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Front Cover: A grey heron *Ardea cinerea* using 'stress & wash' prior to consuming a great crested newt *Triturus cristatus*, photographed in Kent (England), by Clifford Seabrook. There is an article about this species on p. 33.

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Bromeliad rosettes as shelters for hylid treefrogs during a heat wave in the Brazilian Pantanal

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ABSTRACT – During a heat wave in November 2023, we assessed the use of bromeliad rosettes as shelters for hylid treefrogs in the Brazilian Pantanal (area of Nhecolândia). During the day time, four hylid species (genera *Boana, Scinax, Trachycephalus*) were detected sheltering in 40 rosettes of the terrestrial bromeliad *Bromelia balansae*; this was a different species complex from when observations were made in October 2019 when the temperature conditions corresponded to long-term averages. The internal and external day time temperature of each shelter was measured. The mean daytime temperature inside the shelters was 36.1 °C (range 24.0–43.5 °C), this varied depending on the microhabitat conditions, and was 1.1 °C lower than the mean temperature of the leaves of the upper part of the rosettes; the difference was statistically significant. We suggest that during this very dry and hot period the main advantage provided by the bromeliad shelters was to enable frogs to have behavioural control of overheating so that they could avoid excessive evaporative water loss.

INTRODUCTION

The Pantanal is an ecological sub-region of the Cerrado formed by flat plains of Quarternary sediments covered by seasonally flooded grassland and Cerrado vegetation (Griffith et al., 1998). The climate of the Pantanal is characterised by humid and hot summer months (December to January) and dry and colder winters (June to August) with mean monthly temperatures in the range of 19.9–27.4 °C (Tarifa, 1986; Uetanabaro et al., 2008). However, in recent years due to climatic change, the Pantanal is experiencing prolonged periods of drought accompanied by extreme heatwaves (Campos et al., 2020; Marengo et al., 2021).

The Pantanal is well known for the diversity and abundance of its wildlife, in particular a very rich amphibian fauna comprising more than 50 anuran species (Strüssmann et al., 2007; 2010; Uetanabaro et al., 2008; Valério et al., 2016). Amphibians generally play an important role in ecosystem food webs and contribute significantly to various ecosystem services (Hocking & Babbitt, 2014). However, they are experiencing a global crisis of decline and current climate change is one important contributing factor (Beebee & Griffiths, 2005; Corn, 2005). It has been predicted that increased temperature, increased length of dry season, decreased soil moisture and increased inter-annual rainfall variability will negatively affect amphibian populations (Donnelly & Crump, 1998; McMenamin et al., 2008; Walls et al., 2013). Drought and drastic environmental changes have also recently been reported from the Pantanal (Campos et al., 2020; Campos & Mourão, 2020; 2021). Therefore, from the perspective of the conservation of the Pantanal herpetofauna, it is important to know how local amphibian populations are responding to these changes.

In general, the appropriate choice of retreat sites and good timing of retreat appears to be fundamental for survival under hot and dehydrating conditions (Navas et al., 2004). In the area of Nhecolândia (sub-region of the Brazilian Pantanal) an important source of anuran retreats is the terrestrial bromeliad *Bromelia balansae* Mez, 1891 (Bromeliaceae) and at least two hylid treefrogs, *Dendropsophus nanus* and *Scinax nasicus*, frequently use the rosettes of *B. balansae* as diurnal shelters (Moravec & Campos, 2020). In the current study, we evaluate the role of bromeliad rosettes as shelters for treefrogs during a heatwave in Nhecolândia.

MATERIALS & METHODS

From 1–12 November 2023, we surveyed bromeliad rosettes for the presence of treefrogs in the territory of the Fazenda Nhumirim and nearby Fazenda Campo Dora, in the Brazilian Pantanal (Nhecolândia, state Mato Grosso do Sul). Anuran species were identified using Uetanabaro et al. (2008). The research coincided with unusually hot, dry weather in the first half of November (maximum daily air temperatures ranged 40–42.5 °C) which lasted until the beginning of December 2023. Average maximum October and November air temperatures for the Corumbá area (period 1991–2020) located ca. 150 km west of Nhumirim, are 34.1 and 33.8 °C (World climate guide, 2024). Average air temperature recorded in Fazenda Nhumirim in October 2019 was 29.1 °C (B. Soriano, personal communication, 24 April 2024).

The area of Nhecolândia is covered by a mosaic of three major habitats: seasonally flooded grassland (floodplains), permanent or temporary lagoons and pockets of forest. The marginal understory of the forest 'islands' is often formed by dense growths of the terrestrial bromeliad *B. balansae*

Figure 1. Hylid treefrogs sheltering in the terrestrial bromeliad *Bromelia balansae* in the Brazilian Pantanal (area of Nhecolândia)- **A.** Patch of *B. balansae* at the Lagoon B, **B.** Diurnal shelter of *Trachycephalus* cf. *typhonius* in the centre of the bromeliad rosette, **C.** Two individuals of *Scinax nasicus* in the mutual contact in the bromeliad centre, **D.** Two individuals of *Boana raniceps* and one individual of *T.* cf. *typhonius* sharing the same shelter, **E.** *B. raniceps* having their ventral and dorsal surfaces pressed against the bromeliad leaves, **F.** *B. raniceps* with light body colour in the leaf axil (at 41 °C), **G.** *S. nasicus* adopting water-conserving posture on the bromeliad leaf during the night, **H.** Subadult individual of *Leptodeira pulchriceps* exploring the bromeliad centre

(Fig. 1A). These sharply delimit the forest margin from the grassland lying between the forest pockets and the lagoons (Moravec & Campos, 2020). The stiff leaves of *B. balansae* form dense rosettes, which do not accumulate rainwater and lack phytotelmata (Romero, 2006). Nevertheless, a small amount of water can be present in the deepest part of the rosettes after rainfall (Moravec & Campos, 2020). In the surveyed localities, the rigid thorny leaves of the individual rosettes usually reached the height of 700–1,500 mm (maximally 3,000 mm) and were 25–60 mm wide (up to 90 mm at the rosette base). Due to the heatwave, no traces of water were detected in any of those bromeliad rosettes that were inspected.

The study areas were three bromeliad patches growing at the forest margins in the vicinity of three permanent lagoons: Lagoon A (Fazenda Campo Dora, 18° 53’34’’ S, 56°

43’49’’ W), Lagoon B (Fazenda Campo Dora, 18° 57’24’’ S, 56° 44’48’’ W) and Lagoon C (Fazenda Campo Dora, 18° 58’43’’ S, 56° 43’36’’ W). The straight distance between the Lagoons A and B was ca. 7.2 km and between Lagoons A and C ca. 9.3 km. Additional diurnal and night observations were made in bromeliad patches at a fourth permanent lagoon in Fazenda Nhumirim (Lagoon D, 18° 59’03’’ S, 56° 36’58’’ W) lying ca. 16.0 km straight from the Lagoon A. The distances of bromeliad patches from the nearest water margins of the respective lagoons ranged between 20–40 m. In total, more than 800 rosettes of *B. balansae* were inspected around Lagoons A–D during the 12 days of the investigation.

On 6–9 November 2023 between 08:00–14:00 h, rosettes being used as hylid shelters were documented in detail at the bromeliad patches of Lagoons A–C (150 bromeliad rosettes inspected). For each bromeliad containing a hidden hylid we measured (i) the surface temperature of the shaded leaves of the open upper part of the bromeliad rosette ca. 30 cm above the hidden hylid, and (ii) the inner temperature of the funnel-shaped central part of the rosette containing the hidden hylid. The temperatures were measured with a Benetech non-contact infrared digital thermometer (temperature extent -50 to 420 °C) from the distance 50–100 mm. Control measurements of air temperature inside and outside the bromeliad rosette were made with a digital thermometer EMOS RS8471 with an external sensor. Each measurement was repeated three times, and the mean value was rounded to the nearest 0.5 °C. In addition, maximum temperatures of the sunlit surface of the ground at the edges of the bromeliad patches and the maximum surface temperature of the bromeliad leaves exposed to the sun were measured to document temperature conditions at the study area.

Paired t-test was used to evaluate the possible difference between average temperatures of the upper open part of the bromeliad rosette and the inner central part of the rosette containing the hidden hylids.

RESULTS

From 6–9 November 2023, around the Lagoons A–C, 150 rosettes of *B. balansae* were inspected during the daytime, of which 40 (26.7%) were occupied by 53 hylids of four species. We observed 18 *Boana raniceps*, 7 *Trachycephalus* cf. *typhonius*, 1 *Scinax acuminatus* and 27 *Scinax nasicus*. The local occupancy on the outer edges of the bromeliad growths facing the lagoons reached up to 56.0% (n = 25 inspected rosettes). Usually only one individual hylid occupied a bromeliad centre (Fig. 1B). However, in eight cases, 2–4 individuals shared the same shelter (Fig. 1C). In three cases, two different species (*B. raniceps* and *T.* cf. *typhonius* or *B. raniceps* and *S. acuminatus*) were hidden in the same shelter with bodies in mutual contact (Fig. 1D). The hylids were hidden in the deepest parts of the centres of the rosettes (exceptionally also in the near leaf axils). Their ventral and dorsal surfaces were usually pressed against the leaves (Fig. 1E).

The highest temperatures of the sunlit surface of the ground at the edge of the bromeliad growths reached 50–54 °C and the maximum surface temperature of the bromeliad leaves exposed to the sun reached 50–56 °C. The mean temperature of the shaded leaves of the upper part of the rosette was 37.2 °C (range 28.0–45.0, SD = 4.06, n = 40), while the mean temperature of inner occupied central part of the rosettes was 36.1 °C (range 24.0–43.5 °C, SD = 4.23, n = 40), i.e. 1.1 °C lower. This difference was statistically significant $t = -4.119$, $df = 39$, $p < 0.001$).

The distribution of treefrogs was not even, as they were more numerous on the outer edges of the bromeliad growths, which were closer to the lagoons, but they were less numerous in bromeliads that were exposed to the sun for longer parts of the day (e.g. whole morning). In such sunlit shelters the temperature reached 40–43.5 °C and the hylids lightened their colour to reflect the light energy (Fig. 1F). The hylids were not found in bromeliads covered with a layer of leaf litter, which filled the centres of rosettes. The same was true for bromeliads growing under trees frequented by herons and other water birds, as the rosettes of these bromeliads were thickly covered with bird droppings.

At the time of the investigation, the hylids using bromeliad shelters were not breeding or vocalising. After dark when the air temperature was still 30–31 °C, some individuals remained hidden in bromeliad shelters. Others were observed perching on leaves outside the bromeliad centre, some adopting a water-conserving posture (limbs tucked in close to the body and the chin resting against the substrate; sensu Heatwole et al., 1969) to control evaporative water loss (Fig. 1G). The expected nocturnal movement of hylids into the lagoons to replenish water was not observed, but insufficient effort was made to confirm this movement.

During night inspections of the control bromeliad patches at the Lagoon D, three individuals of the frog-eating colubrid snake *Leptodeira pulchriceps* were observed exploring the bromeliad rosettes (Fig. 1H).

DISCUSSION

Bromeliad rosettes are commonly used by Neotropical frogs as diurnal shelters (Peixoto, 1995; Silva et al., 2011; Sabagh et al., 2017). However, the present data indicate that, depending on climatic conditions, the species spectrum of treefrogs using bromeliad shelters may vary. In October 2019, the bromeliad rosettes were frequently occupied by subadult and adult *D. nanus* and *S. nasicus* (Moravec & Campos, 2020). However, during the heatwave of November 2023, the same bromeliad growths also served as diurnal shelters for three physically larger hylid species - *B. raniceps, S. acuminatus* and *T.* cf. *typhonius*. Interestingly, the physically smallest species, *D. nanus*, which is more sensitive to desiccation than the other species, did not shelter in bromeliads in November 2023 but survived the hot days in the moist littoral vegetation on the shores of the lagoons.

We originally assumed that the observed hylids could profit by occupying the rosettes of *B. balansae* in three ways: (i) the thorny leaves of rosette centres protect the frogs from larger predators, (ii) the diverse groups of arthropods associated with bromeliads provide food, and (iii) the deep basal parts of rosette centres provide shady and humid shelters (Moravec & Campos, 2020) and certainly in the semi-arid Brazilian Caatinga, wetter and cooler conditions

have been recorded inside the bromeliad *Aechmea aquilega* (species with phytotelmata) and inside the plots of the rupicolous bromeliad *Encholirium spectabile* (species lacking phytotelmata) (Protázio et al., 2013; Jorge et al., 2020). Our findings from November 2023 show that rosettes of *B. balansae* are completely dry at high ambient temperatures. On the other hand, the average temperature inside the shelters was statistically significantly lower than outside the bromeliad rosettes. Therefore, the question is what is the actual role of the bromeliad shelters?

The temperature in bromeliad shelters varied considerably depending on the microhabitat conditions – from 24.0 °C (deeply shaded rosette at 08:20 h) to 43.5 °C (rosette fully exposed to the sun at 10:00 h). Some bromeliads were exposed to varying lengths of partial or even full sunlight during the day. Consequently, the temperature inside the shelters could be the same or even higher than outside the bromeliad. When compared with the results of other studies on terrestrial bromeliads in semi-arid Brazilian Caatinga (Protázio et al., 2013; Jorge et al., 2020), the difference between the average temperatures inside and outside bromeliad rosettes was 0.5–2.9 °C lower for *B. balansae* in the Pantanal. The fact that in *B. balansae* a small but statistically significant difference (1.1 °C) was detected despite changing microhabitat conditions indicates that evaporative cooling from the skin of the hidden frogs likely contributes to maintaining a lower temperature in the shelter. Evaporative cooling has been reported for different anuran species including the African genera *Chiromantis* and *Hyperolius* and South American genera *Phyllomedusa* and *Pithecopus* (Geise & Linsenmair, 1986; Shoemaker et al., 1987; 1989).

It appears that none of the five hylid species seeking out *B. balansae* as diurnal shelters has any specialisations that enables them to withstand hot and desiccating conditions. They are all bromelicolous species that breed and develop in stagnant water and use the bromeliads as shelters and foraging places (Peixoto, 1995; Gordo & Campos, 2003; Uetanabaro et al., 2008; Jorge et al., 2020). Further, they do not hide in holes and bar access to the shelter with their heads (phragmotic behaviour) as reported in the hylid *Corythomantis greeningi* in the Brazilian Caatinga (Navas et al., 2004; Jared et al., 2005) nor do they wipe cutaneous lipid secretions over the body to reduce evaporative water loss as do the species of the neotropical genera *Phyllomedusa* and *Pithecopus* (Brattstrom, 1979; Shoemaker et al., 1987; Gomez et al., 2006). Nevertheless, despite the absence of such specialisations, the bromeliad shelters enabled four of the observed species to overcome unusually hot and dry daily conditions. Therefore, the following observations suggest that the bromeliads provided to these treefrogs shelters suitable for behavioural control of overheating and excessive evaporative water loss: (i) The species in question were able to tolerate high temperatures (up to 43.5°C in the case of *S. nasicus*), which reach or even exceed the maximum body temperatures reported for some other South American or African anurans inhabiting seasonally dry and hot ecoregions – e.g. around 40 °C in *Chiromantis xerampelina*, *Phyllomedusa sauvagii* and *Pithecopus azureus*, 43–44 °C in *Hyperolius nitidulus*, 45 °C in *Rhinella granulosa* (Geise & Linsenmair, 1986; Shoemaker et al., 1987; 1989; Navas et al., 2004); (ii) They use colour change, probably to reduce radiation absorption; (iii) Observed crowding in the shelter can contribute to the evaporative water loss reduction; (iv) Individuals staying in the tight centres of bromeliads or in the limited space of the leaf axils can reduce evaporative water loss by pressing their dorsal and ventral surfaces against the leaves. Although evaporative cooling is limited in such situations, an individual can easily increase it by changing its position.

Longer-term and more thorough research will be needed to understand all aspects of the association of frogs with bromeliads in the Pantanal. For example, it would be appropriate to focus in detail on the changes in humidity conditions in bromeliad shelters during different climatic conditions. Also, repeated night observations of *L. pulchriceps* and others anuran predators exploring the bromeliad rosettes (e.g. Sabagh et al., 2020) raise the interesting question of the extent to which closer association of anuran with bromeliads during hot periods may increase snake predation pressure.

The importance of *B. balansae* for maintaining the high biodiversity of the Pantanal is already well established in a number of groups of vertebrate and invertebrate species (e.g. Campos, 1993; Medri & Mourão, 2005; Romero, 2006; Campos & Mourão, 2015; Antunes et al., 2016; Paulino-Neto et al., 2016; Menezes et al., 2018) and the results of the current study suggest that this is also the case for hylid treefrogs.

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RESEARCH ARTICLE

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Reproduction and displacements of known-age caimans *Caiman yacare* in the Pantanal of Brazil

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ABSTRACT – We recaptured 26 female and 24 male Pantanal caimans *Caiman yacare* of known-age up to 36 years after marking. The relationship between clutch size and age for known-age females was highly variable although one female captured multiple times between 18 and 26 years of age showed little variation in clutch size. Captured known-age females attending nests varied from 73 cm to 89 cm snout-vent length and from 9 to 36 years old. These females continued to grow long after their first capture, so cessation of growth does not appear to be related to reproduction. Most known-age animals were recaptured within 10 km of where they hatched, but usually on a different ranch, so ranches cannot be used as autonomous management units. Our data indicate that the ratio of snout-vent length (SVL) at first reproduction (73 cm) to mean asymptotic SVL reported for this species (85.7 cm SVL) is much higher in female Pantanal caimans (0.85) than has been reported for most other reptiles (0.7).

INTRODUCTION

Many organisms can be placed on a continuum between species with short life spans combined with a large number of offspring (r selected) and long life spans with a small number of offspring (K selected) (Pianka, 1970). However, crocodilians are long-lived but also produce large numbers of relatively small offspring (Magnusson, 1986), raising the question as to whether they also differ in other life-history traits. Many reptiles start to reproduce at about 70% of maximum length, and these are often referred to as having indeterminate growth, i.e. growth continues throughout life (Andrews, 1982; Shine et al., 2016). Like other reptiles, crocodilians start reproducing long before they reach their maximum size, and are described as having indeterminate growth, though the evidence for this is controversial (Wilkinson et al., 2016). There have been no studies of the ratio of size at first reproduction and maximum size in crocodilians.

Generalities about the size at first reproduction are based on individual growth models (Charnov et al., 2001). However, data are usually not based on individuals, but are estimated from the smallest recorded size at reproduction and maximum asymptotic size in a large number of individuals. This assumes that individuals vary little in age at first reproduction and maximum size can be estimated from growth models (Shine & Iverson, 1995). However, frequently used sigmoidal models of growth are often imprecise (Campos et al., 2014), and data are not usually presented to indicate whether individuals follow the mean trajectory or remain parallel to it for most of their life (Magnusson, 2012).

Life-history data are essential for demographic studies and wildlife management, but long-term studies of individual crocodilians are rare due to the difficulty of marking large numbers of individuals and recapturing them (Bayliss, 1987). Demographic studies of most organisms suffer from the problem of defining the biological population being investigated (Magnusson, 2013), but this is even more difficult for crocodilians, which may make round-trip movements of over 1,800 km (Fukuda et al., 2019). On the other hand, the mean size of nesting female caimans may vary between areas within tens of km of each other (Campos & Magnusson, 1995). Such scale discrepancy indicates the importance of registering the movements of animals used in demographic studies to define the area in which the estimated population parameter may apply.

Individual crocodilians of the species for which long-term studies have been undertaken, such as *Crocodylus johnstoni* studied for 20 years (Tucker et al., 1997), *Caiman latirostris* studied for 22 years (Viotto et al., 2020) and *Alligator mississippiensis* studied for 46 years (Wilkinson et al., 2016), live long after reaching sexual maturity and have life spans that far exceed the duration of most studies. Indirect methods can be used to estimate mean age at first reproduction, displacement from natal areas and reproductive life spans, but these may have little precision, especially when derived from estimates of age based on size (Campos et al., 2014; Magnusson, 2012). Wilkinson et al. (2016) estimated that *A. mississippiensis* has a reproductive life span of 46 years, and individuals may live for more than 70 years in the wild. However, those intervals were based on estimates of age based on size. The longest period of nesting they recorded for an individual female was 31 years. Viotto et al. (2020) studied known-age *C. latirostris* individuals, or individuals captured at small sizes when age-size relationships are precise, and estimated first reproduction at about 8.1 years for females in the wild. Age at first reproduction based on known-age individuals is not known for other crocodilian species in the wild.

Campos & Magnusson (1995) related clutch size to mass of female *Caiman yacare*, and Campos et al. (2006) reported the

size-age relationship for the same species, but there has been no study of the direct relationship between age and clutch size. Wilkinson et al. (2016) did not find evidence of senility in *A. mississippiensis*, except for one emaciated individual. They reported determinate growth in the same species but growth ceased long after the estimated age at first reproduction.

Campos et al. (2014) concluded that age-size relationships based on the relationship between growth rate and size are biased for both males and females, because they differed from the age-size relationships of known-age animals. However, it is expected that an empirical relationship derived from direct observations could predict values for the dependent variable better than those modelled from a relationships between growth rate and size, and the bias would be opposite in direction for males and females. Therefore, it is important to obtain the independent data needed to test this relationship.

Adult *Crocodylus johnstoni* have home ranges that cover a linear distance of about 1 km (Tucker et al., 1997) and adult *Paleosuchus trigonatus* also have small home ranges that generally cover less than 1 km of stream (Magnusson & Lima, 1991), but juveniles of both species appear to wander over large distances. Small *C. c. yacare* cover much larger areas, but individuals with snout-vent lengths (SVL) >40 cm had generally moved less than 10 km when recaptured after 5 to 15 years (Campos et al., 2006). However, in that study, few of the caimans were recaptured after reaching sexual maturity.

Caiman yacare is one of the most intensively studied crocodilians (Campos et al., 2020). It is often considered a full species, even though its range extends well beyond the Pantanal and intergrades with the spectacled caiman, *Caiman crocodilus crocodilus*, over a wide area in the Amazon (Hrbek et al., 2008). While there is dissension about the number of species within the *C. crocodilus* clade, in the Amazon there is consensus that there is only one species in this clade in the Pantanal (Campos et al., 2020). There are no intensive studies of the species in the Amazon, so to avoid confusion we will refer to *Caiman yacare* in this study by its common name, the Pantanal caiman.

Here, we report data on growth, reproduction and long-term movement of known-age Pantanal caimans that were captured up to 36 years after hatching, in the same area investigated by Campos & Magnusson (1995), Campos et al. (2006) and Campos et al. (2014). Our working hypothesis was that analysis of this long-term data would confirm determinate growth in the species and show that individuals vary in their growth trajectories. These data would also allow us to assess whether the ratio between size at sexual maturity and maximum size for the Pantanal caiman is about 0.7, as in other reptiles.

MATERIALS & METHODS

Between 1987 and 2013, caimans were first captured at Nhumrim (18° 59′ S, 56° 39′ W), Campo Dora (18° 55′ S, 56° 40′ W), and Dom Valdir ranches (18° 55′ S, 56° 35′ W) (see Campos et al., 2020 for details). From 2014 to 2022, we continued to recapture caimans in the same areas. Recaptures were made during the day, mainly during the dry season (September to November), when caimans are concentrated in pools (Campos et al., 2011) or moving between pools and thermoregulation sites in the forest (Campos et al., 2006). During the high-water season most waterbodies are connected and forests and pastures are inundated. Few animals were recaptured under these conditions, so the movements reported is almost exclusively between dry-season refuges.

Between February 2004 and November 2010, we captured 1,272 new individuals, resulting in a total of 7,831 caimans marked in the study area since 1987. Only data for these new recaptures were used for this study. Hatchlings were marked by removal of tail scutes and/or application of a numbered aluminum tag (National Band & Tag™ 1005-1) attached to the interdigital membrane of the hind foot. Adults were marked by removal of tail scutes and with numbered plastic cattle ear tags fixed on the tail scutes or with a numbered aluminum tag (National Band & Tag™ 1005-3) attached to the interdigital membrane of the hind foot. Tail scutes were removed quickly with a surgical scalpel, and caimans showed no evidence of distress, such as struggling. These methods have been used on many species of crocodilians (e.g. Manolis & Webb, 2016), are regarded as effective, with no evidence of stress or infection. All procedures for capturing, manipulating and marking of caimans were approved by the EMBRAPA Ethics Committee (No. 009/2016) and authorised under SISBIO license (No. 13048-1) and IBAMA permits (No. 017/02).

Locations of caimans were recorded with a GPS (Garmin GPSMAPS). Surveys were not undertaken in all areas in all years (see Supplementary Material, Table 1S), but all areas were surveyed on several occasions over the study period. Snout-vent length (SVL) of captured caimans was measured with a tape measure graduated in mm, and sex determined by inspection of the cliteropenis (Campos et al., 2006)

Using growth curves giving the size and growth-rate relationships for known-age caimans (see S1 Table 2 in Campos et al., 2014), we compared the size of newly captured known-age caimans to the values predicted by growth curves using t-tests. Multiple regression was used to investigate the independent effects of size and age on clutch size. This analysis was done using only the first data point for each of those females captured more than once and repeated with the data including recaptures. The relationship between distance from hatching site and age was nonlinear and we modeled it with a power curve, which was linearised by taking the logs of both dependent and independent variables. All statistical analyses were done in the R statistical environment (R Core Team, 2021), and we used the K means algorithm of Spring (2018) to classify the water bodies and map the study area based on a Sentinel 2 satellite image.

RESULTS

The permanent marking by scute-clipping (removal of a combination of single and double vertical tail scutes) made it possible to identify recaptures, which extended up to 36 years. We recaptured 26 females and 24 males that had been marked as hatchlings or at such small size (SVL < 24.2 cm) that we could estimate hatching year with confidence. The data for animals captured when more than 25-years-old

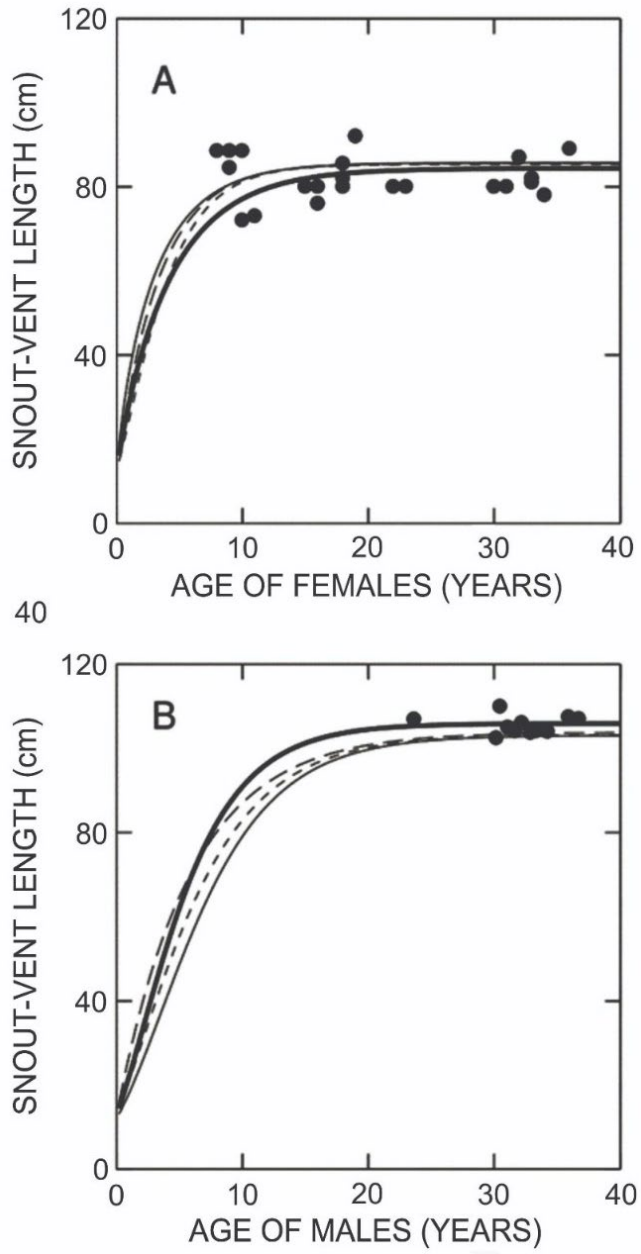

Figure 1. Relationship between size and age for known-age female **A.** and male **B.** Pantanal caimans based on the Richards curve (thick continuous line, from Campos et al., 2014), the filled dots are data from the current study indicating known-age caimans captured between 1987 and 2021. Models based on growth rate-size relationships for animals of unknown age are given by the thin continuous line (full Richards model), short dashes (von Bertalanffy, m = 0.667) and long dashes (monomolecular, m = 0) use the parameter values provided by Campos et al. (2014).

confirms negligible growth of older animals and that the empirical asymptote for known-age individuals from Campos et al. (2014) fits the data well for older animals (Fig. 1). T-tests comparing the observed SVL to that predicted by the model for animals captured subsequently were consistent with all models (P > 0.45 in all cases) given by Campos et al. (2014) for males (Fig. 1). Data from subsequent recaptures were not consistent with the model based on known-age animals for females (t_{48} = -3.1263, P = 0.0003), but the observed data were not significantly different from the other models

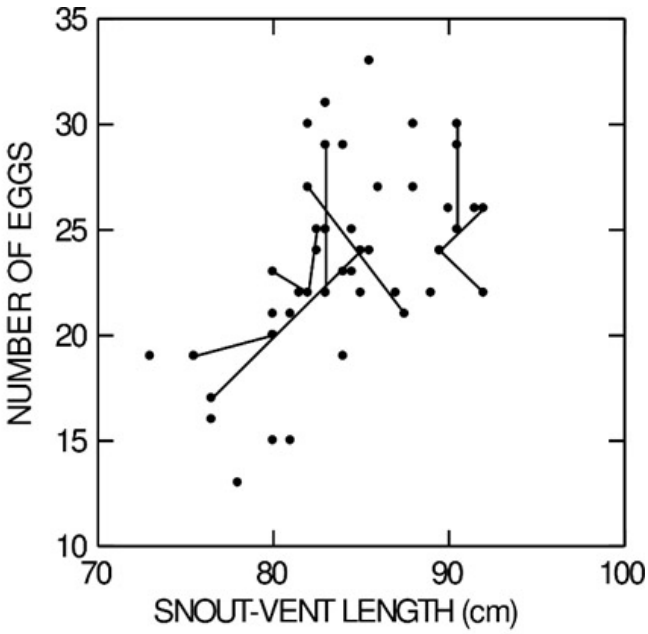

Figure 2. Clutch size in corresponding nests of female Pantanal caimans captured next to nests. Lines connect data points for individuals captured multiple times.

(P > 0.11 in all cases). There was large scatter around the predicted values for all models (Fig. 1).

The number of eggs per clutch generally increased with female size, indicating that clutch size more than doubles over the lifespan of females (Fig. 2). However, individual females that were captured at nests did not necessarily show that relationship. Three females exhibited little or no growth between clutches (almost vertical lines on Figure 2), clutch size increased with SVL for three females, and it decreased with size for another three. The three females that did not grow had presumably reached their asymptotic sizes. The ratio of snout-vent length (SVL) of the smallest reproducing female in the study (73 cm) to mean asymptotic SVL 85.7 cm SVL), as estimated by Campos et al (2014), was 0.85.

There was a very weak relationship between age and SVL of known-age females (r^2 = 0.09, P = 0.233). The relationship between clutch size and age for known-age females showed large scatter, and one female captured multiple times between 18 and 26 years old showed little variation in clutch size (Fig. 3). Including only the first capture for the female captured three times, multiple regression indicated a positive effect (P = 0.012) of SVL on clutch size (CS), but a negative effect of age (P = 0.047) on clutch size (CS = -6.627 + 1.226*SVL – 0.581*AGE, N = 13, R^2 = 0.492, P = 0.034). Including all data for the female captured multiple times gave similar results (SVL, P = 0.011; AGE, P = 0.063).

Most known-age animals were recaptured within 10 km of where they hatched (Fig. 4). Although this distance might be a reflection of the size of the study area, recaptures of some individuals over much larger distances indicates that it probably reflects individual movement patterns. The overall relationship between distance from hatching site (DIST) and age (AGE) could be modeled with a power curve [ln(DIST) = 3.04 - 0.41*ln(AGE), N = 51, r^2 = 0.17, P = 0.003]. Inclusion of sex did not significantly improve the fit of the model (P =

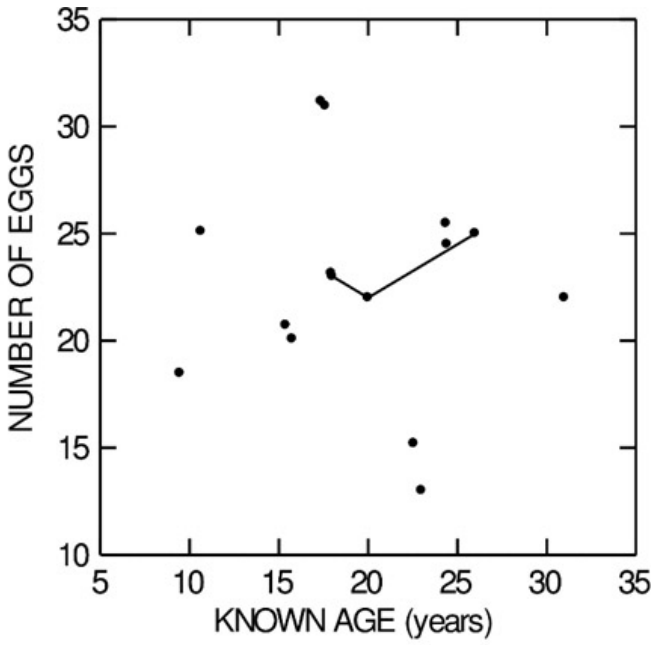

Figure 3. Relationship between the number of eggs in nests and the known ages of female Pantanal caimans. Lines connect data points for one female captured three times.

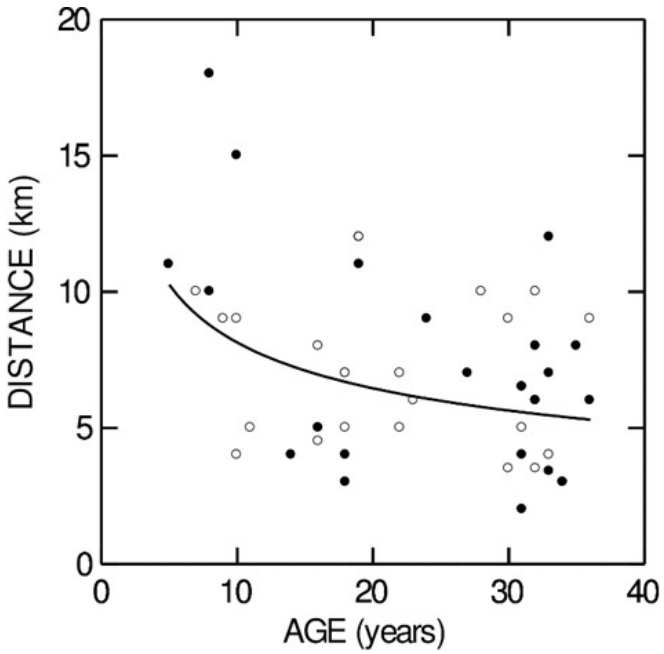

Figure 4. Distance from hatching site at which known-age female (open circles) and male (filled circles) Pantanal caimans were recaptured.

0.33), but few females less than 10 years old were captured. There was no statistically significant relationship between distance from hatching site and age for animals older than 10 years (P = 0.33).

There was a continuous displacement of animals away from nesting areas (Fig. 5), which resulted in a net movement from Nhumirim Ranch in the lake area to the other ranches near the rivers. However, animals showed two distinct displacement patterns; some moved within the ranches (lines parallel to the border between Nhumirim ranch and the other ranches on Figure 5) and others moved from Nhumirim to riverside areas on the other ranches (lines perpendicular to the Nhumirim ranch border on Figure 5). Displacement patterns were similar for males and females, with individuals of both sexes showing the two movement patterns.

DISCUSSION

Long-term data on growth and movement of crocodilians are difficult to obtain (Bayliss, 1987). In this study, we recaptured 50 individuals from a total of >6000 that were marked since 1987, but that required an intensive recapture program over 34 years. The data presented in Campos et al. (2014) suggested that all growth models fit the data well for females but seemed to underestimate growth of males. In contrast, the extended data for animals with ages up to 36 years show that for males all models appear to be unbiased, even if imprecise, but for females the empirical size-age relationship presented by Campos et al. (2014) is biased upward for females. Therefore, conclusions based on such relationships should be used with caution.

One of the major problems with the interpretation of size-age relationships is that there may be large individual variation, which cannot be accounted for without repeated recaptures of individuals (Magnusson, 2012). Growth of crocodilians tends to be deterministic, with negligible growth in large individuals (Wilkinson et al., 2016). This is reflected in the distinct asymptotes for the size-age relationships in Pantanal caimans. However, individual caimans differ greatly in their maximum potential sizes. Three females captured multiple times at nests varied imperceptibly in size among years, and two of those were captured three times, so it was not due to measurement error. Two of those females had snout-vent lengths (SVL) slightly larger than 80 cm, and one was slightly larger than 90 cm. Many females were captured at larger sizes, some of which had multiple recaptures at sizes that spanned the lengths of these three caimans. Therefore, asymptotic size is a characteristic of individuals rather than the species.

Females were found attending nests from 73 cm SVL and 9 years of age, but they continued to grow long after, so cessation of growth does not appear to be related to reproduction. One female was recorded breeding when 31 years old, so reproductive life span is greater than 20 years, and probably much longer, as it is in *A. mississippiensis* (Wilkinson et al., 2016). Larger nesting females tend to be older, and size has a positive effect on clutch mass, though this may be mediated through egg volume rather than clutch size (e.g. Larriera et al., 2004; Campos et al., 2008; 2015). Data on 13 known-age individuals indicates that age has a negative effect on clutch size independent of size, and the very weak relationship between age and size for those animals indicates that this is not because larger females tend to produce fewer larger eggs. This aspect needs further research, but the tendency may indicate the onset of reproductive senility.

Of the five individuals (four of which were male) that were recaptured when less than 8 years old, all had moved more than 10 km from their hatching site. In contrast,

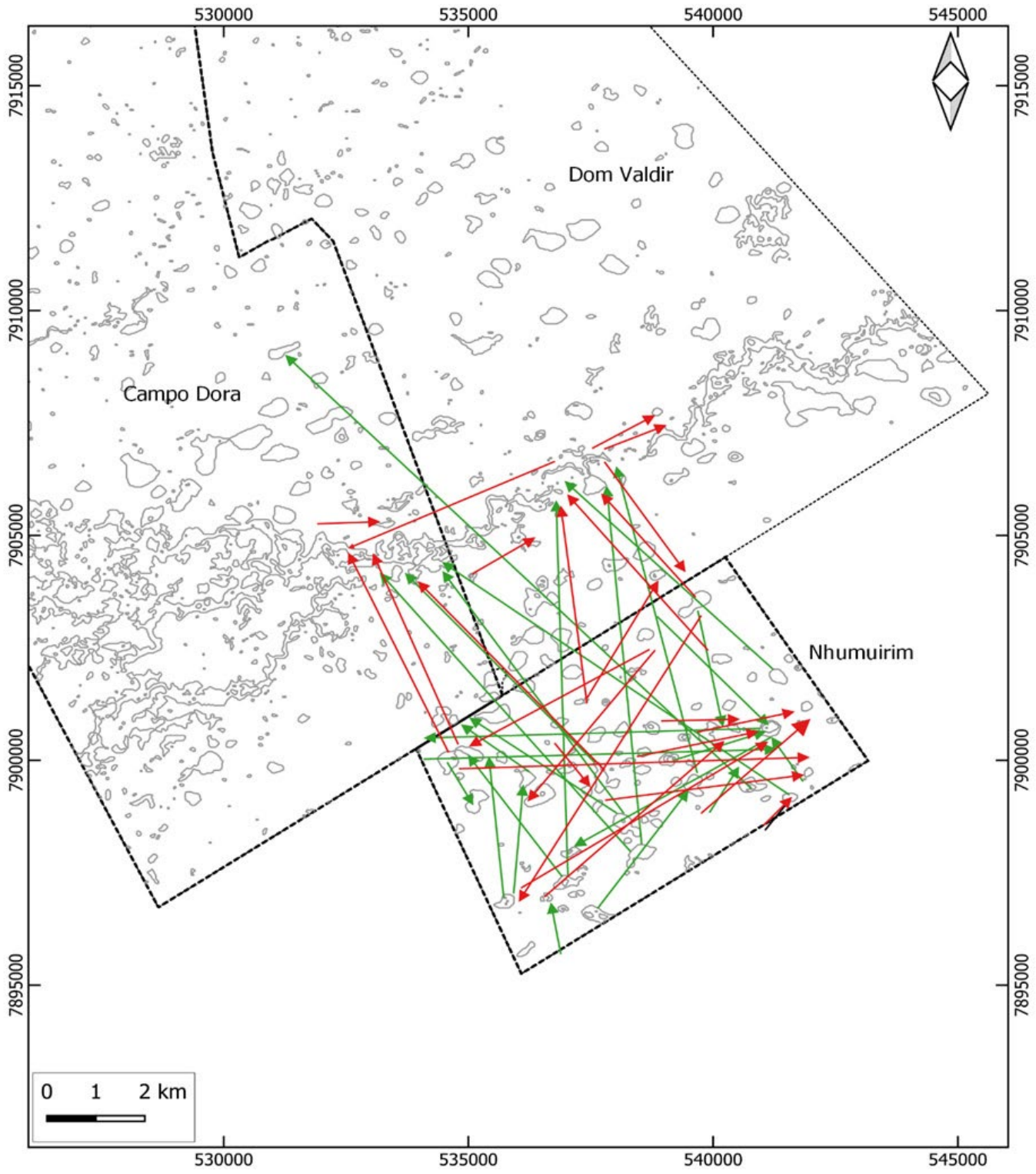

Figure 5. Map based on a Sentinel 2 satellite image of the study area (https://scihub.copernicus.eu/dhus/#/home). Polygons represent water bodies and the arrows indicate the capture and recapture sites from each caiman between 2007 and 2021. The displacements of male caimans are shown as green lines and the females as red lines.

most individuals recaptured when more than 10 years old had moved less than 10 km from the original nest site. This is consistent with the findings of Campos et al. (2006) that smaller animals move greater distances than larger individuals. The sharp cutoff in distances moved at about 10 km, especially for females, indicates that management units of these dimensions may be functionally autonomous, but movements of this order indicate that many or most individuals may not establish in the ranch in which they hatched, an important consideration for the definition of management units in the Pantanal (Campos et al., 2006).

Campos et al. (2006) reported a tendency for movement of animals away from nesting areas, which resulted in a net movement from Nhumirim Ranch in the lake area to the other ranches near the rivers. This tendency continued over the following 14 years, the animals showing two distinct

movement patterns; some moved within the ranches and others moved from Nhumirim Ranch to riverside areas on the other ranches. This indicates a possible distinction between the principal areas used for nesting and areas where most growth of juveniles occurs. The area of isolated lakes may be less suitable for the maintenance of adults, as indicated by the smaller sizes of females captured near nests on Nhumirim Ranch than on other ranches (Campos et al., 2006). This is also reflected in smaller clutch sizes on Nhumirim Ranch (Campos & Magnusson, 1995). Despite a general tendency for juveniles to move away from the area, there was a much greater proportion of juveniles on Nhumirim Ranch than on the ranches in the river area (Campos et al., 2006). Perhaps nest success or survivorship of hatchlings compensates for the apparent lower productivity of the area.

It has been suggested that for female Pantanal caimans the minimum age at reproduction was 13 years (Campos et al., 2014), this was based on the size-age relationships and known size at reproduction. However, the long-term data clearly show first reproduction can occur at 9 years old. This reinforces the warning by Campos et al. (2014) that size-age relationships are unreliable and that care should be exercised when making extrapolations based on them, especially estimates of age based on size.

The short- and long-term studies of the Pantanal caiman all point to heterogeneity in individual life-history characteristics, such as growth, asymptotic size and clutch size, combined with large-scale heterogeneity in movement patterns associated with habitat selection. The long potential reproductive life span may reduce the effect of this heterogeneity on density variation, and most of the fluctuations in nesting effort between 1985 and 2015 were not related to environmental variables (Campos et al., 2015), but generic population models for the whole Pantanal will probably be unrealistic and modeling of local situations will be necessary to understand fluctuations in caiman numbers. This is especially important because the Pantanal appears to be moving from a relatively stable wet period that started in the 1970s and lasted until 2018, and is now returning to a more variable and dryer regime that was typical of most of the period of monitoring from 1900 (Marengo et al., 2016; 2021).

We will discuss the relationship between size at first reproduction and asymptotic size only for females, as males are probably physiologically capable of breeding long before they can get access the reproductive females to sire offspring (Coutinho et al., 2001). Based on the ratio of the size of the smallest reproductive female and asymptotic size, female Pantanal caimans first breed at about 86% of maximum size. However, that does not take into account the fact that many females stop growing long before reaching this size. For them, size at first breeding would be a much larger fraction of maximum size, especially if they started nesting at sizes larger than the smallest female we recorded.

The issue of how to estimate maximum size is not trivial. Use of mean asymptotic size and mean size at first reproduction (Shine & Iverson, 1985), would lead to estimates of the ratio of size at reproduction to maximum size in the Pantanal caiman much larger than that reported for other reptiles. Based on large samples of nesting females the ratio of maximum and minimum recorded size, which is a much more conservative index than that of Shine & Iverson (1985), the ratio differs between *C. yacare* (0.77) and *C. crocodilus* from central Amazonia (0.72) (Campos et al., 2008). To determine whether crocodilians in general have ratios of size at first reproduction to maximum size greater than 0.7 will require data on more species, all with population parameters estimated in the same manner.

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RESEARCH ARTICLE

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Effects of prey-based and non-prey-based scent enrichment on two zoo-housed monitor lizards

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ABSTRACT – Environmental enrichment is a powerful tool in maintaining positive welfare for captive animals but investigation of this in reptiles has been limited. Monitor lizards are active, intelligent animals that represent high priority targets for enrichment in a captive setting, but more data are required to develop evidence-based recommendations and to understand variation in the responses to enrichment of both individuals and species. We exposed two monitor lizards, *Varanus cumingi* and *Varanaus macraei*, both adult females, to olfactory enrichment comprising prey-based and non-prey-based scent trails and then measured changes in activity and tongue-flicking versus a control. Randomisation analysis, employed to deal with small sample size, showed that the *V. cumingi* significantly increased both behaviours in response to both enrichment types, versus control, while the *V. macraei* responded significantly only to the prey-based scent for both behaviours. These findings provide an evidence-based case study demonstrating the potential effectiveness of enrichment for captive monitors, but also the need for context-specific evaluation of enrichment strategies to ensure maximal benefit for a given individual animal.

INTRODUCTION

Enrichment is an animal husbandry principle aiming to enhance the psychological and behavioural well-being of captive animals (Burghardt, 2013). This can take many distinct forms though a core principle is the encouragement of species-specific natural behaviour. Enrichment strategies may include behavioural management (especially animal training), provision of novel objects and rearranging enclosures, modified presentation of food and olfactory stimulation (Swaisgood & Shepardson, 2005). The effectiveness of these interventions is usually assessed by the measurement of behavioural indicators (Zieliński, 2023).

Reptiles are a taxon devoid of domesticated species and elements of the natural behaviour exhibited by many species are often not appropriately catered for in captivity (Waterman et al., 2021). This, in combination with life in what are, relative to natural habitats, small and homogenous enclosures, means that reptiles are often susceptible to stereotypical behaviours (Warwick et al., 2013). In particular, many of the challenges of life in the wild are not presented (Van Waeyenberge et al., 2018). The apparently sedentary lifestyle shown by many reptile species may have, in part, led to the misconception that they do not require complex habitats or enrichment to ensure appropriate welfare (Warwick et al., 2019; Getsy et al., 2022). In reality, reptiles do have complex cognitive demands that require enrichment in order to avoid potential welfare issues that may arise from under-stimulation in a captive environment (Hoehfurtner et al., 2021). Consequently, environmental enrichment for reptiles has been found to improve longevity, physical condition, problem solving behaviour and enhance their behavioural repertoire; it also reduce the occurrence of abnormal behaviours (Waterman et al., 2021).

Environmental enrichment is one of the most effective and appropriate ways to increase behavioural development and plasticity (Almli & Burghardt, 2006) and encourage species-specific behaviours (Bashaw et al., 2016). The positive intended impact of enrichment may be maximised through careful selection of enrichment stimuli to suit the preferred sensory modalities of species and individuals (e.g. Clark & King, 2008; Januszczak et al., 2016; Londono et al., 2018; Waterman et al., 2021). However, it must be noted that not all attempts at providing enrichment are successful. Rosier & Langkilde (2011) showed no effect of environmental enrichment on several measured behavioural and physiological indicators of *Sceloporus* lizards, Januszczak et al. (2016) show only certain indicators of improved welfare are affected by the provision of an enrichment feeding device, and Michaels et al. (2020) describe abnormal repetitive behaviours in a false water cobra *Hydrodynastes gigas* resistant to strategies employed to reduce them.

Members of the genus *Varanus* are active foragers with excellent eyesight. They are capable of rapid learning and problem solving (e.g. Manrod et al., 2008), so unsurprisingly there have been several enrichment studies on the monitors (Cooper et al., 2020; Waterman et al., 2021; reviewed by Howard & Freeman, 2022). However, research on these lizards is limited when compared to, for example, similar studies on mammals or birds; indeed, research of this kind is limited for all reptiles, representing <10% of zoo and aquarium-based research between 2008 and 2017 (Binding et al., 2020). Therefore, more data are required to properly inform practice in order to provide meaningful information

relevant to both more taxa and more enrichment types (Eagan, 2019). Given the small numbers of most monitor lizards maintained in zoological collections (Ziegler et al., 2016), an accumulation of small sample studies may be the most practical means of developing sufficient evidence to properly inform captive husbandry (Waterman et al., 2021). Monitor lizards are equipped with sensitive chemosensory organs and olfactory enrichment has been demonstrated to provide the most effective stimuli across several monitor species (Waterman et al., 2021). The present study adds to this literature by identifying the behavioural responses of two further species of monitor lizard in response to prey and non-prey scent-based olfactory enrichment.

MATERIALS & METHODS

Ethics

All methods were compliant with the British Herpetological Society Ethics Policy.

Animals and husbandry

Singly housed adult female *V. macraei* (9 years old, n = 1) and *V. cumingi* (9 years old, n = 1), both captive bred, were maintained in the herpetological collection at London Zoo. Husbandry followed best practice for the species, including heating, lighting and humidity management as deemed appropriate at the time. Both enclosures had themed, climbable walls, branching and both live and artificial plants. The enclosures measured 210 x 160 x 170 cm for *V. macraei* (snout-vent length [SVL] = 29 cm) and 540 x 220 x 230 cm for *V. cumingi* (SVL = 59 cm), length x width x height. Both animals had been historically exposed to a variety of enrichment without documentation.

Enrichment and data collection

An experimental period, comprising two five-weekday blocks either side of a weekend, was established for both the *V. cumingi* (January 2022) and *V. macraei* (November 2022). Both animals were fed twice weekly, resulting in four feeding days within the experimental period. Feed- and non-feed- days were randomly and equally allocated to either prey and non-prey scent trails. The scent trails were tracks of scented water within an enclosure, designed to stimulate olfactory senses and thereby activity and cognition. This type of enrichment is frequently employed in monitor and other groups of lizards in captivity (Loñdono et al., 2018; Waterman et al., 2021).

Both enrichment types were prepared by trained zookeepers. The scent object, a perforated frozen-thawed mouse for the prey scent and crushed basil leaves for the non-prey scent, was soaked in 1L of distilled water for one hour. The scent object was then removed, and the scented water decanted into a drinks bottle with a dripper cap. Bottles were sterilised between uses and a separate bottle was used for each scent type across observations to avoid cross contamination.

On each day, an observer (CS for *V. cumingi* and FN for *V. macraei*), who had been previously trained in observing the monitor lizards through practice sessions, watched the lizard in question from the public viewing window of the enclosure. Each observation session began with a 30-minute control phase, in which the lizard was observed prior to any enrichment. This was followed by an experimental phase in which the allocated enrichment scent was haphazardly dripped in a trail around the enclosure by a keeper. The *V. macraei* was present in the enclosure as the trail was laid. This was not the case with *V. cumingi* which, being a potentially hazardous animal, was recalled under trained behaviour to a locked compartment of the enclosure while the scent trail was laid. As soon as the trail was complete, typically in about 1 minute, the enclosure was closed and the locked den opened, giving the animal access to its enriched enclosure. The observer then monitored the lizard again for a further 30 minutes. The observer recorded two types of behaviour: activity was measured with a stopwatch as cumulative time, while tongue flicks were counted with a clicker-counter. A lizard was considered active when its centre of mass was in motion. A tongue flick was defined as a rapid protrusion and retraction of the forked tongue. Tongue flicking is the means by which monitor lizards engage their olfactory senses and is therefore a proxy for engagement with olfactory stimulation (Howard & Freeman, 2022; Loñdono et al., 2018; Waterman et al., 2021). Each observation session began at 11:00 h once lizards had had ample opportunity to thermoregulate and reach optimal body temperature for activity. On feed days, animals were fed at least two hours following the conclusion of the session.

The total time spent active and the total number of tongue flicks within each phase of each observation formed the dataset for analysis.

Statistical analysis

For both lizards, the alternative hypothesis was that enrichment would increase activity and tongue flicks compared with the baseline established during the control phase. Randomisation analysis was used to test the hypothesis. Randomisation is a valid strategy for analysing small- and single-n samples, where assumptions of traditional statistical analyses are violated (Dugard et al., 2012; Michaels et al., 2020). Paired analyses were used, with each control-experimental pair forming a datapoint, to control for daily variation in baseline behaviour. For each lizard, each scent-behaviour combination was analysed separately. All analyses were conducted in R 4.2.2 in RStudio 2023.03.1, using base R (R Core Team, 2022). For each analysis, a test statistic was calculated as the observed mean difference between control-experimental pairs. Treatment labels were then randomly shuffled 9,999 times and, after each shuffle, the simulated mean pairwise difference was again calculated. A seed was set prior to this stage to permit repeatability between code runs. The randomised simulations formed a frequency distribution of mean pairwise difference under the null hypothesis that there is no difference between enriched and control phases. The observed test statistic, forming the 10,000th observation, was then compared to this frequency distribution to derive a two-tailed p value as the proportion of absolute values greater than or equal to the test statistic. A one-tailed p value was then calculated as half the two-tailed value. A one-tailed p value was used due to the directionality of the alternative hypothesis.

Table 1. Mean and standard deviation (sd) duration of activity and counts of tongue flicks under control and enriched conditions for *Varanus macraei* and *Varanus cumingi* monitor lizards, with associated one-tailed p values derived from paired randomisation analyses. Significant p values are in bold.

Species	Behaviour (units)	Scent vs. control	Mean (sd) before enrichment	Mean (sd) after enrichment	One-tailed p
Varanus macraei	Activity (seconds)	Prey	424.7 (371.1)	1069.6 (577)	**0.031**
		Non-Prey	471.3 (427.6)	693.3 (579.2)	0.125
	Tongue flicks (count)	Prey	215 (188.4)	973.2 (552.2)	**0.032**
		Non-Prey	248 (230.8)	539 (538.9)	0.157
Varanus cumingi	Activity (seconds)	Prey	32.6 (59.4)	732.4 (231.8)	**0.031**
		Non-Prey	40 (54.8)	470.8 (182.9)	**0.032**
	Tongue flicks (count)	Prey	29 (47.8)	1766.4 (774.9)	**0.031**
		Non-Prey	27.6 (41.2)	1124.2 (1155.3)	**0.031**

We did not compare prey and non-prey scents in head-to-head comparisons due to substantial heterogeneity in baseline activity and tongue flicking. The paired analyses controlled for this but, given that the processes driving daily baseline variation could not be modelled, it was inappropriate to compare enrichment types in unpaired analyses. Relative efficacy of scent types can only be inferred qualitatively relative to the control condition.

RESULTS

Randomisation analysis showed that for both *V. macraei* and *V. cumingi*, prey-based scent trails were associated with a significant increase in both activity and tongue flicks (p = 0.031–0.032; Table 1; Fig. 1). Non-prey scent trails were associated with a significant increase in tongue flicks for *V. cumingi* (p = 0.031, Table 1; Fig. 1) and in activity (p = 0.032; Table 1; Fig. 1), but in neither behaviour for *V. macraei* (Table 1).

DISCUSSION

In this study, we evaluated the behavioural response of two zoo-housed species of monitor lizard to exposure of prey- and non-prey based scent enrichment. These forms of enrichment were chosen due to their suitability for use with varanid lizards, being the only group of lizards that use their tongues exclusively for sensory function (Smith, 1986; Murphy et al., 2019) and the ease of preparation and delivery to target recipients, which make scent-based enrichment an attractive strategy (Clark & King, 2008). Our results showed a difference between animals in responses, such that while the *V. cumingi* significantly increased target behaviours

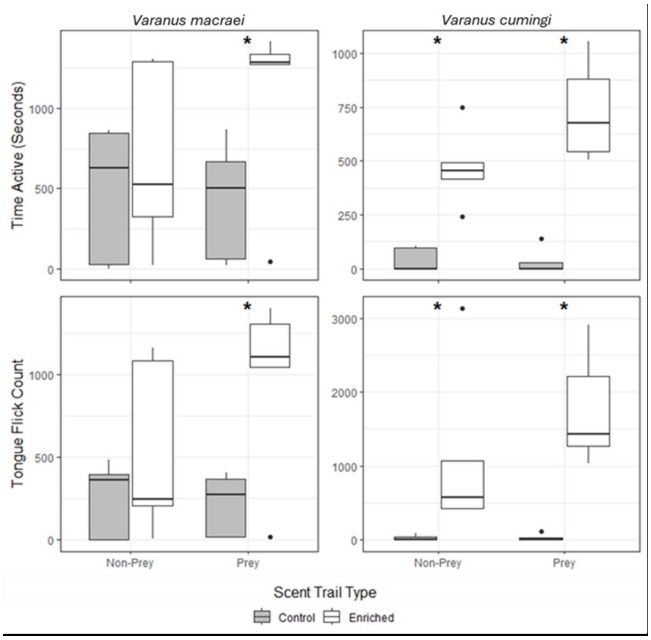

Figure 1. Boxplots of time spent active and tongue flick count before and after enrichment with prey nor non-prey scent trails in *Varanus macraei* and *Varanus cumingi* monitor lizards. Asterisks indicate a significant increase between control and enriched phases.

associated with physical and cognitive stimulation (activity and tongue-flicks) in response to both scent types, the *V. macraei* responded significantly only to the prey scent in terms of both behaviours, despite the basil scent being novel to both of these lizards.

These results, combined with those of other studies (Waterman et al., 2021; see review by Howard & Freeman, 2022) reinforce the utility and broad applicability of prey scents in enrichment strategies for monitor lizards. Under the prey-based scent enrichment, the *V. macraei* increased its average proportion of time spent active within the 30-minute observation window from approximately 25% to approximately 70%, while the *V. cumingi* increased from engaging in little to no activity on average to spending approximately 35% of the observed time active. Both species approximately tripled their counts of tongue flicking. The increase in both tongue flicking and activity strongly associates the behavioural impact of enrichment specifically with the presence of olfactory stimuli and improves health, welfare and physical fitness through increased movement, and likely cognitive stimulation through the processing of sensory information (Howard & Freeman, 2022). Given that obesity and other pathologies resulting partly from reduced activity levels are a concern in captive reptiles and, specifically in monitor lizards (Mitchell, 2007; Latney, 2016), the value of this increase in activity may be substantial.

While it is useful to extend data concerning response to prey scents to two as yet unstudied *Varanus* species, the behavioural response of predators to prey-based scents is unsurprising. The comparison of prey- and non-prey-based scents in this study was designed to investigate the use of scents not associated with food as a means to stimulate cognition and exploration beyond the elicitation of hunting behaviour, and of accessing a much broader array of

available scents to incorporate in enrichment strategies. The difference between animals in response, or lack thereof, to the non-prey scent illustrates that enrichment strategies may not be transferable between monitor lizard species or individuals. The reason for differences between individuals in this study is not clear and cannot be investigated with the current data given the conflation of individual and species; trends may be driven by aspects of personality, species adaptation, individual history and learning or other factors (Clark & King, 2008; Akhund-Zade, 2019; Waterman et al., 2021). However, from a pragmatic perspective, the data demonstrate that scents may be drawn from a wider palette for the benefit of the *V. cumingi* in this context but might be better limited to prey-based scents for the *V. macraei*. This reinforces the need to evaluate the impact of enrichment at an individual level (Clark & King, 2008). Further investigation of more scents, individuals and species would be beneficial, and such data collection may be easily accommodated in long-term husbandry. Additionally, a better understanding of the duration of response to enrichment would be useful to inform enrichment management, but due to limited resources this was not feasible in the present study.

The presented data are subject to limitations associated with small sample size and incomplete individual histories, which are typically unavoidable in the context of opportunistic data collection from small numbers of long-lived and uncommon animals forming part of a long-standing zoological assemblage (Waterman et al., 2021; Getsey et al., 2022). Consequently, while the within-study conclusions may be considered to be valid due to the use of appropriate statistical methods, it may not be robust to extrapolate the results of this study and assume transferability to other individuals of the included species. Rather, findings should be treated as a case study of potential responses to enrichment and combined with other data to provide accumulated insight into relevant trends and patterns that may collectively inform enrichment strategies for monitor lizards in zoos. To facilitate this, further investigation of enrichment for captive reptiles, even in the context of small sample size, is therefore encouraged.

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RESEARCH ARTICLE

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The effects of commercial diets on the growth of diamondback terrapins *Malaclemys terrapin* in head-start programmes

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ABSTRACT – Populations of diamondback terrapins *Malaclemys terrapin* are declining. Consequently, head-start programmes, in which hatchling terrapins are reared in captivity for 6–9 months and then released into their natural habitat, are needed to help stabilise wild populations. As a contribution to the development of optimal husbandry conditions for future generations of diamondback terrapins in head-start programmes, we examined the effects of two widely available commercial turtle foods (Reptomin® and Mazuri®) on the growth of juvenile terrapins over a period of 12 weeks. While terrapins did well on both diets, we show that terrapins consuming the Mazuri® diet had a significantly greater increase in mass and carapace length compared to terrapins on the Reptomin® diet.

INTRODUCTION

Diamondback terrapins *Malaclemys terrapin* are a brackish-water species found along the eastern and Gulf coasts of the United States. Considered a keystone predator regulating species that can degrade habitats such as the periwinkle snail *Littorinidae littorea* (Silliman & Bertness, 2002), they are also a bioindicator of environmental levels of mercury and other toxins (Basile et al., 2011; Blanvillain et al., 2007). Unfortunately, terrapin populations have suffered declines due to pressures from the food and pet trades, residential development, vehicle interactions and climate change (Gibbons et al., 2001; Rowe et al., 2020; Szerlag-Egger & McRobert, 2007; Wood, 1997; Woodland et al., 2017) and are listed as Vulnerable by the International Union for the Conservation of Nature (IUCN, 2024). To mitigate this decline, conservation efforts have been initiated to limit losses, including laws to limit collection, mandating crab-trap excluders, the installation of traffic barriers and the establishment of nesting sites.

As an additional conservation effort, there are head-start programmes that involve rearing hatchlings in captivity before releasing them into the wild (Gibbons et al., 2001; Haskell et al., 1996). In captivity, juvenile terrapins are not exposed to environmental stressors such as predators and so can direct more metabolic energy into growth (Koper & Brooks, 2000; Holliday et al., 2009). When released these larger terrapins may have a better chance of surviving the harsh conditions of the wild and will thus strengthen wild populations.

In 1989, Richard Stockton College (now Stockton University) initiated a long-term head-start programme for terrapins in southern New Jersey, USA (Herlands et al., 2004). This current study utilised hatchlings from this programme to examine the effects of diet on captive growth rates.

MATERIALS & METHODS

Hatchling collection

In August and September 2021, *M. terrapin* hatchlings were collected as part of a conservation project at the Long Beach Township Marine Field Station, NJ. The hatchlings were transported to the Biodiversity Laboratory at Saint Joseph's University, Philadelphia, Pennsylvania, USA, in 1.5L plastic containers with 2.5 cm depth of fresh water.

Housing

After arriving at SJU's Biodiversity Laboratory, hatchlings were randomly assorted into tanks, and marked with dots on their carapaces for identification purposes using non-toxic nail polish (L.A. Colors®, Fresh Paint® and Wet n Wild®). These markings were refreshed when needed, and no damage was observed to the carapace scutes from the markings.

All hatchlings were initially housed in glass aquaria with fresh water to become acclimated to the lab, and begin eating regularly. When the experiment began, hatchlings were moved into aquaria in groups of four. Water depths started at approximately 5 cm and were increased as the hatchlings grew. During the 12-week experimental period, a swimming space of 74,331 cm^3 (45.72 x 91.44 x 17.78 cm) was maintained in all tanks, with a basking area (bricks) of 869.35 cm^2. Lighting was provided by 60-watt incandescent bulbs with aluminium reflectors. Two lights were placed over the basking areas within each tank, and maintained on a 12:12 LD cycle, switching on at 08:00 h EST each day. UVB lighting was not provided during the trial period (see Discussion). Filtration was provided initially by small internal filters (Aqueon) but changed to external filters (Whisper) when the water depth was increased. Filter material was cleaned weekly and tank water was replaced biweekly to maintain water quality. Room and water temperature were maintained at 22–26 °C.

Table 1. Guaranteed analyses of the Reptomin® and Mazuri® diets

Guaranteed Analysis	Reptomin®	Mazuri®
Crude protein, min	42.5%	40.0%
Crude fat, min	8.5%	10.0%
Crude fibre, max	2.0%	5.00%
Moisture, max	8.0%	12.0%
Ash, max	Not reported	9.50%
Calcium (Ca), min	2.0%	1.85%
Calcium (Ca), max	Not reported	2.35%
Phosphorus (P), min	1.8%	1.00%
Sodium (Na), min	Not reported	0.55%
Vitamin E, min	Not reported	250 IU/kg
Ascorbic acid (vitamin C), min	100 mg/kg	Not reported

Table 2. Comparison of ingredients listed for the Reptomin® and Mazuri® diets

Reptomin ®	Reptomin ® & Mazuri ®	Mazuri ®
Wheat starch	Fresh meal	Ground corn
Corn flour	Dried yeast	Corn gluten meal
Shrimp meal	Dehulled soybean meal	Chicken meal
Wheat gluten	L-Ascorbyl-2-Polyphosphate (Vitamin C)	Porcine meat and bone meal
Potato protein	D-Calcium	Fish oil
Soybean oil	Pantothenate	Salt
Monobasic calcium	A-Tocopherol- Acetate (Vitamin E)	Calcium iodate
Phosphate	Thiamine mononitrate (B1)	Biotin
L-Lysine monohydrochloride	Pyridoxine	Choline chloride
Lecithin	Hydrochloride (B6)	Magnesium oxide
Algae meal ascorbic acid (Vitamin C)	Menadione sodium	Riboflavin supplement
D-Calcium pantothenate	Bisulfite (Vitamin K)	Vitamin A acetate
Vitamin A palmitate	Zinc sulfate	Zinc oxide
Manganese sulfate monohydrate	Cholecalciferol (D3) (Vitamin D3 supplement)	Cobalt carbonate
Ferrous sulfate monohydrate	-	Nicotinic acid
Cobalt acetate	-	Copper sulfate
Food Colour: Beta-carotene, blue 2 lake, and yellow lake	-	DL-Methionine sodium selenite

Diet protocol

In the Autumn of 2021, 20 hatchlings were divided into two diet groups. Hatchlings were divided randomly based on the mixing of two different clutches to minimise clutch effect. One group (8 terrapins, housed in two tanks, in groups of four) was fed Reptomin® Floating Food Sticks (Tetra) while the other (12 terrapins, housed in three tanks, in groups of four) was fed Aquatic Turtle Diet (Mazuri®). Table 1 shows the nutritional content of each food and Table 2 provides a comparison of the composition of both feeds. Food was measured before feeding with a top-loading electronic scale (Ohaus CS 200; + 0.1 g) and provided to each group Monday–Saturday, ad libitum. After allowing the hatchlings to eat for an hour, the excess food was removed by siphoning the water through netting and allowing it to dry. The dry food was weighed the next day. Each hatchling was measured biweekly with a digital caliper (+ 0.1 mm) for carapace straight length (CSL); the measurement from the nuchal to the pygal scute of the carapace in a straight line. Mass was measured biweekly.

Statistical methods

CSL and mass were compared between diet groups using 2-tailed independent sample t-tests (IBM SPSS Statistics Subscription for Microsoft Windows 64-bit). Tests were run to ensure the groups met the assumptions for heteroskedasticity (Levene's Test) and normality (Shapiro-Wilk Test). Data were found to be normal in all tests, however the change in carapace and mass showed significant differences in variance so that the two-sample t-test for unequal variance was required when comparing treatment groups for both parameters. To account for the family-wise error rate resulting from multiple tests of the same treatments for different hypotheses (parameters) we used the Bonferroni p value correction for multiple tests (α/n where alpha is the chosen significance level and n is the number of hypotheses tested) to determine significance of each test. Finally, the same independent sample t-test was used to compare the amount of food consumed in both treatments.

RESULTS

There were no statistically significant differences with respect to initial mass across terrapins from each diet group (Reptomin: 45.8 ± 2.87 g vs. Mazuri: 50.02 ± 5.6 g; t-test for equal variance, $t_{15.84} = -0.68$, $p = 0.508$). Likewise there were no significant differences with respect to initial CSL across terrapins from each diet group (Reptomin: 59.6 ± 1.52 mm vs. Mazuri: 59.33 ± 2.7 mm, t-test for equal variance, $t_{16.54} = 0.09$, $p = 0.926$).

With respect to growth, terrapins that were fed Mazuri® showed a significantly greater change in mass than terrapins fed Reptomin® (Reptomin: 64.8 ± 2.14 g vs. Mazuri: 98.0 ± 5.95 g, t-test for equal variance, $t_{13.7} = -5.26$, $p < 0.001$). Terrapins that were fed Mazuri® also showed a significantly greater change in CSL than terrapins fed Reptomin® (Reptomin: 21.7 ± 1.03 mm vs. Mazuri: 28.9 ± 0.91 mm, t-test for equal variance, $t_{16.1} = -5.23$, $p < 0.001$).

There was no statistically significant difference in the amount of food consumed by terrapins in the two diet groups (Reptomin: 25.6 g ± 2.0 vs. Mazuri: 34.0 g ± 5.54. independent samples t-test, $t_3 = -1.147$, $p = 0.335$).

DISCUSSION

This study presents a comparison of two commercial turtle foods (Reptomin® and Mazuri®), utilised in a diamondback terrapin head-start programme. During a 12-week period (within the 6-9 months the terrapins were maintained in captivity), we determined that Mazuri® led to a significantly greater increase in both CSL and mass.

One potential limitation to these findings was the use of incandescent lighting, rather than lights providing UVB radiation that are essential to vitamin D3 synthesis in reptiles (see Acierno et al., 2006). Vitamin D3, in turn, is crucial to calcium metabolism. In captive settings reptiles without UVB lighting may require dietary supplementation of calcium and vitamin D3. Analysis of the Reptomin® and Mazuri® diets (Tables 1 and 2) show that they contain similar amounts of calcium, and both contain vitamin D3 (although the amounts are not specified). During our study we did not note any clinical signs of D3 or calcium deficiency (such as deformed or soft shells), but we recognise this as a limitation and plan to use UVB lights in the next phase of this study.

Another potential limitation was housing our terrapins in groups of four, which may lead to competition for food and space, and the possibility of aggression. Our stocking density was 18,582.8 cm^3 swimming space/terrapin, and 217.34 cm^2 basking space/terrapin. We regularly examined each terrapin, and found no signs of aggression (wounds), and excess food was collected after each feeding, assuring that each terrapin had enough to eat.

Reptomin® has a higher percentage of crude protein, while Mazuri® has a higher percentage of crude fat and crude fibre. In terms of protein sources, both diets have fish and dehulled soybean meal. Mazuri® also includes chicken meal, porcine meat, bone meal and fish oil, while Reptomin® includes shrimp meal and potato protein. It has been shown that juvenile slider turtles *Trachemys scripta* fed diets with 25% or 40% crude protein grew significantly faster than turtles receiving a diet with only 10% crude protein (Avery et al., 1993). However, the diets used in our study both had at least 40% crude protein. Another noteworthy ingredient was biotin, which has been shown to increase keratin production, possibly affecting the growth of hair, bone and shell (da Silva et al., 2010). Although we did not measure the levels of biotin (only listed as an ingredient in the Mazuri® diet) within the hatchling's shells, it is possible that this improved CSL growth for the Mazuri® group.

While head-start programmes have been shown to help terrapins avoid many of the issues they face during early life stages, the approach is controversial. There is concern that head-start hatchlings may outcompete wild hatchlings because of their enhanced size. Since size is associated with age (Gibbons & Semlitsch, 1982; Haskell et al., 1996) there are additional concerns of ageing hatchlings faster. In fact, hatchlings in head-start programmes have been noted to be the size of 2–3-year-old juveniles in the wild (Holliday et al., 2009; Rowe, 2018; Ashley et al., 2021). Successful head-start terrapins could, in theory, go on to produce the next generation faster than terrapins that were not in head-start programmes. Growing at a faster rate may result in the hatchlings being sexually mature earlier which raises concerns of limiting genetic diversity, which can result in inbreeding, and other genetic complications (Dodd & Seigel, 1991; Frankham, 2005).

Comparisons of captive growth rates for terrapins, while important, can be limited by differences in experimental methodologies. For instance, Holliday et al. (2009) studying *M. terrapin* show notable differences in final terrapin sizes when compared to our study. However, in their study, the terrapin hatchlings where exposed to toxins (PCB) and/or different levels of salinity, their treatments began eight months after terrapin hatchlings emerged from eggs, their terrapins were housed individually, and fed a different diet (frozen brine shrimp). Our terrapins were raised in groups of four, in fresh water and under incandescent lights. It is likely that these differences in methodology are responsible for the differences in terrapin sizes across the two studies.

In summary, despite their potential disadvantages, head-start programmes may be one of the best tools to help stabilise declining populations of turtles. The adoption of better husbandry techniques, including potentially better diets as described in this study, can help to improve the efficiency of head-start programmes.

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SHORT NOTE

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Snakes on the menu of free-range chickens: Incidents in smallholder traditional poultry farming systems in Greek rural areas

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INTRODUCTION

Snakes, as a taxonomically diverse group of reptiles, face predation risks from a wide range of vertebrate and invertebrate species (Schalk & Cove, 2018). Concurrently, the anthropogenic impact on snake populations, despite deviating from natural predation processes, is conspicuously widespread, evident through both direct killing, whether intentional (Larson et al., 2024) or unintentional (Zevgolis et al., 2023).

Beyond these threats, domesticated vertebrates with access to a wide range of food sources in their natural environment, such as the domestic cat, can also contribute to snake mortality (Dickman & Newsome, 2015). Another noteworthy domesticated vertebrate is the chicken *Gallus domesticus* L., 1758. Originating from the jungle fowl lineage (Lawal & Hanotte, 2021) this avian species has undergone significant dietary transformations since its ancestral days. In contemporary settings, domestic chickens' dietary habits are influenced by their living conditions and housing system. Compared to the predominantly plant-based diet of cereal grains, animal-based protein sources, soy and vegetable residues consumed by chickens in barns or industrial farming systems (Coletta et al., 2012; Bryden et al., 2021), free-range chickens exhibit a significantly more diverse diet (Singh & Cowieson, 2013), which can include seeds, fresh leaves and small stems from a wide variety of flora (Dal Bosco et al., 2014), as well as organic household waste. Additionally, free-range chickens adapt their diets to include a broad spectrum of fauna, including a substantial intake of invertebrates such as arthropods and earthworms (Clark & Gage, 1996) and vertebrates such as snakes.

Despite anecdotal reports suggesting such interactions, a lack of formal documentation of snake consumption by domestic chickens, particularly within free-range systems, has limited our understanding of this potential dietary behaviour. In this study, we provide six documented cases within the confines of smallholder traditional poultry farming systems.

MATERIALS & METHODS

Our study formed a component of the Amaltheia Network research programme to assess the losses and conservation opportunities of the indigenous productive and working animals in Greece. From 2012 to 2022 we investigated multiple smallholder traditional poultry farming systems across diverse regions in both the mainland and islands. Using a combination of photographic and observational methods, we documented predation events involving domestic chickens and snakes. Direct field observations were made during routine visits to poultry farms, where each predation event was recorded by documenting the date, location, species involved (both chicken and snake) and the observed behaviour of the chicken during the event. All field observations adhered to ethical guidelines for animal research and welfare, ensuring minimal disturbance to the natural behaviour of the animals under study.

RESULTS

Natrix natrix

On 26 August 2012, in a smallholder local bantam farm in the village of Lianokladi (Fthiotida), mainland Greece, we recorded a direct observation of predatory behaviour by a domestic chicken. The individual, a young female bantam, was observed preying upon a juvenile grass snake *Natrix natrix* in a grassy area using its beak (Fig. 1A–C). Upon approaching the scene, we observed the bantam seize the snake in its beak and retreat a short distance before stopping. The bantam then proceeded to subdue and kill the snake with several forceful pecks before initiating consumption. The breeding of poultry followed a traditional free-range, semi-enclosed farming method, with the birds belonging to the native Greek population of Aegina Bantam.

On 23 May 2014, in Proastio (Karditsa), mainland Greece, a hen was observed having killed and consumed a juvenile grass snake *N. natrix*, which it quickly swallowed when approached further. The poultry farming followed a

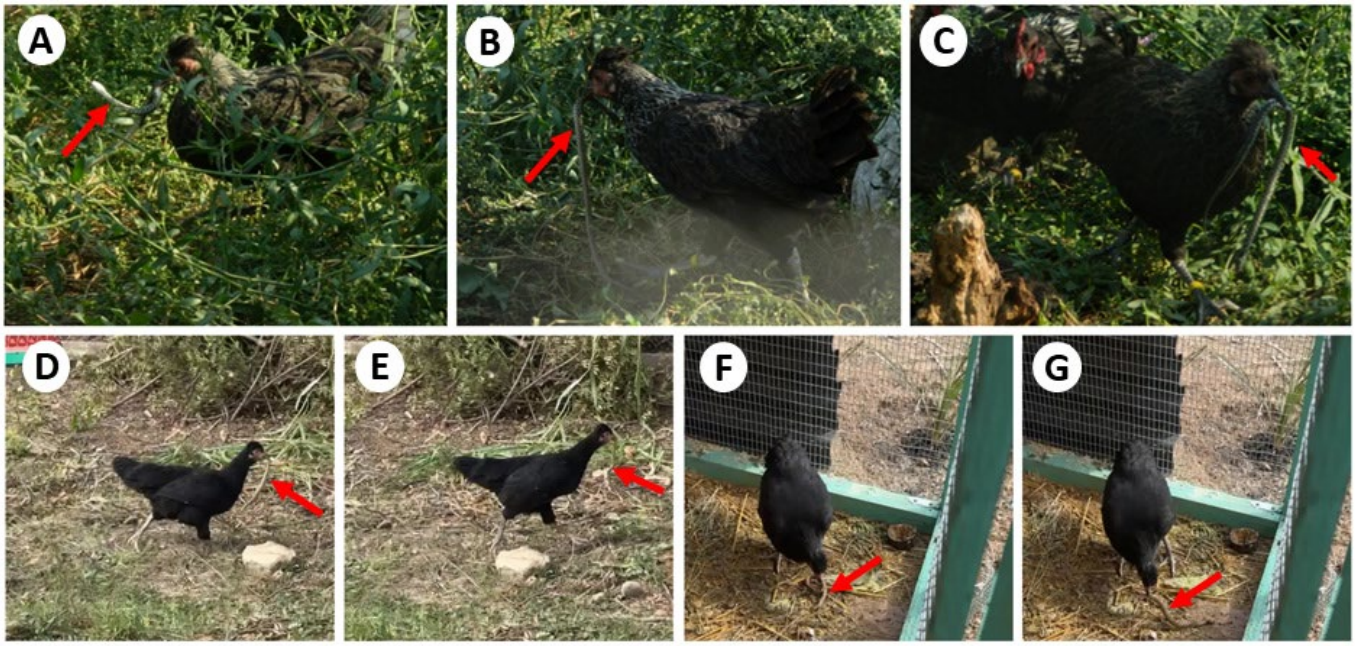

Figure 1. Sequential photographs of predatory behaviour by domestic chickens capturing- **A.–C.** A juvenile grass snake *Natrix natrix* in Lianokladi (Fthiotida), and **D.–G.** A juvenile nose-horned viper *Vipera ammodytes* in Rafina, Attica, mainland Greece. Red arrows indicate the positions of the snakes.

traditional free-range method within a large enclosed area with dense grassy vegetation, located within the settlement. The birds belonged to the local indigenous population of Thessaly Plain Chicken, which is bred in many rural villages, primarily in western Thessaly.

Malpolon insignitus

On 22 April 2013, in Megalo Evydrio (Larissa), mainland Greece, a hen was observed consuming a juvenile eastern Montpellier snake *Malpolon insignitus*, which likely had been killed moments before, as the snake still exhibited nervous reactions. Poultry farming followed a traditional free-range method, situated in an unfenced area near agropastoral facilities close to the settlement. The birds on the farm were hybrids of commercial poultry breeds as well as individuals belonging to the local native population known as the Thessaly Plain Chicken.

Dolichophis caspius

On 5 May 2013, in Sykia (Elassona, Larissa), mainland Greece, a hen was observed running with a small snake in its beak. The snake was alive and attempting to escape. When the hen stopped, it dropped the snake to the ground and attempted to kill it by striking it with its beak. An attempt to approach the hen revealed that the snake was a juvenile Caspian whipsnake *Dolichophis caspius*. The hen retrieved its prey and disappeared into a cluster of brambles *Rubus fruticosus*. The poultry farming followed a traditional free-range method, situated in an unfenced area on the outskirts of the settlement. The birds belonged to the local indigenous population of Potamia Chicken, which is bred in the area of Potamia, Elassona.

Xerotyphlops vermicularis

On 7 March 2019, in the broader area of Antissa, Lesvos, insular Greece, within a setting with free-ranging local chickens, a hen was observed executing a similar predatory behaviour. In this instance, the prey was a European blind snake *Xerotyphlops vermicularis*, and the hen employed the same procedure of killing and subsequent consumption.

Vipera ammodytes

On 27 February 2024, in the area of Rafina, Attica, mainland Greece, another instance of similar behaviour was observed at a farm raising local line chickens. A hen was observed killing and consuming a juvenile nose-horned viper *Vipera ammodytes* (Fig. 1D–G). Notably, the method employed by the hen in this case mirrored the behaviour observed in the other five incidents.

DISCUSSION

These documented instances of domestic chickens actively preying upon and consuming five different snake species (*N. natrix, M. insignitus, D. caspius, X. vermicularis* and *V. ammodytes*), present a noteworthy addition to our knowledge of predation dynamics within small-scale traditional farms, highlighting the diverse diet of free-range poultry. Moreover, the observed resilience of domestic chickens to the defensive strategies employed by the consumed snakes prompts intriguing questions about the coevolutionary dynamics between prey and predator within these ecosystems. For instance, while some snakes utilise foul odour and feigned death (e.g. *N. natrix*) (Hagman et al., 2015) or rely on bite-and-release tactics to escape, stand up, hiss and even pursue their attackers (e.g. *Malpolon* spp.) (Martín-Sierra et al.,

2018; Ballouard et al., 2022) to evade predation, chickens clearly have adaptive mechanisms to overcome these defences. Similarly, the jumping at the attacker, hissing, biting and tail waving of snakes such as *D. caspius* (Bjelica et al., 2024), or the venomous defence of *V. ammodytes* (Paolino et al., 2020), is likely not successful against the predatory prowess of chickens, at least in the instances we observed. It is noteworthy that, in most cases, the chickens involved were local populations from old traditional lines specific to each respective region, especially in Thessaly area.

The observed predation events contribute to our broader understanding of the intricate predator-prey dynamics that shape local ecosystems and the intricate relationships between domesticated animals and their environments. Further research, employing methods such as questionnaires, hold promise in revealing the frequency with which snakes or other reptiles are consumed by domestic chickens, to give a more nuanced understanding of their dietary patterns and ecological impact. Future research should strive to unravel the broader ecological implications of these findings, delving into the multifaceted interactions within rural landscapes and exploring potential parallels with issues related to super-predators, such as the domestic cat.

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SHORT COMMUNICATION

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First confirmed record of the snake genus *Xenodon* from Sierra Nevada de Santa Marta, Colombia, supports the morphological distinctiveness of *Xenodon angustirostris* and *Xenodon rabdocephalus*

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The Sierra Nevada de Santa Marta (SNSM) in northern Colombia harbours a high proportion of the endemic biota of northern South America. It is an isolated mountain massif with a broad altitudinal gradient (0–5,800 m a.s.l) giving it wide variations in climatic and ecological conditions encompassing páramo, montane forest, xerophytic forest, and rainforest. Lower elevation dry forests, xeric shrublands and wide alluvial plains isolate the SNSM from other Andean wet forests (Rangel-Ch et al., 1997; Sánchez-Pacheco et al., 2018). Most previous herpetological studies of the SNSM have focused on the ecosystems/species of the western versant of this mountain massif so leaving the eastern versant poorly explored. However, the signing of the peace agreement in Colombia has allowed the return of field scientists to vast rural areas, including the SNSM, that were inaccessible due to the internal armed conflict. Since the peace agreement, biological recording at the National Biodiversity System of Colombia has spiked (Salazar et al., 2021; 2022).

Thirty four snake species are known to occur in the SNSM (Rivas et al., 2021), of which 17 taxa have known distributions on the eastern versant (Rodríguez-Mahecha et al., 2008; Meza-Joya, 2015). Although there are records for dipsadid snakes of the genus *Xenodon* in the SNSM, *Xenodon rabdocephalus* (Carvajal-Cogollo et al., 2020) and *Xenodon severus* (Rivas et al., 2021), and two further claims about the occurrence of *Xenodon* spp near the SNSM (Blanco-Torres et al., 2013; Blanco-Torres & Renjifo, 2014), these are all unsubstantiated as no voucher specimens or data on specific localities were registered in biological collections.

The available geographical records of *Xenodon* nearest to the SNSM with specific localities and voucher specimens are from Municipio Sabanas de San Ángel, Departamento de Magdalena (*X. rabdocephalus*; Angarita-M et al., 2015) and Serranía del Perijá (*Xenodon angustirostris*; Angarita-Sierra & Manco-Jaraba, 2023) (Fig. 1). We document the first confirmed record of *Xenodon* from the SNSM based on two specimens collected from the eastern versant of this isolated mountain massif. On 16 January 2024 at 09:00 h PAL found a freshly killed male *Xenodon* during his routine farm duties at the settlement of Potrerito, Corregimiento La Junta, Municipio San Juan del Cesar, Departamento de La Guajira, Colombia (10,80638889 °N, -73,22361111 °W, WGS84; 685 m a.s.l; Fig. 1), and on 15 March 2024 at 08:40 h found a conspecific female. Both specimens were collected and fixed following the procedures described by Pisani (1973), and exhibit similar colour pattern, scutellation, and head-scales

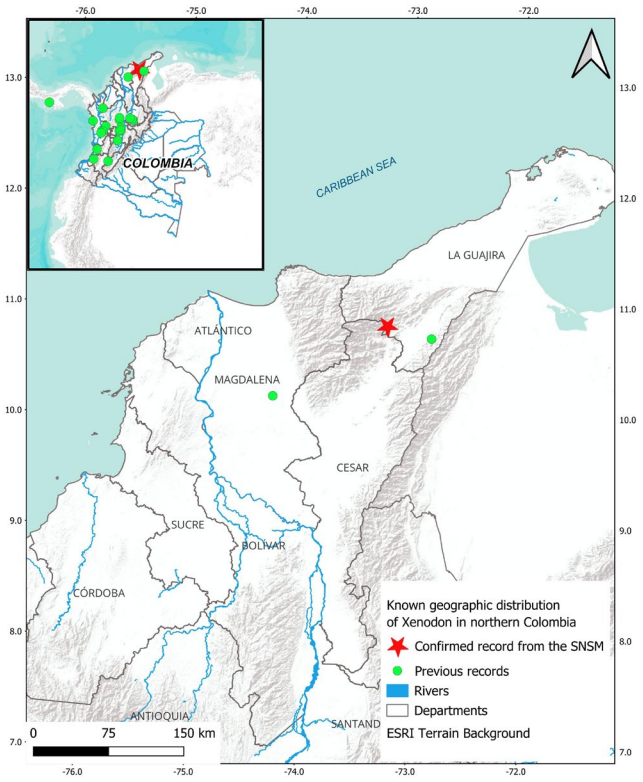

Figure 1. Geographical distribution of the snake genus *Xenodon* in northern Colombia. Green dots depict previous substantiated records (Angarita-M et al., 2015; Angarita-Sierra & Manco-Jaraba, 2023). Red star indicates the first confirmed record of *Xenodon* (*X. rabdocephalus* sensu Myers & McDowell [2014]) from the Sierra Nevada de Santa Marta.

Figure 2. *Xenodon rabdocephalus* from Potrerito, San Juan del Cesar, La Guajira, Sierra Nevada de Santa Marta, Colombia and *Xenodon angustirostris* from Corraleja, San Juan del Cesar, La Guajira, Serranía del Perijá, Colombia. Colour pattern in life of **A.** *X. angustirostris* (male, INSZ 281) and **B.** *X. rabdocephalus* (female, INSZ 247). **C.** Dorsal and **D.** Ventral views of *X. rabdocephalus* (male, INSZ 246). **E.** Dorsal and **F.** Ventral views of *Xenodon angustirostris* (male, INSZ 281). Black bars represent 10 mm.

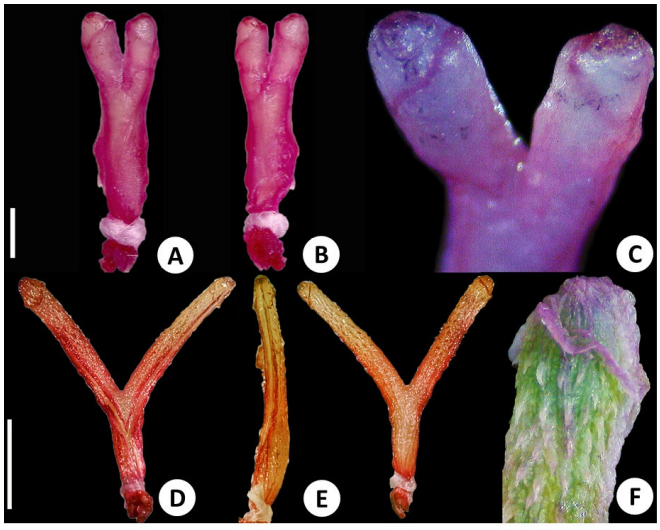

Figure 3. Hemipenial morphology of *Xenodon* spp: *Xenodon angustirostris* (INSZ 281)- **A.** Sulcate and **B.** Asulcate views, **C.** Apices of lobes showing the absence of apical discs with free edges. *Xenodon rabdocephalus* (INSZ 246)- **D.** Sulcate and **E.** Asulcate views, **F.** Apices of lobes showing the presence of apical discs with free edges. White bars represent 10 mm.

Table 1. Meristic and morphometric (mm) data of the specimens of *Xenodon rabdocephalus* (INSZ 246 and 247) from the Sierra Nevada de Santa Marta, Colombia. Abbreviations: snout-vent length (SVL), tail length (TL) and total length (TTL).

Character	INSZ 246 (male)	INSZ 247 (female)
SVL	440	727
TL	86	100
TTL	526	827
TL/SVL	19.5%	13.8%
Ventral scales	133	145
Subcaudal scales	44+spine	40+spine
Dorsal scale rows	19/19/17	19/19/17
Supralabial scales	7/7	7/8
Infralabial scale	9/9	9/8
Preocular	2/2	1/1
Loreal	1/1	1/2
Temporal formula	1+2/1+2	1+2/1+2
Head length	20.85	30.16
Head width	17.17	22.77
Parietal scale length	7.80	10.81
Parietal scale width	4.87	7.11
Frontal scale length	5.80	7.84
Frontal scale width	4.65	6.65
Prefrontal scale length	2.44	2.98
Prefrontal scale width	3.27	3.66
Internasal scale length	2.47	2.82
Internasal scale width	2.66	3.38
Eye diameter	4.05	7.18
First temporal scale length	5.14	8.50
First temporal scale high	1.49	3.02
Interorbital length	8.41	12.36
Rostro-orbital length	5.01	11.23
Naso-orbital length	5.68	8.59
Hemipenis length	12th subcaudal scales	N/A

measurements (Table 1, Fig. 2). Hemipenial eversion followed Pesantes (1994). Based on hemipenial morphology, we identified the male as *X. rabdocephalus* since it possesses the distinctive characteristics described by Myers & McDowell (2014), such as hemipenial lobes deeply divided (>50% of the hemipenial body), sulcus spermaticus centrifugal and strongly grooved, each branch extending onto the tip of lobe, intersulcar area nude, apices of lobes ornamented with smooth calices and presence of apical discs with free edges, and hemipenial body with medium-sized spines arranged in longitudinal rows (Fig. 3). The specimens were deposited in the Colección Zoológica del Instituto Nacional de Salud (INSZ, Bogotá) under the numbers INSZ 246 (male) and 247 (female). The new locality of *X. rabdocephalus* is located 139 km north-east from the record of this taxon nearest to the SNSM (Angarita-M et al., 2015) and 47 km west from the report of *Xenodon* nearest to the SNSM (Angarita-Sierra &

Manco-Jaraba, 2023), and represents the highest altitude at which *X. rabdocephalus* has been recorded.

Based on hemipenial morphology, Myers & McDowell (2014) tentatively resurrected *X. angustirostris* from synonymy with *X. rabdocephalus* for Central American and western Colombian populations but cautioned "...in applying the name *angustirostris* until comparative hemipenial and other data can be accrued from populations throughout western Colombia and especially Middle America". Recently, Angarita-Sierra & Manco-Jaraba (2023) reported the occurrence of *X. angustirostris* in the Serranía del Perijá, northern Colombia. Although the specimen described by them (INSZ 281; Fig. 3A–C) is not from western Colombia, it is in general agreement with the hemipenial characteristics attributable to *X. angustirostris* sensu Myers & McDowell (2014). Similarly, our newly collected male (INSZ 246; Fig. 3 D–F) possesses the distinctive hemipenial characteristics of *X. rabdocephalus* as described by Myers & McDowell (2014). Specifically, it differs from Angarita-Sierra & Manco-Jaraba's (2023) male *X. angustirostris* (INSZ 281) by having hemipenial lobes deeply divided (vs. moderately divided), sulcus spermaticus strongly grooved (vs. moderately grooved), apices of lobes ornamented with smooth calices and the presence of apical discs with free edges (vs. nude, lacking apical discs), and hemipenial body with medium-sized spines arranged in longitudinal rows (vs. with several medium-sized spines positioned laterally on each side, lacking spines arrangement in longitudinal rows) (Fig. 3). In addition to differences in hemipenial morphology, both specimens of *X. rabdocephalus* also differ from that of *X. angustirostris* in having dorsal scale formula 19/19/17 (vs. 21/21/17), 9/9 (male) and 9/8 (female) supralabial scales (vs. 10/11), 3rd supralabial scale entering into the eye orbit (vs. 4th and 5th supralabial scales entering into the eye orbit), temporal scale formula 1+2 (vs. 1+3), and ventral surface of the body cream (vs. dark, Fig. 2). Therefore, comparison between these Colombian specimens supports Myers & McDowell's (2014) hypothesis that the morphological distinctiveness of *X. angustirostris* and *X. rabdocephalus* warrants the resurrection of the former from synonymy with the latter. This work expands our knowledge of the distribution and morphology of *Xenodon* spp, which are rare dipsadid snakes poorly represented in biological collections.

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A case of melanism in the horseshoe whip snake *Hemorrhois hippocrepis* from Algeria

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Snakes of the western Palearctic display a broad spectrum of phenotypic variation, sometimes mimicking other distinct species (Jablonski et al., 2017; 2023). This resemblance can lead to misidentification by local people (Beddek, 2017; Bakhouche & Escoriza, 2017). *Hemorrhois hippocrepis* (Linnaeus, 1758) has a predominantly west-Mediterranean distribution, spanning North Africa, the Iberian Peninsula, and the islands of Ibiza, Formentera, Sardinia, Pantelleria and Zembra where it was introduced (Mateo et al., 2011; Faraone et al., 2020). The dorsal colouration of *H. hippocrepis* is quite variable across its geographic range, where its ground colour can have diverse hues. A form of partial melanism, where the overall dorsal colour is blackish except for small light dots that surround the elements of the pattern, is fairly common in this species, especially in some of its eastern populations (Bruno & Hotz, 1976; Cattaneo, 1985). This dark morph appears to be purely ontogenetic, as it is exclusively present in adults, whereas juveniles are typically light coloured (Fig. 1) (Cattaneo, 1985; Feriche, 2017). Partially or totally melanistic juveniles are quite rare in *H. hippocrepis* (Garcia-Marsà et al., 2015), as is the case in juveniles and adults in congeneric species (Tuniyev et al., 1997; Jablonski & Soran, 2023). Here, we describe for the first time a melanistic juvenile *H. hippocrepis* from its African geographic range.

As part of an investigation into people's perception of snakes, we recovered the individuals killed by the local population in Algiers region. After examination, we identified 13 individuals of *H. hippocrepis* and six *Natrix maura*. In the same context, on January 2024, we found a black, small snake at the USTHB university campus in the locality of Bab Ezzouar (36° 42'47" N, 3° 10'45" E). The snake was collected for further examination, due to its unusual colouration. The observation took place in a habitat that was formerly a marshland but has since been heavily urbanised.

Upon further morphological examination, the snake was determined as *H. hippocrepis*. The specimen had a snout-vent length of 298.1 mm and tail length of 76.9 mm. Consistent with our specific determination (Feriche, 2017) the specimen had the following head scalation characters (right side): 10 supralabials, 8 infralabials, 1 preocular, 2 postoculars, 3 suboculars, 1 loreal, 2 nasals, 3 anterior temporals and 3 posterior temporals. Based on its size and according to

Figure 1. Recurrent colour patterns of *Hemorrhois hippocrepis* from the population of Pantelleria (Italy) – **A.** Typical juvenile, and **B.** Dark morph adult

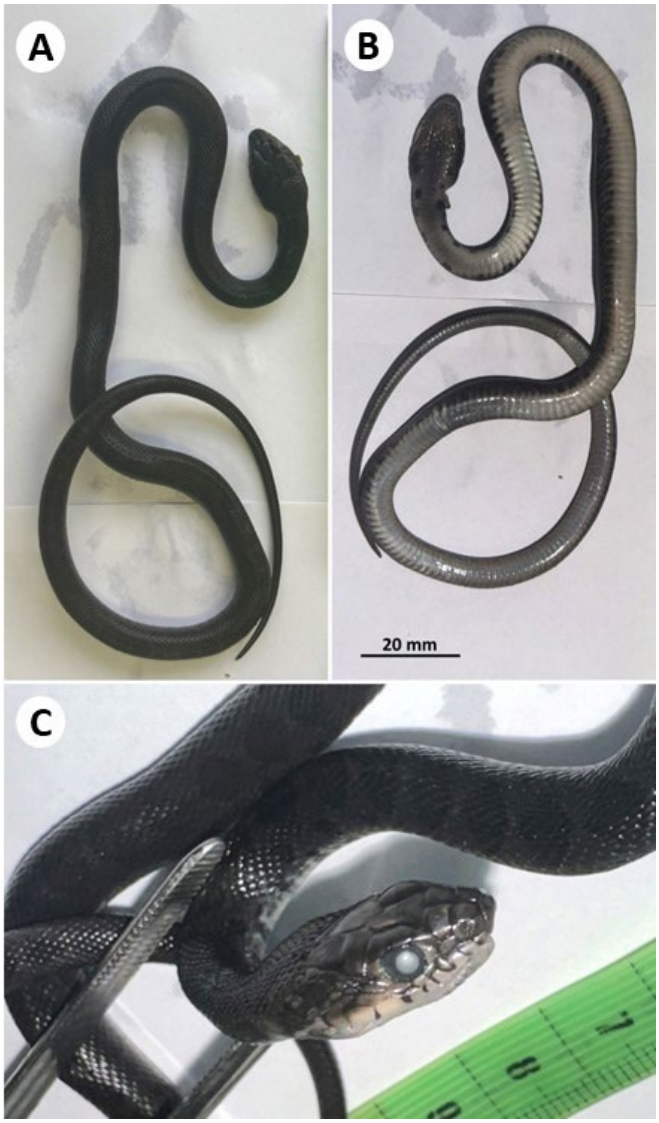

Figure 2. Melanistic juvenile *Hemorrhois hippocrepis* from Bab Ezzouar, Algeria - **A.** Dorsal view, **B.** Ventral view, and **C.** Head and dorsal pattern detail

available data (Cattaneo, 1985; Pleguezuelos & Feriche, 1999), our specimen is likely a yearling. Its overall colouration is almost uniformly blackish (Fig. 2A). However, the typical dorsal pattern of the species is barely visible, made up of a dorsal row of large round blotches and a lateral row of small dark dots (Fig. 2C). The dorsal colour fades towards the belly, which appears uniformly whitish, except for dark spots which alternate on the external margins of the ventral scales (Fig. 2B). Similarly, the ground colour fades on the sides of the head, lightening on the supralabial scales, which are thinly outlined in black in their posterior margin (Fig. 2C). The darkening pattern of the specimen resembles the "charcoal" morph reported for the barred grass snake, *Natrix helvetica* (Di Nicola et al., 2023).

Melanism is widespread in snakes both as a rare chromatic aberration (Benito et al., 2022) and as the most frequent colour morph in a given taxon or population (Schwaner, 1989; Storniolo et al., 2023). In *H. hippocrepis* the darkening of the dorsal pattern can manifest itself both as a widespread ontogenetic process, considered predominant and advantageous for some populations (Cattaneo, 1985), and as a rare mutation, apparently non-ontogenetic as in the present case (see also Garcia-Marsà et al., 2015). In ectothermic animals such as snakes, melanism is considered an advantageous condition as it allows greater efficiency in thermoregulation and protection against the damaging effects of UV rays (Fu et al., 2022; Goldenberg et al., 2024). On the other hand, melanistic individuals are sometimes considered to be at a disadvantage where they are less cryptic than individuals with normal colour patterns (San-Jose et al., 2008). The great diffusion of the ontogenetic form, as opposed to the rarity of the non-ontogenetic melanic morph, probably depends on a set of these factors. In fact, in *H. hippocrepis*, as well as in other snakes, melanism is usually preceded by a cryptic or warning-coloured juvenile (Vanni & Nistri, 2006; Arquilla & Lehtinen, 2018), which could decrease mortality in the early life stages. The observation reported here expands knowledge on the phenotype variability of this species and, moreover, represents an interesting starting point to delve deeper into the function of melanism and its different variations.

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‘Stress and wash’ may make great crested *Triturus cristatus* and smooth newts *Lissotriton vulgaris* palatable for grey herons *Ardea cinerea*, with a link to video evidence

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The smooth newt *Lissotriton vulgaris* is a widespread amphibian species widely distributed across western Europe, and notably common throughout most of Great Britain (Speybroeck et al., 2016). Growing up to 11 cm in length, *L. vulgaris* occupies a diverse range of aquatic and terrestrial environments. In contrast the great crested newt *Triturus cristatus*, Britain’s largest newt species reaching 16 cm in length, is found predominantly in deeper and more mature fish-free environments across northern Europe (Beebee & Griffiths, 2000; Speybroeck et al., 2016). In England, both species return to ponds to breed typically in February, and then in about June they leave water for terrestrial habitats, while the metamorphs leave water bodies later (Beebee & Griffiths, 2000). *Triturus cristatus* is known to produce defensive toxic secretions from glands within its skin, which are used to deter predators in combination with corresponding aposematic colouration (Kupfer & Teunis, 2001). The toxic secretion is often seen as a white foamy liquid that is released when the newt is agitated. It is known that the skin secretion of *T. cristatus* contains a heavy (long chain compound) proteinaceous toxin (Jaussi & Kunz, 1978) and that in both species there are low concentrations of tetrodotoxin and 6-epitetrodotoxin (Yotsu-Yamashita et al., 2007).

In the case of birds preying on amphibians with toxic skin secretions, it is known that some species use a ‘stress and wash’ technique to rid their prey of their toxins before swallowing them whole. Comparable behaviours have also been reported for bird species when predating on toxic amphibian species, such as the Australasian swamphen *Porphyrio melanotus* when feeding on cane toads *Rhinella marinus* (Wilk, 2018). The grey heron *Ardea cinerea* is known to be a predator of amphibians such as *T. cristatus* and *L. vulgaris*, fish, small mammals and other species that inhabit wetlands (Draulans et al., 1987; Jakubas & Mioduszewska, 2005; Inns, 2009). It is found in a variety of wetland habitats across Europe, Asia and parts of Africa. They stalk their prey within shallow water bodies and the surrounding terrestrial habitat (Cook, 1978; Draulans et al., 1987) and are extremely adaptable in their diet, being able to shift feeding strategies to exploit seasonally available food sources including ducklings (Marquiss & Leitch, 1990) and water voles *Arvicola amphibius* (Reid et al., 2022). However, there are no known written descriptions of *A. cinerea* using ‘stress and wash’ when preying upon amphibians, although the behaviour has been recorded in videos posted on YouTube, the earliest of which is by Linklater (2017) filmed at Dungeness in England.

From 2–18 April 2024, a juvenile *A. cinerea* was recorded in a pond by camera trap (Browning BTC-5DCL) feeding on

Figure 1. A juvenile grey heron *Ardea cinerea*, photographed by a camera trap, feeding on a great crested newt *Triturus cristatus*, using the ‘stress and wash’ technique

Table 1. Details of observations of a juvenile grey heron *Ardea cinerea* feeding on great crested *Triturus cristatus* and smooth newts *Lissotriton vulgaris*, at a pond in Shropshire using a Browning camera trap

Date	Time	Species consumed
2 April 2024	14:15 h	Smooth newt
2 April 2024	14:18 h	Great crested newt
2 April 2024	15:08 h	Great crested newt
8 April 2024	15:30 h	Smooth newt
18 April 2024	14:36 h	Great crested newt
18 April 2024*	22:43 h	Smooth newt

* indicates the observation of an adult heron feeding using the same technique

both *T. cristatus* and *L. vulgaris* (Fig. 1, Table 1). The pond, located in Acton Scott, Shropshire (52.4897679, -2.7982975), measured approximately 70 m by 25 m and approximately 2 m deep, with a mix of plant and animal species inhabiting it. This juvenile *A. cinerea* was apparently using the 'stress and wash' technique, whereby it can be seen agitating the captured newts by shaking them around, and then using the pond to wash the toxins released by the newts (BHS video, 2024). Additionally, an adult *A. cinerea* was photographed on 18 April 2024 at the same pond at night (22:43 h) feeding on an *L. vulgaris* using the same technique.

This is the first written record of *A. cinerea* using the 'stress and wash' technique when predating newts, although oddly, all of the observations of the juvenile *A. cinerea* predation on the newts were made in the afternoon (Table 1) and the one observation of an adult was at night. Herons are opportunistic predators of newts, and may consume toxic prey when they are more abundant, such as in the breeding season (Roulin & Dubey, 2013). These observations suggests careful behaviour in *A. cinerea* to reduce the concentration of toxin ingested when consuming the newts. Now while we cannot be sure that the newts were not regurgitated later, no newts were found around the area of the pond during the retrieval of the camera trap or routine monitoring, and given that Inns (2009) states that *A. cinerea* is a prodigious predator of great crested newts it very likely that the prey was digested.

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Not so fast: Two observations concerning slow worm *Anguis fragilis* antipredator behaviour

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Slow worms *Anguis fragilis* are a legless lizard of the family Anguidae which is common and widespread in Britain and mainland Europe (Arnold & Ovenden, 2002; Inns, 2009). Despite substantial literature on the ecology of slow worms (e.g. Beebee & Griffiths, 2000; Smith, 1990), there are relatively few published reports describing predation attempts on the species and the effectiveness of antipredator defences. Although a wide range of animals may occasionally prey upon slow worms, the major predator groups on slow worms are likely birds and reptiles (Martín & López, 1990; Smith, 1990; Vacher & Wendling, 2019). Described antipredator behaviours include caudal autotomy, crypsis, rapid escape by burrowing or fleeing into nearby vegetation and immobility (Beebee & Griffiths, 2000; Capula et al., 1997; Smith, 1990).

Here I describe a successful predation attempt on a slow worm despite use of caudal autotomy, and also provide a record of association with ants alongside a proposal that this serves an antipredator function.

While teaching on an undergraduate field course at Mumbles Hill Nature Reserve (51.569259, -3.984648) on 22 April 2021, a student alerted me to an adult female slow worm on an open section of short grass and bare soil which was being attacked by a magpie *Pica pica*. The attack took place ca. 13:30 h on a sunny and dry, but relatively cool day (temperature ca. 14 °C). The magpie noticed the exposed slow worm, flew down, and started pecking at it focusing on the front half of the body. After a few seconds the slow worm shed its tail, but this did not effectively distract the magpie, which continued its attack. Within a minute or so the magpie had grasped the slow worm (minus tail) in its beak and flew off to a nearby tree where I presume it was consumed. The magpie would not have been feeding chicks at this time of year (they lay first clutches in mid-April to early-May and the eggs take 20–22 days to hatch; Madge, 2009). The isolated tail continued to wriggle with slowly decreasing activity for ca. 5 minutes. Soon after the tail stopped moving, the same magpie came and carried off the tail to a nearby tree.

Although magpies are known as predators of slow worms (e.g. see predation of a juvenile slow worm in this video https://www.youtube.com/watch?v=GbN-GPgD0zI) there appear to be few described observations and slow worms rarely appear in studies of magpie diets. Hence this observation contributes a new record to the literature of a successful predation event by a magpie on an adult slow worm and an unsuccessful deployment of a major antipredator defence by slow worms (caudal autotomy). It is notable here that the predation event occurred on open ground, which might explain the failure of autotomy to prevent predation, since escape following autotomy would be facilitated by thick vegetation to hide in (particularly if the tail was more exposed than the body). However, as the magpie was very focused on the body (not the tail) throughout, it is unclear whether this would have prevented predation in this instance.

On 25 May 2023 at 17:41 h, I uncovered two slow worms while carrying out a routine check of a 0.5 x 0.5 m corrugated roofing tile made of bitumen-soaked organic fibres placed in Three Crosses (51.628867, -4.061703) as an artificial refugium. For several months this refugium was home to an active colony of small black ants (presumed to be *Lasius niger*), and these were still occupying the refugium when the slow worms were under it (Fig. 1). I have commonly found ants nests under artificial refugia that

Figure 1. Two slow worms, a subadult (above) and a large juvenile (below) found under an artificial refugium alongside an ant nest (bottom)

are also occupied by slow worms, such that this does not seem to be a rare event. Moreover, several previous reports mention associations between slow worms and ants under reptile refugia, which has variously been attributed to a food source (though rarely; Parry, 2023a), or shared habitat requirements and use of ant tunnels for burrowing (Beebee & Griffiths, 2000; McInerny, 2014).

Despite rare records of slow worms feeding on ant larvae (Parry, 2023a), the specific use of ant nests as a feeding resource currently seems unlikely. Although slow worms appear capable of feeding on a wide range of prey, including occasional records of vertebrates (Capizzi et al., 1998; Gleed-Owen, 2012), the diet is heavily biased towards molluscs and earthworms in most populations investigated, with hymenopterans in general and ants specifically almost never a major diet component (Beebee & Griffiths, 2000; Capizzi et al., 1998; Mollov, 2010; Pedersen et al., 2009; Smith, 1990). Hence, the lack of ants as prey of slow worms, and a degree of specialism on molluscs and earthworms which don't have a particular association with ant nests, makes it very unlikely that any association of slow worms and ant nests is related to feeding.

I have yet to encounter the proposal that slow worms might be actively seeking out shelters occupied by ants as a defensive behaviour, but this is an idea which I believe is very plausible. First, Smith (1951) reported that slow worms are often found in association with the nests of multiple species of ants, often under stones, and emphasised that they are not common prey items of slow worms. Second, McInerny's (2014) observation that slow worms specifically (despite this study also considering northern vipers *Vipera berus* and common lizards *Zootoca vivipara*) often co-occurred under refugia with ants is consistent with my own casual observations; slow worms seem to share refugia with ant nests more commonly than other reptiles. Third, slow worms possess osteoderms under their skin which provide a degree of armour that presumably protects against predators (Beebee & Griffiths, 2000; Parry, 2023b; Williams et al., 2022). Fourth, ants are widely recognised as formidable prey that possess effective defences such as venomous stings or combining biting with spraying formic acid into wounds, sufficient to deter predators including lizards and birds (Cloudsley-Thompson, 1995; Dornhaus & Powell, 2010; Hasegawa & Taniguchi, 1993). Finally, other lizards with osteoderms have been found to specifically flee to shelters containing ants (Arbuckle, 2008). The latter report found five-lined skinks *Plestiodon fasciatus* showing preferential fleeing to natural cover objects housing ants, and although no analysis was performed in that note a binomial test on the presented data does reveal a significant association ($P = 0.0001$).

Taken together, I propose that ants potentially present a general opportunity for boosting the defence of lizards which have sufficient armour to avoid being harmed themselves by the ants. I suggest that additional investigation of this possibility is worthwhile, for instance by quantifying whether slow worms are more likely than other reptiles to use refugia occupied by ant's nests, whether slow worms co-occurring with ants are slower to flee once uncovered (consistent with a perceived reduction in risk), or whether reptile behaviour during interactions with ants differs between slow worms and other species. Such questions have the potential to reveal insights into the wider ecological context within which reptiles function.

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The advertisement call of the robber frog *Pristimantis peraticus* in a population from the eastern slope of the Colombian central Andes

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Acoustic communication is widely used by anurans in different social contexts, such as male-male agonistic interactions and mating. Among the diverse acoustic signal types in anurans, the advertisement call is the most conspicuous signal. It serves to attract mates and transmit territorial information to conspecifics (Wells, 2007; Köhler et al., 2017). Moreover, knowing the advertisement call traits may be useful for studying taxonomic and phylogenetic relationships, natural history, behaviour, ecology, and eventually, conservation (Myers & Daly, 1976; Dias et al., 2019; Patiño-Ocampo et al., 2022a; Zaffaroni-Caorsi et al., 2023). However, for many anurans the advertisement call is still unknown. Colombia has one of the richest anuran faunas in the world (818 spp, Acosta-Galvis, 2024), the advertisement call is only known for about 39% of anuran species, and of the 225 species of *Pristimantis* known in Colombia it is known only for 25 of them (Rivera-Correa et al., 2021; 2022; Patiño-Ocampo et al., 2022a; 2022b; Cuellar-Valencia et al., 2023). This is of concern since most species in this clade have a restricted distribution in the Andean region of the country, which is subject to high rates of deforestation and transformation of its original vegetation cover with the concomitant negative consequences on species diversity (Mesa-Joya & Torres, 2016; Arnesto & Señaris, 2017; Agudelo-Hz et al., 2019).

Pristimantis peraticus (Lynch, 1980) is strambomantid frog distributed between 2600 and 3460 m a.s.l. in the central Andes of Colombia (Lynch, 1980; Castro-Herrera & Vargas-Salinas, 2008; Buitrago-González et al., 2016). Individuals of this species are usually found on herbaceous vegetation, bromeliads and the necromass of frailejones (*Espeletia* spp.), at 0–30 cm height above ground (Buitrago-González et al., 2016). Little has been published about the natural history of this species, including its activity pattern and acoustic signalling. Herein, I describe for the first time the advertisement call of *P. peraticus* based on seven males recorded in a population located on the eastern slope of the central Andes of Colombia.

In July 2023, I undertook an 11 day field trip to Paramo La Yerbabuena, in the 'Loros Andinos' natural reserve (4° 4'34.3'' N, 75° 42'54.9'' W; altitude 3420 m a.s.l.), municipality of Roncesvalles, department of Tolima, central Andes of Colombia. Three people performed visual and auditory encounter surveys (Crump & Scott, 1994), looking for anurans in all available microhabitats (e.g. leaf litter, necromass of frailejones, leaves) from 8:00–16:00 h and 19:00–00:00 h. When a calling male was observed, I recorded its advertisement calls from a maximum distance of one metre, using a Sennheiser ME62/K6 unidirectional microphone connected to a handheld recorder Marantz PMD661. The body size (snout-vent length, SVL) of the signaller was measured with a digital calliper (± 0.1 mm). Recordings were digitized with 16-bit resolution and a sampling frequency of 44.1 kHz. Oscillograms and spectrograms were analysed with a 512-point Fourier Transformation window and the Blackman algorithm using the software RAVEN Pro 1.6.5 (Bioacoustics Research Program, 2024). The procedures and terminology used for the following measures and descriptions of call traits were according to Köhler et al. (2017) using a call-centered definition to describe the call. The unit for the descriptive analysis was the individual recorded. Digital copies of the calls (in WAV format) were deposited at the Colección de Sonidos Ambientales of the Instituto Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia (see Table 1 for voucher numbers). Three individuals euthanised with 2% lidocaine, fixed in 10% formalin and preserved in 70%

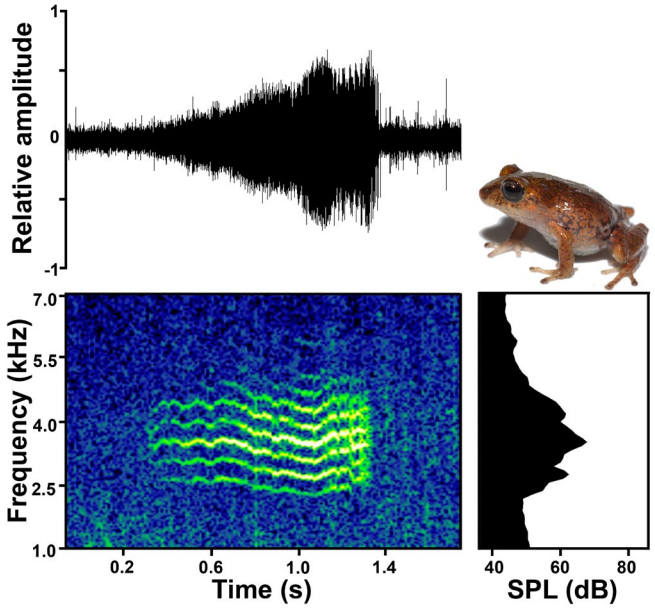

Figure 1. Oscillogram, spectrogram and power spectrum for one advertisement call of *Pristimantis peraticus*. This call was emitted by the male #1 (Table 1). SPL = sound pressure level

Table 1. Advertisement call features for each male of *Pristimantis peraticus* recorded at municipality of Roncesvalles, department of Tolima, Central Andes of Colombia. Values are reported as mean ± standard deviation (minimum-maximum). Body size (snout-vent length, SVL), voucher numbers of the Colección de Sonidos Ambientales of the Instituto Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia (IAvH-CSA), and Colección de Anfibios y Reptiles de la Universidad del Quindío, Colombia (ARUQ) are shown.

Male ID	Voucher IAvH-CSA	Voucher ARUQ	Number of calls recorded	SVL (mm)	Call duration (ms)	Fundamental frequency (Hz)	Dominant frequency (Hz)	Number of harmonic bands
1	37825	1557	7	15.74	0.9 ± 0.01 (0.9–1.0)	2745 ± 246 (2343–3000)	3535 ± 279 (2906–3656)	6 ± 0.8 (5–7)
2	37826	-	2	-	1.27 ± 0	3093 ± 132 (3000–3187)	3515 ± 66 (3468–3562)	6.5 ± 0.7 (6–7)
3	37827	1558	1	19.18	1.27	2625	3562	7
4	37828	1559	5	18.76	1.6 ± 0.21 (1.2–1.8)	2669 ± 320 (2096–2812)	3449 ± 78.4 (3375–3562)	5 ± 0.7 (4–6)
5	37829	-	2	-	0.8 ± 0.06 (0.8–0.9)	3093	3609 ± 198 (3468–3750)	5
6	37830	-	1	-	1.05	2531	3281	5
7	37831	-	4	-	0.9 ± 0.14 (0.7–1.0)	2929 ± 89.7 (2812–3000)	3679 ± 309 (3375–4031)	8.2 ± 0.1 (7–10)

ethanol and deposited at the Colección de Anfibios y Reptiles, Universidad del Quindío, Armenia (ARUQ), Colombia (see Table 1 for voucher numbers).

A total of 71 individual *P. peraticus* were recorded (62 males, 2 females and 7 unsexed individuals). From 10:00–15:00 h we recorded 22 calls emitted by seven males calling from the base of the frailejón (*Espeletia hartwegiana*). The advertisement call of *P. peraticus* consisted of a pulsatile call composed of a dense harmonic single note with multiple harmonic bands (Fig. 1). The note or whole call lasted 1.1 ± 0.2 (0.8-1.5) s, and had a mean dominant frequency of 3599.5 ± 246.5 (3281.2-3679.6) Hz, and a fundamental frequency of 2812.5 ± 227.6 (2531.2-3093.7) Hz. Ninety percent of the call energy was located between 2496.8 ± 292.6 (1968.7-2929.6) Hz and 4888.8 ± 861.9 (3281.2-6656.2) Hz of the call. In the recordings it was possible to detect five to eight harmonic bands (Fig. 1).

This is the second description of the advertisement call for a species of the *P. leptolophus* group which is composed by nine species (sensu Lynch, 1991; González-Duran et al., 2017; Rivera-Correa et al., 2017). The other species of this group for which the advertisement call has been described is *P. acatallelus* (Lynch & Ruiz-Carranza, 1983), which has a very different call structure consisting of a group of 6 to 11 tonal notes (Cuellar-Valencia et al., 2023). The dominant frequency and call duration in *P. peraticus* is higher than in *P. acatallelus* (2265.6 Hz and 0.5 ms, respectively; Cuellar-Valencia et al., 2023). It should be noted that Romero-García et al. (2015) describe the advertisement call of what is alleged to be *Pristimantis uranobates*, a species nested within the *P. leptolophus* group. However, when comparing the photograph and the call provided by the authors, it is observed that it does not coincide with the external phenotypic characteristics of *P. uranobates* (González-Durán, unpublished data), but rather with those of *Pristimantis boulengeri* (Rios-Soto & Ospina-L, 2018), a species of the group *P. boulengeri* (sensu Gonzalez-Durn et al., 2017). Clearly, more call descriptions are necessary before establishing patterns of the call structure within the *P. leptolophus* species group.

The advertisement call of species belonging to genus *Pristimantis* are predominantly composed of multiple tonal notes (e.g. *P. crepitaculus*, Fouquet et al., 2022; *P. campinarana*, Mônico et al., 2023) or a single pulsed note (e.g. *P. silverstonei* and *P. alius*, Arriaga-Jaramillo et al., 2023). The structure of the advertisement call of *P. peraticus* (i.e. dense harmonic single note) is unusual in the advertisement call of anurans, and tends to be more similar to an anuran distress call (Köhler et al. 2017) such as the tree frog *Smilisca baudinii* (Mendoza-Henao, 2021) and the rainy frog *Pristimantis racemus* (Pisso-Florez et al., 2023). To the best of my knowledge the advertisement calls of *P. peraticus* and *Pristimantis molybrignus* (Cuellar-Valencia et al., 2023), a species not yet assigned to any *Pristimantis* group, represent the first examples of advertisement calls with a dense harmonic single note structure in species of *Pristimantis* (608 spp, Frost, 2024).

Last but not least, *P. peraticus* is a species found below the necromasses of frailejones and it is very difficult to locate individuals. In the field, it was necessary to invest between 15 to 30 minutes by three people to find a former calling male. With a knowledge of the *P. peraticus* males call, we were able to detect other individuals quickly, obtaining 78% of our records from their calling. This underlines the effectiveness of passive acoustic monitoring as a crucial technique for the monitoring of populations of this and other similarly cryptic anuran species.

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NATURAL HISTORY NOTE

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Photographic record of subaudible vibration (SAV) in the American crocodile *Crocodylus acutus*

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The American crocodile *Crocodylus acutus* is widely distributed in coastal and lowland wetlands in the northern Neotropics (Thorbjarnarson et al., 2006; Rainwater et al., 2022). For this species, courtship and mating are exclusively aquatic activities where the courtship is usually initiated by the female, and typically consists of a somewhat stereotyped sequence of behaviours with the female snout-lifting, swimming in slow circles around the male, or placing her head on the snout or back of the male (Thorbjarnarson, 1989). The main advertisement display of the male is a series of one to three headslaps, also males frequently respond to the female by emitting a very low frequency sound, which is below 100 Hz and even in the infrasound below the limit of human hearing at around 10 Hz (Dinets, 2013). This is termed subaudible vibration or SAV (Thorbjarnarson, 1989; Grigg & Kirshner, 2015) and is created by rapid contraction of the male's trunk muscles beneath the water surface (Lang, 1989; Boucher, 2017), but at the water surface, this creates 'dancing' water droplets caused by Faraday waves that can result when a liquid overlies a solid surface (Dinets, 2013; Grigg & Kirshner, 2015). It is thought that SAVs may be sexually stimulating during courtship and are a good predictor of further courtship (Garrick & Lang, 1977; Grigg & Kirshner, 2015). The SAV is released from a typical 'head oblique, tail arched' (HOTA) posture, a behaviour well known in the American alligator *Alligator mississippiensis*, where it is significant in courtship and in the establishment of territories (Vliet, 1989; Grigg & Kirshner, 2015).

Figure 1. American crocodiles *Crocodylus acutus* from Puerto Vallarta, Mexico - Female head (left) and male (centre) in 'head oblique, tail arched' posture with water dance droplets on its back resulting from subaudible vibration

On 8 May 2018 at 11:10 h, in the 'water hazard' at Marina Vallarta Golf Club (20° 40'00.1" N, 105° 15'46.4" W; altitude < 5 m) in Puerto Vallarta, Jalisco, Mexico, we observed and photographed an adult male *C. acutus* (total length ≤ 3 m) in the presence of a smaller female. The male was in HOTA posture and a 'water dance' was visible over its dorsal surface (Fig. 1). The crocodile held the pose for 2 minutes during which time we observed only one 'water dance' for a few seconds.

Garrick & Lang (1977) described in detail the social signals and reproductive behaviour of *C. acutus* and present a drawing of a male *C. acutus*, traced from movies and still photographs, with SAVs radiating from the body. To our knowledge, this note represents the first published photographic record of subaudible vibration (SAV) and visible 'water dance' in the American crocodile. On this occasion, mating was not observed but it has occurred on this golf course as, every year for the last 25 years, we have observed four to six nests with hatchlings. Thus, this man-made habitat helps to conserve the American crocodile on the west coast of Central Mexico (Mc Cann et al., 2016).

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A case of suspected paedomorphosis in a captive Asian lentic salamander *Hynobius leechii*

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Paedomorphosis is a condition in which juvenile characteristics are retained into adulthood. It may take two forms, neoteny where the juvenile form remains even in adulthood due to the delayed development of somatic cells, or progenesis where the growth rate is fast and the development of gonads is accelerated, leading to early adulthood (Wakahara, 1996; Box & Glover, 2010). In some amphibians, including salamanders, paedomorphosis occurs depending on environmental conditions including population density, water level, competitors, habitat changes, genetics, water temperature, mutations, stress, and hormones (Sasaki, 1924; Tompkins, 1978; Moriya, 1980; Semlitsch, 1987; Voss & Shaffer, 1997 Whiteman et al., 2012; Bendik et al., 2013; Johnson & Voss, 2013).

We report here a case of suspected paedomorphosis in the Wosan salamander *Hynobius leechii*. On 15 March 2022, under local government collection permit (approval number: Goheung 2022-1, Uiryeong 2022-1), we collected ten male specimens from Jukjeon-ri, Yongdeok-myeon, Uiryeong-gun (35° 21’17’’N, 128° 16’35’’E, 79 m a.s.l.) and on 16 March 2022 ten females from Bongnae-myeon, Goheung-gun (34° 27’27’’N, 127° 28’31’’E, 34 m a.s.l.). On 16 March 2022, to induce reproduction, one male (snout-vent length, SVL 58.9 mm, tail length, TL 47.6 mm) and one female (SVL 58.4 mm, TL 49.1 mm) were placed in a vivarium (L 320 × W 180 × H 200 mm) at Ewha Womans University. The water depth in the vivarium was kept at about 10 cm so that any scattered eggs would not dry. Spawning was confirmed the next day (17 March) and on 23 March a total of 52 larvae hatched from the eggs. The hatchlings were kept in the vivarium within which sponge filters (SF2822, Amazon, China) were installed for aeration. The temperature in the rearing space was kept at approximately 15 °C. Twice weekly, the young salamanders were fed with frozen mosquito larvae (BBVSR0001, Hyangsan, South Korea) with multivitamins (PT-1861, Hagen, USA). This study was approved by the Institutional Review Board (IRB) affiliated with Ewha Womans University (EWHA IACUC 23009t). We followed the ARRIVE guideline for salamander breeding and management (Percie du Sert et al., 2020).

By 30 May, 38 salamanders had metamorphosed and left the water except for one. Thereafter, the remaining individual in the water were fed thrice weekly. The growth rate of this specimen is shown in Figure 1. At approximately 23 months after hatching (15 January 2024), external gills were still present and thin fins were visible (Fig. 2). However, the sex of the individual still could not be determined.

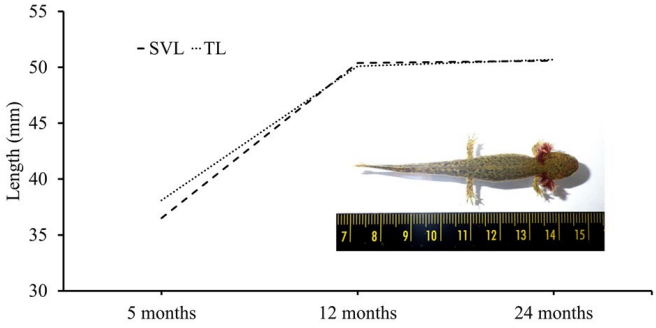

Figure 1. Changing body (SVL) and tail length (TL) in a potentially paedomorphic *Hynobius leechii* reared in captivity (August 2022 to February 2024). The salamander was 5 months old when the photo was taken.

Figure 2. The external appearance of a suspected paedomorphic *Hynobius leechii* 23 months after birth in captivity, the photo was taken on 15 January 2024

Paedomorphosis in salamanders is common in North America, but very rare in Asia (Sasaki, 1924; Okamiya et al., 2021). In addition, this is the first case of suspected paedomorphosis in an individual born and reared in captivity. Salamanders in the genus *Hynobius* usually become adults 3 to 5 years after hatching (Ento & Matsui, 2002; Kusano et al., 2006). However, it took only about 12 months from hatching for a paedomorph-like individual to become adult-sized. Denöl et al. (2005) suggested that neotenic individuals have a size similar to that of adults when they reach adult age, while progenetic individuals reach adult size long before they reach adult age. We suspect the current case to be one of progenesis, i.e. based on early growth, but it is difficult to confirm this because we do not know whether the specimen is yet capable of reproduction.

It remains unknown why this individual is paedomorphy-like. All the larvae were fed in the same way and were kept in the same environmental conditions. In previous studies, approximately equal proportions of metamorphosis and paedomorphosis were identified among offspring from paedomorphic *Ambystoma mexicanum* (Tompkins, 1978; Voss & Shaffer, 1997). In the current case, neither parent was paedomorphic, which reduces the likelihood that this case is related to intergenerational genetics. Sasaki (1924) who discovered the first case of paedomorphosis in the *Hynobius* salamander, associated it with low-temperature conditions (0–10°C) that lasted for a long period together with a rich food supply. In our study, the temperature was kept constant at a room temperature of about 15 °C, so low-temperature conditions may also be excluded as a cause.

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NATURAL HISTORY NOTE

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European common frog *Rana temporaria* carcass scavenged by the planarian *Schmidtea polychroa*

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Parasitic flatworms are well known to cause serious harm to amphibians (Imai et al., 2009) but there have been few observations of interactions between amphibians and free-living flatworms (planarians), which could act as either scavengers or predators (Vila-Farre & Rink, 2018).

On 16 March 2014 in central Cambridgeshire (England, 52.215028, 0.142833) the carcass of a common frog *Rana temporaria* was discovered on the vegetated edge of a pond being scavenged by approximately 20 planarians (Fig. 1 A&B). The planarian species in question is believed to be *Schmidtea polychroa* (Tricladida: Dugesiidae). This was distinguished from the closely related species *Schmidtea ugubris* based on shape and colour (Reynoldson & Bellamy, 1970). Moreover, *S. polychroa* has been previously recorded in central Cambridgeshire, whereas there are no current records of *S. lugubris* in that area (NBN Atlas, 2024a; 2024b). Species of the planarian genus *Schmidtea* can be found in freshwater, growing to sizes of approximately 10 mm; they are grey, black or brown in colour with a diet that includes molluscs, algae and detritus (Reynoldson & Davies, 1970; Reynoldson & Young, 2000; Macan & Worthington, 1990).

It is rare for planarians to feed by scavenging (Reynoldson & Young, 1963) and this is the first recorded instance of a *Schmidtea* sp. scavenging on an amphibian although *Schmidtea nova* has been observed predating the eggs of *R. temporaria* in the laboratory (Segev et al., 2015).

Figure 1. Free-living flatworms scavenging - **A.** *Schmidtea polychroa* scavenging on the carcass of a European common frog *Rana temporaria*, **B.** Close up photo of *Schmidtea polychroa*

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Observation of nuclear-follower foraging behaviour between a snapping turtle *Chelydra serpentina* and a smallmouth bass *Micropterus dolomieu*

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Nuclear-following behaviour is described as an interaction among aquatic animals where one 'nuclear' species forages on the benthos by disturbing substrate and one or more other 'follower' species follows for the purposes of consuming prey that are purposely or incidentally displaced by the nuclear species (Lukoschek & McCormic, 2002). Although this phenomenon has commonly been described in marine species (Lukoschek & McCormic, 2002; Krajewski, 2009) few observations appear to have been published involving freshwater turtles. Platt & Rainwater (2021) observed instances of nuclear following behaviour among spiny softshell turtles *Apalone spinifera*, largemouth bass *Micopterus salmoides* and sunfish *Lempomis* spp. Herein, I describe an observation of nuclear-following behaviour between a snapping turtle *Chelydra serpentina* and a smallmouth bass *Micropterus dolomieu* in eastern Pennsylvania, USA.

On 3 July 2024 at approximately 15:00 h, I observed a behavioural interaction consistent with nuclear-following behaviour between an adult *C. serpentina* (estimated carapace length 30 cm) and an adult *M. dolomieu* (estimated total length 30 cm) in the North Branch Susquehanna River in the village of Mifflinville, Columbia County Pennsylvania, USA (41° 02'06.1" N, 76° 18'38.5" W). While bicycling across a bridge spanning the river at this location, I stopped to view the river and noticed the *C. serpentina* in the river directly below the bridge in a shallow sand/gravel bar submerged in approximately 30 cm of water. I observed the turtle for approximately five minutes, and during this entire time it slowly probed the benthos with its mouth, stirring up sediment in the process, apparently foraging for an unidentified food source (possibly aquatic molluscs, which are common in the North Branch Susquehanna River and are a known food source for *C. serpentina*; Ernst & Lovich, 2009; Dillon et al., 2019). While engaged in this behaviour, a single adult *M. dolomieu* closely followed the turtle during the entire duration of this observation, and consistently appeared to consume small aquatic organisms displaced by the turtle's disturbance of the substrate (possibly crayfish, a typical dietary item for *M. dolomieu* in Pennsylvania; Stauffer et al., 2016). The turtle did not interact aggressively with the bass and appeared undisturbed by its presence. Both species moved together along the substrate approximately 10 m during the course of this observation, before both became obscured from my view as they moved underneath the bridge.

To the best of my knowledge, this observation appears to be the first report of nuclear-following behaviour between *C. serpentina* and *M. dolomieu* and may be the first report of this phenomenon in *C. serpentina*. This observation, along with those published for *Apalone spinifera* by Platt & Rainwater (2021) may suggest that nuclear following behaviour is more common among freshwater turtles and centrarchid fishes than was previously realised and warrants further study.

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Multiple tail furcations in a common house gecko *Hemidactylus frenatus* from Thailand

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The common house gecko *Hemidactylus frenatus* Duméril & Bibon 1836, is a relatively small (SVL 60 mm), arboreal, nocturnal lizard. It is native to south-east Asia with a widespread distribution in the Pacific islands; it has also been introduced widely elsewhere by anthropogenic means (Rodda, 2020). There are numerous records of various lizard species detailing tail furcations following caudal autotomy (Baum & Kaiser, 2024), including *H. frenatus* with bifurcated or/and duplicated tails (e.g. Heyborne & Mahan, 2017; Maria & Al-Razi, 2018; Khandakar & Sultana, 2020; Caicedo-Martínez et al., 2022).

On 27 April 2024 at 16:17 h, an adult (approx. 60 mm) common house gecko was observed with multiple furcations of the tail, on the wall of the veranda (Fig. 1). The observation was made in a house at Rang Ka Yai (Nakhon Ratchasima province), Thailand (15° 12.987540 N, 102° 33.793860 E; 158 m a.s.l.). This gecko exhibited typical behaviour for its species by hunting insects on the wall near the ceiling. At the observation site, and the surrounding environment, geckos of the same species are observed, as well *Hemidactylus platyurus* and *Gecko gecko*.

To the best of our knowledge, this is the first documented observation of multiple tail furcation in this species. Although the cost of tail loss has been studied extensively (e.g. Clause & Capaldi, 2006; García-Rosales et al., 2023), understanding the possible impact of abnormal tail regeneration on individual survival merits study. Observations such as these, even as single events, can broaden the scope of information about the natural history and autotomy of lizards and their tail abnormalities.

Figure 1. An adult common house gecko *Hemidactylus frenatus* with supernumerary tails

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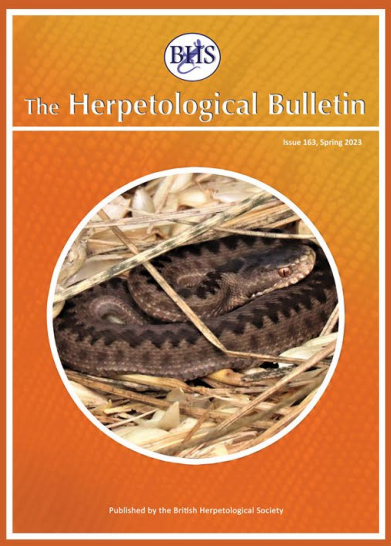
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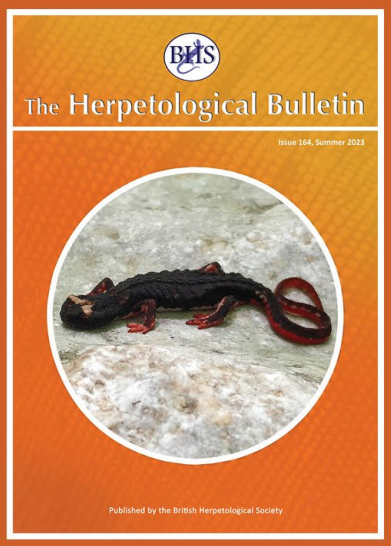
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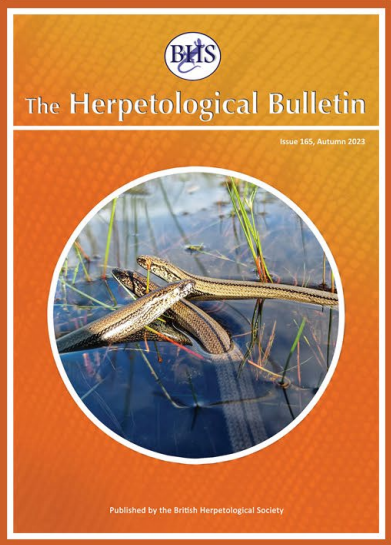
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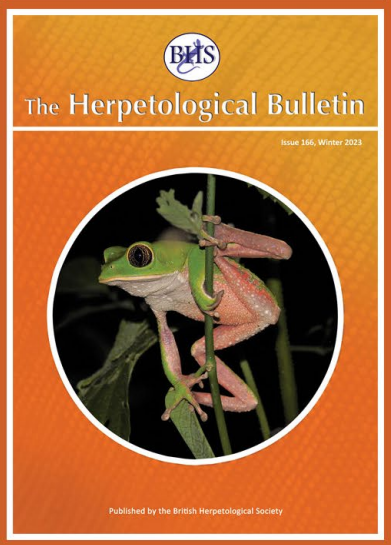
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