

**THE EFFECT OF PHYSICAL CHARACTERS ON FORAGING IN
PACHYDIPLAX LONGIPENNIS (BURMEISTER)
(ANISOPTERA: LIBELLULIDAE)**

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The foraging behavior, comparing sexes foraging on and off the pond in a large enclosure is described and the effect of physical characters is shown. Foraging rate in the enclosure was considerably lower than previously reported for this sp. in the wild. The sexes did not differ in foraging rate. Phenotypic characters were correlated only weakly with foraging rate, but weight was significantly positively correlated with how often males foraged, while fat content correlated negatively. Foraging rate was also correlated with time of day.

INTRODUCTION

Energetic costs and benefits determine the feasibility of feeding territory defense (e.g.: BROWN, 1969). However, many species defend mating territories where they do not feed. If individuals do not forage on the mating territory, energy reserves may also be important for maintaining mating territories. For example, FRIED & MAY (1983) suggested that in a species of libellulid dragonfly, *Pachydiplax longipennis*, males need to spend most of the day foraging off their mating territories in order to ingest enough food to balance the energy they expend in territory defense. Males may be forced to leave territories at a pond after only a few hours in order to replenish their energy reserves. Males that are able to forage more efficiently may therefore be able to remain on their territories longer, and will probably achieve greater reproductive success.

Food consumption has been quantified in a few species of adult Odonata (e.g.: HIGASHI et al., 1979; SHELLY, 1982; FRIED & MAY, 1983; MICHIELS &

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DHONDT, 1989; ANHOLT, 1992; J.M. Baird, unpubl.). Male size has been shown to affect success at defending territories in some odonates (FINCKE, 1992), but not in others (MARDEN & WAAGE, 1990). The effects of male size on foraging behavior are not known. If large males must maintain higher body weight, they may need to forage more than smaller males. I hypothesized that, because size and weight affect metabolism and energy requirements, they would affect foraging in individual males and females. Large, heavy dragonflies are expected to take in more food than small, light dragonflies, all else being equal.

I observed foraging behavior in marked individual *Pachydiplax longipennis*, a medium-sized (24-35 mm hindwing) libellulid dragonfly common throughout the United States. All individuals were confined to a large enclosure, similar to that used by MICHELS & DHONDT (1989).

METHODS

I carried out this research between 23 April and 6 June 1990 at the Austin Cary Memorial Forest near Gainesville, Florida in Alachua County, and between 27 June and 17 August 1990 at the Jencks' farm in Seekonk, Massachusetts in Bristol County. I collected additional data between 15 May and 31 July 1992 at the University of Florida Research and Education Center (UFREC) in Welaka, Putnam County, Florida. Adult *P. longipennis* were caught, individually marked, and released into a large enclosure (10 x 20 x 3 m) for observation. In Massachusetts in 1990, the enclosure was built along the edge of an existing pond, in which *Typha*, *Salix* and algae grew. In Florida in 1992, the enclosure contained a year-old man-made pond 5 x 10 x 1 m in size. *Typha* had been transplanted along the edge of the pond the year before, and later in the season algae grew as well. In each cage, dowels were placed every 1 m along the edge of the pond. These dowels were often used as perches by the dragonflies.

I weighed individuals to the nearest 0.1 mg and measured hindwing length to the nearest 0.1 mm within 2 h of capture. Hindwing length is correlated with other measures of size in insects (SOUTHWOOD, 1968). Although weight changes from day to day (DUNHAM, 1993), I did not weigh dragonflies daily. Therefore I used weight at initial capture in analyses. Fat (MARDEN & WAAGE, 1990) and flight muscle ratio (MARDEN, 1989) can affect contest outcome or mating success in odonates. In 1992, therefore, males were recaptured and killed after 4 days in the cage. They were held at 0-4°C for up to 3 months, dried at 70°C to a constant weight, and weighed to the nearest 0.1 mg. I extracted fat from the dried head, thorax and abdomen using chloroform in a Soxhlet apparatus (MARDEN, 1989). Flight muscle ratio (FMR) was calculated as $(\text{wet thorax mass} \times 0.95) / \text{total wet body mass}$ (MARDEN, 1989).

Observations were made between 0800 and 1600 EDT. Individual males and females were observed for 20 min focal periods. The following behaviors were recorded: chases (focal individual flew towards another dragonfly), patrol (distinctive slow circling flight close to water), foraging flights (short flight upward at a 45-80° angle), and survey flights (longer flights, takeoff usually horizontal, often ending in a perch change). Focal individuals were considered to be off the pond if they were at least 1 m from the water's edge. Usually dragonflies off the pond were more than 2 m from the water. Successful capture of prey was not noted because of the distance at which observations were made.

I measured temperature every 30 s in 1990, and every 15 min in 1992. I measured light intensity in foot-candles with a General Electric light meter type 214 every 15 min in 1992.

Results are given as mean \pm standard deviation.

RESULTS

Males showed no significant difference in foraging rate between Florida ($\bar{x} = 3.07 \pm 3.68$ foraging flights/20 min, $N = 125$) (in 1992) and Massachusetts ($\bar{x} = 3.13 \pm 4.12$, $N = 45$; $t = 0.093$, $p = 0.93$) (in 1990). Males were significantly more active in Florida in 1990 ($\bar{x} = 1.99 \pm 2.40$ s in flight/20 min, $N = 46$) than Massachusetts ($\bar{x} = 1.10 \pm 1.41$, $N = 52$; Fisher's PLSD = 422, $p < 0.0001$), and males were more active in Massachusetts than in Florida in 1992 ($\bar{x} = 0.23 \pm 0.37$, $N = 257$; Fisher's PLSD = 0.317, $p < 0.0001$).

1990 (Massachusetts) – In a 3-way ANOVA, there were no significant relationships between temperature and foraging rate ($F = 0.337$, $p = 0.88$, $N = 28$), between time of day and foraging rate ($F = 2.131$, $p = 0.16$), or between hindwing length and foraging rate ($F = 2.934$, $p = 0.10$). Similarly, there were no significant relationships between temperature and total activity ($F = 3.532$, $p = 0.065$, $N = 72$), between time of day and total activity ($F = 1.745$, $p = 0.19$), or between hindwing length and total activity ($F = 0.379$, $p = 0.54$). Time of day was correlated with temperature (quadratic $r^2 = 0.35$, $p = 0.0001$, $N = 94$).

1992 (Florida) – Males made 3.64 ± 4.75 foraging flights/20 min ($N = 50$) off the pond; females made 4.0 ± 3.06 foraging flights/20 min ($N = 25$) off the pond. Males made 1.4 ± 1.84 foraging flights/20 min ($N = 270$) on the pond, whereas females made 2.8 ± 1.81 foraging flights/20 min ($N = 14$) on the pond. In a 2-factor ANOVA using sex and location (on or off the pond) as factors, location had the only significant effect on foraging rate, with no significant interaction term. Thus, both males and females foraged less on the pond than they did off the pond.

In an ANCOVA of foraging rate against date, time of day, hindwing length, weight, flight muscle ratio (FMR), fat, location on or off pond, density of dragonflies in cage, temperature, and light intensity, foraging rate was significantly negatively related to fat content, and significantly positively related to time of day. Individuals away from the pond foraged significantly more often than those on the pond (Tab. I). Nearly significant relationships existed between hindwing length and foraging rate and between weight and foraging rate. The model explained 31.6% of the variance in foraging rate. Removing non-significant factors from the ana-

Table I
Results of stepwise multiple regression against the number of foraging flights/20 min focal period

Source	df	Mean square	P-value
Date	1	0.758	0.7846
Time of day	1	69.113	0.0103
Hindwing length	1	39.321	0.0512
Body mass	1	39.188	0.0516
FMR	1	4.128	0.5240
Fat content	1	50.760	0.0271
Male density	1	2.262	0.6370
Temperature	1	9.281	0.3399
Light intensity	1	2.104	0.6490
Location	1	1053402	0.0017
Residual	100	10.094	

lysis increased the power enough to show a significant negative relationship between hindwing length and foraging rate, and a significant positive relationship between weight and foraging rate, without otherwise changing the results.

In an ANCOVA of total activity against date, time of day, hindwing length, weight, FMR, fat, location on or off pond, density of dragonflies in cage, temperature and light intensity, activity was nearly significantly positively related to temperature ($F = 3.71$, $p = 0.059$). When location on or off the pond ($F = 0.001$, $p = 0.977$) was removed from the model, the relationship between temperature and activity became significant (Tab. II). This model explained 30.0% of the variance in total activity.

DISCUSSION

In this study, *P. longipennis* foraged at a low rate in the enclosure (0.15 flights/min). In contrast, MAY (1984) observed that male *P. longipennis* make 1.04 ± 0.4 flights/min, during which they catch as much food as FRIED & MAY (1983) estimated they eat in a day. J.M. Baird (pers. comm.) found an average foraging rate of 0.67/min for unmarked individuals in the wild in Florida, observed using similar methods to mine. In Baird's study, *P. longipennis* were observed away from the pond, where their behavior may have differed from behavior near the pond, or prey density may have been higher. However, dragonflies were able to maintain body weight in the cage (DUNHAM, 1993) and survived longer than in the wild, despite their low foraging rate. Caged individuals rarely made long flights, did not often need to evade predators, and experienced lower intrusion on territories in the cage. Therefore, they may not have expended as much energy each day as wild individuals. Caged individuals may also be less time constrained than in the wild, because they spend little time hiding from predators.

Foraging rate was also low in another study done in a large enclosure (MICHIELS & DHONDT, 1989). The *Sympetrum danae* they studied made 0.038 flights/min (males) or 0.073 flights/min (females). Both males and females survived significantly longer in the enclosure than in the wild in their study (MICHIELS & DHONDT, 1988), so they were apparently able to maintain body weight despite their low foraging rate. In comparison, *Sympetrum frequens* in Japan made 0.53-1.00 flights/min, depending on time of day (HIGASHI, 1978).

Table II

Results of stepwise multiple regression against seconds active during 20 min focal period

Source	df	Mean square	P-value
Date	1	0.262	0.1883
Time of day	1	0.245	0.2027
Hindwing length	1	0.010	0.7958
Body mass	1	0.042	0.5951
FMR	1	0.195	0.2559
Fat content	1	0.268	0.1831
Male density	1	0.144	0.3276
Temperature	1	0.617	0.0457
Light intensity	1	0.362	0.1232
Residual	57	0.148	

Heteragrion erythrogastrum, which forage in the shade in lowland neotropical forests, make only 0.36 flights/min (range 0-1) in the wild, also a low rate (SHELLY, 1982). Shelly contrasted this damselfly to another species of the same size, *Argia difficilis*, which makes 1.77 flights/min (range 1.07-2.47) in the sun in the same forest. He does not indicate the mating system of the two species, nor how they budget time when not foraging.

The damselfly *Mnais pruinosa* made 0.02-0.5 foraging flights/min, depending on the time of day (HIGASHI et al., 1979). *Calopteryx cornelia* made 0.02-0.82 foraging flights/min, again depending on the time of day (HIGASHI, 1973). In both cases low foraging rates were recorded in territorial individuals.

Although dragonflies can be maintained and manipulated in large enclosures, they do not forage as often as in the wild. Although they are still able to survive, and indeed survive longer in the enclosure than in the wild, their energy balance is likely to be different in the enclosure.

PHENOTYPIC EFFECTS ON FORAGING RATE

Three of the four phenotypic characters I measured were related to foraging rate. Large (i.e. long-winged) males forage less often than small males. They also lived longer in the wild than did small males, suggesting that active foraging may be dangerous (see also ANHOLT, 1992), or that large size protects against predation.

The weak relationship between foraging rate and weight was positive in sign. Weight was measured on capture, and would have changed daily thereafter (DUNHAM, 1993). Possibly heavier males foraged more often in order to maintain high body weight, but it is also possible that heavier males were heavy because they foraged more often. Heavy males suffer higher mortality rates, at least under some conditions, again suggesting that high rates of foraging may be risky.

Fatter males foraged less often. Fat was measured at the end of the study, so this relationship may be causal. That is, fatter males forage less often than leaner males and still have greater fat reserves after 4 days of observation. It is unlikely that males foraging at a high rate would therefore use up fat reserves. Alternatively, males may have started with the same amount of energy, but some were less active than others, both in foraging and in territorial defense. These less active males could have maintained or even increased fat reserves, while more active males suffered negative energy budgets. However, activity was not correlated with mass change from day to day.

J.M. Baird (pers. comm.) found that when prey availability was high, female *P. longipennis* foraged less often than males, whereas when prey availability was low, there was no difference between male and female foraging rates. In the cage in my study there was no difference between male and female foraging rates,

although both males and females foraged at an overall much lower rate than the *P. longipennis* Baird studied. Because prey availability had the strongest effect on foraging rate in Baird's study, it seems reasonable to conclude that the availability of prey was low in the cage, although I did not measure prey availability.

ENVIRONMENTAL EFFECTS ON FORAGING RATE

J.M. Baird (pers. comm.) found foraging rate correlated with hour of day, date (biweekly interval), site, prey availability, dragonfly density, and sex (multiple ANCOVA). In my study of caged dragonflies, time of day was correlated with foraging rate, but neither density nor date had an effect on foraging rate. Males foraged at different rates in different places and in different years.

MICHIELS & DHONDT (1989) and HIGASHI et al. (1979) found a peak in foraging rate at the end of the day (*Sympetrum danae* and *Mnais pruinosa*). In my study, foraging rate also peaked in the evening. However, foraging rate peaked at solar noon in J.M. Baird's unpublished study and in *Sympetrum frequens* (HIGASHI, 1978). HIGASHI et al. (1979), MICHIELS & DHONDT (1989), and I observed individuals at or near water, whereas Baird and HIGASHI (1978) observed dragonflies away from water, only foraging. Reproductively active dragonflies may budget their time differently, placing more emphasis on reproductive activity at midday, and only foraging after reproductive activity has ceased. Alternatively, prey density may peak at different times in different places. Indeed, J.M. Baird (pers. comm.) found that prey density peaked at noon.

SHELLY (1982) found a positive correlation between light intensity and foraging rate in damselflies foraging in a forest, and a stronger correlation between thoracic temperature and foraging rate. He believed that the thoracic temperature was determined by light intensity and in turn determined foraging rate. Baird found a correlation between foraging rate and time of day, and showed that the correlation between time of day and light intensity caused the correlation between light intensity and foraging rate.

ANHOLT (1992) found that adult male *Enallagma boreale* away from the pond had fuller guts than males at the pond. Assuming that foraging results in a fuller gut, my finding is consistent with his — males and females away from the pond foraged more often than individuals at the pond. However, *P. longipennis* males caught in the wild away from the pond weighed less than males at the pond at the same time of day (DUNHAM, 1993), in contrast to his study. I also found no difference between males and females in foraging rate, whereas ANHOLT (1992) found that females had fuller guts than males. Anholt suggested that foraging effort should be more similar between the sexes in territorial odonates than in non-territorial odonates. *Enallagma boreale* are non-territorial, whereas *P. longipennis* are territorial. My results therefore are consistent with this hypothesis. However, Anholt's study was carried out in the wild, where prey was probably

more abundant than in the enclosure I used, so I am not able to reject the alternative hypothesis that caged dragonflies are not able to forage at their preferred rate.

In conclusion, both phenotypic and environmental characteristics can affect foraging in *Pachydiplax longipennis*. Short-winged, heavy males foraged most frequently. Because this was a correlative study, it is not possible to determine whether males that were heavy therefore foraged more often, or were heavy because they had foraged more often before capture. However, size is fixed at emergence, so it seems plausible that small males forage more often because they are small. As expected for these ectotherms, activity increased with temperature. Activity also increased with time of day, which was correlated with temperature. The correlation between time of day and activity was stronger than the correlation between temperature and activity. Therefore it seems likely that other factors that also vary with time of day, such as wind speed, light intensity, or prey activity, also affect odonate activity patterns.

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