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Partial submergence: An undescribed behavioral adjustment for thermoregulation at high ambient temperature in Aeshnidae

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Abstract: Many insects including odonates thermoregulate using a combination of behavioral and physiological mechanisms. At high ambient temperature (T_a), these mechanisms include decreased heat production and increased heat loss. Heat production can be reduced by decreasing activity. Heat loss can be enhanced by perching in a shaded microhabitat where temperature is cooler than in the surrounding environment. Aeshnids, which are intermittent endotherms, increase heat loss at high T_a also by increasing hemolymph circulation from the thorax, where most metabolic heat is produced, to the abdomen, where it dissipates to the environment by convection. While studying two aeshnid species (*Anax junius* and *Rhionaeschna multicolor*) at a Sonoran Desert (Arizona, USA) stream, I observed partially submerged mature individuals of both sexes of these species. This heretofore undescribed behavior was seen only at $T_a \geq 43^\circ\text{C}$ and almost exclusively during the hottest part of the day (15:00–17:00 hr), when the daily difference between T_a and water temperature (T_w) was, on average, largest. A cooling effect of partial submergence behavior on body temperature would, therefore, presumably be most effective also during this period. Several percher species of libellulids were present at the study site. These dragonflies are not known to use endothermy for thermoregulation or to increase hemolymph circulation to the abdomen to dissipate heat at high T_a , and none was ever observed to partially submerge. It is suggested in aeshnids that partial submergence at high T_a serves a thermoregulatory function by facilitating body heat dissipation from the abdomen.

Keywords: Common Green Darner, *Anax junius*, body temperature, Blue-eyed Darner, dragonfly, Odonata, endothermy, Libellulidae, *Rhionaeschna multicolor*, Sonoran Desert

Introduction

Many insects, including a number of odonates, can thermoregulate (May 1976; Corbet 1999). The physiological bases of thermoregulation have received considerable attention in dragonflies of the family Aeshnidae and within this family, particularly in *Anax junius* (Drury), Common Green Darner, which has long served as a model species for studies on this subject (Heinrich & Casey, 1978; Marden, Kramer, & Frisch, 1996; May, 1976, 1995a, 1995b). Aeshnids and at least some gomphids (*Arigomphus villosipes* (Selys); May, 2017) can regulate their body temperature by intermittent endothermy, i.e., the generation of internal body heat by metabolic processes. At relatively low ambient temperature and during warm-up, for example, heat is produced by rapid wing muscle contractions that result in wing whirring. When flying at such temperature, *A. junius* can also regulate its body temperature by increasing heat production through decreased gliding, during which flight muscles are inactive, and increased wing-beat frequency (May, 1995b). As a result of endothermic temperature regulation, large species such as *A. junius* may be able to extend the duration of their daily period of activity compared to smaller species, for which endothermy is energetically prohibitively expensive (May, 1977).

At high ambient temperature ($> 30^\circ\text{C}$), mechanisms must intervene to facilitate heat loss so as to avoid hyperthermia. One such mechanism in *A. junius* consists in heat transfer from the thorax, where muscle activity generates heat, to the abdomen, where it is dissipated to the environment by convection. This transfer is mediated by increased hemolymph circulation to the abdomen which, therefore, serves as a “thermal window” facilitating heat loss (May, 1995a). Heat transfer from the thorax to the abdomen may be particularly effective for cooling in species with a long, slender abdomen, which is characteristic of aeshnids and results in a high surface area/volume ratio (May, 1976; Corbet, 1999). At elevated temperature, odonates commonly regulate their body temperature also by

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behavioral adjustments: reduced activity, which decreases metabolic heat production, postural changes (e.g., Tracy, Tracy, & Dobkin, 1979), and selection of shaded microhabitats where temperature is lower than the body temperature.

While surveying odonates in the Phoenix, Arizona, area during a hot (47 °C [117 °F]) mid-August afternoon, I noticed numerous *A. junius* and *Rhionaeschna multicolor* (Hagen), Blue-eyed Darner, perched in low vegetation along the shady side of a local stream. Intriguingly, several mature males and females of both species were perched with their abdomen dipping to half its length in water and immobile for several minutes. I did not find any published description of or reference to this behavior for any odonate species. May (1976) measured the thermal tolerance threshold, defined as the temperature approaching that at which it can cause dangerous thermal stress and paralysis, in multiple odonate species held in the laboratory. He determined in *A. junius* that this threshold equals 45.6 ± 0.98 °C. The study did not include *R. multicolor*. Given my above observations, the role of the abdomen as thermal window (May, 1995a), and the results of this author's studies on heat tolerance, do aeshnids partially submerge to enhance heat loss at ambient temperatures approaching or exceeding their thermal tolerance threshold? If so, this heretofore undescribed behavior would add to the list of adjustments already known to be used by these insects for thermoregulation.

The hypothesis of a thermoregulatory role for partial submergence in aeshnids would be supported if:

- (a) this behavior is associated with periods of particularly hot temperature within a same day;
- (b) it is associated with such temperature also across days with varying high temperature;
- (c) water temperature is lower than ambient temperature, thereby promoting heat dissipation from the abdomen during submergence;

and (d) we do not observe partial submergence at high temperature in percher species of libellulids. Indeed, these dragonflies have similar thermal tolerance thresholds as aeshnids (May, 1976), but they are not endothermic and are not known to transfer heat from the thorax to the abdomen for thermoregulation. The main objective of this field study was to test these predictions through behavioral observations of *A. junius* and *R. multicolor*.

Materials and methods

The study took place along a 120-meter-long stretch of a perennial, slowly flowing artificial stream in the Phoenix, Maricopa Co. (Arizona) area (33.27° N; 111.67° W; 629 m a.s.l.). The stream flows roughly in northwest to southeast direction through Sonoran desert. Banks are lined with vegetation consisting mostly of sedge (*Carex sp.*) and cattail (*Typha sp.*) that grow up to approximately two meters high (Figure 1). Surrounding trees are mostly mesquites (*Prosopis glandulosa*, *P. pubescens*, and *P. velutina*) and Blue Paloverde (*Parkinsonia florida*). The surveyed section of stream bank is exposed to direct sunlight in the morning and partially or completely (after 15:00 hr) shaded during the rest of the day (Figure 1).

I used 10 x 42 binoculars to count the number of male and female *A. junius* and *R. multicolor* - the only aeshnids that are regularly encountered at the study location - perched in herbaceous vegetation on the opposite bank of the stream, from a distance not exceeding 20 meters, during 66 surveys between 25 August and 20 September 2020. The weather during all surveys was sunny and calm or with light breeze. All surveys took place during daytime (08:00 - 18:30 hr; Figure 2) and individual surveys took, on average, 22 ± 1 min (mean \pm standard error [s.e.]) to complete. I surveyed the stream 1 - 4 times per day to cover a range of times as well as ambient (T_a) and water (T_w) temperatures (Figure 2 and see below). At least 1 hr 12 min separated consecutive surveys done on a same day (average: 2 hr 34 min \pm 12 min (mean \pm s.e.)). During each survey, I recorded local T_a (weather.com; ± 0.5 °C) and measured T_w at a depth of 10 cm using an alcohol thermometer (average of two measurements; ± 0.5 °C). I used these data to calculate differences between T_a and corresponding T_w .

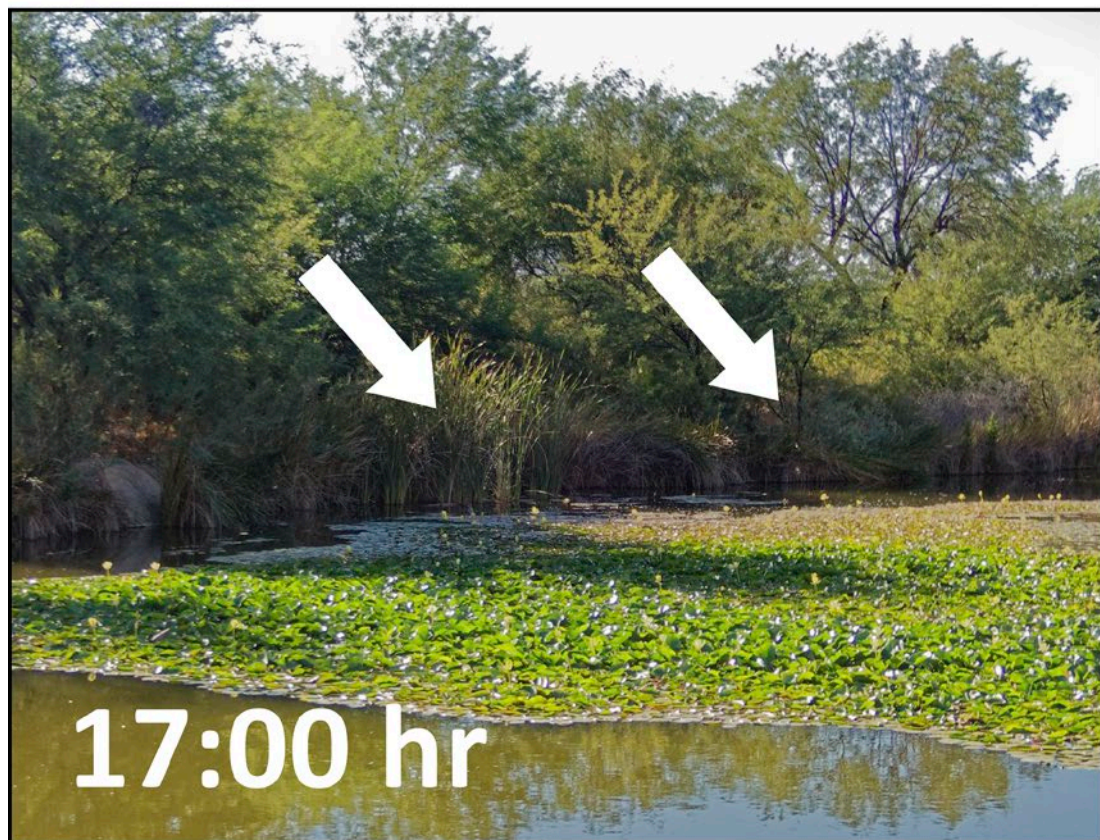


Figure 1. Study site showing a representative section of the stream that was surveyed and was exposed to direct sunlight in the morning (upper panel), but shaded in the afternoon (lower panel). Arrows point to the layer of herbaceous vegetation where darters perched and were counted.

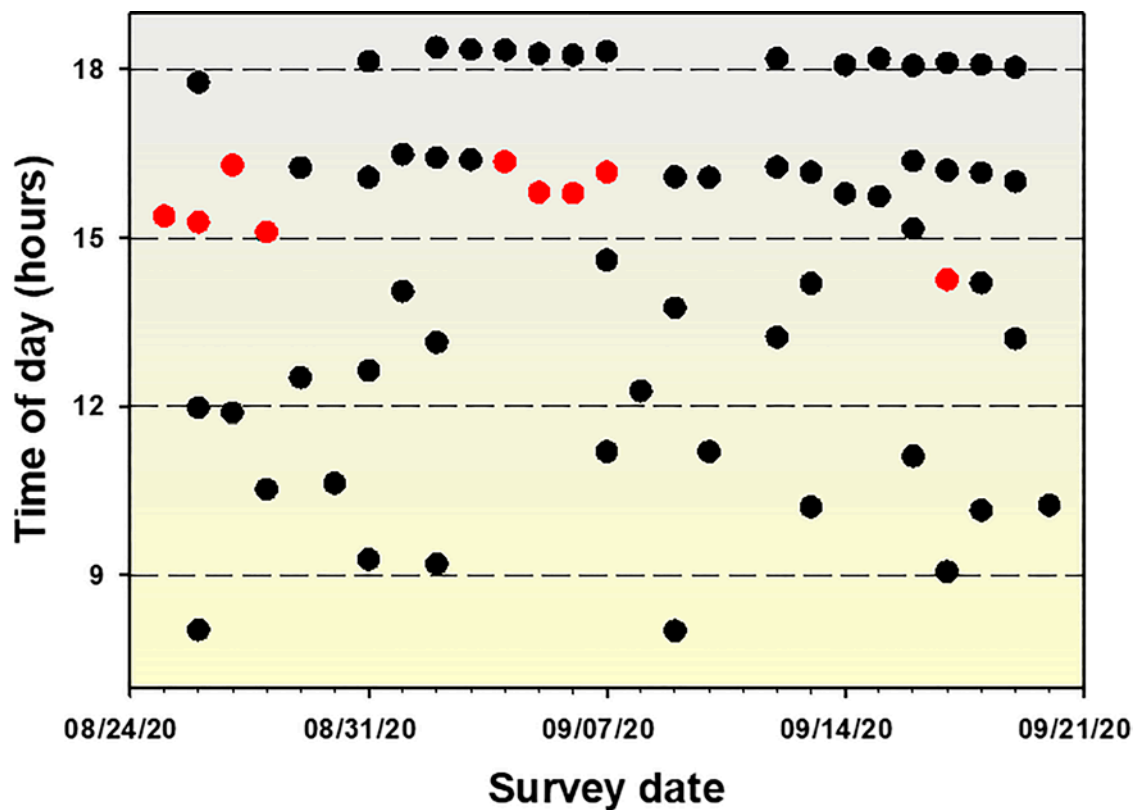


Figure 2. Dates and times of day that surveys were conducted. Each dot corresponds to one survey and red dots represent surveys during which partially submerged darners were observed (see text for details).

Only mature darners were encountered. During each survey, I counted the numbers of individuals (two species combined) that were perched with their abdomen partially submerged. Females that were hanging on low vegetation and ovipositing by themselves or in tandem ($N = 0$ to 15, depending on the survey) were excluded from the study. Results for *A. junius* and *R. multicolor* were generally similar (see below). However, the latter species was much less abundant than *A. junius* and so I statistically analyzed results obtained only for *A. junius*. Regularly observed percher species of libellulids included *Pachydiplax longipennis* (Burmeister), Blue Dasher; *Erythemis collocata* (Hagen), Western Pondhawk; *Brachymesia furcata* (Hagen), Red-tailed Pennant; *Sympetrum corruptum* (Hagen), Variegated Meadowhawk; and *Perithemis intensa* (Kirby, Mexican Amberwing).

Statistical analyses

I analyzed data statistically using SigmaPlot 13.0 (Systat Software, Inc., San Jose, CA). I determined the relationship between T_a and $T_a - T_w$ using linear regression. Correlations between variables were calculated using the Spearman's rank coefficient. I compared groups of paired data using paired Student's t-tests or, when data were not normally distributed, the Wilcoxon signed rank test. The statistical significance threshold of all tests was set at $\alpha = 0.05$.

Results

Ambient temperatures during surveys ranged from 21 °C to 47 °C. On average, T_a increased gradually from morning to mid-afternoon and then began to decline (Figure 3). Water temperature ranged from 26 °C to 36 °C and followed a similar pattern of changes to that of T_a , but of smaller amplitude. Consequently, the $T_a - T_w$ difference increased as a function of T_a , up to a maximum of 13 °C ($N = 66$; $r^2 = 0.746$, $P < 0.001$; Figure 4).

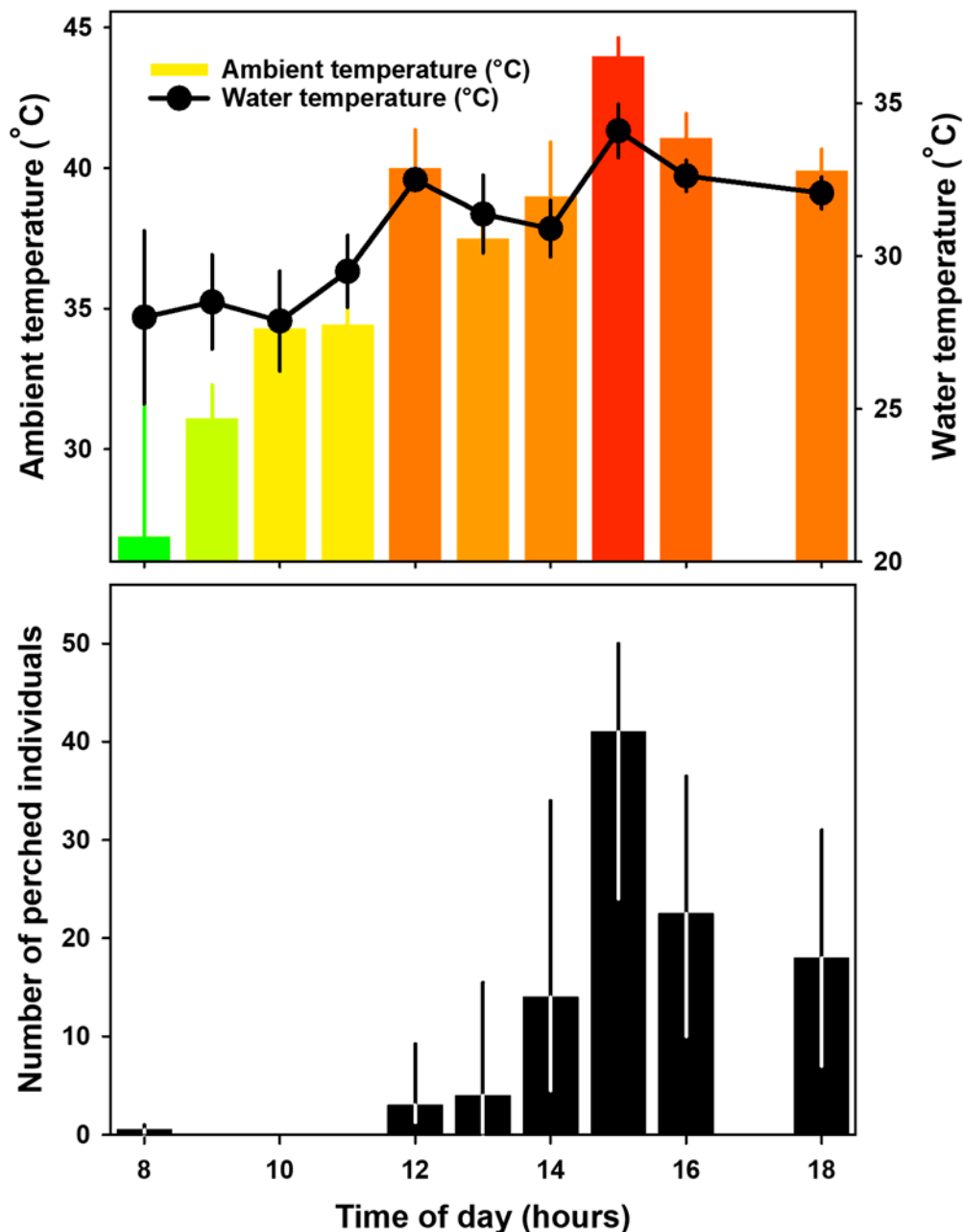


Figure 3. Upper panel: Ambient and water temperatures (means \pm standard errors) recorded during surveys as a function of time of day. Lower panel: Number of *Anax junius* (medians \pm interquartile intervals) found perched as a function of time of day.

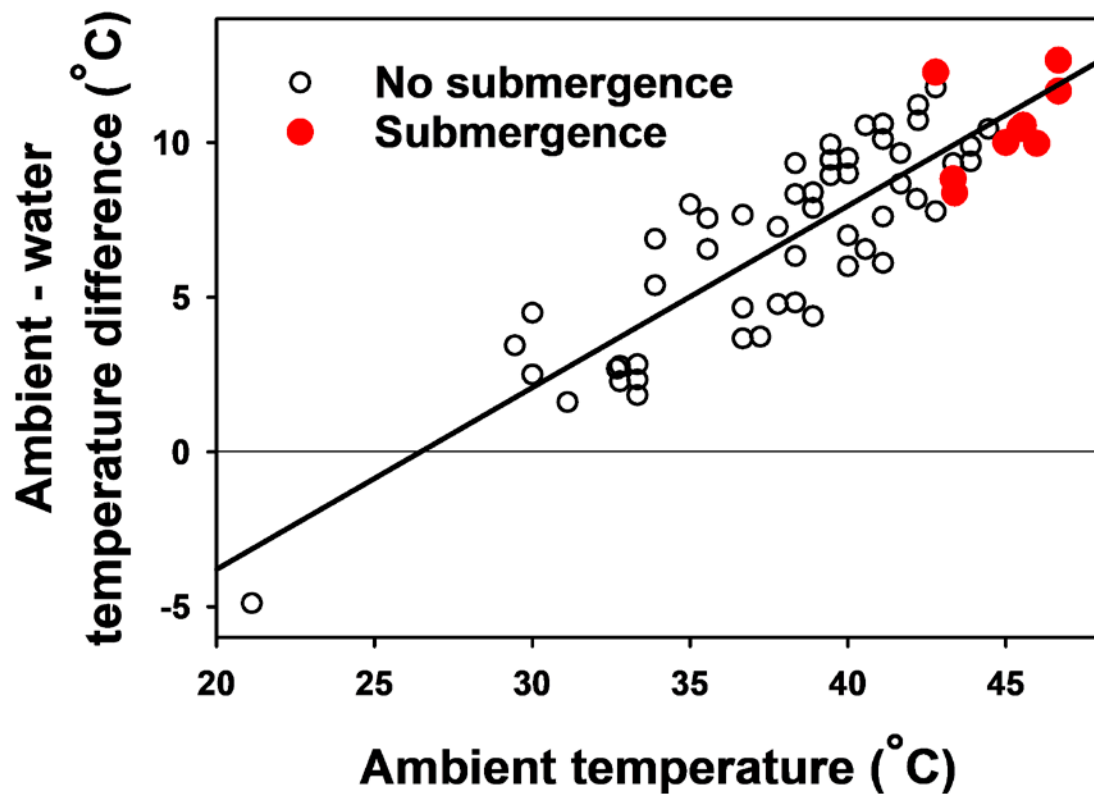


Figure 4. Relationship between ambient temperature and difference between ambient and water temperature. Each dot represents one survey. Red dots show surveys during which partially submerged darners were observed.

The number of darners found perched in herbaceous bank vegetation ranged from 0 to 96 (two species combined). Only a single darner was ever found perched before noon, when the stream bank was exposed to direct sunlight (Figures 1 and 3). As sections of the bank became shaded, the number of perched individuals gradually increased, reaching a maximum in mid-afternoon (15:00 hr), and then declined (Figure 3). Over the course of the study, T_a , $T_a - T_w$ differences, survey times, and the numbers of perched *A. junius* all correlated positively to each other (Table 1).

Most darners seen perched along the stream were a few centimeters to one meter above water (Figure 5). In addition, during nine surveys, each on a different day (Figure 2), some individuals of either or both species were found perched with their abdomen almost touching the water surface (Figure 6a) or partially submerged (Figure 6b–d). Males and females of both species exhibited partial submergence behavior. Partially submerged females, being completely immobile, could be readily distinguished from actively ovipositing (moving) females. One to 10 darners (median: 2) engaged in partial submergence during surveys when this behavior was observed, which represents 1 % – 44 % (median: 6.3 %) of the number of darners perched in bank vegetation during these surveys. Partial submergence was limited to the hottest time of the day; with one exception (17 Sept., 14:20 hr, $T_a = 43^\circ\text{C}$), this behavior was observed only between 15:00 and 17:00 hr (Figure 2). Furthermore, partial submergence occurred only at T_a equal to or above 43°C (Figure 7). As $T_a - T_w$ correlated positively to T_a (Figure 4), partial submergence was most frequent also at large $T_a - T_w$ differences ($> 8^\circ\text{C}$; mean \pm s.e.: $10.5 \pm 0.5^\circ\text{C}$, $N = 9$). No libellulid was ever observed to partially submerge.

Table 1. Spearman's rank correlations (ρ) and corresponding probabilities (P) showing associations between ambient temperature (T_a), difference between ambient and water temperature ($T_a - T_w$), and numbers of perched *Anax junius* over the course of the study ($N = 66$ surveys).

		$T_a - T_w$	Number of perched <i>A. junius</i>	Survey time
T_a	ρ	0.821	0.810	0.456
	P	< 0.001	< 0.001	< 0.001
$T_a - T_w$	ρ	—	0.739	0.328
	P		< 0.001	0.007
Number of perched <i>A. junius</i>	ρ	—	—	0.539
	P			< 0.001



Figure 5. *Anax junius* perched in aquatic vegetation along the edge of the stream in the middle of the afternoon. Also note horizontally perched male *Pachydiplax longipennis* above the darners.

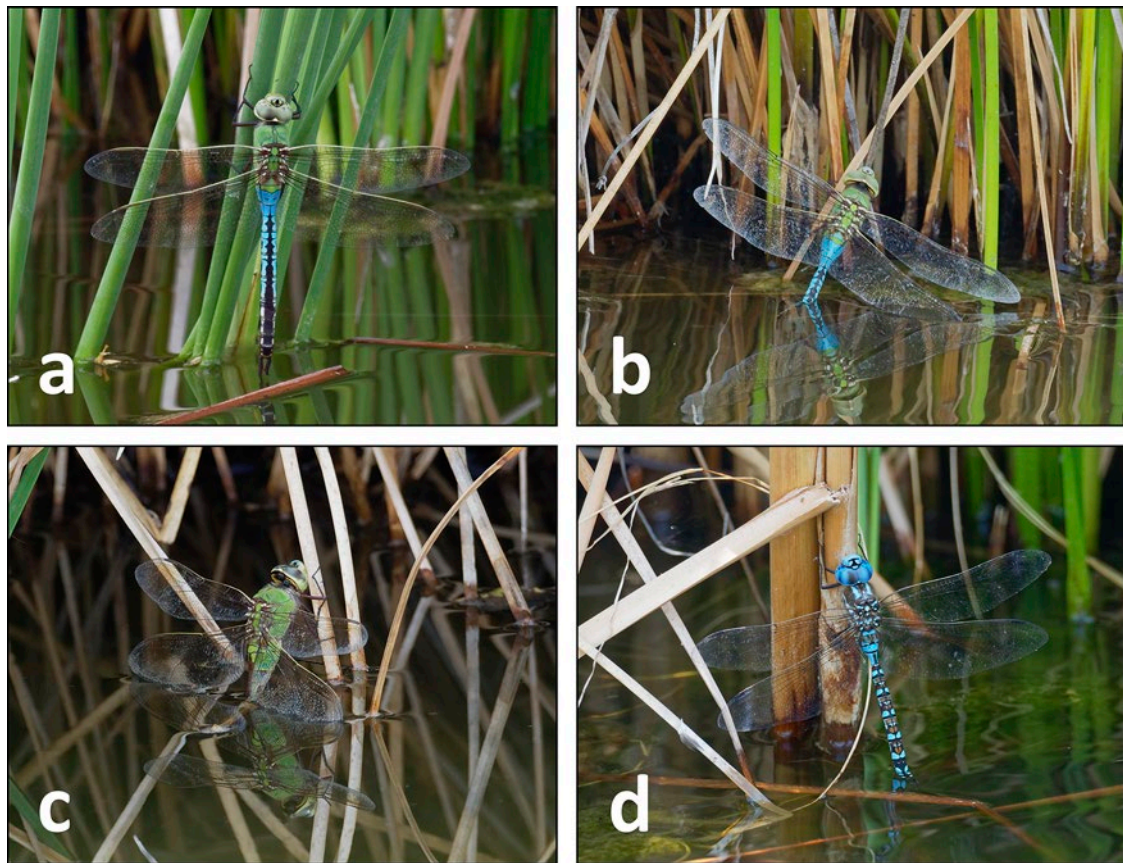


Figure 6. (a): Male *Anax junius* perched just above water. (b – d): Male (b) and female (c) *Anax junius* and male *Rhionaeschna multicolor* (d) showing partial submergence behavior.

To further characterize the use of stream bank vegetation microhabitat for perching and partial submergence behavior, I compared data collected during two periods: 15:00–17:00 hr vs. after 18:00 hr. During these periods, fewer than 10 *A. junius* were found perched at T_a below or equal to 37 °C (Figure 7). At T_a above 37 °C, this number increased with increasing T_a . Thus, during each period, the number of perched individuals was T_a -related. The number of perched *A. junius* appeared to decrease at T_a above approximately 43 °C, but whether this was actually the case could not be confirmed statistically based on the available data. I surveyed the stream between 15:00 and 17:00 hr and again after 18:00 hr on the same day on 14 occasions. During these surveys, T_a , the $T_a - T_w$ difference, and the number of perched *A. junius* all declined significantly ($P \leq 0.02$) between the two time periods (Table 2).

Table 2. Ambient temperature (T_a ; °C), difference between T_a and water temperature (T_w ; °C), and number of perched *Anax junius* as a function of time of day.

	15:00 - 17:00 hr	18:00 - 19:00 hr	Probability
T_a	41.7 ± 1.9^a	39.7 ± 1.9^a	$< 0.001^c$
$T_a - T_w$	9.4 ± 0.6^b	7.8 ± 0.5^b	$< 0.001^d$
Perched	32 ± 12^a	18 ± 12^a	0.021^c
^a : Median \pm 0.5 interquartile interval; ^b : Mean \pm standard error; ^c : Sign rank test; ^d : Paired Student's t-test.			

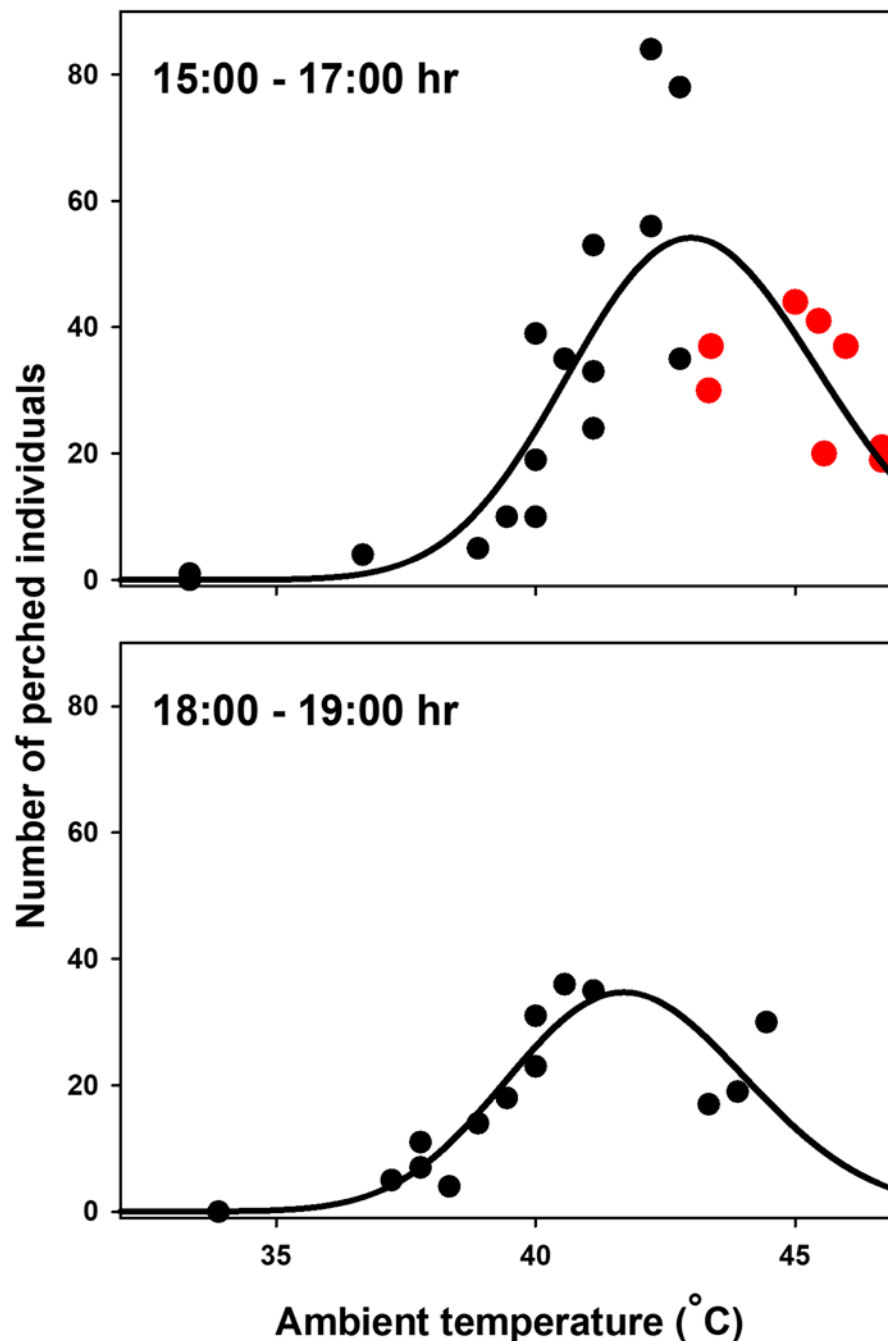


Figure 7. Numbers of perched *Anax junius* during two periods (15:00 – 17:00 hr; 18:00 – 19:00 hr) and as a function of ambient temperature. Each dot represents one survey and red dots show surveys during which partially submerged darters were observed.

Discussion

Previous observations documented that at high T_a many odonates decrease their activity and avoid excessive heat exposure by selecting shaded, cooler microhabitats. The present study confirms and extends these observations. During 66 surveys conducted over the course of three weeks, *A. junius* and *R. multicolor* made extensive use of herbaceous microhabitat lining a stream for perching. This usage was, however, time of day- and temperature-dependent; darners perched there almost exclusively during the afternoons, when the stream was shaded and T_a highest. In addition, during the hottest times of the day (mid-afternoon and early evening) and despite the stream being shaded, few darners perched on streamside vegetation when T_a was below 36 °C, but did so increasingly at T_a above this threshold. Darners do not use stream vegetation microhabitat for perching at T_a below 36 °C possibly because in these conditions they preferentially perch elsewhere, such as in trees. Alternatively, at T_a up to 36 °C heat dissipation mechanisms (see Introduction) may be sufficiently efficient for darners to remain active without having to perch in shady, cooler locations for thermoregulation. This conclusion would be consistent with the finding that the abundance of flying *A. junius* did not change during the day at T_a up to approximately 32 °C (Marden, Kramer, & Frisch, 1996).

The present study also describes a behavior – partial submergence – that had to my knowledge not been reported for any odonate: At high T_a , a small number (1–10 depending on the survey) of darners of both species and sexes perched with the abdomen partly submerged, immobile for prolonged periods (at least several minutes). During the time of the day (15:00 – 17:00 hr) that partial submergence was most prevalent, it occurred only at $T_a \geq 43$ °C. Thus, the behavior was associated with elevated T_a or an environmental factor varying concurrently with T_a , and did not represent the manifestation of an intrinsic daily pattern of activity. Intriguingly, even at $T_a \geq 43$ °C, darners did not exhibit partial submergence during surveys conducted after 18:00 hr (within one hour of sunset). Partial submergence may normally occur in such conditions but was perhaps not detected due to small sample size because T_a equaled or exceeded 43 °C during only three of 15 surveys conducted after 18:00 hr. Also, the number of darners perched at the stream decreased between 15:00 – 17:00 hr and 18:00 – 19:00 hr irrespective of T_a (Table 2). Thus, even at high T_a , many darners appear to leave the stream in late afternoon, presumably to overnight elsewhere.

Temperatures at which partial submergence was observed (≥ 43 °C to 47 °C) approach or exceed the thermal tolerance threshold (45.6 °C) of *A. junius* as determined by May (1976). As the $T_a - T_w$ difference correlates positively to T_a , the effectiveness of partial submergence as a heat loss mechanism would increase with increasing T_a . Yet even at T_a close to or above 45.6 °C, only a minority (average: 6.3 %) of perched darners engaged in partial submergence. This may be for several reasons. First, the thermal tolerance threshold of freshly caught *A. junius* belonging to a Mohave Desert, California, population (52.5 ± 0.6 °C; Polcyn, 1994) was considerably higher than measured in the laboratory by May (1976), who investigated the species in central Florida. Thus, this threshold may be higher in free-ranging than in captive individuals and/or it is regionally variable. If it is similar in populations of *A. junius* living in the Sonoran and Mohave deserts, these dragonflies in Arizona may be able to tolerate higher body temperatures without resorting to partial submergence for thermoregulation, even at the highest T_a (47 °C) measured during the present surveys. Second, on the days that partial submergence was seen, but not other days, individuals were often observed that were perched with their abdomen almost (i.e., within less than one cm) touching the water surface (Figure 6a). Air is likely cooler just above water than higher in the air column. Thus, perching just above water may result in more heat loss than perching higher in vegetation and may suffice to meet thermoregulatory needs at T_a close to the thermal tolerance threshold. Third, at high T_a , many species reduce but do not completely suspend flight activity. At T_a approaching or exceeding the thermal tolerance threshold, darners may use partial submergence as a heat dissipation mechanism only after a period of flight. In this case, only relatively few individuals would be expected to show this behavior at any given time. Finally, partial submergence may increase the risk of predation by aquatic predators. Predators seen at the study site include Fishing Spiders, Rio Grande Leopard Frogs, *Lithobates berlandieri* (Baird), and Pond Slider Turtles, *Trachemys scripta* (Thunberg). If partial submergence assists with body heat loss but also increases the predation risk, few dragonflies may engage in this behavior because it constitutes a trade-off between the benefit gained from cooling and the risk of predation.

Several percher species of libellulid also used streamside vegetation during the afternoons, but were never observed to partially submerge. Libellulids can thermoregulate but, contrary to aeshnids, do not use endothermy and are not known to use the abdomen as a thermal window for heat dissipation. That aeshnids, but apparently not percher libellulids, use partial submergence during hot weather is consistent with the hypothesis that this behavior serves a thermoregulatory function.

These results both support the hypothesis that partial submergence behavior is a thermoregulatory adaptation and raise new questions. Do aeshnids inhabiting cooler regions use partial submergence and if so, at what minimum T_a do they do so? If partial submergence is, indeed, used for thermoregulation, how effective is this behavior to dissipate body heat compared to perching above water? If intermittent endothermy is widespread in gomphids, do members of this family, especially those living in hot climates, use partial submergence? And will additional observations confirm that libellulids, which are not known to thermoregulate by endothermy, never use partial submergence? Many libellulids perch horizontally (see, e.g., *Pachydiplax longipennis* in Figure 5), but others (e.g., *Pantala* (Hagen), gliders; *Brechmorhoga* (Kirby), clubskimmers) hang vertically when perched. It would be particularly illuminating to investigate whether species in these genera ever engage in partial submergence.

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