Social and spatial patterns of two Afromontane crag lizards (*Pseudocordylus* spp.) in the Maloti-Drakensberg Mountains, South Africa

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Abstract Understanding the evolution of vertebrate sociality requires comparative data on social associations across the vertebrate phylogeny. In the case of group-living lizards (i.e. species that live in stable social aggregations often associated with a shared resource), most work has focused on the Egerniinae in Australia, resulting in a taxonomic and geographic skew to our understanding of reptile sociality. The African cordylid lizards (Cordylidae) are also a promising system to study the evolution of sociality because grouping behaviour varies across the clade. Here, we studied the conspecific grouping behaviour of two crag lizards, *Pseudocordylus langi* and *P. melanotus subviridis* that occur at high elevations in the Maloti-Drakensberg Mountains of South Africa. To better understand their social organisation and mating system, we also present data on their spatial distribution, sexual dimorphism, and bite force. Both *Pseudocordylus* spp. were sexually dimorphic in morphology (males had larger heads than females of similar body size), colouration (males were more colourful) and female *P. langi* had a weaker bite force than males. Both *P. langi* and *P. m. subviridis* were associated with rocky habitat on the mountainside (e.g. cliffs, rock buttresses, and rock outcrops) and both were spaced apart and rarely in groups (79% of *P. langi* and 90% of *P. m. subviridis* were observed alone). Based on our findings, we hypothesise that both *Pseudocordylus* spp. have a territorial social structure and a polygynous mating system. This novel natural history information about crag lizards supports the assertion that Cordylidae is another model system for examining the evolution of sociality.

Key words: aggregation, bite force, polygyny, sexual dimorphism, social behaviour, squamate.

INTRODUCTION

Social life is fundamental to the emergence of complex behaviours across many animals, including birds, mammals, and invertebrates (Ward & Webster 2016). In a recent synthesis on social evolution, sociality was defined as co-operative group living (Rubenstein & Abbot 2017). More broadly, sociality can be thought of as the degree to which individuals within a species interact with one another and the complexity of these social interactions (i.e. the number of individuals in a social unit, the nature of their interactions, as well as their mating and care systems) all of which vary greatly across the animal kingdom (Whiting & While 2017; Kappeler 2019). Cooperation, cognitive ability, and complex vocal repertoires are all behaviours that may have evolved as an outcome of a species' sociality (Byrne & Bates 2007; Sussman & Cloninger 2011). Lizards are an

emerging taxon that, over the last few decades, have been documented to exhibit a wide range of sociality. To date, some form of social grouping has been documented in 94 species from 22 taxonomic families (Whiting & While 2017). An important dimension of sociality is social organisation, which refers to the size, demographic composition, stability, and genetic structure of a social unit (Kappeler 2019). An Australian lineage of skinks, the subfamily Egerniinae, may be the most extensively studied taxonomic group of reptiles to date in terms of their sociality. This group contains species that are largely solitary and promiscuous, others that form long-term monogamous pairs, and even species that live in large communal family-groups (Chapple 2003; While *et al.* 2015; Whiting & While 2017). These recent insights into the diversity of lizard social life, coupled with the presumption that the ancestral state (i.e. traits of basal common ancestors) of squamates was solitary (O'Connor & Shine 2003) and the fact that lizards are amendable to both behavioural observation and experimental manipulation, suggests they may be a

source of valuable insights into to the diversity and evolution of animal sociality.

The cordylid lizards of Africa are a promising model for understanding the evolution of sociality because they represent a different, albeit closely related, clade to the comparatively well-studied social egerniinae skinks (Pyron *et al.* 2013). A well-supported phylogeny exists for Cordylidae (Stanley *et al.* 2011) and studies have shown that at least four species live in stable aggregations and more are anecdotally reported to be gregarious (Fig. 1, Appendix S2). One of these species is Lang's Crag Lizard (*Pseudocordylus langi*), for which anecdotal observations in the wild have noted this species lives in 'colonies' at high elevations in the Maloti-Drakensberg Mountains (Broadley 1962). Depending on the source, the terms used to describe aggregations of this species vary between 'small groups' and 'colonies', however, definitions of these terms or further description of this species' behaviour were not detailed in the original account (Broadley 1962). A closely related, sympatric lizard within this region is the Drakensberg Crag Lizard (*Pseudocordylus melanotus subviridis*), which has similarly been anecdotally reported to live in 'colonies' (Bates *et al.* 2014). In general, the term 'colony' can be used to refer to a group of animals that live and interact closely with one another – it is often applied to eusocial insects or seasonal breeding congregations of birds or pinnipeds. A more detailed study of the aggregations of these two crag lizards would help to clarify their nature (i.e. determining if aggregations of *P. langi* are similar to other group-living lizards) and increase our knowledge of sociality across the Cordylidae phylogeny. Information such as this would greatly inform future research regarding the evolution of sociality within the Cordylidae, as well as predictions about the nature of other cordylid lizards' sociality, for example, whether they could be family-living and potential phylogenetic constraints.

We investigated whether, and to what degree, both species (*P. langi* and *P. m. subviridis*) aggregate. Our focus was to collate data on the natural history of these lizards in order to gain insights into their potential social systems. Known group- and family-living lizard aggregations often (1) consist of a mating pair and their offspring, and (2) share a limited resource with one another, which forms an initial base for their interactions and preferential associations (Whiting & While 2017). Thus, we focused on surveying the gregariousness (i.e. the frequency of grouping) and social organisation (defined as the size and demographic composition of a group; Kappeler 2019) of crag lizard conspecific groups, as well as determine if lizards share retreat sites, which would establish an understanding of the potential proximate causes behind aggregations.

We also collected data on sexual dimorphism in these species, since the degree to which it is expressed can reflect a species' social structure and mating system (Whiting & While 2017). Family-living and long-term, stable social aggregations, as well as monogamous mating systems, typically occur in sexually monomorphic lizards because there is less sexual conflict (Table 1). Conversely, territorial lizards are often polygynous and males are often more colourful, have larger heads than females, and have greater bite force in response to male–male contest competition (Fox et al., 2003). In general, montane cordylid lizards vary in their degree of sexual size dimorphism (SSD) between species (Mouton & Van Wyk 1993; Van Wyk & Mouton 1998; Mouton *et al.* 2005; Costandius & Mouton 2006; Bates 2007). Previous work has shown that male-biased body and head size dimorphism occurs in *P. m. subviridis* (Mouton & Van Wyk 1993). Male *P. langi* tend to be larger than females, yet differences in head size and colouration have not been adequately described in wild populations (Bates 2007). We examined individuals of both species and quantified their morphological traits, documented colouration, and measured bite force. Thus, if there is further evidence for sexual dimorphism in both crag lizards, this would suggest that some aspect of contest competition is playing a role in their social interactions. By combining these multiple lines of natural history information, we aimed to provide insights into the social system of two crag lizards, which will contribute to our understanding of both lizard and vertebrate sociality.

METHODS

Study Species

There are five described crag lizards (*Psuedocordylus* spp.; Stanley *et al.* 2011), of which four taxa (species and subspecies of this genus) reside in the central and northern regions of the Maloti-Drakensberg (Bates *et al.* 2014) (see supplementary materials for more details). *Pseudocordylus langi* is found in Lesotho and the Free State and KwaZulu-Natal provinces of South Africa (Bates 2007). They are a medium-sized, viviparous cordylid lizard (maximum recorded snout-vent length, SVL, is 106 mm; Reissig 2014) and are found within crevices and on cliffsides at the escarpment edge and rocky buttresses of the Maloti-Drakensberg Mountain range. Their habitat is limited as they only occur over 2600 m a.s.l. (Reissig 2014). *Pseudocordylus langi* is endemic to southern Africa and globally listed as 'Near Threatened' (Bates & Cunningham 2017). Its persistence is potentially threatened by their limited ability to disperse, particularly in the face of global climate change, and may be affected by over-collecting and disturbance at some hiking trails in the Maloti-Drakensberg (Bates *et al.* 2014).

Pseudocordylus m. subviridis is also a medium-sized, viviparous cordylid lizard (maximum recorded SVL is 140 mm; Bates 2007). They are more abundant than *P.*
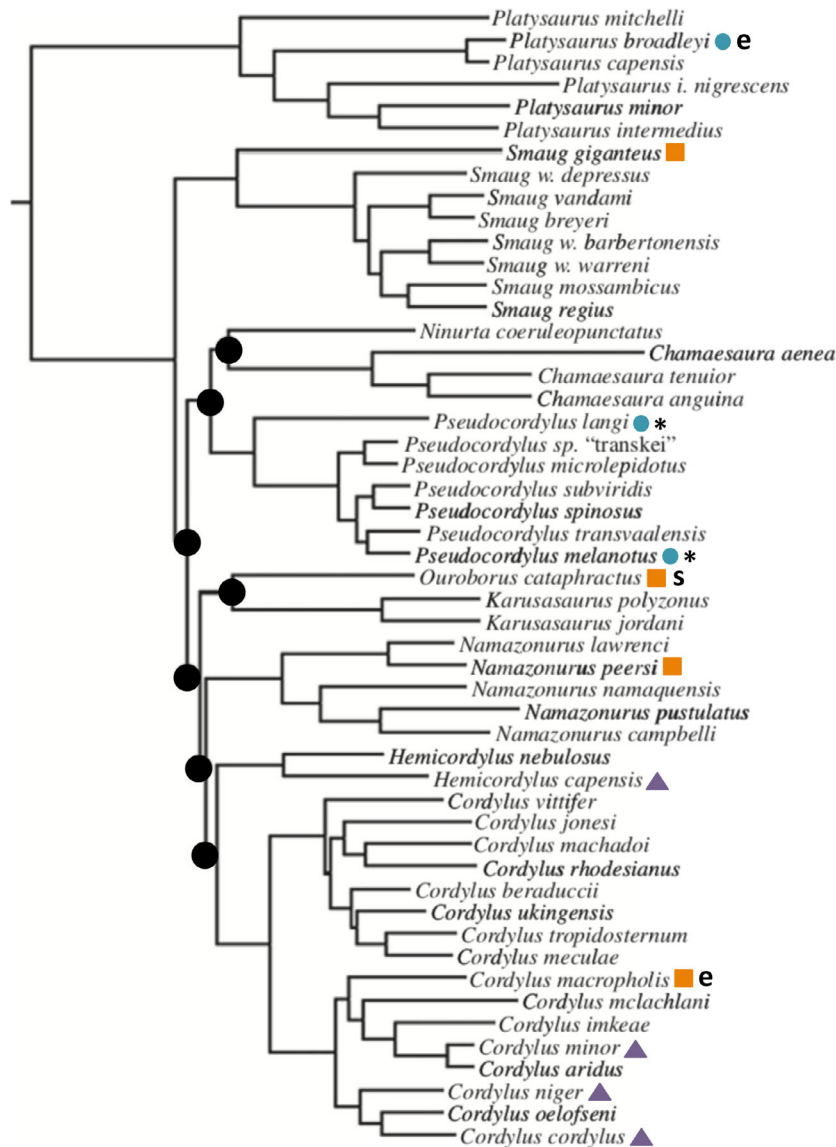
Fig. 1. Phylogeny of Cordylidae (adapted from Stanley *et al.*2011) with species that exhibit year-round stable aggregations (orange squares following the species' name) and species that anecdotally have been observed in groups (purple triangles). We represent if the species is grouping for ecological or social factors using a black 'e' or 's', respectively. We also highlight species that have are known or hypothesised to have a territorial social structure (blue circles), including the two *Pseudocordylus* spp. in this study (indicated with a black asterisk). The other species, to the best of our knowledge, lack data on their sociality, and a detailed account of the literature this figure is based on can be found in our supplementary material (Appendix S2).

langi and range widely across Lesotho and south-eastern South Africa (Bates 2007; Bates *et al*. 2014). They are a saxicolous lizard inhabiting rock outcrops, mountainsides and rock crevices, and can be found in several high elevation areas. As such, within suitable habitat in the Maloti-Drakensberg, they co-occur with *P. langi* (Broadley 1962).

Fieldwork

In October 2019, we conducted our fieldwork within the central and northern regions of the Maloti-Drakensberg

Transfrontier Park, which are part of the uKhahlamba-Drakensberg World Heritage Site. There were two aspects to our fieldwork: (1) capture and measurement of lizards to examine sexual dimorphism, and (2) transects observing lizard spatial and social patterns.

Documenting Crag Lizard Phenotypic Traits

Before our transect surveys, from 14 to 15 October, we captured lizards by lassoing (i.e. a loop of fishing line at the end of a pole). Once captured, we measured each lizard's head length, width, and height using digital callipers

Table 1. Sexual dimorphism of family-living lizards or lizards with kin-biased associations. The definition of sexual dimorphism is a distinct difference in size or appearance between the sexes, in addition to the sexual organs themselves. In this table, we are specifically interested in if lizards are visually distinguishable from one another, and do not consider fine differences (e.g. slight differences in head measurements researchers might use to identify sex through analyses after fieldwork) as sexual dimorphism

Family	Species	Sexually Dimorphic	Description	References
Agamidae	*Intellagama lesueurii*[†]	Yes	The abdomens and chests of large males are covered with orange–red to reddish-black colouration that is absent in females	Piza-Roca *et al.* (2019); Thompson (1993)
Liolaemidae	*Liolaemus leopardinus*	No	–	Brito (2017)
Scincidae	*Liopholis kintorei*	No[§]	–	McAlpin *et al.* (2011); Chapple (2003); Dennison (2015)
Scincidae	*Liopholis whitii*	No	–	Chapple and Keogh (2006), While *et al.* (2009)
Scincidae	*Tiliqua rugosa*[‡]	No[§]	–	Bull and Pamula (1996), Bull (2000), Bull and Lindle (2002)
Scincidae	*Bellatoris major*	No	–	Osterwalder *et al.* (2004), Shea (1999)
Scincidae	*Bellatoris frerei*	No	–	Fuller *et al.* (2005)
Scincidae	*Egernia kingii*	No[§]	–	Masters and Shine (2003)
Scincidae	*Egernia cunninghami*	No[§]	–	Stow and Sunnucks (2004)
Scincidae	*Egernia saxatillis*	No	–	O'Connor & Shine (2003)
Scincidae	*Egernia striolata*	No[§]	–	Duckett *et al.* (2012)
Scincidae	*Egernia stokesii*	No	–	Gardner *et al.* (2001)
Scincidae	*Gnypetoscincus queenslandiae*	No[§]	–	Sumner (2006); Sumner *et al.* (1999)
Scincidae	*Corucia zebrata*	No	–	Hagen *et al.* (2013)
Xantusiidae	*Xantusia vigilis*	No	–	Davis *et al.* (2011)

[†]Rather than family-living (residing in long-term stable, social aggregations with relatives), conspecifics have kin-biased social associations within a territorial social system.

[‡]Largely solitary-living, but pairs up with long-term mates before and during the breeding season.

[§]Species exhibits dimorphism in morphology, which through analyses, can be used to identify sex. But, the degree to which this can be observed by eye is subjective.

(±0.01 mm), as well as SVL using a clear plastic ruler (±1 mm). We used a cut-off of 80 cm to delineate between adults and juveniles of both species (Mouton & Van Wyk 1993; Bates 2007). We were able to determine the sex of both species visually using descriptions in Mouton and Van Wyk (1993) and Bates (2007) for *P. m. subviridis* and field guides for *P. langi* (Alexander & Marais 2007; Reissig 2014). In general, male crag lizards are brighter in colouration and have obviously wider heads and larger bodies than females and juveniles (Mouton & Van Wyk 1993; Alexander & Marais 2007; Reissig 2014). We also verified our visual assessments by sexing males through hemipenal eversion. We took photographs to document each individual's colouration, but appreciate that visually scoring colour is subjective and biased by human perception. It will fail to take into account any colouration such as ultraviolet, which is not detectable by humans. However, our aim was simply to document wholescale visual differences between the sexes and not take into account spectral (chromatic and achromatic contrast) characteristics. Bite force (N) was measured using an isometric force transducer connected to a Kistler charge amplifier (type 5995; Kistler Inc. Winterthur, Switzerland). Lizards were coerced to bite on two parallel plates (fixed at a distance of 1 mm), by stroking both sides of their jaw simultaneously with our index finger and thumb (Baxter-Gilbert & Whiting, 2018). Each individual was tested five consecutive times, and the maximum bite force was used in analyses (Anderson *et al.* 2008; Baxter-Gilbert & Whiting, 2018). Lizards were released at their location of capture within 24 h. One day elapsed between our capture period and the beginning of our transect surveys to allow lizards to re-acclimatise to their surroundings.

Transect Surveys to Observe Social and Spatial Patterns

We observed *P. langi* and *P. m. subviridis* along the Sentinel Trail (a hiking trail) in the Maloti-Drakensberg Mountains of South Africa. We used the hiking trail as a transect (Fig. 2) that we surveyed once per species to avoid repeat sampling of the same individuals (see below for more details). Along each transect, we used binoculars to visually observe lizards within 5 m of either side of the trail and recorded each lizard's location using a GPS (± 3–5 m), demographics (i.e. male, female or juvenile), the habitat they were sighted on, their behaviour (i.e. basking, moving, hiding within a refuge or foraging), and whether or not they were observed in a group.

We were able to determine each species' demographics (i.e. male, female, or juvenile) visually using binoculars, so

lizards were not captured during transect sampling. We familiarised ourselves with the visual differences between species and sexes during the capture period (see details above). Lizards that were classified at juveniles from visual observations were obviously smaller than adults, exhibited juvenile colouration, and had less-developed bulbous jowls (Appendices S3 and S5). Males were visually differentiated from females by their pronounced, bulbous jaw muscles (i.e. larger and wider heads), and brighter colouration (e.g. head and flanks were yellow, orange, and orange–red in *P. m. subviridis*, and yellow, green, and turquoise in *P. langi*; Appendices S3 and S4).

Lizards were recorded as within a group if they met three criteria: (1) they were less than 3 m from one another, (2) they were in visual (i.e. line of sight) or physical contact (i.e. touching each other), and (3) not exhibiting aggressive behaviour towards each other (e.g. biting, chasing, or posturing with head-bobbing, push-ups, or badge displays; Fox *et al.* 2003). Lizards in social groups may still act aggressively towards one another (Riley *et al.* 2017), but they are more likely to exhibit aggressive behaviour towards non-group members (Fox *et al.* 2003). Further, our third criterion did not play a large role in our study, as we only observed one aggressive encounter (i.e. head-bobs and chasing) during the transect surveys, which occurred between an adult male *P. langi,* that appeared to be guarding a water spring on a cliff face, and a juvenile conspecific. Also, although our first criterion (i.e. a 3 m limit) is subjective, we based it on our previous observations of other cordylids in the field in which individuals either show tolerance to familiar group members close to a shared resource or display at rivals. Also, our criteria for designating if lizards were within a group or not are also similar to other studies of lizard sociality (Whiting & While 2017) and are intended to reflect that lizards were aware and tolerant of one another. There were a few cases where lizards were less than 3 m from a conspecific but were unaware of each other due to the presence of rocks or grasses obstructing their view; in these cases, we recorded these lizards as solitary and visually estimated the distance between them (to the nearest 10 cm).

If lizards were observed in a group, we recorded if individuals were in visual or physical contact (see definitions above), if individuals were sharing a shelter site (i.e. rock or cliff crevice, burrow), and a visual-estimation of the distance (nearest 10 cm) between individuals within the group. Also, if they retreated during observations, we noted what habitat they retreated to (i.e. rock or cliff crevice, burrow, space between two rocks, or a space within an artificial structure like a fence or brickwork), and if their retreat site was shared with other group members. This allowed us to establish if lizard groups were associated with a particular resource (i.e. shelter site).

Along the Sentinel Trail, the transects we hiked were species-specific. We were able to visually-distinguish between species using their distinct dorsal patterning (Bates 2007). These two lizards co-occur along the hiking trail after 2915 a.s.l. (Fig. 2), but *P. m. subviridis* also occurs at lower elevations, so we decided to survey each species separately and focus on conspecific groups. On 17 October 2019, we walked our *P. m. subviridis* transect, from the Sentinel Trail parking lot to the base of the chain ladders (4.38 km in length). We sampled *P. langi* along a 1.42 km transect on 19 October 2020. This transect began at the base of the chain ladders (2954 m a.s.l) and extended down the hiking trail to the point where we observed our last *P. langi* (2922 m a.s.l.). We also included eight additional sightings of *P. langi* collected while climbing the chain ladders (maximum elevation of 3014 m a.s.l.) on the previous day (18 October 2020). These transects spanned an elevational gradient from 2543–3014 m a.s.l., and all occurred within the lizard's active period (i.e. mid-morning to early afternoon). Daily average ambient temperatures were also similar (20 to 21°C), and we passed a similar number of hikers on our transects (ranging between 35 to 44 people).

As opportunities presented themselves, we also noted the grouping behaviour of both species in two additional locations. These are separate to the transects we describe above, so no repeated sampling of lizards occurred. On 20 October 2020, we ascended the mountain again and searched the Phofung Plateau for lizards. We also hiked the same pathway as outlined in Broadley (1962) along the Organ Pipes Pass near Cathedral Peak in the Maloti-Drakensberg on 23 October 2019. Approaching Organ Pipes Pass, we began noting the presence of both *P. m. subviridis* (*n* = 50 total) after reaching an elevation of 2358 m a.s.l., and *P. langi* (*n* = 13 total) after reaching 2743 m a. s. l. We have included a description of our observations from these additional surveys below.

Statistical Analyses

Behavioural and spatial observations were summarised and compared between species qualitatively. We used R version 3.5.0 to test for differences in morphological traits and bite force between males and females for each species (R Core Team 2018). All morphological traits and SVL were log_{10}-transformed before analyses to ensure a scalar linear relationship (Lailvaux *et al.*, 2004; Baxter-Gilbert *et al.* 2020). First, we used a Type I analysis of variance (ANOVA) to test for a difference in SVL between sexes, which was performed using the R package 'car' and the function 'aov' (Fox & Weisberg 2019). Then, we analysed differences in head morphometrics (i.e. head width, length, and height) between sexes using an analysis of covariance (ANCOVA) that also included SVL to control for sex-specific differences in body size (using the function 'Anova' specifying 'type="III"' from the R package 'car'; Fox & Weisberg 2019). Before performing the ANOVAs, a Levene's test (using the 'Levene Test' function in the R package 'car') was performed to check for homogeneity of variance. If variance did not fit this assumption, then we used a heteroscedasticity-corrected coefficient (also termed a 'White-corrected' or 'White-Huber'; White 1980) covariance matrix to run ANOVAs (Type II) or ANCOVAs (by specifying 'white.adjust = TRUE' in the 'Anova' function of the R package 'car'; Fox & Weisberg 2019). Additionally, we used a principle components analysis (PCA) to summarise measurements of SVL, head width, head length and head height. We used the function 'prcomp' from the R package 'factoextra' to perform the PCAs (Kassambara & Mundt 2020). All means are reported ± 1 standard deviation and summarised from raw data.

Ethical Statement

Research methods were approved by the Stellenbosch University Animal Ethics Committee (Protocol # ACU-2019-6766) and were permitted in the Free State (Permit No. 201910000003314) and KwaZulu-Natal (Ezemvelo KZN Wildlife, Permit No. OP 3486/2019).

RESULTS

Observations of Aggregations

Along the Sentinel Trail, 10% ($n = 12/115$) of *P. m. subviridis* were observed in groups. In total, we observed 45 females, 44 males, 24 juveniles, and two of unknown sex and age class. Only groups of two individuals were observed, and the demographics of groups varied (Table 2). Of these groups, most lizards were basking on rock outcrops, but one group was observed refuging together within a rock crevice. *P. m. subviridis* within groups ranged from 0.15 to 2.00 m from one another (average of 0.9 ± 0.7 m, $n = 6$). Only one group was found sharing a rock crevice, all other groups were observed in visual contact with one another while basking on the same rock ($n = 5$). All individuals, when disturbed, retreated to separate locations (other than the group that was already sharing a crevice). Similarly, we did not observe any *P. m. subviridis* groups on the Pofung Plateau, while 16% (8/50) were in groups along Organ Pipes Pass where we observed 21 females, 20 males and 9 juveniles (Table 2).

Along the Sentinel Trail, 21% ($n = 15/72$) of *P. langi* were observed in groups. In total, we observed 27 females, 19 males, 23 juveniles, and three of unknown sex and age class. We observed six groups of two individuals and one group of three individuals, all of which occurred while lizards were basking on cliffs. The demographics of groups varied greatly among observations (Table 2). Within groups, *P. langi* ranged from 0.1 to 3.0 m from one another (average of 1.4 ± 1.1 m, $n = 7$), and were observed in visual contact on the same cliff face. Of groups where we observed their retreats, two out of five groups retreated to the same location. On the Pofung Plateau and Organ Pipes Pass, *P. langi* were never observed in groups (Table 2).

Spatial Observations

The nearest neighbour distance between individual *P. m. subviridis* was, on average, 46.5 ± 57.2 m (median = 22.7 m), and ranged between 2.8 to 321.3 m for individuals that were solitary ($n = 103$). For *P. langi*, the nearest neighbour distance between lizards was 22.6 ± 32.2 m (median = 8.1 m), and ranged between 1.0 to 122.3 m for individuals that were solitary ($n = 57$).

Morphology and Bite Force

We captured 12 *P. m. subviridis* (5 females, 3 juveniles, and 4 males) and 15 *P. langi* (4 females, 5 juveniles, and 5 males). Male *P. m. subviridis* were significantly larger than females ($F_{1,7} = 8.60$, $p = 0.02$). From raw data, the SVL of female *P. m. subviridis* averaged 84.80 ± 2.17 mm, while male SVL was on average 97.25 ± 10.05 mm (Fig. 3a). Juvenile *P. m. subviridis* averaged 75.67 ± 1.15 mm in SVL. Male *P. langi* (93.00 ± 9.80 mm) tended to
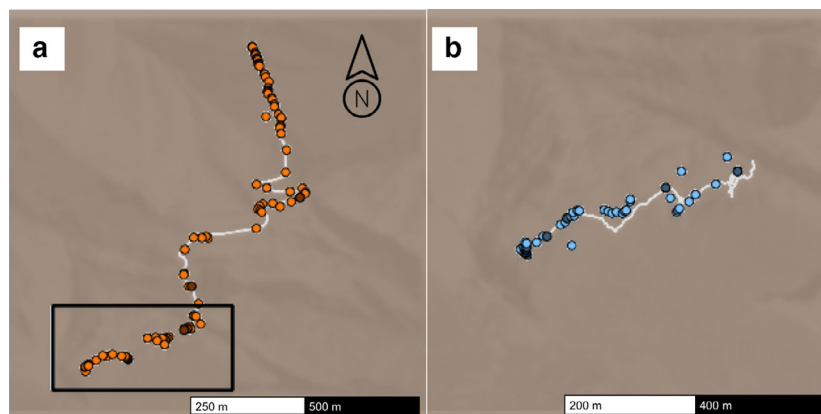

Fig. 2. Locations of (a) *Pseudocordylus m. subviridis* and (b) *Pseudocordylus langi* along their respective transects (indicated by the white path). The black inset box in the left map indicates the border of the right map. In both species, the lighter fill indicates individuals observed alone, and the darker fill shows individuals that were observed in a group. The map's details have been blurred to protect the exact location data.

Table 2. Group size and composition for the aggregations of two crag lizards (*Pseudocordylus langi* and *P. melanotus subviridis*) we observed along the Sentinel Trail and Organ Pipes Pass, and on the Pofung Plateau in the Maloti-Drakensberg Mountains, South Africa

Species	Number of individuals in groups/Total observations	Group size	Group composition
Sentinel Trail (Fig. 2)			
P. m. subviridis	12/115 (6 groups)	2 (*n* = 6)	1F and 1J (*n* = 3)
			1F and 1M (*n* = 2)
			2J (*n* = 1)
P. langi	15/72 (7 groups)	2 (*n* = 6)	2F (*n* = 2)
		3 (*n* = 1)	1F and 1J (*n* = 2)
			1F and 2J (*n* = 1)
			1F and 1M (*n* = 1)
			1J and 1M (*n* = 1)
Pofung Plateau			
P. m. subviridis	0/8	–	–
P. langi	0/7	–	–
Organ Pipes Pass			
P. m. subviridis	8/50 (3 groups)	2 (*n* = 2)	1F and 1M (*n* = 2)
		4 (*n* = 1)	4J (*n* = 1)
P. langi	0/13	–	–

be larger than females (82.00 ± 1.41 mm; Fig. 3b), and this difference was significant ($F_{1,8}$ = 6.12, p = 0.04). Juvenile *P. langi* averaged 72.25 ± 8.34 mm in SVL.

Pseudocordylus m. subviridis head length, but not their head width or height, was significantly related to their SVL (length: $F_{1,6}$ = 9.71, p = 0.02, width: $F_{1,6}$ = 5.14, p = 0.06, height: $F_{1,6}$ = 0.33, p = 0.59). Male *P. m. subviridis* heads (22.66 ± 2.98 mm) were wider than females (16.93 ± 1.35 mm), yet this trend was not significant ($F_{1,6}$ = 3.46, p = 0.11). Head length (female = 22.97 ± 0.77 mm, male = 29.69 ± 3.19 mm; $F_{1,6}$ = 8.81, p = 0.03) and head height (female = 8.11 ± 0.52 mm, male = 10.31 ± 0.68 mm; $F_{1,6}$ = 9.91, p = 0.02) was significantly larger in males than females. Our PCA shows clear differentiation in head measurements between *P. m. subviridis* females, juveniles, and males (Appendix S1, Fig. 4a).

With respect to *P. langi*, head width (female = 15.29 ± 0.77 mm, male = 21.08 ± 3.03 mm; $F_{1,7}$ = 40.44, p < 0.01) and head length (female = 20.87 ± 0.26 mm, male = 216.32 ± 3.17 mm; $F_{1,7}$ = 27.98, p < 0.01) differed between sexes. Yet, head height did not differ between females (8.16 ± 0.65 mm) and males (9.77 ± 1.66 mm) ($F_{1,7}$ = 0.06, p = 0.82). *Pseudocordylus langi* head morphology was significantly related to their SVL (length: $F_{1,7}$ = 53.34, p < 0.01, width: $F_{1,7}$ = 46.04, p < 0.01, height: $F_{1,7}$ = 22.99, p < 0.01). Our PCA shows differentiation in head measurements between *P. langi* males and females, as well as males and juveniles, but not females and juveniles (Appendix S1, Fig. 4b).

Maximum bite force was not related to *P. m. subviridis* SVL ($F_{1,4}$ = 0.01, p = 0.94), but it was significantly related to *P. langi* SVL ($F_{1,6}$ = 26.16, p < 0.01). Male *P. m. subviridis* maximum bite force (36.37 ± 5.54 N) tended to be greater than female maximum bite force (17.53 ± 3.36 N), but this difference was not significant ($F_{1,4}$ = 5.09, p = 0.09). This is likely due to our limited sample size. For *P. langi*, maximum bite force was significantly lower in females than males ($F_{1,6}$ = 15.97, p = 0.01). Maximum bite force of *P. langi* females was, on average, 13.28 ± 2.04 N and for males was 26.58 ± 8.42 N (Fig. 5b).

Colouration

Both species' colouration differed between sexes. This has previously been well-documented in *P. m. subviridis* (Mouton & Van Wyk 1993; Bates 2007). This species has smooth dorsal scales with small, wide granular black scales patterning their dorsal surface. Males and females have black mottling and striping on their backs, due to stippling from these raised micro-scales (Appendix S3). On males, the background to this dorsal patterning can vary between light green to yellow, whereas in females the background is often yellow-brown to olive-brown. The central, ventral scales of both males and females are white. The male's flanks are very colourful (varying from yellow, orange, and orange–red). Females also can have small amounts of colouration on their sides, but the colouration is not as deeply saturated as males (i.e. light yellow and orange instead of
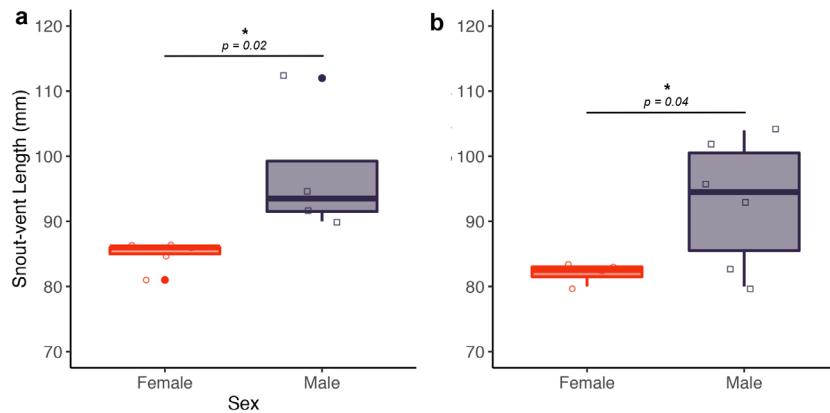
Fig. 3. Differences between sexes in snout-vent length (mm) of (a) *Pseudocordylus m. subviridis* and (b) *P. langi* captured along the Sentinel Trail, Maloti-Drakensberg Mountains, South Africa. Raw data is plotted. *P*-values are shown between sex-specific comparisons and significant differences are denoted using an asterisks.
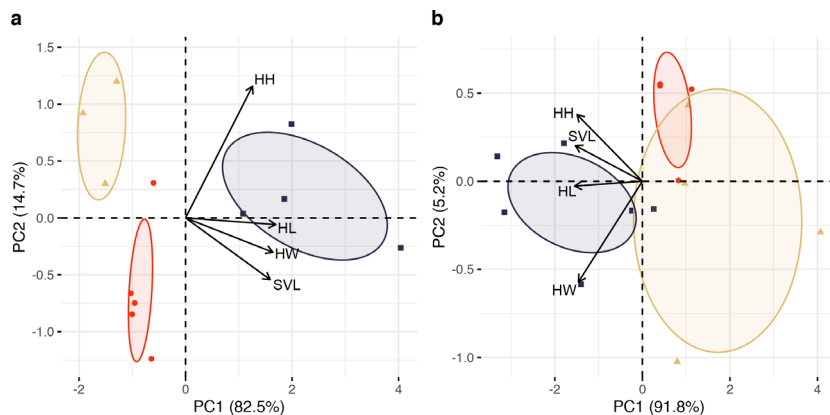

Fig. 4. Biplot of the first and second principles components assessing differences in snout-vent length (SVL), and head measurements (HW = head width, HL = head length, and HH = head height) in (a) *Pseudocordylus m. subviridis* and (b) *P. langi* among juveniles (represented using triangles and a beige colour), males (represented using squares and a blue colour), and females (represented using circles and a red colour).

deeper orange to red). No juveniles we observed had colouration on their sides or distal ventral scales. Some males also had light blue to turquoise colouration on their heads, central ventral scales, and on their arms.

Pseudocordylus langi also differed in the colouration between sexes (Appendix S4). Their dorsal surface was very smooth and was patterned with black stripes and blotches. This dark patterning was often interspersed with light crossbars. The background colour of their back varied between yellow, olive, and greenish-grey, and often the males appear brighter in their colouration than females. This species' also have two to six bright blue, almost iridescent, spots extend from the neck posteriorly along the back of the body in two lines (Appendix S5). The ventral colouration varies from light grey to blue, and males often had more saturated blue on their venter. Males also had yellow to

green colouring on the distal ventral sides, red-blueish centrally on their undersides, and had a blueish-grey tinge to the base of their heads. Interestingly, both species had a black throat patch that also has been noted by Bates (2007), which we observed being extended during social signalling (Appendix S6).

DISCUSSION

Our observations suggest that *P. m. subviridis* and *P. langi* are not group-living, which is further supported by their sexual dimorphism in body size, colouration and bite force – traits often consistent with territoriality and polygynous mating systems in lizards. Both *Pseudocordylus* spp. were typically associated with specific habitat types that are clumped on the landscape-scale, which resulted in the localised presence
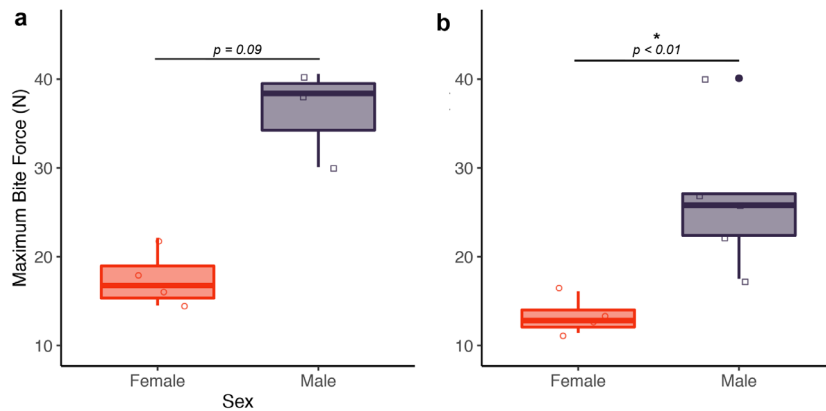
Fig. 5. Differences between sexes in maximum bite force (N) of (a) *Pseudocordylus m. subviridis* and (b) *P. langi* captured at along the Sentinel Trail, Maloti-Drakensberg Mountains, South Africa. Raw data is plotted. *P*-values are shown between sex-specific comparisons and significant differences are denoted using an asterisks.

of lizards in patches along our transects. For *P. m. subviridis* their preferred habitat was typically rock outcrops on mountain slopes, while *P. langi* were almost exclusively seen on cliffsides and rock buttresses. The habitat type preferences we observed for both species support what has been previously described (Broadley 1962; Bates 2007; Reissig 2014; Bates *et al.* 2014). Habitat did not appear to be limited, and thus we would not expect lizards to be driven to aggregate due to a lack of resources (i.e. the ecological constraints hypothesis; Hatchwell & Komdeur 2000). Our behavioural observations support this; within areas of suitable habitat, lizards were spaced apart, and a low percentage of lizards were grouping (i.e. individuals were less than 3 m to one another, in visual or physical contact, and not exhibiting aggressive behaviour). Specifically, 10% of *P. langi* and 21% of *P. m. subviridis* were observed in groups and rarely shared refuges. Also, groups were small – the majority were pairs. Most commonly, *P. m. subviridis* groups were either a male and female or a female and juvenile, while *P. langi* groups were composed of an adult and juvenile(s). We also observed a similar lack of aggregative behaviour on the Phofung plateau and along the Organ Pipes Pass, which further supports our finding that both species are not group-living.

The behaviour we observed in both *Pseudocordylus* spp. differed from group- and family-living lizards that typically bask near their shelters (i.e. rock or tree crevices, plants, or burrows) in small to large groups that are in close visual and physical contact with one another (e.g. cordylids like Armadillo Lizards, *Ouroborus cataphractus*, and egerniinae skinks like the Cunningham's Skink, *Egernia cunninghami*, and the Great Desert Skink, *Liopholis kintorei*; Whiting & While 2017). Instead, their fine-scale spacing was more akin to Australian Water Dragons (*Intellagama*

lesueurii; Piza-Roca *et al.* 2019) and Augrabies Flat Lizards (*Platysaurus broadleyi*; Whiting 1999, Whiting *et al.* 2003); whereby individuals are regularly spaced within suitable habitat. In these examples, regular social interactions between individuals do occur; including aggressive encounters during territorial disputes, as well as social tolerance for shared shelter sites in *Platysaurus broadleyi* when habitat is limited (Schutz *et al.* 2007) and kin-based social associations in the case of *I. lesueurii* (Piza-Roca *et al.* 2019). Thus, although we expect the social systems of crag lizards to differ from lizards that have been described as group-living and/or gregarious (Whiting & While 2017), we are not suggesting they are asocial. Rather, below, we provide a hypothesis as to the nature of their sociality. Further, and based on our observations of *P. langi* and *P. m. subviridis*, we assert that although these species have previously been described as living within 'colonies' (Broadley 1962; Bates *et al.* 2014; Reissig 2014), this term was likely originally used in reference to the clumped distribution of lizards on the landscape rather than as a description of the nature of their sociality.

Both *Pseudocordylus* spp. were sexually dimorphic in morphology and colouration with a male-bias for larger size and 'brighter' colouration. Our limited sample size prevented us from making comparisons of the morphology between species. Yet, an interesting avenue for future research would be comparing the morphology of crag lizards occurring within the Maloti-Drakensberg Region, and assessing if that may relate to their species-specific habitat use. For example, is the morphology of *P. langi* constrained in some way (i.e. head or body height, limb or foot morphology) by their predominant use of vertical cliffs and narrow crevices? In this study, we restricted our comparison of crag lizard morphology between sexes within a species. The majority of the differences we detail herein,

especially in their colouration, are visually distinguishable from a distance with binoculars.

Pseudocordylus m. subviridis females were smaller in SVL, head length, and head height than males. We did not find a significant sex-difference in *P. m. subviridis* head width or bite force, but non-significance is likely due to our limited sample size. Other studies have established that females have smaller heads and body size than males (Mouton & Van Wyk 1993), and our PCA demonstrated clear differentiation in morphology between demographic groups. Further, female *P. m. subviridis* colouration could be considered as 'drab' in comparison with males, because they do not have the same bright, intense orange–red venters or blue–green heads as males. Similarly, *P. langi* females were smaller in SVL and their heads were also smaller in head width and length than males, but not head height. Bates (2007) also found that female *P. langi* were smaller in SVL than males, but did not find sex-specific differences in colouration in preserved museum specimens. We assert that in the wild, female *P. langi* are less colourful than males. Although, the degree of sex-specific colouration differences in *P. langi* is lower (i.e. more subtle) than in other crag lizards. The differences we observed in *P. langi* morphology also translated into a difference in bite force, with females having a lower maximum bite force than males. This sexual dimorphism suggests there may be a territorial basis to these species' social structure. The greater size and bite force observed in males, may suggest males are more territorial than females. During our observations we saw that males of both species had a tendency to perch or bask on elevated locations (e.g. on a cliffside or at the top of a rock or outcrop) with a raised body posture (Fox *et al.* 2003), appearing to be monitoring and maintaining a territory. Also, females were more often observed in groups with juveniles or males, and we never observed two males in a group; suggesting a lack of tolerance for one another. Our observations on these crag lizard's social organisation, spatial patterns, and sexual dimorphism have led us to hypothesise that both *Pseudocordylus* spp. have a territorial social system and a polygynous mating system (for a similar assertion for *P. m. subviridis* see Mouton & Van Wyk 1993), yet more behavioural observations and experiments are needed to confirm this.

Although informative, our study is limited because it was conducted at a single point in time (October 2019) and at, largely, one study site. From this, it is not possible to determine if group-living is facultative in either species. Our observations that crag lizards were predominately observed alone does not discount the possibility that these *Pseudocordylus* spp. could be group-living under a different set of circumstances. One factor that can affect social behaviour is a

species' reproductive behaviour, cycle, and mode (Halliwell *et al.* 2017). For example, some lizards have delayed dispersal when habitat is limited and risks of infanticide are high (O'Connor & Shine 2003), which can increase the association between parent(s) and offspring and set the stage for family-living. Also, Timber Rattlesnakes (*Crotalus horridus*) group with relatives while gestating their young (Clark *et al.* 2012). In our study, adults were most-often observed in groups with juveniles and occurrence of these groups may increase during the breeding season or following birth. One of the female *P. m. subviridis* we captured gave birth and other females appeared gravid (i.e. a distended abdomen and high mass). So, our sampling may have overlapped with female parturition at this site. Although, this does not follow the reproductive cycle described in Flemming (1993), where *P. m. melanotus* (a closely related subspecies; Bates 2007) was reported to give birth in January (during the Austral summer), which is also typical of most southern African lizards. Our understanding of *P. langi* and *P. m. subviridus* sociality would benefit from repeated surveys across seasons or years to establish the proper timing of parturition and its potential effect on social organisation.

Based on our findings it would appear that social group-living is not the ancestral state of the *Pseudocordylus* clade, as we hypothesise that the basal species of within this genus (*P. langi*) has a territorial social system and a polygynous mating system. Future research is needed to test our hypothesis, and it could involve (1) observing grouping behaviour of lizards repeatedly across the year, (2) conducting experiments that provide individuals with unlimited shelters to tease apart potential drivers of grouping, like ecological or social factors (as per Visagie *et al.* 2005; Schutz *et al.* 2007), and (3) carrying out behavioural assays in the field or lab to study the territorial response of a resident lizard to an intruder lizard (as per Fox & Baird 1992; Whiting 1999). The presence of stable group-living in other cordylid lizards (Van Wyk 1992; Mouton 2011) suggests it may either have evolved multiple times or been lost within this clade, but we need data on more species in order to test this using ancestral state reconstruction. Nevertheless, we have mapped cases of confirmed social grouping to indicate the spread across the cordylid phylogeny (Fig. 1) to help future researchers select taxa to examine the diversity of sociality within this group, and the degree to which sociality is plastic or fixed.

Overall, African cordylid lizards have a number of benefits that make them a suitable model for studying sociality – a known phylogeny, overt and simple behaviour that is easily observable in open habitats, and a number of natural- and life-history characteristics that may select for family-living (i.e. viviparity, a *K*-selected life history, longevity; Whiting & While 2017). Our collection of natural history observations

provides insights into the social behaviour and spatial ecology of two cordylids, *P. langi* and *P. m. subviridis*, and we hope our study prompts further research of the diversity and evolution of sociality within this group.

CONFLICT OF INTEREST

All authors declare they have no conflict of interest.

AUTHOR CONTRIBUTION

Julia Riley: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (equal); Methodology (lead); Project administration (lead); Writing-original draft (lead); Writing-review & editing (equal). **James Baxter-Gilbert:** Conceptualization (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Writing-review & editing (equal). **Martin Whiting:** Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Writing-review & editing (equal).

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Component loadings for the principle component analyses (PCA) for head morphology of (A) *Pseudocordylus m. subviridis* and (B) *P. langi*.

Appendix S2. A summary of grouping behaviour that has been reported in Cordylidae and that Figure 1 is based on.

Appendix S3. A range of colouration that can be observed in *Psuedocordylus melanotus subviridis* that varies between age classes and sexes of this species.

Appendix S4. A range of colouration that can be observed in *Psuedocordylus langi* that varies between sexes of this species.

Appendix S5. Close-up view of the blue spots along a *Psuedocordylus langi* individual's back, as well as a clear view of the males enlarged head and jaw muscles.

Appendix S6. A male *Psuedocordylus langi* with his throat extended and the black patch in view.

Social and Spatial Patterns of two Afromontane crag lizards (*Pseudocordylus* spp.) in the Maloti-Drakensberg Mountains, South Africa

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Supplementary Materials

Additional Details about Crag Lizards in the Maloti-Drakensberg Mountains

There are a total of five described species within this genus (*Psuedocordylus* spp.; Stanley et al. 2011), three of which reside in the central and northern regions of the Maloti-Drakensberg (Bates *et al.* 2014). This includes one species that is taxonomically separated into subspecies (*Psuedocordylus melanotus*; Bates 2007), resulting in four distinct crag lizards in the area. The two other crag lizards, the Spiny Crag Lizard (*P. spinosus*) and the Common Crag Lizard (*P. m. melanotus*), occur in different habitats than this study focused on (Bates et al. 2014). They did not co-occur with our two study species at the locations we sampled. In fact, during our fieldwork, we only haphazardly observed two *P. spinosus* individuals, at 1897 and 1877 m a.s.l. respectively, along Organ Pipes Pass (see manuscript for location details), which were both solitary and basking on rock outcrops on a roadside within grassland.

Appendices

Appendix S1. Component loadings for the principle component analyses (PCA) for head morphology of (A) *Pseudocordylus m. subviridis* and (B) *P. langi.* The PCA included $\log_{10}$-transformed snout-vent length (mm), head height (mm), head width (mm), and head length (mm) measurements. We also present the standard deviation of the principle components, as well as the proportion of variance they explained in our data. See Fig. 4 for a graphical representation.

(A) *P. m. subviridis*				
Morphological Variables	**PC1**	**PC2**	**PC3**	**PC4**
Snout-vent length	0.511	-0.412	-0.640	-0.400
Head width	0.528	-0.230	0.759	-0.304
Head length	0.545	-0.044	-0.058	0.836
Head height	0.404	0.881	-0.104	-0.224
Standard deviation	1.817	0.769	0.284	0.168
Proportion of Variance	0.825	0.148	0.020	0.007
(B) *P. langi*				
Snout-vent length	-0.508	0.283	-0.520	-0.625
Head width	-0.484	-0.799	0.290	-0.210
Head length	-0.513	-0.038	-0.419	0.748
Head height	-0.495	0.529	0.685	0.072
Standard deviation	1.916	0.454	0.301	0.177
Proportion of Variance	0.918	0.052	0.023	0.008

Appendix S2. A summary of grouping behaviour that has been reported in Cordylidae and that Fig. 1 is based on. The two *Pseudocordylus* spp. in this study are bolded, and on the phylogeny (Fig. 1) are denoted as exhibiting territorial social structure according to our hypothesis, although we report in this table the anecdotal reports this study was following up on. We include a description for each species' sociality as per the literature cited; we include a range of group sizes for aggregative species if provided (if not, this lack of information is denoted using [††]). We also specify if a species' grouping behaviour was explicitly studied or if it was reported anecdotally, as well as if grouping behaviour is thought to be driven by social or ecological factors – represented by supplying a citation within the appropriate column.

Species	Description of Sociality	Type of Report		Drivers of Sociality[§]	
		Studied in the Field	*Anecdotal Report*	*Social*	*Ecological*
Platysaurus broadleyi	Territorial social structure	Whiting 1999, Whiting *et al.* 2003			Schutz *et al.* 2007
Smaug giganteus	Groups of two to seven lizards	Van Wyk 1992, Ruddock 2000			
Pseudocordylus langi	**Small colonies[††]**		**Broadley 1964**		
Pseudocordylus melanotus subviridus[†]	**Small groups[††]**		**Reissig 2014**		
Ouroborus cataphractus	Large, stable groups of two to 60 lizards	Mouton 2011		Visagie *et al.* 2005	
Namazonurus peersi	Groups of up to six lizards	Mouton 2011			
Hemicordylus capensis	Small, diffuse colonies[††]		FitzSimons 1943, Branch 1998		
Cordylus macropholis	Groups of up to 13 individuals sharing a *Euphorbia caput-medusae* plant	Mouton 2011			Visagie *et al.* 2005
Cordylus cloetei[‡]	Groups of up to three lizards		Mouton & Van Wyk 1994		
Cordylus niger	Dense colonies[††]		Cordes & Mouton 2011		
Cordylus cordylus	Dense colonies in some areas[††]		Reissig 2014		

[†] Positioned on the phylogeny (Fig. 1) as part of the *P. melanotus* complex (Bates 2007).
[‡] Positioned on the phylogeny (Fig. 1) beside *Cordylus minor* as it was described as a geographical isolate of this species (Mouton & Van Wyk 1994).
[§] All studies that investigated whether grouping was due to social or ecological factors were experiments.
[††] In the case of species reported to aggregate, this denotes that data on group sizes was lacking.

Appendix S3. A range of colouration that can be observed in *Psuedocordylus melanotus subviridis* that varies between age classes and sexes of this species.
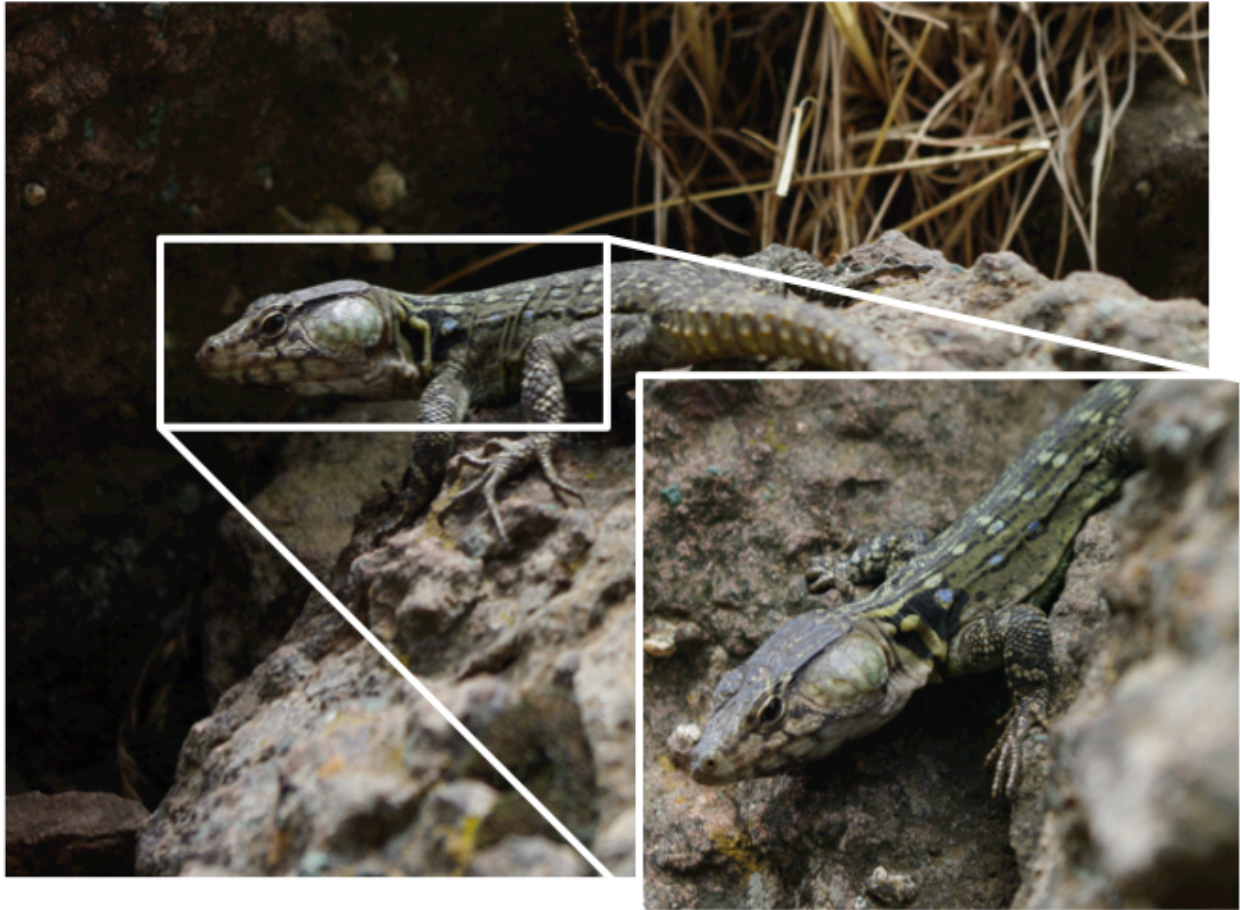
Appendix S4. A range of colouration that can be observed in *Psuedocordylus langi* that varies between sexes of this species.

Appendix S5. Close-up view of the blue spots along a *Psuedocordylus langi* individual's back, as well as a clear view of the males enlarged head and jaw muscles.

Appendix S6. A male *Psuedocordylus langi* with his throat extended and the black patch in view.

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