“Riding” behaviour by males of *Conops quadrifasciata* (Diptera: Conopidae): Do females set up “riders” as targets for takeovers by larger males?

KEN PRESTON-MAFHAM

*Bodmin, Cornwall, UK*

*(Accepted 12 May 2005)*

Abstract

Males of *Conops quadrifasciata* “claim” females in late morning and then spend the rest of the day exposed as “riders” to attacks by other males. Male riders can respond to an attack by performing an abdomen-lift which denies the attacker access to the female’s genitalia. Attacking males can tailor their behaviour to suit the prevailing conditions. If a rider is engaged in a “repeat” copulation (as he does at regular intervals), the attacker “waits” beside the rider. If the rider is not in genitalic contact with the female, the attacker tries to mate with her immediately. It is proposed that females deliberately expose their riders to takeovers in order to gain the fittest mate.

Keywords: Conopidae, Diptera, flies, mating behaviour, post-copulatory guarding, riders

Introduction

The family Conopidae contains some 800 species of flies which are generally only rarely encountered. Many species mimic wasps, while the larvae are often endoparasites of bumble bees, passing through three instars within the host before finally killing it after 10–12 days. In at least some species the parasite’s final act before pupation is to manipulate the host’s behaviour so that it digs into the ground, providing a more secure overwintering site for the conopid pupa within (Müller 1994).

There are few descriptions of sexual behaviour in conopids, and these consist mainly of short anecdotal comments. Uffen (1998) noted “delayed” mating in a trio of *Conops quadrifasciata* in which two males were mounted side-by-side upon a female (troilism), but failed to interpret this behaviour. Jones (1999) noted troilism in *Sicus ferrugineus* and the frequent occurrence of non-copulatory “riding” behaviour by males of *C. quadrifasciata* and *Conops ceriaeformis*. Until the present study, no attempt has been made either to describe fully or to interpret these two most characteristic and puzzling aspects of conopid behaviour, i.e. troilism and prolonged episodes of riding.
Male conopids usually greatly outnumber females, both in the field and in collections. In polyandrous insects multiple copulations give rise to sperm competition, so that the last male to mate has the highest chance of siring any progeny (Parker 1970). If the sex ratio at a given site is strongly skewed in favour of males, selection to be the last male to mate will be especially strong. This did not seem to be the case in *C. quadrifasciata*, and was complicated by the fact that females appear to subject males to a prolonged “fitness test”.

**Study area and methods**

The study, totalling 17 h, was carried out over three consecutive warm sunny days in early September 1993. It was not possible to mark individual males and females for recognition purposes. This was not a major drawback, as it was often possible to maintain observation of a riding pair, plus one or more single males, for periods in excess of 2 hours. The study site was Oversley Wood near Alcester in Warwickshire, England. This wood has been highly modified for forestry purposes, and presently consists of a mixture of deciduous and coniferous trees.

I conducted the study along a 30m stretch of track bordered on one side by coniferous plantations and on the other by mixed deciduous woodland. The study stretch was densely bordered by flowering plants, interrupted at either end by trees. Both sexes of *C. quadrifasciata* visited the dense stands of creeping thistle (*Cirsium arvense*) and marsh ragwort (*Senecio palustris*) which grew alongside the track. As many as 16 individuals of both sexes were often present simultaneously along this 30 m stretch. In a concurrent survey of the rest of the track through the wood (just over 2.5 km), only five more *C. quadrifasciata* were located, despite an abundance of suitable flowers.

**Results**

*Male–female interactions—establishing contact*

I did not see any riding pairs before 11:06 h, after which they started to appear frequently. I noted the first males just after 10:00 h, working their way back and forth along the 30 m study stretch, turning back when they reached the trees at either end. They frequently jumped upon and briefly “tested” a wide variety of insects. Targets reasonably similar to conspecific females, i.e. with black and yellow banding, included conspecific males, males of *C. flavipes*, *Vespula* spp., social wasps, and hoverflies (Syrphidae) in the genera *Syrphus* and *Helophilus*. Targets which did not much resemble conspecific females either in size, shape or colour included honey bees (*Apis mellifera*) and several kinds of large and medium-sized flies, especially the tachinid *Tachina fera*. This large, plump bristly brown fly does not resemble a female *C. quadrifasciata* in any respect. All contacts between males of *C. quadrifasciata* appeared to be cases of mistaken identity, and there was no evidence of physical rivalry.

I made only a single observation of the initial contact between male and female. Without any prior courtship the male dropped on to the female’s back and “pinned” her to the flower on which she was feeding. He fell slightly to one side of the female, so that he only grasped her with the legs on his right side; the rest of his body and legs remained in contact with the flower. The female responded by assuming a very strange posture, with her body pressed down closely on the flower and her legs spread outwards almost horizontally. She remained immobile in this “spreadeagled” posture while the male inched his way slowly
across her body so that he could mount the dorsal surface of her thorax. He appeared to take considerable care to keep the female “pinned down”, always keeping all three right-hand legs in firm contact with her. Once mounted, he reached backwards over the tip of the female’s abdomen with his posterior abdominal segments and clasped the apex of the female’s abdomen between his theca and his genitalia. The female’s much larger theca, which she uses to get a firm grasp on a host when ovipositing, was not involved. The female made no attempt to resist, and resumed feeding as soon as genitalic contact was fully established.

Once a female has gained a rider, she appears to spend the rest of the day carrying him around as she feeds. On the warm, sunny days covering the study period, riding pairs began to disappear between 17:30 and 18:00 h, with none seen after 18:08 h. The maximum likely period during which a female carries a rider is therefore around 7 h. I kept one pair under observation for 4 h 52 min, and three more pairs for 2–3 h each. Males spent the majority of their riding time in non-genitalic contact, but made regular repeat copulations (mean interval between copulations $43.14 \pm 7.1$ min, $n=14$). These 14 repeat copulations lasted 2–14 min, with 11 in excess of 10 min. In two instances males extended copulation beyond 14 min, upon which the female almost immediately started to struggle. One female struggled so violently that she fell off the flower on to the leaf below. This caused the male to disengage his genitalia, after which the female quickly resumed her position on the flower, complete with rider. In neither case did the female appear capable of forcing the male to uncouple.

Response of male searchers to females with riders

A searching male apparently locates riding males visually. On several occasions a riding pair and a searching male were on opposite sides of a creeping thistle capitulum, only some 1 cm apart but invisible to one another. Despite such close proximity, the searching male remained unaware of the pair’s presence, making it unlikely that pheromones play any role in mate location. Searching males which locate a riding couple usually make an immediate attempt to dislodge the rider. Observations on four pairs over 11 h indicated that each pair on average receives a takeover attempt every 14 min. However, these are not distributed evenly throughout the day, but are concentrated in the late morning and early afternoon, when the interval can drop to 6 min. Frequency and intensity of takeover attempts then diminish towards evening, such that after 16:00 h, they are normally more than 50 min apart.

The sequence of events which follows contact between an attacking male and a rider is fairly stereotyped. “Attackers” always make an initial attempt to dislodge a rider by ramming him, followed by a brief struggle to pull him off his mount. What happens next depends on the circumstances prevailing, and there are two possibilities:

1. The riding male is not engaged in one of his regular repeat matings. This means that the female’s genitalia are available to the anal claspers of the attacking male. He attempts to establish genitalic contact by mounting the dorsal surface of the riding male’s thorax. The attacker then tries to thrust his abdominal tip past and over the posterior segments of the rider’s abdomen, so that the female’s genitalic segment can be grasped and lifted upwards into the correct position for copulation. The rider responds to these actions by abruptly lifting his abdomen upwards at an angle of almost $90^\circ$ (Figure 1), raising the attacker away from the female. The rider will respond with any number of
“abdomen-lifts” until the attacker gives up. Abdomen-lifts were always successful in denying access to the female’s genitalia, even when the attacking male was visibly larger than the incumbent (Figure 2).

2. The female’s genitalia are occupied in a repeat mating. It is impossible for the attacker to gain access to the female’s genitalia, a situation that he seems to recognize at once. He immediately adopts the alternative strategy of perching alongside the riding male (Figure 3), remaining quiescently in this “waiting” position for $3.34 \pm 0.78$ min, $n=7$. In every observed instance the waiting male eventually flew off, without any attempt at establishing genitalic contact with the female.

The variable intensity of takeover attempts

The intensity of an attacker’s takeover attempt varies noticeably according to a number of factors. These are:

1. The relative sizes of attacker and rider. When the attacker is visibly smaller than the rider, the attack is pressed home with little vigour. The attacker just momentarily mounts the rider before flying off ($n=9$).

2. When both attacker and rider are evenly matched in size. Under these circumstances the degree of intensity of the attack varies according to two further subsets of criteria, namely:

   (a) If the attacker is making contact for the first time with a previously “unknown” pair. This most often happens from around 11:15 h until around 14:30 h. Takeover
attempts are usually intense, but seldom last for more than 2 min \((n=26)\); none was seen to be successful.

(b) If the attacker has previously made fruitless attempts to displace a rider, and has therefore learned by experience that this particular opponent is “unbeatable”. Because riding pairs and searching males do not move far, I could often keep them in view for an hour or more after a failed takeover attempt. On one occasion two males first made “serious” attempts, and upon their return 23 min later they mounted attacks on the same ‘riding’ pair, still on the same flower on which the original attacks had taken place. The new attacks were much briefer \((3\text{ and } 5\text{ s instead of }42\text{ and }55\text{ s})\) and less vigorous. Both attackers moved away, but returned a few minutes later and again encountered the same pair (still on the same flower). This time the two males made only perfunctory contact with the rider before moving on. One of the males returned 5 min 6 s later, but this time he ignored the riding pair (still on the same flower), despite stopping to feed on a flower only a few centimetres away.

3. When the attacker is considerably larger than the rider. This only occurred once during the study period and resulted in the sole example of a successful takeover. The attacking male rammed the riding pair with such force that he knocked them off their flower on to the leaves below. The female instantly adopted the same spreadeagled stance as when first claimed by her rider. She maintained this immobile stance for the next 10–15 min. She did not attempt to struggle free, even though at times contact with both males was probably sufficiently loose to enable her to do so. During this time the attacker

Figure 2. Despite being some 20% larger than the incumbent rider, this attacker has failed to establish genitalic contact with the female, having been thwarted by repeated abdomen lifts. ‘Ramming’ seems to be the only effective way of making a takeover.
gradually forced his body in-between rider and female (Figures 4, 5), upon which the rider released his grip and flew off. The new rider then immediately copulated with the female, who made no attempt to resist (Figure 6). This lack of resistance is important, because her former rider had made a repeat copulation only 9 min 23 s earlier. She should therefore have resisted any attempt at a repeat mating so soon. It thus appears that females recognize a “victorious” newcomer and immediately permit a first copulation when a repeat from an existing rider would be denied. By contrast, whenever an existing rider tries to re-mate immediately after resisting an unsuccessful takeover attempt, the female resists by violently shaking her body ($n=7$).

Figure 3. A male attacker waiting beside a rider who is engaged in a repeat copulation. Both males are about the same size.

Figure 4. This attacking male (on left) has rammed a riding couple with such force that they were knocked off their flower on to a leaf. The female remained stationary for the several minutes needed for a successful replacement of her partner. Comparison of head-widths indicates that the attacker is considerably larger than the rider.
Female behaviour on flowers

A solitary female will spend from a few seconds to several minutes on a thistle capitulum before moving on to another, quickly rejecting any which are past their prime and therefore offer few nectar rewards. By contrast, a female with a rider will spend up to 90 min on a single capitulum, even when this is well past its prime.

Discussion

There are a number of ways in which female insects can acquire “fit” mates. Intrasexual competition between males usually ensures that not all of their number end up by mating,
and often it is only the biggest which do so (Alcock et al. 1977; Alcock 1990). Males can compete to gain access to females in a number of ways. They can compete among themselves to monopolize resources which are of value to females, such as food-sources or oviposition sites. Examples of such resource defence polygyny (Emlen and Oring 1977) are found in insects as diverse as grasshoppers (Otte and Joern 1975), neriid flies (Mangan 1979), and bees (Frohlich and Parker 1985). When resources cannot be economically monopolized, males may engage in scramble competition (Thornhill and Alcock 1983), fighting directly over access to females around nesting, resting, or feeding sites.

Males of *C. quadrifasciata* search for females on flowers. They have no other viable option, as females emerge unpredictably from parasitized hosts (a bumble bee, *Bombus lapidarius*) which die at random. Searching on flowers ought to be an unprofitable strategy, as females usually occur at very low densities and visit many kinds of very common flowers. However, the daily 6–7 h concentration of 12–14 individuals of both sexes of *C. quadrifasciata* in the short 30 m study strip seems significant, especially when compared with only five more individuals recorded along a further 2.5 km of flower-filled trackside. It therefore seems that some kind of rendezvous mechanism is in operation. This could involve some intrinsic quality of the site itself, recognizable to both sexes.

In *C. quadrifasciata* the first male to “claim” a female on a flower then has to guard her for the rest of the day against competing males. This would seem to be scramble competition followed by extended contact-guarding, a common category within insects (Hughes 1979; McLain 1989). However, the prolonged nature of the riding behaviour seen in *C. quadrifasciata*, and the very exposed situation in which the male finds himself, invite a further question. Do females of this species ensure that they acquire fit mates by “offering up” their riders as “sitting targets”, inviting repeated attacks by rival males?

Most female insects are able to exercise a certain degree of “choice” by refusing to mate with any given male. They can do this in a number of ways, for example by making it physically impossible for a male to mount by kicking him away (Hancock et al. 1990), or to stay mounted, by shaking him off (Bland 1987); by refusing to adopt a specific posture necessary for mating (Grant and Brady 1975; Freidberg 1981); by bending the genitalia inwards to deny access to them (Pinto 1975); by refusing to open a genitalic pore (Conner 1989); or by performing a stereotyped rejection display (Alcock 1977). One alternative strategy that does not require female co-operation, namely rape, is relatively rare in insects (Thornhill 1980). Thus it appears that female co-operation is normally essential.

It seems that females of *C. quadrifasciata* are unable to deny genitalic access to males. Females can make life difficult for a rider by shaking, but are unable to force males to dismount.

As males do not compete directly with one another while searching for mates, a female’s best way of obtaining a fit partner may be to expose her existing mate to competitive “testing”, by adopting a conspicuous and almost fixed feeding position on flowers for much of the day. Evidence for this being a “deliberate policy” is based on the considerable difference between the behaviour of solitary females and those with a rider. The lengthy periods that females with riders will spend on semi-withered flowers makes it unlikely that they are feeding all the time. A better interpretation is that they are exposing their rider to competitive view in a place where other males are likely to be searching. Females seem reluctant to move to better-quality forage-sources, even when these are very close by and the move (even given the “penalty-weight” of her rider) would incur little extra cost.

For a mating system to evolve and become fixed the benefits must outweigh the costs. The female *C. quadrifasciata* has to endure the energy costs of carrying a male’s weight
around all day, but this is easily compensated for by increasing nectar-intake, given that the whole day can be spent on flowers. The benefits of acquiring a fit male are therefore probably acquired at comparatively low cost. Females with riders could incur an extra cost by exposing themselves for such long periods to potential predators. However, C. quadrifasciata is a convincing mimic of various common wasps which are generally shunned by most predators, thereby minimizing any risk.

Female-operated mating systems in which males are subjected to a prolonged fitness test are also known in some other insects. In the tenebrionid beetle Onymacris rugatipennis, females will not mate until late evening. During the day males undergo a testing marathon by shadowing the female and attempting to keep rival males away (Hamilton et al. 1976). In the otitid fly Physiphora demandata, the females seem to demand a long and complex courtship, performed in the face of numerous interruptions from rival males (Alcock and Pyle 1979).

The behaviour of the males of C. quadrifasciata is also complex, and reasonable interpretations based on observed actions can be proposed. Testing these at some future date is desirable, but is liable to be difficult, given the rarity of these flies. Why should so many repeat copulations be necessary, and why do the females refuse to allow them at reduced intervals? This could be linked to sperm priority patterns in this species. Takeover attempts become rarer and less aggressive towards late afternoon. If last-male sperm priority were to apply, then the opposite should be the case, as the last male to mate would have everything to gain. Takeover attempts should therefore become more frequent and intense as the day progresses. Last-male sperm priority therefore seems unlikely in this species. The function of the repeat matings would therefore more likely be to swamp the spermatheca with sperm. The behaviour of the males supports this conclusion, as they will try to reduce the time interval between matings and to extend each act of copulation. This would fill the spermatheca more rapidly, reducing exposure to takeovers by rivals.

The females’ refusal to reduce the intervals between repeat matings, or to permit copulations that extend beyond the mean, increases the chance that a fitter male will replace a rider. The ability of females to measure mating times and react accordingly has also been observed in Scatophaga stercoraria (Borgia 1981). Takeover attempts in C. quadrifasciata probably diminish towards late afternoon because by then the spermatheca would be almost full, leaving little to gain in terms of eggs fertilized. Females with riders remained in the study-site all day, and did not leave until late afternoon, giving little or no time for oviposition before evening fell. Females of many conopids wait near flowers and pursue bees that arrive, laying eggs on the back of the host in flight.

Female intolerance of repeat copulations that are extended beyond the mean probably explains the waiting behaviour observed when a rider is engaging in a repeat copulation. A rider threatened by a rival faces two choices. Firstly, he can release the female's genitalia after the mean duration of copulation, in which case the rival can then attempt to seize them. The rider will attempt to negate this with an abdomen-lift, which in all observed cases \( n = 23 \) was successful, even when the attacker was larger than the incumbent. Secondly, the rider can choose to prolong a copulation beyond the mean. This will cause the female to react violently, possibly increasing the chance of a successful takeover. In fact females seem to tailor their response to fit the circumstances. When opposing males are evenly matched, the female continues to feed, ignoring the struggles taking place on her back. When an attacker knocks a riding pair off a flower, the female adopts the spreadeagled posture, facilitating a takeover by an obviously larger intruder. It seems that ramming is therefore the only tactic likely to succeed.
A waiter has to make a trade-off between time spent waiting for the female to shake (possibly up to 14 min) and the chance that by resuming searching he might find an unoccupied female, or one occupied by a smaller rider. By waiting too long he risks the possibility that a rival might get there first. This probably explains why waiting seems to be limited to around 3 min.

Searching males quickly learn to recognize the location of unbeatable riders and economize on unprofitable effort by gradually reducing their attack response to zero.

The present study was cut short by bad weather, before any statistical evidence could be amassed to back up the theories which were beginning to emerge in the light of the observations being made. Since 1993 the author has seldom seen this species, making it impossible to make further measurements, such as the amount of sperm in the spermatheca at various times of day. The admittedly incomplete results and untested interpretations presented here are offered on the basis that they are vastly more comprehensive and enlightening than the few words of unelaborated anecdotal observation available hitherto. Given the rarity both of these flies and of expert observers, this may have to be the last word on the subject.

Acknowledgements

I should like to thank Professor John Alcock of Arizona State University for reading through the initial draft and making many helpful comments. Similar thanks are due to Dr John Ismay of the University Museum, Oxford, and two anonymous reviewers.

References

Alcock J. 1977. The courtship behavior of Heteropogon stonei (Diptera: Asilidae). Journal of the Kansas Entomological Society 50:238–243.
Alcock J. 1990. A large male competitive advantage in a lekking fly, Hermetia comstocki Williston (Diptera: Stratomyiidae). Psyche 97:267–277.
Alcock J, Jones CE, Buchmann SL. 1977. Male mating strategies in the bee Centris pallida Fox (Anthophoridae: Hymenoptera). American Naturalist 111:145–155.
Alcock J, Pyle DW. 1979. The complex courtship behaviour of Physiphora demandata (Diptera: Otitidae). Zeitschrift für Tierpsychologie 49:352–362.
Bland RG. 1987. Mating behaviour of the grasshopper Melanoplus tequestae (Orthoptera: Acrididae). Florida Entomologist 70:483–487.
Borgia G. 1981. Mate selection in the fly Scatophaga stercoraria: female choice in a male-controlled system. Animal Behaviour 29:71–80.
Conner J. 1989. Older males have higher insemination success in a beetle. Animal Behaviour 38:503–509.
Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–222.
Freidberg A. 1981. Mating behaviour of Schistopterum moebiusi Becker (Diptera: Tephritidae). Israeli Journal of Entomology 15:89–95.
Frohlich DR, Parker PD. 1985. Observations on the nest-building and reproductive behaviour of a resin-gathering bee: Dionthidium ulkei (Hymenoptera: Megachilidae). Annals of the Entomological Society of America 78:804–810.
Grant GG, Brady UE. 1975. Courtship behaviour of phycid moths: I. Comparison of Plodia interpunctella and Cadra cautella and role of male scent glands. Canadian Entomologist 53:813–826.
Hamilton WJ, Buskirk RE, Buskirk WH. 1976. Social organization of the Namib desert tenebrionid beetle Onynacris rugatipennis. Canadian Entomologist 108:305–316.
Hancock RG, Foster WA, Yee WL. 1990. Courtship behaviour of the mosquito Sabethes cyaneus (Diptera: Culicidae). Journal of Insect Behavior 3:401–412.
Hughes AL. 1979. Reproductive behaviour and sexual dimorphism in the white spotted sawyer Monochamus scutellatus (Say). Coleopterist’s Bulletin 33:45–47.
Riding behaviour by males of Conops quadrifasciata

Jones RA. 1999. Troilism in Sicus ferrugineus (L.) (Diptera: Conopidae). British Journal of Entomology and Natural History 11:138.

Mangan RL. 1979. Reproductive behaviour of the cactus fly, Odontoloxozus longicornis, male territoriality and female guarding as adaptive strategies. Behavioural Ecology and Sociobiology 4:265–278.

McLain DS. 1989. Prolonged copulations as a post-insemination guarding tactic in a natural population of the ragwort seed bug. Animal Behavior 38:559–564.

Müller CB. 1994. Parasitoid induced digging behaviour in bumblebee workers. Animal Behaviour 48:961–966.

Otte D, Joern A. 1975. Insect territoriality and its evolution: population studies of desert grasshoppers on creosote bushes. Journal of Animal Ecology 44:29–54.

Parker GA. 1970. Sperm competition and its evolutionary consequences in insects. Biological Review 45:525–568.

Pinto JD. 1975. Intra- and interspecific courtship behaviour of blister beetles of the genus Tegrodera (Meloidae). Annals of the Entomological Society of America 58:275–284.

Thornhill R. 1980. Rape in Panorpa scorpionflies and a general rape hypothesis. Animal Behaviour 28:52–59.

Thornhill R, Alcock J. 1983. The evolution of insect mating systems. Cambridge (MA): Harvard University Press.

Uffen RWJ. 1998. Delayed mating in a trio of Conops quadrifasciatus (Diptera: Conopidae) and the functional male theca. British Journal of Entomology and Natural History 11:30.