The Ins and Outs of Odonata Mating Behavior
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Abstract

Odonata is a very diverse order. Dragonflies and damselflies are very difficult to observe due to their skittish nature. Tracking them to conduct field studies is very difficult especially in order to get the necessary replications one would need.

There are a wide number of mating behaviors exhibited by the Odonata. Among these are the pre-copulatory courtship displays, the copulatory and sperm displacement behavior patterns which are varied depending on species, and the post copulatory behaviors. These are very dominant behaviors and are discussed broadly. Topics include the various types of mate guarding and the effects both to the males and the females. Behavioral protandry is discussed for those species having non-overlapping generations. Fluctuating wing asymmetry was found to be a controversial topic as to whether or not mating success and body size were effected. Also how ectoparasitism affects reproductive and mating behaviors and success. An interesting behavior is the communication that goes on between the males and females and the signals they use with each other, as well as other cues. There are the unusual discoveries, such as the night roost mating aggregations in Mexico.

The Odonata take us on a journey of wonder and discoveries as we weave in and out of their mating behaviors.
Introduction

Most Odonatas spend time in flight skimming along streams and pond edges looking for mates. Some prefer more off water sites, but most are near water. The females lay eggs in or near water as the immatures are aquatic. These immatures are also predaceous feeding on various aquatic organisms. Adults have compound eyes that take up most of the head, with antennae that are small and bristle-like. They have chewing mouthparts. Their thorax consists of a prothorax and a pterothorax. The abdomen is long, slender, and 10 segmented. The four wings are elongate membranous and have many veins. Their legs are long and used for perching or holding prey. The length varies from about 20mm to over 135mm. Odonatas are large and beautiful, and usually very colorful.

Copulation and Sperm Displacement

Prolonged copulations had many positive effects on the mating and fertilization of the damselfly (Andres, et al., 2000). The Andres group believed that prolonged copulations could have evolved from a cryptic female choice, by which male fertilization success is increased by female responses, or by the female-mediated process. After long copulations became fully evolved the male fertilization success was greater. They theorized that long copulations evolved as a consequence of the sexual selection, which favored male adaptations. They also discovered that male density was positively correlated with copulation duration For example this would have evolved to avoid sperm competition. The Andres group also found that copulations are statistically longer with mated females and being able to remove almost all of the sperm from a female’s bursa. Evidence shows us that once and twice mated females had close to the same amount of sperm in the bursa and in interrupted females it was empty nine out of ten times. Also
males spent more time with mated females than with interrupted females and more with these than with the virgin females.

Andrew, 2001, theorized that the damselfly, *Ischnura aurora* (Brauer), exhibited an unusual transitional reproductive behavior with regards to sperm competition. The females of this species are polyandrous, in that they provide opportunities for sperm competition. This then leads the male to exhibit behavior in order to protect the female and their sperm. *I. Aurora* has the unusual behavior of pre-copulatory guarding. The male carries the female around in tandem for more than an hour until they form the copulatory wheel. The male displaces any sperm in the female’s vagina by pulling out the sperm mass from the bursa copulatrix, using its backward directed spines on the flagella of the penis, and then mates with the female.

**Post-Copulatory Behavior**

The North American dragonfly, *Libellula pulchella* Drury, females receive non-contact guarding after copulation. They receive minimal protection from their copulatory, mates who are busy chasing off intruder males. Females then faced frequent harassment during oviposition by unpaired males seeking copulation. Sometimes this harassment led to termination of the female (McMillan, 2000). The females have developed some tactics for avoiding male harassment, which interferes with their ovipositing. McMillan, 2000, discovered that the tactics females employed to minimize the interference include rapid escape flights, repeated return visits to the water, perching when harassed, and when clasped, proceeding with mating. When there are high male densities, and increased interference, the females may not be able to lay all their eggs at a single visit to the water. In order to adapt to the high male densities in which intense interference occurs utilizing both rapid escape and repeated visits to the water is a valid tactic
used. This conclusion can be drawn simply from the fact that less time ovipositing provides a reduced amount of time when the female is especially vulnerable to harassing males. As McMillan pointed out, multiple ovipositor attempts are potentially energetically costly to the female *L. pulchella* by increasing the risk of injury or death resulting from predators or male harassment. Remating when clasped has potential fitness benefits, in that the female can take the opportunity to exercise mate choice. Perching when severely harassed only provides a temporary solution; because ultimately the female must still finish the ovipositing process thus this tactic offers no overall benefit except preventing termination. Regardless of the negative and positive aspects of any of the tactics these behaviors do help to reduce interference during both initial and return visits to the oviposition site. The female post-copulatory tactics including male protection is not only found in Libellulide.

*Behavioral Protandry*

Protandry is known in most insects having non-overlapping generations, where the males emerge before the females (Watanabe and Taguchi, 2000). The male *Minais pruinosa costalis* have a reproductive strategy where the goal is to maximize the amount of females mated. The males of the species have wing color dimorphism, where one form has orange wings and the other form has hyaline wings, these resemble female wings. Watanabe and Tagchi theorized that each color of wings has a different objective. The hyaline wing damselfly is mostly non-territorial and it uses sneak tactics to secure the mates in the orange winged damselfly territories. The orange winged *M. p. costalis* will become sexually mature before the females. This is to ensure that the reproductive success is at its maximum. The hyaline winged damselflies have a different reproductive maturity, in that they mature after the females; this difference is due to the
fact that the hyaline winged *M. p. costalis* utilizes the orange wing’s territory. The orange wing and hyaline wing damselflies have different mating strategies, which explain the difference in sexual maturity and territory. The orange winged males defend their territory, however, while the orange wing is defending his perching site the hyaline wing will sneak in and copulate with the females along the periphery of the territory. The orange wing and the hyaline wing mature at different times for a reason. Due to the orange wing damselfly defending the territorial sites, the hyaline wing is dependent on the orange wing and his territory. The hyaline wing males need to mature after the orange wing males because females are receptive for mating at the oviposition sites as well as the roosting sites after a certain period of sexual maturity. Watanabe and Taguchi, 2000, found that this behavioral protandry is a reproductive behavioral strategy for the orange winged males to get on the scene first and establish territories.

**Mate Guarding**

There are two types of mate guarding. one is contact-guarding, which is when the males remain in tandem with the female during the mating process. The second being non-contact guarding which is when the males stay with the female but do not attach themselves to the females but perch near them. They spend most of their time chasing intruders away from the oviposition sites.

According to Alcock, 1982, not only do males of the damselfly *Hetaerina vulnerata* remain with their mates after copulation, they also exhibit two very unusual behaviors of post-copulatory mate guarding. The first is that a male, flying in tandem with the female, will leave his territory to accompany her to the appropriate oviposition site. The second behavior is that the male perches and watches over the female, guarding her at the oviposition site while she lays her
eggs. Alcock suggests two reasons for this. First, so an intruder own male will not copulate with
the female, remove his sperm and replace it with his and own, and second to protect her and their
eggs from predators. These activities may have two potential costs for the male. One, while
mate guarding he may miss opportunities for mating with other females, and two, he runs the risk
of loosing his territory to an interloper. The costs of these things are low as Alcock discovered
that a territorial male can mate once about 3.6 days on average, depending on the male density of
the area. Also, those territorial males can reclaim their territories after being gone 30-60
minutes. *H. vulnerata* females submerge when egg-laying. During that time another male
cannot capture her. Therefore, one gain from post-copulatory guarding is to catch the female if
she decides to fly out of the water when she rejects the oviposition site. The chance of a female
leaving one site to search for another is about 40%.

During mate guarding sequences, observations have been made that male-male tandems
occur (Switzer and Shultz, 2000). When one male initiates this tandem he grabs the other male
by the head and flies with him, behavior much resembling male-female tandem flight. Switzer
and Schultz found this behavior to be one of mate guarding intruder aggression. While a non-
contact mate guarding is in process and an intruder comes into the territory, the male will grasp
the intrude in a tandem flight and remove him from the territory. This has been considered a
very rare behavior compared to other territorial aggression. Switzer and Schultz noted that the
territorial aggression part of sexual behavior has not really been explored. They found that
among Odonates, two components of this aggressive behavior seem to vary. First, the species
will differ in whether discrete stages exist within territorial contests. These contests can consist
simply of the males chasing other males away from their territory or be of more complex
behaviors. Second, the species will differ in whether there is direct physical contact in guarding
their territory, some will have “physical battles” (Switzer and Schultz, 2000). Some of this physical contact may include two males flying at each other and having a clattering of wings, or bite and grasp at each other. Those males who don’t come into direct contact with each other may have contests of chases and hovers or “energetic battles” (Switzer and Schultz, 2000). The species *Perithemis tenera* has a rare way of guarding its territory. The *P. tenera* has contests in which the males will not make any physical contact, the males are usually chased. However a *P. tenera* male was observed flying in tandem with another male like the male female mating position. After the tandem is broken, Switzer and Schultz reported that the two males immediately had either a fight or pursued a fight. This suggests that the other male did know that the pursued male was in fact a male and not a female. This also is in conjunction with the mate choice behavior.

*Fluctuating Asymmetry*

According to Beck and Pruitt-Jones, 2002, wing asymmetry could negatively affect the ability for the male dark-winged damselflies to mate with a female; the females tend to discriminate against the different wing asymmetry. Fluctuating asymmetry can also have an affect on territoriality and the mating success of the male with the female. The male wing asymmetry alters their flight agility and maneuverability, which is a crucial part of protecting their territory. Beck and Pruitt-Jones found that the asymmetry of the forewing was a significant factor in male mating success. They found there was no correlation between trait size and fluctuating asymmetry. Carchini, 2000, found that the male mating success of *Ischnura elegans* (Vander Linden) is negatively related to the body size. Also that a low level of fluctuating asymmetry for both the wing size and body size, may produce a higher mating success rate.
However, they didn’t find this to be true for the males of *C. resolutum*. This conflicts with, Rivera, et al., 2002, who found that the mating success of *Ischnura graellsii* (Rambur) is related to body size and not to the fluctuating asymmetry. The Rivera group believes that body size is positively correlated to male reproductive success.

*Parasite Behavior*

Andres, et al., 1998, discovered that the water mite, *Arrenurus cuspidator*, on its host, *Coenagrion puella*, would detach only during host oviposition. Although there was a significant effect on male mating success there was no effect on female mating success. However, this conflicts with what Cordoba-Aguilar, et al., 2003, found. They discovered that the female sexual behavior of the damselfly, *Calopteryx haemorrhoidalis* is affected by parasites. Their studies found that the female’s wing pigmentation color significantly effected by parasite burden. Also effected were egg production, mating success, mate choice, mate courtship, and were guarded less. They found that the wing pigmentation was a signal for the female’s reproductive value. Rolff, et al., 2000, on the other hand, found no correlation between ectoparasitism, by the water mite, *Arrenurus cuspidator*, and the number of male matings in the damselfly, *Coenagrion puella*. It was thought that males in tandem had significantly fewer mites than those males that were single, however, they found no correlation for this.

*Communication*

Thompson, 2004, found that although female damselflies have the option to refuse to copulate with males they don’t, because just one mating will fertilize about fourteen clutches of eggs, similar to *Ischnura graellsii* (Rambur). A cost a female will need to pay in order to avoid
continual harassment from males is to copulate while they themselves are ovipositing. However, if the female is in a contact mate guarding tandem harassment by males is almost non existent. The advantages for females to be in tandem are that the male can pull them out of danger if an aquatic predator tries to get them. For the females that oviposition under the water the male has the power to pull the female out of the water if needed. On the other hand, there are advantages to females having more than one mate, mainly by increasing genetic variation in the offspring. Males can also sense signals from females Thompson found that female coenagrionid damselflies give honest signals to males. For example, if a female enters a site with a full clutch of mature eggs she is harassed until she enters tandem and tip their abdomen for the tandem clasp. If a female is leaving the breeding site without eggs she will signal the male by bending their abdomens in an almost 90 degree angle. The males get the message. When the female is weighted down with eggs she can’t bend at this angle and so it is impossible to cheat with this signal.

Gibson, 2003, discovered wing communication among three species of Anisoptera. In male migrant hawkers, Aeshna mixta, using a camcorder, he observed wing clapping behavior during copulation. The male perched upright with the female below, “the male raises his abdomen until it is nearly at right angles to the vertical and this raises the females head to just below that of the males second abdominal segment. The male slowly brings his hindwings back until they mantle or envelop the head and thorax of the female. Then he brings his forewings back very quickly to ‘clap’ against hindwings. The forewings are then returned very quickly to their normal position. The hindwings are returned more slowly.” Gibson observed this same behavior on other occasions right before uncoupling. This behavior was also observed in the common hawkers, A. juncea. The female was also observed to have a
wing communication behavior. Females exhibited a wing touching behavior by holding “the abdomen of the male with her front and middle legs, used her hind legs to make stroking movements under the hindwings of the male”. The female common darter, *Sympetrum striotum* was observed in wing lifting behavior just prior to uncoupling. “The female disengaged her hind legs and tapped the left hindwing of the male twice, moving it upward a short distance before lifting it and holding it in a significantly raised position. Then she let the wing droop before twice tapping it upwards and raising it again”. Gibson interpretation of the wing communication is that the males may be signaling to the females that “I have finished sperm transfer”, while the females then are signaling that “I am ready to oviposit”, with uncoupling and flight soon following. In 2004, Gibson did another study on the wing clapping behavior of the blue-tailed damselfly, *Ischnura elegans*.

**Behavioral Displays**

Male *Calopteryx haemorrhoidalis* face the female and give behavioral displays by showing off their pigmented wings. This behavior was found to be both a pre- and post-copulatory behavior by Cordoba-Aguilar, 2002. It is thought this might be a function of sexual selection or species recognition. These males were found to have a higher proportion of wing pigmentation, fewer parasites, and higher matings success. The males exhibit a complex flying courtship display. Before copulation they use two courtship displays for the female. The first is “a cross display in which a male lands on the water surface and allows himself to be taken by the current for a few centimeters while keeping his wings open” and, two, “the courtship arc, in which the male used his forewings to sustains flight while keeping his hindwings open.” Then, after copulation, when the female is moving to oviposition sites the male “carries out the cross
display at any flying movement of the female”. Cordoba-Aguilar determined that the results suggested that the wing pigmentation was due to sexual selection, also it was found that territorial males were more pigmented than non-territorial males.

*Roosting Behavior*

Grether and Switzer, 2000, discovered that in relation to sex and territorial status the males were more roost site faithful when they held mating territories. Their study was of the aggregation night roosting behavior of the rubyspot damselfly. They found that mating does not occur at this site, that these sites are not rendezvous for sexual behavior. Some odonates will go where there is an opportune place to mate whether it is near the water or on land. However, some Anisoptera will congregate in flight and prey on the insects, which is called “swarm feeding” or “swarm foraging” by Gonzales-Soriano, 2001. It was found that some species will use the foraging sites as mating rendezvous sites. The libellulid fliers, *Miathyria marcella* and *Tuarihila azteca*, were discovered in copulating pairs and were occasionally detected within the foraging aggregation. The Mexican protoneurids fly along streams and rivers. The males will patrol the surface in search for ovipositing females, called “cruising” by Gonzalez-Soriano. These males go from one perch to another with out territories. This species mates in aerial tandem aggregations. Also in tandem they will look for oviposition sites flying along streams and rivers in search for a safe site. Some of these sites may include; submerged grasses, living roots, and floating objects such as lily pads. The male remained erect during this process and beat his wings. Gonzalez- Soriano video recorded a small aggregation. They observed males hovering 4-5 meters from the ground and 2-3 meters from the edge of the stream. The area was surrounded by small trees no more than ten meters high, in a forest opening. All of the hovering
*Protoneura cara* were facing the same direction, which appeared to be against the wind. The males were exhibiting strange behavior as they were visiting small trees and bushes that were along the streams edge and then darted into the foliage. This behavior could have been a result of few females that were receptive. This is believed because there was no foraging activity observed during the time watched. *Neoneura amelia* was also observed, they formed aggregations that were 2-3 meters above the ground, located below the top of a tree, at 40 meters from the edge of the water. An unusual observation that Gonzalez-Soriano made was that males had the ability to stay in place while hovering, a very high cost of energy. In contrast to the *Hataerina americana* roost aggregations, he determined that the only reason for the roost aggregations of these species was to mate.

**Conclusion**

As we can see, Odonata is a very diverse order. They are very difficult to observe with their flight patterns. Tracking them to conduct any of these field studies was very difficult and long hours of perseverance would have been needed to gather all the valuable information collected in this paper.

There are a wide number of mating behaviors exhibited by the Odonata. Among these are the pre-copulatory courtship displays, the copulatory and sperm displacement behavior patterns, and the post copulatory behaviors. These are very dominant behaviors and were discussed broadly. Topics included the various types of mate guarding and their effects. Behavioral protandry is discussed for those species having non-overlapping generations. Fluctuating wing asymmetry was discussed as to whether or not mating success and body size were effected. Also, how ectoparasitism affects reproductive and mating behaviors and success.
An interesting behavior is the communication that goes on between the males and females, and the signals and cues they use with each other. Let’s not forget the night roost mating aggregations in Mexico. This is an amazing order, one to enjoy watching on a lazy afternoon by a stream.

Bibliography


