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The Role of Landmarks in Territory Maintenance by the Black Saddlebags Dragonfly, Tramea lacerata

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The role of landmarks in territory maintenance by the black saddlebags dragonfly, Tramea lacerata

(TITLE)

BY

Jeffrey Lojewski

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

Master of Science in Biological Sciences

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

2014

YEAR

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Abstract

Territoriality can reduce competition for resources, but territorial defense can be costly. Therefore any behavior that reduces territorial costs may increase the net benefit of territoriality. Some species will align their territory boundaries with conspicuous landmarks that may serve to reduce defense costs. Dragonflies, including black saddlebags (*Tramea lacerata*), defend territories at breeding sites, keeping rival males away to allow themselves access to females. We used three treatments to investigate whether *T. lacerata* used landmarks: constraining landmarks (an object that provided a physical barrier to flight), non-constraining landmarks (an object of the same dimensions and construction that did not impede flight), and a control without landmarks. We observed patrolling male black saddlebags and recorded the locations of turns at their territory boundary and interactions with other dragonflies. When either type of landmark was present, individuals placed their boundary at the landmark far more often than any other location. In addition, individuals that used landmarks had a significantly narrower range of turn locations than those that did not. Unlike other studies the use of a landmark did not seem to reduce defense costs, and interestingly not all individuals used landmarks when they were provided. The lack of an observed reduction in defensive costs could be due to the collection of data during territory maintenance rather than territory establishment, when the costs may have been higher, or landmarks may be important as part of a spatial reference system that aids male dragonflies in efficiently searching for females.

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Chapter 1: General Review of Territorial Behavior

Summary

My thesis deals with the establishment of territorial boundaries in a species of dragonfly (*Tramea lacerata*). In this chapter, I first review important concepts in territoriality, and then I highlight different types of territories. I briefly discuss the different definitions of territoriality in order to explain what is meant by a "territory" and show how different definitions have arisen over time. Territories can be classified into different types based on the degree of exclusivity maintained within them and the type of resources defended. Territoriality evolves when it is possible for individuals or groups to defend a particular resource that enhances their survival and reproductive success. Aggression is a necessary component of defense as individuals or groups struggle to prevent others from exploiting their area, utilizing a variety of methods to settle disputes. The settlement of disputes influences the spatial aspects of territories. The first spatial aspect of a territory considered is its size and shape because these properties influence the location of boundaries. The size and shape of a territory is set during the process of establishment, which may involve spatial learning and fighting. After the general discussion of territoriality and boundaries is complete I narrow my focus to dragonfly territoriality. The organization of the dragonfly section mirrors the larger territoriality section, including sections on the types of territories, defense, and spatial aspects of territories. The mechanism of territorial establishment in dragonfly territories is still unknown, and one possibility is that dragonflies use landmarks to help identify the location of boundaries. In my study I set up landmarks and analyzed whether they led to

more clearly defined boundaries and fewer agonistic interactions in dragonflies compared to boundaries without landmarks.

Types of Territories

Definitions of Territoriality

The oldest definitions of territoriality focus on an animal defending an area in order to exclude other animals (Noble 1939), specifically around the time when mating occurs (Tinbergen 1936). In its most general form a territory is simply a defended area (Tinbergen 1957). Over time many definitions of territoriality have been used (reviewed in Maher and Lott 1995). The definitions vary in the number of criteria used and whether they are conceptual or operational. Conceptual definitions focus on what attributes are used to define a territory and are more theoretical than operational definitions, which can easily be applied to field settings. Maher and Lott (1995) grouped the conceptual definitions of territoriality into three categories, defended area, exclusive area, and site-specific dominance. Maher and Lott (1995) found that when territoriality was studied in fish, 'defended area' was often the only criterion used. A few other studies used two or three criteria, including factors such as site specific dominance and the spatial distribution of home ranges in addition to a clearly defended area. A defended area was also the most common criteria used when studying birds, reptiles, and mammals. Over time territoriality has come to be recognized as one part of a continuum of spacing behavior (Craig and Douglas 1986). Craig and Douglas (1986) showed the importance of including dominance in considerations of territoriality. However current definitions of territoriality continue to rely on the defense of an area that does not overlap with another animal's area (Lacey and Wieczorek 2001).

Exclusivity in Territories

Differences in the definition of territoriality have led to the recognition of many types of territories that vary in the degree to which an individual excludes others. Maher and Lott (1995) divided territories into three major groups, a defended area, an exclusive area, and an area defined by site-specific dominance. Exclusive areas are perhaps the clearest form of territoriality. In exclusive territories the resident forces all unwanted intruders out of the territory. In *Anolis aeneus* juveniles defend territories against intruders so that there is little overlap (Stamps and Krishnan 1998). When territories are tied to reproduction the resident may exclude members of the same sex but not ones of the opposite sex, so there is sex-specific exclusivity (Butchart et al. 1999). When a territory is tied to foraging the resident may exclude all other individuals. For example limpets (*Patella caerulea*) show almost completely exclusive foraging paths (Keasar and Safriel 1994). Male white rhinoceroses (*Ceratotherium simum*) use scent marking to identify exclusive territories (Rachlow et al. 1999). Exclusivity does not necessarily imply that there is only one individual on a territory. Groups can maintain exclusive territories where members of any other group are kept out. Flocks of willow tits reside in exclusive territories that contain only one adult pair and several juveniles (Hogstad 1999). Pairs of butterflyfish (*Chaetodon austriacus*) defend exclusive territories against conspecifics (Righton et al. 1998), whereas ant communities defend exclusive foraging areas against heterospecifics (Adams 1994).

It is important to note that residents may not maintain exclusive territories across time or space. Wolf pack territories tend to overlap more when resources are poor (Tallents et al. 2012). In an experiment manipulating the distribution of food for dunnocks (*Prunella modularis*), Davies and Hartley (1996) showed that changing the food supply from abundant to patchily distributed caused territories to become larger and have greater overlap. Juvenile *Anolis aeneus* defend territories against unwanted intruders, but they may tolerate the presence of subordinate individuals that lack territories, especially when densities are high (Stamps and Krishnan 1998).

A definition of territoriality based simply on a defended area implies that an animal actively defends against intruders but does not or cannot completely exclude them. Simply defining a territory as an area that is defended is the least stringent form of territoriality. Some investigators may use this definition so that territoriality does not imply complete exclusivity, which would prevent them from calling a species territorial if exclusivity was not maintained. Therefore the degree of exclusivity may vary when comparing territorial studies. Reviews of territoriality may clump together territories that are nearly exclusive with other less exclusive territories under the definition of defended area. One example in which territoriality has been defined in terms of a defended area involves pupfish (Kodric-Brown 1988). Males defend suitable oviposition sites for females. In small productive habitats dominance hierarchies may develop in place of territoriality, revealing once again that territoriality is a flexible process (Kodric-Brown 1988). Some lizards show a territorial pattern similar to pupfish. Many lizards display territory defense except against individuals with different food-gathering strategies, and a dominance hierarchy develops in place of territoriality at high densities (Brattstrom 1974). Territorial defense is also seen in pied wagtails (*Montacilla alba*), although owners may tolerate the presence of wandering non-territorial individuals known as satellites (Davies and Houston 1983). Many mammals show territoriality based on defense of an area. There are many examples (reviewed in Maher and Lott 1995), one of them being chimpanzees (*Pan troglodytes*) (Wilson and Wrangham 2003). A special type of defended area may result if the resident chases intruders less frequently when they are farther away from the center of the territory, in which the territory may be called a dominion. Evidence for dominions has been seen in dragonflies (Wolf and Waltz 1984).

A third type of territory is defined by site-specific dominance. In this form territoriality is achieved because one individual or group is dominant in a certain area. Even though other individuals may be present in the territory, the dominant one will get preferential access to the resource held on the territory, whether it is food, mates, or some other resource (Kaufmann 1983). As seen previously, site-specific dominance may develop in place of territoriality when densities are high, such as the case in pupfish (Kodric-Brown 1988). Dunnocks show territoriality most of the time, but occasionally two unrelated males will defend a territory together and a dominance hierarchy develops (Davies and Hartley 1996). Resident flocks of black-capped chickadees almost always defeat intruding flocks, suggesting that resident flocks are dominant at that particular site (Desrochers and Hannon 1989). Female strawberry poison frogs also show site-specific dominance within their core area (Meuche et al. 2011).

Resources Defended In Territories

In addition to variation in the degree of exclusivity, territories can also be broken into types based on the resources defended within the territory. Individuals and species defend territories because they provide some benefit. Usually the benefit is in the form of some type of resource, such as food, mates, or shelter. For insects the defended area is often a mating site, so the location of their territory depends on the location where they are able to find a female. Thornhill and Alcock (2001) thoroughly review the different orders of insects that seek out territories in particular locations, and a few examples from their work are presented here. In the Order Hymenoptera, jewel wasps (*Nasonia vitripennis*) seek out female emergence sites to mate with virgin females, as do crabhole mosquitoes (*Deinocerites cancer*), and many species of Ephemeroptera. Some insects defend female oviposition sites including many species of Odonata, *Gryllus*, and *Oxybelus*. Other insects defend female foraging sites including some species of *Xylocopa*, tsetse flies (*Glossina pallidipes*), blister beetles (*Pyrota postica*), creosote-bush grasshoppers (*Bootettix argentatus*), and consperse stink bugs (*Euschistus conspersus*). The fourth area defended by insects is conspicuous landmarks that may be used by females to orient themselves while travelling. If females are not clumped at emergence sites or oviposition sites and they travel over large ranges, males that wait at landmarks may be at an advantage because they may have greater visibility, or females may be likely to travel by these landmarks in order to orient themselves. Examples of insects that use this method are honey bees (*Apis mellifera*), some carpenter bees, *Papilio zelicaon* and other butterflies, and *Quesada gigas* and other cicadas.

Maher and Lott (2000) published a comprehensive review of ecological variables that determine territoriality in vertebrates, and that is the source of most of the information in the following paragraphs. They found 20 variables that were related to territoriality. The most common variable was food, which was divided into assessibility (how individuals can identify food characteristics), density, distribution, predictability, quality, quantity, renewal rates, and type. Food quantity was the most common of all the variables, described in 24% of all papers. The other variables were listed as resources (distribution, quantity, predictability, and quality), population density, habitat features, mates, space, refuges/spawning/home sites, predation pressure, host nests, and energy availability.

The most common variables determining territoriality in fish are population density and space, making up 31% of all papers. For example agonistic interactions in rainbow trout (*Salmo gairdneri*) tend to increase as density increases, although the effect becomes clearer in fast-moving water (Cole and Noakes 1980). Manipulations of tank sizes have shown that dominance hierarchies in pupfish (*Cyprinodon pecosensis*) develop in smaller habitats at low densities in place of territoriality (Kodric-Brown 1988).

The most common determinants of territoriality in amphibians and reptiles were food quantity and food distribution. Stamps (1973) examined both in female *Anolis aeneus* and found that differences in the distribution and quantity of food could lead to the formation of a dominance hierarchy. When food becomes more clumped or more scarce individuals may become more clumped together, leading to greater overlap in territories and necessitating a dominance hierarchy. In contrast a study on salamanders (*Plethodon vehiculum*) revealed that food distribution did not lead to territoriality, potentially because food was so available that the cost of defending a territory was not worth the benefit (Ovaska 1988).

In birds, food quantity is the most cited territorial determinant, whereas among other variables habitat features and host nests are the most common. Pied wagtails (*Montacilla alba*) switch between foraging on territories and foraging in a flock depending on the amount of food available. If food is scarce on the territory an individual is more likely to join a flock, and if a flock cannot find a lot of food an individual may try and invade a territory (Davies and Houston 1983). Even when an individual is a part of a flock it will occasionally go back to its territory to ensure that the territory is not stolen, so territoriality is not completely abandoned (Davies and Houston 1983). Habitat features affect lek behavior in sage grouse (*Centrocercus urophasianus*). Territoriality has been observed to break down following harsh winters when the lek site is still covered in snow (Gibson and Bradbury 1987). Evidence for territoriality based on host nests is mixed in brown-headed cowbirds (*Molothrus ater*). In some studies no evidence of territoriality has been found (Elliott 1980), but other studies showed indications of territoriality by demonstrating that females responded aggressively to female calls, suggesting that females are seeking to defend a territory by excluding others (Dufty 1982).

In mammals, food dispersion, food quantity, and population density were the most important factors affecting territoriality. Kruuk and Parish (1987) suggest that as food quantity declines European badgers (*Meles meles*) may switch away from strictly territorial behavior. The dispersion of food determines whether territoriality is present in primates or not. Some insectivorous species are not territorial even though they move around enough each day so that the defense of an area would be possible (Mitani and Rodman 1979). Population density is related to the presence of territorial behavior in woodchucks (*Marmota monax*). In populations with low or intermediate densities territoriality occurs, whereas at high densities territoriality breaks down as home ranges overlap more, and a dominance hierarchy develops (Ferron and Ouellet 1989).

Territory Defense

Evolution of Territoriality

Territoriality evolves when an organism is able to defend a particular resource that increases its fitness, such as food or mates (Brown 1964). When the benefits of obtaining exclusive (or nearly exclusive) access to a resource outweigh the costs of defending the territory, individuals should become territorial (Brown 1964, Hinsch and Komdeur 2010). The butterfly *Lycaena hippothoe* has been shown to defend territories around nectar sources because that is where females aggregate (Fischer and Fiedler 2001). Females of this species tend not to be clumped except when around a source of nectar, so defense of females is not practical in other areas.

Territorial species may act aggressively toward conspecifics as well as heterospecifics (e.g. Lehtonen et al. 2010, Resende 2010). Conspecific aggression occurs because of a conflict over resources. If a conspecific invades a territory it may steal food, mates, shelter, or some other resource from the resident. The evolution of heterospecific aggression is less clear, and it is explored in a review by Peiman and Robinson (2010). They examined non-adaptive and adaptive explanations for heterospecific aggression. As support for a non-adaptive explanation of heterospecific aggression, they found that heterospecific aggression was greater among species within the same genera, which suggests that misidentification is the reason for heterospecific aggression. In support of adaptive explanations, they found that heterospecific aggression increased as the amount of resource overlap increased, indicating that heterospecific aggression occurs because of resource conflict similar to the conflict between conspecifics. Their results suggest that territorial individuals should defend an area against heterospecifics when the heterospecifics look similar to the territorial individual or they share a lot of resources.

In cases where territories are defended against conspecifics, not all conspecifics may be equal. Johansson (1996) noted that interactions between neighboring roe deer (*Capreolus capreolus*) were less intense than other interactions. This pattern is known as the "dear enemy effect" and it has been observed in a wide variety of taxa (fiddler crabs, Booksmythe et al. 2010; convict cichlids, Leiser and Itzkowitz 1999; lizards, Whiting 1999; yellow-bellied tits, Wei et al. 2011; ants, Santini et al. 2011; beavers, Rosell and Bjorkolyi 2002). The dear enemy effect is a flexible phenomenon that can change temporally (Briefer et al. 2008) and has been found primarily in breeding territories as opposed to feeding territories. Most data support the hypothesis that individuals respond more severely toward strangers because they present a greater threat (Temeles 1994). The reason that strangers pose a greater threat than neighbors is because over time neighbors may learn to respect each other's boundaries, resulting in lower defensive costs and therefore greater net benefits for each neighbor. Strangers may not have a territory and could pose a greater threat to residents because the stranger may not only steal mating opportunities but the territory itself (Temeles 1994).

Mechanisms of Territorial Defense

Disputes over territories are fairly common as individuals struggle to gain access to resources. In order to successfully defend a territory, there must be a way to settle disputes. The winner of a dispute may be determined based on several factors that depend on the species. The factor that decides a dispute is asymmetric, so that one individual has an advantage over the other. In cichlids, gonad weight and body size can predict the winner of contests (Neat et al. 2008). In tarbush grasshoppers (*Ligurotettix planum*) disputes are settled using calling behavior, in short contests winners depended on call rate and length, but in longer contests call length was more important (Greenfield and Minckley 1993). In the damselfly *Calopteryx splendens xanthostoma* the individual with greater fat reserves, indicating that it has more stored energy, wins disputes, and the amount of fat stored changes with age (Plaistow and Siva-Jothy 1996). In butterflies, the resident almost always wins disputes (e.g. Kemp and Wicklund 2001). The effect of prior residence is strong and does not seem to decay quickly over time (Beaugrand and Beaugrand 1991). Unlike body size and calling behavior, which may be tied to the quality of the individual, residence is not necessarily tied to individual quality. A territorial resident may still win disputes even if its opponent is larger (Koivula et al. 1993).

Spatial Aspects of Territoriality

Territory Size and Shape

Territories vary in their size and shape depending on the species and its environment. Understanding territory size and shape is an important first step in studying territory boundaries because boundaries are the features that define the size and shape of a territory. Adams (2001) recognized three different types of models that determine territory shape. The most common is the focal resident model. In this model only the actions of one focal individual are considered. The individual's decisions about the size and shape of the territory that it defends are usually determined by optimality theory. An individual may be an "energy maximizer" or a "time minimizer", which involves selecting a territory that gives the greatest net energy benefit or requires the least amount of time to defend or find food. In an interesting example, juvenile salamanders

(*Plethodon cinereus*) act as energy maximizers whereas adults act like time minimizers (Jaeger et al. 1995). If the individual does not maximize its energy intake or minimize time, it may defend as large an area as possible as long as the benefits outweigh the costs, or it may choose an area where it is least likely to starve (Adams 2001). In rare cases territory size may not be determined by an individual assessing the environment. For example heterozygosity can be correlated with territory size. In a study of the mesite (*Monias benschi*), it was found that groups with greater heterozygosity had larger territories (Seddon et al. 2004). They found that the same pattern held for males but not females. Males with greater heterozygosity also showed differences in song structure, allowing other individuals to assess the quality of the male.

The second type of model considers interactions between neighbors. Territory boundaries are determined by asymmetries between individuals. These asymmetries vary between species and may include factors such as body size and prior residency. Adams (2001) describes mechanistic and game theory models that determine the resulting territory size and shape in detail, so only a few will be highlighted here. One of the most significant mechanistic models predicts hexagonal territories when individual densities are high, territory sizes are similar, and individuals are equally spaced (Grant 1968). Another significant model is outlined in Huxley's elastic disc hypothesis, which Adams (2001) describes as an increase in incentive and ability of an animal to resist encroachment as territory size decreases. A result of this hypothesis is that if pressure is applied to one side of a territory then the territory may expand on opposite sides, which has been shown to occur experimentally in fire ants (Adams 1998). Adams (1998) showed that pressure was the result of agonistic interactions between ants, however positive pressure in the form of increased prey interactions can also cause shifts in territory shape (Steingrimsson and Grant 2011). Game theory models examine the costs and benefits associated with defending territories against neighbors. One example is Tullock's (1983) model that describes a conflict between two birds with territories surrounding a nest. The value of the territory decreases as the distance away from the nest increases, and eventually there is a point when the two competitors are equal (see also Mesterton-Gibbons and Adams 2003). This point and all others where the competitors are equivalent form the boundary between territories. Another game theory model indicates that taking larger-than-optimal territories is evolutionarily stable when population sizes are small and individuals compete over patchily distributed resources that are essential for reproduction (Knowlton and Parker 1979).

The third model of territory size and shape considers interactions between residents and intruders. These models often consider the distribution of animals in a habitat (Adams 2001). In an ideal free distribution (IFD), individuals select the habitat that is best suited for their survival and reproduction and they are not restricted by any other individuals (Fretwell and Lucas 1970). Adams (2001) connected IFD to territoriality by explaining that in systems in which the IFD is seen territoriality may allow individuals to regulate density, although no one is forced out of their "ideal" place. Under the IFD, territory size and shape are determined by each individual assessing the density in each patch and then choosing the available space that provides the greatest net benefit. When territorial behavior begins to restrict certain individuals from gaining access to particular areas, variations of the IFD develop, such as the ideal despotic distribution in which dominant individuals prevent subordinates from choosing the best habitat (Harper 1982). For example in yellow-legged gulls (*Larus michahellis*) younger subordinate individuals were found almost exclusively in a poor patch of habitat and prevented from breeding by dominant individuals (Oro 2008). Organisms may switch distributions depending on the predictability of the environment. When the predictability of convict cichlids receiving food is high they follow an ideal despotic distribution, and when it is intermediate they follow an ideal free distribution (Grand and Grant 1994). Models of interactions between residents and intruders emphasize the distribution of animals, possible strategic interactions among neighbors, and establishment effects (Adams 2001).

The Influence of Territory Establishment on Territory Size and Boundaries

In their model of territorial establishment, Stamps and Krishnan (1999) describe how animals can rely on spatial learning to associate areas with positive or negative experiences. The animals learn to avoid areas associated with negative experiences and return to areas with positive experiences. The establishment of a territory is a critical period for studies of territorial boundaries because that is when boundaries begin to take shape. Assuming that Stamps and Krishnan's (1999) learning model holds, boundaries may develop at the site of negative interactions as individuals learn to avoid these areas. In roe deer the establishment of territories coincides with an increase in agonistic interactions between individuals. The interactions serve to eliminate overlap between territories (Johansson 1996). The lack of overlap between territories clearly shows that a boundary has developed due to a response to negative agonistic interactions.

Stamps and Krishnan's (1999) model also predicts that animals should be able to respond to positive experiences and establish their territories accordingly. Leks represent a special type of territory, and they display unique establishment patterns that provide evidence for a response to positive factors. In lek mating systems, territories may be established around "hotspots" or "hotshot" males. In the "hotshot" model males distribute themselves around a successful male and may fight with the successful male to attract females onto their territory (Partecke et al. 2002). The "hotshot" model reveals how other males establish their territories around a centrally-located successful male. They are able to recognize that a lot of receptive females are located near this male and establish their territories accordingly, providing support Stamps and Krishnan's (1999) model. In the prairie mole cricket (*Gryllotalpa major*) attractive males that separate themselves from the group may gain an advantage in attracting females (Howard et al. 2011), which reveals that individuals are responding not only to negative effects (the presence of male competitors that reduce mating opportunities), but also positive ones (an increase in mating opportunities when away from the group) when establishing their territory. In the "hotspot" model, males distribute themselves in areas containing a lot of females. In the European beewolf (*Philanthus triangulum*), territories are established through scent-marking by releasing a sex pheromone at "hotspots" near female nest sites (Kroiss et al. 2010). Hotspots may occur near locations where females are already foraging. Males utilizing territories at these locations hope to mate with females as they seek out the food. Lek sites have been shown to contain larger amounts of food than non-lek sites (Ryder et al. 2006).

The establishment of feeding territories is frequently tied to the amount of available food in an area. The abundance and spatial distribution of food determines the size and shape of a territory, and three hypotheses have been proposed to explain the relationship (Marshall and Cooper 2004). The "direct monitoring" hypothesis describes how territory size directly follows the amount of food available. The "intraspecific competition" hypothesis predicts that territory size is limited by the number of competitors. The "structural cues" hypothesis shows that habitat structure can predict territory size. Evidence exists for all three hypotheses (direct monitoring, Gill and Wolf 1975; intraspecific competition, Hixon 1980; structural cues, Smith and Shugart 1987). Whereas many studies have shown an inverse relationship between food abundance and territory size (e.g. Hixon 1980 and its references), food availability also affects the rate of territory establishment. When food density is high, limpets (*Patella caerulea*) expand their territory more rapidly than when food is scarce (Keasar and Safriel 1994). In feeding territories strict boundaries may be defended during harsh times to ensure survival (van der Heide et al. 2012). These boundaries may be stable from year to year when conditions are good (Spear 1993) or territories may be used repeatedly if they contain good resources (Mason and MacDonald 2000). In other cases the territory may remain in the same area but with slight boundary modifications (van Riper 1995). When food becomes scarce, hyenas (*Crocuta crocuta*) have been shown to forage outside their territories (Honer et al. 2005). In badgers, adults are involved in territory defense, so they visit boundaries more often than subadults (Kowalczyk et al. 2006).

Territory Defense and Territory Boundaries

Territory boundaries are established and maintained in a variety of ways. For example, territory boundaries may be determined by a switch in dominance. The mechanisms by which territory boundaries are established are the same as the mechanisms by which they are defended. It is not surprising that the mechanisms are the same because defense can simply be considered a fight against the establishment of new territorial boundaries. Therefore defense and establishment are inextricably tied. The first mechanism that will be considered is fighting ability. Individuals or groups with greater fighting ability hold larger territories than weaker individuals or groups. One important note is that fighting ability is not always constant. Individuals may be less likely to win disputes when they are farther away from the center of their territory (Campanella and Wolf 1974). When individuals were removed from fire ant colonies, reducing their fighting ability, those colonies lost greater amounts of territory than unmanipulated colonies (Adams 2003). Since fighting is costly, individuals may use other signals to indicate fighting ability and settle disputes. Vocalizations can indicate fighting ability in bats (Davidson and Wilkinson 2004), toads (Arak 1983), and gibbons (Mitani 1988, Cowlishaw 1992). Birds also use singing in territorial defense (Ball and Hulse 1998, Schmidt et al. 2007). Other traits may be used to assess fighting ability and the specific trait depends on the species. Body size is used as a signal in *Anolis* lizards (Jenssen et al. 2005). Color may be used to assess fighting ability in some bird species (Pyrke et al. 2001) but not in others (Stutchbury 1992). Body size can also determine the outcome of contests (Moore et al. 2009). Other traits that are correlated with fighting ability are reviewed in Arnott and Elwood (2009).

The establishment of boundaries can be affected by the presence of predators (LaManna and Eason 2007). The presence of a predator is simply another cost to consider when establishing a territory. While holding a larger territory may give an individual greater access to resources, it also increases the area over which they risk encountering a predator. LaManna and Eason (2007) found that fish exposed to a predator accepted smaller territories than fish that did not see a predator.

Territory boundaries may be established on the basis of asymmetries such as fighting ability, but the costs of establishing boundaries through fighting are high. Disputes are particularly intense near territorial boundaries, especially when the boundaries are first established (Stamps and Krishnan 1997). One way in which the costs of territorial disputes may be reduced is through the adoption of landmarks (Eason et al. 1999, LaManna and Eason 2003). Landmarks may either be natural features in the environment (Reid and Weatherhead 1988, St. Louis et al. 2004) or features made by the organism such as the scent marks made by wolves (Sillero-Zubiri and MacDonald 1998) and badgers (Roper et al. 1993). Landmarks reduce defensive costs and allow more individuals to establish territories in an area than would be possible without landmarks (LaManna and Eason 2003). Heap et al. (2012) thoroughly review all studies that document the use of landmarks as territory boundaries. They provide evidence indicating that boundaries with landmarks persist longer than those without landmarks. They differentiate between two types of landmarks, constraining ones that physically restrict the visibility or movement of an organism, and non-constraining ones that serve only as conspicuous indicators of where a territory ends.

Heap et al. (2012) also describe two hypotheses that can explain how landmarks reduce the cost of defending territories. The first is the clear boundaries hypothesis. A landmark serves as a clear boundary when it is clearly visible and allows the resident to easily identify where its territory ends. Having clear boundaries can reduce defense costs either by allowing the resident to restrict its defense to the area defined by the landmark, reducing accidental intrusions onto territories, or reducing the need for repeated contests to re-establish territory boundaries. A constraining landmark may serve as a clear boundary because intruders may not be able to see or move past it, but for a non-constraining landmark to serve as a clear boundary both intruders must be able to associate the landmark with the interactions that take place there. The association between landmark and interactions allows the intruder to recognize that it has reached the edge of another individual's territory and not to proceed farther. The second hypothesis regarding the use of landmarks to reduce defense costs is the landmarks-as-convention hypothesis. Unlike the clear boundaries hypothesis, which emphasizes the role of landmarks as reference points to mark where a territory ends, the landmarks-as-convention hypothesis focuses on the role a landmark can play in reducing the costs of boundary establishment. If contests between individuals are very costly, then it may be beneficial for both individuals to adopt an arbitrary landmark as a territory boundary. The system should not work if an individual is unable to gain a sufficiently large territory. As Heap et al. (2012) describe, the individual must also respond to the landmark. A landmark that is adopted as a convention may be constraining, it may exploit an existing sensory bias, or it must be used as a spatial reference (Heap et al. 2012).

Dragonfly Territoriality

Dragonflies (Order Odonata) are a useful system for studying territoriality because they represent a gradient of territorial behavior ranging from aggression without site attachment to defense of an area with strong site attachment (Corbet 1980). Dragonflies are typically classified into two broad groups known as perchers and fliers. Perchers survey their territory from a perch located within it, occasionally making short patrol flights over the territory or flying to repel intruders (Heinrich and Casey 1978). Fliers continuously patrol around the border of their territory looking to intercept females or fend off male intruders (Heinrich and Casey 1978). While classifying dragonflies into two discrete groups is functionally useful, the percher-flier system is actually a continuum made up of some species that perch almost all the time at one end and species that fly almost all the time at the other (Corbet and May 2008). The following sections review important aspects of dragonfly territoriality, eventually focusing on territorial boundaries, an important aspect of territoriality that has received little attention.

Types of Dragonfly Territories

Before focusing on boundaries, it is necessary to understand the attributes of different dragonfly territories. Dragonflies tend to control territories that contain some resource. Most male dragonflies control territories containing suitable oviposition sites for females (Thornhill and Alcock 2001). These oviposition sites occur in an area frequently called the rendezvous because it is where males and females meet to copulate (Corbet 1980). Oviposition sites play a critical role in territory selection because males often choose territories based on the quality of oviposition sites present within them. For example *Nannophya pygmaea* choose their territories based on the quality of oviposition sites within the territory regardless of whether or not they had mated with a female in another territory previously (Tsubaki and Ono 1995). DeMarco and Resende (2004) found that individual *Perithemis mooma* choose sites with vegetation and explained that females may choose sites with vegetation in which to oviposit because the plants provide protection for the larva. In contrast they found that *Orthemis discolor* choose territories with tall perches so that they are better able to see females. DeMarco and Resende (2004) also demonstrate an important point that must be considered when studying habitat selection. While individuals may show a preference for particular features in a territory, that preference can be altered by the presence of competitors. Specifically they found that the presence of the dragonfly *Planiplax phoenicura* caused *O. discolor* to switch its preference from territories without vegetation to territories with vegetation (DeMarco and Resende 2004).

In addition to territories based on resource control, several other types of territorial behavior can be observed in dragonflies. Conrad and Pritchard (1992) classify odonate mating systems into resource-based and non-resource-based types, and these types influence how territory defense is conducted. They subdivide the resource-based group into resource-control and resource-limited systems. Corbet (1999) re-classified odonates into six new categories, all of which can be considered resource-based except for long-range migration. The resource-control system is exemplified by *N. pygmaea* and *P. mooma* as well as many other species of dragonflies in which males defend oviposition sites, and in order for females to gain access to the resource they must mate with the territorial male. Corbet's (1999) short copulation mating system is similar to the Conrad and Pritchard's (1992) resource control system. In the short copulation system there is strong competition for territories and unsuccessful males may adopt a satellite tactic in order to try and gain access to females (Corbet 1999). In contrast in the resource-limited system males cannot defend all possible resources (such as oviposition sites), so females are not forced to mate with territorial males. Territoriality still exists because some clumped resources can be controlled by individual males, but a non-territorial strategy can evolve because not all of the resources (e.g. oviposition sites) can be guarded. For example male *Leucorrhinia intacta* require perches on their territories, but some oviposition sites lack perches nearby. Females may mate with a non-territorial male and then oviposit in one of these sites, allowing non-territorial males to persist (Waltz and Wolf 1984). The resource-limitation system is also found in many Calopterygid damselflies (see Conrad and Pritchard 1992). The resource-limited system closely aligns with Corbet's (1999) long copulation system, except that Corbet (1999) divides the systems on the basis of copulation length to make them easier to distinguish.

Conrad and Pritchard's (1992) non-resource-based mating systems include free female choice, female control, and encounter-limited mating. Free female choice is a system in which females select males on the basis of favorable traits. While originally considered to be an unlikely mating system for dragonflies (Conrad and Pritchard 1992), there is evidence that some female dragonflies select males on the basis of wing pigmentation (Fincke 1997). An example of cryptic female choice is found in the dragonfly *Pantala flavescens*, which ejects sperm following copulation but before oviposition, allowing her to control the fertilization of her eggs (Cordoba-Aguilar 2006). Since females are assessing males on the basis of quality, a mating system based on free female choice does not necessarily require territoriality, and as a result there is very limited evidence for female choice in territorial dragonflies. Female *Plathemis lydia* frequently reject male mating attempts, but female choice does not play a major role in their mating system because females do not show a strong consistent preference for males with certain features (Koenig 1991). In *Diastatops obscura* females choose whether or not to oviposit following copulation (Irusta and Araujo 2007). Indirect female choice can occur when females choose to mate with territorial males and territorial males are of higher quality. Territorial males in species such as *Libellula pulchella* may contain fewer parasites, making them stronger and more able to hold territories, and the choice of females to mate with these males influences reproductive success (Marden and Cobb 2004). The free female choice system does not neatly correspond to any of Corbet's (1999) systems because a degree of intersexual selection is expected in all systems except long migration (see Table 11.21 of Corbet 1999), although it may be most closely related to the nonterritorial, oviposition site rendezvous system.

The next non-resource-based system is female control. Two of the assumptions of the female control system are that females and males encounter each other randomly and males cannot defend a resource that females use (Conrad and Pritchard 1992). Therefore territoriality is not likely to be a component of this mating system. The female control system is most similar to Corbet's (1999) postponed oviposition system because males in that system may patrol a large area not necessarily tied to an oviposition site. However if males can control a resource that allows them a greater ability to get access to females, then intrasexual selection within males can be strong and territoriality can be a component of the female control system. This pattern is exemplified in *Orthemis discolor*, in which males defend tall perches that allow them to see females as they approach the pond (DeMarco and Resende 2004).

The final system to be considered is encounter-limited mating. Encounter-limited mating is not really its own mating system, but rather one aspect of other mating systems in which encounters with females are rare (Conrad and Pritchard 1992). Male-female encounters may be rare when both females and their resources, normally oviposition sites in dragonflies, are widely dispersed. The low probability of finding a female in any given area means that territoriality is unlikely to exist because a territory would have to include large boundaries that likely would not be economically defensible. Infrequent male-female encounters characterize the long migration system and to a lesser extent the postponed oviposition and hinterland rendezvous systems (Table 11.21 of Corbet 1999).

Dragonfly Territorial Defense and Resolution of Conflicts

Regardless of the reason for territoriality or the mating system associated with it, defense is a critical component of territoriality. The oldest and simplest definitions of territoriality simply describe a territory as an area defended against other animals (Noble 1939). Based on this definition, aggressive behavior should be sufficient to determine the boundaries of a territory. It logically follows that wherever a dragonfly stops aggressively defending, indicating that he is no longer dominant, that is the boundary of its territory. However dragonflies can display a more complex system of territoriality in which the probability of being aggressive toward an intruder decreases as the distance away from the center of the territory increases. When this pattern is evident, a territory may be called a dominion (Wolf and Waltz 1984).

Territorial defense involves aggressive interactions against intruding dragonflies. Many factors have been examined to see if they affect the outcome of contests in many different species of dragonflies (see Table 1 in Switzer 2004). Many species of dragonflies show a pattern where the resident almost always wins in conspecific disputes (Van Buskirk 1986). However this pattern may be restricted to low-intensity contests (Switzer 2004). Interestingly residents also frequently win heterospecific disputes (Resende 2010). One possible explanation is that residents may have higher fat content (Raihani et al. 2008). Fat content is correlated with age, with younger individuals having more fat, so age can also play a role in determining residency (Marden and Waage 1990). Residents may also have fewer gut parasites that weaken the dragonfly's ability to defend a territory by reducing its fat content (Marden and Cobb 2004). Residency is also related to the time of day at which a dragonfly arrives (Switzer 2002a).

Space Use and Boundaries in Dragonflies

The previous section discussed territorial defense and the resolution of territorial disputes. Disputes can have profound effects on the size of territories, and therefore the location of territorial boundaries. In *Libellula pulchella* the size of territories decreases as the number of aggressive interactions increases, and therefore the territory boundaries change (Pezalla 1979). *Libellula luctuousa* also show an increase in aggression as the male density increases (Moore 1987), and the same pattern was observed in *Perithemis tenera* (Switzer 2002b). In *P. lydia* territory size increased along with the amount of time spent chasing but decreased with the number of other males on the pond (Koenig 1990). Early studies indicated that *Perithemis tenera* established regularly spaced territories (Jacobs 1955), and later studies have shown that they tend to perch in areas that minimize interactions with male neighbors (Switzer and Eason 2003). Whether territories are altered by a reduction in size or a change in spacing, the purpose appears to function to reduce the need for energetically costly aggressive interactions.

Visibility also plays an important role in shaping space use within territories. Dragonflies can detect intruders more quickly when they approach from certain angles, so if it is possible dragonflies should adjust their territory to maximize intruder visibility (Switzer and Eason 2000). *P. tenera* use perches that are located farther away from the shore than the oviposition site they are defending because they get a better view of approaching females and intruders (Switzer and Walters 1999).

As Pezalla (1979) described, boundaries may be set by aggressive interactions. However aggression is not a necessary component for determining the location of boundaries. Ubukata (1986) developed a model for flier-type dragonflies that describes when frequent turns are beneficial and when they are not, regardless of the presence or absence of aggression from conspecifics. In Ubukata's (1986) model the edge of the territory is not determined by aggression but rather by the chance to increase the probability of encountering a female. Dragonflies may set their boundaries in relation to environmental features such as landmarks. While few studies have directly tested for the use of landmarks in dragonflies, there is some anecdotal evidence to support the idea. Some of the earliest evidence comes from Campanella and Wolf (1974). They observed that territories somewhat aligned with clumps of vegetation on the shore and that the dragonflies followed the shoreline while patrolling. Adding shrubs reduced the size of territories, but removing them did not cause territory sizes to increase. Dragonflies have some capacity for spatial learning, as many of them are able to navigate long distances when travelling from site to site (Eason and Switzer 2006). Dragonflies are visual predators and clearly use vision to navigate around their environment, as evidenced by the strong site specificity of some species (Baird and May 1997, Switzer 1997). Male *P. tenera* will follow the oviposition site that they are guarding if it is gradually moved (Jacobs 1955). *Pantala flavescens and Pantala hymenaea* may use features on the ground as a reference in order to compensate for the wind while migrating (Srygley 2003). Some dragonflies and damselflies return to the same roosting sites for many consecutive nights, and through the manipulation of physical features it has been proposed that they use visual cues to recognize these sites (Miller 1989, Grether and Switzer 2000).

Thus, dragonflies are capable of spatial learning, and that they have the ability to recognize and respond to visible landmarks such as oviposition sites, perches, and even clumps of grass. However, little work has been done to connect territorial establishment in dragonflies to the use of visual cues. While it is clear that dragonflies establish territories, there is no clear mechanism for how these territories are established. Disputes over territories are common as one intruder attempts to move in on a resident's territory. These disputes are frequently settled through residency advantage (Van Buskirk 1986, Switzer 2004, Resende 2010). Therefore one of the simplest operational definitions of territory boundaries could be the location between two adjacent territories where an individual no longer wins disputes. Studies that demonstrate resident advantage often ignore its spatial component that is critical for understanding territory boundaries. They do not explicitly examine where resident advantage ends, or why it ends at that particular location. Understanding why territories end in certain locations is one of the key components of territorial establishment because it reveals how dragonflies respond to their environment when they create their territories. In my thesis I explored several possible ways in which the black saddlebags dragonfly (*Tramea lacerata*) establishes territory boundaries.

Possible Mechanisms for Boundary Establishment in Dragonflies

One possible mechanism by which black saddlebags may establish boundaries is through the use of landmarks. In my observations I have seen black saddlebags patrol long territories seemingly without regard to oviposition sites, rather they seem to try and intercept females as they approach the pond. Using a landmark may help black saddlebags determine their location around a pond so that they know where to turn around and start searching for females in another direction.

Two hypotheses have been developed and related to the use of landmarks to define territories, the clear boundaries hypothesis and the landmarks-as-convention hypothesis (Heap et al. 2012). One problem with these hypotheses is that they are not mutually exclusive (Heap et al. 2012), and manipulations designed to show that landmarks are used may not be able to distinguish between the two.

The clear boundaries hypothesis requires that individuals are able to associate negative interactions with conspicuous landmark and learn to avoid that landmark. The result is that the landmark becomes a boundary for a patrolling individual that encounters another dragonfly near the landmark and loses, so that when it returns to the landmark it remembers that it previously lost a dispute there and turns away.

Another prediction of the clear boundaries hypothesis is that interactions near a landmark should be less intense than those in the absence of a landmark. The presence of a landmark should allow an individual to quickly assess where it is and avoid energetically expensive disputes that it is likely to lose. To test this, aggressive interactions can be classified into different categories and compared in the presence or absence of a landmark. The presence of a landmark should result in lower aggression scores. Removing the landmark should cause an increase in aggression as individuals no longer have the visual cue that allowed them to clearly identify their territory boundary. As a result they may move into another resident's territory more frequently and get chased away more vigorously.

The landmarks-as-convention hypothesis has also been proposed to explain how landmarks can be used in territorial behavior. This hypothesis seems less likely to apply to black saddlebags or other dragonflies because it requires high fighting costs (Mesterton-Gibbons and Adams 2003, Heap et al. 2012). Most dragonfly contests are settled without any physical contact, meaning that the costs of fighting are relatively low (Lutz and Pittman 1970). Some fights may still be very energetically costly as they involve long chases (Marden and Waage 1990). In order for the landmarks-as-convention hypothesis to apply, both individuals in adjacent territories should settle on the same landmark to define the boundary in order to avoid the high cost of fighting. By placing a landmark, or exploiting a naturally occurring one, between two territories and observing the behavior of both individuals it can be determined if the landmarks-as-convention hypothesis applies. If both individuals frequently turn near the landmark that is evidence for the hypothesis, and if they do not the landmarks-as-convention hypothesis can be ruled out. If only one individual frequently turns near the landmark that indicates that one of them is using the landmark as a clear boundary, but the landmark has not been adopted as a convention.

If dragonflies do not appear to use landmarks in the establishment of territorial boundaries there are still several other mechanisms that can be tested. Boundaries may be established in areas where there are frequent contests. For a boundary to be present in these areas dragonflies will have to learn to avoid the area over time. By noting the location where disputes take place and then noting where an individual dragonfly turns as it patrols its territory, it can be determined whether dragonflies avoid areas in which they have previously been involved in contests, establishing these areas as boundaries. In order for boundaries to be established in areas with frequent contests, dragonflies must be able to associate negative interactions with a particular space.

Another possibility is that territory boundaries are continuously reestablished depending on changing factors such as density and temperature. In this case boundaries do not depend on physical space. In my observations I have seen black saddlebags patrol very long territories. They may be using a simple rule such as "fly as long as you can without being disturbed." The rule predicts that territory size should be highly variable, even at a constant density, because the location of the boundary depends on encountering another male. On some occasions one individual may fly to a point and interact with another male, and on other occasions he may not because the other males are off patrolling other parts of their territories. The rule can be tested by arriving early in the day, before any dragonflies have arrived, and recording the size of their territory as an individual arrives on the pond. The first individual should occupy a large space, up to the entire pond, and it should generally decrease as each individual arrives because interactions will become more frequent as density increases. Even though territory size should generally decrease, the location of the boundary and resulting size of the territory should show a lot of variation. One possible confounding factor that may prevent dragonflies from patrolling huge territories is the benefit that it receives from turning around (Ubukata 1986). As long as dragonflies move in one direction they cannot mate with any females that arrive behind them because they cannot see them. If female arrival is non-uniform then it is beneficial for a male to defend smaller territories in order to more frequently patrol a certain area where the male has encountered a female. However if female arrival is uniform (spatially and temporally) then moving forward or turning back makes no difference because the probability of encountering a female is the same. As a result a male may continue to move forward until it is forced to turn around. Given that black saddlebags do not appear to defend certain sites, such as oviposition sites, it seems more likely that female arrival is uniform and males are trying to patrol as large an area as possible in order to intercept females.

Temperature may also play a role in territory establishment. Dragonflies are more active at warmer temperatures, so higher temperatures should lead to larger territories, but increases in temperature also lead to a higher density of dragonflies. Territory size tends to decrease when dragonfly density increases (e.g. Pezalla 1979). Even if density remains constant, there should be an upper limit to territory size as it may decrease if the temperature gets excessively high and the dragonfly's thermoregulatory ability is affected. The relationship between territory establishment and temperature could explain why it does not appear that dragonflies use landmarks. The dragonfly may recognize that a landmark is present but simply choose not to use it because it limits their territory to an unacceptably small size for the given temperature.

The study of territory establishment in dragonflies should not be limited to the effects of conspecific density, landmarks, or abiotic factors such as temperature. Dragonflies must also deal with heterospecifics that are trying to establish their own territories. Heterospecific disputes do occur, although rarely (Resende 2010). It would be interesting to look at what happens when different species meet at the same boundary. Individuals may try to exclude heterospecifics or they may not. Heterospecifics do not pose a threat to steal a male's potential mates, but their larvae may affect each other. While competition for resources between heterospecific larvae may not appear to be strong, the effect is masked because larger larvae prey upon smaller ones, reducing the importance of competition (Johnson et al. 1985, Wissinger 1989). Therefore there may be some pressure to act aggressively toward heterospecifics. By noting whether boundaries are established between heterospecific dragonflies or whether heterospecifics exist within the same territory, it can be determined how the presence of heterospecifics affects territory establishment.

There are many possible factors that can affect territory establishment in a dragonfly. No one has determined whether or not landmarks play a role, but dragonflies are sensitive to visual cues and they possess spatial memory, key components for the use of landmarks. If they do not use landmarks then territories may be shaped by disputes, density, or temperature. While any of these factors appear likely to play a role in territory establishment, it is still possible that other unknown or imperceptible factors could influence the process. By thoroughly investigating one species of dragonfly this study hopes to determine exactly what black saddlebags use to establish territories. A similar framework can be applied to other species to further understand territory establishment in dragonflies.

Project Specifics

Study Organism

The genus *Tramea* has received relatively little attention in studies of dragonflies. Even less attention has been paid to adults, as most studies focus on larvae and their role as predators (e.g. Wissinger and McGrady 1993). A majority of the information collected on adults concerns their natural history. Like other dragonflies, members of the genus

Tramea eat insects such as stableflies (Wright 1945) and damselflies (McPeek and Peckarsky 1998). Fish are the major predators of *Tramea*, and they thrive in ponds where fish are not present (McPeek 1998). Their oviposition behavior is like a dance in which the female releases from the male to tap the water and then they re-engage (Davis 1898, Rosche et al. 2008). Some species found in Florida such as *Tramea abdominalis* and *Tramea insularis* fly all year, while in more northerly latitudes the flight season is more variable but typically between May and September (Paulson 2011). They may be present over land or water (Allison 1919) and are strong fliers able to stay in the air for several hours at a time (Kormondy 1961, Lutz and Pittman 1970).

The species that I used for this study was the black saddlebags dragonfly (*Tramea lacerata*). Like other members of *Tramea* they eat insects, display the typical dancing oviposition behavior, and may be found over water or far away from it (Paulson 2011). They migrate over long distances in large groups (Moskowitz et al. 2001). They patrol long flight paths over water and interact much more frequently with other flier-type dragonflies than perchers (Curry and Kennedy 2010). They tend to fly low over the water (Paulson 2011), so it should be possible to construct landmarks that constrain their movement and observe how they react. Black saddlebags have not been the focus of many studies because they are difficult to catch (Allison 1919). Their flight season is fairly predictable because they tend to emerge at the same time each year (Kormondy and Gower 1965). They have poor thermoregulatory ability like other members of *Tramea* (May 1976), so all aspects of their behavior including territoriality may be affected by temperature. They seem to possess some capacity to assess objects and recognize places they should not cross, as they have been shown to cross roadways less frequently than expected (Soluk et al 2011). Some consider black saddlebags not to be territorial (Wong-Munoz et al. 2011), however black saddlebags simply may not appear territorial because they often patrol very long stretches when over water (Paulson 2011).

Study Overview

The purpose of my study was to 1) assess whether *T. lacerata* use landmarks to help determine their territory boundaries, and 2) determine the effect of landmarks on conspecific interactions. To do this, I used focal sampling to observe the location and size of territories by recording where the dragonfly turned on each side of its territory. I also recorded whether the turn immediately followed an interaction with another dragonfly. On the following day I set up one of two types of landmarks: constraining landmarks (a PVC pipe frame with a screen designed to act as a physical barrier to movement), or non-constraining landmarks (just the PVC pipe frame, which provided a conspicuous feature but no barrier to movement). I placed the landmarks 4 m inside the territory boundaries observed on the previous day and recorded data as I had done on the previous day. Using these data I calculated how close the dragonfly's territory boundary was to the landmark, which indicated whether they used the landmark as a boundary. I also examined the relationship between landmarks and interactions with other dragonflies by determining if the use of landmarks reduced the number of interactions or altered their location.

Chapter 2: The role of landmarks in territory maintenance by the black saddlebags dragonfly, *Tramea lacerata*

Introduction

Animals defend territories when the benefits outweigh the costs (Brown 1964). During the process of territory establishment, potentially costly aggressive interactions can lead to the development of territory boundaries (Johansson 1996; Stamps and Krishnan 1997). Aggressive displays and interactions also serve to maintain territory boundaries once they are established (Savard 1984; Pryke and Andersson 2003). One potential way to reduce the cost of territory defense, thereby increasing the net benefit to the territory holder, is to align a territory boundary with a conspicuous feature known as a landmark. Landmarks have been shown to reduce the number and intensity of interactions at territory boundaries, either because the landmark serves as a clear boundary that is less likely to be crossed accidentally or because multiple individuals agree on the landmark to avoid costly interactions (Eason et al. 1999; LaManna and Eason 2003; Mesterton-Gibbons and Adams 2003). When landmarks are present, individuals may decrease territory size in order to incorporate a landmark as a boundary, which can lead to population level impacts (e.g. higher densities) as a result of this individual behavior (LaManna and Eason 2003; Heap et al. 2012).

In their review of landmark use at territory boundaries, Heap et al. (2012) define two types of landmarks: constraining and non-constraining. Constraining landmarks act as a physical barrier that restricts movement across them, whereas non-constraining landmarks do not restrict movement but are clearly visible. Of these, use of non-constraining landmarks are the most challenging to explain: despite not affecting visibility or movement, a "line in the sand" still can have dramatic affects on an individual's space use and defensive behavior. However, despite their apparent influence on territorial behavior in many taxa, the role of landmarks has received relatively little study, especially for territorial arthropods (Heap et al. 2012). Therefore, we lack a general understanding of the conditions under which territorial animals use landmarks for territory boundaries, as well as the types of landmarks that may be used (i.e. constraining or non-constraining) and whether the use of landmarks is due to lowered defense costs.

In this study, we examine experimentally whether male black saddlebags dragonflies (*Tramea lacerata*) use landmarks as territory boundaries. Male black saddlebags dragonflies patrol linear territories on the edges of lakes and ponds, typically flying within a few meters of the shore approximately 1 m above the water surface (Paulson 2011). While patrolling, they aggressively pursue conspecific males and some heterospecifics in non-contact chases (Lutz and Pittman 1970), and seek to copulate with arriving females (Corbet 1999). As with other territorial taxa, defending a territory is potentially costly for dragonflies (e.g. Koenig 1990; Marden and Waage 1990; Marden and Rollins 1994; Plaistow and Siva-Jothy 1996).

Although territoriality is common in dragonflies (Corbet 1999), no previous study has sought to determine whether dragonflies use landmarks as territory boundaries. However, anecdotal evidence of landmark use in dragonflies does exist; some previous studies have suggested that some dragonflies may align their territories with clumps of vegetation (Kormondy 1961; Campanella and Wolf 1974). In our study we sought to understand the factors that impact the maintenance of territory boundaries in male *T.*

lacerata by providing constraining and non-constraining landmarks on a pond and examining subsequent space use and aggressive interactions by territorial males.

Methods

Study Site

This study covered an entire flight season from 19 May – 2 September 2013 at a pond near the northeastern edge of Charleston, Illinois U.S.A. The pond is approximately 260 m in circumference, with two long edges each approximately 90 m in length and two short edges each 40 m in length. Vegetation around the edge of the pond was clipped to allow for easier visibility and to remove distinctive features that might be used as natural landmarks. Prior to the experiment the edge of the pond was marked every 2 m with small surveyor's flags to record locations of individuals and events.

Experimental landmarks

The experiment included three treatments: constraining landmark, non-constraining landmark, and a no landmark control. The constraining landmarks consisted of a PVC pipe (1.3 cm diameter) frame that had one horizontal pipe approximately 3 m long and two vertical pipes attached to each end extending 1.2 m above the water. We added four legs, two on each vertical pipe, by taking two pieces of pipe 0.3 m long, connecting them at a right angle and connecting them to the pipe. We attached empty plastic bottles (591 mL) to the bottom of each leg and on the bottom of the horizontal pipe so that the horizontal pipe floated on top of the water. We added a charcoal-colored fiberglass insect screen with 35 holes per cm^2 (Phifer, Inc.) that measured 3 m long and 1.2 m tall and attached it to stakes in the ground so that the frame would not tip over. The screen was designed to act as a potential impediment to the dragonflies' movement and vision. For non-constraining landmarks, the structure was exactly the same except without the screen, therefore the PVC pipe frame was still visible but it did not impede movement or vision. We positioned landmarks starting at the pond edge and oriented them perpendicular to the shoreline, and distributed them so that each focal dragonfly would only have one landmark on the left side of its territory. Each day, an experimental location was designated for landmark placement (or no landmark, in the case of the control). This location was approximately 4 m from the boundary of a male from the previous day. Using a location that was near, but not directly at, a previous boundary ensured that the landmark was in a suitable location but not directly corresponding to a previous territory boundary. Landmarks were placed on the pond prior to the arrival of any males. Data collection was organized so that no treatment occurred on consecutive days and no individual was observed more than once.

Observations

Each day, two observers conducted focal sampling on individual male dragonflies, which patrolled essentially linear territories along the edge of the pond within a few meters of the shore. Males would fly in an essentially straight line, occasionally slowing down or stopping to hover, until they reached a point at which they reversed the direction of travel within their territory (i.e. turned). Although males occasionally turned their body perpendicular to the direction of travel and stopped briefly (approx. 1 sec.) before continuing in the same direction it had been travelling, these did not result in a significant reversal in travel direction and therefore were not classified as "turns." Prior to collecting data on a male, we briefly observed it to determine if the male was patrolling the same area repeatedly and if it was aggressively pursuing other dragonflies (i.e. being territorial). Only males exhibiting these behaviors were used for observations. A patrolling male was observed with binoculars for 20 turns, 10 on the left side and 10 on the right. For each turn we recorded the location (to the nearest 1 m) and whether the turn was spontaneous or due to an interaction. A turn was defined as an interaction turn if it occurred immediately (< 1 sec) after the focal dragonfly chased or was chased by another dragonfly, while spontaneous turns had no interaction prior to the turn. For each focal individual we also recorded the time of day and the temperature as reported by a nearby weather station. During the study temperatures ranged from 19-34 °C.

After the turns were recorded we caught and marked the dragonfly using a permanent marker to write a number on its left forewing. Acrylic paint was also used to add 1-3 small dots to the wings so that the marked individual could be detected in flight. We measured the length of the left forewing as a proxy for body size. At the same time we recorded the density of male black saddlebags by counting all individuals currently active on the pond.

Data Analysis

Data were analyzed using SPSS Version 20. Non-parametric tests were used for many comparisons because most variables were not normally distributed. An individual's territory boundary was defined as the median of the turn locations on each side to account for the non-normal distribution of turn locations. Territory size was calculated by taking the difference between the median left boundary and the median right boundary for each individual. We first examined general territoriality patterns related to territory size, density, and temperature. Differences in density between treatments were analyzed using Kruskal-Wallis tests. To examine relationships between temperature, density, the number of conspecific interactions, and territory size we used Spearman rank correlations.

To explore potential differences between individuals that used landmarks and those that did not, we considered individuals to be users of the landmark if they had a boundary less than or equal to 1 m from the landmark location, and then we made comparisons between individuals that used the landmark and those that did not with Mann-Whitney U tests. These comparisons included territory size, the number of conspecific interactions, density, temperature, forewing length (as a measure of body size, e.g. Switzer 2004), and the proportion of turns due to interactions. We also used a Mann-Whitney U test to compare how likely an individual was to intrude on another territory by examining the maximum distance past its territory boundary in individuals that used landmarks and those that did not. To determine if individuals in each landmark treatment turned at the landmark more often than expected we used a chi-square test with the number of dragonflies that had a boundary within 1 m of a landmark for each treatment. For the control (no landmark) treatment we used the experimental location that would have had a landmark, as described above, to determine the number of individuals that had their actual boundary within 1 m of the hypothetical landmark. To determine the variability in territory boundaries we used the location of the shortest and farthest turn on each side to calculate the range of territory boundaries, and then compared the ranges within and among males using Wilcoxon Signed Rank tests and Mann-Whitney U tests. Because interactions with other dragonflies might also play a role along with landmarks in determining where an individual turns, we examined whether the proportion of turns with an interaction differed among different areas of the territory (short of the boundary, at the boundary, and beyond the boundary) between individuals that used landmarks and those that did not with Mann-Whitney U tests. We used the binomial test to compare the actual proportion of turns due to interactions for each individual to the hypothesized proportion of 0.5. We set the hypothesized probability at 0.5 because all dragonflies interacted with other individuals in their territory, and they could choose one of two possibilities following an interaction: turn around or not turn around. All probabilities are two-tailed and all means are reported ± SE.

Results

General Patterns in Territoriality

The average territory size was 69.7 ± 2.6 m (n = 88) without any landmarks, 66.5 ± 3.2 m (n = 59) with constraining landmarks, and 64.6 ± 2.7 m (n=57) with non-constraining landmarks. The difference in territory size between treatments was not statistically significant (Kruskal-Wallis K = 1.77, n = 204, df = 2, p = 0.41). The average black saddlebags density was 4.6 ± 0.2 individuals (n = 204) across all treatments, with no difference between them (Kruskal-Wallis K = 2.11, n = 132, df = 2, p = 0.35). As density increased, the number of conspecific interactions increased significantly (r_s = 0.34, n = 83, p = 0.001) and density increased with temperature for all three treatments (Constraining Landmarks: Spearman Correlation Coefficient r_s=0.33, n=45, p=0.027; Non-Constraining Landmarks: r_s=0.34, n=45, p=0.021; No Landmarks: r_s=0.32, n=42, p=0.042). As density increased territory size decreased (Constraining: r_s = -0.30, n =45, p = 0.046; Non-Constraining: r_s = -0.50, n = 45, p = 0.0005; No Landmarks: r_s = -0.32, n =

42, $p = 0.04$). Finally, as territory size increased, there was a decline in the percentage of turns due to interactions in the constraining landmark treatment, but no significant difference in the other two treatments (Constraining Landmarks: $r_s = -0.41$, $n = 59$, $p = 0.001$; Non-constraining Landmarks: $r_s = -0.20$, $n = 57$, $p = 0.13$; No Landmarks: $r_s = -0.12$, $n = 88$, $p = 0.26$).

Response to Landmarks

Black saddlebags dragonflies often responded to landmarks. In the no landmark treatment the location of the territory boundary (i.e. the median turn location) relative to the hypothetical location of a landmark was normally distributed among males, but in the landmark treatments the location of the territory boundary relative to an actual landmark was significantly non-normal (Figure 1a, No Landmarks: Shapiro-Wilk $W = 0.974$, $n = 71$, $p = 0.14$; Figure 1b, Non-Constraining: Shapiro-Wilk $W = 0.863$, $n = 47$, $p < 0.0001$; Figure 1c, Constraining: Shapiro-Wilk $W = 0.854$, $n = 49$, $p < 0.0001$). When a landmark (either constraining or non-constraining) was present individuals turned far more often near the landmark than expected when there were no landmarks on the pond (Figure 1). On constraining landmark days 38% (19/49) of individuals that had a landmark in their territory set up their boundary within 1 m of the landmark, and on non-constraining landmark days 53% (25/47) set up their boundary within 1 m of the landmark. This yields an overall average of 46% (44/96) of dragonflies that had a boundary within 1 m of a landmark, compared to the control (no landmark) days when only 1% (1/71) of dragonflies had their territory boundary within 1 m of the hypothetical landmark location ($\chi^2 = 43.5$, $df = 2$, $p < 0.0001$).

Consequences of Landmark Use

The use of landmarks did not impact overall territory size or the number of conspecific interactions involving the focal male. On constraining landmark days there was no significant difference in territory size between individuals that had a landmark within 1 m and those that did not ($\bar{x}$(within 1 m) = 60.2 ±5.9 m, $\bar{x}$(not within 1 m) = 70.5 ± 4.4 m, Mann-Whitney U = 229, n = 53, p = 0.19), nor was there any statistically significant difference on non-constraining landmark days ($\bar{x}$(within 1 m) = 71.7 ± 4.0 m, $\bar{x}$(not within 1 m) = 62.1 ± 4.1 m, Mann-Whitney U = 394.5, n = 50, p = 0.09). Likewise, there was no significant difference in the number of interactions with black saddlebags between individuals that used landmarks and those that did not ($\bar{x}$(within 1 m) = 5.9 ± 0.6, $\bar{x}$(not within 1 m) = 4.9 ± 0.4, Mann-Whitney U = 1414, n = 103, p = 0.22).

Individuals that had a landmark, regardless of whether it was constraining or non-constraining, within 1 m of their left boundary had a significantly smaller range of turn locations on their landmark edge as compared to those individuals that did not have a landmark within 1 m of their territory boundary ($\bar{x}$(within 1 m) = 37.8 ±3.3 m, $\bar{x}$(not within 1 m) = 46.7 ± 2.9 m, U = 948.5, n = 103, p = 0.05). The same pattern for a decreasing range of turns occurs when comparing within males (Figure 2); individuals that had a landmark within 1 m of their left boundary had a significantly smaller landmark boundary range than non-landmark boundary range (Wilcoxon Signed Rank W = 467, n = 38, p = 0.035). Individuals that did not have a boundary within 1 m of a landmark showed no difference in their left and right boundary range (W = 1023, n =65, p = 0.74). Individuals that used landmarks were less intrusive into other territories, as their maximum distance beyond the landmark boundary was significantly lower than individuals that did not use landmarks ($\bar{x}$(within 1 m) = 19.6 ± 2.1 m, $\bar{x}$(not within 1 m) = 30.5 ± 2.5 m, U = 514.5, n =82, p = 0.003).

These patterns in the range of turns cannot be explained by differences in body size, the density of individuals on the pond, the percentage of turns due to interactions, or temperature. There was no difference in body size between individuals that had a boundary within 1 m of a landmark and those that did not (forewing length $\bar{x}$ (within 1 m) = 44.3 ± 0.2 mm, $\bar{x}$(not within 1 m) = 44.3 ± 0.2 mm, U = 1215.5, n = 101, p = 0.893), or density ($\bar{x}$ (within 1 m) = 4.8 ± 0.4 individuals, $\bar{x}$(not within 1 m) = 4.8 ± 0.3 individuals, Mann-Whitney U = 817.5, n = 83, p = 0.89), or the percentage of interaction turns ($\bar{x}$ (within 1 m) = 21.7 ± 2.0%, $\bar{x}$(not within 1 m) = 18.4 ± 1.2%, U = 1396, n = 103, p = 0.27), or temperature ($\bar{x}$(within 1 m) = 26.6 ± 0.4 °C, $\bar{x}$(not within 1 m) = 26.5 ± 0.4 °C, U = 1237.5, n = 103, p = 0.93).

Interactions and the Location of Turns

Interactions did not play much of a role in shaping where a dragonfly turned. Individuals had significantly less than 50% of their turns occur with an interaction ($\bar{x}$ = 20 ± 0.9%, Binomial test Z = 7.1, n = 204, p < 0.0001). However, the use of landmarks did have some effect on the location of interactions. The proportion of turns due to interactions that occurred at the territory boundary on the landmark side was significantly higher in individuals that used landmarks compared to those that did not (Figure 3) ($\bar{x}$ (within 1 m) = 0.04 ± 0.008, $\bar{x}$(not within 1 m) = 0.01 ± 0.005, Mann-Whitney U = 1506, n = 103, p = 0.007). No significant difference existed in the proportion of interaction turns that occurred short or beyond the boundary between individuals that used a landmark as a boundary and those that did not (short: $\bar{x}$(within 1 m) = 0.1 ± 0.02, $\bar{x}$(not within 1 m) = 0.12 ± 0.01, U = 1118.5, n = 103, p = 0.42, beyond: $\bar{x}$(within 1 m) = 0.05 ± 0.01, $\bar{x}$(not within 1 m) = 0.05 ± 0.009, U = 1220.5, n = 103, p = 0.91).

Discussion

T. lacerata males usually turned without interacting with a neighboring male. Therefore, they were not simply flying until they encountered another male, as suggested by Davies and Houston (1984) for the dragonfly *Libellula quadrimaculata*. Instead, they were defending discrete areas, as found for other patrolling dragonfly species (e.g. *Cordulia aenea amurensis* Ubukata 1986). We found that *T. lacerata* males often used landmarks as territorial boundaries, even if the landmarks were not physical barriers to movement. The use of landmarks led to a more consistent territory boundary, with a narrower range of turns, but did not significantly affect territory size. This pattern of landmarks reducing boundary variability was not explained by conspecific density, the percentage of turns due to interactions, or ambient temperature. Increases in density did increase the number of interactions and decreased territory size. However, interactions did not decrease for individuals using a landmark, and interactions also did not seem to play a large role in boundary maintenance, as only 20% of turns occurred following an interaction.

To our knowledge, our study is the first to demonstrate landmark use for dragonflies, but similar results have been found in other territorial animals (Heap et al 2012). Previous studies have suggested that one of the main benefits of using landmarks, especially non-constraining landmarks, may be a lowered cost of territory defense (Eason et al. 1999; LaManna and Eason 2003; Mesterton-Gibbons and Adams 2003; Heap et al. 2012), and this hypothesis has received empirical support (Eason et al. 1999; LaManna and Eason 2003). In our study, however, we found no evidence that defense costs were decreased by males that used landmarks, as neither interaction frequency nor the percentage of turns with an interaction decreased for landmark-using males.

At least two possible explanations may explain this lack of an observed reduction in defense costs. First, our data were collected during territory maintenance, rather than territory establishment. Prior to collecting data on an individual it was necessary to determine that it was being territorial. Therefore, we may have missed the process of territory establishment, especially if this process was relatively brief, because we focused on males that were already patrolling repeated areas and defending them against conspecifics. Defensive costs may be highest during territory establishment (van den Assem and van der Molen 1969; Gwinner et al. 1994; Stamps and Krishnan 1997; Switzer et al. 2003). Because males in our study had established territories already, the benefit of landmarks on defensive costs may have occurred by the time our observations began. For example, Mesterton-Gibbons and Adams (2003) argue that the primary benefit of using a landmark as a boundary is that the landmark acts as a stable convention used by both the resident and potential intruder, and that once this convention is established defensive costs remain low. On average only 20% of turns followed an interaction, and these interactions were exclusively non-contact and relatively brief (typically < 3s) (see also Lutz and Pittman 1970), unlike some other territorial species in which physical contact occurs more commonly in disputes (van den Assem and van der Molen 1969; Kruuk and Parish 1987; Sillero-Zubiri and MacDonald 1998; Eason et al. 1999; LaManna and Eason 2003). Therefore, few interactions occurred, and what interactions did occur for *T. lacerata* in our study were not likely to be as costly as in these other species. Future studies should attempt to identify and track individuals prior to territorial establishment, during establishment, and after establishment to more clearly identify differences in defensive costs over time.

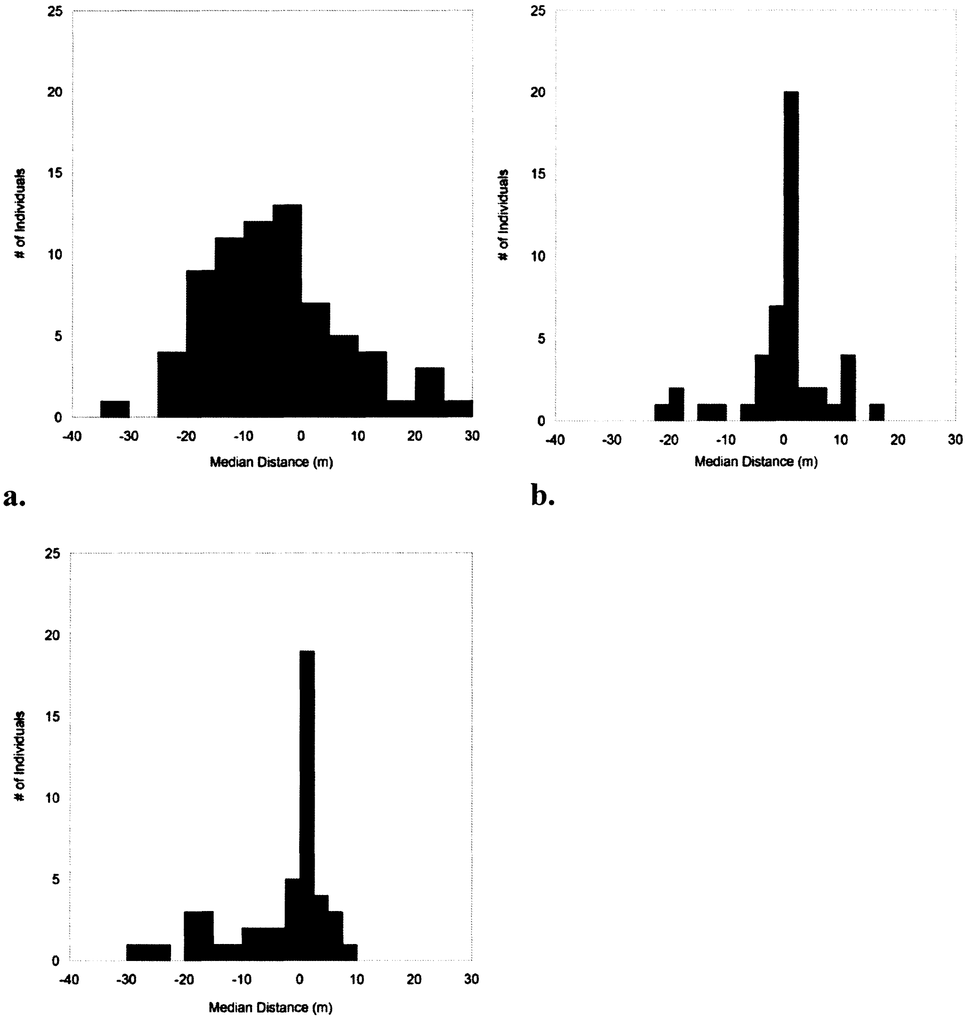
Second, because interactions were of relatively low frequency and likely of low-cost, it is possible that *T. lacerata* benefit from using landmarks in a way other than decreasing defense costs. One possibility is that landmarks serve as a reference point for males that yield an increase in familiarity within a limited area by ensuring he repeatedly patrols the same area without moving excessively beyond the territory boundary. Over time, familiarity with an area may allow the resident to accrue private information, such as areas where females may be found or characteristics of neighbors (Stamps 1987; Piper 2011). In his model of mate searching behavior and territoriality for another flier-type dragonfly, *Cordulia aenea amurensis*, Ubukata (1986) found that turning (i.e. having boundaries) can be beneficial when multiple males are present at a breeding site and spatial variation exists in female arrival, because it increases a male's ability to defend the territory and detect arriving females. Although landmarks were not included in Ubukata's (1986) model, we found that the use of landmarks led to more consistent turn locations at territory boundaries. Consistently returning to the same area allows the individual to become familiar with the area, and landmarks may help an individual develop a mental map that can be used to remember the location of individuals and events, allowing the territorial resident to anticipate positive and negative interactions in a particular space (Jenssen 2002). Therefore, landmarks can be incorporated into models such as Ubukata's (1986) because they promote familiarity within a territory, which may aid in defense and finding females. In addition, Heap et al. (2012) suggest that interactions that occur near landmarks should be more precise, such that if a negative interaction takes place near a landmark the resident will avoid a smaller area in the future than it would if there was no landmark in place. Thus, by limiting the male to a more defined area, landmarks may aid the male in developing a mental map of its territory, allowing it to adjust its behavior quickly in response to positive and negative interactions.

Interestingly, not all individuals in this study used the provided landmark as a territory boundary, unlike some previous experimental studies with landmarks (Eason et al. 1999; LaManna and Eason 2003). Several factors may influence whether landmarks are used as territory boundaries, and they can be broadly categorized as properties of the landmark and properties of the individual (Heap et al. 2012). At least two properties of the landmarks used in this study may have influenced the ability of dragonflies to use them. The first factor is the type of landmark used. Our landmarks were not natural landscape features, and it has been suggested that some species of birds may not respond to anthropogenic roads as landmarks because their lack of a long evolutionary history with roads prevents them from recognizing the roads as barriers (St. Clair 2003). However, this possibility can be ruled out for our study because we found that many *T. lacerata* did establish their boundaries near our landmarks. The second factor that could influence landmark use is placement. Heap et al. (2012) suggest that some landmarks may be used preferentially if they are in a specific location. For example, a male may reject a landmark if it results in a territory that is too small (Mesterton-Gibbons and Adams 2003). We attempted to place landmarks in appropriate areas by putting them in locations near previous territory boundaries, but we could not control male arrival at the experimental location or at other areas of the pond. Therefore, other males had the opportunity to set up territories in areas without landmarks, and the placement of their territories may have affected what section of the pond was available for a territory for the focal male. To defend a territory of a sufficient size, the focal male may have required boundaries in areas other than our landmark location. Finally, even though the male was not using our landmark, that does not preclude the possibility that it was using a different landmark. For instance, other landscape features, either within or beyond the pond, or changes in the pond shape (e.g. a corner) may have served as landmarks for these males.

Individuals differ in their intrinsic properties, and consequently some individuals may be less likely to use landmarks than others (Heap et al. 2012). Males that are better fighters may be less likely to use landmarks as territory boundaries if it is possible for them to get a larger territory by ignoring the landmark (Mesterton-Gibbons and Adams 2003). We found no difference in body size between individuals that used landmarks compared to non-landmark users, however body size may not always be correlated with fighting ability in dragonflies (Wolf and Waltz 1984; Kasuya et al. 1997; Switzer 2004), and future studies should thus study fighting ability in more detail to determine whether it plays a role in landmark use. Individuals also may vary in their willingness to go beyond territory boundaries, and consequently they may use landmarks less often, such as Smith (2011) found for rose bitterlings, *Rhodeus ocellatus*. In support of this possibility, we did find that individuals that did not use landmarks had a greater range of territory boundary turns and showed a greater tendency to go beyond territory boundaries. Consequently, individual variation in intrusion propensity may account for some of the lack of landmark use.

We found that when landmarks were used, a greater percentage of interaction turns occurred at the territory boundary than when landmarks were not used. Similarly, LaManna and Eason (2003) also observed an increase in the percentage of aggressive interactions at the landmark in cichlids. Repeated competition at a particular location can lead to more exclusive access to the location for the individual that initiates the interaction (Stamps and Krishnan 2001). Also, the net benefit of territoriality may be greater when defense can be restricted to the boundary (Holldobler and Lumsden 1980; Holldobler 1983). Some species of insects establish territories near landmarks, not as a territorial boundary but because they are attractive to females that use the landmark to orient themselves while travelling (Thornhill and Alcock 2001). In dragonflies, therefore, it is also possible that the landmark may serve as a location at which males converge for interactions. Alternatively, with more consistent boundary use, perhaps the boundary is simply more likely to be the location at which neighboring, patrolling males would encounter one another. Either way, whether landmarks serve as an active site of convergence or just as the passive primary location where neighboring males meet, when a landmark is present they may have interactions distributed over a narrower region than without a landmark.

In conclusion, we found that *T. lacerata* often use landmarks to define their territory boundaries. Although boundaries do not appear to have significant effects on social behavior during territory maintenance, as seen in other territorial species that use landmarks as territory boundaries, use of landmarks may be important in territory establishment and/or in promoting an efficient search for females. This latter suggestion – focusing on increasing the benefit of a territory rather than decreasing the costs – is unique compared to previous discussions of landmark use (e.g. Heap et al. 2012). We believe that future studies investigating how landmarks might aid in territorial searching efficiency, specifically with respect to the mating success of males that use landmarks compared to those that do not, would prove valuable in species for which this benefit may apply. To that end, because dragonflies as a group have a gradient of mating behavior, ranging from non-territorial species that show aggressive behavior without site attachment to species that are strongly territorial around specific oviposition sites (Poethke and Kaiser 1987; Corbet 1980; Corbet 1999), this taxon is likely to provide a useful model system for investigating the role of landmarks in a variety of territorial modes.



a.

b.

c.

Figure 1 Histograms of distance between the median boundary and the landmark (where 0 m = landmark location) for: **a.** no landmarks (n = 71 individuals) **b.** non-constraining landmarks (n = 47) **c.** constraining landmarks (n =49). The distances in Graph A are based on where the landmark would have been if one had been placed on the pond. Positive numbers represent boundaries that are short of the landmark (i.e. the landmark is not included within the territory) and negative numbers are boundaries beyond the landmark (i.e. landmark is inside the territory)

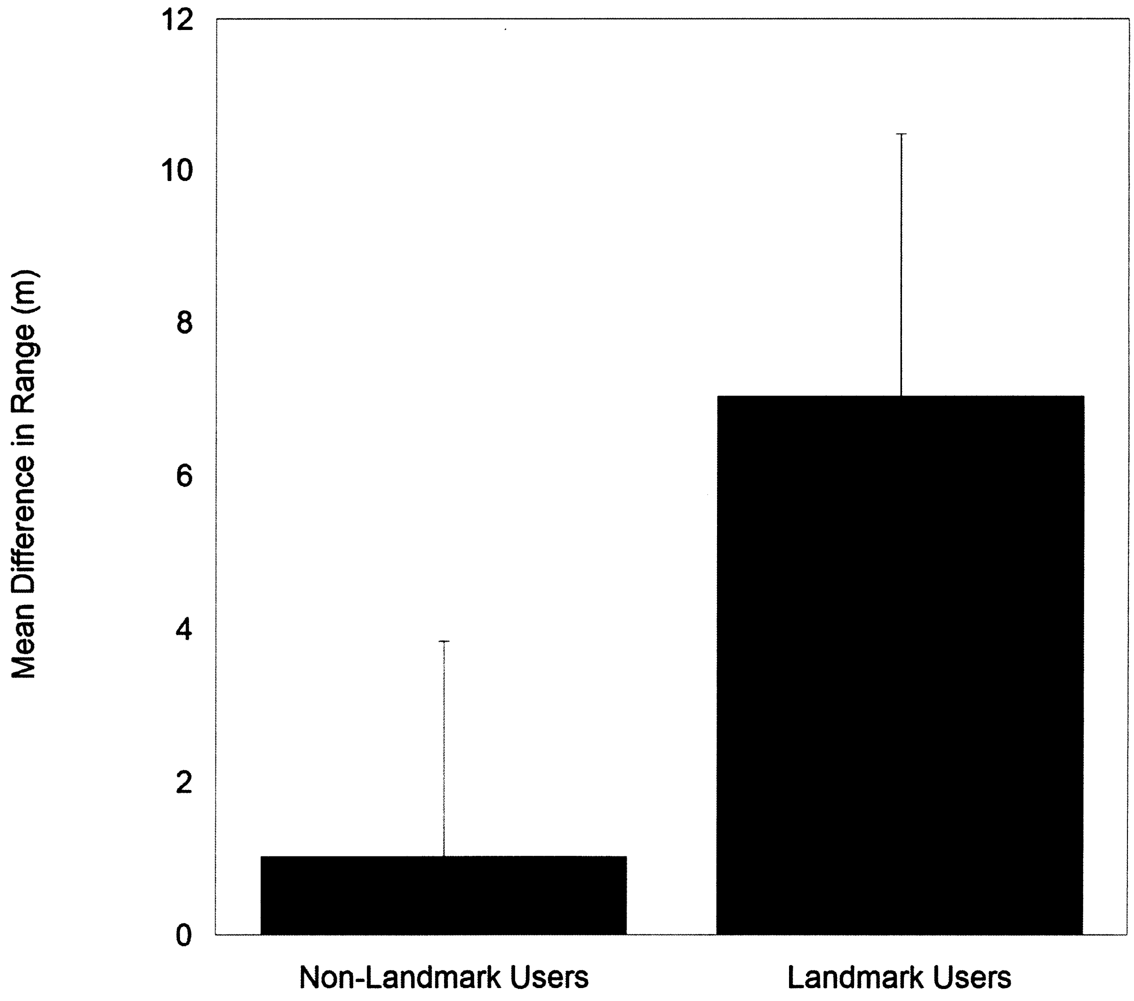


Figure 2 The average difference in territory boundary range (+ SE) between the non-landmark boundary minus the landmark boundary for individuals that used landmarks (n = 38) versus those that did not (n = 65)

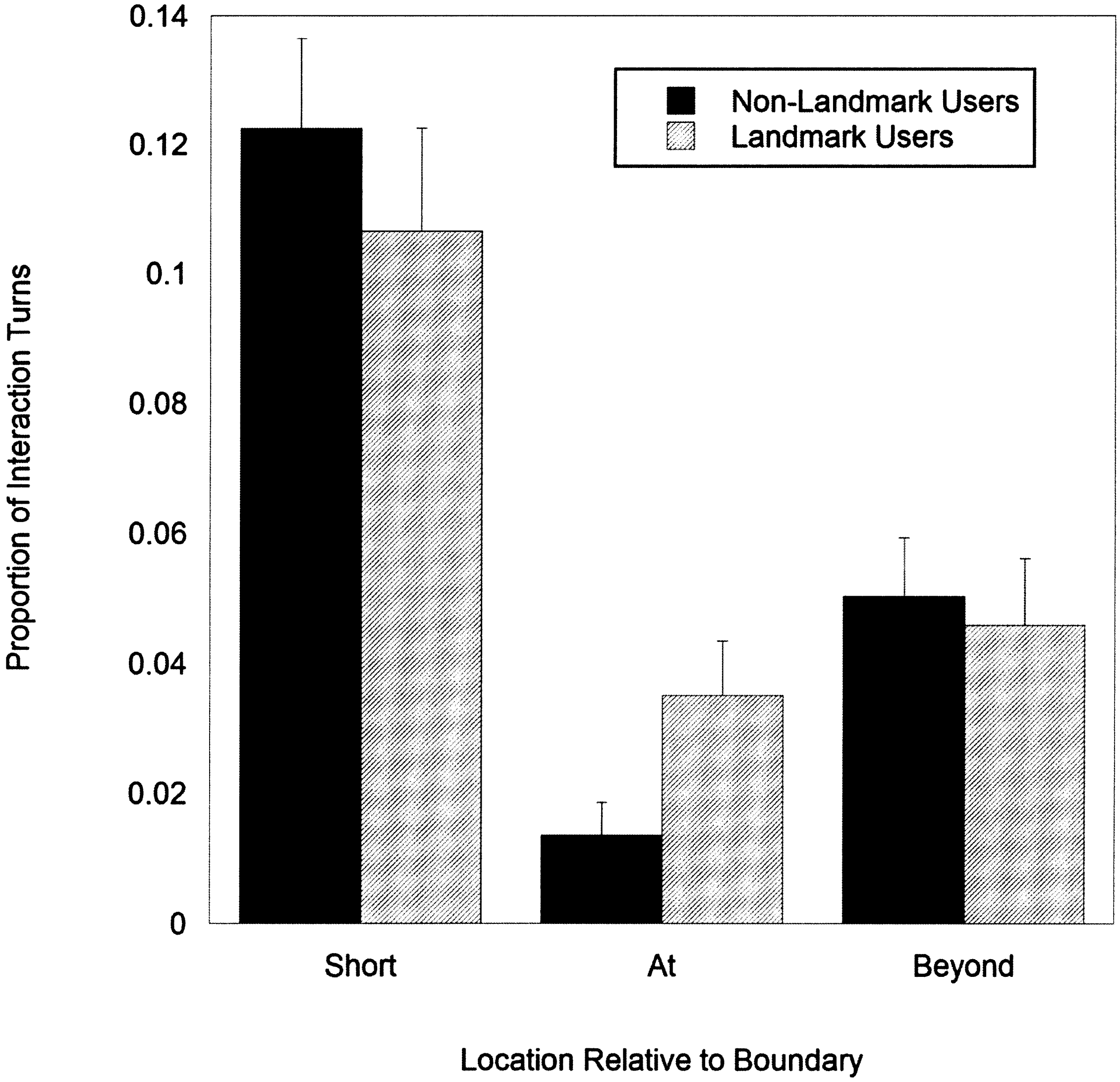


Figure 3 Comparison of the average proportion of turns following interactions (+SE) around the territory boundary for individuals that used landmarks (n = 38 individuals) and those that did not (n = 65 individuals)

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