# MATE CHOICE IS NOT AFFECTED BY MATING HISTORY IN THE SIMULTANEOUSLY HERMAPHRODITIC SNAIL *LYMNAEA STAGNALIS*

## JORIS M. KOENE, MATHIEU J. LOOSE AND LOES WOLTERS

*Department of Animal Ecology, Faculty of Earth & Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands*

## ABSTRACT

Mate choice based on mating history is one way to optimize the distribution of one's sperm. This is especially pertinent when donating semen is costly. Owing to sperm competition many species allocate different amounts of sperm depending on their partners' mating histories. The hermaphroditic *Lymnaea stagnalis* has a preference for inseminating different partners, rather than the same one twice. Moreover, virgin partners receive more sperm than nonvirgins. Here we aim to determine whether these hermaphrodites prefer to inseminate virgins. Therefore, focal animals were offered a choice between one mating partner raised in isolation and one raised in a group. For each rearing condition we also measured individual growth, onset of egg laying (waiting time) and hatching success. Of the growth parameters we found that only the asymptotic size differed, with the virgins attaining a larger size. This coincides with the delayed onset of laying selfed eggs by virgins. Selfed eggs did not differ in hatching success from outcrossed eggs. The choice experiment revealed that focal individuals mated randomly with animals raised in isolation (virgins) and raised in groups (nonvirgins). This leads us to conclude that the decisions about whether to mate with an encountered individual and how much sperm to donate to this individual are two separate processes.

## INTRODUCTION

Sperm and seminal fluid are often costly to produce (e.g. Dewsbury, 1982) and can result in the allocation of different amounts of sperm or inseminations. One determining factor for such strategic sperm allocation seems to be the mating history of the partner. There is, for example, abundant evidence that insects are prudent with their expensive sperm and seminal fluids, despite their relatively high mating rates. Many studies have found an adjustment of the size of the ejaculate according to the level of sperm competition (Gage, 1991; Simmons *et al.*, 1993; Pitnick & Markow, 1994; Cook & Wedell, 1996; Schaus & Sakaluk, 2001; Martin & Hosken, 2002). Moreover, for two invertebrates it has been shown that they prefer to inseminate novel partners over ones that they already inseminated (Arnaud & Haubruge, 1999; Koene & Ter Maat, 2007). Such preferential insemination of a novel mating partner, known as the Coolidge effect, is well known in vertebrates (e.g. Wilson, Kuehn & Beach, 1963; Pizzari *et al.*, 2003).

Furthermore, males of several species provide a larger ejaculate in matings with virgins. Examples include mites (Yasui, 1996), bumblebees (Sauter & Brown, 2001), bedbugs (Siva-Jothy & Stutt, 2003), orbweaving spiders (Bukowski & Christenson, 1997), bushcrickets (Wedell, 1992) and pond snails (Loose & Koene, 2008). Two recent theoretical models provide an explanation for these observations, which were so far contrary to the predictions of most sperm competition models (Engqvist & Reinhold, 2006; Ball & Parker, 2007). Engqvist & Reinhold (2006) showed that when sperm competition level is high and males can distinguish between virgins and mated individuals it pays to invest more in matings with the former, because more paternity can be gained. Ball & Parker (2007) basically supported this finding, although in their sperm competition risk model, matings with virgins result in higher sperm allocation when the sperm competition level is low and females are sperm limited. Since mating history seems to be an important determinant for the allocation of sperm, this indicates that animals may somehow be able to assess the mating history of their partner, and may use this information to decide whether to mate or not. We here investigated whether hermaphrodites base their decision to mate on their partner's mating history, using the Great Pond Snail *Lymnaea stagnalis*.

These snails mate relatively frequently (Koene, 2006; Koene, Montagne-Wajer & Ter Maat, 2006; Koene & Ter Maat, 2007), and can use and store sperm for over 3 months (Cain, 1956). Double matings result in roughly equal paternity for both sperm donors (average $P_2$ is 0.6: Koene *et al.*, 2008). Interestingly, in Engqvist & Reinhold's model (2006) these conditions – high mating rates and equal paternity chances – predict higher allocation to virgins, which is what is indeed found in this species (Loose & Koene, 2008). This hermaphrodite is also known to invest differently in growth and reproduction depending on the conditions in which it is raised: animals reared as virgins delay the production of self-fertilized eggs for several weeks (Van Duivenboden, 1983; Koene & Ter Maat, 2004). This delayed onset of egg laying is referred to as the waiting time (e.g. Tsitrone, Duperron & David, 2003). As a consequence, animals raised in isolation grow larger (Koene & Ter Maat, 2004; Koene *et al.*, 2006; Tsitrone, Jarne & David, 2003). Although body size is a good indicator of female reproductive output in terms of eggs, this does not result in a preference for inseminating larger mates (Koene, Montagne-Wajer & Ter Maat, 2007). Nonetheless, strategic sperm allocation is predicted, because previous research has suggested that acting as a sperm donor is costly in this species (De Visser *et al.*, 1994; Koene, 2006). In addition, two recent studies have indeed found evidence for strategic sperm allocation. The first found that insemination preferentially occurs with a novel partner rather than with the same one twice (Koene & Ter Maat, 2007). The second study found that more sperm are donated to

Correspondence: J.M. Koene; e-mail: joris.koene@falw.vu.nl

virgins than to already-mated partners (Loose & Koene, 2008). The Loose & Koene study (2008) only provided animals with one type of partner and the animals saved male resources by donating less to partners in which sperm competition risk was higher. However, they might have chosen not to inseminate that partner if a more attractive partner had been present. Therefore, we set out to test whether animals also distinguish between partners with different rearing backgrounds and thus different mating histories.

## MATERIAL AND METHODS

### Animals

All specimens of *Lymnaea stagnalis* were obtained from our laboratory culture. In the breeding facility and in the tank in which the experiments were performed, the low-copper water was kept at $20°C$. The light:dark cycle was 12:12 h. Snails in the experiments were each fed one circular disc ($19.6$ cm$^2$) of lettuce per day per animal. This amount is slightly below their maximum food intake and thus completely consumed. Hence, the total energy intake of individuals was equal. To determine the relationship between body weight and shell length under these conditions, we weighed and measured 47 animals that ranged in size between 2.0 and 3.1 cm.

For the experiments immature specimens of *L. stagnalis* with a shell height of approximately 10 mm were selected from one breeding tank, ensuring that they were all of the same age (4 weeks posthatching). The immature animals were randomly assigned to either isolated housing (I, i.e. virgins) in perforated polythene jars (460 ml) or in grouped housing (G, i.e. mated) with 25 animals per large perforated polythene box (5,600 ml). All jars and boxes were placed in the same tank. Under these conditions, the animals were raised to maturity and each individual was only used once.

### Growth

To follow the maturation and growth of immature snails under I and G conditions, we followed 15 I and 25 G animals (10 mm) for several months (101 days). For these animals we determined body weight and shell length at set intervals. Initially this was done three times a week because growth speed was high. Once growth slowed, measurements were taken every 3 or 4 days. For weighing, the animals were first placed on a tissue paper to dry off the excess water and then weighed on a closed scale (Sartorius, model 1712 MP8). Shell heights were measured with callipers. Waiting time, i.e. the average difference between the onset of egg laying in the two treatments, was determined by noting when egg masses were observed in both treatments. Waiting time was then calculated by subtracting the age at first reproduction in G from that in I.

### Hatching

For a separate group of snails which was treated as described above, we compared hatching success between the treatments I and G. The difference in hatching success between the two treatments provides a measure for inbreeding depression. For this purpose, when egg laying had started in both groups, we placed the G animals in individual pots. One week later we collected one egg mass per individual of both treatments ($N = 20$ per treatment). These eggs were then left to hatch in closed pots with low-copper water. After 4 weeks, when hatching was finished, we counted hatched and unhatched eggs.

### Mating trials

For a mate choice experiment, we raised a third set of snails under I and G conditions. These animals were used as potential mates for focal mature animals that were isolated only 1 week prior to the experiment (in order to increase their willingness to mate in the male role; De Boer *et al.*, 1997). One hundred and thirteen focal animals were offered a choice between an I and a G partner by placing them in trios in closed jars filled with 460 ml low-copper water of $20°C$. The different types of snails had been marked in advance with different colours of nail polish. We recorded the mating behaviour, including insemination duration, of the focal individual and measured all three individuals after copulation had taken place.

### Statistics

The data were tested for normality and homogeneity of variance. The statistical analyses were performed with JMP version 5.0.1 (SAS Institute Inc.). The different statistical tests that we used are indicated in the results section.

## RESULTS

### Body size

The measurements of body weight (in grams) and shell length (in centimetres) reveal the close relationship between these two measures. We fitted a third-power line because we are dealing with a one-dimensional and a three-dimensional variable. As shown in Figure 1, body weight and shell length are tightly correlated ($R^2 = 0.98$, $N = 47$, $P < 0.0001$). Hence, shell height can be used as a very reliable measure for body weight under standard conditions.

### Growth curve

During the 101 days that we recorded body weight and shell length of 15 I and 25 G snails, respectively, 5 and 16 individuals died before the end of the period. This difference is just short of statistical significance (likelihood ratio: $\chi^2 = 3.58$, df $= 1$, $P = 0.058$). Animals raised in isolation grew significantly larger than those reared in groups, as was evident from
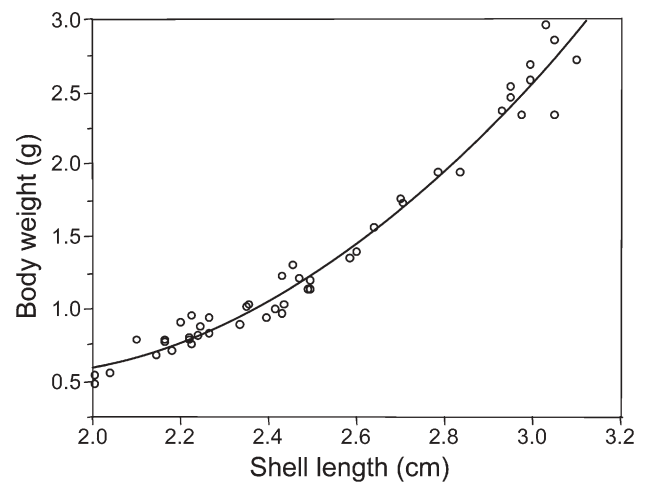


**Figure 1.** The relationship between shell length and body weight of *Lymnaea stagnalis*. The line that is fitted to the data points is based on a third-power function given the one-dimensionality of length and three-dimensionality of weight.
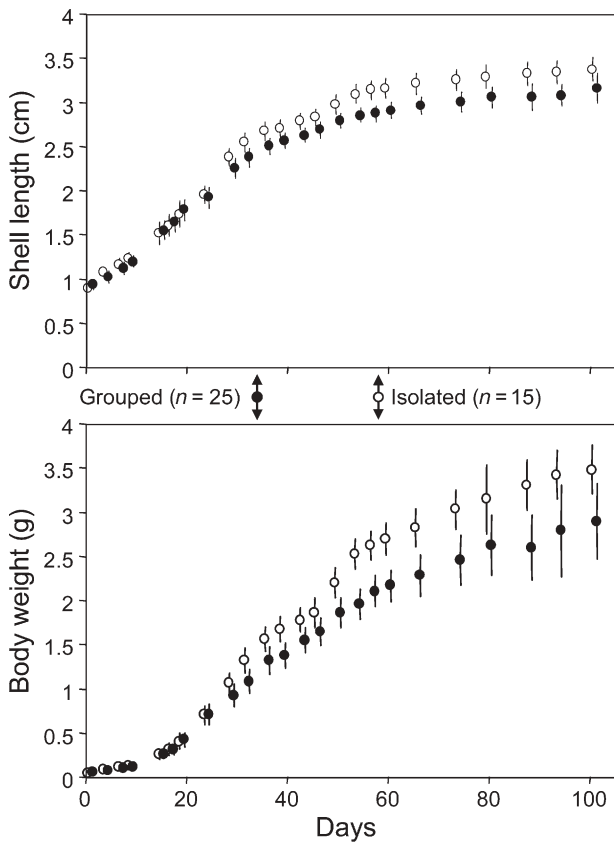
**Figure 2.** Growth curves for *Lymnaea stagnalis* reared in isolation and in a group. The top graph shows shell length and the bottom graph shows body weight of the animals over time. Means with confidence intervals are shown for isolated (open circles) and grouped (closed circles) snails. The measurements for the isolated and grouped snails were taken on the same day, but for visual clarity these open and closed points are slightly offset to, respectively, left and right. The arrows indicate the onset of egg laying in each treatment.

both the shell length (*t*-test: $t = -2.43$, df $= 17$, $P = 0.026$) and body weight (*t*-test: $t = -2.71$, df $= 17$, $P = 0.015$).

Figure 2 summarizes the growth data over the whole period for shell length and body weight. We fitted Von Bertalanffy growth curves to these data using the formula

$$s(t) = \frac{s_0 s_a}{(s_a - s_0)e^{-rt} + s_0}$$

where *s* stands for size (either length or weight), $s(t)$ represents size at time *t*, $s_0$ represents size at time 0, $s_a$ represents asymptotic size and *r* represents growth speed (Zonneveld & Kooijman, 1989). The estimates and confidence intervals for these parameters are shown in Table 1. These curve fits reveal

that the starting size and growth speed are similar for the two treatments (*t*-tests: $P > 0.05$), but that the final, asymptotic size ($s_a$, weight and length) differs between the two treatments (*t*-test: final weight, $t_{17} = 29.20$, $P < 0.0001$; final length, $t_{17} = 7.95$, $P < 0.0001$).

### Waiting time

The arrows in Figure 2 indicate when the first egg masses were found in the two treatments. Evidently, the eggs laid by I individuals, which are virgins, are self-fertilized, whereas the G individuals' eggs are cross-fertilized. For these animals egg laying started between day 36 and 74 of the experiment, with an average onset on day 59 (i.e. 87 days old). The first egg masses of G animals were observed on day 32 (i.e. 60 days old).

The mean waiting time, defined as the difference in onset of egg laying between selfing and outcrossing individuals, was $27 \pm 14$ days. It is striking from the graphs in Figure 2 that right around the onset of egg laying in the G animals, the two growth curves start to deviate.

Hatching success for outcrossed egg masses (G) was $89.9 \pm 16.2\%$. For selfed egg masses this was $89.3 \pm 12.5\%$. These values did not differ significantly (Wilcoxon: $\chi^2 = 1.15$, df $= 1$, $P = 0.28$).

### Mate choice

Sixty-nine of the 113 focal animals chose to inseminate one of the potential mating partners. Before choosing, the animals actively crawled around in the observation jars and thus encountered both of the potential mating partners before commencing courtship. Trios in which the focal animal was itself first inseminated were excluded ($N = 44$) in order to avoid introducing an additional factor, insemination prior to choice. Of the 69 focal animals that did first inseminate a partner 36 chose for G and 33 chose for I. Clearly, this does not reveal a significant preference for one of the mating types (likelihood ratio: $\chi^2 = 0.13$, df $= 1$, $P = 0.72$). To look at the possible effects of body size on copulation duration, we analysed these data in a general linear model with the focal animal's length and its partner's length as factors and copulation duration as dependent variable (for the cases where we were able to measure copulation duration reliably, after excluding four outliers this left 56 data points). This revealed that the length of the focal snail determined copulation duration ($F_{(1,49)} = 5.27$, $P = 0.026$) and that partner length did not ($F_{(1,49)} = 0.37$, $P = 0.55$). The insignificant interaction term was removed from the model. The results were similar when the copulation durations of all the 113 matings were taken into account.

### DISCUSSION

Since the work of Dewsbury (1982) it has been generally accepted that sperm and seminal fluids can be energetically

**Table 1.** Values of Von Bertalanffy growth curve fits.

| Measure | Treatment | $s_0$ | $s_a$ | $r$ |
|---|---|---|---|---|
| Body weight (g) | Isolated | 0.123 (0.005–0.198) | 3.337 (3.062–3.612) | 0.080 (0.063–0.097) |
| | Grouped | 0.119 (0.033–0.206) | 2.676 (2.362–2.990) | 0.078 (0.057–0.100) |
| Shell length (cm) | Isolated | 0.842 (0.711–0.974) | 3.368 (3.216–3.520) | 0.064 (0.053–0.075) |
| | Grouped | 0.849 (0.715–0.983) | 3.086 (2.937–3.235) | 0.066 (0.053–0.078) |

The parameter estimates are given for both the body weight and shell length data; 95% confidence intervals are indicated in brackets. Parameters: $s_0$, size at time 0; $s_a$, asymptotic size; *r*, growth speed.

costly to produce. Especially when animals mate promiscuously and can store received sperm for prolonged periods, donors will be selected to optimally allocate their sperm (to different partners). In accordance with this prediction, two recent studies have found that pond snails prefer to inseminate novel partners over familiar ones and transfer more sperm to virgin partners (respectively, Koene & Ter Maat, 2007; Loose & Koene, 2008). Despite these abilities, we do not find any evidence for mate choice based on rearing condition. In this study we found that focal snails that were given the choice between a virgin and mated individual inseminated one of these at random and did not prefer animals with a particular mating history. This is somewhat surprising because during spring two adult generations overlap in the field (Ter Maat *et al.*, 2007), indicating that encountering virgins is a real possibility.

We did find clear differences in growth between the animals raised in groups and those raised in isolation. Interestingly, the growth curve parameters reveal that the two rearing conditions only differ in the animals' final sizes and not in starting points and growth speeds. We also found no difference between the hatching success of selfed and outcrossed eggs. Furthermore, Figure 2 clearly illustrates that the two curves start to diverge around the time that the grouped animals start laying eggs. Evidently, the isolated animals, which delay selfing for roughly 4 weeks, keep investing their resources into growth while the grouped animals now need to divide their resources between growth and reproduction (see also Koene & Ter Maat, 2004).

Both body weight and shell length were recorded in this study. Because these are, respectively, three-dimensional and one-dimensional measures, for the most realistic fit we used a third-power curve. Our results clearly show that shell length can be used as a very reliable measure for body weight (under standard conditions), given that it explains 97.6% of the variation. Previous modelling of the growth of *L. stagnalis* under mid- and long-day (12L:12D and 16L:8D) conditions also revealed that shell length is a good predictor for body weight (Zonneveld & Kooijman, 1989; see also Zonneveld, 1992). In the latter study, the snail sizes that were tested experimentally were rather categorical; our study therefore confirms the previous findings over a more continuous range of lengths of snails that, importantly, all had the same age. This is useful information considering that this species has indeterminate growth.

The snail's size is also a good indicator of female reproductive output in *Lymnaea stagnalis* (Koene *et al.*, 2007). Nonetheless, previous choice experiments found no preference of focal animals for larger partners. That study did reveal that copulation duration was longer with larger sperm donors. The choice experiment presented here confirms this and shows again that copulation duration is determined by the size of the sperm donor and is independent of the size of the sperm recipient. In connection to this it is interesting to note that unpublished data show that in size-matched pairs the number of sperm transferred is not correlated with copulation duration, but only positively correlated with body weight of the sperm donor (GLM: copulation duration, $F_{(1,41)} = 0.888$, $P = 0.352$; Body weight, $F_{(1,41)} = 155.85$, $P < 0.0001$; M.J. Loose & J.M. Koene, unpubl.). Hence, although in pairs of larger animals more sperm were transferred, the duration of such inseminations does not reflect the amount of sperm transferred.

In conclusion, we find that these hermaphrodites do not distinguish between virgin and mated individuals when deciding to mate. Thus, although differential sperm allocation is found towards such animals (Loose & Koene, 2008), this does not imply a choice prior to copulation. This indicates that although sperm may be costly in this species, donating a smaller quantity of sperm is still more advantageous than donating no sperm at all. And the optimal solution in this case for the male function might be to inseminate both partners and allocate different amounts of sperm to each. Of course, the fact that focal individuals were isolated before the trail, and thus eager to donate sperm, may have reduced their choosiness. However, this would be very much the situation in the field when the animals become sexually active again after winter. The lack of choice is rather striking given the finding that they do donate different amounts of sperm according to these same mating histories (Loose & Koene, 2008). Moreover, the recognition of novel and familiar partners seems to be mediated by a mucus component (Koene & Ter Maat, 2007). All this indicates that the decision to mate as a male with an encountered individual and the decision about the amount of sperm to donate to this individual are two separate processes. The question then arises how these animals are able to differentially transfer sperm to partners with different mating histories? This most likely requires some kind of (chemo)sensory mechanism. Here, the peripheral neurons at the distal tip of the preputium could come into play. It is possible that these sensory neurons, with a dendrite extending through the preputial epithelium and an axon in the penis nerve (Zijlstra, 1972), can sense the mating history of the partner, thus allowing the animal to donate sperm accordingly. It is unclear whether these animals assess such aspects of their partners via chemical or tactile cues – a promising topic for future research.

## REFERENCES

ARNAUD, L. & HAUBRUGE, E. 1999. Mating behaviour and male mate choice in *Tribolium castaneum* (Coleoptera, Tenebrionidae). *Behaviour*, **136**: 67–77.

BALL, M.A. & PARKER, G.A. 2007. Sperm competition games: the risk model can generate higher sperm allocation to virgin females. *Journal of Evolutionary Biology*, **20**: 767–779.

BUKOWSKI, T.C. & CHRISTENSON, T.E. 1997. Determinants of sperm release and storage in a spiny orbweaving spider. *Animal Behaviour*, **53**: 381–395.

CAIN, G.L. 1956. Studies on cross-fertilization and self-fertilization in *Lymnaea stagnalis appressa* Say. *Biological Bulletin*, **111**: 45–52.

COOK, P.A. & WEDELL, N. 1996. Ejaculate dynamics in butterflies: a strategy for maximizing fertilization success? *Proceedings of the Royal Society of London, Series B*, **263**: 1047–1051.

DE BOER, P.A.C.M., JANSEN, R.F., KOENE, J.M. & TER MAAT, A. 1997. Nervous control of male sexual drive in the hermaphroditic snail *Lymnaea stagnalis*. *Journal of Experimental Biology*, **200**: 941–951.

DE VISSER, J.A.G.M., TER MAAT, A. & ZONNEVELD, C. 1994. Energy budgets and reproductive allocation in the simultaneous hermaphrodite pond snail, *Lymnaea stagnalis* (L.): a trade-off between male and female function. *The American Naturalist*, **144**: 861–867.

DEWSBURY, D.A. 1982. Ejaculate cost and male choice. *The American Naturalist*, **119**: 601–610.

ENGQVIST, L. & REINHOLD, K. 2006. Theoretical influence of female mating status and remating propensity on male sperm allocation patterns. *Journal of Evolutionary Biology*, **19**: 1448–1458.

GAGE, M.J.G. 1991. Risk of sperm competition directly affects ejaculate size in the Mediterranean fruit fly. *Animal Behaviour*, **42**: 1036–1037.

KOENE, J.M. 2006. Tales of two snails: sexual selection and sexual conflict in *Lymnaea stagnalis* and *Helix aspersa*. *Integrative and Comparative Biology*, **46**: 419–429.

KOENE, J.M., MONTAGNE-WAJER, K., ROELOFS, D. & TER MAAT, A. 2008. The fate of received sperm in the reproductive tract of a hermaphroditic snail and its implications for fertilisation. *Evolutionary Ecology*, in press.

KOENE, J.M., MONTAGNE-WAJER, K. & TER MAAT, A. 2006. Effects of frequent mating on sex allocation in the simultaneously hermaphroditic great pond snail. *Behavioral Ecology and Sociobiology*, **60**: 332–338.

KOENE, J.M., MONTAGNE-WAJER, K. & TER MAAT, A. 2007. Aspects of body size and mate choice in the simultaneously hermaphroditic pond snail *Lymnaea stagnalis*. *Animal Biology*, **57**: 247–259.

KOENE, J.M. & TER MAAT, A. 2004. Energy budgets in the simultaneously hermaphroditic pond snail, *Lymnaea stagnalis*: a trade-off between growth and reproduction during development. *Belgian Journal of Zoology*, **134**: 41–45.

KOENE, J.M. & TER MAAT, A. 2007. Coolidge effect in pond snails: male motivation in a simultaneous hermaphrodite. *BioMedCentral Evolutionary Biology*, **7**: 212.

LOOSE, M.J. & KOENE, J.M. 2008. Sperm transfer is affected by mating history in the simultaneously hermaphroditic snail *Lymnaea stagnalis*. *Invertebrate Biology*, **127**: 162–167.

MARTIN, O.Y. & HOSKEN, D.J. 2002. Strategic ejaculation in the common dung fly *Sepsis cynipsea*. *Animal Behaviour*, **63**: 541–546.

PITNICK, S. & MARKOW, T.A. 1994. Male gametic strategies: sperm size, testes size, and the allocation of ejaculate among successive mates by the sperm-limited fly *Drosophila pachea* and its relatives. *The American Naturalist*, **143**: 785–819.

PIZZARI, T., CORNWALLIS, C.K., LOVLIE, H., JAKOBSSON, S. & BIRKHEAD, T.R. 2003. Sophisticated sperm allocation in male fowl. *Nature*, **426**: 70–74.

SAUTER, A. & BROWN, M.J.F. 2001. To copulate or not? The importance of female status and behavioural variation in predicting copulation in a bumblebee. *Animal Behaviour*, **62**: 221–226.

SCHAUS, J.M. & SAKALUK, S.K. 2001. Ejaculate expenditures of male crickets in response to varying risk and intensity of sperm competition: not all species play games. *Behavioral Ecology*, **12**: 740–745.

SIMMONS, L.W., CRAIG, M., LLORENS, T., SCHINZIG, M. & HOSKEN, D. 1993. Bush-cricket spermatophores vary in accord with sperm competition and parental investment theory. *Proceedings of the Royal Society of London, Series B*, **251**: 183–186.

SIVA-JOTHY, M.T. & STUTT, A.D. 2003. A matter of taste: direct detection of female mating status in the bedbug. *Proceedings of the Royal Society of London, Series B*, **270**: 649–652.

TER MAAT, A., ZONNEVELD, C., DE VISSER, J.A.G.M., JANSEN, R.F., MONTAGNE-WAJER, K. & KOENE, J.M. 2007. Food intake, growth, and reproduction as affected by day length and food availability in the pond snail Lymnaea stagnalis. *American Malacological Bulletin*, **23**: 113–120.

TSITRONE, A., DUPERRON, S. & DAVID, P. 2003. Delayed selfing as an optimal mating strategy in preferentially outcrossing species: theoretical analysis of the optimal age at first reproduction in relation to mate availability. *American Naturalist*, **162**: 318–331.

TSITRONE, A., JARNE, P. & DAVID, P. 2003. Delayed selfing and resource reallocation in relation to mate availability in the freshwater snail *Physa acuta*. *American Naturalist*, **162**: 474–488.

VAN DUIVENBODEN, Y.A. 1983. Transfer of semen accelerates the onset of egg-laying in female copulants of the hermaphrodite freshwater snail, *Lymnaea stagnalis*. *International Journal of Invertebrate Reproduction*, **6**: 249–257.

WEDELL, N. 1992. Protandry and mate assessment in the wartbiter *Decticus verrucivorus* (Orthoptera: Tettigoniidae). *Behavioral Ecology and Sociobiology*, **31**: 301–308.

WILSON, J.R., KUEHN, R.E. & BEACH, F.A. 1963. Modification in the sexual behavior of male rats produced by changing the stimulus female. *Journal of Comparative Physiology and Psychology*, **56**: 636–644.

YASUI, Y. 1996. Males of mite, *Macrocheles muscadomesticae*, estimate a female's value on the basis of her age and reproductive status. *Journal of Insect Behavior*, **9**: 517–524.

ZIJLSTRA, U. 1972. Distribution and ultrastructure of epidermal sensory cells in the freshwater snails *Lymnaea stagnalis* and *Biomphalaria pfeifferi*. *Netherlands Journal of Zoology*, **22**: 283–298.

ZONNEVELD, C. 1992. *Animal energy budgets: a dynamic approach*. PhD thesis, VU University Amsterdam, The Netherlands.

ZONNEVELD, C. & KOOIJMAN, S.A.L.M. 1989. Application of a dynamic energy budget model to *Lymnaea stagnalis* (L.). *Functional Ecology*, **3**: 269–278.