African Journal of Herpetology, 2000 49(2): 173-174.

Book review

Reptilian sperm wars

Sperm competition and sexual selection. *Edited by T.R. Birkhead & A.P. Møller. 1998. 826 pages, 26 contributors, 17 chapters. Academic Press, San Diego, London. US$ 59.95 (softcover). ISBN 0-12-100543-7.*

The field of sperm competition is now in its 30th year and is therefore a relative neophyte compared with other branches of biology. However, few biological disciplines have had such an immediate impact. The gist of sperm competition is that sperm from multiple males compete to fertilize a single female's ova. Sexual selection therefore involves not just competition for mates, but also postcopulatory competition among gametes. Traditional studies focused on the male role in mating systems and portrayed male strength and aggression as the key ingredients for reproductive success. Recent work paints a very different picture with strong emphasis on the female role (reviewed in Eberhard 1996; recent papers in Evolution 54(3)). The question "why mate multiply?" has therefore attracted considerable recent attention and has culminated in 826 pages on sperm!

This impressive volume details advances in sperm competition theory and summarises the burgeoning number of empirical studies for a multitude of taxa. Why should this volume be reviewed in African Journal of Herpetology? The answer is simple, one chapter deals with amphibians (T. Halliday) and another with reptiles (M. Olsson and T. Madsen). Furthermore, recent work on sperm competition and cryptic female choice (postcopulatory sperm selection) in reptiles has provided startling new insights into mating systems and the direction of evolution. My review focuses on some of these results and the chapters on amphibians and reptiles. Because my own research interests are dominated by lizards and to a lesser degree include snakes, this review may reflect a slight reptilian bias!

Halliday's review of sperm competition in anurans, apodans and urodeles yields mixed results. Apodans are quickly dismissed in a short paragraph, simply because their reproductive biology is so poorly known. Urodeles, however, are shown as promising subjects for sperm competition studies because multiple matings, internal fertilization and sperm storage are all widespread. The most intriguing result reported for urodeles is that females of some taxa actively destroy sperm in the spermatheca. This process is not fully understood, but allows females to destroy excess or "old" sperm once reproduction is complete. A key question is whether females are able to selectively destroy defective sperm. Among anurans, foam nesters (Rhacophoridae) exhibit the most intense sperm competition and southern African *Chiromantis xerampelina* are among the most impressive. Testis size is 14 times that of non-foam nesters of the same body size and can be almost 8% of total body weight! It is clear from Halliday's review that amphibians are employing diverse reproductive tactics that impose strong selective pressures on males with regard to sperm allocation.

Olsson and Madsen review more than just sperm competition in reptiles. Their chapter provides an overview of determinants of reproductive success including among other things the influence of body size on mate acquisition, attributes of lizard territories and home range, and female mate choice. Much of this information reflects a bias towards lizards, largely because lizard mating systems are often easier to disentangle in comparison to those of snakes. However, one key finding regarding the costs of sperm production emerged from work on

adders (*Vipera berus*) by Olsson *et al*. (1997). Their data now suggest that sperm production may not be a trivial matter and may be energetically costly to males. The consequence of this important finding is that we need to re-evaluate how we determine the costs of reproduction for males, at least in squamates.

Reptiles (lizards and snakes specifically) have been important subjects for studies of the fitness consequences of multiple matings and cryptic female choice. Madsen's work on adders (*V. berus*) and Olsson's work on sand lizards (*Lacerta agilis*) clearly demonstrate the benefits of multiple mating. Female adders that mated multiply produced more viable offspring sired by genetically superior males (Madsen *et al*. 1992). Female sand lizards that mated multiply had higher hatching success, a lower incidence of deformities and higher survivorship (Olsson *et al*. 1994). Another key finding for sand lizards is that females actively select sperm following insemination by multiple males (Olsson *et al*. 1996). This challenges the long held belief that the female reproductive tract is simply an arena for sperm competition. The female must now be considered an active participant (selecting sperm) during the postcopulatory phase. Why select sperm? By mating with multiple males, females sometimes mate with close relatives. Active sperm selection reduces the negative effects of inbreeding. What does this mean for measuring fitness? Most importantly, we need to reconsider evaluating reproductive success based simply on number of matings.

These studies suggest complex reproductive tactics in squamates and highlight both snakes and lizards as model organisms for investigating the relative influence of postcopulatory mechanisms (sperm competition and cryptic female choice) on the direction of evolution. For the student of sperm competition and amphibian and reptile behavioural ecology, this book not only identifies areas for future investigation, but also represents a wealth of information. It is a must read.

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Received: 15 November 2000.