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January 2000

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Proximate Constraints on Intruder Detection in the Dragonfly *Perithemis tenera* (Odonata: Libellulidae): Effects of Angle of Approach and Background

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Ann. Entomol. Soc. Am. 93(2): 333-339 (2000)

ABSTRACT The implications of insects' vision for territorial defense have been relatively little studied in the field. In the dragonfly *Perithemis tenera* Say we investigated whether either the angle at which an intruder was viewed by a territorial resident or the background against which it was viewed affected the detection of that intruder. Residents detected intruders at a greater distance if the intruders were directly in front of them; they also detected more intruders in front of them than from other angles. Intruders viewed against distant vegetation were detected more readily than were intruders against near vegetation. Residents detected more intruders viewed against distant vegetation than viewed against near vegetation; however, more intruders than expected were detected against near vegetation. The probability of detecting intruders depends on the angle at which they are viewed and the background behind them. Hence, there may be selection on territorial residents to adjust their orientation and space use to enhance their view of their territory and intruders.

KEY WORDS territoriality, intruder detection, odonates

ALTHOUGH INSECT VISION has been studied extensively in the laboratory (Wehner 1981; Land 1989, 1997), relatively little work has been done on insect vision in the field. As a result, we do not generally know how the activities of insects are influenced by their vision. To begin investigating how visual capabilities might affect behavior in the field, we studied territorial behavior in the Eastern amberwing dragonfly *Perithemis tenera* Say.

We focused on territorial behavior for 3 reasons. First, studies of territorial behavior have generally focused on examining the ultimate benefits of having a territory and have relatively rarely examined the proximate factors such as visual capacity. Second, such proximate factors are known to limit the conditions under which territoriality can occur and may therefore be likely to influence an individual's ability to defend its territory. The effects of proximate factors on the occurrence of territorial behavior have been studied and described in various taxa. For example, it has long been recognized that among lizards, species with relatively good vision are more likely to defend territories than are species that have relatively poor vision (Stamps 1977). Similarly, among insects, visual acuity varies widely, and in general, insect taxa that contain many species that defend territories by sight tend to be those in which visual acuity is relatively high, such as odonates, dipterans, hymenopterans, and lepidopterans (Baker 1983, Thornhill and Alcock 1983). Despite these demonstrated effects of vision on

the occurrence of territoriality, the effects of visual capabilities and limitations on territorial defense by individuals have not generally been examined. There are, however, studies that have examined environmental limitations on vision rather than innate, physical limitations, and not surprisingly, these studies have demonstrated that reduced visibility within a territory can alter an individual's territorial behavior and that individuals tend to select territories with high visibility (Rutowski et al. 1991, Eason 1992, Eason and Stamps 1992, Ravenscroft 1994). Finally, territoriality is a common behavior among diverse taxa, and strong proximal effects on territorial behavior are likely to influence the reproductive success of territorial residents; thus, any conclusions regarding the effects of vision on territorial behavior will be relevant to a wide variety of species and potentially significant for the evolution of territorial behavior and of visual systems.

To discover whether vision might affect territorial behavior, one should examine some component of defense that is critical to maintaining a territory. One such component of defense for all territorial species is the detection of conspecific intruders. Rapid detection of intruders is critical for territorial defense for several reasons. First, the speed with which a territory owner can detect an intruder may have significant effects on defensive costs. In various species, intruders that are not quickly detected and that therefore remain some time on the territory without being challenged by the owner are more costly to evict than intruders that are immediately detected and evicted (Krebs 1982; Beletsky and Orians 1987, 1989; Eason 1992). Successful intruders may also be more likely to

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attempt to take over the territory than intruders that were rapidly evicted (Smith 1978, Arcese 1987). In addition, intruders that have remained undetected on a territory for some time may be more likely to return to that territory, thus effectively increasing the intrusion rate for that territory. Furthermore, intruders that remain undetected have a greater opportunity to steal resources from the territory, such as food or a copulation with a female being defended by a male (Davies and Houston 1981, Moller 1987). Thus, failure to detect intruders rapidly can increase the costs of territorial defense and also decrease the benefits that the owner can derive from that territory.

Laboratory and field studies of vision have clearly identified 2 characteristics of vision that might affect the probability of detecting intruders and that thus could strongly influence how territorial residents behave in the field. The 1st of these is simply what the resident can see, which is determined by the visual field of the territorial resident and variation in acuity across that field. The size of the visual field varies across species. Within insects, for example, the visual field ranges from the somewhat limited field of cockroaches to the extremely wide fields of view found in many dipterans, odonates, and backswimmers (Mazokhin-Porshnyakov 1969, Frazier 1985). Visual acuity also varies across species, and for many species, acuity varies within the visual field (Horridge 1977, Land 1997). For example, acute zones may be located frontally or dorsally in insects that pursue prey, such as dragonflies and mantids, or in insects that pursue mates, such as male mayflies and hoverflies (Land 1997). If the ability of a resident to detect intruders depends in part on the portion of the visual field that is oriented toward the intruder and if the direction from which intruders approach is somewhat predictable, one might expect residents to position and orient themselves in such a way that the greatest proportion of intruders are viewed within the most acute region of the visual field (Pajunen 1964; Rutowski et al. 1991, 1994). Thus, the visual field and variation in acuity within that field may influence the ways in which territorial individuals use the space within their territories.

The 2nd characteristic of vision that could affect the probability of detecting intruders is the background against which a stimulus is viewed, which can determine how readily the stimulus is detected by a focal animal (Rutowski et al. 1991). Studies of predation have demonstrated that birds may more quickly locate approaching predators that are viewed against a plain background than identical predators that are viewed against a more complex background (Lima and Bednekoff 1999). Similarly, insects may more readily detect a small, dark, moving object that is viewed against the bright, uniform sky than an object that is viewed against nearby vegetation (Horridge 1977, Labhart and Nilsson 1995). Whether such effects of background will influence the ability of a territory owner to perceive an intruder in the field has not been examined. If such effects exist, however, the owner's behavior may also be influenced; one might for ex-

ample expect a resident to choose look-out posts that maximize the probability that intruders will be viewed against a plain background when possible (Rutowski et al. 1991, 1994).

Here, we first tested whether the angle at which an intruder is viewed by a territorial resident affects the detection of that intruder. Next, we investigated whether the background against which an intruder is viewed affects its detection. *P. tenera* is ideal for such questions because it is abundant and easily captured and marked, and because both intruders and residents' responses to intruders are readily observed.

Materials and Methods

This study was conducted June–August 1998 on a small farm pond (≈ 175 m in circumference) in east-central Illinois. The pond has a slightly sloping bank, no emergent vegetation, and the shoreline consists of grass kept at a height of 25–40 cm. Males at the pond were captured, individually marked on the right forewing, and released. Individuals marked in this manner could then be identified using binoculars.

A territorial male amberwing defends an area around a single oviposition site. Oviposition sites are generally objects lying on the surface of the water, such as a clump of algae or a stick (Jacobs 1955; Switzer 1997a, b). When few or moderate numbers of males are intruding on the territory, the resident perches on emergent vegetation, algae mats, or sticks, preferring objects that project above the water (Switzer 1995, Switzer and Walters 1999). When conspecific males or females enter his territory, he will fly out from the perch and approach them, attempting to drive intruding males from the territory and to bring females to the oviposition site to mate (Jacobs 1955, Switzer 1997a, Switzer and Walters 1999). At high intrusion levels, males tend to fly constantly rather than perch between flights (unpublished data).

To standardize the perch sites used by males, we provided dowels (5 mm diameter) that protruded identical distances above the surface of the pond; the distance that they protruded varied slightly with fluctuations in the level of the pond but remained within the range naturally used by amberwings (15–30 cm; Switzer 1995, Switzer and Walters 1999). These perches were placed 0.75 m out from the bank, every 1 m along the shoreline. This perch placement made multiple perches available to males.

We collected data by recording residents' responses to naturally approaching males and also by making experimental presentations of males and recording residents' responses to those presentations. For both natural and experimental intrusions, we recorded the distance at which a resident detected the intruder (detection distance); by using our 1-m spaced perches we were able to record this distance accurately. We used the time at which the resident took off in pursuit of the intruder to indicate detection, and we recorded the distance between the resident and the intruder when the resident took off as the detection distance. Some studies have found that detection of a visual

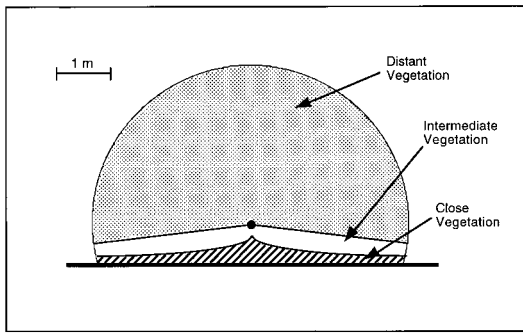


Fig. 1. Amberwing territory. The large dot indicates the resident's perch and the thick straight line represents the shoreline. The proportions of the territory that fall into the background categories of close, intermediate, and distant vegetation are indicated.

stimulus in dragonflies is indicated by head movements (Miller 1995); however, in amberwings, the head movement and take-off occur effectively simultaneously. Furthermore, in the field there are many stimuli that could elicit head movements, which makes the cause of any particular head movement difficult to determine (Miller 1995). In contrast, after a take-off the individual approaches the stimulus for that take-off; thus, the stimulus for a take-off is unambiguous. In addition, take-off is much easier for a human observer to detect in the field than are small head movements. For these reasons, we used the moment of take-off to indicate that the resident had detected the intruder.

Because we took multiple samples on individual males, we were able to use a male as his own control and thus eliminated differences in the reaction time caused by variation in motivation among individuals. The detection distance was recorded to the nearest 0.5 m for both natural approaches and experimental presentations.

For investigating the effects of background on detection, we assumed that the proximity of the vegetation to the conspecific determined the background against which the conspecific was viewed by the resident, i.e., an intruder that is very near vegetation would be viewed against vegetation, but an intruder that is some distance from any vegetation would appear against a simpler background (Horridge 1977, Labhart and Nilsson 1995, Land 1997). Therefore, we measured the distance between the point at which the approaching conspecific was detected and the shoreline vegetation directly behind it from the resident's point of view; we recorded this distance to the nearest 0.5 m. To calculate the expected values for the numbers of intruders detected against different backgrounds, we first divided the backgrounds into close, intermediate, and distant vegetation. For close vegetation, the background was <0.5 m behind the intruder, for intermediate the background was between 0.5 and 5 m behind the intruder, and for distant vegetation the background was >5 m behind the intruder. We made 2 simplifying assumptions. First, we assumed

that the shoreline was straight (Fig. 1), which was approximately accurate at our study site. Second, we assumed that the expected number of intruders in each category of background would be proportional to the area of the territory that was situated at the appropriate distance from the vegetation from the viewpoint of the perched resident. With these assumptions, we then determined the proportion of a territory from which a detected intruder would be viewed in each of the 3 categories of distance from vegetation (Fig. 1) and used that proportion to calculate the expected numbers of intruders. For simplicity in some analyses, we divided the data into only 2 categories, close and distant vegetation; for such analyses, intrusions that fell between these 2 categories in distance to the shoreline vegetation (i.e., between 0.5 and 5 m from the vegetation) were not considered in analyzing the effects of background on intruder detection.

We used naturally occurring approaches to examine the effects of both angle of approach and background. To get data on natural approaches, we made 15-min focal samples of resident males, and during these samples we took data on intrusions that occurred, recording the angle at which the intruder was approaching the resident when it was detected (angle of approach), the detection distance for this intruder, and the distance to the background vegetation. The approach angle was determined to the nearest 45° , with 0° representing an intruder directly in front of the resident and 180° representing an intruder directly behind the resident. We assumed that a resident could see equally well to either side (Wehner 1981, Land 1997), and hence did not distinguish between intruders approaching to the left and right sides of the resident. Data were not recorded if >1 intruder elicited a response from the resident, if the stimulus was not a male amberwing, or if the angle of the intruder's approach was not observed.

Multiple approaches were recorded for most males (55 of 56 males). Three methods were used to take advantage of these multiple observations while minimizing pseudoreplication in our analyses. First, when investigating the relative frequency of approaches from different angles and for different backgrounds, we used for each male only the category (e.g., 0° or close vegetation) with the highest number of approaches for that particular male for each male. If 2 or more categories for a male tied for the highest number of approaches, that male was not included in these analyses. Second, when combining data from all males for analyses involving detection distance, we calculated for each male the average detection distance in each category to decrease the contribution from any particular male. Thus, a male only contributed 1 data point (his average) to an analysis for a particular approach angle and background. Third, to investigate detection distances for different approach angles within individual males, for each male that had approaches from multiple angles, we calculated the Kendall nonparametric correlation coefficients for the approach angle and detection distance. Because of the relatively small number of approaches per male, ob-

taining statistical significance for individual males was unlikely. Therefore, we also conducted a meta-analysis, which allowed us to combine the probabilities of the individual tests and to perform a test for overall significance. Thus, we were able to look at patterns in the overall frequency of positive and negative correlations among males (Tsubaki and Ono 1987). Because not all residents had intruders approaching from all possible angles and against all possible backgrounds, sample sizes differ among some analyses.

To control for characteristics such as intruder behavior and time between successive intruder arrivals, we supplemented our observational data with data from experimental presentations of tethered males, a technique commonly used for studying odonate responses to conspecifics (Frantsevich and Mokrushov 1984, Mokrushov 1991, Gorb 1998). We used experimental presentations to examine the effects of angle of approach on detection distance; to control for the effects of background, all experimental presentations were conducted with the background vegetation >5 m behind the tethered individuals.

To standardize the behavior of the tethered individual, we used dead males that had been mounted in a flying position. These dead individuals were suspended from a length of thin florist's wire attached to a fishing pole. The use of wire allowed us to control the position of the tethered individual precisely even in windy conditions. Furthermore, the wire was inconspicuous to the resident: the mean detection distance \pm SE when using wire without a male attached was 0 ± 0 m with $n = 15$ males. Residents appeared to respond to a tethered individual in the same manner as a natural intruder (unpublished data).

During focal observations, males left their perch an average of 2.1 ± 0.16 times per minute (mean \pm SE; $n = 23$). Accordingly, to approximate the natural conditions and to remove the possibility of changes in motivation caused by the frequency of intrusions, we waited 30 s after any naturally occurring flight before making a presentation. The tethered individual was brought toward the resident at a speed of 2 m/s. This speed mimicked the approach speed of most naturally occurring intrusions (unpublished data) and allowed us to record accurately the distance at which the resident detected the tethered individual.

A given male was presented with a tethered male twice, once from 0° and once from 180° . To ensure that the resident being tested did not habituate to our tethered individual, we waited at least 10 min between presentations (36 ± 6.9 min; $n = 16$). Tethered presentations began 4–5 m from the resident; this distance was well beyond the average natural detection distance (2.0 ± 0.046 m; $n = 458$ approaches) that we recorded.

Because amberwing behavior may be sensitive to weather conditions (Jacobs 1955), we recorded ambient temperature and cloud cover hourly on days that we were collecting behavioral data. We did not take data on cloudy days when the temperature was below 25°C to eliminate periods during which amberwing activity levels could have been reduced (Jacobs 1955).

Table 1. Frequency distribution for intruder approaches relative to the resident

| | Approach angle | | | | | χ^2 | df | <i>p</i> |
|------------------|----------------|------------|------------|-------------|-------------|----------|----|----------|
| | 0° | 45° | 90° | 135° | 180° | | | |
| No. of residents | 11 (4.5) | 11 (9) | 7 (9) | 4 (9) | 3 (4.5) | 13.55 | 4 | <0.01 |

The approach angle was relative to the resident's point of view. The numbers represent the number of males that had the highest number of detections at that angle and the expected values are given in parentheses. Because each male had 2 potential 45° , 90° , and 135° angles (1 on each side of his body) but only one 0° and 180° possibility, the expected values are lower for 0° and 180° than for the other 3 angles.

Means are reported as \pm SE; nonparametric statistics take tied values into account when appropriate, and all *P* values are two-tailed.

Results

Angle of Approach. Most natural intruders were in front of the resident when they were detected (Table 1). Of 36 males, 22 males (61.1%) most frequently detected intruders at either 0° or 45° ; in contrast, only 7 males (19.4%) most frequently detected intruders at 135° or 180° . Residents were better able to detect intruders that were more head-on: as the angle of approach decreased, the detection distance increased (Fig. 2). This difference in detection distance is significant both when the background vegetation is close to the intruder (Kruskal-Wallis, $H = 26.2$, $df = 4$, $P < 0.0001$) and when the background vegetation is distant (Kruskal-Wallis, $H = 78.9$, $df = 4$, $P < 0.0001$).

The trends in detection distance were similar when we analyzed data within individual males. When the

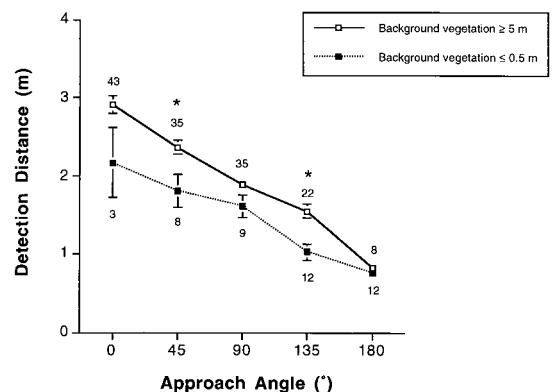


Fig. 2. Mean detection distance (\pm SE) for different angles of approach by naturally intruding males. For each male we used his average detection distance for a particular category; the numbers above or below the symbols refer to the number of males used to calculate the averages at that angle and distance to vegetation. Asterisks refer to angles for which detection distances differed significantly between the 2 categories of distance to vegetation using a Mann-Whitney test (45° , $U = 217.5$, $P = 0.015$; 135° , $U = 217.5$, $P = 0.0016$); $P > 0.12$ for the 3 other pairwise comparisons.

Table 2. Frequency distribution for intruder detections relative to the resident

| | Background vegetation | | | χ^2 | df | P |
|------------------|-----------------------|--------------|--------------|----------|----|--------|
| | Close | Intermediate | Distant | | | |
| No. of residents | 7 (2.8) | 2 (4.6) | 37 (38.6) | 7.62 | 2 | <0.025 |

The distance to background vegetation was relative to the resident's point of view. The numbers represent the number of males that had the highest number of detections in that category and the expected values are given in parentheses. Expected values were calculated based on the proportion of a territory that corresponded to a given background category.

vegetation was close, none of the 13 individual correlations between angle of approach and detection distance were significant (for all, $P > 0.05$). However, when the frequency of positive and negative correlations was examined across all males, a significant trend did emerge. As the angle of approach decreased, 11 of 13 males had increasing detection distances (Kendall $\tau < 0$), and 1 male had decreasing detection distances ($\tau > 0$), and 1 male had no correlation between detection distance and approach angle ($\tau = 0$; sign test, $P < 0.005$). When the vegetation was distant, 15 of the 44 individual correlations between angle and detection were significantly negative at $P < 0.05$ (mean $\tau = -0.78 \pm 0.032$ for these significant correlations). Overall, with decreasing approach angle, 41 of 44 males had increasing detection distances, 0 had decreasing detection distances, and 3 of 44 had no correlation between angle and detection distance (sign test, $P < 0.001$). Thus, the pattern evident within males is consistent with the results presented in Fig. 2: an intruder in front of a resident is detected at a greater distance than is an intruder behind a resident.

Results from experimental presentations also supported the idea that intruders were more quickly detected when they were in front of the resident. In these presentations, a resident tended to detect the presented intruder at a greater distance when the intruder approached from 0° (1.78 ± 0.23 m, $n = 16$) than when it approached from 180° (0.39 ± 0.76 m, $n = 16$; Wilcoxon $T = 0$, $n = 15$, $P < 0.001$).

Background. Of 46 focal males, 80% (37) detected the highest number of intruders when the vegetation was >5 m behind the intruder (Table 2). This result was probably because the territories had more points from which the vegetation was distant; when the proportions of the territories at different distances from vegetation were taken into account, more intruders than expected were detected when they were <0.5 m from the background vegetation (Fig. 2; Table 2).

Residents tended to detect intruders at a greater distance when the background vegetation was far behind the intruder as opposed to when the vegetation was near; this difference was significant for 2 of the 5 approach angles (Fig. 2). To control for potential variation among males in detection distance, we again made within-male comparisons. During focal samples, some residents changed the direction they faced during the observation period, which altered their orien-

tation with respect to nearby vegetation. This gave a sample of 14 males for which we had records of natural intruders that were detected approaching from the same angle to the resident (either 45° , 90° , 135° , or 180°) when the background vegetation was close behind the intruder (≤ 0.5 m) and when the background vegetation was distant (>5 m). We compared the average detection distances when the vegetation was distant versus close behind the intruder, controlling for the angle of approach. Of these 14 males, 9 had greater detection distances when the background vegetation was distant, 1 had a greater detection distance when the background vegetation was close, and 3 had equal detection distances for close and distant vegetation (sign test, $P = 0.022$). Thus, when controlling for angle of approach, an intruder far away from the vegetation seems to be easier for the resident to detect than one close to the vegetation.

Discussion

Both the angle of approach and the background against which an intruder was viewed by a resident had significant effects on the resident's ability to detect the intruder. Residents detected intruders at greater distances when intruders were in front of them (i.e., from 0 to 45°) than when intruders were behind them (from 135 to 180°) residents also detected intruders at greater distances when the intruder was viewed against distant vegetation.

For angle of approach, the most readily detected types of intrusions were also the most common: intruders most frequently were detected approaching residents from in front rather than from behind. This pattern could result from intruders tending to come from predictable directions and residents facing those directions. Alternatively, residents may tend to face the direction from which intruders most commonly come for some other reason; for example, residents might face toward the center of the pond because females approach from that direction or simply because the light is stronger in that direction. If so, and if intruders mostly come from the direction of the pond, then the residents will view most intruders head-on. Finally, a resident may be relatively unlikely to detect intruders until they are in front or nearly in front of the resident; thus intruders that begin to approach from the side may be detected only when they cross in front of the perched resident. This possibility is supported by our data showing that intruders at oblique approach angles tended to approach residents more closely before being detected, indicating that residents apparently could not see as well to the side as to the front.

For background, most residents detected most intruders against distant vegetation. This result may be caused by the location of the territories against the shore and a tendency for residents to face the pond; these 2 conditions meant that a resident viewed a large proportion of his territory and hence of intruders against distant vegetation (Fig. 1). However, intrusions detected against close vegetation, which were

the least readily detected type of intrusions, were more frequent than expected. Several hypotheses can explain these results. First, intruders may tend to approach so that vegetation is close behind them to decrease the chance that they will be detected. Second, intruders may tend to follow the shoreline, perhaps because resources such as oviposition sites tend to be concentrated along the shore. Third, predation risk might be higher over the pond than along the shore. At the study site, this explanation seems unlikely because many of their potential predators, such as larger odonates, lurk in the grass along the shore. Finally, the tendency of intruders to approach against close vegetation may be biased by observations of neighbors intruding, which should be more likely to occur along the shoreline given that the territories rim the shore at our study site.

Our results clearly indicate that the limitations of perception in amberwings could influence territorial behavior in the field. Residents were better able to detect intruders coming from certain angles, and given that rapid detection of intruders is critical, territorial residents should adjust their use of space within their territories so that intruders are most likely to be viewed from the angles from which they are most likely to be detected (Rutowski et al. 1991, 1994). For perching territorial species, this could mean that perch choice within a territory depends on the behavior of intruders; perch choice could also be influenced by the behavior of females (Ravenscroft 1994). Orientation should be similarly affected, with residents facing the direction from which either intruders or females tend to approach, if such a direction exists (Miller and Miller 1985). We are currently examining whether residents' orientation and use of space within their territories is affected by intruders and by the residents' ability to detect them.

Acknowledgments

We thank James and Fran Updegraff for permission to work on their property, JaLana Lewis for assistance in data collection in the field, and I. Switzer, J. Switzer, D.G. Cochran, and an anonymous reviewer for comments on the manuscript. This work was partially supported by a grant from Eastern Illinois University to P.V.S. and by National Science Foundation grant IBN-9707464 to P.K.E.

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Received for publication 11 May 1999; accepted 2 September 1999.
