



Differential longevity in free-living smooth snakes *Coronella austriaca*

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During a 31-year study (1992–2022) of reptiles inhabiting a 10 ha area of lowland heath, within a planted coniferous forest in southern England, UK, smooth snakes *Coronella austriaca* Laurenti, 1768, were individually marked with passive integrated transponder tags. New-born smooth snakes were also captured, measured and weighed to estimate size at birth. Growth curves were estimated for females and males which, combined with their estimated size at birth, provided an estimate of age at the time of death. The estimated mean age at death of females (7.8 years) was significantly lower than that of males (10.1 years), with females and males reaching a maximum age of 15 and 25 years respectively. Reproductive effort was considered as a possible explanation for the observed reduced longevity of females compared to males. Female reproductive success increased between 4 and 10 years of age and then declined in the largest breeding individuals, regardless of age. This finding suggested the possible presence of size/growth-related reproductive senescence. This is the first known study to provide reliable estimates of longevity in free-living smooth snakes. It demonstrated a significant difference between females and males in both mean and maximum ages attained, and the potential impact of breeding stress as an explanatory factor for increased female mortality and reproductive senescence.

Keywords: predicted age, body size, SVL, reproductive output, senescence

INTRODUCTION

The study of wildlife population dynamics relies on the ability to sex and age individuals, determine longevity, fecundity and age at death (Townsend et al., 2003). Due to the lack of long-term, individual-based and species-specific data (Colchero et al., 2018), this has largely been addressed through the use of mathematical modelling techniques. However, it is recognised that determining longevity in wildlife populations remains a problem that requires further reliable data on population parameters data to be collected from populations of tagged individuals that are frequently recaptured (Lind et al., 2005; Colchero et al., 2018; Cayuela et al., 2019). Birth and especially age at death are difficult parameters to determine in cryptic species such as amphibians and reptiles. The age of individual snakes is typically estimated using either growth curves for a given species (Plummer, 1985; Shine & Charnov, 1992; Stanford & King, 2004; Fornasiero et al., 2016; Dick & Mebert, 2017), or skeletochronology techniques to count annual growth rings in selected tissues, the latter of which may require either killing an individual animal or removing a bone/tissue sample from it (Waye & Gregory, 1998; Waye, 1999).

In snakes, an estimate of fecundity can sometimes be obtained by palpation to detect developing eggs or embryos (Reading, 2004). Determining the relationship between the number of eggs and/or embryos versus

snake size and estimated age, has often resulted in positive relationships (Luiselli et al., 1996; Sparkman et al., 2007; Bronikowski, 2008; Cayuela et al., 2020; Tully et al., 2020). However, this relationship was weak in *Thamnophis radix* (Stanford & King, 2004) and may also not occur in all geographic locations for a given species such as the smooth snake, *Coronella austriaca* (Dick & Mebert, 2017). Overall, a common factor is that incorrect age estimation can lead to significant error in all of these reported relationships.

Although it has been postulated that in both European and tropical reptiles there may be an increase in mortality (actuarial senescence) or a decrease in reproductive success (reproductive senescence) of females related to age (Dmi'el, 1967; Cayuela et al., 2020; Tully et al., 2020), female mortality due to other causes such as predation, resulting from a reduction in other physical attributes, such as a decline in response time to external stimuli, reduction in visual acuity and overall muscle strength decline due to actuarial senescence may occur before reproductive senescence is either apparent or detectable (Cayuela et al., 2019).

The current 31-year study of individually marked, and frequently recaptured smooth snakes at a heathland site in southern England, has provided a potential opportunity to address the problems associated with the reliable estimation of age and fecundity in a wild snake species and to test the hypothesis that reproductive senescence may

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occur, and/or can be detectable in the oldest females. The objectives of this study were, therefore to 1) determine the age and longevity of wild female and male smooth snakes *C. austriaca* and 2) determine the relationships between body size and age, with fecundity in wild female smooth snakes.

MATERIALS & METHODS

Study site

The study site is an area of approximately 10 ha of lowland heath within a managed coniferous forest in southern England (50°44' N, 2°08' W). It comprises a mosaic of dry heathland, dominated by a fragmented area of heather (*Calluna vulgaris*) and gorse (*Ulex europaeus* and *Ulex minor*), wet heath, dominated by purple moor grass (*Molinia caerulea*) and cross-leaved heather (*Erica tetralix*). Bristle bent (*Agrostis curtisii*) is also present throughout the study area along with small (< 2 m high) regenerated conifers (*Pinus sylvestris*). Much of the ground surface, beneath the vegetation, is covered with moss. Small areas of open sandy soil were also present within the dry heath (Reading & Jofré, 2020).

Data collection and analysis

Between 1992 and 2022 (31 years) multiple surveys for smooth snakes within the study site were completed annually. With the exception of 2002, when only 3 surveys were completed, surveys were spaced approximately one week apart (mean = 21.27/year, SD = 2.406, n = 30; range: 13–28) between the beginning of May and the end of October (depending on weather conditions) using permanent hexagonal arrays of 37 artificial refuges (corrugated steel sheet: 76 cm x 65 cm; Reading, 1997). In each array, refuges were spaced 10 m apart. The total number of refuges used each year varied between 333 and 488 with 407 used annually between 1997 and 2022. During each survey the sex of all captured individuals was determined using the length and shape of the tail (Reading, 2004), their body mass (g) was determined using a Salter spring balance, snout-vent length (SVL) and tail measured (mm) using a 30 cm ruler. On initial capture, snakes were individually marked with a sterilised (70% isopropyl alcohol) Passive Integrated Transponder tag (PIT-tag: ID100) implanted sub-dermally 3–5 cm anterior to the cloaca, and towards the cloaca so that forward movement of the snake would not massage the PIT tag back to the implant needle puncture site before it had healed. The implant puncture site was also sterilised prior to PIT tag implantation. In addition, the lower abdomen of females was gently palpated to determine if they were gravid and if so, the number of embryos they contained. For fecundity analysis only palpation estimates were used if a gravid female was captured during the late summer (July and August) to reduce the likelihood of mistaking food in the gut for early developing embryos. New born individuals were not PIT-tagged as they were considered to be too small, but their head pattern was photographed for individual identification in case of future recapture. Refuge checks

during each survey also included a visual search along a 360 m transect walk between refuges in each array.

The determination of smooth snake age, at assumed death, was only estimated for individuals that were considered to be resident within the ten-hectare study site. The criteria used for residency depended on whether an individual snake had been captured within the study area for at least three consecutive years thereby eliminating potential transient individuals from the analysis. No dead individuals were found during the 31 years of the survey and therefore if an individual was not captured for at least two consecutive years it was assumed to have died.

Many of the snakes that met these two criteria were not first captured as very young juveniles so their year of birth had to be estimated using von Bertalanffy growth curves which were determined by a) an estimated mean SVL at birth and subsequent annual increases in SVL, for each sex, obtained from growth curves plotted for those individuals that had been first captured at a small size and then subsequently recaptured over many years. This growth curve (one for females and one for males) was then plotted with that for each snake that had been first captured as a subadult/adult, and its position along individual growth curves manipulated to enable the birth year, and subsequent age, for each snake to be estimated thereby enabling a determination of age at death.

A cubic regression analysis was used to determine the relationship between the number of offspring produced by gravid females in relation to either their SVL or estimated age. Data analysis was completed using Minitab software (Version 18.1) with $p = 0.05$ used as the threshold for statistical significance in all analyses.

RESULTS

For comparison with other studies of smooth snake growth, that measured total body length (TBL: SVL + tail length) rather than only SVL, the relationship between these two parameters, for females and males within the study area is shown in Fig. 1.

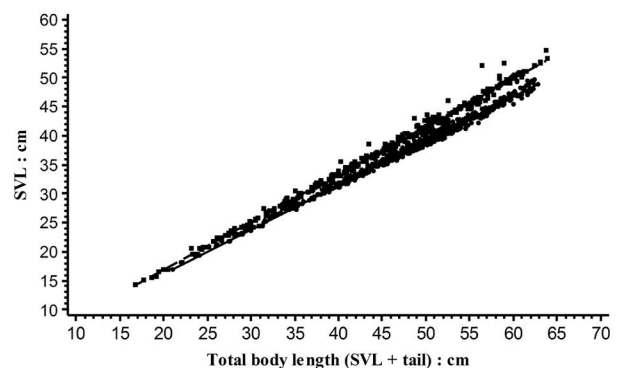


Figure 1. Relationship between SVL and total body length (TBL: SVL + tail length) in smooth snakes in southern England. ●—: mean male SVL = $0.9252 + 0.7635$ mean male TBL; $r^2 = 99.11\%$; $p < 0.001$; $df = 598$. ■---: mean female SVL = $0.1190 + 0.8287$ mean female TBL; $r^2 = 99.47\%$; $p < 0.001$; $df = 338$.

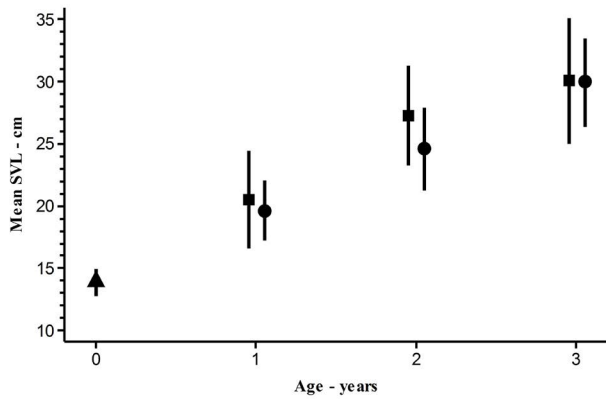


Figure 2. Mean SVL $\pm$ SD against age for female and male smooth snakes (females: ■; males: ●) during their first three full growth seasons plus SVL at birth (▲).

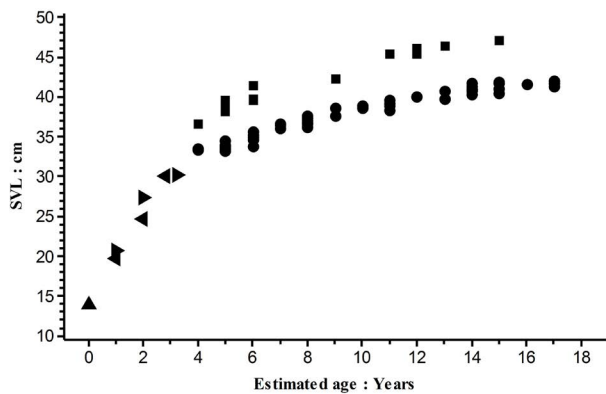


Figure 3. Growth curves for a female and a male smooth snake illustrating how age was estimated from recorded SVL measurements (female: ■; male: ●), mean predicted measurements (female: ◀; male: ▶) and mean SVL at birth (▲).

Between 1992 (14 August) and 2022 (22 September) a total of 298 smooth snakes were captured and individually marked (♀: 127; ♂: 169; undetermined sex: 2). Of these, 102 (♀: 38; ♂: 64) met the criteria for residency (consecutive capture years: ♀: mean = 5.37 years; SD = 2.410; $n = 38$; range = 3–12 years; ♂: mean = 6.94 years; SD = 4.790; $n = 64$; range = 3–24 years) and their age at assumed death estimated after no captures for at least 2 years (♀: mean = 14.71 years; SD = 7.591; $n = 38$; range = 2–27 years; ♂: mean = 14.203 years; SD = 7.622; $n = 64$; range = 2–27 years).

The mean SVL of new born smooth snakes, born in late August/early September (13.84 cm; SD = 1.021; $n = 26$) was determined following captures under refuges where recently gravid females had been frequently found. Following birth, female and male smooth snakes grew at essentially the same rate during their subsequent first three years (Fig. 2). The predicted mean SVL of females and males against age, using the SVL values in Figure 2 to predict the birth year, are given in Figure 3. Female growth subsequently exceeded male growth from the fourth year onwards and also attained a lower maximum age (15 years) than males (25 years; Fig. 4). The oldest female was captured 33 times over 11 years (1993–2003) and the oldest male 167 times over 24 years

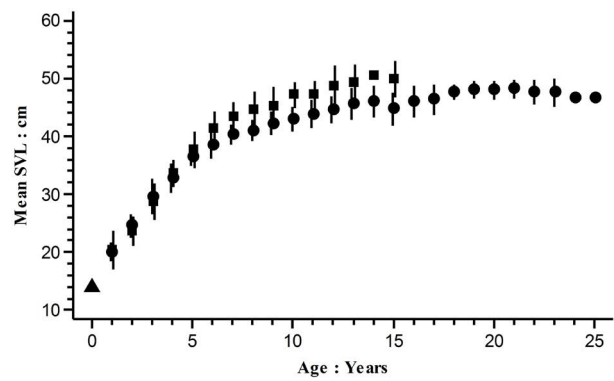


Figure 4. Female (■), male (●) and new born (▲) SVL $\pm$ SD against age.

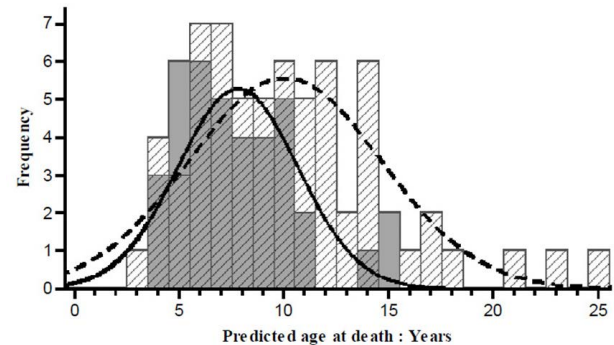


Figure 5. Histogram of female (dark columns) and male (striped columns) predicted age at death with a fitted normal distribution curve (females: —; $n = 38$; males: ---; $n = 64$).

(1997–2020). Overall, the mean age of assumed death for females (mean age = 7.82 years; SD = 2.87; $n = 38$; range = 4–15 years) was significantly lower ($t = 3.04$; $df = 99$; $p = 0.003$) than that attained by males (mean age = 10.06 years; SD = 4.58; $n = 64$; range = 3–25 years; Fig. 5).

One variable possibly correlated with increased female mortality compared to males, is higher reproductive effort. The number of young produced by females of different SVL (Fig. 6a), and estimated age (Fig. 6b) was plotted and analysed using a cubic regression analysis. This showed a significant positive relationship ($p = 0.021$) between the number of young produced by females from an SVL of about 40 cm (approximately when breeding starts), and an estimated age of 4 years, to an SVL of about 49 cm, at an estimated age of 10 years, after which there was an apparent decline in the number of young produced. The fecundity of the largest female (snake #162: ◆) increased with increasing SVL (45.7–49.2 cm) and then declined (SVL: 52.4/52.5 cm; age: 8–15 years). Female #103 (▲), which grew to a relatively large size (SVL: 50.8–51.5 cm) but at a younger age (7/8 years old) than female #162, also showed an apparent decline in fecundity. However, there was no significant relationship ($p = 0.057$) between the number of young produced and the age of females.

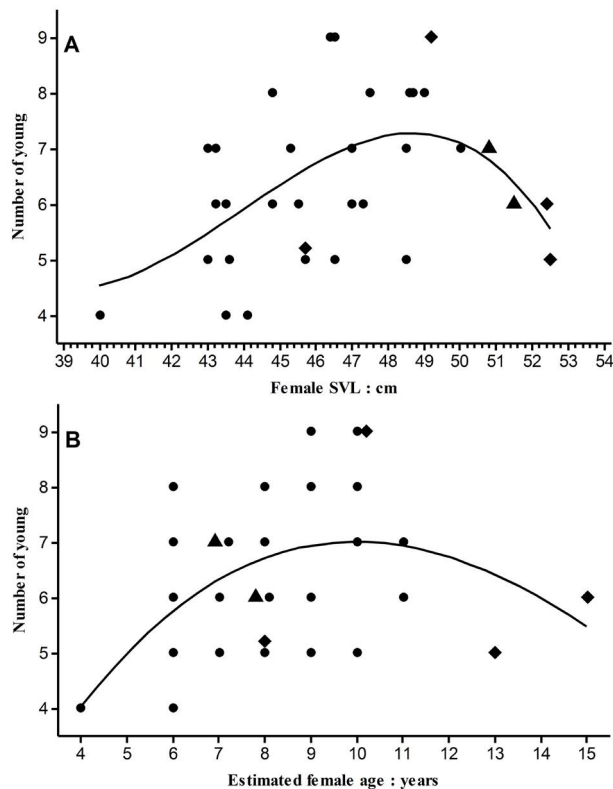


Figure 6. Plots of the number of young produced by female smooth snakes of different SVL – **A.** No. young = $543.5 - 37.59 \text{ SVL} + 0.8656 \text{ SVL}^2 - 0.006566 \text{ SVL}^3$; $r^2 = 27.30\%$; $p = 0.021$; $df = 33$ and estimated age. **B.** No. young = $2.201 + 2.061 \text{ Est. age} - 0.0354 \text{ Est. age}^2 + 0.002143 \text{ Est. age}^3$; $r^2 = 21.83\%$; $p = 0.057$; $df = 33$. $\blacktriangle$: female #103; $\blacklozenge$: female #162; $\bullet$: all other females.

DISCUSSION

Overall, the mean age at death of male smooth snakes was two years greater than that of females, the maximum age attained by males was ten years greater than that of females and, although fecundity generally increased with SVL, there was an indication that it started to decline in the largest females, possibly indicating evidence of size related reproductive senescence.

In this study, smooth snake size was determined by SVL, rather than total body length (SVL + tail), as used in some previously reported studies (Luiselli et al., 1996; Dick & Mebert, 2017; Dalessi et al., 2021; Struijk et al., 2023), as this excludes potential error in determining total body length resulting from tail damage/shortening, an occurrence that was occasionally found in this study.

The largest source of potential error was the determination of death for each individual snake, since dead individuals were never found. This was addressed using the capture data for individuals that had been caught many times over many years. For example, male #89 was first captured on 8 September 1997 and then recaptured for 24 years (mean: 6.87 captures/year; range: 1–13) so its absence in 2021 and 2022 indicates death, after its last capture on 23 July 2020. Similarly, female #87 was first captured on 24 June 1997 and then recaptured annually

for 9 years (mean 5.0 captures/year; range 2–10), so its absence in 2006, and all subsequent years up to 2022, suggests that it died after its last capture on 26 May 2005. The long periods of capture of an individual within the study site were also used to indicate residency within the site, thereby further reducing error in estimating age at death if a ‘transient’ individual simply moved away from the study site. These two examples, along with numerous others, were the basis for reducing error as much as possible in determining both residence and the occurrence of death, for both sexes.

The mean size (SVL = 40 cm) and age (4 years) taken to reach sexual maturity in female smooth snakes in this study differs from some other geographical locations where sexual maturity was reached in one female at two years of age (total body length = 50.9 cm; SVL = 42.2 cm) in the Netherlands (Struijk et al., 2023), but at a longer total body length (mean = 73.4 cm) and probably a greater age in Norway (Dalessi et al., 2021). In the eastern Italian Alps smooth snake females reproduced for the first time with a total body length of 43.5 cm and an estimated age of four years (Luiselli et al., 1996). Apart from the one reported exceptional female from the Netherlands (Struijk et al., 2023), most from that region are similar in size to the females from the UK and suggests that snakes from a similar latitude present with similar growth parameters compared to those from much further north (Norway) and that size at first reproduction in females declines as latitude declines (Norway: 59° N, 10° E; the Netherlands: 51° N, 5° E; UK: 50° N, 2° W; Italian Alps: 46° N, 13° E). Similarly, black rat snakes *Elaphe obsoleta* grew more slowly and matured at a greater age in Canada compared to those further south in the USA (Blouin-Demers et al., 2002) as did garter snakes *Thamnophis elegans* (Bronikowski, 2008).

Sexual size dimorphism in free-living snake populations is not consistent between species. In the smooth snake, females were larger than males in Germany (Dick & Mebert, 2017), Norway (Dalessi et al., 2021) and southern England (Reading, 2004) and also in the plains garter snake *Thamnophis radix* in the USA (Stanford & King, 2004). However, no difference was found between the sexes in the size of European whip snakes *Heirophis viridiflavus* and *H. carbonarius* in France and Italy (Fornasiero et al., 2016).

The attained maximum age of females and males was also inconsistent between species. In meadow vipers *Vipera ursinii* in France, males have a higher adult mortality and a shorter life expectancy than females (Tully et al., 2020) possibly due to increased activity during the mating season and suggested avian predation. In smooth snakes the home range of males is approximately double that of females (Reading, 2012) and suggests that increased male activity does not necessarily result in increased mortality, as males lived to a greater age than females in the present study (females: mean age = 7.8 years; maximum age = 15 years; males: mean age = 10.1 years; maximum age = 25 years). Conversely, life expectancy in female Norwegian smooth snakes was possibly higher than in males (Dalessi et al., 2021). It is

tempting to suggest that reduced female survivorship may be the result of reproductive stress. For example, in a study of a captive colubrid snake *Spalerosophis cliffordi*, old females showed an inability to maintain body weight after successive breeding events suggesting a degree of reproductive senescence (Dmi'el, 1967). Similarly, the mortality rate of Italian smooth snakes was also highest in breeding females and those emaciated following parturition (Luiselli et al., 1996). Conversely, in a 16-year study of garter snakes *Thamnophis atratus* in California, females exhibited a higher survival rate than males, though the need for intensive sampling to gain reliable population parameter estimates was also acknowledged (Lind et al., 2005).

Perhaps the biggest problem that has been recognised with respect to determining senescence in wildlife populations is that mortality may occur before reproductive senescence occurs, or can be detected, (Cayuela et al., 2019). With respect to this study on smooth snakes a significant cubic regression analysis of offspring number against female SVL, indicated that fecundity may have declined in the biggest (SVL > 50 cm), but not oldest individuals. The capture data for females #103 and #162 indicate that reproductive senescence may occur at large size irrespective of age (female #103: SVL = 51.5 cm and 8 years old; female #162: SVL = 52.5 cm and 15 years old). The increase in female fecundity with increasing age/SVL has been reported in many snake species (Luiselli et al., 1996; Stanford & King, 2004; Sparkman et al., 2007; Bronikowski, 2008), whilst in this study SVL appeared to take precedence over age with respect to correlating with reproductive decline. This being the case then it potentially supports the view that senescence may be caused by telomere shortening in relation to increased cell division during rapid growth (Bronikowski, 2008). This was found in garter snakes *T. elegans*, where fast growth resulted in early maturation, production of large annual litters, low annual survival and a reduced lifespan whilst slow growth resulted in late maturation, infrequent production of small litters, increased annual survival and an increased lifespan (Bronikowski, 2008). In the current study both fast and slow growing individual smooth snake females were found, with the fast growing individual (female #103) attaining a lower terminal age (8 years) than the slow growing individual (female #162; 15 years) (Bronikowski, 2008), despite both females being of a similar size.

The length of this individual-based study (31 years) is one of the longest on a wild snake species, and coupled with its high number of annual surveys, has provided a rare opportunity to investigate both sex-related longevity and female reproductive senescence in smooth snakes with potential relevance to other snake/reptile species for which long-term studies are not feasible.

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DATA ACCESSIBILITY

Data is available following an appropriate request to the author.

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