THE EVOLUTION OF SPERM-ALLOCATION STRATEGIES AND THE DEGREE OF SPERM COMPETITION

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Abstract.—The prevailing viewpoint in the study of sperm competition is that male sperm-allocation strategies evolve in response to the degree of sperm competition an ejaculate can expect to experience within a given mating. If males cannot assess the degree of sperm competition their ejaculate will face and/or they are unable to facultatively adjust sperm investment in response to perceived levels of competition, high sperm allocation (per mating) is predicted to evolve in the context of high sperm competition. An implicit assumption of the framework used to derive this result is that the degree of sperm competition is unaffected by changes in sperm-allocation strategies. We present theory based on an alternative perspective, in which the degree of sperm competition and the sperm-allocation strategy are coupled traits that coevolve together. Our rationale is that the pattern of sperm allocation in the population will, in part, determine the level of sperm competition by affecting the number of ejaculates per female in the population. In this setting, evolution in sperm-allocation strategies is driven by changes in underlying environmental parameters that influence both the degree of sperm competition and sperm allocation. This change in perspective leads to predictions that are qualitatively different from those of previous theory.

Key words.—Ejaculate, male-male competition, sperm allocation, sperm competition, sperm precedence.

The study of the evolution of sperm allocation in the presence of sperm competition (Wedell et al. 2002; Parker 1970, 1998; Anderson 1994; Simmons 2001) has received a great deal of attention by both theoretical (Parker 1990a,b, 2000; Parker et al. 1997; Greeff and Parker 2000) and empirical (Gwynne 1984; Birkhead and Møller 1992; Simmons and Siva-Jothy 1998; Evans and Magurran 2001) evolutionary biologists. The prevailing view is that the degree of male investment in sperm at any given mating attempt is expected to evolve in response to the degree of competition that the male can expect to experience with sperm from rival males (Wedell et al. 2002). A universal prediction of current theory states that males should allocate more sperm in each mating (at the expense of having fewer matings) as the degree of sperm competition increases across populations or species (Parker 1993; Ball and Parker 1996, 1997; Parker et al. 1996). Mating system is therefore thought to be a critical determinant of sperm-allocation strategies, with polyandrous populations expected to evolve to invest more in sperm allocation than their less promiscuous counterparts. Several empirical studies have been directed towards testing this prediction (reviewed in Møller and Briskie 1995), with some data being in agreement with this expectation and others being at odds (Pitnick and Markow 1994; Møller and Briskie 1995; Schülke et al. 2004). In either case, the fundamental conceptual underpinning of all of this research is that the degree of sperm competition drives the evolution of sperm-allocation strategies.

In this paper, we suggest an alternative perspective that we believe is more appropriate and that leads to some new insights and predictions about evolution under sperm competition. Specifically, rather than viewing the degree of sperm competition as an important factor driving the evolution of sperm-allocation strategies, we suggest that allocation strategies and the degree of sperm competition are actually two sides of the same coin. For example, if all males in a population allocate a great deal of resources to each ejaculate, and therefore produce very few of them, then we would expect the degree of sperm competition to be relatively weak because competition among the sperm of different males is not very likely to occur. Conversely, if all males allocate very little to each ejaculate, and therefore produce many of them, then we would expect the degree of sperm competition to be relatively strong because competition among the sperm of different males is virtually certain to occur. Thus, the sperm-allocation strategy that predominates in a population is inextricably coupled to the degree of sperm competition. Any evolutionary change in sperm allocation will therefore necessarily lead to a change in the degree of sperm competition and vice versa. As a result, we cannot view the degree of sperm competition as a factor driving the evolution of sperm allocation.

We present a model that incorporates this coupling between sperm allocation and the degree of sperm competition. As in previous theory, we use the model to explore how various factors such as the cost of finding a mate, the presence of sperm precedence, and the availability of resources affect sperm allocation across populations or species. Our results demonstrate that the change in perspective advocated here qualitatively alters some of the predictions from previous theory. We can also use the model to predict the relationship between the degree of sperm competition and sperm-allocation strategies. By varying a parameter (e.g., resource availability) and determining how both the degree of sperm competition and sperm allocation respond evolutionarily, we can predict how the two should covary across populations dif-

fering in this parameter. Again, our results reveal some qualitative differences with previous theory. It is crucial to bear in mind, however, that the difference in perspective taken here means that the predicted relationship between the degree of sperm competition and sperm allocation in the present model is correlative rather than causative. Aside from being an important conceptual distinction, this also means that the relationship between the degree of sperm competition and sperm allocation can depend on which parameter is responsible for the evolutionary differences in each across populations (e.g., resource availability, cost of finding a mate). Our results clearly demonstrate this as well.

MODEL

We use a game theoretic model framework following that of traditional sperm competition models and assume that a male's per mating sperm-allocation strategy is constant across all matings obtained in his lifetime (Parker 1982, 1984, 1990a; Parker and Begon 1993; Parker et al. 1996). Equivalent statements of this assumption are that individual males are either unable to allocate sperm differentially to matings or unable to assess the degree of sperm competition at a given mating. While these are likely to be accurate descriptions of some mating systems (e.g., systems with passive gamete dispersal), a growing body of empirical literature suggests that conditional allocation of sperm in response to perceived levels of sperm competition might also be quite common (Pilastro et al. 2002; Pizzari et al. 2003). Although our model could be extended to account for facultative allocation adjustments, we forgo such complexities in favor of analytic tractability and transparency of the results. In so doing, we focus our analysis on between-species (or between-population) comparisons.

The fitness of a mutant male with per mating sperm-allocation strategy s, in a population with per mating sperm-allocation strategy $\hat{s}$, is denoted by $W(s, \hat{s})$. As in previous models, we take $W(s, \hat{s}) = n(s)v(s, \hat{s})$, where $n(s)$ is the number of matings obtained by a mutant male and $v(s, \hat{s})$ is the expected per mating reproductive success of such a mutant male in a population with resident strategy $\hat{s}$. In what follows we use n, $\hat{n}$, and n^* to denote $n(s)$, $n(\hat{s})$, and $n(s^*)$, respectively, to simplify notation.

Specification of the number of matings, n(s)

Suppose that each male has a total resource budget of R units that is to be devoted to the production of sperm. We follow Parker (1984), Parker and Courtney (1984), and Parker et al. (1996) by supposing the males require c units of resource to obtain a mate, and therefore the expected number of matings obtained by a male with sperm-allocation strategy s is $n = R/(c + s)$, where the denominator is the total per mating resource expenditure.

Specification of the expected reproductive success, v(s, ŝ)

The critical feature of the present model is that changes in sperm allocation alter not only the number of matings that males receive, $\hat{n}$, but also the distribution that describes the probability of a given ejaculate experiencing competition

from a given number of competing ejaculates. This arises via the dependence of this probability on $\hat{n}$, since more matings imply a greater chance of sperm competition and vice versa.

Although the above point remains true for any initial distribution of matings, for simplicity we assume that matings are randomly distributed among all females in the population. If we further assume both a 50:50 sex ratio and large population size, then the probability that a female obtains k matings, where k can be any positive integer, is a Poisson random variable (see Appendix 1 available online only at http://dx.doi.org/10.1554/04-668.1.s1). Mathematically, this means that

$$P(\text{female obtains } k \text{ matings}) \equiv p_k = \frac{\hat{n}^k e^{-\hat{n}}}{k!}, \qquad (1)$$

where $k = 0, 1, 2, \ldots$. From the distribution for p_k, we then need to calculate the probability that a mutant male will mate with a female that has a total of k mates. This probability (which we denote by q_k) is nothing more than the probability that a mutant ejaculate ends up in a female that has mated $k - 1$ other times, and therefore we have

$$q_k = p_{k-1}, \qquad (2)$$

where now $k = 1, 2, 3 \ldots$, since the female must have received at least one mating (the mutant's).

With these considerations we let

$$v(s, \hat{s}) = \sum_{k=1}^{\infty} q_k f_s(s, \hat{s}, r), \qquad (3)$$

where f_k is a function that describes the proportion of total paternity that the mutant sperm obtains when mating with a female who has mated a total of k times. Here r is a weighting parameter that accounts for the possibility of first (or last) male precedence; it takes on values between zero and one, with $r = 1$ corresponding to a fair raffle with no sperm precedence and values closer to zero indicating greater precedence. Assuming that mating order is random, a mutant ejaculate in a female that has mated k times has a $1/k$ chance of being the first mating and $(k - 1)/k$ chance of not being first. Assuming further that a mutant's probability of fertilization is simply its proportion of the total sperm received by a female (i.e., sperm competition obeys a raffle principle) and that all sperm received from donors other than the first male are discounted by the factor r (first male sperm precedence), we can write the following form for v:

$$v(s, \hat{s}) = \sum_{k=1}^{\infty} q_k \left\{ \left(\frac{1}{k}\right) \frac{s}{s + (k - 1)r\hat{s}} \right. \\ \left. + \left(\frac{k - 1}{k}\right) \frac{rs}{rs + [(k - 2)r + 1]\hat{s}} \right\}. \qquad (4)$$

An identical expression is arrived at if we assume last, rather than first, male precedence.

Method of Analysis

The evolutionarily stable strategy (ESS) level of per mating sperm allocation is defined to be a value of s (denoted by s^*) such that, if all males in the population are using this strategy, no mutant strategy can have a higher fitness. Math-

ematically, this requires that $W(s, s^*) \leq W(s^*, s^*)$ for any mutant allocation strategy, s. Local conditions that an ESS must satisfy are therefore given by the first and second derivative of the fitness expression with respect to s (evaluated at s^*):

$$\left.\frac{\partial W}{\partial s}\right|_{\substack{s=s^* \\ \hat{s}=s^*}} = 0, \quad \text{and} \tag{5}$$

$$\left.\frac{\partial^2 W}{\partial s^2}\right|_{\substack{s=s^* \\ \hat{s}=s^*}} < 0. \tag{6}$$

Conditions (5) and (6) are usually supplemented by an additional condition (referred to as the convergence stability condition) to guarantee that the population evolves toward the ESS provided that it starts out close enough. This condition is

$$\left.\frac{\partial}{\partial \hat{s}}\left(\left.\frac{\partial W}{\partial s}\right|_{s=\hat{s}}\right)\right|_{\hat{s}=s^*} < 0 \tag{7}$$

(Bulmer 1994). With the above choices of n and v, both the ESS and the convergence stability conditions are satisfied (Appendix 2; see appendices available online at http://dx.doi.org/10.1554/04-668.1.s1).

RESULTS

We begin this section with a simple example that highlights the differences between the results derived here and those of previous work. Assuming no sperm precedence (so that $r = 1$) expression (A2-1; see Appendix 2, available online) can be rearranged to give

$$s^* = c(\tilde{N} - 1) \tag{8}$$

for the ESS sperm allocation, where $\tilde{N} = 1/E(1/k)$ is the harmonic mean number of competing ejaculates in a female. Similarly, Parker et al. (1996) derived the analogous expression

$$s^* = c(N - 1) \tag{9}$$

where N represents the overall number of competing ejaculates (which was implicitly assumed to be the same for all females). One obvious and relatively minor difference between these two expressions is that ESS sperm allocation is a function of the harmonic mean number of competing ejaculates in (8). More importantly, however, the mean number of competing ejaculates in (9), N, is treated as an independent parameter, so that (9) explicitly defines the ESS sperm allocation. Moreover, equation (9) reveals the classical prediction mentioned in the introduction that a greater degree of sperm competition (i.e., a large N in this case) results in a larger sperm allocation at each mating attempt. In contrast, the harmonic mean number of competing males, $\tilde{N}$, in equation (8) is itself a function of the ESS sperm allocation strategy, s^*, because it is a function of $n(s^*)$. Equation (8) thus defines the ESS sperm allocation implicitly, and therefore it is no longer possible to view the number of competing males (and thus the degree of sperm competition) as a factor that governs the evolution of sperm allocation. This highlights
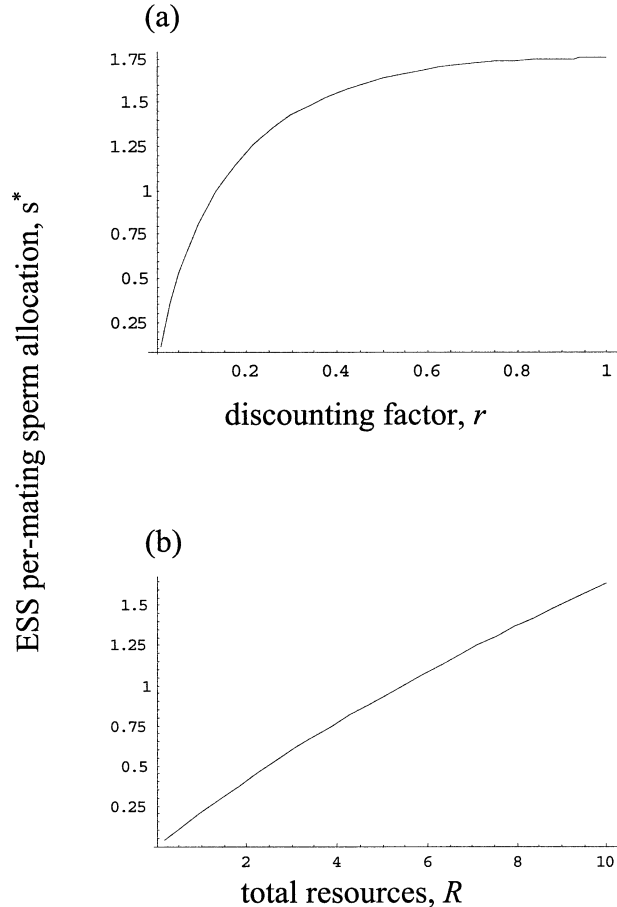

FIG. 1. The evolutionarily stable strategy (ESS) level of sperm allocation, s^*, as a function of (a) sperm precedence, r (with $c = 1$, $R = 10$); and (b) total resources, R (with $c = 1$, $r = 0.5$).

the difference in perspective taken here from that of previous theory.

Predictions for the Evolutionarily Stable Allocation Strategy under Various Conditions

The effect of sperm precedence, r

In Appendix 2 (available online) we show that per mating ESS sperm allocation is predicted to increase with increasing fairness, as was also found by Parker (1990a). In a fair raffle ($r = 1$), the more a male invests in sperm, the greater the chance that his sperm will be used for fertilization. However, as sperm precedence rises (i.e., as r decreases) the payoff to investing in sperm at any given mating decreases. Thus, the best strategy for a male, with no information about mating order, is to produce a larger number of smaller ejaculates (Fig. 1a, Table 1).

The effect of total resources, R

Again by Appendix 2 (available online) we find that, in contrast to Parker's (1990a, 1996) results, where ESS sperm allocation was unaffected by changes in R, here the ESS is predicted to increase with an increase in the total resources. In the present model the amount of available resources now

TABLE 1. Predicted effects of increases in different parameters on the evolutionarily stable strategy (ESS) level of per mating sperm allocation, s^*, and expected across-populations correlation between ESS sperm allocation and sperm competition risk/intensity. The first column gives the predicted direction of change in the ESS level of sperm allocation given an increase in the indicated parameter; classical predictions (left) are presented along with those of the present work (right). Predicted increases are denoted by a plus symbol and decreases by a minus. An asterisk indicates that a result is contingent on the degree of sperm precedence. The second and third columns give the predicted correlation between ESS sperm allocation and sperm competition risk and intensity, respectively. The plus symbols recapitulate the classical prediction of a positive across-populations correlation between sperm allocation and competition risk or sperm allocation and competition intensity. These predictions are upheld under the theory presented here when comparisons are made across populations differing in total resources, R, but can be reversed when comparing across populations differing in mating costs, c (see Discussion for details).

| | Expected effect on ESS sperm allocation, s^* | | Expected correlation between ESS sperm allocation, s^*, and | | | |
| | | | Sperm competition risk | | Sperm competition intensity | |
Parameter	Classical	New	Classical	New	Classical	New
r	+	+	NA	NA	NA	NA
R	no effect	+	+	+	+	+
c	+	+ or − (*)	+	+ or − (*)	+	+ or − (*)

not only affects the number of matings a male achieves, but also the value of each mating through feedback between s^* and the probability of sperm competition. All else being equal, greater resource levels lead to a larger number of ejaculates, which in turn results in heightened sperm competition. This, in turn, leads to the evolution of a greater male investment per ejaculate (Fig. 1b, Table 1).

It must be stressed, however, that this prediction applies to comparisons between populations that have evolved in response to different resource levels. It does not, for example, apply to facultative alterations that individuals make in response to changes in resource levels. Under the present hypothesis an increase in resource abundance would first lead to a facultative increase in the number of matings (and thus a higher average level of sperm competition in the population) with the sperm allocation at each mating remaining unchanged. If this resource increase were maintained over successive generations, then the heightened level of sperm competition would lead to evolutionary changes in sperm allocation. It is this latter evolutionary response that is the focus of the theory presented here.

The effect of the cost of mating, c

Previously it has been shown that, when the probability of experiencing sperm competition is fixed, an increase in the cost of mating leads to the evolution of greater per mating sperm allocation (Parker 1990a, 1996). In the present model, the ESS sperm allocation, s^*, increases with an increased mating cost when sperm competition is fair (or nearly so), but it decreases with an increased mating cost when there is strong first (or last) male precedence (Appendix 3 available online at http://dx.doi.org/10.1554/04-668.1.s1; Fig. 2, Table 1). As in previous models, an increase in the mating cost produces a force favoring greater sperm investment in each ejaculate. Because of the coupling between the degree of sperm competition and sperm allocation, however, this enhanced mating cost also leads to a decrease in the total number of ejaculates in the population, and thus to lower sperm competition. Whether sperm allocation increases or decreases therefore depends on the relative magnitude of these two

effects, and the latter effect tends to be large when sperm precedence is high.

DISCUSSION

The theory presented here takes a fundamentally different perspective on the relationship between the degree of sperm competition and sperm allocation than has been taken in Parker's classic works (1990a, 1996). Aside from being conceptually distinct, this has resulted in a number of important differences in predictions as well. In contrast to previous models of sperm competition, the present results show that resource availability can influence the ESS sperm-allocation strategy of males. Specifically, greater resource availability is predicted to lead to the evolution of greater per mating sperm expenditure. This difference arises because resource availability influences both the number of matings a male obtains and the paternity that this male can expect at each mating.

It should be noted that this result comes with two important caveats. First, it applies primarily to mating systems in which a male's reproductive effort is allocated solely between obtaining mates and guaranteeing paternity. When other mating behaviors, such as paternal care or mate guarding, are possible, changes in resource levels might lead to the evolution of these behaviors while leaving sperm allocation strategies unaltered. Second, our analysis assumes that mating costs do not depend on resource levels. However, competition for mates may often become more intense as resource constraints are relaxed (T. Tregenza, pers. comm.). When this is the case, results will largely depend on the functional relationship between mating costs and resource levels. These caveats apply to most previous theory as well, though, because these factors have been largely ignored in the theoretical literature on sperm competition.

Our results also show that when sperm precedence is high, males are expected to decrease, rather than increase, the amount of sperm they invest in each ejaculate as the cost of mating rises. Here, the benefits associated with obtaining additional matings outweigh the benefits of ensuring a larger share of paternity in the matings already obtained. Impor-
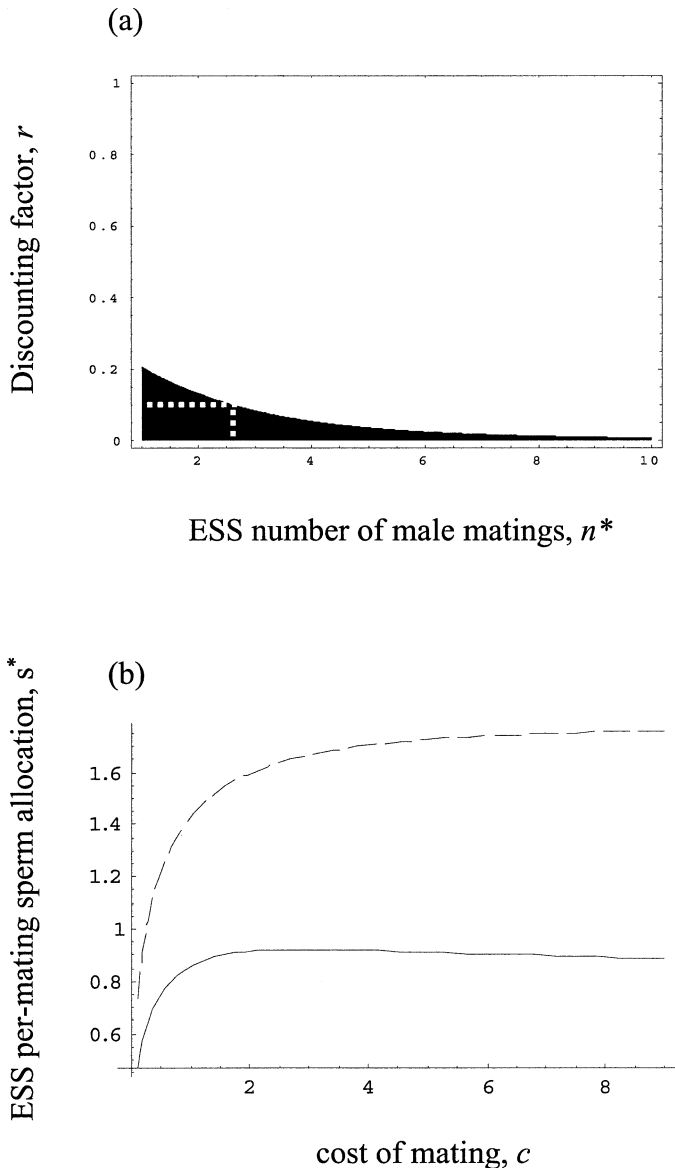
(a)

ESS number of male matings, n^*

(b)

cost of mating, c

FIG. 2. (a) Density plot giving direction of change in evolutionarily stable strategy (ESS) per mating sperm allocation, s^*, given an increase in cost per mating, c, as a function of sperm precedence, r, and the ESS expected number of matings, n^*. The dark area indicates parameter combinations for which a decrease in the ESS is predicted, while light areas give parameter combinations for which increases are expected. For example, when sperm discounting is 90% (i.e., $r = 0.1$), ESS sperm allocation is predicted to decrease whenever the number of male matings, n^* is less than approximately 2.6 (dotted white lines). (b) The ESS level of per mating sperm allocation, s^*, as a function of the cost of mating, c. Dashed curve is for the case when sperm precedence is 70% (i.e., $r = 0.3$), and the solid curve is 90% (i.e., $r = 0.1$). Total resources for both examples was set at $R = 10$. When sperm precedence is 70%, the ESS is always an increasing function of the per mating cost, as predicted in part (a). The decrease in the solid curve starting when mating cost is between 2 and 4 and the ESS sperm allocation is approximately 0.9 corresponds to the point at which the ESS number of male matings drops below the threshold value of approximately 2.6.

tantly, it is the coupling between a population's population-wide sperm allocation strategy and the probability of sperm competition that is the critical determinant of these differences.

The relationship between sperm allocation and the degree of sperm competition

Earlier models (Parker 1990a, 1996) have typically quantified the degree of sperm competition by first distinguishing between the risk of sperm competition and the intensity of sperm competition. Risk refers to the probability of a male experiencing sperm competition at any given mating event, whereas intensity refers to the number of competing males at any given mating event. This dichotomy is no longer tenable within the perspective taken here. As an illustration, consider a population in which the mean number of matings per female is one, so that, on average, males experience little sperm competition. However, because matings are distributed randomly across all females, equation (1) implies that a given ejaculate can expect to experience no competition with probability $(1/e) \approx 0.37$, competition from one other ejaculate with probability $(1/e) \approx 0.37$, two other ejaculates with probability $(1/2e) \approx 0.18$, and so on. In general, risk and intensity cannot be decoupled because variance in the distribution of risk across females necessarily alters intensity as well.

An influential prediction of earlier works is that per mating sperm allocation should increase with both intensity (Parker et al. 1996) and risk (Parker 1990a) in across-population comparisons. As already mentioned, these previous efforts have treated risk and intensity as parameters, and thus these results have implied that risk or intensity drives the evolution of different levels of sperm allocation. In contrast, our results imply that sperm competition risk and intensity will typically be coupled through their dependence on a population's sperm-allocation strategy. We can therefore make predictions about how we expect some measure of sperm competition risk (or intensity) and sperm allocation to covary across populations, as a result of differences among the populations in some environmental parameter of interest. For example, if the cost of mating varies across populations, then we expect different sperm-allocation strategies to evolve in different populations, and consequently different levels of risk or intensity as well.

To explore this issue more fully, we note that, since e^{-n^*} is the probability that a focal ejaculate experiences no sperm competition, $\rho = (1 - e^{-n^*})$ gives the probability of experiencing competition. Consequently, ρ is analogous to Parker's risk parameter, p (Parker 1990a), while n^* plays the role of N, the number competing ejaculates, in Parker et al.'s (1996) treatment of sperm competition intensity. In Appendix 2 (see eq. A2-11; available online) we show that the ESS number of male matings, n^*, increases with total resources, R, and decreases with the per mating cost, c. Therefore, increasing total resources increases s^* (see the previous section) as well as ρ and n^*. As a result, the ESS per mating sperm allocation covaries positively with our analogs of risk and intensity, in agreement with the predictions of Parker (1990a) and Parker et al. (1996) (Fig. 3, Table 1). In contrast, although increasing per mating costs results in decreases in
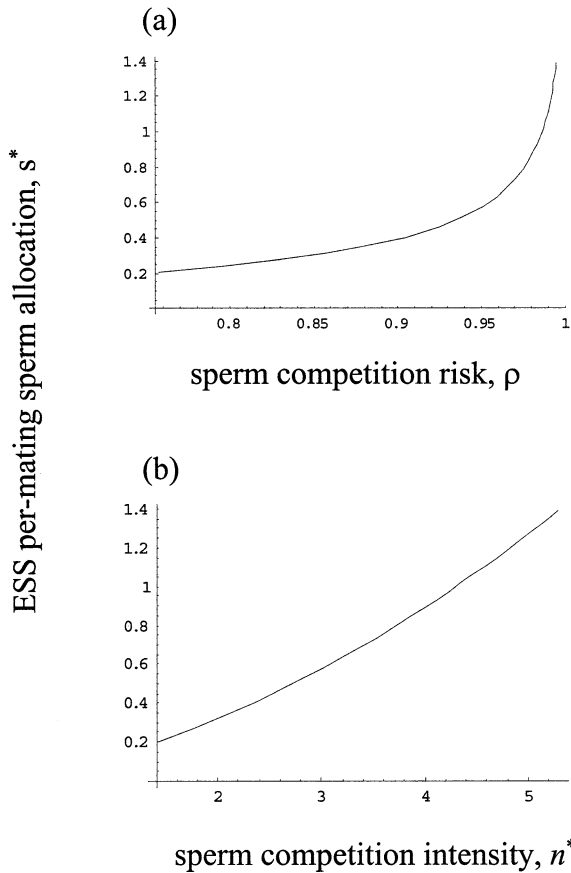
(a)

(b)

FIG. 3. Relationship between the evolutionarily stable strategy (ESS) level of per mating sperm allocation, s^*, and (a) risk of sperm competition, ρ, or (b) sperm competition intensity, n^*, as a function of total resources, R. Risk and intensity both increase with total resources, as does the ESS, so a positive covariance is measured in both cases. Parameter values used in both plots were $r = 0.5$, $c = 0.5$, $1 \leq R \leq 10$.

both ρ and n^* (eq. A2-11; see Appendix 2, available online), it can cause s^* to increase (at least when sperm precedence is not too great; see Fig. 2a). This results in the opposite pattern, in which high sperm competition risk (or intensity) is associated with low per mating sperm allocation. Only when sperm precedence is quite high is it possible to recover the classical predictions (Fig. 4, Table 1).

These findings illustrate the important point that all environmental alterations that increase the probability of experiencing sperm competition need not have equivalent effects on the ESS per mating level of sperm allocation. Additionally, it is crucial to keep in mind that these relationships arise through the mutual dependence of allocation and risk (or intensity) on some underlying parameter, rather than risk (or intensity) being the cause of evolutionary change in sperm allocation. There can be a correlation between allocation and risk (or intensity), but it is not a causal relationship.

One final point to note here is that, while the details of the above discussion do depend on our initial assumption of randomly distributed matings among all females, our results are likely to remain valid for a much broader class of mating systems. This follows from the fact that there will often be
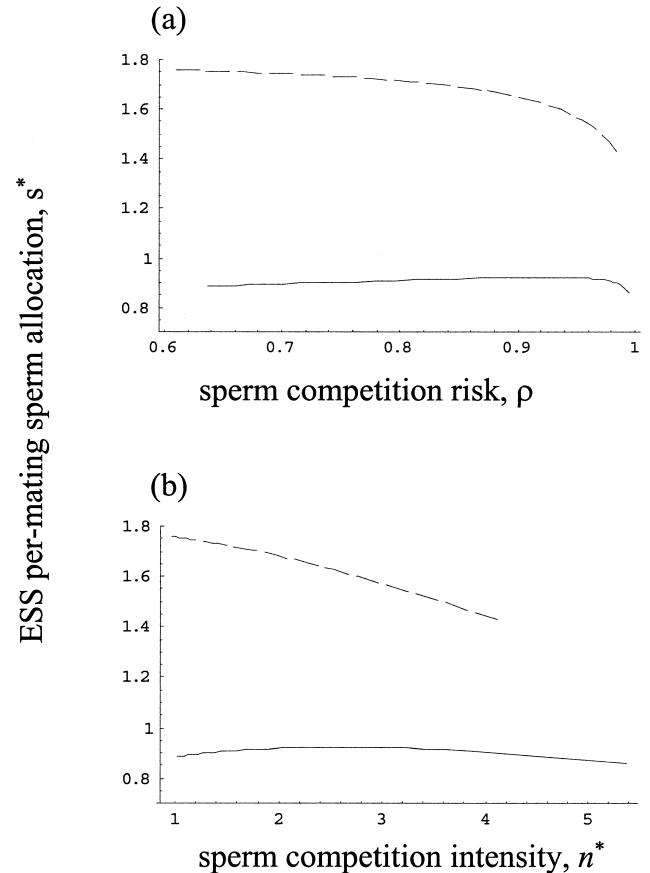
(a)

(b)

FIG. 4. Relationship between the evolutionarily stable strategy (ESS) level of per mating sperm allocation, s^*, and (a) risk of sperm competition, ρ, or (b) sperm competition intensity, n^*, as a function of per mating cost, c. For both plots, dashed lines are for $r = 0.3$, solid lines for $r = 0.1$. When sperm precedence is not too severe (i.e., $r = 0.3$), ESS sperm allocation covaries negatively with measures of risk and intensity, in contrast with classical predictions. Only when sperm precedence is quite high (i.e., $r = 0.1$) is it possible to recover standard results, but this is only possible when the per mating cost is high relative to total resources (corresponding to the region near the plot origins; see Appendix 3 for details). Parameter values used for both plots were $R = 10$, $1 \leq c \leq 9$.

a stochastic component to the number of competing ejaculates faced by a focal ejaculate. While such effects should be particularly evident in species where multiple mating is common, our conclusions can still be applied to situations in which highly structured mating systems constrain stochasticity. For example, if most females of a population typically mate only once, with remaining matings being distributed randomly among some subset of females, then small increases in sperm allocation (e.g., in response to increased resources) will alter sperm competition intensity (by reducing the number of excess matings to be distributed), but not risk. Nevertheless, further increases in sperm allocation will continue to reduce the number of excess matings to the point where all females are mated only once, which corresponds to a decrease in sperm competition risk. Relaxation of the random distribution of matings assumption can thus affect the quantitative degree to which our results apply to a given mating

system without undermining their general qualitative predictions.

Empirical tests of the theory

The classical prediction of a positive relationship between risk (or intensity) of sperm competition and sperm allocation has received considerable empirical attention (reviewed in Møller and Briskie 1995). Much supporting evidence has come from across-population comparative studies that find a positive correlation between testes size (a measure of sperm investment) and the degree of multiple mating (a measure of the likelihood or degree of sperm competition). Nevertheless, several studies have reported results that do not conform to these expectations, and a host of hypotheses have been proposed to account for their apparent failure (Pitnick and Markow 1994; Møller and Briskie 1995; Schülke et al. 2004). Importantly, a corollary of our results is that environmental changes that alter mating system must also directly influence sperm allocation, and so challenges the causal role of mating system in sperm-allocation evolution. We suggest that a careful reexamination of some of these seemingly enigmatic empirical results might be profitable when testing both the validity and generality of the model presented here.

Comparative studies of natural populations that differ in some ecological parameter of interest could also be used to test our predictions. Predation pressure on the Trinidadian guppy, *Poecilia reticulata*, varies geographically (Endler 1978, 1995), a situation that has been exploited in studies of sperm competition (Evans and Magurran 1999; Kelly et al. 1999). These previous investigations found that predation regime may play an important role in shaping across-population differences in courtship displays, sperm reserves (Evans and Magurran 1999), and the frequency of multiple-paternity broods (Kelly et al. 1999). Schooling behavior has also been found to covary with predation risk, with high-risk populations exhibiting greater tendencies to school than low-risk ones (Seghers 1974; Magurran et al. 1992). As a consequence, mate-searching time may be reduced in high-risk populations, suggesting that this system might also prove useful for studying sperm-allocation evolution when the cost of mating is altered. However, this approach is not free of difficulties. High- and low-predation sites also differ in a number of other, possibly confounding, characteristics, the most relevant of which is resource levels. High-predation sites typically have greater abundances of benthic flora and microfauna (Endler 1995), so that teasing apart the contributions of elevated mating costs and altered resource levels to the evolution of sperm allocation becomes problematic. Despite this caveat, some useful insights might be gained by adopting the comparative approach.

A final possibility is to directly manipulate environmental parameters of interest by performing experimental evolution studies. A few such studies have previously been attempted using laboratory populations of the fruit fly *Drosophila melanogaster* (Pitnick et al. 2001), and the yellow dung fly *Scathophaga stercoraria* (Hosken and Ward 2001). However, in both of these experiments treatment groups were polyandrous (vs. monogamous), so that the manipulated parameter was in fact sperm competition, independent of existing levels of sperm allocation. Although this manipulation conforms to the conceptual foundations of previous theory, in natural populations the level of polyandry might well co-evolve with sperm allocation as is assumed in the theoretical approach presented here. If so, then this type of experiment might yield little insight into the evolution of sperm allocation in natural populations. Testing the predictions put forward here would require the manipulation of other factors (e.g., resource availability, cost of mating) that are expected to cause evolutionary changes in both sperm allocation and the degree of sperm competition.

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