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THE REPRODUCTIVE BEHAVIOR OF *ARGIA VIVIDA* HAGEN: AN EXAMPLE OF A FEMALE-CONTROL MATING SYSTEM (ZYGOPTERA: COENAGRIONIDAE)

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At Halcyon Hotsprings in British Columbia, Canada, male *A. vivida* wait for females in the morning at sunlit basking sites on the forest floor, 10-15 m from water. Copulations last for an average of about 40 min, after which the pair remains in tandem for 2-3 hr before arriving at the oviposition site. This long copulation plus the latent period constitute "pre-oviposition guarding", a tactic that serves to keep females from other males until conditions at the water are suitable for oviposition. Males that are unable to capture mates in this way, arrive at the water at about the same time as the tandem pairs. They may then be able to copulate with a female who has escaped or is released from tandem. These afternoon copulations last for about 10 minutes and oviposition starts almost immediately afterwards. — Male *A. vivida* cannot control females' access to oviposition sites by controlling the sites themselves, because oviposition sites are too numerous and too widely dispersed, and males are not able to fly well enough to control them. Instead of resource-control, male *A. vivida* practice female-control, especially away from the water in the morning when the majority of matings occur. While this is the first study to view zygopteran mating behavior in this way, the strategy is probably widespread among zygopterans.

INTRODUCTION

Female animals may be assumed to exercise choice among the number of potential mates in a population. The evolutionary effect of this choice is controversial and largely unresolved (see, for example, contributors to BATESON, 1983). Part of the difficulty of studying the effect of female mate choice lies in discovering the criteria for choice and predicting the relationship between the criteria and the patterns of variation in reproductive success in the population. In attempting to understand these patterns of variation, one must first assume that females, in acting to maximize their fitness, will attempt to choose mates of the highest genetic quality available to them and that the high genetic quality of the chosen mate can be passed on to offspring.

In the simplest form of mate choice, females choose their mates solely on the basis of their genetic quality. Males might be expected to evolve displays of their quality to entice females to choose them over other male competitors. However, when a specific resource significantly determines female reproductive success, males might be expected to evolve tactics that influence female choice through possession of the resource. Or a male may be able to physically keep a female from other males, thereby making itself the highest quality male available. These approaches to female choice, which also involve intrasexual competition for the access to female choice, form the basis of four general types of mating strategies described by BORGIA (1979) as part of a general model of the effect of sexual selection on the evolution of mating systems.

Of the four types of strategy, the "female-control" strategy, whereby the male physically keeps the female from other males, is likely to apply to many zygopteran mating systems. But none has actually been viewed from this framework. We have predicted elsewhere (CONRAD, 1987) that when oviposition sites are numerous and dispersed over a wide area, when males are slow, weak fliers, and when male-female encounters are relatively rare, male damselflies are unlikely to be able to perform resource-control strategies. Instead, males should attempt to limit a female's mate choice by forcibly limiting the female's access to other males, rather than by limiting their access to resources needed for successful reproduction. The female-control strategy in damselflies should be characterized by the absence of courtship display, copulations that occur away from the oviposition site and are of long (>5 min) duration, contact postcopulatory guarding, females rarely ovipositing without a guarding mate, and little active female mate choice. The purpose of this paper is to examine these predictions, using the reproductive behavior of *Argia vivida* Hagen as an example.

METHODS

Argia vivida was studied as Halcyon Hotsprings (117° 52'W, 50° 36'N), 60 km south of Revelstoke, British Columbia, Canada. The area habitable for *A. vivida* larvae is restricted to a section of stream, 85 m long and 1-2 m wide. Nearly all adult activity occurs over the habitable area of the stream, on the adjacent stony slope, and in the forest nearby (Fig. 1).

Three 3-day observation sessions, separated by periods of 3-4 days, were spent at the site between July 10 and July 25, 1985, and six sessions, each separated by 10 to 14 days, from June 10 to August 13, 1986. Adults were captured singly and in tandem with a net, given an individual alpha-numeric mark on the left hindwing with waterproof ink, and released at the point of capture. These marks permitted "recapture" of the insects by observation with a pair of close-focussing binoculars, thereby

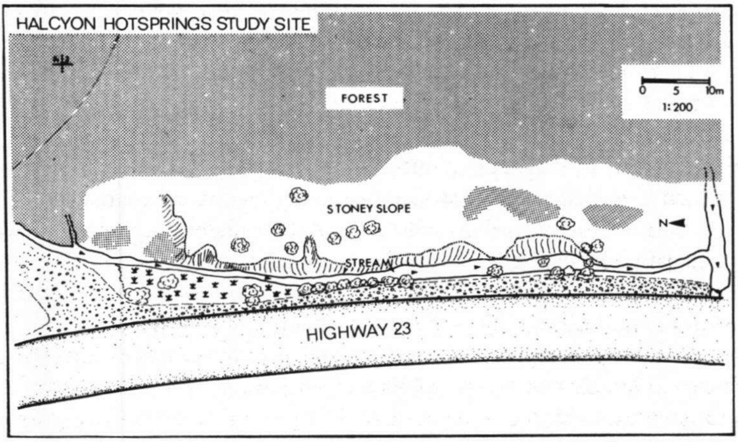

Fig. 1. Map of the Halcyon Hotsprings study site. The boundaries of the study area were defined by the highway and the confluences of the two cold streams with the hot springs effluent. The land slopes sharply uphill to the east (>10% slope) of the stream, far into the forest.

avoiding the need to rehandle them. Mark, mating status (tandem or non-tandem), time and location were recorded for all sightings, which were made while walking continuously during the flight period each day along a specified route, which took the observer throughout the study area every 20 min. These observations allowed daily activities and movements of damselflies to be described. In addition, timings of activities of 12 copulating pairs and 6 ovipositing pairs were made. Times of day are reported on a solar scale; at the time of the study, solar noon occurred about 1 h 50 min after Pacific Daylight noon.

THE PATTERN OF DAILY ACTIVITY IN *A. VIVIDA* AT HALCYON HOTSPRINGS

The pattern of daily movements of *A. vivida* is closely linked to reproductive behavior. At night adults roost high in the trees in the forest and solitary males first appear in patches of sunlight on the forest floor each day at approximately 0800. Females appear at about the same time and begin moving towards the oviposition site, but are intercepted by males who attempt to take them in tandem. By 1030 the majority of receptive females for the day are probably in tandem, and males that have not yet obtained mates continue moving to new basking sites in the grassy areas of the stony slope. Since far fewer copulations occur at ground level than there are pairs that appear at the water later in the day, it is assumed that females are taken in tandem and copulations occur high in the trees as well.

"Morning" copulations occur in the forest or high on the stony slope, 10-15 m from the water, and they last for about 40 min. By 1130 the first tandem pairs have appeared at the water, and within 90 min the density of tandem pairs at the water is too high to count. Solitary males are also abundant at the water from 1130 to 1300. They perch within a few cm of tandem pairs but rarely interfere with their activities.

After 1330 activity begins to decline. Females that escape or are released from tandem frequently fly rapidly and often straight up. Occasionally females that are ovipositing unguarded at the water are captured by males, copulate with them for about 10 min, and continue to oviposit with the new male contact guarding. Other females oviposit secretively and unguarded. A few males and females remain at the water until after 1500 and attempted matings continue to occur, but most of the oviposition at this time is by unguarded females.

DO MALES DEFEND RESOURCES?

It is difficult to decide whether the behavior of male *A. vivida* at sunspots can be called territorial in the sense that they are actively defending particular areas (NOBLE, 1939). These males pursue virtually everything small that flies past and so it cannot unequivocally be said that flights that are made against conspecific males are made in defence of the area. MOORE's (1952) suggestion of misdirected sexual pursuit has been discounted by many authors (including MOORE, 1964), but seems plausible in *A. vivida* where sex recognition by males seems weak at best (CONRAD, 1987). The resident male returns repeatedly to the same spot, but few remain at the same spot for very long. Sunspots are not as permanent as other landscape features such as oviposition sites. They vary in intensity, move and even disappear, and if an *A. vivida* male succeeds in capturing a female he can no longer defend the site. Nevertheless, quibbles over definitions apart, sunspots are clearly resources for males in that they provide locations where males can bask and raise their body temperature and be in a good position to intercept females. But they cannot be so easily construed as an important resource affecting female reproductive success. Although females may be attracted to sunspots early in the morning, they probably never get to use them and so sunspots cannot be considered an essential resource. In BORGIA's (1979) framework, males do not command a resource that is essential to female reproductive success.

ARE OVIPOSITION SITES INDEFENSIBLE?

An "exploratory phase" of oviposition has been observed in many coenagrionids, for example: *Argia apicalis* (BICK & BICK, 1965): *A. fumipennis atra* (BICK & BICK, 1982); *A. plana* and *A. moesta* (BICK & BICK, 1972); *Enallagma aspersum* and *E. exsulsans* (BICK & HORNUFF, 1966); *E. civile* (BICK & BICK, 1963). These species copulate near the water and pairs fly to the oviposition site immediately after copulation. There follows the exploratory phase during which pairs shift about frequently with tandem flights, periods of resting, and periods of probing of vegetation, but little oviposition. Ovipositing *Argia vivida* pairs also move frequently, rest often and probe vegetation, but these activities are interspersed with periods of oviposition, although these periods last for varying lengths of time.

Given the absence of a clear exploratory phase, the variability in proportion of total time actually spent ovipositing and the frequent changes in activity, we believe that oviposition sites for *A. vivida* are of highly variable quality and that high quality sites are unevenly dispersed. Thus it appears that males would have much difficulty defending high quality oviposition sites.

DOES MATING OCCUR AT THE OVIPOSITION SITE?

The two places where the chances of encountering females are highest are near the roosting sites and at the oviposition site. Males active at sunlit patches on the forest floor will have the first chance to capture females as they begin to move towards the water. Sunlit patches in the forest are not numerous and as males become more abundant later in the morning, more and more are forced to search for basking sites further down the slope. However, males on the stony slope after 0900 probably have little chance of intercepting a mate, although it is important to note that unmated males at any location — in the forest, on the stony slope, or at the water — will attempt to mate with any solitary female they encounter. Unmated males continue to move towards the water, arriving there at about 1130. Here they wait amongst the tandem pairs where there is a chance that a mate will become available. Should a pair form at the water, it flies 1-2 m away from the point of encounter (and the swarm of males that converged on the female) before mating. Thus, most mating occurs in the forest well away from the water, and even afternoon pairs remove themselves from the oviposition arena.

THE MATING BEHAVIOR OF *A. VIVIDA* AS A FEMALE-CONTROL SYSTEM

The conditions characteristic of a female-control mating system are present in the population of *Argia vivida* at Halcyon Hotsprings. The population itself is isolated and restricted to the study site by the lack of neighboring hot-springs within flight distance. Individuals are slow-flying and easily disturbed in flight by light winds. Oviposition sites are numerous but dispersed, and the weakly flying males are not able to defend them.

Males can be defined as territorial at sunny spots in the forest, although the territories are ephemeral and turnover of owners is high. It is not clear whether these territories are solely for mating purposes, but they do not appear to be used to control a resource needed by females. This distinguishes their function from territories in BORGIA's (1979) other mating system types.

Male-female encounters in the forest are infrequent. Males appear to have evolved the practice of pre-oviposition guarding as a means of holding females from the time they are first encountered until conditions are suitable for oviposition. "Morning" copulations occur far from the water and last much longer than "afternoon" copulations that occur nearer the water.

Postcopulatory guarding is of the contact type and females only infrequently oviposit unguarded. Females are very limited in their choice of mates, especially in the morning when they are forced to mate with almost any male that is able to capture them. They may not be so limited in afternoon matings, and the existence of afternoon strategies is important to male control of females in morning matings. Without the potential harassment by males at the water, females possibly could not be so readily forced to mate with males in the morning. The mating system of *A. vivida*, especially in the morning when the majority of matings occur, can be described as a female-control mating system.

The concept of female-control has not been previously recognized among the Odonata. Species practicising the female-control strategy will display a suite of inter-related characteristics which will allow rather detailed prediction of the mating behavior of a species from knowledge of a few characteristics. This suite of characteristics should prove useful in modelling the reproductive interactions of odonate species. In addition, BORGIA (1979) has provided the theoretical framework for modelling and understanding the role of mate choice in the evolution of female-control mating strategies.

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