Behav Ecol Sociobiol (1995) 37: 39–44 © Springer-Verlag 1995

Michael T. Siva-Jothy · David Wingfield Gibbons
Deborah Pain

Female oviposition-site preference and egg hatching success in the damselfly *Calopteryx splendens xanthostoma*

Received: 30 April 1994 / Accepted after revision: 18 March 1995

Abstract By removing males and controlling the rate of water flow past oviposition patches in an experimental area, we showed that female *Calopteryx splendens xanthostoma* preferred to oviposit in fast flowing water rather than slow flowing water. A series of manipulations revealed the fitness benefits to females for this preference: eggs placed in fast-flowing water developed significantly faster and showed significantly lower mortality than eggs placed in slow-flowing water. A major factor determining this difference was the deposition and growth of encrusting algae which prevented the successful hatching of eggs in slow-flowing water.

Key words Female choice · Oviposition · Damselfly
Water flow rate · Egg survival

Introduction

The question of whether females are choosing males or the resources those males defend has been addressed in a variety of systems, most notably birds. Examples of two systems where females do not appear to base their reproductive decisions on resource quality are the polygynous marsh wren *Cistothorus palustris* (Leonard and Picman 1988) and the socially monogamous swallow *Hirundo rustica* (Møller 1990). In such species females choose between males on the basis of male secondary sexual traits (Alatalo et al. 1990; Møller 1990; Aarvidsson and Neergaard 1991). However, even when selection favours the evolution of male secondary sexual traits they do not necessarily influence choice independently of resource quality (Searcy 1979) and there is evidence that both male and resource characteristics interact to determine choice (e.g. Moss et al. 1988; Yasukawa 1981). Even when it is possible to untangle the interaction between male traits and resource quality, it is often difficult to determine the components of the resource on which females base their decisions.

Female *Calopteryx splendens xanthostoma* oviposit endophytically into the stems of several freshwater angiosperms, e.g. *Ranunculus penicillatus* and *Potamogeton nodosus*. As with other calopterygids, males guard patches of weed from conspecific males and, after a period of courtship, attempt to copulate with females that visit their patch (Zahner 1960; Pajunen 1966; Heymer 1973; Waage 1973, 1987; Gibbons and Pain 1992). In order to oviposit, females must gain access to a suitable patch (which is usually preceded by copulation with the resident male). Two studies have shown that calopterygid damselflies have very high levels of last male sperm precedence achieved via sperm removal during copulation (Waage 1979; Siva-Jothy and Tsubaki 1989): male *C. s. xanthostoma* remove rival sperm from the female's main sperm storage organ before insemination (Siva-Jothy and Hooper 1995) and most of the eggs laid by a female *C. s. xanthostoma* after copulation at an oviposition site are fertilised by the copulating male (R.E. Hooper and M.T. Siva-Jothy, unpublished work). When a female *C. s. xanthostoma* arrives at a defended oviposition site the resident male performs a characteristic display during which he usually lands on the water's surface adjacent to the oviposition patch and floats passively downstream. After a few seconds he flies off the water, back to the starting point and often repeats the performance several times. The female either eventually accepts his copulatory advances, or flies away.

M.T. Siva-Jothy (✉)
Dept. of Animal and Plant Science, University of Sheffield, Sheffield S10 2UQ, UK

D.W. Gibbons[1]
Station Biologique de la Tour du Valat, Le Sambuc, Arles 13200, France

D. Pain
RSPB, The Lodge, Sandy, Beds., SG19 2BR, UK

Present address:
[1]RSPB, The Lodge, Sandy, Beds., SG19 2BR, UK

Observations of a population of *C. s. xanthostoma* on the river Vidourle in southern France suggested (i) that females preferred to oviposit in those patches of weed found in the fastest-flowing parts of the river and (ii) that males fought most frequently for the patches in the fastest-flowing water (Gibbons and Pain 1992). If the best-quality males gained access to the patches in the fastest-flowing water, the female preference for oviposition site could be due to preference for either male quality or territory quality, or both. There are at least three ways in which some of the criteria for female choice could be experimentally determined whilst controlling for variation in male quality. Firstly males could be assigned to territories at random, as done by Alatalo et al. (1986). Secondly territory quality could be manipulated whilst keeping the same male in residence throughout. Finally, female preference could be measured whilst territory quality was manipulated in the absence of males. The last option is only apt in situations where the female can exploit the resource in the territory without the presence of the male.

Because male calopterygid damselflies are highly mobile it was not possible to assign males to territories or to manipulate territory quality whilst keeping the same male resident, since males often deserted following a decrease in flow rate (Gibbons and Pain 1992). However, females are able to utilise oviposition sites in the absence of males because most have sperm stored from previous copulations. *C. s. xanthostoma* is therefore amenable to the third type of manipulation.

If a female preference for a particular flow rate is demonstrated, the next logical question is "what fitness advantage does that preference confer?". Female calopterygids lay their eggs into plant material, so the eggs are fixed in the oviposition substrate until they hatch. The larvae, on the other hand, are mobile and so can move into favourable, or out of unfavourable, parts of their habitat. Oviposition site selection will therefore have a profound effect on egg development and/or hatching success, and little effect on larval survival. We would therefore expect any female preference for flow rate parameters to be correlated with some aspect of egg survival.

We manipulated egg clutches to determine the effect of flow rate on egg development rate and hatching success and measured several abiotic and biotic parameters that might influence development and hatching success. These manipulations allowed us to evaluate the phenomena which influence egg survival and which are correlated with flow rate.

Material and methods

Sites

Observational data from 63 territories of *P. nodosus* were collected between 1 and 18 July 1986 at a site (site 1) on the river Vidourle in southern France (see Gibbons and Pain 1992 for full details of methods). The experimental fieldwork on female choice was conducted between 1 and 18 July 1989 on the same river but at a site further upstream (site 2). Experiments on egg hatching success and development were conducted in 1990, 1992 and 1993.

Natural variation in female oviposition site preference

We measured flow rate ($m s^{-1}$), depth (m), and area of substrate (m^2) for each territory (as described below) at site 1 and scored the total number of oviposition events (one or more females ovipositing simultaneously) per oviposition patch between 10 30 and 18 00 hours EST during 41 sampling events through the area during this period.

Female oviposition site preference experiment

A 16 m (long) × 4 m (wide) dam system (site 2a) was constructed which consisted of two channels: one experimental and one bypass. The channels ran parallel to the direction of the current and the rate of flow of water through the experimental channel was controlled by the placement of wooden sluice gates. When the experimental channel was designated "slow flow" a series of upstream gates deflected the water into the bypass channel. When the channel was designated "fast flow" the sluice gates were placed across the bypass channel.

The experimental channel contained 25 oviposition patches of *R. penicillatus*: approximately half were transplanted from other parts of the river without any apparent effect on the plants' health during the course of the experiment. A 10 m (long) × 7 m (wide) stretch of river (site 2b) approximately 50 m upstream of site 2a was used as a control area which consisted of a central belt of 18 natural oviposition patches with a 1-m strip on each bankward side devoid of oviposition sites.

The experiment was conducted over 9 days. During the first 2 days the dam system was fixed for "slow flow" and during the second 2-day period the dams were altered for the "fast flow" treatment. There was then a 1-day break (to allow females access to males) followed by two more 2-day experimental presentations of "fast flow" followed by "slow flow" (reversal of first protocol). No manipulations were performed at site 2b.

Immediately prior to each daily experimental period all *C. s. xanthostoma* males were removed from the experimental and control areas with nets (mean = 88 males day^{-1}; range 59–194). Any male which moved into either of these areas during observations was immediately removed. Captured males were kept in a darkened cool box and released at the end of each daily observation period.

Both the experimental and control areas were watched continuously during each experimental day from 1200 to 1800 hours EST and the number of females ovipositing in each was recorded. A female was considered to be ovipositing if she held the distal portion of her abdomen under water in the characteristic calopterygid oviposition position for more than 1 min. Once scored as having commenced oviposition the female was removed from the site and kept in a darkened cool box before being marked and released at the end of the observation period: females caught and marked during the experiment were not observed ovipositing on subsequent experimental days. Females were removed after 1-min of oviposition because ovipositing female calopterygid damselflies are known to attract others to a site (Waage 1987): our protocol ensured that each oviposition was statistically independent.

We did not make observations of oviposition behaviour in the presence of males at sites 2a and 2b, however we did observe this behaviour at an additional upstream site (site 3). Observations at site 3 (10 m × 5 m, 19 territories) were made continuously from 1030–1800 hours for 2 days and were undertaken to determine whether the timing of ovipositions was similar in the presence and absence of males. The number of males holding territories and the number and duration of ovipositions were recorded.

Measurement of abiotic parameters

The maximum surface flow rate past each oviposition site in the experimental area (site 2a) was measured using a impeller driven "Ott Minor" laboratory current meter (calibrated by Hydraulics Research, Wallingford, Oxford, UK). The depth of water beneath each experimental site was measured daily whilst the area of each patch was measured once under slow conditions, and once under fast conditions.

Maximum surface flow rate was measured at ten randomly chosen sites in the control area (site 2b) to determine how the flow rate in the river varied during the course of the experiment. Measurements of temperature and dissolved oxygen were made at fast and slow flow sites to determine how these abiotic parameters fluctuated over the diel cycle. Measurements were made with a thermocouple device accurate to 0.1 °C (Jenway 2003) and a dissolved oxygen meter (Bibby), respectively.

Effect of water flow rate on egg development/hatching

Experiment 1

We collected stems of *R. penicillatus* immediately after females had laid eggs into them. These stems were tethered with thin nylon mono-filament and randomly assigned to one of two treatments, either "fast flow" (~ 0.4 ms^{-1}) or "slow flow" (< 0.04 ms^{-1}). The stems were left for 14 days (the average duration of development to hatching in unmanipulated ovipositions) and then removed for scoring the relative development index (RDI) of the eggs in each stem. (All stems were removed and cleaned of debris by one experimenter, and presented to another who scored egg development, hatching success/predation with no knowledge of the experimental treatment). Stage of development was scored against eggs of known age collected from natural stems in high quality territories (i.e. territories that were most fought over): diagrams of the developing embryos were made for each day, and these were used as the standards by which other developing embryos were scored (Fig. 1). Eggs were scored as hatched if they showed a terminal split in the chorion (hatching line) and an empty transparent egg shell. Eggs were scored as dead if they were opaque and white, or if they showed any form of chorion rupture other than a hatching split. Our measurement of development, RDI, looked at developing eggs over a 14-day period: we scored a hatched egg (nominal 15-days) as 100% developed, a dead egg as 0% developed and, for eggs showing reduced development, the appropriate daily fractional percent of their development (e.g. an egg showing only 10 days development after 14 days would be scored as (10/15) × 100% = 66% developed). RDIs for each stem in each treatment were calculated using this method. Although RDI obscures certain aspects of the data, it provides a single, realistic measure of overall development rate.

Experiment 2

Experiment 2 was identical to experiment 1 except that it was run for 18 d (i.e. until all eggs had either hatched or died) and that stems were not cleaned of debris. We measured % death for each stem in each treatment.

Deposition rate of encrusting algae

We attached several 10-cm strips of 1-mm diameter nylon monofilament in "fast flow" and "slow flow" enclosures. These monofilaments were collected after 14 days and placed in 5% paraformaldehyde solution. All material (mainly algae) attached to the monofilament was removed by sonicating the strands for 2 h: the debris was then centrifugally washed and subsequently dried in a 40 °C oven for 24 h.

The length of each strip of clean monofilament was measured and extrapolated to a surface area. The dry weight of algae deposited per unit surface area was then calculated for each strip in each treatment.

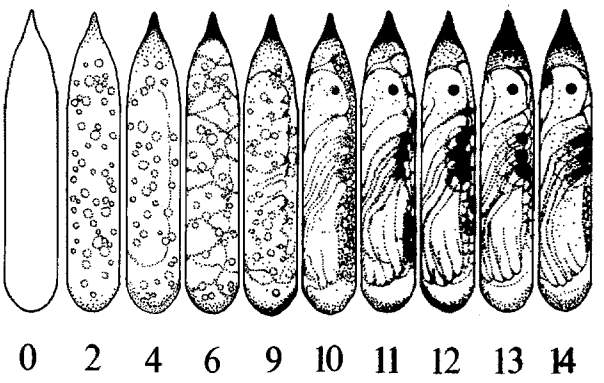


Fig. 1 Morphological changes in embryos with time used to evaluate relative development index (RDI). *Arabic numerals* denote days since laying: the development occurred in *Ranunculus penicillatus* placed in fast-flowing water . Day 0 – translucent egg; day 2 – droplets visible in egg, micropyle darkening; day 4 – outline of embryo evident, tip of micropyle dark brown; day 6 – evidence of segmentation in embryo; day 9 – embryo clearly visible with evidence of major body divisions; day 10 – eye-spot visible, disappearance of large droplets, tightly packed "cells" on dorsum of embryo; day 11 – evidence of labial mask, "cells" on dorsum break down, darkening on dorsal surface of thorax evident; day 12 – eye-spot complete, legs clearly distinguishable, labial mask apparent but incomplete; day 13 – labial mask complete, but teeth unsclerotised; day 14 – all body features clearly identifiable, including labial mask with sclerotised teeth and frontal margin

Scanning electron microscopy

Stems were collected from different experimental treatments and fixed and stored in 3% glutaraldehyde. They were subsequently washed, post-fixed in osmium tetroxide, washed, critical-point-dried and sputter-coated in gold. Micrographs were taken with a Philips PSEM 500.

Results

Unmanipulated oviposition events

There was no significant correlation between substrate area and oviposition events ($P = 0.19$) or depth and oviposition events ($P = 0.29$) at site 1. However, flow rate showed a highly significant correlation with oviposition events ($r = 0.58$, $df = 61$, $P = 0.0001$).

Female oviposition site preference and water flow rate experiment

During "fast" presentations in our experimental enclosure we were able to increase the flow rate by approximately 5.5 times its value during "slow" presentations (Table 1). In the experimental enclosure the number of ovipositions recorded during fast presentations was twelve times that during slow

Table 1 Abiotic and biotic parameters during the 9-day experiment on female oviposition preference. Means are presented ±SD

Day of experiment	1–2	3–4	6–7	8–9	1.2.8.9	3.4.6.7	*P*
Presentation	Slow	Fast	Fast	Slow	Slow	Fast	
Flow rate (ms^{-1})							
Experimental ($n = 25$)	0.07 ± 0.04	0.37 ± 0.16	0.40 ± 0.20	0.07 ± 0.03	0.07 ± 0.03	0.39 ± 0.18	< 0.0001[a]
Control ($n = 10$)	0.30 ± 0.11	0.33 ± 0.14	0.36 ± 0.12	0.30 ± 0.10	0.30 ± 0.10	0.34 ± 0.12	< 0.01[a]
Water depth (cm)							
Experimental ($n = 25$)	12.6 ± 2.8	11.0 ± 2.9	10.5 ± 2.6	13.7 ± 2.9	13.3 ± 2.8	10.8 ± 2.7	< 0.0001[a]
Patch area (m^2)							
Experimental ($n = 25$)					0.52 ± 0.51 Days 1–4	0.60 ± 0.49 Days 6–9	< 0.1[a]
Number of ovipositions							
Experimental	2	13	11	0	$\chi^2 = 10.1$	$\chi^2 = 9.3$	
Control	29	19	8	10	Combined $\chi^2 = 19.4$ with 2 *df*		< 0.0001

[a]Paired *t*-test, two tailed

presentations (Table 1). It is highly unlikely that the differences in oviposition bouts between the "slow" and "fast" presentations in the experimental enclosure were due to daily variation in the number of gravid females in the population since the number of ovipositions in the control area (site 2b) showed a decreasing trend during the experimental period: overall there was a highly significant difference between the number of oviposition events in fast flow and slow flow, taking into account the fluctuations in the control area (Table 1). Moreover the temporal distribution of oviposition behaviour in the absence of males (site 2a) was not significantly different from that when males were present (site 3; Kolmogorov-Smirnov test, $z = 1.06$; $P = 0.61$) suggesting that our experimental data reflected the normal temporal pattern of oviposition behaviour.

Our manipulations of flow rate in the experimental area (site 2a) had two unforeseen consequences. Firstly, when the flow rate was slowed in the experimental area there was a "knock on" effect in the control area upstream (site 2b) which also slowed down (by 0.04 $m\,s^{-1}$). This effect was significant (Table 1) but small in comparison to the difference between the two experimental set ups. Secondly, slowing the rate of flow through the experimental area resulted in a significant increase in water depth during the slow presentations (Table 1). However, this change did not result in a significant change in the area of the oviposition substrate during the slow presentations.

Egg RDI, mortality and water flow rate experiments

Experiment 1

The daily water flow rate through the fast enclosure was 0.39±0.02SD $m\,s^{-1}$ ($n = 27$), and showed no significant difference between day 1, day 5 and day 9 of the experiment (Kruskal-Wallis test, $H = 0.089$, 2 *df*, $P = 0.89$). The water flow rate in the slow enclosure was too slow to detect with our flow meter (< 0.04 $m\,s^{-1}$, $n = 27$). The differential between fast and slow treatments was maintained at this level in all subsequent experiments.

There was a significant effect of water flow rate on the development rate (RDI) of eggs (arcsine transformed data, 2-tailed *t*-test, $t = 2.1$, 45 *df*, $P = 0.041$): eggs in the fast flow treatment had a higher RDI (87.3 ± 3.3 SD, $n = 23$) than eggs in the slow flow treatment (77.5 ± 4.3, $n = 24$).

Experiment 2

There was a significant difference (Mann-Whitney *U*-test, $U' = 22$, $z = 2.17$, $P = 0.034$) in percentage mortality of egg clutches between the fast flow (1.32 ± 1.3, $n = 5$) and slow flow (36.2 ±17.6, $n = 5$) treatments in this experiment. The reason for the elevated death rate in the slow treatment was that although the larvae developed to hatching and actually emerged from their egg shells, they could not break through the mucilage and algae on the stem surface, and died in the space between the egg and the encrusting algae.

Deposition of encrusting algae and flow rate

There was a highly significant difference (2-tailed *t*-test, $t = 2.78$, 16 *df*, $P = 0.013$) in the amount of encrusting algae deposited (dry weight per unit surface area) on nylon monofilament over a 14-day period between fast flow (1.55 ± 0.43 $\mu g\,mm^{-2}$, $n = 8$) and slow flow (63.4 ± 19.8 $\mu g\,mm^{-2}$, $n = 10$).

The effect of water flow rate on algal deposition is illustrated in Fig. 2, which shows stems (with eggs) kept for 14 days in fast and slow enclosures: the emergence holes in the "slow flow" stem have become obscured with algae and debris.

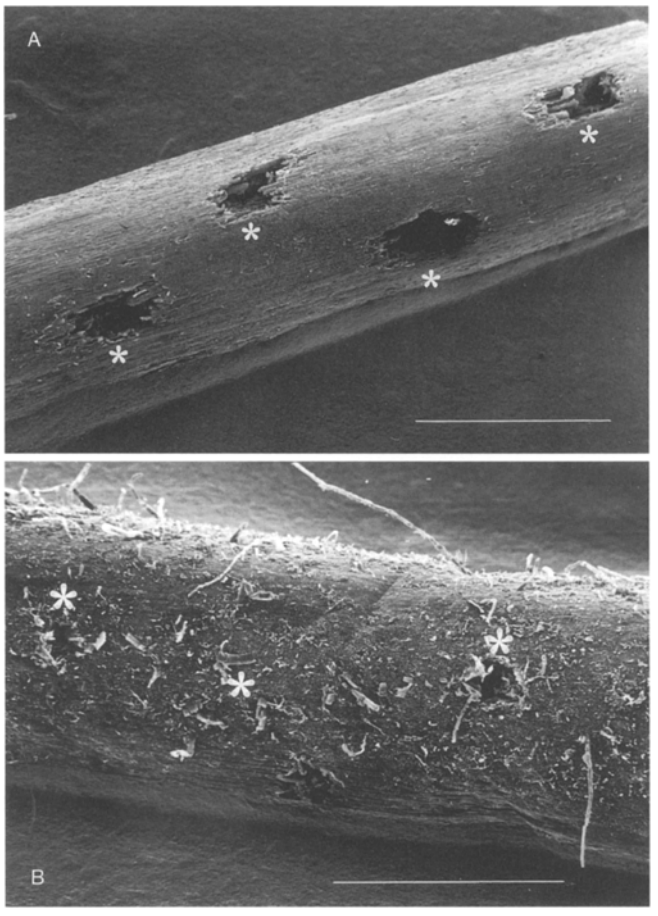


Fig. 2 Scanning electron micrographs of the vegetative stems of *R. penicillatus* containing eggs of *C. s. xanthostoma* **A** stem kept in fast-flowing water (~0.4 m s^{-1}) for 14 days: the *oviposition scars* (*), through which the larvae emerge, are clearly visible and the stem is clean and free of detritus. **B** Stem kept in slow-flowing water (< 0.04 m s^{-1}) for 14 days: the surface of the stem is covered in algae and detritus to the extent that the *oviposition scars* (*) are only just visible and the emergence hole is greatly reduced in size. *Scale bars* 1 mm

Diel fluctuation in temperature and O_2 with flow rate

Measurement of these variables through the day and night revealed considerable variation through the diel cycle in both parameters (dissolved O_2 max/min = 8.5/5.2 mg l^{-1}; temperature max/min = 24.3/19.5 °C), but no significant difference in the diel variation in dissolved oxygen concentration (Kolmogorov-Smirnov test, $z = 0.204$, 2 *df*, $P = 0.84$) or temperature (Kolmogorov-Smirnov test, $z = 0.408$, 2 *df*, $P = 0.68$) between each flow rate treatment.

Discussion

The results strongly suggest that female *C. s.xanthostoma* prefer to oviposit in fast-flowing water. Female oviposition-site preference was influenced by increasing the rate of water flow through an area in which the number, and mean area, of potential oviposition patches remained constant. The preference for fast water was not a consequence of male phenotype (since males were excluded) nor was it the result of females being attracted to suitable oviposition sites by already ovipositing females (since females were removed soon after commencing oviposition).

It is possible that females preferred to oviposit in shallow water, regardless of the flow rate, since our manipulation resulted in significantly shallower water in the fast treatment. Female damselfly oviposition preference is influenced by water depth in *Enallagma hageni* (Fincke 1986) where females prefer to lay in deep water because the vegetation in the pools that this species utilise are less liable to dry up when the water level drops: in contrast, females of our study species preferred to lay in substrates during the fast treatment, during which water levels dropped. More importantly, the observational data on flow rate, depth and area of 63 oviposition sites suggests that water depth, and oviposition area are not critical factors for oviposition site choice in *C. s.xanthostoma.*

The most conspicuous part of courtship in *C.s.xanthostoma* is the male's "floating" display where he lands on the water surface adjacent to the oviposition site and floats downstream for a few seconds. Gibbons and Pain (1992) suggested that this display provides females with information about the flow rate past the oviposition patch, thereby enabling the female to make a decision on the suitability of that site. The results presented here indicate that females can assess the flow rate without recourse to the male or his display: we suggest that if the male display functions to indicate water flow rate then it "amplifies" this environmental signal (*sensu* Hasson 1989). Such amplification would enable females to rapidly assess the suitability of oviposition sites whilst exposing themselves to fewer risks, and might also provide information about the quality of the displaying male.

The submerged egg is the only non-mobile stage in the life-cycle of this damselfly: it spends approximately 14 days at the site of placement before the larva hatches. During this time the embryo is highly susceptible to adverse fluctuations in the biotic and abiotic environment. Females will consequently be under strong selection pressure to deposit their eggs in sites which are unlikely to be subjected to adverse conditions during the period of egg development and hatching. Eggs which developed in fast-flowing water showed a significantly higher RDI (overall development rate) than eggs in slow-flowing water. As well as developing more slowly, the presence of encrusting algae on the surface of stems in slow-flowing water resulted in significantly greater mortality (35%) of the larvae during hatching compared to hatchlings in fast-flowing water. Both of these effects are likely to be important

factors influencing female oviposition-site preference and possibly the male "floating" display which may have evolved to allow females to rapidly assess the rate of water flow through an oviposition patch.

Although the temperature and dissolved oxygen content of slow- and fast-flowing water showed no difference in the pattern of variation throughout the diel cycle, there will be a difference in oxygen availability to the embryo because of the difference in the "boundary effect" caused by the difference in water flow (fast-flowing water supplies oxygen to the egg at a faster rate than a similar slow-flowing medium because the layer of stationary water around the egg is thinner when water flows fastest; e.g. Fox et al. 1937). This difference will be greatest at night, when the plant in which the egg is laid is not undergoing photosynthesis. Restricted access to oxygen during embryonic development (as a consequence of the boundary effect and the encrusting algae) may account for the difference in development rates between eggs in fast- and slow-flowing water.

Acknowledgements This work was supported by travel grants from The British Ecological Society and The Royal Society. We would also like to thank Tim Birkhead, Alex Hanford, Rowan Hooper, Nico Michiels, Kate and Peter Miller and Mary-Anne Rose for their advice and assistance.

References

Aarvidsson BL, Neergard R (1991) Mate choice in the willow warbler – a field experiment. Behav Ecol Sociobiol 29:225–229

Alatalo RV, Lundberg A, Glynn C (1986) Female pied flycatchers choose territory quality and not male characteristics. Nature 323:152–153

Alatalo RV, Glynn C, Lundberg A (1990) Singing rate and female attraction in the pied flycatcher: an experiment. Anim Behav 39:601–603

Fincke OM (1986) Underwater oviposition in a damselfly (Odonata: Coenagrionidae) favors male vigilance, and multiple mating by females. Behav Ecol Sociobiol 18:405–412

Fox HM, Wingfield CA, Simmonds BG (1937) The oxygen consumption of ephemerid nymphs from flowing and from still waters in relation to the concentration of oxygen in the water. J Exp Biol 14:306–320

Gibbons DW, Pain D (1992) The influence of river flow-rate on the breeding behaviour of *Calopteryx* damselflies. J Anim Ecol 61:283–289

Hasson O (1989) Amplifiers and the handicap principle in sexual selection: a different emphasis. Proc R Soc Lond B 235: 383–406

Heymer A (1973) Beiträge zur Ethologie und Evolution der Calopterygidae. J Comp Ethol 1973 Supp II:4–94

Leonard ML, Picman J (1988) Mate choice by marsh wren: the influence of male and territory quality. Anim Behav 36: 517–528

Møller AP (1990) Male tail length and female mate choice in the monogamous swallow *Hirundo rustica*. Anim Behav 39: 458–465

Moss R, Watson A, Parr R (1988) Mate choice by the hen red grouse *Lagopus lagopus* with an excess of cocks – role of territory size and food quality. Ibis 130:545–552

Pajunen VI (1966) Aggressive behaviour and territoriality in a population of *Calopteryx virgo* L. (Odonata: Calopterygidae). Ann Zool Fenn 3:201–213

Searcy WA (1979) Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). Am Nat 114:77–100

Siva-Jothy MT, Hooper RE (1995) The disposition and genetic diversity of stored sperm in females of the damselfly *Calopteryx splendens xanthostoma* (Charpentier). Proc R Soc Lond B 259:313–318

Siva-Jothy MT, Tsubaki Y (1989) Variation in copulation duration in *Mnais pruinosa pruinosa* Selys (Odonata: Calopterygidae). 1. Alternative mate-securing tactics and sperm precedence. Behav Ecol Sociobiol 24:39–45

Waage JK (1973) Reproductive behaviour and its relation to territoriality in *Calopteryx maculata* (Beauvois) (Odonata: Calopterygidae). Behaviour 47:240–256

Waage JK (1979) Dual function of the damselfly penis: sperm removal and sperm transfer. Science 203:916–918

Waage JK (1987) Choice and utilization of oviposition sites by female *Calopteryx maculata* (Odonata: Calopterygidae). Behav Ecol Sociobiol 20:439–446

Yasukawa K (1981) Male quality and female choice of mate in the red-winged blackbird (*Agelaius phoeniceus*). Ecology 62:922–929

Zahner R (1960) Über die Bindung der mitteleuropäischen *Calopteryx* Arten (Odonata, Zygoptera) an den Lebensraum des strömenden Wassers. II. Der Anteil der Imagines an der Biotopbindung. Int Rev Hydrobiol Hydrogr 45:101–123

Communicated by R. Montgomerie