THE UNIVERSITY OF CALGARY

COMPLEMENTARY MALE AND FEMALE MATING STRATEGIES OF

ARGIA VIVIDA HAGEN (ODONATA: COENAGRIONIDAE): AN EXAMPLE

OF A FEMALE-CONTROL MATING SYSTEM

BY

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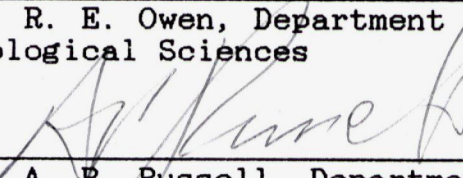
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "Complementary male and female mating strategies of <u>Argia</u> <u>vivida</u> Hagen (Odonata: Coenagrionidae): an example of a female-control mating system" submitted by Kelvin F. Conrad in partial fulfillment of the requirements for the degree of Master of Science.

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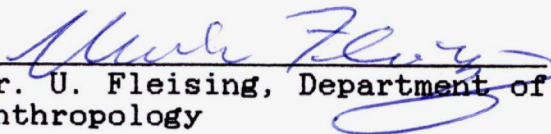## ABSTRACT

Following Borgia (1979: in Blum M. S. and N. A. Blum
(eds.) Sexual selection and reproductive competition in
insects. Academic Press, New York. pp. 19-80), the mating
systems of odonates are divided into four groups. The
feasibility of this classification rests on two assumptions:
(1) that female choice can be a potent evolutionary force,
and (2) that males can evolve mechanisms to limit female
choice. It was postulated from the mating system model,
that the species studied, Argia vivida, has a mating system
dominated by male control of female choice. That is, males
physically control females and do not permit them a choice
of mates. The reproductive behaviour of A. vivida was
recorded in an attempt to discern if males actually are able
to control female choice.

Female A. vivida occur as two colour morphs and both
sexes experience physiological colour change. Females of
either colour morph do not differ in body size and males
capture mates at random with respect to colour. The
hypothesis that the male-like female colour morph is more
attractive to males (pseudo-sexual selection) is discounted
but the hypothesis that the male "mimics" use their
appearance to avoid undue harassment while ovipositing
cannot be dismissed without further study. Males attempt to

seize almost anything moving and of the correct size, making both hypotheses unlikely. No reasonable function for the two female morph colours was found.

Female A. vivida mate more than once in a day and reproductive behaviour is divided into "morning" and "afternoon" matings. Morning matings involve long duration copulations far from the water while afternoon matings involve brief copulations with previously mated females and occurr near the water. The presence of morning and afternoon copulations suggests that both sexes might be practicing alternative reproductive behaviours. Males are not believed to alter their behaviour for morning and afternoon matings. They merely seek mates at a different time and place and so are not considered to be using two distinct reproductive behaviours. The idea that females practice alternative reproductive behaviours requires further study. Tentative reasons why females might want to give up the protection of their guarding mates to find others or oviposit alone are suggested.

It is concluded that males are able to physically control females to limit their mating descisions and that the classification scheme adequately describes the mating behaviour of A. vivida. The importance and implications of applying the scheme to other species is discussed briefly.

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I wish to thank my supervisor, Dr. Gordon Pritchard, for his valuable comments and kind advice, and for allowing me to follow my hunches and test my ideas freely, as strange as some of them may have been. I am greatly indebted to him for his support.

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I am grateful to Dr. Lawrence Harder for untangling several statistical Gordian knots, to Greg Fletcher for surveying the study sites and providing the original maps used in the study, and to Brent Dixon for having the patience to listen to so many of my ideas and help me sort them out.

Finally, I would like to thank Heather Proctor for helping me to stay organized and to stay on top of things, for her proofreading and useful comments and for always providing the right word when my thesaurus was out of reach.

DEDICATION

This work is dedicated to my parents

who never told me I couldn't or should

who taught me the joy of understanding how things happen

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INTRODUCTION

SEXUAL SELECTION AND THE EVOLUTION OF MATING SYSTEMS

A mating system may be loosely defined as the general behavioural patterns members of a population use to obtain mates (Emlen and Oring 1977). The behavioural patterns consist of a sequence of tactics, usually considered to have evolutionarily determined genetic components, and a sequence of these tactics is organized into a behavioural strategy (Dominey 1984). It is generally recognized that sexual selection has played an important role in the evolution of mating systems (Trivers 1972, Blum and Blum 1979, Bateson 1983, Thornhill and Alcock 1983).

Darwin (1859) coined the term "sexual selection" to explain differences between the sexes within a species. Because both sexes are subject to the same natural selective pressures, differences between them must result from another source. Darwin reasoned that the exaggerated armaments of males were used in combat between them for mates, and that extreme male adornment had as its purpose the attraction of females. The price of being poorly adorned or armed was not death to the individual (as would be the case of a trait selected against by natural selection) but rather was leaving few or no offspring (Darwin 1859).

Sexual selection has been implicated in the evolution of mating systems in both theoretical and empirical studies (Otte 1979, Searcy 1982). However, the role that the two components of sexual selection, intrasexual competition and intersexual mate choice, play in the evolution of mating systems is controversial. Theoretical studies often conflict (O'Donald 1980, Kirkpatrick 1982, Searcy 1982, contributors to Bateson 1983) and empirical studies (Bateman 1948, Thornhill 1979, 1980, Andersson 1982, Johnson 1982, Spiess 1982, Arnold 1983, Cade 1984, Boake 1986, Burley 1986, Finke 1986a, Majerus 1986, Houde 1987, Jones 1987, Pomiankowski 1987) have produced diverse results. How mate choice and intrasexual competition have influenced the evolution of reproductive behaviour, for the most part, remains to be resolved.

Wade and Arnold (1980) observed that research into sexual selection was directed toward one of three broad goals: (1) prediction of mating systems from environmental variables; (2) reconstruction of the phylogeny of sexually selected traits, including behaviours; and (3) discovery of the general principles governing the interactions between members of the same and opposite sex within a population.

Borgia (1979) studied the patterns of male-female interaction and incorporated these and resource structure into a general equilibrium model of mate choice. Borgia's

scheme is based on the criteria females use to choose their mates. In the simplest case, females base their choice on the genetic quality of males. Females are free to choose the "fittest" male as their mate from a number of males. Presumably the high genetic quality of the male can be passed on to offspring and this increases the chance of their survival.

On the other hand, males may evolve to restrict the females' freedom in their mating decisions. In situations where a resource is necessary to the female for the successful production of offspring, males may obtain control of the resource. It is then possible for males to completely dominate females in determining viable reproductive strategies. A male makes genetic representation in a female's offspring a requirement for access to the resource. The mating system used in the population is then largely determined by the degree of control males can exert over the resource needed by the females.

Four general strategies emerge, based on female mate choice and male strategies to limit it by controlling necessary resources (Figure 1). In the first strategy (Figure 1A), males are unable to use resources to limit female choice and have no relationship to the resources. Females base their choice on the genetic quality of

potential mates. Males have very limited influence on females' choices.

In the second strategy (Figure 1B), males attempt to limit female choice by controlling resources but are able to obtain control of only some of all that are available. Females are able to acquire the resource themselves but are not able to obtain it as easily or get as much as when males provide it. Females base their choice on male genetic quality and the quality of the resource he holds. They may compromise male genetic quality in favour of the quality of the material benefits a male possesses. A male can attempt to increase his attractiveness to females by controlling desirable high quality resources.

In the third strategy (Figure 1C), males are able to directly control all of the needed resource available and female options are severely limited. A female must mate with a male that is controlling the resource, or sacrifice a great deal of her own reproductive success. Female choice in this situation should be centered on the quality of the resource a male holds, rather than the male's genetic quality.

The fourth strategy (Figure 1D) is for males to control females directly. Males deny females the opportunity to freely choose a mate. While resources are not directly involved in this strategy, they often serve as a focal point

of activity and a place where males can capture females. While females may be able to avoid male control, this practice is energetically costly and this cost is translated into lower reproductive success for the females.

Among these four general reproductive systems, male control of resources or direct control of females dominate over the others. When neither of these systems is possible for males, a system of resource gathering should be dominant, and when this system is not possible for males, a pure strategy of genetic choice by females should prevail (Borgia 1979). This hierarchy permits the prediction of which type of mating system will be used in a population providing knowledge of male ability to control the needed resource is available.

Borgia's classification scheme for male-female interactions and the predictions made by his model for each class are valuable to this study because the required elements of all four of the types of mating strategy in Borgia's scheme can be found among the mating systems of odonates.

ODONATE REPRODUCTIVE BEHAVIOUR

Naturalists and behavioural ecologists have been

interested in the reproductive behaviour of odonates for many years. Corbet (1962) notes that Swammerdam correctly described odonate copulation in 1669. The sequence of events that comprise copulation is similar in both the dragonflies (Suborder Anisoptera) and the damselflies (Suborder Zygoptera). The male grasps the female with his terminal abdominal appendages. Male damselflies grasp a female's first thoracic segment; male dragonflies grasp the top of a female's head. In most species, sperm translocation follows. The male's gonopore is on the venter of the ninth abdominal segment, but the male's accessory genitalia (the penis and sperm vesicle) are on the second and third segments so sperm must be moved from the ninth segment to the vesicle before copulation. When sperm translocation is complete, the male straightens his abdomen and the female curls hers forward and up to engage the male's copulatory organs with her own. A female odonate must actively curl her abdomen forward to copulate. This means that males cannot physically force unwilling females to mate (Finke 1984a, Waage 1984a). The resulting heart-shaped arrangement is referred to as "the wheel" and copulation ends when the wheel is broken.

Most research dealing with the behaviour of odonates has focussed on the elaborate territorial, courtship and postcopulatory behaviours many of them display. These

behaviours often rival those of vertebrates in complexity (Corbet 1962, 1980; Thornhill and Alcock 1983).

Jacobs (1955) believed that territorial interactions between male Plathemis lydia caused the dispersal of males but also prevented other males from interfering with ovipositing females. When males are very numerous at the breeding site they may attempt to copulate with every female present and make oviposition impossible (Pajunen 1966a). Jacobs' interpretation of the value of territoriality was significant because it could also be implicated in the evolution of the elaborate postcopulatory behaviour of many species. Most male dragonflies and damselflies display some sort of postcopulatory guarding behaviour (Corbet 1962, 1980) which has been interpreted as an attempt to keep other males from interfering with oviposition by their mates.

Parker (1970a, 1974) was probably first to suggest that sperm competition (Parker 1970b) and the resulting strong male-male competition could lead to the evolution of guarding behaviour in odonates through intrasexual sexual selection. Sperm competition is widespread among insects (Thornhill and Alcock 1983). Potentially, sperm competition occurs whenever a female is inseminated by more than one male during a single reproductive bout (Parker 1970b). Female insects lay their eggs over a relatively long period of time, fertilizing them internally with sperm they have

stored in their spermathecae and bursae copulatrix. If a male insect can displace or replace a female's store of sperm from a previous mate or even if his sperm will mix thoroughly with those of the previous mate, then it is advantageous for him to mate with that female.

Waage (1979a) showed that sperm competition operates in the damselfly Calopteryx maculata. Males of this species can replace up to 100% of a female's previous mate's sperm by removing it from the female's spermatheca and bursa copulatrix using barbed horns on their penes. The removed sperm are then replaced with their own. Several observers have reported that sperm transfer only occurs in the last few minutes or seconds of copulation (Rowe 1978, Waage 1979a, Miller and Miller 1981). During most of the remaining time, males display rhythmic abdominal movements, and it seems likely these movements are involved with sperm removal (Miller and Miller 1981, Miller 1987). The result is that the last male to mate with a female odonate before she oviposits fertilizes a very large proportion of the eggs she lays. Hereafter, the term "sperm competition", when used with reference to the Odonata, will be used to mean the sort of "last male advantage" created by sperm removal or displacement. Work subsequent to Waage's (1979a) has shown that sperm competition is quite widespread in the Odonata (Miller and Miller 1981, Miller 1982, 1987, Waage 1982,

1984a, 1986a, 1986b, Finke 1984a, McVey and Smittle 1984, Siva-Jothy 1985, 1987).

The potentially intense intrasexual competition between male odonates that results from sperm competition can be used to explain the evolution of territoriality and postcopulatory guarding behaviour. Territorial behaviour provides an area attractive to females for the exclusive use of a particular male and therefore increases his likelihood of encountering females. It also decreases the probability that a mate he has recently copulated with will be taken over and copulated with by another male. Postcopulatory guarding reduces the interference of other males with oviposition and decreases the chance that a male's mate will be taken over by a competing male.

Postcopulatory guarding in the Odonata may take two forms. In "non-contact guarding", a male detaches his terminal appendages from his mate after copulation but remains near her while she oviposits, dashing out at and displaying to other males that approach her. In "contact guarding" the male does not detach his terminal appendages from his mate following copulation and he remains attached to her while she oviposits. Contact guarding is the most common system of postcopulatory guarding used by temperate zone Zygoptera (Waage 1984a). In some species, females may oviposit unguarded following an initial bout of contact

guarded oviposition (e.g. Bick and Bick 1965a) and in other species females may submerge entirely beneath the surface of the water during oviposition (e.g. Finke 1982). In species that submerge during oviposition, males may contact guard their mates until they are submerged and then release them. These males perch nearby and defend the sites as if the females were still visible and vulnerable to takeover. Such males often re-seize their mates when they emerge from oviposition (Bick and Bick 1963, Finke 1982).

Alternatively, in some species, females may oviposit unguarded. Usually these species oviposit at times or places different from those at which copulation occurs, have effective "refusal displays" or are able to oviposit very rapidly (Waage 1984a, Buskirk and Sherman 1985).

Corbet (1962) distinguishes three types of odonates, based on the duration of their copulations. "Short" copulation duration odonates have copulation times ranging from 3-17 s and most are dragonflies that copulate on the wing. "Medium" copulation duration odonates copulate for 1.5 to 5 min. Members of this group are mostly zygopterans that display elaborate courtship and territorial behaviour. "Long" copulation duration odonates have copulation durations that range from 5 - 300 min. and the group consists mostly of species that copulate far from the oviposition site. Most members of this group are those

Zygoptera that practice contact postcopulatory guarding.

Waage (1984a) presents a similar classification of odonate reproductive systems, dividing them according to the way in which males encounter females. He cites the dispersion and defensibility of oviposition sites and population density as being two major determinants of the variations in odonate reproductive behaviour. Waage's three general classes of odonate mating systems are as follows: (A) opportunistic encounters by searching, non-localized males; (B) generally localized encounters at or near oviposition sites; and (C) encounters at territories localized at oviposition sites. Species in groups A, B, and C correspond well with Corbet's (1962) groups "long", "medium" and "short", respectively.

Campanella (1975) provides a similar classification of odonate mating systems. He identifies three types of mating systems based on the distribution and abundance of mates and mating or ovipositing sites. The three types are characterized by the degree of territoriality males display. For example, in situations where oviposition sites are clumped these sites may become predictable sources of mates. If the density of competitors is low, then males can energetically afford to defend a territory at the oviposition site (Emlen and Oring 1977).

Buskirk and Sherman (1985) argue that the ecological

requirements of larvae determine where and how females should oviposit. This determines the distribution of oviposition sites and the spatial dispersion of females. They propose that knowledge of larval requirements and female oviposition behaviour can be used to predict male reproductive behaviour. They present data on seven species of pond Anisoptera and the mating systems of these species fall into three groups, distinguished by how scattered oviposition sites are and how males guard their mates following oviposition. When oviposition sites are clustered males are able to defend territories at the sites, meet females in these territories and non-contact guard the females during oviposition. When oviposition sites are scattered males may contact guard their mates while they oviposit (presumably such males cannot defend mating territories), or if oviposition sites are very scattered males may abandon postcopulatory guarding completely (Buskirk and Sherman 1985). This view ignores the influence that the density of males at the mating site can have on the mating system.

In essence, Buskirk and Sherman (1985) present an extended version of Campanella's observations. The idea that mating behaviour is related to distribution of necessary resources (food, mates, nest or oviposition sites, etc.) is widely accepted in sociobiology. Their ideas and

Campanella's do serve to emphasize the importance of the distribution of resources such as oviposition sites in determining successful male mating strategies. The relationship between degree of territoriality and type of guarding behaviour is also illustrated in Buskirk and Sherman's work.

Any classification of odonate mating systems should take into account all of the relationships apparent in the classification schemes already mentioned. Taking an overview of the different classifications of odonate reproductive behaviour by Corbet (1962), Waage (1984a), Campanella (1975) and Buskirk and Sherman (1985), the following patterns emerge:

1. In species having oviposition sites with a clumped distribution, males are territorial.

2. Territorial species copulate within or very near the territory.

3. Species that copulate at or near the oviposition site have brief copulations.

4. Species having long duration copulations display either contact guarding, or no guarding at all (see also Bick and Bick 1963).

Obviously the distribution of oviposition sites, degree of male territoriality, copulation duration and type of postcopulatory guarding are inter-related. The goals of any

classification scheme should be to be consistent with these inter-relationships and to gain insight into the evolution of odonate mating systems.

I have adopted Borgia's (1979) classification scheme for this purpose. Knowledge of general odonate reproductive behaviour in conjunction with the assumptions and conditions of Borgia's model allows the classification of mating systems of various odonate species, taking into account the interdependent characteristics of the mating systems. This permits the prediction of the type of mating system used by a species from a limited number of ecological parameters.

APPLICATION OF BORGIA'S MODEL TO ODONATES

Males of species such as <u>Aeshna</u> <u>canadensis</u> (Buskirk and Sherman 1985), that are unable to control female access to oviposition sites (Figure 1A) because females are far-ranging, oviposition sites are widely dispersed on a geographical scale, and male-female encounters are infrequent, should not become territorial at a particular oviposition site. Rather they should seek mates in areas near a number of potential oviposition sites. The energetic costs of postcopulatory guarding are not justified because of the low probability that the female will encounter another male before she has laid a batch or batches of eggs.

This sort of mating system should be restricted to species that are powerful fliers. These species tend to mate far from the oviposition site and spend relatively long periods in copulation (Corbet 1962, 1980, Waage 1984a). Mate choice for male quality alone is most likely to be found in these species. However, if the encounter rate between males and females is extremely low, then females should not be selective and should mate with the first male they find (Borgia 1979).

In species in which males are able to practice a resource gathering strategy (Figure 1B), female choice becomes only slightly more restricted than in a system where males are unable to control resources. Males practicing this strategy do not "gather" oviposition sites, but rather are unable to control female access to all of them (e.g. Waage 1978, Conrad and Herman, in press), perhaps because not all oviposition sites are suitable for territories (Waltz and Wolf 1984). If a female needs an oviposition site she may find one that is not controlled by a male, but at some cost of energy or site quality which may ultimately result in lower reproductive success for her. The resource gathering strategy is typical of many of the calopterygid damselflies (Johnson 1962, Pajunen 1966b, Waage 1973, 1984b, Miyakawa 1982, Conrad and Herman, in press). Oviposition sites are clumped but clumps are fairly regularly dispersed,

permitting males to localize around them and defend them against competitors. The territories thus formed provide a place to encounter females as they come to the water. However, the price of territoriality is constant vigilance (Alcock 1979) and copulations are relatively brief (Corbet's (1962) "medium" copulation duration). This may either permit, or be because of, territoriality since it allows males to return quickly to territorial defence. Postcopulatory guarding is of the non-contact type. This also permits males to return quickly to territorial defence and to acquire additional mates (Alcock 1979).

A female may choose her mate on the basis of his genetic quality or the quality of the territory he holds, or any combination of the two. Behavioural displays of both male quality and territory quality may be expected to arise. These displays apparently have evolved in Calopteryx maculata (Waage 1973), C. virgo (Pajunen 1966b) and C. v. japonica, C. cornelia and C. atrata (Miyakawa 1982). Territorial males deliver an elaborate courtship display in two parts. The first part is a "cross display" over the oviposition site, thereby associating the male with the territory (Waage 1973). If the female perches, the male then begins a "courtship arc" which may be some display of the male's quality, since non-territorial males use this only and still obtain copulations (Waage 1973 and pers. obs.

of C. maculata).

A non-territorial mating strategy may also be expected to arise because females can obtain access to some non-territorial oviposition sites. A female may accept a high quality non-territorial male as a mate and attempt to oviposit at an unguarded oviposition site.

When oviposition sites are clumped and males are extremely mobile, territorial males may be able to control all female access to oviposition sites (Figure 1C). This is less likely to happen in species that oviposit in streams because males are able to view only a limited area of a stream at a time (Waage 1984a).

Male density and the probability of male interference with oviposition are important to the degree of control males have over female access to oviposition sites. If the probability that males will attempt to interfere with oviposition is high, then even if non-territorial oviposition sites are available, females are unlikely to be able to use them and should only copulate with territorial males to obtain their postcopulatory guarding services. Copulation typically occurs at the oviposition site and is very brief. Oviposition is also very brief and guarding is by the non-contact method. This permits almost constant male vigilance and allows males to take advantage of the high encounter rates with females that occur in this

situation. It also minimizes the time females can be subjected to male harassment while ovipositing. Females are most likely to choose males for their territory quality. The resource control mating system is exemplified by Libellula (Plathemis) lydia (Campanella and Wolf 1974, Jacobs 1955, Koenig and Albano 1985, 1987).

When oviposition sites are numerous but scattered in a restricted area and the species is not very mobile (e.g. most Zygoptera), males have little opportunity to control female access to oviposition sites. Males may, however, directly control the females and physically prevent other males from mating with them (Figure 1D). Males intercept females as they approach the oviposition area. Copulation times are in Corbet's (1962) "long" duration group. Males remain in tandem with females until they have finished ovipositing or submerge to oviposit and are no longer susceptible to takeover by other males. The amount of time a male and female are in association with one another is long and multiple matings within a day should be extremely rare (see, for example, Bick and Bick 1965a). Female choice in a female-control mating system is very limited.

Borgia's classification scheme, though developed as a general model, seems quite consistent with the schemes presented by Corbet (1962), Campanella (1975), Waage (1984a) and Buskirk and Sherman (1985) in classifying odonate mating

systems. A summary of the characteristics of each of the four types of mating systems appears in Table 1.

Specific examples have been offered for mating systems in which males use no resources, practice resource gathering or control female access to oviposition sites. Key assumptions in the evolution of the types of mating systems as described by Borgia (1979) are that female choice is a potent evolutionary force and that males are able to control female activity, either by controlling a needed resource, or by controlling females themselves. Among the Odonata, the influence of female choice is best studied in those species in which males practice no control of resources. The study of male ability to control female mating decisions, if they are indeed able to do so, is best directed at species expected to be performing the female-control strategy. This study deals with a species believed to be practicing this strategy.

THE STUDY SPECIES, _ARGIA VIVIDA_ HAGEN

The genus _Argia_ is believed to be of neo-tropical origin. Only eight species of the genus are known to occur as far north as Canada and then only in the southern-most parts (Pritchard 1982). All of the well-known Canadian

populations of <u>Argia</u> <u>vivida</u> and many of the populations throughout the species' range occur in thermally heated springs. The use of hot springs as an adaptive mechanism in the northward extension of the range of the species has been addressed in several studies of the larvae (Leggott 1984, Leggott and Pritchard 1985a, 1985b, 1986, Pritchard 1980, Pritchard and Pelchat 1977).

A number of studies of the population ecology and behavioural ecology of adults of various <u>Argia</u> species have been performed (<u>A</u>. <u>moesta</u>: Borror 1934, Bick and Bick 1972; <u>A</u>. <u>apicalis</u>: Bick and Bick 1965a,b; <u>A</u>. <u>plana</u>: Bick and Bick 1968, 1971, 1972; <u>A</u>. <u>fumipennis</u>: Bick and Bick 1982; <u>A</u>. <u>sedula</u>: Robinson et al. 1983), including one on <u>A</u>. <u>vivida</u> (Garrison 1978).

The emergence period and pattern of <u>A</u>. <u>vivida</u> are not known but records of collections (Walker 1953) indicate that it is a "summer species" (having an asynchronous emergence pattern, Corbet 1954) in southern Alberta and British Columbia. This is supported by larval collections (Leggott 1984, G. Pritchard Pers. comm.) as well as by limited records of adult activity (Leggott 1984).

Leggott and Pritchard (1986) performed laboratory experiments and found that the threshold temperature for flight in <u>A</u>. <u>vivida</u> was high (26 °C -- though they caution this may be an overestimate because of the

techniques used) and pointed out that this might limit the northern or altitudinal limit of the species by limiting the time available for flight and reproduction. They noted that A. vivida's habit of sun-basking seemed necessary for it to maintain the body temperature necessary for flight on cool days.

Garrison (1978) found that female A. vivida preferred the riffle areas along his study stream for oviposition and that A. vivida preferred areas of moving water in general. Pritchard (1982) considered this preference for moving water to be important in the northern extension of the range of the species. He also proposed that the choice of oviposition sites in hotspring areas was important for the same reason. Leggott and Pritchard (1986) found that A. vivida larvae showed a preference for high temperatures when placed in a temperature gradient. The problems of adult thermoregulation and placement of eggs so that larvae can develop in thermally appropriate sites may place severe constraints on the time and locations available for reproductive behaviour.

The reproductive behaviour of Argia vivida has not previously been studied intensively. From the data available on other North American species of Argia (Table 2), A. vivida is expected to display copulations of durations characteristic of Corbet's (1962) "long" group (>

5 min). From the studies of _Argia_ reproductive behaviour cited, _A_. _vivida_ males are expected to perform contact postcopulatory guarding. The mating system of _A_. _vivida_ is most likely to be of the female-control type (Figure 1D, Table 1).

Two important conditions must be satisfied before Borgia's model can be applied to _A_. _vivida_. The first is that females are able to mate more than once within a single breeding period. The only study of individually marked _A_. _vivida_ (Garrison 1978) does not report multiple matings of individuals within a day, but reproductive behaviour was not an important topic in the study. Female _Argia_ _moesta_ (Bick and Bick 1972) and _A_. _apicalis_ (Bick and Bick 1965a) have been observed to mate more than once in a single day, but _A_. _plana_ does not (Bick and Bick 1972). It is still likely that most damselflies mate more than once in a lifetime, with the exception of a some members of the genus _Ischnura_ (Rowe 1978, O. M. Finke, pers. comm.).

The second requirement is that sperm competition should be highly effective in _A_. _vivida_. Last male advantage is implied in all the strategies of the classification scheme (Borgia 1979).

Waage (1984a) has studied the structure of the male genitalia and female sperm storage organs (bursa copulatrix and spermatheca) of _Argia_ _fumipennis_ _violacea_ and has

concluded that males of this species are able to remove "virtually all" the sperm stored in the bursa. He found that previously mated females carried large amounts of sperm prior to copulation, little if interrupted during copulation, and large amounts immediately after copulation. He also noted that previously mated females returning to the water for a second day already carried a "substantial" quantity of sperm; presumably enough for a second bout of oviposition without remating.

Subsequently, Waage (1986a) studied the structure of the genitalia and sperm storage organs of A. moesta and A. sedula. He found that the degree of sperm precedence was high (> 85%) in both species.

The penis structure of A. vivida is not known and there is a great deal of interspecific variation in penis structure in the genus (Kennedy 1920 in Eberhard 1985). However, the reproductive behaviour of A. vivida indicates that the species is also capable of sperm replacement (Waage 1986a).

Dimorphism in female A. vivida has been noted by Paulson (1974) and Garrison (1978) but was not mentioned by Walker (1953) or Cannings and Stuart (1977). Both Walker (1953) and Cannings and Stuart (1977) described female A. vivida as varying from yellow or green-grey to pale brown or blue. Kennedy (1915) believed that the brown form represented an

intermediate age that matured to blue later, though blue morphs were rare in the populations he sampled. Garrison's (1978) recaptures of females were insufficient to rule out the possibility that the dimorphism was age related. It is also possible that, as in A. apicalis (Bick and Bick 1965b), multidirectional colour changes occur.

Two reproductive colour morphs existing in a population may affect the type of mating system that occurs because each colour morph may be valued differently by males as mates (Johnson 1975). Two colour morphs were observed in this study; females were either blue or red-brown (referred to as "red") and no yellow-grey or green-grey individuals were seen.

Much of the work on sex-limited colour dimorphism has dealt with butterflies. In many cases, one or more of the morphs mimics a distasteful species and another morph resembles the male and is assumed to be the primitive form (Turner 1978, reviews in Vane-Wright and Ackery 1984). Presumably this polymorphism is balanced by differential predation on the female morphs and differential mate selection by males (e.g. Levin 1973).

Two sociobiological theories have recently been applied to explain the existence of female-limited dimorphism in insects. The first, which originated with studies of the Lepidoptera, has been referred to as "pseudo-sexual

selection" (Vane-Wright, 1984). Vane-Wright has argued that in day-flying butterflies, which locate mates largely by visual stimulus, as do odonates (Corbet 1962), andromorphic females (mimicking the brightly coloured males) may provide a stronger sight-stimulus for males and therefore gain a selective advantage in mating over the cryptically coloured heteromorphs. This polymorphism is balanced by greater predation of the more colourful female morph.

Male _Leucorrhinia_ _dubia_ (Pajunen 1964) appear to attack all similar dragonflies only switching to sexual behaviour when they are close enough to identify the other individuals as females. _A_. _vivida_ males may treat andromorphs similarly.

The second theory has resulted from a study of _Ischnura_ _ramburi_, a small member of the same family as _A_. _vivida_. Sperm replacement is probably not very effective among members of the genus _Ischnura_ and postcopulatory guarding is not performed (Waage 1984a) in many species such as _I_. _elegans_ (Miller 1987). Robertson (1985) demonstrated that the female morphs of _I_. _ramburi_ represent two different strategies for avoiding an excessive number of time-consuming matings and male harassment. Andromorphic females "pretended" to be males and aggressively chased males. Heteromorphic females relied on their cryptic colouration to avoid harassment while ovipositing.

Both of these theories present female dimorphism as a product of male-female encounters. The two theories are not mutually exclusive since each applies to different parts of reproductive behaviour. The facility with which a female attracts a mate or how easily she can avoid males depends to some extent on how frequently she encounters males. Therefore the relative numbers of red and blue females mating each day should respond to large-scale manipulations of male densities. A change in the ratio of red to blue females mating on a day following such a manipulation would indicate that some sociobiological mechanism is involved in maintaining the female dimorphism in the population.

The presence of two female colour morphs may indicate that females are employing two mating strategies. Male $\underline{A}$. $\underline{vivida}$ may also practice alternative reproductive behaviours (as defined by Austad 1984). Preliminary investigations have shown that $\underline{A}$. $\underline{vivida}$ roost fairly far from the oviposition site at night. The next day they begin moving toward the site when it becomes warm enough to fly. Females are intercepted on their way to the water by waiting males while they are still far from the oviposition site. Not all males are successful with this tactic and continue to move toward the water. They may obtain a mate that has escaped another male while ovipositing. Thus males that obtain mates "away from water" and males that obtain mates "at

water" could be considered to be using different mating strategies. Such a system has been described for *Enallagma hageni* by Finke (1985).

The study of the reproductive behaviour of *Argia vivida* was carried out with two general goals in mind: to record and describe the reproductive behaviour of *A. vivida*, and to examine the reproductive behaviour of *A. vivida* in light of Borgia's (1979) model. The pursuit of the second goal will require answering the following questions:

1. How important is sun basking to male and female activity?

2. Do females frequently mate more than once per day or once per lifetime?

3. Do males show a preference for either female morph?

4. Does obtaining mates "at water" entail different behaviour from obtaining them "away from water"? If it does, how can the alternative tactics be explained within the framework of Borgia's model?

Since I have adapted Borgia's (1979) female-control strategy to the Odonata with the reproductive behaviour of coenagrionids such as *A. vivida* specifically in mind, attempting to test the "fit" of the expected strategy to the observed behaviour of *A. vivida* is not a true test of an *a priori* hypothesis. Rather, this study is an attempt to see how specifically the stated characteristics of the

female-control strategy can be applied to the reproductive
behaviour of A. vivida and to examine the explanatory value
of the classification.

STUDY SITES

Study of _Argia_ _vivida_ was carried out at Albert Canyon
(abbreviated "AC") and Halcyon Hotsprings (abbreviated "HH")
in British Columbia, approximately 500 km west of Calgary.
Both sites are at a similar latitude and altitude but differ
in the temperature of the hotsprings that feed them.

The Albert Canyon site is located beside a forestry road
near the Canyon Hotspring Campground, about 30 km east of
Revelstoke, B. C., and is fed by several small streams
leading from the hotsprings (Figure 2). The main stream is
about 75 cm wide and 5-50 cm deep, with a silt and gravel
substrate. The soil of most of the area south of the
forestry road, including that overgrown by trees and shrubs,
is limey silt and the area is swampy. North of the road,
the ground is more solid. The main stream leaves the study
area by plunging underground into a cavity formed beneath a
fallen log. The vegetation consists primarily of _Chara_ sp.
which is very abundant in deeper areas of the stream, and
Equisetum spp. which dominate the swampy areas. _Argia_
larvae were extremely abundant in all sections of the study
area including the swampy area south of the main stream.
Adult _A_. _vivida_ were seen throughout the study area and also
in the shrubs and bushes surrounding the site.

The only other zygopteran seen ovipositing in the area

was _Amphiagrion abbreviatum_. Several anisopterans also oviposited at the study site including _Cordulegaster dorsalis_, _Somatochlora_ sp., _Sympetrum danae_, and at least two species of _Aeshna_.

Water temperatures range from a summer maximum of about 20 °C to winter temperatures of about 5 °C. Daily fluctuations of about 2 °C occur in summer so it is assumed that the temperatures are fairly stable on a diel basis year-round (Leggott and Pritchard 1985a).

The Halcyon Hotsprings site is located on B. C. Highway 23, 60 km south of Revelstoke. The habitable area for _A. vivida_ larvae is restricted to a section of the stream 85 m long and 1-2 m wide (Figure 3). The upstream limit is determined by the confluence of a colder stream with the hotspring effluent. The water is too hot for _Argia_ larvae above this point. The habitable area extends downstream to a point where the stream enters a larger cold stream. Water temperatures in the habitable area are warmer than at Albert Canyon. Summer temperatures are around 30 °C over most of the length of the stream, but in the fall and winter the temperature at the north confluence stays in the mid-twenties and can be 10 °C colder just upstream of the south confluence. Stream temperature appears to vary both with distance from the upstream confluence and air temperature.

Adult <u>A</u>. <u>vivida</u> are most abundant in July and August and may be seen flying in the forest, on the stoney slope or at the water at various times of day. Tandem pairs were seen flying and perching in the vicinity of the north cold stream but none were seen ovipositing. Individuals were not seen at the south cold stream which was deep, fast flowing and not suitable for damselflies to oviposit in. Other odonates are rare in the area. A teneral <u>Aeshna</u> sp. and three <u>Leucorrhinia</u> <u>hudsonica</u> were the only anisopterans seen. Occasionally large Anisoptera made a few passes up and down the stream but did not stay in the area. <u>Amphiagrion</u> <u>abbreviatum</u> was the only other zygopteran noted and it was very rare.

Based on the number of aquatic degree days available for larval development, the Halcyon population should have a one-year life cycle (univoltine) (G. Pritchard Pers. comm.) and the Albert Canyon population should have a three-year life cycle (merovoltine) (Leggott and Pritchard 1985a).

METHODS

SAMPLING PROGRAM AND ESTIMATION OF ABUNDANCE

In 1985 field study of A. vivida began on July 10 and continued until July 25 when the forestry district containing both study sites was closed because of the high risk of forest fires. Three days were spent at Albert Canyon followed by three days at Halcyon Hotsprings and so on, alternating between each site. Each three day period at each study site was called a "session".

The field study of A. vivida during summer 1986 took place at Halcyon Hotsprings only. A study session consisted of a visit to the study site that included three to four days of good weather. A total of 6 sessions were conducted, each separated by 10 to 14 days from June 10 to August 13.

The HH study area was divided into three sections designated as "far" (in the forest), "near" (on the stoney slope or the shoulder of the highway) and "at the water" (over the stream bed)(Figure 3).

Daily abundances of adults were monitored using capture-mark-recapture (CMR) techniques. Adults were captured singly and in tandem at each study site with an aerial insect net, given an individual alpha-numeric mark on the left hindwing with waterproof ink and released at the

point of capture. These marks permitted the "recapture" of the insects with a pair of close-focussing binoculars, thereby avoiding the need to re-handle them. Mark, mating status (tandem or non-tandem), time and location were recorded for each sighting. In 1985, the left forewing length of the first 100 individuals marked in each session was measured to the nearest 0.1 mm with vernier calipers and recorded, but in 1986 an attempt was made to obtain the forewing lengths of all individuals handled. In 1986 a female's colour or the colour of a male's mate was also recorded for each sighting.

Daily abundances were determined from the CMR data using the Manly-Parr method (Manly and Parr 1968, Manly 1971, Southwood 1978) and comparative estimates were provided by the Jolly-Seber method (Jolly 1965, Southwood 1978). Animals removed from the study site were not included in the calculations.

Mean values from frequency distributions of the number of days between marking and last capture of individuals (minimum days alive or MDA) were used as indices of adult longevity.

COLOUR MORPHS AND COLOUR CHANGES

Sexually mature male A. vivida appeared as only one

colour morph which was mostly blue, but females occurred in two different colour forms. One colour form was mostly blue and resembled male colouration. The other female colour form was similar in its markings to the blue form, but was mostly red-brown.

On June 21, 24, July 6, 19 and August 1, 1986, between 3 and 8 females of both colour forms were placed in a 60 cm X 30 cm X 30 cm holding cage and kept overnight to see if any changes occurred in female colour. Usually these females were used for other experiments the following day. On both dates in June, 10 males were also captured and held in the cage. The damselflies captured on June 24 were brought into the lab and kept in an incubator at 20 °C until the last one died 4 days later. The six females captured on July 6 were held for 4 days. The damselflies held in the field were kept in the shade until they were released, except for those captured July 19 and August 1 which were placed in the sun on the stoney slope in an attempt to induce them to mate. It was noticed that A. vivida appeared brighter on warm sunny days. In order to monitor possible temperature-related colour changes, the brightness of each captive individual was scored as either bright or dark when it was captured and released.

On August 13, 1985, 22 tandem pairs, consisting of 11 pairs containing red females and 11 pairs containing blue

females, were captured in mid-afternoon at Halcyon Hotsprings. Each pair was numbered according to its order of capture and placed in an individual insect envelope. Three-quarters of an hour later, the insects were killed in ethyl acetate and preserved in acetone. These specimens are referred to as the "acetone pairs".

Left forewing length, abdominal length and total length of both males and females of the "acetone pairs" were measured using vernier calipers accurate to 0.1 mm. The same calipers were used for all measurements of forewing, abdominal and total length in the lab and field. Ocular width and left mesofemur length were measured using an ocular micrometer in a dissecting microscope. The specimens were dried at 60 °C to constant mass in a drying oven and then weighed to the nearest 0.1 mg on an electronic balance. Correlations were obtained among all the parameters for both sexes to see which parameter would be the best index of body size. Student's t-tests were performed on each of the parameters to see if any differed significantly between red and blue females.

On July 21 1986, 31 pairs containing 15 red and 16 blue females were captured between 1530 and 1630 hrs. The females were numbered on their left forewing according to their order of capture and placed in a holding cage. Two hours later they were killed in ethyl acetate and preserved

in formalin.   In the lab, forewing length, ocular width, abdominal length, length of the mesofemur, nodal width, length of the pterostigma, and whether or not the antehumeral stripe was bifid and the shape of the ventral arm of the stripe were recorded.   A stepwise discriminant analysis was performed to see if red and blue females could be separated on the basis of size and antehumeral markings.

On each study day in 1985, the first five unmarked tandem A. vivida sighted were captured and preserved in formalin.   The colour of females in these pairs was not noted.   It was assumed that these pairs had not begun ovipositing and so the females carried a full complement of eggs.   These specimens are referred to as the "formalin pairs".

Between 1600 and 1630 each day, five males that were not observed mating during the day were also captured and preserved in formalin.   These males are called the "non-tandem formalin males" when compared to males from the "formalin pairs", which are then called "tandem formalin males".   All specimens were taken to the laboratory and left forewing length and total length were measured.   The males were then dried in a drying oven to constant mass and weighed to the nearest 0.1 milligram using an electronic balance.   Females were dissected and the number of eggs in each female was counted.   The females were stored in

formalin for six months before the dissections were performed. The formalin had dissolved some of the connective tissues around the eggs so they were easy to remove from the abdomen and tease apart. Some of the eggs counted may not have been mature enough to be laid on the day the female was captured.

Correlation analysis was performed among all parameters within pairs to see if there was any size-assortative mating and if female body size could be related to the number of eggs they carried.

A two-way analysis of variance was performed to see if "tandem formalin males" differed in body size from "non-tandem formalin males" and if the relationship changed between sites.

DAILY MOVEMENT PATTERNS

Movement of individuals at Albert Canyon in 1985 was monitored during the CMR sampling. This sampling was performed while walking a circular route which passed within an insect-net-handle-length of nearly all the suitable mating and oviposition habitat within the study area. A complete circuit of the route took about 20 min.

A similar route was used at Halcyon Hotsprings in 1985 but the whole study area was not covered as effectively and

densities at the water were so high at mid-afternoon that only one or two passes were made through the forest and along the stoney slope each afternoon. The position of individuals was recorded by using a grid overlay on a 1:200 scale map.

Individuals at Halcyon Hotsprings were found earliest in the morning in the far sector so sampling was started there each morning in 1986. As individuals began appearing nearer and nearer the water as the day progressed, the emphasis of sampling activity was moved toward the water. Individuals and tandem pairs were not seen approaching the site from west of the highway and there was little suitable habitat there, so this area was not sampled.

"Quick surveys" were made at approximately 1630 on June 10 and 22, July 31, and August 1, 11 and 12, and at approximately 1300 on June 22, July 21 and August 12 and 13, 1986 at Halcyon Hotsprings to obtain an index of the number of pairs and non-tandem males at the water at these times. A "quick survey" consisted of beginning at the south confluence and walking slowly upstream at a steady pace while counting all tandem and non-tandem individuals encountered.

EXPERIMENTAL OBSERVATIONS OF BEHAVIOUR

To see if sexually mature males at Halcyon Hotsprings behaved differently when they were basking at sunspots in the forest in the morning or at the water in the afternoon, 13 males were observed in the forest in the morning and 4 males were observed at the water in the afternoon for 10 minutes each. Observations took place on various study days from June 22 to August 2. Males were observed in the forest between 1000 and 1130 and so are called "morning males". Males were observed at the water from 1300 to 1500 and so are called "afternoon males".

Both morning and afternoon males spent most of their time perching and only made very brief flights. Their behaviour was recorded by writing down the time between flights and the purpose of each flight. Time between flights was determined with a stopwatch. The flights themselves were divided into two main types: short flights, which were too brief to be recorded using the stopwatch and so effectively took no time at all, and long flights, which took more than one second and covered about two meters or more.

Flights were recorded as having one of five purposes: (1) changing perches, (2) feeding, (3) inspecting insects, (4) pursuing other males, and (5) pursuing tandems. Pursuit

of teneral A. vivida was included in the "inspect insect"
category. Feeding was usually verified by viewing the
damselfly's moving mouthparts with binoculars after it had
landed. Records of males followed for less than 10 minutes
are not reported.

The activity of ovipositing pairs was recorded in a
fashion similar to that of males. The activities of pairs
were divided into four general groups: flying, perching,
probing, and ovipositing. Flight, which almost always
lasted less than one second, was considered to have taken a
negligible amount of time. It was regarded as a form of
transition between the other activities. Six pairs were
observed between July 21 and August 12 for periods of time
ranging from 517 to 3551 s. The observation time was
determined by how long the pair could be kept in sight.
Several other pairs were only followed for two to three
minutes and these records are not reported.

To see if males showed a preference for either colour
morph, live females were pinned to two long grass stems held
together with a piece of tape. Using this arrangement, two
females, one of each morph, were simultaneously presented to
individual males. The females were first waved back and
forth once about one meter from the male, then were moved at
about the same speed as slow damselfly flight toward the
male. If the male had not responded by the time the females

were about 10 cm away from him, the females were held at that distance for 10 s. The females were bounced gently to cause them to flick their wings and then quickly moved away. One hundred forty-five presentations of the pinned females were made, each in the same ritual manner. Additional experiments were also performed using various combinations of mature males, females of either morph and tenerals. Some presentations of single pinned individuals were also performed.

Males that left their perches and hovered very near the pinned females were said to have "inspected" the females. Those that landed on a female and attached their terminal appendages were said to have "mounted" the female. Some of the males that mounted pinned females had to be removed by force.

To test if the ratio of red to blue female colour forms that appeared in tandem at the water each day was influenced by male mating behaviour, a male removal experiment was performed. It was predicted that if female polymorphism was related to male mating behaviour, and the number of males available to mate with females was reduced, then the ratio of red to blue female morphs mated each day would change.

Each study day in June and July 1986, between 1430 and 1530, tandem pairs were captured at random and placed in a holding cage in a shady area. The number of females of each

colour form were counted and then all captive damselflies were given individual marks and were released after 1600.

On selected days (see Table 19 for dates), every male encountered in the woods or on the stoney slope from the time of arrival until 1300 was captured. These males were placed in a holding cage and were released at the same time as the captive tandem pairs.

The ratio of red to blue females at Halcyon Hotsprings was determined to be 1:2, red to blue in 1985. A replicated G-test (Sokal and Rohlf 1981) was used to see if the ratio deviated from 1:2 on any day in 1986.

Miscellaneous observations of behaviour, including copulations, were made throughout the field seasons. Such observations were usually made with the aid of a pair of close-focussing binoculars and were timed with a stopwatch.

All statistics were performed with a critical level of p = 0.05. Exact probability values are reported (e.g. p = 0.673) for statistical tests performed with computer statistical packages (SPSS version 9.1, Nie et al. 1975; STATS PLUS for the Apple II™, Madigan and Lawrence 1982). Approximate probability values (e.g. p > 0.50) are reported for statistical tests performed using programs I wrote, some of which were modified from the FORTRAN programs presented in Sokal and Rohlf (1969). Large-sample approximations to Z-scores are presented for non-parametric

test results whenever sample sizes are large enough to permit their calculation. Means are reported $\pm$ 1 standard error, unless stated otherwise.

RESULTS

FEMALE DIMORPHISM AND PHYSIOLOGICAL COLOUR CHANGE

On all occasions that male and female damselflies were placed overnight or longer in holding cages, no females changed colour from blue to red or from red to blue. Females of both morphs were seen mating and ovipositing, and pristine, probably virgin females of both morphs were seen, so the colour is not age-related. Red females are clearly distinguishable from the pale tan tenerals of both sexes. Females that are not quite mature and only have developed some of their mature colouration can also be clearly distinguished as red or blue. No red male was ever seen.

A runs test performed on the order of capture of red and blue females in tandem indicated that the sequence of capture was random (n = 100, runs = 50, Z = 0.6375, p = 0.524).

Both sexes of <u>A</u>. <u>vivida</u> experience temperature-related physiological colour change (O'Farrell 1963). When activity first begins each day with the shade temperature at about 18 °C, individuals are observed to be in the "dark phase". Most of the dorsal and lateral surfaces of the abdomen and thorax are dull purple to dark blue in males and blue females and are dull grey-brown to brown in red

females. The black markings on the thorax and abdomen are not distinct. After individuals have been sun-basking and the shade temperature increases to 25 °C or more, they change to the "bright phase". The sides of the abdomens and thoraces of males and blue females lighten to bright blue with pale blue or light blue-grey markings. In red females these areas become red-brown or brown with tan or grey-tan markings. The black markings on the dorsum of the abdomen and thorax become distinct. It is not known if tenerals experience similar colour changes.

"Bright phase" individuals placed in holding cages overnight developed the "dark phase" colouration. Individuals placed in a rather heavy-mesh holding cage in the sun on a warm day remained in the "dark phase" but attempted to mate, and the females in this cage oviposited. Free-ranging males and females on cool cloudy days remained in the "dark phase" but attempted to mate. One female that was captured while ovipositing late in the day displayed the "dark phase" colouration on the part of her abdomen that had been submerged and the "bright phase" colouration on the rest of her abdomen and thorax.

The transition between colour phases is apparently abrupt. It is temperature regulated and does not reflect willingness to mate.

Six "bright phase" and six "dark phase" *A. vivida* males

were killed in ethyl acetate, briefly preserved in acetone,
then dried in a drying oven at 60 °C. The "bright
phase" and "dark phase" groups were placed under a U.V.
light and three uninformed observers were asked to view both
groups and select the more reflective of the two. The
damselflies were rearranged and the observers were asked to
choose again. The observers picked the "bright phase" males
as the most reflective in all but one of the trials.
"Bright" and "dark" phase females of either morph were not
available for testing. "Bright" and "dark" phase males
differ not only in their brightness in visible light but in
their degree of U.V. reflectance as well.

DEMOGRAPHY

Imaginal _Argia_ _vivida_ were present at Albert Canyon and
Halcyon Hotsprings on June 8 in 1985 and from June 4 to
October 10 in 1986. Since these sightings involved mature
individuals in June and tenerals in October, earliest
emergence probably occurs in late May and some individuals
may fly in late October, though the fall of 1986 was
unusually mild. This represents a considerable extension of
the flight season reported by Cannings and Stuart (1977).

A few newly emerged tenerals were captured daily at
either AC or HH from July 10 to 25, 1985. It appears

emergence is dispersed throughout the summer. In 1985 at Albert Canyon, 54 male and 51 female newly emerged tenerals were captured. Forty male and 35 female newly emerged tenerals were captured at Halcyon Hotsprings. The ratio of males to females at either site is not significantly different from 1:1 (Fisher's exact test: AC, p = 0.107; HH, p = 0.120). Similar results were obtained from larvae captured from both sites on 16 November 1985 and reared in the lab. Sixty-one males and 61 females were obtained when adults and final or penultimate instars were sexed. Tenerals were not counted in the field in 1986.

Among sexually mature individuals, more males than females were sighted (marked or recaptured) in both 1985 and 1986 (Table 3). Few non-tandem females were ever captured at either site and at Halcyon in 1986, when particular attention was given to searching for non-tandem females, sightings of non-tandem females made up only about a quarter (133/516) of the sightings of females. All other captures or recaptures of females occurred when they were in tandem.

Manly-Parr estimates of the population size (Manly and Parr 1968, Manly 1971) of males at Halcyon in 1986 ranged from 77 ± 30 on July 21 to 526 ± 273 on July 20 (Figure 4). Jolly-Seber estimates (Jolly 1965) from the same data provided consistently higher values (Figure 5). Maximum population size is estimated to have occurred on July 19

(947 ± 317) and the minimum size estimated is from July 22
(189 ± 47). Daily estimates of variance were high and
values varied greatly between days. Estimates of sampling
intensity for the Jolly-Seber (α) and Manly-Parr
(p_4) methods were sufficiently large for reliable
estimates (Southwood 1978). However, both indices remained
less than 50% on nearly all days and the reliability of the
Manly-Parr method is probably affected more by low levels of
sampling intensity than is the Jolly-Seber method. The
higher estimates of the Jolly-Seber method seem to be more
in agreement with the numbers of animals observed in the
field. The number of recaptures of females was insufficient
to permit estimation of female population size in 1985 or
1986 and the data did not permit reliable estimates of male
population size in 1985.

Among those individuals captured on more than one study
day, on average, fewer days passed between the captures of
males ($\bar{X}$ = 7.47 days, N = 349 captures) than females ($\bar{X}$ =
11.73 days, N = 40 captures; Mann-Whitney $Z_{(approx.)}$ =
-2.06, p = 0.030). These figures are undoubtedly biased
upward by the nature of the sampling program but should
serve as an indication that both sexes are not likely to
come to the water daily and that females appear at the water
less frequently than males.

Argia vivida appears to be a fairly long-lived species.

The longest time between the first and last capture of a male (MDA) was 62 days and for females it was 47 days. Considering only individuals captured more than once, the mean MDA for males of 13.03 days (N = 234) was not significantly different from the mean MDA of 11.25 days (N = 36) obtained for females (Mann-Whitney $Z_{(approx.)}$ = -0.89, p = 0.187). These values are probably biased toward 10-12 days by the sampling program but the similarity of the distributions between the sexes is apparent (Figure 6). If individuals captured only on the day of marking are included, the mean MDAs drop to 3.89 days for males and 2.01 days for females.

The two female morphs of A. vivida appear at each site at different frequencies. From July 19 to 21, 1985, 50 blue and 28 red females were recorded at Halcyon Hotsprings. Seventeen red and 16 blue females were recorded at Albert Canyon from July 22 to 25 of the same season. The ratio of blue to red females was not significantly different from 1:1 at Albert Canyon (X^2 = 0.030, p > 0.9) nor was it significantly different from 2:1 at Halcyon Hotsprings (X^2 = 0.130, p = 0.677).

In 1986, 294 blue and 154 red females were marked at Halcyon. Ten additional females were marked without recording their colour. The ratio of blue to red females sighted did not differ from 2:1 (Table 4) and daily ratios

were not different from 2:1 except on July 7 (G = 4.23, df = 1, p < 0.05). Also, the blue to red ratio of sightings of solitary females in 1986 did not differ from the blue to red ratio of sightings of tandem females (X^2 = 0.054, p = 0.681). The red and blue morphs appeared in the same frequencies relative to each other whether in tandem or not.

Of males sighted in tandem on two days (34), the colour of mates for both days are known for only eight. Of these eight, only three males mated with the same colour female (blue) on both occasions. Among those males mating on more than one day, where the colour of at least one of the mates was known, 6 had blue mates, 9 had red mates, 5 mated with both morphs and 13 were in tandem with morphs of unrecorded colour on all the occasions they were sighted. Males do not prefer one female colour morph throughout their lives.

MORPHOMETRICS

Significant correlations were obtained between female forewing length and the other body measurements of females of the 22 "acetone pairs" captured at Halcyon on 13 August 1985 (Table 5), though these correlations were not particularly strong. Male forewing length correlated well with all the other measurements except ocular width, and was particularly well correlated with body mass (Table 6).

Among females, total length was the measurement most strongly correlated with each of the other female parameters and male abdominal length was most strongly correlated with the other male parameters measured. However, both of these measurements are difficult to obtain from live specimens in the field, so forewing length was regarded as the most useful index of size for both sexes.

The females used were captured mid-afternoon and probably had laid various numbers of eggs, therefore, strong correlations between female mass and any of the body measurements were not expected.

Measurements of the 11 red and 11 blue females from the pairs were examined with t-tests. None was significantly different ($p > 0.50$).

The discriminant analysis performed using parameters determined from red and blue females captured July 21, 1986, generated a discriminant function with nodal width, forewing length, abdominal length, and length of the mesofemur. Inclusion of any of the other parameters did not significantly increase the amount of variance explained. This function mis-classified 10 of the 31 females and most (15/21) of the classification probabilities for those classified correctly were less than 75%. There is no obvious difference between red and blue females, at least on the basis of body size as described by the parameters

measured.

Strong correlations were obtained from the measurements of "formalin pairs" among the male parameters and also between female forewing length and female total length (Tables 7 and 8). Female body sizes did not correlate well with the size of their mates or with the number of eggs they carried.

The mean number of eggs carried by females at Albert Canyon was 471 ± 14 and was 465 ± 17 at Halcyon Hotsprings. The variances of the numbers of eggs carried (F = 1.223; df = 34,29; p > 0.05) and the means (t = 0.310, df = 63, p > 0.50) were not significantly different at either site. The distribution of eggs carried per female, pooled from both sites (Figure 7) was not significantly different from a normal distribution (K-S one sample, D = 0.060, n = 65, p > 0.10). Males probably do not discriminate among receptive females on the basis of the number of eggs they are carrying.

When comparisons are made between sites, Albert Canyon tandem males have longer forewings and greater dry masses but have similar total lengths to Halcyon Hotsprings tandem males (Table 9). Measurements for non-tandem males and females do not differ between sites. However, when tandem and non-tandem males are grouped together, there is a significant difference in forewing length (AC $\bar{x}$ = 2.41 cm,

HH $\bar{x}$ = 2.37 cm, 2-way ANOVA F = 7.828, df = 1, p = 0.006)
and dry mass (AC $\bar{x}$ = 14.93 mg, HH $\bar{x}$ = 14.22 mg, 2-way ANOVA
F = 8.815, df = 1, p = 0.004) between sites. Tandem males
had shorter wing lengths ($\bar{x}$ = 2.37 cm) than non-tandem males
($\bar{x}$ = 2.41 cm, 2-way ANOVA F = 6.243, df = 1, p = 0.014) but
did not differ in total length or dry mass. There is also a
significant interaction effect between mating status and
location for both forewing length and dry mass. Albert
Canyon tandem males, non-tandem males and Halcyon Hotspring
non-tandem males have similar forewing lengths, but Halcyon
tandem males have shorter wings (2-way ANOVA F = 4.236, df =
1, p = 0.042)(Table 10).

Halcyon tandem males weigh less than Halcyon non-tandem
males and Albert Canyon tandem males are heavier than Albert
Canyon non-tandem males, but non-tandem males have similar
dry masses at each site (2-way ANOVA F = 8.422, df = 1, p =
0.004)(Table 10). That is, tandem males are smaller than
non-tandem males at Halcyon, but larger than non-tandem
males at Albert Canyon.

However, data obtained from males in the field
contradict this. Males that were seen in tandem at least
once at Halcyon Hotsprings 1986 had longer forewings than
males that were never seen in tandem (Table 11). There were
no other significant differences of forewing length between
tandem and non-tandem males or females at both sites in 1985

or Halcyon Hotsprings in 1986 (Table 11).

While male forewing length did differ between tandem and non-tandem males from day to day (2-way ANOVA F = 2.419, df = 7, p = 0.021, log-transformed data), there was no significant interaction of day and mating status (F = 0.716, df = 6, p = 0.637) and no pattern in day to day variation in mean forewing length. Only days for which greater than three tandem and non-tandem forewing lengths were available were used in this analysis.

The 1985 pairs and non-tandem males measured in the lab were collected at two different times of day. Pairs captured for lab measurements were taken before many males or females had reached the water. Thus, these pairs could not contain males that had captured mates at the water. The sample of non-tandem males probably consisted entirely of males waiting for females at the water. Males that wait at the water for females may be different in size from males that capture mates early in the day away from the water. This would bias the size of males in the lab-measured samples. To test to see if such a condition existed, field forewing measurements were divided into morning (< 1300 hrs) and afternoon (> 1300 hrs) captures. Males first captured in the morning did not have different wing lengths from those first captured in the afternoon at either Albert Canyon (t = 1.04, df = 223, p = 0.299) or Halcyon Hotsprings

(t = 1.77, df = 138, p = 0.079) in 1985. In 1986, sample size was sufficient to test the effect of time of day on the forewing length of males captured either in tandem or as solitary males. Tandem and non-tandem males did not differ in the morning or afternoon (Table 12). Males found in the forest at Halcyon Hotsprings in the morning do not differ in size from males captured at the water in the afternoon.

Forewing measurements obtained in the field at Halcyon in 1986 of males that were first sighted mating with blue females ($\bar{x}$ = 2.36 ± 0.02 cm) were compared with those males first sighted mating with red females ($\bar{x}$ = 2.38 ± 0.01 cm) and were found to be not significantly different ($t_{(adj.)}$ = 0.66, df = 48, p = 0.511). There is no size difference between males mating with either female morph.

A paired-comparison t-test shows that females are larger than their mates (Table 13). The correlation coefficient of female forewing length with that of their mate is not significantly different from zero in all cases. Regressions of male forewing lengths on their mate's forewing lengths in all cases produced slopes that were not significantly different from zero. It seems reasonable to state that mating is random with respect to size.

DAILY MOVEMENT PATTERNS

The first individuals to appear each day at either site were males. In 1985 at Albert Canyon the first males sighted appeared at about 1000 hrs ($\bar{x}$ = 1001 ± 5.5 min). The earliest sightings of males at Halcyon Hotsprings were slightly later at about 1030 ($\bar{x}$ = 1025 ± 10.6 min). The Halcyon site is shaded by tall trees and is on a west-facing slope, so the sun does not reach it as early as it does the more or less flat, exposed Albert Canyon site. The time of arrival of males at either site was remarkably consistent on fine days. The times reported are for males appearing at the edge of the study site at Albert Canyon (Figure 2) or at the edge of the forest at Halcyon Hotsprings (Figure 3). In 1986 when males were actively sought early in the morning at Halcyon Hotsprings, they were found as early as 0945 hrs, basking in patches of sunlight that streamed through the trees, high on the slope in the forest. The temperature in these sunspots can be 6 - 18 °C higher than the surrounding shade. Occasionally non-tandem females were found at sunspots high on the slope but such sightings were rare. Only 31 of the 516 sightings of females were of non-tandem females in the forest before noon.

The first tandem pairs appeared at about 1215 daily at both sites in 1985 (AC $\bar{x}$ = 1213 ± 13.6 min; HH $\bar{x}$ = 1216 ±

25.0 min). At Halcyon in 1986, with more intensive
searching, the first copulating pairs were found in patches
of sunlight in the forest at about 1150 ($\bar{x}$ = 1151 ± 9.4
min). The first ovipositing pairs recorded at the water at
Halcyon were found at about 1320 ($\bar{x}$ = 1321 ± 27.5 min).

The number of pairs found at the water during the four
early afternoon "quick surveys" ranged from 2 to 15; no
non-tandem females were seen and non-tandem males numbered 5
and 6 on the two days their numbers were recorded. All
activity before 1300 was concentrated in the forest.
However, by 1430, the number of pairs and non-tandem males
at the water was too great to count and the amount of
activity in the forest was greatly reduced.

The number of pairs found during the 6 "quick surveys"
performed between 1600 and 1700 ranged from 2 to 6 and the
number of non-tandem individuals ranged from 2 to 28 with
about 2 to 8 non-tandem females. A number of individuals of
both sexes were seen perched in bushes on the slope, making
occasional feeding flights at this time. Presumably A.
vivida spend the night roosting high in the trees in the
forest. Several individuals were seen taking refuge there
during sudden showers.

Non-tandem males are most abundant in the forest before
1300 and most abundant at the water thereafter until
1600-1700. Non-tandem females were rarely sighted and the

distribution of sightings throughout the day is bimodal
(Figure 8). Sightings were divided into "morning" and
"afternoon" (before and after 1300 hrs, respectively). Blue
non-tandem females were seen earlier in the morning
(median = 1150 hrs, n = 40) than were red non-tandem females
(median = 1246 hrs, n = 24, Mann-Whitney $Z_{(approx.)}$ =
10.2, p < 0.001) and were also seen earlier (median = 1406
.hrs, n = 49) in the afternoon than were red non-tandem
females (median = 1427, n = 20, Mann-Whitney
$Z_{(approx.)}$ = 12.9, p < 0.001).

OBSERVATIONS OF BEHAVIOUR

At Halcyon, male _Argia_ _vivida_ first appear daily at warm
sunlit basking spots in the forest. It is quite likely that
the males are also basking on sunlit limbs higher in the
trees. The activity of male _A_. _vivida_ seems to depend
greatly on the opportunity to sun-bask. On cool cloudy
days, though individuals of both sexes remained active,
sexual activity ceased and the number of individuals seen
was fewer than usual. Pairs that were observed attempting
to copulate separating and took shelter in the trees when
showers began.

It is not known why females seem to become active later
in the morning than males. I found females quite early in

the morning when I carefully searched basking sites far from
the oviposition site. Tenerals of either sex seem not to
need to bask in the sun and are active early each day.
Females may be prevented from basking near the oviposition
site by male activity so that the appearance of females in
the study area each day later than males may be a result of
spatial separation, rather than a temporal one created by
different temperature thresholds for activity between the
sexes.

Males basking at sunspots pursue virtually everything
small that flies past, so it is difficult to see if they are
actively defending their basking sites. Of the 68 occasions
that live pinned males were presented to basking males, only
one resulted in a clearly aggressive encounter. Certainly
other males are chased from the area and males return
repeatedly to a single sunspot, but few remain at a sunspot
for very long. Males show no inclination to return to a
sunspot after being netted and removed from it. They often
do fly to another sunspot after being released and this new
sunspot is often downhill and toward the sun (i.e.
southwest) from the old one. At the water later in the day,
males display less site fidelity, possibly because they are
able to bask virtually anywhere.

Males at all locations show an affinity for white
surfaces on the ground. Sheets of writing paper folded to

form shallow slopes and placed at various conspicuous places
amongst green vegetation where <u>Argia</u> <u>vivida</u> males were not
seen perching before attracted males within a short time.
At Albert Canyon, cedar logs, large stones and small stones
on the hauling road provided the majority of basking sites.
The most frequently used of these have been included on the
map shown in Figure 2.

Females do not appear to reach the water except in
tandem. If they do reach the oviposition site without a
male, they must do so by flying directly to it from a great
distance. Once pairing activity has begun each morning it
is extremely difficult to find non-tandem females anywhere
in the study area. Paired females separated from their
mates, marked and released were quickly beset by other males
attempting to take them in tandem.

Late in the afternoon (> 1530 hrs) the density of
tandem pairs and non-tandem males decreased but non-tandem
females became easier to find. It might be expected that
because time for oviposition is limited in late afternoon
and most females present have already deposited a large
portion of their eggs, males should be more likely to leave
females alone and not attempt to mate late in the day.
However, males were seen attempting to mate at 1715 hrs.
Oddly enough, females were seen ovipositing, not in tandem,
within a few centimeters of perched males at this same time

of day.   After 1600 hrs females that congregate in bushes
along the stream and feed are ignored by males.

Females are able to escape males that attempt to take
them in tandem.   One blue female seen in the morning flew
rapidly to avoid the pursuit of two males and then turned
and flew aggressively at a third.   Males usually responded
sexually to the presence of the pinned live females (if they
responded at all) but one male aggressively attacked one of
the females that was presented to him.   Another tactic
females used to escape males was dropping to the ground when
contacted in the air by a male and then twisting around a
stem of vegetation to prevent the male from attaching his
abdominal claspers.   If males did manage to attach their
claspers, the females could avoid copulation by not curling
their abdomens forward or refusing to fly when the males
took off.   Even the most persistent males eventually
released females that behaved in this way.

Males also attempted to take tenerals in tandem.   Young,
very soft tenerals did not resist and males quickly released
them.   Older, more hardened tenerals attempted to avoid the
males by rapid flight and one was seen to turn on a pursuing
male and curl its abdomen upward in an "S" shape (similar to
the "threat display" described for Ischnura verticalis by
Bick 1966) which caused the male to turn away.   In addition
to live tenerals of either sex, males were observed trying

to form tandems with other males, with males already in tandem, and with dead tenerals, males or females in spider webs. On one occasion a male at Halcyon Hotsprings was seen attempting to mount a male _Leucorrhinia_ _hudsonica_. Despite this apparent indiscrimination, males rarely interfered with tandem or copulating pairs. Pairs that made any movements near non-tandem males were invariably investigated by the males but were usually left alone after a brief inspection.

Female _A_. _vivida_ do not normally copulate immediately after the tandem has formed and the pair has landed in a place suitable for copulation. Females were often seen making curling stabs with their abdomens at their mate's accessory genitalia prior to copulation. These movements were performed repeatedly for up to 40 s. Such behaviour has been called "genital touching" by Robertson and Tennessen (1984). Males were also seen rubbing the heads of their unwilling mates against their accessory genitalia between attempts at wheel formation. Males with females unwilling to curl their abdomens forward were seen bending their abdomens at the joints of the third segment and forcing their accessory genitalia against their perch.

If a male obtains a mate in the morning (before 1300 hrs), he must remain with her for a considerable time. Since many copulations were completed by 1230 and few tandem pairs were seen ovipositing before 1330, males may spend at

least one hour in tandem with their mates before they begin to oviposit. The times of the first daily sighting of copulating pairs and the first daily sighting of ovipositing pairs are remarkably consistent for sunny warm days. Complete oviposition, based on attempts to follow pairs during oviposition and estimates from pairs seen later in the day as individuals, probably requires at least one hour. A male taking a receptive female in tandem in the morning probably remains in tandem with her for a total of at least three and one-half hours. Obtaining a mate in the morning must represent a considerable investment of time and energy for males.

Tandem pairs, including copulating pairs, move frequently. Logging trucks passing on the highway at Halcyon Hotsprings caused tandem pairs to change position even though they were at least 20 m away. One pair that was mating on a sunlit limb at the border between the sun and shade moved three times as the shade overtook them. Copulating pairs were able to fly great distances without breaking the wheel position.

Pairs also move frequently during oviposition. It seems almost essential that the female of a pair should be directing the pair's flight since it is she that ultimately determines where eggs are laid. Males are often suspended by their terminal appendages only, above the ovipositing

females with their legs and wings folded. These males can be seen to take flight in response to their mates' movements. At other times it is the male that first takes flight and the female usually flies with him. However, females are not always willing to fly with their mates and these females were seen grasping their perch until, after several attempts to pull the female off, the males detached their terminalia and flew away. In late afternoon, pairs were often seen flying erratically in a "zig-zag" flight, as described for Enallagma civile by Bick and Bick (1963). Of three such pairs successfully followed, one pair separated in mid-flight, the others landed and the females refused to fly again until the males detached. These two females were captured, preserved in formalin and dissected later. Both carried about the same number of eggs (475, 278; points lettered "E", Figure 9) as non-tandem females captured early in the morning ($\bar{x}$ = 467 ± 56), but more than females captured late in the afternoon ($\bar{x}$ = 96 ± 32) that were presumed to have finished ovipositing (Figure 9). The number of eggs deposited in a single day by a female, estimated by the difference between the means of numbers of eggs carried by pre- and post-oviposition females, is 371 (Figure 9).

The number of eggs carried by females ovipositing unguarded, including the two females that escaped their

mates ($\bar{X}$ = 323 ± 134) was not significantly different from the number of eggs carried by females prior to oviposition (Duncan's multiple range test, critical mean = 302, p > 0.05; Figure 9).

Other instances were observed where males simply detached from females with no apparent change in the pair's behaviour, either while flying, perching or ovipositing. .Some females that were ovipositing when their mates detached continued to oviposit and one such female was seized and mated by a second male within five minutes of her first mate's leaving. At Albert Canyon pairs frequently separated while attempting to fly up from the tangle of _Equisetum_ sp. in which they had been ovipositing. The clatter of the wings of these pairs could be heard from several meters and the pair sometimes emerged in tandem, but usually separately, from the vegetation.

Females that became non-tandem at the water either quickly left the area by flying rapidly, continued ovipositing in dense vegetation without a guarding mate, or were captured and possibly mated by a second male. At Halcyon Hotsprings in 1986 only 16 females were captured more than once in a single day. Ten of these were captured at least once in tandem and all of these females were captured after 1400 hrs. Four of the 10 females were captured in tandem only once and two of these four were seen

first in tandem and then not in tandem. The other two
females were first sighted not in tandem and then were taken
in tandem by males. Because none of the females sighted in
tandem more than once in a single day were mated with marked
males it cannot be said for certain that they were with the
same mates for both sightings. The two females seen first
not in tandem and later in tandem, for reasons given
previously, must have already mated with another male, have
left him, or have been left by him, and then must have been
captured by a second male. One of these two females
remained at the water and oviposited without a guarding male
after separating from this second male. One female that was
used for timed behavioural observations also behaved in a
similar manner. These limited data and observations of
females separated from their mates during marking show that
female A. vivida are capable of mating more than once in a
single day and that they may oviposit with or without
guarding males.

Direct observations of predation on Argia vivida were
rare. At Albert Canyon, a sparrow nesting near the study
site was seen several times with three to four newly emerged
tenerals dangling from its beak. On another occasion a
sparrow was observed to take an adult male. A Sympetrum sp.
was seen taking an adult. At Halcyon Hotsprings spiders
were responsible for most of the observed predation. On

arrival one morning, 24 A. vivida wings were found in spider
webs. Non-tandem individuals were found dead in spider webs
each day, but webs were not seen with more than one
damselfly in them, suggesting that one or both members of a
tandem pair may be able to escape capture. Because of the
proximity of the oviposition site to the highway, many
individuals are probably killed by passing cars and trucks.
.Predation by birds was not observed at Halcyon Hotsprings.

EXPERIMENTAL OBSERVATIONS OF BEHAVIOUR

Ten minute observations of males in the forest in the
morning and of males at the water in the afternoon revealed
that the behaviour of males at both locations was similar.
Following males at the water in the afternoon proved to be
more difficult than observing males localized at sunspots in
the forest in the morning. Males at the water rarely
settled near the same perch twice in a row and they were
subject to the disturbance of passing cars. With the large
numbers of non-tandem males and tandem pairs at the water,
males in flight were quickly confused with others. Also,
the bright blue colour and black markings of males combined
with their erratic flight made them very difficult to follow
in bright sunlight.

The data obtained were pooled for individuals in the groups "morning" (away from water) and "afternoon" (at the water) with the assumption that the individuals observed were representative of these groups (Table 14). Comparing both groups, males away from the water flew less frequently and at greater intervals than males at the water (Table 14). However, this does not take into account that it was cooler in the morning, meaning males would be less active, nor does it take into account the fact that density of conspecifics is greater at the water in the afternoon and therefore there is a greater potential for interactions with them. Comparing the proportion of flights devoted to each activity (changing perch, feeding, pursuing males, and investigating insects), the behaviour of males at the water does not differ from males at sunspots in the forest (X^2 = 6.519, df = 3, p = 0.09). The activity "pursuing tandems" could not be included in the analysis because there were no tandem pairs present in the forest at the times when males were observed.

Males at the water in the afternoon and away from the water in the morning did not behave differently. In general, _Argia_ _vivida_ males tended to fly out at any insect their own body size or smaller that flew by.

Ovipositing pairs changed their location quite frequently. The average time between perch changes for the

six pairs observed was about one minute (Figure 10). The percentage of observed time spent ovipositing ranged from 0 - 44% (Figure 10). Of twenty-five recorded oviposition bouts 16 (64%) lasted less than one minute. For the majority of the time that all pairs were observed they were perching and probing.

If the number of transitions between probing, perching and ovipositing are examined (Figure 11) then most activity can be seen to have centered on seeking and sampling oviposition sites. This, when considered with the variability of the time spent ovipositing, suggests that high quality oviposition sites are patchily distributed and that pairs spend a great deal of time looking for acceptable sites.

The responses of males to live pinned females (including only the "mount red", "mount blue" and "inspect" categories) did not differ between study days (Table 15). Results were pooled for the three days and the ratio of responses to red versus responses to blue live pinned female models was found not to be significantly different from 1:1. Males showed no preference for either colour morph. The data were regrouped according to whether the presentations were made to males at or away from the water. Males showed no preference for either female morph whether they were at the water or away from it (Table 16).

In fact, males showed little discrimination for what type of _Argia_ they attempted to form a tandem with, provided that the pinned individual was moving. Although a trend toward mounting females rather than males or tenerals is apparent (Tables 17 and 18), sample sizes were too small for reliable statistics so this cannot be proposed with confidence.

Five marked males were offered red and blue females simultaneously more than once (with greater than 10 min elapsed between presentations). Of these five, only three responded on all occasions by mounting a female. One of these males attempted to mount the red female on both occasions it was presented to him. Another male attempted to mount the blue female the first time a pair was presented to him, and attempted to mount the red female the second time the pair was presented. The third male was presented with a pair of pinned females four times. Twice he attempted to mount the blue female and twice the red female. Males do not appear to have an inherent preference for either female colour morph.

The removal of males from forest sunspots in the morning did not affect the ratio of red to blue female morphs appearing in tandem at the water between 1430 and 1530 hrs on the day of removal (Table 19). Although the number of males removed may seem insignificant in light of the

population densities estimated for the site, the number of males captured was not limited by the time allotted for the removal, but by the number of males visible at sunspots in the forest. By the time the removal of males was completed each day, virtually no males were visible at sunspots in the forest. All had either been captured or harassed into leaving the area.

Females were regrouped according to whether they had oviposited on a previous day (stained abdomen) or not (unstained abdomen) to see if experience gave females an advantage in either attracting or avoiding males. The ratio of red females with stained abdomens to red females with unstained abdomens to blue females with stained abdomens to blue females with unstained abdomens was independent of study day ($X^2 = 16.41$, df = 21, p = 0.688), suggesting that male mating pressure was equal for both experienced and inexperienced females of both morphs.

The duration of copulation for _Argia_ _vivida_ was initially believed to be long when compared to other _Argia_ spp. (Table 2). Observations of three copulations which occurred in early mornings in 1985 ranged from 28 min to over an hour. Subsequent observations at Halcyon Hotsprings in 1986 showed that copulations occurring in the morning took approximately 40 min while copulations observed in the afternoon took approximately 5 min to complete (Figure 12).

While it might be expected that copulation duration would decrease with increasing temperature from morning to mid-afternoon, the copulations were timed on a number of days and therefore at a wide range of temperatures. The late morning temperatures of some days were not different from the late afternoon temperatures of others. Intuitively, temperature could not be responsible for the great difference between the duration of copulation in the morning and late afternoon.

Since temperatures were not recorded for all times of day and dates when copulations were timed, a multiple linear regression on available data was performed using time of day, time of day squared and date to predict temperature. The equation obtained was:

$$\text{temperature} = 17.19 + -0.0063(\text{date}) + 0.0569(\text{time}) + -0.0000981(\text{time})^2$$

The fit of this equation to the data was significant (multiple $r = 0.683$; $F = 9.633$; $df = 33,2$; $p = 0.0001$). The equation was then used to estimate temperatures for the times of day and dates at which copulations were timed. These predicted temperatures were used in a stepwise multiple linear regression of time, date and temperature against copulation duration. A significant fit of the

regression line was obtained (F = 25.1; df = 10,1; p < 0.0005). Time of day was the only variable which explained a significant portion of the variation in copulation duration. The partial correlation of time of day on copulation duration, controlling for the effects of temperature and date was −0.696 (df= 8,p = 0.013). The partial correlation of temperature on copulation duration, controlling for the effect of time of day and date was only 0.231 (df = 8, p = 0.260). Diel changes in temperature cannot account for the great variation in copulation duration seen between morning and afternoon.

SUMMARY OF RESULTS

1. <u>Argia</u> <u>vivida</u> females occur as two colour morphs; one is blue and looks similar to males, the other is red-brown. Morph colour is not affected by age or temperature.

2. Both sexes experience "physiological colour change". Males and both colours of females display "dark phase" colouration at cool temperatures (< 24 °C) and "bright phase" colouration at warm temperatures. Individuals mate while displaying either colour phase.

3. The flight season of <u>Argia</u> <u>vivida</u> near Revelstoke, British Columbia, is from late May to late September or early October.

4. The sex ratio of emerging tenerals is 1:1. At both Albert Canyon and Halcyon Hotsprings, the sex ratio of sexually mature individuals favoured males. Non-tandem females were rarely seen.

5. The maximum abundance of males at Halcyon Hotsprings in 1986 is estimated to be about 1000 individuals (by the Jolly-Seber method).

6. Males come to the water (oviposition site) more frequently than females.

7. The mean minimum number of days alive (MDA) of sexually mature individuals was about 12 days for both males and females.

8. The ratio of red to blue morphs was 1:2 at Halcyon Hotsprings in both 1985 and 1986, but was 1:1 at Albert Canyon in 1985.

9. At Halcyon Hotsprings in 1986, the ratio of non-tandem red to blue females was equal to the ratio of red to blue females sighted in tandem. The female morphs were mated in proportion to their frequency in the population.

10. Males may mate with either or both morphs over their lifetime.

11. Strong correlations were obtained between body length and mass among females and abdominal length and mass among males. Forewing length, though strongly correlated with mass, was not correlated as strongly as these

measurements but was used as a fairly good index of body size because it was easy to measure accurately in the field.

12. No body-size correlates of 11 red and 11 blue females preserved in acetone from Halcyon Hotsprings were significantly different.

13. A discriminant analysis using eight size and morphological characters failed to distinguish between red and blue female morphs.

14. Female body size does not correlate well with the number of eggs the female is carrying prior to oviposition.

15. The number of eggs carried by females prior to oviposition is randomly distributed. Males probably are not selecting females on the basis of the number of eggs they are carrying.

16. In 1985, Albert Canyon tandem males had longer forewings and greater body masses than Halcyon Hotspring tandem males. Measurements of non-tandem males did not differ between sites.

17. Tandem males were smaller than non-tandem males at Halcyon Hotsprings, but non-tandem males were smaller than tandem males at Albert Canyon in 1985.

18. Measurements of forewing length taken in the field at Halcyon Hotsprings in 1986 showed males seen at least

once in tandem had longer wings than males never seen in tandem. No other comparisons of field-measured forewing lengths between tandem and non-tandem males or females in either year were significantly different.

19. There was no pattern of seasonal variation of male forewing length in 1986.

20. In either study season there was no difference in forewing lengths between males captured in the morning and those captured in the afternoon. As well, tandem or non-tandem males first captured in the morning or the afternoon were not different in 1986.

21. There was no difference in forewing lengths of males first captured mating with either female colour morph.

22. Female _Argia_ _vivida_ have larger forewings than males but there is no correlation between forewing lengths of females and the forewing lengths of their mates.

23. The activity of _A_. _vivida_ begins at about 1000 hrs each day. Nearly all of the earliest daily sightings were of non-tandem males far from the water.

24. The first copulating pairs were seen at about 1150, the first tandem pairs near the water at 1215 and the first ovipositing pairs at 1320 at Halcyon in 1986.

25. Daily sightings of blue non-tandem females were, on average, earlier in the morning and afternoon than those of red non-tandem females.

26. Females are able to avoid males that attempt to take them in tandem.

27. The habit of sun-basking seems important in determining the behaviour of A. vivida.

28. Non-tandem females become more abundant (or are easier to find) after male density at the water decreases late in the afternoon (> 1600 hrs). Some of the males remaining at the water attempt to mate with females, others do not.

29. Several incidents of males attempting to mate with tenerals, other males or even other species occurred.

30. Pairs formed in the morning probably remain in tandem for three and one-half hours.

31. Female A. vivida may mate more than once in a single day and are capable of ovipositing with or without a guarding mate.

32. The behaviour of males in the morning away from the water is not different from the behaviour of males at the water in the afternoon. Males fly out to investigate almost any insect that flies by.

33. Ovipositing pairs devote much of their time to moving about and sampling new oviposition sites. Approximately 2/3 of the recorded oviposition bouts (25) lasted less than one minute.

34. Males showed no preference for either female morph when

presented with live pinned models and when presented with the pinned models more than once, a male's choice of morph was independent of previous choices.

35. Removal of males from forest sunspots early in the morning on a number of days in an attempt to reduce male mating pressure on females failed to alter the ratio of red to blue females in tandem in the afternoon of the same days.

36. Copulations begun in the morning at Halcyon Hotsprings take about 40 min to complete, while those begun in the afternoon take only about 6 minutes. This difference in copulation time cannot be adequately explained by differences in temperature alone.

DISCUSSION

FEMALE POLYMORPHISM

Female _Argia_ _vivida_ occur in two distinct colour morphs in the populations studied. The taxonomic data presented by Walker (1953) and Cannings and Stuart (1977) suggest the possibility of three colour morphs: blue, brown (= red in this study) and a yellow-grey or green-grey morph. However, Garrison (1978) and Paulson (1974) recognized only brown and blue morphs in populations of _A_. _vivida_ in California and Washington which, is consistent with my observations.

Males do not show any preference for either morph. This was illustrated by observation of marked individuals and by experiments using live pinned individuals. Paulson (1974) presented _A_. _vivida_ males with live pinned female heteromorphs of various species, one at a time. He found that _A_. _vivida_ responded sexually to females of a very wide range of species and body sizes. Bick and Bick (1965b) found that male _A_. _apicalis_ reacted sexually more often to brown female morphs than "turquoise" females, "grey-black" females or other males when presented with various dead, pinned _A_. _apicalis_ models. The present study, however, is the only study to offer males a choice of two live pinned specimens simultaneously.

Garrison (1978) found, by observing individually marked damselflies, that _Enallagma cyathigerum_ males showed no preference for either female morph in the population he studied. He (Garrison 1979) obtained similar results for a population of _E. civile_, as did Finke (1982) for _E. hageni_. Robertson (1985) also found no evidence of colour-assortative mating in a population of _Ischnura ramburii_ but Johnson (1975) showed that male _I. demorsa_ and _I. damula_ possessed an inherent, but not irreversible preference for a particular female morph. Johnson (1975) did not discuss the evolutionary significance of the preference and it appears to be atypical among the Odonata.

For _A. vivida_ males, the cost of remaining in tandem with a mate for so long must be high. In species where the cost of mating is high to males, males might be expected to become choosey (Dewsbury 1982) and show a preference for a particular morph. This presupposes that the different female colour morphs are of different value to males as mates. For instance, one morph could produce more eggs than the other. This possibility was not investigated in _A. vivida_. However, in light of the size similarity of the morphs and the fact that a sample containing a random mixture of red and blue morphs (the "formalin" pairs) had a random distribution of egg counts, it is reasonable to assume that one morph is not more fecund than the other.

However, if egg production is similar for both morphs, one may be more successful at laying fertile eggs than the other.

On the other hand, when competition for mates is intense or the male-female encounter rate is low, males might evolve to mate with any female they encounter and no preference should be observed. Data for male selectivity among odonates, at least on the basis of colour, remains inconclusive.

In all populations of Ischnura damula and I. demorsa that Johnson studied (1964, 1966, 1975), andromorphs occurred at lower frequencies than the heteromorphs (2-42%). Robertson (1985) reported that andromorphs occurred at a frequency of 31% in the population of I. ramburii he studied. In studies of Enallagma spp. heteromorphs usually outnumber andromorphs (E. hageni, Finke 1982; E. cyathigerum, Garrison 1979). One exception is the population of E. civile studied by Garrison (1979) where the ratio of andromorphs to heteromorphs was 3:1. Populations such as those of A. vivida in this study, with andromorphs equalling or outnumbering heteromorphs, may be rare. In fact, Kennedy (1915) found so few andromorphs in the populations of A. vivida he studied in Oregon and Washington that he believed he had sampled the populations shortly after a mass emergence and the brown morphs represented

immatures. A study of the variation in andromorph frequency in a far greater number of populations over the species' range is needed. Ideally, breeding experiments should be performed to determine the inheritance patterns of the female colour morphs. The major stumbling block is the extreme difficulty in rearing the damselflies in the lab.

Johnson (1964, 1966) found that Ischnura female dimorphism is controlled by a single autosomal sex-controlled gene that is inherited in simple Mendelian fashion. The andromorph represents the recessive homozygote. The populations of A. vivida studied were fairly large and isolated with little chance of immigration or emigration and mating was random with respect to colour. If the inheritance pattern of female dimorphism in A. vivida is assumed to be the same as Johnson found in I. demorsa (Johnson 1966) and I. damula (Johnson 1964), then the populations of A. vivida studied can be considered to have reached Hardy-Weinberg equilibrium with respect to the female dimorphism and genotypic and allelic frequencies may be calculated. At Halcyon in 1986, the frequency of the hypothetical "andromorph allele" was 0.801 ± 0.032 and was not significantly different from the allele frequency at Halcyon in 1985, which was 0.810 ± 0.014 ($Z = 0.348$, $p > 0.36$). The frequency of the "andromorph allele" at Albert Canyon in 1985, 0.696 ± 0.219, was significantly different

from the frequency at Halcyon in that year (Z = 2.003, p < 0.02).

Since the populations are isolated and relatively small, it may be postulated that the difference in gene frequencies has resulted from the stochastic processes of a founder effect or genetic drift. Both of these hypotheses are untestable and the allele frequencies are based only on a hypothetical genetic relationship. In butterflies, female morph colour may be Y-linked (males are homeochromatic), autosomal dominant or autosomal recessive as in Papilio glaucus (Lepidoptera), P. polytes and P. dardanus, respectively (Turner 1978). It may not be reasonable to extend the inheritance mechanism to other members of the genus Ischnura, much less to other genera of the same family.

Little can be said about the function of the two female colour morphs from the observations and experiments presented here. Among butterflies displaying female-limited polymorphism, the heteromorphs are usually mimics of an unpalatable species (Emmel 1973, Turner 1978, Vane-Wright and Ackery 1984). This does not appear to be the case among odonates, since heteromorphs are drab and andromorphs, like males, are more brilliantly coloured. To my knowledge, no one has performed studies of the palatability of odonates. Should some form of Batesian or Müllerian mimicry be

operating, it would most likely be the brightly coloured andromorphs and males that are the mimics, rather than the drab heteromorphs. This situation is opposite to that of butterflies and is somewhat less plausible (Turner 1978).

Male A. vivida are smaller than females and a male could be a less profitable prey item than a female laden with nutritious eggs. Andromorphic females may be mimicking the less profitable males to help reduce predation pressure; an alternative tactic to being cryptic. This is an extension of the "unprofitable prey hypothesis" of Baker and Parker (1979), originally applied to the evolution of conspicuous colouration in male birds. The hypothesis has received some convincing criticism (Lyon and Montgomerie 1985, and references therein) but provides an intriguing possibility in this specialized application. While Hafernick and Garrison (1986) have found evidence that this does not operate in Ishnura gemina, it is still worthy of investigation as an alternative to the classical Batesian/Müllerian mimicry hypothesis.

In terms of population genetics, the simplest explanations for the presence of a balanced dimorphism of female colour involve frequency dependent selection. This has been dicounted for at least one species of butterfly (Levin 1973, but see Burns 1966) and does not successfully explain why the polymorphism is sex limited.

Turner (1978) has provided linear models indicating that the greater intensity of intersexual selection on males prevents the formation of multiple male morphs because any new morph arising will be rejected by females. In A. vivida, where males have no courtship display and females are seemingly captured by force, it is unreasonable to assume that female choice could exert such an influence.

Johnson (1975) and Garrison (1979) have postulated that the presence of andromorphic females enhances species isolation because in the species of Ischnura and Enallagma they studied, andromorphs were more abundant in populations that were sympatric with similar species. The populations of A. vivida studied were isolated from any similar species but the frequency of andromorphs was higher than in any of the populations of Ischnura that Johnson (1964, 1966, 1975) studied. The high density of andromorphs cannot be linked to species isolation for A. vivida.

Neither of the sociobiological functions for the polymorphism proposed in this study appears to be operating. Males did not discriminate between the female morphs and the male removal experiment failed to alter the daily ratio of red to blue morphs. The hypothesis that male mating behaviour affects the relative numbers of each morph at the water each day may be rejected. Important observations are missing from both the male removal experiment and the

presentations of pinned females. If females do indeed use their colour to avoid harassment during oviposition (Robertson 1985), then the effects of decreased male density would not show up among tandem ovipositing females that are protected from harrassment by their mates. It would be more likely to be expressed as a change in the relative numbers of a morph ovipositing without guarding males. The numbers of unguarded females of each morph ovipositing daily was not recorded because of the difficulty of locating unguarded females at the water.

If andromorphs enjoy an advantage in attractiveness to males because of their visibility, males responding to blue pinned females might be expected to do so from a greater distance. An experiment testing the response distance to pinned females of either morph was not performed.

Since males are indiscriminate in their mating preferences it is not likely that Vane-Wright's (1984) pseudo-sexual selection can be applied to A. vivida. Because few males were removed during the removal experiments, and numbers of females ovipositing unguarded were not recorded, Robertson's (1985) male avoidance hypothesis cannot be dismissed. However, pretending to be a male does not seem to be a good way to avoid harrassment when males attempt to copulate with almost every other damselfly they encounter. Also, red females could be

mimicking tenerals, which are just as likely to be ignored by males as other males are. This possibility was not explored.

Robertson (1985) does point out that the male-mimicking system is frequency dependent in that if andromorphs become more abundant than heteromorphs, males should be selected to be less discriminating to avoid deceit. He does not discuss how the andromorphs might become more abundant but this may well have happened in the populations of A. vivida studied.

The function and evolution of female polymorphism are complex problems. Much more information on the genetics of the polymorphisms, the palatability of damselfly species, the effect of predation of adults on damselfly population dynamics and the social interactions of the morphs are needed before the significance of the colour differences can be determined.

PHYSIOLOGICAL COLOUR CHANGE

In addition to having two female morphs, Argia vivida also undergoes a physiological colour change. Physiological colour change is regarded as having a thermoregulatory function (May 1976, O' Farrell 1963, Vernon 1974) and is widespread among odonates (Corbet 1980). In general, the background colour of individual odonates changes from dark

to light as temperature increases and from light to dark as it decreases.

Vernon (1974) showed that "dark phase" _Austrolestes annulosus_ were more sensitive to sunlight which allowed them to orient themselves to obtain the maximum warmth from the sun. He dismissed the idea that "dark phase" individuals absorb warmth from sunlight more readily (O' Farrell 1963, 1964) after finding that the heating rates of light and dark individuals were the same. O' Farrell (1963) noted that "bright phase" _Diphlebia nymphoides_ were more tolerant of high temperatures.

May (1976) experimented with physiological colour changes in seven species of _Argia_ from Florida and Costa Rica. He suggested that the capability for physiological colour change is widespread in the genus. He also noted, as did O' Farrell (1964), that only the blue portions of the cuticle changed colour in response to temperature changes. In _Argia vivida,_ the blue areas of the thorax and abdomen of males and andromorphic females display physiological colour change, but so do the brown areas of the thorax and abdomen of heteromorphic females.

The threshold temperature for the colour change from "dark phase" to "bright phase" in _A. vivida_ is high (20-24 °C) when compared to the threshold temperature of 12 °C given for _Austrolestes annulosus_ by Vernon (1974)

but agrees with the figures presented for other _Argia_ spp. by May (1976).

Sternberg (1987) noted that the "bright phase" spots of male _Aeshna_ _caerulea_ reflect U.V. light strongly. The blue portions of "bright phase" _A_. _vivida_ males also appear to reflect U.V. more strongly than those of "dark phase" males. Unfortunately, live or recently killed specimens were not available for observation under U.V. light.

I propose that in addition to aiding in thermoregulation, physiological colour change aids in intrasexual signalling in _Argia_ spp. Robertson (1984) found that the whitish exudate, or pruinosity, of many odonates is highly U.V. reflective. The entire dorsal surface of the abdomen of mature male _Libellula_ _lydia_, for example, is covered with pruinosity. Jacobs (1955) recognized that this might serve a signal function and performed a number of experiments that indicated this was the case. Regardless of the white colour, the pruinose abdomen may serve as an ultraviolet flag.

Bick and Bick (1965b) presented male _A_. _apicalis_ with various combinations of female _A_. _apicalis_ body parts, sometimes painted different colours. They found that the "minimum stimulus" required for sexual response was a wing and thorax. They also found that the stimulus of a wing and thorax was enhanced when the thorax was painted white,

despite the fact that males showed a preference for brown female morphs. A bright reflection, as might be obtained from white paint or a highly U.V. reflective surface appears to be an important cue in releasing sexual behaviour in the species.

Likewise, a bright appearance (with or without high U.V. reflectance) might be important in determining the outcome of intrasexual aggression in A. vivida. The importance to individuals of having bright "bright phase" colouration may be implicated in what seems to be the genus' almost universal habit of sun-basking. Argia difficilis in Panama (Shelly 1982) and several of the Argia species studied by May (1976) in Florida and Costa Rica all practice sun-basking. This behaviour is probably not needed to raise their body temperatures high enough for daily activity in such warm climates. Perhaps it aids in producing bright colouration which increases an individual's success in social competition.

The literature on female (and male) polymorphism is undoubtedly confounded by earlier worker's ignorance of physiological colour change. "Polymorphisms" which were recognized in earlier works (see, for example, Bick and Bick 1965b, Borror 1934, Parr 1965) may be the result of a combination of a simple dimorphism, ontogenetic colour change and physiological colour change. May (1976)

presented this argument to explain discrepancies between his observations of colour polymorphism in A. apicalis and those of Bick and Bick (1965b). Such may be the case with the many colours of A. vivida females recognized by Kennedy (1915) and Walker (1953).

DAILY MOVEMENT PATTERNS AND REPRODUCTIVE BEHAVIOUR

Since the majority of the observations of mating behaviour occurred at Halcyon Hotsprings, my discussion will be concentrated on the behaviour of Argia vivida at that site. Each day activity does begin earlier at Albert Canyon, but this is most likely because sunlight reaches the flat, more exposed site earlier than it does at Halcyon Hotsprings. Qualitatively, the activity of A. vivida seems similar at both sites.

A. vivida roost high in the trees in the forest east of the stream at Halcyon and in the shrubs and bushes surrounding the study site at Albert Canyon. At Halcyon, individuals are only able to approach the water from one direction. At Albert Canyon, they may move from anywhere around the perimeter of the study site toward scattered oviposition sites within the study area. Movement patterns are much easier to interpret at Halcyon but similar, more

complicated patterns appear at Albert Canyon.

Solitary male _Argia_ _vivida_ at Halcyon Hotsprings first appear in the forest each day at approximately 1000 hrs. The earliest male activity occurs at sunlit patches high on the slope. Males possibly defend these sunlit patches against conspecific males. Their behaviour is similar to that of the butterfly _Pararge_ _aegeria_, which Davies (1978) described as being territorial. Unlike the males of _P._ _aegeria_ that remain in the area of specific sunspots, those of _A._ _vivida_ migrate in a slow wave toward the water.

Females become active at about the same time as males and begin moving toward the oviposition site. It is possible that blue females become active earlier in the morning than do red females, though this result may be created by the difficulty of seeing red females on the shadowy forest floor.

On their way to the water, females are intercepted by the sun-basking males. Males fly toward almost any passing object of appropriate size, including other males and immatures. Males grapple with the females in flight and attempt to take them in tandem. By 1230 hrs the majority of the receptive females for the day are probably in tandem. Males that have not yet obtained mates continue moving to new basking sites in the grassy areas of the stoney 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. This is also similar to the
behaviour of P. aegeria (Davies 1978).

Light patches in a forest may attract many insects
(Finke 1984b) and the habit of intercepting females at light
patches has been described for other damselfly species
(Megaloprepus coerulatus, Finke 1984b; Platycnemis
echigoana; Watanabe and Oshawa 1984).

It is difficult to decide if the behaviour of males at
sunspots may be called territorial. Males do defend the
sunspots against other males. Whether or not defence is the
"intention" of males that fly out at other males from
sunspots is not known. The encounters between males may
just be cases of misdirected sexual pursuit (Moore 1952).
Moore's observations have been discounted by many authors
(including Moore 1964) but seem plausible in A. vivida where
sex recognition by males is weak. Sunspots cannot be
defended by males as easily as some particular feature of
the land or an oviposition site. Sunspots vary in
intensity, move, or even disappear as the sun arcs across
the sky. Taking the simplest, generally accepted definition
of territory as "any defended area" (Noble 1939), A. vivida
males may be considered territorial. The territories they
defend are ephemeral so their localization at a particular

site is brief. Also, if they succeed in capturing a female they can no longer defend the site.

A. vivida does not fit the requirements for territoriality that Waage (1973) applied to Calopteryx maculata because its method of territorial defence does not involve ritual displays. A. vivida fits into the category "intermediate in territory" which Bick and Bick (1971) used to describe the behaviour of A. plana and A. apicalis. These species displayed spacing, slight localization and superiority in their territories, but did not use complex flight maneuvers in territorial display.

A "morning" copulation occurs in the forest or high on the stoney slope, far from the water, and takes about 40 min. By 1330 hrs the first tandem pairs begin to appear at the water. Within 90 minutes the density of tandem pairs at the water becomes too high to count. Solitary males are also abundant at the water from 1330 to 1500 hrs. They perch within a few centimeters of tandem pairs but never interfere with their activities.

After 1530-1600 hrs activity begins to decline. Females that escape or are released from tandem frequently fly rapidly and often straight up. Occasionally unguarded females at the water are captured by males, copulate with them and continue to oviposit with the new male guarding. Other unguarded females oviposit secretively. Oddly enough,

these unguarded ovipositing females are sometimes ignored by
males at the water.   A few males and females remain at the
water until after 1700 hrs.   Oviposition and attempted
matings continue to occur but most of the oviposition at
this time is by unguarded females.

Few studies of zygopteran behaviour have reported the
mating behaviour of species that mate at sites far from the
water.   Most are concerned with the activity of the species
at the water and report that mating must take place away
from water since most pairs arrive at the oviposition site
in tandem.   Mating far from the oviposition site is not
common among coenagrionids, making A. vivida unusual in this
respect.   Male A. vivida are also unusual in defending
territories far from the water.   Platycnemis echigoana
(Watanabe and Oshawa 1984) is the only other damselfly I
know of that is reported to do this.   The New Zealand
dragonfly Diplacodes bipunctatus holds territories away from
water but these are concerned primarily with feeding (Parr
1983).   The dragonfly Nesciothemis nigeriensis defends
territories at a communal roosting site away from water
where mating may occur (Parr 1983).

The two places where the chances of encountering females
are the best are at the oviposition site and near the
females' roosting sites.   Males attempting to capture
females before they reach the water should prefer areas as

close as possible to the females' roosting sites. Males active at sunlit patches on the forest floor will have the first chance to capture females as they begin to move toward the water. Sunlit patches in the forest are not numerous and as males become more abundant later in the morning, more and more males are forced to search for basking sites further down the slope. Males on the stoney slope from 1100-1200 hrs probably have little chance of intercepting a mate. Nearly all mating activity occurs at the sunlit patches in the forest.

I believe males that are still unmated at noon move toward the water and seek mates at the second place where the chances of encountering females is high -- the oviposition site. It is important to note that unmated males at any position -- in the forest, on the stoney slope, or at the water -- will attempt to mate with any female they encounter.

Most of the copulations observed intensively in the forest concluded before 1230 hrs, yet no pairs appeared at the water until 30-60 min. later. There is some latent period during which pairs remain in tandem following copulation, but do not fly to the water and begin ovipositing. _Enallagma_ _exsulsans_ displays similar behaviour (Bick and Hornuff 1966).

Tandem and copulating pairs cannot fly rapidly or

maneuver well. It would seem prudent for pairs to copulate quickly and oviposit as soon as possible thereafter. Miller and Miller (1981) have suggested that the duration of copulation will vary with the body temperature of the individuals involved. Assuming the body temperature of A. vivida is strongly correlated with air temperature, the great variance in duration of copulation observed in this study cannot be explained by changes in temperature alone. Robertson (1985) found that I. ramburii tended to copulate until mid-afternoon, regardless of when the copulations began. He believed that since males did not practice postcopulatory guarding, the prolonged copulations served to hold females until it was too late in the day to copulate again (see also Bick and Bick 1965a) and this reduced the possibility of sperm competition.

Miller et al. (1984) proposed that male Sympetrum depressiusculum were performing "precopulatory guarding" when they held females in tandem for long periods in the morning prior to copulating with them. This precopulatory guarding allowed males to seek mates early in the morning, take advantage of an opportunity to capture a mate when they encountered one, and still avoid the possibility that their sperm will be displaced by another male before conditions are good for oviposition.

The long copulation time and postcopulatory latent

period probably serve a similar function in A. vivida. Miller and Miller (1981) found that Enallagma cyathigerum remained in tandem for some time before beginning copulation. This was not the case with A. vivida in which pairs began copulating soon after forming a tandem. A. vivida practices "preoviposition guarding" rather than precopulatory guarding.

Males encounter females in the forest infrequently. It is to a male's advantage to capture the first female he encounters, whenever he encounters her. Since males are capable of quick copulations later in the day, it may be assumed that the long copulations performed in the morning are a form of preoviposition guarding. However, the precise timing of the various phases of copulation (Miller 1987, Miller and Miller 1981) was not recorded, so the proportions of time devoted to sperm removal, sperm transfer and resting cannot be estimated.

Long duration copulations may provide a greater degree of sperm removal (Siva-Jothy 1987) but this relationship may not hold true for all species (Waage 1986b). Alternatively, females encountered at the water in the afternoon have already laid part of their clutch of eggs and males may be lowering their investment of time and sperm accordingly (Wiklund and Forsberg 1985, Svard and Wiklund 1986) by engaging in short copulations at this time.

This does not explain why pairs do not copulate briefly and oviposit immediately. McVey (1984) has found that egg release rate in Libellulid dragonflies increases with temperature. A. vivida begins ovipositing at almost the warmest part of the day, when the sun is directly overhead and providing the fewest shadows in the vegetation where females oviposit. Pairs may be starting to oviposit as soon as it is warm enough at the oviposition site to do so (Finke 1985). Males, in performing a lengthy copulation, are holding their mates in tandem until it is warm enough to oviposit. To begin the investigation of this hypothesis, an estimate of the minimum body temperature at which females will oviposit is needed. Comparable data do not exist for any species of odonate, to my knowledge.

Interpretation of the observations of ovipositing pairs is difficult since no pair was followed from the end of copulation to the end of oviposition. Pairs shifted frequently and did not oviposit for long at any site. An "exploratory phase" of oviposition has been observed in many coenagrionids (A. fumipennis atra, Bick and Bick 1982; A. plana and A. moesta, Bick and Bick 1972; Enallagma aspersum and E. exsulsans, Bick and Hornuff 1966, A. apicalis, Bick and Bick 1965a; Enallagma civile, Bick and Bick 1963). These species copulate near the water and pairs fly to the oviposition site immediately following copulation. During

the exploratory phase these pairs shift about frequently and the females probe vegetation for a period of time roughly equivalent to that which I have called the latent period. If A. vivida has an exploratory phase in addition to a latent period, it could explain why the pairs observed shifted so frequently. However, the behaviour of the individuals observed did not appear to be similar to the exploratory behaviour of other species. According to Bick and Bick (1963) and Bick and Hornuff (1965), exploratory activity consisted of frequent tandem flights, periods of resting, probing of vegetation and little ovipositing. The A. vivida pairs observed did move frequently, rest often and probe vegetation, but these activities were interspersed with periods of oviposition. Also, two of the pairs were followed until they were observed to break their tandems. One of these pairs spent the longest period in continuous oviposition, the other pair did not oviposit at all in the time it was watched.

I believe that I did not observe any pairs during an exploratory phase. Instead, the frequent movements of pairs are an indication that oviposition sites are of highly variable quality and that high quality sites are unevenly dispersed.

In addition, the frequent rest periods and short flights may allow A. vivida to thermoregulate. The average time

between flights of non-tandem males at the water and of ovipositing pairs is similar. Ovipositing pairs probably do not always have the opportunity to orient themselves properly, which may affect their ability to regulate body temperature (Corbet 1962, May 1979, Miller and Miller 1981). Both resting and flying may aid pairs in maintaining the proper body temperature. There must also be an energetic cost to a female associated with plunging her abdomen into the water while ovipositing. Heat loss to both members of a tandem pair during oviposition should be measured and the orientation of resting pairs to the sun should be recorded in future studies of this species.

The remating of females within a day is unusual among Argia species (Bick and Bick 1965,1968,1972,1982). Bick and Bick (1965a) attributed this to the fact that reproduction took so long and few receptive females were available at the water for the numerous unmated males. A second lengthy copulation is apparently not needed for rematings in the afternoon in A. vivida. Copulation takes place near the water and lasts less than ten minutes.

In summary, the daily activity of Argia vivida at Halcyon Hotsprings begins when morning sunlight reaches the slope in the forest. The centers of activity are spots of sunlight on the forest floor. Males may be considered temporarily territorial at these sites. Males capture

females passing near these sites and begin lengthy copulations with them. Copulation may be followed by a tandem "latent" period, during which the pair does not oviposit and remains away from the water. The first ovipositing pairs appear at the water between 1300 and 1330 hrs and peak oviposition activity does not occur until about an hour later. Ovipositing pairs remain in tandem for an hour or more, making the total time a pair may spend in tandem greater than three hours. Oviposition is punctuated by frequent shifting, resting and probing. These activities are not characteristic of the "exploratory phase" described for other species. When the tandem eventually splits, it may be the result of the actions of the male or the female. Females released or escaping from their mates may stay at the water and continue to oviposit unguarded. They may also be captured by one of the many males at the water and perform a complete mating sequence again. The duration of copulation for this second mating is much shorter than for a first mating.

The general pattern of daily activity for $\underline{A}$. $\underline{vivida}$ is similar to that of other $\underline{Argia}$ spp. reported in the literature, with minor differences in timing which may be accounted for by differences in temperature and insolation at other sites. In fact, the daily pattern of activity is similar to that of other zygopterans (e. g. $\underline{Platycnemis}$

echigoana, Watanabe and Ohsawa 1984; Cercion calamourum, Ueda 1985; Enallagma exsulsans and E. aspersum, Bick and Hornuff 1966). I believe that if the data for the other species of Argia that have been studied are carefully re-examined, some of the characteristics I have presented as peculiarities of A. vivida, may prove to be widespread in the genus.

ALTERNATIVE MATING STRATEGIES IN ARGIA VIVIDA

Finke (1985) described two alternative reproductive tactics for male Enallagma hageni which she called "searching" and "waiting". "Searching" males seize females away from the water, copulate with them and fly in tandem with them to the water, guarding them while they oviposit. Oviposition in this species occurs under water. Males release the females as they submerge and guard them by driving conspecifics from the area where the female submerged. "Waiting" males seize females at the water as they emerge from an incomplete oviposition, copulate with them at or near the oviposition site and then guard them during oviposition in the same way that "searching" males do.

Male Ishnura ramburii do not perform postcopulatory

guarding (Robertson 1985). Their tactic for avoiding sperm competition is to hold females in the wheel position until it is too late in the day for the females to have a good chance of remating (Robertson 1985). Robertson found that there are some males that release their mates early. He believed this might be an alternative male tactic to obtain an additional mate. For convenience I will refer to the common, long copulation duration tactic as "holding" and the shorter copulation duration tactic as "deserting".

Males practicing the searching and waiting or the holding and deserting tactics (or all four) may be present in the Halcyon Hotsprings population of A. vivida. Either pair of tactics could explain the daily pattern of mating behaviour observed. Discussion of the tactics will center on two questions: (1) Are the tactics described applicable to A. vivida? and (2) Can they logically be considered "alternative reproductive behaviours"?

Since males accompany their mates during at least part of oviposition, the holder and deserter strategies of Robertson cannot be strictly applied to A. vivida males. No males were seen to desert their mates at the waterside following a brief copulation at any time of day. Instead a "holder" may be taken to be a male that remains guarding his mate through the laying of all or nearly all of her eggs. A "deserter" may be considered to be a male that stops

guarding a mate before she has laid most of her eggs, and then deserts her to find a new mate at the water. Presumably the probability of another male finding the female before she finishes ovipositing, the probability of a male finding a new fecund mate, the time the male spends guarding the female before deserting her and the number of eggs the female lays before she is deserted should all interact to determine the success of the deserting tactic relative to the holding tactic. The necessary parameters, such as egg deposition rates and probabilities of encounter could be obtained in the field and a model predicting when males should desert could be generated. This model could be tested in the field.

Such a model would test to see if either tactic is genetically determined or the expression of behavioural plasticity under the control of circumstance. If one group of males is observed to practice the holding tactic and another the deserting tactic, each exclusively, then the two tactics may be considered as alternative behaviours.

The present study, however, only provides the suggestion that these two tactics might exist. More careful monitoring of males in tandem pairs, especially after they have left their mates, is needed before conclusions may be drawn.

Of the two groups of tactics, the searching and waiting tactics presented by Finke (1985) are the most descriptive

of the behaviour of A. vivida. Males found at sunspots in the forest practice the searching tactic, attempting to seize females before they reach the water. Males that are unsuccessful in the forest move toward the water after 1300 hrs and attempt to seize females there are using the waiting tactic.

Within a day, a male may take up the waiting tactic through one of two similar behavioural pathways (Figure 13). In the first part of the flow diagram (Figure 13A) daily activity begins with males sun-basking in the forest, seeking mates and moving toward the water. The time that they are successful at seizing a female determines the "tactic" they use to acquire a mate. If they capture a mate before they reach the water, they are searchers, if they reach the water before they capture a mate, they are waiters.

In the second part of the flow diagram (Figure 13B) daily activity begins with males sun-basking in the forest and seeking mates by the searching tactic. If, by a certain time (about 1300 hrs at the Halcyon site), the males have not found a mate, they switch their tactics, fly to the water and become waiters. Finke (1985) discusses possible cues for this change in behaviour.

In the first case (Figure 13A), males are not altering their behaviour, but rather are changing their location to

be where the chances of encountering females are the best.
They are making the proverbial "best of a bad situation".
Since all males are capable of performing both tactics, and
their tactic is determined by their location (and the
location of females) the two tactics cannot be considered
alternative reproductive behaviours, but are merely two
names for the same behaviour.

In the second case (Figure 13B) males are responding to
some cue which is correlated with their potential
reproductive success by altering their mate seeking
behaviour. This change in behaviour has presumably arisen
in response to selective pressure, is a distinct change in
behaviour and the presence of the response will have a
discontinuous distribution within the population (Austad
1984). Under these conditions the searching and waiting
tactics may be considered to be alternative reproductive
behaviours. The principal determinant that is observable in
the field is the presence of a distinct behavioural switch
from searching to waiting in some individuals and the
absence of this change in behaviour in others.

Observations of $\underline{A}$. vivida correspond most closely with
the first behavioural pathway of the diagram (Figure 13A).
At Halcyon in 1986, 106 individuals were sighted more than
once on at least one day. Forty-two of these males were
sighted before and after 1300 hrs. Of these 42, 30 (71%)

were sighted away from the water in the morning and at the water in the afternoon. Two males were sighted at the water in the morning and in the afternoon, but the morning sightings occurred after 1200 hrs. Of the 10 males sighted only away from the water in the morning and afternoon, all but one moved nearer the water as the day progressed. Since the "near" sectors began almost at the water's edge, some of these males may have been searchers at the water without being in the "at water" sector.

No males at Halcyon Hotsprings are waiters before 1300 hrs. There are no pairs at the water until then and therefore no females at the water. There are no searchers in the forest after 1400 hrs, because all the receptive females that are unmated for the day have already been taken in tandem.

Males migrate slowly between their roosting site in the forest and the water. If they are fortunate enough to capture females in the forest they copulate with them and fly together to the water. Males not so fortunate reach the water at about the same time as the first pairs to continue their search for mates where females are most likely to be found. Males at the water in the afternoon and in the forest in the morning did not behave differently, nor did either group show any preference for either female colour morph.

Males can be both waiters and searchers on a single day or over their lifetimes. Finke (1985) found similar results in _Enallagma_ _hageni_: "Of the 55 males which I saw mate at least twice in their lifetime, 41 (75%) obtained mates by both tactics while one male mated only by the waiting tactic and 13 males (24%) mated only by the searching tactic. All of these last 13 males were seen perching at oviposition sites on days when they were unsuccessful in obtaining a ·mate."

If it can be shown that males actively make a "decision" to switch tactics, in response to some environmental or physiological cue (Figure 13B) then the searching and waiting tactics can be considered to be meaningful alternative reproductive behaviours. The evidence to date suggests that this cue does not exist. The waiting and searching tactics in _A_. _vivida_ are simply a case of males behaving the same way at a different time and place. Since all males can apparently practice either tactic, a discussion of how natural selection can act to maintain both tactics in the population (Finke 1985) is moot.

Concomitant with the two male mating tactics are a number of female tactics. If all males guarded their mates until oviposition was completed, the waiting tactic would be useless. If females can cause their mates to leave before oviposition is completed then females may be considered to

be using mixed oviposition tactics. They may oviposit unguarded, though it is generally accepted that male harassment will make this inefficient. They may seek other mates at the water in an attempt to find a higher quality mate, or to increase the genetic variability of their offspring but must suffer the costs of another copulation.

The data presented in Figure 9 suggest females are exercising some control over the time they spend in tandem with their mates. Females found ovipositing alone, or seen escaping their mates carried a number of eggs not significantly different from females that had not oviposited. If males were always in control of the tandem they would be expected to retain their mates until a greater proportion of eggs were laid. Females in the "unguarded oviposition" group lay at least 2/3 of their eggs after leaving their original mates.

Presumably females remain in tandem so that they may oviposit efficiently while guarded by their mates. The male's presence prevents harassment from non-tandem males and theoretically allows the female to oviposit more quickly (see Waage 1979b, for example). The more non-tandem males that are present at the water, the greater the value of the guarding male to the female.

Since males rarely interfere with tandem pairs, the mean oviposition efficiency of ovipositing in tandem may be

assumed to be constant, regardless of the density of
non-tandem males at the water (solid line, Figure 14). When
females oviposit unguarded, the relationship between their
mean efficiency and the density of non-tandem males may be
described by either of two hypothetical types of curves
(broken and dotted lines, Figure 14). In both types of
relationship the mean oviposition efficiency of ovipositing
unguarded is low when the density of males is high and
increases as male density decreases (as it gets later in the
afternoon).

If it is assumed that males and females are equally good
(or bad) at finding high quality oviposition sites and there
is perfect communication between members of a tandem pair,
then the efficiency of ovipositing unguarded will never
exceed the efficiency of ovipositing in tandem (dotted line,
Figure 14). Females should not leave their mates until they
have completed oviposition.

However, both of these assumptions are unrealistic. It
is more likely that there will be some threshold male
density below which females can oviposit more efficiently on
their own than when guarded. Late in the afternoon when the
density of non-tandem males at the water decreases,
potential male interference with ovipositing females also
decreases and the efficiency of ovipositing unguarded should
increase. Once the potential efficiency of ovipositing

unguarded exceeds the efficiency of ovipositing in tandem, females should be willing to escape their mates (broken line, Figure 14).

In this study, both sexes were observed to initiate the termination of a tandem during oviposition. Whereas males need only to release their hold on a female, females are able to break a tandem only after strong resistance which must be costly to them. The costs to females of practicing mixed oviposition tactics are costs directly affecting their repoductive success. The analysis of the costs and benefits or even the possibility of different female oviposition tactics requires much more research into mate choice, female oviposition behaviour and the physiology of oviposition.

SIZE EFFECTS ON MATING SUCCESS AND SIZE-ASSORTATIVE MATING

There are two reasons why larger-sized males might be expected to have increased mating success. Large males might be better able to hold territories (Harvey and Corbet 1985) or females (Johnson and Hubbell 1984) against smaller conspecifics, or perhaps large males are simply preferred by females. Koenig and Albano (1987) found that lifespan was strongly correlated with lifetime reproductive success and that large males tended to live longer.

Mated males at Halcyon Hotsprings, from data obtained

from the "formalin pairs" in 1985, were smaller than males obtained at random from the population. Field measurements at Halcyon in 1985 showed no significant difference between males captured at least once in tandem and males never captured in tandem. Field measurements at Halcyon in 1986 showed that males captured at least once in tandem were larger than males never captured in tandem. Whether a male was practicing a searching or waiting tactic (i.e. was captured in the morning in the forest or in the afternoon at the water) had no effect, nor did the colour of the female the male mated with. At Albert Canyon in 1985, data obtained from the "formalin pairs" showed that males captured in tandem were larger than males selected at random from the population but field measurements revealed no significant difference. In view of the conflicting data and mixture of results, it is most likely that mating success is not dependent on male size.

In species of flying insects where slightly smaller males of a species may enjoy increased maneuverability and therefore be better able to capture mates (Banks and Thompson 1985), a form of size dis-assortative mating might be expected, especially when larger females carry more eggs. On the other hand, where male size and strength is important in capturing and controlling females in flight, size assortative mating might be expected, even if it is only

because larger males are better able to cope with larger females (Johnson 1982). There is no evidence in the populations of $\underline{A}$. $\underline{vivida}$ of size assortative or dis-assortative mating and although the data are poor, female size as estimated by forewing length is not a good predictor of fecundity. There is no evidence of males choosing mates on the basis of female fecundity.

A number of recent studies (Banks and Thompson 1985, Finke 1982, 1986b, Koenig and Albano 1987) have measured various correlates of size, survivorship and behaviour in an attempt to quantify the most important factors in determining the variation in lifetime reproductive success of the odonate species studied. The principal component in each study was lifespan. In this study, though lifetime reproductive success for any individual was not observed, a simple, weak but significant correlation exists between the MDA of males and the number of times they mated (Kendall's tau = 0.181, p < 0.001). The simplest explanation for this correlation that is consistent with the other data presented here is that mating in $\underline{A}$. $\underline{vivida}$ is the result of random encounters between individuals. This can only be presented as a hypothesis and not a conclusion. Lifetime mating data obtained from daily observations with a more intensive sampling program are needed before this can be tested.

THE EVOLUTION OF MATE GUARDING AND SPERM COMPETITION IN
ODONATES

In much of the recent literature on sperm competition a
great deal of emphasis has been placed on the advantages to
females of sperm competition and of mating multiply (e.g.
Finke 1984a, 1986a, Waage 1984a, Walker 1980). This is, no
doubt, to compensate for the lack of attention it was given
previously. From this attempt to concentrate on female
involvement in the evolution of sperm competition, an aura
of misconception has arisen. It is argued that sperm
competition could not evolve without having a benefit to
females. In effect, in anthropomorphic shorthand, "If sperm
competition is not selected for in females, the females
won't allow it". The author most often cited in this
context is Walker (1980). However, Walker actually implies
that females should be receptive to multiple matings only
when the benefits of multiple matings exceed those of
monogamy. He acknowledges that in a population where
efficient sperm-removing males have become dominant, it may
become advantageous for females to accept multiple matings
(Walker 1980, p 790). He does not say how sperm removal
might become dominant in the population.

Implicit in the argument that multiple female mating and sperm competition could not have evolved without benefit to females is the assumption that the population is evolving from monogamy to polygamy; that multiple mating is the most derived behaviour. This does not explain why Ischnura verticalis, a member of a genus regarded as one of the most derived, is the only species known to date in which females mate only once per lifetime (O. M. Finke, Pers. Comm.). This assumption is usually supported with references to two generalizations: (1) Males cannot force females to mate, and, (2) Females need to be inseminated only once to be able to lay fertilized eggs for the rest of their lives. The validity of point (1) will be addressed later. The reference most often cited in support of point (2) is Grieve (1937). Grieve worked with Ischnura verticalis, which is the only species that would be expected to have the ability to store sperm for a lifetime, given that females mate only once in their lifetimes. Evidence is needed that females of species that mate multiply within a day can fertilize all eggs they will lay in their lifetime with the sperm from a single mating.

In virtually all species in which males perform post-copulatory guarding it may be argued that this is a service males provide females in exchange for fertilization of the female's eggs (see Alcock 1979, 1983, Waage 1979b).

Evolution of sperm competition and multiple mating is favoured in females because guarded females are more efficient at ovipositing than those that attempt to oviposit without guards, that is, without "trading" a copulation for a male's protection. Finke (1984a, 1986a) has pointed out that this leads to a circular argument because if there was no sperm competition there would be no advantage to males in harassing ovipositing females, no advantage to females in being guarded and therefore, no advantage to females in mating multiply or evolving the physiology which permits sperm replacement.

There is a simple and reasonable argument against the premises of this circular argument. This begins with the assumption that the polygamous mating system of odonates has not evolved from a monogamous one where sperm competition did not operate but, rather that the present polygamous system evolved from a more primitive polygamous one where sperm competition was not as intense.

Consider a population of ancestral odonates in which males have simple intromittent organs and females have simple sack-like bursae copulatrix and spermathecae. In such a population, males stand to gain at least some fertilizations by copulating with females that have mated previously, because their sperm will at least mix with that already present. Under these conditions, males should still

harass females that have already mated.

In this population, males that are able to achieve more effective sperm precedence will gain a selective advantage over males with poor sperm precedence. If this increase in sperm precedence is brought about by, for example, a sperm removal mechanism, then as sperm removal ability spreads in the population, so should some form of guarding behaviour. In this way female receptivity, male mate guarding, and sperm replacement efficiency evolve together influenced mainly by male intrasexual selection, in the manner originally described by Parker (1970a). During this evolutionary process, the reproductive success of females is not affected (or perhaps it is enhanced) and sperm competition is not selected against in females (see also Prout and Bundgaard 1977).

DO MALE ARGIA VIVIDA CONTROL FEMALE MATING DECISIONS?

Argia vivida was used in this study to provide an example of a "female-control" mating system (Table 1). Whether or not males are truly able to control females remains to be decided.

Male Argia vivida may obtain control of females via two non-mutually exclusive routes. The first is by simple physical strength which I will call "physical control", the

most extreme form of which is rape. The second method of control involves making the cost of resistance too great, which I will call "energetic control". Physical control involves direct physical manipulation, while energetic control requires males to persist until the females yields.

Male _A_. _vivida_ obtain physical control of females by grasping them with their terminal appendages to form the tandem position. Females may refuse to form the tandem or later, the wheel, but they apparently cannot escape the tandem once it is formed. Hilton (1984) observed female _Nehalennia gracilis_ in tandem with severed male abdomens. Miller (1987) and Miller and Miller (1981) found that only male _Ischnura elegans_ could initiate or terminate the tandem position.

Once seized in the tandem position, females must expend a great deal of energy to escape males. The time and energy females devote to escaping males is detrimental to their reproductive success. When the cost of escaping exceeds the benefits females would gain by finding another mate or just avoiding the male, males are exerting energetic control.

To produce offspring, females must be fertilized and they must reach the water to oviposit. Males capitalize on this by placing themselves between the females and the water. Once a male encounters a female and seizes her, he controls her ability to choose another mate during that

particular mating period. If a male is more persistent in his control of a female than the time and energy cost of mating to the female, the female will gain an advantage by mating with the male.

It is commonly accepted that male damselflies are unable to force females to mate because females must take an active role in the formation of the wheel position. In the absence of any as yet undiscovered "hard-wired" response to male courtship or the tandem, males indeed cannot force females to copulate by means of physical control. However, they may be able to force them to mate by means of energetic control.

A female approaching the water is captured by a male. She has the options of remaining in tandem with him, copulating with him and ovipositing with him guarding, or, she may resist him, escape the tandem and mate with another male or continue to the water and attempt to oviposit unguarded. Because there are so many "waiting" males at the water, the female that avoids all matings with "searchers" will not be able to oviposit unharassed. Furthermore, an individual male probably encounters few females, if any, during a morning. A male that allows a female that he has taken in tandem to escape has lost a great deal in terms of potential reproductive success. Selection against males that are not tenacious in maintaining the tandem position or persistent in their mating attempts should be very strong.

Males have more to lose by releasing the female than the female gains by being released and the female is forced to mate by means of energetic control. These arguments are similar to those presented by Parker (1970a) for the evolution of female receptivity to multiple matings.

Without greater knowledge of the processes involved in the splitting of tandems later in the day and the remating of females with "waiting" males, it is difficult to postulate whether or not female-control is still effective. Males may be releasing mates when the potential benefits of keeping a mate fall below the potential benefits of finding another. Perhaps they guard until the guarding behaviour becomes too energetically costly for the number of the female's remaining eggs.

Evidence has already been presented that females may be responsible for the splitting of tandems (Figure 9). From the female's point of view, after she has oviposited for a period, perhaps her value drops below the benefits needed for the male to maintain energetic control. Male ability and need to control females drops as male density at the water drops in late afternoon. A decrease in potential male interference with unguarded oviposition means a decrease in benefits of guarding to females but also a decreased probability that a female's mate will be subjected to sperm competition.

No matter what the reason, it seems that later in the day the degree of control males exert or are willing to exert decreases and more females are found ovipositing alone or remating. In the primary "morning" mating system, males are able to exert a great deal of control over female mate choice. In the secondary "afternoon" mating system (involving "waiting" males and females that have already mated) males do not exert as much contol.

BORGIA'S CLASSIFICATION SCHEME AND THE MATING BEHAVIOUR OF A. VIVIDA

The conditions characteristic of a female-control mating system (Table 1) are present in the populations of Argia vivida studied. Oviposition sites are numerous and dispersed at the water. The population itself is isolated and restricted to the area by lack of neighboring hotsprings within dispersal distance. The species is slow flying and is easily disturbed in flight by light winds.

Males give the impression of being territorial at sunspots, though the territories are ephemeral and the turnover of owners is high. Deciding if these territories are solely for the purpose of mating requires more observation. Nevertheless, the territories are not established at oviposition sites, nor do they appear to be

used to control a resource needed by females. This distinguishes their function from territories in Borgia's other mating system types.

Male-female encounters in the forest are infrequent, occurring at random with respect to body sizes, number of eggs a female carries and female morph colour. "Morning" copulations occur far from the water and pairs that form in the afternoon at the water move away from it before copulating. The duration of a "morning" copulation falls into the group considered "long" by Corbet (1962). "Afternoon" copulations are much more brief but may still be considered to be in the "long" group.

Postcopulatory guarding is of the contact type and females oviposit unguarded infrequently, though much more frequently than was expected at the outset of the study. Multiple matings for females within a day were also more common than was expected. Females are very limited in their choice of mates, especially in "morning" matings since they are forced to mate with any male that is able to capture them. They may not be so limited in "afternoon" matings.

The discovery of the "afternoon" mating strategies was one of the most surprising aspects of this study. The existence of the "afternoon" strategies is important to male control of females in "morning" matings. The possible availability of females to mate with and the concomitant

presence of "waiting" males at the water are important in determining "searching" males' ability to control female access to oviposition sites.

Calling the mating system of A. vivida "a female-control strategy" accurately describes "morning" matings, but does not include the possibility of the "afternoon" strategies. Like any general classification scheme, Borgia's is useful on a broad scale, but requires additional qualifiers for specific systems.

THE GENERAL UTILITY OF BORGIA'S CLASSIFICATION SCHEME

Borgia's classification of mating systems, as I have adapted it to odonates, is different from previous classification schemes of mating systems in that it acknowledges the importance of resource distribution, physiological limitations of a species, female choice and male ability to limit female behavioural options. The scheme is based on female choice, the methods of males to limit that choice and the resulting patterns of variation in reproductive success. Most importantly, the scheme acknowledges that some male odonates are able to control female reproductive behaviour by controlling females themselves. Emlen and Oring (1977) recognized this male strategy of animals in general, but it has not been applied

to odonates, probably because it has long been common
knowledge that female odonates cannot be physically forced
to mate. I have proposed that males can force females to
mate with them by using what I have called energetic
control. Unfortunately, male ability to control females
energetically has not been proved in this study, only
hypothesized.

The four strategies of the classification should not be
considered to be four distinct points on a quadrangle. No
doubt species can be found that are intermediate between at
least two of the four strategies. Strategies on the
diagonals of Figure 1 show the closest relationship between
each other. Within reasonable limits, the mating system of
a species is not likely to be altered to another type by
changes in population density or dispersion of oviposition
sites, though the behaviour of the population may become
more like another strategy (see Ueda 1979, for example).

Changes in oviposition site dispersion and male density
may alter the patterns of reproductive success of
individuals in a population of A. vivida, but the mating
system would not, for example, change to a resource
gathering strategy, because of the physiological constraints
on the species. In other words, the general class of mating
system a species uses is species specific.

My modification of Borgia's classification scheme has

three advantages. It allows the prediction of the type of mating system a species is using based on a limited number of characters, it emphasizes the interrelationships between a number of behavioural and ecological features common to odonate mating systems and it illustrates the relative importance of intra- and intersexual selection in the various types of odonate mating systems.

In the field, one might expect to find female choice based on territory quality in a resource control system, female choice based on territory quality and male quality in a resource gathering system and no female choice at all in a female-control system. Studies expecting to find female choice based on male quality exclusively should be directed at species that are wide-ranging, powerful fliers, since it is among these species that males are most likely forced to influence female mate choice by displays of their quality alone.

The classification scheme is internally coherent. Each component of a particular type of mating system complements the others. The scheme fails to predict the existence of the "afternoon" strategies of Argia vivida, but these can be explained within the tenets of the female-control strategy.

There has been a trend in recent years to place a great deal of importance on the oviposition behaviour of females in determining the reproductive behaviour of males (Sherman

1983, Finke 1984a, 1985, Waage 1984a, Buskirk and Sherman 1985, Van Buskirk 1986). Certainly there is little benefit for males to be where females are not, but there is little benefit for females to be where there are no oviposition sites. Females must oviposit when and where oviposition sites are available to them. Males are then able to modify their behaviour to take advantage of the predictability of female behaviour (Emlen and Oring 1977). Ultimately it is the environment and the physiology of the species that determines the mating system, not the behaviour of females alone. Borgia's classification places a more appropriate emphasis on the importance of environment and physiology and promotes the view that mating systems have evolved as the result of compromise between male and female behaviour.

Table 1. Classification of odonate reproductive systems according to Borgia's (1979) scheme. See "Introduction" for details.

MALES MAKE NO USE OF RESOURCES

- Oviposition sites widely dispersed, possibly along a stream or at a number of different pools.
- Species highly mobile, strong fliers.
- Male-female encounters rare.
- Males do not form mating territories.
- Males do not perform courtship displays
- Copulation rarely occurs at the oviposition site.
- Copulation duration long.
- No post-copulatory guarding.
- Female mate choice based on genetic quality of male, or possibly the female mates with the first male she ecounters.

MALES USE A RESOURCE GATHERING STRATEGY

- Oviposition sites clumped but males are not able to prevent females from gaining access to all of them.
- Species not very mobile, relatively slow flying.
- Males territorial
- Male-female encounters are relatively frequent at the oviposition site.
- Males perform elaborate courtship displays
- Copulations usually occur at waterside, usually within the territory.
- Copulations of medium duration.
- Postcopulatory guarding usually of the non-contact type.
- Females may oviposit at a number of sites, either guarded or unguarded.
- Multiple matings within a day common for both sexes.
- More than one mating strategy may be practiced in the population.
- Female choice may be based on male, genetic quality, male territory quality, or any combination of both.

MALES USE A RESOURCE CONTROL STRATEGY

- Oviposition sites are clumped and all clumps are easily accessible to males.
- Species very mobile, rapid fliers
- Male-female encounters frequent at the oviposition site.
- Males territorial
- Males do not perform courtship displays.
- Copulations occur very near the oviposition site, usually in flight above it.
- Copulations of very short duration.
- Postcopulatory guarding of the non-contact type.
- Females oviposit quickly at a guarded site.
- Multiple matings within a day common for males, less common for females.
- More than one mating strategy may be practiced in the population
- Female choice based mostly on male territory quality.

MALES USE A FEMALE-CONTROL STRATEGY

- Oviposition sites numerous, dispersed but in a limited area.
- Species not very mobile, slow flying.
- Males do not form mating territories.
- Male-female encounters relatively infrequent.
- Males do not perform courtship displays.
- Copulations occur away from the oviposition site.
- Copulations of long duration.
- Postcopulatory guarding of the contact type, or females may submerge to oviposit after being contact guarded.
- Females rarely oviposit unguarded.
- Multiple matings within a day are very rare for either sex.
- Female choice is very limited.

Table 2.   Duration of copulation for different species
of damselflies (mean in minutes, with range or standard
error in parentheses).

Species	Time	Source
Argia plana	26.9 (19-40)	Bick and Bick 1972
A. apicalis	15.9 (10-27)	"
A. moesta	22.2 (14-31)	"
A. fumipennis atra	24.4 (18-37)	Bick and Bick 1982
Enallagma aspersum	13.5 (10-19)	Bick and Hornuff 1966
E. exsulsans	75.8 (55-119)	"
E. civile	18.7 (11-44)	Bick and Bick 1963
E. cyathigerum	(10-47)	Miller and Miller 1981
E. hageni	22.4 (3)	Finke 1982
Chromagrion conditum	36.0 (24-54)	Bick et al. 1976
Coenagrion puella	28 (1)	Banks and Thompson 1985
C. pulchellum	– (10-15)	Robert 1958 (in Corbet 1962)
Platycnemis pennipes	– (13-27)	Buchholtz 1956 (in Corbet 1962)
Ischnura elegans	– (180-340)	Krieger and Krieger-Loibl 1958 (in Corbet 1962)

Table 3. The number of animals marked and sighted of each sex from both study sites in 1985 and from Halcyon Hotsprings in 1986.

	Marked	sightings	sightings/ individual
Albert Canyon, 1985			
Females	113	118	1.04
Males	486	531	1.42
Halcyon Hotsprings, 1985			
Females	156	162	1.04
Males	330	412	1.25
Halcyon Hotsprings, 1986			
Females	458	516	1.13
Males	917	1426	1.56

Table 4. The number of females of each morph sighted daily
at Halcyon Hotsprings in 1986.

Date	Blue	Red
June 10	17	8
June 11	19	9
June 12	25	19
June 21	22	18
June 22	11	4
June 23	22	10
June 24	11	9
July 6	23	8
July 7	25	5
July 8	3	3
July 9	6	1
July 19	26	17
July 20	22	11
July 21	2	4
July 22	2	1
Aug. 1	17	9
Aug. 2	6	6
Aug. 3	11	6
Aug. 4	7	4
Aug. 10	12	5
Aug. 11	13	7
Aug. 12	8	3
Aug. 13	8	3
Total	318	169

Replicated G-test (Sokal and Rohlf 1981) with the null
hypothesis that there is a 2:1 ratio of blue to "red"
females: G(heterogeneity) = 17.658, df = 22, $p > 0.70$;
G(total) = 18.065, df = 23, $p > 0.30$. The ratio is homo-
geneous between days and the observed ratio is not dif-
ferent from 2:1 (the ratio in 1985).

Table 5.   Correlation matrix for body size measurements obtained from Halcyon Hotspring "acetone" pairs (see methods).   (Pearson r / probability, N = 22).

MALES

	Abdomen Length	Total Length	Ocular Width	Femur Length	Dry Mass
Wing Length	0.781 < 0.001	0.435 0.021	0.144 0.261	0.408 0.033	0.827 < 0.001
Abdomen Length		0.701 < 0.001	-0.034 0.436	0.462 0.018	0.875 < 0.001
Total Length			0.702 < 0.001	0.310 0.086	0.677 < 0.001
Ocular Width				0.106 0.324	-0.004 0.493
Femur Length					0.581 0.003

Table 6. Correlation matrix for body size measurements obtained from Halcyon Hotspring "acetone" pairs (see methods). (Pearson r / probability, N = 22).

FEMALES

	Abdomen Length	Total Length	Ocular Width	Femur Length	Dry Mass
Wing Length	0.718 < 0.001	0.644 0.001	0.528 0.006	0.436 0.021	0.380 0.040
Abdomen Length		0.872 < 0.001	0.501 0.009	0.169 0.225	0.446 0.019
Total Length			0.593 0.002	-0.001 0.500	0.674 < 0.001
Ocular Width				0.158 0.241	0.484 0.011
Femur Length					-0.102 0.325

Table 7. Correlation matrix for body size measurements obtained from Albert Canyon "formalin" pairs (see methods). (Pearson r / probability, N = 35).

	Male Total Length	Male Dry Mass	Female Forewing Length	Female Total Length	Number of eggs
Male Forewing Length	0.448 0.004	0.727 < 0.001	−0.078 0.328	0.051 0.386	0.294 0.043
Male Total Length		0.646 < 0.001	−0.197 0.128	−0.111 0.263	0.312 0.034
Male Dry Mass			−1.660 0.170	0.013 0.471	0.274 0.056
Female Forewing Length				0.510 0.001	0.190 0.137
Female Total Length					0.076 0.332

Table 8.   Correlation matrix for body size measurements obtained from Halcyon Hotsprings "formalin" pairs (see methods).   (Pearson r / probability, N = 30).

	Male Total Length	Male Dry Mass	Female Forewing Length	Female Total Length	Number of eggs
Male Forewing Length	0.800 < 0.001	0.705 < 0.001	-0.191 0.156	0.177 0.175	-0.167 0.189
Male Total Length		0.699 < 0.001	-0.234 0.105	-0.054 0.389	-0.032 0.433
Male Dry Mass			-0.007 0.486	0.157 0.203	-0.294 0.058
Female Forewing Length				0.449 0.006	-0.069 0.359
Female Total Length					0.122 0.260

Table 9.   Mean body size parameters for individuals captured
daily in 1985 at each site and preserved in formalin
(lengths in cm, masses in mg).

	Albert Canyon			Halcyon Hotsprings			
	Mean	S.D	n	Mean	S.D.	n	t
Non-tandem males							
Forewing length	2.41	0.080	30	2.40	0.071	30	0.51
Total length	3.59	0.223	30	3.59	0.112	30	0.00
Dry mass	14.5	1.067	30	14.5	1.322	30	0.32
Tandem males							
Forewing length	2.41	0.089	35	2.34	0.083	30	3.24*
Total length	3.61	0.124	35	3.60	0.099	30	0.47
Dry mass	15.3	1.468	35	14.0	1.293	30	3.90*
Tandem females							
Forewing length	2.55	0.086	35	2.51	0.081	30	1.92
Total length	3.56	0.107	35	3.56	0.104	30	0.00

t - results from a two-sample t-test between sites.

*denotes significant difference at the $p < 0.01$ level,
all others not significant.

Table 10. Comparison of tandem and non-tandem male body size parameters from males captured daily at each site in 1985 and preserved in formalin.

	Albert Canyon			Halcyon Hotsprings		
	Parameter					
	frwng	ttl	mass	frwng	ttl	mass
Tandem	2.41	3.61	15.3	2.34	3.60	14.0
Non-tandem	2.41	3.59	14.4	2.40	3.59	14.5

frwng = forewing length (cm), ttl = total length (cm), mass = dry mass (mg)

Table 11. Forewing lengths of tandem vs. non-tandem individuals captured in the field at Halcyon Hotsprings in 1985 and 1986 and Albert Canyon in 1985.

| | Tandem | | | Non-tandem | | | |
	Mean	S.D.	n	Mean	S.D.	n	t
Halcyon 1985							
Males	2.41	0.106	48	2.36	0.087	92	2.82*
Females	2.54	0.078	44	2.51	0.086	9	1.07
Albert Canyon 1985							
Males	2.41	0.098	54	2.42	0.095	171	1.02
Females	2.55	0.103	47	2.54	0.165	12	0.31
Halcyon 1986							
Males	2.37	0.083	108	2.37	0.096	321	0.08
Females	2.52	0.085	69	2.52	0.086	74	0.31

Animals designated as "tandem" were seen at least once in tandem; those designated as "non-tandem" were never seen in tandem.

t - Results of a two-sample t-test between tandem and non-tandem samples. Where variances are not equal, an adjusted t-value is reported

*Denotes significance at the $p < 0.01$ level. All others are not significant

Table 12.   The effect of time of capture and mating status on field-measured male forewing lengths obtained at Halcyon Hotsprings in 1986.

	Tandem	Non-Tandem
Morning (< 1300 hrs)	2.37 cm	2.37 cm
Afternoon (> 1300 hrs)	2.36 cm	2.37 cm

Only first captures are considered. Males seen at least once in tandem were considered "tandem". Males never seen in tandem were termed "non-tandem".

Table 13. Forewing measurements of tandem pairs obtained in the field at Halcyon Hotsprings in 1985 and 1986 and at Albert Canyon in 1985.

	Males		Females				
	Mean	S.D.	Mean	S.D.	n	t	r
Albert Canyon	2.41	0.093	2.57	0.093	40	7.13	-0.086
Halcyon 1985	2.41	0.082	2.54	0.087	42	6.78	-0.078
Halcyon 1986	2.37	0.083	2.53	0.082	55	10.13	0.056

t - Results of a paired-comparison t-test. All values significant at $p < 0.001$.

r - Pearson's correlation coefficient. All correlations not significant.

Table 14. Comparison of behaviour of "morning" and "afternoon" males during 10 min observation periods at Halcyon Hotsprings.

MORNING (n = 13)

	Perch Changes	Feeding	Pursue Male	Pursue Tandem	Inspect Insect
Short flights	47	37	11	0	5
Long flights	27	9	4	0	0

Mean no. flights/individual = 9.15
Mean time between flights   = 65 s

AFTERNOON (n = 4)

	Perch Changes	Feeding	Pursue Male	Pursue Tandem	Inspect Insect
Short flights	15	5	5	11	3
Long flights	9	0	1	2	0

Mean no. flights/individual = 11.0
Mean time between flights   = 54 s

Table 15. Response of males simultaneously presented with live "pinned" females of each morph on three study days.

	Response			
Day	Mount Red	Mount Blue	Inspect	Ignore
June 22	4	3	6	19
July 21	11	9	15	25
Aug. 02	11	7	10	25
TOTAL	26	19	31	69

Male choice (not including males that ignored the females) is independent of study day (X^2 = 0.667, df=4, p = 0.293).

The ratio of blue to red females chosen (pooled data) is not different from 1:1 (X^2 = 0.80, p = 0.375).

Table 16. Response of males "at water" and "away from water" simultaneously presented with live "pinned" females of each morph.

Position	Mount Red	Mount Blue	Inspect	Ignore
		Response		
At Water	11	5	15	37
Away	15	14	16	32

Male choice (not including males that ignored the females) is independent of the male"s position in the study area (X^2 = 1.565, df = 2, p = 0.462).

Table 17. Response of males presented with pairs of live
·"pinned" <u>Argia</u> which contained at least one individual of
an age or sex not suitable as a mate.

Pair presented	Mount(A)	Mount(B)	Inspect	Ignore
(A) Adult Male (B) Blue Female	2	12	15	39
(A) Teneral Female (B) "Red" Female	1	3	4	9
(A) Adult Male (B) Teneral Male	2	4	4	7

Table 18.   Response of males presented with single live "pinned" damselflies.

Sex/Morph	Response		
	Mount	Inspect	Ignore
Red Female	6	3	4
Blue Female	1	4	7
Male (blue)	2	8	2

Table 19. Number of tandems captured between 1430 and 1530 hrs containing red or blue females during the male removal experiment (dashes indicate days when no males were removed).

Date	Red	Blue	Males Removed
June 04	8	11	—
June 09	7	12	—
June 10	4	7	—
June 11	6	16	—
June 12	20	25	27
June 21	20	29	—
June 22	3	6	—
June 23	11	21	—
June 24	14	18	23
July 06	9	22	25
July 07	9	27	35
July 19	12	26	—
July 20	13	20	43

The ratio of red to blue females is independent of study day ($G = 6.946$, df $= 12$, $p > 0.50$). The male removals had no effect.

Figure 1. Borgia's classification of mating systems (redrawn from Borgia 1979). This figure illustrates the relationship between female mate choice and male ability to control female mating decisions. (A) Males have no control over females' access to needed resources. Females may choose their mates freely on the basis of genetic quality. (B) Males control access to some of the resources and are able to increase their attractiveness by "gathering" high quality resources. Females may choose mates on the basis of genetic quality, quality of the resources "gathered", or any combination of both. (C) Males completely control the needed resources. If females wish to reproduce they must mate with a male that controls the needed resource. (D) Males directly control females and do not permit them to mate with other males. Resources may still be important because they may serve as a place for males to capture females.

(A)

RESOURCE

FEMALE   M   M

M

M   M

M

NO USE OF RESOURCES

(B) RESOURCE GATHERING

M + RESOURCE

FEMALE   M   M

M   M

RESOURCE

(C)

M   RESOURCE

FEMALE   M   M

M

M

RESOURCE CONTROL

(D) FEMALE-CONTROL

M   RESOURCE
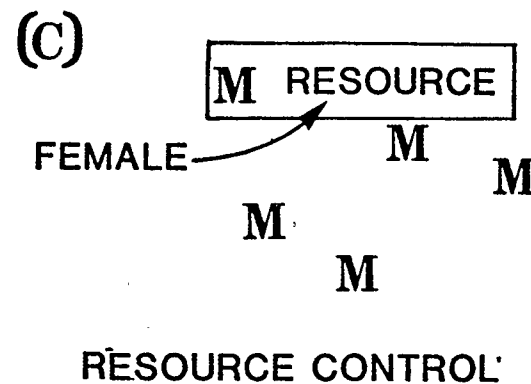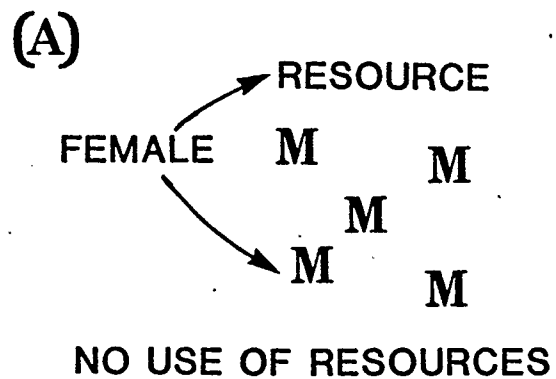
FEMALE   M   M

M   M
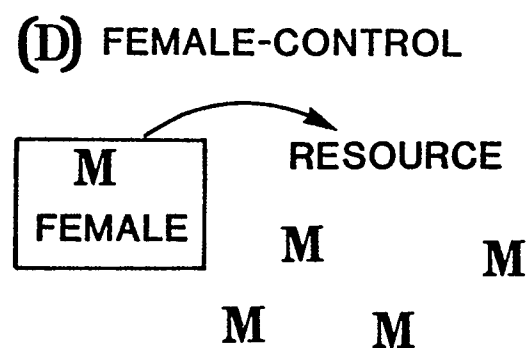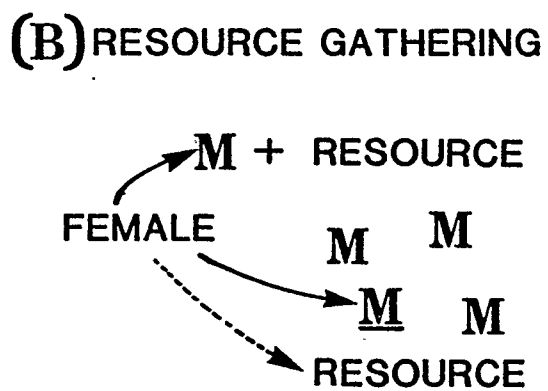
Figure 2.   Map of the Albert Canyon study site.   The study
was conducted in the areas not covered by forest or bushes
and small shrubs.   Basking sites frequently used by males
are shown on the map and included large rocks, logs, stumps
and pieces of split cedar.

ALBERT CANYON STUDY SITE

FOREST

GRASS

0 5 10m

THISTLES

FORESTRY ROAD

MAIN STREAM

SWAMP

BUSHES AND SMALL TREES

N
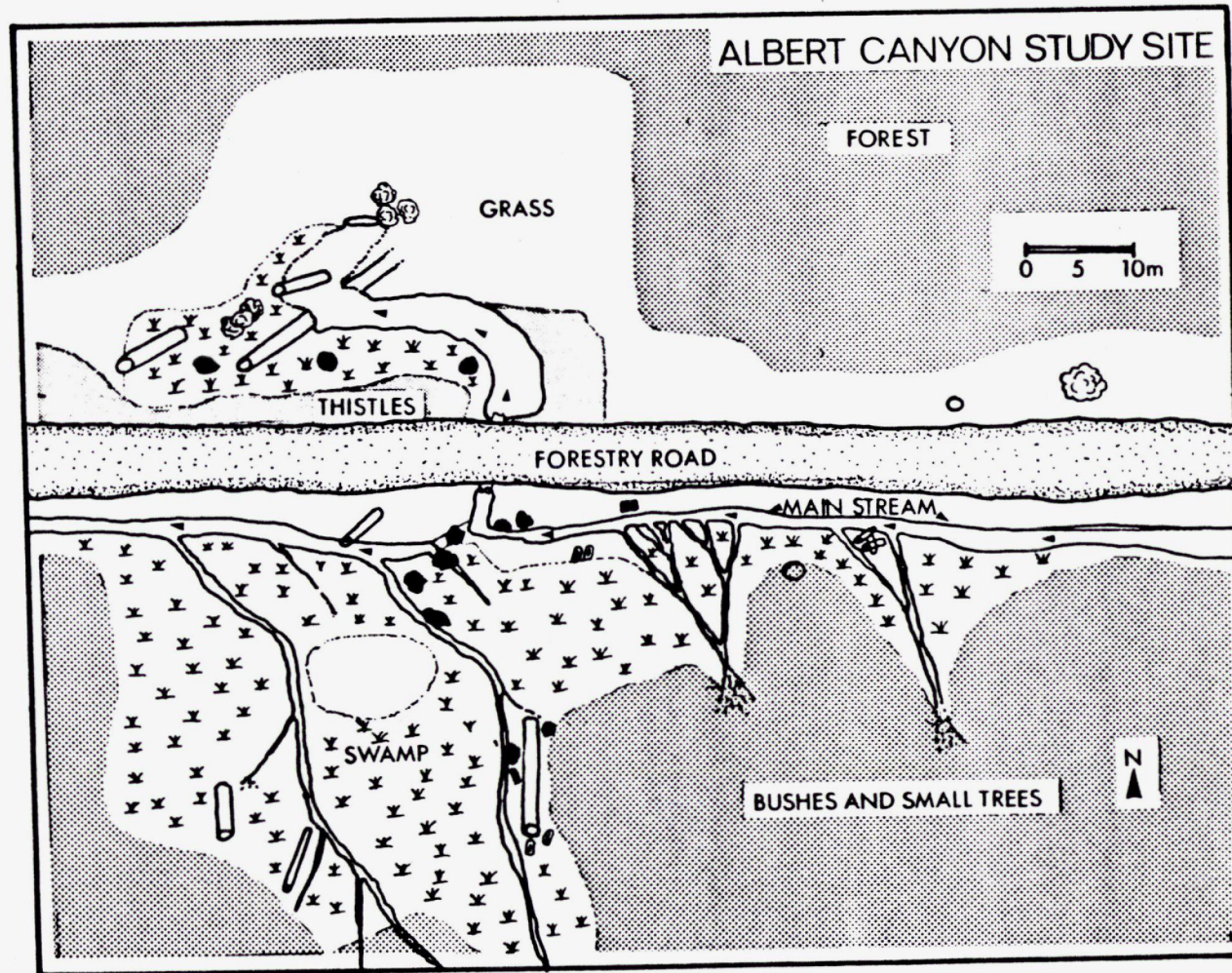
Figure 3.   Map of the Halcyon Hotsprings study site.   The
boundaries of the study area were defined by the highway and
the confluences of two cold streams at the north and south
ends of the map.   The land slopes sharply uphill to the east
(> 10% slope) and this steep grade continues far into the
forest.

HALCYON HOTSPRINGS STUDY SITE

FOREST

0   5   10m

STONEY SLOPE

N

STREAM

HIGHWAY 23
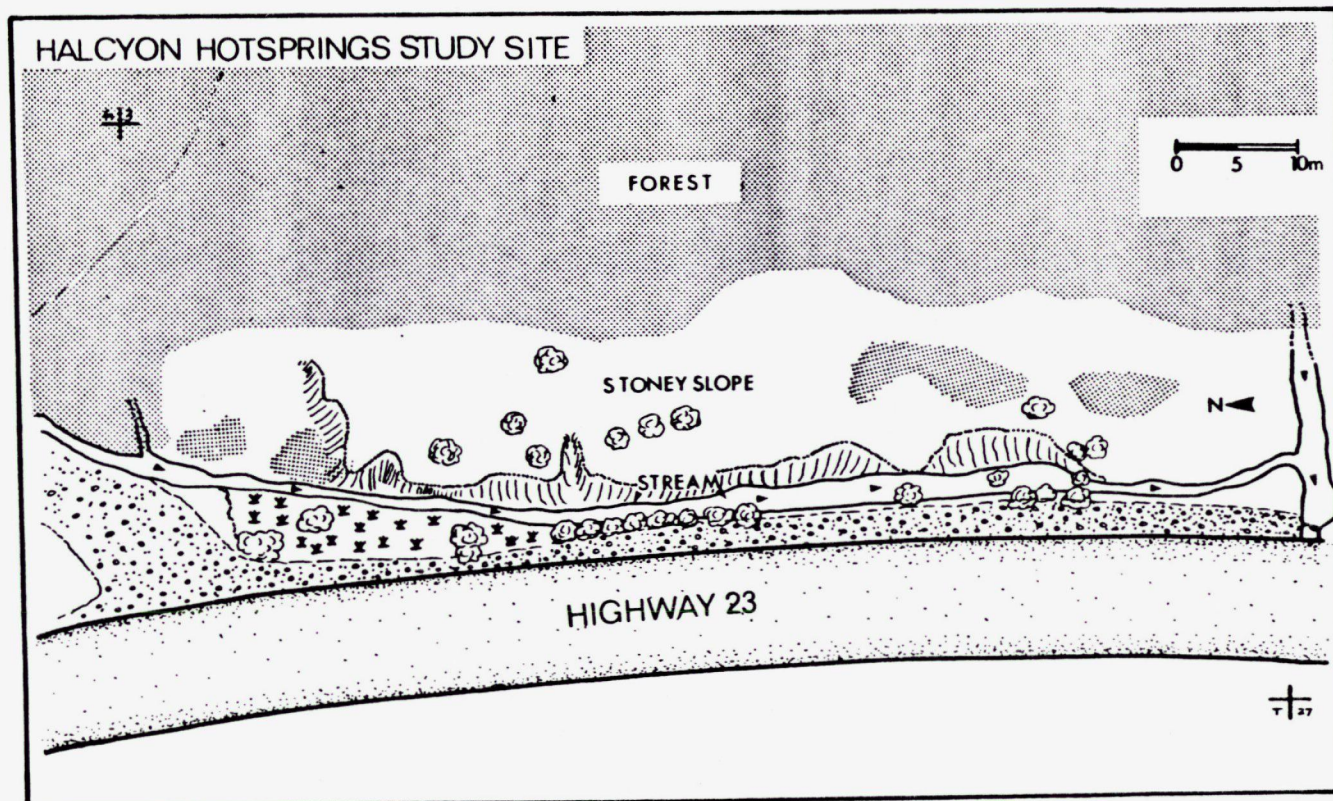
Figure 4.   Male population size estimates by the Manly-Parr
method for Halcyon Hotsprings, 1986.
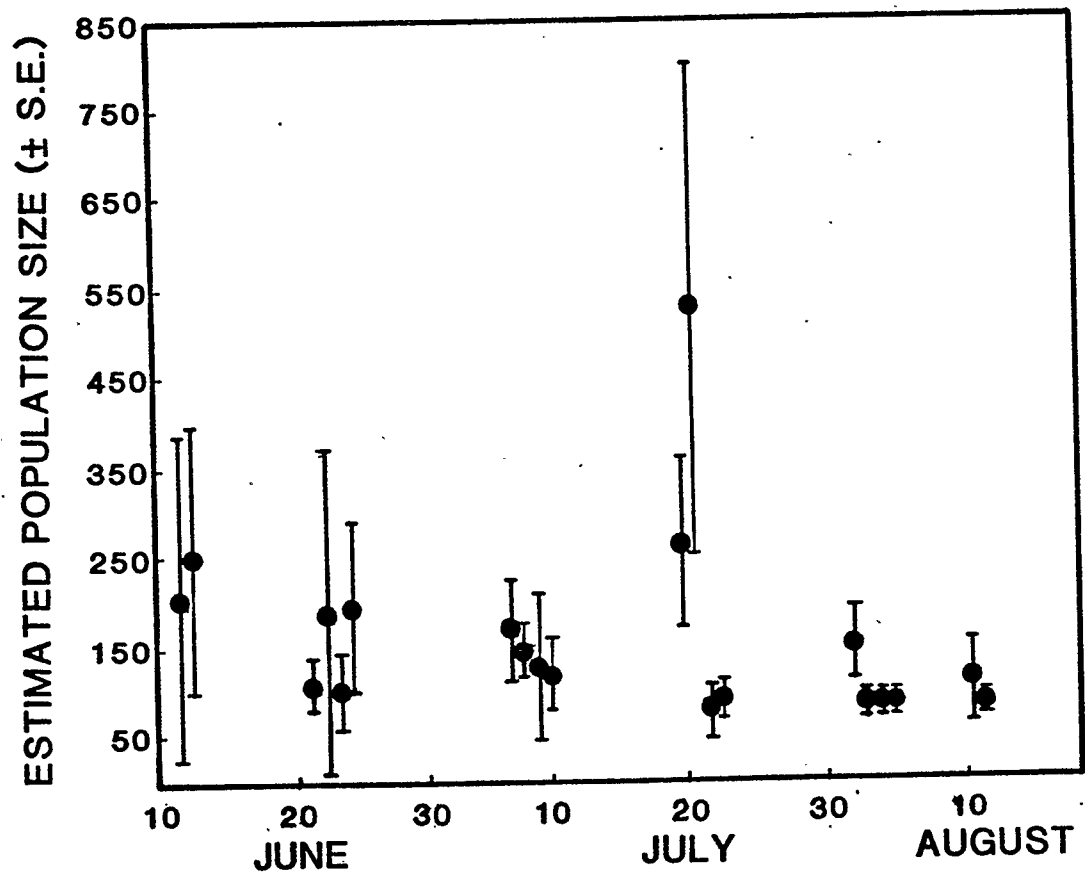
Figure 5.   Male population size estimates by the Jolly-Seber method for Halcyon hotsprings, 1986.
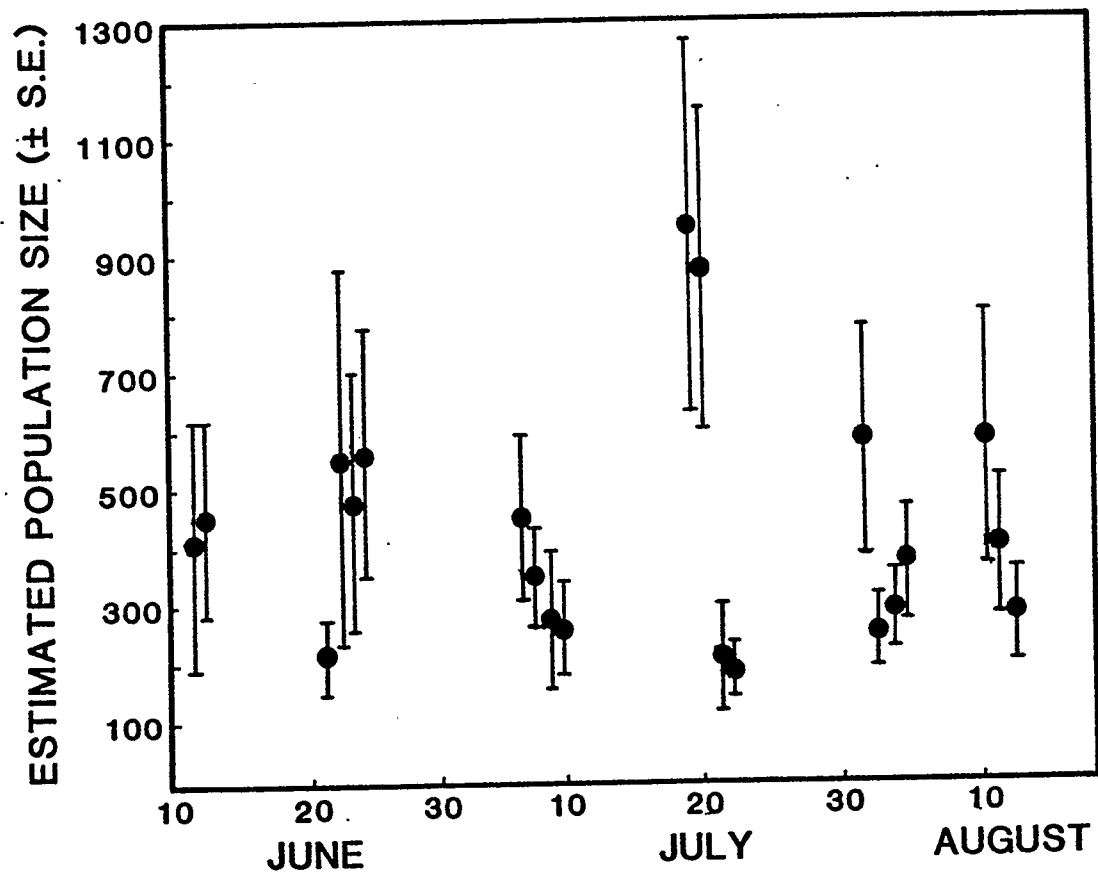
Figure 6. Frequency distributions of the minimum days alive (days between first and last capture) of females (above) and males (below) captured at Halcyon Hotsprings in 1986. The distributions are not significantly different (Mann-Whitney $Z_{(approx.)} = -0.89$, $p = 0.187$).
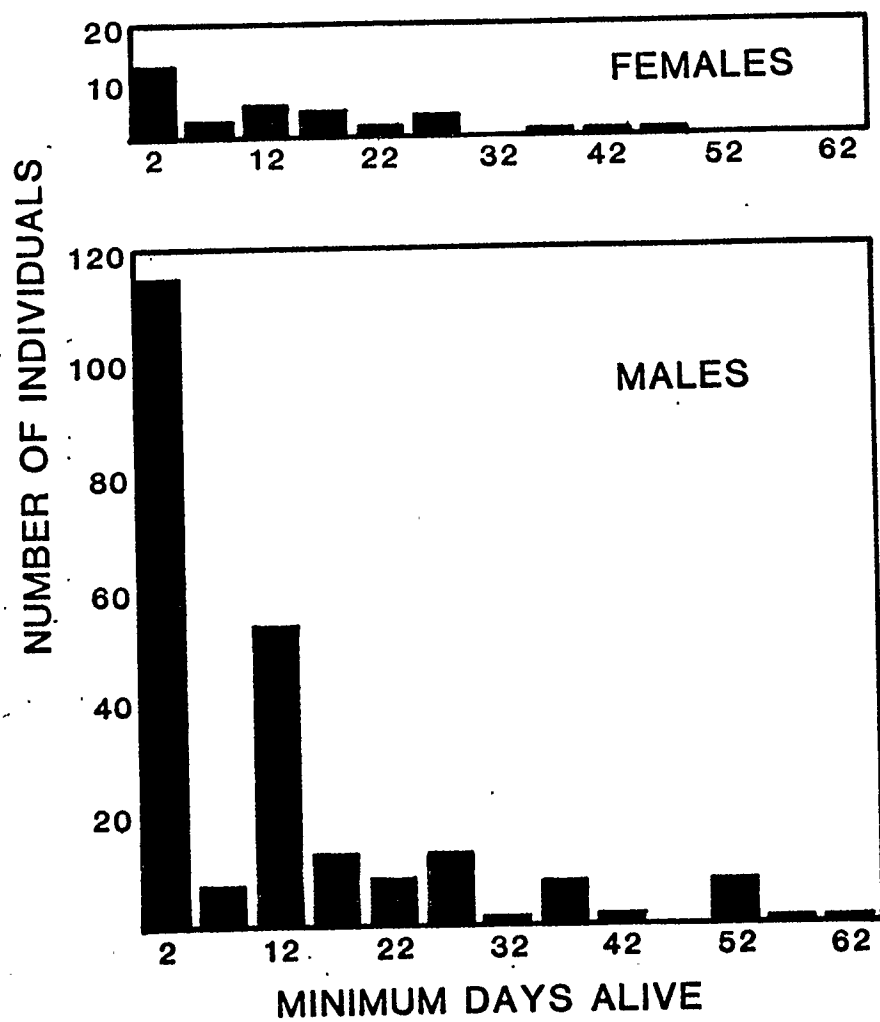
Figure 7.   Frequency distribution of the number of eggs
carried by females captured prior to oviposition at Halcyon
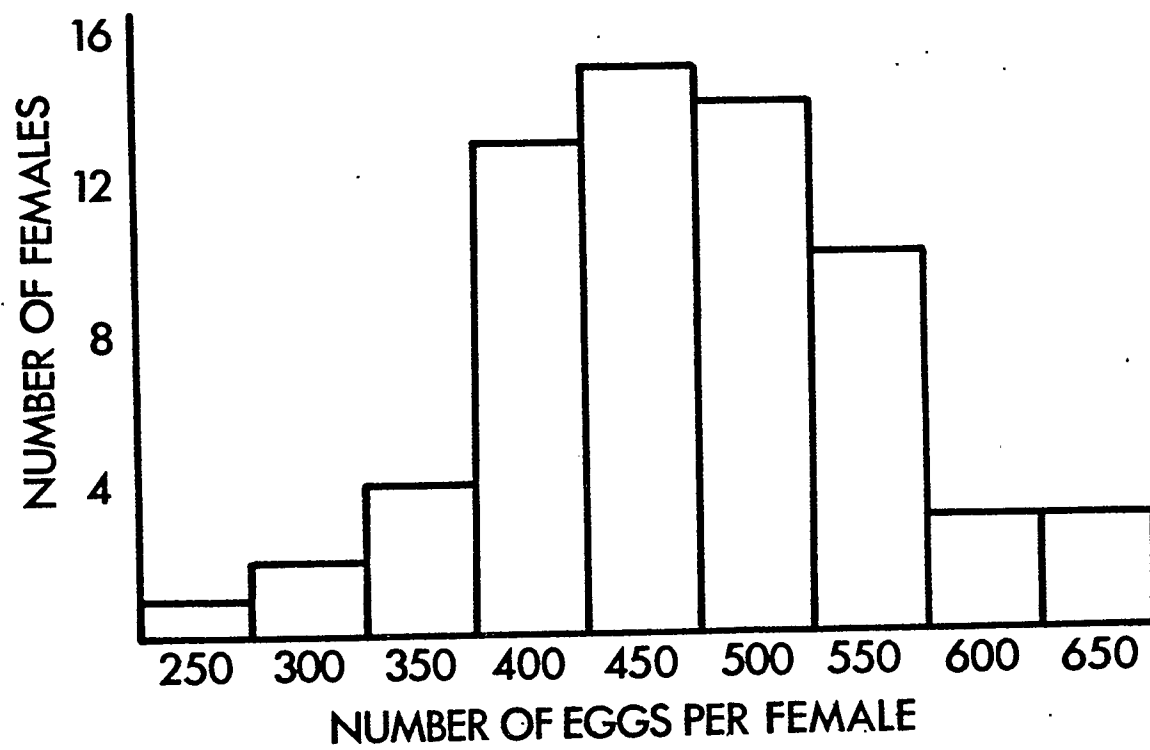Hotsprings and Albert Canyon in 1985 (from the "formalin
pairs").

Figure 8.   Frequency distributions of the time of sighting of non-tandem females. Total Females = Red Females + Blue Females.   To compare red and blue females, the data were divided into morning (< 1300 hrs) and afternoon sightings (> 1300 hrs).   Note that the scale on the vertical axis of each graph is different.
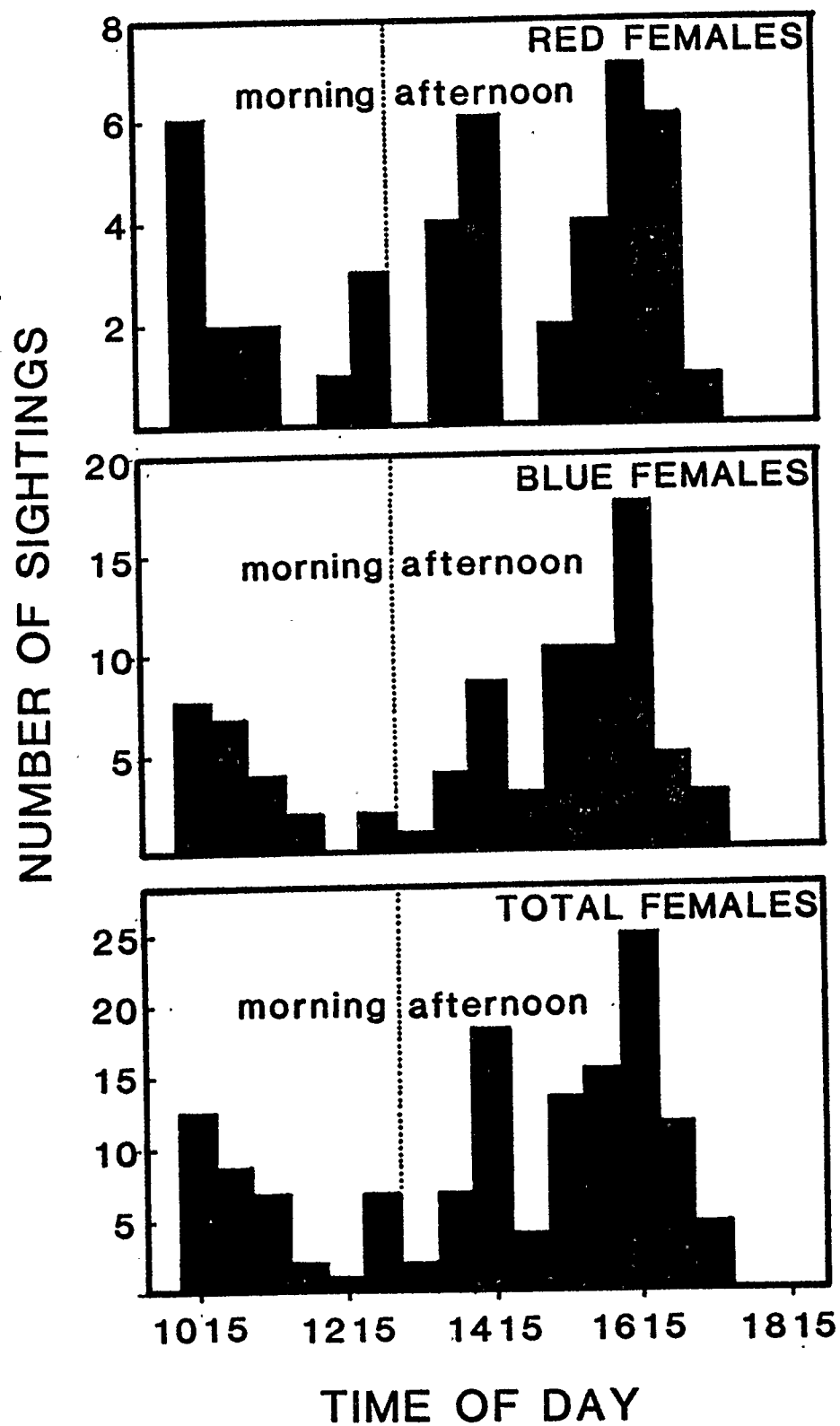
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Figure 9. The number of eggs carried by non-tandem females captured at Halcyon Hotsprings in 1986 prior to oviposition, during unguarded oviposition and following oviposition. The two letter "E"s indicate the number of eggs carried by females captured just after they aggressively escaped their guarding mates. These values were included in the "unguarded oviposition" sample. The number of eggs carried does not differ between the pre-oviposition and unguarded oviposition groups but both are larger than the post-oviposition group (Duncan's multiple range test, critical mean = 302, $p > 0.05$).
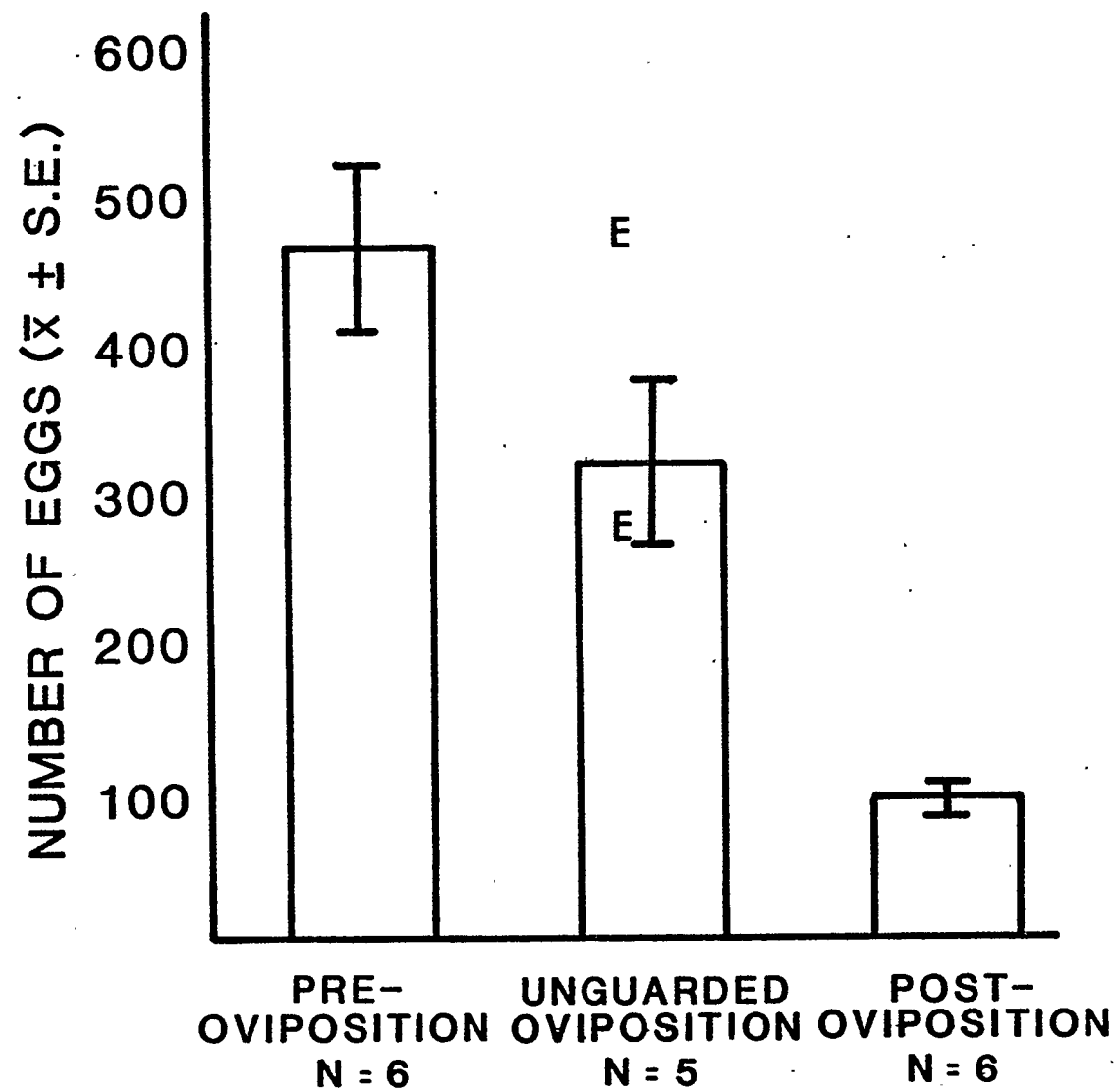
Figure 10. Percentage of total time observed that six
ovipositing pairs spent perching, probing and ovipositing at
Halcyon Hotsprings in 1986. The bar labelled "TOTAL"
represents the sum of all six pairs. The row labelled
"TIME" indicates the total time a particular pair was
observed, in seconds. The "NPC" row gives the number of
changes of perch a pair made while observed and the row
labelled "ATBC" indicates the average time between changes
of perch (calculated as TIME/NPC) for each pair.

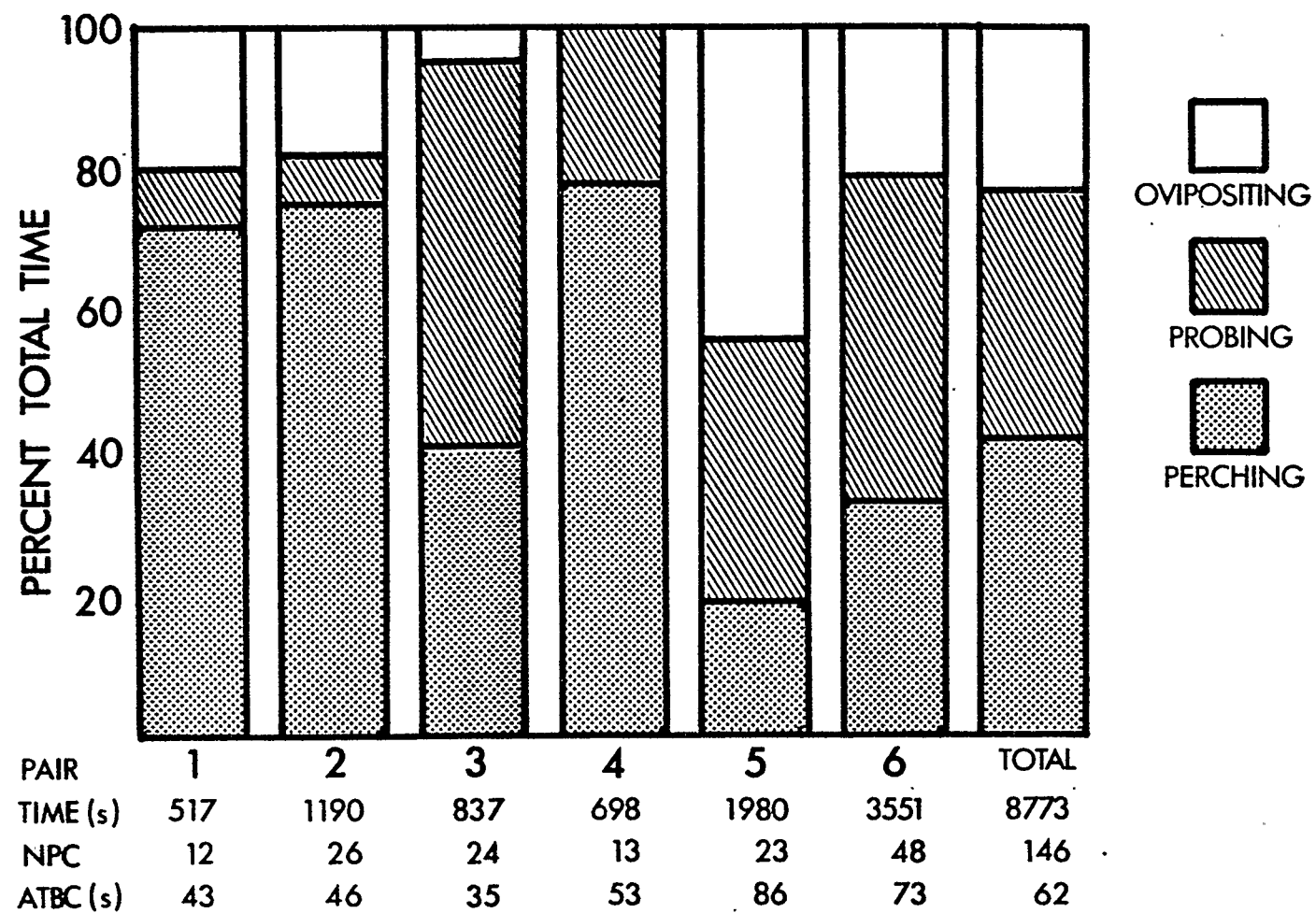|	PAIR	1	2	3	4	5	6	TOTAL
	TIME (s)	517	1190	837	698	1980	3551	8773
	NPC	12	26	24	13	23	48	146
	ATBC (s)	43	46	35	53	86	73	62

Figure 11. Transition flow diagram summarizing changes in
activity of six ovipositing pairs observed at Halcyon
Hotsprings in 1986. This figure is based on the same data
as Figure 10, but presents the number of transitions between
perching, probing and ovipositing made by the six tandem
pairs. Pairs changed perches and females probed potential
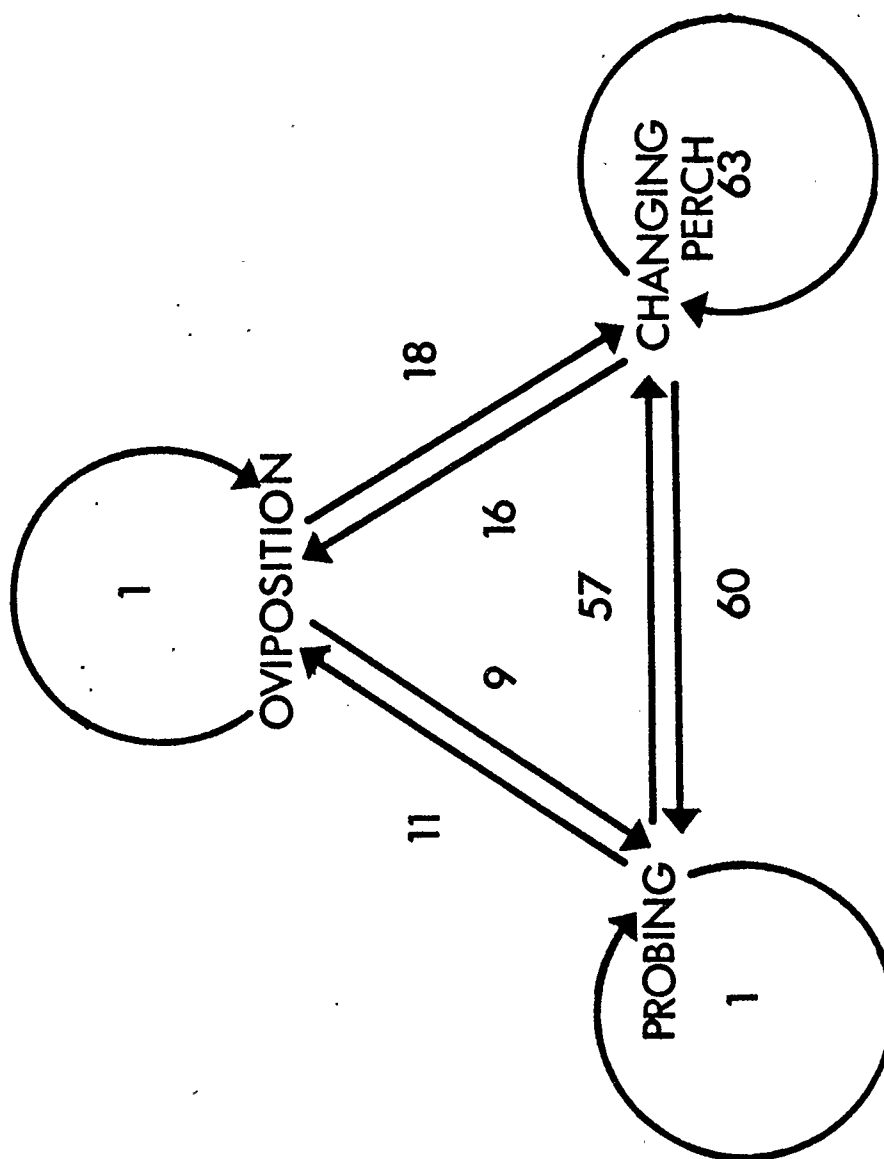oviposition sites frequently.

Figure 12. Duration of copulation of pairs observed at Halcyon Hotsprings in 1986 versus the time of day the copulation began. Copulations of long duration invariably began at patches of sunlight in the forest or high on the stoney slope. Copulations of shorter duration occurred near the water late in the afternoon.
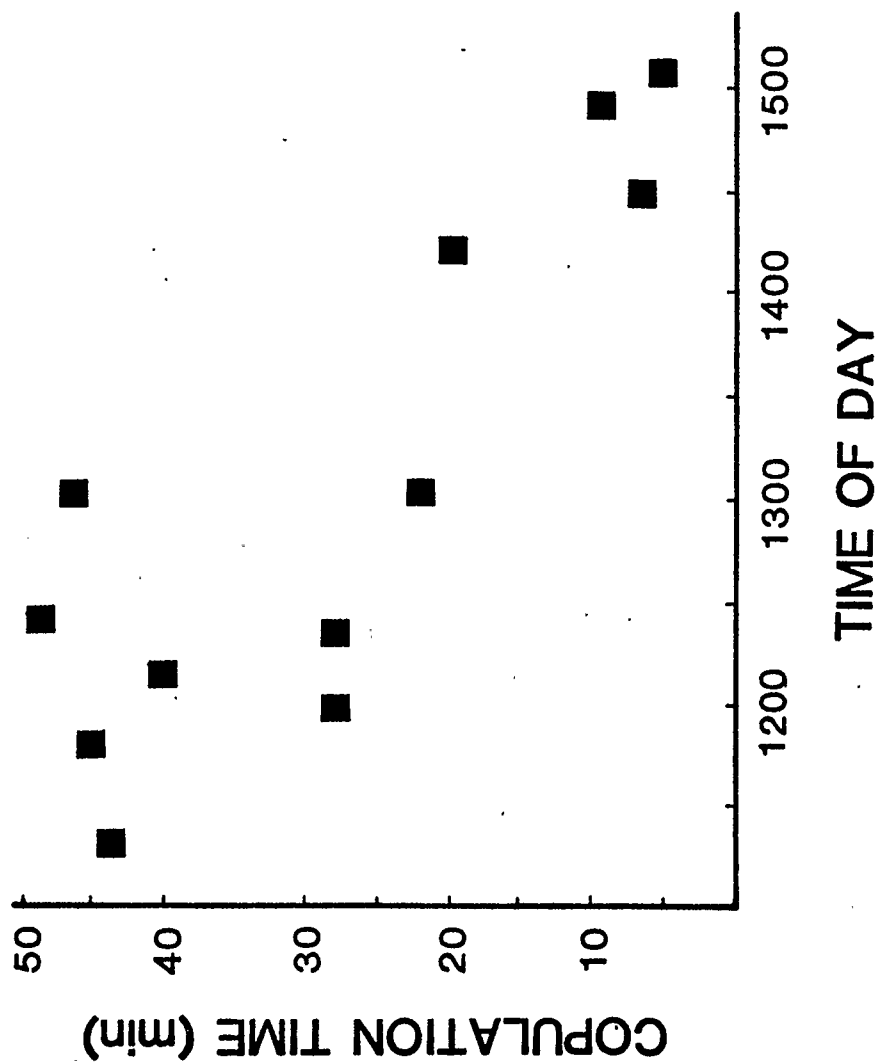
Figure 13. Two possible pathways to describe the mating tactics of male A. vivida at Halcyon Hotsprings. (A) Each morning males that have roosted in the forest begin basking at sunlit patches on the forest floor and seeking mates while simultaneously moving toward the water. (B) Males begin seeking a mate at basking sites in the forest. Later in the day, in response to some unknown cue, if they have not found a mate, they move direcly to the water and begin seeking mates there.
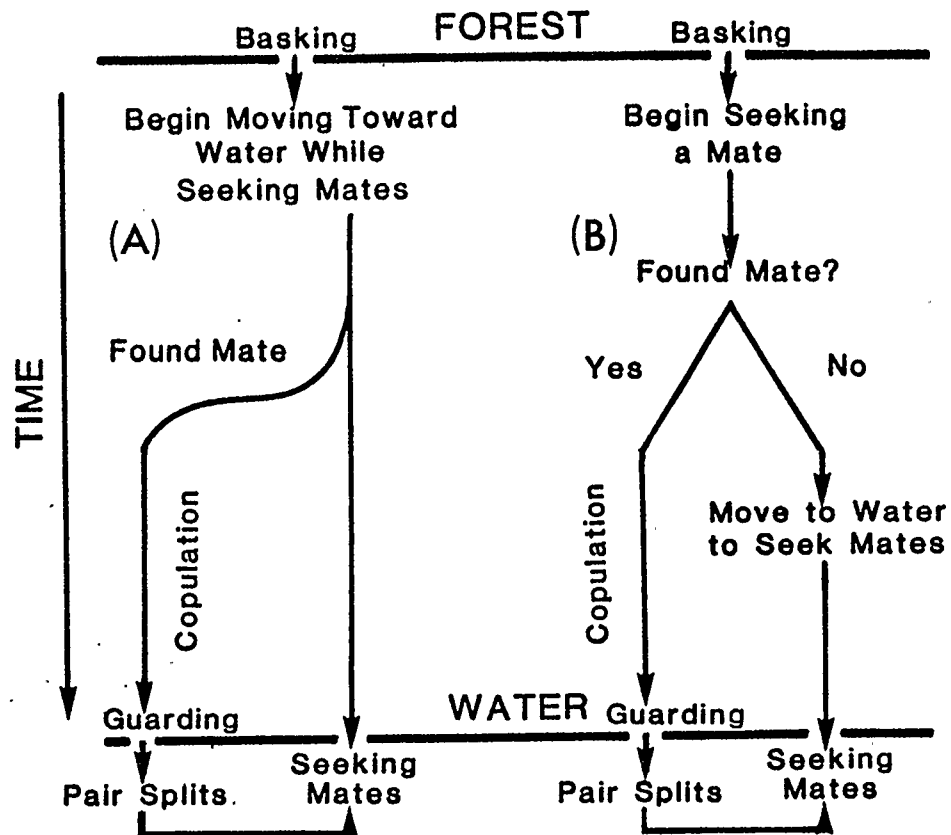
Figure 14. Theoretical relationship between the density of male <u>Argia</u> <u>vivida</u> at the water and mean egg-laying efficiency of tandem and non-tandem females. Since males do not interfere with tandem pairs, oviposition efficiency does not change regardless of the number of non-tandem males present (solid line). If communication within a tandem pair is perfect and both members of the pair are equally good at finding high quality oviposition sites, then the efficiency of unguarded oviposition can never be expected to exceed that of tandem oviposition (line B). However, it is more likely that there is a threshold density of males below which females ovipositing unguarded are more efficient than females ovipositing in tandem (line A). Note that the difference between lines A and B has been exaggerated for clarity.
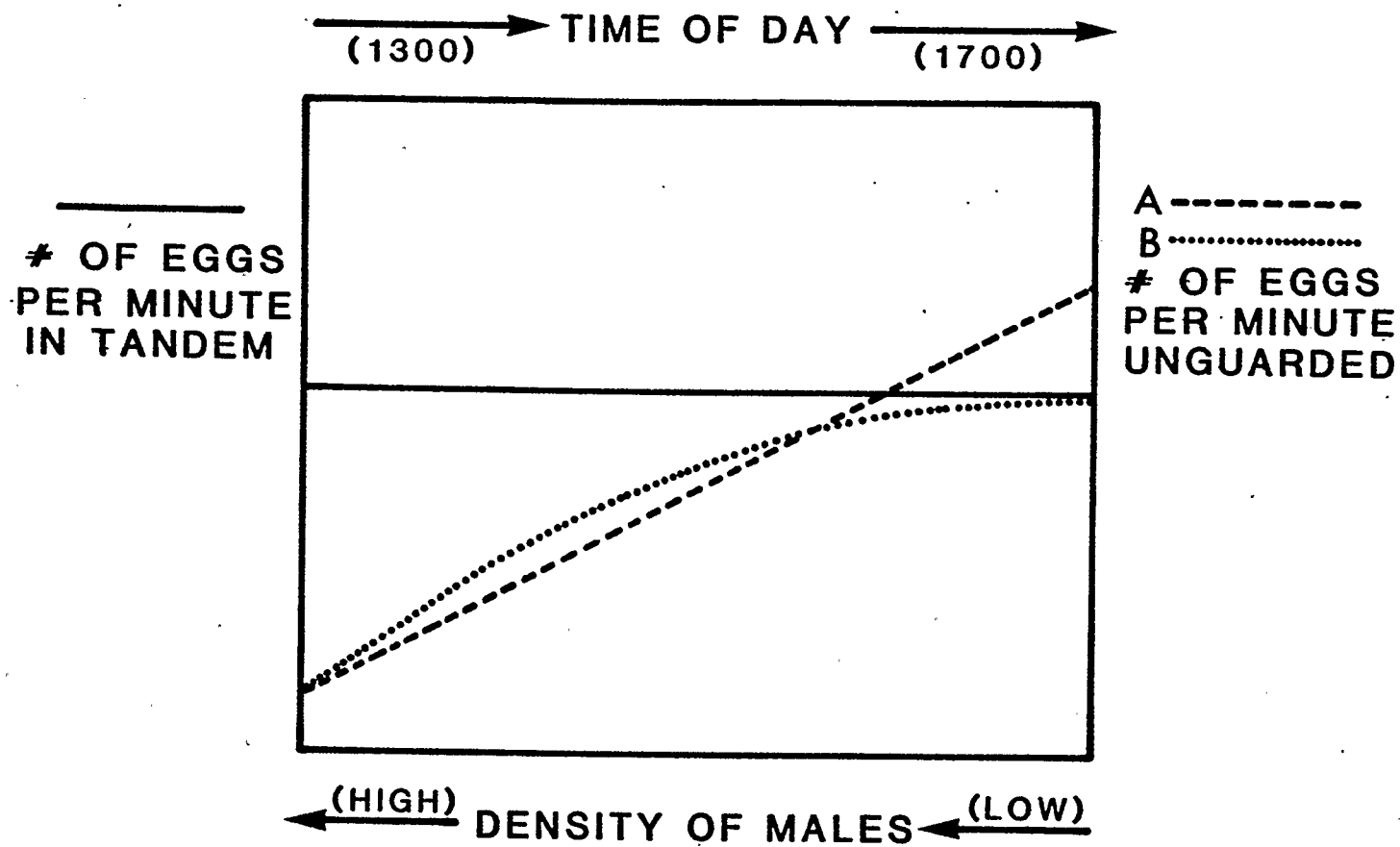
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