may also have consequences for the clutch size game because sex allocation strategies affect the pay-offs from additional eggs. Offspring can both positively and negatively affect each other's reproductive success, which results in (additional) role dependencies in the net pay-off. The joint analysis of both games that is presented in this article shows that mating interactions between the offspring on a patch can alter predictions about the evolutionary stability of ADO.

Under local mate competition a second female may actually profit from the presence of a first female's clutch. When very female-biased sex ratios are favoured in the absence of DO, it is very attractive to add a single son. As a consequence, factors that reduce the female bias of single clutches will also diminish the attractiveness of DO; of these we have discussed (1) small clutch sizes, which have a moderating effect on the sex allocation game, and (2) migration of males between patches, which makes mating more random. Any mechanism that diminishes the degree

of local mate competition, such as migration of females before mating, is likely to have the same effect. Other factors favouring less female-biased single clutches are a limited insemination capacity of sons, mortality among males (Green *et al.*, 1982, Nagelkerke and Hardy, 1994) and imprecise control of the mother over the sex of individual eggs (Green *et al.*, 1982).

The influence of sex allocation strategies is highly dependent on the degree of developmental asynchrony between the two clutches. Asynchronous development actually decreases the profitability of DO because sons of a second female are prevented from mating with daughters of the first female. This is another reason, apart from asymmetries in the competition for resources, why a time interval between the oviposition of the two clutches will make DO less likely. However, the effect of a time interval on mating chances will depend on the amount of variation in the development time between and within sexes. When males develop faster than females, as is the case in many parasitic wasps (Griffiths and Godfray, 1988; Nadel and Luck, 1992) and in spider mites (Sabelis, 1981; Carey and Bradley, 1982), such a time interval must be sufficiently large to have an effect on mating chances. In most phytoseiid mite species, the mean developmental times of males and females are approximately the same (Sabelis and Nagelkerke, 1993) but individual variation is in the order of 1 day. Such variation will reduce the effect of a small time interval.

The migration of males diminishes the effect of sex allocation strategies. Therefore it discourages DO in the case of synchronous development and promotes it in the case of asynchronous development. Migration may well occur in predatory mites because the male locomotory activity and maximum fertile life expectancy can be substantial (Amano and Chant, 1978; Schulten *et al.*, 1978; Bonde, 1989). Such 'out of patch mating' also occurs in many parasitoid wasps (Hardy, 1994).

#### *Discrete eggs*

In contrast to what is often assumed (cf. Wilson and Lessells, 1994) our analysis shows that predictions of oviposition models can be qualitatively different when clutches are represented by discrete instead of continuous variables.

In general, small clutches or, rather, large eggs, compared to the carrying capacity of the patch, favour ADO. Two factors are responsible. First, the magnitude of the drop in profitability of subsequent eggs is larger when eggs are large and few than when they are small and numerous (Fig. 3). Second, small clutch sizes constrain sex allocation, thereby limiting male reproductive success. These results are evidently relevant for solitary parasitoids, with 'clutches' of only a single egg, but also for predatory mites, who produce only a limited number of eggs per day.

#### *What may happen if ADO is not an ESS*

For the (isolated) clutch size game there exists an evolutionarily stable ratio of clutch sizes, dependent on the possibility of a second visit (Strand and Godfray, 1989). Ives (1989) demonstrated that details of the competition between offspring (affecting the net and gross marginal pay-offs) determine whether this ratio will be smaller or larger than unity.

Analysis of the isolated sex allocation game predicts that a small second clutch will have a lower proportion of females than the first (Suzuki and Iwasa, 1980; Werren, 1980). The combined game has as yet only been investigated for the case without survival differences (Nagelkerke, 1994), as will be discussed below in the section on phytoseiids.

#### *Pre-emptive measures*

In our analysis, the evolutionary stability of ADO is determined by the answers to two independent questions: (1) what is the single-clutch optimum? and (2) is it profitable for a second

female to oviposit on a patch containing the single-clutch optimum already? One may wonder why the problem can be decomposed so conveniently. For example, one could think of a solution in which the first female enlarges her clutch to deter subsequent females. However, our analysis does not predict such 'pre-emptive measures'.

This is due to a crucial assumption of our analysis: we assumed that females are able to assess a patch only qualitatively, i.e. whether it is occupied or not. Even though a pre-emptive strategy will indeed favour ADO when resident, it is vulnerable to invasion by females producing the single-clutch optimum, because these profit from the second females' unsophisticated responses. However, if females are able to assess the state of a patch quantitatively, they will be selected to distinguish between patches with the single-clutch optimum and patches on which pre-emptive measures have been taken. In that case the oviposition game becomes more complex and pre-emptive measures are indeed among the possible outcomes (Sjerps and Haccou, 1993; M. van Baalen, unpublished manuscript). The present analysis therefore only applies to those cases where ovipositing females are not able to count or sex the eggs of earlier females, but only have qualitative information, for example due to the presence or absence of a marking pheromone.

#### *Phytoseiid mites*

Female predatory mites (of the family Phytoseiidae) tend to avoid or leave areas where other females are present or that have been visited before by other females (Hislop and Prokopy, 1981; Sabelis, 1981; Janssen *et al.*, in press; M.W. Sabelis, unpublished data). A marking pheromone of the predator and/or an alarm pheromone of the prey may be involved in eliciting the avoidance response. Can such responses be explained as 'ADO'? Many aspects of the biology of phytoseiid mites do favour ADO (e.g. large eggs, male migration and time intervals between the arrival of different females). However, their often strongly female-biased sex ratios are more likely to promote DO. Whether ADO occurs or not will therefore depend on the balance of these factors and these will vary with species and circumstances.

Phytoseiids differ widely in their biology, which is strongly correlated with their characteristic prey density (Sabelis and Janssen, 1993). Nagelkerke and Sabelis (1996) distinguished between 'island' species, with a relatively constant population structure over time and 'haystack' species, with locally unstable population dynamics. Predictions with respect to ADO will differ for the two categories.

'Haystack' species specialize on prey that form clusters of (high-density) colonies on infested leaves. Rapid growth of a local predator population causes extermination of the prey within a few generations (Sabelis and van der Meer, 1986; Janssen and Sabelis, 1992). Predictions with respect to ADO depend on the phase of the local exploitation cycle. In the initial phase the number of unoccupied colonies will be large and resource competition between juveniles will be weak. This will promote ADO. However, the extremely female-biased sex ratios they produce favour DO (in particular when density increases; see Nagelkerke, 1994). In the last phase, DO will be favoured by a scarcity of unoccupied patches and by the rapid succession of visits that will diminish the developmental lag of second clutches.

'Island' species are generalists, whose food is widely dispersed. As prey abundance limits local predator densities for the larger part of the seasonal cycle, the scarcity of unoccupied patches is likely to favour DO. Yet several characteristics of island species may promote ADO when unoccupied patches are more abundant (e.g. just after winter). First, because their prey occur in low densities they tend to produce small clutches. Second, a low density of predators is likely to increase the degree of asynchrony between clutches. Third, they produce less female-biased sex ratios than 'haystack' species, because mating is more random, clutches are smaller or because of the absence of selection at the haystack level (Nagelkerke, 1993). In conclusion, we predict that

under some circumstances it may well pay predatory mites to avoid DO. Experimental work on ADO is needed to test the predictions. However, there may be an additional force at work, in particular in cases where there are few unoccupied patches. It turns out that when ADO is not the ESS, the interaction between the oviposition game and the sex allocation game may force the females to distribute their eggs over the largest number of patches as the costs of travel allow, because females with the smallest contribution to mating groups have the highest fitness per egg (Nagelkerke, 1994). This suggests that observed responses to the presence or traces of other females are not necessarily attempts to avoid DO altogether, but may result from the females trying not to lay too many eggs in one place.

### Acknowledgements

The manuscript benefitted from comments by L. Hemerik. C.J. Nagelkerke was supported by The Netherlands Foundation for Fundamental Biological Research (BION-NWO/ZWO).

### References

- Amano, H. and Chant, D.A. (1978) Some factors affecting reproduction and sex ratios in two species of predacious mites, *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius andersoni* (Chant) (Acarina: Phytoseiidae). *Can. J. Zool.* **56**, 1593–607.
- Bonde, J. (1989) Biological studies including population growth parameters of the predatory mite *Amblyseius barkeri* [Acarina: Phytoseiidae] at 25°C in the laboratory. *Entomophaga* **34**, 275–87.
- Carey, J.R. and Bradley, J.W. (1982) Developmental rates, vital schedules, sex ratios, and life tables for *Tetranychus urticae*, *T. turkestani* and *T. pacificus* (Acarina: Tetranychidae) on cotton. *Acarologia* **23**, 333–45.
- Charnov, E.L. (1976) Optimal foraging: attack strategy of a mantid. *Am. Nat.* **110**, 141–51.
- Charnov, E.L. and Skinner, S.W. (1984) Evolution of host selection and clutch size in parasitoid wasps. *Fla. Entomol.* **67**, 5–21.
- Fiske, W.F. (1910) Superparasitism: an important factor in the natural control of insects. *J. Econ. Entomol.* **3**, 88–97.
- Green, R.F., Gordh, G. and Hawkins, B.A. (1982) Precise sex ratios in highly inbred parasitic wasps. *Am. Nat.* **120**, 653–65.
- Griffiths, N.T. and Godfray, H.C.J. (1988) Local mate competition, sex ratio and clutch size in bethylid wasps. *Behav. Ecol. Sociobiol.* **22**, 211–17.
- Hamilton, W.D. (1967) Extraordinary sex ratios. *Science* **156**, 477–88.
- Hardy, I.C.W. (1994) Sex ratio and mating structure in the parasitoid Hymenoptera. *Oikos* **69**, 3–20.
- Hislop, R.G. and Prokopy, R.J. (1981) Mite predator responses to prey and predator-emitted stimuli. *J. Chem. Ecol.* **7**, 895–904.
- Howard, L.O. (1897) A study in insect parasitism. *US Dept Agric. Tech. Ser.* **5**, 5–57.
- Ives, A.R. (1989) The optimal clutch size of insects when many females oviposit per patch. *Am. Nat.* **133**, 671–87.
- Janssen, A. and Sabelis, M.W. (1992) Phytoseiid life-histories, local predator–prey dynamics, and strategies for control of tetranychid mites. *Exp. Appl. Acarol.* **14**, 233–50.
- Janssen, A., Bruin, J., Jacobs, G., Schraag, R. and Sabelis, M.W. (in press) Predators use volatiles to avoid prey patches with conspecifics. *J. Anim. Ecol.*
- Nadel, H. and Luck, R.L. (1992) Dispersal and mating structure of a parasitoid with a female-biased sex ratio: implications for theory. *Evol. Ecol.* **6**, 270–78.
- Nagelkerke, C.J. (1993) Evolution of sex allocation strategies of pseudo-arrhenotokous predatory mites (Acari: Phytoseiidae). Dissertation, University of Amsterdam, Amsterdam.
- Nagelkerke, C.J. (1994) Simultaneous optimization of egg distribution and sex allocation in a patch-structured population. *Am. Nat.* **144**, 262–84.

- Nagelkerke, C.J. and Hardy, I.C.W. (1994) The influence of developmental mortality on optimal sex allocation under local mate competition. *Behav. Ecol.* **5**, 401–11.
- Nagelkerke, C.J. and Sabelis, M.W. (1991) Precise sex-ratio control in the pseudo-arrhenotokous phytoseiid mite *Typhlodromus occidentalis* Nesbitt. In *The Acari: Reproduction, Development and Life-history Strategies* (R. Schuster and P.W. Murphy, eds), pp. 193–207. Chapman & Hall, London.
- Nagelkerke, C.J. and Sabelis, M.W. (1996) Hierarchical levels of spatial structure and their consequences for the evolution of sex allocation in mites and other arthropods. *Am. Nat.* **148**, 16–40.
- Nunney, L. (1985) Female-biased sex ratios: individual or group selection? *Evolution* **39**, 349–61.
- Nunney, L. and Luck, R.F. (1988) Factors influencing the optimum sex ratio in a structured population. *Theor. Pop. Biol.* **33**, 1–30.
- Parker, G.A. and Courtney, S.P. (1984) Models of clutch size in insect oviposition. *Theor. Pop. Biol.* **26**, 27–48.
- Sabelis, M.W. (1981) *Biological Control of Two-spotted Spider Mites Using Phytoseiid Predators. Part I. Modelling the Predator–Prey Interaction at the Individual Level*. Pudoc, Wageningen.
- Sabelis, M.W. (1985) Predation on spider mites. In *Spider Mites, Their Biology, Natural Enemies and Control* (W. Helle and M.W. Sabelis, eds), pp. 103–29. Elsevier, Amsterdam.
- Sabelis, M.W. and Janssen, A. (1993) Evolution of life-history patterns in the Phytoseiidae. In *Life History and Reproductive Patterns of Mites* (M.A. Houck, ed.), pp. 70–98. Chapman & Hall, New York.
- Sabelis, M.W. and Nagelkerke, C.J. (1993) Sex allocation and pseudoarrhenotoky in phytoseiid mites. In *Evolution and Diversity of Sex Ratio in Insects and Mites* (D.L. Wrensch and M.A. Ebbert, eds), pp. 512–41. Chapman & Hall, New York.
- Sabelis, M.W. and van der Meer, J. (1986) Local dynamics of the interactions between predatory mites and two-spotted spider mites. In *The Dynamics of Physiologically Structured Populations* (J.A.J. Metz and O. Diekmann, eds), pp. 322–44. Springer-Verlag, Berlin.
- Schulten, G.G.M., Arendonk, R.C.M., Russell, V.M. and Roorda, F.A. (1978) Copulation, egg production and sex-ratio in *Phytoseiulus persimilis* and *Amblyseius bibens* (Acari: Phytoseiidae). *Entomol. Exp. Appl.* **24**, 145–53.
- Sjerps, M. and Haccou, P. (1993) Information determines the optimal clutch sizes of competing insects: Stackelberg versus Nash equilibrium. *J. Theor. Biol.* **163**, 473–83.
- Stephens, D.W. and Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ.
- Strand, M.R. and Godfray, H.C.J. (1989) Superparasitism and ovicide in parasitic Hymenoptera: theory and a case study of the ectoparasitoid *Bracon hebetor*. *Behav. Ecol. Sociobiol.* **24**, 421–32.
- Suzuki, Y. and Iwasa, Y. (1980) A sex ratio theory of gregarious parasitoids. *Res. Pop. Ecol.* **22**, 366–82.
- van Alphen, J.J.M. and Visser, M.E. (1990) Superparasitism as an adaptive strategy for insect parasitoids. *Ann. Rev. Entomol.* **35**, 59–79.
- Waage, J.K. (1986) Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In *Insect Parasitoids* (J. Waage and D. Greathead, eds), pp. 63–95. Academic Press, London.
- Waage, J.K. and Ng, S.M. (1984) The reproductive strategy of a parasitic wasp. I. Optimal progeny and sex allocation in *Trichogramma evanescens*. *J. Anim. Ecol.* **53**, 401–15.
- Werren, J.H. (1980) Sex ratio adaptations to local mate competition in a parasitic wasp. *Science* **208**, 1157–9.
- Wilson, K. and Lessells, C.M. (1994) Evolution of clutch size in insects. I. A review of static optimality models. *J. Evol. Biol.* **7**, 339–63.

### Appendix: male migration and relative reproductive success

Assume that all females avoid DO and that the environment is constant. If resident females produce a proportion of daughters  $f_1^*$ , and males visit  $M$  patches later in life, by symmetry a female may expect  $(1 - f_1^*)M$  older males from other patches for every egg she produces. Then, the reproductive success of a male ( $R$ ) is equal to the reproductive success in his native patch,

$$R_{\text{in}} = R(S, S^*) = \frac{f_1}{1 - f_1 + (1 - f_1^*)M} \quad (31a)$$

plus the fitness later in life, given by

$$R_{\text{out}} = M R(S^*, S^*) = M \frac{f_1^*}{(1 - f_1^*)(M + 1)} \quad (31b)$$

Therefore Equations 23 and 24 become

$$F_1(S, S^*) = f_1 + (1 - f_1)[R_{\text{in}} + R_{\text{out}}] \quad (32a)$$

and

$$F_2(S, S^*) = f_2 + (1 - f_2) [pR_{\text{in}} + R_{\text{out}}] \quad (32b)$$

Substituting the ESS sex ratio (Equation 29) into Equations 31a and 31b gives

$$R_{\text{in}} = \frac{1}{M} \quad (33a)$$

$$R_{\text{out}} = \begin{cases} 1 & M > 0 \\ 0 & M = 0 \end{cases} \quad (33b)$$

Interestingly, the reproductive success of males later in life is unity, independently of the amount of migration as long as it is not zero. A decrease in the number of patches visited is compensated by an increase in the pay-off from each patch, which is due to the increasing  $f^s$ .

It follows that

$$F_1 = 2 \frac{M + 1}{2M + 1} \quad (34)$$

and

$$F_2 = f_2 + (1 - f_2) \left[ \frac{p}{M} + 1 \right] \quad (M > 0) \quad (35)$$

According to Equation 35, the second female should add sons, as long as  $M > 0$  and  $p > 0$ . When  $p = 0$ , non-zero migration means that both sexes in the second clutch confer an equal pay-off (cf. Equation 26). Setting  $f_2 = 0$  results in Equation 30 for the relative reproductive success.