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LIFETIME REPRODUCTIVE SUCCESS, WEATHER AND FITNESS IN DRAGONFLIES*

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There are more studies of mating or reproductive success of dragonflies than of any other insects; their size and ability to be marked and watched renders them particularly suitable for such studies. – Laboratory studies on feeding and development rates of larvae indicate that well-fed larvae moult into larger animals and do so sooner than poorly fed individuals. – This trend is reflected in a decline in size at emergence through the season and in those adults arriving at a particular rendezvous to breed. – For many early emerging species the best weather for reproductive activity is at the end of their flying period, a time likely to be encountered by smaller adults. Weather is known to have a major influence on lifetime reproductive success of dragonflies. – It seems that the "best" larvae, those that emerge first, suffer reduced reproductive activity because later emergers experience better weather and consequently obtain more matings. – The present paper explores this apparent paradox and attempts to resolve it.

INTRODUCTION

There have been more studies of lifetime mating or reproductive success in dragonflies than any other insect order (e.g. FINCKE, 1982, 1986; BANKS & THOMPSON, 1985, 1987; HAFERNIK & GARRISON, 1986; KOENIG & ALBANO, 1987; McVEY, 1988). Studies of lifetime mating success are usually accomplished by marking as many individuals of a population as possible, and noting through the whole breeding season, which animals mate together. Because they are relatively big, easy to mark and watch at discrete breeding sites, and in temperate regions at least they are relatively short-lived, dragonflies and damselflies are particularly suitable subjects for the study of lifetime mating success.

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Estimates of lifetime mating or reproductive success are important from the point of view of an evolutionary biologist because they enable something rather close to fitness (the "Holy Grail" of evolutionary biology) to be estimated. This is not the case with the more usual short-term measures of mating success (e.g. THOMPSON & BANKS, 1989). In *Coenagrion puella*, BANKS & THOMPSON (1985a) showed that small males achieved a higher daily mating rate than large males, but that large males live longer than small males, and living longer compensates for reduced daily mating rates. Anyone simply studying short-term mating success in this species would have concluded, wrongly, that small males did better than large males. FINCKE (1982) and THOMPSON (1989) have intimated that there may be stabilizing selection on male size and FINCKE (1988) showed that to be true for *Enallagma hageni.*

Dragonfly biologists have been particularly successful in obtaining estimates of lifetime mating or reproductive success. These estimates have exposed deficiencies in short-term measures of reproductive success and have been obtained in a few weeks, whereas comparable data for birds and mammals may take years to gather. Thus dragonflies are apparently ideal animals in which to study lifetime reproductive success.

However, there are problems for entomologists, in general, and odonatologists, in particular, in estimating anything between reproductive success and fitness. The main one is that it is not possible to track the fates of the offspring. This is certainly the case for insects with aquatic larval stages and a large number of instars, like dragonflies. The aim of this paper is to explore some of the consequences of this problem, and in particular a paradox that exists for some northern European species.

LARVAL FEEDING, DEVELOPMENT AND EMERGENCE

Laboratory studies on feeding and development rates of damselfly larvae indicate that there are a number of responses to variations in prey consumed during an instar (LAWTON, et al., 1981; PICKUP & THOMPSON, 1984, 1990). The most obvious is that well-fed larvae complete any given instar faster than poorly-fed larvae. In addition, well-fed larvae show a greater percentage increase in head width at the moult than poorly-fed larvae.

So we might think of "good" larvae developing quicker and moulting into progressively relatively bigger larvae than "poor" larvae. Poor larvae are poor for a number of reasons, but one is likely to be that they are not able to establish themselves in areas of high prey density.

This trend is continued as far as emergence and beyond. A number of studies have demonstrated that larger animals emerge sooner than small animals and that consequently larger adults arrive at the breeding site before smaller adults (e.g. BANKS & THOMPSON, 1985b; GRIBBIN & THOMPSON, 1991a, 1991b).

WEATHER

Table I shows the 28-year mean temperature (1953-1980) from Bidston Observatory, Wirral, northern England. Although the weather in England is notoriously unpredictable, on average there are higher temperatures and more sunny days in July than June. This means that the adults that emerge from "good" larvae experience worse weather conditions than those from "poor" larvae.

Table I
28-year mean temperatures from Bidston Observatory, Wirral, northern England (1953-1980)

June	17.35°C
July	18.35°C
August	18.25°C
September	16.36°C

Weather is known to influence lifetime mating success in damselflies in at least 2 ways. THOMPSON (1990) showed that each 1°C rise in temperature within the range experienced added about 12 eggs to a clutch of eggs of *Coenagrion puella*. A clutch produced at an average temperature of 10°C contains 71% of the eggs produced at 15°C (around 200 eggs). As well as temperature, the number of sunny days experienced in adult life plays a major part in determining egg production, because reproductive activity only takes place on sunny days.

THOMPSON (1990) simulated the effects of weather on lifetime egg production using field estimated parameters for *C. puella*. Using the best field estimates of daily survival for *Coenagrion* of 0.85, it was possible to look at the effects of different weather conditions, specifically proportion of sunny days, on lifetime egg production. The results were that in good months lifetime egg production was around 750 eggs but in bad months it was under 350. The bad months are more likely to be Junes than Julys. Thus the "poor" larvae, those that did not feed well and developed slowly and emerged later, produced on average rather more offspring than the better fed, faster developers.

THE PARADOX

So the question we might ask then is, "Does it pay to be a poor larva, if this means emerging later in the season and experiencing weather conditions more suitable for reproductive activity?"

One of the problems with working with insects for those who would study lifetime reproductive success is that it is not possible to mark the larvae and follow them through the life cycle. But, we can guess at the fates of the larvae of early and late emerging adults from the results of laboratory experiments.

LARVAL COMPETITION

GRIBBIN & THOMPSON (1990) compared the development rates and head width increases at the moult of two larval instars of *Ischnura elegans*, (F-1) and (F-3), the two instars that early and late larvae might be expected to reach by autumn when growth stops. Larvae were maintained with a superabundance of food and either larvae from the same or the larger/smaller instar. The experiments were performed in small containers with either one or four perches, that is either "low" or "high" perch availability. The mean development times, and percentage head width increases at the moult, of small larvae in 4 treatments: (1) isolation, (2) in combination with other small larvae, (3) with small and large larvae, and (4) with large larvae, were measured. Small larvae suffered increased development times in the presence of large larvae, but not when in the presence of other small larvae. Development times of large larvae were not affected by the presence of small larvae. There was a significant reduction in percentage head width increase when small larvae were maintained with three large larvae. These interference effects were both reduced when there were more perches available so the mechanism of competition is likely to be that large larvae force smaller larvae into inferior fishing sites.

These experiments describe asymmetric intraspecific competition when there is an abundance of food available. They reflect what we might think of as one end, the more subtle end, of the spectrum of intraspecific effects. The other end of the spectrum, and the most extreme intraspecific effect, is cannibalism, which has been reported in odonate populations in the field from analysis of faecal pellets. Although not as terminal as cannibalism, a second phenomenon that can befall late larvae is that they miss the window of emergence altogether and have to spend a second winter as larvae. The survival prospects of the later part of a split cohort are unlikely to be high.

CONCLUSION

It is likely that the increased lifetime mating success of adults of late emerging larvae is more than counterbalanced by a combination four things:

(1) cannibalism – some offspring are likely to be cannibalised,
(2) small larvae being forced from preferred (safe) fishing sites, and following from that,
(3) the general high probability of being eaten by something, be it other odonates or fish, is higher the more time is spent in larval life.
(4) One more direct way in which late adults may suffer against early adults is in choice of oviposition substrate. At the end of the season many oviposition substrates are simply saturated with eggs so that late adults are forced to lay in sub-optimal locations (A. Martens pers. comm.; FINCKE, 1985, 1988). It is not clear how widespread this phenomenon is.

The resolution of the paradox is that success as a larva is more important in fitness terms than increased lifetime mating success as an adult. It may be that dragonfly behavioural ecologists will have to grasp the nettle and learn some DNA fingerprinting techniques to find whose larvae develop rapidly to emergence in the field. It is likely that RAPD fingerprinting results will soon be available for the tree-hole breeding species *Megaloprepus coerulatus*, in which FINCKE (1992) has already demonstrated that many 'successful' males, in terms of mating success, get zero fitness, in terms of offspring produced, from the tree holes they defend (O.M. Fincke, pers. comm.).

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