

Fights at the Dinner Table: Agonistic Behavior in *Pachydiplax longipennis* (Odonata: Libellulidae) at Feeding Sites

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Aggressive behavior of Pachydiplax longipennis during foraging was quantified by observing focal individuals on arrays of artificial perches. Pachydiplax apparently aggressively defend, for up to several hours at a time, one or a few feeding perches. Seventeen percent of all behaviors included agonistic actions, e.g., chasing or physical contact. The frequency of interactions was correlated positively with ambient temperature, solar radiation, prey density and density of other dragonflies. Both sexes initiated and responded to intra- and interspecific aggression; intraspecific interactions were more intense, however. Males had significantly higher interaction rates and fighting success than females, and intraspecific male–male contests were particularly intense. When prey were visibly localized, contest winners commonly gained perches closer to the prey swarm, and aggressive behavior was apparently correlated with feeding opportunity. Despite the frequency of aggression, these dragonflies allocated only about 19 s, on average, to agonistic behavior during 30-min observation periods. This and other costs appear small compared to foraging benefits of occupying a favorable perch, although at a very high interaction intensity high energy costs and lower intake reduce the net energy gain.

KEY WORDS: aggressive behavior; dragonfly; feeding territory; foraging; Odonata.

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INTRODUCTION

Faced with limited resources or limited time to acquire them, animals compete by diverting resources from others to themselves for their own reproductive advantage, often by interfering directly with competitors (Wolf, 1978). Interference competition may range from peaceful display to severe fights depending on the value of the resource, the disparity in fighting ability between opponents, and the energy and damage costs associated with alternative tactics (Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981). When resources are economically defendable and localized, interference may take the form of territoriality (e.g., Brown, 1964). Territories frequently secure more than one important resource, but few animals defend, over short time periods, separate territories associated with different resources. Some dragonflies may do so, however.

Adult male Odonata often are territorial at breeding sites (Corbet, 1999). As in other animals (e.g., Gill and Wolf, 1975), territoriality can entail high energetic costs. In at least one damselfly, *Calopteryx maculata*, contests usually are won by the male with higher fat reserves (Marden and Waage, 1991). *Plathemis lydia* males rapidly shunt energy accumulated during feeding to flight muscle during maturation, improving aerial performance and short-term mating success but possibly risking reduced survival due to low energy reserves (Marden, 1989) or limitation of time devoted to mating (Koenig, 1990). Fried and May (1983) inferred that for male *Pachydiplax* the energy cost of flight and the increased agonistic contest frequency associated with increased dragonfly density may limit individuals' territorial defense and dictate alternative mating strategies or curtailment of mating in favor of feeding. Sherman (1983) noted shortened territorial tenure as a correlate of increased male density.

Despite the importance of energy in reproductive activity and the large proportion of time spent feeding, foraging behavior in adult Odonata has received scant attention (reviewed by Corbet, 1999). Individual behavior at feeding sites has only recently been studied closely (e.g., Gorb, 1994; Baird and May, 1997). Gorb (1994) described agonistic behavior in female *Sympetrum sanguineum* at feeding sites but did not measure its impact on feeding rate or efficiency. The high energy cost of reproduction suggests that the foraging behavior of individual *Pachydiplax* might be important in reproductive success and that interruptions may be costly (Fried and May, 1983; Baird and May, 1997).

The abundance, size, and perch-based foraging mode of *Pachydiplax longipennis* facilitate observation and quantification of behavior, and its reproductive behavior has been studied extensively (Johnson, 1962; Robey, 1975; Sherman, 1983; Fried and May, 1983; MacKinnon and May, 1994). It

is a common, medium-sized (0.1- to 0.25-g) libellulid and, like other adult dragonflies, is an obligate, generalist carnivore (Corbet, 1999), usually feeding on small flying insects. Foraging flights typically originate and terminate at a perch and are short and oriented directly toward individual prey. Males are highly territorial at reproductive rendezvous sites, which are located on the margins of lakes or ponds where females oviposit, but they feed very little there (Fried and May, 1983). Males and females feed together at woods edges or in fields with vegetation that provides suitable perches.

Individual *Pachydiplax* at feeding sites frequently behave agonistically toward nearby conspecific and heterospecific dragonflies. Contests range from brief displays to extended chases to physical clashes. Since prey are small and apparently widely dispersed most of the time, the function of this aggression is not immediately obvious. It might, however, represent defense of perches near which the average prey abundance is high and/or prey "bonanzas" (swarms) are likely to occur. Perch occupation, as in some larval Odonata (Convey, 1988), might thereby increase prey intake.

Our specific objectives here are (1) to describe the nature and outcomes of aggressive encounters at the feeding site; (2) to assess how aggressive interactions vary with extrinsic variables such as physical environmental factors, sex, prey availability, and dragonfly density; and (3) to discuss possible benefits and costs of this behavior. More broadly, we address the questions of whether aggressive behavior is consistent with our hypothesis that *P. longipennis* is under strong selection to maximize energy intake, whether density and behavior of competitors restrict food intake, and whether aggression at feeding sites is likely to enhance energy intake and, ultimately, reproductive success.

MATERIALS AND METHODS

Study sites and methods were described by Baird and May (1997). In brief, adult *P. longipennis* were observed from 20 April to 31 July 1987 in Gainesville, Florida (FL; 29°38'N, 82°21'W), and from 5 August to 8 September 1987 in Plainsboro, New Jersey (NJ; 40°21'N, 74°36'W). Three hundred twenty-seven focal observations (Altmann, 1984) were conducted at arrays (two at FL, designated FE and FN) of nine uniform, artificial perches, usually for 30-min intervals (never <5 min). Of these, unless otherwise stated, observations at FE when rainwater had accumulated next to the array are excluded ($N = 58$) because standing water apparently caused some males to intensify aggression (Baird, unpublished data). Arrays were about 75 m (NJ) to 250 m (FL) from breeding sites.

Perches in arrays were similar in configuration and volume density to natural perches in the area but differed in their uniform spacing, two-dimensional character (i.e., the tips were nearly in one plane), lack of interspersed vegetation, and relative isolation, by 10–20 m, from other perches. Perch arrays were placed far enough from one another and from natural clusters of perches to avoid frequent interactions of focal individuals with dragonflies from outside the arrays. Perch density was manipulated ($1\text{--}5\text{ m}^{-2}$) by altering the dimensions of the array. We define dragonfly density as the total number of Anisoptera m^{-2} at the array, so it is a function of both the perch density and the number of occupied perches.

Focal individuals were selected as much as possible from those at an array at a given time to balance samples by sex and position. For each we recorded the date, observation start time, perch array, perch density, position within the array, sex, air temperature (T_a), operative environmental temperature (T_e ; temperature of a dried specimen of *P. longipennis* with an implanted Cu–Cn thermocouple, placed at the top of a perch in the sun), solar radiation intensity, wind speed, and relative humidity. For each behavioral event we recorded the initiation time, the duration, the flight type (see Results), whether prey were captured (as indicated by rhythmic movements of the mandibles after return to the perch), the estimated flight distance from the perch to the most distant point, and whether the individual changed perches.

During agonistic behavior, the species, sex, and perch position of the nonfocal contestant(s) were noted, as were the number of discrete encounters, whether the focal or a nonfocal individual initiated the contest, and the contest outcome. A “contest” was one or a continuous sequence of agonistic actions (“encounters”), initiated at the perch or in flight and terminating in a return to a perch for at least 1 s or in departure from the perch array. The term “interaction” refers to aggressive behaviors more generally or indicates durations and rates of contests summed or averaged over entire observation periods. We assessed the intensity of individual contests using three criteria: duration, distance flown, and number of separate encounters per contest.

At the beginning of each observation, prey availability at the perch array was assessed visually and assigned to one of three distinct qualitative levels (Baird and May, 1997): normal (dispersed prey, low prey density), intermediate (dispersed, moderate density), and swarm (concentrated, high density; mostly chironomid swarms). In the last case, the position of the focal individual relative to the swarm was recorded as near (on the same side of the array as the swarm), far (far side of the array), or middle (middle row of the array); swarms almost invariably formed 1–2 m outside the array along its south side and, when present, normally persisted at approximately the same location throughout a focal observation period.

Energy costs of flight were calculated from time budgets assuming a rate of 330 J h^{-1} of flight from Polcyn's (1988) regression describing the relationship between body mass and flight metabolism for dragonflies. Metabolism during perching (3.9 J h^{-1}) was based on average resting metabolism (May, 1979) corrected for variation in body temperature. Energy balance was calculated by assuming an energy content of insect prey of $24,500 \text{ J (g dry mass)}^{-1}$ (Slobodkin, 1962) and an apparent digestibility of 0.76 (Fried and May, 1983; May and Persky, unpublished data). Net energy for a successful flight then is effective intake (=prey energy content \times apparent digestibility) minus expenditure (=flight metabolism \times duration). For unsuccessful or nonforaging flights, intake = 0.

Data were analyzed using SAS (SAS Institute, 1990). Differences among statistics were considered significant at $\alpha = 0.05$. Multiple means were compared using Scheffe's test. All proportions were analyzed after arcsine-square root transformation.

We analyzed behavioral variables, such as interaction rate and duration, in relation to characteristics of the physical (e.g., T_a) and biotic (prey availability, dragonfly density) environments, time (hour, date), and sex of the focal individual. Analyses were complicated by multicollinearity among predictor variables. To reduce or eliminate mutually correlated variables we performed a stepwise series of multiple ANCOVAs or ANOVAs, using the SAS GLM procedure, with successively more restricted models, as described by Baird and May (1997). This procedure removed most colinearity but may have masked significant effects of some variables. In practice, however, important predictors were usually easy to distinguish. Because of the very large number of possible interaction terms, only main effects were tested unless we had reason to suspect, after inspection of the data, that statistical interactions might be important. Frequencies of behavioral alternatives were analyzed using the FREQ procedure and significance assessed with log-likelihood ratio chi-square tests. We know from observation of marked or physically distinctive individuals that we included multiple observations of some individuals, but we previously (Baird and May, 1997) showed that repeated observations, from the same data set analyzed here, of foraging *P. longipennis* were statistically independent (i.e., individual identity had no significant effects) and therefore have treated all observations as independent here.

RESULTS

Behavior at the Feeding Site

Flight behaviors were classified as foraging, survey, and interaction flights (Table I) according to criteria described by Baird and May (1997).

Table I. Frequency, Duration, and Distance of Various Flight Types During Foraging by *P. longipennis*^a

| Flight type | N | Proportion | Flight duration (s) | Flight distance (m) |
|------------------------------|------|------------|---------------------------|---------------------------|
| Interactions | | | | |
| All | 1007 | 0.168 | 3.67 ± 0.25 ^{CD} | 2.46 ± 0.14 ^C |
| With conspecific opponent | 333 | 0.056 | 4.75 ± 0.29 ^D | 3.59 ± 0.25 ^D |
| With heterospecific opponent | 665 | 0.112 | 3.10 ± 0.35 ^{BC} | 1.88 ± 0.17 ^{BC} |
| Foraging | 4404 | 0.732 | 1.05 ± 0.007 ^A | 0.76 ± 0.006 ^A |
| Multiple foraging | 288 | 0.048 | 2.64 ± 0.15 ^B | 1.79 ± 0.10 ^B |
| Survey | 315 | 0.052 | 1.30 ± 0.17 ^A | 0.74 ± 0.13 ^A |
| All flights | 5948 | 1.000 | 1.55 ± 0.043 ^A | 1.07 ± 0.025 ^A |

^aDurations and distances are given as mean ± SE; means within a column that share a superscript are not significantly different.

More than 82% of the 327 focal observations included at least one contest, accounting for about 17% of all recorded behaviors. For convenience, we use the term “flights” for all contests even though 7.5% ($N = 75$) involved only a postural change or wing flutter by the focal individual. Contests involved significantly longer mean durations ($F = 186.0$, $P < 0.0001$) and flight distances ($F = 241.1$, $P < 0.0001$) than any other flight type and therefore were relatively energetically costly. Most contests (88.0%, $N = 883$) comprised a single encounter, with 7.9% ($N = 79$) including two and 4.3% ($N = 43$) three or more encounters.

Contests ranged from flights toward other individuals, to chases usually lasting 1–10 s but sometimes a minute or more, to contact in the air or even physical removal of individuals from perches by bumping or grasping. Most agonistic behavior of *Pachydiplax* at feeding sites was like that already described for males at breeding sites (Johnson, 1962; Robey, 1975; Sherman, 1983), including displays and mutual hovering with individuals in close proximity, chases, “sky dances” (a combination of hovering and display [Sherman, 1983]), and physical clashes. Others have not, however, recorded actual removal of individuals from perches. Contests usually were resolved quickly, but one remarkable instance involved 15 separate encounters. Thus, aggression, when it occurred, could be as intense as that seen at waterside breeding territories, although generally it occupied a much smaller proportion of time (cf. Fried and May, 1983).

Contests were categorized by outcome in five groups (Table II). The first two resulted in perch retention: (1) retain—focal individual not displaced from its perch; and (2) regain—focal initially displaced but regained the

Table II. Frequency Distributions of Outcomes of Agonistic Contests, Separated by Various Categories of Intrinsic and Environmental Characteristics

| Category | Outcome | | | | | Total |
|--|----------------------|----------------------|----------------------|----------------------|----------------------|---------------|
| | Usurp | Retain | Regain | Displace | Retreat | |
| All contests | 51 (0.051) | 423 (0.42) | 365 (0.37) | 140 (0.14) | 19 (0.019) | 998 |
| Sex of focal ^a | | | | | | |
| Male | 41 (0.061) (0.80) | 300 (0.44) (0.71) | 246 (0.36) (0.67) | 89 (0.13) (0.64) | 6 (0.009) (0.31) | 682 (0.68) |
| Female | 10 (0.032) (0.20) | 123 (0.39) (0.29) | 119 (0.38) (0.33) | 51 (0.16) (0.36) | 13 (0.041) (0.69) | 316 (0.32) |
| Prey availability ^b | | | | | | |
| Low | 18 (0.054) (0.35) | 167 (0.48) (0.39) | 101 (0.30) (0.27) | 46 (0.14) (0.33) | 8 (0.024) (0.42) | 336 (0.34) |
| Intermed. | 13 (0.042) (0.25) | 132 (0.43) (0.31) | 118 (0.38) (0.32) | 45 (0.14) (0.32) | 2 (0.006) (0.10) | 310 (0.31) |
| Swarm | 20 (0.057) (0.39) | 128 (0.36) (0.30) | 146 (0.42) (0.40) | 49 (0.14) (0.35) | 9 (0.025) (0.47) | 352 (0.35) |
| Dragonfly density (m ⁻²) ^c | | | | | | |
| 0–0.99 | 0 (0.0) (0.0) | 33 (0.45) (.076) | 23 (0.32) (0.063) | 8 (0.11) (0.057) | 4 (0.055) (0.21) | 73 (0.072) |
| 1–1.99 | 13 (0.051) (0.25) | 113 (0.45) (0.27) | 96 (0.38) (0.26) | 22 (0.087) (0.16) | 7 (0.028) (0.37) | 253 (0.25) |
| 2–2.99 | 18 (0.048) (0.35) | 165 (0.44) (0.39) | 131 (0.35) (0.36) | 60 (0.16) (0.43) | 2 (0.005) (0.11) | 378 (0.37) |
| 3–3.99 | 15 (0.069) (0.29) | 82 (0.38) (0.19) | 74 (0.34) (0.20) | 40 (0.18) (0.28) | 5 (0.023) (0.26) | 217 (0.21) |
| ≥4 | 5 (0.056) (0.098) | 33 (0.37) (0.078) | 41 (0.46) (0.11) | 10 (0.11) (0.071) | 1 (0.011) (0.053) | 90 (0.089) |
| Opponent ^d | | | | | | |
| <i>Pachydiplax</i> | 17 (0.051) (0.33) | 165 (0.50) (0.39) | 104 (0.31) (0.28) | 38 (0.11) (0.27) | 9 (0.027) (0.47) | 333 (0.33) |
| Males ^e | 9 (0.041) (0.53) | 85 (0.043) (0.52) | 70 (0.036) (0.67) | 26 (0.13) (0.68) | 7 (0.036) (0.78) | 196 (0.59) |
| Females ^e | 8 (0.066) (0.47) | 80 (0.058) (0.48) | 34 (0.025) (0.33) | 12 (0.088) (0.32) | 2 (0.015) (0.22) | 137 (0.41) |
| Heterospecific | 34 (0.051) (0.67) | 258 (0.39) (0.61) | 261 (0.39) (0.72) | 102 (0.15) (0.73) | 10 (0.015) (0.53) | 665 (0.67) |
| Encounters per contest ^f | | | | | | |
| 1 | 36 (0.041) (0.71) | 411 (0.47) (0.96) | 310 (0.35) (0.85) | 111 (0.13) (0.79) | 12 (0.014) (0.63) | 880 (0.88) |
| 2 or more | 15 (0.12) (0.29) | 15 (0.12) (0.035) | 55 (0.45) (0.15) | 30 (0.25) (0.21) | 7 (0.057) (0.37) | 122 (0.12) |

Note. Proportions in rows are given in parentheses after the frequency; proportions in columns are given in parentheses below the frequency.

^aDistribution of outcomes differs by sex ($G = 17.4$, $P = 0.002$, $df = 5$).

^bDistribution of outcomes differs by prey availability level ($G = 18.0$, $P = 0.021$, $df = 10$).

^cDistribution of outcomes differs by density ($G = 35.6$, $P < 0.003$, $df = 16$).

^dDistribution of outcomes differs by identity of opponent (conspecific vs. heterospecific; $G = 17.4$, $P = 0.002$, $df = 4$).

^eDistribution of outcomes differs by sex of conspecific opponent ($G = 12.2$, $P = 0.016$, $df = 4$).

^fDistribution of outcomes differs by number of encounters per contest ($G = 88.2$, $P < 0.001$, $df = 4$).

perch. The other three categories involved focal movement to a new perch: (3) displace—focal removed or chased from its perch and settled on another perch within the array; (4) usurp—focal individual displaced a nonfocal interactor and took over its perch; and (5) retreat—focal left the perch array entirely, apparently in response to aggression by another individual (this category excludes spontaneous departures without interactions; $N = 13$). For outcomes 2–5, series of 10 or more displacement and recovery encounters might occur before the contest ended. Retreats followed contests that were significantly more intense (Fig. 1) than those preceding other outcomes. Contests involving two or more encounters were significantly more frequent, compared to single encounters, for displacements

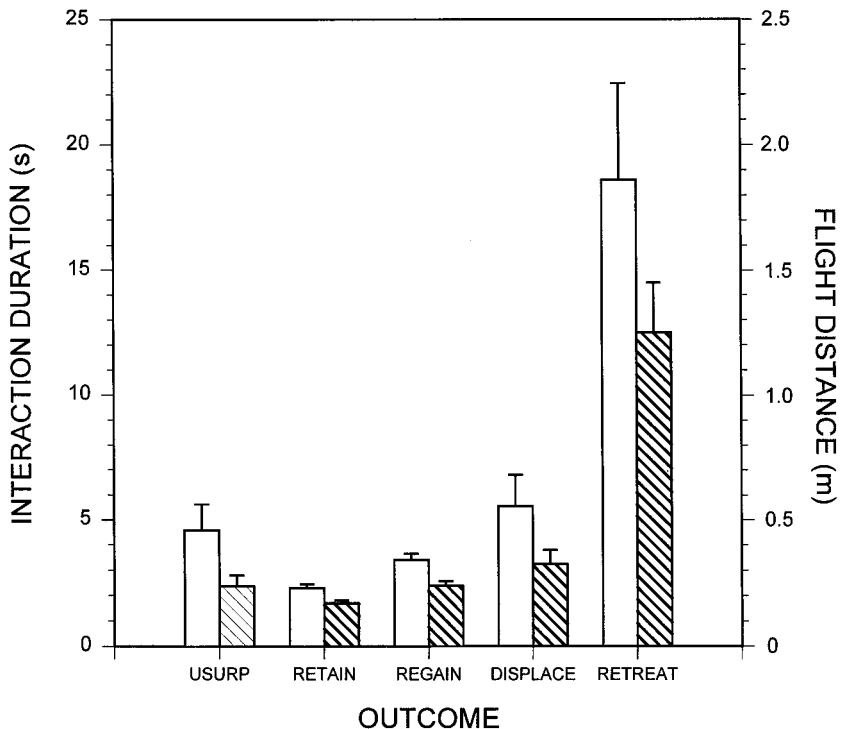


Fig. 1. The relation of contest outcome to intensity, measured as flight duration (open bars) or distance (hatched bars). Intensity differed among outcomes by both measures (duration, $F = 26.1$, $P < 0.0001$, $df = 4$; distance, $F = 34.7$, $P < 0.001$, $df = 4$) as well as for number of encounters per contest (data not shown; $F = 18.3$, $P < 0.0001$, $df = 4$). Interaction intensity during Retreat was significantly higher than during any other outcome by all criteria (Scheffe's test, $P < 0.05$), while the Retain outcome was lower in duration and number of interactions than all others and involved shorter distances than Displace.

(21.3%; log-likelihood ratio, $G = 9.15$, $P < 0.01$), usurpations (29.4%; $G = 10.7$, $P < 0.01$), and retreats (36.8%; $G = 7.65$, $P < 0.01$) than for all interactions (12.2%). Contests ending in usurpations or retreats were much more likely to be instigated by their eventual winners, i.e., the focal or the nonfocal interactor, respectively, than by the loser ($G = 27.9$, $P < 0.001$, $df = 1$, for usurpations; $G = 12.5$, $P < 0.01$, $df = 1$, for retreats).

Aggression and the Physical Environment

Like other behaviors in ectotherms, agonistic encounters in *Pachydiplax* are affected by thermal conditions, but in multiway ANOVAs only T_e had significant independent effects using our stepwise procedure (Table III). To a considerable extent the lack of other effects may be due to the intercorrelation among environmental parameters; solar radiation and T_e ,

Table III. Variables Affecting Agonistic Behaviors in *Pachydiplax longipennis*

| Behavior | Model r^2 ^a | Predictor variable ^b | F^c | P^c | df of predictor variable |
|---|--------------------------|---------------------------------|-------|---------|--------------------------|
| Rate of interaction (agonistic flts.) per min | 0.491 | Operative temperature (+) | 7.72 | 0.006 | 1 |
| | | Prey availability (+) | 13.07 | <0.0001 | 2 |
| | | Dragonfly density (+) | 7.05 | <0.0001 | 4 |
| | | Sex of focal | 3.17 | 0.053 | 1 |
| Cumulative duration of interactions ^d (s per focal observation period) | 0.227 | Prey availability (+) | 5.94 | 0.0031 | 2 |
| | | Dragonfly density (+) | 5.39 | 0.0004 | 4 |
| | | Biweekly interval | 2.02 | 0.045 | 8 |
| Total flight duration ^d (s per focal observation period) | 0.517 | Prey availability (+) | 38.32 | <0.0001 | 2 |
| | | Dragonfly density (+) | 8.02 | <0.0001 | 4 |
| | | Biweekly interval | 5.76 | <0.0001 | 8 |
| Proportion of flight time devoted to aggression | 0.203 | Operative temperature (+) | 11.12 | 0.001 | 1 |
| | | Dragonfly density (+) | 6.20 | 0.001 | 4 |
| | | Sex of focal | 4.97 | 0.027 | 1 |

^aFraction of total variation explained by predictor variables.

^bSee text for explanation; only variables with significant effects are included. Symbols in parentheses indicate direction of effect of predictor variable.

^cType III regression (SAS Institute, 1989); effect of each independent variable is independent of order of entry.

^dCumulative durations normalized to 30-min interval in cases in which actual observation period was <30 min.

and in some cases T_a or hour of the day, could be interchanged with little change in overall r^2 . Interaction rate and duration, like other behaviors, were sensitive (two-way ANOVAs) to both T_a and solar radiation (Fig. 2). Both also had distinct midday peaks (Fig. 3), although the peak for interaction duration occurred several hours later than that for total time in flight, owing to an earlier peak of foraging flight duration (Baird and May, 1997).

Effects of Prey Density and Localization

Increased prey availability enhanced most measures of agonistic behavior (Table III). Rates and durations of interactions did not differ significantly during swarm and intermediate prey conditions but in both circumstances differed from the means for normal prey (Fig. 4); all three levels differed for total flight time. The proportion of flight time spent interacting did not vary in response to prey (Table III). As a result of the more frequent and intense agonistic behaviors, the frequency of displacement from a perch during any given focal observation period was greater during intermediate and swarm conditions than when prey availability was low ($G = 44.9$, $P < 0.001$, $df = 2$) and the relative frequency of retreats from the array was higher during swarms than at other times ($G = 6.77$, $P < 0.02$, $df = 2$).

Feeding rate ($t = 4.75$, $P < 0.01$; $N = 73$ at arrays, 53 on natural perches), prey capture rate ($t = 3.76$, $P < 0.01$), and rate of interactions ($t = 2.57$, $P < 0.02$) were all higher at the pole arrays during April and May 1987 than at natural perches in 1986, even if data when swarms were present at arrays are excluded (May and Baird, 2002); these differences correspond to substantially higher prey availability near the arrays (Baird and May, 1997).

When prey were localized in swarms, a focal's position relative to, but not its absolute distance from, a swarm was monitored. After contests, focals were more likely to perch either nearer to (5.1% of flights) or farther from (17.0% of flights) the swarm than after other flights (<1.5% of flights in either case; $G = 192.1$, $P < 0.001$, $df = 4$). After displacement, individuals were most likely to end up farther away from the swarm ($G = 22.5$, $P < 0.001$, $df = 1$) than after all interactions. Conversely, usurpations resulted in movement nearer to a swarm more often than expected for interactions in general ($G = 9.42$, $P < 0.01$, $df = 1$). The net effect was that usurpers usually gained more profitable perches, while displacement generally resulted in a less favorable perch (Table IV).

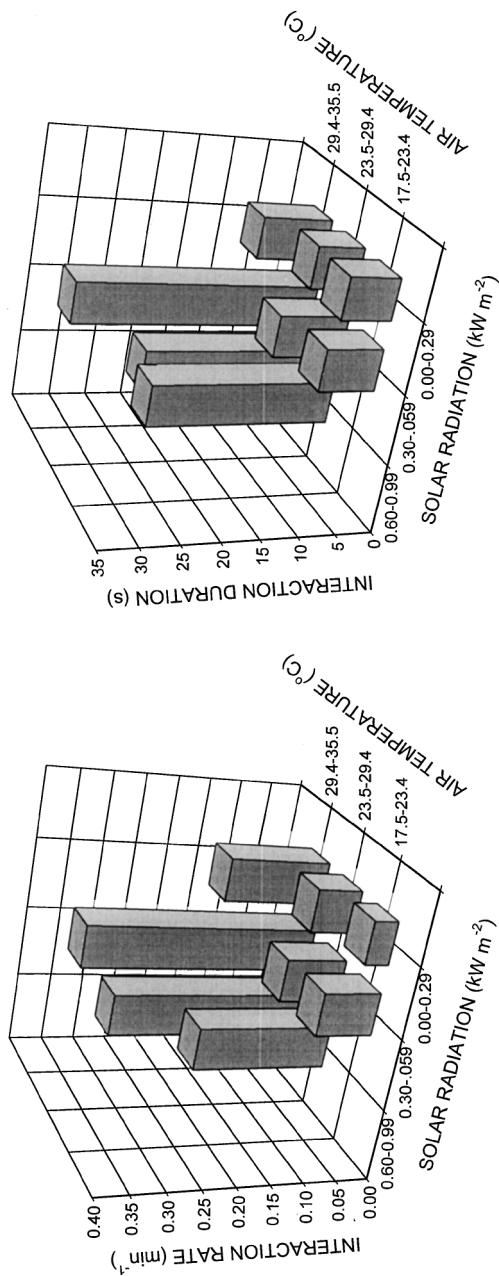


Fig. 2. Effects of solar radiation intensity and air temperature on interaction rate (solar radiation, $F = 35.4$, $P < 0.0001$, $df = 1$; temperature, $F = 49.0$, $P < 0.0001$, $df = 1$) and cumulative duration of interactions (solar radiation, $F = 19.0$, $P < 0.0001$, $df = 1$; temperature, $F = 13.2$, $P = 0.0003$, $df = 1$).

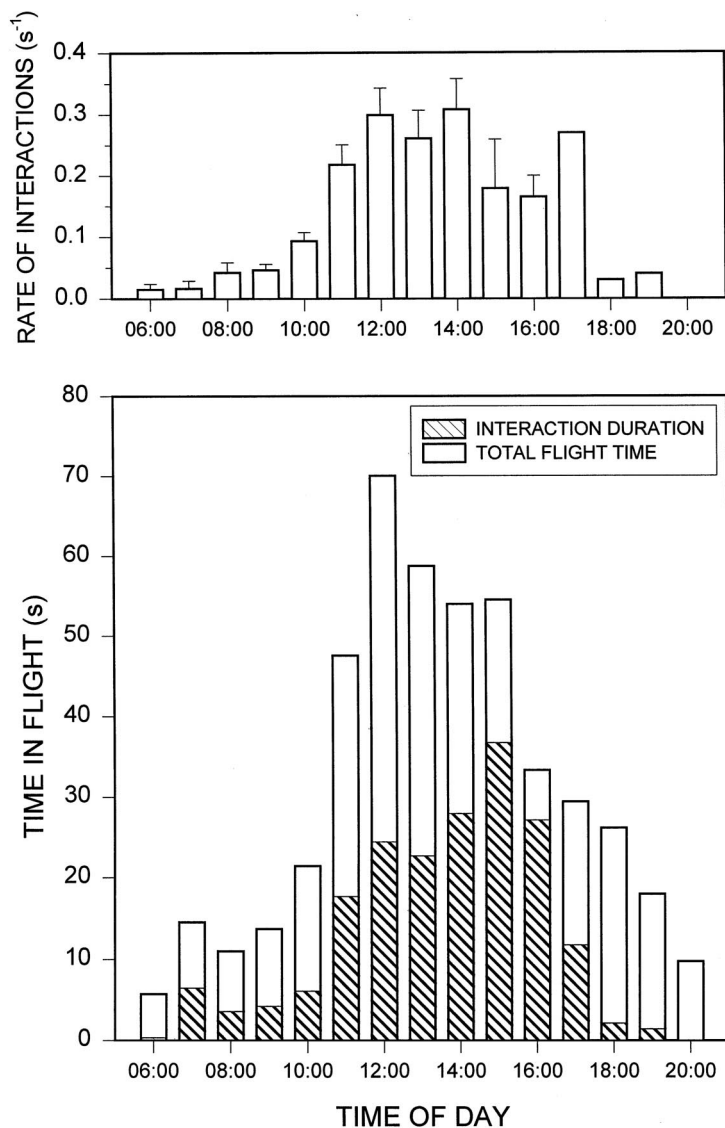


Fig. 3. Effects of time of day, considered alone, on interaction rate ($F = 4.65$, $P < 0.0001$, $df = 14$), cumulative duration of interaction ($F = 3.23$, $P < 0.0001$, $df = 14$), and total flight time ($F = 8.69$, $P < 0.0001$, $df = 14$); note that total flight time is indicated by the total height of the bar. Error bars for interaction rates indicate \pm SE.

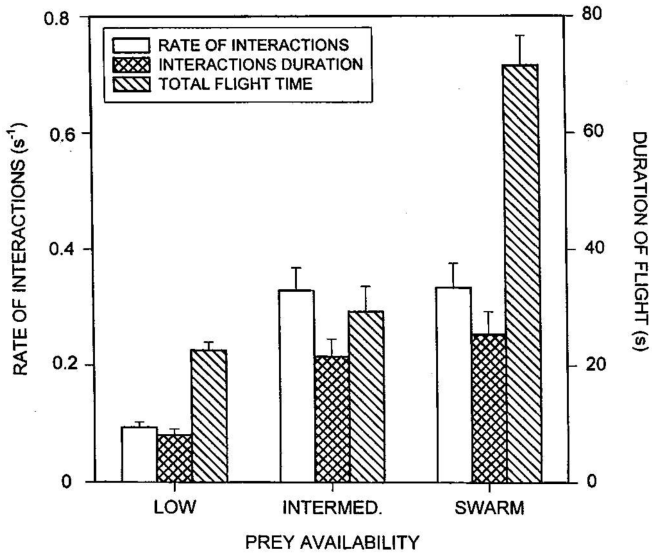


Fig. 4. Effects of level of prey availability on interaction rate, cumulative duration of interaction, and total flight time. All effects are highly significant ($P \leq 0.001$; cf. Table III); error bars indicate \pm SE. All three responses were lower during periods of low (normal) prey availability than at other times, but only total flight time differed between intermediate and swarm levels of availability.

Position within the array did not significantly affect any measured behavioral rate or duration, either within or among individuals, because all were extremely variable. Nevertheless, almost all were substantially higher for the positions closest to the swarm than for middle or far positions; e.g., mean feeding rate was 1.77 min^{-1} when close vs. 1.25 and 1.39 min^{-1} for middle and far positions, respectively; prey capture, 1.81 min^{-1} vs. 1.19 and 1.27 min^{-1} ; and cumulative duration of interactions, 25.6 vs. 12.2 and 16.6 s per standard 30-min observation. Furthermore, the mean intensity of interactions was much higher at the closer positions, although, again, the differences are not significant owing to the high variance; mean contest duration was 17.7 vs. 4.1 and 3.4 s and mean number of interactions per contest was 2.17 vs. 1.26 and 1.13 . Among 24 individuals that were observed in two or three different relative positions, aggressive interactions were likely to continue longest from the closest position (10 of 16 observations) and least likely from the farthest (4 of 17; 10 of 22 from middle positions); the difference again

Table IV. Distribution of Movements Relative to Prey Swarms That Resulted from Aggressive Interactions, According to Interaction Outcome and Sex of Focal Individual

| Position after interaction | Outcome | | | | | Total |
|----------------------------|-----------|-------------|---------------------|-----------|------------|------------|
| | Usurp | Retain | Regain ^a | Displace | Retreat | |
| All focals ^b | | | | | | |
| Farther | 3 (0.14) | 0 (0.0) | 24 (0.13) | 30 (0.52) | 28 (100.0) | 85 (0.15) |
| Nearer | 7 (0.32) | 0 (0.0) | 11 (0.061) | 5 (0.086) | 0 (0.0) | 23 (0.041) |
| Same distance | 12 (0.55) | 164 (100.0) | 145 (0.81) | 23 (0.40) | 0 (0.0) | 452 (0.81) |
| Males ^c | | | | | | |
| Farther | 2 (0.12) | 0 (0.0) | 14 (0.12) | 16 (0.43) | 13 (100.0) | 45 (0.12) |
| Nearer | 6 (0.38) | 0 (0.0) | 9 (0.074) | 3 (0.081) | 0 (0.0) | 18 (0.049) |
| Same distance | 8 (0.50) | 115 (100.0) | 98 (0.81) | 18 (0.49) | 0 (0.0) | 302 (0.83) |
| Females ^c | | | | | | |
| Farther | 1 (0.17) | 0 (0.0) | 10 (0.17) | 14 (0.67) | 15 (100.0) | 40 (0.27) |
| Nearer | 1 (0.17) | 0 (0.0) | 2 (0.034) | 2 (0.095) | 0 (0.0) | 5 (0.033) |
| Same distance | 4 (0.67) | 49 (100.0) | 47 (0.80) | 5 (0.24) | 0 (0.0) | 105 (0.70) |

Note. Proportions are given in parentheses.

^aSome "regain" outcomes resulted in positions farther from or nearer to swarms because of shifts in swarm position.

^bResulting positions differed significantly by outcome ($G = 238.9$, $P < 0.001$, $df = 8$).

^cResulting positions differed significantly by sex from the combined distribution ($G = 52.7$, $P < 0.01$, $df = 8$); summed across all outcomes; males were more likely than females to move nearer to and less likely to move farther from the swarm ($G = 15.9$, $P < 0.01$, $df = 4$).

is not significant ($G = 2.95$, $P > 0.05$). Mean single and multiple feeding flight distances and durations varied by less than 35% among positions, and except for multiple feeding flight durations were, if anything, shortest for the close positions. Feeding success, however, was slightly but significantly higher for individuals foraging from close or middle positions (0.94 in each case) than from far positions (0.90; $G = 8.58$, $P = 0.014$, $df = 2$).

Heterospecific Aggression

A distinctive feature of these clashes was that they involved other dragonfly species much more frequently than those at breeding sites (Table II); 66% of interactions were with heterospecifics. The majority of the latter were with *Libellula needhami*, the most common species at the perch arrays at FL after mid-May. Other species with which *Pachydiplax* interacted include *Libellula vibrans*, *L. incesta*, *L. axilena*, *Anax junius*, *Tramea carolina*, *Erythemis simplicicollis*, and *Orthemis ferruginea*. Most other species were larger than *P. longipennis*, and contests were disproportionately more often initiated by heterospecific than by conspecific intruders ($G = 17.3$, $P < 0.001$). *Pachydiplax* nevertheless frequently initiated interactions, and focals were

no less successful against heterospecific than conspecific dragonflies. Regardless of initiator, however, contests with conspecifics were significantly more intense by distance and duration criteria than those with other species (Table I). There was no evidence for differences in intensity of interaction to different heterospecific dragonflies.

Effects of Competitor Density

Increased density of dragonflies at the array typically resulted in sharp and significant increases in agonistic behavior (Fig. 5) and had highly significant effects on cumulative duration of interactions and ratio of duration of aggressive flight to all flight (Table III). Both interaction duration and total flight time dropped at the highest density level for reasons that are not clear; the sample size at this level was low ($N = 10$). The frequency of various types of flight varied significantly with density ($G = 229.0$, $P < 0.001$, $df = 16$), largely due to the lower than expected frequency of interactions at $<1 \text{ m}^{-2}$ (7.5% of flights, vs. 16.7% of flights averaged over all densities) and higher frequency of interactions (32.5 vs. 16.7%) and concomitantly lower foraging frequency (52.4 vs. 73.2%) at densities $\geq 4 \text{ m}^{-2}$. The frequency at which agonistic encounters, especially multiple encounters, occurred during a foraging flight was lower than expected under the assumption of no density effect at densities $<1 \text{ m}^{-2}$ ($G = 10.5$, $P < 0.01$, $df = 1$) and higher at densities $\geq 4 \text{ m}^{-2}$ ($G = 33.3$, $P < 0.001$, $df = 1$).

Successful prey capture was significantly less likely if interactions, especially multiple interactions, occurred during foraging flights (Fig. 6). Perhaps as a result, foraging success declined significantly at very high densities (Fig. 5). Partial polynomial regressions (with prey availability and other significant predictors of foraging behavior accounted for [Baird and May, 1997]) of foraging rate, prey capture rate (number of prey actually captured, estimated by observation of mastication), and foraging success on density all had significant, positive linear terms but negative quadratic terms; all declined at densities $\geq 4 \text{ m}^{-2}$. Rate of interaction had no significant negative effects on foraging statistics, however. Thus, overall activity increased with density over most of the range we investigated, possibly in response to undetected changes in prey abundance within our broad categories of availability, but aggressive behavior may have interfered with foraging at the highest density levels.

Effects of Sex

At breeding sites aggressive behavior is almost entirely between conspecific males. At feeding sites, both sexes of *Pachydiplax* initiate agonistic

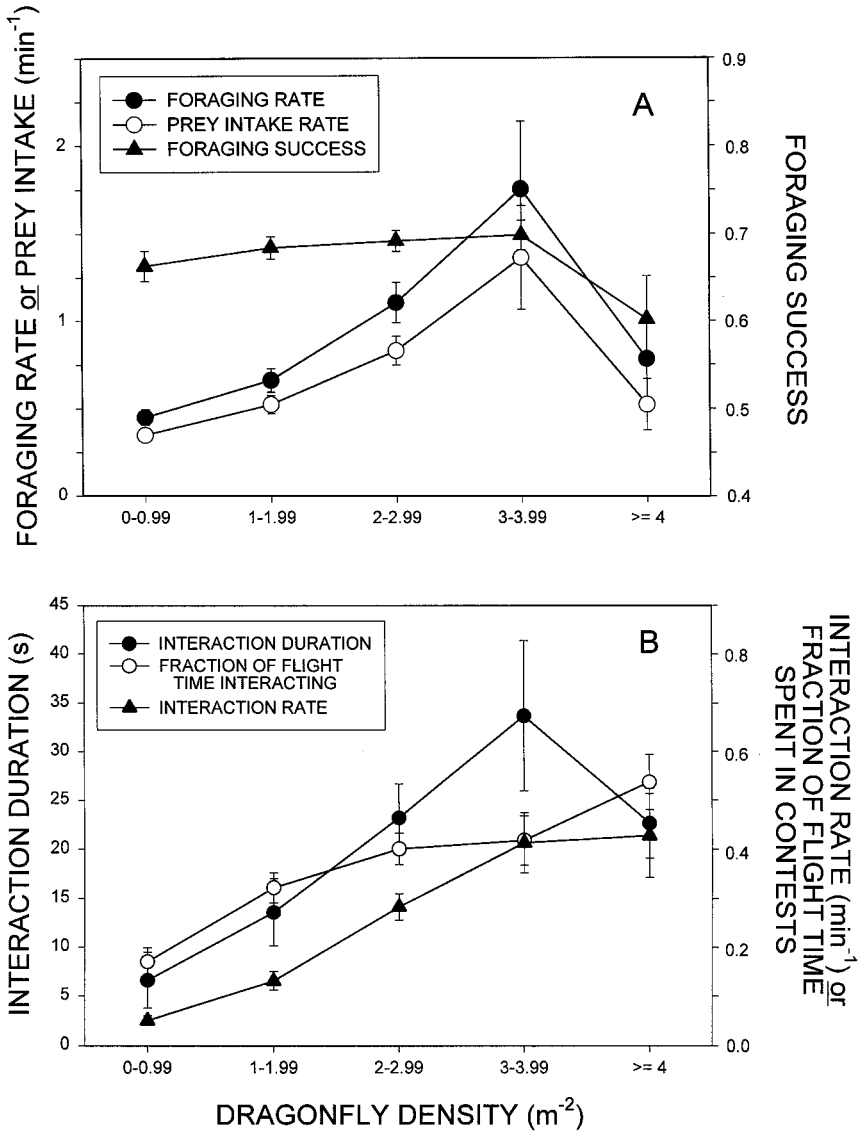


Fig. 5. Effects of dragonfly density at perch arrays on foraging (A) and aggressive (B) behaviors. All effects are highly significant ($P \leq 0.001$; cf. Table III); quadratic terms are also significant for foraging rate ($F = 5.14$, $P = 0.024$, $df = 4$), prey intake rate ($F = 5.46$, $P = 0.020$, $df = 4$), foraging success ($F = 7.81$, $P = 0.0056$, $df = 4$), and interaction duration ($F = 6.11$, $P = 0.014$, $df = 4$). Error bars indicate \pm SE.

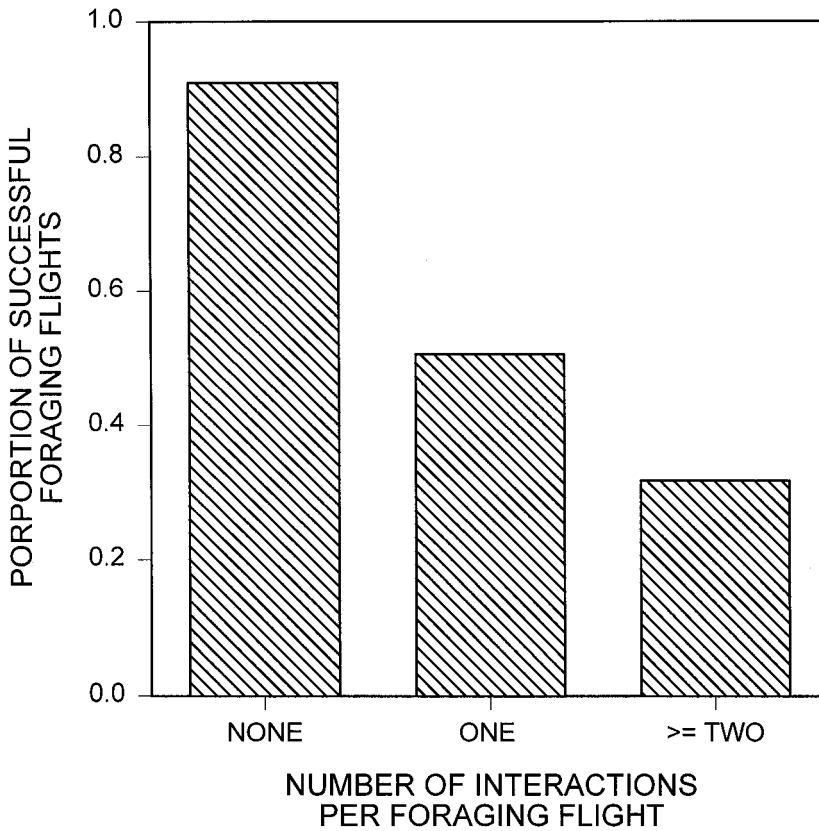


Fig. 6. Change in probability of successful prey capture in foraging flights that included no aggressive encounters ($N = 4402$ flights), one encounter ($N = 168$), or more than one encounter ($N = 22$). The effect of number of encounters is highly significant ($G = 210.1$, $P < 0.001$, $df = 2$).

encounters. Males were relatively more likely to interact aggressively (68% of contests vs. 62% of all flights) at the feeding site ($G = 15.6$, $P < 0.001$, $df = 1$; Table II) and to initiate interactions ($G = 8.9$, $P < 0.003$, $df = 1$) than were females.

Males and females were equally likely to attack conspecifics of either the same or the opposite sex ($G = 0.543$, $P > 0.5$, $df = 2$). The duration ($F = 3.45$, $P = 0.0047$) and flight distance ($F = 3.60$, $P = 0.0035$) of intraspecific contests were significantly longer for male–male than for male–female or female–female interactions (Fig. 7). Males and females were about equally likely to retain, regain, or be displaced from a perch (Table II), but males

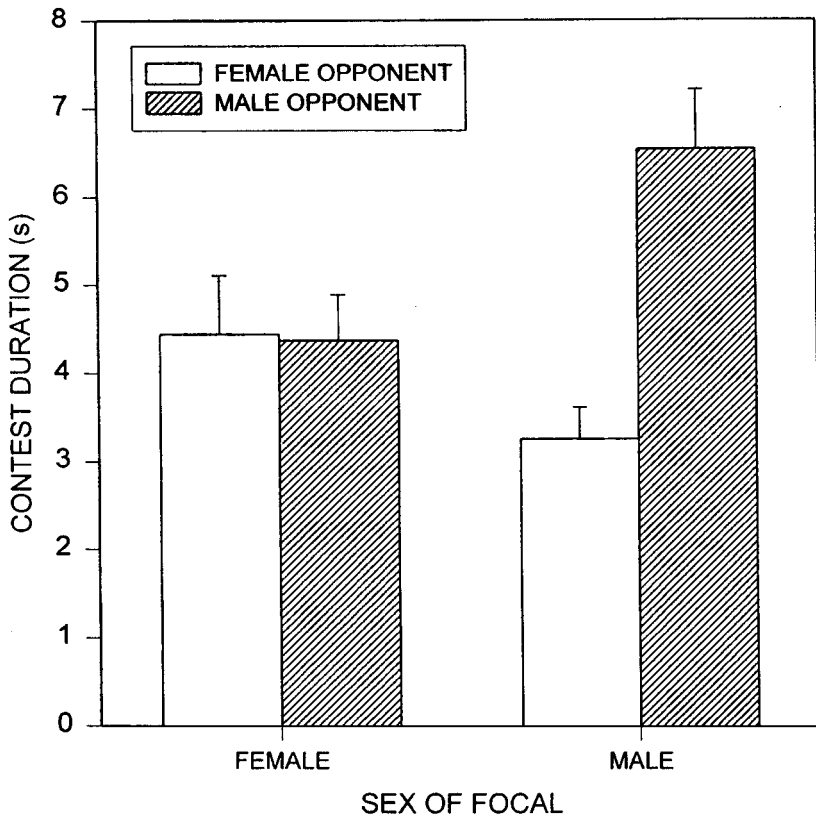


Fig. 7. Variation in duration of intraspecific contests as a function of sex of focal individual and its opponent. The effects of sex of opponent and of the statistical interaction of sex of focal with sex of opponent are significant (sex of opponent, $F = 3.79$, $P = 0.024$, $df = 2$; sex of focal by sex of opponent, $F = 4.22$, $P = 0.016$, $df = 2$). Error bars indicate \pm SE.

were more likely to usurp another occupied perch ($G = 3.80$, $P = 0.05$, $df = 1$) and females more likely to retreat from the array after an interaction ($G = 10.8$, $P < 0.01$, $df = 1$).

Rates of interaction were higher in males (0.218 ± 0.02 ; $N = 144$) than in females (0.143 ± 0.159 ; $N = 101$), and males also responded more strongly to prey availability and dragonfly density considered simultaneously (Fig. 8), although the sexes did not differ in average response to density alone. Parallel differences in sensitivity to prey occur in the foraging rates of the sexes (Baird and May, in preparation).

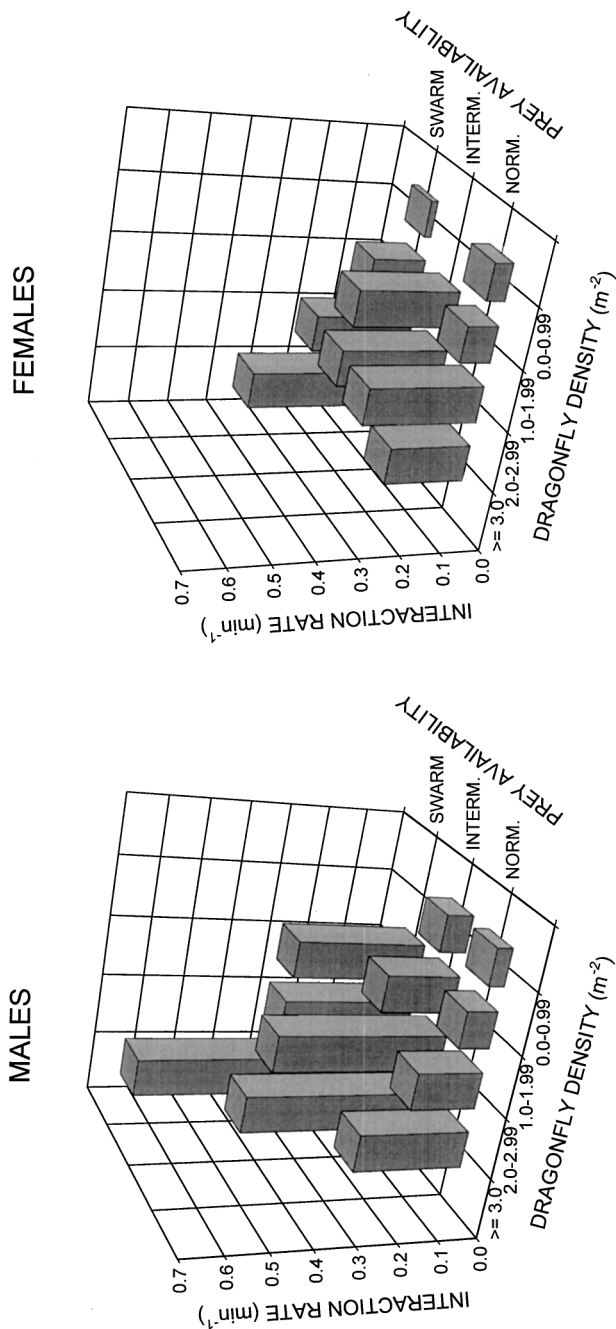


Fig. 8. Comparison of simultaneous effects of dragonfly density and prey availability level on interaction rate in male and female *Pachydiplax*. Sex, prey availability, and dragonfly density all had significant effects (Table III), as did the statistical interaction of sex with prey availability ($F = 4.86$, $P = 0.086$, $df = 3$) but not of sex with density.

Energetics

About 45% of the total flight time, on average, or about 19 s per 30-min observation, was allocated to interaction, so the average energy expenditure for aggression must have been low relative to the intake (see Discussion). A few individuals, however, flew for much longer periods, up to 220 s per observation period. Aggression might, in some circumstances, also affect energy intake adversely. When all observations, including those with enhanced aggressive behavior due to the presence of standing water, were included in the analysis, and when prey availability (which affects both interaction duration and prey capture rate) was taken into account, a significant negative correlation of expected prey capture rate (i.e., feeding flight frequency times capture success) with interaction duration occurred ($F = 10.8$, $P = 0.001$).

Net energy gain increased over the range of total interaction duration that most individuals experienced (Fig. 9), although it decreased sharply if

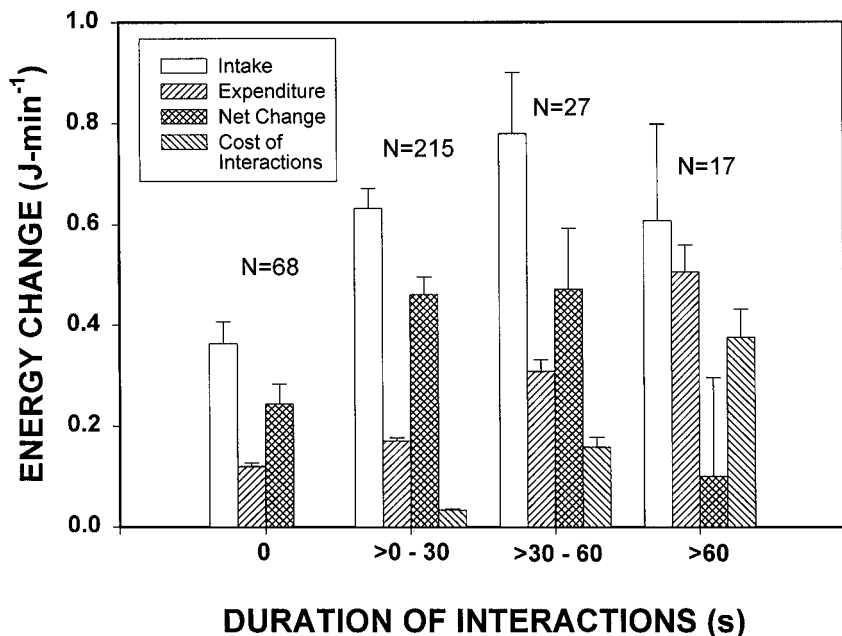


Fig. 9. Effect of duration of aggressive interactions on estimated energy intake and expenditure. Duration had significant effects on feeding (energy intake; $F = 5.35$, $P = 0.0013$, $df = 3$), metabolic expenditure ($F = 88.86$, $P < 0.0001$, $df = 3$), net energy gain ($F = 5.23$, $P = 0.0015$, $df = 3$), and energy costs of aggressive behavior ($F = 199.17$, $P < 0.0001$, $df = 3$). In all cases, energy changes were greater for individuals that engaged in aggressive behavior than those that did not ($P \leq 0.006$). Numbers of observations for each duration class are shown above the corresponding group of bars. Error bars indicate \pm SE.

interactions were very lengthy; individuals behaving aggressively ($N = 259$) gained significantly more energy than nonaggressive individuals ($N = 68$). In part the increase reflects the fact that energy intake as well as interaction intensity increased when prey availability was highest, during prey swarms. Net gain, however, still changed with interaction duration ($F = 2.99$, $P = 0.031$, $df = 3$) even when variation due to prey availability ($F = 39.97$, $P < 0.0001$, $df = 2$) and the interaction of duration and availability ($F = 4.30$, $P = 0.0003$, $df = 6$) were accounted for. The pattern of change was essentially as in Fig. 9 for both low and swarm prey levels; at intermediate prey availability the estimated gain continued to increase at the highest interaction intensity, but only two observations were made under these conditions.

DISCUSSION

With one exception (Gorb, 1994) aggression among Odonata has previously been studied only in males at sexual rendezvous sites. Nevertheless, agonistic interactions like those described here are frequent among *Pachydiplax* and some other species at unmanipulated feeding sites as well as at our artificial arrays (May, 1984; May and Baird, 2002), despite the almost-complete absence of overt sexual behavior (Baird, 1991). We doubt that this phenomenon is merely a nonadaptive reflection of inherent aggressiveness, because it differs in several important respects from aggression in a mating context. Although the elements of behavior are similar in both circumstances, the general pattern during foraging is distinctive in (1) the prevalence of interspecific interactions, (2) the frequent participation of both sexes of *P. longipennis*, and (3) the nature of the defended resource. In addition, agonistic behavior during foraging is not free of costs, although these may be substantially less than at sexual rendezvous sites (Fried and May, 1983).

Resource Defense

At feeding areas the possibly defendable resources include prey and the perches from which individuals forage. Since individual prey are usually quite small and, except during ephemeral swarms, widely dispersed, their defense is unlikely to be profitable. In addition, the costs of defending exclusive rights to a feeding area may not be warranted when a predator can use only a small portion of the prey occurring within the territory at one time (Morrison, 1978). Finding or defending exclusive patches may cost more than tolerating others in the patch, particularly for predators of

ephemeral prey such as aggregations of small, flying insects. Defense of a perch seems more likely to be economically feasible.

What potential benefits accrue to perch occupants? Perches might be in short supply simply as places to sit—not all possible substrates qualify as suitable perches for *Pachydiplax*. They use, almost exclusively, tips of slender, more-or-less erect branches or twigs, usually within 3 m of the ground. Numerous apparently suitable natural perches were always unoccupied, however, and empty perches usually were available at the arrays, suggesting that perches are not absolutely limited.

Perches provide places to thermoregulate and consequently may affect the ability of a dragonfly to maximize flight readiness, alertness, and/or rates of digestion and energy assimilation. Undoubtedly, perches differ in suitability as sites for thermoregulation, and these differences may contribute to assessment of perch benefits by *Pachydiplax*. At least within the arrays, however, all perches were usually about equal in temperature and exposure to sun.

Perches also afford access to prey, and defense of a perch may represent the defense of areas where prey abundance is likely to be high. Dragonflies close to swarms fed at higher rates and could accumulate energy about 20% more rapidly and consequently may have been able to mature gametes more rapidly and/or spend less time at feeding sites (Baird and May, 1997, in preparation). The movement of *Pachydiplax* toward perches nearer to swarms suggests that they assess current perch suitability and act to gain better access to prey. Preferential use of poles in the arrays compared to nearby perches supports the same conclusion, because prey density and swarm frequency were higher at the arrays (Baird and May, 1997), resulting in higher rates of prey capture and correspondingly higher levels of aggression.

Higher levels of aggression are predicted in the presence of a richer prey resource (Charnov *et al.*, 1976; Ewald and Orrians, 1983), at least up to a point, and in fact, the rate and cumulative duration of interactions increased significantly at high levels of prey availability (Fig. 4). Nevertheless, aggressiveness did not increase in proportion to foraging activity or overall flight activity at the highest levels of prey availability. The fraction of flights that involved contests was elevated during intermediate prey conditions (31.3% of contests occurred during this situation, vs. 25.3% of all flights) but was significantly reduced during swarms (35.2 vs. 40.9%; $G = 20.4$, $P < 0.001$, $df = 2$), despite the fact that swarms were more localized and thus, one might think, more defensible. Moderation of aggressive behavior in the presence of abundant prey could be explained by a resource-threshold model of feeding (Gill and Wolf, 1975; Carpenter and MacMillen, 1976) if the relative benefit of resource defense declines above some maximum resource density. On the other hand, fairly high levels of aggression still persisted,

a fact perhaps more consistent with a “distraction” model (Crowley and Martin, 1989), in which a predator’s attention is divided between prey and rivals.

We regard continued occupation of a perch in the circumstances described here as a special form of territoriality. Perch tenure may be brief and occupants may change alternately or successively, but since the benefit of aggressive interaction is dependent on maintaining location within the habitat, the behavioral strategy of these dragonflies is essentially territorial rather than defense of individual-centered space or maintenance of a dominance hierarchy. The territory holder gains exclusive use of a fixed position in space, the perch, at least partly through aggressive defense. The value of this position is principally that it provides access to a spatially separate but nearby resource. The latter provides the ultimate benefit accrued but is not itself defended, and the perch holder gains improved but not exclusive access to this ultimate resource.

Costs of Aggression

The potential costs of agonistic interactions, and therefore of perch defense, are those commonly enumerated: (1) loss of time and energy that could be allocated to other activities, including energy acquisition and reproduction; (2) missed foraging opportunities and reduced foraging success (Fig. 6); (3) injury and mortality as a direct result of interaction; and (4) increased predation risk. Heightened intensity of encounters increases all these costs.

Despite the relatively long duration of intense contests, the average time and energy costs are comparatively low. A typical individual allocated only about 3 J h^{-1} to agonistic behavior, vs. roughly 20 J h^{-1} for all foraging costs or 100 J h^{-1} for a male defending a mating territory. Mean net energy intake during foraging was nearly 0.5 J min^{-1} , depending on prey availability (Baird and May, in preparation). Figure 9 shows that the average energy spent in aggression by individual *Pachydiplax* during foraging, as in spiders (Riechert, 1988) and larval coenagrionid damselflies (Anholt, 1990) but unlike *Pachydiplax* males at breeding territories (Fried and May, 1983), was low compared to the total energy budget. Net energy gain was higher on average in individuals that engaged in aggressive behavior than those that did not (Fig. 9), although this conclusion is complicated by effects of other correlated factors. Interaction duration was highly variable, however, and some individuals allocated almost 7.4 min per hour to aggressive interactions, at significant cost (up to 40 J h^{-1}) and reduced net energy gain or sometimes even a net loss.

Aggressive interaction may also affect foraging directly. Retreat (Table II), e.g., probably reduced energy intake rates owing to lower prey availability away from the arrays (Baird and May, 1997). Thus contests would have reduced feeding opportunities for some individuals chased from the arrays. The lower foraging success associated with interactions occurring during foraging flights likewise indicates that aggression may interfere with foraging activity in the short term. Increasing density of other dragonflies at the arrays was accompanied by increasing aggression (Fig. 5). At the highest density, however, this effect seems to level off or even decline. Foraging rate also was reduced under the same density conditions, so reduced aggressiveness could be a consequence either of prey depletion or, since the number of observations was small ($N = 10$), simply of unmeasured variation in prey availability. These possibilities are somewhat unlikely, however, because intermediate ($N = 5$) or swarm ($N = 1$) prey conditions occurred in an unusually high proportion of these 10 observations. Alternatively, interference could reduce foraging success (Fig. 5), in part because of increasing numbers of multiple interactions and interactions during foraging flights (e.g., Fig. 6); i.e., a high competitor density may reduce the net value of the resource. Thus we speculate that high density resulted in reduced foraging efficiency, most likely due to interference competition. This is reflected in the reduced intake seen at the highest level of interaction duration (Fig. 9).

Multifunction flights were infrequent, however. Moreover, interaction rate had no significant negative effect on foraging rate or success or prey capture rate in one-way or multiple ANOVAs, although these analyses necessarily exclude foraging by focal individuals after retreats from the arrays. Very prolonged interactions apparently depressed energy balance, but this occurred in only a small minority of individuals. Thus it is plausible that aggressive behavior interferes with foraging and net energy gain only at rarely observed levels of intensity.

Agonistic interactions may carry some risk of injury, although we saw no unequivocal evidence of this. Predation on *P. longipennis* at these feeding sites also was quite rare, regardless of the level of agonistic activity. We noted only two cases of attempted predation, both by *E. simplicicollis* and both unsuccessful. Four other *E. simplicicollis* were observed feeding on previously captured *P. longipennis* at the FL site. Again, the average costs of these occurrences over the entire population seems trivial.

For the most part, then, the potential costs of perch defense by an average *P. longipennis* individual seem relatively low. Only in infrequent (at our artificial perch arrays) combinations of low foraging success and high interaction rates is energy balance likely to be so unfavorable that failure to defend a perch is of net benefit.

Interspecific Encounters

Interspecific aggression is rare among dragonflies at mating sites (but see Moore, 1964; May, 1980). Singer (1989) hypothesized that tradeoffs occur between assessment costs when the intruder is a conspecific and the benefit of avoiding conflict when the intruder is a heterospecific, so dragonflies that often encounter conspecifics should defend against all intruders, while those that rarely encounter conspecifics should be more discriminating.

Although foraging *Pachydiplax* did discriminate, in that contests with conspecifics were more intense than with other species, most interactions involved heterospecific opponents, especially *L. needhami*. The latter are much larger than *Pachydiplax*, quite different in color, and lack uv-reflecting pruinescence that may characterize other species attacked by male *P. longipennis* at breeding sites (Robey, 1975). They use similar perches, however, and seem to feed on much the same prey. Moreover, heterospecific encounters were very frequent later in the season, when *P. longipennis* were relatively less common and thus might be expected to be more discriminating. We therefore believe that these interactions usually represent genuine interspecific competition rather than mistaken identity. Gorb (1994) also reported that female *S. sanguineum* attacked heterospecific intruders.

We cannot completely discount the possibility that some "contests" were actually predation attempts, but *P. longipennis* and *Libellula* spp. usually take only much smaller prey; *E. simplicicollis* did, on rare occasions, prey on *P. longipennis*, however (see above).

Effects of Sex

Females typically avoid agonistic interactions at breeding sites, but both sexes initiated contests when foraging. Males and females feed at the same times and places and use similar prey, so the function and the costs and benefits of aggressive behavior at foraging areas are probably similar. Still, important differences exist. Males interacted aggressively more frequently and more intensely than females, especially with conspecifics (Gorb [1994] also found *S. sanguineum* males to be slightly more aggressive than females) and were more likely to usurp a perch and less likely to retreat from the array. Males also occurred at the arrays during periods of slightly but significantly higher mean dragonfly density ($1.85 \text{ individuals m}^{-2}$) than did females (1.50 m^{-2}). Possibly because males were more successful in maintaining a position at the array at higher densities, males had more opportunity for aggressive interactions, although not enough to account entirely for the higher frequency of aggression in males.

Stronger agonistic responses of males might simply be an extension of their behavior at breeding sites or a result of their slightly larger average size (Dunham, 1993). On the other hand, sexual differences may also reflect adaptive differences in foraging strategy. Males spend much longer periods than females at breeding sites (Sherman, 1983), where they rarely feed but expend a great deal of energy (Fried and May, 1983; Baird and May, in preparation). Time constraints on prey capture by males may magnify the importance of acquiring energy rapidly and thus of defense of favorable perches.

Conclusions

Most studies of spatially based resource defense in animals focus exclusively on either feeding or mating territoriality, without explicitly relating one to the other except when both functions occur concurrently in the same area (Alcock, 1993). In *Pachydiplax* and many other Odonata, however, feeding and mating are spatially and temporally separated, so costs and benefits of defending space for one function are not confounded by the other. Feeding nevertheless has direct and important reproductive benefits—energy and materials for egg maturation in females and energy for mating territory defense in males. This situation provides an opportunity to relate foraging behavior and success to reproductive strategy (Baird and May, 1997, in preparation).

So far we have not been able to observe the same individual during foraging and mating activity. We infer, however, that to maximize reproductive opportunities both sexes probably must feed throughout most of the day when not actually ovipositing (females) or defending a mating territory (males). In this context, aggressive defense and/or appropriation of favorable perches from which to feed ultimately is an adaptive aspect of reproductive strategy. Because other dragonfly species may use the same perches and prey, interspecific aggression is an important foraging tactic. Finally, males may be subject to stringent energetic and time constraints on reproduction (May and Baird, 2002; Baird and May, in preparation), so their heightened aggressiveness during foraging could stem from conflicting selective pressures to maximize energy gain while simultaneously minimizing time away from mating sites.

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