

A state-based model of sperm allocation in a group-breeding salamander

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We developed a dynamic program of optimal sperm allocation for group-breeding species. Using the small-mouthed salamander, *Ambystoma texanum*, as a model organism, we considered how spermatophore deposition is affected by sperm reserves, male and female number in breeding aggregations, and time during the breeding season. Parameters for part of the model were based on field data of breeding-pond arrival times for both sexes and on laboratory spermatophore deposition data. Our model included simulations of three different seasonal patterns of female arrival rate: decreasing (as in *A. texanum*), increasing, and uniform. General predictions are (1) Increased male competitor numbers at breeding aggregations should cause a reduction in spermatophore allocation. (2) Increased female numbers at breeding aggregations should increase spermatophore allocation. (3) The effect of current sperm reserve levels on sperm allocation depends on the seasonal distribution of the mean number of females per male during the breeding season: (3a) If relative female availability decreases over time, males with low sperm reserves should limit allocation early in the season but should deposit maximal sperm loads late in the season; (3b) if female availability increases over time, males with low sperm loads should limit allocation throughout the entire breeding season; and (3c) if female availability is constant, sperm reserves are predicted to have little effect on spermatophore allocation tactics. We discuss model predictions in the context of current sperm allocation theory. *Key words:* *Ambystoma texanum*, dynamic programming, ejaculate evolution, group breeders, mate competition, mating system, salamanders, sexual selection, sperm allocation, sperm competition. [*Behav Ecol* 13:705–712 (2002)]

Sperm competition occurs when gametes from more than one male compete to fertilize a female's ova (Parker, 1970). The form and intensity of sperm competition may depend on factors such as characteristics of the female reproductive tract and sperm-storage organ anatomy, male sperm density or total ejaculate volume, and the propensity for multiple mating by both males and females (Birkhead and Parker, 1997; Parker, 1990a,b, 1998). Consequently, a variety of morphological, physiological, and behavioral adaptations have evolved in both sexes (Birkhead and Møller, 1992, 1998; Birkhead and Parker, 1997; Parker, 1984; Smith, 1984).

Although sperm are generally small compared to ova, ejaculates in some species may contain so many sperm (or accessory materials) that male reproductive success is limited by their production (Dewsbury, 1982). Empirical studies in a variety of taxa suggest that males do become sperm depleted (e.g., fish: Nakatsuru and Kramer, 1982; Warner, 1997; insects: Gage and Cook, 1994; amphibians: Arnold, 1976; Smith-Gill and Berven, 1980; Verrell, 1986; mammals: Dewsbury, 1981). Also, sperm expenditure may be costly because the energetic expenditure of producing sperm may limit the energy spent searching for mates (Birkhead and Parker, 1997; Parker, 1982). Due to these constraints, males may be expected to economize when allocating sperm to ejaculates (Parker, 1998).

Two recent game theory models have been proposed that focus on sperm allocation strategies: Risk models apply to species in which sperm competition is rare and in which males risk the chance that they compete with another single male for reproductive access to ova (Parker et al., 1997); intensity models apply to species in which sperm competition is com-

mon, but numbers (intensity) of competitors vary among breeding opportunities (Parker et al., 1996). Under the assumptions of the risk model (i.e., rare sperm competition), males are predicted to produce larger ejaculates as the risk of sperm competition increases. In addition, if sperm competition between two males does occur and one male has a lower expected reproductive payoff than the other (e.g., because of sperm precedence), the disadvantaged male is predicted to allocate relatively more sperm per ejaculate than the male with the higher expected payoff (Parker et al., 1997).

The intensity model of sperm competition (Parker, 1998; Parker et al., 1996) yields different predictions than the risk model. Males are predicted to ejaculate a small amount of sperm when there are no competitors (i.e., just enough to fertilize ova), a relatively large amount of sperm when there is one competitor, and a monotonically decreasing amount of sperm as the number of competitors increases. The reason for this result is that, as the number of competitors increases, the reproductive payoff expected from each unit of sperm because since there are more males competing for the ova (i.e., as occurs as the number of players increases in a lottery). The predictions assume that males can assess the number of competitors and that paternity for a given male is proportional to the sperm he allocates relative to the total amount of sperm competing for access to ova.

Neither the risk nor intensity game theory models consider all potentially important components of the fitness consequences of sperm utilization. For example, the optimal allocation of sperm may depend on the specific sequence of mating opportunities experienced by the male in species where males mate multiply and sperm supply is limited (Galvani and Johnstone, 1998). The optimal sperm allocation decision at each mating may also depend on several factors other than competition intensity, such as female quality or future mate availability (e.g., Gage, 1998; Gage and Barnard, 1996; Shapiro et al., 1994; Weddell, 1992). For example, larger sperm expenditures may be predicted if environmental conditions correlate with a reduction in future female availability or if risk of sperm competition is higher for more reproductively

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valuable females (e.g., Gage, 1998; Gage and Barnard, 1996; Shapiro et al., 1994). These additional factors generate conditions where the payoff to sperm allocation changes dynamically with the reproductive state (e.g., sperm reserves) of the male and with time. These issues are addressed best using dynamic optimization (Mangel and Clark, 1988).

Galvani and Johnstone (1998) used dynamic programming to model sperm allocation based on female quality and probability of obtaining future mates. They explicitly modeled a finite, depleting supply of sperm for males encountering sequential mating opportunities. The situation they modeled is analogous to the sperm competition risk models of Parker et al. (1997), while incorporating sperm depletion and mate choice. An important assumption of the Galvani and Johnstone (1998) model was that female availability and the level of sperm competition does not vary over time. Their model predicted that males should allocate fewer sperm when future mating opportunities are uncertain. Also, they found that sperm allocation should interact with female quality and female mate choice. That is, males were predicted to allocate fewer sperm to high-quality females due to a risk of future sperm competition or sperm rejection. We extend these previous models and focus our model on sperm allocation in a group breeder.

Here we present a dynamic optimization model of sperm allocation for *Ambystoma texanum*, the small-mouthed salamander, that incorporates the effects of sperm depletion as well as variation in the mean number of females per male through time (i.e., operational sex ratio [OSR]; after Emlen and Oring, 1977). Pond-breeding urodeles, such as *A. texanum*, exhibit postnuptial gametogenesis, such that males begin a breeding season with a full complement of sperm and do not replenish their supply until after the breeding season ends (Plummer, 1977; Verrell et al., 1986). This property makes the economics of sperm allocation critical to male reproductive success in this species. Our model differs from that of Galvani and Johnstone (1998) in that it is constructed for group breeders (and thus is analogous to sperm competition intensity models; Parker et al., 1996) and incorporates competition intensity and different distributions of the OSR during the breeding season. Seasonal variation in mate availability is apparent in *A. texanum* (see below) and may be characteristic of many species.

Our model explicitly considers sperm supply at each mating opportunity when predicting the optimal sperm allocation decision. This approach is different from that of Parker (1998). In Parker's model, energy allocated to sperm is traded off against energy spent searching for mates. Thus, total sperm allocated to ejaculates (which determines paternity in the context of sperm competition) is traded off against the number of mates a male can obtain. An advantage of our approach (and that of Galvani and Johnstone, 1998) is that we can examine the time-dependent effect that variation in sperm supply may have on sperm allocation (as a result of variation in body size or condition among males for example). Below we first present field data and laboratory experiments that provide an empirical basis for several components of the model. We then develop the model and describe predictions derived from it.

Methods

Study organism

Most ambystomatid salamanders, such as *A. texanum*, exhibit a short, intense breeding season in early spring (Krenz and Sever, 1995; Petranka, 1998). *A. texanum* at our observation pond bred in temporally and spatially discrete aggregations

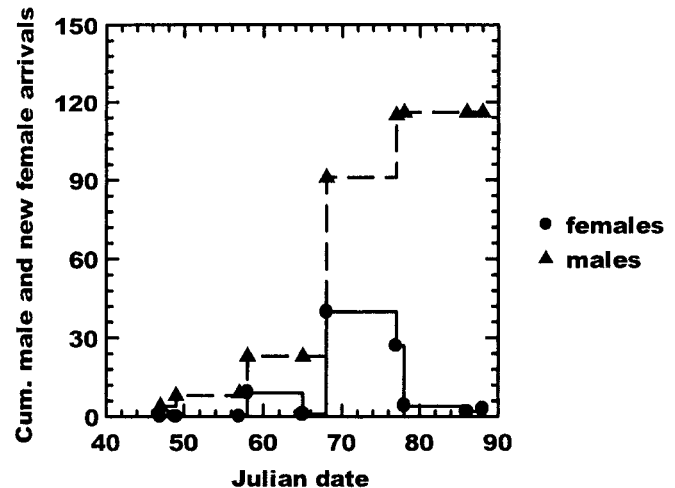


Figure 1

Male and female *A. texanum* arrival times to the breeding pond in 1998. Male arrivals (circles and dashed line) are cumulative; female arrivals (triangles and solid line) refer only to new females. These values were used to estimate temporal variation in the operational sex ratio for *A. texanum*. The pattern of female availability per male decreases through time as the cumulative number of males arriving at the breeding pond increases.

(~1 m or less in diameter) in vernal ponds that contained multiple males and at least one female. The bulk of the breeding season lasts about 30 days (Figure 1; Harris and Lucas, personal observations). Based on laboratory observations, the number of spermatophores each male deposits in an aggregation is variable (mean = 45.6, SD = 15.7, range = 22–85; $n = 18$ males), and males may participate in multiple aggregations during a breeding season. These results are similar to *A. texanum* spermatophore depositions observed by McWilliams (1992) in similar experiments (mean = 73.8, SD = 31.4, range = 23–128; $n = 21$ males). In our model we assume spermatophore deposition rates intermediate to these values (i.e., 60 spermatophores per male per breeding aggregation). Aggregations last for approximately 2 h with spermatophores deposited during a shorter period of 0.5–1.5 h (McWilliams, 1992). *A. texanum* exhibit little courtship behavior compared to other salamanders (e.g., Arnold, 1976). Instead, males deposit spermatophores on the substrate and females pick up these spermatophores with their cloaca later. Thus, females mediate male–male competition through the uptake of spermatophores.

Dynamic program

We modeled spermatophore allocation decisions in *A. texanum* using a state-based dynamic program (Galvani and Johnstone, 1998; Mangel and Clark, 1988), with state defined as the number of spermatophores a male has available at any time during the breeding season. We assume that a focal salamander chooses how many spermatophores to deposit and that these decisions maximize reproductive success over the course of a single reproductive season. Reproductive success, in turn, is determined by the number of reproductively active females available to the focal male and by competition with other males for access to the females' eggs. Similar to Galvani and Johnstone (1998), we assume that survival rates are not affected by the decision to enter a breeding aggregation and that there is no fitness carryover from one breeding season to the next. Under these assumptions, maximization of reproductive success over the course of a single season is a realistic measure of fitness.

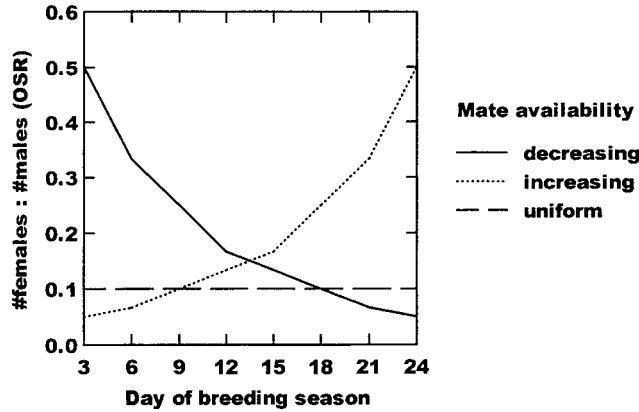


Figure 2

Different distributions of mean females per male (operational sex ratio) modeled. The solid line indicates decreasing mean females per male during the breeding season and was estimated using field data collected on *A. texanum* (see text for details). The dotted line indicates increasing mean females per male (as may occur in *A. talpoideum*) and is the inverse of the decreasing pattern. The dashed line indicates uniform, low mean females per male throughout the breeding season.

We divided the breeding season into 10 discrete time intervals, each about 3 days in length. We assume that a male may participate in at most a single breeding aggregation in any given time interval. Males enter the breeding season with a finite and non-renewable quantity of spermatophores. The state variable, $X(t)$, denotes the number of spermatophore units a male has remaining to deposit at the beginning of time period t . We assume all spermatophores contain equal amounts of sperm. We assume that males begin the breeding season with a maximum of 250 spermatophores. Because males do not deposit spermatophores in the absence of females (Harris and Lucas, personal observation), we assume that $D(t) = 0$ [where $D(t)$ = the number of spermatophore units deposited during time period t] when no females are present. If females are present, we model males as choosing to deposit between 0 and 100 spermatophores (in increments of 10), with the constraint that the male cannot deposit more spermatophores than he currently has stored at time t :

$$D(t) = \begin{cases} \{0, 10, \dots, 100\} & \text{if } X(t) \geq 100, \\ \{0, \dots, X(t)\} & \text{otherwise.} \end{cases} \quad (1)$$

If males receive an equal payoff for any two alternative spermatophore decisions, we assume that the default decision will be the lower number of the two. Note that the allocation of 100 spermatophores approximates the maximum number of spermatophores that males are observed to deposit in a single breeding aggregation (McWilliams, 1992).

We model breeding aggregation size by assuming that the number of females and males at a given aggregation can be approximated with a truncated Poisson distribution (Pielou, 1969). The mean encounter rates of females and males are denoted by λ_f and λ_m , respectively. Male mean encounter rate was modeled using estimates of the OSR through the breeding season. Three different distributions were modeled: decreasing, increasing, and uniform (Figure 2). The decreasing distribution approximates the pattern of the number of breeding females per male observed in *A. texanum* during the breeding season (Figure 1), and in our model is generated by a reduction throughout the breeding season in male arrival rate at individual breeding aggregations. The increasing distribution simulates the opposite pattern of OSR, a pattern found in species such as *A. talpoideum* (Krenz and Sever, 1995;

Verrel and Krenz, 1998). The uniform distribution approximates a constant, low degree of mate availability (1 female per 10 males) such as may occur in species with longer breeding seasons. Because aggregations likely form around individual sexually receptive females, we assume the average encounter rate of females per time unit is one over the entire breeding season (i.e., $\lambda_f = 1$ for all simulations). The tails of the distributions were truncated when the probability of occurrence of the largest class was $< .0001$. Thus, the maximum number of males modeled was 45 for the decreasing and increasing distributions and 30 for the uniform distribution; the maximum number of females used was 9 for all distributions.

The number of clutches fertilized during the breeding season measures focal male fitness. The increment in this value for time t will be denoted by $W(d, x, f, m, t)$ when d spermatophore units are deposited and spermatophore state $X(t) = x$ in an aggregation consisting of f females and m males. Thus, the number of spermatophore units expended is the decision variable that will be determined at each state, time, and combination of males and females at the current breeding aggregation.

We assume that females take in sperm from spermatophores at random with respect to the male that produced them; as a result, the number of selected spermatophores of a particular male depends only on the proportion of the total spermatophores that he deposits in a breeding aggregation. We also assume that each male competitor deposits 60 spermatophores. The number of spermatophores deposited by the focal male is denoted by d , and $C_m(t)$ is the number deposited by competing males. Thus the total current number of spermatophore units selected by females at time t belonging to the focal male is:

$$W_C(d, x, f, m, t) = f[d/(d + C_m(t))]. \quad (2)$$

Equation 2 is the increment in the focal male's fitness at the present time interval resulting from decision d . The future component of fitness depends, in part, on the decrement in spermatophore level (the state variable) resulting from the current decision and on the availability of mates and abundance of competitors in the next time period. The future portion of fitness is calculated as:

$$\begin{aligned} W_F(d, x, t) &= \sum_{f=0}^{N_f} \sum_{m=0}^{N_m} p_{fm} [W_C(D_{fm}^*(t+1, x + \Delta x), x + \Delta x, f, m, t+1) \\ &\quad + W_F(D_{fm}^*(t+1, x + \Delta x), x + \Delta x, t+1)], \end{aligned} \quad (3)$$

where N_f and N_m are the maximum number of male and female participants at a given aggregation at time $t+1$, respectively; Δx is the change in state resulting from the current decision, and therefore $x + \Delta x$ is the expected state at time $t+1$; $D_{fm}^*(t+1, x + \Delta x)$ represents the optimal spermatophore allocation decision at time $t+1$ (this is a function of the number of males, m , and females, f , and state, $x + \Delta x$, at time $t+1$), and $W_F(D_{fm}^*(t+1, x + \Delta x), x + \Delta x, t+1)$ represents the future reproductive success at time $t+1$. The optimal decision at time t , $D_{fm}^*(t, x)$, can be solved by maximizing the sum of Equations 2 and 3.

Forward simulation

The dynamic program generates a decision matrix that provides information about the optimal decision at each combination of state and time, but it does not provide information about the net results of this decision-making process. For this

Table 1
Sperm allocation predictions arising from dynamic program results

Factor	Temporal pattern of mean OSR (females per male) during the breeding season		
	Decreasing	Increasing	Uniform
Sperm reserve level	Strong effect: early in season males are conservative when sperm reserves are low	Strong effect: throughout the breeding season males are conservative when sperm reserves are low	Weak effect: throughout the breeding season males are slightly conservative when sperm reserves are low and competition intensity is high
Time during the breeding season	Strong effect: early in the breeding season males are much more conservative when sperm reserves are low	Weak effect: early in the season males are slightly more conservative	Weak effect: early in the season males are slightly more conservative
Male competitor number (competition intensity)	Moderate effect: more conservative when more competitors present early in the season, especially at low sperm reserves	Same as decreasing	Same as decreasing
Female number	Strong effect: much less conservative as female number increases	Same as decreasing	Same as decreasing

Predictions are organized by state-decision factors; number of females competed for, number of competing males, sperm reserves, and time during the breeding season. Columns are arranged by the temporal pattern of mean females per male during the breeding season.

we use a forward simulation of the decision matrix (Mangel and Clark, 1988). A forward simulation generates conditional probability distributions for each state variable under consideration in the dynamic program. These may be viewed as predictions about the distribution of decisions or distributions of states resulting from decisions made by a population of salamanders.

To initiate the forward simulation at the beginning of the breeding season, the probability distribution of states must be seeded with initial values across all states. Thus, $P(x, t, f, m)$ is the probability of the focal male having x sperm reserves at time t in an aggregation with f females and m males. For our simulation, we simulated mean male spermatophore complement at two different starting complements of spermatophores: 250 (full) and 125 (half). By varying the starting complement of spermatophores, we attempted to model the effects of variation in spermatophore supply on sperm allocation decisions (see below). For the simulation, males start with either complement of spermatophores at time 0 and the breeding season starts at time 1 (i.e., $f = m = 0$ at time 0):

$$P(x, 0, f, m) = \begin{cases} 1 & \text{if } x = 25 \text{ or } x = 12.5, \quad f = m = 0, \\ 0 & \text{otherwise.} \end{cases} \quad (4)$$

Mating trials

To obtain data on sperm allocation characteristics in *A. texanum*, W.E.H. collected adults during spring breeding migrations in 1998 using a drift fence of aluminum flashing and pitfall traps. The population is located in Tippecanoe County, Indiana, USA, near Purdue University. Field data were used to estimate population sizes and OSR. All animals collected were returned to the lab, measured, weighed, and stored at 4°C until used in breeding trials (usually within 24 h).

Breeding trials were conducted in 40-l aquaria containing about 10 cm of well water chilled to 4°C. Males and females were added to the tanks in one of the following sex ratios 1 F:1 M, 3 F:1 M, and 1 F:3 M. In multi-male trials, male salamanders were marked for individual identification by attaching a small piece of colored flagging to their heads using cyanoacrylic glue. Tags did not appear to affect male behavior and were usually shed with skin within 24 h. Spermatophore

depositions were recorded for each male. In single-male trials, spermatophores were counted after courtship and deposition; in multi-male trials, mating was audiotaped to record observations of mating behavior and spermatophore deposition.

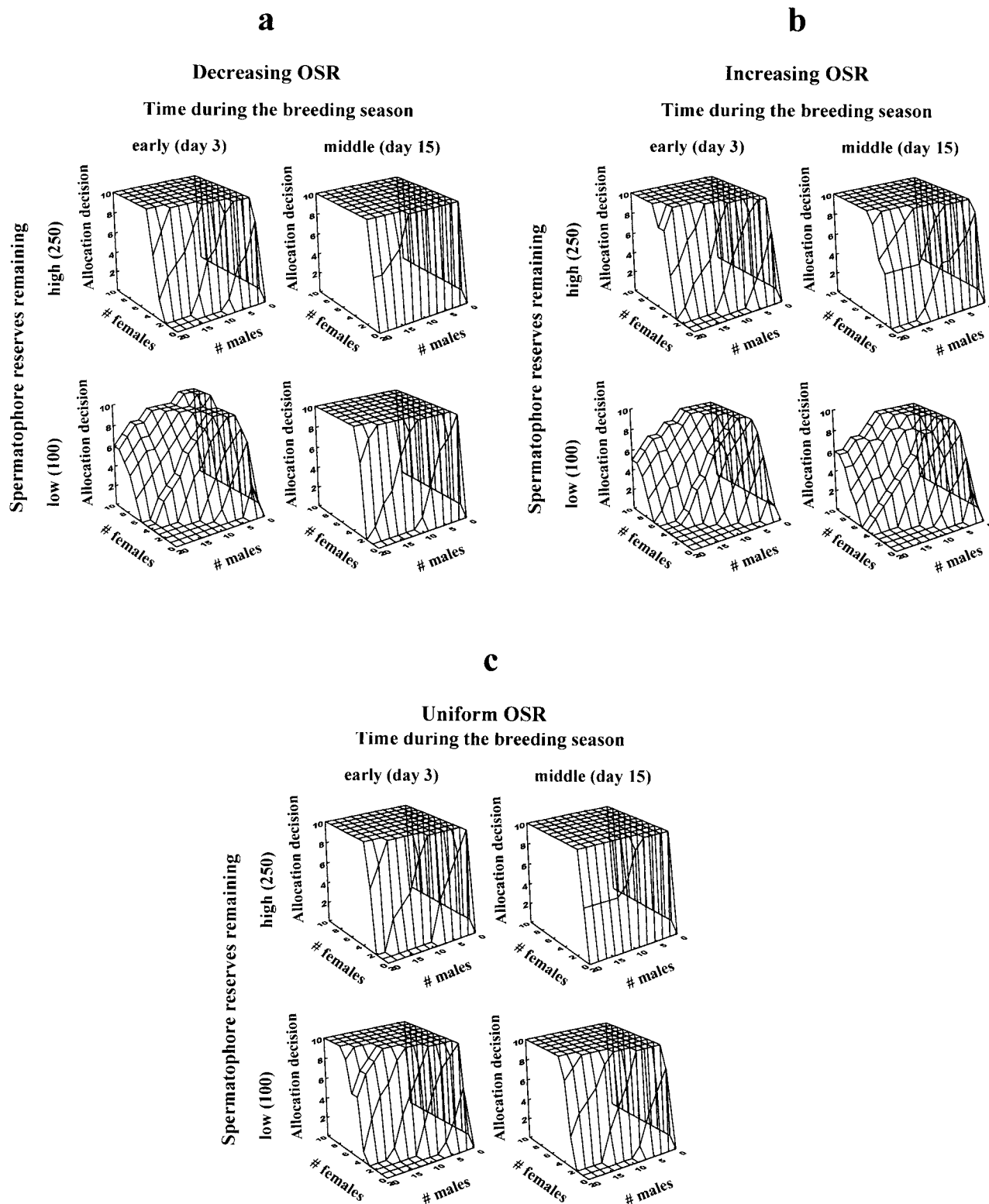
RESULTS

Sperm reserves and seasonal OSR patterns

Dynamic program predictions are summarized in Table 1. Seasonal patterns in the OSR should strongly affect the relationship among sperm reserves, time during the breeding season, and sperm allocation. If the OSR decreases over the course of the season, males are predicted to deposit the maximum number of spermatophores possible if they have high sperm reserves and when many females are present in an aggregation (Figure 3a). As sperm reserve level declines, so too does the number of spermatophores males are predicted to deposit. Near the middle of the breeding season, males are predicted to deposit the maximum number of spermatophores possible (i.e., constrained only by sperm supply or physiological limits), regardless of how many females are present. Similar to predictions of Parker (1998), males should be more conservative with sperm allocation as competition intensity increases. Competition intensity has a moderate influence on male allocation decisions when the OSR decreases through the breeding season.

If the OSR increases during the breeding season, males with low reserves are predicted to limit sperm allocation under conditions of high competition for females (low female number and high male number at a breeding aggregation). In contrast, unless there are very few females, males with high reserves are predicted to deposit a maximal number of spermatophores. Surprisingly, the time during the breeding season has little effect on spermatophore allocation in this case (Figure 3b).

When the OSR is uniform throughout the breeding season, spermatophore reserve level and time during the breeding season have only a weak effect on spermatophore allocation (Figure 3c). Males' allocation decisions are usually constrained physiologically and become conservative with sperm allocation only when the number of females is low and number of competitors is high in an aggregation. Surprisingly,

**Figure 3**

Dynamic program results for the effect of male and female numbers at breeding aggregations on sperm allocation. Allocation decisions are given for 2 different days in the season (early in the season: day 3; at the middle of the season: day 15), and for 2 different levels of sperm reserves (low sperm reserves: 100 spermatophores; high sperm reserves: 250 spermatophores). (a) Decisions for decreasing female availability. (b) Decisions for increasing female availability. (c) Decisions for uniform female availability.

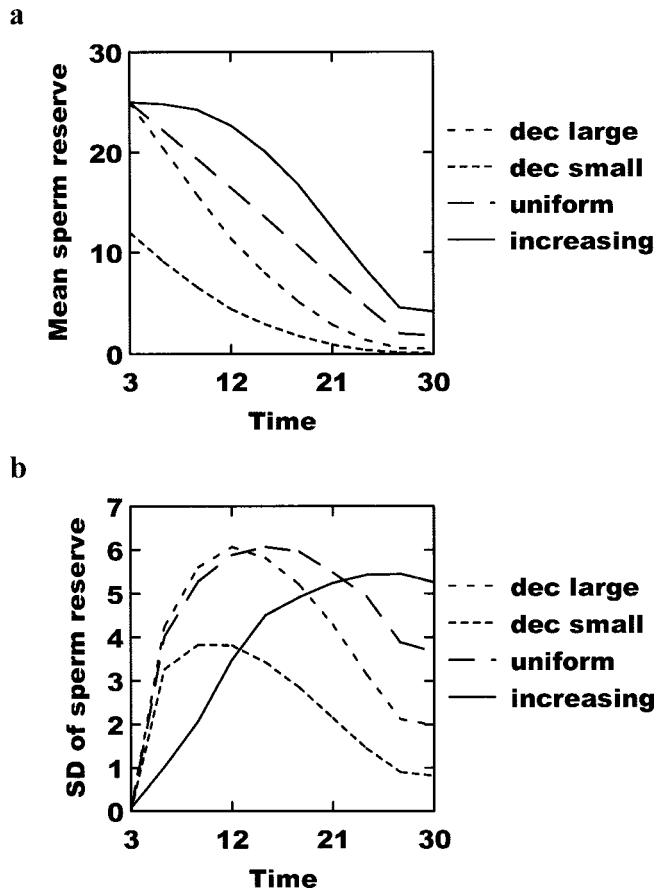


Figure 4

For both panels, “dec large” is the population mean sperm reserve for decreasing OSR with males starting at 250 spermatophores (large males), and “dec small” is decreasing OSR with males starting at 125 spermatophores (small males). “Uniform” and “increasing” are for uniform and increasing OSR, respectively, for males starting the season with 250 spermatophores (large males). (a) Forward simulation results for mean sperm reserves expected day by day during the breeding season as predicted by decisions arising from the dynamic program. (b) Forward simulation results for the SD of mean sperm reserves expected day by day during the breeding season as predicted by decisions arising from the dynamic program.

when mate availability is constant, competition intensity is predicted to have a relatively minor effect on optimal sperm allocation.

Population profiles from forward simulations

Forward simulations predict different temporal patterns of mean sperm-reserve state depending on the temporal pattern of the OSR. Sperm reserves are predicted to decline relatively rapidly during the breeding season for a species with a decreasing OSR (Figure 4a). When males begin the breeding season with few expendable spermatophores (small males compared to large males), their mean sperm reserve state is predicted to be lower at all times than it is for males beginning with more spermatophores. Also, mean sperm reserve state decreases more slowly for small males than for large males. In contrast, sperm reserves are predicted to decline linearly for large males when OSR is uniform and decline relatively slowly for large males when mean OSR increases during the breeding season (Figure 4a).

Temporal patterns of variability in sperm reserve level also

differ depending on the seasonal pattern of female availability during the breeding season (Figure 4b). In general, variance is a unimodal function of time in season. The location of the peak of this function depends on the pattern of the OSR during the breeding season and therefore the opportunity to expend spermatophores; an early peak in sperm reserve variability characterizes environments with decreasing female availability, and a late peak characterizes environments with increasing female availability. The basis of this pattern is straightforward: males that deposit spermatophores early in the season (i.e., with decreasing female availability) will show a more rapid decline in spermatophore reserves compared to males that delay spermatophore deposition. Males that deposit spermatophores earlier will also show an earlier environment-induced increase in variance in spermatophore reserves because spermatophore production is partially dependent on stochastic variation in the number of males and females found in any given breeding aggregation. Males faced with decreasing access to females are predicted to deposit virtually all of their sperm by the end of the season (Figure 4a), causing a concomitant end of season reduction in the population sperm-reserve variance (Figure 4b). With increasing female availability during the breeding season, males are predicted to delay deposition of spermatophores early in the season, causing a shift in the peak population variance in spermatophore reserves to later in the season. The result of this delay in spermatophore deposition is that some males will fail to deposit all of their spermatophore stores by the end of the season because they are unable to find females (whose arrival is assumed to be a Poisson process) before the season ends. Also, when initial male sperm reserve is low (small males), the corresponding variance is small across the breeding season relative to large males (shown for decreasing OSR males; Figure 4b).

Mating trials

For small-mouthed salamanders, the number of spermatophores deposited was correlated with male body weight across all three sex ratio treatments ($R^2 = .35$; $p < .03$; $n = 18$; Figure 5). When treatments were analyzed separately, however, the correlation was only significant in the high competition (1 F:3 M) trials ($R^2 = .74$; $p < .03$; $n = 6$). Assuming that body weight is related to sperm stores (see Discussion), the positive correlation for this trial supports a key prediction of the dynamic program (Table 1): Males with lower sperm reserves should be more conservative in sperm allocation when competition intensity is high. We found no significant effect of sex ratio on average spermatophore production ($F_{2,15} = 1.45$; $p = .27$; ANOVA; Figure 6). However, the power of this test was low ($1 - \beta = 0.25$, for $\alpha = 0.05$; effect size = 15 spermatophores), and more data are required to elucidate the pattern of sperm allocation in response to competition intensity and sex ratio for *A. texanum*.

DISCUSSION

The results from our model suggest that sperm reserves and time during the breeding season, as well as the temporal OSR pattern, should strongly influence decisions for sperm allocation in group breeders. The reason for this is that mate availability affects future reproductive payoffs expected by males and thus should affect allocation of sperm as a limiting commodity. We also show that the relative importance of sperm competition intensity for optimal sperm allocation is sensitive to the particular pattern of mate availability. This result is intuitive, yet most current models assume that mate availability is constant through time and focus on sperm com-

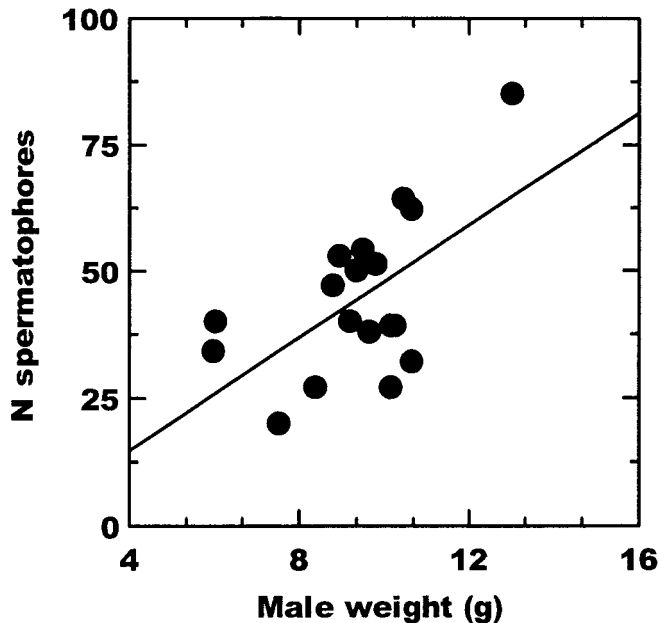


Figure 5
Relationship between male mass and number of spermatophores deposited across breeding trials ($R^2 = .35$; $p < .03$; $n = 18$).

petition intensity as the main factor affecting sperm allocation decisions. These effects will be most important for species in which these factors are likely to interact, such as species containing males that mate multiply during a short breeding season (e.g., pond-breeding salamanders: Verrell, 1989; insects with short adult phases: Engelman, 1970; ground-squirrels: Schwagmeyer and Parker, 1987; red-winged blackbirds: Westneat et al., 1998), although sperm depletion appears to be a common phenomenon in many taxa (Dewsbury, 1982).

In general, males should be more conservative with sperm expenditure early in the breeding season compared to late in the season, especially when the intensity of competition for a given mating is high and expected reproductive payoff is low. The basis for this prediction is the trade-off between current and expected future reproductive success. Early in the season future reproductive success is a large component of fitness, and thus male sperm allocation should be positively correlated with current expected reproductive success. Late in the breeding season future reproductive success is negligible; thus large sperm expenditures on present mating opportunities is predicted. This is similar to predictions of Galvani and Johnstone (1998) for conditions when sperm competition is rare. These results underscore the importance of evaluating time-based solutions to sperm-allocation decisions.

Our model explicitly considers the effect of sperm supply on sperm allocation for individual mating events. Forward simulation results indicate that initial sperm supply has a relatively strong effect on sperm reserve level during the breeding season and consequently will influence predicted sperm allocation decisions. Males with lower sperm reserves are generally predicted to deposit fewer spermatophores in a given set of competitive states. Our breeding trial results support this prediction: We found a positive relationship between male mass and the number of spermatophores deposited across breeding trials (Figure 5). The relationship between male body size and testis size in salamanders has been documented (Verrell et al., 1986); thus it is likely that larger males begin the breeding season with larger sperm stores.

To interpret these results for different species, one must consider the temporal pattern of sperm depletion and mating

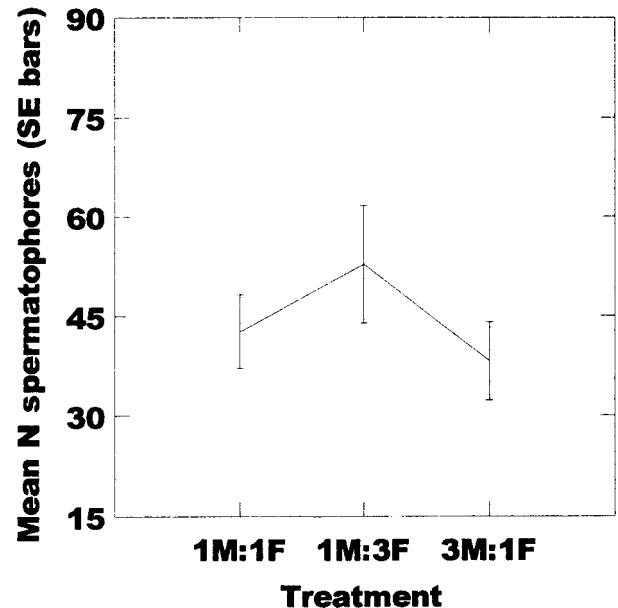


Figure 6
ANOVA results for spermatophore allocation across three sex ratio treatments ($F_{2,15} = 1.45$; $p = .27$).

opportunity in males. That is, multiple mating opportunities (resulting in depletion of immediate sperm reserves) must occur during the period of time required for a male to replenish sperm supplies. In pond-breeding salamanders (such as *A. texanum*) sperm are depleted during a short breeding season and not replenished until after the breeding season has ended (Verrell, 1989). Thus, the relevant time course for sperm depletion is the breeding season itself, during which males mate multiply and no new sperm are produced.

Results presented here provide a framework to construct predictions regarding sperm allocation in group breeders and compliment the models of Parker et al. (1996). Both the dynamic program and the game theory models make similar sperm allocation predictions when female availability is uniform through time: Males should become more conservative with sperm allocation as the number of competitors increases at a given breeding aggregation. In this case, the effects of sperm reserve level and time during the season, which we considered in our dynamic program, are relatively weak. These predictions suggest that both dynamic programming and game theory approaches generate robust and potentially complementary insight into this problem *when mean females per male is temporally uniform*. However, when female availability changes through time, males are predicted to allocate much less sperm when their sperm reserves are low. In contrast, a strong time effect is only evident when female availability decreases during the course of the breeding season. In this case males are predicted to allocate much more sperm per mating later in the breeding season. Empirical studies of sperm allocation are lacking for group breeders (Parker, 1998), and therefore more data are needed to determine the importance of factors such as sperm reserves and mate availability to sperm allocation.

Fundamentally, sperm allocation in group-breeders is a dynamic game. Sperm allocation tactics in such systems have game aspects in that the payoffs to males are likely to be frequency-dependent (as discussed in Parker et al., 1996). Sperm allocation is dynamic because both environmental conditions and sperm supply may change stochastically over the course of the breeding season, and these shifting conditions should

be incorporated into a male's sequential allocation of resources (sensu Alonzo and Warner, 2000; Lucas et al., 1996). Thus, we see both our dynamic programming model and that of Galvani and Johnstone (1998) as necessary steps toward a more complete tool set for asking questions about evolution of sperm allocation strategies.

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