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Growth and longevity of *Nebo hierichonticus* in the laboratory; a long-term study (Scorpiones, Diplocentridae)

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Summary

During a long-term study of scorpions, it was possible to follow for 15 years the growth (increase in mass) in the laboratory of adult *Nebo hierichonticus* (Simon, 1875). The growth rate is highest during the first years (0.75 g/yr), dropping with age to 0.1 g/yr. During this long captivity period it also became possible to study their longevity. Longevity of two females was 15 and 18 years. Problems involved in the various methods used to assess growth and to estimate longevity are discussed.

Introduction

Growth

In many studies the calculation of growth curves is based on Bertalanfy's (1938) growth equation, which is essentially the calculation of addition in linear dimensions at two different ages (t_0 and t_1). However, since age can only be estimated, growth rate calculated based on age cannot be entirely accurate. Adult scorpions grow by increasing their mass, since they do not moult after their last nymphal moult.

Technical problems involved in studying growth

Several techniques have been used in studying growth in adult (non-moulting) scorpions:

1. Some studies on growth of adults and the calculation of growth curves are based largely on frequencies of size classes at different ages. This enables the creation of a size-frequency curve based on field collections and matching the scorpion's dimensions (mass) to the time it takes to moult and grow. Growth can be followed this way between moults. However, it is based on two assumptions: that scorpions grow throughout their life, and that their growth is largely correlated with age.

It is well known that extrapolations from size-frequency in a population with age cannot be accurate, since scorpions stop growing and reach a plateau when at a certain age. Using this method does not enable a growth curve to be obtained. Moreover, extrapolating from size-frequency data is based on the assumption that all sizes have an equal chance of being captured, which may not be true (since females are much more secretive than males, as a result of which they are less frequently captured (discussed in Warburg, 1997). The main faults are the assumptions that age and size are statistically related, and the difficulties in assigning the right age to either the smallest or the largest size classes. Furthermore, variance in body size within a particular age-class can be high, especially during their first five years of life, ranging between 16 and 22% (Warburg, in prep.). Although body size increases with age, this relationship is so weak that size cannot be used to predict growth at a certain age with any confidence.

2. A second way of studying growth is by adding up annual growth increments into a single growth curve. In discussing growth it may be better to express it per unit time (days, months, years) rather than as a function of age, since the birth date is hardly ever known for an animal found in nature and if it is raised in captivity there are additional problems that need to be considered as a result of these artificial conditions. The gain in dimensions (Δmass) per unit time (year) is much easier to calculate. These increments in growth can be joined in sequence to obtain a growth curve by adding up annual growth increments of individual animals in the wild (or in an enclosure) to form one curve. The advantage is that the data are obtained from animals under natural conditions, and each time the same animal is recaptured it is possible to obtain their mass and linear dimensions and calculate the increase in both. By adding this series into a single curve, a theoretical, cumulative growth curve, based on the average annual growth increments of individual animals arranged in different weight classes, can be constructed. One drawback is that this method is entirely dependent on recapture rates which are usually low (in nature, not in an enclosure), and in some animals (scorpions included) depend on the gender. Another disadvantage is that the scorpion's growth curve is not exponential but flattens out when growth slows down with age, reaching a plateau. To my knowledge, this method has so far not been applied to scorpions.

3. A third way to measure growth is by raising the scorpions from birth to death. This is the only way that growth can be followed with any accuracy. Thus, growth can be determined but only under non-natural conditions in the laboratory or in an enclosure. Alas, the few reports available on laboratory-raised scorpions did not record their growth after maturation. Francke & Jones (1982) raised six litters of *Centruroides gracilis* (Latreille, 1804) from birth to maturity (on average 235.7 days) but no record of their dimensions after maturation.

The drawbacks are that in the laboratory they are protected from predation and possibly exposed to parasites, as is not uncommon in cultures. On the other hand, an enclosure may not provide sufficient shelter against predation. Moreover, artificial food conditions may be either maximised if fed *ad libitum*, or there may not be sufficient food because of limitations caused by the enclosure. The advantage of this method lies in keeping the animals captive under presumably optimal conditions.

In conclusion: techniques used for measuring growth all have their drawbacks. Since these problems do not arise in all methods at the same time and may involve only one or two methods, it would be best to use all three measurements.

One of the objectives of this long-term study was to follow growth in adult scorpions. What is meant by "growth" is the increase in mass rather than (and independent) of moulting which is generally absent in adult scorpions. Since *Nebo hierichonticus* (Simon, 1872) can be maintained readily in captivity for many years, this report is confined to that species.

Longevity

Three terms are in use to describe longevity. The first two terms, longevity and life-span, both imply the maximal age an animal may reach under optimal conditions either in the wild or in captivity. The third term, life expectancy, is the average number of years an individual may expect to live, thereby implying that life-expectancy drops with age. None of these terms can be actually verified, consequently the age of an animal (scorpions included) can only be estimated.

Four methods have been used to estimate longevity, the first two of which involve following growth:

1. The first method (most commonly used) involves creating a size-frequency curve based on field collections and matching the scorpion's dimensions to the time it takes to moult and grow. In this way growth can be followed between moults, but it is based on the wrong assumption that scorpions grow throughout their life, and that their growth is highly correlated with age. The advantage in this technique is that it provides an idea of the size (i.e. age?) of the majority of animals in a population. However, in many cases, correlating size frequency with age cannot be accurate since scorpions stop growing after reaching a certain size (i.e. age), and their growth curve assumes a plateau. Moreover, extrapolating from size-frequency data is based on the assumption that all sizes have an equal chance of capture, which may not be true in many cases (discussed in Warburg, 1997). The main faults are the wrong assumptions that age and size are statistically related, and the difficulties in assigning the right age to either the smallest or the largest size classes. Furthermore, variance in body size within a particular age-class can be high, especially during the first five years of life. In addition, due to the great inter-individual variability in body size, in spite of the fact that body size increases with age, this relationship is so weak that size cannot be used to predict age with any confidence. The main difficulty is the fact that in some scorpions the moulting stage does not necessarily correspond to age.

In addition, scorpions in general stop growing when older, thus preventing the deduction of age from size. Under field conditions the longevity of scorpions (and indeed any other taxa) can at best be only estimated, since neither the time of their birth nor of their death can be known with any accuracy.

2. The second method of estimating age uses the construction of a growth curve by adding up annual growth increments of individual animals in the wild, to form a single curve. The advantage is that the data are obtained from animals under natural conditions. Each time the same animals are recaptured, it is possible to obtain their mass and linear dimensions and calculate the increase in both. By adding this series into a single curve, a theoretical, cumulative growth curve, based on the average annual growth increments of individual animals arranged in different weight classes, can be constructed. One drawback is that this method is entirely dependent on recapture rates which are usually low (in nature, not in an enclosure), and in some animals (scorpions included) depend on the gender. Another disadvantage is that the scorpion's growth curve is not exponential but flattens out when growth slows down with age, reaching a plateau. To my knowledge, this method has so far not been applied to scorpions.

3. The only way to know longevity with any accuracy is by raising scorpions (individually) in captivity from birth to death. Thus, age can be determined, but only under non-natural conditions in the laboratory or in an enclosure. This was partly achieved by Francke & Jones (1982) raising *Centruroides gracilis* from birth to maturity (on average 300 days, ranging between 214–348 days). The drawbacks are that in the laboratory they do not suffer from food shortages since they are fed *ad libitum*, and they are protected from predation. There is also the possibility of being exposed to parasites, as is not uncommon in cultures. The advantage of this method is that by keeping the animals captive under presumably optimal conditions one knows the time of death. It may, however, not be the actual maximum life span since the cause of death could be due to various factors other than old age. Again, unless the animal is raised from birth the life span can only be guessed.

All these three methods enable the estimation of longevity.

4. Another method of estimating longevity is an indirect one, by deducing longevity from the number of post-partum diverticulae and their colour (Smith, 1966; Warburg & Elias, 1998). Four different kinds of post-partum diverticulae can be distinguished by their different coloration and length. Warburg & Elias (1998) suggested that the life expectancy of *Scorpio maurus fuscus* (Ehrenberg, 1829) is between 9–17 years. This subject has been recently reviewed (Warburg, 2010).

Methods

Scorpions were collected over a period of 25 years (1974–1999), largely in northern Israel. Adult *N. hierichonticus* (generally weighing over 2 g) were hand-picked from under stones, logs and other refuges during the day, and with the aid of an ultraviolet lamp on suitable moonless, windless nights (Warburg, 1997). Animals were brought back to the laboratory, sexed and weighed on a Mettler electronic balance at ± 0.1 mg. (This method was used since adult scorpions do not moult and thus allometric linear changes in dimensions are not likely to yield any results.) Adult *N. hierichonticus* were kept separately in spacious containers (25×50 cm) containing soil, bark refuges and water, under a seasonally temperature- and light-regulated regime, in a room without windows. They were fed *ad libitum* on mealworm larvae (*Tenebrio*). These conditions enabled some scorpions to live for many years. All scorpions were weighed periodically at least once yearly during the study period. Generally, the mass of adult *N. hierichon-*

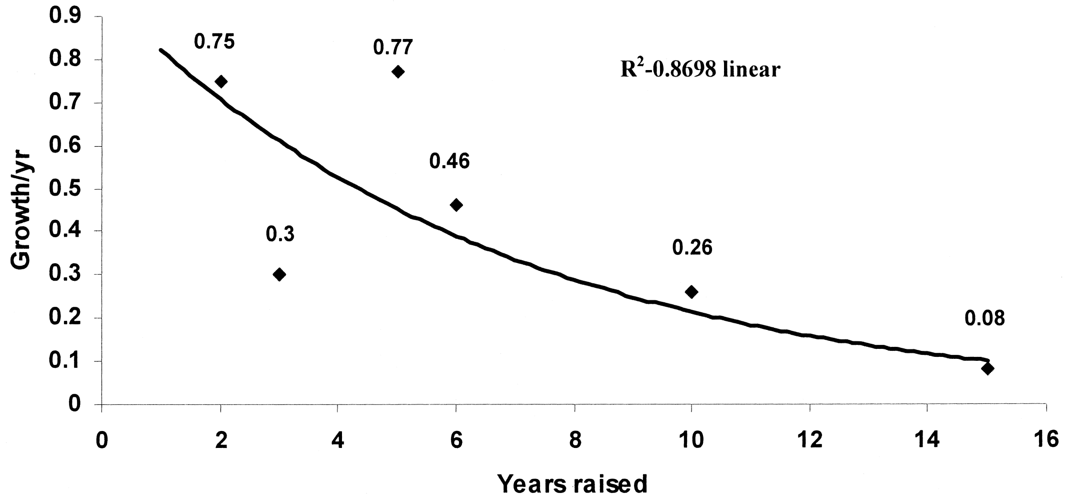

Fig. 1: Average annual growth rate in six adult *N. hierichonticus* raised in the laboratory over 15 years. Growth (g/yr) declined from 0.75 g after 2 years to 0.08 g after 15 years. Growth rate declined markedly (from 0.46 to 0.08 g) after the 6th year.

ticus ranged between 2.5–10.6 g but some scorpions matured when smaller, probably because of the variability in the juvenile's size (Warburg, in prep.).

Regression analysis was used to compare between the different growth rates and scorpions' age.

Since other research on the reproductive system (Warburg, 2010) and cycle required the sectioning of some animals, their ovariuteri were excised and oocytes or diverticulae were counted and measured to distinguish different stages of development (for details see Warburg & Elias, 1998; Warburg, 2001). All the remaining living scorpions were eventually released back to their place of origin on my retirement.

Results

Growth in adult N. hierichonticus

The growth of 33 adult *N. hierichonticus* was followed in the laboratory for several years. These fully grown, mature adults were captured when mature and did not moult in the laboratory. They were probably 4–5 years old when captured, and six were raised for 15 years (Fig. 1).

The average annual gain in mass (Δg) was 0.75 g/yr for a scorpion raised for two years, dropping thereafter to Δ<0.08 g/yr after 15 years (Fig. 1). Growth slowed down considerably (R^2=8698) to less than 0.5 g/yr after six years, and some years later to Δ<0.1 g/yr (Fig. 1).

The average annual gain (Δg) in six mass classes ranged between 0.5–2 g/yr. In the larger mass classes (5–11 g), the gain dropped to Δ<0.1 g/yr (Fig. 2).

The growth rate of seven adults was not related to their initial mass (ranging between 1.55–5 g). There was no relationship between the female's initial size and growth. Nor was their growth related to the number of years they were raised (Fig. 3).

Estimating longevity of N. hierichonticus

As an example of how to estimate longevity indirectly, a female *N. hierichonticus* (weighing 5.73 g) that gave

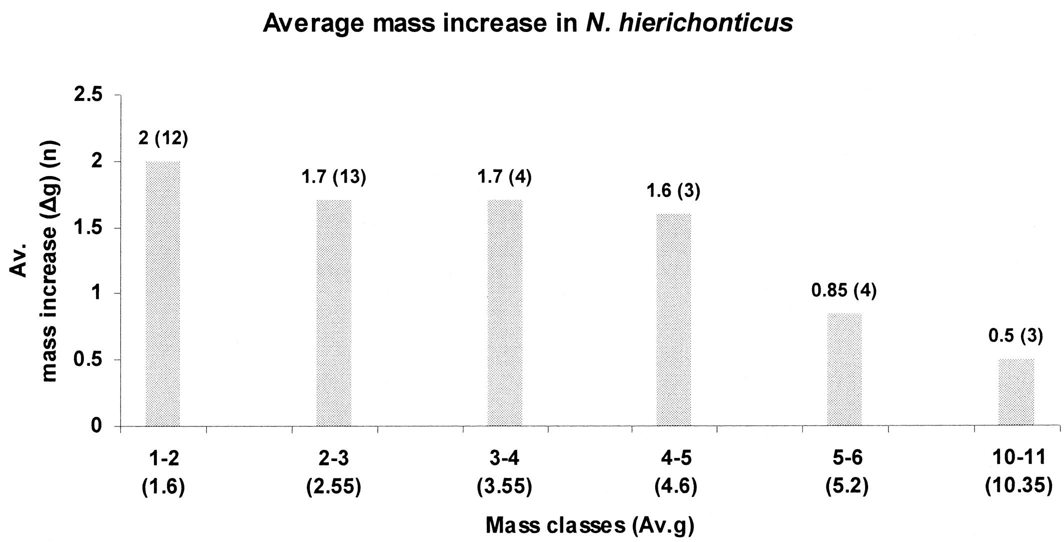

Fig. 2: Average increase in mass in six mass classes of *N. hierichonticus*. Number of scorpions (*n*) in brackets after figure for mass increase. The increase in mass (Δg) drops significantly from 2 g in the lower mass classes, to 0.5 g in the higher mass classes (5–11 g).

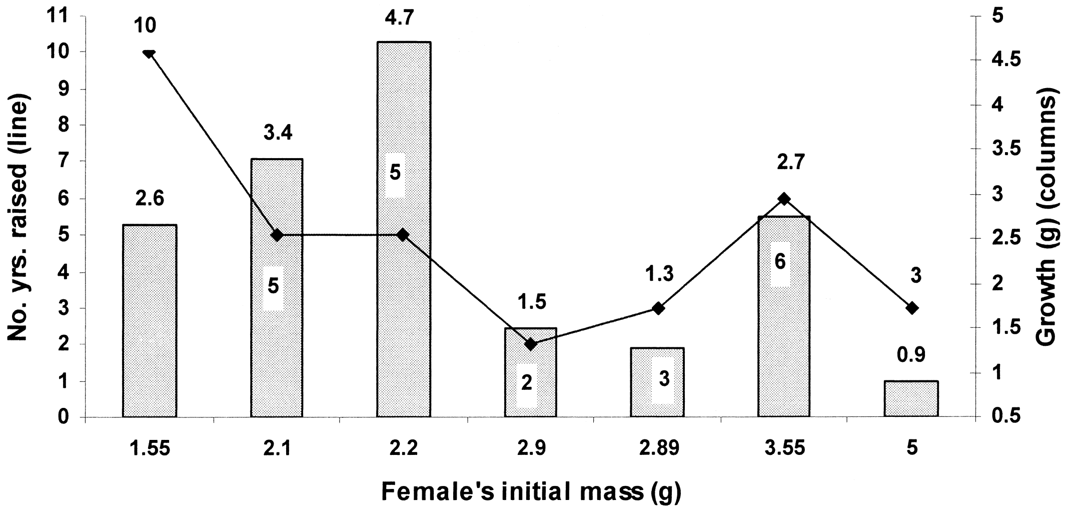

Fig. 3: Relationship between growth rate and the female's initial mass when captured for seven scorpions. The initial mass of the female had no effect on the growth rate.

birth to 25 juveniles was dissected three months later. Altogether, the ovariuterus of that female contained 25 large post-partum diverticulae, 11 half-sized ones, 23 smaller yellow, post-partum diverticulae, and 35 dark coloured, very small ones. From this it can be concluded that this female gave birth three or four times before the present parturition. Since it also contained two generations of small rudimentary diverticulae, it can be assumed that it was capable of giving birth at least 6–7 times to a total of over 100 juveniles. Assuming that it matured at the age of three years and bred only in alternate years, its life span could reach 18 years (see Table 1).

Another *N. hierichonticus* female was captured when about 3-years old (judged from its size). It was raised in the laboratory for another 15 years, reaching the age of 18 years. (With my retirement and the loss of my research facilities, this scorpion among many others, was released back to its original habitat where it was captured 15 years before.)

Discussion

Estimating growth in adult scorpions

There are no published data available on long-term growth in adult scorpions. Most available data refer to growth of juveniles between moults.

Two methods can be used to follow growth:

Species	Age (years)	Source
Urodacus yaschenkoi	10	Shorthouse & Marples, 1982
Urodacus mordax	1.6	Francke, 1976
Centruroides gracilis	4	Francke & Jones, 1982
Centruroides sculpturatus	5	Stahnke, 1966
Tityus bahiensis	3.9	Matthiesen, 1969
Tityus serrulatus	4	Matthiesen, 1971
Isometrus maculatus	5	Probst, 1972
Pandinus gambiensis	8	Vachon *et al.*, 1970
Nebo hierichonticus	18	This study
Scorpio maurus fuscus	17	Warburg & Elias, 1998

Table 1: Longevity in some scorpions.

1. Raise scorpions in the laboratory from birth to death. This way both growth and longevity can be studied. At present this can be done with only a few species [*Pandinus imperator* (Koch, 1841), and *Liocheles australasiae* (Fabricius, 1775)]. The problem is the fact that these laboratory-raised scorpions will never suffer from starvation, predation and other hazardous ambient conditions, and experience nothing resembling the normal, ambient conditions prevailing in the habitat.

2. Another method that overcomes this problem is marking juveniles that were born in the laboratory after their maturation, and releasing them to be recaptured during the following years. The marking technique needs to be such that will neither stress nor harm the scorpion. One difficulty is the differential growth of a scorpion brood. Offspring belonging to the same sibling cohort (=brood or age class, born to a single female during the same parturition) grow at different rates. Thus, in some scorpion species some juveniles are born larger and grow faster than others, consequently they will mature sooner to become larger adults, and breed sooner. Therefore, a population study alone cannot accurately provide an estimate of a cohort's growth. Size (or mass) alone is not a reliable indication that a scorpion (or any other invertebrate) belongs to a certain cohort (or age class). Laboratory observations (supplemented by field studies) should be able to provide additional information.

Estimating longevity in adult scorpions

Longevity or life span is a subject that definitely needs urgent attention. It bears on our evaluation of a species' reproductive potential (Warburg, in prep.), and therefore on the species' vulnerability and whether it is endangered. There are only two ways that I know that could be used:

1. Raise scorpions in the laboratory from birth to death. Currently this can be done with only a few species (*Pandinus imperator* and *Liocheles australasiae*). The problem is the fact that these laboratory-raised scorpions will never suffer from starvation, predation and other hazardous ambient conditions.

2. The above problem can be overcome by marking juveniles born in the laboratory after their maturation, and releasing them to be recaptured during the following years. The marking technique needs to be such that will neither stress nor harm the scorpion. One difficulty is the differential growth of a scorpion brood. Offspring belonging to the same sibling cohort (=brood or age class, born to a single female during the parturition) grow at different rates. Thus, in some scorpion species some juveniles are born larger and grow faster than others, consequently they will mature and breed earlier. Therefore, a population study alone cannot accurately provide an estimate of a cohort's growth. Most data available on longevity are based on population studies estimating the number of individuals, and their size- (or age- ?) class. At the same time the number (and proportion) of females in the population is estimated. Size (or mass) alone is not a reliable indication that a scorpion (or any other invertebrate) belongs to a certain cohort- (or age-class). Laboratory observations (supplemented by field studies) should be able to provide additional information.

Data available on longevity estimates in 16 scorpion species belonging to four families have been summarised up to 1988 (see table 4.4 in Polis & Sissom, 1990). These authors concluded that most scorpions are short-lived organisms that live 2–5 years on average: buthids survive on average 3.2 years, ischniurids 1.3 years and scorpionids eight years. More recently, Lourenço (2002) summarised data on life span in 45 species (including those listed by Polis & Sissom, 1990) belonging to seven families (see table 1 there). The data on longevity do not specify how it was estimated. More accurate data were obtained by D. Mahsberg (pers. comm.) who estimated longevity in laboratory cultured *Pandinus imperator* to reach 15 years (see also Mahsberg & Warburg, 2000). Some species may live for almost a quarter of a century; the Australian *Urodacus yaschenkoi* could live up to 24 years (Shorthouse, 1971).

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