

SEXUAL COMBATS, MATINGS, AND REPRODUCTIVE PHENOLOGY IN AN ALPINE POPULATION OF THE SLOW WORM, *ANGUIS FRAGILIS*

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Abstract. The reproductive pattern and mating system of *Anguis fragilis* were studied in natural populations from a mountain territory of northeastern Italy (Sella Nevea, Tarvisio Forest, Carnic Alps). Mating occurs between April and May, while parturition takes place from mid-August to mid-September. In most cases, females reproduce in alternate years. Courtship and mating are usually stationary events which take place within bushes. The most spectacular characteristic of this mating system is the occurrence of sexual combat between males for access to females. Male body size is shown to be a crucial determinant of mating success, as body size of males defeated during sexual combats was always smaller than that of the winners. The fact that (1) large males win over small males during sexual combats, and (2) fighting time tends to increase when two similarly-sized males engage in a fight, suggest the existence of size-based male dominance in the studied populations.

Key Words. *Anguis fragilis*; Intrasexual competition; Male combats; Male hierarchy; Mating system; Carnic Alps; Northeastern Italy

Recently, Malkmus (1995) reported the occurrence of a possible aggressive display behavior by two male slow worms (*Anguis fragilis*), stating that his finding was the first one of male-male aggression in *A. fragilis*. He also reported that the interaction lasted at least 45 min, and that one male clenched its teeth on the side of the rival just in front of the cloaca. Malkmus (1995) concluded that it was still unknown whether the observed behavioral interaction was related to reproduction, foraging, or territoriality, and suggested that the first of these hypotheses was more likely than the others. Following Malkmus' contributions, Girolla (1996)

interpreted the interaction reported by Malkmus as a mating prelude (see also Fretey 1987, for additional observations on this issue). This controversy in the interpretation of behavioral displays of slow worms can be resolved only by considering the semi-fossorial and very elusive habits of this species, which, despite its enormous distribution across Europe, is considerably less known than other wide-ranging European lizards, such as *Lacerta agilis* (Olsson 1992a,b, 1993, 1994a,b,c; Olsson et al. 1994), *Lacerta vivipara* (Heulin 1988), or *Podarcis muralis* (Stewards 1965; Edsman 1986). The occurrence of combat between male *A. fragilis* seems to have simply escaped the attention of many field researchers and also of careful reviews (e.g., Dely 1981).

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During long-term field research on the behavioral ecology of some snake species in a mountain locality of the eastern Italian Alps, we had the opportunity to carry out several behavioral observations on free-ranging slow worms. The aim of this paper is (1) to present some findings on reproductive phenology (including both copulations and male-male combats) of this alpine population of *A. fragilis*, and (2) to discuss these data in the light of current theories on reptile mating systems, with special reference to other well-known European species, such as *Lacerta agilis* (Olsson 1992a,b, 1994a,b,c; Olsson et al. 1994), *Vipera berus* (Andr n 1986; Madsen et al. 1993; Capula and Luiselli 1994a; Luiselli 1995), and *Natrix natrix* (Luiselli 1996).

MATERIALS AND METHODS

Study Area

All data were collected at a high altitude site of the northeastern Italian Alps (Sella Nevea, Tarvisio Forest, Carnic Alps, province of Udine, elevation 1100 m), where *Anguis fragilis* is widespread and extremely abundant. The study site is characterized by a mosaic of grassy patches interspersed with stones at the edge of mixed forests (*Abieti-Fagetum*), and has already been used by us for eco-ethological studies on *A. fragilis*, *Coronella austriaca*, *Natrix natrix*, and *Vipera berus* (e.g. Capula and Luiselli 1993; Capula et al. 1992, 1997; Luiselli 1992a,b; Luiselli et al. 1995). The climate of the study area is typically alpine, with cold winters, prolonged snow covering, and mild and rainy summers.

Observations and Analysis

Field observations on combats and copulations were done between 1991 and 1997, when the study area was also used for long-term studies on sexual selection in *Vipera berus*. In each year, field trips were conducted on each day between April and June with weather that allowed reptile activity. We spent as long as possible in the field on each day, but rainfall often interrupted our research. Every year the sampling effort was constant (see Capula and Luiselli 1994b), so that annual differences in observed patterns would not just reflect observation intensity. All times indicated here are in European Standard Time.

When a combat or a copulation was seen, the number of interacting individuals was noted, the behavioral displays and the mating or combat outcome were recorded, and the individuals involved in such behaviors were sometimes captured at the end of the behavioral interactions. This was normally easy, due to the site-tenacious, careless attitude and the slow escape speed of *Anguis fragilis*. All captured individuals were sexed, their snout-vent length (SVL) measured to the nearest 0.1 cm, marked by ventral scale-clipping for permanent individual identification, and dorsally painted with a white number for visual identification at a distance. Statistical analyses were performed using the STATISTICA personal computer package (version 4.5, 1993), with α set at 5%. All tests were two-tailed.

RESULTS

Reproductive Phenology of *Anguis fragilis* in the Tarvisio Forest

The populations of *A. fragilis* from Sella Nevea are subjected to the severe constraints of the alpine climate in the Carnic Alps region. *Anguis fragilis* leave the hibernacula shortly after the onset of the snow melt, usually in mid-April. Slow worms and common lizards (*Lacerta vivipara*) are the earliest reptiles of Sella Nevea to leave the hibernacula (Table 1), followed by adders (*Vipera berus*), grass snakes (*Natrix natrix*), and smooth snakes (*Coronella austriaca*). During the early above-ground activity phase *A. fragilis* spend much time in basking on warm substrates, sometimes forming small "balls" of 3-13 individuals (maximum number observed: 16 individuals on 8 April 1997). In total, we observed 44 slow worm balls between 1991 and 1997, constituted by an average of 5.3 ± 8.8 individuals. Twenty-nine of 44 balls consisted only of males. Since these "balls" often include only males, they cannot be considered "mating balls" (*sensu* Joy and Crews 1988; Luiselli 1996; Madsen and Shine 1993). The basking phase is followed by the reproductive season, which is characterized by frequent combats between males, mating attempts, and later by the pregnancy phase of the reproductive females. Most females reproduce in alternate years. Parturition occurs between

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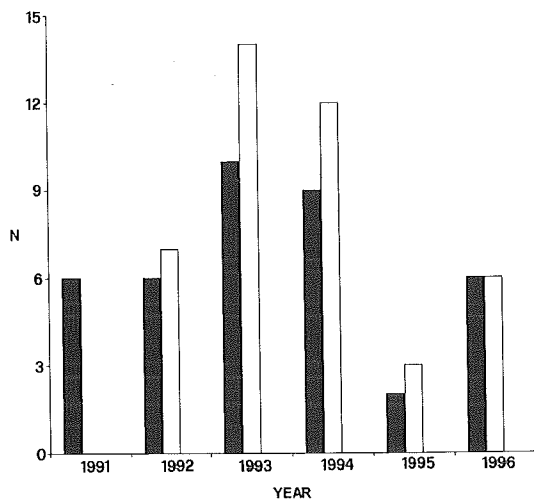


Figure 1. Numbers of mating (white bars) events and male-male combat (black bars) observed in *Anguis fragilis* from Sella Nevea (Tarvisio Forest, Carnic Alps, Northeastern Italy), between 1991 and 1996. In the term "matings," both completed copulations and unsuccessful courtships are included

mid-August and mid-September, with minor variations across years. Hibernation begins between mid-October and early November, depending on the proximate external temperatures. *Anguis fragilis* feed throughout the whole activity period, although some females suspend feeding during pregnancy.

Timing of Occurrence of Male-Male Combats and Copulations

We recorded 39 male-male combats and 42 copulation events (Fig. 1). Despite the low number of regression points ($n = 6$ yr), there was a positive correlation between numbers of observed combats and number of observed copulations in each year ($r = 0.793$, adjusted $r^2 = 0.537$; ANOVA: $F = 6.795$, $df = 1,4$, ordinate intercept = 3.55, $P < 0.05$).

The distribution of numbers of observed combats and copulations in relation to the monthly date is also of significance (Fig. 2). All male-male combats occurred between 5 May and 3 June, whereas all copulations occurred between 15 May and 3 June. The first male-male combats occurred earlier than copulations, but both fight and copulation behaviors peaked in mid-May. There were statistically significant differences in the distribution of combats and matings in relation to monthly date

(Mann-Whitney U test, $P < 0.05$).

We also recorded the diel distribution of the numbers of combats and matings (Fig. 3). Both types of interaction were observed almost exclusively during daylight hours despite regular nighttime surveys. The hourly distribution of combats was bimodal, with a morning peak (1000–1200h) and an afternoon peak (1400–1600h). The distribution of copulation events was unimodal (Fig. 3), with the peak in the early afternoon hours (1400–1600h). The distribution of combats and matings in relation to diel time differed significantly (Mann-Whitney U test, $P < 0.05$).

Behavioral Components of Male-Male Combat and Copulation

During combat males bite each other vigorously and for prolonged times (10–30 min or even longer). During mating attempts, the male bites the female (usually her anterior body parts, either head or neck) and tries to oppose his vent to that of the female. Courtship and mating are usually stationary events which take place within bushes. However, in

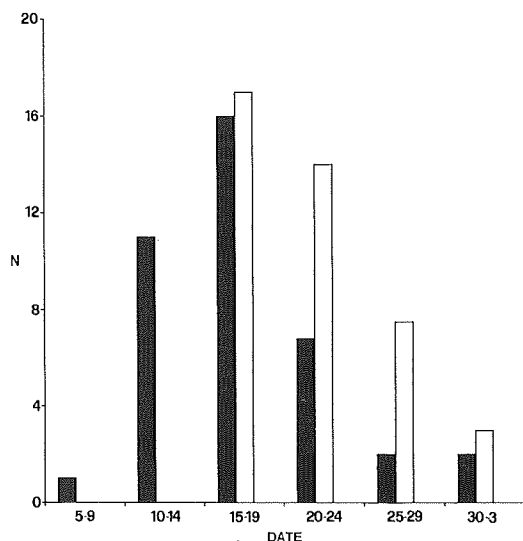


Figure 2. Distribution of matings (white bars) and male-male combat (black bars) in relation to date in *Anguis fragilis* from Sella Nevea (Tarvisio Forest, Carnic Alps, Northeastern Italy). In the term "matings," both completed copulations and unsuccessful courtships are included. The months of May and June are included in this figure.

Table 1. Date of spring emergence (after hibernation) of some reptile species in Sella Nevea (Carnic Alps, northeastern Italy). The emergence date given in the table indicates the first time in which at least five different individuals of a given species have been observed above-ground during spring. Note that *Anguis fragilis* emerged earlier than the sympatric snakes *Vipera berus* and *Coronella austriaca*, and shortly after the lizard *Lacerta vivipara*.

Species	1991	1992	1993	1994	1995	1996	1997
<i>Anguis fragilis</i>	23 Apr	13 Apr	10 Apr	16 Apr	5 Apr	12 Apr	30 Mar
<i>Lacerta vivipara</i>	19 Apr	10 Apr	7 Apr	11 Apr	25 Mar	10 Apr	24 Mar
<i>Coronella austriaca</i>	6 May	8 May	1 May	3 May	11 May	12 May	7 May
<i>Vipera berus</i>	28 Apr	23 Apr	22 Apr	23 Apr	17 Apr	21 Apr	20 Apr

a few cases the female has been seen moving away from a courtship site, immediately followed by the courting male.

Male Hierarchy During Sexual Combats

Body sizes of males defeated during combats (number of complete combats monitored = 21) were always lower than those of the winner (Table 2). The mean differences between body sizes of winners (16.4 ± 0.6 cm, $n = 21$) and losers (15.3 ± 0.5 cm, $n = 21$) was statistically significant (Student t test, $df = 40$, $P < 0.0001$). Furthermore, the mean length of the males courting and successfully mating with females (17.3 cm, $n = 42$) was significantly higher (one-way ANOVA, $P < 0.005$) than the mean length of the male *Anguis fragilis* occurring in the study area (15.6 cm, $n = 183$). This

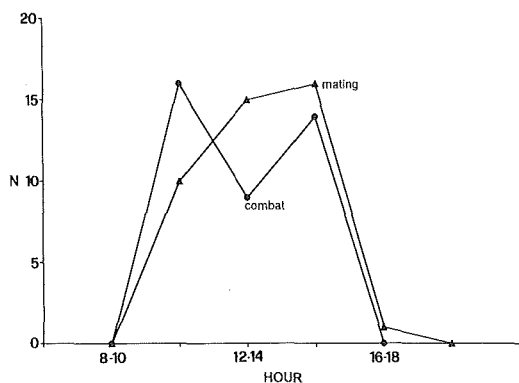


Figure 3. Diel distribution of matings and male-male combats in *Anguis fragilis* from Sella Nevea (Tarvisio Forest, Carnic Alps, Northeastern Italy). In the term "matings," both completed copulations and unsuccessful courtships are included.

suggests that access to reproductive females is almost monopolized by the larger males in the population. Moreover, fighting time tended to be negatively correlated with the ratio of mass between the contestants, however, due to the small sample size, relationships did not attain statistical significance (correlation of size difference in % against time in log sec, Spearman's $r = -0.364$, $n = 8$, ANOVA $F_{1,6} = 0.917$, $P = 0.37$)

DISCUSSION

Information available in the scientific literature on the mating system of free-ranging *Anguis fragilis* are not detailed (see Patterson 1983; Saint Girons 1963), but certain features are becoming clear and our data can probably be considered as the most detailed available. With regard to reproductive phenology, there is considerable similarity between *A. fragilis* and sympatric snakes. This similarity is apparent in (1) the simultaneity of mating periods of slow worms and adders (*Vipera berus*), (2) the nearly identical parturition dates of slow worms, adders, and smooth snakes (*Coronella austriaca*), (3) the similar lengths of reproductive cycles of female slow worms, adders, and smooth snakes, and (4) the existence of an intense basking period during early spring in both slow worms and sympatric snakes (cf. Capula and Luiselli 1994b; Luiselli 1995; Luiselli et al. 1996). This pronounced similarity in various traits can best be interpreted by convergence, as these taxa are phylogenetically distant. The similarity in reproductive pattern may be related to the peculiarities of the alpine climate, an important external constraint on reptile natural history, as demonstrated by the high

reproductive costs experienced by reptiles of this geographic area (Luiselli 1992b; Luiselli et al. 1996, 1997).

The most obvious feature of the mating system in *Anguis fragilis* was the occurrence of combat between males for access to females, with an observed advantage of large-sized males for mating success. This is another similarity between *A. fragilis* and sympatric snakes, including both adders (Luiselli 1995) and smooth snakes (Capula and Luiselli 1997). It would be interesting to know whether the male *A. fragilis* can monopolize females via mate guarding by dominant males, as is the case in sympatric adders (Luiselli 1993a, 1995) and some lizard species (e.g. Bull 1988; Carpenter 1977; Deslippe and M'closky 1991; Olsson 1993; Stamps 1983). Alternative reproductive components could be present but were not detected during our study. Saint Girons (1963) demonstrated that viable spermatozoa could only be present in genital tracts of female *A. fragilis* for less than 30 days. This precludes long-term sperm storage as alternative reproductive component for slow worms, the same being true for *Vipera berus* (Hoggren 1995; Luiselli 1993b, 1995).

In the study area, *Anguis fragilis* occur at high densities (>80 individuals/ha; Capula et al., unpubl. data) and are found practically everywhere (Capula et al. 1997; Darsa 1972; Stergulic 1987). Such densities may favor the establishment of hierarchical rather than territorial social structures (Torr and Shine 1996). This seems to be true in the case studied. In fact, we have rather firm evidence of male hierarchy in Sella Nevea *A. fragilis*, as (1) large males win over small males, and (2) fighting time tends to increase when two similarly-sized males engage in a fight. However, more data are necessary to demonstrate whether males aggressively excluded other males from their home ranges, and if this is so, to suggest absence of territoriality.

Taking into account the effect of size of outcomes of combat, it is likely that smaller males may sometimes be excluded from copulations each season, since slow worms have small home ranges and tend to have high site-fidelity year after year (Capula et al., submitted). This is exactly what happens in Sella Nevea adders (Luiselli 1993a, 1995).

Detailed studies on *Lacerta agilis* provided

Table 2. Body size (snout–vent length in cm) of *Anguis fragilis* males involved in sexual combats at the study area. Note that the winner of each fight was always the bigger individual.

Winner	Loser
165	148
162	153
177	155
161	157
159	159
164	155
168	165
155	155
158	150
167	155
162	153
169	152
173	148
154	148
170	147
172	155
168	159
160	148
165	159
159	157
160	143

evidence that coloration is important for assessing dominance (Olsson 1994b) and for reducing costly interactions with predictable outcome between individuals meeting repeatedly during mate search (Olsson 1994c). In *Anguis fragilis* the sexes do not differ greatly in dorsal colouration and the males do not become particularly bright during the nuptial phase. Therefore it is likely that in *A. fragilis* dorsal coloration serves less in a nuptial context than it does in *L. agilis*. However, blue-spotted coloration, especially bright during the mating season, is present in a few large males (see Capula et al. 1997), suggesting that dorsal pattern could also have some communication value in alpine *A. fragilis*.

The behavior of male *A. fragilis* which follow females for prolonged time is quite similar to that of European vipers, in which the female retreats a few metres within her activity area as a response to an approaching male, and the male immediately follows the female without losing body contact (see Andrén 1986; Capula et al., unpubl. data).

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