Belg. J. Zool. — Volume 124 (1994) — issue 1 — pages 11-19 — Brussels 1994

Manuscript received on 16 November 1993

THE INFLUENCE OF SPERM PRECEDENCE PATTERNS AND MATING COSTS ON COPULATION DURATION IN ODONATES : PREDICTIONS AND SUPPORTING DATA.

by

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SUMMARY

NUYTS and MICHIELS (1993) developed a model that predicts how insect copulation duration should vary under varying conditions of intra-male competition, mating systems and copulatory mechanisms in order to optimize the male's reproductive success. In this paper, we compare the predictions of this model with data of odonates. In general, the data seem to support the predictions, especially the prediction that territoriality, a lower take-over probability, a higher female encounter rate or a shorter time between copulation and first oviposition bout shorten copulation. We conclude that the model is well-suited for odonates, and point out how it can have some practical use.

Key-words : optimality model, copulation duration, Odonata, sperm competition, reproductive success, territoriality, take-over, encounter rate, oviposition.

INTRODUCTION

Copulation duration varies widely in odonates, both within one species (UÉDA, 1979 ; MILLER, 1983 ; NOMAKUCHI *et al.*, 1984 ; SIVA-JOTHY, 1987 ; ALCOCK, 1988 ; SIVA-JOTHY and TSUBAKI, 1989a ; WOLF *et al.*, 1989 ; MICHIELS, 1992) and between species (WAAGE, 1984a, 1986). The authors listed discuss many different explanations for these differences. Only few of them show that some of these hypotheses are evolutionarily stable. In this paper, we present the (relevant) predictions of a theoretical model (NUYTS and MICHIELS, 1993 ; NUYTS and METZ, unpublished) and use these to explain the observed differences in copulation duration. The strength of our model is threefold :

(i) The model assumes that males optimize copulation duration to maximize their reproductive success. As a results, the predictions are both causal and evolutionarily stable. By adding stability we reinforce the importance of existing hypotheses.

(ii) All but one of the results presented in the literature can be explained by this model. Hence, it seems to provide a unifying theory on the influence of parameters on the copulation duration of odonates. It is, however, sufficiently flexible to be applied to a wide range of different taxa.

(iii) All this suggests that the model can be used to indicate new research avenues in dragonfly copulatory behaviour.

TABLE 1

Abbreviations used in the text

t : copulation duration.
h : time between copulation and first oviposition.
ovi + : copulation duration increases with increasing time between copulation and oviposition.
take + : copulation duration increases with increasing probability of take-over between copulation and oviposition.
enc + : copulation duration increases with increasing time to encounter the next receptive female.
cost − : copulation duration decreases with increasing territorial or energetic costs of a copulation.

THE MODEL OF NUYTS AND MICHIELS (1993)

The model assumes that male reproductive success is a monotone increasing, concave or sigmoid function of copulation duration (Fig. 1). It also assumes that copulation duration is not limited because of sperm depletion and that it has no effect on the probability of a take-over, nor on the time between encounters with receptive females. This implies, amongst other things, that rival males never interrupt a copulating pair. In several odonates, a short copulation can yield a high immediate second male's precedence (P_2), since the last male's sperm initially has a positional advantage. But, due to long term sperm mixing, this advantage may decrease with time. Hence, P_2 decreases in time even without rematings. In such a species longer copulations are necessary to maintain a high P_2 over time, since longer copulations increase the volume of the male's sperm and/or decrease the volume of the rival's sperm within the female sperm stores.

If every male has only one optimal copulation duration (only inter-individual differences between conspecific males), the following predictions can be made.

(1) Males that face higher risks will copulate longer. It is as if they make the best of a bad job, by exploiting their opportunities more extensively. More precisely :

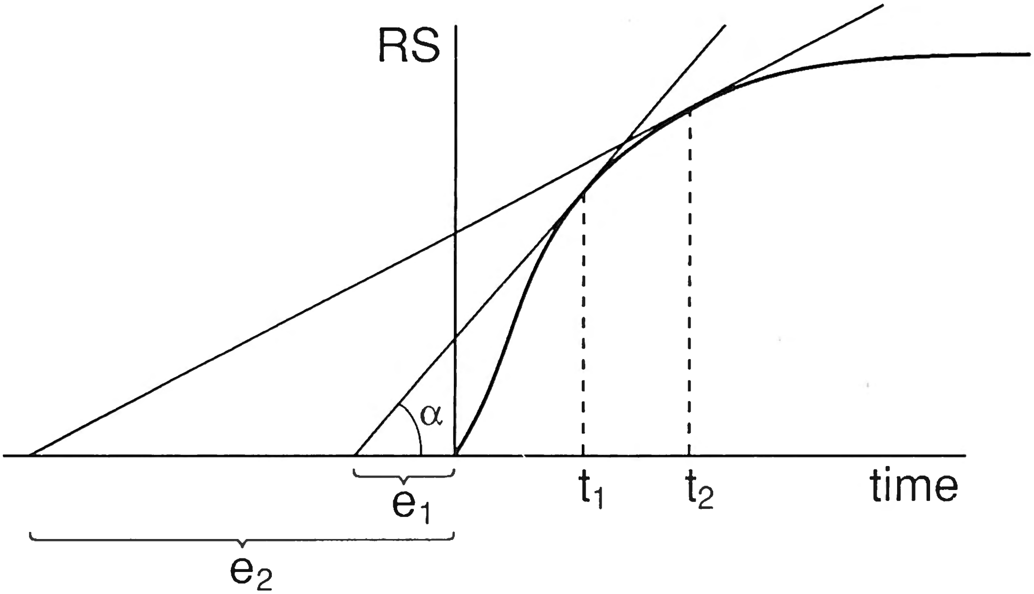

Fig. 1. — A simple representation of the maximization principle. The only costs taken into account are the encounter time to the next receptive female (e) and the copulation duration (t) (cfr PARKER and STUART, 1976). Copulation duration is optimised if

$$\frac{\text{reproductive succes}}{\text{costs}} = \frac{\text{RS}}{\text{e} + \text{t}} = \text{tg}\ (\alpha) \text{ is maximized.}$$

A larger encounter time increases optimal copulation duration. The optimal duration, associated with e_1 (e_2) is noted as t_1 (t_2).

(1a) If P_2 decreases in time due to long term sperm mixing, a male that can expect a longer time between copulation and the first oviposition, will copulate longer. (Prediction *ovi*+).

(1b) A higher take-over probability before or during the first oviposition bout will result in an increase of the optimal copulation duration for individual males, if long term sperm mixing occurs. (Prediction *take*+).

(1c) The optimal copulation duration will also increase with the female encounter time for the male. (Prediction *enc*+). Courting is included as part of the encounter time. If guarding duration is independent of the copulation duration, it has two contradictory effects. As guarding needs time, it has the same influence on t as the encounter time, and so it prolongs copulation. But since guarding reduces the probability of a take-over, it should also shorten copulation duration.

(2) Males that face higher energetic and territorial costs copulate shorter. As an essential difference between costs and risks, risks are independent of the copulation duration, whereas the costs depend on the copulation duration. If guarding duration is positively correlated with copulation duration, in the same way as are the energetic costs, it has only a negative effect on t. (Prediction *cost*−).

If every species has only one optimal copulation duration the predictions (ovi +), (enc +) and (cost-) stand firm. For mathematical reasons with biological relevance, the model does not allow a prediction on (take +) in this situation (NUYTS unpublished).

DISCUSSION OF ODONATE EXAMPLES

In the following discussion, abbreviations are used according to Table 1.

Within species

MILLER (1983) found significant differences in copulation duration between territorial (190.6 ± 330s) and nonterritorial (1699s ± 1398s) *Orthetrum chrysostigma* (BORM) males. Since territorial males encountered females nine times more often than nonterritorial males, this difference is in agreement with prediction (enc+) of the general model. Also, post-copula take-overs were less common in territorial than in nonterritorial males, since the former guard ovipositing females (MILLER, 1983). If sperm mixing occurs in *O. chrysostigma*, this lower number of take-overs for territorial males will also shorten t (take+). Finally, territorial costs must be taken into account (cost-), since twice a territorial male was seen to terminate copulation abruptly in order to chase an intruder (MILLER, 1983). This suggests that a male shortens t in response to the increased risk of a successful take-over of his territory. Continued copulation would make it increasingly difficult to chase away the intruder.

In *Orthetrum cancellatum* (L.), territorial males at the water have short copulations (21.0 ± 13.5 s) resulting in 10-15 % removal of rival sperm (SIVA-JOTHY, 1987). Wandering males mated for 894 ± 142 s, resulting in almost 100 % removal. SIVA-JOTHY (1987) attributed this difference to the very short encounter time for territorial males relative to the opportunistic males (16 times longer) (enc+), and, secondly, the short time between copulation and a mate's first oviposition for territory holders ($h \approx 0$) (ovi+). A third possible reason might be a difference in the number of take-overs. According to SIVA-JOTHY (1987) females deposited on average half their clutch before being grasped by a territorial male. Hence, if there are no take-overs by opportunistic males away from the water, both territorial and opportunistic males had a take-over probability of aprox. 0.5 per female. If there were unnoticed take-overs by opportunistic males, the number of take-overs could lead to increased copulation duration in opportunistic *O. cancellatum* (take +).

Mnais pruinosa pruinosa SELYS males show three alternative mating tactics, each characterized by a specific copulation duration (SIVA-JOTHY and TSUBAKI, 1989a, b). Territorial males defend pieces of wood, have copulations of intermediate length and guard their ovipositing females. Nonterritorial, wandering males have long matings at feeding sites. Sneaky males secure females that are ovipositing in another male's territory. Their copulations are short. Probably to avoid discovery by the territory owner, as this invariably results in remating of the female with the territory owner (SIVA-JOTHY and TSUBAKI, 1989a,b). In our notation this means that the number of take-overs depends on t, which we assumed not to be so. Hence, the model is not valid for sneaky *M. p. pruinosa* males. Under natural conditions, the time between copulation and the first oviposition is longer for nonterritorial males than for territory owners (SIVA-JOTHY and TSUBAKI, 1989a). Since long term sperm mixing has been demonstrated (SIVA-JOTHY and TSUBAKI, 1989a), a smaller h is predicted to result in a shorter copulation duration (ovi+). Territory owners experience fewer take-overs than nonterritorial ones (SIVA-JOTHY and TSUBAKI, 1989a). Since mixing has been demonstrated and more than one oviposition bout can be taken into account (NOMAKUCHI, 1988 ; SIVA-JOTHY and TSUBAKI, 1989a), fewer take-overs will shorten t (take+). By experimentally introducing males and females, SIVA-JOTHY and TSUBAKI (1989b) found that t did not depend on the number of territorial intrusions by other males, nor on the female encounter rate. Only the place where a female was captured and copulated with explained variation in t. From this, we have the feeling that insects don't measure encountertime, but the presence or absence of an oviposition site and that they use this as an on/off trigger to adjust their copulation duration. Both in *Mnais pruinosa* (SIVA-JOTHY and TSUBAKI, 1989b) and in yellow dungflies *Scatophaga stercoraria* (L.) (WARD and SIMMONS, 1991) males do not adapt their copulation duration when the encountertime is reduced in an experimental way. But under natural conditions the encountertime is smaller in presence of an oviposition site (*S. stercoraria* : PARKER, 1971 ; *M. pruinosa* : SIVA-JOTHY and TSUBAKI, 1989b). As a result males adapt their copulation duration if females are presented near versus away from the ovipositon site (*M. pruinosa* : SIVA-JOTHY and TSUBAKI, 1989b ; *S. stercoraria* : WARD and SIMMONS, 1991). The influence of the encountertime seems only to exist in copulations at versus away from the oviposition site. Independence of the rate of territory intrusions seems to disagree with the model (cost−).

In *Sympetrum danae* (SULZER) a large variation in copulation duration exists (MICHIELS, 1992). Copulations shorten with increasing temperature, with time of the day, and for each additional mating of the male. The correlation with temperature probably has a physiological origin and has been mentioned earlier for insects (PARKER, 1971 ; UÉDA, 1979 ; LARSSON, 1989 ; PETERSSON, 1990). At high temperatures, males mate more rapidly with the same results than at low temperature. The time effect is most probably due to an increasing mating probability during the first half of the day (MICHIELS, 1992), which is equivalent to a decreasing encounter time (enc +). *S. danae* pairs mate before 13h00 (mean solar time), and hardly afterwards. Apparently, males become sperm depleted when mating several times a day (MICHIELS, 1992). PARKER (1992) modelled a comparable situation, and showed that it is adaptive to decrease copulation duration with each additional mating.

In all the former examples, males « make the best of a bad job », by adapting their copulation duration to a worse situation. In *Leucorrhinia intacta* (Hagen), the situation is different. WOLF *et al.* (1989) found a significant difference in t between territorial and nonterritorial males. The short copulations (t_1) of territory owners resulted in less than 100 % immediate precedence, whereas the longer copulations of nonterritorial males (t_2) ensured 100 % immediate precedence. But territorial males that left their territory while in copula copulated as long as nonterritorial ones. Apparently, the territorial cost in *L. intacta* is high, and this cost shortens copulation. According to WALTZ and WOLF (1984) the overall gain per cost was equal for both tactics :

$$\frac{G(t_1)}{TC(t_1) + C(t_1)} = \frac{G(t_2)}{0 + C(t_2)},$$

with G(t) denoting the reproductive success when copulating during time t, TC(t) the costs due to copulating while territory owner, and C(t) all the other costs of copulating. If we assume that the probability of intrusions is greater in a territory than in the nearby grass, copulating in a territory will require more energy ($TC(t) > 0$). Occasionally, territory holders in copula chased away intruders (WOLF *et al.*, 1989), again increasing TC(t). When the territorial cost exceeds the benefits (the higher probability of meeting another female the same day), males will abandon their territory and become nonterritorial, resulting in diminished costs. We conclude that the two tactics are part of a mixed Evolutionary Stable Strategy (ESS), whereas two different ESS's, one with a lower pay-off, were concerned in the other species. Also in this species, the predictions (cost-) and (enc+) are fulfilled.

In *Calopteryx maculata* (de Beauvois) the conditions for an intraspecific difference in copulation duration exist. Territorial males have territorial costs (cost-) that result from mating due to a temporary absence from the territory (WAAGE, 1973). They encounter as much or more receptive females than wandering males (WAAGE, 1973) (enc +) and have a smaller take-over probability (WAAGE, 1979) (take+). But an essential assumption of the model is not fulfilled by this species. There is a biological limit for the copulation duration : after 1.0-1.5 minutes, 88-100 % of previous inseminated sperm is removed, and own sperm is inseminated (WAAGE, 1979). This means that the P_2-function is not concave everywhere, but it becomes horizontal after some copulation duration t_0 (for $t > t_0 : P_2(t) = 1$). Hence it is simply useless to copulate longer than this duration.

Between different species

WAAGE (1984a, 1986) compared different species, and suggested that short copulations are related to high mating rates, territoriality and non-contact guarding, intermediate copulation durations are related to low mating rates, nonterritoriality or opportunism and oviposition in tandem, and long copulations with infrequent mating and no postcopulatory guarding. This is in agreement with the predictions (enc+) and (cost−) of the model useable for interspecific comparison.

Males that have on average energetically more costly copulations should copulate shorter than males that copulate energy-efficiently (cost−). Costs can be higher when copulation takes place in flight or at a less optimal temperature. Male dragonflies that copulate in flight do so for a few seconds only (SAKAGAMI *et al.*, 1974), while copulations on a perch last a few minutes to several hours (CORBET, 1980).

CONCLUSION AND FURTHER SUGGESTIONS

From the examples above, we conclude that our model is appropriate to predict copulation behaviour for odonates. Only one (experimental) result was in contradiction with the model (*M. pruinosa* (cost−)). Therefore the model can be used to generate or contradict hypotheses and to point out experiments to be done, such as :

(a) UÉDA (1979) interprets the long copulation duration of wandering relative to territorial males in *Sympetrum parvulum* BARTENEFF as a kind of postcopulatory guarding. His major argument is that at low densities the copulation duration of both types of males is the same. This hypothesis might be correct, but a part of the longer duration at high densities can also be caused by *e.g.* higher encounter time (enc+) and increased take-over risk (take+) for wandering males (UÉDA, 1979), and probably a higher territorial cost (cost−) for the territory owners.

(b) In *Erythemis simplicicollis* (HAGEN) territorial males copulate more frequently (enc+), they have a higher probability of immediate oviposition (ovi+), and they guard their mates more effectively than nonterritorial satellites (take+) (MCVEY, 1981). Long term sperm mixing has been proven (MCVEY and SMITTLE, 1984). Hence, we strongly expect a difference between territorial and nonterritorial males. Data to support this prediction are not yet available.

(c) WAAGE (1984b) found the same restriction in *Calopteryx dimidiata* BURMEISTER as in *C. maculata*. Therefore we predict no different copulation durations.

(d) In order to see if an on/off trigger is a good explanation for the independence between copulation duration and artificially decreased encountertime, it might be interesting to decrease experimentally the encountertime for males at and away from the oviposition site in other species.

(e) If a species doesn't fulfill several predictions, it might be worthwhile to look for an overriding factor, such as a very large difference between males, rather than between groups of males, or a strong female influence.

(f) If the encounter time is very large, relative to lifetime, the optimisation principle as such may not be fulfilled. Then the right currency to optimize is lifetime reproductive success, rather than gain per unit of time. Time loss is not important anymore. Then we expect the copulation duration to be limited by other factors, such as sperm depletion, the maximal P_2 being reached after some time, an external physical constraint or female unwillingness to continue. Large encounter times are reported for *Hetaerina vulnerata* Selys (e = 3.5 days (ALCOCK, 1982)). Analogously, no variation in copulation duration will be caused by the parameters in the model if the mating system limits the males to one mating a day, as is the case in *e.g. Argia apicalis* (Say) (BICK and BICK, 1965), *Ischnura graellsii* RAMBOR (CORDERO, 1990), and *Ischnura elegans* (van der Linden) (MILLER, 1987). We expect the parameters of the model not to influence the copulation duration.

ACKNOWLEDGMENTS

We are grateful to Hans Metz, André Dhondt and two anonymous referees for helpful comments on an earlier draft of the manuscript. Nico K. Michiels was supported by a Senior Research Assistantship of the Belgian National Fund for Scientific Research.

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