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# Life History Patterns of *Gambusia marshi* (Poeciliidae) from Cuatro Ciénegas, Mexico

GARY K. MEFFE

**The life history and ecology of *Gambusia marshi*, a poeciliid fish endemic to the Cuatro Ciénegas basin and Rio Salado drainage of Coahuila, Mexico, is virtually unknown. Fishes collected in different seasons from natural lakes, rivers and an artificial canal were analyzed for reproductive patterns, food choice and parasitism. *G. marshi* reproduced seasonally, with fecundity increasing as a function of female size. Reproduction is not strongly habitat dependent, although reduced reproductive activity was noted in the canal. Superfetation was infrequent. Major food items of *G. marshi* were detritus and insects, with other invertebrates, plant material and juvenile fish also represented. Somatic condition was little affected by habitat or season and most individuals were robust. Parasites included two nematodes, a trematode and an acanthocephalan. *G. marshi* is a habitat and food generalist, which perhaps accounts for its local abundance and success within its limited range.**

THE Cuatro Ciénegas region, an intermontane basin west of Monclova, Coahuila, Mexico, is well known for its high degree of biological endemism (Taylor and Minckley, 1966; Marsh, 1984). Aquatic endemics include species of crustaceans, molluscs, fishes and turtles (Minckley, 1969). Despite intense interest in this biota, particularly in the fishes (reviewed by Minckley, 1984), few comprehensive studies have been conducted on basic ecology and life histories of its component species. With growing awareness of the scientific value of this area, potentials for human-induced changes and resultant conservation concerns (Contreras-Balderas, 1984), it is appropriate to assemble life history information regarding Cuatro Ciénegas fishes.

*Gambusia marshi* Minckley and Craddock (Poeciliidae) is native to the Cuatro Ciénegas basin and the Rio Salado drainage of Coahuila. Occurring in two color morphs, a light, spotted phase and a striped, melanistic phase (Minckley, 1962), it is "... perhaps the most abundant fish in the Cuatro Ciénegas basin ..." (Minckley, 1969). Despite its abundance and general representation in collections, little has been published on *G. marshi* since its description more than 20 years ago (Minckley, 1962). Included are reports on laboratory hybridization with *G. affinis* (Minckley, 1964), laboratory study of mate choice by males (Arnold, 1966), a discussion of distribution and occurrence within the Cuatro Ciénegas basin (Minckley, 1969, 1984), chromosome morphology (Campos and Hubbs, 1971) and details of male and female genital morphologies (Peden, 1972a, b).

I investigated reproductive parameters, food utilization and parasite occurrence in spotted phase *G. marshi* over four seasons from three major habitats of Cuatro Ciénegas: shallow lakes (lagunas), rivers and an artificial canal. Seasonal and spatial (habitat) variation in life history of *G. marshi* was thus obtained for a gross analysis of its ecology.

## Materials and Methods

*Specimens used.*—All analyses were conducted on preserved specimens housed in the Arizona State University (ASU) Museum, collected by various personnel from 1964–1970, but mostly 1964–1965. Because collections were not made specifically for comprehensive life history studies, I selected habitats best represented and for which the largest number of specimens was available. Consequently, two habitat categories included collections from several different localities, while the seasonal analysis included collections from several years. Seasonal designations are: winter = Dec.–Jan.; spring = April; summer = June; autumn = Aug.–Sept.

The following collections were utilized (listed are localities as in Minckley [1969], ASU museum number and collection date): Lagunas—San Pablo Laguna, 625, 24 Jan. 1964; Laguna Grande, 1746, 15 Apr. 1965; Ferriños Laguna, 955, 9 June 1964; Laguna Grande, 5967, 2 Sept. 1970. Rivers—Rio Salado, 2852, 21 Dec. 1966; 1725, 13 April 1965; Puente Colorado, 967, 10 June 1964; 5989, 4 Sept. 1970. Canals—La Angostura, 620, 23 Jan. 1964; 1731, 13 April 1965; 934, 7 June 1964; 2260, 13 Aug. 1965.

*Length-frequency analysis.*—All specimens from each collection were sexed and placed in 1 mm (standard length, SL) size categories. One to three mature females were randomly selected from each category for further analysis, so that a total of 20–30 females representing the size range of maturity were selected (three small collections allowed analysis of only 18, 18 and 11 individuals). These fish were used in all subsequent procedures. Most collections were made by 3.2 mm mesh seines, but some were by 6.3 mm mesh and mesh sizes may have influenced size distributions in collections.

*Reproductive and somatic analysis.*—Females were measured to the nearest 0.1 mm SL with a dial caliper. Ovaries were removed and contents counted under a dissecting microscope (7×). Eggs and embryos were placed into one of six categories, primarily for detection of superfetation: 1) immature ova—ova in the process of yolking, but sub-mature in size; 2) mature ova/fertilized egg—full-sized ova, unfertilized or recently fertilized; 3) primitive streak—primitive streak present, but eyes not yet distinguishable; 4) early eyed—eyes present, but not full sized; little dorsal pigmentation; 5) middle eyed—eyes full sized; moderate to extensive dorsal pigmentation; and 6) late eyed—little yolk remaining; near parturition.

Categories 2–6 were summed to obtain total number of eggs and embryos carried, or "total reproduction" (TR). Category 1 was considered preparatory to actual reproduction since it included immature members. Subsequent to counting, ovaries and their contents were placed into individual tared aluminum pans, dried to constant weight at 85–90 C for 24–28 hr and weighed to the nearest 0.1 mg on a Mettler analytical balance. The remainder of the fish, minus the digestive tract (below), was similarly treated and weighed. I thus obtained reproductive and somatic dry weights (RDW and SDW), respectively. Since all fish were preserved in 10% formalin and stored in 35% isopropanol, potential effects of preservation on length or weight should be equivalent among groups.

A somatic condition factor was calculated for

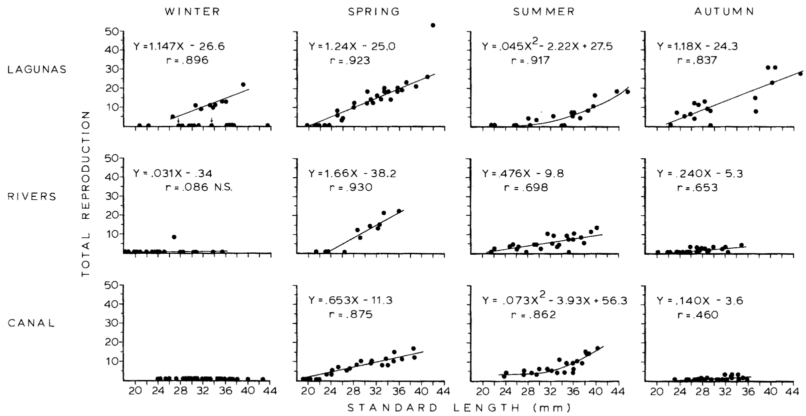


Fig. 1. Regressions of total reproduction on standard length for *Gambusia marshi* by habitat and season. The winter laguna regression included only reproductively active fish. The spring laguna regression does not include the extreme value at 41 mm SL, considered an outlier. A regression was not conducted for the winter canal sample, since all observations were zero and thus collinear. N.S. indicates statistically non-significant product-moment correlation coefficients; the remainder are significant at $P < .05$ or better. Small arrows indicate two identical observations.

each fish as SCF = (SDW/SL) × 100 and reproductive effort was calculated as RE = (RDW/SDW + RDW) × 100, or the percentage of total weight invested in reproduction. The relationship between dependent variables TR, SCF, or RE and the independent variable SL was investigated using a regression analysis program (BMDP5R, Dixon et al., 1981) on the ASU IBM system. A linear model was used as a descriptor of the relationship between the dependent variable and SL. In four cases a second order polynomial was used instead since it improved the correlation coefficient by at least 10%. These models are included simply as aids in visualizing relationships between variables.

*Food habits.*—The entire length of the digestive tract was removed (above) and opened lengthwise and contents were examined under a dissecting microscope (7–21×). Contents were broadly classified as detritus, invertebrates, vascular plant material, turbellarian flatworms (planarian-like), or fishes. Detritus consisted of a variety of organic and inorganic materials including mud and debris, but was frequently invested with diatoms and unicellular or filamentous algae, as revealed under higher power (40–100×). Invertebrates consisted primarily of insects, but also included spiders, ostracods and small unidentified crustaceans. Vascular plants included small seeds and broken stems. Food contents were quantified by visually estimating, at 5% intervals, the percentage of gut filled by each category.

*Parasites.*—Gut and coelom parasites were collected as encountered. No systematic search was made for parasites.

## RESULTS

*Length-frequency analysis.*—Male *G. marshi* generally matured between 18 and 20 mm SL, with the smallest mature male 17.6 mm and the largest in the 31 mm size class. Females matured at 20–22 mm and ranged upward to 47 mm SL. Fish from rivers were generally smaller than those from canals or lagunas, but no consistent seasonal size trends were noted.

*Reproductive and somatic analyses.*—Numbers of ova/embryos carried by *G. marshi* were positively related to female size (Fig. 1). The smallest individual carrying an embryo was 22.0 mm SL, but fish typically began to yolk ova in the 20–22 mm range. Reproduction was strongly seasonal, with little activity in winter and autumn and peaks in spring and summer. An exception was females from lagunas, which were reproductively active in all seasons although less so in autumn and winter (Fig. 1). All embryos in the winter (Jan.) laguna sample were in stage 2, indicating reproduction for that year was just commencing.

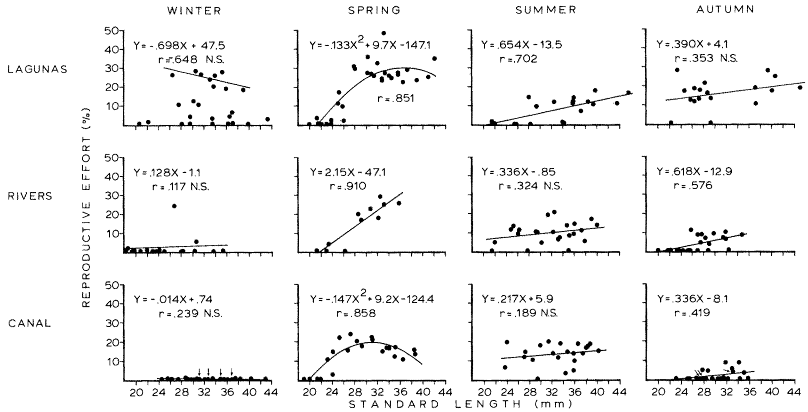


Fig. 2. Regression of reproductive effort on standard length for *Gambusia marshi* by habitat and season. Protocol as in Fig. 1.

Superfetation, for purposes here, is defined as carrying ova/embryos in two or more nonconsecutive stages of development. Consecutive stages (i.e., #2 and #3) were not considered instances of superfetation since they may represent slow development by some embryos, or an error in classification by the observer. With this definition only 6 of 251 (2.4%) mature females superfetated; it was observed once in the canal (spring, stages 1 and 6), four times in lagunas (summer, stages 1, 2 and 6; autumn, stages 2 and 4, 2 and 5, and 1 and 5) and once in rivers (spring, stages 1, 2 and 6). Superfetation is thus rare in *G. marshi.*

Reproductive effort as a function of SL is plotted in Fig. 2. The relation between RE and SL, although inconsistent, is usually positive. A low reproductive investment occurred in autumn and winter in all habitats except lagunas, where the reproductive season was extended. Generally low coefficients of determination ($r^2$) indicate that SL is a poor predictor of RE, or conversely that RE is somewhat independent of length.

Somatic condition factor as a function of SL is plotted in Fig. 3. SCF's were consistent among seasons and habitats, indicating that somatic condition was little influenced by spatial or temporal change.

*Food habits.*—*G. marshi* is primarily a detritivore/insectivore (Fig. 4). The dominant item

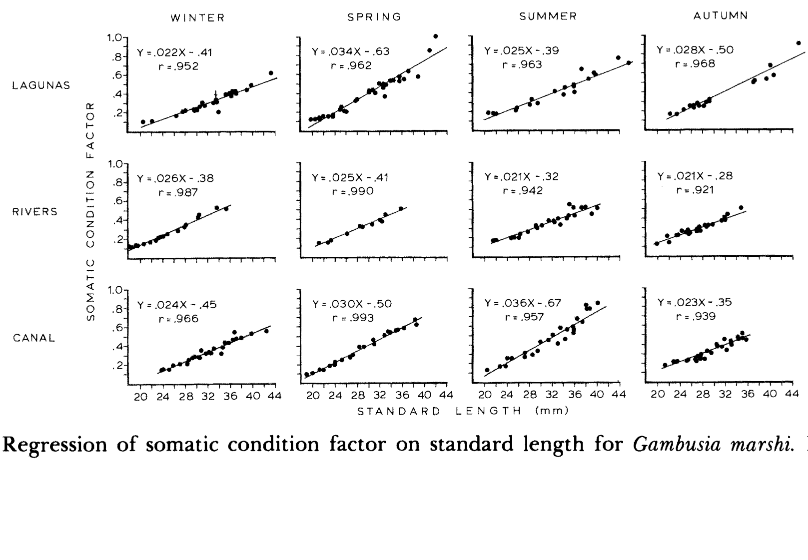


Fig. 3. Regression of somatic condition factor on standard length for *Gambusia marshi.* Protocol as in Fig. 1.

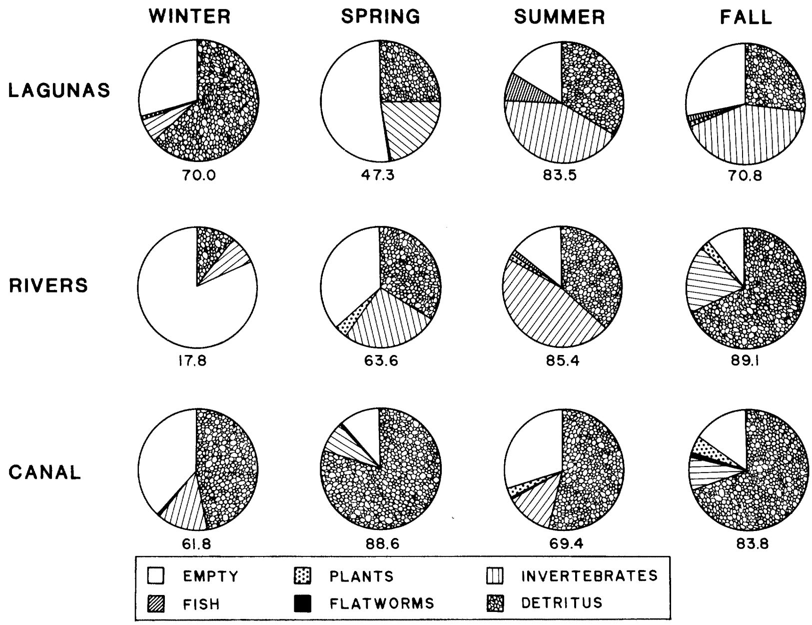


Fig. 4. Pie diagrams showing average proportion of alimentary tracts filled with each food item. Numbers under diagrams are average percentage fullness of tracts.

in 9 of 12 populations was detritus, with invertebrates occasionally a major food item in summer or autumn. Other categories were sparsely and intermittently represented.

The amount of each food item as a percentage of total food in guts is a better indicator of actual food choice by *G. marshi* (Table 1) since it ignores empty portions of the digestive tract. Detritus constituted 37 to 90% of the diet, while invertebrates made up 9 to nearly 60%. No seasonal trends were obvious other than an increase in utilization of invertebrates through the year in lagunas. Overall food choice was remarkably similar in lagunas and rivers, two natural habitats, while detritus was more important in the artificial canal (Table 1). Invertebrate prey were identified whenever possible and at least 12 taxa were utilized: Platyhelminthes (Planariidae), Arthropoda (Arachnida, Ostracoda, unidentified crustaceans), Insecta (Ephemeroptera, Odonata, Megaloptera, Hemiptera [Corixidae, Naucoridae], Coleoptera, Diptera, Hymenoptera [red ants]).

Fishes as prey items were detected only from lagunas and rivers and in quantifiable amounts only in summer and autumn (Fig. 4). Based on scale structure and pigmentation patterns, fish eaten were almost certainly juvenile *G. marshi.* Although the species is thus cannibalistic the behavior appears to be rare.

*Parasites.*—Four parasite species were collected from *G. marshi*: an intestinal trematode, a small (5–10 mm) intestinal nematode, a large (20–100 mm) encysted coelomic nematode (possibly *Contracaecum* sp.), all unidentified and an acanthocephalan of the genus *Paulisentis* (Hoffman, 1967). Incidences of parasitism by season and habitat (Table 2) indicate more heavily infected fish in lagunas and lowest incidence of parasitism in the canal. The small nematode, when present, often numbered several to 20 individuals per fish; other parasites generally occurred singly. The only other report of *G. marshi* parasites is by Guajardo-Martínez (1984) who found ". . . encysted and intestinal nematodes . . . ."

## Discussion

*G. marshi* is an abundant fish in the Cuatro Ciénegas basin and adjacent drainages (Minckley, 1962, 1969, 1984). It tolerates a wide range of environmental conditions and adapts to a variety of situations, with relatively little effect on life history parameters. The fish is by all measures a generalist, feeding on a variety of items

TABLE 1. PERCENTAGE OF *Gambusia marshi* DIET CONSISTING OF EACH FOOD CATEGORY, LISTED BY HABITAT AND SEASON.

| Habitat | Season | Detritus | Invertebrates | Flatworms | Plants | Fish |
|---|---|---|---|---|---|---|
| Laguna | Winter | 90.3 | 8.9 | 0 | 0.8 | tr |
| | Spring | 52.4 | 46.9 | 0.7 | 0 | 0 |
| | Summer | 40.1 | 50.3 | 0 | 0 | 9.6 |
| | Autumn | 37.7 | 59.1 | 0 | 1.6 | 1.6 |
| | Mean | 55.1 | 41.3 | 0.2 | 0.6 | 2.8 |
| River | Winter | 57.9 | 42.1 | 0 | 0 | 0 |
| | Spring | 52.8 | 41.5 | 0 | 5.7 | 0 |
| | Summer | 42.8 | 54.2 | 0 | 1.5 | 1.5 |
| | Autumn | 76.3 | 21.0 | 0 | 2.7 | 0 |
| | Mean | 57.4 | 39.7 | 0 | 2.5 | 0.4 |
| Canal | Winter | 76.6 | 22.3 | 1.1 | 0 | 0 |
| | Spring | 90.5 | 9.3 | 0.2 | 0 | 0 |
| | Summer | 77.5 | 18.7 | 0.3 | 3.5 | 0 |
| | Autumn | 83.1 | 10.6 | 1.3 | 5.0 | 0 |
| | Mean | 81.9 | 15.3 | 0.7 | 2.1 | 0 |
| | Grand mean | 64.8 | 32.1 | 0.3 | 1.7 | 1.1 |

and existing in all major habitats of Cuatro Ciénegas, from natural streams, marshes and lakes to artificial canals.

Fish from three habitats exhibited similar patterns with respect to reproductive activities, but with slightly different lengths of reproductive season. Reproduction in lagunas began in Jan., when about one-third of the females contained yolked ova or early embryos (Fig. 1). Reproduction was at a peak through autumn (Sept.) and presumably declined thereafter. The reproductive season in lagunas apparently spans 9+ months.

Fish in rivers were reproductively inactive in Dec. except for one individual beginning to yolk ova and another with early embryos. Most fish were reproducing in spring and summer (Fig. 1), while only half remained active in Sept. River fish also appear to be reproductively active from Jan.–Sept. but with smaller broods at the beginning and end of the season.

Fish in the canal were all inactive near the end of Jan., while full reproductive activity occurred through spring and summer (Fig. 1). By mid-Aug. reproduction was on the decline, with about two-thirds of the fish no longer carrying offspring. Reproductive season in the canal was shorter than elsewhere, probably lasting from Feb. or March until Aug.

Overall, fish were reproductively active longest and carried the largest broods in lagunas, while both parameters were depressed in the

TABLE 2. PARASITES COLLECTED FROM *Gambusia marshi* AT CUATRO CIÉNEGAS. Total number of fishes examined is in parentheses, below which is number of individuals infected by trematode, small nematode, large nematode and acanthocephalan parasites, respectively.

| | Season | | | |
|---|---|---|---|---|
| | Winter | Spring | Summer | Autumn |
| Lagunas | (25) | (32) | (20) | (18) |
| | 8, 0, 0, 0 | 1, 0, 0, 0 | 4, 13, 0, 0 | 0, 0, 0, 1 |
| Rivers | (18) | (11) | (24) | (23) |
| | 0, 0, 1, 0 | 0, 0, 0, 0 | 0, 9, 0, 0 | 1, 0, 0, 0 |
| Canal | (26) | (25) | (25) | (27) |
| | 0, 0, 0, 0 | 0, 0, 0, 0 | 0, 0, 0, 0 | 1, 0, 3, 0 |

canal. This is curious since fish in canals had the highest average slope for SCF (.0283 vs .0274 and .0233 for lagunas and rivers, respectively) and thus were not in poor somatic condition. Reproduction in *G. marshi* is probably not primarily limited by energetic contraints, but is rather a function of local environmental conditions.

SCF's were remarkably consistent among seasons and habitats (Fig. 3). Other than minor mean differences just mentioned (not statistically significant) there was no clear evidence of seasonal or habitat effects on robustness and most fish examined appeared to be in good condition. There was, however, an unmeasured seasonal effect on amount of fat present. Visceral fat was generally absent or at low levels in reproductively active females (spring and summer) and was prevalent along the alimentary tracts in autumn and winter. Storage apparently begins when reproduction declines making high-energy fats available for the next reproductive season.

Patterns of RE were erratic, but generally paralleled total reproduction. In most cases, RE increased with SL, although this was not always significant (Fig. 2). RE was generally less dependent upon SL than was total reproduction, indicating that energetic commitments to reproduction in *G. marshi* may be flexible.

Life history patterns of *G. marshi* are typical of gambusiines in general (Krumholz, 1948, 1963; Hubbs and Springer, 1957; Hubbs, 1971; Peden, 1973). Most examined to date reproduce seasonally, are generalists in food choice and exhibit increased fecundity with increased female size. *Gambusia marshi* is more of a habitat generalist than species such as *G. amistadensis* (Peden, 1973), *G. gaigei* (Hubbs and Brodrick, 1963), *G. geiseri* (Hubbs and Springer, 1957), *G. georgei* (Hubbs and Peden, 1969), *G. heterochir* (Hubbs, 1957), *G. krumholzi* (Minckley, 1963) or *G. longispinis* (Minckley, 1962), which are restricted to limited habitats or are otherwise rare in Coahuila or adjacent southern Texas, but probably is not as generalized as the cosmopolitan *G. affinis.* The apparently flexible nature of *G. marshi* is likely responsible for its abundance within its limited geographic range.

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W. L. Minckley's pioneering studies of the Cuatro Ciénegas fauna made this analysis possible. I thank him for introducing me to this amazing region, for allowing me to exploit hard-earned specimens collected by himself, his colleagues and students and for critically reviewing the manuscript. The paper was improved by the comments of Clark Hubbs and an anonymous reviewer. Financial support during analysis of fishes was provided by the Department of Zoology, ASU; manuscript preparation was aided by a postdoctoral appointment at the University of Florida. I thank Grace Kiltie for typing the manuscript and B. DeMarias for assistance in data analysis.

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# An Experimental Demonstration of the Species-Recognition Role of *Anolis* Dewlap Color

JONATHAN B. LOSOS

**Inter- and intraspecific encounters were staged in the laboratory between adult males of the sympatric sibling species *Anolis marcanoi* and *A. cybotes* which differ morphologically only in dewlap color. Levels of intraspecific aggression among *A. marcanoi* were high, but little interspecific aggressive behavior was observed. The importance of dewlap color for species-recognition was assessed by changing the color of the dewlap of *A. marcanoi* to appear like that of *A. cybotes* and vice-versa. *A. marcanoi* in interspecific encounters between altered individuals exhibited an intermediate level of aggressive behavior. Intraspecific encounters between pairs of *A. marcanoi* with altered dewlaps revealed no higher level of aggression than the normal interspecific encounters. A system of species-recognition signals is proposed in which lizards examine more obvious signals, such as dewlap color, at greater distances and more subtle signals, such as head-bobbing patterns, at closer distances.**

THE sibling species *Anolis marcanoi* and *A. cybotes* are trunk-ground ecomorphs (Williams, 1972) found sympatrically throughout much of *A. marcanoi*'s limited range in southwestern Dominican Republic. They are consistently separable morphologically only by the color of the dewlap of males and the throat of females: red in *A. marcanoi,* yellow or white in *A. cybotes* (Williams, 1975). Electrophoretic studies, however, show them to be quite distinct and reveal no hybrids (Webster, 1975). How the species coexist is a puzzle. In some areas, they are found on adjacent fenceposts (Hertz, 1980), whereas in other localities only one species is present. Although Hertz (1980) suggests that *A. marcanoi* may be adapted to hotter, more open microhabitats, field observations have failed to discover any obvious difference (Williams, 1975; Hertz, 1980; pers. obs.). The existence of two such closely related species in sympatry raises two questions amenable to laboratory investigation: does interspecific territorial behavior occur and, if not, how do males distinguish conspecifics from non-conspecifics?