The Adaptive Significance of Non-contact Mate Guarding by Males of the Dragonfly, *Nannophya pygmaea* Rambur (Odonata: Libellulidae)

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Abstract — In *Nannophya pygmaea*, ovipositing females were frequently disturbed by conspecific males. Disturbed females often copulated with one of these males or flew away from the pool. Females which flew away from the pool due to male disturbance often returned later the same day and mated with different males. A territorial male would guard his ovipositing mate by hovering above her, presumably trying to prevent her from moving out of his territory. A non-territorial male would also guard his mate in a similar way, both at a vacant water area which was not occupied by any territorial males, or within the territory of a resident male. In addition, both territorial and non-territorial males chased intruding males in an attempt to prevent their mates from being stolen. Territorial males defended their mates better than non-territorial males. Both males and females often mated more than once in the course of a single day. Some territorial males copulated with a new female while another mate oviposited in their territories. This observation supported the "multiple mating hypothesis" proposed by Alcock (1979) and Ueda (1979) but other evidence suggested that this is an inadequate explanation for the non-contact guarding of *N. pygmaea*.

Among the odonates there is a great diversity in the extent to which males guard their mates after copulating with them (Sakagami et al. 1974; Corbet 1980). Males may a) release females after mating and consequently ignore them when ovipositing (non-guarding), b) perch or hover near ovipositing females, repelling other males from the immediate area (non-contact guarding), or c) remain in tandem with ovipositing females (contact guarding).

Despite the fact that tandem guarding seems to offer a male the best security against takeover of his mate (Ueda 1979), males of many dragonflies use non-contact guarding to protect their ovipositing mates (Sakagami et al. 1974; Corbet 1980). Three hypotheses have been proposed to explain the evolution of non-contact guarding: (1) it permits a male to acquire new mates even while guarding previous ones (multiple mating hypothesis; Alcock 1979 and Ueda 1979); (2) it allows a male both to maintain his territory and to guard mates (territory maintenance hypothesis; Sherman 1983 and Waage 1984); (3) it lowers the risk to males of predation during oviposition (Waage 1984). Although these 3 hypotheses are not mutually exclusive, their relative importance may differ with different dragonflies and their ecological environments.

During the course of a study on *N. pygmaea*, we collected data on post-copulatory mate guarding by males, and multiple mating by males and females of this species. Based on these data, we discussed the adaptive significance of non-contact mate guarding in *N. pygmaea*.

Methods

The study was performed on a moor near the campus of Kinjo Gakuin University, Omori, Nagoya, Japan. Within this area, we chose one of several small pools present for behavioural observations on dragonflies. The study site and methods have been described in more detail by Tsubaki & Ono (in press). Data collected on 9 sunny days between 8 and 25 July 1982 were used for the analysis since the density of males, excluding tenersals, was fairly constant (8–11 males...
in the study area) during this period. This density appeared to be neither extremely high nor extremely low compared with other seasons (personal observations from 1981 to 1985). We spent about 5 h, from 9:00 h until 14:00 h, each day watching the dragonflies. Almost all sexual activities take place during these hours (Nakamuta et al. 1983; Tsubaki & Ono, in press). In order to facilitate individual identification, marking was carried out from late May to September. Males and females found for the first time were captured in a net and were individually marked with small dots of colour paint on their forewings. As a result, almost all males and females in the study area were individuals which had already received marks during the observation periods.

We attempted to observe the sexual behaviours of all mature males simultaneously. We recorded the individual numbers of copulating pairs, the presence of mate guarding, whether a male copulated with a female while a previously mated female(s) was still ovipositing, whether the oviposition was disturbed by other males, and whether the female left the pond due to male disturbance.

Results

The mating system of N. pygmaea is considered to be a resource defence polygyny (Emlen & Oring 1977), in which males defend oviposition sites, such as pools or shallow rivulets. Sexually receptive females arrived at these sites to oviposit and were usually intercepted by these territorial males (Yamamoto 1968; Fujita et al. 1978; Nakamuta et al. 1983; Tsubaki & Ono, in press). After mating, both males and females perched on emergent grass separately (usually with a distance of 20 cm or less) for a while (usually 30–60 s), and then females usually oviposited within their mates territories, repeatedly penetrating the water surface with the tips of their abdomen. While the female oviposited, the male usually guarded her by hovering above her. Females stroke the water surface 8.9±7.4(S.D.) times (n=187) in an average oviposition bout of 6.2±5.0(S.D.) s (Nakamuta et al. 1983). Oviposition was completed after a sequence of 1 to 11 bouts (Nakamuta et al. 1983). Oviposition bouts were separated by periods of inactivity (perching), generally lasting 10–60 s. Duration of copulation was 32±7(S.D.) s (n=11) and a complete reproductive event (from the female arrival to female departure) took 314±95(S.D.) s (n=16) on average when pairs were not disturbed.

Non-territorial males adopted surreptitious mate acquiring behaviour on some territorial sites in the observation area: they attempted to perch as near as possible to another male's territory, often while the territory owner was mating or was occupied in defending the territory against other intruders. Usually a non-territorial male would be seen in several different territories during the course of a day. They tried to intercept females which were approaching territorial sites before the territorial male noticed the females. Thirteen of 21 observed copulations by non-territorial males (see Table 2) were made in this way. The females which mated with non-territorial males began oviposition either at vacant areas (14 of 21 copulations) or within territories of other males (4 of 21 copulations).

Multiple Mating

On each observation day, there were 8–11 mature and 0–3 immature (teneral) males in the study area. Among mature males, 5–8 males were territorial and others were non-territorial on each day.

Males almost always responded sexually to a newly arriving female, even while guarding a female recently mated. On 10 occasions, a territorial male copulated with a new female while another male oviposited in his territory (Table 1). In one case, a male (No. 132 on 8 June) guarded 3 females simultaneously.

In addition, a male would re-mate successively with the same female in a single day (n=16). In 9 cases, the re-mating occurred after the male chased the intruders and left his mate unprotected for a while (a few seconds). However, it was difficult to say whether the territorial male treated her as a new female or mated with her again because she might have mated with another male while he was absent. In other cases, the re-mating occurred when his mate, after mating, was inactive for a while (usually more than 3 min).

A female also often mated with 2 or more males in a single day (mean=1.49, S.D.=.76, range=1–4, n=107). Non-territorial males tried to steal ovipositing females from their mates. Successful mate stealings usually occurred in the following manner. When 2 or more intruding males approached an ovipositing female in her mate's territory, the territorial male chased one of the intruding males. This usually resulted in the female being unprotected for a while and the female was often stolen by one of the other intruders. We observed 6 females stolen by non-territorial males. Non-territorial males took females away from the territory to vacant sites in tandem and mated there.

Territorial males also often tried to steal females which were ovipositing at neighbouring territories. Moreover, females usually moved around within the mates territory while ovipositing but they sometimes approached or moved