Singer, F. 1987.

<u>Animal Behaviour</u> 35:

1575 - 1577.

A Physiological Basis of Variation in Postcopulatory Behaviour in a Dragonfly Sympetrum obtrusum

Male dragonflies show two forms of mate-guarding behaviour: (1) tandem guarding, in which the male holds the female by the head during oviposition, and (2) non-contact guarding, in which the male hovers or perches above the female during oviposition and chases away intruding males.

Most hypotheses for differences between species have focused on the fitness consequences of each form of mate-guarding behaviour. Tandem guarding reduces the chances of take-over but males are less free to pursue other matings and to defend

territories. Non-contact guarding increases the chances of take-over, but males are free to pursue other activities, while possibly incurring reduced predation risks (Ueda 1979; Sherman 1983; Waage 1984).

Within-species variation in mate-guarding behaviour is rare in dragonflies. However, Ueda (1979) showed that in Sympetrum parvulum, territorial males always used non-contact guarding, while those without territories used non-contact guarding at low densities but switched to tandem guarding at high densities, presumably in response to a high risk of take-over.

Sympetrum obtrusum males also use both types of mate guarding. This variation in mate-guarding behaviour is surprising, as tandem guarding affords greater protection against take-overs in this species (1) out of 41 taken over during tandem guarding in contrast to 5 out of 45 taken over during non-contact guarding; P = 0.035, Fisher exact test). In this paper I consider three factors that may determine which form of mate-guarding behaviour is used: (1) conditions of high male-male competition may favour the more secure tandem guarding, (2) conditions of high female availability may favour the less constraining non-contact guarding (to afford access to more females), and (3) unfavourable thermal conditions (low air temperature and strong winds) may impose high physiological costs that restrict males to using non-contact guarding. Using a statistical model, I present evidence supporting the hypothesis that the type of mate-guarding behaviour a male uses is determined by his physiological state.

S. obtrusum is a small libellulid dragonfly that mates and oviposits in tall vegetation on the periphery of ponds and marshes. My observations of mating pairs were made in 1984 and 1985, on a small shallow pond at Cedar Creek Natural History Area in East Bethel, Minnesota. For each observation I recorded mating time (time from first sighting until end of mating), type of mate-guarding behaviour, duration of oviposition period and time in tandem (if applicable).

In 1984, I watched pairs until the end of oviposition or until I lost sight of them. Observations from 1984 indicated that males that tandem-guarded for 20 s continued to do so for at least 60 s, although not necessarily until the female finished ovipositing. Thus for most observations in 1985, I captured mating pairs 20 s after the end of mating. Oviposition was scored in tandem only if the pair remained in tandem for that entire 20-s period. I immediately measured the thoracic temperature (T_{th}) of the male (T_{thn}) and female (T_{thr}) with a thermister probe, and then measured the thoracic temperature of the nearest unmated male (T_{thr}) as a

control. By restricting oviposition to 20 s. I reduced the possible impact of tandem flight on T_{th} . A comparison of T_{thm} with T_{th} , showed no difference in T_{th} , thus it is unlikely that 20 s of tandem flight significantly elevated T_{thm} .

After each observation I calculated local density by counting dragonflies in the 3×3 -m quadrat in which oviposition occurred. Total dragonfly density was estimated every hour from counts in six quadrats chosen at random.

Models of the best predictors of the type of postcopulatory behaviour were formulated using logistic regression (an analogue to least squares regression for a binomial response variable). The first variable incorporated into the model had the maximum effect on baseline deviance (ΔG^2) defined as $2\Sigma\{[v\log_e(v/p)] + (1-v)\log_e[(1-v)(1-p)]\}$ (McCullagh & Nelder 1983) with y = the observed value and p = the fitted value from the model (probability of non-contact guarding). Then additional variables were added only if they significantly reduced the deviance (criterion $\Lambda(i) = 3.84$). Thus the first variable introduced was the one most highly correlated with the type of mate-guarding behaviour, and subsequent explanatory variables were introduced only if they significantly improved the predictive ability of the model after the effects of the first explanatory variable were accounted for.

Possible explanatory variables for the logistic regression analysis in 1984 included the following: date, time, quadrat, radiant energy, ambient temperature (T_a), wind speed, local male density, local female density, total male density, total female density, male weight, female weight, distance from shore and vegetation density. In the 1985 analysis I also considered T_{thm} and T_{thf} .

In 1984, when theoracie temperatures were not measured, the best predictors of mate-guarding behaviour were wind speed ($\Delta G^2 = 10.85$, P < 0.001) and T_a ($\Delta G^2 = 8.08$, P < 0.005). These two effects are independent of each other, as T_a was added to the regression equation after the variation explained by wind speed was accounted for. The 1984 model was

$$p = \frac{e^{(2.51 - 0.33(T_a) + 0.45(wind))}}{1 + e^{(2.51 - 0.33(T_a) + 0.45(wind))}}$$

where p = probability of non-contact guarding. Thus the probability of non-contact guarding was greatest when T_a was low and wind speed was high

In 1985, when thoracic temperatures were measured, T_{thm} was the best predictor of mate-guarding behaviour ($\Delta G^2 = 25\cdot12$, P < 0.001); when T_{thm} was below 30 C, non-contact guarding was used almost exclusively, and when T_{thm} was above 33 C, tandem guarding was used almost exclusively. At interme-

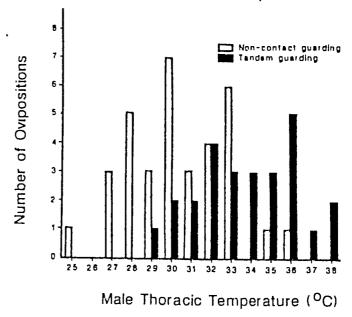


Figure 1. Frequency of each type of mate guarding in relation to thoracic temperature of the mated male (1985 data). The regression model is

$$p = \frac{e^{(11/27 - 0.62(I_{\text{thm}}) + 0.32(\text{wind}))}}{1 + e^{(11/27 - 0.62(I_{\text{thm}}) + 0.32(\text{wind}))}}$$

where p = probability of non-contact guarding.

diate temperatures both behaviours were used at high frequencies (Fig. 1). Adding wind speed to the regression after accounting for the effects of T_{thm} improved the fit somewhat ($\Delta G^2 = 5.44$, P < 0.025).

Low T, will constrain flight output most severely in dragonflies lacking thermoregulatory abilities (May 1976). The regression of T_{th} on T_{s} for S, obtrusion is linear and has a slope of 0-97, indicating that S, obtrusion is a poor thermoregulator. High wind speed may reduce flight output by interfering with the mechanics of flight, or by reducing thoracic temperature so that efficient flight is physiologically impossible (Church 1960).

Insect flight muscles have enormous fuel requirements (Weis-fogh 1964), thus a flying dragonfly requires more fuel than a perching dragonfly (Fried & May 1983). I measured flying time and perching time in ovipositing dragonflies on 2 consecutive days with little variation in T_a . Mean flying time $(\bar{X} \pm \text{SD})$ was much greater for males $(201.8 \pm 59.9 \text{ s})$ and females $(193.5 \pm 58.0 \text{ s})$ ovipositing in tandem than for males (71.9 + 33.5) and females $(46.7 \pm 29.6 \text{ s})$ using non-contact guarding, as both members of the pair are free to perch during oviposition after they detach (N=11) for tandem guarders. N=8 for non-contact guarders). This indicates that tandem guarding is energetically more expensive than non-contact guarding

Pairs that oviposit in tandem often detach before the female completes oviposition. Thus if tandem guarding is constrained energetically, time in tandem (TT) should vary in response to changes in environmental factors that permit extended flight. There was a significant positive correlation between TT and air temperature for dragonflies who used tandem guarding in 1984 (r_{19} =0.53, P=0.010), and a significant negative correlation between TT and wind speed (r_{19} =-0.60, P=0.026). The multiple regression model is TT=-66.90+10.64(T_a)-7.52(wind)($T_{2.10}$ =4.76, T_a =0.043).

The logistic regression shows no relationship between local or total male population density and variation in postcopulatory behaviour. This is inconsistent with the first hypothesis that males are changing their behaviour in response to the probability of take-over. The regression analysis also shows no correlation between non-contact guarding and female density. This opposes the second hypothesis that males use non-contact guarding to take advantage of periods of high female availability ($\Delta G^2 < 3.84$, Ns for all cases).

In many insect species, population density is correlated with ecological factors such as $T_{\rm a}$, radiant energy and wind speed (Heath et al. 1971; Wolf & Waltz 1984). Unless these factors are measured and analysed in a way that separates out these potentially confounding effects, differences in behaviour resulting from physiological constraints may be incorrectly attributed to social factors.

I thank P. Abrams, D. Blockstein, D. Bruggers, B. Eliason, J. Haarstad, L. Keuchle, K. Larntz, M. May, F. McKinney, B. Schmid, E. Waltz and L. Wolf for contributions to this manuscript. This study was supported with funds from the Department of Ecology and Behavioral Biology and the Field Biology Program at the University of Minnesota, the Minnesota Zoological Society and the Wilkie Fund for Evolution and Behavior of the Bell Museum of Natural History.

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(Received 9 February 1987; revised 5 March 1987; MS. number: As-454)