

PHYSIOLOGICAL COLOR CHANGE IN NEW WORLD DAMSELFLIES (ZYGOPTERA)

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Temperature dependent physiological color change in several species of New World Zygoptera is described. The phenomenon is probably widespread in the genus *Argia* and possibly other genera. Within the former group the capability may be correlated with the thermal environment of the species and may have a thermoregulatory function. Preliminary data on physiological control of color change are presented.

INTRODUCTION

Reversible (physiological) color change occurs in a number of Australian Zygoptera in response to different temperature and light regimes (O'FARRELL, 1963, 1964, 1968; VERON, 1973) and O'FARRELL (1964) and VERON (1974) suggest a thermoregulatory function for the phenomenon. BICK & BICK (1965) noted reversible color changes in the North American *Argia apicalis* but concluded that the various color phases were not correlated with temperature. The present paper shows that several North American and Neotropical damselflies are capable of physiological color change and that temperature is probably the major factor controlling such change.

METHODS

Most studies were performed at Gainesville, Florida, USA. I collected 20-30 individuals of a species for each experiment, which commenced on the day of

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collection. The damselflies were divided into two groups of 8-12 individuals and each group placed in an approximately 10 liter glass tank closed at the top with aluminum foil and lined with moist paper toweling to prevent desiccation. The insects moved about freely within the containers. Both groups were placed in a lighted constant temperature chamber at 30°C, for 3-4 hours. Then I examined each individual and scored its color on a scale of 1-5, modified after VERON (1973): (1) – light areas of cuticle entirely bright colored, (2) – these areas mostly bright but with dark patches, (3) – bright and dark patches approximately equal, (4) – dark areas predominant, (5) – entirely dark. After this initial scoring one group was returned to the 30°C chamber as a control and the other group placed overnight in another chamber at a present temperature between 3°C and 25°C. Transfer to the cool chamber was at 2000-2200 hrs. Each pair of control and experimental groups was kept under the same light regime, constant light or constant darkness. At 1000-1100 the next morning I again examined and scored each individual of both groups, then placed both at 30°C and constant light for 1-4 hrs, scoring them again at the end of that period.

A few individuals of several species were examined at various sites in Costa Rica. Here I merely placed specimens, collected the same day, in envelopes in a refrigerator or icebox for several hours and noted whether or not darkening occurred. I then allowed them to remain at room temperature for several hours and again noted color.

Preliminary experiments to elucidate the mechanism of physiological control of color change in *Argia bipunctulata* were modeled on VERON's (1973) studies. In one set I ligated the third abdominal segment of both controls and an experimental group left overnight at 10°C. Then each abdominal segment of each individual was scored separately. In another experimental regime I excised with a razor blade whole tagmata or individual abdominal segments or groups of segments and placed these in dishes of physiological saline (0.8% NaCl). Each part was scored immediately after excision, then placed at 10°C or 30°C overnight and scored again, then all were placed at 30°C for several hours before final examination.

RESULTS AND DISCUSSION

A number of species darken markedly at low temperatures (Table I), resuming normal bright colors after being returned to a warm environment. The ability is apparently present in several species of *Argia* and *Enallagma*, two of the dominant genera in North and Central America, suggesting that the phenomenon may be widespread. The absence of darkening in many Costa Rican species may in part be due to the very poorly controlled conditions of cooling and warming used there.

As would be predicted from the work of O'FARRELL (1964) and VERON, et al. (1974) only blue areas of cuticle change color. For example, in females of *Argia sedula*, darkening was restricted to the pale bluish or blue-green areas of the thoracic and abdominal venter and did not occur on the rest of the mostly tan cuticle. In *A. tibialis* males, which have violet antehumeral areas, only the blue dorsal areas of abdominal segments 9 and 10 changed color. Females of this species were either tan or turquoise when captured. Only turquoise specimens darkened in the cold.

Table I
Occurrence of temperature dependent physiological color change

Species	Location	Darkening at low temperature	
		♂♂	♀♀
Platystictidae			
<i>Palaemnema nathalia</i> Selys	Costa Rica (CR)	0	0
Protoneuridae			
<i>Neoneura amelia</i> Calvert	CR	0	...
Coenagrionidae			
<i>Argia apicalis</i> (Say)	Florida (F)	+	...
<i>A. bipunctulata</i> (Hagen)	F	+	...
<i>A. extranea</i> (Hagen)	CR	+	...
<i>A. moesta</i> (Hagen)	F	0	+
<i>A. oculata</i> Hagen	CR	+	...
<i>A. sedula</i> (Hagen)	F	+	+
<i>A. tibialis</i> (Rambur)	F	+ ^a	+ ^b
<i>Argia</i> sp.	CR	+	+
<i>Enallagma cardenium</i> Selys	F	...	+
<i>E. civile</i> (Hagen)	CR	0	...
<i>E. durum</i> (Hagen)	F	+	...
<i>Ischnura ramburii</i> Selys	F, CR	0	0 ^c
Lestidae			
<i>Lestes forficula</i> Rambur	CR	0	0
<i>L. sigma</i> Calvert	CR	0	0
Hetaeriniidae			
<i>Hetaerina caja</i> (Drury)	CR	0	0

+ - reversible darkening; 0 - no darkening; ... - not tested;

^a tip of abdomen only; ^b blue phase only; ^c in one homeochromatic ♀ from Florida a small patch on the blue area of abdominal segment 8 darkened reversibly.

The last finding differs from the conclusions of BICK & BICK (1965) on *A. apicalis*, which shows a similar range of colors. One of their individually marked females, tan when initially captured, was later discovered in the dark phase. Their data can be reconciled with mine, however, if changes from brown to

turquoise are age-related and if the female had turned turquoise between observations; the Bicks apparently never observed a turquoise female that was later brown. This is not to say that all brown females eventually become turquoise. Bick and Bick also concluded that reversible changes between bright and dark phases in *A. apicalis* are not related to temperature. My results on males of the same species show that cold exposure does cause darkening. Nevertheless, under field conditions other, unknown factors may play a part. Also, field observations may be confused by the fact that color change is rather slow. I did not time the darkening process, but according to O'FARRELL (1964) it may take several hours. In species studied here, bright colors were resumed usually within two hours at 30°-33°C, but after one hour many individuals were still largely dark. Thus the color at a given moment in the field need not exactly reflect thermal conditions at that time.

If, as suggested by O'FARRELL (1964) and VERON (1974), temperature-mediated color change in Zygoptera has a thermoregulatory function, one might expect the property to be correlated with behaviour or habitat likely to incur exposure to a broad range of temperature. Such a correlation has not emerged clearly heretofore (O'FARRELL, 1964, 1968). In this study an unidentified species of *Argia* from the lowlands of Costa Rica, a thermally very equable area, changed color reversibly. The other Costa Rican *Argia* were studied at an elevation of about 1200 m, where nights may be quite cool. On the other hand, most *Argia* species perch during the day in sunlight on the ground or other broad surfaces where temperatures might be quite high. Thus in any habitat members of this genus may be exposed to extremes of temperature and are likely to be among the most thermophilic of damselflies. Moreover, species of *Argia* may be

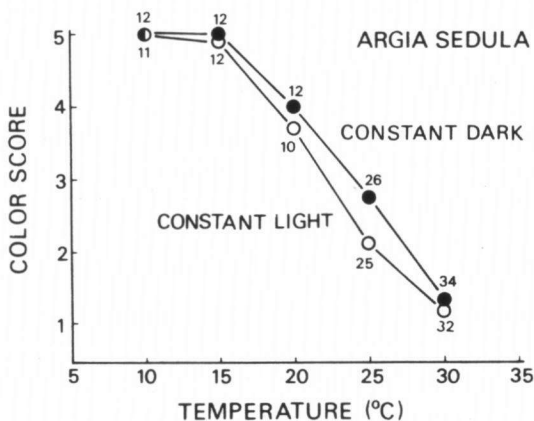


Fig. 1. Mean color score after overnight exposure at the indicated temperatures in male *Argia sedula*. Number by each point is the sample size.

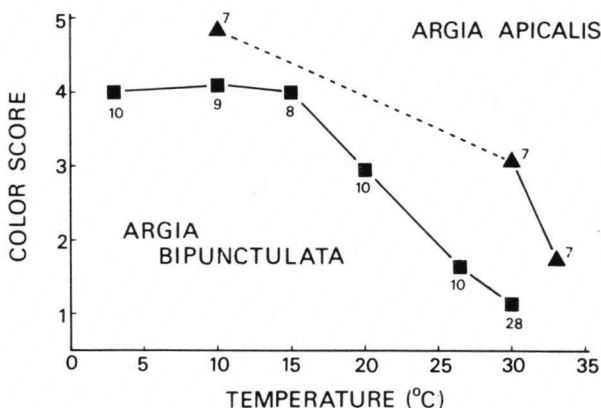


Fig. 2. Mean color score after overnight exposure at the indicated temperatures in male *Argia apicalis* and *A. bipunctulata*. Number by each point is the mean sample size.

adapted in their color responses to their particular habitat. Figures 1 and 2 show the mean color scores after overnight exposure to the indicated temperatures in three species. At any given temperature between 15°C and 30°C, *A. bipunctulata* is the brightest, *A. sedula* intermediate, and *A. apicalis* darkest. In *A. bipunctulata* darkening is less marked in intensity, as well as in relative extent, than in the other species. The sequence of response is consistent with adaptation to increasingly warm and/or variable habitats. *A. bipunctulata* commonly occurs in weedy areas and has the rather atypical habit of perching most often on vegetation. *A. sedula* perches primarily on the ground but also sometimes on vegetation and in shaded or semi-shaded areas. *A. apicalis* males, at least in Florida, are practically restricted to exposed perches on bare, often highly reflective sand (JOHNSON, 1972; and personal observations).

Figure 1 suggests the possibility that light may contribute to brightening of the cuticle in *A. sedula*. The effect is consistent but not statistically significant at any temperature for the sample sizes tested. It appears improbable, in any case, that so small a change is of much functional importance. On the other hand, the light levels used during constant light exposure were almost certainly less than levels to be expected outdoors after sunrise on a clear day.

The correlation of color change with habitat in *Argia* must be viewed with caution in light of the limited data and the partially subjective nature of the scoring system. Nevertheless, I accept, at least as a working hypothesis, the suggestion that color change in Zygoptera is an adaptation to enhance thermoregulation. The hypothesis is rendered more plausible by VERON's (1974) suggestion that cuticular darkening acts primarily to enhance sensitivity of thermoreceptors rather than directly to increase absorption of solar radiation.

Some of the species studied here, notably *A. sedula*, have such restricted blue areas that darkening probably has little effect on the overall heat load on the thorax.

One incidental observation on an anisopteran is of interest here. *Anax junius* normally is blue on the basal abdominal segments. In the laboratory at 15°C, however, this region turns dull mauve. *Anax* regulates thoracic temperature but probably not abdominal temperature. I have suggested (MAY, 1976) that this species does not orient itself relative to incident sunlight during flight, but in view of VERON's (1974) observations on orientation during flight in dark phase Zygoptera, it would be interesting to re-examine my earlier conclusions and consider the possible role of darkening of the basal abdominal segments in *Anax*.

I studied control of color change in *Argia bipunctulata* because, unlike other available *Argia* species, the abdomen is almost entirely blue. At present only the most rudimentary data are available. Ligation of the third abdominal segment had no apparent effect. Abdominal segments darkened and brightened as usual. Whole dead animals changed color readily, darkening at 10°C and brightening at 30°C. Isolated tagmata and abdominal segments could change in both directions at appropriate temperatures, but the ability both to brighten and to darken was reduced. Possibly the use of unsatisfactory medium (mammalian physiological saline) adversely affected the isolated parts. In living *A. sedula* males, the blue dorsal areas of abdominal segments 8-10 always darkened at lower temperature than blue areas of the thorax, and in *A. bipunctulata* males the lateral blue areas of these segments rarely if ever darkened, even at 3°C (thus the maximum color score is near 4, Fig. 2). This makes unlikely, although certainly not impossible, a control mechanism involving a "darkening factor" produced distally in the abdomen, as in *Austrolestes annulosus* (VERON, 1973).

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