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Phenology and life history of the cavernicolous isopod, *Venezillo tenerifensis* Dalens 1984, endemic to Tenerife (Isopoda: Armadillidae)*

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RESUMEN: El isópodo cavernícola *Venezillo tenerifensis*, endémico de Tenerife, exhibe características típicas de los isópodos hipógeos. Es una especie iterópara, tiene una longevidad cercana a los 8 años, y sólo produce tres grandes descendientes por cría. Bajo la influencia de condiciones controladas (oscuridad y 17,5 °C), la duración del ciclo reproductor oscila entre 9 y 11 meses.
Palabras clave: *Venezillo tenerifensis,* isópodos terrestres, islas Canarias, Tenerife, fenología reproductora, historia, estrategias reproductoras.

ABSTRACT: The cavernicolous isopod, *Venezillo tenerifensis*, which is endemic to Tenerife, exhibits typical characteristics of hypogean isopods. This species is *iteroparous*, has a longevity of about 8 years and produces only three large offsprings per brood. Under the influence of constant laboratory conditions (darkness, 17.5 °C), the duration of the breeding cycle ranges from 9 to 11 months.
Key words: *Venezillo tenerifensis*, terrestrial isopods, Canary Islands, Tenerife, breeding phenology, life history, reproductive strategies

INTRODUCTION

The genus *Venezillo* Verhoeff 1928 (Crinocheta: Armadillidae) is common to America and Africa (Schmalfuss & Ferrara, 1983). Numerous species from the southern part of Africa have been described by Ferrara & Taiti (1979). In addition, several

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species can be found in north-west Africa. *V. trifolium* (Dollfus 1890) is endemic to the Cape Verde Islands (Schmalfuss, 1982), *V. crassus* (Budde-Lund 1904) is restricted to Sao Tomé and Principé (Schmalfuss & Ferrara, 1983), and *V. berlandi* (Paulian de Félice 1940) was found at the northern west coast of Africa (Schmalfuss, 1982; Schmalfuss & Ferrara, 1983). Two further species inhabit the Canary Islands: *V. canariensis* Dollfus 1893 (cf. Schmalfuss, 1982) and *V. tenerifensis* Dalens 1984. The latter was first found in a cave („Cueva Los Roques", Tenerife) in 1981 (Dalens, 1984). The distribution of the genus *Venezillo* in America and Africa is mainly of biogeographical interest. However, our studies concentrated on the phenology and the life history of one of the species inhabiting the west-african islands: *V. tenerifensis* is one of the most widespread cave-dwelling species in Tenerife and occurs in numerous caves in remarkably low population densities (pers. comm., J.J.H. Pacheco).

Darkness and constant temperatures force animals to exhibit reproduction cycles which are endogenously synchronized. By contrast, species that develop under the influence of changing abiotic conditions usually respond to these factors (Topp, 1994). In a stable environment, such as caves, with a lack in seasonal variation of abiotic factors and with low comparably predation pressure, phenological strategies different from those of soil dwelling or litter colonizing species can be expected. Our studies on reproduction and growth of *V. tenerifensis* were performed to reveal information about its previously unknown ecology.

MATERIAL AND METHODS

In May 1994, one female and one male of the endemic isopod species *Venezillo tenerifensis* were captured in the volcanic cave, „Cueva del Viento Sobrado", on Tenerife (*leg.* W. Topp). These individuals were brought to our laboratory and maintained at constant conditions of 17.5 °C, darkness and nearly saturated air moisture, coinciding with the conditions of their natural habitat. The isopods were kept in small Petri dishes (45 mm diameter) the bottoms of which were covered with plaster (cf. Zimmer & Topp, 1997). Filter paper in the lids of the dishes served as an additional source of moisture. A mixture of leaf litter of palearctic trees was offered as food *ad libitum*. Feces remained in the Petri dishes to allow coprophagy (cf. Hassall & Rushton, 1982), but the isopods were placed into new Petri dishes monthly.

We observed individuals of *V. tenerifensis* to reveal information on moulting cycles, reproduction, and growth rates. The latter parameter was described by changes in head width (cf. Sutton, 1968; Sunderland *et al.*, 1976). Moulting activity was indicated by exuviae that appeared not to be fed on by the isopods. The time intervals between observations on the isopods were chosen at random within the range of 10-20 days. By this, we intended not to influence the endogeneous rhythms of these presumably blind isopods. Furthermore, these observations outside of the breeding chamber were performed at low light intensities.

RESULTS

During our observations from May 1994 to November 1997, one female of *V. tenerifensis* reproduced four times, in October 1994, in July 1995, in June 1996, and in May 1997. Each time, three juveniles with a head width of (0.56 ± 0.04) mm were released from the brood pouch. The duration of breeding cycles ranged from 9 to 11 months.

Moulting appeared more frequently in juveniles than in adults. The latter individuals (that have been captured in Tenerife) moulted every 90 to 210 days (n = 7; median: 189 days), while intermoults lasted only 50-70 days in juveniles (n = 17). Consequently, juveniles grew much faster than adults (Fig. 1). Data on juvenile growth were used to calculate non-linear regression that could deliver information on the adults' age when taken to the laboratory (cf. Fig. 1). Moreover, these analyses revealed a maximum size (head width) of about 1.5 mm.

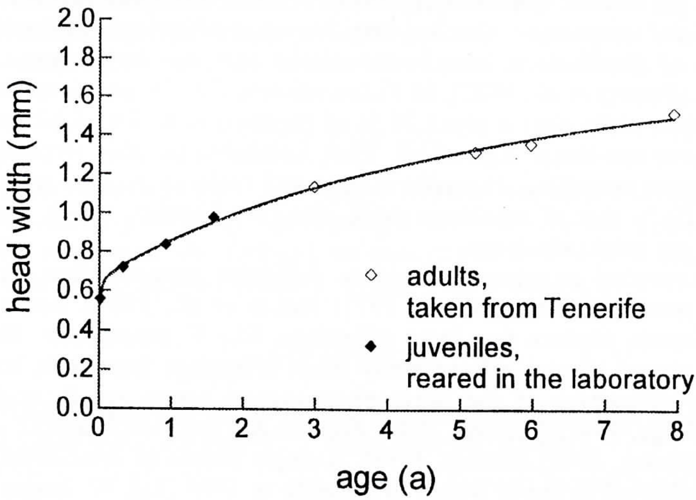

Fig. 1. Growth of individuals of *Venezillo tenerifensis* under constant darkness (17.5 °C) in the laboratory.

Taking these data into account, longevity of *V. tenerifensis* appears to be up to 8 years. However, we did not succeed in rearing the juveniles to maturity. Hence, the slow development may as well be an artefact due to suboptimal conditions. In this case, development might be faster, and longevity might be less extended in the field.

DISCUSSION

Inside the taxon of terrestrial isopods (Isopoda: Oniscidea), both iteroparity and semelparity occur wide-spread. Comparing these phenological strategies, the spreading of risk in iteroparous species is obvious. This strategy appears to be adaptive for inhabitants of unstable environments. However, no regularity can be found in taxonomically contrasting isopod species of these habitats (summarized in: Warburg, 1993).

The cavernicolous isopod, *Venezillo tenerifensis*, is iteroparous, and thus contrasting to *Venezillo arizonica* that was described to be semelparous (Warburg, 1993) while producing 2-4 mancae per brood in a cryptic habitat (Warburg, 1965). Concluding from our observations during four years of maintenance at darkness and constant temperature, the endogenous breeding cylce of *V. tenerifensis* takes 9-11 months (n = 4). Each brood (n = 4) produces three mancae with a head width of about 0.56 mm (n = 12). The extremely low number of juveniles per brood appears to be typical for hypogean and endogean isopods.

The reproductive success of an endogean isopod, *Platyarthrus hoffmanseggii* (living in ant nests), ranges from 2 to 8 mancae per female (Sutton *et al.*, 1984). Females of different myrmecophilous species of the genus *Exalloniscus* produce between 3 and 5 (Taiti & Ferrara, 1988) or 6 and 11 embryos (Ferrara *et al.*, 1987). Similar values have been reported for the small endogean synochetes, *Trichoniscus pusillus* (4-10 mancae per female: Heeley, 1941; Sutton *et al.*, 1984) and *T. pygmaeus* (2-9 mancae per female: Sutton *et al.*, 1984). Another endogean trichoniscid isopod, *Haplophthalmus montivagus*, also has very few large offsprings (Schmalfuss, 1977), and females of *Exalloniscus maschwitzi* release only one large manca from their brood pouch (Ferrara *et al.*, 1987). In *V. tenerifensis*, the size (head width) of freshly released mancae (0.56 mm) is about 35 % of the maximum size of adults (1.56 mm, calculated from non-linear regression). Thus, compared to other terrestrial isopods, e.g. the common woodlice, *Porcellio scaber* and *Oniscus asellus*, with mancae of only about 20 % size of maximum adult size (cf. Zimmer, 1998), mancae of *V. tenerifensis* are relatively large.

The presented examples elucidate different reproductive strategies of iteroparous species (cf. Schmalfuss, 1977; Sutton *et al.*, 1984). Some species of terrestrial isopods produce few large offsprings, like *V. tenerifensis*. On the other hand, some isopod species release many small offsprings from their brood pouch. Typical representatives of the latter phenological group are *P. scaber* (25-40 mancae: Collinge, 1941; Hatchett, 1947; Zimmer & Topp, 1997) and *O. asellus* (20-50 mancae: Heeley, 1941; Zimmer, 1998). A single female of *Armadillidium vulgare* which was collected in laurel woods in Tenerife in 1994 (*leg.* W. Topp) released as much as 264 mancae in the laboratory.

The low number of offsprings in endogean (Sutton *et al.*, 1984) and hypogean isopods, as in *V. tenerifensis*, is interpreted as a strategy when predation is negligible (Schmalfuss, 1977). Furthermore, unpredictable climatic events, such as droughts, floods and extremely high or low temperatures, which influence development and may incresase mortality in epigean species, are mostly insignificant for hypogean and endogean species. In a comparative study on canarian roach species of the genus *Loboptera* (Blattodea: Blattelidae), Izquierdo *et al.* (1990) described ovarian reduction related to progressive adaptation to underground habitats. Cavernicolous isopods can investigate their reproductive efforts into few mancae that, consequently, are relatively large (cf. Sutton *et al.*, 1984). For these individuals, the risk of death during juvenile development is comparably small, while in many other isopods juvenile mortality is extremely high (Sutton 1968, 1970; McQueen & Carnio, 1974; Sunderland *et al.*, 1976) due to low humidity in the field (Al-Dabbagh & Block, 1981).

We estimated the longevity of *V. tenerifensis* to be about 8 years, calculating from our data on juvenile growth and the size of captured adults, including their life span in the laboratory (cf. Fig. 1). This value appears to be very high compared to other terrestrial isopods with longevities of 1-4 years (summarized in Warburg, 1993). The mediterranean species *Armadillo officinalis* is thought to have a longevity of about 9 years (Warburg, 1993, after Cohen, 1988), and the myrmecophilous isopod, *Platyarthrus hoffmanseggii*, reaches an age of 5 years (Collinge, 1946). In contrast to the latter species and the above-mentioned endogean and hypogean species, *A. officinalis* is semelparous and produces about 50 (Shereef, 1970) or up to 90 mancae (Warburg & Cohen, 1991). Thus, low numbers of offsprings seem to be typical for endogean isopods, but long-lived species are not consistently iteroparous.

From the present results we conclude that the small, blind and white, conglobating, armadillid isopod, *V. tenerifensis*, is a typical representative of hypogean isopods with high longevity and few large offspring. The breeding cycle of 9-11 months appears to be endogeneously controlled, as can be expected in species from seasonally stable environments (cf. Topp, 1994). As a true cavernicolous species, *V. tenerifensis* is well-adapted to its hypogean habitat.

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