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Cover: Coromandal Sacred Langur *Semnopithecus priam* - made with acrylic paint. © P. Kritika.

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COMMUNICATION

Communal egg-laying by the Frontier Bow-fingered Gecko *Altiphylax stoliczkai* (Steindachner, 1867) in Ladakh, India

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Abstract: Communal egg-laying behaviour in the Frontier Bow-fingered Gecko *Altiphylax stoliczkai* was investigated within Ladakh's Indian trans Himalayan region during the summer of 2019. The findings present the first documented evidence of communal egg-laying in the species. Distinct egg-laying sites were identified with crevices containing between four and 10 eggs. Confirmation of species identity was achieved through post-hatching visual identification and genetic tests. Contrary to prevailing notions of one to two eggs per female gekkonid, the observation suggests that communal egg-laying involves multiple females. This behaviour attributes to the unique environmental challenges of high-altitude mountainous terrain, proposing significant reproductive benefits for the species.

Keywords: Adaptation, agama, Baltistan Gecko, behaviour, cold-desert, ectotherm, high-altitude specialist, mountain herpetofauna, oviposition, trans Himalaya.

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Author contributions: DP—carried out the fieldwork, analysed the data, wrote the paper, coordinated with co-authors, and edited the manuscript. CR—provided comments, inputs, and feedback on the manuscript. SG—Provided comments, inputs, feedback on the manuscript, helped with the analysis, and edited the manuscript. PR—provided support and resources for fieldwork and provided feedback on the manuscript.

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INTRODUCTION

Animal aggregations have received considerable attention regarding their adaptive value (Hamilton 1971; Treisman 1975; Turner & Pitcher 1986; Inman & Krebs 1987). In comparison, aggregation for egg-laying has received relatively less attention (Danchin & Wagner 1997). Laying eggs with conspecifics is one of the oviposition strategies used by many reptilian species. This behaviour has been documented in many species including dinosaurs and, in contemporary times, about 481 species of reptiles and amphibians around the world (Plummer 1981; Graves & Duvall 1995; Brown & Shine 2005; Radder & Shine 2007; Doody et al. 2009).

The phenomenon of communal egg-laying, observed in various reptilian species globally, has prompted the formulation of several hypotheses to elucidate its drivers. These hypotheses include the notion that scarcity of optimal egg-laying sites with stable thermal and humidity conditions might influence this behaviour. However, none of these proposed hypotheses has achieved conclusive establishment as the definitive explanation. Despite multiple hypotheses aiming to explain the communal egg-laying behaviour in different species, consensus remains elusive, as underscored by the work of Doody et al. (2009).

Each species uses specific strategies for oviposition based on a combination of biological and environmental factors. Current literature has identified 'adaptation' and 'constraint' as two critical factors with high correlation with female lizards laying eggs with conspecifics. In this context, the term 'adaptation' refers to fitness benefits for young individuals and 'constraint' refers to the scarcity of favourable environmental conditions for laying eggs (Radder & Shine 2007). It is assumed that high-altitude cold deserts are one such place where environmental constraints have a significant influence on the ecology of various species, especially ectotherms/poikilotherms (cold-blooded) animals though this has been very poorly studied so far. Here, we elaborate on the egg-laying habits of one such high-altitude specialist reptile – the Frontier Bow-fingered Gecko *Altiphylax stoliczkai* in Ladakh, of the western Himalaya.

The Frontier Bow-fingered Gecko, also referred to as the Baltistan Gecko, belongs to the Gekkonidae family and thrives in high-altitude regions. Its global presence is confined to the Palearctic zones of northern India and Pakistan, specifically in central Asia and the trans Himalayan region within the *Altiphylax* genus, as highlighted in Bauer et al.'s (2013) work. In India, this gecko species is identified in the union territories of Ladakh and Jammu & Kashmir, formerly known as Jammu & Kashmir State, as documented by Smith (1935). The measurements align with Smith's (1935) data, indicating an average snout-to-vent length (SVL) and tail length (TL) of approximately 50 mm. Despite its presence, knowledge about the biology of *Altiphylax stoliczkai* remains limited. Displaying nocturnal behaviour, the species seeks shelter under small rocks for thermoregulation during daylight hours and is often found near human settlements. Although established as oviparous based on Auffenberg et al.'s (2004) work and Sharma's (2002) findings, there is a notable absence of documented proof or published records detailing its egg-laying strategy or preferred elevation range. This study contributes significant insights, presenting original observations from Ladakh, India, which provide the inaugural documented evidence of communal egg-laying behaviour exhibited by the Frontier Bow-fingered Gecko.

Study area

Ladakh (32.15–34.38 °N & 75.36–78.22 °E) is located in the rain shadow region to the north of the Himalayan ranges and the annual precipitation ranges 90–110 mm (Srivastava et al. 2009). The elevation in the region varies, ranging from an altitude of 2,600 m to over 7,000 m. The temperature ranges from an average of -30 °C in winter to 30 °C in the summer. The landscape in Ladakh is undulating, arid, and resource-scarce due to the lack of precipitation, short growing seasons and harsh, long winters. Ladakh is included in the trans Himalayan biogeographic region (Rodgers & Panwar 1998). Most of the region is treeless except for plantations, cultivated lands and areas along water sources (Kachroo et al. 1977; Hartmann 1983). The herpetological diversity and richness of Ladakh are similar to neighbouring regions of Gilgit-Baltistan (Ficetola et al. 2010) with which it shares geographical, topographic, and climatic characteristics. Currently, Ladakh has been documented to host four lizard species, one snake species, and one amphibian species (Patel et al. 2023).

MATERIALS AND METHODS

A series of comprehensive herpetological surveys were undertaken across diverse Ladakh habitats (Image 6) between March and September 2019. A cumulative 220 h were dedicated to surveying 150 km of randomised trails, averaging 6 km daily. The survey hours spanned 0800–1700 h. The primary objective centred on documenting reptile and amphibian diversity and abundance. Captured specimens underwent manual handling, with recorded metrics including snout-vent length (SVL) and total length (TL).

In this period, 61 randomly chosen sites were surveyed, each representing one of six distinct habitat types classified based on topography, ecology, and local insights. These encompassed riverine settings, rocky outcrops, plains of both sandy and rocky terrain, agricultural lands, sand dunes, and grasslands. Survey activities spanned both sunny and cloudy days, with limited nocturnal surveys due to logistical constraints.

RESULTS

During the survey, we obtained 119 sightings of *Altiphylax stoliczkai* in 24 of 61 sites in relatively dry areas. The observed individuals displayed morphological characteristics consistent with established literature. Specifically, this gecko species is medium-sized and often exhibits a shorter tail. Its body and head show slight dorso-ventral compression, with the dorsal surface featuring greyish colouring and dark brown wavy cross-bars, while the ventral surface appears greyish-white. The extent of tail swelling varies among individuals, being more prominent in recently regenerated tails.

In addition to morphometric measurements, a genetic analysis was performed on a tail segment collected from one of the sites, confirming the gecko species' identity. The corresponding genetic sequence has been submitted to the National Centre for Biotechnology Information (NCBI) with accession numbers MZ293046, MZ293045, MZ293047, and MZ293044.

Since the species is nocturnal, it was observed hiding under rocks during the day and foraging during the night (Image 1). The survey encompassed a sample size of 119 adult *A. stoliczkai* individuals, yielding mean snout-vent length (SVL) and tail length (TL) values of 51.27 ± 14.99 mm and 72.60 ± 34.65 mm, respectively.

During the survey in early August (1–10 August 2019), clusters of eggs were found at four sites (Table 1). These sites were located near the villages of Ney (six eggs), and Phyang (four eggs) in Leh District; and Chiktan (four eggs), and Wakha (10 eggs) in Kargil District, in the Union Territory of Ladakh. The egg measurements at the site in Ney ranged 11.7–12.87 mm in length and 8.84–9.91 in width. Eggs measurements at the site in Phyang ranged 12.3–12.88 mm in length and 9.89–9.93 mm in width whereas at the sites in Chiktan and Wakha, they ranged 12.41–12.86 mm in length, 9.93–9.94 mm width and 11.9–12.81 mm length, 8.85–9.88 width, respectively. No adult *Altiphylax stoliczkai* or hatching was observed near these egg-laying sites during multiple visits to the same sites. In Ney, Phyang, and Chiktan- the eggs were located beneath medium-sized boulders covered with loose soil. The Ney and Phyang sites were relatively flat with small to medium-sized boulders (Images 2 and 4). The site in Wakha was located on a steep south-facing mountain slope with rocky outcrops. Here, the soil was relatively compact and 10 eggs were observed through a narrow fissure in a rock (Images 3 and 5). On closer inspection, we found a broken egg. We were able to identify the premature neonate inside of the broken egg as *Altiphylax stoliczkai* by its physical features that match with literature descriptions. We cautiously measured, and photographed the eggs at all the sites to avoid embryo damage. Though this species has been recorded near human settlements, all the above-mentioned sites were at least three to four km from the nearest human habitation with minimal disturbance and no flowing water in the immediate vicinity. Since all survey sites were located away from human habitation, currently fewer data are available on egg-laying behaviour near human settlements. Common vegetation in these areas included Ephedra *Ephedra gerardiana* and wormwood *Artemisia* spp.

DISCUSSION

Upon the eggs' discovery, the identity of the species responsible was unequivocally determined only at the Wakha site, as previously mentioned. To establish the egg layer at the other three sites, we employed deductive reasoning and indirect indicators. Despite the presence of Theobald's Toad-headed Agama *Phrynocephalus theobaldi* Blyth, 1863 at the Ney and Phyang sites, the viviparous nature of this species ruled it out as the egg layer. Consequently, *Altiphylax stoliczkai* emerged as the likely candidate. Similarly, the Himalayan Agama *Paralaudakia himalayana* Steindachner, 1867 was observed at the Wakha and Chiktan sites It is oviparous but the eggs of agamas are leathery and ellipsoidal in shape making them distinctly different from the eggs of geckos. Also, most agamid species dig small burrows to lay their eggs. The ones we observed were spherical and hard-shelled (Table 1), which is typical of eggs laid by members of the Gekkonidae family (Andrews 2004). Further egg comparison among the three

Image 1. An adult Altiphylax stoliczkai from Ladakh, India.

Image 2. Rocky plain habitat.

Image 3. Rocky outcrop habitat in Ladakh.

Image 4. Broken egg shells covered with soil in rocky plain habitat.

sites and the confirmed Wakha identification showed notable consistency. Subsequent validation occurred by revisiting the sites at least twice after the initial discovery, culminating in hatching around mid-August and confirming *Altiphylax stoliczkai* as the egg layer.

A review of the current literature suggests that this is the first record of such an en masse, communal egg-laying strategy used by *Altiphylax stoliczkai.* Auffenberg et al. (2004) allude to the possibility that this species might be laying eggs communally based on observations of eggs near Skardo in Baltistan but did not provide any

Image 5. Egg clutches in rock fissure supported by old egg shells.

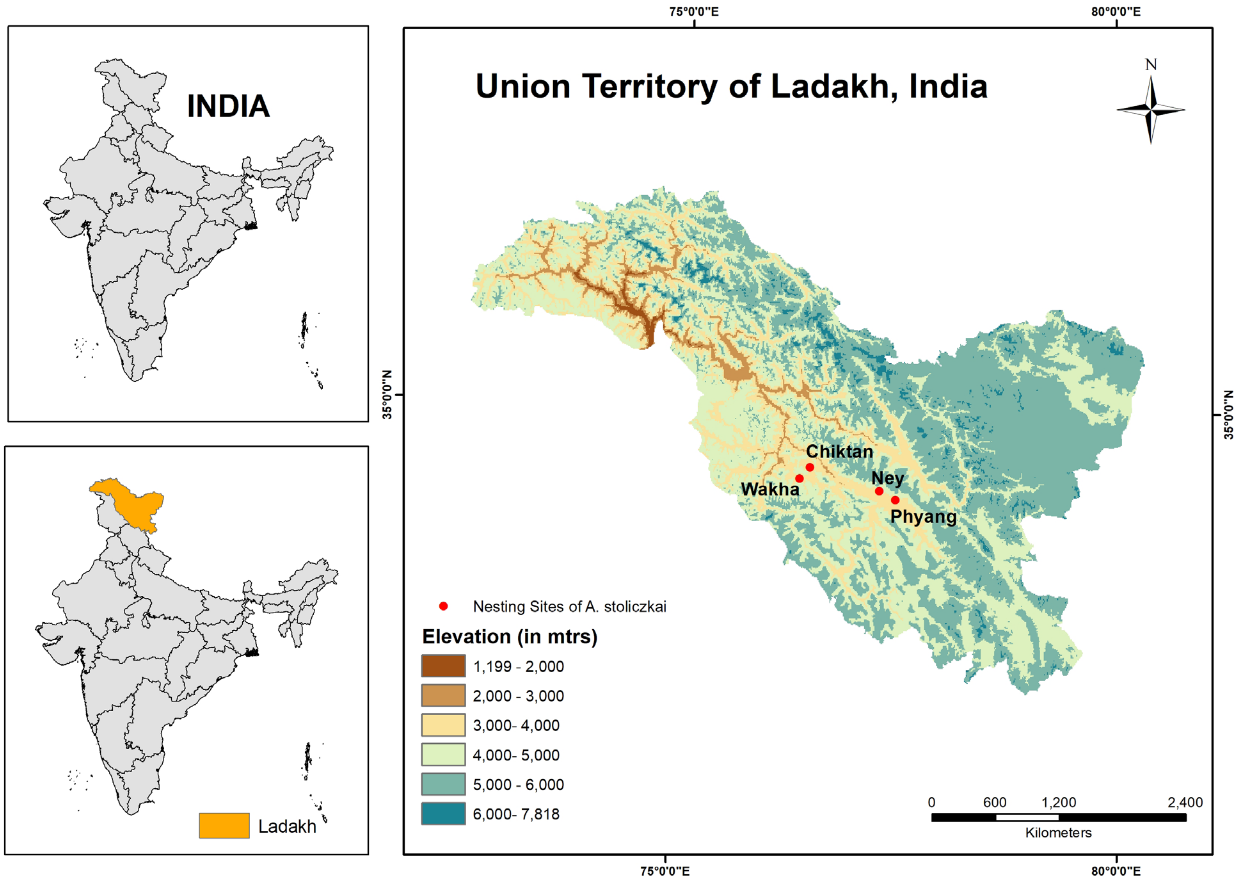

Image 6. A map of the study area.

Table 1. Details of eggs, egg-laying sites and other lizard species recorded in the habitat along with egg clutches of *Altiphylax stoliczkai* in Ladakh, India.

Site name, GPS, and elevation (m)	Habitat type	No. of eggs (n)	Range of egg measurements (mm)		Average size of eggs (mm)		Type of shell	Presence of old eggshells	Sympatric lizards and their reproductive strategies	
			Length	Width	Length	Width				
Wakha N 34.369381 E 76.382559 3396 m	Rocky outcrop	10	11.9–12.81	8.85–9.88	12.15	9.23	Spherical, hard	Yes	*P. himalayana*	Oviparous agamid
Chiktan N 34.4751306 E 76.4962916, 3337m	Rocky outcrop	04	12.41–12.86	9.93–9.94	12.63	9.94	Spherical, hard	Yes	*P. himalayana*	Oviparous agamid
Ney N 34.265275, E 77.295730 3575m	Rocky pains	06	11.7–12.87	8.84–9.91	12.16	9.23	Spherical, hard	Yes	*P. theobaldi*	Viviparous agamid
Phyang N 34.1838889, E 77.482666 3551 m	Rocky plains	04	12.3–12.88	9.89–9.93	12.59	9.91	Spherical, hard	Yes	*P. theobaldi*	Viviparous agamid

details or confirmation. The measurements of the three eggs collected by them ranged 9.7–11.1 mm in length and 7.6–8.5 mm in width which is smaller than the eggs we recorded. This difference is probably a reflection of body size as our largest recorded adult (SVL = 59.27 mm) was larger than the largest adult (SVL = 46.5 mm) reported from Baltistan. The species was documented within sites positioned at altitudes ranging 3,000–4,026 m, a higher elevation than the previously reported range of 2,300–3,700 m documented by Auffenberg et al. (2004).

Neither the process of egg-laying nor genetic tests to ascertain distinct female contributors per egg-laying site were observed or conducted. Nonetheless, it is noteworthy that the majority of gecko species tend to yield a maximum of one or two eggs during a given time frame (Shine & Greer 1991; Doughty 1996; Mesquita et al. 2016). Additionally, a relationship exists between the size of a gecko and its clutch size, with the former serving as a constraining factor on the number of eggs a female can produce (Doughty 1996).

Thus, communal egg-laying in geckos might be a behavioural adaptation to cope with the constraint of clutch size, as it increases female fitness by improving the performance of hatchlings (Blouin-Demers et al. 2004; Radder & Shine 2007). Current literature correlates this behaviour with social factors (Brown & Shine 2005; Radder & Shine 2007; Refsnider et al. 2010), scarcity of suitable egg-laying sites (Rand & Dugan 1983) and reduction of predation risk (Martin 1998; Spencer 2002). Of these, the scarcity of suitable egg-laying sites is the most commonly cited factor to explain communal egg-laying. In this regard, suitable sites provide desired thermal and humidity conditions. This is perhaps even more important for species that do not show post-egg-laying parental care, especially reptiles and turtles. While this could be one of several factors, it contributes to the adoption of communal egg-laying behaviour in certain species (Bustard 1968; Shine & Greer 1991; Doughty 1996; Doody et al. 2009).

Most oviparous lizards generally do not engage in parental care, and the success of their reproduction depends primarily on choosing optimal egg-laying sites (Pike et al. 2011). The scarcity of suitable egg-laying sites, as determined by optimum temperatures and moisture conditions are important factors that influence the success of the communal egg-laying strategy among reptiles and amphibians (Graves & Duvall 1995; Rand 1967). In addition, communal egg-laying provides many adaptive benefits including reduced predation risk. The larger the group of eggs, the smaller the probability of predation risk faced by each egg (Mateo & Cuadrado 2012). Furthermore, egg-laying sites located under large boulders are assumed to have stable conditions required for the incubation of eggs due to stable microclimatic processes (Garcia-Roa et al. 2015). Also, proximity with other eggs is known to alter moisture and thermal exchange to reduce water intake and produce healthier offspring (Radder & Shine 2007; Dees et al. 2020).

A substantial quantity of old and new eggshells was observed at all four egg-laying sites, implying their recurrent utilization. There were no egg-laying sites for this or any other species nearby. Adverse climatic conditions in the region might have incentivized individuals of this species to select previously successful sites. This not only increases the likelihood of success but also reduces the energy expenditure needed to locate new sites with unfamiliar microclimates (Doody et al. 2009). Mountain herpetofauna species, in particular, could be more susceptible to climate change impacts (Sinervo et al. 2010). Furthermore, limited optimal egg-laying sites, harsh weather conditions, and unpredictability could contribute to these adaptive strategies. Ladakh's demanding climate conditions create challenges for ectotherms/poikilotherms reliant on external heat sources and adaptive behaviours for temperature regulation. Extended periods of cold weather and intense solar radiation due to elevation make the region unsuitable for ectotherms. The existing species have developed energy-efficient strategies to meet nutritional needs and adjust to the environment, potentially explaining the region's diminished species diversity. While these reptilian species evolve physiological adaptations over time, behavioural adjustments are less resource-intensive and time-consuming (Hertz 1981). Communal oviposition might well represent one such adaptation.

The precise cues guiding individual geckos' selection of egg-laying sites and whether this decision-making occurs independently or collectively remain uncertain. An intriguing possibility is that geckos acquire familiarity with these sites through individual observation, potentially coupled with site-specific cues such as the presence of aged eggshells and optimal microclimatic conditions. However, a comprehensive investigation of these factors is essential for deeper comprehension. Additionally, as mentioned earlier, another oviparous species, the Himalayan Agama, was observed at two sites without the discovery of their nests. This observation suggests that *Altiphylax stoliczkai* and *Paralaudakia himalayana* likely do not engage in site competition due to distinct egg-laying strategies and site preferences, presumably influenced by inherent variations in egg size and clutch size.

Communal egg-laying behaviour has been observed in certain species where egg-laying sites are inherited across generations. This phenomenon, known as natal homing, has been documented in various species, including sea turtles and snakes (Meylan et al. 1990; Graves & Duvall 1995; Brown & Shine 2005;). For instance, in Morton National Park, located in south-eastern Australia, a mark-recapture study focusing on Lesueur's Velvet Gecko *Oedura lesueurii* revealed that hatchlings return to their natal nests as gravid females (Webb et al. 2008). A similar pattern was identified among Oudri's Fan-footed Gecko *Ptyodactylus oudrii* in northern Africa, where the presence of eggshells plays a pivotal role in selecting egg-laying sites (Mateo & Cuadrado 2012). Additionally, Pike et al.'s (2011) experimental study involving *Oedura lesueurii* showcased the geckos' reliance on both biotic (eggshell presence) and abiotic (thermal and moisture conditions) cues when choosing egg-laying sites. Interestingly, they showed a preference for sites with hatched eggshells and stable, cooler temperatures over warmer alternatives. Notably, these aspects remain unexplored in the context of *Altiphylax stoliczkai*, particularly regarding its biological requirements and the environmental constraints unique to the Ladakh region.

While these observations are significant, they also highlight the large knowledge gap that exists about the ecology of reptiles in cold regions such as Ladakh. The findings of this paper point to several lines of investigation to gain further insights into various strategies employed by ectotherms in response to various environmental challenges in Ladakh. The study findings will help design further long-term studies to understand various behavioural choices and this, in turn, will help develop appropriate conservation strategies for herpetofauna in Ladakh and regions with a similar climate.

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