



The Herpetological Bulletin

Issue 158, Winter 2021



Published by the British Herpetological Society



THE HERPETOLOGICAL BULLETIN

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Front Cover: An Asian water monitor *Varanus salvator* photographed by Rudi Delvaux (Danau Girang Field Centre) in the Lower Kinabatangan Wildlife Sanctuary Sabah, Malaysia. See article on p. 37

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Mating behaviour of the lizard *Ameiva ameiva* in Brazil

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ABSTRACT – The courtship and copulation behaviours of the lizard *Ameiva ameiva* is described from field observations made at various locations in Brazil. In males, the main behaviours observed during one observation of courtship were head bobbing, circling and walking over the females, rubbing his body against the female, mounting, and dismounting. Females generally remain passive throughout courtship. The reproductive behaviour of *A. ameiva* resembles that of other teiids, however males exhibit some behavioural peculiarities, such as circling the female to restrict her movements, no cloacal rubbing against the ground, and no biting during copulation.

INTRODUCTION

The most common mating system reported for lizards, including non-territorial lizards such as teiids, is polygyny, in which males move over wide areas actively searching for multiple mates (sequential polygyny; Pianka & Vitt, 2003; Vitt, 2003). In these non-territorial species, the mere presence of a male is insufficient for mating to occur, instead females select males based on the size and shape of their bodies (Pianka & Vitt, 2003).

Courtship and copulation in lizards involve a series of ritualised behaviours (Vitt, 1983; Costa et al., 2010; Gogliath et al., 2010; Ribeiro et al., 2011). Examples of these behaviours in teiid lizards include chase, cloacal rubbing and head bobbing (Carpenter, 1960, 1962; Quesnel, 1978; Costa et al., 2013; Sales & Freire, 2021). Sexual size dimorphism, sexual dichromatism, and behavioural displays are intricately linked to courtship and copulation and are fundamental to sexual selection (Noble & Bradley, 1933; Vitt, 1983; Censky, 1997).

Copulation in teiid lizards may involve some behaviours performed by the male, such as biting the female's flank or pelvic region and posture patterns during the intromission

phase (Carpenter, 1960; Crews, 1987; Mahrtdt, 1976; Ribeiro et al., 2011; Alfonso & Torres, 2012; Sales & Freire, 2021). Mate guarding after copulation seems to be common in teiid lizards, which reduces the opportunity for female to mate with other males. The occurrence of mate guarding lasting for days indicates that male-female associations may be longer than previously thought, even in lizards practising sequential polygyny (Quesnel, 1978; Anderson & Vitt, 1990; Censky, 1995; Colli et al., 1997; Zaldívar-Rae et al., 2008).

The teiid lizard *Ameiva ameiva* is widely distributed in Brazil, inhabiting areas of the Caatinga, Amazon, Cerrado, and Atlantic Forest, where it exhibits diurnal and terrestrial habits and forages actively in open areas with high solar exposure (Vitt, 1982; Magnusson, 1987; Colli, 1991; Vitt & Colli, 1994; Rocha, 2008). Males grow larger than females (Rocha, 2008); this may relate to sexual selection (Anderson & Vitt, 1990). Despite advances in behavioural ecology, descriptions of the reproductive behaviour of teiid lizards remain scarce (Censky, 1995; Zaldívar-Rae & Drummond, 2007; Sales & Freire, 2021). Here we describe the courtship and mating behaviour of free-ranging *A. ameiva*.

Table 1. Location and date of the available records of courtship and copulation of *Ameiva ameiva* in Brazil

Location	Date	Season	Source	Observed event
Ribeirão Preto, São Paulo state	March 2005	Summer	This study	Mating
Parque Pedra da Cebola, Vitória, Espírito Santo state	7th October 2012	Spring	This study	Mating
Cariacica, Espírito Santo state	3rd December 2018	Spring	This study	Mating
Vale do Capão, Palmeiras, Bahia state	17th December 2018	Spring	This study	Mating
Cantá, Roraima state	29th May 2019	Autumn	This study	Mating
Sítio Córrego do Areião, Brodowski, São Paulo state	10th January 2020	Summer	This study	Courtship and mating
Parque Nacional da Serra do Cipó, Minas Gerais state	22nd October 2001	Spring	Manata & Nascimento (2005)	Courtship
Tabajara, Inhapim, Minas Gerais state	12nd March 2009	Summer	Costa et al. (2010)	Courtship

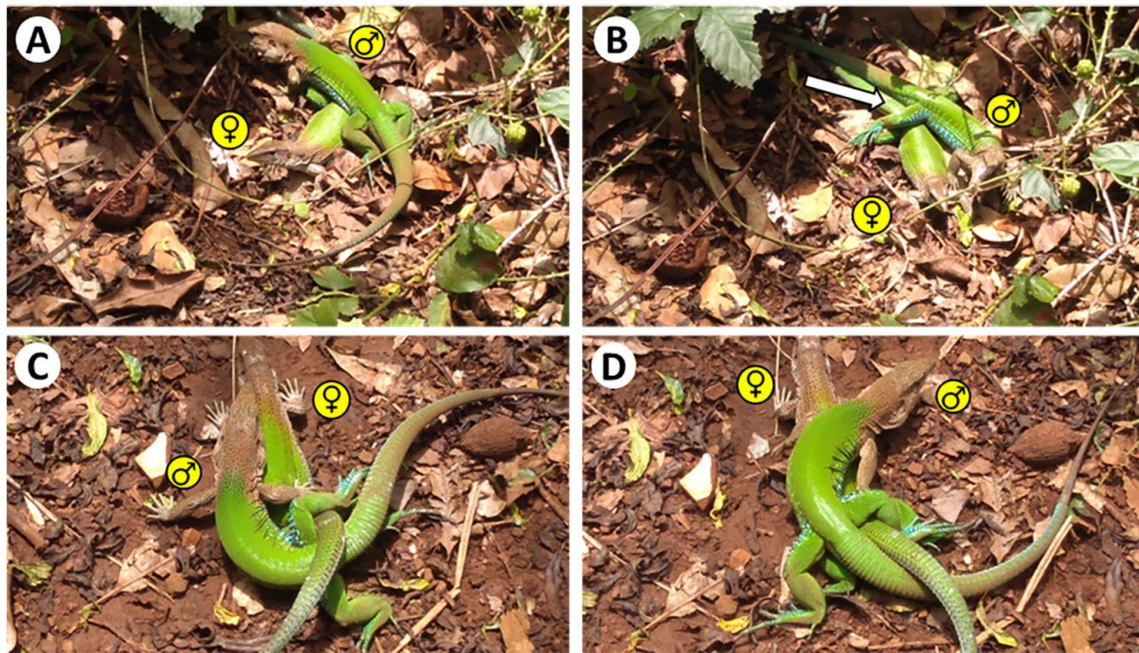


Figure 1. Courtship behaviour and position shift during copulation of the lizard *Ameiva ameiva* observed in Brodowski, São Paulo, south-eastern Brazil- **A.** Male circling the female and moving over the female's body at the base of the tail, **B.** Male rubbing his cloacal region over the base of the female's tail (arrow), **C.** Initial position during copulation, **D.** The male shifted position during copulation, moving over the female's body as she gradually lowers her tail

MATERIALS & METHODS

We described courtship and copulation behaviours based on six fortuitous encounters videotaped by lay people between 2005-2020 at different locations in Brazil (Table 1). The description of the behavioural repertoire is based on Quesnel (1978). In each observation, we assumed that the largest individuals were males until the sex of each individual became evident during copulation, which refers to the moment the female arches her tail and male positions his cloaca in opposition to hers so that the intromission of the hemipenis can occur. To view one example of the courtship and copulation of *A. ameiva* watch our video (BHS, 2021).

RESULTS

We identified four distinct phases during courtship behaviour, which can occur successively or alternately: (1) approach on a spiral route, (2) circular movements around the female, (3) body contact, and (4) rubbing against the female's body. The complete courtship and mating sequence was recorded only once. In the other observations, the couples were either at the end of courtship or copulating when they were found (Table 1). Therefore, the description of the entire courtship behaviour was based on a single observation.

The male began the courtship by approaching the female in short spurts followed by head-bobbing displays. This sequence resulted in a direct approach, with the male continually circling and moving over the female's body at the base of the tail (Fig. 1A). At this time, the male rubbed his cloacal region over the female's tail base (Fig. 1B). The male then stopped courting the female, and both individuals foraged for 50 s. The courtship was then resumed, with the male again circling the female. However, the female, which

had previously remained static, started to move over the male's body to continue foraging. To restrain the female and regain her attention, the male placed his left forelimb over the female's pectoral girdle and rubbed the side of his body against hers. The male mounted and dismounted the female three times while rubbing his cloacal region against her body until she became receptive. The female then arched the tail base, and the male placed his tail under the female so that both cloacae were opposed. We could neither see the eversion of the hemipenis nor its insertion into the cloaca. The complete courtship sequence lasted about 270 s. The tongue-flicking rate was high during courtship.

We were unable to identify the exact position of the individuals when copulations began. Although some body adjustments occurred, males and females remained immobile for most of the copulation. The males positioned themselves parallel to the females and placed their right fore- and hind limbs over the females' pelvic girdle and tail, respectively, thus resting on their left fore- and hind limbs. Moreover, males placed their tails under females' tails to bring their cloacae into close apposition (Fig. 1C). On some occasions, males shifted position during copulation, placing their bodies over females' bodies as they gradually lowered their tails (Fig. 1D). After copulation, the couple remained close to each other. Males resumed courtship behaviour by performing head-bobbing displays after each step forward.

One of the copulations occurred near an underground shelter. A female was seen leaving the shelter and being pursued by a male (Fig. 2A). After reaching the female, the male immediately mounted her and rubbed his ventral and cloacal regions on her back. This behaviour was followed by copulation (Fig. 2B). In one of the videos, we observed a third individual next to a mating pair. This individual approached the female after the copulation ended but the female



Figure 2. Copulation of the lizard *Ameiva ameiva* observed in Vale do Capão, Bahia, north-eastern Brazil (**A, B**), and Cariacica, Espírito Santo, south-eastern Brazil (**C, D**) - **A.** Female leaving an underground shelter while being pursued by a male, **B.** Copulation occurred immediately after the couple left the underground shelter (courtship behaviour probably occurred within the shelter), **C.** Male and a female copulating, **D.** A second individual (*) approaches the female after the copulation ended

quickly moved away after noticing the approach (Fig. 2C, D). Copulations lasted 22-164 s (mean = 94.5 s). All observations were made during the daytime, and no aggressive behaviour was noticed.

DISCUSSION

The phases of the courtship behaviour of *A. ameiva* are in general similar to those of other lizard species, including other *Ameiva* (Quesnel, 1978; Manata & Nascimento, 2005). In *A. ameiva*, the movements performed by males seem to go unnoticed by females. However, this apparent disinterest may indicate a positive response from the female and that she is tolerating his presence (Quesnel, 1978). The female passivity seems to be important for a successful approach and may be caused by the circular movements performed by the male. By circling the female, a courting male may restrict her movements (thus allowing body contact to occur) and suppress biting behaviours during copulation that have been reported in other teiids (e.g., Carpenter, 1962; Anderson & Vitt, 1990; Zaldívar-Rae & Drummond, 2007; Ribeiro et al., 2011; Alfonso & Torres, 2012; Sales & Freire, 2021), but have not been observed in *A. ameiva* (Manata & Nascimento, 2005; this study) and other congeners (Quesnel, 1978). Moreover, cloacal rubbing against the ground, a behaviour already reported in male teiids (Carpenter, 1962; Sales & Freire, 2021), was not observed.

The duration of courtship is variable in teiid lizards. Male *Pholidoscelis auberi* spend about 32 minutes pursuing and courting females (Alfonso & Torres, 2012), while male *Ameivula ocellifera* court females for 0.8-121 minutes (Sales & Freire, 2021). Costa et al. (2013) reported that a male *Kentropyx calcarata* stayed about 13 minutes close to a female before copulating. However, these authors observed

no visual signalling between the specimens or any other behaviours reported here, such as head-bobbing displays, circular movements or cloacal rubbing over the female's body. The duration and number of repetitions of each courtship phase are variable (Quesnel, 1978).

The male position of *A. ameiva* during the intromission phase of copulation is similar to other teiid lizards that do not usually follow the arched posture pattern and bites during this phase (Quesnel, 1978; Censky, 1995; Costa et al., 2013). On the other hand, some male teiids from smaller species adopt the arched pattern, biting the female's pelvic region close to her hind limbs, in a ring shape that Crews (1987) called the 'doughnut posture' (Carpenter, 1962; Mahrtdt, 1976; Anderson & Vitt, 1990; Ribeiro et al., 2011; Alfonso & Torres, 2012; Sales & Freire, 2021).

In lizards, copulation is often interpreted as an isolated event. However, some records of multiple copulations in a short period suggest that copulation may be a serial event (Quesnel, 1978). Mate guarding has been observed in *Ameiva* (Quesnel, 1978; Manata & Nascimento, 2005) and several teiids, such as *Aspidoscelis* (Anderson & Vitt, 1990; Zaldívar-Rae & Drummond, 2007; Zaldívar-Rae et al., 2008; Ancona et al., 2010), *Pholidoscelis* (Censky, 1995), and *Ameivula* (Ribeiro et al., 2011; Sales & Freire, 2021). Male lizards can spend days guarding females. During this period, they copulate several times and chase away other males that try to approach the females (Censky, 1995, 1997; Zaldívar-Rae & Drummond, 2007). By guarding the female as much as possible, males decrease the opportunity for rival males to access the female, which may increase their reproductive success (Bull, 2000; Ribeiro et al., 2011; Sales & Freire, 2021). However, this behaviour is not always successful (Olsson et al., 1996). Our observation that the larger male moved away from the female shortly after copulation is similar to

the observation of Sales & Freire (2021) in which a male *Ameivula ocellifera* moved away and did not return to guard the female in the burrow that she had entered shortly after copulation, even though mate guarding or guarding of the female's burrow seems widespread in teiids (Quesnel, 1978; Censky, 1995, 1997; Alfonso & Torres, 2012; Sales & Freire, 2021).

Reproductive behaviour in *A. ameiva* occurs during both the spring-summer (rainy season) and the autumn (dry season) and varies geographically. It is continuous or extended in the Amazon forest, Caatinga, and the restingas of the Atlantic Forest but is more seasonal in the Cerrado and Amazonian savannas (Vitt & Colli, 1994; Rocha, 2008). In summer in the Atlantic Forest, Costa et al. (2010) described courtship behaviour and attempted copulation between an adult male and a dead conspecific female that had six oviductal eggs. However, the size of these eggs resembles that of enlarged vitellogenic follicles (R.A. Ramalho, unpublished data) suggesting that the dead female was in late vitellogenesis.

Our observations show that *A. ameiva* shares some aspects of courtship and copulation behaviour with other teiids. However, the species exhibits some peculiarities, such as performing circular movements around the female to restrict her movements but does not engage in cloacal rubbing against the ground or biting during copulation. Further studies could focus on the dynamics of other reproductive strategies in *A. ameiva*, such as reproductive cycle and sperm storage, and relate them to interactions between males and females during and after the mating season.

ACKNOWLEDGEMENTS

We thank Alexandre Gois, Jorge Calazans, Luiz Antonio Rufato, Michael Siernandes, Willyam Belo de Oliveira, and the Cineryna-TV staff for providing us with the video recordings used in this work, and Henrique B. Braz for the translation. This study was funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (process no. 135518/2020-2) for Ramalho, R.A.

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Accepted: 4 May 2021

Husbandry and captive reproduction of the giant Mexican leaf frog *Agalychnis dacnicolor*

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ABSTRACT - The giant Mexican leaf frog, *Agalychnis dacnicolor*, is a large arboreal frog endemic to Mexico. This species was previously under-represented in European zoological collections and specific techniques for reproductive management under vivarium conditions little known. A group of four males and one female *A. dacnicolor* were maintained in captivity at Chester Zoo (Great Britain). To bring them into reproductive condition, they were subjected to three simulated environmental phases that differed in temperature, humidity and feeding regime. This proved successful so that two clutches of spawn, each containing 150-300 eggs, were deposited on leaves overhanging water. Tadpoles hatched from 4 days following oviposition with approximately 80 % success rate. They were reared at a water temperature of 27 °C to 29 °C and displayed no negative effects from living in high density. All tadpoles metamorphosed successfully and froglets with resorbing tails left water after about 32 days. Their tails were resorbed in a further 4 to 5 days at which time they began to feed; at least in the case of males, sexual maturity was reached after 10 months. This methodology will enable zoological collections in Europe to breed this species for potential conservation, research and educational purposes.

INTRODUCTION

The giant Mexican leaf frog *Agalychnis dacnicolor* (Cope, 1864) is a large hylid frog endemic to Mexico and on the IUCN red list is shown as of Least Concern (IUCN, 2021). It belongs to the subfamily Phyllomedusinae, previously placed within the monotypic genus *Pachymedusa*. Following a review by Faivovich et. al (2010) this species was consequently included within the genus *Agalychnis*, which currently comprises 14 species distributed widely throughout Mexico, Central America, and northern South America (Frost, 2021).

Agalychnis dacnicolor inhabits semi-arid subtropical Pacific lowland forest in Mexico (Duellman, 1970; Weiwandt, 1971). It is especially adapted to survive in hot environments with prolonged dry periods and in some instances has been observed to use humid rodent burrows to escape the heat (Weiwandt, 1971). The breeding cycle of this species is highly seasonal and has been reported to take place during the summer rains that begin in June and extend into August (Weiwandt, 1971). The seasonal rains bring temporary breeding ponds and a higher relative humidity, although day time ambient temperatures remain high and may reach 40 °C or above (Weiwandt, 1971). As with all species of *Agalychnis*, the spawn is attached to vegetation overhanging water where upon hatching the tadpoles drop into the pools below (Duellman, 1970). *Agalychnis dacnicolor* has also been observed laying eggs on land close to the water's edge; the hatching tadpoles use rapid movements of the tail to make their way over ground to water (Weiwandt, 1971).

As suggested by the common name, this is a large species; females have been recorded with snout to vent lengths of up to 103.6 mm, and males up to 73.1 mm (Duellman, 1970). When compared to other species of *Agalychnis*, it is

noticeably heavy bodied, as highlighted in the naming of the previous genus *Pachymedusa*, of which *A. dacnicolor* was the only member; the etymology refers to the thick body of this species (Duellman, 1970). The species is also sexually dimorphic; the snout of the male is more pointed and narrow than that of the female (Duellman, 1970), and in the breeding season males develop dark brown to black triangular nuptial thumb pads (Bagnara & Rastogi, 1992).

Weiwandt (1971) made detailed field observations of the reproductive biology of this species in Sonora, Mexico. The species was also bred in captivity during the 1980s and early 1990s at the University of Arizona during a time when it was more readily exported from Mexico. The physiological processes of both sexes during their reproductive cycles have been described (Bagnara & Rastogi, 1992), as well as pigmentation (Iga & Bagnara, 1975; Bagnara, 1985) and aspects of endocrinology (Bagnara, 1990). However, the specifics of a methodology to bring this species into breeding condition in captivity when maintained within an indoor vivarium are lacking, as the population maintained at Arizona University were maintained and reproduced under semi-natural conditions within a greenhouse, where temperatures and light cycles were similar to that of the natural habitat in Mexico (Bagnara & Rastogi, 1992). The current study provides details of husbandry and environmental conditioning required to induce captive breeding in *A. dacnicolor*.

MATERIALS & METHODS

In 2018, a group of adult *A. dacnicolor* consisting of four males and one female was donated by the Manchester Museum to Chester Zoo. In order to bring them into breeding condition, they were subject to three distinct environmental phases

(summarised in Table 1) from October 2019 to June 2020. Since the frogs were of unknown origin these environmental phases were developed following previous observations of reproduction in this species (Weiwandt, 1971; Bagnara & Rastogi, 1992).

Environmental phases to induce breeding

Phase 1

From October 2019 to April 2020, the group were maintained in a 90 cm (H) x 60 cm (W) x 45 cm (D) Exo Terra vivarium (Rolf C. Hagen Inc.). Thick branching was provided for perching and climbing areas, no substrate was used and a potted *Dracaena fragrans* was used to provide cover and additional arboreal perching. The floor of the enclosure contained a large water tray measuring 24 cm x 18 cm x 8 cm which was replaced daily along with the removal of waste from any glass surfaces within the enclosure. The vivarium was illuminated with a 6 % T5 Arcadia fluorescent lamp (Arcadia Products, Monkfield Nutrition Ltd) providing an ambient UVB index gradient of 0 – 3 (Readings taken using a Solar Meter® 6.5). The ambient daytime temperature fluctuated between 24 °C – 28 °C with a nighttime drop in temperature reaching 18 °C – 20 °C. In addition to this, a basking site was provided consisting of a Solar Raptor 50 W high output lamp (©ECONLUX GmbH) combined with a 50 W Arcadia deep heat projector positioned over branching. This provided a localised area (approx. 25 cm²) of increased heat and UVB during daytime hours. The temperature range in this area was between 29 °C – 35 °C and UVB index range accessible at the level of the dorsum of a basking frog was 2.0 (outer basking zone) to 4.0 (central basking zone). The frogs were provided with a 12:12 photoperiod and the enclosure was lightly misted with water every second day; ambient relative humidity of 40 % – 50 % was maintained during this period. Food was offered three times per week and consisted of Dubia cockroaches (*Blaptica dubia*), black field crickets (*Gryllus bimaculatus*), banded crickets (*Gryllodes sigillatus*) and locusts (*Schistocerca gregaria*). All live foods were gut loaded with fresh vegetables and Repashy Super Load gel (Repashy Specialty Pet Products ©) 24 h prior to feeding, and supplemented directly by dusting with Repashy Calcium Plus.

Phase 2

For the month of May 2020, the group were subjected to an increase in temperature and ambient humidity. They were moved into a larger custom made glass vivarium (dimensions 120 cm H x 120 cm W x 45 cm D) with one third mesh ventilation on the roof. The vivarium was furnished with thick branching to provide perching and with live potted plants (*Ficus elastica* and *Philodendron* sp.) for cover, additional perching, and potential oviposition sites. The ambient temperature was increased to 28 °C – 34 °C during the daytime, with a night time drop in temperature to 20 °C – 22 °C. To raise the temperature in the basking zone the original basking lamp was replaced with a 160 W Arcadia D3 lamp as before positioned over the branching to give a basking zone (now approx. 30 cm²) with temperatures of 38 °C – 42 °C and a UVB index of 3.0 – 4.0. The general enclosure lighting was provided as detailed in phase one. The ambient humidity was increased to 60 % – 70 % by providing a daily misting with water in the afternoon, and fresh water was provided in a large water tray which was

replaced daily. This enclosure did not contain substrate and surfaces were cleaned on a daily basis. During this phase, the frogs were fed more frequently (4 – 5 times per week) using the same food items as detailed previously. The photoperiod also remained the same.

Phase 3

The final environmental phase simulated the rainy season and commenced on 1st June 2020 for two weeks. In this phase, the frogs were not fed and the base of the enclosure was filled with 10 cm of water at room temperature (20 °C – 21 °C). All water was filtered (HMA - Heavy Metal Axe) tap water with a pH of 7.4 at source (tested with API® Freshwater Master test kit and colour chart). The enclosure was not misted during this time and after the first 48 h the water was heated to 27 °C – 29 °C using a 100 W submersible aquarium water heater. The increase in water temperature resulted in an increase in ambient humidity to above 80 %, causing condensation to form inside the enclosure. Further 'rain' sessions over the frogs were created manually using a hosepipe. This increased the water depth of the enclosure to 20 cm. The water was allowed to drain away completely and was then re-filled using the hose rain method up to four times in one rain session. Rain sessions lasted approximately 30 minutes and were provided twice daily for five days, and subsequently every second day for the following nine days. Upon successful oviposition this phase was terminated.

Table 1. A summary of the parameters used for three sequential environmental phases leading to breeding in captive *Agalychnis dactylicolor*

	Phase 1 (Oct 2019 - April 2020)	Phase 2 (May 2020)	Phase 3 (June 2020 for 2 weeks)
Ambient temperature	Day: 24 – 28 °C Night: 18 – 20 °C	Day: 28 – 34 °C Night: 20 – 22 °C	Day: 28 – 34 °C Night: 20 – 22 °C
Feeding	3 times weekly	4-5 times weekly	Not fed
Basking temperature	29 – 35 °C	38 – 42 °C	38 – 42 °C
Relative humidity	40 – 50 %	60 – 70 %	> 80 %
UVI range	0.0 - 4.0	0.0 - 4.0	0.0 - 4.0
Water provision	Localised water bowl, light misting on alternate days	Localised water bowl, light misting daily	Flooded enclosure base, hose rain method 30 minutes twice daily
Photoperiod	12:12	12:12	12:12

Care of eggs, tadpoles and metamorphs

Following oviposition the adult frogs were removed from the enclosure separated by sex, and then housed as detailed in Phase 1. The spawn was left in situ to develop in the breeding enclosure. The first developmental stages of the eggs could be observed within 12 h of oviposition. Development was completed by the fourth day when tadpoles began to hatch. The hatching was aided by lightly misting the spawn with water which promoted tadpole emergence from the egg capsule. This process took place over a 24 h period after which all tadpoles were free swimming and had begun to feed.

Tadpoles remained within the flooded breeding enclosure for rearing in 110 L of filtered (HMA) tap water, giving an estimated density of three tadpoles per litre.

Tadpoles were fed twice daily on a mixed diet of Repashy Soilent Green gel, tropical fish flakes, tinned spinach leaves, Arcadia Amphibigold Pellets and frozen thawed bloodworm (Chironomidae). Tadpoles also grazed on algae growing on the glass walls of the aquarium. Daily water changes of up to 50 % were undertaken to manage the waste produced by tadpoles and the uneaten food. Water temperature was maintained between 27 °C – 29 °C and the pH between 7.4 – 7.6. Due to the density and metabolic rate of the tadpoles a large amount of nitrogenous waste was produced consistently, with levels of nitrates routinely recorded at 80 – 160 ppm (tested using API® Freshwater Master test kit and colour chart).

Metamorphosed young were housed in 45 cm (H) x 45 cm (W) x 45 cm (D) glass Exo Terra vivariums each with a small water bowl, branching, and potted *Spathiphyllum* sp. and *Epipremnum aureum*. Enclosure lighting, UVB and ambient temperature range was provided as detailed in Phase 1, a high temperature basking area of approximately 35 °C was provided via a 35 W halogen spot lamp. For food, 2nd and 3rd instar brown crickets, dusted with Repashy Calcium Plus, were offered daily.

RESULTS

During environmental Phase 1 the group maintained good health and body condition but showed no signs of reproductive readiness or activity. Males did not develop dark nuptial thumb pads or attempt amplexus with the female. It was presumed that nocturnal activity was minimal due to the lack of signs of activity within the enclosure, such as prints



Figure 1. Adult male *Agalychnis dacnicolor* actively basking during the daytime at 41.3 °C



Figure 2. *Agalychnis dacnicolor* spawn attached to a *Ficus elastica* leaf hanging above water



Figure 3. Metamorphosing *Agalychnis dacnicolor* at Gosner stage 44 (Gosner, 1960) following 32 days aquatic larval development

and waste on the glass of the enclosure. Individuals were also often found positioned in the same refugia for consecutive days. Despite low activity during this phase, food was readily consumed after each feeding event.

After being transferred into Phase 2, activity appeared to increase within the group. Individuals were positioned in different resting areas on a daily basis and there was an increase in the amount of waste produced within the enclosure. During day time hours individuals were regularly observed resting in the basking area for prolonged periods at 40 °C – 42 °C (Fig. 1). Although nuptial thumb pads were not evident at the start of this phase, by one week these pads were observed, initially as light brown patches on the thumb of each male and by the third week as dark brown/black swollen nuptial thumb pads.

During Phase 3, males in the group were observed making advertisement calls during the daytime, and amplexus was initiated with the female intermittently during the initial rain events. After five days a male initiated a prolonged amplexus, during this time the female appeared noticeably swollen and began to display restless behaviour, pacing the enclosure carrying the male in amplexus during daytime hours. On the fourteenth day two clutches of spawn were found attached to the leaves of *F. elastica* 10–15 cm above the water level. Each clutch contained approximately 150–300 eggs (Fig. 2) and about 80 % of the eggs gave rise to tadpoles.

Development of the tadpoles was rapid and froglets with resorbing tails emerged from the water from as early as 32 days post hatching (Fig. 3) and in the following 4–5 days tails were fully resorbed. All tadpoles metamorphosed successfully. Once tails had been resorbed, the froglets started to feed readily, began congregating in the high temperature basking area during daytime hours, and grew rapidly. After ten months, individuals reached adult size and the males developed dark nuptial thumb pads, indicating sexual maturity, however these young adults were not exposed to Phase 3 conditions as we did not wish them to spawn at this time.

DISCUSSION

In nature, *A. dacnicolor* requires extreme seasonal changes before it will reproduce. Until males are maintained at above 33 °C the hormonal processes that enable spermatogenesis are not triggered (Bagnara & Rastogi, 1992) and in the current study it was not until during Phase 2, when males were maintained consistently above this temperature, that nuptial thumb pads developed. The presence of these nuptial pads was used as an indicator of readiness to begin Phase 3, the 'rainy season'. Similarly, the maturation of ova in females is also linked to seasonal temperature cycles (Bagnara & Rastogi, 1992).

This prolonged period of reproductive development is unlike other members of *Agalychnis*, which are often opportunistic and explosive in their breeding habits (Scott & Starret, 1974; Roberts, 1994), with females in captivity capable of producing spawn several times annually (Bland, 2013). The dependence on a specific and quite extreme seasonal cycle illustrates the environmental pressure upon this species, which is likely only able to reproduce once per annum. This appears to be mitigated by producing a large amount of spawn and subsequently many offspring before seasonal ponds dry out. When compared to congeneric species of *Agalychnis*, *A. dacnicolor* produces on average larger clutches of eggs, with the mean recorded clutch size being 467 (Duellman, 1970). This dependence on seasonality is also a limitation to the frequency with which the species can be bred in captivity, as it would appear that a full seasonal cycle is required for successful breeding.

Experience based on this group of frogs suggests that this species is relatively hardy when maintained in captivity providing that its environmental needs are met. In the case of the tadpoles, regular partial water changes were sufficient for managing the biological load of the rearing aquarium. In nature, tadpoles would become more crowded as temporary

breeding ponds start to dry out (Weiwandt, 1971). This predisposes them for situations in captivity where tadpoles may be maintained in high densities, in water containing a significant nitrate load, as this appeared not to have negative impacts. Indeed, the tadpoles of this species display adaptations such as unusually long gills, likely in response to the environmental constraints of the natural breeding ponds (Morrisett, 1986).

Following an analysis of record data from the Zoological Information Management System (ZIMS), which is used by zoological collections worldwide, it appears that this breeding success represents the first captive reproduction of this species in a European zoo. It is also the only reproduction amongst all current ZIMS users within the last eighteen years. The methodology detailed herein will be of use to zoological collections wishing to maintain populations of this species, and perhaps even to collections wishing to work with *A. dacnicolor* as a model species for research (Bagnara, 1990).

Given the specific environmental needs of *A. dacnicolor*, this species will become vulnerable in the future if climate change results in prolonged droughts in Mexico (Seagar et. al., 2008; Sodhi et. al., 2008). This research to gather knowledge about captive maintenance of *A. dacnicolor* may benefit future conservation efforts and will enable zoos to maintain educational exhibits that raise awareness of the global amphibian crisis.

ACKNOWLEDGEMENTS

The authors would like to thank Andrew Gray and Matthew O'Donnell of the Manchester Museum for the donation of *Agalychnis dacnicolor* specimens to Chester Zoo herpetological collection, and the herpetology team at Chester Zoo for their support in working with this species.

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Accepted: 8 July 2021

Diet of the southern ravine salamander *Plethodon richmondi*

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ABSTRACT - The diets of many small North American *Plethodon* species are poorly studied despite their important roles in forest ecosystems. Using a non-lethal gastric lavage method, we examined the spring-season diet of 31 southern ravine salamanders (*Plethodon richmondi*) from a second-growth forest in south-eastern Kentucky (USA). We recovered and identified a total of 452 prey items from 14 different prey groups. The three most important prey groups were Formicidae (ants), Acari (mites and ticks), and Collembola (springtails). Together, these groups accounted for more than 80 % of all prey items. Examining the diets of terrestrial salamanders may help us better understand their roles in the regulation of invertebrate communities and the transfer of accessible nutrients back to the soil.

INTRODUCTION

Terrestrial lungless salamanders (Plethodontidae) are an integral component of many forested ecosystems. In the eastern United States, terrestrial salamanders are often abundant (Bailey et al., 2004; Dodd & Dorazio, 2004), with recent density estimates of up to 5.26 individuals/m² (Hernández-Pacheco et al., 2019). Thus, terrestrial salamanders can play an important role in the top-down regulation of invertebrate populations (Hairston, 1987; Davic & Welsh, 2004; Walton et al., 2006; Semlitsch et al., 2014). In turn, terrestrial salamander populations can influence the rate of detritus and leaf litter decomposition (Wyman, 1998; Hickerson et al., 2017), which regulates the amount of CO₂ released from forest floors into the atmosphere each year (Wyman, 1998).

Salamanders typically employ a euryphagous feeding strategy (but see Paluh et al., 2015), where the diversity, amount, and frequency of prey acquired is directly dependent on the spatial and temporal availability of prey in the salamander's microhabitat (Jaeger, 1981). Numerous studies have examined the diets of large (i.e., adult snout-vent-length, SVL > 60 mm), terrestrial, eastern North American plethodontid salamanders (i.e., Oliver, 1967; Rubin, 1969; Whitaker & Rubin, 1971; Powders & Tietjen, 1974; Jensen & Whiles, 2000; Lewis et al., 2014; Hutton et al., 2017). However, the diets of most small (i.e., adult SVL < 60 mm) North American *Plethodon* species are unknown or poorly studied. Furthermore, the majority of previous *Plethodon* dietary studies only identified prey items to the taxonomic level of order and only provided percent occurrence or raw numerical count data. While this dietary information can be useful, identification of prey to the lowest taxonomic level, along with estimates of individual prey volumes, can provide researchers with the data resolution necessary to examine specific differences in ontogenetic, seasonal, and inter-species diet composition.

Plethodon richmondi (southern ravine salamander) is a small (less than 138 mm total length, TL; Petranks, 1998) terrestrial lungless salamander with a broad distribution in eastern Kentucky, northern North Carolina, north-eastern Tennessee, western Virginia, and southern West Virginia. The species is commonly found under flat rocks, damp rotting logs, and in leaf litter on rocky wooded slopes in tracts of mature forest. In Kentucky, these animals are generally active on the forest floor during periods of damp, mild weather from fall through spring and they are particularly abundant on the forest floor from March through May.

In this study, we examined the spring (March - May) diet of *P. richmondi*, from a second growth forest in south-eastern Kentucky. We used a non-lethal gastric lavage technique to identify stomach contents to the lowest possible taxonomic resolution, with these data we have been able to report 1) the first description of *P. richmondi* diet, and 2) evaluate the importance of prey groups/types to the overall diet.

MATERIALS & METHODS

Our study area was located in the University of Kentucky's Robinson Forest (RF), a 5983 ha experimental forest located in the interior rugged section of the Cumberland Plateau in Breathitt and Knott Counties, Kentucky USA. Robinson Forest is a 90-year-old, second growth forest with vegetation consisting of typical, mixed mesophytic forests of the region; dominant tree species included white oak (*Quercus alba*), tulip tree (*Liriodendron tulipifera*), Eastern hemlock (*Tsuga canadensis*), and chestnut oak (*Quercus prinus*) (for more details, see Phillippi & Boebinger, 1986).

In the spring (March-May) of 2016 and 2017, *P. richmondi* were located by sifting through dense leaf litter, as well as by turning over logs, rocks, and other cover objects near first-order streams. Upon capture, the salamanders were placed in individual containers and brought back to the dry lab at RF for processing. Salamanders were anesthetised in a solution

of 1 g Maximum Strength Orajel®/1 liter of aged tap water (Cecala et al., 2007). They were removed from the solution when they could no longer right themselves after being flipped over. Then to obtain their stomach contents the salamanders were subjected to a non-lethal gastric lavage technique (Fraser, 1976a; Hantak et al., 2016; Hutton et al., 2017). Salamanders were placed on their dorsum on a folded paper towel, and an approximately 6.0 cm long piece of water-lubricated tubing (1.3 mm OD PTFE tubing were used, Zeus Inc., catalog number AWG24) was slowly inserted into the esophagus until there was resistance. Distilled water was then pumped (Nipro® 3 mL syringes with 22-gauge needles) into the tubing. As in previous studies, salamander stomachs were pumped at least two additional times after the last prey item was extracted to verify removal of all contents (Cecala et al., 2007; Bondi et al., 2015). After lavage, each salamander was measured for snout-vent length (SVL: from the tip of the snout to the posterior angle of the vent) and total length (TL: from tip of the snout to the tail's terminus) to the nearest 0.01 mm with a digital caliper, and mass to the nearest 0.1 g with a digital scale. If possible, sex was determined based on the presence of mental glands in males, or eggs visible through the abdominal walls in females. Salamanders were then placed in a recovery container of aged tap water until they could right themselves and responded to tapping, which took approximately 15 minutes. Salamanders were returned to their exact location of capture within 1.5 h.

Stomach contents were retained on the paper towels and immediately identified to family, genus, and species, if possible, using a dissecting microscope along with appropriate keys and guides (Peckarsky, 1990; Merritt & Cummins, 1996; Fisher & Cover, 2007; Bradley, 2012; Evans, 2014). Additionally, invertebrate life stage (larval or adult) was reported, if applicable. The individual prey items were then grouped based on order/class and life stage.

To calculate prey volume, we measured the length and width of each prey item to the nearest 0.01 mm using a digital caliper and estimated volume as a prolate spheroid using the equation (Dunham, 1983):

$$\text{Prey Volume } (v_x) = \left(\frac{4\pi}{3}\right) \left(\frac{\text{length}}{2}\right) \left(\frac{\text{width}}{2}\right)^2$$

The relationship between individual *P. richmondi* size (i.e., mass, SVL, and TL) and total consumed prey volume were analyzed using individual linear regressions in the statistical program R (Version 3.4.3). The Shapiro-Wilk test was used to assess the normality of the data residuals. Salamander size (SVL and TL) were log-transformed to meet the normality assumption of linear regression.

Relative occurrence (RO) of each prey group was calculated using the equation:

$$\text{RO} = (P \times 100) / T$$

where P is the total number of occurrences of a given prey type, and T is the total number of prey items recovered (Loveridge & Macdonald, 2003).

Individual prey volumes and RO were used to calculate importance values (I_x) for each prey group (Holomuzki, 1980; Davic, 1983). Specifically, I_x values estimate the relative weight of importance of a particular prey type or group to the overall diet in the animals sampled. To estimate group I_x values, the volumetric and relative occurrence (RO) data of each prey item and type are calculated. Importance values (I_x), ranging from 0 to 1, were calculated for each prey group/type using the equation (Powell et al., 1990; Anderson & Mathis, 1999):

$$I_x = \frac{\left[\left(\frac{n_x}{N}\right) + \left(\frac{v_x}{V}\right) + \left(\frac{f_x}{F}\right)\right]}{3}$$

Where n_x , v_x , and f_x represent the number of a prey type, the volume of the prey type, and frequency or the number of stomachs containing that prey type, respectively, and N, V, and F represent their sums across all prey types (Hantak et al., 2016). These importance values were used to compare the overall importance of a particular prey group/type to the overall diet of *P. richmondi*. After processing, prey samples were placed into individually labeled vials containing 70 % ethanol. Samples are stored in the Branson Museum collection at Eastern Kentucky University, Richmond, Kentucky.

RESULTS

We stomach flushed a total of 31 *P. richmondi*, SVL ranged from 20.00–57.20 mm (mean \pm SD = 40.86 \pm 7.93), TL ranged from 38.54–101.07 mm (mean \pm SD = 76.46 \pm 17.33), and mass ranged from 0.1–1.2 g (mean \pm SD = 0.75 \pm 0.31). Overall, 14 individuals were identified as adult females, 3 were reproductive males, and 14 were of unknown sex. All individuals had at least one prey item in their stomachs. We recovered a total of 452 prey items, and on average, individuals contained 14.6 \pm 10.1 prey items in their stomachs. We found no relationship between total consumed prey volume and salamander mass ($R^2 = -0.028$; $P = 0.683$), SVL ($R^2 = -0.034$; $P = 0.891$), or TL ($R^2 = 0.013$; $P = 0.249$).

Overall, we found 49 distinct prey types from 14 invertebrate prey groups. These results are summarised in Figure 1 and shown in detail in Supplementary Materials (Table S1). The three most important prey (I_x), which made up 62% of the overall importance (1.519 of 2.419 total I_x) and 82% of the total prey occurrence, were Formicidae (ants: $I_x = 0.659$, RO = 29.20%), Acari (mites/ticks: $I_x = 0.514$, RO = 28.76%), and Collembola (springtails: $I_x = 0.346$, RO = 24.56%; Fig. 1, Table S1).

Among the ants, prey from the genus *Pheidole* contributed to approximately 50 % of both the overall Formicidae I_x and RO. *Pheidole* also comprised 12 % of the overall prey importance and 15.3 % of all prey items consumed. Mites from the superfamily Galumnoidea, were the most important and frequent among the Acari (34 % and 42 %, respectively), comprising 7.1 % of the overall prey importance and 12 % of all prey items. Lastly, springtails from the family Isotomidae, were the most important and frequent among the Collembola

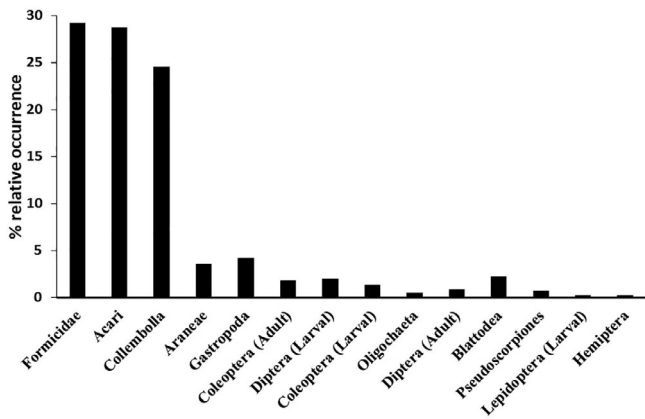


Figure 1. Prey groups found as stomach contents in *Plethodon richmondi* (n=31), expressed as percent relative occurrence, from south-eastern Kentucky (USA) from March-April 2016 and 2017

(62 % and 55 %, respectively) and comprised 8.9 % of the total prey importance and 13.5 % of all prey items.

Arachnids (Acari, Araneae, and Pseudoscorpiones) accounted for approximately 30 % of all prey importance and occurrence. Araneae were found to be the fourth most important prey group ($I_x = 0.178$) in terms of volumetric importance (i.e., I_x), although they only comprised 3.5 % of all prey items. Unfortunately, many of the spiders could not be identified further than order due to advanced digestion, but of those that could be identified, most were either cobweb (Theridiidae) or ground (Gnaphosidae) spiders. The fourth most common prey were gastropods (snails) and comprised 4.2 % of all prey and were the fifth most important group ($I_x = 0.170$). Overall, larval prey comprised Coleoptera (beetles), Diptera (flies), and Lepidoptera (moths), accounted for 8.4 % of the total importance and just 3.5 % of all prey items.

DISCUSSION

This is the first study to describe the spring diet of *P. richmondi* and calculate individual prey group importance values. We reported the importance values for 14 prey groups to adult *P. richmondi* from a population in Kentucky to the taxonomic level of family, genus, and species, and our data demonstrate that *P. richmondi* spring diet is primarily composed of adult-staged, terrestrial invertebrates, with Formicidae, Acari, and Collembola being the three most volumetrically important and frequently consumed prey.

We found ants to be both the most important and numerous prey ($I_x = 0.659$, RO = 29.20 %) consumed by *P. richmondi*. Previous studies have similarly reported ants as one of the most important prey groups in many eastern North American *Plethodon* (Cochran, 1911; Duellman, 1954; Oliver, 1967; Rubin, 1969; Whitaker & Rubin, 1971; Powders & Tietjen, 1974; Hall, 1976; Fraser, 1976b; Camp & Bozeman, 1981; Bailey, 1992; Bellocq et al., 2000; Jensen & Whiles, 2000; Milanovich et al., 2008; Lewis et al., 2014; Paluh et al., 2015; Hantak et al., 2016; Hutton et al., 2017). King et al. (2013) estimated that ants can account for more than 95 % of the macroinvertebrate population in eastern temperate hardwood forests. Thus, the general importance of ants to

Plethodon species is likely a result of their abundance and availability in salamander microhabitats relative to other potential invertebrate prey.

We identified ants in the spring diet of *P. richmondi* from nine species/genera, with members of *Pheidole* and *Lasius* comprising 53 % and 23.5 % of all ants, respectively. Similar to our results, Hutton et al. (2017) reported 12 species/genera of ants in the south-eastern Kentucky spring diet of *P. kentucki*, 43 % were *Pheidole* and 24 % were *Lasius*. Unsurprisingly, studies conducted outside of Kentucky or in other seasons have produced somewhat different results. Paluh et al. (2015) reported ants in the north-eastern Ohio fall (September and October) diet of *P. cinereus* from ten species/genera with *Aphaenogaster picea*, followed by two species from the genus *Lasius* comprising the majority of ants consumed. Lewis et al. (2014) reported ants in the south-western North Carolina summer diet of *P. shermani* from ten species/genera with *Aphaenogaster* comprising up 46 % of the ant prey and 27 % of all prey items consumed. In our study, *Aphaenogaster* comprised only 0.8 % of the ants consumed by *P. richmondi*. Differences in regions, sampling seasons, species distributions, species assemblages, and microhabitats are likely responsible for the observed differences in the species of ants in the diets of these eastern *Plethodon* salamanders.

In this study, Acari (mites) were found to be the second-most important and frequently consumed prey group ($I_x = 0.514$, RO = 28.76 %). Despite their importance in *P. richmondi*, Duellman (1954) reported only three mite prey items in the diet of the closely related *P. electromorphus*. Acari have been found to feature prominently in the diets of *P. amplus*, *P. glutinosus*, and *P. wehrlei* (Rubin, 1969; Hall, 1976) and have been reported as the second-most consumed prey in *P. jordani*, *P. serratus*, and *P. websteri* (Powders & Tietjen, 1974; Camp & Bozeman, 1981). Numerous studies throughout the eastern range of *P. cinereus*, have also reported Acari to comprise a large portion of their diet (Cochran, 1911; Maglia, 1996; Bellocq et al., 2000); specifically, Hantak et al. (2016) found Acari to comprise 26 % of the diet of this species. Similarly, Hutton et al. (2017) reported Acari in 27% of *P. kentucki* diets. It is uncertain if seasons, species assemblages, and or microhabitat are responsible for the variation of Acari in the composition of the diet.

We found Collembola (springtails) to be the third-most important and frequently consumed prey group ($I_x = 0.346$, RO = 24.56 %) in the diet of *P. richmondi*. In the diet of *P. electromorphus*, Duellman (1954) reported Collembola to constitute just 2 % of the diet. However, Collembola (springtails) have been reported to constitute a significant portion of diet in *Plethodon* (Cochran, 1911; Fraser, 1976a; Powders & Tietjen, 1974; Camp & Bozeman, 1981; Jensen & Whiles, 2000; Bellocq et al., 2000). Specifically, Hantak et al. (2016) found Collembola to comprise 17 % of the dietary importance in *P. cinereus* and Hutton et al. (2017) reported Collembola in 42 % of *P. kentucki* stomachs and comprised 10% of all prey. In addition to differences in Acari and Collembola in the diet of *P. electromorphus* and *P. richmondi*, Duellman (1954) reported that Isopoda (isopods) were the second-most abundant prey, however, we failed to detect isopods in any *P. richmondi*. Overall, the differences in the

diet compositions between these two closely related species are likely due to the influence of sampling season and site conditions on invertebrate prey diversity, abundance, and availability.

Plethodon richmondi is a euryphagous salamander that during spring time consumes a diverse assemblage of primarily mid-sized, terrestrial, adult invertebrates, principally consisting of Formicidae, Acari, Collembola, Araneae, and Gastropods. Additional studies should prioritise evaluating the diet of *P. richmondi* during other times of the year. Further, the non-lethal gastric lavage technique should be used to examine the diets of other small *Plethodon* salamanders to identify prey to the lowest taxonomic level and so better understand the role of these salamanders in the regulation of invertebrate communities. These studies should include the estimation of prey volumes to allow for the calculation of importance values, which can be used to make a more discerning examination of spatial and temporal variation in salamander diets among species, age groups, and between sexes.

ACKNOWLEDGEMENTS

Funding for this project was provided by the Kentucky Academy of Science, University of Kentucky Tracy Farmer Institute for Sustainability and the Environment, University of Kentucky Appalachian Center, Eastern Kentucky University Division of Natural Areas, the Society for the Study of Amphibians and Reptiles, Foundation for the Conservation of Salamanders, the Society of Freshwater Science, and the McIntire-Stennis Research Program (accession number 1001968). The Department of Forestry and Natural Resources at the University of Kentucky provided resources, facilities, and permission for use of Robinson Forest. Research was performed under the University of Kentucky Institutional Animal Care and Use Committee protocol number 2012-1054 and Kentucky Department of Fish and Wildlife Resources permit number SC1711117.

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Accepted: 9 July 2021

Please note that the Supplementary Material for this article is available online via the Herpetological Bulletin website:
<https://thebhs.org/publications/the-herpetological-bulletin/issue-number-158-winter-2021>

Agonistic and mating behaviour of the endemic lizard *Trachylepis atlantica* from the Fernando de Noronha archipelago, Brazil

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ABSTRACT - The skink *Trachylepis atlantica* is endemic to the Fernando de Noronha archipelago. Although this species is abundant in the archipelago, it is increasingly threatened by invasive species, predation, and anthropic interference. However, little is known about its natural history. Here we report on territory use, male-male combat, and mating behaviour of free-ranging *T. atlantica*. During the dry season, we observed two bouts of male combat and two copulations, which suggests some mating seasonality. In male combat, *T. atlantica* displays ritualised agonistic behaviour with escalated aggressiveness that include - i) visualisation, approaching or following, ii) visual display, iii) bite and body confrontation, and iv) dominance. Adult males were always alert to invaders within their territories. After combat, resident males showed scars on their heads resulting from agonistic encounters. During the two copulations, we observed courtship, immobilisation, and mating.

INTRODUCTION

Skinks of the genus *Trachylepis* occur mainly in Africa, but a single representative, the Noronha skink *Trachylepis atlantica* (Schmidt, 1945), occurs in the New World, on the Fernando de Noronha archipelago, off the north-eastern coast of Brazil (Travassos, 1946; Mausfeld et al., 2002; Carranza & Arnold, 2003). The ancestors of *T. atlantica* are suggested to have reached the archipelago about nine million years ago by natural transoceanic dispersal of rafting vegetation (Mausfeld et al., 2002; Carranza & Arnold, 2003). The Noronha skink is an opportunistic generalist, feeding on insects, plant material, and even nectar from the flowers of the mulungu tree (*Erythrina velutina*) (Sazima et al., 2005; Rocha et al., 2009). Although the species has not yet been classified by the International Union for the Conservation of Nature, it was recently reclassified locally as 'threatened' (unpublished data, State Environment Agency - AEMA, 2017). *Trachylepis atlantica* is abundant in the Noronha archipelago but many aspects of its biology remain unknown and, despite the increasing knowledge of lizard behaviour, studies on the agonistic behaviour of skinks are scarce (Torr & Shine, 1994). Some species show elaborate social behaviours and complex interactions associated with reproduction (Sánchez-Hernández et al., 2012). Here, we provide the first report of male competition and mating behaviour of free-ranging *T. atlantica*.

MATERIALS & METHODS

The Fernando de Noronha archipelago (area = 18.2 km²) is located 350 km off the north-eastern coast of Brazil and comprises 21 islands and islets (Carleton & Olson, 1999; Almeida, 1995). Temperature is constantly warm throughout the year (~ 27 °C). Rainfall is highly seasonal, with the rainy season occurring from March to August and the dry season from September to February (Almeida, 1955). Field observations were made on the main and secondary islands in February, April, October, November, and December of 2015, 2016, and 2018 (Fig. 1). Observations were made from 10:00 to 15:00 h, when lizards are most active (Rocha et al., 2009), inside a capture-mark-resight parcel (main island) and in point transects on the main island and on four smaller islands Rata, Meio, Morro da Viúva, and Chapéu (for population density methodology see Gasparotto, 2019). The first author filmed the social interactions using a Nikon Coolpix P610 digital camera; care was taken to keep a distance that would not disturb the lizards. We recorded the date, time, location, and duration of each combat and copulation (Fig. 1; Table 1). We considered 'territory defence' any behaviour that caused escape or avoidance of rival individuals so that an area became of exclusive use to the resident male (Martins, 1994). We defined combat as any aggressive act involving physical contact (e.g., biting, wrestling) that may cause injury (Martins, 1994). Because of the evident male-biased sexual size dimorphism (Rocha et al., 2009), it is possible to identify the sex of adult individuals without capturing

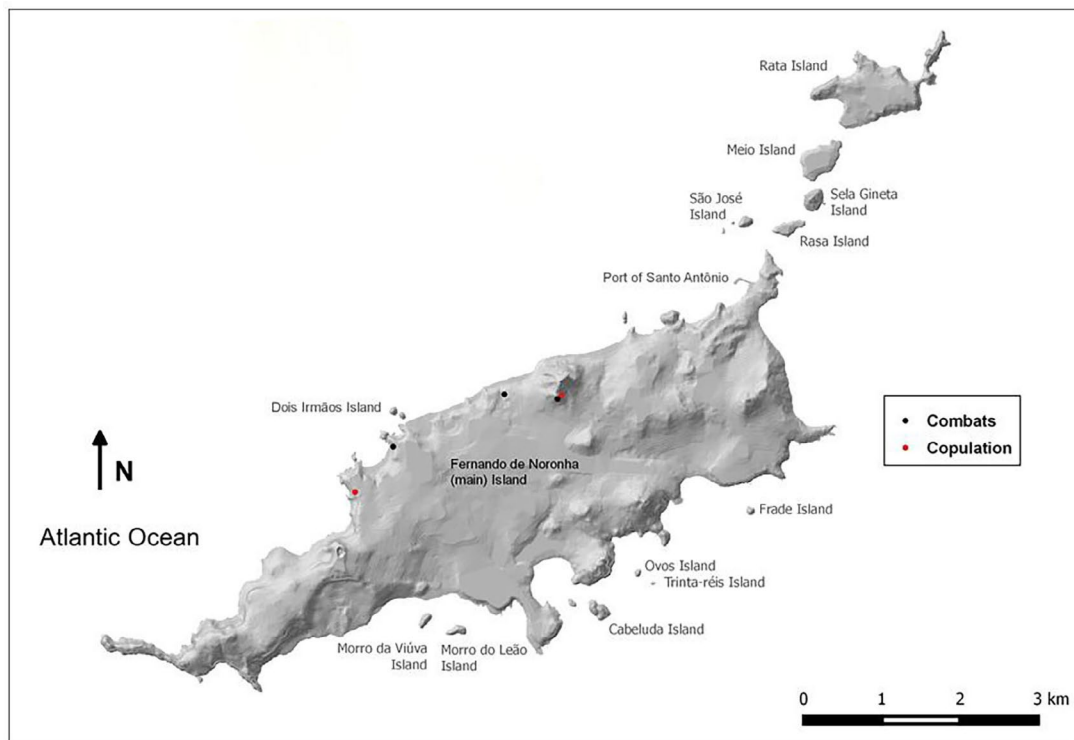


Figure 1. Map of the Fernando de Noronha archipelago indicating the locations of behavioural observations

Table 1. Metadata for observations made on the social interactions of the Noronha skink, *Trachylepis atlantica*, recorded in the Fernando de Noronha archipelago

Record	Interaction	Date	Site	Interaction duration (min)	Start time	End time	Season	Record
1	Mating	02/23/2015	Piquinho	1	10:53	10:54	Dry	Photo
2	Male-male combat	02/23/2015	Boldró	15	14:24	14:39	Dry	Photo and video
3	Territory defence	02/26/2015	Boldró	< 1	10:01	10:01	Dry	No media
4	Territory defence	11/25/2015	Golfinho	< 1	11:40	11:40	Dry	No media
5	Territory defence	02/06/2016	Tejuaçu	< 1	9:14	9:14	Dry	No media
6	Territory defence	02/06/2016	Piquinho	6	14:47	14:53	Dry	Photo and video
7	Courtship	02/06/2016	Piquinho	< 1	14:52	14:52	Dry	Video
8	Territory defence	02/10/2016	Tejuaçu	< 1	10:32	10:32	Dry	No media
9	Male-male combat	02/11/2016	Sancho	3	15:16	15:19	Dry	Photo and video
10	Territory defence	02/17/2016	Americano	< 1	9:40	9:40	Dry	No media
11	Territory defence	02/19/2016	Americano	< 1	9:55	9:55	Dry	No media
12	Territory defence	11/02/2016	Leão	< 1	11:58	11:58	Dry	No media
13	Mating	12/29/2018	Golfinho	2	9:10	9:12	Dry	Video



Figure 2. An adult male *Trachylepis atlantica* using a hole in a tree as a shelter (November 25th, 2015, at Golfinho, Fernando de Noronha archipelago). The male was alert to the approach of other conspecifics.

them. The study was conducted under the approval of the Instituto Chico Mendes de Conservação da Biodiversidade (Brazilian Ministry of Environment, permit number 41682-1) and the Animal Ethics Committee of the School of Veterinary Medicine of the University of São Paulo (1827250515)

RESULTS

Agonistic behaviour

We identified the following behavioural repertoire during interactions between males.

Alert – The resident male is alert to possible invaders in his territory. When a male enters an occupied territory, the resident male runs towards the invader, chasing and expelling him from the territory.



Figure 3. Male combat behaviour of *Trachylepis atlantica* observed on February 23rd, 2015, at Boldró, Fernando de Noronha archipelago – **A.** Two adult males positioned parallel to each other while compressing the body laterally and lifting the four limbs, **B.** One of the males opens his mouth to intimidate and eventually bite his opponent, **C. – E.** Body confrontation and attacks directed at the head and tail of the rival, followed by body rotation, **F.** The combat ends with the pursuing male expelling the rival from the territory

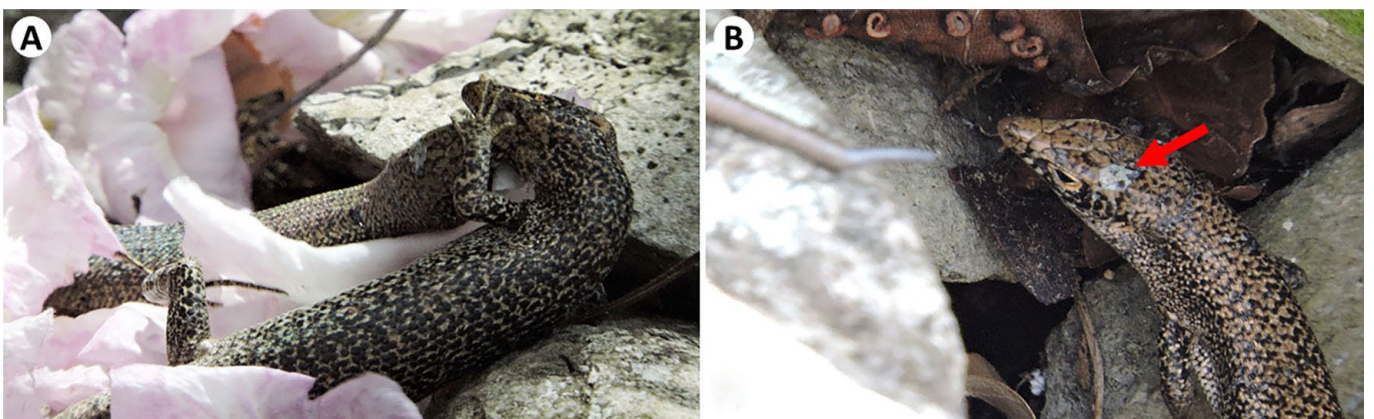


Figure 4. Male combat of the *Trachylepis atlantica* (February 23rd, 2015, Boldró, Fernando de Noronha archipelago) – **A.** A male biting his rival's head, making it impossible for the opponent to open his mouth, **B.** A male with a head injury (red arrow) after the combat

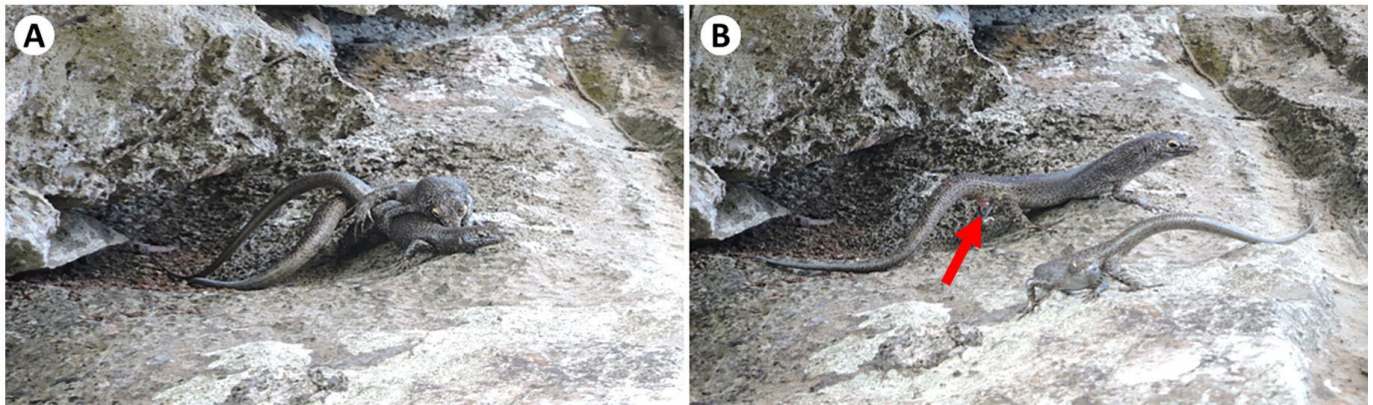


Figure 5. Mating behaviour of *Trachylepis atlantica* (February 23rd, 2015, Piquinho, Fernando de Noronha archipelago) – A. The male bites and holds the female while inserting his hemipenis into her cloaca, B. Post-mating, note that the male's hemipenis (red arrow) remains everted

Body (visual) display – This consists of visual contact and body alignment. Males position themselves parallel to each other and switch positions frequently, directing their heads parallel to the opponent's tail.

Slow-motion walk – Lizards stand on tiptoes, arch their bodies upwards, walk in slow motion arching their necks. In some cases, the opponent keeps its venter and head on the substrate.

Bite and body confrontation – This consists of bites directed at the tail, cloacal region, neck, and head. As the combat continues, the males become breathless and decrease the frequency of attacks.

Dominance – The submissive male flees the territory, followed by the dominant male, which continues to attack.

To view some details of these agonistic behaviours watch our video (BHS video, 2021).

Description of the observed combats

All observations of agonistic interactions were made only on the main island during the dry season in February and December (Table 1). Seven resident males showed territorial defence behaviour. The resident males were alert most of the time. Male territories were usually associated with shelters and feeding sites. Locations with many rocks or tree trunks provide safe hiding places and often had greater numbers of lizards (Fig. 2). On two occasions (23rd February 2015 and 11th February 2016), the invading male remained in the territory even after the resident male approached; consequently, the lizards engaged in combat. These agonistic interactions had already started when we first detected them (Figs. 3 and 4). The males moved around while slightly arching their bodies (slow motion walk), inflating the gular region, and compressing the trunk laterally (Fig. 3A). These behaviours proceeded for a while, with the males often switching positions and positioning themselves parallel to each other. Shortly before the attack, the individuals opened and closed their mouths. Next, the lizards moved slowly towards the opponent with short and abrupt movements. All individuals performed slow and side-to-side undulations of the tail end to direct the opponent's attack to that region (Fig. 3B, C). Individual males often exhibit tail injury or breakage and in one agonistic interaction, a male ripped

and ingested the tip of his rival's tail (VPOG, pers. obs.). The attacker bit the opponent while rotating its own body (Fig. 3C, D). Throughout the combat, both rival males launched sequential attacks that alternated with body displays. Fighting males had scars on their heads (Fig. 4A, B). In the third observation (6th February 2016), we noticed only body displays (without attacks) and that both individuals were panting, suggesting that the agonistic interaction was ending or that the resident male was just defending the boundaries of his territory. Tongue-flicking occurred a few times throughout this behaviour. In all combats, we identified the same behavioural repertoire described above.

Mating behaviour

We identified the following behavioural repertoire during male-female reproductive interactions.

Courtship – The male approaches the female performing rapid and frequent head bobs.

Immobilisation – The male bites the female's neck or limb and holds her body with his hindlimb.

Mating – The male inserts the hemipenis into the female's cloaca.

Description of the observed mating

We observed two copulations on the main island during the dry season (Table 1). When a female entered an occupied territory, the resident male approached and started to court her. Females moved through the territories of several males. The first copulation occurred on 23rd February 2015 (late dry season). The male immobilised the female by biting her on the neck and holding her body with his right hindlimb. Then, the male positioned himself so that the female's tail was lifted, thus allowing the insertion of the hemipenis into the female's cloaca (Fig. 5A). Although copulation was underway when we began our observations, the male still took 30 seconds to release the female and retract his hemipenis. After copulation, the male stayed close to the female, following her for some time. The second copulation occurred on 29th December 2018 (mid-dry season). The male chased the female, started the courtship and bit her near the left forelimb to immobilise her. While the male tried to insert the hemipenis into the female's cloaca, another male approached, causing the first male to move away holding the

female by her neck. Next, the male immobilised the female by biting her on the left forelimb and then rubbed his left hindlimb on hers. After a few seconds, the female lifted her tail, allowing the male to insert his hemipenis into her cloaca. The mating was recorded for only 12 seconds, but it lasted approximately two minutes.

DISCUSSION

We report for the first time male-male agonistic interaction and mating in *T. atlantica*. Because male combats occurred in the same season as mating, we infer that male-male agonistic interactions in *T. atlantica* are related to territory defence and probably access to females. Indeed, vitellogenic females have also been observed in the same period as mating (Rocha et al., 2009).

Territoriality is often correlated with access to females (Koenig, 2017), and combat ability strongly predicts species fitness (Cooper, 1999). Male body size is related to better territories (i.e., greater availability of resources); thus, the larger the male, the better its territory (Olsson & Madsen, 1995; Sacchi et al., 2009). These observations may explain the male-biased sexual size dimorphism recorded in *T. atlantica* (Travassos, 1946; Rocha et al., 2009). Territory defence is favoured when the payoffs, such as access to females and territorial exclusivity, are higher than the costs of expelling potential competitors (Stamps, 1994). Experienced male individuals are more likely to succeed in agonistic encounters with other males, resulting in greater access to females (Kim & Zuk, 2000). Besides the three agonistic interactions observed, resident males also attacked other males that entered their territories during courtship. Occasionally, male and female individuals were seen close to each other (VPOG, pers. obs.), suggesting that male and female territories overlap or that females move through the male territories.

Agonistic interactions are common in reptiles and usually associated with the reproductive season (Brattstrom, 1974; Shine, 1978; Gillingham et al., 1983; Denardo & Licht, 1993; Almeida-Santos et al., 1998). Agonistic behaviour seems uncommon in skinks (Cooper & Vitt, 1987a, b; Cooper, 1999; Chapple, 2003; Langkilde et al., 2003) but common in varanids (Murphy & Mitchell, 1974; Thompson & Withers, 1997), helodermatids (Beck & Ramírez-Bautista, 1991), iguanids and agamids (Moehn, 1974; Rand & Rand, 1976), and even in the tuatara (Gans et al., 1984). Agonistic interactions usually exhibit varying degrees of ritualisation, which may culminate in high energy costs and potentially fatal injuries (Langkilde et al., 2005).

Several male *T. atlantica* had mutilated or regenerated tails. These observations corroborate previous descriptions that lizards may autotomise only the tip of the tail when facing a predator (Cooper & Smith, 2009). The “economy of tail autotomy” may be advantageous because it allows the rest of the tail to be autotomised in later events (Cooper & Smith, 2009). Another proposed advantage is that the tail portion left intact functions as a lateral counterbalance that keeps the individual stability during flight (Ballinger et al., 1979). However, frequent tail bites may contribute to a decrease in territorial dominance, as observed in the phrynosomatid lizard

Uta stansburiana. Dominance decreases after individuals lose their tails in agonistic interactions (Fox & Rostker, 1982; Fox et al., 1990). Many lizard species also use tail undulation during agonistic interactions as an antipredatory tactic and in social interactions to direct the rival's attention to the tail (Murphy & Mitchell, 1974; Cooper, 2001). Making the tail visible deflects the attack away from the body, thus avoiding injury to the head and vital organs (Fox et al., 1990). However, tail undulation has also been described as submissive and evasive behaviour in subordinate individuals of some species, such as *Tropidurus semitaeniatus* and *Chalcides viridanus* (Sánchez-Hernández et al., 2012; Bruinjé et al., 2019). We suggest that the Noronha skink uses tail undulation to divert the rival's attention and direct attacks to the tail.

The aggressive behaviour of *T. atlantica* is similar to that described for other skinks (Done & Heatwole, 1977; Torr & Shine, 1994; Torr & Shine, 1996; Sánchez-Hernández et al., 2012). In *Trachylepis*, agonistic interactions have been observed in *T. margaritifera* (Wymann & Whiting, 2002) and *T. sechellensis* (Brooke, 1983). In *T. margaritifera*, male combat seems to be associated with the maintenance of territories during the reproductive season (Wymann & Whiting, 2002).

Carpenter (1963) observed that iguanids and agamids that inhabit areas where sight is of limited importance exhibit less elaborate behaviours and more discrete displays. As skinks are less territorial and many are fossorial, they are believed to lack social display (Stamps, 1977a). Evans (1961) suggested that the limited repertoire of agonistic and courtship behaviours in skinks derives from greater dependence on olfactory stimuli than visual signals for interspecific recognition. In several lizard species, pheromones that mediate agonistic interactions, mate attraction, and territory demarcation are released from femoral pores (Cooper, 1994; Bruinjé et al., 2020). Although we observed some tongue-flicking, we observed no femoral or cloacal pores, suggesting that male *T. atlantica* rely heavily on visual signals during agonistic behaviour, similar to that observed in the skink *Carlia jarnoldae* (Langkilde et al., 2003).

Lateral compression of the body is performed when individuals are close to each other and often precedes bites. This behaviour has also been described in the skinks *C. viridanus* and *Lampropholis guichenoti* (Torr & Shine, 1994; Sánchez-Hernández et al., 2012). Unlike several lizard species that commonly perform head bobs and tongue flicks during male-male combat and courtship (Langkilde et al., 2003; Coelho et al., 2018; Bruinjé et al., 2019), a male Noronha skink performs these behaviours most of the time that a female is in its territory. Slow-motion behaviour also occurs in the skink *Carlia jarnoldae*, mainly during courtship (Langkilde et al., 2003). Torr and Shine (1994) suggested that the slow-motion behaviour in the skink *L. guichenoti* is an assertion display in agonistic interactions. Biting has also been reported during male-male combat in several lizard genus, such as *Anolis* (Vanhooydonck et al., 2005) and *Crotaphytus* (Husak et al., 2006). Biting, chasing, and approaching are considered intimidating postures, performed mainly by dominant males (Bruinjé et al., 2019). In *T. atlantica*, many individuals showed head scars and regenerated tails, possibly caused by bites during male combat.

The mating behaviour of *T. atlantica* is similar to that described for several skinks (e.g., Fitch, 1954; Evans, 1961) and unrelated lizards (Barreto-Lima & Sousa, 2006; Sánchez-Hernández et al., 2012; Migliore et al., 2014). Prolonged neck bites are likely to be advantageous and suggestive of mate guarding in other lizard species, including skinks (Bull, 2000). In conclusion, our observations on the agonistic behaviour of *T. atlantica* contribute to the understanding of ritualised combat behaviour and the use of visual signals during agonistic interactions in the Scincidae. We suggest that the high density of lizards in the Fernando de Noronha archipelago, the absence of femoral pores, and the scarce tongue flicking during agonistic interactions corroborate the greater use of visual than chemical signals. The occurrence of male combat and mating in the same season (dry season) suggests that such behaviours are associated with the reproductive season of this species.

ACKNOWLEDGMENTS

We thank the administrations of the State District of Fernando de Noronha, Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Parque Nacional Marinho de Fernando de Noronha, Área de Proteção Ambiental de Fernando de Noronha-Rocas-São Pedro e São Paulo, Centro Nacional de Pesquisa e Conservação de Répteis e Anfíbios (RAN/ICMBio), and Fire Department of Fernando de Noronha for allowing this study to be conducted. We also thank Mauro Teixeira Jr. for valuable suggestions during the manuscript preparation. We are thankful to The Rufford Foundation (grant number 18890-1), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (PVE Project number 88881.065000/2014-1), Fundação de Amparo à Pesquisa do Estado de São Paulo (project number, 2016/16433-1) for the financial support and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for research fellowships (#310357/2018-7). This study was partially financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001.

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Accepted: 29 July 2021

Captive husbandry and breeding of the Nguru spiny pygmy chameleon *Rhampholeon acuminatus*

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ABSTRACT - The Nguru spiny pygmy chameleon (*Rhampholeon acuminatus*) is endemic to the Nguru mountains in Tanzania. It is assessed as Critically Endangered and is collected from the wild for the pet trade. An ex-situ population of this species was recently established at The Wild Planet Trust, Paignton Zoo, in the hope of learning more about the husbandry and biology of this species. We report on the captive husbandry of adults and the successful breeding, hatching and rearing of juveniles. Females carried four eggs but laid them in pairs. When eggs were incubated at 19.2-22.8 °C, hatchlings emerged roughly 180 days after laying. The hatchlings had a total length of about 30 mm and weighed 0.2-0.3 g. To our knowledge, this is the first published account of captive breeding for this species. The husbandry methods described could be used to establish populations of this and other *Rhampholeon* species in captivity, which in turn would reduce the demand for wild caught (*Rhampholeon*), as well as inform future conservation breeding programmes for this species.

INTRODUCTION

The genus *Rhampholeon* (family Chamaeleonidae) comprises 19 species (The Reptile database, 2021). These are distributed across West Africa (parts of Nigeria), Central Africa and East Africa in savannah, forests and woodland habitats usually restricted to highland areas. *Rhampholeon acuminatus* Mariaux & Tilbury 2006, commonly known as the Nguru spiny pygmy chameleon, occurs in the subtropical/tropical montane forest of the Nguru Mountains in the Morogoro region of Tanzania, at 1500-1600 m a.s.l. (Mariaux & Tilbury, 2006; Tilbury, 2010). The species is assessed as Critically Endangered by the IUCN (Tolley et al., 2014). It is also considered a global priority for conservation on account of its evolutionary distinctiveness and global endangerment (EDGE, 2020).

Rhampholeon acuminatus is a crepuscular chameleon living on the lower levels of the forest in leaf litter or perching on low vegetation between 50 cm and 700 cm high (Tilbury, 2010). They are sexually dimorphic; the males are more slender and longer than females, up to 63-71 mm total length with a longer tail that accounts for 25-30 % of this length, and when mature have a larger downward pointing rostral extension (Fig. 1) (Mariaux & Tilbury, 2006; Hildenhagen, 2007). Females have a shorter and more rounded body and when gravid are extremely round due to the large size of the eggs. The mating behaviour of this species is not documented but is likely to be similar to *Rhampholeon spinosus* in which males will chase the females. If the females are receptive then they will remain a light colour, while unreceptive females will change to darker colours and will display aggressive postures at approaching males. Gravid females *R. spinosus* carry 3-4 eggs (each 11 x 6 mm) and descend to the ground to lay them in leaf litter and soil; females may lay several clutches a year and once laying is finished the females' bloated shape will reduce significantly (Hildenhagen, 2007). Although *R.*

acuminatus has been kept and bred by private breeders, the methods used to breed them and keep them successfully have not been reported.



Figure 1. Adult female (left) and adult male (right) *Rhampholeon acuminatus* showing the larger rostral extension of the male

MATERIALS & METHODS

Origin of captive specimens

On 25th October 2019, a group of 17 *R. acuminatus* were donated from a private collection in the United Kingdom that had held the founders of the group in captivity since 2016. The founder animals were acquired before CITES was in place for protecting this species; the species was added to CITES appendix II in 2017 (Species+, 2021). The group comprised one adult male, three large adult females, three subadult males and four small adult females, with the remaining six of undetermined sex. Two of the large adult females appeared to be gravid on arrival given their swollen abdomens and

because they displayed aggressively when approached by the male. The largest female weighed 4.24 g on arrival and the male weighed 3.81 g. Within the adult group, one male and one female were of wild origin and came into captivity in 2016 as subadults.

Captive enclosure

To form a breeding group, the adult male, three large adult females and the largest two of smaller adult females were housed together in a 65 x 127 x 55 cm aluminium-framed mesh enclosure (Fig. 2) (Chameleon World Muji). To help maintain humidity, the ventilation rate was reduced by replacing the mesh on the left side of the enclosure with a solid foamex panel and the mesh at the back of the enclosure was pressed against a vinyl wall. The enclosure was placed on a shelf in a 20 cm-deep tray made of foamex to allow for a deep substrate of leaf litter, soil and moss. The soil was a mixture of coir and organic compost with a layer of sphagnum moss on top covered with a thin layer leaf litter. The enclosure was simply furnished with plants such as *Ficus microcarpa* and *Ficus benjamina* with lots of thin twigged branching and vines. A water dish was not provided as the enclosure was heavily sprayed once in the morning and again in the early evening (for roughly 10 minutes) with aged tap water. The water used to spray the chameleon enclosure was warm (19–23 °C), approximately neutral (pH 6.8–7), with carbonate hardness (KH: 3–6 °d) and general hardness (GH: 8 °d).



Figure 2. Enclosure used to house the breeding group of *Rhampholeon acuminatus*

Lighting and heating arrangements

Rhampholeon acuminatus is reported to occur in forests with canopy cover and in the wild hides in low vegetation under the canopy (Tilbury, 2010). We provided full spectrum lighting, including UV, with plenty of plant cover to create dappled light. UV light was provided by using a 55 cm lamp

(Arcadia T5 D3 6 % Reptile Lamp 24watt) with a reflector, placed directly on the mesh top of the enclosure, covering around 50 % of the top with a gradient extending to the enclosure floor. The lamp was set to turn on at 10:00 h and off at 19:00 h. The UV index was measured monthly with a Solarmeter 6.5 UV index meter (Solartech Inc., Harrison Township, MI); UVI gradients were measured through the mesh and ranged 0–3 UVI at the level of the branches where the chameleons were perched. An Exo Terra Daylight Basking Spot (25 W in a 14 cm Arcadia Ceramic Reflector Dome Clamp Lamp) was used to create a small basking zone and temperature gradient giving a surface temperature of up to 29 °C. Temperature was measured using a mini RayTemp infrared thermometer (Electronic Temperature Instruments Ltd, Sussex, UK). The basking lamp was placed as close to the UV lamps as possible so the lights overlapped in the enclosure. The basking lamp was controlled by a dial timer set to turn on at 10:00 h and off at 19:00 h. Ambient full colour lighting was provided by a GroBeam 800 ND Natural Daylight LED (Tropical Marine Centre Ltd, Rickmansworth, UK) placed above the UV light, controlled by a AquaRay SmartControl 8 (Tropical Marine Centre Ltd, Rickmansworth, UK) so that the light came on at 07:30 h, ramping up from 1 % to 100 % in 20 minutes to give a 'dawn', and vice versa to give a dusk that finished at 20:00 h. Photoperiod was the same throughout October–April and set according to data from Tanzania on the season's day length and sunlight hours (Time and Date, 2019). Ambient temperature in the room where the enclosure was maintained was controlled by a wall mounted air-conditioning unit set to 19 °C which gave a temperature range in the room of 19–23 °C and relative humidity range of 30–50 %. Two thermometers were installed in the breeding enclosure, one at substrate level the other at the top of the enclosure. In a 24-hour period, the night / day temperature range at substrate level was 16.7–21.4 °C while the top of the enclosure was 19.0–29.0 °C. These temperature ranges were not altered by changes to air conditioning unit settings or the installation of additional heating or cooling equipment from the time of the chameleons' arrival to the hatching of young, between October–April. There was a night time temperature drop of 2–3 °C degrees as a result of lighting going off at night.

Feeding arrangements

The diet consisted of crickets (*Gryllus assimilis* and *Gryllus bimaculatus*), fruit flies (*Drosophila melanogaster* and *Drosophila hydei*), bean weevils (*Callosobruchus maculatus*), grain weevils (*Sitophilus granarius*) and hatchling hoppers (*Schistocerca gregaria*). Chameleons were fed three to four times a week. The food was dusted 1–2 times/week with Repashy Calcium Plus, vitamin and calcium supplement (Repashy Ventures, Inc., 4135 Avenida, De La Plata, Oceanside, USA).

RESULTS

Four days after arrival, the two smallest adult females were removed from the breeding enclosure and moved to an enclosure with the other two smaller adult females, as we noticed that they were showing signs of stress, indicated by a change in colour and black lateral stripes on the body (Fig. 3).

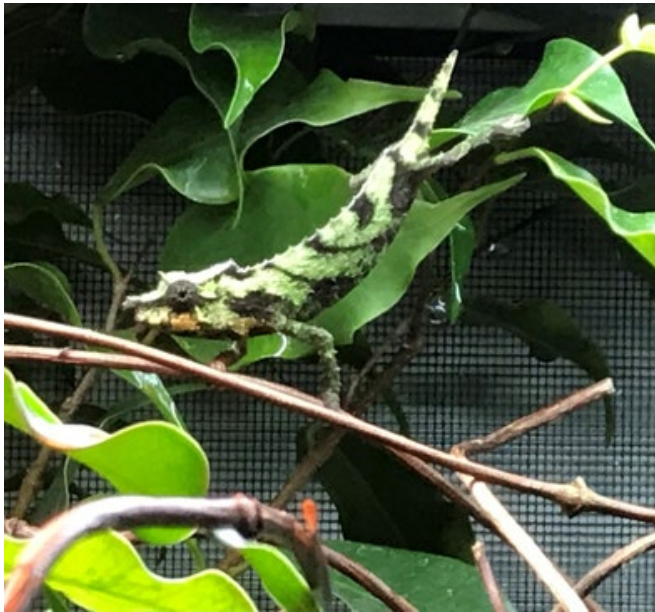


Figure 3. Adult female *Rhampholeon acuminatus* showing dark lateral markings to warn off a pursuing male

Since receiving the chameleons, we have never observed copulation in our breeding group. The first hatchling was discovered on 17th April 2020 in the breeding enclosure, with a second found in the afternoon on the same day. They both weighed 0.3 g and measured 30 mm total length (Fig. 4). The hatchlings were left in with the adults for the first three days before they were transferred to a smaller enclosure, setup in the same way as the adults, so they could be monitored during rearing. All subsequent hatchlings were also moved to smaller enclosures. On 23rd April 2020, a hatchling was found in the single sex group of the four young adult females, this individual was only 0.2 g and unfortunately only survived for two days. All eggs were incubated and hatched naturally within the enclosure so we are unable to determine the exact length of incubation. However, given that two of the adult

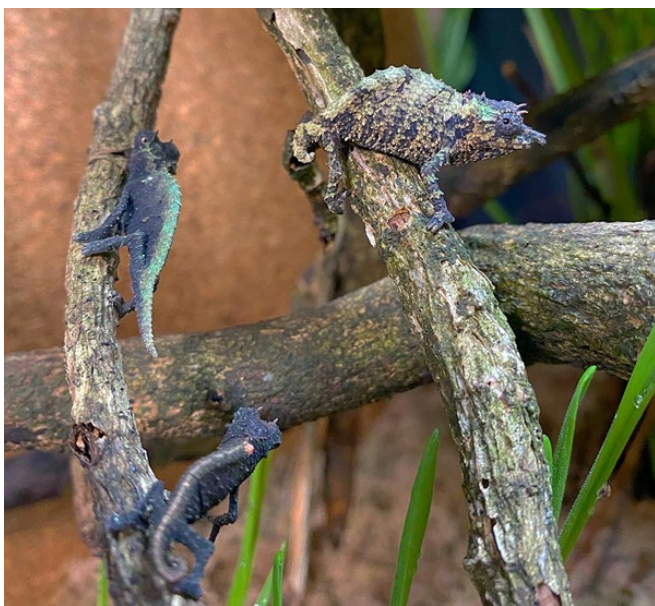


Figure 4. Recently hatched young *Rhampholeon acuminatus* (left) and a specimen that is about 2-weeks older (right)

females appeared to be gravid on arrival and that the two smaller adult females spent four days with the male before being separated (and had previously never been housed with a male) we would estimate an incubation period of no longer than 180 days.

Since the 23rd April 2020 we have successfully raised 12 juveniles from the three large adult females and the four small adult females (that previously had been considered to be sub-adult). When finding juveniles in the enclosure we almost always found them in pairs. Newly laid eggs measured 10 mm whilst more developed eggs measured 14 mm and the young all hatched weighing about 0.3 g and measuring 30 mm total length. Females laid eggs beneath moss and leaf litter in the first 1 cm of soil; they favoured certain locations laying several clutches in the same spot (Fig. 5). Remnant egg shells were found just below the surface of some moss which had a probed temperature of 19.2–22.8 °C. Clutch sizes are assumed to be four eggs but are possibly laid two at a time as juveniles hatched in pairs. However, when searching through the substrate we sometimes found up to 8 eggs laid in the same location. This suggests that females shared laying sites.



Figure 5. Several eggs of *Rhampholeon acuminatus* found under moss, at varied developmental stages

DISCUSSION

As anticipated, the breeding activities of *R. acuminatus* were similar to those described for *R. spinosus* (Necas & Schmidt, 2004). During courtship, male *R. acuminatus* will chase the females, which if receptive will remain a light colour. If unreceptive, females will change colour, adopt darker markings, and will display aggressive postures; similar responses have been reported for *R. spinosus* (Hildenhagen, 2007). Female *R. acuminatus* also appear to show signs of swelling when gravid (Hildenhagen, 2007). We assume that copulation in *R. acuminatus* occurs during dawn / dusk as we did not observe this behaviour between 08:00 h and 18:00 h. The females lay eggs in leaf litter and soil on the ground and appear to be able to lay several clutches a year (Necas & Schmidt, 2004). Based on our findings, *R. acuminatus* has a similar incubation period to *Rhampholeon spinosus* (Necas & Schmidt, 2004). Our recommendation is that breeding adults

are housed together in small groups with three females housed per one male as this reduces the stress on them. The male can then be removed periodically for a couple of months to give the females a break.

At emergence, hatchlings weigh only 0.3 g and are 30 mm long; they reach sexual maturity after 8-9 months. This is comparable to reports for *Rhampholeon spinosus* which also measure 30 mm at hatching and reaching sexual maturity at 9 months (Hildenhagen, 2007). Eggs can be left in situ to develop and do not need to be removed and placed in an incubator. Hatchlings should be removed from the adult enclosure as soon as they are found, as this makes them easier to monitor closely and keep track of their development. They can be reared in small mesh enclosures with cork bark covering the sides to increase humidity. We housed up to 8 hatchlings in a 38 x 51 x 38 cm aluminium framed mesh enclosure (Chameleon World Muji). The enclosures were setup with lots of thin branching and vegetation to create visual barriers and hiding places for them. They should be fed every other day on small food items such as fruit flies (*D. melanogaster*) and springtails (*Entognatha*). Juveniles can be reared in groups and separated once males and females can be identified then raised in single sexed groups. We have had no obvious issues raising males together however once they were fully mature, we house them individually.

The methods described here can be used for ex-situ management for species conservation to increase the captive population of this species. Given the similarities between *R. acuminatus* and *R. spinosus* it seems likely that the approach we have taken to captive breeding may well be suitable for other threatened species within the same genus.

ACKNOWLEDGEMENTS

We extend our thanks to Julian Tovey from Muji chameleon cages for donating the animals to Paignton Zoo and his invaluable advice on their care and husbandry; to Lucy Herbert, Joe Ross, Pete Amphlett and Frazer McDade, our volunteers that helped with the care of the species; and to Benjamin Tapley (Zoological Society of London) for his assistance in the development of this manuscript.

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Accepted: 4 August 2021

Distribution of the alpine newt *Ichthyosaura alpestris* in Great Britain updated using social media

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ABSTRACT - The alpine newt (*Ichthyosaura alpestris*) is an alien species in Great Britain. Using location information derived from photographs posted on social media we have updated its known distribution, validated previously unconfirmed populations, and present an updated distribution map. Comparison of the records collected from social media with those in the National Biodiversity Network Atlas indicates eleven new confirmed populations, although three of these had previously been shown as unconfirmed records in the NBN Atlas. The new records have been deposited with NBN.

INTRODUCTION

The alpine newt (*Ichthyosaura alpestris*) is a medium-sized newt that is an alien species in Britain (Speybroeck et al., 2016). In the second half of the twentieth century, alpine newts were popular as pets. It is likely that introductions of this species stem from intentional releases or accidental escapes from private collections (Beebee & Griffiths, 2000). A number of populations are known throughout Britain, from Scotland and Wales to southern England (Beebee & Griffiths, 2000), although it is likely that further populations exist, which are yet to be discovered. The true extent of the alpine newt's distribution in Britain is always changing and it has been some time since the population was assessed, despite some efforts to document where they can be found (Banks, 1989).

The impacts of alpine newts on native species are not currently known, although alpine newts may threaten native newt species through competition, or by acting as vectors of disease (Bell, 2016). Alpine newts are known vectors of the lethal amphibian chytrid fungus (*Batrachochytrium dendrobatidis*), which may be spread to native species through both direct and indirect contact. Alpine newts are also susceptible to a different species of chytrid fungal disease, *B. salamandrivorans*, which is yet to be recorded infecting wild newts in Britain (Cunningham et al., 2019). Being an alien species, alpine newts should be removed from any habitats where they are caught, which would facilitate the taking of samples to check for disease. Management of introduced species is vital to reduce their impact on native species. To assist this, the distribution of a non-native species must be known in order to monitor populations, or control them if necessary.

Digital images posted on the internet are increasingly becoming a source of useful data for conservation science (Chamberlain, 2018; Toivonen et al., 2019). Public user-generated content, uploaded to social media, can provide valuable information about both where and in what context certain species are found, and this method has proven a reliable approach to recording the presence of introduced

species, such as terrapins (Allain, 2019). In the current study, online data about alpine newts in Britain were collected from social media websites and, together with pre-existing records, used to plot an up-to-date map of alpine newt distribution to aid the future management of this species.

METHODS

Following the same methodology as Allain (2019), we used a number of standard keyword phrases (Table 1) to search for social media posts that included alpine newt photographs. The searches were for images of newts taken only between 2008 and 2020 on the image-sharing platforms Flickr and Instagram and the social media platforms Facebook and Twitter. On Flickr, the date a photograph was taken was determined with reference to the image metadata; for posts from Facebook, Instagram, and Twitter, the photograph date was assumed to be within two months of the date of the online post. All results from these searches were checked to capture information from photographs taken only in Britain. Any locations stated in the photograph description or metadata were recorded, along with any other metadata, including the photographer's username and the post URL; this was necessary to minimise the chance of duplications within the dataset.

Search results were then subjected to a data cleaning process, which involved manually sorting and removing photographs of captive individuals, duplicate images, and other non-relevant photos. For each keyword search, dozens of hits were returned; however, each search returned only a small number of posts containing relevant photographs. In cases where it was unclear where the photograph was taken, contact was made with the user who had posted the photograph to verify the sighting location. Locations listed were georeferenced, and the location's grid reference, latitude, and longitude estimated using UK Grid Reference Finder (<https://gridreferencefinder.com/>). In some instances, this was a water body, but in others the location was terrestrial habitat, which would be expected as alpine newts spend part of the year on land.

Using the data collected, a map was created to compare with the dataset available from the National Biodiversity Network (NBN Atlas, 2021). A full listing of the NBN citations can be obtained from the corresponding author on request. Differences between the two datasets were noted, and used to infer new records of the species. Data from Record Pool was omitted from our study, due to a lack of any significant difference from the NBN Atlas data. A standard spatial analysis approach was used to plot photograph location points on a map. All mapping was completed using QGIS 3.12 (QGIS Development Team, 2020).

RESULTS

The searches on Flickr demonstrated a negative relationship between the precision of a search term and the number of results yielded (Table 1). There was considerable variability in the number of records found between the four social media platforms (Fig. 1) with Flickr returning the largest number of posts (20) and Facebook returning the highest proportion of usable posts (75 %). No posts were found that were duplicated between the platforms. Despite our best efforts to contact the photographers of alpine newts on these platforms, individual photographers were not always available or willing to provide the information.

Table 1. Numbers of photographs returned by Flickr in response to various search terms for new British records of alpine newts and the number of photographs that were actually of alpine newts

Search term	Total no. of photos returned by search	No. of photos of alpine newts
Alpine newt*	1353	1131
Alpine newt UK	21	21
Alpine newt Britain	40	39
Alpine newt England	56	1
Alpine newt Wales	55	0
Alpine newt Scotland	63	8
<i>Ichthyosaura</i> UK	1	1
<i>Ichthyosaura</i> Britain	7	7
<i>Ichthyosaura</i> England	0	0
<i>Ichthyosaura</i> Wales	0	0
<i>Ichthyosaura</i> Scotland	8	8

* This search term returned photos of alpine newts within their wider European range, as well as a number of captive individuals

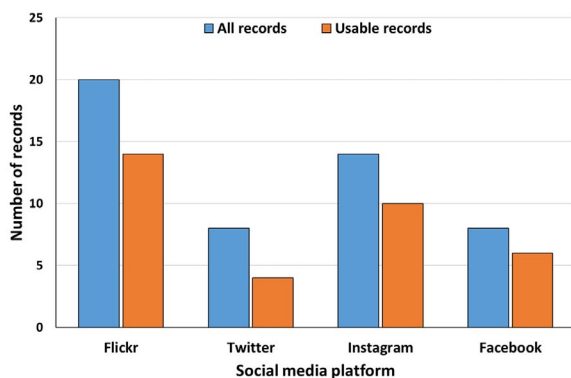


Figure 1. Total number of records and number of 'usable' records of alpine newts obtained from various social media platforms. Flickr provided the most records whereas Facebook provided the highest proportion of usable records.

Considering all observations collected from the four social media sources, the period from 2008 to 2012 yielded no more than a single record per annum, but from 2013 there was a sharp rise with returns averaging 5.4 per annum (range 2 to 9) (Fig. 2). Comparisons of observations collected from social media with records on the NBN Atlas, indicate eleven

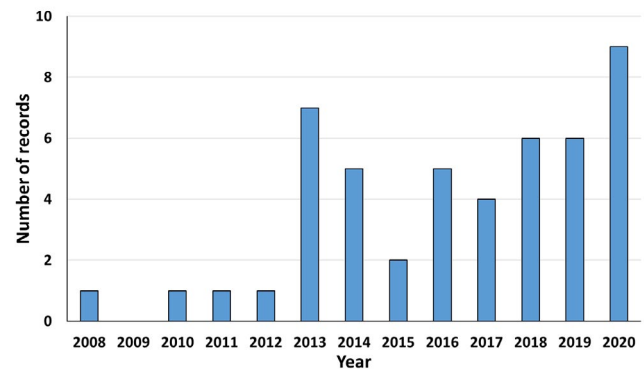


Figure 2. The number of alpine newt records (N = 48) dated from 2008 to 2020 retrieved from four social media platforms in 2020. There was a noticeable increase in records from 2013 onwards. Each of the four single records from 2008 to 2012 represent different populations.

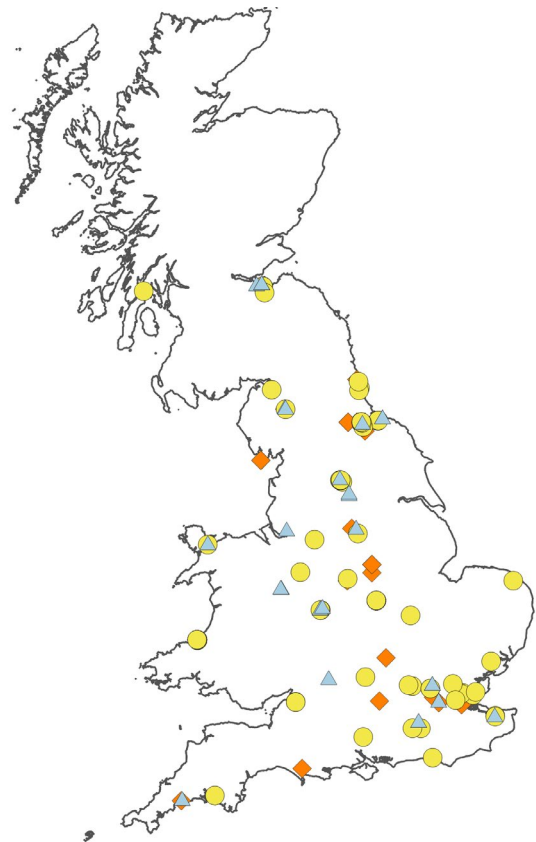


Figure 3. An updated distribution map of alpine newt (*Ichthyosaura alpestris*) populations in Britain: yellow circles – current confirmed NBN records; orange diamonds – current unconfirmed NBN records; blue triangles – new records from the current study. Eight of the 16 populations identified in the current study have no overlap with any previously recorded alpine newt populations.

new populations (Fig. 3). Three of these are at locations that were previously unconfirmed on the NBN Atlas (Barrow-in-Furness, Fowey, and Lewisham). Other newts photographed were all from previously-known populations.

DISCUSSION

Using the methods described above, new alpine newt populations within Britain were successfully confirmed. This additional data highlights the substantial potential of social media as a data source, to identify populations and track the spread of a non-native species. The limitations of this approach include the assumptions that the social media user can correctly identify the animal photographed, and that in the caption or description social media users would employ standard English, English common names, or scientific names, and the correct spelling. In addition, certain search terms, for instance 'Alpine Newt Britain', returned a large number of relevant results. However, a large proportion of these results were multiple photos of a single individual, and therefore these results were not included in the final dataset, after manual data cleaning. The previous scientific names for alpine newts, *Mesotriton alpestris* and *Triturus alpestris*, were not included in searches, because the widespread use of *Ichthyosaura alpestris* predates the earliest year of the study period, 2008 - 2020.

At the time of writing, the National Biodiversity Network (NBN) Atlas held 134 pre-existing British records of *I. alpestris*. However, not all of these records date from within the study search period, 2008 - 2020. Sixteen NBN records between 1972 and 2007 were removed from the dataset before it was mapped. Of the pre-existing records dating from 2008 - 2020, only 86 records had been accepted by NBN, with the further 32 being unconfirmed. The current study increases the number of confirmed records by 40 % and it is hoped this data will assist land managers and conservation organisations in the future, should it be necessary to manage alpine newt populations. With this in mind, it is likely that further populations remain to be identified; conservation organisations must continue to encourage the public to look for and submit records of this species to recording schemes. All data collected in this study were submitted to the NBN Atlas.

Our results indicated that from 2013 to 2020, there were significantly larger annual numbers of posts containing photographs of alpine newts (Fig. 2). This may result from a number of factors, such as increased awareness of alpine newts, or annual conditions being unfavourable to alpine newt breeding and dispersal, therefore making them more conspicuous. The noticeable lack of records before 2013 may be a consequence of older online content being removed by the original content creator. However, this explanation is uncertain, as very little research has examined the patterns of removal of online content. Therefore we feel it is more likely a consequence of the sudden rise in the popularity of social media platforms, among the general public.

Methods for collecting presence-absence data from social media may make use of automation. Such techniques may include automated text mining (e.g. web scrapers),

for analysing photo descriptions and other text associated with each photo (Hernandez-Castro & Roberts, 2015). These could be used to search for a specific phrase such as 'alpine newt', alerting the user to that post on a target website. However, the expertise and time needed to create a web scraper may not be required when targeting a single species, on a single platform (Stringham et al., 2021), and, in this context, a manual search approach would be more appropriate. Automated image classification can be used to filter the search results, helping to speed up the process of data cleaning when coupled with manual image sorting. These methods could be also used to create an 'early warning' system for new uploads of alpine newt photos (or another target species) to social media platforms such as Flickr.

Through this study, it has become apparent that not every social media user is willing or able to provide the data needed to map the distribution of the species they have photographed. If the photographs were taken a significant time ago, it may be that users simply cannot recall the location in which they photographed the individual in question. It is also worth noting that previous website users may no longer be active on websites; this may mean that contacting them for their data is very difficult. These are important considerations when using this methodology for future studies.

Future research should make the most of other national recording schemes, to increase knowledge of alpine newt distribution in Britain. Efforts must continue to record the distribution of alpine newts in Britain, while researchers must also establish the threats they pose to our native amphibians.

ACKNOWLEDGEMENTS

We would like to thank everyone who has recorded an alpine newt through one of the schemes that has contributed to the National Biodiversity Network Atlas. We would also like to thank all the photographers who were happy to share additional details about where they photographed or observed alpine newts within Britain.

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Accepted: 30 August 2021

Diet of the Malabar pitviper *Trimeresurus malabaricus*

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The Malabar pitviper *Trimeresurus malabaricus* (Jerdon, 1854) is endemic to India, distributed in the tropical rainforests of the Western Ghats from Mahabaleshwar to Kanyakumari (Whitaker & Captain, 2004). This polymorphic species is active nocturnally on rocks, trees, bushes and occasionally on the ground (Whitaker & Captain, 2004; Sawant et al., 2010), often inhabiting riparian habitats (Whitaker & Captain, 2004; Ganesh et al., 2010). Its diet is known to include small mammals, frogs, toads, lizards, birds and their eggs, moreover cannibalism has been observed (Whitaker & Captain, 2004; Khaire, 2006). Sagar (2016) highlighted variation in the dietary preference among the life stages of *T. malabaricus* with adults and sub-adults eating rodents, birds and bird eggs, whereas the young and juveniles feed on small frogs and lizards, and sometimes on insect larvae and the eggs of birds and lizards.

Analyzing the diets of snake species provides a basis to understand their natural history and provides a broader ecological and evolutionary context (Greene, 1983; Mushinsky, 1987). Furthermore, it gives an understanding of both resource partitioning (Schoener, 1965) and competition within an ecosystem (Toft, 1985) that pave the way for the development of species-specific conservation approaches (Greene, 1994). No detailed study on the diet of *T. malabaricus* has been published previously, consequently we have prepared an inventory of the recorded prey items of *T. malabaricus* from the following information sources:

1. Social media records

We searched Facebook using the keywords- "*Trimeresurus malabaricus*", "Malabar pit viper", "*Trimeresurus malabaricus* eating", "Malabar pit viper eating", "*Trimeresurus malabaricus* feeding", "Malabar pit viper feeding", "*Trimeresurus malabaricus* kill" and "Malabar pit viper kill" and Instagram using the hashtags- "#trimeresurusmalabaricus" and "#malabarpitviper" and compiled all records along with photographic evidence of *T. malabaricus* feeding only in the wild. The observations were verified through their captions and photographs. Information including identity of the prey, the observer's name, location of sighting, direction of ingestion and the colour morph of *T. malabaricus* were recorded. Additionally, we searched YouTube and Flickr using the same keywords and compiled records that met the above criteria.

2. Citizen science records

Records of *T. malabaricus* feeding were collected from various citizen science websites such as Reptiles of India (Kamdar et al., 2021) and iNaturalist (2020).

3. Records from literature

Records of *T. malabaricus* feeding were reviewed in published literature and were added to the list. These were compiled from Google Scholar and ResearchGate.

All the above-mentioned records were collected and arranged in a Numbers v.11.1 spreadsheet. Before finalising the data, records of the same observation posted across multiple platforms by the same observer were deleted (literature and citizen science websites taking priority over the duplicate social media records) as were multiple records of the same observation posted by different observers (which were identified based on the images). From the records collected, we first created separate data frames, i.e. type source of records and type of prey consumed. We then broke down the prey by morph to reveal trends/ patterns (if any) and tested the statistical significance of the relationship between the morph of *T. malabaricus* and its prey items using the Chi-Square test. Data obtained from crowdsourcing is accurate but has some obvious biases that have been listed by Kalki & Weiss (2020). These included observers naturally photographing events of personal interest and photographs being restricted to easily accessible spaces, closer to the ground, on or near forest trails etc. that have a higher probability of catching the observer's eye.

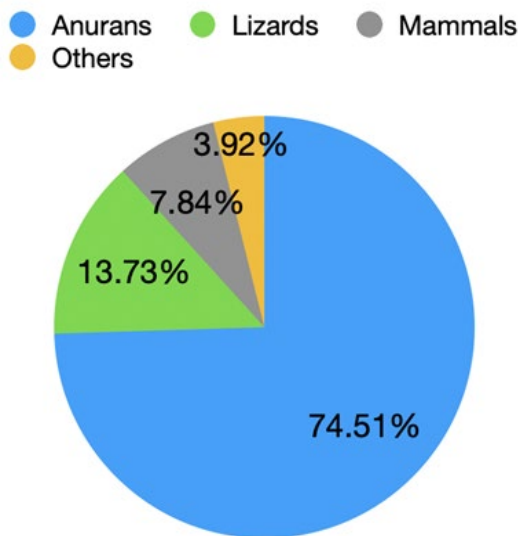
A total of 51 observations of *T. malabaricus* feeding in the wild were compiled (Table 1). Of these, most were social media records (88.2 %), followed by citizen science (9.8 %) and then published literature (2 %). Of the total social media records, Facebook contributed 51.1 %, Instagram 33.3% and the rest came from YouTube and Flickr. According to the data collected, *T. malabaricus* primarily feeds on anurans (74.5 %), occasionally on lizards (13.7 %) or mammals (7.8 %) and quite rarely on other prey types (3.9 %; there was one instance each of feeding on a land snail and an eel) (Fig. 1). The direction of ingestion was determined for 78.4 % of the total records, out of which 75 % prey were consumed head-first and only 25 % were consumed feet-first.

Out of all the feeding observations, most were recorded for the brown-green (olive) morph of *T. malabaricus* (45.1 %), followed by the green morph (35.3 %) and then by the other

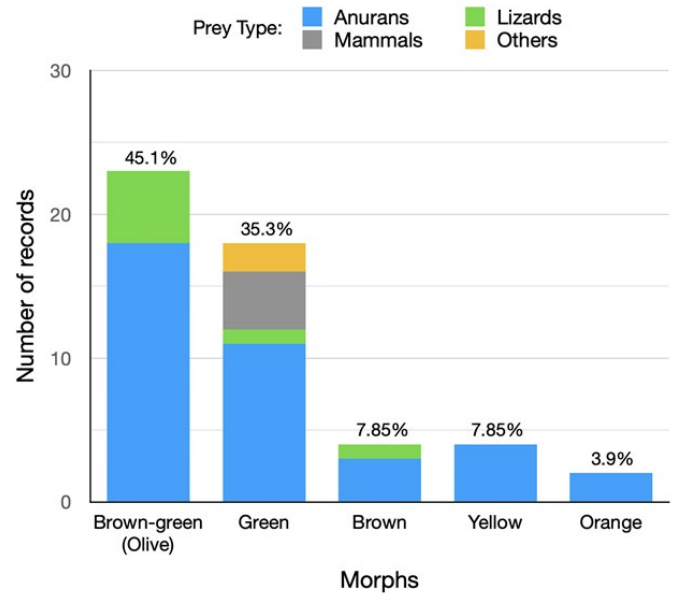
Table 1. List of prey items* recorded for *Trimeresurus malabaricus* along with their source type

	Social media	Citizen Science	Literature
Anura			
<i>Clinotarsus curtipes</i>	1		
<i>Euphylyctis</i> sp.	1		
<i>Hoplobatrachus tigerinus</i>	1		
<i>Indirana</i> sp.	1	1	
<i>Indosylvirana intermedia</i>	4	1	
<i>Minervarya</i> cf. <i>rufescens</i>	1		
<i>Nyctibatrachus</i> sp.	5		
<i>Polypedates</i> sp.	1		
<i>Pseudophilautus</i> sp.	1		
<i>Rhacophorus malabaricus</i>	16	2	
<i>Uperodon marmorata</i>	1		
Unidentified anuran	1		
Fish			
<i>Monopterus</i> sp.	1		
Lizards			
<i>Cnemaspis</i> sp.	2		
<i>Hemidactylus</i> sp.	4	1	
Mammals			
<i>Vandeleuria oleracea</i>	2		
Unidentified rodent	2		
Invertebrates			
Land snail			1**
% Total observations	88.2	9.8	2.0

*Identifications were visual and based on the images examined by us. None of the prey items were keyed out ** from Lele & Chuneekar (2014)

**Figure 1.** Types of prey eaten by *Trimeresurus malabaricus* as observed in the study

morphs (19.6 %) (Fig. 2). There was also an interesting pattern in the relationship between the morph of the *T. malabaricus* and the prey items consumed; only the green morphs were recorded consuming mammals (n=4) and the two unusual prey items (land snail and eel) while the orange and the yellow morphs were only observed feeding on anurans. However, the apparent differences between morphs were not statistically significant ($\chi^2=15.151$, $p=0.233$).

**Figure 2.** Types of prey eaten by different colour morphs of *Trimeresurus malabaricus* as observed in the study

Of all the listed trophic interactions, 16 have not yet appeared in scientific reports and 12 have been sourced solely through social media, demonstrating social media to be a significant repository for such natural history data (Maritz & Maritz, 2020). The collected data suggest that *T. malabaricus* feeds primarily on frogs, occasionally on lizards and mammals, and rarely other taxa. Its diet is also said to include small birds but examples of avian predation were not collected in this study; perhaps the result of the aforementioned observer bias. There has only been one record of *T. malabaricus* attempting to feed on a land snail. This might be a more common prey item but as feeding events involving small sized prey, such as land snails, involve shorter feeding times, the probability of them being observed is relatively low. An adult *T. malabaricus* in captivity was recorded eating a juvenile conspecific on two occasions (Whitaker & Captain, 2004) but no observations of cannibalism or even ophiophagy have yet been reported in the wild. It is clear that *T. malabaricus* can be an opportunistic predator, as illustrated by the two observations of predation on unusual prey. The captive scenario, unlike the natural one, may have provided the right conditions for *T. malabaricus* to indulge in ophiophagy.

ACKNOWLEDGEMENTS

We thank the teams responsible for the maintenance of the various citizen science websites and also the uploaders of the numerous natural history observations on social media, which made this study possible.

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Accepted: 26 August 2021

First record of Peter's caecilian *Epicrionops petersi* from Colombia

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On 31st March 2016 in Colombia, one of us (JPL) collected a specimen of the caecilian *Epicrionops petersi* Taylor 1968 (Fig. 1). This was found at about 1200 m a.s.l. at Serranía de La Concepción, Vereda Buenos Aires, Mpio. Santa Rosa, Dpto. Cauca (01° 24'49.53" N, 76° 26'45.98" W; Fig. 2 & Supplementary Material Table S1) in the water of the El Borrachero stream (Fig. 3). This stream contained much decaying vegetation such as fallen trees and leaf litter; epiphytes were abundant on stones. The vegetation in the area is typical of the rainforest of the Colombian Andean-Amazonian foothills when in good condition. We deposited the specimen at the Amphibian Collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN 55790).



Figure 1. Dorsal view in life of *Epicrionops petersi* (ICN 55790), from Serranía de La Concepción, eastern Andes of Colombia

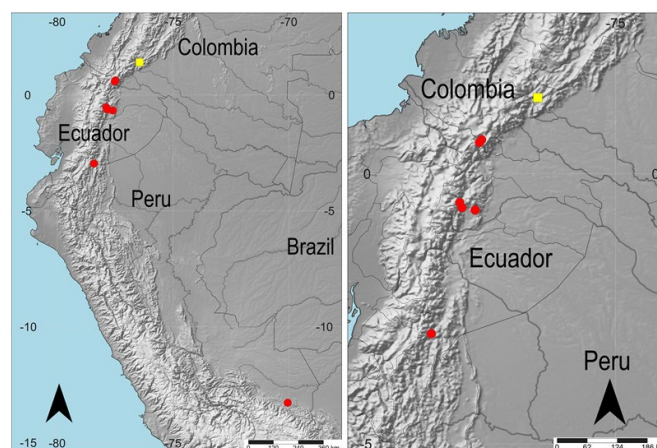


Figure 2. Known distribution of *Epicrionops petersi*: red circles - previous records, yellow square - new record in Colombia

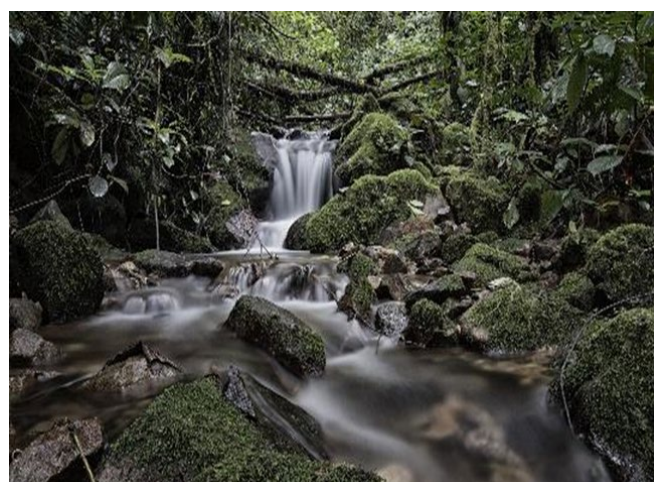


Figure 3. Habitat and record location of *Epicrionops petersi* in a stream in the Colombian Andean-Amazonian foothills

The caecilian (ICN 55790) was examined under a Zeiss stereoscope using entomological pins to facilitate counting the numerous grooves found throughout the body. The total groove count was made twice by JDF and JDL in order to avoid miscounting. Dentition (i.e. the number of teeth per series) was examined directly with the mouth opened and all counts were made clock-wise from left to right postero-anteriorly; any teeth that were not fully exposed outside the gums were not counted. All meristic data was determined using a Neiko digital calliper rounded to the nearest 0.1 mm with the exception of total body length, which was measured to the nearest mm using a plastic ruler and straightening the body of the specimen.

Our detailed observation, compared with the data available from specimens of *E. petersi* from elsewhere, are presented in Supplementary Material (Table S2). Our specimen had a total body length of 205 mm, a body width of 8.9 mm at mid-body point, a length divided by width (i.e. attenuation index) of 23 times and a mainly dark grey body coloration in preservative (70 % ethanol) (Fig. 4). A total of 271 grooves are along the total body length of the specimen, the last 16 of which are 'postcloacals' that include 5 grooves interrupted by the vent plus 11 grooves posterior to the vent (Table S2). Dentition and the number of teeth per series are smaller than those indicated in the original description by Taylor (1968) but this

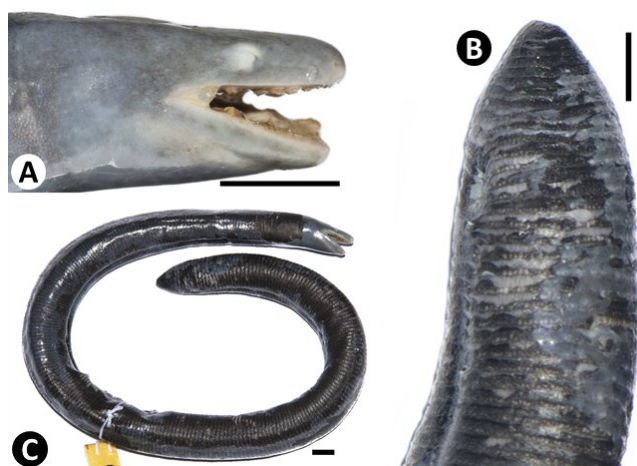


Figure 4. *Epicrionops petersi* from Serranía de La Concepción, eastern Andes of Colombia (ICN 55790) - **A.** Lateral view of the head, **B.** Lateral view of the tail, and **C.** General view of the specimen. Scale bars: 4 mm

is to be expected given that this is the smallest size individual known to date and some teeth are missing or concealed by the gums hence were not counted; premaxillary-maxillaries 12 left - 1 medial - 14 right, vomeropalatines 12-1-13, dentaries 10-1-11, and splenials 7-1-7. Taking into account that the meristic data of ICN 55790 falls well within the range provided by Taylor's (1968: 226) original description, we can confirm this is an individual of *Epicrionops petersi*. Before this new record, the caecilian genus *Epicrionops* was represented by three species in Colombia, namely *E. bicolor* Boulenger, 1883 (western Cordillera, also in Ecuador and Peru), *E. columbianus* (Rendahl & Vestergren, 1939) (endemic to the western Cordillera) and *E. parkeri* (Dunn, 1942) (endemic to the Central Cordillera) (Lynch, 2000; IUCN, 2021). This new record increases the number of Colombian caecilian species to 34 (Frost, 2021) and extends the distribution of *E. petersi* by over 150 km northward from the nearest previously known locality in the province of Sucumbios, Ecuador.

Taylor and Peters (1974) reported finding individuals of *E. petersi* in sympatry with *Caecilia orientalis* Taylor, 1968, which were found under a layer of thick moss and detritus growing on the surface of a fallen tree trunk inside a very humid forest where tree logs had fallen and had begun to rot. In 2018, GCP also found a specimen of *C. orientalis* (ICN 58444) in Serranía de la Concepción which suggests that these two species are sympatric and very closely associated along the Amazonian foothills of western Andes of Colombia and neighbouring provinces of Napo and Pastaza, Ecuador. The Andean-Amazonian foothills possess some of the greatest floral and faunal biodiversity in Colombia owing to their structural connectivity to the lowlands of the Amazon basin and Andean region, thus forming a mosaic of landscapes, vegetation and water resources. Consequently, the national government has declared three natural national parks: Serranía de los Churumbelos Auka Wasi NNP, Alto Fragua Indi Wasi NNP and Cueva de los Guacharos and the development of conservation programs and proper use of natural resources (Restrepo & Naranjo, 2007). Sadly, biological surveys and monitoring of amphibian populations have not taken place in these

protected areas since their designation as such.

There is an urgent need to design and develop more effective ways to improve the detection of amphibians with fossorial and aquatic habits. This will generate more information about their natural history and increase the collection of voucher specimens that will help to resolve taxonomic uncertainties and identification difficulties (Gower & Wilkinson 2005).

ACKNOWLEDGEMENTS

This finding is framed in the BIOCUENCAS project led by Conservation International Colombia (CI). Our thanks to José Vicente Rodríguez and Andrés Páez Ortiz of CI Colombia for their support and advice. Dr Santiago R. Ron generously allowed us to use the records of *Epicrionops petersi* deposited at QCAZA collection, Pontificia Universidad Católica del Ecuador, Quito, (www.bioweb.bio) for us to include in this note. Thanks to Gladis Calvache and the community of San Juan de Villalobos for assistance during our fieldwork, and Héctor E. Ramírez Chaves for his comments in the preparation of this manuscript. Biological collections for this study were authorized by permit No. 404 (April 30th 2014) for Universidad Nacional de Colombia by the Autoridad Nacional de Licencias Ambientales (ANLA).

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Accepted: 26 August 2021

Please note that the Supplementary Material for this article is available online via the Herpetological Bulletin website: <https://thebhs.org/publications/the-herpetological-bulletin/issue-number-158-winter-2021>

Homing: a case-study on the spatial memory of the Asian water monitor lizard *Varanus salvator* in the Kinabatangan floodplain

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Translocation may be used to improve the biological health of animal populations (Wolf et al., 1996) or to mitigate the impact of human-wildlife conflicts (Fisher & Lindenmayer, 2000). However, wildlife species may respond differently to translocations; they can show a tendency to either travel long distances in an attempt to return to their original location (homing), or to exhibit larger home ranges compared to resident individuals (Bradley, 2005; Wolf et al., 2009). Homing behaviour is negatively correlated with translocation distance (Bowman et al., 2002; Villaseñor et al., 2013), and it is associated with several factors such as the identification of landscape landmarks and resource availability in the original home range (Powell & Mitchel, 2012). Thus, understanding the spatial memory and navigation skills of an organism can be fundamental to predict the success of management actions, such as translocations. This report describes the response of an Asian water monitor lizard (*Varanus salvator*) translocated within the Kinabatangan floodplain in Sabah (Malaysian Borneo) and its return journey to its home territory.

In February 2018, a message was received that a monitor lizard, GPS-tagged as part of a long-term telemetry study, had been feeding on poultry in an oil palm plantation estate (Hillco, Felda Global Ventures Sdn. Bhd.; 5° 25'02" N, 118° 01'46" E). The 17 kg individual (presumably male) was subsequently translocated to a forested area (Lot 6 of the Lower Kinabatangan Wildlife Sanctuary; 5° 24'05" N, 118° 04'27" E), 5.27 km away from its original home range, which had been previously estimated using 2472 locations over 299 tracking days with a fix success rate of 75 % (Guerrero-Sanchez et al., unpublished data). A new GPS tracker (Advanced Telemetry Systems Inc., North Isanti, MN, USA) was deployed in order to monitor its adaptations to the new environment (Fig. 1).

The new tracker was set to record one GPS location every 90 minutes during day time; night time was not recorded as water monitors are not active nocturnally. The lizard was tracked for 11 weeks post-translocation, collecting a total of 621 GPS locations. The data show that the lizard took about seven weeks to return to its original home range, but instead of traveling in a straight line or following the river, it travelled through the forest by way of three different plantation

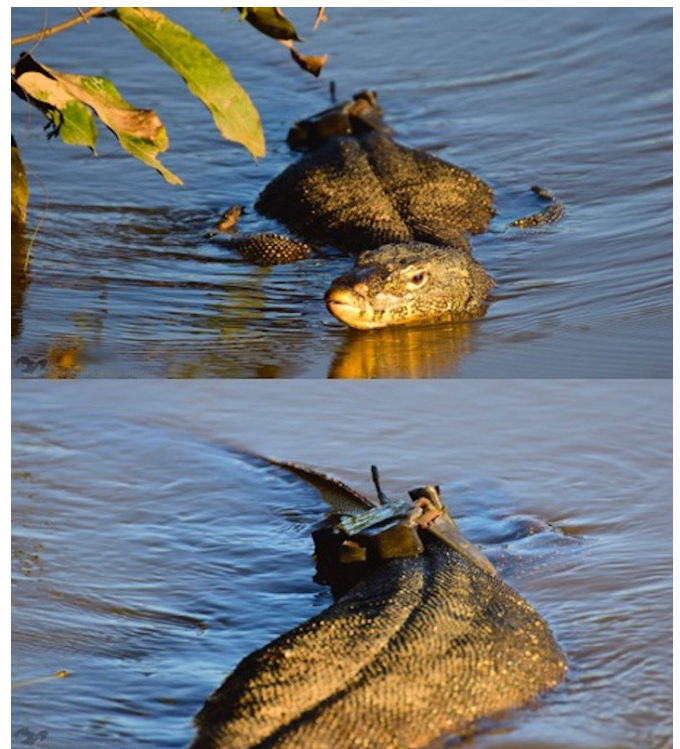


Figure 1. The Asian water monitor with GPS tracker navigating the Kinabatangan river, Sabah, Malaysian Borneo

"spots" (Fig. 2). The last two of these spots were on the same side of the river as the home range, with which there was contiguous plantation habitat, but to reach the home range the monitor instead went through the forest and made further river crossings. This route may have been chosen as unpublished data suggest that forested area offers more protection to the monitor lizards than oil palm plantations and has prey in equal abundance.

Homing behaviour is not rare in reptiles (Read et al., 2007; Pittman et al., 2014); it has been reported that the saltwater crocodile (*Crocodylus porosus*) can travel up to 400 km back to its original home range after being translocated (Read et al., 2007). Burmese pythons (*Python bivittatus*) possess a well-developed bearing ability that allow translocated individuals

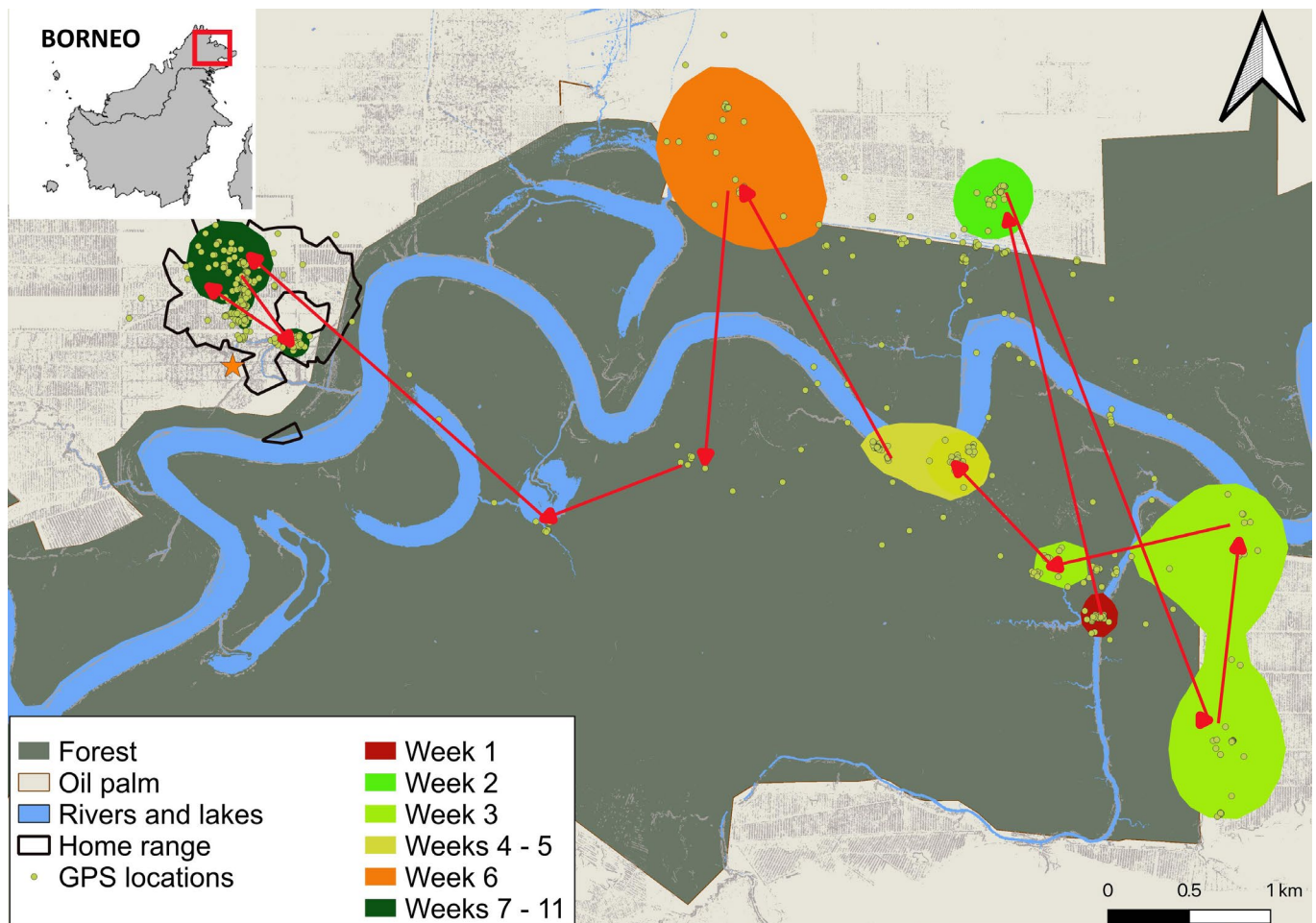


Figure 2. Weekly occupied areas of the translocated monitor lizard in the Kinabatangan floodplain. Polygons represent a 95 % home range (kernel density estimate; KDE). Release spot is within the “week 1” polygon. Arrows show the flow of the lizard’s movements and the orange star marks the location of the chicken house. KDE was fitted using the package *Animove HR* for R.

to head back home without the need to follow straight lines (Pittman et al., 2014). The natal habitat preference induction theory suggests that when translocated individuals of certain species are looking for a new home they search for habitat attributes similar to those encountered early in life (Davis & Stamps, 2004). Furthermore, the length of time a released individual spends at a release site can be informative about its acceptance or rejection of a new home, while the overall distance travelled during its return can indicate the degree of preference for the special features of its original habitat (Hayward et al., 2007). The time taken by the lizard in this study to return to its original home range, as well as the time spent in certain key areas, (i.e. a different location of an oil palm plantation), suggest that this particular individual was willing to look for a suitable ‘new home’ with similar features to its original one, but ended up rejecting these areas, possibly due to the presence of other individuals, or unsuitable environmental features (i.e. prey and shelter availability, intense human activity). This report suggests two main drivers influencing the lizard’s behaviour: (1) the well-identified habitat of its original home range as a source of predictable food resources and safety, and (2) the discontinuous distribution of these features within the landscape, forcing this individual to avoid these areas and keep moving towards its original home range. We cannot

discard the role of the navigational ability and spatial memory that might help the lizard to locate itself within the landscape and find the safest route to his original range (Pittman et al., 2014).

Although it is unclear whether monitors exhibit strictly territorial behaviour (Pascoe et al., 2019), antagonism is likely to occur between males, not only as territorial defence but also as competition for both food and reproductive females (Pascoe et al., 2019). Interestingly, after the return of the lizard to its original home range it was tracked for four more weeks and the data show that it remained within the boundaries of its home range. This behaviour suggests that the lizard not only recognised its home but also that probably no other large individual occupied it during the monitor’s absence. Hence, what we witnessed could be part of a territorial behaviour, which should be taken into consideration in further studies of human-monitor lizard conflict mitigation.

The water monitor’s knowledge of the most relevant elements in its original home range, such as absence of other lizards and the features associated with food and cover, might work as a stimulus for its return to its original home. All these findings suggest that the species may have a well-developed spatial memory, as well as a strong attachment to the well-known features of its home range. These

characteristics should be considered in areas where there are human-lizard conflicts and whenever translocated lizards are moved to areas already abundant in monitor lizards. The presence of large monitors in these selected areas can have a counterproductive effect if they result in translocated individuals fleeing and returning to their original homes. In order to get a better understanding of territoriality and habitat preferences of monitor lizards, we recommend carrying out long-term experiments on translocations, using GPS telemetry and considering treatments with varying translocation distance and varying habitat similarities, especially for areas where human-lizard interactions are a burden.

ACKNOWLEDGEMENTS

This study was financially supported by Danau Girang Field Centre and Cardiff University. SGS was supported by the National Council for Science and Technology (CONACYT; Mexico; scholarship No. 235294). Safety and animal welfare protocols were reviewed and approved by Sabah Wildlife Department and the Sabah Biodiversity Centre (permit JKM/MBS.1000-2/2 JLD.3-7). The authors would like to thank students and staff members of the Danau Girang Field Centre for their support with the fieldwork, as well as the Director of Sabah Wildlife Department for his support on this project, and Felda Global Holdings Sdn. Bhd. for granting permission to conduct part of the fieldwork within their plantation estates. We would also like to thank our colleagues Rudi Delvaux, for the two photos in Figure 1, and Liesbeth Frias, for her comments on early versions of this manuscript and proofreading.

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Accepted: 14 September 2021

An axanthic common frog *Rana temporaria* from Great Britain

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Axanthic animals have skin that may lack the xanthophores and erythrophores that produce yellow, orange and red pigments or lack light reflecting iridophores; alternatively xanthophores may be present but unable to produce pigment. Consequently, such animals have blue or grey coloured bodies with dark patterning and dark eyes. For a review of axanthism in amphibians see Jablonski et al. (2014).

In June 2021, an axanthic common frog *Rana temporaria* L. (Fig. 1) was found in a garden in The Wirral area of north-west England (53° 37'03" N, 3° 05'46" W) under vegetation in a flower bed. This species has long been known to have variable colouration (Smith, 1951), and colour aberrations have also been reported (Smallcombe, 1949; Nicholson, 1997; Allain & Goodman, 2017; Baker & Biddle, 2020). Nevertheless, we believe that this is the first record of axanthism in this species, although 'black eyes' have been described in other ranids, including moor frogs (*Rana arvalis*) (Vershinin, 2004), and in *R. temporaria* in Poland (Kolenda et al., 2017). However, in all reported cases of black eyes in ranid frogs, the animals appeared to have normal coloured bodies.



Figure 1. An axanthic common frog showing typical blue skin (left) and black eyes (right)

Although axanthism is genetically determined, environmental factors including temperature, disease, UV-irradiation or chemicals may be responsible for its expression (Henle et al., 2017). Since the 1960s, many of the reports of axanthism have been from urban areas in industrial countries (Dandová et al., 1995) which suggests that pollution may play a role in this aberration. It may be no coincidence that the current observation of an axanthic *R. temporaria* was from a relatively industrialised area of The Wirral. It seems

possible that this body colour could render the animal more conspicuous, leading to a higher chance of predation and consequently lowered reproductive success. This may be why axanthic frogs are so rarely observed in the wild (Childs, 1953; Dubois, 1979).

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Accepted: 14 July 2021

Puffing up as a defensive reaction of the yellow-bellied toad *Bombina variegata*

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Amphibians have evolved a wide range of adaptations to minimise the risk of predator attack, including aposematic colouration. It is generally accepted that predators receive advance warning of apparent toxicity when potential prey items present bright and contrasting colours (Vitt & Caldwell, 2014). This is in line with the hypothesis of venom optimization (Wigger et al., 2002), according to which the successful deterrence of a predator may not require the use of venoms or poisons. These consist of hundreds of protein and non-proteinaceous compounds, and their production comes at a high metabolic cost. As a result, adaptations have evolved to minimise toxin expenditure, for example by behavioural control (Morgenstern & King, 2013).

A well-known way of displaying aposematic colouration is the unken reflex, first described in amphibians of the genus *Bombina*, but also demonstrated in other amphibians, including newts and salamanders (Löhner, 1919 as cited in Telea et al., 2021). This reflex involves arching the body, presenting the undersides of the brightly coloured limbs and partially exposing the ventral surface, while at the same time remaining still and closing the eyes. In addition to the full unken reflex, there may be a partial reflex, with markedly less flexion. Then, the limbs are detached from the ground so as to display the brightly coloured side, and the eyes are open. Both *Bombina bombina* and *Bombina variegata*, are found in Poland and both exhibit this reflex. Besides the unken reflex, *Bombina* toads may also react to a threat by immobilising, running away or inflating their bodies. The last of these reactions has apparently not been reported previously in *B. variegata* and has been suggested as a feature that distinguishes this species from *B. bombina* (Bajger, 1980).

On 15 August 2008 in the village of Makowa (southern Poland; GPS 49° 38'33.85" N, 22° 40'24.55" E), I approached a *B. variegata* standing on the flat edge of a small puddle, near the waterline of a shallow stream. As I approached the toad, it first became motionless (this lasted for about 30 seconds), then it jumped into the stream, at the same time turned over on to its back and inflated its body (Fig. 1). It remained perfectly still in this position for almost 5 minutes, after which it deflated, returned to its 'normal' shape and calmly moved away. The locality of this observation lies well to the south of the known distribution of *B. bombina* thus the individual observed must be *B. variegata*. The observation shows that, in exceptional situations, *B. variegata* may use the antipredator defensive strategy of flipping over onto its back and puffing up its body. This makes it visually larger and more difficult for predators to overpower and swallow. Also, the fact that the



Figure 1. Puffed up body of *Bombina variegata*

bright colouration of *Bombina* covers the entire underparts and not just the legs and body margins suggests that it plays an important role in defensive behaviour.

ACKNOWLEDGEMENT

I would like to thank Professor Tadeusz Zajac for our interesting conversations on the defensive behaviour of animals and for encouraging me to further research on this topic.

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Accepted: 8 August 2021

Arboreal behaviour in a population of Geniez's wall lizard *Podarcis virescens*

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The wall lizard *Podarcis virescens* Geniez, Sá-Sousa, Guillaume, Cluchier & Crochet (2014) is endemic to central and southern areas of the Iberian Peninsula (Caeiro-Dias et al., 2018; Geniez et al., 2014; Harris & Sá-Sousa, 2002; Kaliontzopoulou et al., 2011). Like many other *Podarcis* species from the *Podarcis hispanicus* complex (Harris & Sá-Sousa, 2002), *Podarcis virescens* have been characterised mainly as having saxicolous habits, both associated with human habitats (villages, bridges, stone walls, etc.) or in more natural habitats with rocky outcrops (Geniez et al., 2014). However, incidental arboreal behaviours have been reported for this species, either basking, hibernating (Malkmus, 2004) or hiding (Vega, 1988). Particularly, Malkmus (2004; see also references therein) reported three cases from 1976 where a single tree, in each case, was used by several individuals for basking, and another case from 2003 where several individuals were observed using also a single cork oak (*Quercus suber*) for hibernation or limited activity during the winter. This last observation was the first one to report the use of a single tree by a *P. virescens* during several consecutive days. Arboreal behaviour has been reported for other species of the *P. hispanicus* complex. Several *Podarcis bocagei* were observed using a number of olive trees (*Olea europea*; Ayres, 2020), eucalyptus (*Eucalyptus globulus*), English oak (*Quercus robur*) and black alder (*Alnus glutinosa*; Galán, 2011) for basking and seeking refuge in north-western Spain. Similar observations were reported for *Podarcis lusitanicus* in the same geographical area (Ayres & Domínguez-Costas, 2021). The authors still refer to this form as *Podarcis guadarramae*, but the observation was reported before the recent validation of *P. lusitanicus* as a species by Caeiro-Dias et al. (2021). Individuals of the Tunisian form of *P. hispanicus* complex (see Kaliontzopoulou et al., 2011 for further information on systematics) were repeatedly observed climbing cork oak or European chestnut (*Castanea sativa*) for basking and feeding or in response to disturbance, in several locations (spanning more than 90 km between the most distant locations) during several consecutive days (Kaliontzopoulou et al., 2009). These observations constituted the first report of extensive arboreality in the *Podarcis* genus (Kaliontzopoulou et al., 2009). Unlike the reported cases in Malkmus (2004), all these observations involved multiple individuals on distinct trees.

On 3rd and 4th March 2007, I observed several *P. virescens* basking on cork oak trunks, below 1 meter height

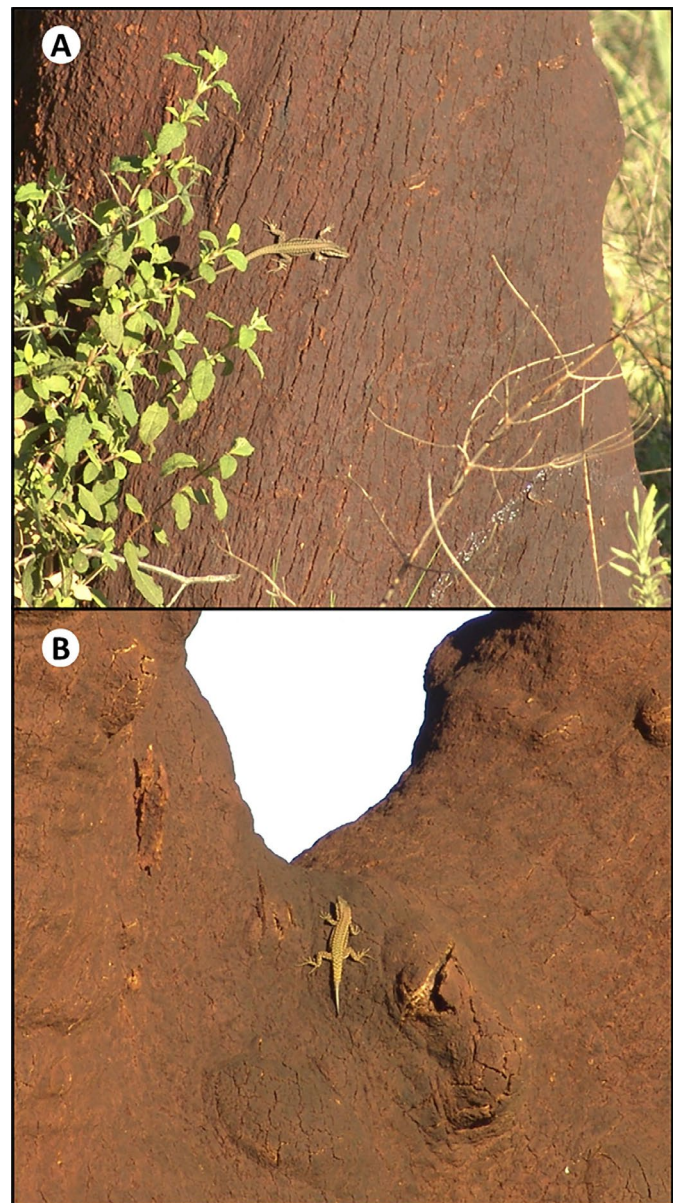


Figure 1. Adults of *Podarcis virescens* on cork oaks (*Quercus suber*) in Mora (Portugal)- **A.** Basking on the lower part of the trunk, and **B.** Climbing a tree, seeking refuge

(Fig. 1A), and/or climbing the trees as a response to my presence (Fig. 1B). These behaviours were observed in the same area (about 64,000 m²) on both days in Mora, Portugal

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(38° 56'13.47" N, 8° 10'44.61" W), by adult males and females. In some cases, the individuals fled from the soil to the trees. When the individuals were on the tree and were approached by me, they climbed to a height approximately between 1 to 2 m, and continued to climb as I got closer, until about 5 to 6 m above the ground when I could not see them anymore. Although scattered observations exist of several *Podarcis* species utilising trees in Iberian Peninsula, it has been reported mainly as incidental. By reporting these observations, I am the first to document an arboreal behaviour of several individuals on several trees, in more than one day and in the same population of *P. virescens* during the active season, contrasting to the previously mentioned hibernation case from Malkmus (2004).

The apparently common arboreal behaviour in the reported population of *P. virescens*, when the observations were made, may reflect microhabitat availability. The observations were made in a Portuguese 'montado' (a traditional human managed wood-pastoral system dominated by more or less sparse *Quercus* spp. trees and a mosaic of bush coverage), where rocky outcrops or stony refuges were non-existent. Also in this area, two other lacertid species, the spiny-footed lizard *Acanthodactylus erythrurus* and the Algerian sand racer *Psammotromus algirus*, were frequently detected during these two days. Both lizard species grow to be larger than *P. virescens* and used the ground as basking sites, and bushes or holes in the soil as refuges, and thus could be important competitors reducing ground basking opportunities for *P. virescens*. Although these observations are 14 years old, they were not previously published or reported, but are still important, since to date only the observations on Tunisian form reported by Kalintzopoulou et al. (2009) shows extensive arboreal behaviour in the *P. hispanicus* complex. Kalintzopoulou et al. (2009) also stated that "we have never observed its (the Iberian species from the *P. hispanicus* complex) regular use of trees in the Iberian Peninsula, even though oaks and other large trees are often available." However, it is possible that the arboreal behaviour may be more common in some *P. virescens* populations than reported in the literature, which deserves further investigation, particularly in this region of Portugal. Two of the cases reported in Malkmus (2004) were observed in Ponte de Sôr and Fóros do Arrão, which are relatively close to the population reported here (about 38 km to north and 23 km to north-west, respectively).

ACKNOWLEDGEMENTS

Thanks to Jacob A. Trujillo for the English revision of the manuscript.

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Accepted: 1 September 2021

A first case of polymely in the northern pool frog *Pelophylax lessonae* from a translocated population in Norfolk, England

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The northern clade of the pool frog *Pelophylax lessonae* (Camerano, 1882) is a warmth-loving water frog restricted to England, Estonia, and Scandinavia (Zeisset & Hoogesteger, 2018). Following extirpation from England in 1995, individuals collected from Sweden were translocated to a confidential site in Norfolk in 2005. Head-starting has been used to re-establish the species at a second site, Thompson Common, the last recorded location of the pool frog in England (Foster et al., 2018).

Here we describe the first known record of polymely in the northern clade pool frog observed during a monitoring survey on the 18th August 2021 at Thompson Common, Norfolk, England. A recent metamorph (Gosner [1960] stage 45; tail stub still evident) was observed basking on vegetation in a pond with a supernumerary leg bent parallel to the left hindlimb. We netted, photographed, and measured the metamorph (snout-urostyle length = 28.5 mm; see Fig.1), before releasing it at the place of capture. The supernumerary limb emerged from the base of the left hindlimb, caudal to the acetabulofemoral joint. The muscles of the limb appeared atrophied and although the limb was initially observed bent alongside the left hindlimb, the individual demonstrated no motor control. The individual appeared capable of normal movement with the additional limb causing no obvious hinderance. As it had recently metamorphosed, it is clear that the individual could survive the late larval period with polymely, but the impact on longer term post-metamorphic survival is unknown.

The Institute of Zoology's Disease Risk Analysis and Health Surveillance (DRAHS) project team has monitored the health of free-living northern pool frog populations in Norfolk since 2006. Over 500 metamorph and adult northern pool frogs have received veterinary health examinations. Infrequently, individuals have been identified with absent or abnormal limb extremities however there have been no recorded cases of polymely. The presence of supernumerary limbs has been reported in other free-living anurans and has been attributed to hyper-regeneration subsequent to physical damage, such as traumatic lacerations, musculoskeletal injuries, and cyst formation within tissues caused by trematode parasites (Session & Ruth, 1990; Johnson & Chase, 2004; Svinin et al., 2020). Chemical pollution and radiation have been considered contributing factors where mass occurrences of developmental aberrations have been reported, however



Figure 1. Supernumerary limb present in a *Pelophylax lessonae* metamorph - **A.** Dorsal view, **B.** Hind view with supernumerary limb extended

these causative factors are less likely in an isolated case as described here (Kiesecker, 2002; Taylor et al., 2005; Henle et al., 2017). As the individual would have been descended from a restricted wild-breeding population established through head-starting and translocation, a genetic component is important to consider, yet also seems unlikely where a single case is observed. Further investigation using radiography, parasitology and histopathology techniques may have elicited a diagnosis however this was not possible in the case of this northern pool frog due to licence restrictions and the ethical implications of removing an otherwise fit and functioning, free-living individual from a small population.

ACKNOWLEDGEMENTS

With thanks to Chris Michaels, John Baker and Tony Sainsbury for their comments on the manuscript and Ben King for assistance in the field. Surveying was conducted under licence from Natural England as part of the Pool Frog Recovery Project funded by the Government's Green Recovery Challenge Fund. The fund was developed by Defra and its Arm's-Length Bodies and is delivered by The National Lottery Heritage Fund in partnership with Natural England, the Environment Agency and Forestry Commission. We thank

Norfolk Wildlife Trust for their assistance with pool frog recovery at Thompson Common.

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Accepted: 23 September 2021

Predation of *Vipera ammodytes* by the eastern Montpellier snake *Malpolon insignitus*

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Ophiophagy in snakes is common and it seems to be a good option for a gape-limited predator. The prey is forced into the stomach in a concertina-like fashion so that it can fit into the predator's gastrointestinal tract; long thin snake-like prey apparently provide a bigger payoff per prey item (Wiseman et al., 2019).

In Europe, the eastern Montpellier snake *Malpolon insignitus* (Geoffroy Saint-Hilaire, 1827) is distributed from Croatia to eastern Greece, following the Balkan coast, and often lives in sympatry with the nose-horned viper, *Vipera ammodytes* and the Ottoman viper *Montivipera xanthina*. The eastern Montpellier snake is one of only two representatives of the species in Europe the other being *Malpolon monspessulanus*; neither species usually exceed 200 cm in length and both eat a wide range of prey including reptiles, birds, and mammals (Speybroeck et al., 2016). To date the two *Malpolon* spp have been recorded as predators of at least seven snake species (Corti et al., 2014; Amr & Disi, 1998; Safaei-Mahroo et al., 2017) and even cannibalism has been recorded (Ottonello et al., 2006).

On 21st August 2019 at 09:10 h on the road from Platani to Galatas, Peloponnese (342 m a.s.l.), the author observed a dead male *Malpolon insignitus* (Fig. 1). This had a *V. ammodytes* protruding from its gastrointestinal cavity. The

viper had evidently been swallowed head-first. The length of the snakes were estimated to be about 120 cm (*M. insignitus*) and about 60 cm (*V. ammodytes*), suggesting that both were adults. The sex of the *Malpolon* was established by the everted hemipenes and by its dorsal colouration as *Malpolon* spp are sexually dimorphic (Speybroeck et al., 2016).

No differences in dietary spectrum have been recognised between *Malpolon* spp, not least because since 2006 they were considered the same species (Carranza et al., 2006). The current observation is the first record of a *Malpolon* sp preying on a viper. Given the similarity between the two *Malpolon* spp it might be expected that both consume vipers.

ACKNOWLEDGEMENTS

I am very grateful to Andrea Pozzi, Tom Major and Wolfgang Wüster (University of Bangor, Wales), who helped me writing this manuscript by giving their advice and reviewing it.

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Accepted: 13 November 2021

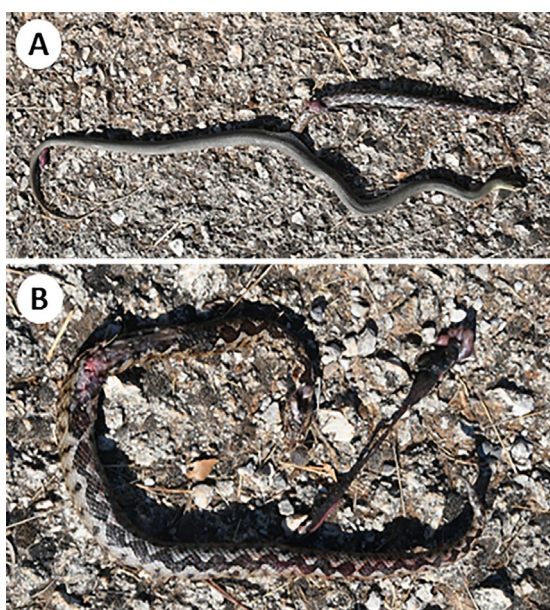
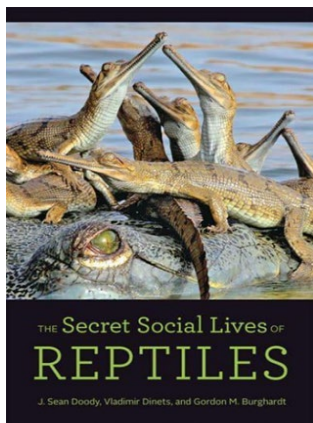


Figure 1. A road-killed *Malpolon insignitus* found with a *Vipera ammodytes* protruding from its intestinal tract **A**. The two snakes as they were found on the road, **B**. Close up of the *V. ammodytes*

The Secret Social Lives of Reptiles

J. Sean Doody, Vladimir Dinets & Gordon M. Burghardt
Johns Hopkins University Press, ISBN 9781421440675, pp. 440



Why is it so difficult for us to imagine that reptiles might have intricate social lives? We have long studied and appreciated the complex social lives of birds (who are just one branch of the extant archosaurian reptiles). Could it be because we share endothermy and the resultant hyperactivity with birds? Like birds, we are stuck in high gear, burning fuel even when idling. We buzz quickly through

the lives of the more patient ectothermic reptiles, and then peevishly conclude that there's nothing interesting going on there.

The prevailing view of reptiles as less intelligent and socially stunted is not supported by evidence, as is made clear in this important new book. Rather the opposite is true: in many cases where researchers have taken the time to conduct careful observations and experiments, ectothermic reptiles exhibit clear signs of social complexity and other sophisticated cognitive feats. The stated goal of this book is not to present new analyses, but rather "...to present, with many examples and extensive literature, the remarkable diversity and complexity reptiles possess and to stimulate both wonder and creative new explorations in field, zoo, and laboratory." This book definitely succeeds on that level (and many others, as well). For example, did you know that the Australian sleepy lizard forms long term pair bonds that can last over 27 years? Or that American alligators participate in complex group courtship dance-displays that can involve 30 or more individuals? Or that within a vast woodland, dozens of individual female black rat snakes may all seek out the same rotting stump in which to lay their egg clutches? Or that adult New Zealand common geckos will hold branches belonging to different trees to form living 'bridges' that can be used by the very small neonates to move safely away from the daytime group shelter they all share? These and many similar examples are arresting, yet there is a deeper level. This book lays bare a broad gap in our understanding of our fellow terrestrial vertebrates and provides a summary of how we can start filling in that gap.

This is not a textbook—you can tell by the morphology: at 22 X 14 cm and 400 pages you can carry it around to read on

the bus, like your favorite hardcover novel. Its function is also not that of a textbook—it is not meant to lay out all details of all relevant research on the social behaviour of reptiles. Instead, it is meant to inspire. It is a call to action. Biologists studying social behaviour have largely created an inaccurate narrative about reptiles, and the authors have good reason to be dismayed. Their book is an extended argument that reptiles behave in ways much more complex and interesting than even professional herpetologists generally assume.

Although this is not a textbook, it is also not necessarily aimed at the casual reader. Rather, the intended audience includes researchers, dedicated amateurs, and others with a deep interest in the science of herpetology. The authors do an admirable job of explaining complex concepts from the scientific literature, but these discussions require familiarity with some terminology and a basic understanding of evolutionary biology. The book is mainly organised by taxonomy. Most of the chapters introduce a behavioural concept, and then discuss what is known in that field of study within tetrapods. Mammals, birds, and amphibians are discussed in brief, usually as an aspirational comparison to highlight the yawning gap in what we know about the social behaviours of those taxa in comparison to ectothermic reptiles. The social behaviours of the remaining tetrapod groups (the tuatara, snakes and lizards, crocodilians, and turtles) are reviewed thoroughly, with extra detail provided on systems where study of these animals may facilitate broader insights into the evolution of sociality. In addition, information that paleontologists have been able to glean from extinct lineages of non-avian reptiles is summarised and discussed throughout these chapters.

The book begins with two excellent introductory chapters which give a rather masterful short summary of the evolution of reptiles, including discussions of recent findings and debates regarding phylogenetic relationships and major evolutionary events. I found myself making notes throughout this chapter on the informed perspective provided by the authors—notes I plan on incorporating into my own Herpetology classroom the next time I offer the course (as an aside, I really loved the seamless inclusion of the Anthropocene into the evolutionary history of the reptiles). After this introduction there are specific topical chapters which offer detailed discussions of mating systems, social structure, communication, reproductive behaviour, communal egg laying, parental care, hatching, behavioural development, and a catch-all of additional social behaviours that are too sparsely studied to warrant full

chapters. The book is closed out by a forward-looking chapter that revisits the major topics and lays out the authors' vision for how to move research forward in these areas.

As the authors themselves note repeatedly, the level of detail provided concerning the social behaviours of different ectothermic reptile taxa is unbalanced. Although (excepting the tuatara) crocodiles are the smallest of these taxa, they have perhaps received the most attention in regard to social behaviour, and several sections of the book provide in-depth reviews and first-hand accounts of crocodilian behaviour. Because crocodilians are large, less secretive, and more active than most other ectothermic reptiles, we probably are better able to observe and understand their social lives. Perhaps this is not surprising—they are not only the most closely related to birds, but also seem behaviourally similar, with extensive auditory communication and a style of egg-laying and nesting that requires some level of parental care. However, the authors address the taxonomic imbalance by pointing again and again to the huge diversity of other reptiles about which we know basically nothing. The fact is, relatively few of the 10,000+ species of snakes and lizards are known to science beyond a basic description (and of course many thousands of additional species have not been described at all). The behavioural variety hidden in that vast unknown is sure to be staggering.

The book is full of broader insights. For example, at the beginning of Chapter 5, the authors point to three trends in the practice of science that have had a detrimental effect on our understanding of reptile behaviour and other natural systems: the concept of a 'model species'; the overemphasis on experimentation in a controlled laboratory setting; and the increasing focus on preregistration of scientific studies that lay out all the details of the planned experiment in advance. Of course these practices have a central place in scientific research, but, as the authors compellingly argue, they can never be used as a substitute for descriptive studies, opportunistic observation, and detailed accounts of natural history. All too often studies in captive laboratory environments fail to recreate the context that is necessary to see and understand the way animals interact with their environment in nature. Controlled studies are only applicable when scientists have developed enough understanding of a natural system to be able to formulate very specific hypotheses. And that understanding has to be developed from observational, quantitative natural history research that has (somehow) found a route to dissemination. Those routes are being choked off in most modern scientific journals, and if that trend continues, the raw material that scientists need to refine into controlled experiments will also dry up.

Another crucial insight that the authors highlight repeatedly is the value of variation in behavioral traits across ectothermic reptiles. The comparative method of examining the form and function of traits across different species of known relationship is the most powerful tool we have for understanding behavioural evolution, and this method requires variation across those traits to be present. In ectothermic reptiles, parental care is rarer and far more variable than in birds and mammals, arising and disappearing repeatedly across different taxonomic groups—the ideal setup for a detailed comparative analysis.

The book has other bonuses as well: an insightful foreword by Gordon W. Schuett does an excellent job of whetting the palate for the engaged reader. The colour plates in the center of the book are a nice addition, too, but if a picture is worth a thousand words, a video of behaviour is worth a thousand pictures (especially if it's at least 34 second at 30 fps...). The authors refer to video examples throughout, often referencing Youtube, which made me long for a digital supplement, some sort of repository where all these clips of interest had been assembled and annotated (a few URLs are given in the text).

All three authors of this landmark volume are accomplished researchers with dozens upon dozens of their own scientific publications, and a deep, collective grasp of the currently dispersed and idiosyncratic literature on reptile social behaviour. They have collaborated to produce a real gem of a book—a clearly written, logically organised, and impassioned (but deeply informed) scientific call to arms. Although anyone with an interest in reptiles or their natural history would benefit from reading this book, perhaps its greatest impact will be on the up-and-coming next generation of scientists. If you are still developing your own expertise or are casting about for an area of scientific inquiry in which to focus, this book is a treasure map—it highlights case after case of compelling (but often preliminary) observations that need further investigation. You should buy it, read it, and start marking up the margins, as I did, with excited exclamations and notes to yourself about the rich and complex and unexplored social world of some of the most misunderstood animals in nature.

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Received: 5 October 2021

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