INQUIRY & INVESTIGATION

Flying Dragons: A Colorful Field Experiment in Resource Partitioning

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Abstract

Several common dragonfly species perch at different heights. Using dowels as perches and simple chi-square tests, this pattern of resource partitioning can be described quickly and easily. Additional experiments can examine the effect of interspecific competition on perch selection, and the relationships between perching height, body size, and wing aerodynamics.

Key Words: *Dragonfly; competition; territoriality; resource partitioning; community structure.*

Stroll near a pond on a warm sunny day between late spring and early autumn and you will undoubtedly see the shimmering wings of darting, dancing dragonflies. On closer inspection you will probably see several species of dragonflies dashing across the pond and along the perimeter; and in the reedy vegetation at the margins you will spy delicate damselflies floating from one stalk to another. You may first be struck by the beauty of these colorful animals and the apparent chaos of their acrobatic flights. But a small amount of time and careful study will reveal interesting patterns relevant to important ecological principles such as niche partitioning and territoriality. For example, many species of dragonflies perch at different heights (Worthen & Patrick, 2004; Worthen & Jones, 2006, 2007). Here, I describe a field-based laboratory activity that I developed from this research. I have used this activity in ecology courses and introductory biology courses for majors and nonmajors at the university level, but I think that aspects of the activity could be used throughout K–12. Students observe perch-height selection by different dragonfly species. They test for perch-height preferences with simple chi-square tests. Mounted "decoys" can be added to the design to examine interspecific and intraspecific aggression and territorial behavior. Finally, if dragonflies are netted and photographed, differences in size and wing morphology can be correlated with differences in perch-height preferences. It is a simple system that can address interesting and important questions in ecology and the biomechanics of flight in a short time, using beautiful and charismatic organisms that students enjoy watching and handling.

> *These field exercises… progress from describing a simple but interesting ecological pattern to examining the ecological and morphological causes of the pattern.*

Male dragonflies perch along the margins of ponds and lakes. Almost any water body – even catchment basins or borrow pits along roadways – will attract a variety of dragonfly species. Dragonflies perch to thermoregulate (May, 1978) and to scan their territory for intruders, prey, and mates (Moore, 1952; Ottolenghi, 1987; Gorb, 1995). Several species also "display" from their perches, raising their abdomens high above their heads to ward off conspecific males and attract mates. Acquiring and maintaining a territory attractive to females for egg laying is critical to male reproductive success (Parr, 1983; Switzer, 2002), so males often battle for territories in spectacular dogfights, and for perches that provide the best access to these territories. If high-quality perches are a limiting resource, ecological theory suggests that competing species might partition this resource, with different species preferring different types of perches to decrease the energetic and physical costs of interspecific competition. If taller perches provide a better view of the surrounding area, and if competitive ability correlates with size, then progressively smaller species would be relegated to progressively shorter perches in a competitive hierarchy. There have long been anecdotal observations suggesting that dragonfly species may partition this resource by perching at different heights, with larger species perching higher than smaller species (Warren, 1964).

However, several other factors could contribute to the relationship between body size and perch height. Because wind speed increases with height above the ground, large species may prefer tall perches to gain lift. Or, because they must fly faster to remain aloft, large species may avoid dangerous landings on short perches that are precariously close to the water. Conversely, small species may gain some protection from larger predators (larger dragonflies and birds) by flying and perching close to the water's surface. Or dragonfly size may be correlated with prey size, and their prey may fly at different heights. Although the predation hypothesis has not been addressed, wind speed does not seem to be a contributing factor (Worthen & Jones, 2007). However, there is a competitive hierarchy based on body size; interspecific battles for perches are frequent, and the larger species usually wins (Worthen & Jones, 2007).

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In this experiment, students test this hypothesis by placing standardized perches along the margin of a water body and observing perch-height selection by different dragonfly species. After describing the basic design and analysis, I will describe modifications that can be used in subsequent activities or in more advanced courses to test hypothetical causes of this pattern.

○ Basic Design & Analyses

"Perching stations" are established at least 5 m apart along the margin of the pond. There should be one perching station per student or pair of students. At each perching station, use four dowels (6 mm diameter) to create standardized artificial perches. The perches should extend 10, 20, 40, and 80 cm above the water line and should be approximately 50 cm from the bank. They should be approximately 10 cm apart and arranged in random order with respect to height. If time allows, the students can place their own dowels. They can discuss various reasons why a randomized order is appropriate, and they can determine a method for randomization. However, planting dowels can be a time-consuming procedure for a class of 20–30 students (requiring multiple meter sticks, hammers, and waders), so I have found it best to place the dowels myself before the lab period. This also allows the dragonflies time to acclimate to the presence of these new perches.

The first 10–15 minutes of observation should be used to familiarize the students with the common species in the area. There are several excellent field guides for identifying dragonflies and damselflies, such as *Dragonflies through Binoculars* (Dunkle, 2000), *Common Dragonflies of the Southwest* (Biggs, 2004), *Dragonflies and Damselflies of Georgia and the Southeast* (Beaton, 2007), and *Dragonflies and Damselflies of the West* (Paulson, 2009). Most species perching at ponds and lakes will be in the family Libellulidae, and the males will be fairly easy to distinguish by color and size. I will introduce a few species common to the eastern United States, but even within this region one or more of these may be absent and other species will be present at a given time or at a given locality. Two of the most common species, found everywhere in the continental United States except the states of the Northern Rockies, are the Blue Dasher (*Pachydiplax longipennis*) and Common Pondhawk (*Erythemis simplicicollis*, with eastern and western subspecies). Male Blue Dashers are approximately 5 cm in length, with a powder blue abdomen, dark terminal appendages at the end of the abdomen, a thorax striped in green and brown, a white face, and wings that are often lightly stained near the tips (Figure 1A). In addition, they often hold their wings down and forward. They also frequently lift their abdomen over their head while perching, in a display posture called "obelisking." Male Common Pondhawks are entirely powder blue when mature, with white terminal appendages and a green face (Figure 1B), but they have a green thorax when immature. East of the Rockies, another common summer species is the Eastern Amberwing (*Perithemis tenera*). It is easily identified by its small size (~2.5 cm) and orange wings and body (Figure 1C). Slaty Skimmers (*Libellula incesta*) are large (~6 cm), dark, eastern species with clear wings (Figure 1D). Widow Skimmers (*L. luctuosa*) are also dark and large and have wings banded in black and light blue (Figure 1E). Another species common east of the Rockies is the Halloween Pennant (*Celithemis eponina*), a beautiful orange species with brown bands on the wings (Figure 1F). Again, while these species are very common throughout most of the United States, there will probably be other species that are equally or more abundant in your area. A reconnaissance should be conducted the day before the field activity to familiarize yourself with the species flying in your area. If possible, take digital photos that can be copied and distributed as a quick reference for the students.

Once the perching stations are established and the students can identify the most abundant species, they can begin the observation period. The students should observe their perches for 1 hour, recording every instance of a dragonfly landing on a perch, even if it is the same individual dragonfly perching repeatedly. Ideally, the students should only record perch events at unoccupied perching stations, so that the dragonfly has all perches available. For instance, if a dasher occupies the 40-cm perch, another dragonfly that approaches the station has only the 10-, 20-, and 80-cm perches available. However, because dragonflies can displace one another from perches, it is also defensible to count all perch events, regardless of occupancy. Perching activity will probably be patchy; some perching stations may be in poor-quality areas and may have no perch events in an hour. Other students may be writing constantly in an effort to record every event. The students can be rotated between stations to increase the chances that everyone sees some activity sometime during the hour. After 1 hour, pool the data across species and across perch heights (Table 1).

These data should be analyzed in two ways. First, a chi-square goodness-of-fit test should be performed on the data for each species separately, to test the null hypothesis of no preference for each species (Table 1). Next, a chi-square test of independence should be conducted to determine whether species show statistically significant differences in their preferences (Table 1). Ideally, analyses should be limited to species that have been observed perching more than 24 times to meet a principal assumption of the chi-square tests (expected values >5), and goodness-of-fit alpha levels should be adjusted for multiple comparisons with a modification like the Bonferroni correction. In this correction, the corrected alpha level is determined by dividing the desired alpha level by the number of contrasts. So, if you want to maintain an alpha level of 0.05 across five contrasts, you should evaluate the statistical significance of each contrast at the 0.01 level (0.05/5). Results like those in Table 1 falsify the null hypotheses of no preference and independence and will be consistent with the hypothesis that species partition resources by perching at different heights.

Students enjoy this lab for a variety of reasons. First, it gets them outside on a pretty day. There is a relaxed feel to any outdoor lab as students escape the anxieties often associated with breakable glassware, technological "black boxes," or the frustrations that can occur with microscopy or long recipes of reagents. This is a conceptually and methodologically simple activity that provides a nice break from the stress of the lab environment and encourages students to slow down and observe nature, taking time to see the patterns amid the apparent chaos. Students enjoy watching these charismatic and personable animals. Here are some typical comments:

"I have walked around this lake every day but have never paid attention to what lived here. There is a lot going on."
"I thought all dragonflies were the same, but now I see that they are so different and so beautiful."
"Dragonflies are cool."

As Yogi Berra said, "You can see a lot just by watching." Students will probably see a variety of interesting behaviors. They will see aggressive interactions between and within species. They will see males "charging" their secondary sex organs with sperm, they will see pairs in "tandem," and they may observe males and females in the mating "wheel" position. So, this lab will naturally lead to discussions about the unique reproductive biology of dragonflies and the evolutionary significance of territoriality and mate guarding. In addition, you can dispel the rumor that dragonflies sting!

○ Extension 1: The Effect of Other Species on Perch Selection

One reason why co-occurring species might partition resources is to reduce interspecific competition. This hypothesis can be tested by placing dead, mounted decoys at some of the stations and recording whether other species avoid those stations, shift their pattern of perch use within stations, or attack the decoys. To prepare a decoy, you must

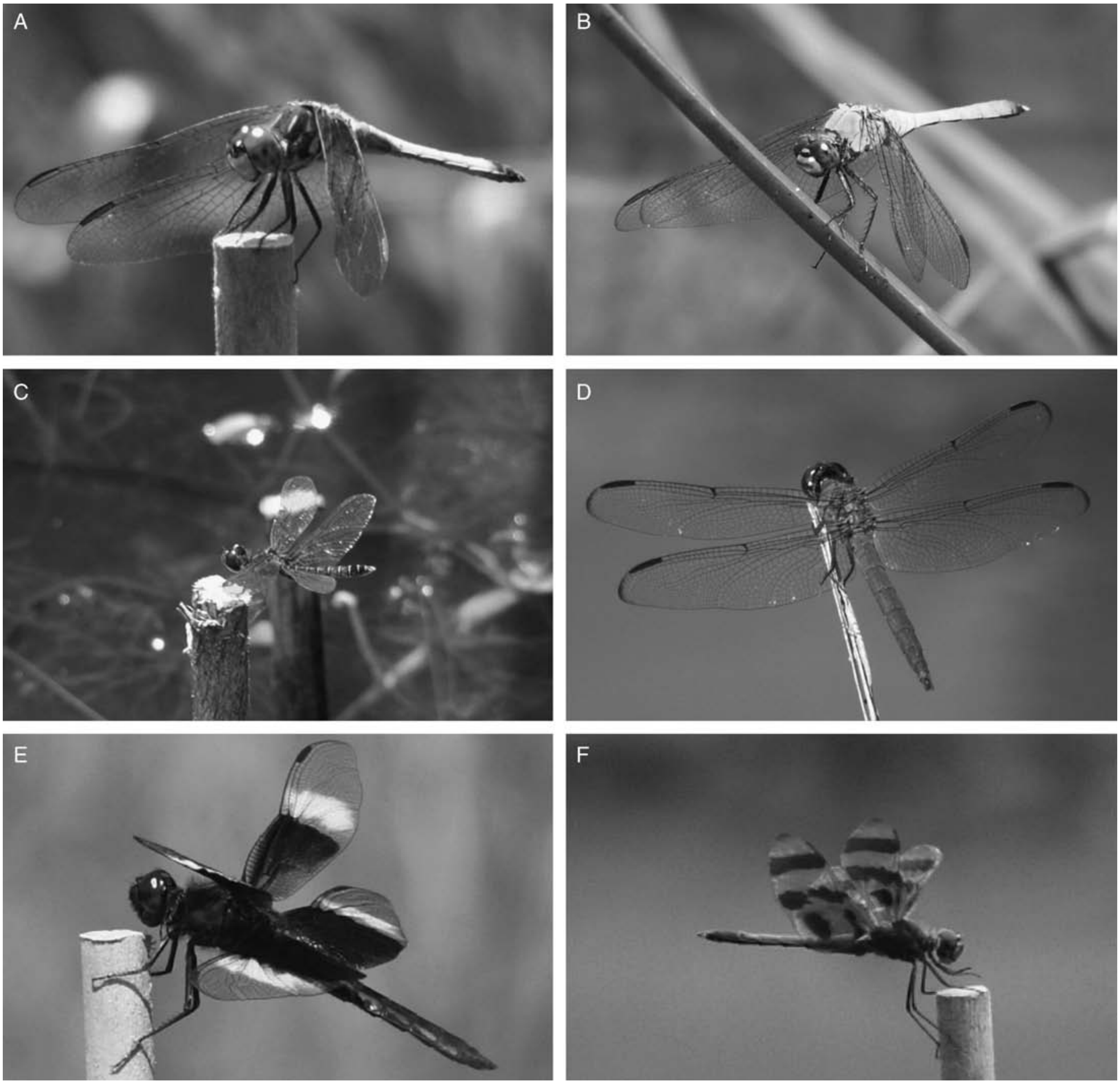

Figure 1. Common perching dragonflies: **(A)** Blue Dasher, **(B)** Common Pondhawk, **(C)** Eastern Amberwing, **(D)** Slaty Skimmer, **(E)** Widow Skimmer, and **(F)** Halloween Pennant.

Table 1. The frequency of perch events at different heights by four dragonfly species, and chi-square tests comparing these distributions against even distributions of no preference. Data from an introductory biology course for nonmajors, conducted in summer 2007. The chi-square test of independence = 344.70, p < 0.0001.

	Perch Height					
Species	**10 cm**	**20 cm**	**40 cm**	**80 cm**	**Total**	**Chi-square, p**
Halloween Pennant	0	0	0	41	41	123.00, p < 0.0001
Widow Skimmer	0	0	1	10	11	25.72, p < 0.0001
Blue Dasher	0	42	73	19	134	88.51, p < 0.0001
Eastern Amberwing	53	16	0	0	69	108.68, p < 0.0001

catch a few male dragonflies of one or a couple species. (Just catch a couple, at first, to practice the decoy-preparation techniques. Do not collect in state parks or other protected areas without a permit.) I recommend a large aerial ("butterfly") net with a 45-cm-diameter hoop and at least a 2-m handle. Wait until they perch and then slowly move the net to within about 1 m – then swing fast! Once a dragonfly is caught, hold its wings together above the back. You can place specimens in envelopes (secured with a paper clip) until you return to the lab. Use a "kill jar" charged with ethyl acetate to kill the specimens. Then use folded paper and paper clips to position each specimen with wings outstretched (Figure 2A), and submerge them in acetone. After 24 hours, remove the dragonflies from the acetone and let them dry for 15 minutes. The specimens will harden in their "life-like" positions. Acetone will bleach their eyes, so paint the eyes their natural color. Then affix each specimen to a thick wire bent to support the head, thorax, and abdomen (Figure 2B). I have found that a quick-drying epoxy works well. The specimens are still fragile, so be gentle. This wire can now be bound to a dowel with tape or rubber bands and positioned at a perching station (Figure 2B). I have used these decoys in previous experiments (Worthen & Patrick, 2004; Worthen & Jones, 2007), and they can be used repeatedly if they are well cared for.

To test for interspecific competitive effects, add a decoy to a random subset of perch stations (half would be ideal). Place the decoy 10 cm behind the perch appropriate for that species. For example, Common Pondhawks typically use the 20-cm perches. A Pondhawk decoy should be placed on its own dowel, 10 cm behind the 20-cm perch at the station (so the station still has four perches available to visiting dragonflies). Then record perch events at the stations, as before. The effects of interspecific competition can be assessed in two ways. First, chi-square goodness-of-fit tests can be used to compare the total frequency of perch events by a species at stations with and without decoys, to test the hypothesis that dragonflies of a given species avoid stations with a decoy. Second, the patterns of perch-height selection can be compared between stations with and without decoys, to test the hypothesis that a species will shift its pattern of perch selection in the presence of a decoy. In our research, we found asymmetrical effects at both scales. Smaller species avoided stations with larger decoys and perched lower at stations with decoys than at stations without decoys (Worthen & Jones, 2007). Larger species were unaffected by the presence of small decoys (Worthen & Jones, 2007). In addition, smaller species were attacked and displaced from perches by larger species more frequently than the reverse. So, it appears that the pattern of resource partitioning may be driven by asymmetrical aggressive interactions among species, whereby larger species drive smaller species to shorter perches.

○ Extension 2: Relationships between Body Size, Wing Morphology, & Perch Height

As mentioned above, there has long been anecdotal evidence that perch height is correlated with body size. If the diversity at your pond is fairly high (8–10 perching species), you can test for this relationship with a little additional information. In this experiment, you don't need to use dowels as perches if there are many natural perches of various heights (0.1–1.5 m) present. Have each student (or pair of students) responsible for a particular 5-m stretch of shoreline, and have them use a meter stick to measure the perch height of dragonflies that land in their areas. This may require that the students have waders or boots to walk out into the pond to measure the perch heights. If natural perches are rare or equal in size, employ the dowels. Natural perches are preferable, because their heights will be a continuous variable more appropriate for calculating means than the discrete variable of standardized dowel heights. After the 1-hour observation period, have the students use aerial nets to catch as many dragonflies of as many different species as possible. Instruct them to be careful with the animals and instruct them on how to hold them properly. After the dragonfly is carefully removed from the net, label its wing with a number or series of colored dots so that you do not resample individuals. Place an index card between the wings and hold the wings in a plexiglass "folder" with a scale in view (Figure 3). Then take a digital picture; be sure to include the entire animal and the scale in the frame. If possible, place each dragonfly in an envelope and weigh each specimen using an analytical balance (0.0001 g resolution). Release the dragonflies as quickly as possible.

Calculate the mean perch height for each species. Then measure the length, width, and surface area of the fore- and hindwing visible in each picture. A free, easy-to-use image analysis package is ImageJ software. It can be downloaded from the National Institutes of Health (http://rsbweb.nih.gov/ij/). Wing lengths can be used as a direct index of body size, so mean perch height can be correlated with mean body mass or mean wing lengths using Pearson or Spearman correlations. These correlations should be statistically significant; larger dragonflies use taller perches, on average, than smaller dragonflies (Worthen & Jones, 2006, 2007).

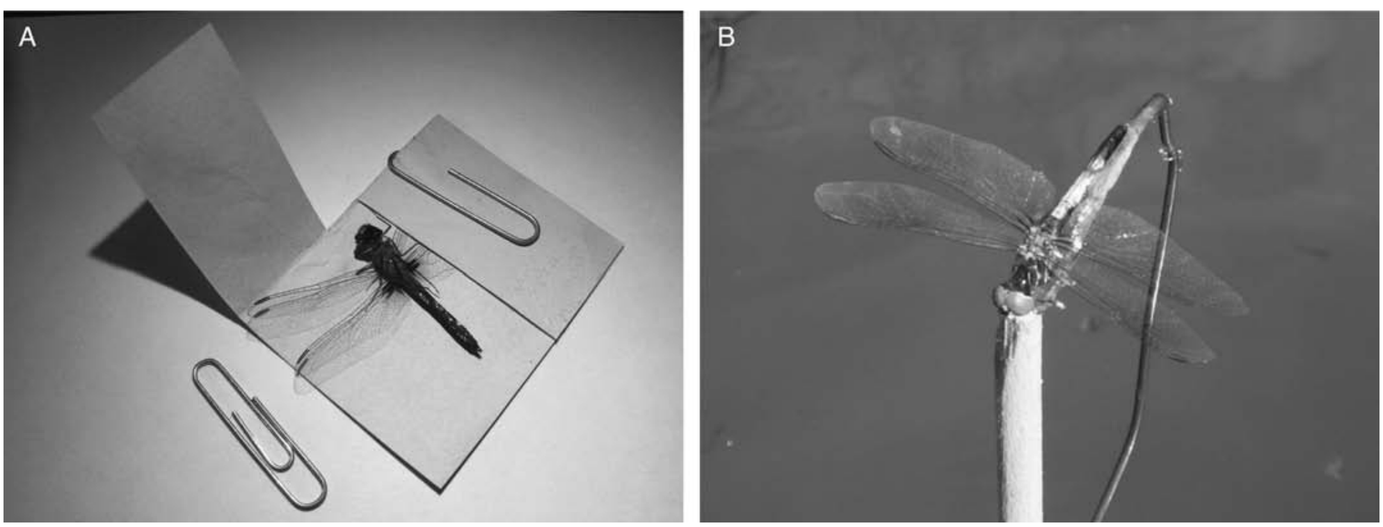

Figure 2. Constructing a decoy: **(A)** Positioning the dead specimen for the acetone bath; **(B)** Blue Dasher decoy with painted eyes, glued to a wire and positioned above a perch.

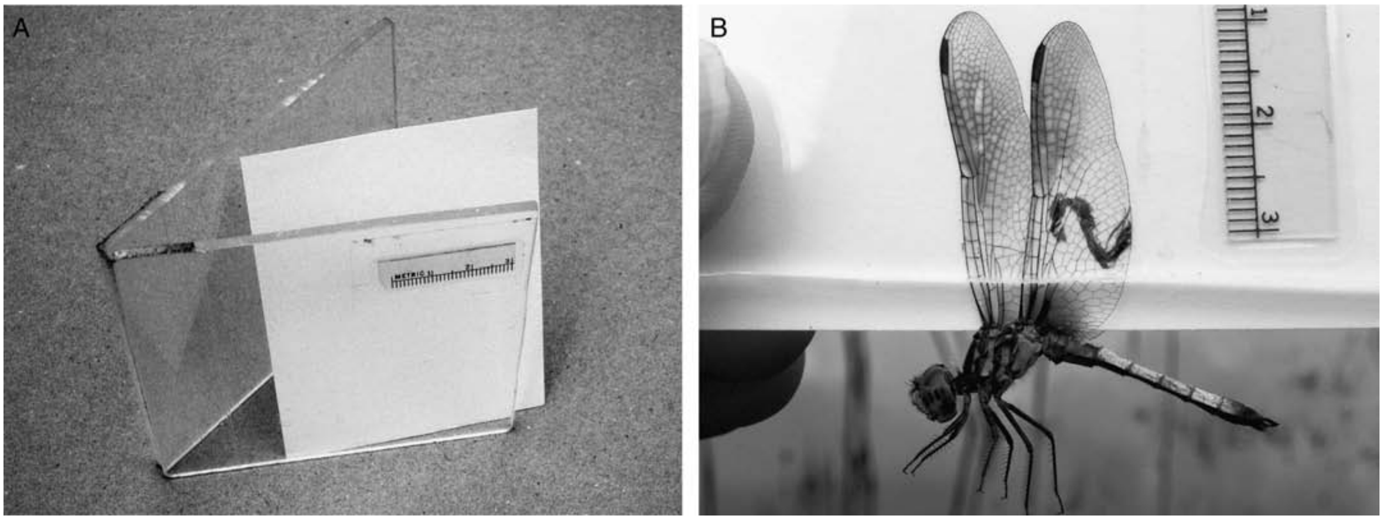

Figure 3. Preparations for wing analyses: **(A)** plexiglass holder; **(B)** Blue Dasher photographed between plexiglass (with scale) for wing measurements.

The photographs and measurements can also be used to compute more interesting aerodynamic characteristics, such as aspect ratio and wing loading. Aspect ratio is calculated as $L^2 \times SA^{-1}$, where L = wing length and SA = wing surface area. Basically, this yields a length:width ratio for the wing. A long, narrow wing (like that of a falcon) has a high aspect ratio and is adapted for fast flight. A low aspect ratio indicates a short, broad wing (like that of an owl) that maximizes maneuverability, especially at slow speeds. If you measured body mass, you can calculate wing loading: the mass (gravitational force in Newtons m^{-2}) supported by each unit area of the wing surface, as $N \times m^{-2} = (9.807\ m\ second^{-2}) \times [(\text{mass in kg}) / 2\ (SA_{forewing} + SA_{hindwing}\ \text{in}\ m^2)]$. Because surface area increases as a squared function of body length but mass increases as a cubic function of body length, larger dragonflies have greater wing loading than smaller dragonflies. Wing loading must be offset by lift to fly. Lift can be created by beating the wings and increasing the amount of air that crosses the wing by flying faster (increasing thrust) or by placing the body in an environment with increasing headwind speed. Air speed increases with height, so larger species may prefer taller perches because greater wind speed offsets their increased wing loading. And through aggressive interactions they outcompete smaller species for these taller perches, relegating small species to low perches.

These field exercises are fun and instructive. They progress from describing a simple but interesting ecological pattern to examining the ecological and morphological causes of the pattern. Students examine species in their natural context and see an aspect of biodiversity of which most are unaware. In addition, simple statistical tests and the principles of hypothesis testing are involved. Finally, the wing analyses open the door to the complex but tractable issues of ecomorphology and flight. Like most good field experiences, the students should leave this activity with an enhanced appreciation for nature and biodiversity.

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