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SKELETOCHRONOLOGICAL ANALYSIS OF AGE IN THREE ‘FIRE-SPECIALIST’ LIZARD SPECIES

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ABSTRACT:

Adverse fire regimes threaten the persistence of animals in many ecosystems. ‘Fire-specialist’ species, which specialise on a particular post-fire successional stage, are likely to be at greatest risk of decline under adverse fire regimes. Life history data on fire-specialists, including longevity, are needed to develop tools to assist fire management for conservation. We used skeletochronology to estimate the age of individuals of three South Australian fire-specialist lizard species: *Amphibolurus norrisi* (Agamidae), *Ctenotus atlas* (Scincidae) and *Nephrurus stellatus* (Gekkonidae). Bone samples were sourced from specimens captured in mallee vegetation predominantly on the Eyre Peninsula, South Australia. Transverse sections of femora were prepared using a standard histological procedure. We counted the minimum and maximum number of lines of arrested growth (LAG) in each sample to provide a conservative and non-conservative estimate of age for each individual. Our results showed that *A. norrisi* may live for at least five and up to seven years, *C. atlas* for at least three and up to four years and *N. stellatus* for at least four and up to seven years. The assumptions that one LAG was deposited per year and that endosteal resorption was minimal must be considered before using these estimates in further research. Our results provide a guide to the potential longevity of the three species which can be used in simulation modelling and genetic studies to improve fire management for animal conservation.

KEYWORDS:

Fire management; life history; lines of arrested growth; longevity; reptile

INTRODUCTION:

Fire is a natural driver of disturbance and succession in ecosystems globally (Pausas & Keeley 2009) but changes in fire regimes, particularly in the last century, have threatened the persistence of many animal species (Gregory *et al.* 2010; Sanz-Aguilar *et al.* 2011; Woinarski *et al.* 2011). The species at greatest risk of decline under adverse fire regimes are ‘fire-specialists’, defined as those which specialise on a particular post-fire stage (e.g. early or late successional) (Driscoll & Henderson 2008). Complete fire suppression can lead to declines of early-successional species (e.g. Templeton *et al.* 2011) while widespread, frequent burning can threaten late-successional species (e.g. Lyet *et al.* 2009). Observations of contrasting needs among animals in fire-prone ecosystems often result in recommendations to maintain a fire mosaic, or successional heterogeneity in vegetation (e.g. Lowe *et al.* 2012). Unfortunately, few studies have quantified the spatial and temporal scales of

fire mosaics that will allow species to persist in an ecosystem (Clarke 2008; Driscoll *et al.* 2010).

Simulation modelling and genetic studies can assist with predicting how animal species will respond to spatial and temporal variation in fire regimes. For example, Bradstock *et al.* (2005) used a spatial simulation model to determine which prescribed burning regimes would allow the persistence of the mallee fowl, *Leipoa ocellata*. This model required detailed life history data on the mallee fowl including time to maturity, fecundity, longevity, territory size and dispersal. Unfortunately, this kind of information is not available for most animals in fire-prone ecosystems (Clarke 2008). Genetic studies also have great potential to inform fire management. For example, Schrey *et al.* (2011) used genetic data from the Florida sand skink, *Plestiodon reynoldsi*, to understand how dispersal and population structure changed after fire. The interpretation of such genetic data relies on a strong understanding of the life history of the target species. In particular, knowledge of the time to maturity and longevity is needed to realistically estimate how long it takes for ecological barriers to influence gene flow (Landguth *et al.* 2010). A detailed understanding of life history parameters, including longevity, is needed for fire-specialist species so that simulation modelling and genetic studies can be effectively used in conservation management.

We aimed to estimate the age of individuals in a sample of three South Australian fire-specialist lizard species using skeletochronology. When lizards undergo seasonal growth deceleration (e.g. torpor), lines of arrested growth develop in their bones which appear distinct from rapidly growing bone when viewed on a histological section (Castanet 1994). The number of lines of arrested growth can indicate the number of seasons a lizard has been inactive, giving an estimate of its age. The lizard species examined were *Amphibolurus norrisi* Witten & Coventry (Agamidae), *Ctenotus atlas* Storr (Scincidae) and *Nephrurus stellatus* Storr (Gekkonidae). *Amphibolurus norrisi* has a mid- to late-successional response to fire which depends on its location (Driscoll & Henderson 2008). The abundance of *C. atlas* usually increases with time since fire in response to the growth of its *Triodia* grass habitat (Driscoll *et al.* 2012) and *N. stellatus* specialises on recently burnt vegetation (Smith *et al.* 2012).

METHODS:

Study system & sample collection

All but one of the 28 bone samples used in this study came from lizards captured in four areas on the Eyre Peninsula, South Australia (**Table 1, Fig. 1**). Sample no. 4 (**Table 1**) was from an *A. norrisi* individual captured approximately 10 km north-east of Border Village, South Australia, west of the Eyre Peninsula. The study areas on the Eyre Peninsula are semi-arid with an annual mean rainfall of 361 mm at Heggaton, 296 mm at Munyaroo, 340 mm at Hincks and 303 mm at Pinkawillinie (Xu & Hutchinson 2011). Most of the rainfall occurs in the cool winters (mean maximum temperature = 16° C) while summers are typically hot and dry (mean maximum temperature = 28° C) (Bureau of Meteorology; Schwerdtfeger 1985). Lizards were captured in mallee vegetation which is characterised by multi-stemmed *Eucalyptus* species. The dominant mallee species on the Eyre Peninsula are *E. costata* and *E. socialis* which are commonly associated with the shrubs *Melaleuca uncinata* and *Callitris verrucosa* and the spiky hummock grass *Triodia irritans*

(Specht 1972). The main topographic features in the region are white sand dunes, occurring in either large, parabolic fields or longitudinal ridges interspersed by swales of heavier, reddish-brown soils (Twidale & Campbell 1985). Summer lightning is the most common ignition source of mallee typically resulting in large, severe wildfires on a decadal (10–100 yr) time scale (Bradstock & Cohn 2002). However, mallee can remain unburnt for over 100 years (Clarke *et al.* 2010).

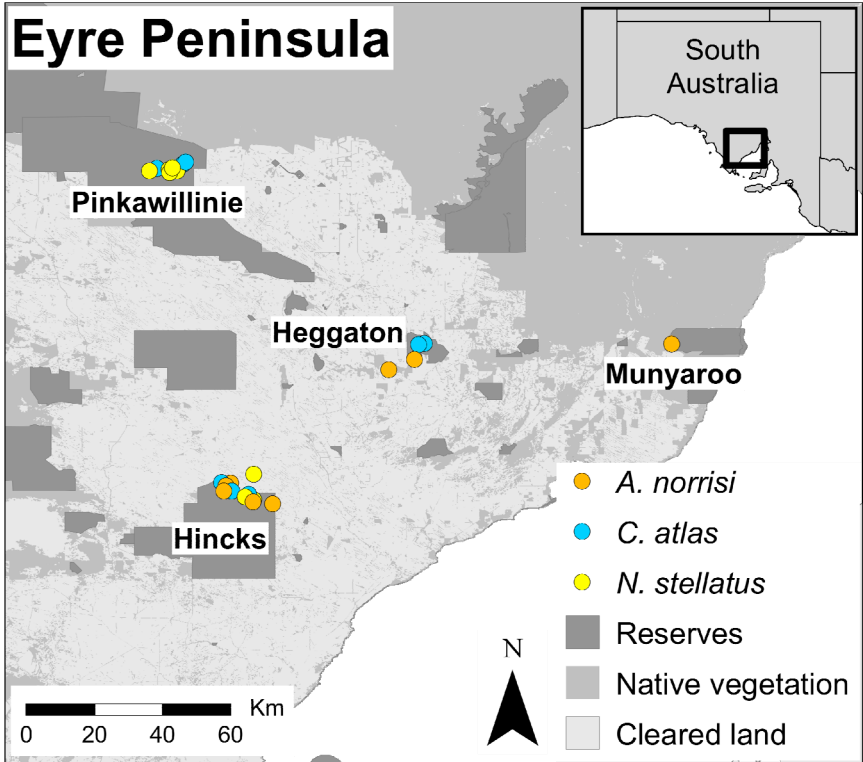


Fig. 1: Location where lizards used in skeletochronological analysis were captured on the Eyre Peninsula, South Australia. One additional sample (*Amphibolurus norrisi*, not shown) was captured approximately 10 km NE of Border Village, SA.

Bone sample numbers 3 and 4 (**Table 1**) came from specimens held in the South Australian Museum (Registration Numbers: R13926 and R26266, respectively) and were collected in October 1972 and September 1984, respectively (spring). The other 26 individuals were collected between December 2004 and January 2010 during a broad-scale study of reptile fire ecology using pitfall trapping (details in Driscoll & Henderson 2008; Driscoll *et al.* 2012; Smith *et al.* 2012). During these studies, occasional trap deaths occurred and, in those cases, specimens were preserved in 95% ethanol and subsequently used for skeletochronology analysis.

In order to determine how well our sampled individuals represented a general lizard population we compared the size (snout-vent length) distribution of our sample to the size distribution of lizards recorded during ecological field surveys. The surveys were conducted at Hincks Wilderness Area and Pinkawillinie

Conservation Park (**Fig. 1**) and full details of the protocol were reported by Smith *et al.* (2012). Briefly, we surveyed 14 sites (six at Hincks and eight at Pinkawillinie) in mallee vegetation ranging from two to 48 years after fire. At each site 25 pitfall traps were set in a 1 ha plot with five rows of five traps spaced at 25 m intervals. Traps were 20 litre buckets buried flush with the ground surface and intersected by a 10 m long, 30 cm high plastic drift fence. We conducted surveys over two consecutive spring/summer seasons: November 2008–February 2009 and November 2009–February 2010. In each season, three trapping sessions were conducted ranging from 5–15 days (mean = 8 days) giving a total trap effort of 17 000 trap nights (8 400 at Hincks and 8 600 at Pinkawillinie). In each trapping session, traps within reserves were opened and closed at the same times and checked every morning while open. We recorded the snout-vent length of each captured individual and applied a unique mark to identify lizards upon recapture (toe clips for *C. atlas* and *A. norrisi* and fluorescent implants for *N. stellatus*). Lizards were released the following day, approximately 5–10 m from their capture location. Only initial captures were used to calculate the size distribution.

Table 1. The number of lines of arrested growth (LAG) in the lizard bone samples and details of individuals sampled. The minimum and maximum number of LAG give a conservative and non-conservative estimate of age in years, respectively.

Sample No.	Life stage	Snout-vent length (mm)	Sex	Number of LAG		Collection location	
				Min.	Max.	Latitude	Longitude
<i>Amphibolurus norrisi</i>							
1	Adult	71	F	1	1	33° 47' 20" S	136° 08' 33" E
2	Adult	72	F	3	3	33° 22' 01" S	137° 11' 55" E
3	Adult	116	F	5	7	33° 25' 60" S	136° 26' 60" E
4	Adult	114	F	3	5	31° 36' 50" S	129° 06' 20" E
5	Adult	74	F	1	1	33° 24' 27" S	136° 31' 05" E
6	Adult	86	M	4	6	33° 45' 18" S	136° 00' 51" E
7	Adult	83	M	3	5	33° 46' 59" S	136° 05' 25" E
8	Juv.	34	Unknown	1	1	33° 44' 30" S	136° 01' 11" E
9	Juv.	38	Unknown	1	1	33° 44' 01" S	136° 01' 58" E
<i>Ctenotus atlas</i>							
10	Adult	68	F	2	2	33° 45' 48" S	136° 04' 47" E
11	Adult	71	F	3	3	33° 21' 53" S	136° 32' 39" E
12	Adult	68	F	1	3	32° 53' 27" S	135° 54' 21" E
13	Adult	69	F	1	1	32° 53' 08" S	135° 54' 47" E
14	Adult	63	M	1	1	33° 45' 48" S	136° 04' 47" E
15	Adult	70	M	3	4	33° 22' 05" S	136° 31' 43" E
16	Adult	66	M	2	4	32° 54' 05" S	135° 50' 15" E
17	Juv.	37	Unknown	1	1	33° 43' 60" S	136° 00' 27" E
18	Juv.	40	Unknown	1	1	33° 45' 16" S	136° 02' 05" E
<i>Nephrurus stellatus</i>							
19	Adult	79	F	2	5	33° 46' 14" S	136° 04' 13" E
20	Adult	75	F	3	3	32° 54' 01" S	135° 52' 41" E
21	Adult	76	M	2	2	32° 54' 16" S	135° 52' 10" E
22	Adult	79	M	3	6	32° 54' 17" S	135° 52' 12" E
23	Adult	75	M	3	4	32° 54' 33" S	135° 53' 24" E
24	Adult	72	M	4	7	33° 42' 39" S	136° 05' 32" E
25	Juv.	54	F	1	3	33° 46' 41" S	136° 05' 34" E
26	Juv.	42	M	2	2	33° 46' 12" S	136° 04' 15" E
27	Juv.	49	M	1	4	32° 54' 47" S	135° 52' 17" E
28	Juv.	38	M	1	1	32° 54' 32" S	135° 49' 03" E

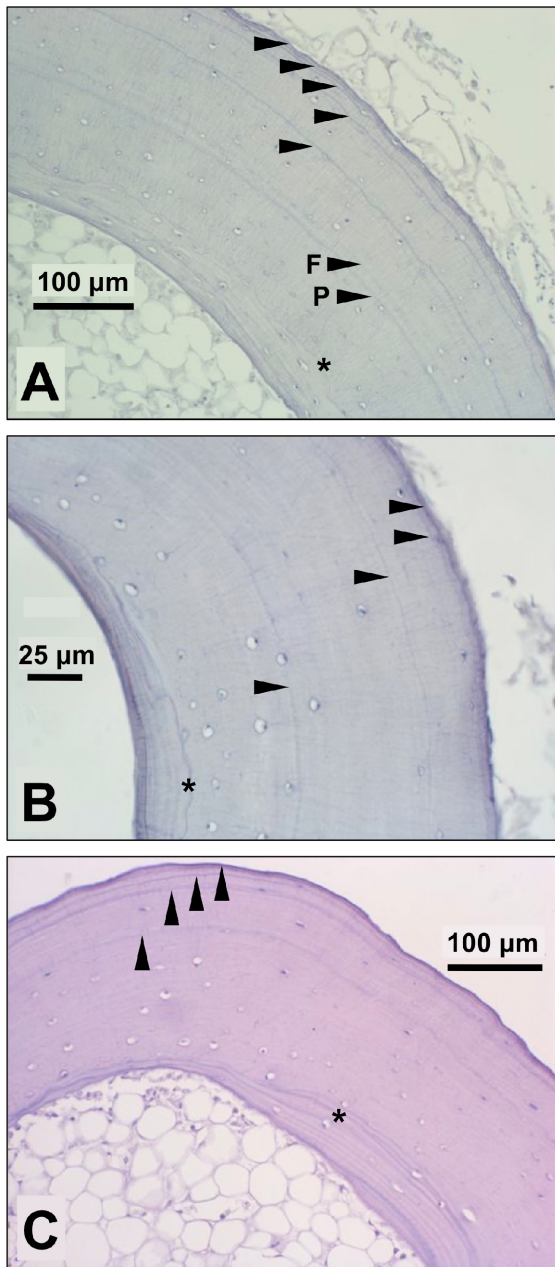


Fig. 2: Examples of bone sections used to estimate age from the number of lines of arrested growth (LAG, arrows) in **(A)**. *Amphibolurus norrisi* (sample no. 3), **(B)**. *Ctenotus atlas* (sample no. 15) and **(C)**. *Nephurus stellatus* (sample no. 23). Examples of LAG scored as faint (F) and prominent (P) are shown on panel A. *Endosteal resorption may have masked some LAG in the bones of adult lizards.

Skeletochronology

We extracted one femur from each lizard specimen (*Amphibolurus norrisi*, N = 9; *Ctenotus atlas*, N = 9; *Nephrurus stellatus*, N = 10; **Table 1**). Compared with other long bones, femora are reported to have clearer growth patterns (Piantoni *et al.* 2006) and less endosteal resorption (Wapstra *et al.* 2001) making them suitable for our study. Femora were decalcified in 5% aqueous nitric acid for seven hours then embedded in paraffin wax. Transverse sections of 5 μ m were cut through the central diaphysis with a Leica rotary microtome and sections were stained in haematoxylin. We viewed sections on an Olympus BH-2 Brightfield microscope and captured images with a Nikon digital camera using NIS Elements 3.2 software. Lines of arrested growth (LAG) were counted from the images.

The LAG in our samples showed variation in clarity so we scored each line as either prominent or faint (**Fig. 2**). This allowed us to calculate a minimum (prominent lines only) and maximum (prominent and faint lines) number of LAG for each sample. Under the assumption that a single LAG is deposited in each inactive season, these values provided a conservative and non-conservative estimate of age in years for each individual. We plotted the minimum and maximum number of LAG against the snout-vent length of each sampled lizard. To examine the relationship between estimated age and body size in each species we used Pearson's correlation tests. We compared the size (snout-vent length) distribution of our bone sample specimens with the size distribution of individuals from our survey data. This allowed us to determine the extent to which our bone samples represented the size range of a general population.

Table 2: Results from Pearson's correlation tests between snout-vent length and number of lines of arrested growth (LAG) for each species. The minimum and maximum number of LAG were analysed separately.

Species	<i>r</i>	<i>P</i>
<i>Amphibolurus norrisi</i>		
Min.	0.777	0.014
Max.	0.814	0.008
<i>Ctenotus atlas</i>		
Min.	0.526	0.146
Max.	0.578	0.103
<i>Nephrurus stellatus</i>		
Min.	0.689	0.028
Max.	0.599	0.067

RESULTS:

Across all individuals, the minimum and maximum number of LAG in our samples, respectively, was five and seven for *A. norrisi*, three and four for *C. atlas* and four and seven for *N. stellatus* (**Table 1**), indicating the potential age in years of the individuals analysed. There were five *A. norrisi*, six *C. atlas* and four *N. stellatus* individuals with equal estimates for minimum and maximum LAG, indicating a similar level of precision among species (**Table 1**). The number of LAG increased with snout-vent length in *A. norrisi* (**Fig. 3a**) and *N. stellatus* (**Fig. 3e**) but the relationship was not significant for the maximum LAG in *N. stellatus* (**Table 2**). There was no correlation between the number of LAG and snout-vent length in *C. atlas* (**Fig. 3c, Table 2**).

Our two largest *A. norrisi* specimens (samples 3 and 4, **Table 1**) were larger than any individuals caught during field surveys (**Fig 3b**), indicating that our bone sample data for this species may represent the upper limit in size (and possibly age) for this species. The largest *C. atlas* specimen (sample no. 11, 71 mm) was smaller than five individuals caught during field surveys, with the largest being 75 mm. However, the size distribution of our *C. atlas* specimens was close to that of the field data (**Fig. 3d**). The largest *N. stellatus* specimens (sample no. 19 and 22, 79 mm) were smaller than 63 individuals caught during field surveys, the largest being 96 mm. Our bone sample data therefore do not represent the largest and potentially oldest *N. stellatus* individuals in a general population (**Fig. 3f**).

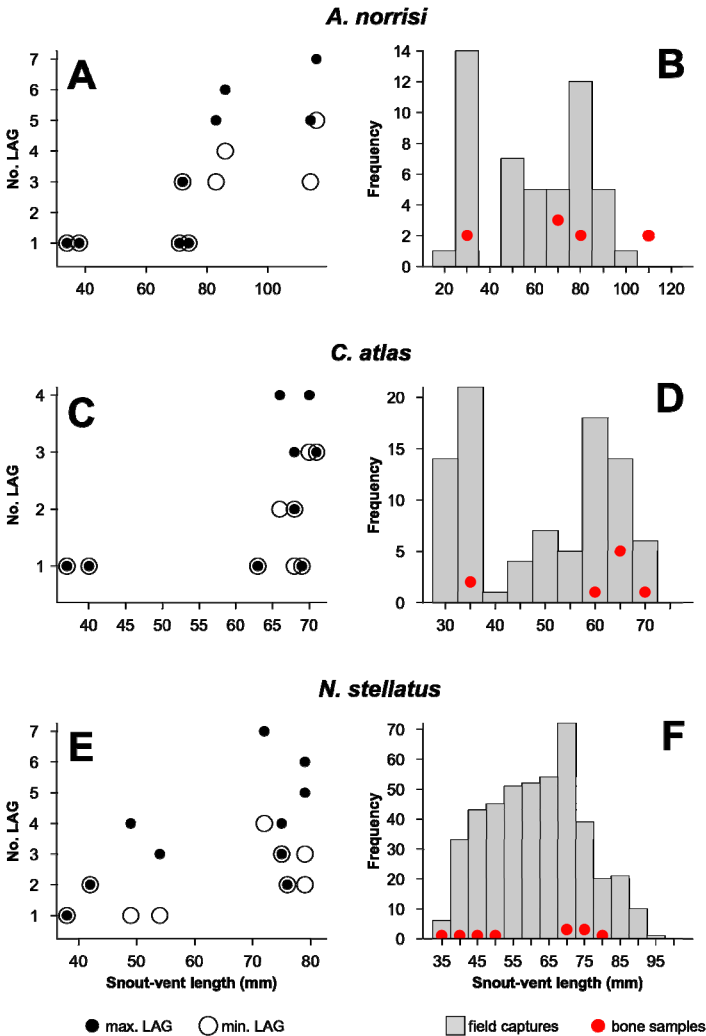


Fig. 3: The relationship between snout-vent length and the minimum and maximum number of lines of arrested growth (LAG) in (A). *Amphibolurus norrisi*, (C). *Ctenotus atlas* and (E). *Nephrurus stellatus*. See **Table 2** for correlation coefficients. (B, D, F) The size (snout-vent length) distribution of a general population is shown in grey bars with the size distribution of the bone samples in red dots.

DISCUSSION:

Under the assumption that a single LAG is deposited in each inactive season, our skeletochronology analysis revealed that *A. norrisi* may live for at least five and up to seven years, *C. atlas* for at least three and up to four years and *N. stellatus* for at least four and up to seven years. These estimates will enable future simulation modelling and genetic research on these fire-specialist species, ultimately improving fire management for conservation. The assumptions made in our analysis must be taken into account when using these estimates in further research and we discuss these before considering the ecological implications of our results.

In some reptiles, more than one LAG can be deposited per year. For example, McCoy *et al.* (2010) found that the number of LAG in the Florida sand skink, *Plestiodon reynoldsi*, often exceeded its probable lifespan. This was attributed to the lack of regular seasonality in the region and to the spatially clustered prey (termites) of the lizards which can lead to bursts of feeding activity throughout the year (McCoy *et al.* 2010). Most studies on herpetofauna report an annual accumulation of LAG (e.g. Castanet & Smirina 1990; Driscoll 1999; de Buffrénil & Castanet 2000). In our temperate, seasonal study region, it seems likely that one LAG would be deposited per year. Furthermore, all samples were collected in the spring/summer period when mallee lizards are most active so it is likely that the first LAG would have been deposited in the winter following their first active season. However, confirming annual LAG accumulation using mark-recapture techniques is important. Long-term mark-recapture studies are also important to confirm upper estimates of age, particularly for longer lived species (>20 years) in which outer LAG may become indistinguishable (Castanet 1994). The maximum estimated longevity in any of our target species was seven years, but we can not rule out the possibility of outer LAG being indistinguishable in some of the older individuals.

Endosteal resorption during expansion of the medullary cavity can remove some of the inner LAG in reptiles leading to an underestimation of age (Castanet 1994). Endosteal resorption of between one and two LAG is commonly reported in lizards (Chinsamy *et al.* 1995; de Buffrénil & Castanet 2000; Curtin *et al.* 2005; Kolarov *et al.* 2010) and resorption of up to three LAG was found in a long-lived (17 yr) gecko (Piantoni *et al.* 2006) and an African cordylid (Curtin *et al.* 2005). Wapstra *et al.* (2001) found resorption of a single LAG was common in the skink *Niveoscincus ocellatus*, while two LAG were sometimes resorbed in older individuals. In *Lacerta agilis boemica* resorption of more than one LAG was rare and the highest resorption rates occurred in two-year old lizards (Roitberg & Smirina 2006). Our sample size was not large enough to reliably estimate resorption rates but we observed endosteal tissue surrounding the medullary cavity on sections from most adult lizards (Fig. 2). Endosteal resorption may have removed LAG so our LAG counts should be considered conservative estimates of age. The studies cited above indicate that resorption of one to three LAG can occur in lizards and this gives a guide to the potential error in our estimates.

The observation that some LAG had greater clarity than others prompted us to provide both conservative (prominent LAG only) and non-conservative (all LAG) estimates of age. The data we present are likely to be useful for future genetic and simulation modelling studies and different analyses may require different levels of conservatism. Our results enable researchers to consider the level appropriate for

their question. One explanation for the observed variation in LAG clarity is that environmental conditions during the inactive period varied among years (Castanet & Smirina 1990). For example, variation in winter temperatures that affect metabolic rates of the lizards may have led to variation in the appearance of the LAG. Inter-annual variation in seasonal conditions may also explain differences in the width of the actively growing bone (e.g. **Fig. 2**) although these differences are also affected by age-related growth rates (Leclair & Leclair 2011).

Lizards typically undergo rapid juvenile growth rates which slow after reaching maturity, and such patterns have previously been reported using skeletochronology. For example, Wapstra *et al.* (2001) examined bone sections of 158 individuals to analyse environmental and demographic effects on longevity in *Niveoscincus ocellatus*. Such a detailed analysis was not possible on our limited data set but some growth patterns were evident in our results. For example, the lack of significant linear relationships between snout-vent length and the number of LAG for *C. atlas*, and the maximum number of LAG for *N. stellatus*, may reflect rapid juvenile growth rates which slow after maturity. A larger data set would have allowed us to explore more complex, non-linear models (e.g. the von Bertalanffy model) to describe growth in these species. There was a stronger relationship between snout-vent length and the number of LAG in *A. norrisi*, possibly reflecting a slower growth rate in this species. Investigating growth rates with larger data sets (e.g. mark-recapture data) will be important for understanding the ecology of the target species and their relationship with fire.

Despite the limitations of the skeletochronology method, our results provide a general guide to the potential longevity in our three target species. We found that *A. norrisi* may live for five to seven years, two to three years longer than its congener *A. muricatus* which has a lifespan of three to four years (Warner & Shine 2008). Our results suggested that *C. atlas* may live for three to four years which is close to the range of estimates derived from growth rates of five other *Ctenotus* species (3.6–5.4 yr, James 1991). Read (1998) derived similar estimates from recaptured *C. schomburgkii* (5 yr) and *C. regius* (4 yr), while *C. leonhardii* had a longer lifespan (5–7 yr). At the time of this report, two captive *N. stellatus* individuals were still alive after eight (male) and seven (female) years of age (D. Hossack, pers. comm.), longer than our estimate of four to seven years for this species. Cessation of breeding in the past year indicated these animals were reaching old age (D. Hossack, pers. comm.). Although captive-reared animals tend to live longer than wild animals, our results suggested that we did not sample the largest, and possibly oldest, geckos in the population. Lifespans of eight or more years therefore seem possible for wild *N. stellatus*. Our study of longevity in three fire-specialist lizards will be important for continued research into appropriate fire regimes for biodiversity. Skeletochronology can also be useful in other areas of conservation biology, for example to inform habitat management for threatened species (e.g. de Buffrénil & Castanet 2000) or to examine the effects of contrasting climatic conditions on population age structure and longevity (e.g. Wapstra *et al.* 2001).

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