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Biting in the Salamander *Siren intermedia intermedia*: Courtship Component or Agonistic Behavior?

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In salamanders, biting serves three potential purposes: subduing prey (e.g., Reilly and Lauder, 1990), repelling competitors and predators (e.g., Jaeger, 1981; Brodie et al., 1989), and stimulating the opposite sex during courtship (Arnold, 1977). In *Siren intermedia*, nonpredatory biting was first reported by Gehlbach and Walker (1970), who observed it while recording underwater vocalizations. Bitten individuals often fled while emitting yelps that could be submissive or alarm calls, suggesting that biting was an agonistic behavior. Later, Godley (1983) demonstrated with convincing photographs and illustrations that distinctive epidermal marks on six female sirens matched the cornified beaks and vomerine teeth of conspecifics. No bite scars were observed on females outside the breeding season, nor on any males in the 489 specimens necropsied, leading him to suggest that "biting is a vigorous and important component of courtship in this species." Additional indirect evidence supporting this view was the sexual dimorphism characteristic of some populations of *S. intermedia* and *S. lacertina* (Davis and Knapp, 1953; Martof, 1973; Gehlbach and Kennedy, 1978; Hanlin and Mount, 1978), particularly the enlarged masseter muscles of males, which could be important in social or reproductive behavior. However, neither this morphological evidence nor the small number of females with bite scars (<1.5% of the sample) conclusively demonstrate that biting is related or restricted to courtship. Here, we present data from field sampling and a field experiment that bear on this question.

We sampled 105 *S. intermedia intermedia* from two Carolina bays in Scotland and Richmond Counties, North Carolina, USA from May 1987 through November 1989. The sites are described elsewhere (Harris et al., 1988; Resetarits and Fauth, 1998). Sirens were captured on 14 dates using dipnets and minnow traps, then transported to the laboratory, where they were anesthetized in 2% chloretone solution, checked for bite scars, and measured (snout–vent length [SVL] and total length [TL]) before being returned to their natal pond. We were unable to sex individuals because this population lacked sexually dimorphic external characters. We used a Welch ANOVA in JMP version 3.2.2 (SAS Institute, Inc., 1998) to test for differences

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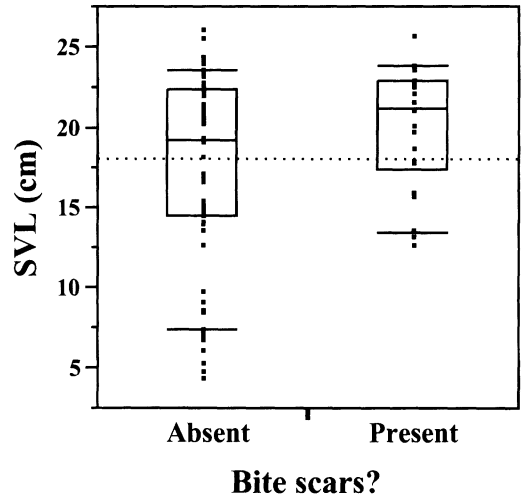

FIG. 1. Quantile box plots of the snout-vent length (cm) of 105 field-caught *Siren intermedia intermedia* from Scotland and Richmond Counties, North Carolina, USA, as a function of the presence or absence of bite scars. These epidermal injuries were inflicted by the keratinized beak and/or vomerine dental array of conspecifics. Lower and upper ends of the quantile boxes are 25th and 75th percentiles, respectively; the solid horizontal bar within each box is the median. The upper and lower hash marks denote the 10th and 90th percentiles, respectively. The dotted horizontal line indicates the overall sample mean. Solid squares are individual data points.

in the mean SVL of individuals with and without bite scars, and a G-test of independence (Sokal and Rohlf, 1995) to determine if bite scars were equally prevalent during and after the November–March breeding season (Collette and Gehlbach, 1961; Petranka, 1998; J. E. Fauth and W. J. Resetarits, Jr., pers. obs.) in this field sample.

Scarred individuals were significantly larger than those without bite marks, even after adjusting for unequal variances (Welch $F_{1,51.3} = 6.04$, $P < 0.018$; Fig. 1). No sirens smaller than 128 mm SVL had bite scars. Frequency of bite scars varied with season ($G^2 = 9.561$, $P < 0.002$; Table 1). Individuals with bite scars were more prevalent than expected during the breeding season (cell $\chi^2 = 4.20$), but sirens also had fresh bite scars during the nonbreeding season.

We also observed bite scars in an experiment investigating competition between juvenile *S. intermedia intermedia* and adult broken-striped newts, *Notophthalmus viridescens dorsalis* (Resetarits and Fauth, unpubl. data). The subset of experimental treatments relevant to the issue of biting by sirens involved raising two juvenile *S. i. intermedia* either alone, or with three male *N. v. dorsalis*. Densities of both *S. i. intermedia* (1.12 yearlings/m²) and *N. v. dorsalis* (1.6 adults/m²) were within the range of densities observed in natural populations (Gehlbach and Kennedy, 1978; Sugg et al., 1988; Harris et al., 1988). We used only male *N. v. dorsalis* to prevent newts from reproducing. Sirens could not be sexed based on external characters, so the distribution of males and females among ponds resulted

TABLE 1.   Frequency of bite scars in 105 *Siren intermedia intermedia* sampled from two Carolina bays in Scotland and Richmond Counties, North Carolina, USA, as a function of season. Entries are total number of individuals observed with and without scars during the breeding (November–March) or nonbreeding (April–October) season, plus expected values. The frequency of bite scars varied significantly with season ($G^2 = 9.561$, $P < 0.002$).

Season	Condition	# individuals observed	# individuals expected
breeding	no scars	30	36.4
breeding	scars	16	9.6
nonbreeding	no scars	53	46.6
nonbreeding	scars	6	12.4

from randomly assigning field-collected individuals to the experimental units.

We conducted the experiment in an array of twelve artificial ponds (1.5 m diameter, 0.5 m deep) at the Duke Zoology Field Station, Durham, North Carolina from April–October 1986. Our method of reconstructing pond communities closely followed that of Morin (1983). Briefly, tanks were filled with 1000 L of water, and 1.0 kg of dried pond litter was added to provide spatial complexity and nutrients. Two 1 L inoculations of a pond water suspension on 28 and 29 April added phytoplankton, periphyton and microorganisms. Fifty grams of rabbit food were added to provide a burst of nutrients, and ten stems of an aquatic macrophyte (*Myriophyllum* sp.) provided additional structure and realism. Six amplexed pairs of asellid isopods, 17 planorbid snails, and 100 hatchlings of Cope's gray treefrog (*Hyla chrysoscelis*) also were added to each pond to diversify the prey community. Tightly fitting lids of fiberglass window screening prevented colonization by insects and ovipositing treefrogs, and retained experimental organisms.

We collected *S. i. intermedia* and *N. v dorsalis* for the experiment by dipnetting ponds in Scotland County, North Carolina during late April, 1986. Individuals were weighed, measured (SVL for *N. v dorsalis* and TL for *S. i. intermedia*), examined for bite scars, and housed in separate containers before being assigned randomly to the appropriate treatments. No sirens had bite scars before being released into the experimental ponds on May 6. Yearling *S. i. intermedia* ranged from 101–116 mm TL (105 ± 4.9 mm TL, $\bar{X} \pm 1$ SD) and from 1.65–2.51 g (1.90 ± 0.26 g). In *S. i. intermedia*, sexual maturity is reached in two years, when females average 150 mm and males 180 mm SVL (about 220 and 270 mm TL, respectively: Cagle and Smith, 1939; Davis and Knapp, 1953; Martof, 1973). Adult *N. v dorsalis* ranged from 31–43 mm SVL (37 ± 3.20 mm SVL) and from 0.99–2.13 g mass (1.52 ± 0.37 g). Ponds were drained after 178 d (on 30–31 October 1986), and the surviving *N. v dorsalis* and *S. i. intermedia* were anesthetized, weighed, and measured before preservation in 10% formalin. Preserved *S. i. intermedia* were examined for bite scars, then dissected to determine gender and reproductive condition. We used a log likelihood ratio test (SAS Institute,

Inc., 1998) to determine whether scarred individuals were distributed independently of sex and experimental treatment.

All 16 of the experimental *S. i. intermedia* survived until the end of the experiment, and dissection revealed that seven were male and nine were female. Most of the females fully matured during the experiment; eight had at least some mature follicles, while one had only vitellogenic follicles. Seven of the 16 individuals (44%) bore distinctive scars inflicted by conspecifics on the trunk and tail. Bite scars were independent of the presence and absence of *N. v dorsalis* ($G^2 = 2.075$, $P > 0.10$). The smallest individual with bite scars in the experiment was 128 mm SVL, the same lower size limit as in the natural population. More male (4 of 7:57%) than female (3 of 9:33%) sirens had bite scars, but the difference was not statistically significant ($G^2 = 0.907$, $P > 0.34$). However, every experimental pond that contained at least one male siren yielded at least one individual with scars, while the three ponds containing only female sirens had no individuals with scars. The exact probability of this outcome is $(3/8)^3 = 0.053$. Thus, the presence of males may have been necessary to elicit biting, and six of the seven (86%) sirens that inflicted the bites were males.

Sirens in natural ponds displayed bite marks throughout the year, and data from our experiment demonstrated that both male and female sirens receive bites from conspecifics outside the breeding season, indicating that biting is not solely associated with courtship. In videotaped laboratory encounters (A. J. Pappas and J. E. Fauth, unpubl. data), we observed more than 30 biting incidents without any indication of courtship behavior. The bitten individual usually fled, often emitting high-pitched yelps as reported by Gehlbach and Walker (1970). We suggest that, as in many other salamanders (reviewed by Jaeger and Forester, 1993; Mathis et al. 1995), biting is a form of aggressive behavior. It is unlikely that bite scars indicate failed predation attempts, as paired individuals were very similar in body size and cannibalism (except for predation on eggs) has not been reported in sirens.

The available data on biting in sirens suggests four testable hypotheses, which are not mutually exclusive. (1) Biting is an agonistic behavior that is infrequent until sirens near maturity. Our data are consistent with this hypothesis. We found no bite scars on larval *S. i. intermedia* in a previous experiment (Fauth et al., 1990), and the scars on our experimental sirens, which were just reaching sexual maturity, were not as numerous or severe as those depicted in Godley (1983). The smallest individual with bite scars in the experiment had the same SVL as the smallest siren with epidermal injuries in the natural ponds, further evidence of a size threshold. Similar results have been found in the semiaquatic plethodontid *Desmognathus quadramaculatus*; larger salamanders were more aggressive and had more bite scars than smaller individuals (Camp, 1996). (2) Biting and other agonistic behavior increases during the breeding season. Because sirens are most active during this period (Gehlbach and Kennedy, 1978), increased biting may reflect reproductive behavior (Godley, 1983) or be an artifact of increased activity. Our data also support this inference. The bite marks on our experimental sirens were

fresh, indicating recent infliction, and field sampling showed that bite scars were more common during the cooler months when sirens were apparently more active (as indicated by capture frequency in traps). (3) Female sirens are bitten while coiled around their nest, guarding eggs from oophagous conspecifics. Our data do not address this point, but this hypothesis could explain Godley's (1983) report of heavy scarring on female sirens. Of the six females with bites he described, two were collected while attending nests, three were spent females and the other was an ovulating female. Adults of *S. intermedia* commonly feed on the eggs of conspecifics (Scroggin and Davis, 1956; Collette and Gehlbach, 1961), and exposed nests (Godley, 1983) could leave brooding females vulnerable to bites. (4) Male sirens are more aggressive than female sirens. This is consistent with our finding that most bites in the experimental ponds were inflicted by males. It is also consistent with Godley's (1983) suggestion that larger body size and masseter muscles in male sirens may be advantageous in territorial defense or competition for females. In terrestrial species of plethodontid salamanders, males often are more aggressive than females (Ovaska, 1987; Staub, 1993; Wiltenmuth, 1996) although studies on the semi-aquatic desmognathines found no sexual variation in aggressiveness (Keen and Sharp, 1984; Camp, 1996).

Sirens are enigmatic and poorly understood salamanders (e.g., Dunn, 1924; Scroggin and Davis, 1956; Altig, 1967) that play an important role in many temporary pond communities (Fauth and Resetarits, 1991; Resetarits and Fauth, 1998; Snodgrass et al., 1999; Fauth, 1999). Their unique life history and complex ecology deserve greater attention from herpetologists. For example, their mating system remains undescribed, but likely includes complex courtship behavior, external fertilization, and parental care (Ultsch, 1973; Godley 1983; Sever, 1994 and references therein). Our data indicate that biting cannot be restricted solely to courtship in *Siren intermedia intermedia*. Biting appears to be a male-biased agonistic behavior observed in male-female and male-male encounters, both during and outside the breeding season.

LITERATURE CITED

ALTIG, R. 1967. Food of *Siren intermedia nettingi* in a spring-fed swamp in southern Illinois. Amer Midl. Natur. 77:239–241.

ARNOLD, S. J. 1977. The evolution of courtship behavior in New World salamanders with some comments on Old World salamandrids. *In* D. H. Taylor and S. I. Guttman (eds.), The Reproductive Biology of Amphibians, pp. 141–183. Plenum Press, New York.

BRODIE, E. D., JR., T. G. DOWDEY, AND C. D. ANTHONY. 1989. Salamander antipredator strategies against snake attack: biting by *Desmognathus*. Herpetologica 45:167–171.

CAGLE, F. R., AND P. E. SMITH. 1939. A winter aggregation of *Siren intermedia* and *Triturus viridescens*. Copeia 1939:232–233.

CAMP, C. D. 1996. Bite scar patterns in the black-bellied salamander, *Desmognathus quadramaculatus*. J. Herpetol. 30:534–546.

COLLETTE, B. B., AND F. R GEHLBACH. 1961. The salamander *Siren intermedia intermedia* LeConte in North Carolina. Herpetologica 17:203–204.

DAVIS, W. B., AND F. T. KNAPP. 1953. Notes on the salamander *Siren intermedia*. Copeia 1953:119–121.

DUNN, E. R. 1924. *Siren*, an herbivorous salamander? Science (NS) 51:145.

FAUTH, J. E. 1999. Interactions between branchiate mole salamanders (*Ambystoma talpoideum*) and lesser sirens (*Siren intermedia*): asymmetrical competition and intraguild predation. Amphibia-Reptilia. *In press.*

———, AND W. J. RESETARITS, JR. 1991. Interactions between the salamander *Siren intermedia* and the keystone predator *Notophthalmus viridescens*. Ecology 72:827–838.

———, W. J. RESETARITS, JR., AND H. M. WILBUR. 1990. Interactions between larval salamanders: a case of competitive equality. Oikos 58:91–99.

GEHLBACH, F. R., AND S. E. KENNEDY. 1978. Population ecology of a highly productive aquatic salamander, *Siren intermedia*. Southwest. Natur 23:423–430.

———, AND B. WALKER. 1970. Acoustic behavior of the aquatic salamander, *Siren intermedia*. Bioscience 20:1107–1108.

GODLEY, J. S. 1983. Observations on the courtship, nests and young of *Siren intermedia* in southern Florida. Amer. Midl. Natur. 110:215–219.

HANLIN, H. G., AND R. H. MOUNT. 1978. Reproduction and activity of the greater siren, *Siren lacertina* (Amphibia: Sirenidae), in Alabama. J. Alabama Acad. Sci. 49:31–39.

HARRIS, R. N., R. A. ALFORD, AND H. M. WILBUR. 1988. Density and phenology of *Notophthalmus viridescens dorsalis* in a natural pond. Herpetologica 44:234–242.

JAEGER, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. Amer. Natur. 117:962–974.

———, AND D. C. FORESTER. 1993. Social behavior of plethodontid salamanders. Herpetologica 49:163–175.

KEEN, W. H., AND S. SHARP. 1984. Responses of a plethodontid salamander to conspecific and congeneric intruders. Anim. Behav. 32:58–65.

MARTOF, B. S. 1973. *Siren intermedia*. Cat. Amer. Amphib. Rept.: 127.1–127.3.

MATHIS, A., R. G. JAEGER, W. H. KEEN, P. K. DUCEY, S. W. WALLS, AND B. W. BUCHANAN. 1995. Aggression and territoriality by salamanders and a com-

parison with the territorial behavior of frogs. *In* H. W. Heatwole and B. K. Sullivan (eds.), Amphibian Biology, Vol. 2, pp. 633–676. Surrey Beatty and Sons, New South Wales, Australia.

MORIN, P. J. 1983. Predation, competition, and the structure of larval anuran guilds. Ecol. Monogr. 53: 119–138.

OVASKA, K. 1987. Seasonal changes in agonistic behavior of the western red-backed salamander, *Plethodon vehiculum*. Anim. Behav. 35:67–74.

PETRANKA, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington.

REILLY, S. M., AND G. V. LAUDER. 1990. The evolution of tetrapod feeding behavior: kinematic homologies in prey transport. Evolution 44:1542–1557.

RESETARITS, W. J., JR., AND J. E. FAUTH. 1998. From cattle tanks to Carolina bays: the utility of model systems for understanding natural communities. *In* W. J. Resetarits, Jr. and J. Bernardo (eds.), Experimental Ecology: Issues and Perspectives, pp. 133–151. Oxford Univ. Press, New York.

SAS INSTITUTE, INC. 1998. JMP Version 3 Statistics and Graphics Guide. SAS Institute, Inc., Cary, North Carolina.

SCROGGIN, J. B., AND W. B. DAVIS. 1956. Food habits of the Texas dwarf siren. Herpetologica 12:231–237.

SEVER, D. M. 1994. Observations on regionalization of secretory activity in the spermathecae of salamanders and comments on phylogeny of sperm storage in female amphibians. Herpetologica 50:383–397.

SNODGRASS, J. W., J. W. ACKERMAN, A. L. BRYAN, JR., AND J. BURGER. 1999. Influence of hydroperiod, isolation and the occurrence of heterospecifics on the distribution of aquatic salamanders (*Siren* and *Amphiuma*) among depression wetlands. Copeia 1999: 107–113.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. W. H. Freeman, New York.

STAUB, N. L. 1993. Intraspecific agonistic behavior of the salamander *Aneides flavipunctatus* (Amphibia: Plethodontidae) with comparisons to other plethodontid species. Herpetologica 49:271–282.

SUGG, D. W., A. A. KARLIN, C. R. PRESTON, AND D. R. HEATH. 1988. Morphological variation in a population of the salamander, *Siren intermedia nettingi*. J. Herpetol. 22:243–247.

ULTSCH, G. R. 1973. Observations on the life history of *Siren lacertina*. Herpetologica 29:304–305.

WILTENMUTH, E. B. 1996. Agonistic and sensory behaviour of the salamander *Ensatina eschscholtzii* during asymmetrical contests. Anim. Behav. 52: 841–850.

Winter Activity of Juvenile Desert Tortoises (*Gopherus agassizii*) in the Mojave Desert

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The desert tortoise, *Gopherus agassizii*, is a large, herbivorous turtle which inhabits parts of the Mojave and Sonoran deserts of the southwestern United States and the northwestern Sinaloa region of northwestern Mexico (Iverson, 1992). Populations west of the Colorado River currently are listed as Threatened under the U.S. Federal Endangered Species Act (U.S. Fish and Wildl. Serv., 1990). Juvenile desert tortoises, like juveniles of most chelonians, are often under-represented in biological studies because of their low survivorship and cryptic nature (Morafka, 1994). Based upon previous research, it appears that the behavior and physiology of hatchling and juvenile tortoises may differ from that of adults partly because of their small body size, increased mass specific metabolic rates, and high demands for protein and macronutrient-rich forage for growth (Naegle and Bradley, 1974; MacDonald and Mushinsky, 1988; Adest et al., 1989; Morafka, 1994). The ecological requirements of young and adult tortoises may, therefore, differ, and proper management of threatened populations of desert tortoises likely must encompass a thorough understanding of the ecological needs of all age classes (Tom, 1994).

Studies reporting daily and seasonal activity patterns of desert tortoises have focused on adults (e.g., Marlow, 1973; Burge, 1977; Rautenstrauch et al., 1998) and subadults (Nagy and Medica, 1986) largely because juveniles are cryptic and very difficult to locate and observe. Although studies have been done on survivorship, microhabitat utilization, activity, and thermal preferences of juveniles (Berry and Turner, 1986; Hillard, 1996; Spangenberg, 1996), data are limited to the period from when juveniles emerge from winter hibernation in early spring to when they reenter hibernation the following fall. Daily activity of juvenile desert tortoises during this time period has been shown to be unimodal in early spring, gradually changing to a bimodal pattern as midday temperatures increase in the late spring to summer (Hillard, 1996). Little knowledge exists on activity patterns of juvenile tortoises during the winter season, because they were assumed to retreat below ground. Here, we report on the activity of juvenile desert tortoises from 22 October 1996 to 18 February 1997 (Julian dates 295 to 49).

Our study was conducted at the Fort Irwin Study Site (FISS) located within the boundaries of the U.S. Army National Training Center, San Bernardino County, California (35°06'49"N, 116°29'27"W; 650 m elevation). Two large, fenced enclosures were con-