

ENERGETICS OF ADULT ANISOPTERA, WITH SPECIAL REFERENCE TO FEEDING AND REPRODUCTIVE BEHAVIOR

MICHAEL L. MAY

Department of Entomology and Economic Zoology
New Jersey Agricultural Experiment Station
Cook College, Rutgers University, New Brunswick, NJ 08903, U.S.A.

Current information on energy intake and on respiratory metabolism in adult Anisoptera is reviewed. Daily food consumption has been found to be about 10-15% of body mass in several species. *Pachydiplax longipennis* requires at least 7.3 h of feeding time and 38 J of energy to acquire this food. Metabolic rate during rest and endothermic warm-up have been reported previously, but accurate data on flight metabolism are lacking. A method of calculating the latter is tentatively proposed. Results using this method show that flight metabolism may be extremely high in some species but may vary markedly with flight behavior.

Such data could eventually permit construction of accurate energy budgets for Anisoptera. I suggest that energy requirements may place important constraints on reproductive behavior of these insects, and I present a series of testable hypotheses, some supported by preliminary data, about the nature of adaptations of mating behavior to energy requirements. Further studies of both male and female energetics may prove fruitful in efforts to gain a general understanding of reproductive behavior.

INTRODUCTION

Energy is an essential resource for all organisms and is limiting for many. Thus acquisition of energy and its allocation among physiological and behavioral functions are among the most important problems of adaptation that an animal must solve. The energy requirements of immature stages of Odonata have been investigated by several authors (e.g. LAWTON, 1970; BENKE, 1976). However,

adult dragonflies have received little attention in this regard, despite many studies of their behavior (CORBET, 1963, 1980) and the obviously high energetic cost of much of this behavior. Although quantification of energy metabolism and food consumption in adults has been difficult, some progress has been made in recent years. My objective here is to review current information, add some preliminary data from my own studies in progress, and indicate how studies of energy utilization and allocation may illuminate various aspects of the biology of Anisoptera.

FOOD INTAKE

For an organism to maintain energy balance, its energy intake must equal its rate of energy expenditure. Thus food intake sets the outer limits of the energy available to an individual, unless stored reserves are depleted. This relationship may be described by the energy balance equation, $C = P + R + FU$ (where C is consumption, P is growth, R is respiratory metabolism, and FU is losses as feces and excreta; PETRUSEWICZ & MACFADYEN, 1970.) (All symbols are fully defined in the Appendix). Since growth is probably negligible in post-teneral male dragonflies, and since assimilation efficiency can be measured in the laboratory (FRIED & MAY, 1983), only C and R need to be determined to evaluate energy balance of these insects; for females, P, as eggs, must also be measured. The need to avoid a severe or long-sustained negative energy balance may force increases in foraging time or reductions in the allocation of energy to mating behavior (e.g. by reduced territorial defense effort). Such effects have been demonstrated in nectarivorous birds (STILES, 1971; WOLF, 1975). CAMPANELLA & WOLF (1974) and CORBET (1980) suggested that the ability to mobilize energy may likewise limit effectiveness of territorial defense in Odonata.

Because the adult lifespan of dragonflies is short compared to that of birds, the possibility exists that energy reserves built up during the larval or teneral adult period may account for a substantial portion of energy utilized as mature adults, and the role of energy stored as fat or glycogen needs to be determined. However, adults feed extensively; males may feed opportunistically while defending their territory or may leave the breeding site to feed (PARR, 1980, 1983). Also, maximum reproductive life is at least 30 days in *Pachydiplax longipennis* (B. MACKINNON, pers. comm., 1982) and up to 13 weeks in some other species (CORBET, 1980). Since, as seen below, some dragonfly males require the equivalent of at least 10% of their body mass during a typical day when they defend a territory, stored reserves probably account for only a small fraction of their energy needs.

Quantification of consumption is also necessary to understand the role of dragonflies in the trophic structure of communities. Odonate larvae may be extremely important elements in energy flow in some aquatic systems (BENKE, 1976). Similar studies of adults will require accurate estimates of population

density in feeding areas, which may prove very difficult, considering the mobility of these insects. Preliminary marking experiments with *P. longipennis* suggest that individuals do not return to the same feeding site on successive days; of 22 individuals marked, only 1 was seen again, 11 days later. However, much more extensive work is needed on the dispersion and density of dragonflies in feeding areas.

Food consumption has been quantified in very few adult Odonata. HIGASHI and his colleagues (HIGASHI, 1973, 1978; HIGASHI *et al.*, 1979) measured food intake in three species by several techniques: Frequency and success rate of feeding flights; variation of gut contents throughout the day, coupled with laboratory measurements of gut clearance rates; and rate of production of feces throughout the day. All three species consumed about 10-15% of body mass per day. Likewise, FRIED & MAY (1983) found that male *P. longipennis* consumed the equivalent of 12-15% of their body mass per day. Since Odonata feed almost exclusively on insects, their food is of relatively uniform energy content (GOLLEY, 1961; SLOBODKIN & RICHMAN, 1961), and mass consumption can thus be converted to caloric values.

Table I
Quantification of food consumption and feeding behavior by *Pachydiplax longipennis*.

Consumption (J day ⁻¹) ^a		Mean Flight Frequency (h ⁻¹) ^b	Mean Time in Flight (s h ⁻¹) ^b	Success Rate (%)	Mean Dry Mass of Prey (mg) ^b
Gut Contents	Feces				
144-183	151-184	62.4 ± 24.0	110 ± 38	62	0.030

^a Estimates from FRIED & MAY (1983) based on changes in gut contents throughout the day or on total production of feces through the day (assuming assimilation efficiency = 76%); data given as range.

^b Unpublished data, given as mean or mean ± S.D.; see text for methods.

Data from FRIED & MAY are summarized in Table I, along with preliminary results based on observations of feeding behavior of *P. longipennis* (mostly females — data for males do not differ significantly). Individuals were observed closely for periods up to 15 min at feeding sites in a partly overgrown field and wood's edge about 10-50 m from a breeding pond. The number of flights during an observation period was recorded and their total duration timed with a stopwatch. When possible, the proportion of successful flights, as indicated by regular movements of the mouthparts after an individual returned to its perch, was noted. Some flights were not elicited by prey but were chases of other male or female *P. longipennis* or were due to other disturbances. Since the reason for the flight could not always be determined unambiguously, no attempt was made to distinguish among these. A rough estimate of prey size was made by capturing 20 specimens immediately after successful feeding flights, decapitating them and preserving the heads in 70% EtOH, then later the same day removing the prey, drying and weighing it (Table I). The average dry mass of prey was about half that estimated from sticky trap samples by HIGASHI (1978). The discrepancy

may be due to regional differences in size of available prey, selectivity on the part of the dragonflies, or loss of prey mass in my samples owing to ingestion or wastage.

From data in Table I, I calculated the time and energy necessary to satisfy the minimum energy requirements of a male *P. longipennis*. The mean dry mass of males studied by FRIED & MAY (1983) was about 0.07 g. In order to consume 12% of this mass, equivalent to roughly 170 J of assimilable energy, an individual would have to capture 280 prey, requiring 452 flights. At a rate of 1.04 flights per min, the dragonfly would have to devote 7.3 h per day to feeding behavior. *P. longipennis* were observed feeding from at least 07:30 to 20:00 hr Eastern Daylight Time, but in the absence of data from marked specimens, the actual daily duration of feeding by individuals remains uncertain. Feeding continued later than the last daily samples obtained by FRIED & MAY (1983), so their estimates of intake may be low. Nevertheless, frequency of feeding flights was apparently reduced late in the afternoon (although data are insufficient for statistical analysis), so the error is probably small.

The energetic cost of feeding should be closely related to the total duration of feeding flights. Based on Table I, the latter should be about 110 s per h, *i.e.*, 13.4 min during 7.3 h of feeding or 22 min if 12 h were devoted to feeding. The cost of 13 min of flight would be about 38 J according to FRIED & MAY (1983); however, they may have substantially underestimated flight metabolism — see below. This leaves a net profit of about 130 J, which at best would be barely sufficient to supply the energy required by males for territorial defense. Females presumably devote much of the energy excess to egg production.

RESPIRATION

MAY (1979) determined resting metabolism of Anisoptera over a wide range of size and temperature. The magnitude and variation with temperature and size was similar to other insects. Data were from eleven libellulids and one aeshnid, *Anax junius*, all collected in central Florida, and although there may be some undetected taxonomic or geographic variation in metabolism, data from other insects suggest these are probably minor. "Fliers" (CORBET, 1963) had slightly higher metabolism than "perchers", and females of *P. longipennis* had slightly higher rates than males, possibly correlated with the energy demands of vitellogenesis. Diel and seasonal variations were small. Size and body temperature are evidently the primary determinants of resting metabolism. The latter increased approximately exponentially with temperature ($Q_{10} = 2.5$). At 30°C the mean rate of metabolism per individual varied with the 0.91 power of mass. The range of mass-specific metabolism is shown in Table II. Resting metabolic rate is generally only a few per cent of the rates characteristic of flight or endothermic warm-up. As a result, the energy costs of perching and nocturnal roosting (assumed to be equivalent to rest) may be comparatively minor in many dragonflies (FRIED & MAY, 1983).

Table II

Summary of respiratory metabolism during rest, endothermic warm-up and flight in Anisoptera. Values given are the range of mean values for different species ($W \text{ g}^{-1}$).

Rest ^a		Warm-up ^a		Flight ^b
$T_b = 20^\circ\text{C}$	$T_b = 30^\circ\text{C}$	$T_{th} = 30^\circ\text{C}$	Max. Rate	
0.0018-0.0031	0.0044-0.0085	0.13-0.29	0.11-0.39	0.25-0.76

^a From MAY (1979).

^b Unpublished data; see Table III.

Much higher rates of metabolism occur during certain vigorous activities other than flight, such as wing-shivering (wing-whirring). In those Anisoptera that are capable of this behavior, maximal rates of metabolism may approach those of flight (MAY, 1979; see Table II). Since the duration of warm-up is usually brief, the overall daily energy expenditure is probably small for most species. However, certain species may shiver for extended periods while perched under cool, cloudy conditions (MILLER, 1964; MAY, 1976), and females of some aeshnids shiver during oviposition (unpublished observations). Data on metabolic rate and total duration of shivering are lacking, but maintenance of endothermy might require a sizable portion of the total energy budget in these species, especially under cool conditions. Respiratory rates associated with some other activities, *e.g.* endophytic oviposition, even without shivering, might also be high enough to constitute an important energy drain.

Flight cost may make up a large fraction of the energy budget of many insects, including Odonata (HANEGAN & HEATH, 1970; MAY, 1977; FRIED & MAY, 1983). Insect flight is probably more demanding energetically than any other metazoan activity (KAMMER & HEINRICH, 1978; CASEY, MAY & MORGAN, in prep.). Since flight energetics are closely coupled to flight mechanics (CASEY, 1981), data on energy expenditure are an integral part of analysis of the entire flight system. Knowledge of flight metabolism also can be important to an understanding of the ecological energetics of insect populations and individuals.

Flight energetics of hovering insects have been measured by allowing an insect to initiate flight, then placing it in a closed vessel in which it hovers continuously, and measuring the change in O_2 content of the vessel after a known interval (*e.g.* HEINRICH, 1971; BARTHOLOMEW & CASEY, 1978). This method appears to give accurate results, but it suffers from two important limitations. First, many insects, including dragonflies, do not hover for sufficient periods in a confined space. Second, energy requirements for flight depend on several factors, *e.g.* forward speed and extent of climbing or other maneuvers (PENNYCUICK, 1969), which may differ markedly between field and laboratory conditions. Thus methods of estimating metabolism in the field are desirable, even though they may be less precise than O_2 consumption measurements.

WEIS-FOGH (1964a, b) estimated flight metabolism in desert locusts, wasps, and aeshnid dragonflies by measuring the difference between their thoracic temperature and air temperature and using heat exchange coefficients to infer rates of

“dry” heat loss. Since thoracic temperature was constant in his experiments, heat loss was equivalent to heat production or, when corrected for estimated evaporative losses and work output, to flight metabolism. He failed to account for heat transferred to the head and abdomen and so probably significantly underestimated heat loss. Nevertheless, by calculating heat loss in a like manner from all three tagmata (*i.e.*, head, thorax, and abdomen) of sphinx moths flying in the laboratory at low air temperature, HEGEL & CASEY (1982) accounted for 90-100% of flight metabolism as measured by O₂ consumption. MAY & CASEY (1983) found a similar degree of agreement between the two techniques in slowly flying bees at deeply shaded locations in the field. Thus, despite errors due to variations in flight speed and environmental air movements and to variation of temperature within a body region (HEINRICH & CASEY, 1978), there is evidence that reasonable approximations of flight metabolism can be obtained from field measurements of the temperatures of the head, thorax, and abdomen and of flight speed, coupled with laboratory measurements of corresponding heat exchange coefficients.

This approach depends on the approximation, $dT_b/dt = K(T_b - T_a)$, so that $dH/dt = sKm(T_b - T_a)$, where T_b is body temperature, T_a is air temperature, K is a cooling constant (HEATH & ADAMS, 1969), H is heat content, s is the specific heat of dragonfly tissue (MAY, 1979), and m is mass. The value of K will depend primarily on size and insulation of the organism and on wind speed and turbulence. Since convection is the predominant mode of heat loss for a flying insect (CHURCH, 1960), this heat exchange model is a good approximation unless solar radiation contributes to heat input. The temperatures of the thorax (T_{th}), head (T_h), and abdomen (T_{ab}) typically differ sharply during flight (MAY & CASEY, 1983). If each of these temperatures is measured and if K is determined for each tagma individually, then total heat loss is approximately the sum of losses calculated independently as above for each tagma. For insects at thermal equilibrium, flying in the shade or at dusk, metabolism, $M = dH/dt + W$. Therefore

$$M = sK_h m_h (T_h - T_a) + sK_{th} m_{th} (T_{th} - T_a) + sK_{ab} m_{ab} (T_{ab} - T_a) + E + W$$

where E is evaporative heat loss and W is mechanical work; together E and W make up about 20% of M (WEIS-FOGH, 1964b; CASEY, 1981).

Making these assumptions, I can characterize flight metabolism as a function of body mass in dragonflies that are active when solar heat input is negligible. Only with fliers can one be reasonably confident that the criterion of thermal equilibrium is met; the intermittent flight of perchers may often not allow for stabilization of body temperature during flight. I assume that the results can be extrapolated to most perchers because their basic morphology is similar to that of fliers, so the mechanical demands of flight and thus the metabolic power required for flight should be similar (CASEY, 1981). I also assume that body temperature *per se* does not affect flight metabolism, since it does not affect mechanical requirements (CASEY, 1981; HEINRICH, 1971). Nevertheless, in dragonflies gliding flight may occur in response to high body temperature (MAY, 1978) or

as an energy saving mechanism (GIBO, 1981). Therefore, average flight metabolism might vary markedly under different circumstances.

Sufficient data are in hand to calculate M as described above for *Tetragoneuria cynosura* and *Anax junius*. Specimens of the former were all males collected on territory, while the latter were in feeding swarms of mixed sex. Temperatures for all tagmata of these species are shown in Fig. 1. These are the first data on T_h and the first field measurements of T_{ab} to be reported for Odonata. Note that T_h is well below T_{th} but always distinctly elevated and usually higher than T_{ab} . Other evidence (unpublished observations) suggests that T_h may be maintained by active circulation of hemolymph from the thorax.

Table III shows mean values of K and mass for each tagma of these species, as well as calculated flight metabolism. The latter was calculated for each individual using that individual's masses and temperatures but average K values for the species, since K was measured in different specimens. K is dependent primarily on mass and flight speed (Fig. 2 shows this relationship for the thorax of several species). The average flight speed of *T. cynosura* is not known but was estimated to be about 0.25 m sec^{-1} , because, except during occasional chases, most of their time was spent hovering or in very slow flight, and hovering individuals were most likely to be captured. Flight speed of territorial *A. junius* was determined to be about 2 m sec^{-1} by filming patrolling males from several metres above their plane of flight and measuring average frame-to-frame displacement. This figure was used in the present case, even though feeding rather than territorial flight was involved.

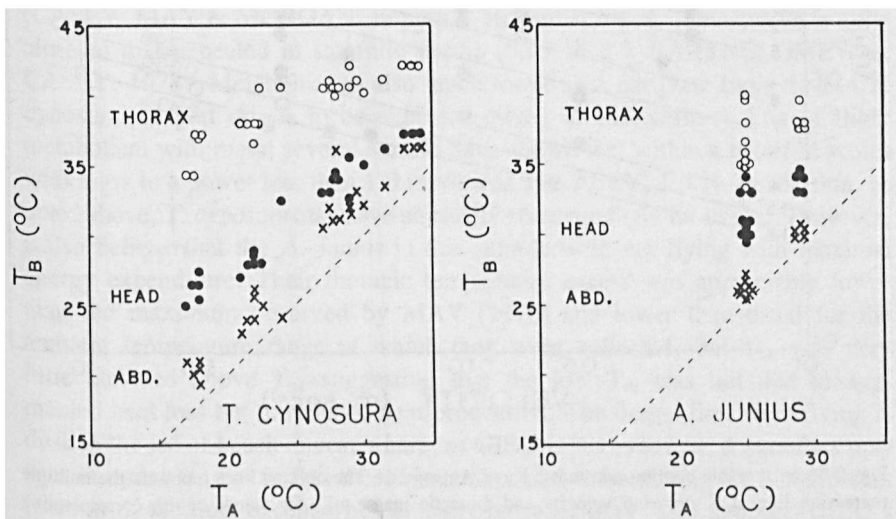


Fig. 1. Temperatures of the head, thorax, and abdomen, recorded in the field under conditions of ambient solar radiation intensity of less than 200 W m^{-2} , in *Tetragoneuria cynosura* and *Anax junius*. Temperatures were measured as described by MAY (1976) and MAY & CASEY (1983).

Table III

Estimates of respiratory metabolism during flight, and relevant morphometric and heat exchange parameters for two species of Anisoptera.

Species	<i>Tetragoneuria cynosura</i>		<i>Anax junius</i>
T_a (°C)	<20	>30	25-29
Mean $m_h/m_{th}/m_{ab}$ (g)	0.029/0.089/0.069	0.027/0.079/0.046	0.12/0.53/0.32
Estimated Flight Velocity (M s ⁻¹)	0.25		2.0
Mean $K_h/K_{th}/K_{ab}$ (min ⁻¹)	2.95/0.78/1.92		1.18/0.31/1.38
Mean Heat Loss (W g ⁻¹)	0.63	0.34	0.21
Mean metabolism (W g ⁻¹) (= heat loss + 20%)	0.76	0.41	0.25

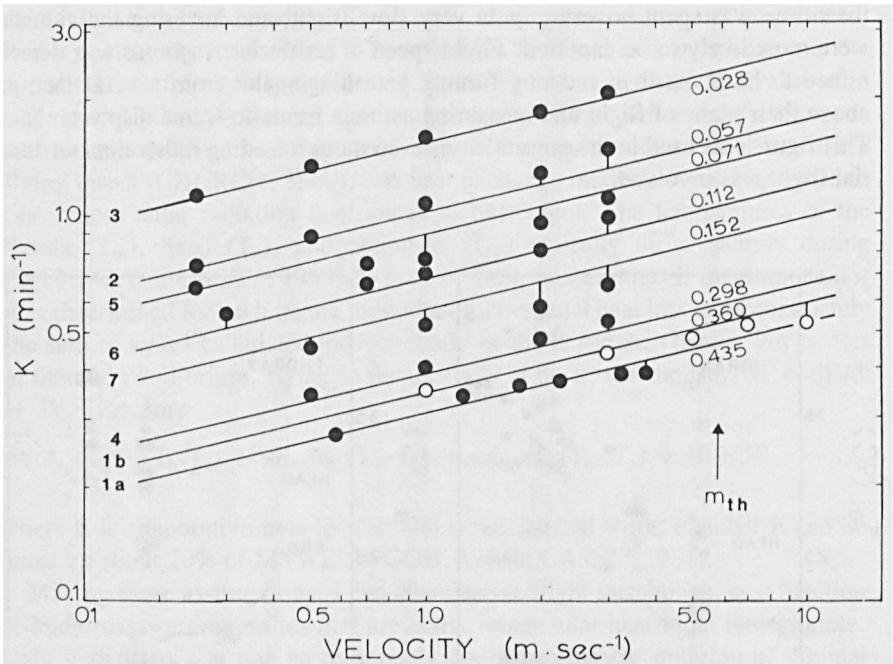


Fig. 2 Mean thoracic cooling constants, K , of Anisoptera. The oblique lines represent the multiple regression line of K on wind velocity and thoracic mass, m_{th} , for values of m_{th} corresponding to the mean values for each species ($\log K = 0.23 \log \text{velocity} - 0.59 \log m_{th} - 0.73$). Filled points are actual values used to calculate the regression. Species are: 1a - *Anax junius* collected in Florida; 1b - *Anax junius* collected in Illinois (data not used to calculate regression but to test its predictive value - note K is below predicted at very high velocity); 2 - *Erythrodiplax berenice*; 3 - *Erythrodiplax connata minuscula*; 4 - *Libellula needhami*; 5 - *Miathyria marcella*; 6 - *Pachydiplax longipennis*; 7 - *Tramea carolina*.

Estimates of M are temperature dependent in *T. cynosura* (Table III). A real reduction at high T_a is possible, but I noted no increase in gliding. More likely the discrepancy is the result of inaccuracy in measuring T_{ab} owing to the small size of the abdomen, and to the increasing inadequacy at high T_a of the assumption that the temperature of each tagma, especially T_{ab} , is uniform. These insects probably regulate T_{th} by increasing circulation of warm hemolymph to the abdomen at high T_a (HEINRICH & CASEY, 1978), and this complicates the model of heat loss. Thus the calculations of M should be most accurate at low T_a , when the simplified model is likely to be most realistic.

Maximum estimated M is surprisingly high in *T. cynosura* (Table III), about twice the maximum value during shivering (cf. Table II), which itself is exceptionally high compared to shivering in other Anisoptera (MAY, 1979). Calculated M is also slightly higher than in other very vigorous fliers of comparable size, e.g. sphinx moths (0.56 W g^{-1} ; BARTHOLOMEW & CASEY, 1978) and euglossine bees (0.66 W g^{-1} ; CASEY, MAY, & MORGAN, in prep.). Further work is needed to confirm the accuracy of these data, but it seems certain that flight metabolism in *T. cynosura* is very high, especially considering its relatively low wing loading. The fact that maximum temperature excess (i.e., $T_{th}-T_a$) is appreciably greater than in other comparably-sized fliers (e.g., *Micrathyria atra*; MAY, 1977; *Miathyria marcella*; MAY, 1976) suggests that M is higher in *T. cynosura* than in these species.

Results for *A. junius*, by contrast, are lower relative to other insect taxa; e.g. a 1 g sphinx moth would be expected to expend about 0.40 W g^{-1} (BARTHOLOMEW & CASEY, 1978) and a euglossine bee of similar size about 0.36 W g^{-1} (CASEY, MAY & MORGAN, in prep.). However, the *A. junius* value is quite close to that expected in saturniid moths (0.25 W g^{-1} ; BARTHOLOMEW & CASEY, 1978). Metabolism is also much lower on a per gram basis than in *T. cynosura*. In part this is to be expected owing to allometric scaling of flight metabolism with mass; several studies have shown that within a taxon M scales with mass to a power less than 1.0 (reviewed by CASEY, 1981). In addition, as noted above, *T. cynosura* may have unusually energetic flight for its size. However, I also believe that the *A. junius* in this sample were not flying with maximal energy expenditure. Their thoracic temperature excess was appreciably lower than the maximum observed by MAY (1976) and lower than usual for the ambient temperature range at which they were collected, but T_{ab} was very little elevated above T_a , suggesting that the low T_{th} was not due to augmented heat loss but to reduced heat production. The dragonflies were flying at dusk in the lee of beach dunes, where, as GIBO (1981) showed, dragonflies may soar in updrafts, and in fact these *Anax* appeared to be gliding for a significant fraction of the time except when actually pursuing prey. This supports GIBO's suggestion that Odonata may take advantage of "slope soaring" to reduce energy expenditures in flight. Such behavior probably would not occur in dragonflies during territorial defense. Its occurrence does re-emphasize the need for caution in interpreting data on flight metabolism and also suggests that the present method of calculating M is sensitive to alterations in flight behavior.

Clearly, the data presented here are only a beginning. Additional information is needed on temperatures and heat exchange coefficients of these and other species, as well as on possible effects on body temperature of low levels of radiant heat input, implicitly assumed to be negligible here. Finally, it would be extremely valuable to obtain estimates of M that are independent of temperature and heat exchange data; this might be done by measurements of O_2 consumption during tethered flight in a container or possibly by means of heavy water exchange, as has been done with birds (UTTER & LEFEBVRE, 1973).

ACTIVITY AND ENERGY BUDGETS

Time/energy budget analysis makes it possible to quantify energy expenditure during different behaviors that occur in rapid and irregular sequence, and thus to discriminate subtle differences in the ways that energy is used by different species and individuals under different circumstances. Concurrent data can be gathered that reveal correlations of behavior patterns with energy requirements. This technique has been used with a variety of birds, especially nectarivorous species (*e.g.*, STILES, 1971; WOLF & HAINESWORTH, 1971; GILL & WOLF, 1975; WOLF, 1975), which are relatively easy to observe and lend themselves to quantitative estimates of energy intake as well as expenditure. Statistical estimates of uncertainty (TRAVIS, 1982), comparisons with energy intake estimates (WOLF, 1975), and comparisons with independent measurements of energy expenditure (UTTER & LEFEBVRE, 1973) confirm that time/energy budgets give an accurate picture of energy expenditure.

Male dragonflies, like birds, are easily observed at breeding sites, and their behavior can be quantified. Their activities encompass two distinct energy states — perching and flight. However, in contrast to birds, dragonflies defend mating territories for relatively short periods and often do not use them for feeding (PARR, 1980); parental care is non-existent. Males almost invariably outnumber females, as the latter generally appear only briefly to mate and oviposit. Because feeding and mating areas are often separate and because resting metabolism of insects is much lower than in birds, most energy costs associated with territoriality are probably devoted directly to territory defense (FRIED & MAY, 1983).

A few previous studies have produced quantitative time budgets of male Anisoptera at mating sites; these are summarized in Table IV. Some investigators only discriminated between flight and perching time, while others divided flight into functional subcategories. Although it is presently impossible to determine the differences, if any, in flight metabolism during, *e.g.*, chasing vs. patrolling, it is nevertheless useful to have a general idea of how flight time, and hence, approximately, energy, is allocated to different behavioral functions.

Table IV
Time budget data for male Anisoptera at breeding sites.

Species	% Time in Flight				Remarks	Reference
	Total	Patrol	Chase	Other		
<i>Aeshna cyanea</i>	100	—	—	—	Flier, averaged about 45 min/day at observed breeding site	KAISER, 1974
<i>Cordulia aenea</i>	100	—	—	—	Flier, aver. < 20 min/day at observed breeding site	UBUKATA, 1975
<i>Libellula luctuosa</i>	16	—	—	—	Range 7-18% throughout day	CAMPANELLA, 1975
<i>Libellula pulchella</i>	75	32	43	—	Total flight and chase time incr. w/ incr. in male density	PEZALLA, 1979
<i>Micrathyrina aequalis</i>	19	—	—	—	Range 8-25% throughout day	MAY, 1977
<i>Micrathyrina atra</i>	45	—	—	—	100% at T < 24°C to about 25% at T _a > 28°C	MAY, 1977
<i>Micrathyrina ocellata</i>	23	—	—	—	100% at T < 22°C to about 15% at T _a > 25°C	MAY, 1977
<i>Orthetrum coerulescens</i>	13	8	2	3	Included appreciable feeding; total incr. w/ incr. in temperature	PARR, 1983
<i>Orthetrum julia</i>	5	—	3	2	Included appreciable feeding	PARR, 1980
<i>Pachydiplax longipennis</i>	34	8	25	<1	Incr. from 10-40% w/ incr. in male density, due to incr. in chasing	FRIED & MAY, 1983
<i>Plathemis lydia</i>	49	—	—	—	At high density site (6% at low density); range 36-68% throughout day, highest at peak density	CAMPANELLA & WOLF, 1974

ENERGY BUDGETS AND REPRODUCTIVE BEHAVIOR

Predation on mature adult Anisoptera is infrequent (CORBET, 1963), and since they are carnivores, nutrients probably are not in shorter supply than energy. Thus, energy availability may limit gamete production or mating effort, and energy expenditure should be closely related to fitness costs. The data presented above suggest that in male *P. longipennis* most daylight hours not spent defending a territory are devoted to feeding. Confirmation by observations of marked

individuals would lend support to the hypothesis that reproductive effort is energy limited in this species and hence that energy requirements may be a major selective force on reproductive strategy.

How might variations in energy supplies and/or expenditures affect reproductive behavior? Concrete information is scanty, but I have tried to review the available data and to formulate some preliminary predictions about how adult dragonflies allocate energy and how this impinges on reproductive strategy. These are often very speculative and are perhaps best regarded as guides for future research. Table V lists the principal energy requirements for reproduction and indicates my best estimate of the relative magnitudes of each component for males and females. The terminology for major categories generally follows that of ALEXANDER & BORGIA (1979), but it should be borne in mind that I am concerned here with energy *per se* and only incidentally with other fitness costs and benefits.

Table V
Probable avenues of energy allocation and their estimated relative magnitude in male and female Anisoptera

Nature of Allocation	Relative Magnitude	
	Male	Female
Somatic effort (maintenance and feeding)	variable ^a	variable ^a
Gametes and associated structures	low	high
Other parental effort	nil	variable
Travel to oviposition area	nil	variable ^b
Site selection and oviposition	nil	variable
Post-copulatory interaction	nil	low
Other mating effort	high	low
Travel to mating area	variable ^b	nil
Mate searching and courtship	mod./high	low
Territory defense	mod./high	nil
Copulation and defense of mate	variable ^c	nil

^a Low in perchers, possibly high in fliers.

^b High for migrants, otherwise probably very low to moderate.

^c Probably low for the great majority of species.

Feeding should occur only if it results in a net gain in energy. When an energy profit is only possible at restricted times or locations there should be strong selection to feed at those times and/or places, with possible concomitant restrictions on the timing and location of reproduction. Profitability will also depend on

the energetic cost of feeding; the latter may constitute a large proportion of total somatic effort, *i.e.* the energy required for individual maintenance and for acquisition of resources.

Somatic effort is probably a small fraction of the total energy budget for most perchers, as in *P. longipennis*, owing to low resting metabolism and short total duration of feeding flights. Thus, at least in males, nearly all the energy intake is expended in reproductive effort (FRIED & MAY, 1983). The balance could be altered if prey were extremely scarce or hard to capture or if a more or less fixed lifetime reproductive effort were spread over an unusually long period of time (*e.g.* because of limitation of reproductive activity by weather, or to hedge against rapid and unpredictable changes in suitability of oviposition sites), during which the individual would have to maintain itself.

Fliers, on the other hand, remain constantly on the wing during both feeding and reproduction. The few available data suggest that precopulatory male mating behavior is of short daily duration (Table IV), although some species have long copulatory and post-copulatory associations that may represent major energy investments. There is no particular reason to think that investment in gametes differs greatly from that of perchers. Therefore, if feeding occupies much time its energy cost may be proportionately much higher than in perchers. To prove this, however, will require determination of total daily duration of feeding by marked individuals and assessment of the importance of reduction of flight metabolism by gliding during feeding. Also, fliers may feed during reproductive behavior; present evidence suggests that such feeding occurs but is infrequent (KORMONDY, 1959; KAISER, 1974; UBUKATA, 1975; but see HILTON, 1983). Another difficult but essential task will be to quantify rates of prey capture; these must almost certainly be far greater during a given feeding session than in the perchers studied heretofore.

Male dragonflies apparently do not contribute nutrients to their mates or offspring via ejaculates, and there is little to suggest that sperm itself is a major energy cost (although under exceptional circumstances sperm supply may limit fecundity; JACOBS, 1955). Thus I assume that ejaculate cost is minor. Females, by contrast, probably allocate most of their reproductive effort to gametes (ALEXANDER & BORGIA, 1979). This allocation has evidently never been quantified in energetic terms, but it is clearly high. Exophytic Anisoptera may produce 150 to over 5000 eggs in a single oviposition bout (KORMONDY, 1959; CORBET, 1963; McVEY, 1981; SHERMAN, 1984a; some of the highest totals probably represent the maximum possible production rather than the number normally deposited in nature). Females typically oviposit repeatedly during their life, sometimes several times in a single day (JACOBS, 1955; WAAGE, 1978; SHERMAN, 1984a). Eggs vary in size but often have an average radius of roughly 0.2 mm (TILLYARD, 1917; KORMONDY, 1959), suggesting an approximate volume of $3-4 \times 10^{-5} \text{ cm}^3$. Density must be at least 1 g cm^{-3} since eggs generally sink, so production of 1000 eggs represents 0.03 g, about 10% of the fresh mass of an average-sized libellulid female; this is obviously a major energy drain even if oviposition only occurs at intervals of several days (JACOBS,

1955; SHERMAN, 1984a). Females of endophytic species oviposit much more slowly and produce fewer eggs during their lifetime (CORBET, 1963; WAAGE, 1978).

Reproductive effort aside from gametes is conveniently divided into parental and mating efforts (ALEXANDER & BORGIA, 1979). Parental effort by males can be disregarded. Although territorial defense might result in protection of sites that are particularly suitable for larval development, it seems virtually impossible in practice to determine whether a male defends a territory in part to benefit his offspring or only because it is a good place to encounter females, which in turn select sites partly on the basis of their effect on larval success.

Non-gametic parental energy expenditure of females is very poorly known and probably quite variable. Daily movements between feeding or roosting sites and breeding sites (Table V) are probably not very costly for most species, as the former are often quite close to the latter (FINCKE, 1982; MILLER, 1982; personal observations), although feeding may also occur several miles from apparently suitable oviposition sites. Dispersal during the maiden flight, while occurring during the prereproductive period, is properly considered here and may be of greater significance in some cases. Certainly in migratory species, dispersal is probably a major energetic drain.

Energy costs of copulatory and post-copulatory interactions with males will depend on their length, on whether or not the female flies during them, and on the cost of flight, which may be quite different if in tandem than if alone. Since most species that copulate for long periods do so while perched (CORBET, 1963), and since during post-copulatory tandem females are generally ovipositing or resting, energy expenditures other than for oviposition are probably slight. They could be somewhat higher when oviposition is not in tandem and females must avoid interference from males, sometimes by leaving the oviposition site and returning later. Transfer of gametes may itself elevate metabolism, but this is probably negligible, especially for females, in the overall energy budget.

Oviposition and selection of oviposition sites may often represent the greatest energetic cost for females, apart from gametes. Many exophytic species hover while ovipositing and must then have high flight metabolism, but single oviposition bouts typically last only 1-3 min (e.g. JACOBS, 1955; SHERMAN, 1984a). Endophytic oviposition, as already noted, may last much longer, and the associated metabolic costs are entirely unknown. In addition to direct energy costs, prolonged oviposition might limit the time available for feeding and so have widespread indirect consequences for energy budgeting. The energy or time required to discover or move among oviposition sites might be significant in some cases, depending on the dispersion of suitable sites or substrates and perhaps on the presence of predators (WAAGE, 1979a; SHERMAN, 1984a) or, as noted above, on density of potentially interfering males.

Since females almost always have a full sperm complement when they appear at breeding sites (WAAGE, 1979b), the cost of getting there is properly parental rather than mating effort, as in males, except possibly for the initial copulation. Little is known about mate searching when mating and oviposition are spatially

separated (CORBET, 1963, 1980), but ordinarily these activities occur at the same place, and females generally are found at once by males, unless the female actively evades detection to allow undisturbed oviposition. Courtship is rare, and when it occurs it is generally brief and, as expected, the male is usually the more active partner (e.g. JACOBS, 1955; WILLIAMS, 1977).

In contrast to the cost of gametes and parental effort, mating effort is expected to predominate in males (ALEXANDER & BORGIA, 1979), and practically all observations of Anisoptera are consistent with this prediction. Access to females probably limits male reproductive success (CAMPANELLA & WOLF, 1974; PEZALLA, 1979; WAAGE, 1979a; see THORNHILL & ALCOCK, 1983, for a general discussion), so mate acquisition must usually receive the greatest allocation of energy (Table V). In most species females are most readily located at oviposition sites, so male mating effort should be critically dependent on the predictability in time and space of females at such sites (THORNHILL & ALCOCK, 1983). Fig. 3A outlines some of the factors, including energy constraints, that may influence female predictability.

Fig. 3B shows the major postulated determinants of male energy allocation. Female predictability primarily affects the benefits obtainable from a particular territory. If females are widely dispersed in space and time, maximum mating frequency is likely to be low and the opportunity to secure a disproportionate number of matings is slight. Very low population density coupled with random dispersion of females could necessitate high energy expenditure for mate searching, but males would be slightly if at all localized (KAISER, 1982), and little energy would be devoted to territory defense. On the other hand, if females are highly predictable in time and space, males that dominate favorable sites at the right time may enjoy considerably enhanced mating opportunities (CAMPANELLA & WOLF, 1974). Then a large expenditure of energy to secure control of a good territory at the optimum time may well be worthwhile. Consequently, average energy expenditure, and the proportion of energy devoted to aggressive interactions, should be correlated with maximum mating frequency and with variance in mating frequency, hence with female predictability. The scant available evidence supports this. Females are more predictable in time and space in *Plathemis lydia* than in *Libellula luctuosa*, and the former employs a more energetically expensive mating system (CAMPANELLA & WOLF, 1974; CAMPANELLA, 1975). The effect should be amplified if individual females carry large numbers of mature gametes, as this increases the stakes for each mating.

Within species, the effort devoted to territorial defense should be greatest at the times and places where females are most abundant, as CAMPANELLA & WOLF (1974) showed for *P. lydia*. In *P. longipennis* also, high male density, which entails high energy costs (FRIED & MAY, 1983), is correlated with high frequency of female visitation (SHERMAN, 1984b). Comparison of costs of territorial maintenance to spatial and temporal distribution of females might be used to test these hypotheses for both between and within species variation. It would also be of interest to know whether differences in energy expenditure

among males simultaneously present in the same small area are correlated with mating success.

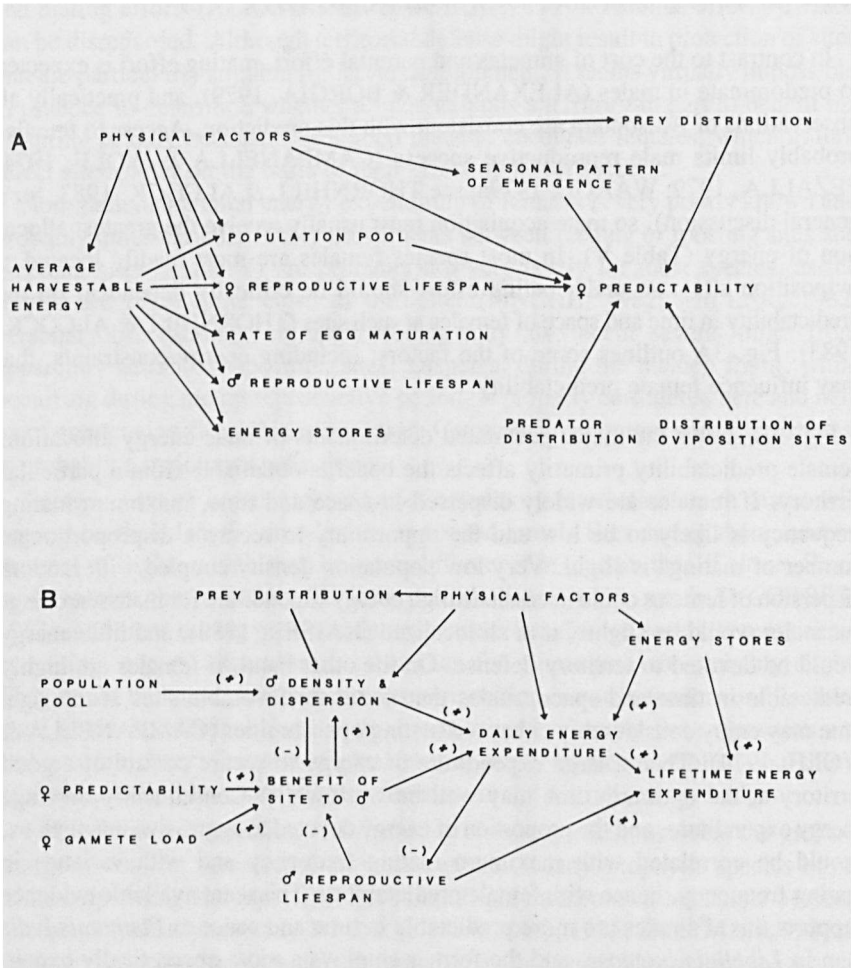


Fig. 3 A: Suggested influence of environmental, population, and life history characters on the predictability of female Anisoptera at mating sites. Both temporal and spatial aspects of distributions and predictability are to be considered. Also shown are possible effects of energy availability and the physical environment, especially temperature, on relevant biological properties of dragonflies. Not all possible parameters or interactions are indicated (e.g., distribution to prey will certainly be related to average harvestable energy), nor are all suggested relationships supported by data. For example, the population pool contributing to a given breeding site may well be determined by limitations acting on the larval population from which it arose rather than energy available to adults. B: Suggested determinants of male mating strategy and energy expenditure. Where appropriate, a (+) or (-) indicates that the driving parameter typically has a positive or negative effect, respectively, on the driven parameter; thus, e.g., it is suggested that long reproductive life reduces the benefit of any particular site at a given time, since time is available to search for alternative sites. Where no symbol is indicated, the direction of the effect is unpredictable or variable.

Mating sites of high potential benefit are likely to attract large numbers of conspecific males, which may in turn affect the realizable benefits of the site. In order to maintain territorial integrity, more energy must be devoted to defense as more intrusions occur (STILES, 1971; WOLF, 1975). FRIED & MAY (1983) showed that in *P. longipennis* the energy expended in territorial defense increases asymptotically with density owing to increased time spent chasing other males. Population density appears to be the primary determinant of energy expenditure in this species, and its importance has been documented also in *L. luctuosa* and *P. lydia* (Table IV). High male density might either increase attractiveness of a site to females, and thus its benefit to males, by increasing the likelihood of mating with a dominant male (THORNHILL & ALCOCK, 1983), or decrease attractiveness owing to excessive interference with oviposition. If energy expenditures and/or other associated costs exceed benefits, territories may be reduced in size or break down entirely (KORMONDY, 1959; PAJUNEN, 1966; CAMPANELLA, 1975; WALTZ, 1982). In the latter event expenditures might fall again, commensurate with the reduction in possible benefits as favorable mating sites are no longer defended.

In addition, excessive pressure from rival males may reduce male mating success (WARNER & HOFFMAN, 1980; E. WALTZ & L. WOLF, pers. comm., 1982; B. MACKINNON, pers. comm., 1984) by making copulation and mate guarding more difficult. If these behaviors are fairly lengthy and involve flight, especially hovering or support of the female in tandem by the male, energy expense is potentially significant (SAKAGAMI *et al.*, 1974; SHERMAN, 1983). However, since copulation and guarding are usually short compared to total duration of activity at the mating site, the effect on the male energy budget is probably slight (FRIED & MAY, 1983). Other costs, such as possible loss of mates or territories (THORNHILL & ALCOCK, 1983) may be more important.

Given a fixed energy intake, several kinds of tradeoffs are possible for males in the face of increasing energy demands of mating. For example, high energy mating behavior might require compensatory reduction in time devoted to reproduction. Among the closely related species, *Libellula pulchella*, *P. lydia*, and *L. luctuosa*, per cent time in flight (Table IV) is inversely correlated with total duration of time at breeding ponds (CAMPANELLA, 1975; PEZALLA, 1979). *Micrathyria atra*, with relatively high energy expenditure, has shorter daily tenure at mating sites than *M. ocellata* or *M. aequalis* (MAY, 1980). In male *P. longipennis* (FRIED & MAY, 1983; SHERMAN, 1983) and *Cordulia aenea* (UBUKATA, 1975) tenure decreases as density, and hence energy expenditure, increases. It is also possible that daily energy expenditures or other costs of mating have negative effects on reproductive lifespan (Fig. 3B). Then reductions in daily tenure at territories might increase longevity, so that total time devoted to mating would be relatively constant but, along with associated energy costs, spread over a longer period. Observations of marked males over a sufficiently long period of time could provide information on the relation of energy expenditure to daily tenure and longevity. FINCKE (1982) found that in *Enallagma hageni* mating frequency, and thus presumably mating effort, did not adversely

affect survivorship, but the mating system of these Zygoptera may be less energetically demanding than that of many Anisoptera.

If high rates of energy expenditure shorten the duration of mating efforts but are not always completely compensated by increased reproductive success, there might be selection for some or all males to reduce or abandon territorial defense, conserve their energy, and perhaps extend their reproductive life. This could explain the existence of the non-territorial, or wandering, strategy exhibited by a fraction of the males of some odonate species (HIGASHI, 1969; WAAGE, 1979a; PARR, 1980; E. WALTZ & L. WOLF, pers. comm., 1982; WALTZ, 1982, presents a different, but not incompatible, analysis of this strategy).

Distribution of prey could affect male mating costs by its effect on cost of travel to mating sites and by its possible effect on dispersion of male territories (NOMAKUCHI & HIGASHI, 1983), although I expect both effects to be small, again excepting migratory species.

Finally, physical conditions may restrict mating activity (LUTZ & PITTMAN, 1970) and influence male density (E. WALTZ & L. WOLF, pers. comm., 1982). In species that regulate body temperature endothermically, energy costs of territory maintenance can vary sharply with temperature (MAY, 1977). This may affect temporal distribution of males and females, male:female ratio, and male tenure at breeding sites (MAY, 1980). Ectothermic species, on the other hand, may be forced to spend most of their time perched and basking at low temperature (PARR, 1983; PEZALLA, 1979) or may have to perch to avoid overheating at high temperature (MAY, 1976; HEINRICH & CASEY, 1978; PEZALLA, 1979); in either case the ability to defend a territory and interact with potential mates must be affected. Solar radiation intensity and wind velocity might also alter activity patterns. Since oviposition rates may be extremely temperature sensitive (MCVEY, 1981), the value to a male of a given mating and the cost of mate guarding might also depend on thermal conditions. In other words, the physical environment affects the costs of territory maintenance, the benefits, and the physiological ability to capitalize on benefits. Thus the mating strategies of these insects operate under significant physical constraints and the latter must be determined to understand the former.

ACKNOWLEDGEMENTS

I wish to acknowledge the kindness of Mr. B.I. MACKINNON, Dr. K.J. SHERMAN, and Dr. E.C. WALTZ for access to their unpublished data or manuscripts. Thanks also to Dr. JON WAAGE for valuable criticism and advice and to Dr. T.M. CASEY for discussions of the heat exchange model and for reading an earlier version of part of this paper. Dr. H.T. STREU, Chairman, Department of Entomology & Economic Zoology, Rutgers University, made funds available for me to attend the VII International Symposium on Odonatology. New Jersey Agricultural Experiment Station Publication No. F-08001-02-83, supported by State funds.

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APPENDIX

Definition and dimensions of symbols used in text.

Symbol	Definition	Dimensions
C	Energy equivalent of food consumed	(Joules)*
E	Rate of evaporative heat loss	Watts
FU	Energy equivalent of feces and excreta	(Joules)*
H	Heat content	Joules
K**	Cooling constant	minutes ⁻¹ or seconds ⁻¹
M	Rate of energy metabolism	Watts
m**	Mass	grams
P	Energy equivalent of growth, including reproduction	(Joules)*
Q ₁₀	Approximately equivalent to ratio of values of M at 10°C intervals	dimensionless
R	Energy equivalent of respiration	(Joules)*
s	Specific heat of tissue	Joules gram ⁻¹ °C ⁻¹
t	Time	minutes or seconds
T _a	Air temperature	degrees Celsius
T _b	Body temperature, body region not specified	degrees Celsius
T**	Temperature	degrees Celsius
W	Rate at which work is performed	Watts

* Units are not stated or implied in text, but those given in parentheses are appropriate for the parameter defined.

** Subscripts ab, h, and th indicate that the parameter is a property specifically of the abdomen, head or thorax, respectively.