Female preference for nests with many eggs: a cost-benefit analysis of female choice in fish with paternal care

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In several fish species with paternal care, females prefer males guarding many eggs in their nest. This preference might be advantageous because the presence of many other eggs dilutes the risk of newly laid eggs being eaten by the father. To evaluate this hypothesis quantitatively, we constructed a simulation model that mimics the breeding biology of the blenny *Aidablennius sphynx*. In contrast to earlier verbal models, the costs of choice are explicitly taken into account. We systematically varied factors such as the stringency of choosiness and the level and nature of the costs of choice. For realistic parameter values female choosiness may result in a fitness advantage of more than 50%. The optimal choice strategy created a distribution of eggs over the nests which resembles that found in the field for *A. sphynx*. Our model shows that the relative fitness of a choice strategy is not constant but frequency dependent in a complicated way. If most females are choosy, a bimodal distribution of eggs over the nests results, with many nests containing few and some nests containing many eggs. In such a situation choosiness is profitable, since randomly laying females will often lay their eggs in nests with few eggs, producing a high mortality per egg due to filial cannibalism. If, on the other hand, only few choosers are present, their influence on the egg distribution is limited. A unimodal distribution results which is profitable for nonchoosers, since the average egg mortality is low and nonchoosers do not bear the costs of choice. The positive relation between chooser frequency and chooser fitness makes it easy to understand why choosiness is evolutionarily stable. However, it is not obvious how the trait is established by selection in the first place. *Key words: Aidablennius sphynx*, costs of choice, dilution effect, fish, evolutionary stability, female choice, frequency dependent selection, paternal care, simulation model. *[Behav Ecol 7:353–361 (1996)]*

I n a variety of fish species where males care for eggs in a nest, females show a strong preference for males that have already accumulated many eggs (Gronell, 1989; Knapp and Sargent, 1989; Kraak and Videler, 1991; Marconato and Bisazza, 1986; Marconato and Rasotto, 1983; Petersen, 1989; Ridley and Rechten, 1981; Sikkel, 1989; Unger and Sargent, 1988). In four of these species and in *Oxylebius pictus* (DeMartini, 1987), it has been shown that the hatching percentage, or the survival of eggs, increases with brood size (number of eggs present in the nest) (Marconato, 1985; Sargent, 1988; Gronell, 1989; Kraak, 1996a). Part of the mortality of eggs in the nest appears to be due to filial cannibalism, meaning that males entirely or partly cannibalize the brood they care for (DeMartini, 1987; FitzGerald and van Havre, 1987; Hoelzer, 1988, 1992; Kraak, 1996a; Loiselle, 1983; Marconato and Bisazza, 1988; Petersen, 1990; Petersen and Marchetti, 1989). Rohwer (1978) formulated a model addressing the phenomenon of filial cannibalism and its consequences for female choice in fishes with paternal care for eggs. According to this model, it may pay males to consume a number of eggs from their brood in order to compensate for the restrictions in foraging opportunities while guarding the nest. If the number of eggs that males cannibalize per day is limited, the risk per egg to be cannibalized decreases with brood size at a diminishing rate (Figure 1). All other things being equal, this "dilution effect" implies that a female minimizes the per capita mortality of her eggs by laying in a nest that contains many eggs.

It is, however, difficult to estimate quantitatively the net benefits of female preference for males guarding many eggs. Certainly eggs laid into a nest with few eggs present have a higher mortality than eggs laid in a nest containing many eggs, but it depends on the subsequent fate of the nest whether the mortality risks accumulate in time. In fact, the probability of being cannibalized will drop significantly as soon as the nest receives additional batches of eggs from other females. Furthermore, choosy females may lose time and energy or they may incur a higher predation risk when exerting their choice. The consequences that such costs may have on the processes of mate choice and sexual selection have recently received much attention in theoretical (e.g., Crowley et al. 1991; Parker, 1983; Pomiankowski, 1987; Real, 1990; Sullivan, 1994) as well as empirical studies (e.g., Alatalo et al., 1988; Berglund, 1993; Forsgren, 1992; Milinski and Bakker, 1992). These studies show that when costs of mate choice increase, the level of choosiness decreases. Therefore, when such costs of choice play a role, it is no longer obvious whether preference for nests with many eggs is indeed advantageous. A thorough cost-benefit analysis is required to explain the evolutionary origin, fixation, and maintenance of the trait.

It is the aim of this study to perform such an analysis by means of a simulation model. To keep the model as realistic as possible, we tried to mimic some basic aspects of the breeding biology of the blenny *Aidablennius sphynx*. Females of this fish prefer males when they have many eggs in their nest (preference rises at nest contents of 100–1000 eggs; nests can contain up to 7000 eggs) (Kraak and Videler, 1991). Moreover, male *Aidablennius sphynx* have been shown to cannibalize on average 36 eggs per day from their brood, resulting in a dramatic increase of egg survival with brood size (Kraak,
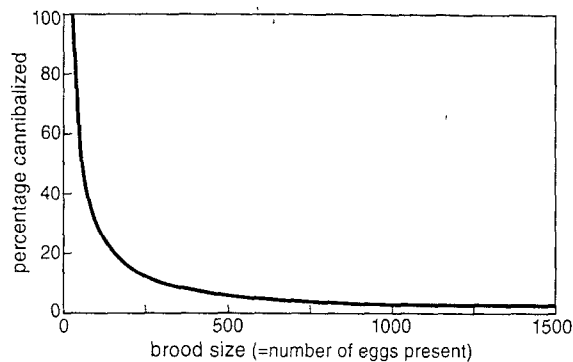
Figure 1
Visualization of the dilution effect. If a fixed number of eggs is cannibalized (here 30 eggs), the per capita risk of being cannibalized decreases with brood size at a diminishing rate.

1996b). We want to investigate how the net advantage of choosiness is influenced by such factors as the prevalence of choosiness, the stringency of choosiness, and the costs of choice.

METHODS

The model species

Our model is based on the following empirical knowledge of *Aidablennius sphynx* (see Kraak, 1996b,c; Kraak and van den Berghe, 1992; Kraak and Videler, 1991). The breeding season starts at the end of April and extends into August. Males continuously occupy the same nest; they receive eggs and care for eggs throughout the breeding season without any cyclical pattern. Males and females both mate promiscuously. Males can mate with up to seven females per day. Females usually lay 200–300 eggs every 2 or 3 days. During the peak hours of sexual activity, the number of nests visited per hour by individual females ranged from 1 to 9 (N = 228 female hours, mean = 1.6, SD = 1.1; Kraak SBM, unpublished data). The development of eggs into free-swimming larvae, which receive no further care, takes 15–18 days in May when water temperature is low (15°C–20°C). Developmental time decreases to 7–8 days in July when the water is much warmer (20°C–26°C).

The simulation model

Our model keeps track of the reproductive output of a population of males and females throughout one breeding season. Each female produces batches of ripe eggs at fixed time intervals. When a female has ripe eggs, she randomly picks a nest (guarded by a male). If the female is a "nonchooser" she will deposit her batch of eggs into the first nest she encounters. A "choosy" female will only deposit her eggs if she finds the nest acceptable according to a threshold criterion (see below). If the nest is not acceptable, the female will randomly pick another nest. Once being laid into a nest, an egg needs a fixed number of days until hatching. The father (the male guarding the nest) cannibalizes a fixed number of randomly chosen eggs from his nest per day. Hence, the daily risk per egg of being cannibalized is inversely proportional to the number of eggs present that day (see Figure 1). If an egg survives until hatching, it is transformed into a larva. Larvae immediately leave the system. The number of larvae produced by a female is considered a measure for the fitness of the female's choice strategy. The structure of the simulation model is illustrated by the flow chart in Figure 2.

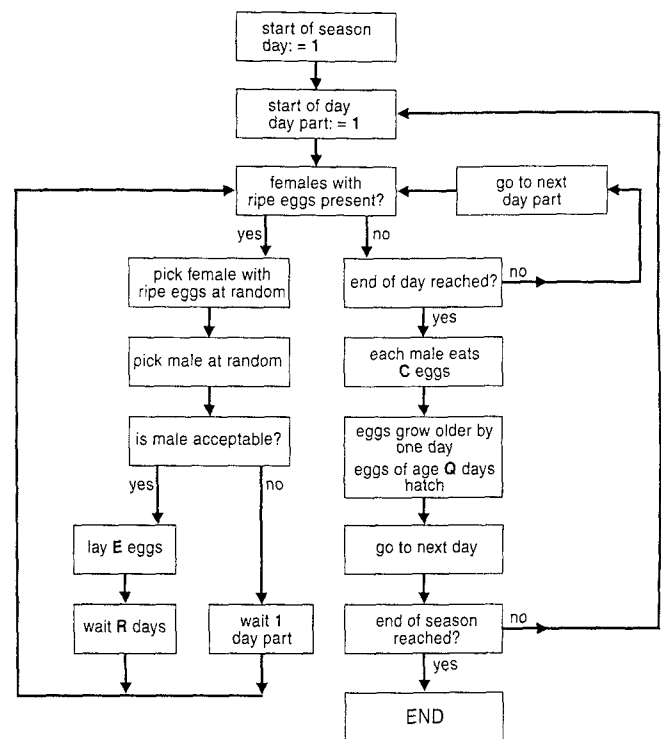The model includes a number of parameters that were var-

Figure 2
Flow chart of the simulation model. A simulation run corresponds to one breeding season. Each day of the breeding season is divided into a fixed number of "day parts." Each female with ripe eggs gets one opportunity per day part to randomly encounter a male's nest. For a nonchoosy female the randomly encountered nest is always acceptable; for a choosy female the nest is acceptable only if it contains more than T eggs, or if the female has already visited V males ("fixed threshold strategy with last chance option"). The box "wait 1 day part" only applies to the "time cost model"; in the "energy cost model" and the "mortality risk model" this box is skipped. In the "energy cost model" the batch of E eggs that choosy females lay is reduced by L for every rejection, and in the "mortality risk model" a female has a probability, μ, of dying at every visit.

ied systematically in order to investigate their effects. We consider a population of F females, and M males collecting eggs in their nest throughout the breeding season of S days. Eggs need Q days until hatching. Each male randomly cannibalizes C eggs per day (or all eggs if less than C eggs are present in his nest). A proportion, p, of the females consists of choosers and a proportion, $1 - p$, of nonchoosers. It takes a female R days to develop a batch of E ripe eggs. If the eggs are ripe, a female gets D opportunities per day to inspect nests. Hence, a day is split into D fractions, and such a "day part" is the time unit of our model. Choosy females use a "fixed threshold strategy with last-chance option" (sensu Janetos, 1980): such a female will only accept a nest if it already contains more than T eggs; otherwise she will go on and visit another randomly picked nest. A choosy female has, however, a fixed maximum of V options. If she does not find a nest meeting the threshold criterion within V visits, she will deposit her eggs in the last nest. Notice that a large value of V essentially means that the female is using a "fixed threshold strategy without last-chance option." Table 1 lists the model parameters, their default values, and the parameter ranges that were investigated. The choice of the default values was motivated by the breeding biology of *A. sphynx* (see above).

For each parameter combination, a simulation run (corre-

Table 1

Parameters of the model[a]

Parameter	Symbol	Default value	Values investigated
Number of males	M	20	20, 40, 80
Number of females	F	20	20, 40, 80
Development time of eggs	Q	10	10[b]
Number of eggs eaten	C	30	30[b]
Length of breeding season	S	100	10, 100
Number of eggs per batch	E	200	200[b]
Number of opportunities to lay eggs per day (day parts)	D	4	1, 2, 4, 8, 16
Time needed for egg riping (in days)	R	2	2[b]
Threshold number of eggs used as criterion	T	500	100, 250, 500, 1000, 1500
Maximum number of visits allowed before last chance option	V	6	2, 6, 10, 100, 500
Number of eggs lost per rejection (energy costs model[c])	L	25	12, 25, 50
Mortality risk (mortality risk model[c])	μ	0.25%	1%, 0.5%, 0.25%, 0.125%, 0.0625%

[a] For each parameter combination, the proportion of choosers, p, was systematically varied from 0 to 1 in steps of 0.05.

[b] Parameters Q, C, E, and R were varied in an earlier study to test the robustness of the model (Kraak and Weissing, 1994); variation of these parameters has only trivial effects and will therefore not be considered here. We also performed simulations in which C and E were drawn from a Poisson distribution or a normal distribution.

[c] See Methods.

sponding to one breeding season) was replicated 100 times. For each simulation the following was registered: the total number of eggs laid per chooser and per nonchooser, the total number of larvae hatched per chooser and per nonchooser, and the egg contents of the nests on each day. The relative fitness, W, of choosers was calculated as the number of larvae per chooser divided by the number of larvae per nonchooser (if $W > 1$ choosers have a fitness advantage, if $W < 1$ choosers have a fitness disadvantage).

Three models for the costs of choice

Not much is known about the nature of the costs of choice in *A. sphynx*. Studies on other animals suggest that time and energy spent while searching (Alatalo et al., 1988; Milinski and Bakker, 1992; Slagsvold et al., 1988) and predation risk (Berglund, 1993; Forsgren, 1992) may be major costs of choice. Therefore, three alternative cost models were investigated.

In the "time cost model," which is considered the standard model, each rejection of a nest leads to the delay in the production of a new batch of ripe eggs by one time unit, that is, by $1/D$ day. By having to wait for 1 day part per rejection, choosy females lose reproductive opportunities. The time cost model appears to be plausible if sampling of nests and developing a new batch of ripe eggs are mutually exclusive in time. However, it will also apply to a situation where energy loss or restricted foraging opportunities during sampling retard the production of a new batch of eggs.

In the "energy cost model," the rejection of a nest by a choosy female leads to a reduction in the next batch of eggs to be laid by this female by a fixed number of L eggs per rejection. In other words, the energy spent for nest visiting is not available for the ripening of eggs.

In the "mortality risk model," choosers as well as nonchoosers have a fixed probability, μ, of dying each time a nest is visited. Since choosers generally make more visits than nonchoosers, mortality is higher for choosers. As a consequence, the proportion of choosers will decline over the season. The mortality risk can be interpreted as the risk of being predated while visiting nests.

In all three cost models the actual costs that choosers experience depend on the number of rejections, and therefore on the abundance of suitable nests. The costs of choice in

terms of the loss of reproductive opportunities are reflected by the numbers of eggs laid by choosers relative to the number of eggs laid by nonchoosers. We quantified this "relative reduction in egg production" by the quotient between the difference in total egg production per nonchooser and per chooser, and the number of eggs laid per nonchooser.

RESULTS

The frequency dependence of chooser fitness

Let us first consider the time cost model with all parameters at their default values (see Table 1) in order to illustrate the general properties of the system. The outcome of the simulations are presented in Table 2, Figure 3, and Figure 4. The number of choosy females is systematically increased from 0 to 20. Figure 3 shows that the relative fitness of chooser females increases with the proportion of choosy females. The same type of frequency dependence is obtained for most other parameter combinations (see below). This can be explained by the fact that the ratio of choosers to nonchoosers influences the distribution of eggs over the nests. If mainly randomly laying nonchoosers are present, all nests have an equal chance of obtaining a given batch of eggs. This results in a unimodal distribution of the number of eggs per nest, with few nests remaining empty (Figure 4a). Conversely, when mainly choosers are present, nests with many eggs receive more eggs than average, whereas nests with few eggs are rejected by choosy females, resulting in a bimodal distribution of egg numbers with many nests remaining empty (Figure 4b). At an intermediate proportion of choosers, the shape of the egg distribution lies in between these two extremes. This shift from a unimodal to a bimodal distribution of egg numbers with increasing chooser frequency is reflected by a considerable increase in the standard deviation of egg numbers between nests (see Table 2).

The shape of the egg distribution has important consequences for nonchoosers as well as for choosers. With a unimodal distribution such as in Figure 4a, nonchoosers have a high probability of laying eggs in nests where they benefit from the dilution effect, whereas with a bimodal distribution, such as in Figure 4b, nonchoosers have a high probability of laying eggs in nests where many will be lost by cannibalism. Accordingly, the probability that nonchooser eggs survive to

Table 2

Outcome of the time cost model with parameters at their default values

Chooser frequency (%)	Eggs laid per chooser	Eggs laid per nonchooser	Relative reduction in chooser egg production	Larvae per chooser	Survival per chooser egg	Larvae per nonchooser	Survival per nonchooser egg	Relative chooser fitness	Mean nest contents at end of season (± SD)
5	9478	10,000	0.05	6816	0.72	6827	0.68	1.00	826 (424)
25	9362	10,000	0.06	6812	0.73	6708	0.67	1.02	820 (478)
50	9092	10,000	0.09	6805	0.75	6329	0.63	1.08	799 (557)
75	8624	10,000	0.14	6721	0.78	5257	0.53	1.28	773 (739)
95	8123	10,000	0.19	6323	0.78	3818	0.38	1.66	741 (960)

hatching decreases with the increasing proportion of choosers (see Table 2). For the choosers the shift to bimodality of the egg distribution implies that nests are rejected more often, resulting in a lower egg production (Table 2). At the same time choosers have a higher probability of laying eggs in nests where they benefit from the dilution effect. Hence, the shift to bimodality results in higher costs and higher benefits for choosers. For the parameters considered here, the higher costs are almost compensated for by the higher benefits, as can be seen from the number of surviving chooser larvae (Table 2). Taken together, the effects on choosers and nonchoosers result in a greater fitness advantage for choosers relative to nonchoosers (see Table 2 and Figure 3).

Notice that with all parameters at their default values, female choosiness is selectively neutral in a population of nonchoosers. In contrast, choosiness provides a fitness advantage of 66% if mainly choosers are present. The positive relation between chooser fitness and chooser frequency implies that once the trait gets established it will easily spread to fixation and it will be evolutionarily stable against nonchoosers. This result seems to be independent of population size, since simulations with $M = F = 40$ or $M = F = 80$ gave almost identical results.

The stringency of choosiness

In our model the stringency of choosiness is determined by two parameters: the level, T, of the threshold criterion, and the number, V, of nest visits until the last chance option is used. We investigated the influence of both parameters separately.

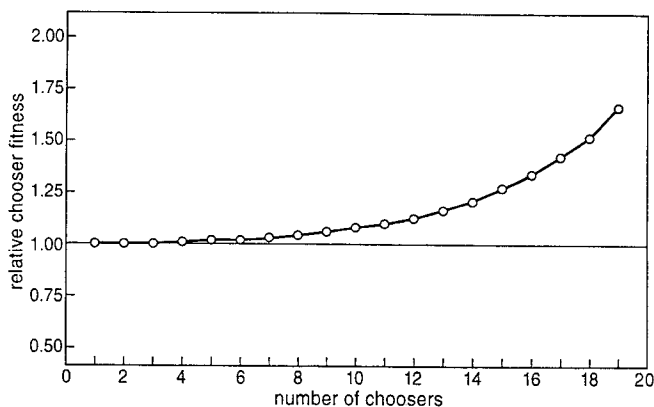Figure 5 illustrates the effects of varying the threshold, T,

in the time cost model. The relative fitness of choosers appears to be strongly dependent upon T, and $T = 500$ seems to be optimal for choosers. With increasing T, the bimodal distribution of nest contents becomes more and more extreme. This results in greater losses due to cannibalism for the nonchoosers, while choosers have greater benefits from the dilution effect. On the other hand, the costs of rejection for the choosers also increase with T. At $T = 1000$ choosers reject so often that at low chooser frequency they have a fitness disadvantage and at high chooser frequency only a slight fitness advantage compared to nonchoosers. At $T = 1500$ choosers have a fitness disadvantage at all chooser frequencies. In fact, very few nests contain more than $T = 1500$ eggs. Therefore choosers have high rejection costs and often use their last chance option to lay in unfavorable nests: choosiness is too stringent.

The fact that a choice strategy with $T = 500$ appears to be optimal, seems intuitively plausible since Figure 1 shows that the marginal benefits, in terms of lower egg mortality gained by preferring larger broods, are insignificant.

When V, the maximal number of visits per chooser female, is increased choosers have more opportunities to find nests with many eggs, but also reject nests more often. This results in more extreme bimodality of the distribution of nest contents and lower mean nest contents. As a consequence nonchoosers have greater losses, while choosers bear greater costs of choice. In general, the fitness advantage of choosers at high proportions of choosers increases with the maximal number
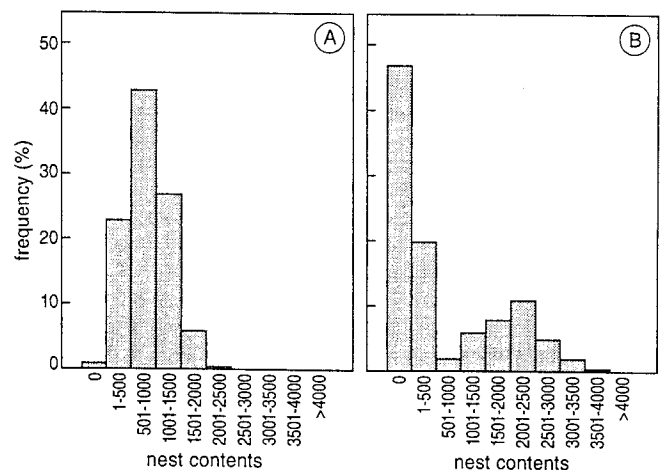

Figure 3
Relative chooser fitness as a function of the number of choosers. (All parameters are at their default values.)

Figure 4
Frequency distribution of nest contents at the end of a breeding season ($S = 100$) when only (A) nonchoosers are present, or (B) only choosers are present. (All parameters are at their default values.)
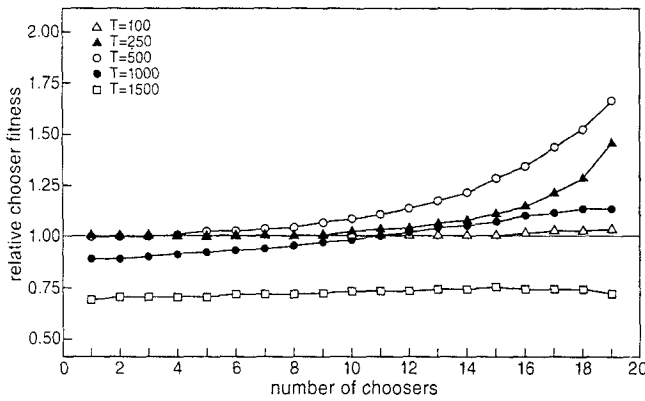
Figure 5
Effect of the threshold criterion, T, on the relative fitness of choosers. (All other parameters are at their default values.)
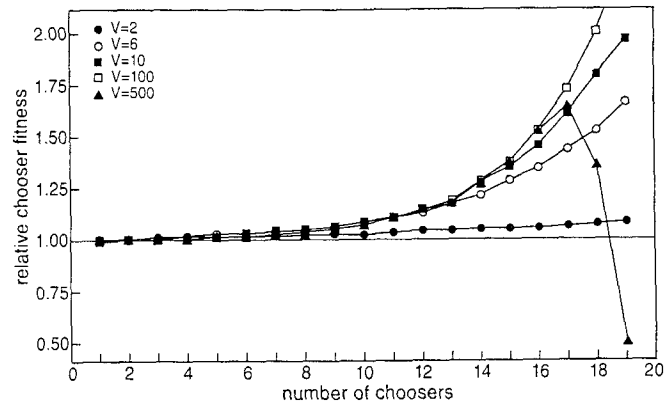

Figure 6
Effect of the maximum number of visits, V, on the relative fitness of choosers. (All other parameters are at their default values.)

of visits, V, and it becomes more than twofold for $V = 100$ (Figure 6). However, at $V = 500$ this advantage drops at the highest chooser frequencies (Figure 6). It is important to realize that relative fitness does not necessarily reflect "absolute fitness" (here defined as reproductive success in terms of the number of larvae produced). In fact, with increasing V the absolute fitnesses of both choosers and nonchoosers decrease dramatically, because very few eggs are laid and many nests remain empty. Despite this, relative chooser fitness increases with V, up to a certain point, because the choosers still have their benefits from the dilution effect. Notice that $V = 500$ effectively means a fixed threshold strategy without last-chance option: since $V/D > S$, the choosers continue to search for nests that meet their criterion. In a population with 100% choosers, choosers will never find a nest that meets the threshold criterion, and therefore they will never lay eggs (and have a fitness of zero). Yet, a frequency of 10% non-choosers is sufficient to give choosers using a fixed threshold strategy without last-chance option a fitness advantage over nonchoosers (Figure 6).

The nature of the costs of choice

Up to now all simulations were based on the time cost model. Let us now illustrate the influence of the type of costs on the evolutionary success of choosiness. To make the different cost models comparable, we had to adjust the parameters that determine the costs of choice in the three models (D for the time cost model, L for the energy cost model, and μ for the mortality risk model). In the time cost model, the default value of $D = 4$ day parts means that $1/D = \frac{1}{4}$ day is lost per rejection. Since the potential rate of egg production is $E/R = 100$ eggs per day ($E = 200$ eggs per $R = 2$ days), a loss of $\frac{1}{4}$ day corresponds to a reduction of the reproductive potential by 25 eggs. Therefore we chose the default value of L in the energy cost model to be $L = 25$, meaning that the batch of eggs to be laid is reduced by $L = 25$ eggs per rejection. For the mortality risk model a comparable default value of μ, the mortality risk per visit, was chosen as follows. With a season length of $S = 100$ days, the total reproductive potential of a female is $S = 100$ days times $E/R = 100$ eggs per day $= 10,000$ eggs. The loss of 25 eggs therefore represents a reduction of the total reproductive potential by 0.25%. We chose this as our default value of μ. With $\mu = 0.25\%$, a rejection of a nest by a chooser female leads to death in 0.25% of all cases. If death means the loss of the total seasonal production of 10,000 eggs, on average $\mu * S * E/R = 25$ eggs are lost. Notice, however, that the total seasonal production is only lost when

death occurs at the start of a breeding season. Since mortality toward the end of the season has only minor effects, the total costs of the mortality risk model with $\mu = 0.25\%$ are somewhat smaller than in the time cost model with $D = 4$ or in the energy cost model with $L = 25$.

The outcomes of the energy cost model and the mortality risk model are depicted in Figure 7 (compare with Figure 5 for the time cost model). With low T, the results of all three cost models are similar. However, with higher values of T significant differences between the cost models appear.

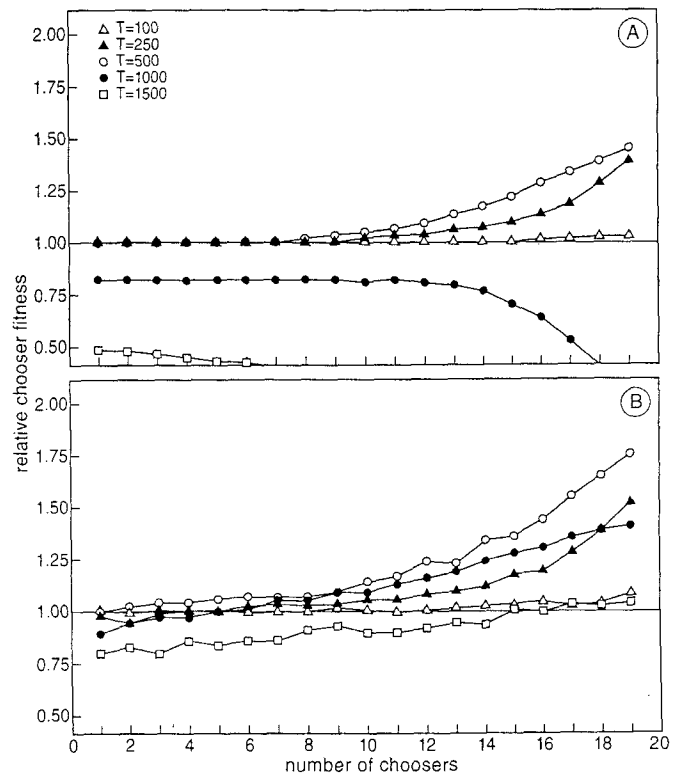In the energy cost model, costs become very severe when

Figure 7
Effects of the cost model on relative chooser fitness. For the energy cost model (**A**) and the mortality risk model (**B**) the threshold value of choosy females is varied (all other parameters are at their default values). Compare with Figure 5 which shows the corresponding results for the time cost model.
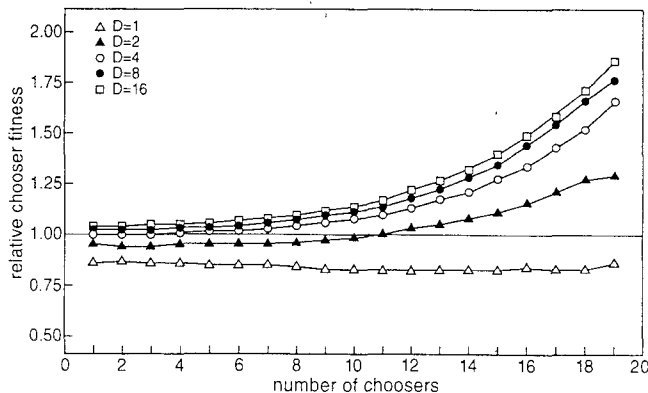
Figure 8

Effect of the time lost per rejection, $1/D$, on the relative fitness of choosers. (All other parameters are at their default values.)

choosiness is stringent. With higher T ($T = 1000$, 1500) relative chooser fitness is no longer positively related to chooser frequency (Figure 7a). The severity of the costs in the energy cost model can be explained as follows. Notice that a female's batch of eggs to be laid next becomes smaller with each rejection. With many stringent choosers, nests accumulate eggs at a low rate and have a low probability of reaching the threshold. This in turn leads to many rejections and few eggs being laid. In general, in the energy cost model, choosers do not contribute much to the distribution of nest contents because they often lay few eggs, and therefore choosers profit little.

In contrast, in the mortality risk model, costs appear to be less severe. Even with $T = 1500$, choosers have a slight relative advantage at high chooser frequencies (Figure 7b). The higher profitability of choosiness in the mortality risk model can be intuitively seen as follows. As long as the choosers are alive they have not experienced any costs yet, meaning that they lay as many eggs and as often as nonchoosers. As a consequence, the distribution of nest contents has a higher tendency toward bimodality early in the season than in the other cost models. This implies that the choosers profit more from the dilution effect early in the season. Moreover, only if a female dies at the start of the season is her entire reproductive potential lost; if she dies later in the season she loses only part of her total reproductive potential (as was mentioned above, the value of $\mu = 0.25\%$ is not fully comparable to $D = 4$ or $L = 25$ in the other cost models). Another characteristic of the mortality risk model is a large variation between replicate simulations (the standard deviation of the mean relative chooser fitness is typically 10 times higher in the mortality risk model than in the other two models). This is because the dying of females is a chance process, whereas the losses caused by rejection are deterministic in the other cost models; at the same time the consequences of loss are more far reaching in the mortality risk model since a dead female remains dead for the rest of the season.

The level of the costs of choice

To investigate the effect of the level of the costs of choice in the time cost model we varied D, thereby varying the fraction $1/D$ of a day that is lost per rejection. As expected, the relative chooser fitness decreases with increasing costs (Figure 8). When $D = 1$ (1 day is lost per rejection), choosers never reach a fitness advantage. With high costs, choosers lay few eggs resulting in low mean nest contents. As a consequence nonchoosers lose many eggs to cannibalism, as do choosers (who at the same time lay few eggs). Hence, raising the costs of

choice has negative consequences for both choosers and nonchoosers because of the lower egg production by choosers.

We varied the level of costs in the energy cost model by varying L, the number of eggs lost per rejection, and in the mortality risk model by varying μ, the probability of dying at each visit. The results are qualitatively similar to those presented for the time cost model: relative chooser fitness decreases with increasing costs, as expected. However, in the energy cost model, costs appear to be very severe, as we have seen before. When choosiness becomes too stringent, this often results in females laying no eggs at all (for example, with $L = 50$ if four nests have been rejected). In the mortality risk model, costs again appear to be less severe.

DISCUSSION

The model assumptions

We first discuss to what extent the assumptions of our model are realistic and hence applicable to empirical systems. Our model centers around the assumption that the presence of many eggs dilutes the risk per egg of being cannibalized, and that choosy females exploit this dilution effect. At least three other benefits for a female preference for nests containing many eggs have been proposed. First, by laying her eggs among many others a female may secure greater paternal investment for her eggs, since males are expected to increase their level of shareable care with the size of their broods (Coleman et al., 1985; Hoelzer, 1988, 1992; Petersen and Marchetti, 1989; Sargent, 1988; Sikkel, 1989; van Iersel, 1953). Second, a female spawning with a male that already guards many eggs may choose a father of proven "good parental quality" (Ridley, 1978). Third, by spawning in a nest containing many eggs a female mates with a male that has proven to be attractive to other females. This might result in the production of attractive offspring or offspring of good genetic quality (see discussions on copying, e.g., Gibson and Höglund, 1992; Kraak, 1996a; Losey et al., 1986; Ridley, 1978; Wade and Pruett-Jones, 1990). These benefits are not mutually exclusive and they may act in concert, together with the benefits from the dilution effect. In this study we have focused on the dilution effect, since the other benefits are more difficult to implement into a model without making many ad hoc assumptions. Moreover, the dilution effect will always play a role when partial cannibalism occurs. Hence, it is interesting to investigate to what extent the evolution of female preference for nests with many eggs can be explained on the basis of this factor alone.

We modeled female choice by assuming that females use a fixed threshold strategy. However, other mate choice strategies are also plausible (Janetos, 1980; Wittenberger, 1983). For example, the threshold criterion might vary with local circumstances (e.g., the costs of choice or the distribution of mate quality; Real, 1990), or the criterion might become less stringent with each successive trial. Our model also neglects the possibility that females use information that they acquired earlier (see e.g., Dombrovsky and Perrin, 1994). By visiting males, females might assess the actual quality distribution of mates. In some species female preference for a particular male becomes stronger after the female has been exposed to an unattractive male than if the female has been exposed to an attractive male (Bakker and Milinski, 1991; Collins, 1995). Furthermore, females using their last chance option might go back to the best male they have encountered so far. Or females might use a "best-of-n-males strategy" (Janetos, 1980; Real, 1990; Wittenberger, 1983), where they sample a set of n males and then return to the best male encountered. Moreover, it is conceivable that females have expectations about

the contents of a nest from knowledge acquired on previous days, and that they visit nests to verify whether this knowledge is still "up to date." Field observations suggest that this might be the case in *A. sphynx* (Kraak and Videler, 1991). To investigate the effects of other choice strategies, we have also implemented strategies such as "best-of-*n*-males" or "decreasing threshold" in our simulation model (Weissing FJ and Kraak SBM, unpublished data). The results are comparable to those based on a "fixed threshold" strategy, but they will be discussed elsewhere in more detail. In the present study we have concentrated on fixed threshold strategies, since these strategies are particularly simple and can easily be implemented as "rules of thumb." It is intuitively plausible that a last-chance option is used, since at a certain point in time females must get rid of their ripe eggs. The latter is supported by the observation that *A. sphynx* females in aquaria will deposit their ripe eggs even if no male at all is present (Kraak SBM, personal observation).

Several theoretical studies have stressed that the costs of mate choice may have important consequences for the outcome of sexual selection (e.g., Janetos, 1980; Kirkpatrick, 1987; Parker, 1983; Pomiankowski, 1987; Real, 1990; Sullivan, 1994). In fact, females may risk predation and spend time and energy searching and judging males. Empirical studies have shown that females become less choosy when costs of choice are increased (Alatalo et al., 1988; Berglund, 1993; Forsgren, 1992; Milinski and Bakker, 1992). However, the costs of choice, in terms of loss of fitness, are difficult to quantify in empirical systems (but see Gibson and Bachman, 1992). In order to compensate for this lack of knowledge, we considered three models that focus on different aspects of the costs of choice. In all three models, the costs of choice are related to the stringency of choosiness in a natural way: the costs are highest when acceptable nests are hard to find. To compare the different cost models, we chose the relevant parameter values in such a way that the costs per rejection were roughly equivalent. Interestingly, the three models differ significantly in their long-term consequences. With a threshold value of $T = 500$ and 95% of the females being choosy, the total egg production of choosers was reduced by 19% in the time cost model, by 27% in the energy cost model, and by 13% in the mortality risk model. Accordingly, the relative fitness of choosers differed significantly between the three cost models (1.66, 1.45, and 1.75 respectively; see Figures 5 and 7). This discrepancy can be explained by the fact that the costs of choice have a twofold effect: choosy females are not only directly affected by losing time, energy, or their life, but are also indirectly affected via the influence of the cost model on the distribution of eggs over the nests (see Results). In view of such subtle indirect effects, it is of utmost importance to correctly specify the level and the nature of the costs of mate choice in empirical studies.

Our model contains a number of structural assumptions that are not always met in field settings. In a previous study (Kraak and Weissing, 1994) we investigated the robustness of our predictions by varying the population structure, the sex ratio, the number of eggs laid, the time required for egg development, and the number and type of eggs cannibalized. All these variations had quantitative effects, but the general properties of the system were not altered. In particular, the relative fitness of choosers remained positively frequency dependent. Our general conclusions were also not affected when stochastic factors were added to the model. When, for example, the numbers of eggs eaten by a male or the number of eggs laid by a female were no longer assumed to be fixed but were drawn from a probability distribution (Poisson or normal), the variance between simulation runs became larger while the relative fitness of choosers became slightly smaller.

However, the relative chooser fitness remained positively frequency dependent, and it was >1 when mainly chooser females were present. We also considered the possibility that the strategies themselves are stochastic by drawing the threshold, T, and the maximal number of visits, V, from a normal and a Poisson distribution, respectively. Again, the general properties of the model were not altered by these modifications.

Empirical relevance of the model

It was one goal of the present study to investigate whether benefits from the dilution effect are sufficient to explain female preference for nests with many eggs in the blenny *A. sphynx*. The model structure and the default values of most parameters were therefore motivated by the breeding biology of *A. sphynx* (see Methods and Table 1). In contrast to our default assumption of a 1:1 sex ratio, a female biased sex ratio is probably more realistic for *A. sphynx*, since nest sites are likely to be limiting. Unfortunately, not much is known about the nature and the level of the costs of choice in *A. sphynx*. Normally, *A. sphynx* females are rather motionless and are quite cryptically hidden in the vegetation. However, females often swim long distances to sample males for mate choice (Kraak, 1996c), thereby spending time and energy. Furthermore, displaying males are conspicuous to the observer and probably to predators as well. Females might therefore increase their risk of predation by being involved in sexual interactions with conspicuous males. Hence, aspects of all three cost models seem to play a role. However, since our knowledge of the costs of choice and the choice strategy is limited, we assumed for simplicity that a fixed threshold strategy with last-chance option and the time cost model adequately represent the situation of *A. sphynx*.

Our model shows that, under these assumptions, choosiness is indeed highly advantageous when most females are choosy. Hence, the dilution effect alone provides choosiness with a considerable fitness advantage. The fact that we found $T = 500$ to be optimal under most conditions corresponds with the finding that in nature female preference of *A. sphynx* rises at nest contents of between 100 and 1000 eggs (Kraak and Videler, 1991). Moreover, the distribution of nest contents resulting from simulations with a sex ratio of 2 females:1 male and all females being choosy agrees quite well with field data on *A. sphynx*. The simulations yielded at day 100 a mean nest content of 1638 eggs with a 90-percentile range of 4253 eggs and 40.5% of the nests being empty. Field data on eight nests (198 pooled "nest days" between 14 May and 9 June 1986) yielded a mean nest content of 2120 eggs, with a 90-percentile range of 4860 eggs and 36.4% of the nests being empty (Kraak SBM, unpublished data). Therefore we have some confidence in the empirical relevance of our simulations.

Our model can easily be modified to make it applicable to other fish species with a similar breeding biology. Of course the quantitative outcome will depend on species-specific aspects of the breeding biology. In particular, differences may be found if males do not breed continuously over a long breeding season, but instead breed in short repetitive nesting cycles (as, for example, in sticklebacks; van Iersel, 1953; see also Sargent et al., 1995), during which females may oviposit only once. Interestingly, the qualitative features of our model became visible quite early in the breeding season. For example, the distribution of egg contents in a population of choosy females became markedly bimodal after only 5 days. When we decreased the length of the season from 100 to 10 days (during which nonchoosers oviposit five times) the relative fitness of choosers became smaller and more variable. However, it was still positively frequency dependent and >1 when mainly choosers were present.

Evolutionary implications

It is perhaps the main result of the present study that the frequency dependence of chooser fitness is made explicit. In other words, the benefits of choosiness depend on what other females are doing. When many females are choosy, choosiness is strongly favored. In contrast, the net benefits of choosiness are negligible or even negative in the absence of other choosers. This frequency dependence is mediated by the effects of choosiness on the distribution of eggs over the nests. If choosy females are rare, the distribution of nest contents is unimodal with a relatively small variance. In such a situation choosers can hardly exploit the dilution effect. If, on the other hand, choosy females are frequent, the distribution of nest contents becomes bimodal with a large variance. In this situation, the choosers have higher costs but they also have high benefits from the dilution effect. While choosers have higher costs and higher benefits, the nonchoosers are only facing a higher mortality per egg since many nests contain only few eggs. Taken together, these effects generally lead to a positive relation between relative chooser fitness and chooser frequency. Although the total reproductive output of a population is negatively related to the chooser frequency (see Table 2), choosy females will typically gain a selective advantage once their proportion has surpassed a certain critical value. If choosiness gets established at all in a population, it will easily spread to fixation, and it will be maintained by the selection pressure derived from the dilution effect alone.

The question, however, remains how choosiness based on nest contents gets established in the first place. This is not obvious since choosiness appears to be selectively neutral or even disadvantageous in a population of nonchoosers. Several arguments might be given to explain the evolutionary origin of choosiness.

First, we may have underestimated the benefits and overestimated the costs of choosiness. We have already mentioned several additional possible benefits of laying in nests with many eggs (see discussion of the model assumptions above). Moreover, while assessing nest contents females might at the same time consider male traits that are important for mate choice. For example, the level of courtship display might signal male vigor, and male vigor might indicate heritable fitness ("good genes") or a high parental quality (Hoelzer, 1989). Or females might assess a male's body condition, which might be correlated with the level of starvation and hence with the expected level of cannibalism. Furthermore, assumptions concerning the costs of choice are crucial at low chooser frequencies where the benefits of choosiness are small. In our standard configuration, we have assumed rather high costs of choice: in the three cost models, the relative reduction in chooser egg production ranged from about 10% to 30%. The level of the costs of choice in natural settings is largely unknown. We know of only one study that quantifies the costs of mate choice (Gibson and Bachman, 1992): female sage grouse increased energy expenditure by 1% and predation risk reduced their annual survival by <0.1% due to visiting leks. Hence, we may have overestimated the costs of choice.

Second, in small populations natural selection may be overruled by genetic drift. In other words, even if choosiness is selectively neutral or slightly disadvantageous, stochastic processes may lead to an increase in the proportion of choosy females in small, isolated subpopulations. As soon as drift has shifted the proportion of choosy females beyond some critical value, selection may take over and result in the spread and fixation of choosiness. If choosiness is established in some local subpopulations, migration may then lead to the spread of choosiness in the population as a whole. Whether this scenario is realistic depends largely on whether the population is indeed composed of small, relatively isolated subpopulations. Unfortunately, the population structure of species such as *A. sphynx* is largely unknown. In particular, it is not known whether the pelagic larvae mainly disperse locally or over wide areas (Leis, 1991).

Third, choice strategies that are less stringent than the optimal one ($T = 500$) have less costs and might therefore be able to spread in a population of nonchoosers. For example, with $T = 100$ and $T = 250$ choosiness was slightly advantageous (relative chooser fitness = 1.01) at the lowest chooser frequency. One could imagine the initial introduction and establishment of such "moderate" choice strategies, followed by repeated invasions of chooser strategies with more stringent thresholds. Whether such a scenario is indeed plausible cannot be judged on the basis of the present model. We are currently investigating a model for the direct competition between different choice strategies. The study of mutual invasions of these different strategies should shed some light on the fascinating question of which female choice strategy will result as the long-term outcome of natural selection.

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