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Seasonality of prey size selection in adult *Sympetrum vicinum* (Odonata: Libellulidae)

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Abstract

Sympetrum vicinum is a sit and wait predator, which takes off and pursues small flying insects during its long flying season (July to November). We investigated whether foraging individuals become less discriminating regarding prey size selection during the fall season because the changeable fall weather has an impact on the prey population. To investigate the seasonality of prey size selection, we videotaped prey capture flights of females and tenerals chasing artificial prey of known sizes (1-8 mm beads) from September to October in 2002 and 2003 in upstate New York, USA. We calculated the probability of pursuit for each bead size and measured the distance of the bead at the time of takeoff (213 presentations in 2002 and 383 presentations in 2003). We found that 2 mm beads had the highest probability of eliciting takeoff in both years and throughout the study periods. Weather conditions, especially the early first hard frost in 2003, reduced prey abundance. *S. vicinum* opportunistically pursued a wide variety of prey sizes. The probability of pursuit of larger beads (3-5 mm) increased in late fall, but *S. vicinum* never pursued 8 mm beads. The mechanism of distance perception and therefore size detection is not known in Odonata and yet *S. vicinum* in this study is showing a preference for 2 mm beads no matter what the distance of the bead from the perch.

Introduction

Adult libellulids are, for the most part, sit-and-wait predators, perching on the ground or on vegetation and periodically taking off after small flying insects. Once in flight, they swoop upwards from underneath their flying prey, grabbing the prey with their outstretched legs. They are very effective predators with capture rates as high as 97% (Olberg et al. 2000). This complex behavioral act is guided by the odonate's large compound eyes and highly developed visual system as they take off in pursuit of the prey, navigate to intercept the prey (Olberg et al. 2000) and coordinate leg movements to grab the prey.

We have been investigating the first step in the prey capture behavior, what characteristics of potential prey elicit takeoff after a moving object. The selection of prey items of an appropriate size is an important component of the foraging (MacArthur & Pianka 1966; Griffiths 1980; Stephen & Krebs 1986). According to foraging theory, odonates should chase prey items that maximize the energy harvest while minimizing the cost of chasing or handling the prey. In a 2002 study, we presented moving beads of various sizes to adult *Libellula luctuosa* Burmeister and *Sympetrum vicinum* (Hagen) and noted which sizes elicited takeoffs in each species. We discovered that each species has a very specific size preference implying that the foraging odonate can assess distance to moving objects and hence their size (R.M. Olberg et al. unpubl.). The 2002 data also suggested a seasonal trend in *S. vicinum*'s size discrimination.

In this study we investigated the seasonality of prey size preference in *S. vicinum*. First we assumed that the abundance of prey decreases with cooler fall weather and repeated frosts (Ives 1981). Our hypothesis was that as the mean daytime temperature decreased and rapid drops occurred overnight in temperature, the odonates would become less discriminating over time. *S. vicinum* has a long flying season (July to November), and is typically the last libellulid flying in the northeastern USA (Nikula et al. 2003). We predicted that *S. vicinum* would display flexibility in prey size choice in the face of declining prey choices.

Materials and methods

Study site and animals

Female and teneral *Sympetrum vicinum* were videotaped while chasing glass beads from perches in heterogeneous low vegetation surrounding grassy open grassy areas, 10-150 m away from ponds in town parks (Colonie Town Hall Park or Ann Lee Pond, Colonie, New York). This study was conducted from 8 September - 8 October 2002 and from 10 September - 31 October 2003. Weather records for both study periods were obtained from the on-line National Weather Service (NOAA) climate data recorded at the Albany County Airport, less than 2 km from both study sites <www.erh.noaa.gov/aly/climated>. The abundance of small flying insects was not quantified but aerial insect abundance and activity should decline with each night below freezing (Taylor 1963).

Stimulus presentation

Our principal artificial prey items were spherical white shiny glass beads ("Pearls", Jewelry and Craft Essentials, Hischerberg Shuts & Co, Inc.) of six sizes ranging from 2-8 mm diameter. In 2002 we presented six sizes of glass beads (1.5, 2, 3, 4, 5 and 8 mm) and we fabricated smaller beads, 0.5, 0.8 and 1 mm, from a mixture of starch and latex glue (Elmer's), which appeared to our eyes similar in appearance to the glass beads. In 2003 we presented four sizes of glass beads (2, 3, 5 and 8 mm) and 1 mm beads made from crushed milky quartz, which appeared to our eyes similar to the glass beads.

Each bead was affixed with cyanoacrylate adhesive to the end of a fine (75 µm diameter) tungsten wire 50 cm in length. This wire was invisible to our eyes at 2 m but was stiff enough to produce jerky bead movements that mimicked the flight of small insects. The tungsten wire enabled us to control the bead even in a breeze, which was not possible with fine fishing line.

The tungsten wire was glued at right angles to the end of a steel wire (1.8 mm diameter) 50 cm in length, and the steel wire slipped into the hollow end of a fishing rod (1.7 m long, 3.1 mm tip diameter) making it easy to interchange stimuli in the field. With the stiff wire extending the length of the fishing rod, we were able to dangle and move the bead above the perched odonate at a distance of 2.5 m. In no case did we see an escape response to the rod above the animal.

While one person focused a handheld MiniDV digital camcorder (Sony TRV17, shutter speed 1/100 s) on a perched individual, another person slowly brought a moving bead down from directly above the animal. The camcorder was aimed so that the odonate was at the bottom of the visual field, which extended 1 m above the animal. The bead was moved slowly downward in steps of 10 cm, pausing 2-3 s at each level. After each pursuit flight, a 10 cm calibration ruler mounted on another long rod was placed at the perch location and filmed. In a few cases, the odonate pursued a bead beyond the field of the camcorder. In these cases, the distance from the perch to the bead was estimated visually to the nearest 10 cm.

We presented each bead to different perched animals before switching sizes. We made no attempt to identify individuals. It is likely that a previously recorded animal was sampled more than once in one day but not consecutively. We varied the order of bead sizes presented each day. In 2003, we made sure that the number of bead presentations of each bead size was approximately equal each day.

Data analysis

Digital video clips of pursuit flights and calibrations were imported onto a Macintosh G4 computer using Apple's iMovie software. After editing the clips and noting any information on the audio track of the videotape (species, bead size, distance estimate, whether the animal had been tested previously, weather conditions, etc.), the clips were assembled into QuickTime movies (720 x 480 pixels) and imported into a motion analysis program (Videopoint) for frame-by-frame analysis.

For the four frames immediately preceding takeoff (defined as the first frame with the legs off the perch), location of the center of the animal's head and of the bead were digitized, as were the ends of the 10 cm calibration ruler. We calculated the distance from perched odonate to bead before takeoff using the x and y coordinates imported from the Videopoint file.

Results

Sympetrum vicinum took off in pursuit of our beads 43% (91 takeoffs / 213 presentations) of the time in 2002 and 24% (92 / 383 presentations) of the time in 2003. Probability of takeoff after a bead differed with bead size (Fig. 1). Both years, *S. vicinum* showed distinct preferences for beads between 1.5 and 2 mm diameter (Fig . 1). If we compare the distribution of the number of takeoffs after each bead size in 2002 and 2003 (not the probability of taking off after a particular bead size), the frequency distribution of takeoffs as a function of bead size are not significantly different between years (*G*-test of independence, $G = 8.464$, d.f. = 3, $k = 4$, n.s.).

However in 2002, *S. vicinum* was more likely to pursue the larger beads later in the study period (Fig. 2). During the first three days of the study (8-17 September)

S. vicinum took after 3-5 mm beads only 14% (21 takeoffs / 153 presentations of beads that size) of the time, while during the last three days of the study (28 September - 8 October), 3-5 mm beads were pursued 44% (36 / 82) of the time. During the same periods, preference for smaller 2 mm beads remained similar, 83% and 72%, respectively. In 2002 we did not present all bead sizes each day of recordings and we stopped recording well before a hard frost. We hypothesized that the odonates increased their chases of larger beads later in the fall due to the natural decline in the abundance of flying prey as the climate cools.

In 2003, we carefully examined the seasonality of prey preference. This extended the period of observations past the first overnight temperatures below freezing on 3 October 2003 (minimum temperature -0.6°C) and past several significant hard frost, 24 and 25 October (average minimum both nights -2.78°C). Using the weather records from the Albany County Airport <www.erh.gov/aly/climated>, we could separate our observations into three phases of fall weather. From 10-30 September, the days were fair and warm (average maximum temperature 22.7°C, average minimum 11.7°C). The next period, 6-13 October, began after the first mild frost and mild daytime temperatures (average maximum 20°C, average minimum 5.5°C). Our final observation period, 24-31 October, took place after several hard frosts and cooler daytime temperatures (average maximum 14.4°C, average minimum 3.1°C).

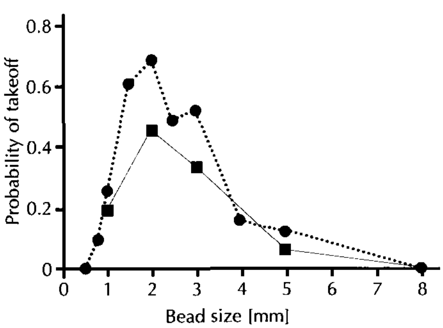

Figure 1: Prey size preference in *Sympetrum vicinum* — probability of pursuit of a bead as a function of the bead size. Probability of takeoff for each bead size equals the number of takeoffs towards bead size *x*/total presentations of bead size *x*. In fall 2002 (solid line with square symbol), each bead size, 1.5-8 mm, was presented an average of 24 times (range 5-56, n = 213 presentations of beads). In fall 2003 (dotted line with black spots), each bead size, 1-8 mm, was presented an average of 77 times (range 50-100, n = 383 presentations of beads).

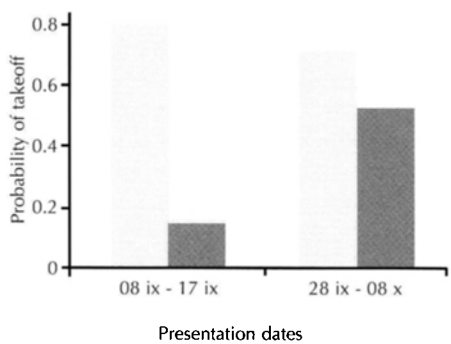

Figure 2: Seasonality of prey size selection in *Sympetrum vicinum* — probability of pursuit of small beads (1.5-2 mm, light grey) and large beads (3-5 mm, dark grey) as a function of season in 2002. Probability of takeoff for each bead size equals the number of takeoffs towards bead size *x*/total presentations of bead size *x*. Bead presentations early in the sampling season (08-17 ix 2002) are contrasted to presentations late in the study season (28 ix - 08 x 2002).

As the fall season progressed, the probability of pursing beads greater than 2 mm increased (Fig. 3). Overall bead pursuit increased from 25.6% (45 takeoffs for all beads / 176 presentations) in the early fall to 29.9% in the late fall (23 / 77 presentations). *S. vicinum* never took off after 5 mm beads until after the first hard frost (after 24 October), although preference for 2 mm beads remained high and increased over time. In the early fall, 43% of 2 mm bead presentations were chased (26 / 60 presentations of 2 mm beads) and, in late fall, 59% (10 / 17 presentations of 2 mm beads, Fig. 3).

The frequency distributions of number of chases of each bead size changed significantly with the seasons (Fig. 4, $G = 16.58$, d.f. = 6, $k = 4$, $p < 0.025$).

S. *vicinum* took off after beads at a distance of 1 m or less (Fig. 5). It showed no tendency to pursue larger beads at greater distances, where larger beads would have smaller visual angles ($R^2 = 0.023$, $F = 2.5$, n.s.). Each bead size was pursued over a wide range of distances. For example, *S. vicinum* chased after 2 mm beads over a range of 3-80 cm (Fig. 5).

The distance from which *S. vicinum* pursued beads did not change with the season (Fig. 6). There is a high variance in the distance that the animals are willing to fly after any bead size (Figs 5, 6). Even for the largest bead (5 mm), chased only at the end of the season, pursuit distance ranged from 10-100 cm.

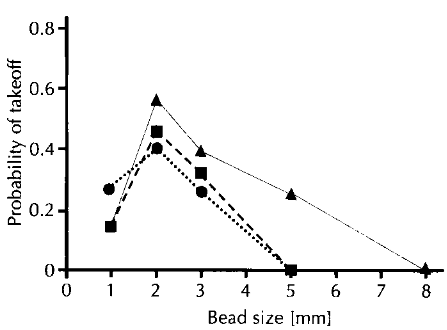

Figure 3: Seasonality of prey size selection in *Sympetrum vicinum* — probability of pursuit as a function of three distinct weather conditions in 2003: sunny and warm (dotted line and black spots, 10-30 ix), after the first mild frost (dashed line and square symbol, 06-13 x) and after a hard frost (solid line and triangle symbol, 24-31 x). Probability of takeoff for each bead size equals the number of takeoffs towards bead size *x*/total presentations of bead size *x*. Each bead size (1, 2, 3, 5 and 8 mm) was presented equally in each period.

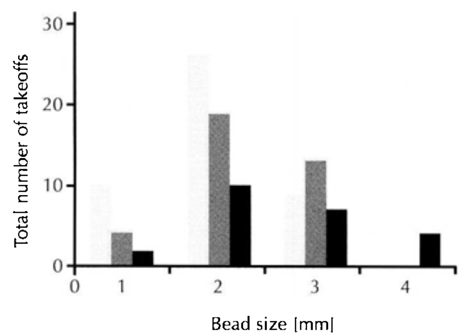

Figure 4: Seasonal changes in prey size chased by *Sympetrum vicinum* — total number of chases of each bead as a function of three distinct weather conditions in fall 2003. Distributions are significantly different (*G*-test of independence, $G = 16.58$, d.f. = 6, $k = 4$, $p < 0.025$). The weather con-ditions in each sampling period are described in caption for Figure 3 (light, 10-30 ix; middle, 10-13 x; dark, 24-31 x).

Discussion

Sympetrum vicinum showed a strong preference for 1.5-2 mm beads throughout the fall. *S. vicinum* began to pursue larger prey items in late fall, while still preferring smaller prey. As the summer ends in the northern hemisphere, there is a seasonal decline in small aerial insect abundance and activity. According to Taylor (1963), if small insect flight activity is at a maximum (100%) at 30°, only 65% of insects are flying at 22°C, 50% at 20°C and 30% flying at 15°C, the average air temperature for each of our observation periods.

The foraging behavior of anisopterans operates within the constraints of both the economics of prey choice – profitability being defined by prey abundance, energy yield per prey and energy expenditure per pursuit – and the resolving power of the visual system. The acuity of the eye is a function of the inter-ommatideal angle. In the zone of highest acuity, the dorsal fovea, Sherk (1978) calculates that the small inter-ommatideal angle provides a resolution of 1/4° of arc. As a rule of thumb, a 2 mm object makes a 1/4° arc at a distance of a 0.5 m. The speed of reaction of the photoreceptors also influences what size and velocity of prey can be detected. Therefore, larger objects can be detected farther away and at higher angular velocities than smaller objects. Very high velocity prey may be undetected.

Prey pursuit varies considerably among species of libellulids. *Libellula pulchella* Drury (R.M. Olberg unpubl.) pursues beads over a wide range of distances (12-209 cm) with a mean distance of 75.6 cm (n = 75 flights, s.d. 36.8). *Pachydiplax longipennis* (Burmeister) has a mean flight distance of 0.76 m (Baird & May 1997, 2003). *P. longipennis* flies farther for larger prey (Baird & May 1997); most large prey, defined as prey that protruded from the buccal cavity, were caught 1.5-2.5 m from the perch. This behavior could be explained by foraging economics or by sensory constraints. Foraging theory would predict that larger prey is worth flying farther for but the design of the odonate visual system makes small prey hard to see at greater distances. R.M. Olberg (pers. comm.) has been making high-speed video recordings of the foraging of *Erythemis simplicicollis* (Say) and *P. longipennis* and he finds that *E. simplicicollis* will chase a 2 mm bead at short range (15 cm) but *P. longipennis* flies after the 2 mm bead before the bead is within the camera's field at distances of 50-100 cm. In this study, *S. vicinum* pursued large and small prey at a wide range of distances (5-100 cm) with a mean distance of 26.5 cm (n = 78 flights, s.d. 19.0 cm). In fact, even 1 mm beads were pursued up to 50 cm. Unlike *P. longipennis*, there was no indication that *S. vicinum* flew farther for larger prey nor did they increase foraging distance when prey abundance declined late in the fall.

All anisopteran species pursue prey of diverse size and taxa (Pritchard 1964; Alonso-Mejia & Marquez 1994; Corbet 1999: 345) with the majority of anisopterans (95%) carrying small Diptera and Coleoptera in their guts (Pritchard 1964). Among the odonates that pursue prey from a perch, each species appears to have its own foraging strategy of what size prey to pursue. Baird & May (1997) find that *P. longipennis* discriminates against abundant small prey (< 1 mm) and that 60% of their successful prey captures are of prey 1-2 mm in size. Prey items of this size (1-2 mm) are the most abundant in their study site in Florida. *P. longipennis* selects larger prey (> 2mm) generally in proportion to its abundance. Large prey items (> 4.5 mm) were rarely pursued. May & Baird (2002) find that *E. simplicicollis* is more likely than *P. longipennis* to take prey large enough to protrude from the buccal cavity. Both species have similar prey capture rates in their study but the magnitude of the gut content (as a proportion of the body mass) is more than two times greater in *E. simplicicollis* than in *P. longipennis*. May & Baird (2002) conclude that *E. simplicicollis* must have been taking larger prey items in each foraging bout.

Prey pursuit is a rapid, highly accurate, visually guided behavior. Capture success rates of *E. simplicicollis* and *Leucorrhinia intacta* (Hagen) are 97% (Olberg et al. 2000) based on video recordings of these anisopterans pursuing insects. *P. longipennis* returns to its perch chewing prey 90% of short pursuit flights (ca 0.5 m) and 70% of pursuit flights greater than 2.5 m (Baird & May 1997).

As adults, odonates harvest energy for reproductive output during their flight season. While foraging theory may suggest that it is profitable to harvest the largest amount of energy per foraging trip (Schoener 1971), an extreme energy maximizer should consume every potentially capturable prey that it encounters (Griffiths 1980). The evolutionary and energetic investment in huge compound eyes and in a high-resolution visual system enables the detection of very small prey items. Why invest in such high acuity if the goal is to chase only large items? Their huge eyes allow them to detect and successfully capture a wide range of prey sizes, especially small and abundant Diptera. From this study, we conclude that *S. vicinum* prefers to chase very small prey and opportunistically chase other size classes as activity and abundance of prey change with the seasons.

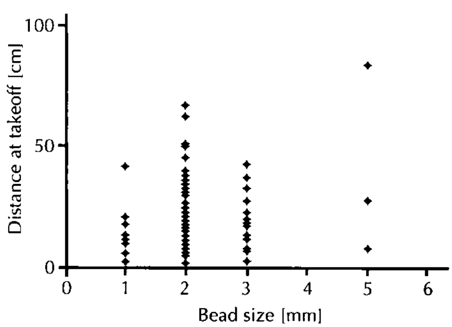

Figure 5: Prey pursuit distance in *Sympetrum vicinum* — distance of bead at takeoff – defined as the first video frame with the legs off the perch – as a function of bead size in 2003 (n = 338 presentations, R^2 = 0.023, F = 2.3, n.s.). Mean distance of beads at takeoff was 26.6 cm (s.d. = 19 cm).

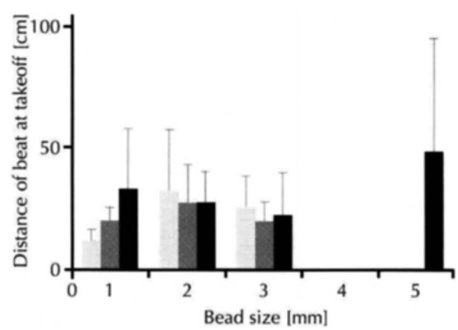

Figure 6. Seasonality of prey pursuit distance in *Sympetrum vicinum* — mean distance of bead at takeoff – defined as the first video frame with the legs off the perch – as a function of seasons (error bars = s.d.). The weather conditions in each sampling period are described in caption for Figure 3; light: 10 - 30 ix; middle: 10 - 13 x; dark: 24 - 31 x.

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References

Alonso-Mejia, A. & M. Marquez, 1994. Dragonfly predations on butterflies in a tropical dry forest. Biotropica 26: 341-344.

Corbet, P.S., 1999. Dragonflies: behavior and ecology of Odonata. Cornell University Press, Ithaca.

Baird, J.M. & M.L. May, 1997. Foraging behavior of *Pachydiplax longipennis* (Odonata: Libelludidae). Journal of Insect Behavior 10: 655-678.

Baird, J.M. & M.L. May, 2003. Fights at the dinner table: agonistic behavior in *Pachydiplax longipennis* (Odonata: Libellulidae) at feeding sites. Journal of Insect Behavior 16: 189-216.

Griffiths, D., 1980. Foraging costs and relative prey size. American Naturalist 116: 743-752.

MacArthur, R.H. & E.R. Pianka, 1966. On optimal use of a patchy environment. American Naturalist 100: 603-609.

May, M.L. & J.M. Baird, 2002. A comparison of foraging behavior in two "percher" dragonflies, *Pachydiplax longipennis* and *Erythemis simplicicollis* (Odonata: Libellulidae). Journal of Insect Behavior 15: 765-778.

Nikula, B., J.L. Loose & M.R. Burne, 2003 A field guide to the dragonflies and damselflies of Massachusetts. Massachusetts Division of Fisheries and Wildlife, Natural Heritage and Endangered Species Program, Westborough.

Olberg, R.M., A.H. Worthington & K.R. Venator, 2000. Prey pursuit and interception in dragonflies. Journal of Comparative Physiology (A) 186: 155-162.

Pritchard, G., 1964. The prey of adult dragonflies in Northern Alberta. The Canadian Entomologist 96: 821-825.

Schoener, T.W., 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369-404.

Sherk, T.E., 1978. Development of the compound eyes of dragonflies (Odonata). III. Adult compound eyes. Journal of Experimental Zoology 203: 61-80.

Stephens, D.W. & J.R. Krebs, 1986. Foraging theory. Princeton University Press, Princeton.

Taylor, L.R., 1963. Analysis of the effect of temperature on insects in flight. The Journal of Animal Ecology 32: 99-117