

Sexual abstinence and the cost of reproduction in adult male water snakes, *Nerodia sipedon*

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Low frequency of reproduction among iteroparous organisms is most often observed among female ectothermic vertebrates and is thought to be a strategy used to defer reproductive costs. We assessed reproductive costs of male water snakes (*Nerodia sipedon*) to determine why half of adult males abstain from reproduction each year. There was no evidence of a short-term energetic cost of reproduction. Change in mass did not differ between reproductive and non-reproductive males during the one-month mating season or during the entire four-month activity season. Changes in mass of reproductive males were similar at two sites in which the spatial distribution of females differed. However, there were size-specific differences in growth and survival between reproductive and non-reproductive males. Among reproductive males growth rate decreased with body size at a lower rate than among non-reproductive males. Survival increased with body size for reproductive males, but decreased with body size among non-reproductive males. Most of the differential survival between reproductive and non-reproductive males did not occur during the mating season but rather during hibernation. Size-related differences between reproductive and non-reproductive males may reflect selection having eliminated low quality males from the larger size classes. Overall our results appear most consistent with there being high variance in male quality, such that the best males can bear the cost of reproducing and still grow and survive as well or better than low quality males that abstain from reproduction.

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Central to life history theory is the assumption that reproduction is costly and thus, investment in reproduction should negatively affect other components of fitness such as growth, future fecundity or survival (Roff 1992, Stearns 1992). Given these trade-offs, selection should favor a schedule of reproduction in iteroparous animals that maximizes fitness. In most iteroparous species, individuals reproduce at each opportunity once they have reached sexual maturity (e.g. annually in seasonally reproducing species). In some iteroparous species, however, some individuals regularly appear to forgo breeding opportunities (Bull and Shine 1979). Females of many species invest more heavily in reproduction than males do (Clutton-Brock

1991). Thus, females may be under stronger selection than males to optimize their reproductive schedule, reproducing only when their own condition and/or the environment allow a high likelihood that reproduction will be successful (Winkler and Wallin 1987, Clutton-Brock 1991). For males, however, the assumed low cost of reproduction should rarely favor abstinence. Here we investigate variation in reproductive schedules in male northern water snakes (*Nerodia sipedon*), an apparent exception to this generalization.

Despite the differences between males and females in their relative investment in reproduction, the cost of reproduction can still be important for males, even with the absence of paternal care. Sperm and semen can be

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energetically expensive to produce (Dewsbury 1982, Olsson et al. 1997), and those costs may be small relative to the costs of finding mates or competing with other males for mates (Vehrencamp et al. 1989, Aldridge and Brown 1995, Yoccoz et al. 2002). Bull and Shine (1979) found that those species in which males sometimes skip reproductive opportunities often have some expensive accessory activity (breeding migration) associated with reproduction. More generally, the more that males must engage in some form of endurance competition to reproduce, the greater should be the likelihood that some males will abstain from reproduction. This prediction follows from the expectation that by skipping reproduction, an individual may increase the probability of surviving to the next reproductive opportunity and/or increase the amount of energy available to invest in the next reproductive event (Williams 1966, Reznick 1985).

The costs and benefits of reproducing or abstaining on a given occasion are specific to the individual. Males that are of 'high quality' may be able to reproduce as well as grow and survive whereas low quality males may be less able to grow and survive even if they forego reproduction. Alternatively, if all males are of similar overall quality, those that abstain from reproduction should survive better and/or have higher reproductive success the following breeding season than those individuals that did reproduce. Evidence of both patterns has been reported (Roff 1992). Our main goal in this study is to test these alternative hypotheses to understand why some male northern water snakes abstain from reproduction.

The cost of reproduction is poorly studied in snakes and particularly so for male snakes. Documenting female reproductive effort generally entails measuring fecundity, a relatively straightforward undertaking for many species. For male snakes, however, one must quantify the effort expended by individuals searching for, and competing for access, to females, a task made difficult by the cryptic nature of most species. Our study population of northern water snakes has several features that make it an exception to this generalization. First, mating aggregations are easy to locate and observe (Barry et al. 1992, Weatherhead et al. 1995). Second, combining mating observations with genetic analysis of paternity in the same population (Prosser et al. 2002, Weatherhead et al. 2002) allowed us to estimate accurately whether or not a male had attempted to reproduce (see Methods). Third, the limited movement of individuals in and out of the beaver pond populations we study (confirmed by radio telemetry (G. P. Brown, unpubl.) and genetic analysis (Prosser et al. 1999)) allowed accurate documentation of survival between years (Brown and Weatherhead 1999a, b). Fourth, a four-fold difference in dispersion of reproductive females in the two populations (Brown and Weatherhead 1999c) allowed us to compare the inci-

dence and consequence of male abstinence in populations in which the cost of locating females should differ substantially. In an experiment that manipulated the intensity of male mating competition in sandgobies (*Pomatoschistus minutus*), Lindström (2001) found reduced survival of males that had to compete more for mates.

The specific predictions we test are that (1) abstinence from reproduction should be more common when females are more dispersed because of the higher costs of reproduction, that (2) the cost of reproduction should result in reproductive individuals losing weight over the mating season relative to non-reproductive individuals and being less likely to survive to the next year than non-reproductive individuals, and that (3) the negative effects of reproduction should be more pronounced where reproductive females are more dispersed. (4) Among those individuals that survive, individuals that abstain should grow more, and/or be in better condition the following year than individuals that are reproductive, and abstinence should increase the probability of being reproductive the following year.

A final prediction we test concerns the way in which reproductive effort should change with age. If males sometimes trade off current reproduction to increase future reproduction, then investment should increase with age because the potential for future reproduction should be lower. Reproductive success in male water snakes is independent of body size (Weatherhead et al. 2002), so older snakes do not achieve a relatively greater benefit from attempting to reproduce because they are larger. This "terminal investment" hypothesis (Clutton-Brock 1984) assumes that survival probability declines with age (i.e. senescence) independent of any increased reproductive effort. There is evidence for decreased survival in older male water snakes (Brown and Weatherhead 1999a), but it is not known whether age-related reproductive effort contributes to that decrease. Here we test the prediction that, independent of other factors that affect whether a male abstains or is reproductive (see predictions above), the proportion of males abstaining should decline with age.

Material and methods

Study species

N. sipedon is a medium sized, viviparous, largely aquatic natricine species. At our study location, mating activity commences in early May, soon after the snakes emerge from hibernation, and continues until early June. Because the annual active period only extends until early September, the mating period comprises approximately 25% of the entire active season. The mating behaviour of *N. sipedon* is characteristic of

other natricine species (e.g. *Natrix*, *Thamnophis*). When a male locates a receptive female he aligns himself on her back until their cloacas are in contact. He then taps her back with his chin and the female allows copulation by opening her cloaca. Male access to females is determined by scramble competition rather than by individual males attempting to monopolise receptive females; often several males court the same female simultaneously. In these aggregations males compete physically with one another (via tail wrestling) for access to the female. There is no evidence that larger males are more successful in these competitions (Prosser et al. 2002). Some individuals of both sexes participate in multiple mating aggregations within the same season. As a result, multiple paternity of litters is common (Barry et al. 1992, Prosser et al. 2002) and some males sire offspring with multiple females within the same year (Weatherhead et al. 2002).

Study site

The study was carried out at two marshes approximately 1 km apart, located 10 km from the Queen's University Biological Station in eastern Ontario, Canada (45°37'N, 76°13'W). Barbs Marsh and Beaver Marsh are 4 ha and 3 ha in area, respectively, and have been illustrated and described elsewhere (Brown and Weatherhead 1999a, c). A difference between the marshes important to this study is the spatial distribution of females during the mating season. At Beaver Marsh the majority of mating occurs on two beaver dams located at either end of the marsh. At Barbs Marsh, reproductive females are more dispersed (mating occurs throughout the marsh) and male home ranges during the mating season are significantly larger than in Beaver Marsh (Brown and Weatherhead 1999c). Estimated mean population sizes are 101 and 84 individuals age one or older in Beaver and Barbs Marshes, respectively (Brown and Weatherhead 1999a).

General methods

Most data for this study were collected from 1994–1996, although long-term marking and monitoring of the population bracketed those years. Each year we searched both marshes intensively at least once each day beginning in mid April and continuing until after all mating activity had ceased. Snakes were captured by hand or in minnow traps and brought to the lab to be sexed, weighed, measured for snout to vent length (SVL) and tail length and have a 100 µl blood sample taken from the caudal vein. We estimated condition using the approach of Weatherhead and Brown (1996), where fat-free wet mass is estimated from SVL. Subtracting this value from total wet mass estimates fat

mass, which is then expressed as a percentage of total mass.

Snakes were permanently marked using subcutaneous passive integrated transponder (PIT) tags. During the mating season we also marked snakes with spots of non-toxic, acrylic paint. Use of unique color combinations allowed us to identify individuals at a distance in the field without disturbing mating aggregations. Most adults were measured and marked soon after emergence from hibernation, before the mating season began. By the latter half of the mating season almost all individuals observed in aggregations were painted and could be identified. If paint marks faded before the end of the mating season, individuals were captured and repainted, reweighed but usually not remeasured.

During August, we resumed intensive searches of the marshes to capture and measure snakes prior to their entering hibernation. We kept all gravid females captured in August in captivity until they gave birth. Because gravid females bask more (Brown and Weatherhead 2000) and are easier to catch than non-gravid females, we are likely to have captured all gravid females. Following parturition we collected approximately 50 µl of blood from the caudal vein of each neonate. We removed the terminal 1 cm of the tail from young that were stillborn. We released mothers and all live neonates at the maternal marsh. Using eight microsatellite DNA loci, we successfully assigned paternity to approximately 93% of neonates from Barbs Marsh and 70% of neonates from Beaver Marsh (Prosser et al. 2002).

Determination of reproductive status and reproductive costs

Of 92 males observed in mating aggregations, 67% sired no young and 33% sired at least one young. Paternity analyses identified an additional 16 males that sired at least one young despite never having been observed attempting to mate (Prosser et al. 2002). Thus, even though males observed attempting to mate were more likely to sire young, observations of mating were obviously incomplete (note that Prosser et al. 2002 found no evidence that females used sperm stored from a previous year to fertilize their ova). Because our interest is in whether or not males attempted to mate, rather than the success or failure of those attempts, we combined observational and molecular methods to determine reproductive status. We classified a male as reproductive in a given year if he had been observed participating in courtship behavior or if paternity analysis identified him as having sired any offspring produced that year. A few of the males that we classified as non-reproductive may actually have attempted to reproduce. However, for them to have avoided detection by both methods (observation and paternity analysis), their reproductive

effort is unlikely to have been substantial, and thus their misclassification should not have a strong effect on our results.

Observations of males participating in mating activity and genetic analysis of paternity both indicated that the minimum size of reproductive males is 42.7 cm SVL. Age estimates of males calculated from growth equations (Brown and Weatherhead 1999a) revealed that most males in the population mature at three years of age, although a small number of two-yr olds are reproductive (Brown and Weatherhead 1999c). Thus, among two year olds, most individuals that our criteria would classify as 'non-reproductive' are likely to be immature rather than mature males that do not attempt to reproduce. To avoid incorrectly classifying immature males as mature non-reproductive males, we restricted our analyses of reproductive costs to males that were at least three years old.

To determine whether reproduction imposed a growth cost on males we compared growth in mass between reproductive and non-reproductive individuals over two intervals. We compared growth in mass over the one-month mating season for individuals that were weighed once prior to 15 May and a second time prior to 14 June. We also compared growth over the entire four-month active season for individuals that were weighed once prior to 31 May and a second time after 7 August.

Our recapture records focussed on 149 males captured between 1994 and 1996. We also included capture data from 1997 to assess survival of males captured in 1996. Our long-term recapture data (1988–1997) indicated that catchability of male water snakes is very high (Brown and Weatherhead 1999a). In the 1994–1996 sample only one individual was not captured during a year when he was known to be alive (i.e. captured in 1994 and 1996 but not in 1995). Thus, if a male was not captured in a given year it reliably indicated that he was no longer in the population. Because it was so rare for a male to avoid capture, we assessed survival of individuals directly from recapture histories rather than adjusting for differential recapture probabilities using mark-recapture methods (e.g. Jolly-Seber analyses).

Results

Frequency of reproduction

We captured 149 adult males three years of age and older between 1994 and 1996 at both sites. Comparisons of body size, growth and recapture statistics between sites and reproductive classes of males are shown in Table 1. Ninety-four males were captured in only one year, 43 were captured in two consecutive years and 11 were captured in all three years. Of the 43 males captured during two consecutive years, 10 were not reproductive during either year, nine were reproductive during both years and 24 were reproductive during one of the two years. Of the 11 males captured in all three years, four were reproductive during only one year, six were reproductive in two years and one male was reproductive in all three years. Contrary to the prediction that males should be more likely to be reproductive following a year of abstinence, reproductive status in a given year was unrelated to reproductive status the previous year ($\chi^2 = 0.11$, $N = 65$, $p = 0.75$).

At Barbs marsh 19 of 34 males (56%) were reproductive in 1994, 7 of 33 (21%) in 1995 and 17 of 31 (55%) in 1996. At Beaver marsh, 20 of 47 males (42%) were reproductive in 1994, 22 of 38 (59%) in 1995, and 21 of 32 (66%) in 1996. At Barbs marsh, the proportion of reproductive males was lower in 1995 than in the two other years ($\chi^2 = 10.39$, $p = 0.006$). At Beaver marsh the proportion of males reproducing did not vary significantly over the three years ($\chi^2 = 4.45$, $p = 0.11$). Contrary to our prediction that more males should abstain from reproduction in Barbs marsh, the proportion of reproductive males did not differ significantly between marshes (site: $\chi^2 = 1.39$, $df = 1$, $p = 0.24$; year: $\chi^2 = 6.03$, $df = 2$, $p = 0.06$).

Consistent with the terminal investment hypothesis, on average reproductive males were significantly longer (53.6 cm vs 50.7 cm, $t = 4.00$, $df = 213$, $p = 0.0001$) than non-reproductive males, and thus, reproductive males were also older (5.2 yr vs 4.2 yr, $t = 3.80$, $df = 213$, $p = 0.0002$) than non-reproductive males.

Table 1. Summary statistics of body size, growth and recapture characteristics of reproductive and non-reproductive male *N. sipedon* at two sites. Values are means with standard deviation in parenthesis.

| | Barbs marsh | | Beaver marsh | |
|---|---------------|------------------|---------------|------------------|
| | Reproductive | Non-reproductive | Reproductive | Non-reproductive |
| N | 43 | 55 | 63 | 54 |
| mass (g) | 103.8 (32.6) | 84.9 (31.4) | 105.2 (31.8) | 89.2 (25.1) |
| % fat | 0.17 (0.08) | 0.15 (0.09) | 0.20 (0.08) | 0.20 (0.09) |
| SVL (cm) | 53.9 (4.9) | 50.7 (5.6) | 53.5 (5.6) | 50.8 (5.0) |
| Rate of mass change during mating season (g/day) | -0.18 (1.10) | -0.02 (0.27) | -0.03 (0.71) | 0.22 (0.77) |
| Rate of mass change during entire activity season (g/day) | 0.18 (0.18) | 0.23 (0.14) | 0.09 (0.21) | 0.37 (0.15) |
| Rate of SVL growth over entire year (cm/day) | 0.007 (0.006) | 0.01 (0.007) | 0.009 (0.006) | 0.009 (0.006) |
| proportion surviving | 0.77 | 0.64 | 0.75 | 0.43 |

Table 2. Multiple regression results of effects of body size, site and reproductive status on growth rates of male *N. sipedon*. Bold type indicates significant relationships at $\alpha = 0.05$.

| Growth variable | Source | F | p |
|--|-----------------------------|-------|-------------------|
| Mating season growth rate in mass (N = 57) | SVL | 0.39 | 0.54 |
| | site | 0.70 | 0.41 |
| | repro. status | 0.40 | 0.53 |
| | site \times repro. status | 0.05 | 0.83 |
| Activity season growth rate in mass (N = 26) | SVL | 0.66 | 0.43 |
| | site | 0.31 | 0.58 |
| | repro. status | 2.28 | 0.15 |
| | site \times repro. status | 2.88 | 0.10 |
| Annual growth rate in SVL (N = 81) | SVL | 27.47 | <0.0001 |
| | site | 0.12 | 0.73 |
| | repro. status | 2.22 | 0.14 |
| | site \times repro. status | 0.01 | 0.97 |

Energetic cost of reproduction

Condition measured at the start of the breeding season did not differ between males that were reproductive or non-reproductive that year (18.5% vs 17.2%, $t = 1.12$, $df = 213$, $p = 0.26$). During the mating season there was also no evidence of an energetic cost associated with reproduction at either marsh. Non-reproductive males gained an average of 0.07 g per day and reproductive males lost an average of 0.08 g per day during the mating season. Approximately 50% of both reproductive and non-reproductive males increased mass over the mating season, indicating that both groups feed during that time to some extent. A two-way analysis of covariance with reproductive status and site as factors indicated that after adjusting for body size, there was no significant difference in rates of weight gain between classes of males or between sites and there was no interaction between site and reproductive status (Table 2).

Changes in condition over the entire active season were similar to the results just for the mating season. Non-reproductive males gained an average of 0.04 g per day and reproductive males gained mass at an average of 0.03 g per day. Results of a two-way ANCOVA indicated no significant differences between reproductive classes or between sites and no interaction (Table 2).

Growth

To test the prediction that abstinence enhances growth, we used ANCOVA to compare the change in SVL of reproductive males and non-reproductive males from early spring in one year to early spring the following year (reproductive status is designated for the first year). We included SVL in year one, and the interaction between initial SVL and reproductive status in the model. Growth was designated as the absolute rather than the relative change in SVL. We had complete data

for 43 reproductive males and 38 non-reproductive males. Growth increased with SVL ($F = 35.73$, $df = 1$, $p = 0.00001$) and reproductive males grew more than non-reproductive males ($F = 4.07$, $df = 1$, $p = 0.047$). There was also a significant interaction between SVL and reproductive status ($F = 4.69$, $df = 1$, $p = 0.034$). Reproductive males grew more than non-reproductive males, and that difference increased with male size (Fig. 1).

Survival cost of reproduction

To test the prediction that reproductive males should exhibit lower survival than non-reproductive males we used a full multivariate logistic regression model. Contrary to that prediction, reproductive males survived significantly better than non-reproductive males (Table 3). Survival of reproductive and non-reproductive males did not differ between sites and did not vary significantly with body size (Table 3). However, there was a significant body size \times reproductive status interaction. Among reproductive males, survival increased sig-

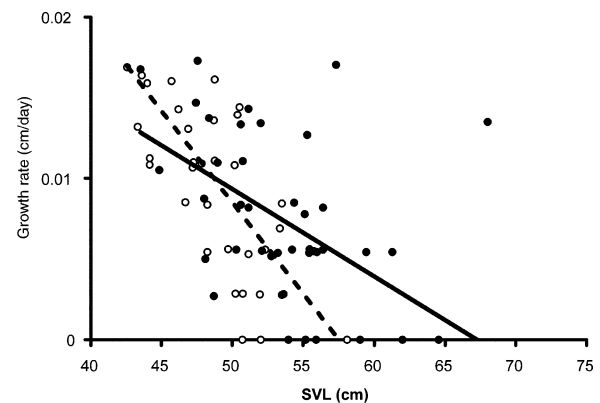


Fig. 1. Relationships between annual growth rate and body size for reproductive (solid line, closed circles) and non-reproductive (broken line, open circles) male *N. sipedon*.

Table 3. Multiple logistic regression results for the effects of body size, site and reproductive status on probability of survival in male *N. sipedon*. Bold type indicates significant relationships at $\alpha = 0.05$.

| Source | χ^2 | p |
|-----------------------------|----------|--------------|
| SVL | 0.32 | 0.57 |
| site | 2.23 | 0.14 |
| repro. status | 6.04 | 0.014 |
| SVL \times repro. status | 7.61 | 0.006 |
| site \times repro. status | 1.73 | 0.19 |

nificantly with body size while among non-reproductive males, survival decreased significantly with body size (Fig. 2).

We have previously determined that peaks in male mortality occur during the mating period (May–early June) and during hibernation (Brown and Weatherhead 1999a). To assess whether the differential mortality of non-reproductive males occurred prior to or subsequent to the end of the active season we examined the composition of our August capture sample. During the mating season, the overall ratio of reproductive to non-reproductive males was 0.97:1 (106 vs 109; 49.3%). In the August capture sample the ratio was 1.13:1 (43 vs 38; 53.1%). The ratio for those subsequently surviving to the next year was 1.37:1 (80 vs 58; 58.0%). Although the change in the ratio was greatest over winter, the differences in these ratios are not significant ($\chi^2 = 2.54$, $p = 0.28$).

Discussion

To understand why some sexually mature male water snakes abstain from reproduction we examined both the short- and long-term correlates of reproductive status. In the short term, there was no support for the hypothesis that males abstain from reproduction for energetic reasons. Differences in condition at the start of a mating period did not distinguish males that were

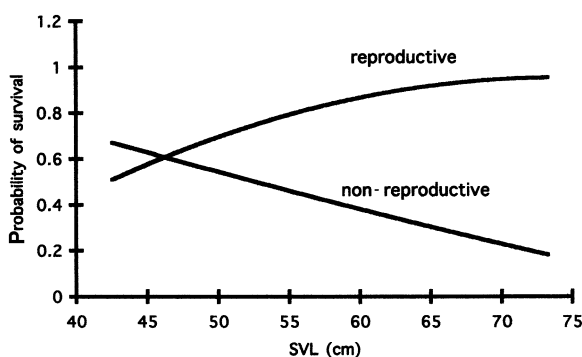


Fig. 2. Relationships between probability of survival and body size for reproductive and non-reproductive male *N. sipedon*. Lines are probability functions from logistic regressions.

reproductive that year from those that were not. During the mating season approximately half of all males improved their condition, whether or not they were reproductive. The proportions of mature males that were reproductive did not differ significantly between the two marsh populations, despite the substantial difference in dispersion of reproductive females, and thus the probable difference in costs of mate searching (Brown and Weatherhead 1999c). Over the entire active season reproductive males increased body condition to the same extent as non-reproductive males. Finally, abstaining from reproduction in one year did not make it more likely that a male would be reproductive the following year.

Our failure to find evidence that energy constrains reproduction in male northern water snakes is consistent with our previous studies of this population (Weatherhead et al. 1995, 2002, Brown and Weatherhead 1999c). The simple explanation appears to be that males forage to some extent during the mating season, and that attempting to mate neither reduces foraging opportunities nor depletes stored fat sufficient to produce condition differences between reproductive and non-reproductive males. A possibility we can not rule out is that reproductive males actually increase foraging during the mating season sufficient to compensate for the energetic costs of reproduction. Reproductive males are seen more often than non-reproductive males during the mating season (Brown and Weatherhead 1999c), which would be expected if they are foraging more. Mate searching also requires that these males be more active, however, so data on rates of food consumption are required to resolve this question. In any case, it is clear that male water snakes are not capital breeders (Drent and Daan 1980) that fuel reproduction with endogenous reserves, as has been documented for males of some other snake species (Madsen and Shine 2000) but not others (Aubret et al. 2002).

Our data on the long-term correlates of reproductive status are more informative about the cost of reproduction, because ultimately the consequences of reproductive decisions must be evaluated by how they affect lifetime reproductive success. We considered two general alternatives. When variation in individual quality is low, individuals that reproduce (or at least attempt to reproduce) should grow and survive less well than individuals that abstain. Alternatively, when quality is more variable, the best individuals may be able to reproduce and still grow and survive as well as or better than lower quality individuals that abstain from reproduction. Our data were most consistent with the latter alternative. Reproductive males grew more and had higher survival than non-reproductive males.

We do not know which factors contribute to variation in quality in male water snakes and account for the lower size-specific growth and survival of non-reproductive males. However, recent research on other

taxa suggests that immune function and infection by parasites is a good candidate. A negative relationship between immune function and male reproductive effort has been documented in birds (Norris et al. 1994, Richner et al. 1995, Merila and Andersson 1999) and *Drosophila* (McKean and Nunney 2001), supporting the hypothesis that suppressed immune function may be an important cost of reproduction (Sheldon and Verhulst 1996). Male water snakes with compromised immune systems may not be able to afford the costs of reproduction, and thus abstain. Interestingly, evidence from the same population of water snakes suggests that all sexually mature males produce sperm during the mating season (A. I. Schulte-Hostedde, pers. comm.), even though some of the males sampled were unlikely to have engaged in mating activity. Such a pattern suggests that the important cost of reproduction for male water snakes is not spermatogenesis, but rather, the heightened activity associated with searching and competing for mates. As with the immune function hypothesis, this hypothesis also awaits testing.

An unexpected result of our study was that the relationship of both growth and survival with body size differed between reproductive and non-reproductive males. Reproductive males grew more than non-reproductive males, but that difference increased with male size. Survival increased with size among reproductive males, and decreased with size in non-reproductive males. Both of these results might be related to the fact that reproductive males survived better than non-reproductive males. Within a cohort of males, selective mortality should steadily increase the difference in quality between reproductive and non-reproductive individuals, so that the difference would be greatest amongst older (i.e. larger) males. This does not explain the specific growth and survival patterns within groups (reproductive and non-reproductive males), but may explain differences between these groups.

Based on the terminal investment hypothesis (Clutton-Brock 1984), we had predicted that reproductive effort should increase with age. Apparently consistent with that prediction, we found that reproductive males were larger, and thus older, than non-reproductive males. While this is consistent with an increase in reproductive effort with age (a greater proportion of older males attempt to mate), it is also consistent with selective mortality increasing the average quality of older males. Furthermore, survival increased with size among reproductive males, contrary to the assumption underlying the terminal investment hypothesis that survival probability declines with age. If our hypothesis of selective mortality is correct, then age-specific patterns of reproduction can not be assessed without considering intrinsic differences between cohorts of different ages.

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