
19 Evidence for a dispersal morph in females of *Dolania americana* (Ephemeroptera: Behningiidae)

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We compare data from reared series of female adults with field data on percentage representation of "light" and "dark" morphs of Dolania americana Edmunds and Traver to show that dark morph representation is best estimated from light trap samples taken shortly after female emergence. Except for days of severe weather, dark morphs were essentially absent from later light trap samples and from drift samples. Dark morphs were occasionally found arriving at the river more than one hour after sunrise. Dark morphs also were found over bridges, flying along roads and ovipositing away from the main river. The dark colouration appears to mark a dispersal morph.

Introduction

Studies on within-species variation of Ephemeroptera include colour variation in *Hexagenia limbata* and *Stenacron interpunctatum* by McCafferty and Pereira (1984) and variations in size and fecundity for many species, for example *Baetis rhodani* and *Isonychia bicolor* (Benech 1972; Sweeney 1978). Colour variation is often attributed to melanization, or the increased deposition of melanin in tissues at lower temperatures (Spieth 1938; Rentz 1991), and size variation to effects of different temperature regimes on growth rates (summarized by Brittain 1982). Within-species variation is termed polymorphism in *Dolania americana* because distinct colour differences are present only in female adults of single populations (Peters and Peters 1977). There is no final molt in females of *D. americana* and the morphological subimago is the functional imago; males have subimaginal and imaginal stages, but no colour polymorphism.

Earlier, Peters and Peters (1977) briefly described female variation. In the present study, the range of colour is illustrated and summarized into eight categories

(Fig. 1); annual variation is presented in Table 1. We use the term “dark morph” to refer to forms nos. five to eight — those with some colouration apparent over all abdominal terga.

The existence of colour polymorphism suggests physiological or behavioural differences. Physiological differences in protein composition from bodies of light and dark morphs were discovered by Basha and Pescador (1984). Peters and Peters (1977) noted differences in percentages of dark morphs collected at light and in drift. In this paper, we examine behavioural differences among females of *D. americana*.

Materials and Methods

Data were obtained from two sites on the Blackwater River, Okaloosa Co., Florida, 1976-1992: Site 1, the primary study site northwest of Holt, and Site 2, a secondary site 1 km south of the Alabama state line (FL1 and FL2 in Sweeney and Funk 1991). The Blackwater is a clean, clear, sand-bottomed river with a pH ca. 6.0 and an average width and depth of 26 m x 1 m at Site 1 and 12 m x 60 cm at Site 2. The sites have been described in Peters and Jones (1973), Peters and Peters (1977) and Peters et al. (1987).

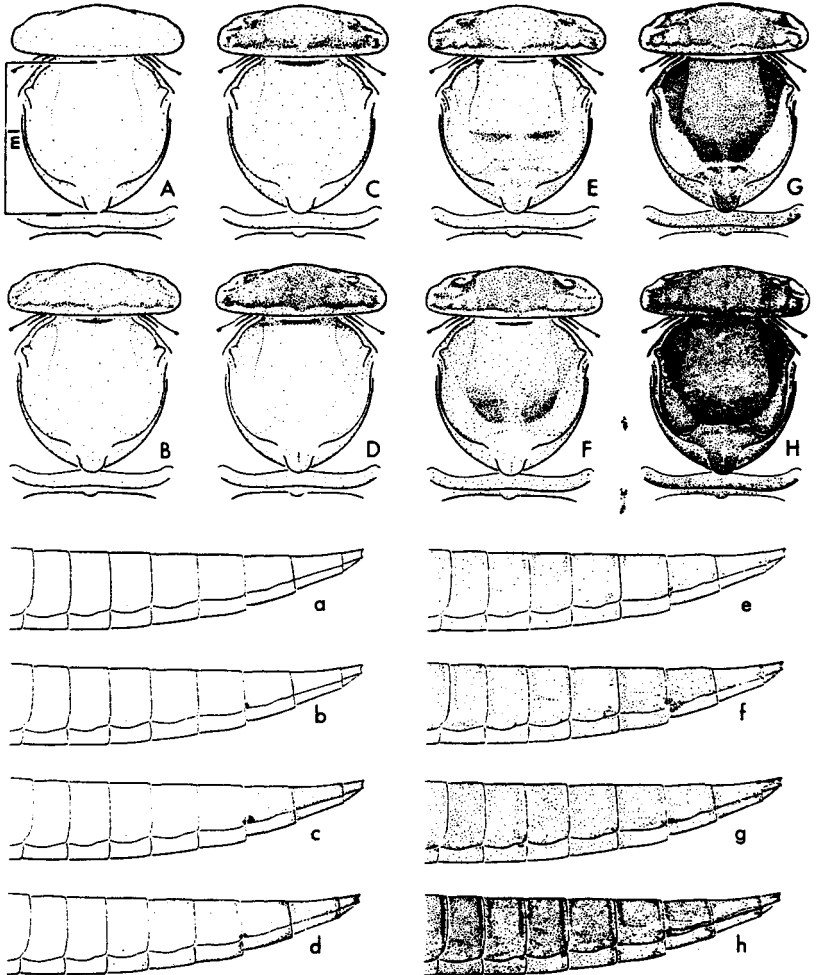
Air temperatures (accuracy $\pm 0.1^{\circ}\text{C}$) were taken 1-1/2 hours before and at sunrise on every date of emergence, as were water temperatures and climatological factors, which will not be discussed here.

Light trap samples were taken on every date using battery or generator-powered fluorescent lights. For females, collections began approximately one hour before sunrise and were discontinued at full light. When numbers were large, lights were extinguished after a sample size of 30-60 was obtained, although a small fluorescent light usually remained. For 1991-1992 comparisons, we used a single light in a fixed position: after a sample ≥ 10 was obtained, the light was turned off, the sample collected and the procedure repeated.

We took samples of surface drift when possible, although high water prohibited sampling on occasion. Drift refers to specimens collected by surface nets (0.25 m or 1 m diameter, mesh size 1.2 mm) in place in the river from about two hours before to 15 min after sunrise. Drift is a standard method of estimating populations as exuviae from emerging nymphs and spent adults float (Peters and Peters 1977; Sweeney and Vannote 1982; Peters et al. 1987).

We used sweep nets to collect females in flight approximately 40-20 minutes before sunrise. Not intended as a quantitative measure, sweep nets were used to collect females for egg studies. Mature nymphs were also collected from Site 1 in advance of emergence and reared through emergence in aquaria (details in Peters et al. 1987).

Figure 1. Colour variation in thorax and abdomen of female *Dolania americana*. Capital letters are used for the thorax, lower case letters for the abdomen, forms #1-8 explained at bottom of figure. Mesothoracic length (mm) size range given on Figure 2; scale for abdomen one-half that of mesothorax.



#1 - Aa	#5 - Ce, De, Ee, Cf, Df
#2 - Ab, Ba, Bb, Cb	#6 - Ef, Ff, Fg, Fh
#3 - Bc, Cc, Dc, Ec	#7 - Gf, Gg, Gh
#4 - Cd, Dd, Ed	#8 - Hf, Hg, Hh

Table 1. Ten-year variation in per cent distribution of colour forms at Site 1 (sample N = 1529). Colour forms are depicted in Figure 1.

Form	Mean %	Range	Form	Mean %	Range
#1	38.0	5.6 - 68.6	#5	2.1	0 - 6.2
#2	30.4	9.8 - 47.8	#6	1.8	0 - 5.7
#3	10.4	0 - 44.4	#7	5.0	0 - 10.8
#4	2.1	0 - 12.1	#8	11.0	1.6-29.2

Table 2. Comparison of dark morphs captured at light traps, Site 1, with those collected by other methods: A, surface drift; B, sweep nets. SE = standard error, df = degrees of freedom, *p* = probability (*) <0.001).**

Air (°C)	A. Surface Drift			B. Sweep Nets			Difference (A + B pooled)		
	Sample method	N	Percentage mean ± SE	Sample method	N	Percentage mean ± SE	df	mean ± SE	<i>p</i>
≥15	Light	16	20.4 ± 2.9	Light	10	27.5 ± 4.3	25	19.3 ± 2.4	***
	Drift	16	1.9 ± 0.5	Sweep	10	6.9 ± 2.1			
11-14	Light	6	21.1 ± 3.0	Light	2	16.4 ± 7.3	7	7.3 ± 5.1	NS
	Drift	6	8.5 ± 3.0	Sweep	2	25.0 ± 5.0			
≤10	Light	1	19.3	Light	2	23.8 ± 13.8	2	-2.1 ± 4.6	NS
	Drift	1	19.4	Sweep	2	26.8 ± 21.6			

Measurements of female morphs were made to an accuracy of ± 0.04 mm from specimens preserved in alcohol. Unless specified, minimum sample size is ten or more females; however, dark morphs in drift represented less than 2 per cent of the total catch, so we used minimum sample size 50 for analysis of drift data.

Results

Samples of reared females from Site 1 were large enough (ten or more individuals) in years 1979-1984 and 1986-1989 to compare annual representation of dark morphs in reared samples with those obtained from light traps and surface drift. The percentage of dark morphs reared (18.9 per cent) was not significantly different from the percentage in light traps (20 per cent). Both were significantly higher than the percentage (2.8 per cent) in drift (Student-Newman-Keuls multiple range test, $p < 0.01$).

Using light trap results, the annual mean percentage of dark morphs (20 per cent) at Site 1 ranged from 3 per cent (1982) to 37 per cent (1984). Because of strong between-year differences, further analyses compare results per day.

For 1991-1992, we separated early and late light trap samples on six days when air temperatures were $\geq 15^\circ\text{C}$. Dark morphs averaged 18.6 per cent at early lights and 4.5 per cent at later lights: mean difference was 14.1 per cent ($\text{SE} \pm 2.4$ per cent, $t = 5.88$, $df = 5$, $p < 0.01$). This apparent loss of dark morphs was confirmed on days when sample size was adequate to compare samples from early light traps with drift or sweep net samples (Table 2): dark morphs were significantly underrepresented in both at air temperatures $\geq 15^\circ\text{C}$. [On rare occasions when male imagos were absent (air $\leq 10^\circ\text{C}$, Peters and Peters 1986), there was no difference (Table 2).] Assuming favourable temperatures (air $\geq 15^\circ\text{C}$), dark morphs were not among females ovipositing immediately after mating — the typical behaviour described by Peters and Peters (1977) and Sweeney and Vannote (1982).

We do not know exactly where the dark morphs went. However, reports of no activity after sunrise (Peters and Peters 1977) are not entirely correct. We monitored post-sunrise activity at Site 1 for one hour after sunrise on days with emergence, 1984-1992. On 14 of 25 days with optimum conditions (air $\geq 15^\circ\text{C}$), there was no activity. Table 3 gives arrival times of females on the remaining days. Almost all females present after sunrise (98.6 per cent of 142 captured) were dark morphs.

Light morphs were usually trapped by their wings when ovipositing on the water surface; in contrast, dark morphs arriving after sunrise actively flapped their wings after landing on the river. All such dark morphs collected have lacked eggs. [We do not include here the rare female of either morph that may continue to fly after sunrise, presumably unmated, with a full complement of eggs and in an "offering" flight pattern (Savolainen 1978).]

Evidence is against these dark morphs necessarily arriving from downriver. First, those observed arriving came from above the trees. Second, there were size differences between post-sunrise females and those that emerged on site based on mesothoracic length (Fig. 2). There was little overlap (dark area) between years for either morph on site (Fig. 2A,B). For the post-sunrise females (Fig. 2C, 99 per cent dark morphs), there was a strong size overlap between 1984 and 1990; however, post-sunrise females (Fig. 2C) were significantly smaller (1984) or larger (1990) than their respective on-site populations (Fig. 2 A,B) (t test, comparison of means, $p \leq 0.01$).

Finally, the 15 V 1984 record occurred at the end of a well-documented emergence season (eight days after peak emergence, no females in drift, none at light, other unpublished data). Most females collected were dark morphs that arrived long after sunrise (Table 3). The Blackwater River is typical in that emergence shifts upstream over the season (Ide 1935; Peters and Peters 1977), so that arriving dark morphs either came from upstream or from outside the system.

To better evaluate females leaving the river, we moved to Site 2 where a bridge crosses the river. On four dates with large emergence, dark morphs began flying over the bridge and along an adjacent road about 30 minutes before sunrise and were found on the river after sunrise (Table 4). In contrast, Site 2 dark morphs collected at light on these dates averaged 19.0 per cent (18 of 95 females).

We tried to collect eggs from females cited in Table 4. Females from the river were void (as at Site 1), and those in puddles were essentially void (25 eggs from nine females, of which 23 developed). Eggs from all but one of the females collected above the bridge developed. Knowing that unfertilized eggs of *Dolania* do not develop (Peters et al. 1987), females must have mated before leaving the river.

Discussion

It appears that under favourable conditions dark morphs of *D. americana* leave the site of emergence and mating to oviposit elsewhere: dark morphs disperse! This type of dispersal does not fit into present theories of the "compensation-cycle" of Müller, although Müller (1982) expanded the closed cycle concept to include "exploitation of different biotopes," referring particularly to the movement from estuaries to freshwater streams, and allowing for other forms of dispersal. Russev (1973) too referred to a tendency towards, rather than an obligatory, upstream flight. Nevertheless, a compensatory flight does not occur for light morphs of *D. americana* that oviposit immediately, and dark morphs do not seem always to follow the river. Further, the flight of dark morphs is not necessarily upstream, although it may be upstream for some. The flights we saw resemble more a

Figure 2. Mesothoracic length. Per cent representation of size classes for all measured specimens at Site 1 (light traps and sweep nets): A, light (#1-4) morphs; B, dark (#5-8) morphs; C, size classes for females arriving after sunrise (104/105 dark morphs), 14-15 V 1984, 1 V 1990. Plain = 1984, light stipple = 1990, dark stipple = area of overlap.

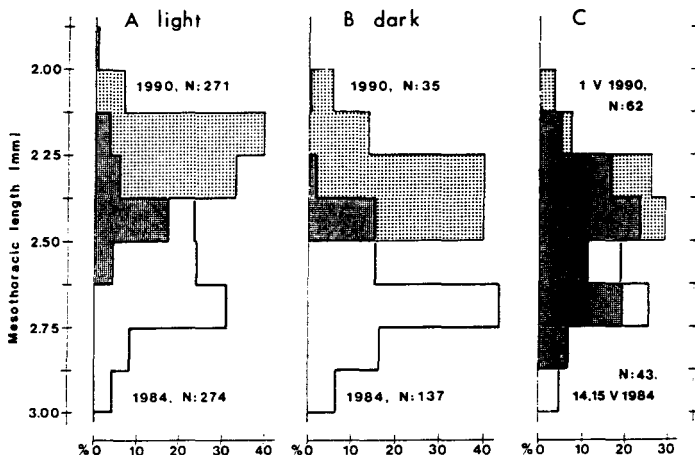


Table 3. Times of activity for female *Dolania* on river after sunrise, Site 1, 1984-1992. Individual dates are those with sample size >10 (air temperatures $\geq 17^{\circ}\text{C}$). Smaller samples are pooled. Other indicates air temperatures $\leq 14^{\circ}\text{C}$ or adverse weather.

Min after sunrise	15 V 1984	1 V 1990	7 V 1985	Air $\geq 15^{\circ}\text{C}$	Other
≤ 5 min	0	6	0	1	2
6-20 min	1	57	4	8	8
21-35 min	1	53	9	12	6
36-50 min	13	26	0	6	3
51-65 min	23	7	0	0	0
≥ 66 min	$>2^a$	$>2^b$	0	1	0

^{a,b} continued past 76 and 71 min

Table 4. Females collected away from river and females after sunrise, Site 2, 1987, 1988, 1991 (air $\geq 14^{\circ}\text{C}$, no rain or wind).

	light	dark
Flying on road, over bridge	1	8
Roadside pools	1	12
On river after sunrise	0	7
Per cent of total	6.8%	93.4%

“migration,” used in the one of the many senses of the word — a unidirectional movement over some distance (Farrow and Drake 1991).

Our data indicate that dark morphs flew above the trees after mating and before oviposition. Depending on weather, air currents and other undetermined factors, they may return to another position on the same river or possibly be carried far from the site of emergence. There are no data for *Dolania*, but other insects take advantage of a nocturnal temperature inversion, frequently with an associated zone of wind, to migrate great distances at speeds of 10-20 m/sec, and stable night-time air conditions (without updrafts and downdrafts) normally continue one to two hours after dawn (Farrow and Drake 1991). A night-time migration was suggested for some mayfly species in Mali based on radar observations of swarms moving upstream 30-130 m above the River Niger (Reynolds and Riley 1979).

The only confirmed record of distance for *Dolania* is at least 2.5 km — the distance up a dry tributary at which one dark morph was found. On an average day at Site 1, most dark morphs are gone from the river 35-40 min before sunrise. Adding this time to the dark morph arrival times (Table 3) and using a flight speed of >4 km/h (Peters and Peters 1977) produces a dispersal of >7 km without hypothesized air currents. Fremling (in Russev 1973) documents an upstream flight of 13.2 km for *Hexagenia bilineata* and suspects that the distance is much greater.

The existence of a dispersal morph is an addition to known forms of mayfly dispersal. Others are the upstream flight as part of the colonization cycle (summary in Müller 1982), an upstream migration before emergence as in *Leptophlebia cupida* (Hayden and Clifford 1974), and dispersal by means of human activity, such as *Cloeon cognatum* or *Pseudocloeon?* from the Rivière Bleue in New Caledonia (Burks 1953; Peters et al. 1978).

The existence of colour polymorphism indicating a dispersal form in *D. americana* may be a fortuitous occurrence, but other species — several species of *Campsurus* for example — are described only on female variations that may, perhaps, indicate dispersal morphs. The type of dispersal may vary under different situations for many mayflies. For these, as for *Dolania*, additional study must include an understanding of factors producing dispersal forms.

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