

Spatial Learning in Dragonflies

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Spatial learning is evident in dragonflies on a variety of spatial scales. Mature dragonflies must be able to locate a variety of features in the habitat that are critical to survival and reproduction, including sites for breeding, foraging, roosting, and thermoregulating. In many species, these sites do not coincide in space. Because individuals may repeatedly use particular sites for different activities, they must learn both the locations of these sites and routes among them. Further evidence of spatial memory in dragonflies is provided by their site specificity on a finer scale. Breeding males, for example, often are faithful not only to a particular area, but to a specific territory site within that area. Males appear to become faithful to a territory site through localization, a process during which they explore the site and develop a spatial map of the location of the territory and its resources. Males also respond to their interactions with other individuals, adjusting both their choice of territories and their space use within their territories to reflect those interactions. In eastern amberwing dragonflies (*Perithemis tenera*), males are not faithful to territories on which they have lost a fight with another male; in contrast, males are more likely to be faithful to territories on which they successfully mated than to territories on which they obtained no matings. Similarly, while on territories, male amberwings adjust their position in response to negative and positive interactions. They move away from the side of the territory from which neighbors most frequently intruded, and they move toward locations from which they pursued a female. Territorial amberwings thus modify their space use at both the territory and within-territory spatial scale in response to their social environment. Their responses are consistent with the hypothesis that they learn from their positive and negative experiences and adjust their future space use accordingly. Further study of spatial learning in dragonflies would greatly enhance studies of dragonflies' behavior and ecology, and help us understand learning in general.

Although dragonflies (Order Odonata) have been the subjects of a great deal of scientific research, relatively little has been published on learning in this taxon, despite the likely importance of learning for animals that are both highly predacious and highly mobile. Work with larval dragonflies has provided clear evidence of learning in foraging behavior, with individuals learning, for example, to avoid noxious prey (Rowe, 1994), to pursue more actively those prey types that they have successfully captured (Bergelson, 1985), and to adjust their behavior to compensate for injury in detecting and capturing prey (Abbott, 1941; Caillere, 1970). Larvae can also learn to recognize predation risk through experience with chemical cues (Chivers, Wisenden, & Smith, 1996; Wisenden, Chivers, & Smith, 1997), and adult males are known to learn to recognize potential mates when females have more than one color pattern (Fincke, 2004; Miller & Fincke, 1999; Van Gossum, Stoks, & De Bruyn, 2001a, 2001b; Van Gossum, Stoks, Matthysen, Valck, & De Bruyn, 1999). Given the natural history and behavior of the dragonflies, however, spatial learning must be one of dragonflies' most critical capabilities, and dragonflies must be capable of spatial learning on a variety of scales.

In this paper we will focus on spatial learning in adult dragonflies, particularly as it relates to finding and using sites of reproduction. We will use the term “dragonfly” when referring in general to a member of the Order Odonata or when referring to a particular species in the suborder Anisoptera. We will use the term damselfly only when referring to a specific example of a member of the suborder Zygoptera. In the sections that follow, we first describe the different spatial scales commonly relevant to dragonflies and briefly review what is known about dragonfly learning on each of these scales. We then discuss how learning might play a role in determining individuals’ location preferences at each scale level. Finally, we apply these ideas in a case study of the amberwing dragonfly, *Perithemis tenera*.

Spatial Learning

Mature dragonflies must be able to locate a variety of features in the habitat that are critical to their survival and reproduction, and in most species, sites providing these features do not coincide in space. First, dragonflies in general have very specific requirements for breeding sites, which are most commonly located along streams or ponds. Males defending breeding territories, however, typically defend those territories for only part of each day (Alcock, 1987, 1989), and females often visit the territories only when ready to mate and lay eggs (e.g., Hilton, 1984). Second, dragonflies need sites for foraging, preferably locations that have abundant arthropod prey. Because breeding areas typically have high densities of dragonflies, the best foraging sites for aggressive species may be at other locations, where foragers will have less interference and competition from conspecifics and where prey density may be higher (Baird & May, 2003). In many species, in fact, males feed little if at all while they are on their territories; in particular, males that spend relatively little time on their territory are less likely to forage there (Parr, 1983). Females, too, rarely forage on breeding territories, presumably due at least in part to interference by males seeking mates. Third, dragonflies typically use roosts, which are sites to which they retreat when light levels are low or when the weather conditions are unfavorable and which may be more than 1.5 km away from their breeding sites (reviewed in Corbet, 1999). Roosting may reduce predation risk either through the formation of aggregations, which might reduce the risk for any one individual, or through the selection of roosting sites at which predation risk is lower than at the breeding sites. Finally, individuals in many species choose specific sites for thermoregulation, for example, by leaving a breeding site to perch in a sunnier location (Clausnitzer, 1998). Such ‘sun-flights’ are likely to be particularly common in the many species that breed in forested habitats, where oviposition sites tend to be shaded.

In most odonate species, then, adults must move among discrete locations that they use for different purposes. For all four of the types of locations mentioned above, there is evidence that individuals make more than one trip to a given site, suggesting that the animals learn the locations of the sites they use. For example, although few data are available for females, male odonates are commonly faithful to one or a few particular areas for reproduction. Substantial evidence for this is provided by numerous studies of marked individuals, which are often resighted at a

particular pond or section of a stream (e.g., Beukema, 2002; Clausnitzer, 1996, 1998; Koenig & Albano, 1987; reviewed in Corbet, 1999; Switzer, 1995). Dragonflies appear to be less faithful to particular foraging areas than they are to breeding areas, and shifting foraging areas between days may be the norm, although too few species have been well studied to draw a firm conclusion. Nonetheless, within a given day individuals may forage in the same location for hours, and some individuals return to the same foraging area over several days, suggesting again that they are capable of learning the location of a particular area (May & Baird, 2002). In addition, dragonflies appear to be able to learn the locations of foraging areas with high prey density. For example, individuals of some species regularly forage near areas containing beehives, and others appear to be able to locate swarms of flies and mosquitoes that persist over several days at the same site (Wright, 1945). In some species that have been carefully observed, individuals also appear to return to the same areas for roosting (Grether & Switzer, 2000; Miller, 1989) and to the same areas for sunning (Clausnitzer, 1998). For example, Grether and Switzer (2000) found that a male rubyspot damselfly (*Hetaerina americana*) tended to return to the same roosting aggregation night after night, but often shifted his roost location if he obtained a new territory in a different part of the stream.

Dragonflies that have long commutes among the locations they frequent probably use both visual landmarks and a sun compass to navigate. Evidence for the latter comes from studies of long-distance migration; however, migrants also follow distinctive, linear features of the landscape, such as roads or stream (reviewed by Corbet, 1999). Dragonflies with shorter commutes may rely primarily on “piloting” (i.e., using familiar landmarks and/or spatial memory to navigate). For example, careful observation revealed that a male traveling between his breeding site and a sun perch repeatedly used the same flight route, suggesting that he followed a learned route when commuting between the two locations (Clausnitzer, 1998). Few experimental studies have been performed to demonstrate that dragonflies use landmarks and spatial memory for commuting. However, in one interesting study, *Leucorrhinia duba* males returned to a pond that had been covered by a cloth, and they even displayed reproductive behaviors there despite the absence of visible water (Sternberg, 1990, cited in Corbet, 1999). These males were probably using cues provided by the surrounding landscape to identify the site of their pond. Similarly, foraging dragonflies presumably relocate an insect swarm by learning the topography around the site of the swarm (Corbet, 1999). Experimental evidence has demonstrated that with increasing distance, the probability that dragonflies will be able to find their way back to the point of their capture is reduced. For instance, in the case of the damselfly *Calopteryx maculata*, 35% of males were able to return to a stream when released 350 m from the stream, but only 10% returned when released 700 m away (Pither & Taylor, 1998). This may reflect dragonflies’ greater familiarity with the areas nearer their breeding areas.

Further evidence for the use of spatial memory in dragonflies is provided by their site specificity on a finer scale. Within the areas used for reproduction, for example, male dragonflies often exhibit site fidelity not only to a particular area (i.e., a given pond or stream), but also to a specific territorial site within that area (Switzer, 1995). Among species, the maximum reported periods over which individuals returned to the same territories range from 10 to 90 days (reviewed in Cor-

bet, 1999). Similarly, male dragonflies sometimes defend feeding territories at different sites than their reproductive territories, and they may return to those feeding territories over periods of days (Baird & May, 2003). In addition, both female and male dragonflies are known to return not only to the same general foraging area, as discussed above, but to the same foraging perches within that area over a period of several days (May & Baird, 2002). Within foraging sites, individuals will adjust their perch locations so that they are closer to locations with higher prey abundance (Baird & May, 1997, 2003). This observation also indicates some spatial learning, as individuals must leave their perches to pursue prey and then return to their preferred locations.

This fine-scale site fidelity has been best studied with regard to males' defense of breeding territories. Males appear to become faithful to a particular territory site through a process called localization. Males first explore a shoreline, investigating various potential oviposition sites, sometimes performing patrolling flights in which they fly about an area that includes a potential territory (e.g., Pezalla, 1979; Ueda, 1979; Wildermuth, 1991). During these maneuvers they appear to develop a spatial map that identifies the location of the territory and to learn the locations of resources in the territory, including oviposition sites and perches. In many species, males occupy several territories during their reproductive lifetimes and learn the locations and features of each (e.g., Fincke, 1992; Robinson & Frye, 1986; Switzer, 2002a; Utzeri & Dell'Anna, 1989; Wolf, Waltz, Klockowski, & Wakeley, 1997). Evidence of their learning is provided by their ability to return to those territories even after bad weather forces a long absence (Corbet, 1999). For example, male *Megaloprepus coerulatus*, which is a neotropical damselfly species in which males defend water-filled tree holes, return to the same site to breed following a dry season of almost two months (Fincke, 1992).

Landmarks on a smaller scale than those used for returning to an area are likely to play a role in an individual's ability to return to his particular territorial site on a pond or stream, although dragonflies defending sites along streams may also use the stream itself as a landmark. Experiments have demonstrated that dragonflies captured and released at some distance from their territories are able to find their way back. In one experiment, for example, half of the individuals that were displaced between 80-240 m along the stream on which they were breeding found their way back. These individuals probably used the stream as a landmark or guide and followed it back to their territories (Beukema, 2002). This experiment also demonstrates that at least on a landscape scale individuals are not restricted to navigating by using familiar routes, as it is unlikely that all displaced individuals had previously flown from the areas to which they were displaced to their territories (or vice versa) and thus established a route (see also Pither & Taylor, 1995).

Patrolling males clearly demonstrate knowledge of their territories. For example, they sometimes interrupt their flights in order to inspect sites where females are likely to be, such as oviposition sites and areas where females perch (Corbet, 1999). Knowing the location of the oviposition sites is vital not only for finding females, who may come in and begin laying eggs without having mated with the territorial resident, but also for courtship. In some species, when a male sees a female entering or near his territory, he flies to the female and then turns, flies back to an oviposition site in his territory, and hovers over it (e.g., Jacobs, 1955). Fur-

thermore, in many species the male will either perch on the oviposition site or land on the water directly over the site, if it is submerged (e.g., Meek & Herman, 1990). Presumably, these behaviors show a visiting female the location of the oviposition site and, perhaps, its quality. It is critical that a male know the location of the site well because he must fly back to it quickly; speed is important both to keep the female's attention and to avoid being disturbed by other potential suitors.

During the period of territorial settlement, dragonflies typically establish boundaries with their neighbors. In some cases the boundary is set simply where two males happen to meet; in other species, however, the boundary is set at some sort of visual landmark, and both neighbors learn to recognize the landmark as a boundary (Pajunen, 1966). Males defending territories defined by landmarks will frequently turn back upon reaching them during a patrol or chase flight, whether or not the neighbor on the adjacent territory is at that boundary and enforcing a retreat.

Learning Location Preferences

The particular location chosen by a territorial male dragonfly may be based on both inherent characteristics of the habitat and his experience in that location (reviewed by Corbet, 1999; see also Eason & Hannon, 1994; Gauthier, 1990; Switzer, 2002b). This is true whether the geographic scale (from largest to smallest) is the dragonfly's entire breeding area, his territory within the breeding area, or his preferred locations within his territory. For example, consider a mature male of a stream-dwelling dragonfly species who is searching for a breeding site for the first time. Even without any prior experience, he will likely search for a suitable creek instead of a pond. Within the creek, he may search for a riffle in which to defend a territory; within this territory, he may choose to perch on rocks rather than sticks, and he may look over several clumps of plants to choose potential oviposition sites. None of these preferences may involve learning. However, males may modify their initial choices based on their experience. In terms of breeding site selection and, particularly for males, preferred locations within breeding sites, relevant experience is likely to be based on males' interactions with predators and conspecifics.

Early theoretical work relevant to questions about spatial patterns in behavior focused on habitat selection and proposed that animals select habitats to maximize fitness. For example, ideal free distribution models predict that individuals in different habitats should have approximately equal fitnesses, given that they are free to move among habitats (Fretwell, 1972; Fretwell & Lucas, 1970). However, such models are unlikely to apply in many of the situations we focus on here, such as the locations of individuals within their territories. Furthermore, these models typically assume that increased densities of conspecifics are deleterious to individual fitness, an assumption that often may not be met. Recent work suggests that individuals may benefit from the presence of conspecifics, both during settlement and later during territorial residency (reviewed by Stamps, 2001). Accordingly, here we make a finer distinction among conspecifics, suggesting that they may have either negative or positive effects. We also consider behavior on a finer scale, looking at site selection within territories rather than only at territory selec-

tion. Because only a few studies have examined such behavior in dragonflies, we offer a general framework for understanding how experience might be expected to affect dragonfly behavior in the following paragraph.

The cost-benefit logic underlying how predators and conspecifics may modify a male's choice of location is consistent regardless of spatial scale. In general, a male should attempt to occupy a location that minimizes his negative interactions with both conspecifics and heterospecifics and maximizes his beneficial interactions. Interactions with predators, for example, are clearly negative. Consequently, one might expect that an individual that survived a predation attempt would move away from the area where the attempt occurred. We predict that such avoidance would be particularly likely in females who do not have the same strong attachment to a particular territory that males do. Similarly, one would predict that a territorial male would position himself within his territory so that he might minimize his interactions with his neighbors, which can be costly in terms of time and energy (Eason & Switzer, 2004; Marden & Waage, 1990). With respect to beneficial interactions, one would predict that on mating territories, residents would locate themselves so that they maximize their ability to detect and interact with females. Similarly, if quickly detecting nonterritorial males is less costly than trying to evict them later, one would predict that residents would occupy a location in which they maximize such detections.

We tested the validity and heuristic value of these ideas in our research on the eastern amberwing dragonfly, *Perithemis tenera* (Libellulidae), a common species found in the eastern United States (Figure 1).



Figure 1. A male amberwing dragonfly (*Perithemis tenera*) in an obelisk (thermoregulatory) posture.

Case Study: Eastern Amberwing Dragonflies

Male amberwings defend small territories (3-5 m in length) around an oviposition site on a still or slow moving body of water such as a pond (Jacobs, 1955). Any small object that extends beyond the water's surface will suffice as an oviposition site, such as small clumps of algae, floating sticks, or parts of floating plants. Although several potential sites may exist within a male's territory, he will use only one. Typically, he perches near the site and pursues both passing males and females (Switzer & Eason, 2000; Switzer & Walters, 1999). The former he attempts to chase away; the latter he attempts to lead back to the site. Because oviposition sites, and the territories in which they reside, are typically located around the edge of a body of water, each resident usually has two neighbors, one to the left and one to the right.

Territorial males have a reproductive lifespan of just about one week (Switzer, 1997a) but spend only a portion of this time within their breeding area near the water (Switzer, 2002a). When not at their breeding site, we have observed them foraging in surrounding fields and up in trees. In fact, males and females are commonly observed flying many (i.e., over 50) meters away from their pond and, even at ponds where amberwings are abundant, densities within 50 m of the pond can be quite low (Switzer, 1995). However, both males (Jacobs, 1955; Switzer, 1997a) and females (Jacobs, 1955) return to the same pond to breed day after day. Furthermore, Switzer (1995) found that territorial males marked at a primary study pond were never seen at three other ponds within a 600 m radius. This means that males can become "attached" to a single breeding pond and navigate back and forth from roosting sites. When leaving a pond, both males and females often fly 5-10 m straight up before flying in a straight line away from the pond (Switzer, 1995); this behavior suggests that they are using key landmarks to navigate.

At a pond, males searching for a new territory examine potential oviposition sites by flying low over the site and occasionally touching the site with their legs (Jacobs, 1955). Once a suitable site is found, they begin to fly in increasingly larger, horizontal circles, each consisting of a flight away from the site and a flight directly back to the site. The final circles may be 2-4 m in diameter. This behavior is similar to that of burrowing wasps learning the location of their burrows (Tinbergen, 1951). Knowing the location of the oviposition site is important for males because a female will abandon him if he does not lead her directly to an appropriate site (Switzer, 1997b).

Jacobs (1955) noticed that individual males tend to use the same types of oviposition sites (e.g., sticks *versus* plants). He attributed this to differences in color preference; darker individuals preferred darker colored sites. However, learning may also be involved. Switzer (2005) observed that males who return to the same territory over a period of days spend less time examining their oviposition site and less time flying in small circles before they begin to behave territorially than do males who settled on a territory for the first time. This suggests that over visits, males learn both the spatial location of their breeding site and the oviposition site within their territory.

We also have more extensive evidence of how experience—in particular social experience—modifies amberwing space use. Male amberwings can exhibit

site fidelity; that is, they typically return to or close to their previous day's territory, and in many cases they repeatedly defend the same oviposition site (Jacobs, 1955; Switzer, 1997a, 1997b). Jacobs (1955) found that females are also faithful to oviposition sites. However, not all males are site-faithful, and a male may be site-faithful on some days but not on others (Switzer, 1997a). Whether a male returns to a site is largely a function of his experience with conspecifics.

As noted above, in territorial systems, nonterritorial males pose a threat for territory takeover, so interactions with these males should affect a territory resident's behavior. For amberwings, territory contests are frequent, and escalated contests tend to be won by younger males and males who have spent less time fighting previously (Switzer, 2004). Given that these territory takeovers are won by males in seemingly better condition, that these new residents are likely to return to the territory the following day, and that a male's condition is unlikely to improve greatly from one day to the next, one could hypothesize that a resident who is evicted from his territory would be unlikely to attempt to reclaim it the next day. In other words, residents who lost their territory would tend not to be site-faithful. In support of this hypothesis, Switzer (1997a) found that males evicted from their territories were much less likely to be site-faithful the following day than males who were not evicted from their territories even when the evicted male returned to the pond on the following day. This strongly suggests that their previous day's experience directly influenced their subsequent site choice.

If success with females at a location is predictable over time, then males should modify their territory selection in response to their experience with females (Switzer, 1993). Success with females should positively affect a male's preference for a territory, and a lack of success should negatively affect a male's preference. In amberwings, mating success in a particular location was weakly but positively correlated (i.e. predictable) from day to day (Switzer, 1997a) and observational studies supported the corresponding theoretical prediction: Males who were successful in obtaining at least one mating were more site-faithful than those who did not mate, and the same male was more site-faithful on days following a mating than on days in which he did not mate (Switzer, 1997a). These results were subsequently confirmed experimentally. Males who were allowed to mate were more site-faithful than their paired counterparts who were experimentally prevented from mating (Switzer, 1997b). Therefore, predictable experience with both males and females affects the territory preference of male amberwings.

We also predicted that a resident male will modify his use of space within his territory based on his experience with conspecifics. Specifically, residents should modify their space use so that they occupy locations that increase their positive and decrease their negative interactions. The former include interactions with females (because these are mating territories) and nonterritorial intruders (because quickly detecting and evicting them will decrease the cost of territory maintenance). The latter include interactions with neighbors. For amberwings, neighbors are rarely threats to one's territory (Switzer, 2004), but the resulting pursuit flights may be costly and interfere with detecting passing females (Eason & Switzer, 2004). Consequently, interactions with neighbors may serve little purpose and residents should benefit by occupying a location that minimizes their frequency.

To test these ideas, we observed territory intrusions during focal samples of residents (Switzer & Eason, 2003). We recorded the number of intrusions as well as the identity of the intruders (female, neighbor, nonneighbor), the location of the intrusion (left or right side of the territory), and where the resident was perched. As predicted, residents tended to perch away from the side of their territory from which they experienced the most intrusions from neighboring males and towards the side of their territory from which they experienced the most intrusions from females. We found no overall relationship between resident location and intrusions by non-neighbor males.

For most residents' territories, the same location provided both minimal interactions with neighbors and maximal interactions with females. For those residents in which this was not the case, their location seemed to reflect an avoidance of neighbor intrusions rather than a maximization of their interactions with females. Hence, their choice of location appeared to be related to minimizing interactions with neighbors. However, residents did modify their space usage in response to both female and neighbor intrusions. When we examined location changes following a single pursuit fight, residents tended to move to a perch closer to the side on which they pursued a female and to a perch further away from the side on which they pursued a neighbor (Switzer & Eason, 2003). A resident's location preference may be more strongly affected by neighbors simply because neighbor intrusions are more common than female intrusions.

The apparent lack of response to non-neighbor male intrusions is interesting. We suggest that this may be a result of the resident's limited ability to distinguish neighbors from non-neighbors. A failure to recognize non-neighbor males, in combination with the much larger number of intrusions by neighbors than non-neighbor males, may result in residents essentially treating most male intrusions as intrusions by neighbors (Switzer & Eason, 2003). Territorial males may simply use the rule, "avoid interactions with males." If this is true, and most intruders are neighbors, males would appear primarily to avoid neighbors, and any effect of non-neighbors may not be apparent, as was the case in our study. In addition, not all of the non-neighbor males in our study were non-territorial males; some were residents of nearby, but not continuous, territories.

Territorial male amberwings, therefore, modify their space use at both the territory and within-territory spatial scales in a set of adaptive responses to their social environment. These responses are consistent with the hypothesis that they learn from both their positive and negative experiences with conspecifics and adjust their behavior accordingly.

Future Directions

We hope that this introduction to what is known about spatial learning in dragonflies will inspire more researchers to work on this subject. Although we have clear evidence that dragonflies are capable of learning, we do not have information about such basic questions as how long their memories persist, how much exposure to a site is necessary for them to learn its attributes and location, or how many spatial features they are capable of learning. Interestingly, recent work on mate recognition in damselflies suggests that the limit of a male's memory for a

female morph is less than one day (Miller & Fincke, 2004). Given that individuals are known to return to breeding sites after up to two months have elapsed (Corbet, 1999; Fincke, 1992), their memory for spatial cues may be much longer lasting than their memory of female images. Investigating the persistence of spatial memory relative to other sorts of memory is one avenue of research that is likely to be productive in this taxon, and future work should also address the evolution of spatial memory and of optimal memory length. It may be, for example, that a memory of the location of a breeding site is particularly critical for males of territorial species. For such males, the cost of defending a territory during settlement is higher than the cost of maintaining residency, and thus there may be a strong selective advantage for retaining a memory of the site's location. All else being equal, non-territorial species may experience weaker selection for spatial memory. Similarly, a relatively stronger ability to remember routes and landmarks should be highly beneficial for species that must travel relatively long distances among sites used for various activities. In contrast, species that are not particularly mobile or that tend to concentrate all of their activities in a small area may have less ability (and less need) to remember as many geographic features. Furthermore, persistent spatial memories may be more commonly found among species that experience long intervals between visits to certain sites, such as forest species that may not return to breeding sites during long droughts (Fincke 1992). In contrast, species that use highly ephemeral resources should be less likely to have long memories for the location of those resources; for example, a member of a species that uses floating vegetation as oviposition sites may retain a general memory for a pond, but no specific attachment to or memory of the location of a particular oviposition site, if the site's location is unpredictable.

Another aspect of dragonfly learning that needs to be investigated is sexual differences in spatial memory. We currently know less about spatial memory in females than in males. This may be partly because the behavior of females has been less studied, so that the movement patterns of individual females are less well understood than are those of males. Further work could include large-scale mark and recapture studies and displacement experiments on both males and females of various species. It seems likely that females may generally return to the same sites for feeding, roosting, and oviposition, although we have information for only a few species.

At least with regard to returning to profitable foraging sites and favored roosting sites, females and males may face similar selective pressures. However, for other kinds of behavior there are likely to be sexual differences in selective pressures on the evolution of spatial learning, and those differences may allow researchers to tease apart the relative value of certain types of information for dragonflies. For example, females clearly do not receive the same advantages for site fidelity as do territorial males. For males, defense costs can be greatly reduced for site-faithful individuals, and those costs may determine the length of a male's territorial tenure. For females, the benefits of re-visiting a particular territory might include re-mating with a favored male or re-using a favored oviposition site; neither of these potential advantages have as yet been demonstrated for dragonflies, and they may not provide as strong a selective force for spatial learning in the context of locating a particular territory as that provided to males by the benefits of

site fidelity. Similarly, it remains to be seen whether females will respond to landmarks on the smaller spatial scales that males use to locate sites within their territories; females have not been reported to make localization flights when leaving an oviposition site, as males do when learning their territories. For males, knowing the location of their oviposition sites is critical so that females can be quickly led to them. Females may also find it advantageous to reach oviposition sites quickly, especially in species in which females are persistently harassed by males. Females that have been disturbed at an oviposition site often leave the site but return to it after perching nearby for a short time; a quick, direct flight back to the oviposition site may allow females to avoid unwanted attention from males. This kind of memory is short term; how long it may persist is not known. In sum, the different selective pressures on males and females may result in interesting and potentially instructive sexual differences in spatial learning and memory.

In addition, the application of techniques used to study learning in other taxa will enhance our understanding of spatial learning in dragonflies. For example, studies of navigation in bees have been transformed by the use of harmonic radar, which allows researchers to track individuals carrying small transponders and flying near the ground (Riley, et al., 1996; Riley et al., 2003; Osborne et al., 1999). This technique would allow researchers to plot a dragonfly's path and to answer questions about the routes dragonflies use and how they learn those routes (Riley et al., 2003).

To date, the only arthropod taxon in which spatial learning has been studied in any detail is the Hymenoptera (bees, ants, and wasps). Dragonflies provide an opportunity to study very different species that, like some Hymenoptera, travel both relatively long distances between specific sites and, repeatedly, back-and-forth between certain sites. Further, territorial dragonflies appear to have evolved spatial memory abilities that function at a variety of geographical or spatial scales, as is the case for many hymenopterans. For example, many bees have to navigate between their nests and resource patches, but they may also become familiar with the locations of patches relative to one another (Fauria, Campan, & Grimal, 2004). In addition, bees may learn plant locations within patches, and individuals may even use the same routes to move between plants (Manning, 1956; Thomson, Peterson, & Harder, 1987). Consequently, dragonflies may provide independent tests for examining some of the ideas and hypotheses that have been investigated in the hymenopterans, such as the selective advantage of using landmarks for navigation. A better understanding of spatial learning and memory in this taxon will inform future research not only in the area of learning in general, but also in odonate behavior and ecology.

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