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Partitioned parturition: Birthing asynchrony in cordylid lizards

J. L. Riley[1,2,3], J. Baxter-Gilbert[4], M. J. Whiting[5] & M. Cherry[1]

[1]Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa
[2]Department of Biology, Dalhousie University, Halifax, NS, Canada
[3]Department of Biology, Mount Allison University, Sackville, NB, Canada
[4]Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa
[5]Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia

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Correspondence
Julia Riley, Department of Biology, Mount Allison University, 62 York St., Sackville, NB E4L 1E2, Canada.
Email: jriley@mta.ca

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Abstract

Hatching/birthing asynchrony, when siblings emerge at least 12 h apart, is thought to be a significant driver of phenotypic variation and group cohesion that is commonly reported in invertebrates and birds, but rarely in squamates. We examined birthing asynchrony in African cordylid lizards (Cordylidae), a clade characterized by a wide range of sociality (a hypothesized evolutionary driver of this unique phenomenon). We monitored parturition from wild-caught mothers from four species, which vary in their conspecific grouping behaviour. In two species, most litters were born asynchronously, over a maximum of 3–4 days respectively. The other two cordylids also exhibited asynchronous birth in all litters with more than one offspring, although this was not applicable for most litters because there was a prevalence of singleton litters. Our study uncovered birthing asynchrony in a novel taxonomic group, which suggests it evolved convergently in at least two social lizard clades from different continents. Furthermore, the function of birthing asynchrony and limiting litter size to a single offspring may be similar in social animals. We discuss the potential significance of this rare phenomenon in this disparate taxon, and compare it with other more well-studied taxa, in order to guide future research directions.

Introduction

The order in which siblings emerge into the world can have profound, lifelong impacts on their behaviour and ecology (Mock, 2006; Schrader & Travis, 2012; Smiseth et al., 2006; Sulloway, 2001). Hatching or birthing asynchrony (aka., prolonged parturition; Chapple, 2003) occurs when a clutch hatches, or a litter is born, over a wide inter-birth interval (e.g. a minimum of 12 h between individuals; While et al., 2007). Although well documented in invertebrates and birds, leading to an array of theorized functions (e.g. as a bet-hedging strategy for phenotypic diversity and survivorship; Amundsen & Slagsvold, 1998; Laaksonen, 2004), hatching/birthing asynchrony in non-avian reptiles has garnered far less attention (While et al., 2007; While & Wapstra, 2008, 2009), which constrains our general understanding of this phenomenon and the selective pressures driving its convergent evolution. Squamate reptiles are typically oviparous (80% of species; Pyron & Burbrink, 2014) and hatching asynchrony has been documented in eastern three-lined skinks (*Bassiana duperreyi*; Radder & Shine, 2007). In addition, asynchronous birth has been reported in viviparous species. For example, it has been anecdotally reported in northern watersnakes (*Natrix sipedon*; Bauman & Metter, 1977) and has been best studied in the social Australian skinks from the subfamily Egerniinae (see Table 3 in Van Dyke et al., 2021). Female egerniine skinks can actively retain fully developed offspring, giving birth to them one at a time over a period of hours to days, even when multiple offspring are within the same uterus (While et al., 2007). Factors relating to complex sociality in these lizards have been suggested to be potential drivers of birthing asynchrony in this group (Chapple, 2003; While & Wapstra, 2008, 2009). Yet even solitary-living species within this clade exhibit asynchronous birth (e.g. the Eastern mourning skink, *Lissolepis coventryi*; Manning, 2002), perhaps due to phylogenetic or physiological constraints imposed by the evolution of social living.

The presence of similar, or convergent, natural and life history traits is often found across social vertebrates (Gardner et al., 2016; Ward & Webster, 2016; Whiting & While, 2017). For example, it has been proposed that the life history strategy of family living and/or cooperative breeding species is characterized by delayed sexual maturity, high adult survival and longevity, and low reproductive and dispersal rates (MacArthur & Wilson, 1967; Ward & Webster, 2016). Evidence from cooperatively breeding birds (e.g. Cockburn, 1998; Edwards &

Naeem, 1993), family living reptiles (e.g. lizards; Whiting & While, 2017), and fishes (e.g. sharks and rays; Jacoby et al., 2012) supports the relationship between these particular life history traits and complex sociality. Thus, knowledge of a species' sociality may also provide insight into other aspects of its biology. For example, sociality has been linked to a species' mating system (Gardner et al., 2016; Lukas & Clutton-Brock, 2013), foraging mode (Whiting & While, 2017), communication (Phillips & Austad, 1996), cognitive ability (Byrne & Bates, 2007; Whiten et al., 2016), parasite transmission (Bull et al., 2012; Kappeler et al., 2015; Rimbach et al., 2015), predation rates (Graves & Duvall, 1995), and space use (Jetz et al., 2004). As such, we can use our knowledge of the natural and life histories of well-studied social taxa to make predictions regarding the biology of understudied species either with close evolutionary associations or convergent social tendencies.

Here, we examine if birthing asynchrony is present in a geographically distinct, but ecologically and socially similar clade of reptiles to the egerniine skinks, the cordylid lizards (Cordylidae) of sub-Saharan Africa (Riley et al., 2021). The family Cordylidae contains 10 genera (Stanley et al., 2011), and like many of the egerniine skinks, cordylid lizards are crevice- or burrow-dwelling, ambush foraging, viviparous lizards with small litter sizes (typically 1–4 offspring, but up to 7 for certain species; Reissig, 2014) that display a varying degree of sociality, ranging from solitary to large social groups (Mouton, 2011; Whiting & While, 2017). Furthermore, conspecific aggression and infanticide occurs regularly in egerniine skinks (family Scincidae) (While et al., 2015) and has been suggested to be an important driver for the evolution of parental care in this clade (e.g. associations between mothers and offspring reduce the threat of infanticide by conspecifics; O'Connor & Shine, 2004). Conspecific aggression has also been hypothesized to be an evolutionary driver of asynchronous birth because it allows offspring to gradually integrate into social groups with parental protection (Amundsen & Slagsvold, 1998; Laaksonen, 2004; Stenning, 1996). Recent observations have similarly noted that infanticide and cannibalism occur in several species of free-living cordylid lizards (van Blerk et al., 2021). Given the behavioural and ecological parallels between these lizard clades, we expect that birthing asynchrony is present in Cordylidae. To test our hypothesis, we monitored the parturition of four cordylid species that varied in their conspecific grouping behaviour. Additionally, we explored whether the inter-birth interval between offspring in cordylids depends on their degree of sociality, and whether there are differences between offspring morphology based on their order of birth. These are both key questions regarding whether birthing order is adaptive and what selective pressures drive the evolution of asynchronous birth.

Materials and methods

Study species and sites

The four cordylid species (representing four genera) we examined vary in their conspecific grouping tendency (Bates et al., 2014; Mouton, 2011). The Southern Karusa Lizard (*Karusasaurus polyzonus*) is typically solitary living within rock crevices (Reissig, 2014). Indeed, we observed *K. polyzonus* basking or sheltering alone most of the time (77% of observations) but also infrequently in groups of two to three individuals (J. Riley unpublished data). Both Peers' Nama Lizard (*Namazonurus peersi*) and the Large-scaled Girdled Lizard (*Cordylus macropholis*) live in medium-sized groups that include both juveniles and adults, and they, respectively, aggregate in crevices within rock outcrops and the succulent plant *Euphorbia caput-medusae* (Mouton, 2011). We observed *N. peersi* and *C. macropholis* in groups of up to 4 and 12 lizards respectively (J. Riley unpublished data). The Armadillo Lizard (*Ouroborus cataphractus*) can live in groups of up to 60 individuals in rocky outcrops (Mouton et al., 2014) and we observed *O. cataphractus* in groups of up to 27 juveniles and adults (J. Riley unpublished data). We studied one population of each of these species in the Western Cape province of South Africa (specific location details are withheld due to the threat of poaching; CITES, 2021).

Fieldwork and captive husbandry

In January 2019, we collected gravid females by hand, lizard lasso, or Elliot trap. We captured 20 K. *polyzonus*, 15 *N. peersi*, 22 *C. macropholis*, and 28 *O. cataphractus*. After capture, we then transported lizards in individual cloth bags to Stellenbosch University where we housed females individually in a climate-controlled room (~26°C) within transparent plastic tubs (28.5 cm $W \times 41$ cm $L \times 18$ cm H) to monitor parturition (see Appendix S1 for husbandry details).

From February to April 2019, we visually checked twice daily (08:00–09:00 h and 15:00–16:00 h) whether females had given birth and recorded the time and date offspring were found. We then measured offspring morphology (see Appendix S1) and uniquely marked them with a toe-clip (Ferner, 1979). Only a subset of females from each species gave birth: 55% (11/20) of *K. polyzonus*, 80% (12/15) of *N. peersi*, 91% (20/22) of *C. macropholis,* and 43% (12/28) of *O. cataphractus*. This suggests that these species may not reproduce annually, which mirrors reproductive trends found in other cordylid lizards (e.g. the Sungazer, *Smaug giganteus*; van Wyk, 1994) and egerniine skinks (Chapple, 2003; While, Uller, & Wapstra, 2009).

Data summary and statistical analyses

We calculated the mean ($\bar{x}$), median, standard error, and range (minimum and maximum) for each species' litter size and the approximate duration of birth (h). The duration of birth was calculated by subtracting when the last offspring within a litter was found from the time when the firstborn was found (i.e. if the last offspring was found at 15:00 and the firstborn was found at 08:00 the day prior, then the duration of birth was calculated to be 31 h). This is a coarse measure of birthing duration that is dependent on our study design. Future research should aim to monitor birthing asynchrony 24/7 remotely using video cameras. We were also restricted in the inter-species comparisons that could be made because only *K. polyzonus*

and *C. macropholis* had more than one litter comprising two offspring or more.

We compared the approximate duration of birth between *K. polyzonus* ($n = 11$) and *C. macropholis* ($n = 20$) using a Type I analysis of variance (ANOVA) that was performed using the R package '*car*' and the function '*aov*' (Fox & Weisberg, 2019) in R version 3.5.0 (R Core Team, 2018). Before performing the ANOVAs, a Levene's test (using the '*leveneTest*' function in the R package '*car*'; Fox & Weisberg, 2019) was performed to check for homogeneity of variance, which was verified in this case. We also calculated the overall effect (η^2) of species – how much variation in duration of birth can be explained by the variation between species – using the R package '*effectsize*' and the function '*eta_squared*' (Ben-Shachar, Lüdecke, & Makowski, 2020). In addition, we tested for differences in morphology of offspring depending on their birth order to explore the adaptive significance of birthing asynchrony. Owing to sample size constraints, we report this morphological analysis in Appendix S1.

Results

Karusasaurus polyzonus gave birth between 17 March 2019 and 3 April 2019 (Fig. 1a). Litter size was, on average, three individuals (median = 3, SE = 0.14, range = 2–3, $n = 11$). The majority (64% or 7/11) of litters were born asynchronously (Fig. 2a). On average, litters were born across 31 ± 9 h (median = 26 h, range = 0–74 h). The interval between birth of the first and second offspring was, on average, 11 ± 6 h (median = 0 h because 8/11 first and second offspring were born at the same time, range = 0–49 h), and the interval between the second and third offspring was, on average, 28 ± 7 h (median = 26 h, range = 0–49 h).

Namazonurus peersi gave birth between 16 March 2019 and 9 April 2019 (Fig. 1b). Litter size was, on average, one individual (median = 1, SE = 0.08, range = 1–2, $n = 12$). In fact, all but one of the litters consisted of a single individual (Fig. 2a); the litter with two offspring was born asynchronously taking 48 h for both individuals to be born (Fig. 2b).

Cordylus macropholis gave birth between 12 February 2019 and 22 March 2019 (Fig. 1c). Litter size was, on average, two individuals (median = 2, SE = 0.07, range = 1–2, $n = 20$). Fifteen per cent (3/20) of *C. macropholis* litters were comprised of one offspring, and, of the two-offspring litters, the majority (60% or 12/20) were born asynchronously (Fig. 2a). On average, litters were born across 42 ± 8 h (median = 47 h, range = 0–96 h); this also represents the average time interval between the first and second offspring.

Ouroborus cataphractus gave birth between 25 March 2019 and 26 April 2019 (Fig. 1d). Litter size was, on average, one individual (median = 1, SE = 0.08, range = 1–2, $n = 12$). All but one of the litters consisted of a single individual (Fig. 2a); the litter with two offspring was born asynchronously and took 25 h (Fig. 2b).

We found no significant difference between the duration of birth of *C. macropholis* and *K. polyzonus* ($F_{1,27} = 0.44$, $P = 0.51$). The overall effect of species was low ($\eta^2 = 0.30$) and non-significant as the confidence level includes 0 (95% CI = 0.00, 1.00).

Discussion

Our findings support asynchronous birth being present within the Cordylidae. The majority of *K. polyzonus* (64%; solitary) and *C. macropholis* (60%; group living) multi-offspring litters were born asynchronously over 1–3 and 1–4 days respectively. The duration of birth in these two species was not significantly different, so there was no evidence that the degree of sociality was moderating birthing asynchrony in cordylids. This is reinforced by the fact that *N. peersi* and *O. cataphractus* litters with more than one offspring were also born asynchronously. Yet, for both species, the identification of asynchronous birth did not apply for the majority of litters as they consisted only of a single offspring. Regardless, we found clear evidence for asynchronous birth in wild populations of cordylid lizards regardless of their degree of sociality. Comparing the occurrence of this phenomenon between African cordylid lizards and Australian egerniine skinks suggests this trait may have convergently evolved in these two clades, and that it appears correlated with a suite of ecological and social traits (While et al., 2007; While & Wapstra, 2008, 2009). Interestingly, the presence of birthing asynchrony for less social species (e.g. *K. polyzonus* in this study or *L. coventryi* from Egerniinae; Manning, 2002), suggests two possibilities. This ability is likely to be ancestral within both clades perhaps due to phylogenetic or physiological constraints potentially associated with species that have litters of few large offspring. Asynchronous birth may then be retained as species became more social (i.e. 'concentrated parental care' hypothesis), or increased phenotypic variation and alternative dispersal strategies (i.e. 'diversity through sibling rivalry' hypothesis) confer advantages regardless of a species' sociality. Since egerniine skinks are capable of delaying parturition of fully developed offspring (While et al., 2007), and birthing asynchrony is present even within 'solitary' species of both lizard clades, selection is either neutral or maintains this ability.

Multiple factors that relate to complex sociality (i.e. family living) in egerniine skinks (e.g. alternative dispersal strategies, parental care trade-offs, and social cohesion) have been suggested to be potential drivers of birthing asynchrony (Chapple, 2003; While & Wapstra, 2008, 2009). One hypothesis asserts that staggering parturition could allow for neonates to gradually integrate into social groups and in doing so may promote group cohesion and reduce aggression by other adults in the group, which lowers the mortality risk of offspring (Chapple, 2003). Furthermore, as parental care in egerniine skinks reduces offspring mortality from conspecifics (O'Connor & Shine, 2004), mothers can prolong the duration between the birth of siblings to 'buy' themselves time to focus their protective behaviour on only a single offspring while the social group is becoming familiarized with the novel individual. This 'concentrated parental care' hypothesis would mean that, through asynchronous birth, mothers increase their litter's survival rate by ensuring their offspring are introduced to their social group in a stepwise fashion. Similarly, the same benefits

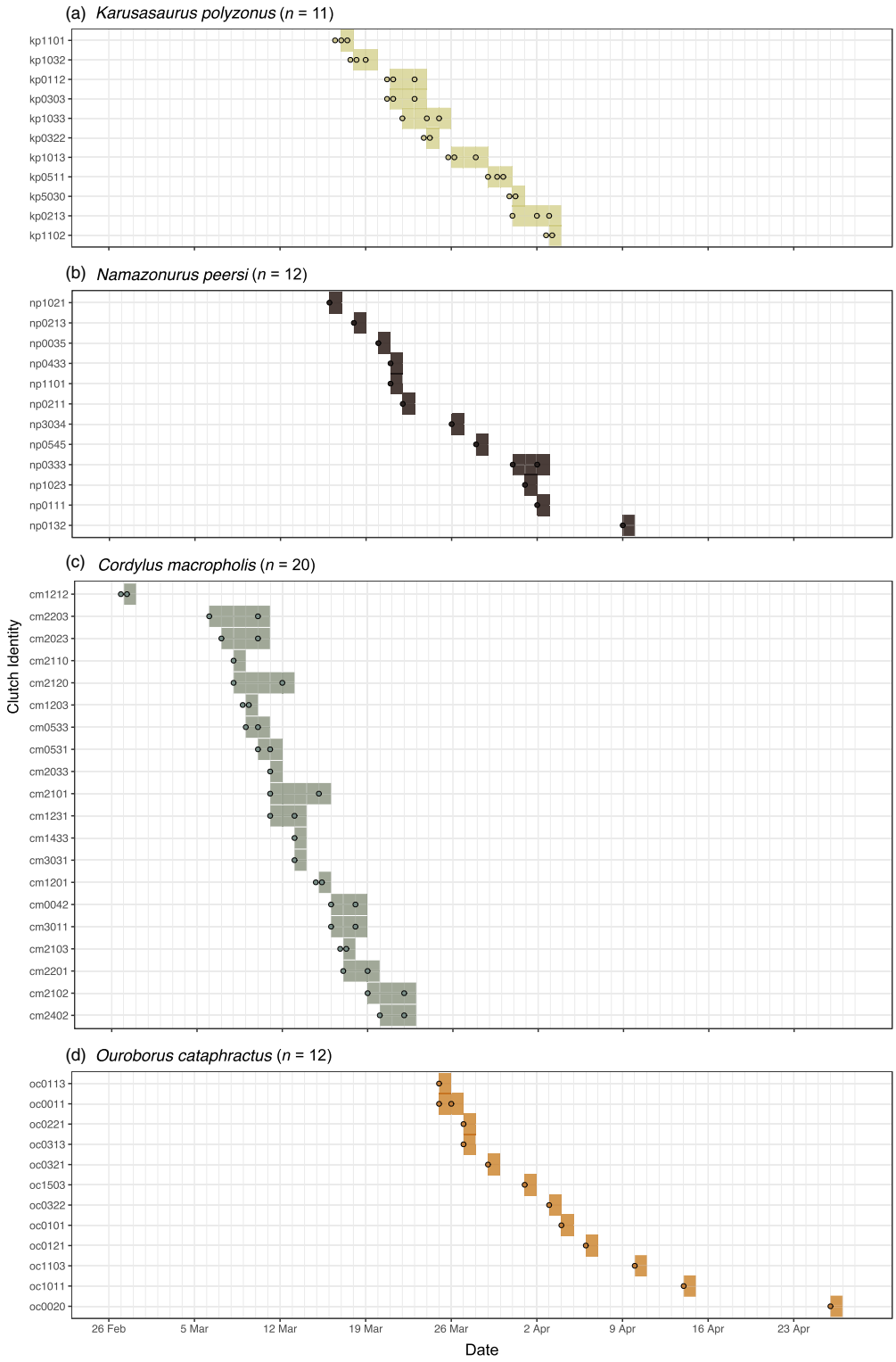

Figure 1 A diagram of the birth timing for each cordylid species litter in our study. The rectangles span the start and end dates for parturition of each litter, and the circles represent the dates on which individuals in the litter were found post-birth. The circles of individuals that were found on the same day are slightly offset the midline. Data are shown for (a) *Karusasaurus polyzonus* (beige), (b) *Namazonurus peersi* (dark grey), (c) *Cordylus macropholis* (light grey) and (d) *Ouroborus cataphractus* (orange-brown).

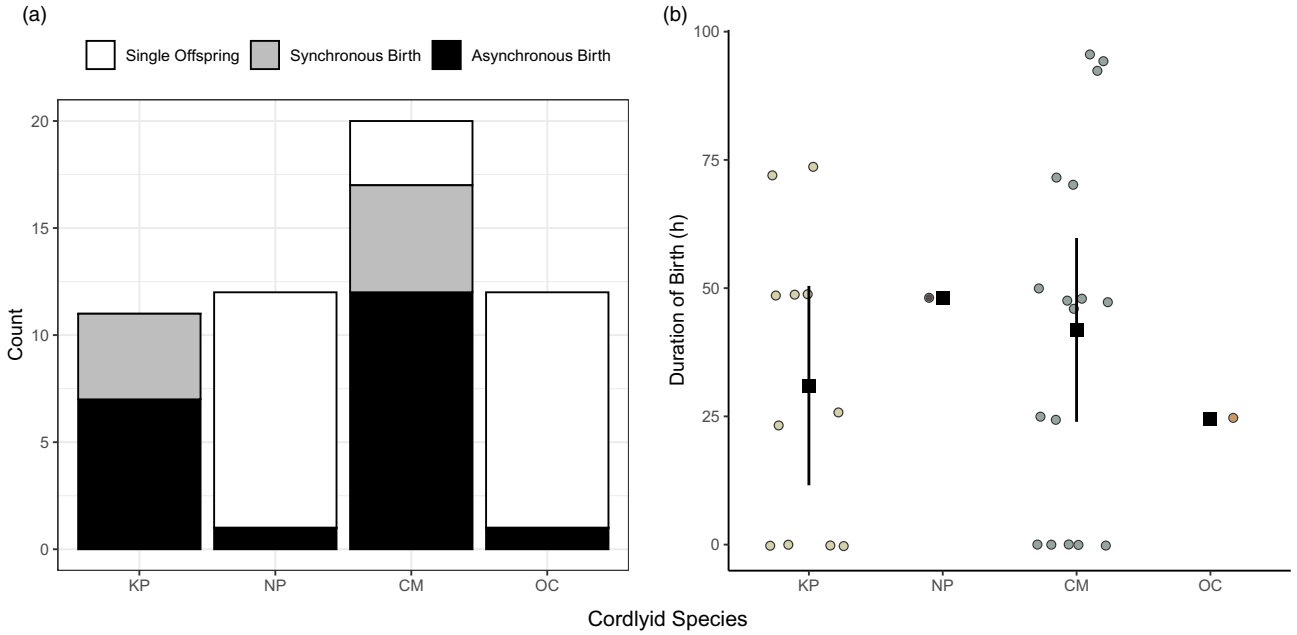

Figure 2 (a) A stacked bar chart of the number of litters for each cordylid species (KP = *Karusasaurus polyzonus,* NP = *Namazonurus peersi,* CM = *Cordylus macropholis* and OC = *Ouroborus cataphractus*) that either contained a single offspring or wherein multiple offspring were born synchronously or asynchronously (i.e. across a period of more than 12 h). (b) The duration of birthing interval observed for each cordylid species. Raw data are shown using circles, and the mean ± 95% confidence intervals are represented with a black square and lines respectively. Note that the sample size of $n = 1$ for *Namazonurus peersi* and *O. cataphractus* precludes the inclusion of confidence intervals.

that asynchronous birth affords – by having to safeguard only one neonate at a time – would be experienced by mothers that have a single-offspring litter, like the majority of *N. peersi* and *O. cataphractus* in our study. Having a single offspring may well be energetically adaptive for particular cordylids; the energetic consequences of producing offspring with extensive osteodermal armour may physiologically limit litter size (Broeckhoven, 2015). Yet, While and Wapstra (2008) also found that, from a parental care perspective, one offspring may be an optimum for both energetic costs and predation risk in the White's skink (*Liopholis whitii*). Also hatching asynchrony in birds and some invertebrates is hypothesized to be a means of brood reduction, similarly echoing that a smaller clutch/litter size reduces parent–offspring conflict (Ento et al., 2010; Forbes, 1993). Thus, the similarities in benefits from both asynchronous birth (i.e. only have one offspring to care for a duration of time) and having a singleton litter may explain its presence in these social lizards. But this hypothesis requires further investigation within both these geographically and evolutionarily distinct lizard clades.

An alternative, but not mutually exclusive, hypothesis regarding the evolutionary drivers of birthing asynchrony suggests that it can increase offspring variation through sibling dominance hierarchies, which promote both phenotypic variation and alternative dispersal strategies (Laaksonen, 2004; While & Wapstra, 2008) – the 'diversity through sibling rivalry' hypothesis. Yet, within-litter timing of birth did not affect growth or survival in *L. whitii* (While, Uller, McEvoy, et al., 2009), and here we did not find that birthing order affected offspring morphology immediately after they were born in *K. polyzonus* or *C. macropholis* (see Appendix S1); albeit this analysis was limited by sample size and was not assessed longitudinally (e.g. growth rate differences generated due to sibling rivalries). However, the impact of birthing order has been observed across the animal kingdom – from beetles (Smiseth & Morgan, 2009; Takata et al., 2015) to birds (Bitton et al., 2006) to humans (Eckstein et al., 2010; Sulloway, 2001). Specifically within many avian systems, birth order is known to impact growth rate, body size and survival, with early-hatching offspring benefiting from increased parental care leading to the formation of sibling dominance hierarchies (Badyaev et al., 2002; Johnson et al., 2003; Stienen & Brenninkmeijer, 2006). Dominance hierarchies are also known to form between neonate egerniine skinks, causing growth and behavioural differences (e.g. in the Tree Skink, *Egernia striolata*; Riley et al., 2017). Furthermore, and particularly for social taxa, sibling dominance hierarchies may result in larger, dominant offspring remaining with the social group, while subordinate individuals may be driven to disperse earlier due to sibling conflict (While & Wapstra, 2008).

Despite hatching asynchrony being common within invertebrates and many avian systems (Amundsen & Slagsvold, 1998; Badyaev et al., 2002; Johnson et al., 2003; Laaksonen, 2004; Marois & Croll, 1991; Smiseth et al., 2006; Stienen & Brenninkmeijer, 2006), our account of birthing asynchrony in a novel clade of lizards suggests that within non-avian reptiles this

phenomenon has convergently evolved in the African Cordylidae and Australian Egerniinae – two groups which concurrently show a suite of similar traits related to sociality. This discovery provides fundamental insights into the behavioural and ecological factors which may relate to hatching/birthing asynchrony, which can further elucidate hypotheses on the selective forces driving this trait, particularly for taxa like insects (Smiseth et al., 2006) and non-avian reptiles (Chapple, 2003; While et al., 2007). We assert that cordylid lizards are a valuable model system, by which future research should examine the physiological mechanisms governing asynchronous birthing and test the hypotheses regarding its function that have been generated from research on egerniine skinks (While et al., 2007; While & Wapstra, 2008, 2009). Overall, it is well established that birth order can significantly impact individuals reared in social groups, with examples being seen in both invertebrate and vertebrate taxa (Mock, 2006; Schrader & Travis, 2012; Smiseth et al., 2006; Sulloway, 2001). We highlight the need for more data on diverse taxa to better understand the evolutionary drivers of birthing asynchrony and whether birthing asynchrony has evolved convergently by similar or different routes in distantly related taxa such as birds and lizards. These early-life-events can set the tone for an individual's remaining years however few or many there may be (e.g. pre-dispersal survival in seabirds; Stienen & Brenninkmeijer, 2006), which is critical to not only advance our knowledge of different species' natural histories but can also significantly further our understanding of some of the fascinating mechanisms shaping the sociality of animals and their ecology more broadly.

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Conflict of interest

The authors declare they have no conflicts of interest regarding the content of this study.

Data Accessibility

The data and R code for this study are available from Open Source Framework (OSF), which can be found at the following link: https://osf.io/myxfh/ (doi: 10.17605/OSF.IO/MYXFH).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary materials.