

**BEHAVIOR OF ADULTS OF DARK-WINGED AND
CLEAR-WINGED SUBSPECIES OF *ARGIA FUMIPENNIS*
(BURMEISTER) (ZYGOPTERA: COENAGRIONIDAE)**

J.C. BICK and G.H. BICK

1928 SW 48th Avenue, Gainesville, Florida 32608, United States

Received December 24, 1981.

The behavior of unpaired males of the dark-winged *A.f. atra* Gloyd and *A.f. fumipennis* (Burm.) was compared with that of the clear-winged *A.f. violacea* (Hag.). The dark and clear-winged subspecies differed primarily in that the former had more wing-clapping episodes per unit of time, more claps per episode, and a greater clap angle. — The reproductive behavior of the dark-winged *A.f. atra* was similar in most respects to that of the clear-winged species of *Argia*. Without courtship, males seized females at water and intramale sperm translocation in tandem ($\bar{X} = 14.6$ sec) and the wheel position ($\bar{X} = 24.4$ min) quickly followed. The wheel consisted of two phases: an initial long period ($\bar{X} = 19.9$ min) of pumping when sperm from a previous mating was probably removed, followed by a brief ($\bar{X} = 4.5$ min) terminal period without pumping when the male probably inseminated the female. After an exploratory period averaging 33.8 min, pairs oviposited in tandem at the water surface for an average of 58.2 min. Unlike clear-winged species of *Argia*, *A.f. atra* males frequently wing clapped during the wheel position, and both sexes clapped during oviposition.

INTRODUCTION

This study continues our efforts to describe the behavior of Nearctic Zygoptera, this time with special attention to possible subspecific differences between the dark- and clear-winged subspecies of *Argia fumipennis* (Burmeister). We previously (BICK & BICK, 1965a, 1971, 1972) recorded behavior of three species of clear-winged *Argia*, viz. *apicalis* (Say), *plana* Calvert, and *moesta* (Hagen).

When GLOYD (1968) united *A. fumipennis* with *A. violacea* (Hagen), she differentiated three subspecies by wing and abdominal color. *A.f. fumipennis*

(Burm.) has smoky to dark brown wings and the dorsum of abdominal segments II-VI in males is violet; likewise, *A.f. atra* Gloyd has very dark brown wings, but abdominal segments III-VII are dark brown to black. Although *A.f. violacea* has abdominal segments II-VI or VII mostly violet, its wings are clear or slightly smoky. There is no study comparing behavior of Nearctic Zygoptera on the subspecific level. We thought it would be significant to compare the behavior of the dark-winged *A.f. atra* and *A.f. fumipennis* with that of the clear-winged *A.f. violacea*.

METHODS

On 16 days in September and October, 1979, we studied *A.f. atra* behavior along a branch of Hatchet Creek, northeast of Gainesville in Alachua County, Florida, USA, near a site described by TENNESSEN (1975). Pairs were observed and timed throughout the reproductive sequence, and the activity of unpaired males at water was recorded during 15 min intervals. Various colors of paint were applied to wings and/or thorax to make field recognition of the individual possible. However, with constant attention, we were able to track some pairs even without marks. Field notes were supplemented by still and cine photography. The angle of wing clap was measured using single frames of 8 mm cine film, an editor viewer, and a protractor.

In addition, the behavior of unpaired *A.f. fumipennis* males was studied near Pass Christian, Harrison County, Mississippi, in May, 1980, and that of unpaired *A.f. violacea* males near Mentone, DeKalb County, and Hamilton, Marion County, both in Alabama in July 1981. Unfortunately, pairs at these localities were too few for a study of reproduction.

BEHAVIOR OF UNPAIRED MALES

Activities of five unpaired *A.f. violacea* males, four unpaired *A.f. fumipennis* males, and seven unpaired *A.f. atra* males were recorded during totals of 75, 60, and 105 min respectively. All observations were on clear days between 1000 and 1500 hours EST. Activities of these three subspecies are compared in Tables I and II.

SHIFTS AND PATROL FLIGHTS

During a patrol flight a male flew out 1-2 m, then quickly returned to the same perch, whereas a shifting male flew and then returned to a perch, 5 cm - 2.1 m away from the original one. In the three subspecies (Tab. I), the average number of patrols was identical and less frequent than shifts. Inexplicably, shifts were twice as frequent in *A.f. violacea* and *A.f. atra* as in *A.f. fumipennis*. *A.f. atra* males showed little attachment to their original perches which usually remained available for reoccupancy. Although *A.f. atra* males frequently shifted, none was more than 5 m from the original perch at the end of the observation period; they remained in the same general area but not at the same perch.

Table I

The number of activities (patrols, shifts, and flights toward) per minute among unpaired males of three subspecies of *Argia fumipennis* (Burm.)

Subspecies	No. of males	Minutes of observation	Number per minute		
			Patrol	Shift	Flight toward
<i>violacea</i>	5	75	0.2	0.6	0.06
<i>fumipennis</i>	4	60	0.2	0.3	0.2
<i>atra</i>	7	105	0.2	0.6	0.2

FLIGHT TOWARD

Wing warnings, in which an adult elevates and separates all four wings in the presence of an intruder (BICK & BICK, 1963), did not occur in unpaired males of any of the three subspecies. Instead, *A.f. atra* males flew vigorously toward intruders or even toward passing males before the latter were close enough for wing warnings to be effective. Also, the occupant sometimes chased intruders or passing males as far as 5.1 m along the Creek. Judged subjectively, they flew more aggressively toward conspecifics than did other species or subspecies of *Argia*. Flights toward, shifts, and patrols spread unpaired *A.f. atra* males along the Creek at average intervals of 2 m. This distance equals the 2 m of pond margin maintained by *A. apicalis* but exceeds the 1 m of Creek margin maintained by *A. plana* (BICK & BICK, 1971).

Unpaired *A.f. atra* males advanced toward 21 conspecific pairs and persistently attempted to separate male from female. One unpaired male succeeded, seized the female, and then engaged in a complete reproductive sequence. These attacks occurred although males of pairs (12 times) or both sexes (4 times) wing warned. We have never seen unpaired males of any other coenagrionid so persistently attempt to separate conspecific pairs.

WING CLAPPING

This activity consists of the separation of right and left wings and a return to the resting position, usually in the absence of intruders (BICK & BICK, 1978). We recorded these claps for unpaired males of Coenagrionidae and Lestidae, and for both sexes of Calopterygidae, erroneously stating that it had not been recorded for any coenagrionid female, when actually we had reported it for a female *A. apicalis* away from water (BICK & BICK, 1965a). Among coenagrionids, wing clapping was particularly impressive in *A.f. atra* and *A.f. fumipennis* perhaps because of the impact which the dark wings have

on the observer. In *A.f. atra* clapping occurred in unpaired males, in males during the wheel position, in both sexes during tandem oviposition, and even in an unpaired female at water.

Clapping was not continuous but in episodes, each with a highly variable number of claps. The number of episodes and the number of claps per episode were greater in the two dark-winged subspecies (Tab. II) than in the clear-winged one, and the angle formed between the anterior margins of the fore wings was much greater in the dark-winged *A.f. atra* than in the clear-winged *A.f. violacea*.

Table II

The frequency, size and duration of wing claps, and the number of activities (patrol, shift, flight toward) not followed by a wing clap in unpaired males of three subspecies of *Argia fumipennis* (Burm.)

Subspecies	Mean no. of episodes per 30 min.	Mean no. of claps per episode	Mean duration of a clap (sec)	Angle formed by fore wings (degrees)	No. of activities not followed by a wing clap
<i>violacea</i>	13.2	1.4	0.4	28	29
<i>fumipennis</i>	19.5	4.1	—	—	7
<i>atra</i>	22.0	3.6	0.5	52	4

Because wing clapping in unpaired males most often occurred after activity such as shifts, patrols, or flights toward, the greater number of claps in *A.f. atra* and *A.f. fumipennis* might be attributed to greater densities of the dark-winged subspecies and hence to more frequent interactions. However, regardless of density or the number of activities, males of the two dark-winged subspecies seldom failed to wing clap after flight, whereas the clear-winged *A.f. violacea* frequently did not clap after a flight (Tab. II).

REPRODUCTION

There is no recorded information (BICK & BICK, 1980) on reproduction in *A.f. atra* and *A.f. fumipennis* and only very general statements (CALVERT, 1893; KELLCOTT, 1895, 1899; NEEDHAM, 1903; MORGAN, 1930; WALKER, 1953; LAROCHELLE, 1979) on oviposition in *A.f. violacea*. The following account is based on *A.f. atra* pairs observed constantly from seizure until the end of oviposition, 83-157 min later (\bar{X} = 124.8, N = 5) and on many other pairs observed briefly during various stages of reproduction.

SEIZURE

As in all coenagrionids and lestids which we have studied, there was no courtship, display, or signal of any kind prior to seizure of the female by the male, which was so quick that few details were noted. We observed five seizures, all between 1016 and 1208 hours. Three were in flight as females arrived at the Creek, two just after arriving females perched on emergent vegetation in the Creek.

INTRAMALE SPERM TRANSLOCATION

As in all Zygoptera species which we have studied, intramale sperm translocation was always in tandem and quickly followed each seizure. Among 10 observations, nine males reached the position on the first attempt, one only after nine attempts. During translocation seven pairs perched among dense bordering vegetation where they were well hidden, but three others perched over water with scarcely any shelter.

The duration of sperm translocation in *A.f. atra* was 7-20 sec ($X = 14.6$, $N = 10$). Previously reported (BICK & BICK, 1965b, 1972) mean durations for *A. moesta* and *A. plana* were 10.6 and 21.4 sec respectively. We have also timed the tandem event in *A. sedula* (Hag.) (8.0 sec, $N = 1$), *A. immunda* (Hag.) (20.0 sec, $N = 1$), and *A.f. violacea* (22.5 sec, $N = 2$).

WHEEL POSITION

The wheel position, observed and timed for 11 pairs, quickly followed every observed sperm translocation at the same spot. Ten reached the wheel on the first attempt, one after a preliminary trial. Six pairs did not change perch but five did, three of the latter maintaining the wheel, two breaking it. Leg positions of females varied from tight against the thorax to extended, and one female assumed both positions. Female eye cleaning and male "kicking" the female abdomen occurred at unpredictable times; kicking could not be used to predict the breaking of the wheel.

The duration of the wheel position in *A.f. atra*, excluding momentary interruptions in two pairs, was 18-37 min ($\bar{X} = 24.4$, $N = 11$), a duration similar to means of 22.2 min and 26.9 min for *A. moesta* and *A. plana* respectively (BICK & BICK, 1972), but considerably longer than the mean (15.9 min) for *A. apicalis* (BICK & BICK, 1965a, 1972).

While in the wheel, females never clapped but seven of 11 males did, even when intruders were absent. Two males clapped almost constantly, three engaged in 10, 11, and 15 episodes, and two in only one episode each. Claps per episode for males not clapping constantly were 1-9.

A significant aspect of the wheel position was the rhythmic up and down movement of the male abdomen which we designated as pumping and which occurred in all *A.f. atra* pairs (BICK & BICK, 1963). ROWE (1978) stated that the male of *Ischnura aurora* (Br.) alternately and rapidly curved and straightened his abdomen, and that sperm was transferred to the female only in the last few minutes of the wheel position. WAAGE (1979) showed that in *Calopteryx maculata* (P. de Beauv.) a long period of pumping early in the wheel position actually resulted in removal of sperm deposited by a previous mate, and that sperm transfer to the female occurred briefly and only late in the wheel position. MILLER & MILLER (1981) described three phases of the wheel in *Enallagma cyathigerum* (Charp.): the first, a pumping phase, resulted in removal of previously deposited sperm; the second and third phases resulted in the transfer of sperm to the female.

In *A.f. atra* we detected only two phases of the wheel position. First was a 13-32 min (\bar{X} = 19.9, N = 10) initial period of pumping, corresponding to the first phase in WAAGE (1979) and MILLER & MILLER (1981), when the pair formed a typical wheel or valentine. Then pumping stopped for 3-6 min (\bar{X} = 4.5 min, N = 10) near the end, when the configuration of the pair changed to an elongated rectangle. This corresponds to the second WAAGE (1979) stage and to the MILLER & MILLER (1981) stage III, figure 1C. Thus the 19.9 min of pumping in *A.f. atra* was probably spent in sperm removal and only the last 4.5 min of non pumping in transfer of sperm to the female.

EXPLORATION

In this phase, pairs in tandem shifted so frequently and females probed so briefly that effective oviposition was not possible. One pair shifted 95 times in 73 min and, by frequent shifting, another moved 44 m from the copula site. On the other hand, one pair shifted only 10 m and another, without exploration, moved directly from the copula site to the effective oviposition site. Exploration lasted 0-73 min (\bar{X} = 33.8, N = 5), a longer period than for other species of *Argia*. We cannot explain this long duration; apparently suitable vegetation was abundant, the population was not very large (1♂ / 2m), and there seemed to be little competition from any other species of Odonata.

EFFECTIVE OVIPOSITION

Effective oviposition was always in tandem. No female of *A.f. atra* oviposited alone, even momentarily after the male of a pair disengaged near the end of oviposition as sometimes occurs in other *Argia* species. All

oviposition was at the water surface where the usually upright male occasionally leaned forward to rest briefly on the substrate.

A.f. atra always oviposited in horizontal material, using almost every species of aquatic plant in the study area. The percent time that seven pairs spent at each substrate during a total of 348 min of effective oviposition was: *Cyperus flavescens*, 38.5 percent; *Fuirena pumila*, 17.5; *Typha latifolia*, 13.8; *Sacciolepis striata*, 12.1; *Ludwigia palustris*, 7.8; plant debris, 5.4; *Hydrocotyle umbellata*, 4.3; *Cyperus strigosus*, 0.6. The figures for *Sacciolepis* and *Typha* probably would be higher if we had not lost sight of several pairs in the dense growth of these plants. Selection of plant species probably was not involved; the most abundant plant was the most frequently utilized. During exploration, pairs seemed to search for sheltered sites rather than for any particular plant species. Effective oviposition lasted 44-88 min ($\bar{X} = 58.2$, $N = 5$), a duration intermediate between means of 47.2 for both *A. plana* and *A. moesta* (BICK & BICK, 1972) and 72.7 min for *A. apicalis* (BICK & BICK, 1965a, 1972).

Both sexes wing clapped during oviposition even when intruders were absent. Following almost every shift, sometimes of only a few cm, one or both members clapped. For seven ovipositing pairs, monitored for clapping, there were 105 episodes, 52 by both sexes, 46 by the male only, seven by the female only. When both sexes clapped during an episode, the male and female did not do so synchronously as we illustrate for *Calopteryx maculata* (BICK & BICK, 1978). Male clapping episodes were more frequent than female ones for five of the seven pairs. The greater frequency of clapping in the male is shown also by the average interval between episodes: 4.1 min for males, 6.6 for females.

DISCUSSION

Unpaired males of the two dark-winged *A. fumipennis* subspecies wing clapped more frequently and with greater magnitude than did *A.f. violacea* and other clear-winged coenagrionids. Also, *A.f. atra* males clapped during the wheel position, and both sexes did so during oviposition, in contrast with clear-winged coenagrionids. The frequently clapping dark wings were very striking to us and presumably to conspecifics and to other species of Zygoptera. The only other Nearctic zygopteran known to us, which claps so frequently and so conspicuously is the dark-winged *Calopteryx maculata*.

If wing clapping is a mere comfort movement, one would expect the clap to be of equal frequency and magnitude in clear and dark-winged species. This is not so. Instead, we hypothesize, as we did in 1978, that wing clapping is a signal, perhaps a territorial declaration. Even if wing claps were large and frequent in clear-winged species, the claps probably still would not be efficient

signals to other odonates, i.e., they would not attract attention sufficient to justify the extra energy expenditure. On the other hand, in *A.f. atra*, the large and frequent claps can serve as efficient signals because the dark wings are so readily visible to other odonates as to justify extra energy expenditure.

As far as we know, only in dark-winged Zygoptera (*Calopteryx maculata*, *A.f. atra*, and *A.f. fumipennis*) do both sexes wing clap during oviposition. Such clapping in dark-winged species but not in clear-winged ones cannot be mere coincidence. Wing clapping in *C. maculata* during non-tandem oviposition appears to be a communication between the sexes (BICK & BICK, 1978). However, a wing clap communication between a male and female which are firmly clasped together in tandem, as in *A.f. atra*, seems scarcely necessary. We hypothesize that wing clapping during tandem oviposition announces occupancy of the site and thus spreads ovipositing pairs along the Creek. We did not observe communal oviposition in the dark-winged *A.f. atra* as we did in the clear-winged *A. apicalis* and *A. plana* (BICK & BICK, 1965a, 1972 resp.), neither of which clapped during oviposition.

KIAUTA & KIAUTA (1980) state that *Argia* is a rapidly evolving genus and that, in the *fumipennis* complex, *A.f. violacea* is the oldest, *A.f. atra* the youngest. Our interpretation of wing color and wing clapping supports their view. It is reasonable to conclude that the widely distributed *A.f. violacea* represents the primitive condition because it has clear wings and infrequent wing claps as do most Nearctic Zygoptera. From this clear-winged type we judge that the dark wings and conspicuous clapping (infrequent in the suborder) of the geographically more restricted *A.f. fumipennis* and *A.f. atra* were derived.

ACKNOWLEDGEMENT

We thank S.W. DUNKLE who gave important comments on an earlier version of the manuscript.

REFERENCES

- BICK, G.H. & J.C. BICK, 1963. Behavior and population structure of the damselfly, *Enallagma civile* (Hagen) (Odonata: Coenagriidae). *SWest. Nat.* 8: 57-84.
- BICK, G.H. & J.C. BICK, 1965a. Demography and behavior of the damselfly, *Argia apicalis* (Say), (Odonata: Coenagriidae). *Ecology* 46: 461-472.
- BICK, G.H. & J.C. BICK, 1965b. Sperm transfer in damselflies (Odonata: Zygoptera). *Ann. ent. Soc. Am.* 58: 592.
- BICK, G.H. & J.C. BICK, 1971. Localization, behavior, and spacing of unpaired males of the damselfly, *Argia plana* Calvert (Odonata: Coenagrionidae). *Proc. ent. Soc. Wash.* 73: 146-152.
- BICK, G.H. & J.C. BICK, 1972. Substrate utilization during reproduction by *Argia plana* Calvert and *Argia moesta* (Hagen) (Odonata: Coenagrionidae). *Odonatologica* 1: 3-9.

- BICK, G.H. & J.C. BICK, 1978. The significance of wing clapping in Zygoptera. *Odonatologica* 7: 5-9.
- BICK, G.H. & J.C. BICK, 1980. A bibliography of reproductive behavior of Zygoptera of Canada and conterminous United States. *Odonatologica* 9: 5-18.
- CALVERT, P.P., 1893. Catalogue of the Odonata (dragonflies) of the vicinity of Philadelphia, with an introduction to the study of this group of insects. *Trans. Am. ent. Soc.* 20: 152-272.
- GLOYD, L.K., 1968. The union of *Argia fumipennis* (Burmeister, 1839) with *Argia violacea* (Hagen, 1861), and the recognition of three subspecies (Odonata). *Occ. Pap. Mus. Zool. Univ. Mich.* 658: 1-6.
- KELLICOTT, D.S., 1895. Catalogue of the Odonata of Ohio. Part I. *J. Cincinn. Soc. nat. Hist.* 17: 195-216.
- KELLICOTT, D.S., 1899. The Odonata of Ohio. *Bull. Ohio St. Univ.* (IV) 1899 (5): 1-116.
- KIAUTA, B. & M.A.J.E. KIAUTA, 1980. Introduction to the cytotaxonomy of the odonate genus *Argia* Rambur (Zygoptera: Coenagrionidae). *Odonatologica* 9: 35-56.
- LAROCHELLE, A., 1979. Observations sur accouplement et la ponte de 22 espèces d'odonates du Québec. *Cordulia* 5: 34-37.
- MILLER, P.L. & C.A. MILLER, 1981. Field observations on copulatory behaviour in Zygoptera, with an examination of the structure and activity of the male genitalia. *Odonatologica* 10: 201-218.
- MORGAN, A.H., 1930. *Field book of ponds and streams*. Putnam, N.Y.
- NEEDHAM, J.G., 1903. Aquatic insects in New York State. Part 3. Life histories of Odonata, suborder Zygoptera. *N. Y. Mus. Bull.* 68: 218-279.
- ROWE, R.J., 1978. *Ischnura aurora* (Brauer), a dragonfly with unusual mating behavior (Zygoptera: Coenagrionidae). *Odonatologica* 7: 375-383.
- TENNESSEN, K.J., 1975. *Reproductive behavior and isolation of two sympatric coenagrionid damselflies in Florida*. PhD Thesis, Univ. Florida, Gainesville.
- WAAGE, J.K., 1979. Dual function of the damselfly penis: sperm removal and transfer. *Science* 203: 916-918.
- WALKER, E.M., 1953. *The Odonata of Canada and Alaska, Vol. I*. Univ. Toronto Press, Toronto.
- WILLIAMSON, E.B., 1902. Additions to the Indiana list of dragonflies with a few notes. No. II. *Proc. Indiana Acad. Sci.* 1901: 119-127.
- WILLIAMSON, E.B., 1906. Copulation of Odonata. I. *Ent. News* 17: 143-148.