

**REPRODUCTIVE BEHAVIOR OF TWO *ARGIA* SPP.  
(ODONATA: COENAGRIONIDAE) AT AN ARIZONA STREAM**

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**Abstract**

Here we provide a first report on the reproductive behavior of *Argia sabino* Garrison and *Argia pima* Garrison from observations at Sabino Creek, Arizona. Both species reproduce in autumn (September-October) following late summer rainstorms. Tandem pairs of *A. sabino* submerge to oviposit on rock substrates. The oviposition substrate is abundant and widespread. Male *A. sabino* defend mate-encounter territories in the morning at boulder fields or rock outcrops away from the stream. Copulation may last 30 minutes or more. Ovipositing females submerge in tandem with males, typically to depths of 10-30 cm, and pairs may remain submerged for over 30 minutes. Male submergence with females can be interpreted as contact mate guarding promoted by sperm competition and/or as a male investment in the female's survival and oviposition success. We discuss evidence for both possibilities based on field observations. Whereas ovipositional resources for *A. sabino* are ubiquitous at Sabino Creek, *A. pima* uses patchily distributed, discrete ovipositional habitats (wetted rootlets of riparian trees at waterfalls and riffles). Males of *A. pima* employ a mixture of contact and noncontact mate-attendance strategies. Females occasionally submerge to oviposit. Often they oviposit along the margins of torrential cascades. Male *A. pima* have been observed to release submerging mates just before their own wings become wetted, and to monitor submerged ovipositing females from a nearby perch thereafter.

**Introduction**

Sources of natural selection interact with dynamics of sexual selection to shape odonate mating systems (Fincke et al. 1997). It should also be recognized that evolutionary history may play a role in constraining adaptation and in providing the raw material for behavioral elaboration. Studies of closely related species and of different local populations within species may help to sort out the influences of selection and history in shaping behavior.

Species within the New World coenagrionid genus *Argia* exhibit a wide range of reproductive behavior traits. For example, there is wide variation in oviposition substrate selection (e.g. Bick & Bick 1972). Some degree of tandem oviposition appears to be universal among *Argia* species (e.g. *A. apicalis* (Say) (Bick & Bick 1965), *A. moesta* (Hagen) and *plana* Calvert (Bick & Bick 1972), *A. vivida* Hagen in Selys (Conrad & Pritchard 1988), *A. fumipennis atra* Gloyd (Bick & Bick 1982), *A. alberta* Kennedy and *A. emma* Kennedy (Provoshna 1975), *A. nahuana* Calvert (H. Greeney pers. comm.), *A. hinei* Kennedy, *A. lugens* (Hagen), *A. pallens* Calvert, *A. oenea* Hagen in Selys (Hoekstra pers. obs.). However, there is often considerable variation within species in the duration of male attendance. As oviposition proceeds, males of many species show an increasing tendency to abandon mates that then continue oviposition alone, as seen for example in *Argia apicalis* (Bick & Bick 1965).

*Argia sabino* and *A. pima* are sympatric in southeastern Arizona at Sabino Creek, a high-gradient canyon stream. Both species mate and oviposit during autumn, a period of stable weather and declining stream flows. *Argia sabino* submerges to oviposit on rock surfaces conditioned with algae, whereas *A. pima* typically oviposits into mats of tree rootlets at shady riffles and cascades. We have characterized the very different oviposition substrate selection strategies of the two species as alternative adaptations to a common environmental stress: habitat drying (Hoekstra 1998). Here we more thoroughly describe and contrast the reproductive behaviors of these two species. We evaluate differences in their behavior in the context of differences in the spatial distribution and abundance of their oviposition substrates. We also discuss the potential adaptive functions of tandem submergence in *A. sabino*.

## Methods

Sabino Creek is a 4th-order intermittent (lower reaches) to perennial (above about 2000 m) stream that originates in the Santa Catalina Mts., with headwaters above 2620 m. Within the known range of *A. sabino* (Fig. 1) the stream is characterized by high-gradient riffles and cascades alternating with large boulder-strewn pools. Pools may be quite large, with maximum depths to over 2 m in March and surface areas often exceeding 200 m<sup>2</sup>. Sabino Creek undergoes seasonal phases of drying and flooding that correspond to winter and summer rainy seasons (Smith et al. 1997). Riparian vegetation is dominated by Arizona sycamore (*Platanus wrightii* S. Watson), Fremont cottonwood (*Populus fremontii* S. Watson), alder (*Alnus oblongifolia* Torrey), and willows (*Salix* spp.).

### *Surveys and observations*

Surveys of *A. sabino* and *A. pima* adult densities were made along the margins of seventeen pools (Fig. 1) in May, June, and September of 1997 (Hoekstra 1998). Many opportunistic observations of adult behaviors were made in May–October 1996 and 1997 at elevations between 910 m and 1210 m. Observations are reported in Mountain Standard Time (MST). (Solar noon ranged from 12:07 to 12:30 MST during the study period.) To investigate *A. sabino* oviposition behavior, seven ovipositing pairs

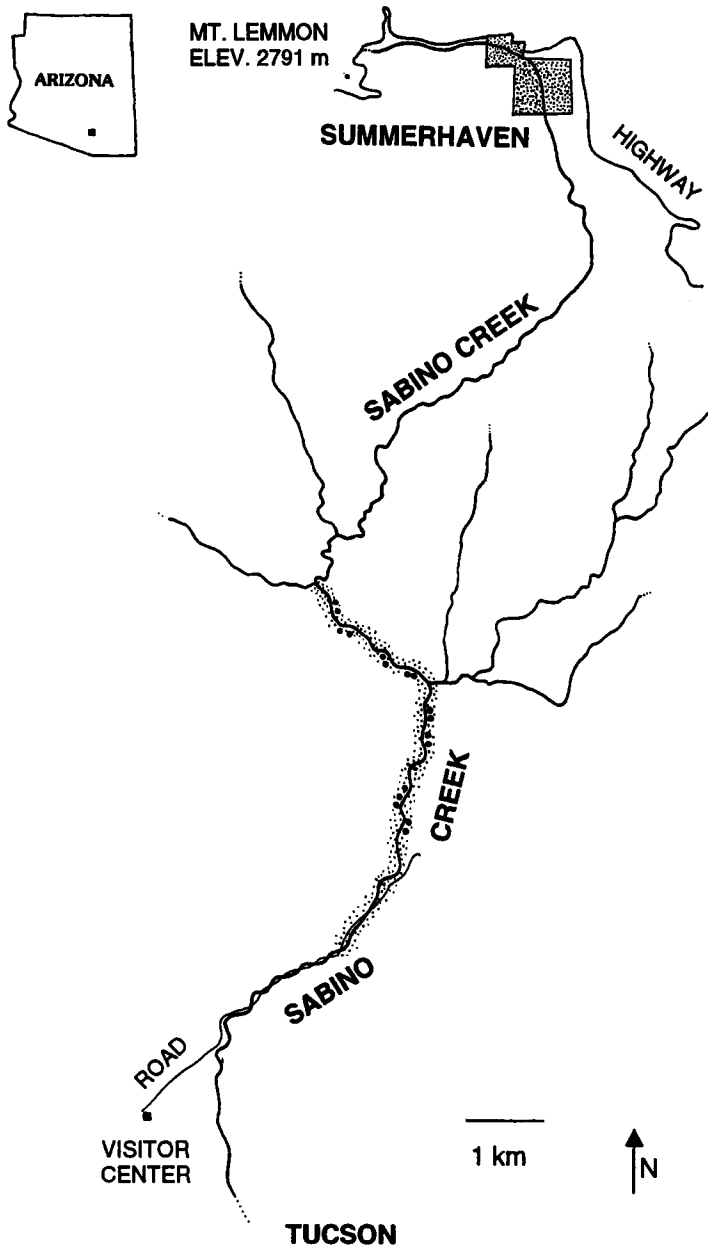


Figure 1. Sabino Creek, Pima County, Arizona, U.S.A. Large dots indicate locations of study pools. Stippled area along stream is known distribution of *A. sabino*. Distribution is similar for *A. pima*. Upstream limit is simply the highest point that has been surveyed, except for a location without *A. sabino* or *A. pima* at 2040 m.

were monitored between 12:30 and 14:30 (MST) (solar noon at 12:16) on 23 September 1997 at a series of small pools and runs at 1070 m. Pairs engaged in submerged oviposition were readily visible in the clear, shallow (<1 m) water. Locations of focal pairs were noted, time of submergence of the male was noted, and locations and depths of pairs were re-checked approximately every 10 min. We calculated the minimum submergence time (time span between first and last observations of the same pair ovipositing) for each pair, and noted the maximum observed submergence depth.

## Results

In September-October 1996 and 1997 reproductive behaviors of *A. sabino* were frequently observed. Reproductive behaviors of *A. pima* were observed in September 1997. A comparative summary of the reproductive behaviors of *A. sabino* and *A. pima* is presented in Table 1.

Table 1. Comparison of reproductive behaviors in *Argia sabino* and *A. pima*.

Behavior trait	<i>Argia sabino</i>	<i>Argia pima</i>
Oviposition substrate:	Rock surfaces conditioned with algae at pools and runs	Clumps of tree roots or dead twigs at waterfalls and riffles
Substrate availability:	Ubiquitous	Localized and infrequent
Oviposition behavior:	Submerged oviposition	Mix of submerged and unsubmerged oviposition
Male mate attendance:	Males consistently submerge with females and remain in tandem throughout ovipositional bout	Males exhibit mixture of contact and noncontact attendance behaviors but do not submerge with females
Male territoriality:	Males defend morning mate encounter territories away from the stream	Not observed. Males may defend territories centered on ovipositional substrates and encounter mates there

### *Pre-oviposition behaviors*

In the morning (10:00-11:30 MST), *A. sabino* males perched in the sun on the tops of large boulders or on rock outcrops where they defended areas of about 2-4 m radius. Males responded to other males entering their territories with swift flights toward the intruder. Territories were clumped in loose aggregations, usually at bedrock outcrops or

boulder fields. These perching arenas were typically located on the canyon slope several meters from the stream. Dozens of males were seen at large arenas. Unpaired males abandoned encounter-site territories and moved to pool margins after about 12:30.

Copulating pairs were observed at and adjacent to perching arenas from 11:10 to 12:22. Tandem and copulating pairs were frequently harassed by unpaired males at the arena, and typically responded to such harassment by shifting to another location closer to the stream. We have not observed pair formation and do not have a complete, continuous record of any copulation event. We made continuous observations of two copulation events that we discovered in progress. These couplings lasted 30.67 and 22.13 min respectively from the beginning of our observation until disengagement.

Precopulatory behaviors were not observed in *A. pima*. One pair was observed in copula (16 September 1997 at 12:02) in a shaded area in the canyon bottom a few meters from water, perching on a boulder.

### *Oviposition behavior*

Following copulation, pairs of *A. sabino* flew in tandem to bedrock outcrops or large boulders along the stream and usually alighted within a meter of the water surface. Pairs then moved downward (walking backward, tails pointed down) until the female's abdomen contacted the water's surface. At this point the female began probing the substrate with the tip of her abdomen and the pair moved downward until the female and male were both submerged. The male was usually completely submerged within 20–40 s of the female's submergence. A silvery film of air was visible between the wings and on the thoraces of both partners.

Females oviposited under water on rock surfaces that were usually covered with a thin layer of algae. As the pair descended, females actively probed rock surfaces with the tips of their abdomens. Females occasionally ceased probing and held their ovipositors pressed against the rock surface for several seconds. In the course of this study we observed over 70 tandem pairs in the process of oviposition and only one lone submerged ovipositing female. The maximum depth recorded for an ovipositing pair was 60 cm, pairs typically submerging to 10–30 cm below the surface. Oviposition was observed between 12:10 and 15:40.

Minimum estimates of submergence time (time interval between sightings of a submerged pair at the same location) made during opportunistic observations of oviposition behavior ranged from 9–37 min. Some pairs were observed to submerge briefly (1–3 min), leave the water, shift to a new location, and re-submerge. Pairs that were monitored systematically ( $n = 7$ ) exhibited minimum submergence times of 1.33–23.12 min (median: 4.53 min).

Pairs ended oviposition or responded to disturbances by releasing their grip on the substrate and floating to the surface where they broke through the surface film and immediately flew away. We observed three cases in which pairs became trapped in the surface film or entangled in algal filaments. In all of these cases, the male retained his tandem grip on the female and after struggling for a few seconds the pair escaped.

We have observed oviposition in *A. pima* between 12:30 and 14:20. Eggs were deposited into/onto organic substrates (submerged dead twigs, more commonly rootlets

of riparian trees) in swift riffles or waterfall splash zones. Oviposition sites were spatially restricted (total area usually just a fraction of a square meter) and were infrequent and highly localized within the study area at Sabino Creek. Sites were most often found at high-gradient, constrained sections of the stream. We observed up to 3 tandem pairs and 2 unpaired males at a single oviposition site.

Submerged tandem oviposition was never observed in *A. pima*, although females were observed ovipositing alone, submerged as much as 5 cm below the surface in turbulent water. Males stayed in tandem with females in early stages of oviposition. However, two different males released their tandem hold on ovipositing females when females submerged deeply, such that the male's wings were in danger of becoming wetted or submerged. After releasing their grip, males flew to perches within 1-2 m of the oviposition site.

Unpaired *A. pima* males perch near oviposition sites and engage in frequent aerial conflicts with other males. Such males may make strong and persistent efforts to interrupt tandem oviposition. We witnessed one case in which an unpaired male vigorously attempted to establish a tandem clasp on a tandem-ovipositing female for at least 3 min. This interaction was concluded when the tandem male lost his hold and was flung into the water. The unpaired male then flew away (perhaps unable to relocate the cryptic female in the complex root-mat substrate), and the female continued to oviposit alone.

#### *Post-oviposition behavior*

In the afternoon (after about 14:30), unpaired males and females of *A. sabino* were frequently seen foraging in close association along pool margins. Males infrequently approached females. Females responded to approaching males by opening the wings sharply and/or curling the abdomen downward. The typical male reaction was to fly away without contacting the female, or to desist after only brief contact.

Post-oviposition behaviors were not extensively observed for *A. pima*. One female was observed to leave the oviposition area immediately following oviposition. This female responded to harassment by two males by opening her wings sharply and flipping the abdomen downward.

## **Discussion**

Male-male competition for fertilizations is intense in the Odonata (Alcock 1994). Male Zygoptera frequently remain in tandem with mates during oviposition or visually monitor their ovipositing mates. Such attendance behavior, also labeled postinsemination association or PIA, is typically interpreted as a form of mate guarding. Male attendance, coupled with last-male sperm precedence (Waage 1986), assure paternity for male damselflies in the face of intense male-male competition for mates, and a general willingness of females to mate multiply (Alcock 1994).

Interpretation of "mate guarding" behaviors in coenagrionid zygopterans is complicated by the fact that females typically mate once in the morning prior to each daily

bout of oviposition (Conrad & Pritchard 1988; Fincke 1997), and males do not retain overnight associations with females. Optimistically assuming 100% last-male sperm precedence, a male's maximum expected reproductive payoff from a single mating (in terms of number of eggs fertilized) is one day's oviposition bout. Opportunities for rival males to co-opt this payoff occur only when females are both vulnerable and receptive to matings by other males during the day's oviposition activity. Thus a willingness to engage in second matings within a daily bout of oviposition is a necessary precondition for sperm competition to promote mate guarding by males. Afternoon matings with second males are frequently recorded in coenagrionids, as in *Argia vivida* (Conrad & Pritchard 1988) and *E. hageni* (Walsh) (Fincke 1986).

An alternative (or perhaps complementary) hypothesis for the function of male attendance is that males may engage in PIAs to enhance the longevity or ovipositional success of their mates. Males engaging in attendance behaviors that benefit mates may enjoy greater reproductive success than males that do not invest in such behaviors. For example, male Odonata may assess and guide females to high-quality oviposition habitats (Thornhill 1984). In *Enallagma hageni*, attending males rescue submerged-ovipositing mates that become trapped in the surface film upon resurfacing during a bout of oviposition. This assistance saves the mate's time and perhaps even her life, thus improving the odds that she will lay a full clutch of eggs fertilized primarily by the aid-giving male (Fincke 1986).

### *Reproductive behaviors of A. pima*

We know relatively little about the reproductive behaviors of *A. pima*. In general, our observations are in accord with the expectation that males should show oviposition-site territoriality and noncontact mate guarding when oviposition sites are rare and defensible (Fincke et al. 1997). Males engage in a flexible system of attendance, showing both contact and noncontact strategies. When female *A. pima* submerge to oviposit, males have been observed to release the tandem grip just before their wings become wetted. Perhaps males release females at this time because submergence in the fast-flowing water is risky or because submerged females are invulnerable to take-over by rivals (Alcock 1994).

### *A. sabino male territoriality*

Male *A. sabino* defend territories at encounter sites away from the oviposition habitat, which is an expected strategy when oviposition substrates are abundant and impossible to defend (Fincke et al. 1997). Male territorial behavior is similar to that seen in *A. vivida*, in which males defend morning mate-encounter territories away from the stream at forest-floor sunflecks (Conrad & Pritchard 1988). Perhaps male *A. sabino* select high points (tops of large boulders, prominences at outcrops) because these vantage points offer the best opportunities to see females moving through the arena.

*Tandem submergence in A. sabino*

Female zygopterans are thought to be invulnerable to take-over by rival males while submerged (encounters and mating do not occur under water); so one might expect that males would cease guarding a mate once she had submerged completely. However, females may resurface before laying an entire clutch of eggs and become vulnerable to takeover by different males at this time (Alcock 1994). Thus male attendance of submerged-ovipositing females may be explained partly as mate guarding behavior.

Does submerging with mates serve such a mate-guarding function for male *A. sabino*? We have never observed late afternoon matings in *A. sabino*, and so might assume that females of the species are willing to mate only once per day. However, because males almost invariably retain tandem with females throughout oviposition, few egg-carrying (physiologically receptive) females are in a position to engage in late afternoon second matings. We can only speculate that male attendance behavior may have been more variable (as in *Enallagma exsultans* (Hagen) (Bick & Hornuff 1966)) in the past and ask the hypothetical question: *would* females remate if males released them? Experiments should be conducted to answer this question directly by interrupting oviposition and presenting females to unpaired males (Fincke 1986), but in the absence of such data we make the educated guess that they would.

Because males have not been observed searching for females under water, second matings with rival males would probably require that females leave the water before depositing a full egg clutch. Typically, *Argia* species engage in a period of exploration and apparent oviposition site assessment before the bulk of oviposition takes place (e.g. Bick & Bick 1982, 1972). We observed several cases in which pairs of *A. sabino* surfaced after a short period of submergence (<4 min) and shifted to another location before resubmerging. Historically, unattended females may have made such exploratory shifts, and they may have been willing to remate with rival males at this time, as seen in *A. vivida* (Conrad & Pritchard 1988). Such past opportunities for afternoon matings (or a continuing low probability of such matings) may explain the observed movement of unpaired *A. sabino* males to the water's edge following the morning competition for mates away from water.

Males of other zygopteran species in which submerged oviposition has been studied typically release the tandem grip and monitor female movements while hovering or perched nearby (Bick & Bick 1963; Alcock 1982; Fincke 1986). Why do male *A. sabino* remain in tandem with females during submerged oviposition? The alternative is monitoring the female from above. In *Enallagma hageni*, for example, males monitor mates from the vantage point of the sedge stem used by the submerging female (Fincke 1986). Monitoring from an aerial perch may not be a viable option for male *A. sabino*, whose mates often oviposit at broad areas of bedrock and engage in considerable lateral movement during oviposition. It would be difficult for males to wait at a specific vantage point and monitor a defined area for a resurfacing mate.

In addition to (or instead of) the mate-guarding function, male attendance of submerged ovipositing females may serve to enhance the survival or oviposition efficiency (and thus the expected reproductive output) of females. In *Enallagma hageni*, attending males may "rescue" females that become trapped at the water surface, thus



allowing their mates to continue a bout of oviposition (Fincke 1986). Our observations suggest that tandem submergence may serve a similar function in *A. sabino*. When we observed cases in which pairs became momentarily stranded at the surface, the male appeared to actively drag the female out of the water.

Males may also assist females in the oviposition process itself. The presence of the male's abdomen may increase the volume and surface area of the gas bubble surrounding the female's thorax, thus improving the bubble's function as a physical gill and extending the dive time. Results of experiments in which submergence times of *Erythromma najas* (Hansemann) were artificially extended in the presence and absence of tandem males supported the plausibility of such a function (Wesenberg-Lund 1913). In addition, males may assist females in retaining their grip on the substrate. Casual observations suggest this may be a challenge for buoyant female *A. sabino* on smooth rock surfaces, and premature "popping up" was reported by Fincke (1986) in lone-submerging female *E. hageni*.

It is difficult to evaluate "mate guarding" and "mate assistance" as alternative hypotheses for the adaptive function of male attendance. A key problem is that, even when they benefit females directly, male attendance behaviors may actually be driven primarily by sperm competition. If females stand to benefit from male attendance, evolution of willingness among females to mate multiply within a bout of oviposition may be favored (Fincke 1986, 1997). Female receptivity, in turn, would be expected to favor intense male mate guarding (Alcock 1994). Unraveling this puzzle will require evaluation of behaviors both from the female and male perspectives (Fincke 1997), and a recognition that fitness payoffs of individual strategies depend partly on the frequencies of alternative strategies in the population.

Use of different oviposition substrates may have driven the evolution of very different reproductive behaviors in *A. sabino* and *A. pima*. Male behaviors of *A. pima* (territoriality at the oviposition site, flexible mate-guarding system including some noncontact guarding) are as expected for a population with relatively restricted, defensible oviposition sites. Male behaviors of *A. sabino* (territoriality at an encounter site away from the oviposition site, strict contact guarding) are as expected for a population for which oviposition sites are widespread (Fincke et al. 1997).

The focal species of our study are probably closely related (R.W. Garrison, personal communication), but their reproductive behavior is quite different. This observation suggests that details of reproductive behavior are quite plastic within the genus. The highly variable behavior of *A. moesta* (Bick & Bick 1972) attests to the high levels of intraspecific geographic variation in behavior that may also typify many *Argia* species. Thus the genus provides many opportunities for the study of local behavioral adaptation and for investigations into the interplay between evolutionary history, natural selection, and sexual selection in shaping odonate mating systems.

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