

**FOOD INTAKE AND ADULT FEEDING BEHAVIOUR
IN *CALOPTERYX SPLENDENS* (HARRIS)
AND *ERYTHROMMA NAJAS* (HANSEMANN)
(ZYGOPTERA: CALOPTERYGIDAE, COENAGRIONIDAE)**

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The gut contents of the 2 spp. were examined at a riverine site near Oxford, U.K., during June and July 1991. Individuals were captured in the field and dissected in the laboratory. The mass of gut contents was found to be a useful measure of feeding activity for the spp. concerned. Daily food intake was highly variable within the populations. A full gut could represent a considerable addition to the fresh body weight. Most feeding occurred from 10.00-16.00 h (BST). Differences between sexes were generally small in comparison with the total variation in feeding activity. Teneral fed less than non-tenerals in both spp. In ♀ *C. splendens* feeding activity increased until reproductively mature. Gut content analyses should prove useful for studying many aspects of feeding behaviour in a wide range of spp.

INTRODUCTION

Foraging constitutes one of the major activities of adult Odonata (CORBET, 1962, 1980; MAY, 1984) but has received relatively little attention from biologists. A more complete knowledge of foraging behaviour (reviewed in CORBET, 1980) is required to understand the constraints on adult behaviour in general. However a broad approach to foraging studies raises difficulties: with the exception of territorial males (see FRIED & MAY, 1983; HIGASHI, 1973; PARR, 1980, 1983) individuals seldom remain active in a single locality. They are thus not easily observed for any length of time.

This study shows that a solution to this problem may lie through the analysis

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of gut contents (e.g. FRIED & MAY, 1983; PRITCHARD, 1964). Here, such analyses are performed on whole populations of two sympatric Zygoptera species. These methods allow not only a broadening of taxonomic scope in foraging studies but also comparisons between individuals of different sex and maturity. Such information could enhance our ability to tackle the major questions in odonatology in the coming years.

METHODS

Individuals of *Calopteryx splendens* and *Erythromma najas* were captured in the field with a butterfly net and killed in a dry killing jar. They were later dissected in the laboratory and the gut removed below the head. The guts were placed on a filter paper to remove extraneous fluid and then weighed (all weights are fresh weights). Measurement errors caused by differential drying and loss of gut contents were small (up to 0.2 mg and 0.7 mg respectively) relative to the total variation in gut weights (up to 45 mg). Such errors helped justify the use of fresh weight measurements. Where appropriate, the sex, body weight and state of maturity were noted. Two indicators of maturity were taken in females. Firstly the weight of the ovary after dissection was measured. Secondly individuals were placed in age categories using morphological features noted by HEYMER (1973) and MCGEENEY (1986). Identifying degrees of maturity in males was more problematic and only teneral and non-tenerals were distinguished. The characters used are summarised in Table I.

Table I
Characters used to denote age class

Age class	Female		Male	
	<i>C. splendens</i>	<i>E. najas</i>	<i>C. splendens</i>	<i>E. najas</i>
I	Pale colour, soft cuticle, opaque wings	Pale colour, soft cuticle, opaque wings	Teneral	Teneral
II	Bright green colour, tough cuticle, glossy wings	Orange thorax, tough cuticle, glossy wings	Not teneral	Not teneral
III	Bright green colour, tough cuticle, matt wings	Orange thorax, tough cuticle, matt wings	Not teneral	Not teneral
IV	Bronze colour, tough cuticle, crisp wings	Olive green thorax, tough cuticle, crisp wings	Not teneral	Not teneral

Sampling was limited to sunny days. Diel activity was studied on 4th June and 6th July (all times are BST). Samples comparing feeding activity in females of different maturity were taken between 13.30 and 17.30 h on 20th, 28-29th June and 17th July. Further samples for measuring the throughput of gut contents were taken on 16-17th & 30th June, and 2nd & 5th July.

HABITAT

Odonate populations were studied on a tributary of the river Thames at Oxey Mead about 4 km NW of Oxford City. There was little surface vegetation on the river in June but in July the river surface became covered with a mat of vegetation comprising filamentous algae (*Spirogyra* sp.), pondweed (*Elodea* sp.) and yellow water lily (*Nuphar lutea* L.). This provided Odonata with territorial and oviposition sites. By the river banks was a zone of thick vegetation up to 2 m tall and 10 m wide comprising mainly emergent vegetation and nettles (*Urtica dioica* L.). Beyond lay a short-grass meadow separating the riverside zone by about 100 m from the nearest tall vegetation. Odonata were abundant in the riverside vegetation, but only rarely were they observed resting in or flying over the meadow. The two subject species formed part of a diverse odonate community at the study site. In June and July 15 species were seen in total, of which 9 showed evidence of breeding.

RESULTS

FOOD INTAKE

There was great variation in the fresh body weights, gut weights, and ovary weights of both species (Tab. II). The weight of the gut plus contents accounted for 44.8% of the variance in body weight in *Calopteryx splendens* (regression $y=118.4+1.69x$, $p<0.01$), and 30.4% of the variance in *Erythromma najas* (regression $y=65.9+2.83x$, $p<0.01$). Maximum gut weight in *C. splendens* constituted 20.6% (males) and 22.5% (females) of the maximum body weight. In *E. najas* the corresponding values were 16.3% (males) and 16.7% (females).

DIEL ACTIVITY

An important assumption in the interpretation of the results was that gut contents represented the feeding activity of the day on which an individual was collected. An experiment was performed to justify this assumption. Individuals were collected in the field

Table II
Body, gut and ovary weights (in mg) by sex over the whole study

Species (sex)		Body	Gut	Ovary
<i>C. splendens</i> (♂)	Mean:	128.7	9.67	
	SE:	1.98	0.56	
	Max:	142.4	29.40	
	Min:	109.4	1.78	
	n:	23	136	
<i>C. splendens</i> (♀)	Mean:	148.6	15.21	9.59
	SE:	3.36	0.68	0.80
	Max:	202.5	45.52	43.90
	Min:	103.9	1.05	0.05
	n:	47	179	122
<i>E. najas</i> (♂)	Mean:	71.91	4.05	
	SE:	0.79	0.19	
	Max:	101.6	16.61	
	Min:	58.22	0.42	
	n:	85	178	
<i>E. najas</i> (♀)	Mean:	86.82	6.42	9.25
	SE:	2.17	0.36	0.62
	Max:	123.6	20.64	21.96
	Min:	55.67	0.47	0.05
	n:	71	141	92

at the end of sunny days, and placed in a cage in the laboratory. They were then killed at intervals to determine whether guts were emptied during a single night. Guts were largely emptied after only a few hours although some contents lingered in the gut for longer periods (Fig. 1). However, these quantities were not great (a maximum of 18.3% of the maximum gut weight after 16.5 h in *C. splendens*, and 25.8% of the maximum after 16 h in *E. najas*). Sampling across several days probably increased the variance in subsamples, giving the appearance of "kinks" in the downward trend in gut weight over time (Fig. 1).

On 4th June (Fig. 2) both species showed significant changes in gut weight during the day (*C. splendens* $F_{(6,6)}=6.69$, $p<0.05$) (*E. najas* $F_{(6,6)}=4.52$, $p<0.05$). This is clear evidence of feeding activity. The greatest changes were from 12.00-15.00 h. The patterns are remarkably similar in both species. There were 12h of sunshine, and no rain occurred. Maximum shade temperature was 15.7°C, and wind speed reached 9.7 km/h⁻¹. (Weather data are from the Radcliffe Meteorological Station in Oxford City). No reproductive activity was seen, presumably because both species were not far enough advanced in their maturation.

On 6th July (Fig. 3) again there were significant changes in gut weight during the day (*C. splendens* $F_{(7,7)}=2.98$, NS but difference between 06.00 and 12.00 h $t=4.26$, $df=18$, $p<0.01$) (*E. najas* $F_{(6,6)}=5.55$, $p<0.01$). *C. splendens* showed great-

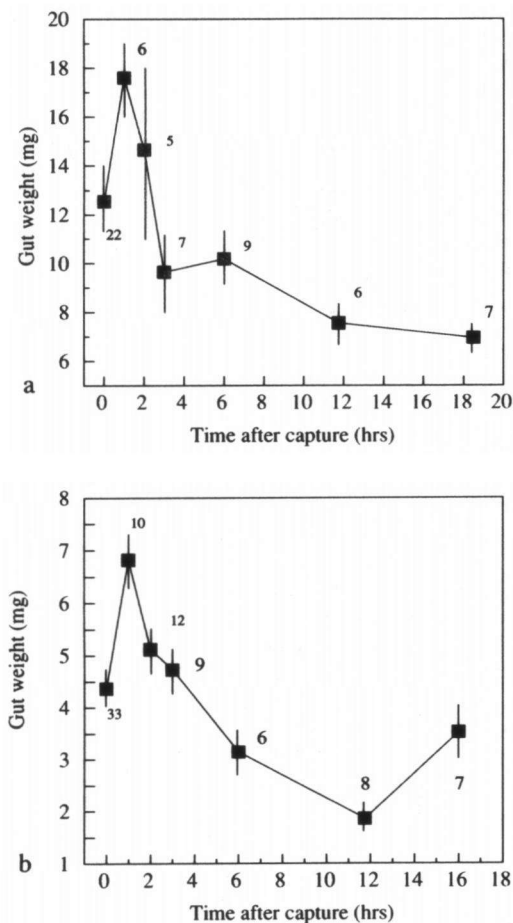


Fig. 1. Throughput of gut contents (mean \pm SE): (a) *C. splendens*; - (b) *E. najas*. - [Numbers denote sample sizes].

est changes 10.00-12.00 h, *E. najas* showed greatest changes 14.00-16.00 h. There were 12.6 h of sunshine, and no rain occurred. Maximum shade temperature was 23°C and wind speed reached 4.8 km/h⁻¹. Table III gives a qualitative measure of reproductive activity through the day. Peak activity was noted at 12.00-13.00 h. Neither species showed evidence of feeding between those times (mean decreases in gut weight).

DIFFERENCES BETWEEN SEXES

No significant differences in peak gut weight between males and females were found for either species on any one day (4th June $t=1.48$, $df=7$, NS [*C. splendens*]; $t=1.41$, $df=7$, NS [*E. najas*]); (6th July $t=1.90$, $df=25$, NS [*C. splendens*]; $t=0.359$, $df=25$, NS [*E. najas*]). The complete data set (Tab. II) suggests that females in general feed more than males, but such data were collected at a variety of times and under different conditions. No significant differences were identified in the timing of feeding between females and males on 4th June ($F_{(1,6)}=0.45$, NS [*C. splendens*]; $F_{(1,6)}=2.72$, NS [*E. najas*]). However, female *C. splendens* fed significantly earlier than males on 6th July ($F_{(1,7)}=5.82$, $p<0.05$). The same trend falls just short of significance in *E. najas* ($F_{(1,6)}=5.62$, $F_{(0.05)}=5.99$).

DEGREE OF MATURATION

On 4th June teneral were found to feed less than non-

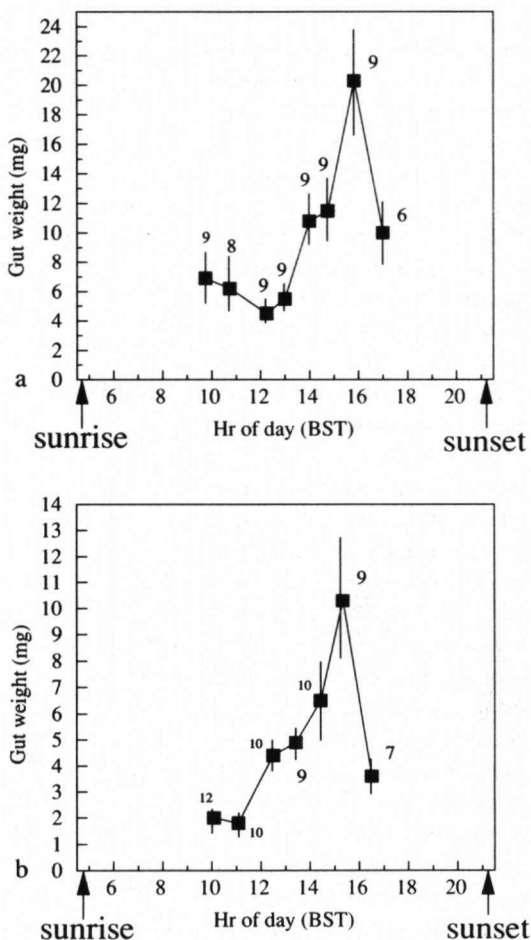


Fig. 2. Change in gut weight over the active period on 4th June (mean \pm SE): (a) *C. splendens*; - (b) *E. najas*. - [Numbers denote sample sizes].

-tenerals in both species (*C. splendens* $t=3.93$, $df=5$, $p<0.05$; *E. najas* $t=2.66$, $df=7$, $p<0.05$). Figure 4 shows the relationship between gut weight after feeding and ovary weight for female *C. splendens* (polynomial regression gives a significantly better fit than linear regression). Feeding activity increases with ovary weight but only up to a point (regression $y=8.48+1.34x-0.03x^2$, $r^2=0.262$, $p<0.01$). Figure 5 indicates that this point corresponds with age class III. This is the class at which reproductive maturity is reached (HEYMER, 1973). No significant relationship between gut weight and ovary weight emerges for *E. najas* (regression $y=5.32+0.14x$, $r^2=0.042$, NS).

DISCUSSION

In this study gut contents have demonstrated many aspects of adult feeding behaviour which would have proved impractical by direct observation. The most consistent theme from the results was the variability in food intake within populations. Two sources of this variability were identified: sex and maturity. Of these the effect of maturity was more marked and widespread than that of sex. Information like this helps to identify the factors which constrain adult behaviour; one of the major challenges in dragonfly biology today (see MAY, 1984).

Previous work on food intake in Odonata has centred on the Libellulidae (FRIED & MAY, 1983), and suggests that daily food consumption is 10-15% of body mass in territo-

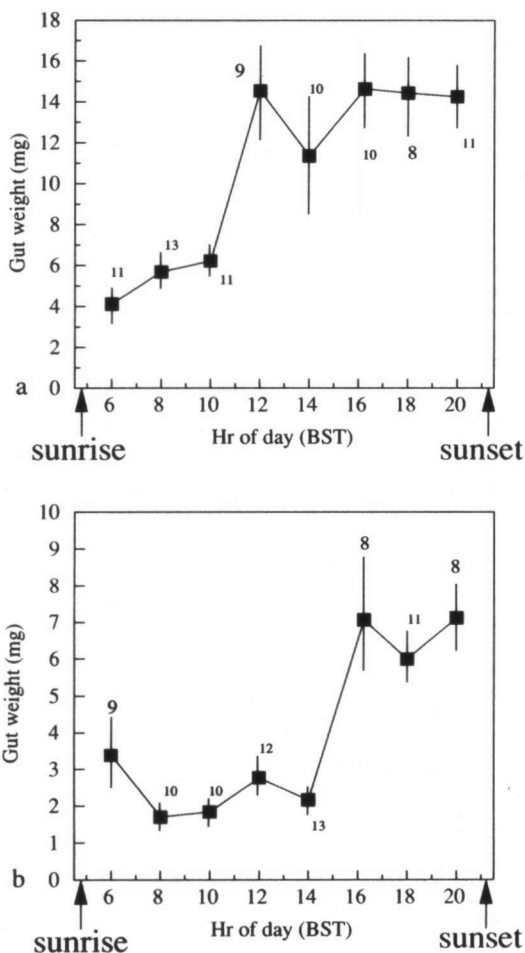


Fig. 3. Change in gut weight on 6th July (mean \pm SE): (a) *C. splendens*; - (b) *E. najas*. - [Numbers denote sample sizes].

Table III
 Presence of reproductive behaviours in *C. splendens* (C) and *E. najas* (E) in a 10 minute observation period each hour on 6th July

Time of day (h)	Flight	In tandem	Territorial aggression	Copulation	Oviposition	Intense activity over water
06.00						
07.00						
08.00	E					
09.00	C & E					
10.00	C & E	E				
11.00	C & E	C & E	C & E	E		
12.00	C & E	C & E	C & E	C & E	E	C & E
13.00	C & E	C & E	C & E	C & E	E	C & E
14.00	C & E	C & E	C & E	C & E	E	
15.00	C & E	C & E	C & E	C & E	E	
16.00	C & E					
17.00	C & E					
18.00	C & E					
19.00	C & E					
20.00	C & E					

rial males. These values do fall within the range of results identified in this study. Fresh weight estimates for *Calopteryx splendens* and *Erythromma najas* suggest maximum values greater than indicated in previous studies, and imply a weight

cost to intense feeding activity. Maximum gut weights (relative to body weight) in *C. splendens* are greater than in *E. najas*, and are consistent within species for males and females. This may be attributable to differences in species metabolic rates such as suggested by SUKHACHEVA et al. (1988).

The food intake of dragonflies reflects both environmental limitations on feeding behaviour and the metabolic needs of the animal (MAY, 1984). In the past there has been a tendency to emphasise the role of environmental limitations (e.g. LUTZ & PITTMAN, 1970;

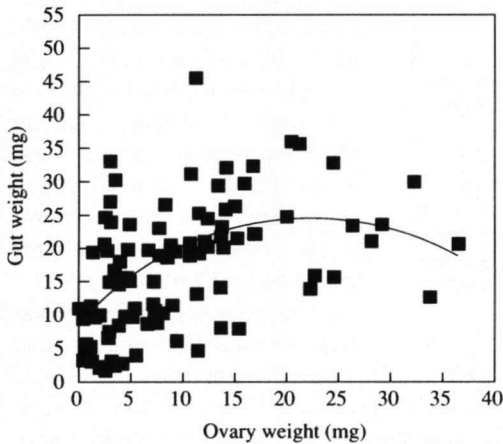


Fig. 4. Gut weight against ovary weight in female *C. splendens*. — [Line fitted by polynomial regression ($y=8.48+1.34x-0.03x^2$, $r^2=0.262$, $p<0.01$).

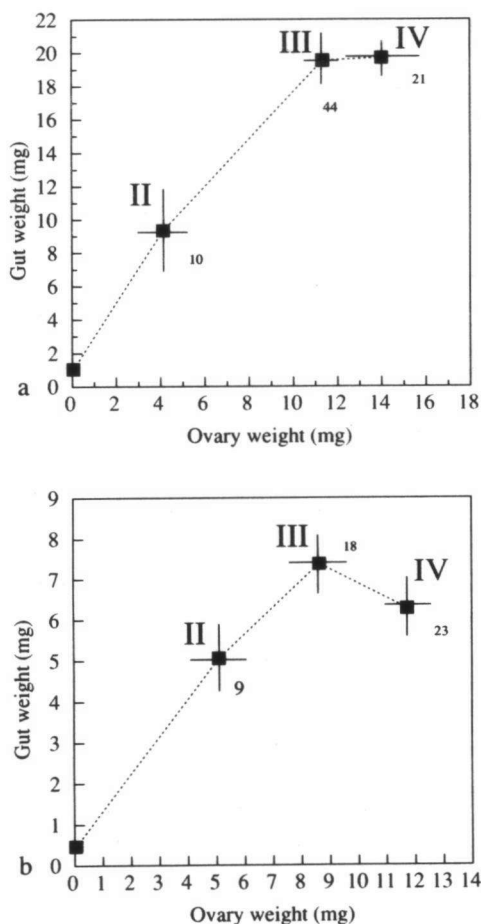


Fig. 5. Gut weight against ovary weight per age class II-IV (mean \pm SE and sample size): (a) *C. splendens*; - (b) *E. najas*. - [Lines originate at smallest recorded ovary and gut weight because adult Odonata emerge with empty guts and immature ovaries; see CORBET, 1962; TILLYARD, 1917].

MAY, 1977), and these play a primary role in regulating diel rhythms in activity (CORBET, 1962). In this study most feeding was from 10.00-16.00 h; times which probably present the optimum environmental conditions for flight.

However feeding activity may often reflect a compromise between the need for a healthy energy budget and the need to perform other activities such as reproduction (see WAAGE, 1988; MARDEN & WAAGE, 1990). The most common activity rhythms probably involve feeding peaks either side of a midday peak in reproductive activity (CORBET, 1962), although markedly different patterns have been reported both in feeding (e.g. MILLER et al., 1984; NEAL & WHITCOMB, 1972; Dr M.J. Parr, pers. comm.), and reproductive activity (e.g. MAY, 1977, 1980; MILLER, 1982). On 6th July neither species showed evidence of feeding activity when reproductive activity was at its height around midday. These patterns therefore conform to the most common patterns identified by CORBET (1962).

Knowledge of how feeding varies with maturation is sparse and based on scattered observations. ASKEW (1988) states that immature individuals spend "much" time feeding and that mature individuals allocate "a part" of each day to feeding. The major energetic requirements in female Odonata probably come from repeated egg provisioning (MAY, 1984). It might, therefore, be expected that feeding activity should peak with reproductive maturity. Results for *C. splendens* conform well to these expectations. However, no definite patterns

emerged for *E. najas*, except that food intake is lower in teneral than non-tenerals.

Failure to identify marked differences in food intake between the sexes suggests either that feeding behaviour is limited by feeding opportunities (unlikely given that they are generalist predators [CORBET, 1980]) or that the metabolic requirements of males and females are approximately equal at a given stage of development. Territorial activity forms the major metabolic requirement in males just as egg provisioning does in females (MAY, 1984). However, small differences between the sexes may have been masked by the total variability in food intake. The timing of behaviour differed between sexes on 6th July, when reproductive activity was prominent (females fed earlier than males). Similar patterns were found by MICHIELS & DHONDT (1989) in the libellulid *Sympetrum danae* (Sulz.), which they related to differences in mate-finding tactics between the sexes. If mate-finding tactics are a primary cause of differences in reproductive activity, and feeding and mate-finding are competing activities, then differences in feeding behaviour may be expected. Males may be constrained to defend a territory at the expense of feeding activity, where females are under no such constraints.

Consideration of feeding activity in this study has shown how a detailed explanation requires a knowledge of environmental conditions, the state of the animal's metabolism, and the influence of competing activities. It is perhaps becoming clearer that to deal successfully with one aspect of dragonfly behaviour involves considering many other facets of their biology.

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