

Ecology of an alpine population of the Slow Worm, *Anguis fragilis* LINNAEUS, 1758. Thermal biology of reproduction (Squamata: Sauria: Anguinae)

Zur Ökologie einer alpinen Population der Blindschleiche,
Anguis fragilis LINNAEUS, 1758.
Einflüsse der Temperatur auf die Fortpflanzung
(Squamata: Sauria: Anguinae)

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KURZFASSUNG

Bei verschiedenen Reptilienarten bestehen Unterschiede in den Temperaturanforderungen trächtiger und nicht trächtiger Weibchen, wobei erstere sich häufiger aufwärmen und/oder eine höhere Körpertemperatur aufrechterhalten. Eine alpine Population der lebendgebärenden Blindschleiche, *Anguis fragilis* LINNAEUS, 1758, wurde auf derartige Unterschiede hin untersucht. Die kloakal gemessene Körpertemperatur war bei trächtigen Tieren höher als bei nicht trächtigen (27,04 °C gegenüber 25,28 °C), und in beiden Fällen waren die mittleren Körpertemperaturen höher als für diese Art im Schrifttum angegeben (etwa 22 °C - 23 °C). Auch war die Körpertemperatur aktiver Tiere bei graviden Weibchen höher als bei nicht trächtigen. Die Korrelation von Umgebungs- und Körpertemperatur war bei trächtigen und nicht trächtigen Individuen schwach. *A. fragilis* scheint eher ein Thermoregulator als ein Thermoconformer zu sein, zumindest während solcher Tage, die zum Sonnen geeignet sind. Trächtige Tiere wärmen sich durch direkte Sonneneinstrahlung auf, nicht trächtige gewöhnlich durch Aufenthalt unter von der Sonne beschienenen Gegenständen. Durch ihr ungeschütztes Sonnen sind gravide Weibchen wahrscheinlich stärker visuell orientierten Fressfeinden ausgesetzt. Dies ist biologisch bedeutungsvoll, da vermehrter Feinddruck auf trächtige Tiere erhöhte "Kosten" in der Fortpflanzung bedeutet.

ABSTRACT

In several reptile species there are differences in thermal requirements of gravid and non-gravid females, the former ones basking more frequently and/or maintaining higher body temperatures. An alpine population of the live-bearing anguid *Anguis fragilis* LINNAEUS, 1758 was studied in this respect. Body temperatures were measured with a cloacal thermometer. Mean body temperature was higher in gravid than in non-gravid females (27.04 °C versus 25.28 °C). Also modal body temperatures of active animals were higher in gravid females. Correlation between ambient and body temperature was weak in both gravid and non-gravid females. *A. fragilis* appears as a thermoregulator rather than a thermoconformer, at least during sunny days suited for basking activities. Gravid individuals bask by exposing their body directly to the sun, while non-gravid ones usually bask by staying under sunwarmed objects. As a consequence, gravid females are probably more exposed to visually orientated predators. This is an important life-history feature, as increased predation on gravid females means increased costs associated with reproduction.

KEYWORDS

Anguis fragilis, ethology, physiology, thermoregulation, activity, Alpine environment, Italy

INTRODUCTION

Developmental rates of reptile embryos are temperature-dependent, embryogenesis being accelerated by increasing temperature (MUTH 1980; SHINE 1980; BEUCHAT 1988; SCHWARZKOPF & SHINE 1991). As period of gestation de-

creases when temperature increases, maintenance of high body temperature appears to be essential for gravid female reptiles. In fact, maintenance of high body temperature seems to be more important to gravid females in terms of reproductive

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energy, growth rate, and increasing survivorship (e. g. TINKLE 1969; SHINE 1980), other than for other reasons (BEUCHAT 1988).

Based on the above considerations, it is not surprising that several authors (see BEUCHAT 1986) found higher body temperatures in gravid than in non-gravid females. In some cases, these higher body temperatures are due to increased basking intensity of the gravid individuals (references in SCHWARZKOPF & SHINE 1991).

Most species with this kind of thermal differences are viviparous day-active heliotherms. They occupy one end of a continuum of specialization that ranges from thermal specialism (narrow range of activity temperature, without significant correlation between body and ambient temperature) to thermal generalism and

thermoconformity (activity temperature passively tracks the ambient temperature) (PATTERSON 1990). Thermal specialists live in low-cost thermal environments, while thermal generalists are usually found in high-cost thermal environments (HUEY & SLATKIN 1976). These latter organisms are little known, but it seems that they:

1. maintain lower body temperatures,
2. keep their body temperatures less constant than species of the low-cost thermal environment (HUEY & WEBSTER 1976).

In the present study field body temperatures of gravid and non-gravid females of the life-bearing anguid *A. fragilis* LINNAEUS, 1758 are analyzed. This semi-fossorial species, that rarely appears in the open and usually is associated with dense vegetation, occurs in high-cost thermal environments (PATTERSON 1990).

MATERIALS AND METHODS

Study area

Data were entirely collected during summer 1992 in the eastern Italian Alps (Sella Nevea, Tarvisio Forest, Carnic Alps, 1100 m a. s. l.), when ecological studies on both *A. fragilis* and *Vipera berus* were carried out (CAPULA & al. 1992). The area is characterized by delapidated walls and ruins at the borders of a coniferous wood (*Pinus mugo*). The most common reptile species in this area are *Lacerta vivipara*, *A. fragilis*, *V. berus* and *Coronella austriaca*.

Field body temperature

Cloacal temperature of females (gravid status determined as in CAPULA & al. 1992) was recorded with a SCHULTHEIS fast-registering mercury thermometer within 40 seconds after capture. Ambient temperature was measured 1 m above ground after each record of cloacal temperature. All results reported refer to observations made on bright sunny days, i. e. under optimum conditions for active thermo-

regulation (PATTERSON 1990). This restriction has been necessary, as ambient thermal conditions significantly (ANOVA $p < 0.001$) affected the body temperature (that ranged from 11 °C to 16 °C on days with "suboptimum" conditions for thermo-regulation).

Basking behaviour

Slow Worms are known to bask either directly exposed to the sun or under sunwarmed objects such as sheets of corrugated iron and flat rocks (ARNOLD & BURTON 1978). Therefore, the basking behaviour of the Slow Worms captured and analyzed for body temperature was assigned to two categories:

1. basking directly exposed to the sun,
2. basking under sunwarmed objects.

There were no difficulties in assigning specimens to category 1, but there were some methodological problems to distinguish individuals which basked under sunwarmed objects from those which simply were inactive. We therefore restricted category 2 to specimens lying under objects that were exposed to the sun.

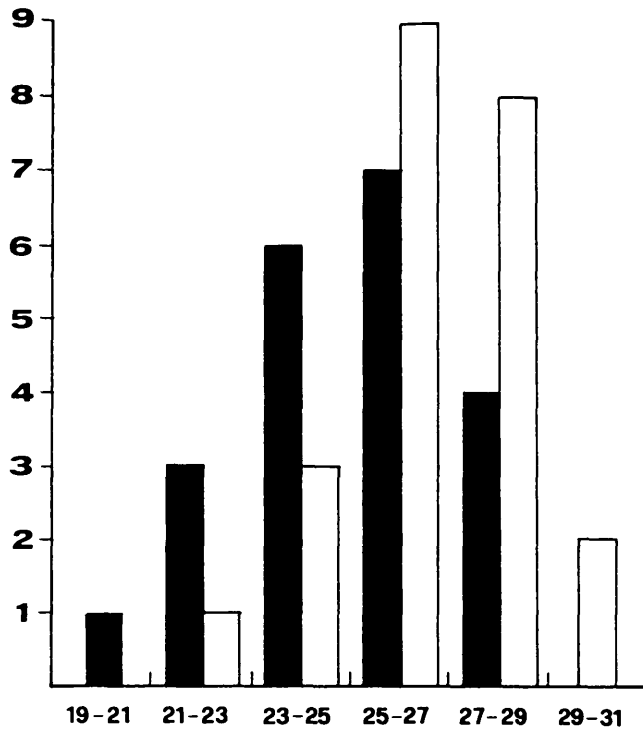


Fig. 1: Body temperature distribution in gravid (white columns) and non-gravid (black columns) females of *Anguis fragilis* at Sella Nevea (Tarvisio Forest, Carnic Alps). Abscissa: Temperatures grouped in 2 °C intervals. Ordinate: number of individuals.

Abb. 1: Die Verteilung der Körpertemperaturen gravider (weiße Säulen) und nicht gravider (schwarze Säulen) *Anguis fragilis* auf der Sella Nevea (Wald von Tarvisio, Karnische Alpen). Abszisse: Temperaturen zu 2 °C-Klassen gruppiert. Ordinate: Anzahl der Individuen.

Statistical analyses

Statistical analyses were computed with the SYSTAT software package (WILKINSON 1988), all tests being two tailed ($\alpha = 0.05$). For the choice of the tests we generally followed recommendations in SNEDECOR & COCHRAN (1980) and ZAR (1984). Frequencies of gravid and non-gravid females basking in two different ways were compared (1) by hypothesizing their ratio to be 1:1, which is typical in biennial breeders such as the present population (CAPULA & al. 1992), and (2) by using Chi^2 2x2 contingency

tables. In this case the correction factor of YATES was used in order to reduce the possible error in p calculation (for $df = 1$), which is true when the distribution in the Chi^2 test is continuous while the series tested including all the eventual values of Chi^2 is not (GLANTZ 1988). Besides this, the following tests were used: STUDENT test for comparing means, regression analysis (linear model: $Y = a + bX$) to correlate two variables, a balanced two-factor ANOVA for analyzing the distribution of body temperature in gravid and non-gravid females, and ANCOVA for comparing two regressions.

RESULTS

Body temperatures

Field body temperatures from 23 gravid and 21 non-gravid female Slow Worms were measured.

Temperatures ranged from 22.2 °C to 31.0 °C (\bar{x} = 27.04 °C \pm 2.01 °C) in gravid, and from 20.0 °C to 28.1 °C (\bar{x} = 25.28 °C \pm 2.28 °C) in non-reproductive females. These differences were significant (equal vars. = 0.45 3.06, df = 42; unequal vars. = 0.44 3.07, df = 40.1; two-tailed STUDENT t = 2.71, p = 0.009).

Variance in body temperature was greater in non-gravid than in gravid females (two-factor ANOVA p < 0.01), and there were significant differences in body temperature distribution (balanced two factor ANOVA p < 0.001).

Modal temperature ranged from 25 °C to 29 °C in gravid, and from 23 °C to 26 °C in non-gravid females (Fig. 1).

Mean difference between cloacal and ambient temperature was 8.95 °C \pm 3.81 °C in pregnant, and 8.14 °C \pm 3.52 °C in non-pregnant females. These means do not differ significantly (equal vars. = -1.43 3.05, df = 42; unequal vars. = -1.42 3.04, df = 42; t = 0.73, p = 0.468), even when temperatures were log-transformed to reduce heterogeneity of variances.

Correlation between body temperature (dependent variable) and ambient temperature was neither significant in gravid nor in non-gravid females (gravid females: r = 0.31, determ. coeff. = 0.096, ANOVA F = 2.225 with df = 1, p = 0.122; DURBIN-WATSON statistics = 2.307; non-gravid females: r = 0.365, determ. coeff. = 0.133, ANOVA F = 2.912 with df = 1, p = 0.093; DURBIN-WATSON statistics = 1.602) (Figs. 2 and 3). Performing ANCOVA analysis either to ordinate intercepts or slopes, regressions did not differ significantly (p > 0.05).

Basking behaviour

We examined a total of 23 gravid and 21 non-gravid females (same individuals as for the body temperature), all of them basking in one of the two different ways described in "Material and methods". 17 out of 23 (73.91 %) gravid and 6 out of 21 (28.57 %) non-gravid specimens basked directly exposed to the sun. Null hypothesis (equal numbers of gravid and non-gravid females are basking exposed to the sun) has to be rejected, as frequencies of gravid and non-gravid females differed significantly (YATES' Chi^2 = 18.18, df = 1, p < 0.0001).

DISCUSSION

As pointed out by PATTERSON (1990), it is more difficult to interpret body temperature data in secretive lizards such as *A. fragilis* than in day-active heliotherms. As a consequence, it is not easy to establish whether these secretive species are thermoconformers or thermoregulators. Our data, however, seem to confirm PATTERSON's (1990) suggestion that Slow Worms are thermoregulators, at least on days which offer optimum basking conditions. If Slow Worms were thermoconformers one would expect ambient temperatures being higher than body temperatures, at least in some cases. This was

found in *A. fragilis* examined on days with "suboptimum" basking conditions (see PATTERSON 1990, Fig. 2), but it was not the case in Slow Worms analyzed on sunny days, both by us in the eastern Alps and by PATTERSON (1990) in England and Wales. Poor correlation between body and ambient temperature in gravid and non-gravid individuals obviously speaks in favour of active thermoregulation during "optimum" basking conditions. In this regard, our data are very similar to those obtained by PATTERSON (1990), although there are some differences. Our observations confirm the existence of a

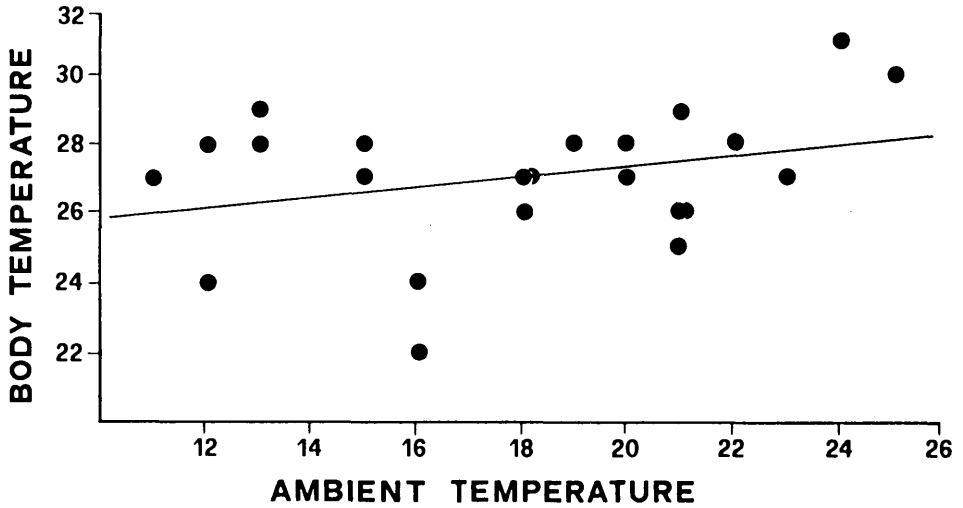


Fig. 2: Relationship between gravid *Anguis fragilis* body temperature and ambient temperature (°C). Note that body temperatures are always higher than corresponding ambient temperatures.

Abb. 2: Die Beziehung zwischen Körper- und Umgebungstemperatur bei trächtigen *Anguis fragilis*. Die Körpertemperaturen liegen in allen Fällen über den Umgebungstemperaturen.

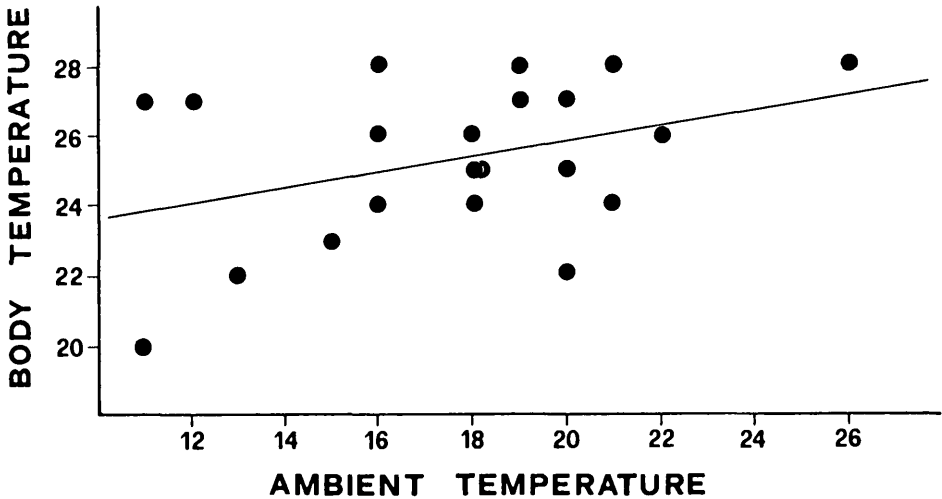


Fig. 3: Relationship between non-gravid female *Anguis fragilis* body temperature and ambient temperature. Note that body temperatures are always higher than corresponding ambient temperatures.

Abb. 3: Die Beziehung zwischen Körper- und Umgebungstemperatur bei nicht trächtigen weiblichen *Anguis fragilis*. Die Körpertemperaturen liegen in allen Fällen über den Umgebungstemperaturen.

wide spectrum of body temperatures in this species, but the mean activity temperature recorded in gravid and non-gravid females is considerably higher than that reported for British Slow Worms (22.6 °C according to PATTERSON 1990).

Moreover, our data show that gravid females are frequently maintaining higher body temperatures than non-gravid ones, and that their body temperatures are significantly lower than those of several day-active heliothermic lizards (see AVERY 1978; POUGH & BUSACK 1978; ARGUELLO & SALVADOR 1988; BRAÑA 1991). These results are different from those of some authors who found no significant difference among mean body temperatures of males, gravid and non-gravid live-bearing female reptiles. (GIBSON & FALLS 1979).

Variance of body temperature was greater in non-gravid than in gravid females. This is in accordance with observations made in other lizards and is possibly due to more precise thermoregulation in the latter ones (see STEWART 1984; BEUCHAT 1986; CHARLAND & GREGORY 1990). Enhanced thermoregulatory capacity of gravid *A. fragilis* may also be due to different basking behaviour. In fact, gravid individuals usually basked by exposing their bodies directly to the sun, while

non-gravid specimens basked more frequently under sunwarmed objects. This diverging basking behaviour possibly reflects different thermal exigencies of the two categories of individuals. As gravid females need higher body temperatures to keep the period of pregnancy short, they gain more heat by direct sun exposure. Non-gravid individuals do not show particular thermal exigencies, and they may choose the other type of basking in order to reduce the risk of predation by visually guided predators. Increased risk of predation in exposed gravid individuals is combined with an increase of speed (e. g. in case of persecution) but also with reduction of locomotive ability (SHINE 1980; GARLAND 1985; SEIGEL & al. 1987). Relative clutch mass (RCM) is negatively correlated with locomotive speed and endurance (SHINE 1980; BAUWENS & THOEN 1981; GARLAND & ARNOLD 1983; HUEY & al. 1984; GARLAND & ELSE 1987; SEIGEL & al. 1987). High RCM therefore means increased "cost" of reproduction. In fact, RCM was hypothesized to be a distinct life-history trait of squamate reptiles, optimized via different mortality in gravid individuals (VITT & CONGDON 1978; VITT 1981; VITT & PRICE 1982).

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