

Delayed Competitive Breeding in Roving Males

HAL WHITEHEAD

Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

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In several species of large mammal, males rove during the mating season, searching for receptive females. In these species, males show considerable sexual dimorphism, and remarkably long delays between sexual maturity and effective competitive breeding. Evolutionarily stable strategies were sought for a model of this breeding system in which large males outcompete smaller males and competitive breeding inhibits growth or survival. The model predicts that roving males should delay competitive breeding until attaining a size at which there are less than a mean of about two to four larger males attending each receptive female. In species in which there are long intervals between the oestrous periods of females, but each can potentially be attended by a number of males, then delayed competitive breeding will be particularly favoured. The conclusions of the model seem consistent with available results on African elephants, sperm whales and polar bears.

Introduction

When males are unable to defend a territory containing the home ranges of one or more females, they often maximize their reproductive success by roving, searching for oestrous females (Clutton-Brock, 1989; Whitehead, 1990). Most of the large mammal species in which males adopt this breeding strategy are characterized by substantial sexual dimorphism. Examples include African elephants, *Loxodonta africana* (males approximately two times the mass of females), sperm whales, *Physeter macrocephalus* ($\delta/\text{f} \approx 3.0$), and polar bears, *Ursus maritimus* ($\delta/\text{f} \approx 2.0$). This strongly suggests size-dependent male competition for mates.

Although these species are generally hard to study, the information available gives a fairly consistent picture of the breeding behaviour of roving males (Barnes, 1982; Ramsay & Stirling, 1986; Poole, 1987; Stirling, 1988; Poole, 1989*b*; Whitehead, 1993). The males generally seem to roam singly, searching for receptive females. When they find a female they may guard her, or sometimes sequester her, trying to prevent access by other males while she is receptive. When more than one male attends a female, they

compete for access by display or fighting, with large males being generally more successful.

In some of these species males appear not to take an effective role in breeding until well beyond the age of sexual maturity in females: both African elephants (Laws *et al.*, 1975; Moss, 1983) and male sperm whales (Lockyer, 1984) are thought to become “sociologically” mature at about age 26 years, even though they are physiologically capable of breeding at about half that age. This is the proximal result of younger males adopting behaviour which excludes them from most breeding opportunities. Younger male elephants do not enter the competitively dominant, but physiologically demanding, “musth” state during the principal mating season (Poole, 1989*a*), and so they do not effectively take part in competitive breeding. Younger male sperm whales remain at high latitudes, away from the breeding grounds which are principally in tropical waters (Best, 1979; Whitehead & Waters, 1990). Although male polar bears become sexually mature at about 6 years of age, Stirling (1988) believes it likely that most mating is probably done by males 8–10 years of age and older. Ramsay & Stirling (1986) found that adult males with adult females were

generally older (median age 10.5 years) than those found alone (median age 8.0 years).

Engaging in mating activity, while potentially increasing the number of offspring fathered, is also likely to have adverse effects for a male: it may increase his mortality and/or retard growth. Then it may be profitable (in terms of the total expected number of surviving offspring) for males to delay breeding, or, if occasional non-competitive breeding opportunities are available, to delay heavy investment in breeding. These delays could occur on the short-term "ecological" time scale, with males not taking part in breeding activities even though physiologically capable of fathering offspring, as seems to be the case with sperm whales and elephants. They could also occur on a longer-term "evolutionary" time scale with selection for later sexual maturity or later development of characters used in competition.

In a competitive environment, the optimal behaviour of a male will depend on that of other males (Maynard-Smith & Brown, 1986). Therefore we might expect evolutionarily stable strategies (ESSs) for maturation which, if adopted by the population, would lead to lowered expected reproductive success for any male using a different strategy.

There have been a number of theoretical studies of the optimal age of first breeding. These have frequently proved successful in predicting maturation ages in real species (e.g. Stearns & Crandall, 1981) but most have principally concerned females and not assumed a size-dependent competitive environment. However, Maynard-Smith & Brown (1986) have modelled the evolutionary consequences of size-based competition for mates or resources using game theory.

In this paper, by means of a model based on the principal features of the mating behaviour of roving males, conditions for EESs are sought which may govern age of first breeding when success in competition for females is size-dependent. The model is applicable for species in which females may be territorial or non-territorial, grouped or solitary. The effects of possible departures from the assumptions of the model are considered and I try to find robust principles governing the deferral of breeding in roving males.

A Model

MALE MATING SUCCESS

The model allows for two states in which males may gain access to breeding females. The first is low cost, and has low expected success which is only

weakly size-dependent. It may correspond the non-musth state in elephants, remaining outside the major female breeding grounds in sperm whales, or sneaking copulations when they are available but not spending a large part of the male's energy budget searching or competing for females. It could consist of refraining from mating entirely. Males in this state will be called non-competitive.

In addition to these opportunities, males may adopt a high cost, competitive breeding strategy. It is also assumed that when a female is ready to mate she is attended by M competitive males, and that M is Poisson distributed with mean m . If $M \geq 1$ she mates with the attending competitive male who has the largest size of some crucial attribute (often, but not necessarily, body size). This could either be a result of female choice or male competition and mate guarding. It is further assumed that the sizes of the competitive males attending a female are randomly and independently chosen from the size distribution of competitive males. Then, when a particular male who is smaller than a proportion p of the breeding population attends a particular female, the number of larger males attending with him is also Poisson distributed with mean $m \cdot p$. The probability that, during an encounter, there are no larger males present is $e^{-m \cdot p}$. If receptive females are encountered at a rate of f per unit time, then the extra (above that of a non-competitive male in the same population) number of females mated per unit time is:

$$s(p) = f \cdot e^{-m \cdot p}. \quad (1)$$

PROPORTION OF LARGER MALES

If all males start breeding competitively at size L , have a competitive breeding mortality of μ , and there are A males in the population (assumed to be stationary with stable age structure) of size L , then the number of competitively breeding males younger than age x (in units past the age of first competitive breeding, i.e. $x = 0$ at length L) is:

$$\int_{x=0}^x A \cdot e^{-x \cdot \mu} \cdot dx = A \cdot (1 - e^{-x \cdot \mu}) / \mu.$$

Then the proportion of larger males for a male of age x is:

$$p(x) = 1 - [A \cdot (1 - e^{-x \cdot \mu}) / \mu] / [A / \mu] = e^{-x \cdot \mu}.$$

SUCCESS WHEN ALL MALES BREED COMPETITIVELY AT SIZE L

From (1) the success rate of a male at age x is:

$$s(x) = f \cdot e^{-m \cdot e^{-x \cdot \mu}}. \quad (2)$$

Then, the expected total breeding success (above that obtained non-competitively, which we assume to be independent of when the male begins to breed competitively) of a male who reaches size L is:

$$R = f \cdot \int_{x=0}^{\infty} e^{-m \cdot e^{-x \cdot \mu}} \cdot e^{-x \cdot \mu} \cdot dx \quad (3)$$

$$= f \cdot (1 - e^{-m}) / (m \cdot \mu). \quad (4)$$

COMPETITIVE SUCCESS WHEN BREEDING AT τ

Let us now consider a male who starts competitive breeding slightly later than the rest, at τ time units past the age at size L . During the time τ he is not competitively breeding when all the other males are, he experiences a lower risk of mortality $c \cdot \mu$ ($c \leq 1$), and a higher growth rate. If the growth rate of a non-competitive male at this size is q , but for competitive males this is reduced to $q(1 - \beta)$ ($0 < \beta < 1$), then at age τ the non-breeding male is of a size equivalent to a normally breeding male of age $q \cdot \tau / [q \cdot (1 - \beta)] = \tau / (1 - \beta)$, and during his competitive years is equivalent in size to a male older by $\tau / (1 - \beta) - \tau = \beta \tau / (1 - \beta)$. Then, modifying eqn (3), the success of this male is:

$$R(\tau, +) = f \cdot e^{-\tau \cdot c \cdot \mu} \int_{x=\tau}^{\infty} e^{-m \cdot e^{-(x + \beta \tau / (1 - \beta)) \cdot \mu}} \cdot e^{-(x - \tau) \cdot \mu} \cdot dk$$

$$= f \cdot e^{-\tau \cdot \mu(c - 1 / (1 - \beta))} \cdot (1 - e^{-m \cdot e^{-\tau \cdot \mu(1 - \beta)}}) / (m \cdot \mu).$$

If competitive breeding at size L is to be an ESS then $dR(\tau, +) / d\tau \leq 0$ when $\tau = 0$, so that there is no advantage to breeding competitively later than the general population.

$$dR(\tau, +) / d\tau = f \cdot e^{-\tau \cdot \mu(c - 1 / (1 - \beta))} \cdot [-\mu(c - 1 / (1 - \beta))] \cdot (1 - e^{-m \cdot e^{-\tau \cdot \mu(1 - \beta)}}) - e^{-m \cdot e^{-\tau \cdot \mu(1 - \beta)}} \cdot m \cdot e^{-\tau \cdot \mu(1 - \beta)} \cdot \mu / (1 - \beta) / (m \cdot \mu).$$

Putting $\tau = 0$:

$$dR(\tau, +) / d\tau = f \cdot [-(c - 1 / (1 - \beta)) \cdot (1 - e^{-m}) - e^{-m} \cdot m / (1 - \beta)] / m.$$

Then, if $dR(\tau, +) / d\tau \leq 0$:

$$-(c - 1 / (1 - \beta)) \cdot (1 - e^{-m}) - e^{-m} \cdot m / (1 - \beta) \leq 0$$

(as $f / m > 0$)

$$c \cdot (1 - \beta) \geq 1 - m \cdot e^{-m} / (1 - e^{-m}). \quad (5)$$

COMPETITIVE SUCCESS WHEN BREEDING AT $-\tau$

Now consider a male who starts breeding competitively slightly earlier than the rest, at τ

time units before reaching L . During the time τ , he is breeding when all the other males are not, he experiences a higher mortality μ (compared to $c \cdot \mu$), and a lower growth rate. This male reaches L at age $-\tau + q \cdot \tau / [q(1 - \beta)] = \beta \tau / (1 - \beta)$. His success, standardized as in eqn (3), is then:

$$R(\tau, -) = f \cdot e^{\tau \cdot c \cdot \mu} \left[\int_{x=-\tau}^{\beta \tau / (1 - \beta)} e^{-m \cdot e^{-(x + \tau) \cdot \mu}} \cdot dx + e^{-(\tau + \beta \tau / (1 - \beta)) \cdot \mu} \cdot (1 - e^{-m}) / (m \cdot \mu) \right].$$

The greater probability of survival to the age of first competitive breeding of the early competitively breeding male is represented by $e^{\tau \cdot c \cdot \mu}$. The first term inside the square bracket represents the success during the period spent growing to size L . During this period all other males are larger, so $p = 1$ in eqn (1). The second term inside the square bracket represents the success subsequently, which is the same as for the standard male, in eqn (4), devalued by the excess mortality during the period $-\tau$ to $\beta \tau / (1 - \beta)$. Then:

$$R(\tau, -) = f \cdot e^{\tau \cdot \mu \cdot c} \cdot [e^{-m} \cdot (1 - e^{-(\beta \tau / (1 - \beta) + \tau) \cdot \mu}) / \mu + e^{-\tau \mu / (1 - \beta)} \cdot (1 - e^{-m}) / (m \cdot \mu)]$$

$$= f \cdot e^{\tau \cdot \mu \cdot c} \cdot [e^{-m} (1 - e^{-\tau \cdot \mu(1 - \beta)}) + e^{-\tau \mu(1 - \beta)} \cdot (1 - e^{-m}) / m] / \mu.$$

If competitive breeding at size L is to be an ESS, then $dR(\tau, -) / d\tau \leq 0$ when $\tau = 0$ so that there is no advantage in breeding competitively earlier than the general population.

$$dR(\tau, -) / d\tau = f \cdot e^{\tau \cdot \mu \cdot c} \cdot \{ \mu \cdot c \cdot [e^{-m} (1 - e^{-\tau \mu(1 - \beta)}) + e^{-\tau \mu(1 - \beta)} \cdot (1 - e^{-m}) / m] + \mu \cdot e^{-m} \cdot e^{\tau \cdot \mu(1 - \beta)} / (1 - \beta) - [\mu / (1 - \beta)] \cdot e^{-\tau \mu(1 - \beta)} \cdot (-e^{-m}) / m \} / \mu.$$

Putting $\tau = 0$:

$$dR(\tau, -) / d\tau = f \cdot \{ c \cdot (1 - e^{-m} / m + e^{-m} / (1 - \beta)) - [1 / (1 - \beta)] \cdot (1 - e^{-m}) / m \}.$$

Then, if $dR(\tau, -) / d\tau \leq 0$:

$$c \cdot (1 - e^{-m}) / m + [e^{-m} - (1 - e^{-m}) / m] / (1 - \beta) \leq 0$$

$$c \cdot (1 - \beta) \leq 1 - m \cdot e^{-m} / (1 - e^{-m}). \quad (6)$$

CONDITIONS FOR ESS

That conditions (5) and (6) are identical, except for the direction of the inclusion, is convenient and perhaps to be expected, but not (to me) intuitively obvious as the processes governing the success

of late and early competitive breeders are rather different. Putting (5) and (6) together, we find an ESS when:

$$c \cdot (1 - \beta) = 1 - m \cdot e^{-m} / (1 - e^{-m})$$

or:

$$\beta = 1 - [1 - m / (e^m - 1)] / c. \quad (7)$$

This relationship [eqn (7)] between β , c and m must hold for there to be an ESS and it not to be more profitable for an individual to breed competitively earlier or later than the standard size. The relationship between these parameters is shown graphically in Fig. 1. It is symmetrical in c and $1 - \beta$ so that a $z\%$ change in mortality during breeding is equivalent to a $z\%$ change in growth.

The relationship in eqn (7) does not directly introduce the age or size at first competitive breeding, but all three parameters may be dependent on it. In particular, m , the mean number of attending males per receptive female will decrease as the age at first breeding increases. Additionally, β and c , the changes in growth and mortality introduced by engaging in breeding competitively, may be dependent on age, with greater deleterious effects for younger, smaller animals. It is also feasible that β and c could be related to m with especially large mortality and low growth when competition is high.

Assumptions

The above model makes use of several crucial assumptions which may not be met for real populations:

- (i) Number of competitive males attending female is Poisson distributed, and
- (ii) sizes of attending competitive males are independently and randomly distributed.

The number of competitive males attending a receptive female might not be Poisson distributed if, for example, the presence of other males attracted or discouraged other males. A more even distribution of competitively breeding males, caused perhaps by males moving away from regions where male density was temporarily higher than average, would result in less opportunity for smaller males and tend to encourage later breeding. Ultimately, standardization of the number of females per breeding male produces a situation equivalent to that for territorial males—males should only breed competitively if there is either a free territory or one being held currently by a smaller male. Conversely a distribution more clumped than random, resulting perhaps from competitive males detecting females by the presence of other males, would lead to more opportunities for smaller males, who might discover otherwise unattended females, encouraging earlier breeding.

Similarly, if large males avoided other large males, earlier breeding would be discouraged, and

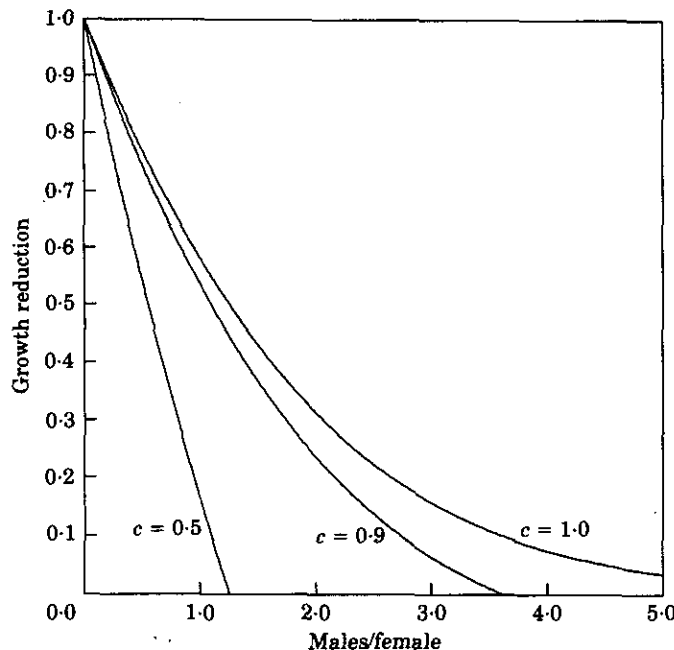


FIG. 1. Necessary conditions for evolutionary stable strategies in size at first competitive breeding: relationship between the mean number of competitive males attending each female and the reductions in growth and survival (c) resulting from competitive breeding.

if they were attracted to one another it would be encouraged.

In general I would expect receptive females to make themselves sufficiently conspicuous to attract competitive males in the neighbourhood (e.g. Moss, 1983). I would also expect attending males to draw as little attention, and therefore potential competition, to themselves as possible. Therefore it seems unlikely that a stable system would evolve in which competitive males discovered receptive females principally by becoming aware of the presence of other competitive males, generally or of a particular size. Spacing of competitive males, and perhaps especially of large males, would intuitively appear more individually advantageous. Therefore, failures of these assumptions would probably tend to encourage later competitive breeding, with lower ratios of breeding males per female (m). In the extreme case, where the same number of males attend each female, including one of the very largest males, males should delay competitive breeding until there is only one male per receptive female ($m = 1$).

(iii) Largest attending competitive male inseminates female

The largest male attending a female may not always be the one that fathers her offspring. If smaller males do sometimes outcompete larger, then earlier breeding would be favoured.

(iv) Constant breeding mortality

The model assumes constant competitive breeding mortality. In some species mortality might be expected to increase with age. This would tend to promote younger breeding and higher numbers of competitive males attending each receptive female (m).

(v) Growth is additive

The model assumes that an advantageous or disadvantageous increment in growth obtained by breeding competitively early or late persists throughout life, so that an early competitive breeder is always comparatively smaller, and a late competitive breeder always comparatively larger, than animals of the same age (past L) who bred competitively at the expected standard size. If this were not the case, so that advantages and disadvantages of competitive breeding to growth do not persist, then younger competitive breeding would be favoured.

(vi) Males have identical values of β , c , q and μ at size L

Although the same size, some males may have greater or lesser expectation of mortality, future growth, or the changes in mortality and growth due to competitive breeding. These will favour individual variation in the size at first competitive breeding. For instance, a particularly well-nourished male may expect little change in growth from participating in competitive breeding, and may thus profit by breeding competitively at a younger age. These types of effects will cause individual variation in the optimal size at first competitive breeding within a population. However, as long as they are not too substantial, population means of β , c and m might be expected to roughly follow the relationship sketched in eqn (7).

(vii) The population is stable in size and age structure

If the population is not stationary, then a term e^{-rx} , where r is the intrinsic rate of increase, should be added to eqn (3) and those derived from it. In general, earlier competitive breeding will be favoured in a growing population and later competitive breeding in a declining one. However, the large mammal species that we are concerned with have low r and so these effects are likely to be small.

(viii) Receptive females are encountered one at a time

The model does not assume any social organization or habitat-use system for the females. They may be solitary or gregarious, roaming or territorial. However, it is assumed that receptive females are encountered one at a time. If there is a reasonable probability of finding, and being able to mate with, a group of receptive females at one encounter, then m should be defined as the mean number of competitive males attending each group of receptive females, and then the model holds as outlined above.

Consequences of Model

The relationships between β , c and m shown in eqn (7) and Fig. 1 have some general consequences for the age at first competitive breeding in roving males:

NUMBER OF COMPETING MALES

In species without male parental care, males are expected to allocate a large part of their resources to mating behaviour. Therefore we would generally expect deleterious effects on either growth or survival once males start competitive breeding. During musth African elephants lose weight, and fights between musth males frequently lead to injury or

death (Hall-Martin, 1987; Poole, 1989a). As a conservative minimum, it would seem likely that either survival or growth should be changed at the onset of competitive breeding by at least 10% of their values before it. As can be seen in Fig. 1, this constrains m , the mean number of competing males, to be less than about 3.6. If both mortality and growth are changed during competitive breeding by more than 10% then $m < 2.8$. Therefore the model predicts that the mean number of males competing for access to a receptive female should almost certainly be less than about 4, and usually less than 3. When competitive breeding is very costly, so that either growth or mortality are changed by a factor of two, then the number of competing males should be less than about 1.2. If the average number of competing males is higher than these limits, it will generally be more profitable for the smaller males to delay competitive breeding until they have a greater chance of success.

In African elephants, more than three males often attend an oestrous female (Moss, 1983; Hall-Martin, 1987). However, in Amboseli National Park, females rarely encountered more than two of the competitively dominant musth males during their oestrous period (Moss, 1983). In sperm whales the number of mature males observed with a group of females can reach five, but is rarely above two (Rice, 1989; Whitehead, 1993), so that the mean number attending an oestrous female is probably less than three. This ratio, however, may have been artificially changed in recent years by the heavy concentration of whaling effort on mature males. Although five to six males can sometimes be seen attending a female polar bear (Stirling, 1988), 92% of the consort female polar bears observed by Ramsay & Stirling (1986) were with only a single male. However, these were virtually instantaneous samples and males remain with females for 7–12 days (Stirling, 1988), so that this may be an underestimate.

In general, then, the available evidence for these three species seems consistent with the prediction that competitive breeding should be delayed until a stage such that there are fewer than a mean of about two to four males competing for each receptive female. In feral goats, *Capra hircus*, males have been found to adjust their willingness to take part in competitive breeding depending on the perceived level of competition among rival males (Dunbar *et al.*, 1990).

AGE AT MATURITY AND NUMBER OF COMPETING MALES

The model suggests that the age of competitive maturity should increase as factors which tend to increase male competition intensify. Therefore,

delayed maturity of roving males might be expected when:

(i) Females have increased inter-birth intervals so fewer females are available at any time.

(ii) Females have longer receptive periods or pre-receptive periods (which the males can monitor) so that more competitive males have the opportunity to find them.

(iii) Females do not synchronize their oestrous periods so that competitive males can attend several females sequentially.

(iv) Females are less spaced and more easily detected so that breeding competitive males spend less time searching.

Examination of these predictions would seem to need good inter-population (or maybe inter-specific) comparative data on delayed male maturity, data which are not available at present.

Conclusion

The model developed in this paper suggests that roving males should delay competitive breeding in favour of increased growth or survival until there are less than a mean of about two to four competitive males attending each receptive female. In species where females breed rarely, but, when they do, they are receptive for reasonably long (but asynchronous) periods so that a number of males can potentially find them, then delayed competitive breeding will be particularly favoured. This scenario is consistent with available results on African elephants, sperm whales and polar bears, so that the model provides a plausible explanation for the long delays in competitive breeding found in these species.

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