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RATES OF COLOR MATURATION IN RELATION TO AGE, DIET, AND TEMPERATURE IN MALE *ERYTHEMIS SIMPLICICOLLIS* (SAY) (ANISOPTERA: LIBELLULIDAE)

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Male *E. simplicicollis* change from female-like coloration to pruinose blue over the entire thorax and the first 7 abdominal segments through a predictable progression of color patterns. 17 stages were delineated in this study. The change occurs over a period of about 2 to 3 weeks in Gainesville, Florida. Males marked within a few hours of emergence were either released or placed in a large outdoor flight cage. Caged individuals were hand fed daily with different amounts of prey. The rate at which a male's colors matured decreased both with decreasing food consumption and declining average air temperatures. A method is described for estimating the postemergence age of reproductively mature males from their color patterns upon arrival at a pond.

INTRODUCTION

The short reproductive life span of many insects makes them appropriate subjects for studies of animal mating systems and the lifetime consequences of different reproductive tactics. Many of the smaller dragonflies and damselflies have average reproductive life spans of 6 to 10 days (FINCKE, 1982; WALTZ & WOLF, 1984; McVEY, 1981; JACOBS, 1955), and males of many species spend their entire breeding lives at a few bodies of water, sometimes defending highly localized oviposition resources, which facilitates observation of individuals over their entire breeding lifespans (CORBET, 1980; JACOBS, 1955; PAJUNEN, 1962, 1966; HIGASHI, 1969; CAMPANELLA & WOLF, 1974; UEDA, 1979; WAAGE, 1979; FINCKE, 1982; MILLER, 1983; McVEY, 1981).

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In many animals breeding tactics are age dependent, performance changing with both experience and effort (LE BOEUF, 1974; HOWARD, 1978; GIBSON & GUINNESS, 1980; PIANKA & PARKER, 1975; WIRTZ, 1982; JARMAN, 1973; HRDY, 1977; HAUSFATER, 1975; KUMMER, 1968). An account of lifetime breeding tactics thus requires knowledge of the ages of most or all animals in a population. For small damselflies, marking individuals at emergence might allow aging of most adult males in isolated populations (FINCKE, 1982); however, in dragonflies, return rates of less than 5% would make this a laborious process (JACOBS, 1955; CORBET, 1980; HIGASHI, 1969; PAJUNEN, 1962). Furthermore, if dispersal following emergence is high (CORBET, 1980), one could not age an entire breeding population by marking tenerals. VERON (1973) was able to age damselflies between 1 to 12 days after the teneral stage by sectioning legs and counting endocuticular layers which were deposited daily, presumably soon following the teneral stage. This operation could interfere with foraging success and breeding performance and would not be useful for most field studies.

In dichromatic libellulid species, males change from their prereproductive female-like coloration to an entirely different male breeding color pattern, often a light powdery (pruinose) blue, purple, or white on parts of the abdomen, thorax, and/or wings. In many species, males complete most aspects of their color change before returning to water for their first breeding attempts (e.g. *Plathemis lydia* (Dru.), *Brachymesia gravida* (Calv.), and *Pachydiplax longipennis* (Burm.) for examples). Others, however, continue the change well into middle age, like *Orthetrum chrysostigma* (Burm.) (P. Miller, pers. comm.) and *Erythemis simplicicollis* (Say).

In this paper, I describe the color changes which occur with age in male *E. simplicicollis*. Two factors, diet and temperature, influenced the rate at which this maturation occurred. This information was then used to age unmarked males in a natural population.

METHODS

Teneral males were obtained on the morning of their emergence from a series of artificial ponds located within the Austin Cary Memorial Forest, University of Florida, 13 km NE of Gainesville, Florida, between 1 May and 30 August 1979. Extensive masses of submergent *Hydrilla verticillata* in two ponds and mats of filamentous green algae in a third provided the larval habitat. A large outdoor flight cage, or odonatary, was constructed from 13 mm nylon fish netting supported by bamboo arches forming a semicylindrical enclosure (length 10.5 m, width 5.0 m, height at top of arch, 3 m). Small trees, bent and staked to fit in the cage, provided shade and visual cover up to 2.5 m high in the middle of the cage. One side of the cage rested at the edge of a clearing bordered by tall pine trees which provided shade late in the day. Dense bushes and undergrowth extended into one third of the cage, and open sandy areas, a favorite perching surface of *E. simplicicollis* on cool days, covered much of the rest. A small pool (1 x 1.3 m, 0.2 m deep) lined with heavy plastic, provided enough water for drinking and thermoregulation, but being free of debris and algae, this was not

suitable for reproductive behaviors.

All emerging individuals captured on one day were marked with the same paint code, using dots of Testors Enamel Paint on the dorsal thorax or abdomen. Males were either released or placed in the cage; no more than 12 were maintained in captivity at the same time. With the help of several assistants, all suitable breeding ponds within a 1.5 km radius were observed all day, every day. Any marked males which returned to the ponds were recaptured and their color patterns described.

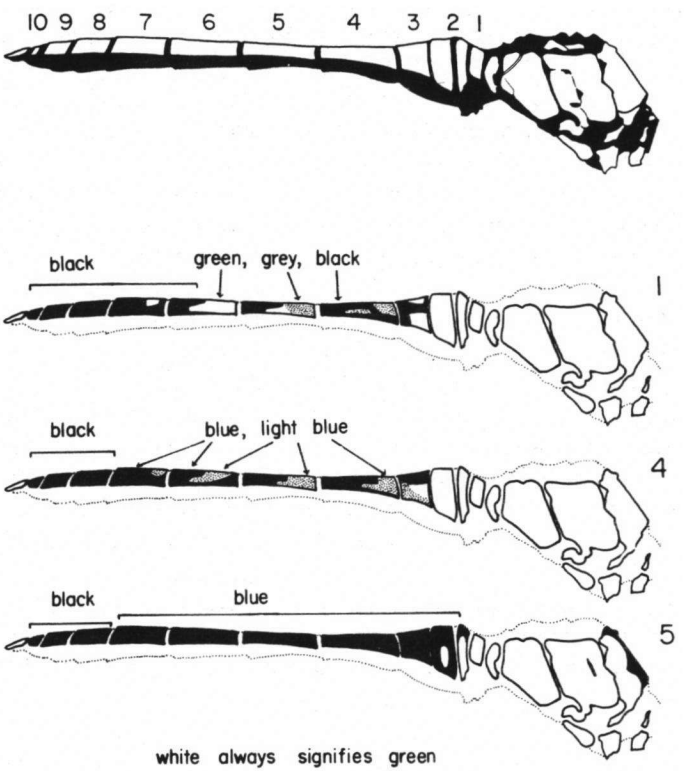

Fig. 1. Diagrams of male *E. simplicicollis* color categories. The top drawing defines the thoracic sutures and indentations which are omitted in the remainder; here white indicates the dorsolateral portions of exoskeleton which exhibit bright colors and which were used to categorize animals. Remaining diagrams of categories 1, 4 and 5 are only of these white areas of the first drawing.

The density of natural prey items for *E. simplicicollis* in the odonatary was low. I could therefore control in large part each male's food intake by hand feeding. Males would not eat for the first two days following emergence. After this stage I used principally the thorax of emerging *Pantala flavescens* (Fab.) and of adult *Pachydiplax longipennis*, the largest natural prey items, to minimize the proportion of cuticle ingested. From the remains of each meal I estimated the fraction eaten to the nearest 20%.

The feeding experiments were conducted with three sets of males. The first set of 7, captured at emergence and added singly to the cage over a 16 day period, received 10 to 80 mg of prey daily. The second set of 7, captured at emergence and added over three consecutive days, received either 70 or 120 mg of prey daily. After two or three weeks of captivity, most males either had escaped or their color patterns had become obscured by frequent handling. To document the food dependence of the later stages of color maturation, the third set of 15 males were captured as young reproductive adults and maintained on 10, 50, 100, or 150 mg of food daily. For all 3 sets, more individuals were originally captured and entered in the experiments than listed here. Due to escape and predation by yellow jackets many males disappeared within a few days; only those surviving in the cage until their color change began (first two sets) or at least 5 days (third set) were used for analysis.

To document color changes in free flying males, a total of 72 males were repeatedly captured, described, and released at 2-3 day intervals for 5 or more days. All were individually paint-marked and the location of blue color was drawn on diagrams of the lateral view of an *E. simplicicollis* thorax and anterior four abdominal segments (Fig. 1).

All caged individuals were both drawn and photographed daily. I created a series of 17 color categories through which males could be expected to mature linearly with time using photographs from two caged males taken around 09.00 hr on 17 consecutive days to create a master set of color drawings. All photographs and capture card diagrams of males were subsequently assigned to a color category by comparison to the 17 master drawings. For categories 1-4, the abdominal segments were used for assignment, for 5-17, only the thorax. Stages intermediate to two color categories were assigned the 0.5 value between the two. After all the category assignments for all photographs and drawings were made, the categories assigned to 91 drawings were compared to those assigned to the photographs taken at the same time. The mean disagreement between drawing and photograph was -0.15 ± 0.76 categories (s.d.).

Air temperature was recorded at 1/2 hr intervals during daylight hours with a mercury glass thermometer at 0.5 m above ground level shaded by a 1 m^2 board located 1.0 m above the ground and covered with aluminum foil to reflected incident radiation. The temperature station was located about 1 m from one pond and 20 m from the odonatary. Hourly recordings of air temperature day and night were obtained from the Federal Aeronautics and Aviation Service (F.A.A.S.) located at the Gainesville Municipal Airport, 13 km SW of the study site. These air temperatures were recorded at a height of 1.5 m above the ground from within a white box equipped with fans to circulate air for several minutes before each reading was taken.

RESULTS

DESCRIPTION OF THE COLOR CHANGE AND COLOR PATTERN CATEGORIES

Both female and prereproductive adult male *Erythemis simplicicollis* have a predominantly green thorax and a green and black abdomen. The first 2 abdominal segments are totally green, the next 5 are black with green patterns giving the illusion of transverse stripes, and the last 3 segments are black. There is geographic variation in the darkness of the black. In Millbrook, New York, the terminal segments are light brown centrally, instead of solid black as in Gainesville, Florida.

Adult male *E. simplicicollis* which have been breeding for three or more weeks are a light pruinose blue over the entire thorax and abdomen, except for the terminal two abdominal segments which tend to remain darkened. Males change

from green and black to blue in a way that is easy to categorize. The first blue appears on abdominal segments 4 and 5 and spreads both anteriorly and posteriorly from there. At the beginning of this change, the striping is still evident in the middle segments, except that grey replaces the former green areas and dark blue replaces the black (Fig. 1). Eventually, a uniform light blue color spreads across all abdominal segments except 8 to 10 which remain darker than the rest of the abdomen for several days. During the first four days or so of the transition, only the abdomen changes color. Around day five, the thorax begins to turn blue beginning dorsally on the mesepisternum (Fig. 1, Tab. I). The colors do not mix;

Table I
Description of early and late color categories for male *E. simplicicollis*

Color category	Description
1	Essentially female-like coloration except light grey has replaced green on abdominal segments 4 and 5
2	On abdomen, blue has replaced black and light blue-grey has replaced green on segments 4-7, terminal 4 segments black
3	Same as above except abdominal segment 7 is half blue and half black, and blue is appearing dorsally on abdominal segment 2 and on the dorsal thorax (not visible in lateral view). Light stripes on abdominal segments 3-7 are still grey-blue
4	Same as above except abdominal segments 3 and 7 are completely blue; terminal three segments only are black. Blue on mesepisternum and abdominal segments 1-2 is visible from lateral view. Stripes on abdomen are only faintly visible as light blue (not grey) areas on segments 3-7 only
5	Striping is no longer visible on abdominal segments which are all blue except 8-10 which are still black. Green is disappearing from abdominal segment 2. Blue on dorsolateral thorax extends further posteriorly
16	Same as 15, except half as much green remains
17	Entire thorax and abdomen are light blue except the terminal two or three abdominal segments which might still be darker than the rest

instead a sharp boundary between the green and blue moves progressively more caudal (Fig. 2). While these drawings are from photographs of only two males, the patterns were similar to the other males in the population. On some, the border between green and blue resembled more closely a straight line without small residual spots of green color. Also, some males changed more quickly than others on the metathorax relative to mesothorax.

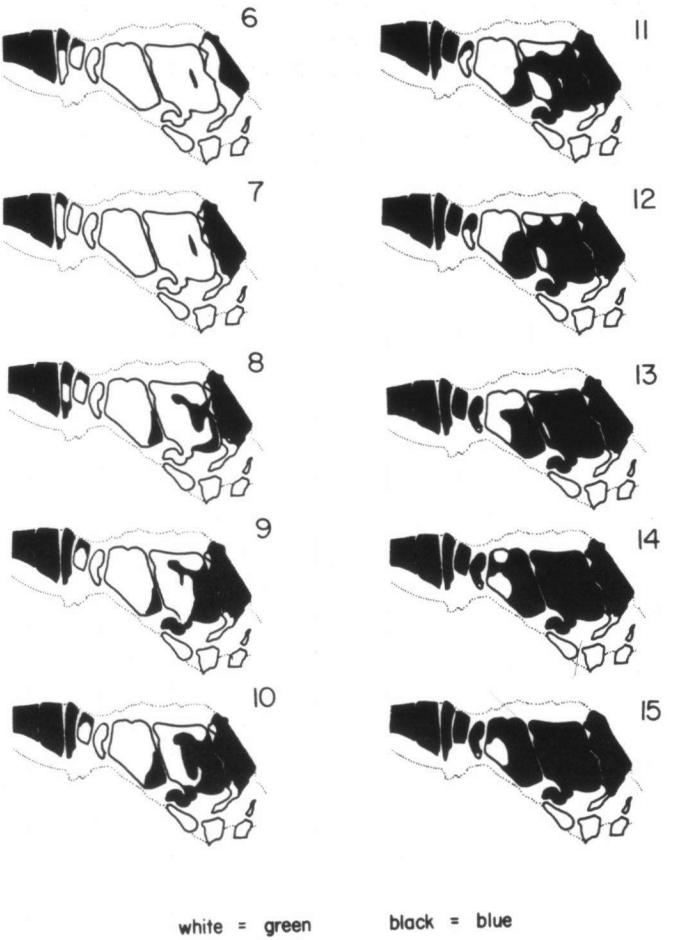

Fig. 2. Diagrams of color categories 6-15. Cf. Table 1 for description of first five and last two categories. Drawings are from photographs of two males taken at 09.00 hr on consecutive days in August. In color categories 6 to 15, the abdomen remains light blue, except segments 8 to 10 which change from black to blue-grey.

FOOD CONSUMPTION AND LATENCY TO COLOR CHANGE

Free *E. simplicicollis* males and females might consume at least as much as 140 mg of prey on some days, sometimes from one prey capture, even though their own mass averages 270 mg (MAY, 1976). I observed many free females to catch teneral *Plathemis lydia* (130 to 150 mg). While on territory, male *E. simplicicollis* sometimes caught 1 or 2 damselflies (30 to 33 mg), rarely 3 in one day. We also

saw 5 captures of adult *Pachydiplax longipennis* (130 to 170 mg) in 600 male days. After these large meals, a male left territory for three or more hours, far longer than the 20 minutes needed to consume the abdomen and thorax of the prey. Males foraged predominantly away from the breeding ponds early and late in the day, and I do not know what their average capture was at these times. The daily food supplement of most caged males thus ranged between the equivalent of a small damselfly, 20 mg, and the largest single prey caught by free animals, 150 mg.

The number of days a male remained in female-like coloration appeared to decrease with increasing food consumption (Fig. 3). The low to medium food group (triangles) lived in the cage a little over a month prior to the medium to high food groups (circles), however. It is possible that they matured more slowly because of cooler body temperatures. Both groups were exposed to partly sunny skies. The low to medium food group experienced 5.8 cm of rain in 16 days (0.36 cm/day) compared to 2.8 cm in 9 days (0.31 cm/day) for the medium to high food groups implying less cloud cover for the latter. To estimate air temperatures experienced by each male, I used the F.A.A.S. records of air temperature for the hours each male was alive. These recordings matched well the air temperatures recorded at the study site during the day (N=35 paired readings taken less than 10 min apart, mean deviation +0.2 ±1.2° C s.d.). The average air temperatures so calculated were not different for the two groups of males and ranged from a low of 26.3 to a high of 27.3° C. Maximum and minimum temperatures experienced were also similar. The difference in the number of days spent in female-like coloration between the two groups of males (Fig. 3, circles and triangles) could have resulted from differences in diet, differences in body temperature as a result of differences in insolation but not average air temperatures, or both.

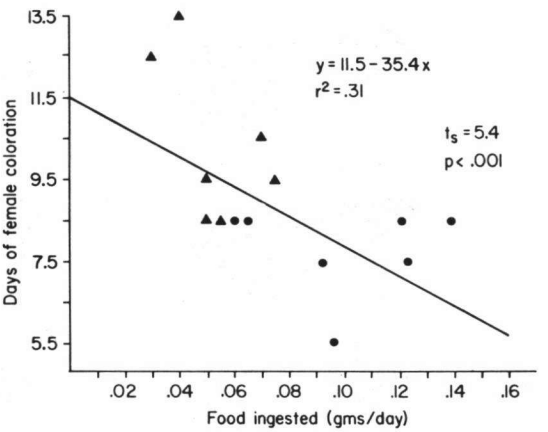

Fig. 3. Latency to male color change with food consumption for males caged the morning of emergence. Circles represent males caged between 16 and 18 August, triangles are males caged between 25 June and 10 July. Maximum error in estimate of total grams of food consumed was ±10%. Average air temperature was 26.3° C for both groups. No correction for error in estimate of food consumption has been made.

FOOD CONSUMPTION AND RATE OF COLOR CHANGE

Despite differences in food consumption and perhaps body temperature, the males caged at emergence did not vary significantly in their rate of color maturation once it had begun (Figs 4a-b). The 15 males captured and caged between color categories 2 to 7 were therefore assigned to a more extreme range of daily food supplements, 10 to 150 mg. In this experiment, the average rate of color change (number of color categories spanned/unit time) increased significantly with increasing food consumption (Fig. 5) in large part because two males receiving less than 0.015 g per day changed at about half the rate of the remaining males. Temperature should not have been a confounding factor because males were assigned to one of the four food supplement groups at random as they were placed in the cage.

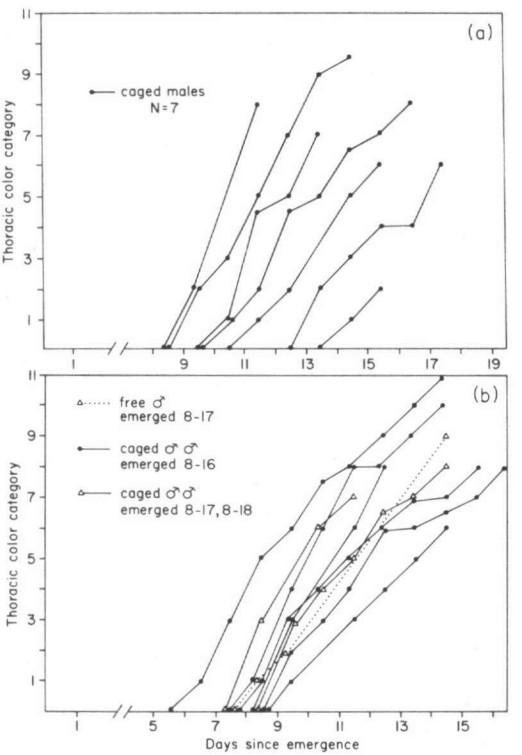

Fig. 4. Color maturation with age for males caged at emergence, same males as in Fig. 3: (a) males caged between 25 June and 10 July, — (b) males caged between 16 and 18 August. One male (8-17) escaped from the cage on day 9 and was recaptured on day 14 (dotted line).

RATE OF COLOR CHANGE WITH AIR TEMPERATURE

Free flying males were studied for effects of ambient temperature on rate of color change. April and May exhibited several cool periods while July and August were consistently warmer. For each male recaptured after an interval of five or more days, I averaged the hourly temperatures encompassed by the dates of his first and last capture. A significant positive relationship was found between average air temperature and an individual's rate of color change (Fig. 6). Average ambient air temperature as measured here accounted for only 21% of the variance in males' maturation rates. During the day

solar radiation, flying activity, and perching position must often elevate a male's body temperature over that of the air a few decimeters above the ground; I have made no attempt here to quantify these factors. At night, however, all males are likely to be close to ambient air temperatures.

AGING MALES FROM COLOR PATTERNS

It should be possible to estimate the age of males which were not marked at emergence from the data on those that were in the same population. Before using data from caged males in addition to free males I needed to compare the two. The age of free flying males might have exhibited a different mean and variance for a given color category than those for caged males. Of 92 males marked at emergence, 7 returned (8%, Fig. 7). All 7 had experienced air temperatures which averaged 3 to 4° C less than the caged males, which could easily have accounted for the fact that free males were on average 1.6 days older for color categories 2 through 5 than caged males[1]. The variance in age of these 7 males (around the mean age of the caged males +1.6 days for each color category) was only +2.0 and -1.8 days compared to +4.0 to -2.9 days for the caged males (from log transforms of the data). Although this difference is not significant (F test), it is possible that free flying males which returned to the breeding

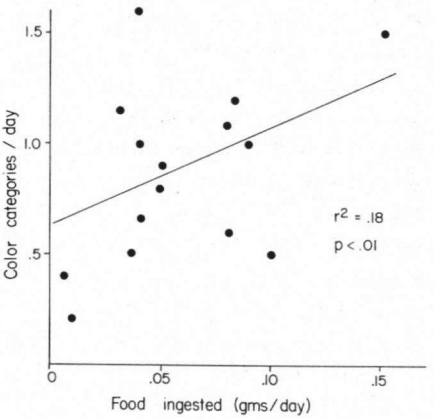

Fig. 5. Effect of diet on rate of male color maturation after color category 1. All males were first captured and caged between 28 June and 11 July exhibiting a color pattern between categories 1 and 7. Only those captive for 5 or more days were used. Average rate of color change = last — first category, divided by time interval. Error of estimates were ±0.24 categories/day (s.d.), and a maximum of ±10% of the total food ingested. Regression equation is $y = 0.46x + 0.61$, student's $t = 3.34$.

[1] In August, males changed color at a rate of one category per day. Thus, 12 days would result in a progression through 12 color categories. If a male experienced cooler average temperatures by 3° C, the regression in Fig. 6 suggests that the male should have progressed at a rate of 0.15 categories/day slower (0.049 categories/day per ° C slower x 3° C). Twelve days x 0.15 categories/day = a backlog of 1.8 categories after 12 days. The rate has thus been 10.2/12 or 0.85 cat/day. In order to span the total 12 categories at this rate 12 cat/0.85 cat per day = 14.1 days, or 2.1 days more than the August values would be required. If the temperature dependence of maturation during the prereproductive phase is similar to that during the reproductive phase it should have taken the free males 2.1 days longer to reach color category 3.5 than it did the caged males.

ponds did not vary as much in their food intake as did the caged males, or that they could choose a more balanced diet, or that they chose their microenvironments, and hence body temperatures, somewhat differently. Thus, using the mean of the caged males to estimate the July and August latency to color change seems reasonable. The variance of that group was, if anything, an overestimate of the variance of wild males.

To estimate the age of males not marked at emergence and breeding in Gainesville in July and August (Fig. 7), I first used the distribution of ages of the 14 males caged at emergence (Fig. 4) up to color category 7. To derive the mean age and variance for color categories 8 to 16, I used 25 free flying males first captured between 28 June and 10 August 1979 when between categories 2 and 7 and which were recaptured 5 to 12 days later. The male's age at first capture was set to the mean age for the 14 caged males caged which displayed that color pattern. This plus the interval between first and last capture then equalled his estimated age at last capture. On a plot of color category against estimated age, a straight line connecting these two points then indicated his estimated age at all intermediate color categories. After all males were so plotted, the mean age for each color category could be estimated from the points of intersection of these lines with each category. The total variance associated with these means was the sum of the variance in the onset of color change of the caged males and the variance in the rate of color change afterwards (or the variance around the mean age derived from 25 graphed trajectories for free males). Note that the drawing error was incorporated in this second variance because all free males' color categories were estimated from drawings. This particular example (Fig. 7) provides estimates only for males living through similar temperature regimes, and would have to be repeated for other temperatures.

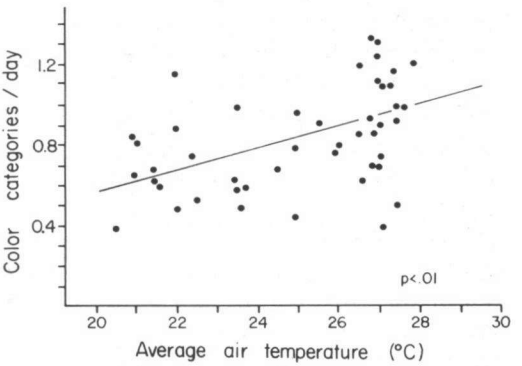

Fig. 6. Average rate of color maturation after color category 1 relative to average air temperature. Color categories / day = last — first category divided by the time interval. Standard deviation of estimate of rate of maturation was ±0.17 categories/day. Regression equation is $y = 0.049x - 0.40$, $N=46$, $r^2 = 0.21$.

DISCUSSION

Male *Erythemis simplicicollis* require around 17 days or longer to change completely from the green and black colors characteristic of females and prereproductive males to the fully pruinose blue of middle aged, breeding males. Depending on temperature and diet, this change can begin at least as early as 5.5 days and as late as at least 13 days postemergence; the average of the caged males in August was 8.4 days. Free males returned to the ponds to breed as reproductively mature individuals no sooner than in color category 3, and 85% did not return until category 7 or older, that is around 14.5 days post-emergence or later (McVEY, 1981). Thus most males had a fully blue abdomen on their first day at the ponds. Few males (< 5%) arrived after category 17 (McVEY, 1981); thus in a well isolated population one can estimate the age of perhaps 95% of newly arriving males from their color patterns.

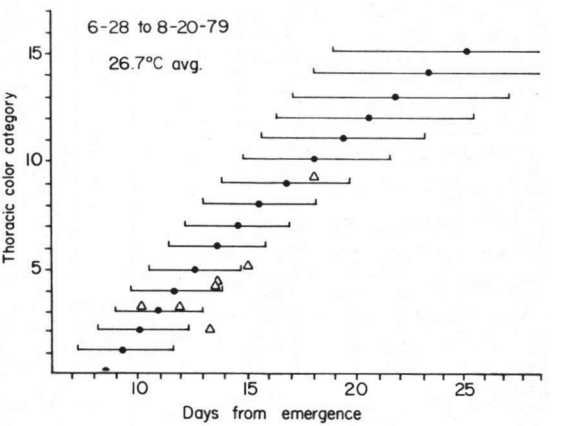

Fig. 7. Estimated male ages in relation to color categories as the mean male age (filled circles) ±1 s.d. (bars). This figure was constructed from the 14 males caged at emergence surviving until category 7 and from 25 free flying males first captured between categories 1 and 7. All caged males were part of feeding experiments. Open triangles represent free flying males marked at emergence between 6 and 17 May. Average air temperatures for these males were 3-4° C cooler than for the caged males.

The latency to the onset of color change in caged male *E. simplicicollis* decreased with either increasing food consumption, increasing body temperature, or both. The rate of color change after category 1 depended on food consumption independent of temperature. Although the males captured at emergence began to change color between 5.5 and 13.5 days post-emergence depending perhaps in part on food consumption, their rate of maturation for 9 days afterwards appeared largely independent of differences in insolation and food consumption for daily diets of between 30 and 150 mg. Only males on near-starvation diets (10 mg/day), which could fly only weakly and for brief intervals, slowed markedly in their progression through the color categories.

As has been reported for other dragonflies (CORBET, 1960; BUCHHOLTZ, 1951; CORBET, 1980), the rate at which free flying males progressed through

their maturational stages increased with increasing ambient temperatures. Whether average air temperature, temperature plus insolation, some other correlate of air temperature, or time spent flying was more important is not known. The temperature effect was not large, however, probably because males did thermoregulate during the day by choosing perching locations (MAY, 1976). Plotting thoracic temperature of perched male *E. simplicicollis* against air temperature under sunny skies, MAY (1976) found a slope of 0.38 instead of 1.0 indicating significant thermoregulation. Thus, while males probably cannot maintain a body temperature below ambient, they can maintain higher temperatures by perching in the sun, adopting specific orientations with respect to incident radiation, and perching in surface boundary layers of warmer air. As a result, the body temperatures of fully adult breeding males and hence their rate of maturation might fluctuate even more with cloud cover than it did with the average daily air temperatures.

A group of free flying males began to change color on average 1.6 days later than the caged males did. Different ambient temperatures during the prereproductive phase could have accounted for the difference between these groups. The variance in the onset of color change for the 7 free males marked at emergence (+2.0 to -1.8 days) was less, though not significantly less, than the variance for the caged males (+4.0 to -2.9 days). CURRIE (1961) also found that free flying male *E. simplicicollis* in a population in Ohio began to change colors within a narrow window of ages. Ten males marked at emergence were recovered between 6 and 11 days later in the equivalent of color categories 2 or 3. This implies a range of 4 or 5 days for the onset of the color change which is similar to the range of 4 days for 7 free flying males reported here. The 14 caged males might have exhibited a larger range in rate of color maturation than the Ohio and Florida populations of free males because I could keep them alive in the protected cage environment when they were too weak to fly well. Free males on near-starvation diets might not live long enough to return to a breeding pond or might have to return to ponds of lower male density than the ones under observation.

In this study an unmarked male entering the population between color category 1 and 8 could be aged with 96% confidence to within +2.8 to -2.7 days (free males) or conservatively +4.0 to -3.4 days (caged males). The confidence limits were somewhat larger for animals first captured between color categories 9 and 17. Because color maturation is sensitive to temperature, it is necessary to follow part of a population to be able to age the remainder for a given locality and season.

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