Extinction of lizards in Sri Lankan: geographically isolated locations

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Author contributions
Buddhi Dayananda conceived this study, carried out this study, and drafted the manuscript. Thilina Surasinghe, Suranjan Karunarathna and Buddhika Madurapperuma collected and analyzed the data. Buddhi Dayananda, Thilina Surasinghe, Suranjan Karunarathna, Buddhika Madurapperuma and Lin Zhang were responsible for this manuscript and reviewed the article critically. All authors read and approved the final manuscript.

Competing interests
The authors declare no conflicts of interest.

Abstract
Climate warming is projected to drive the extinction of approximately one-fifth of the world’s lizard species within the next 60 years (by 2080). However, it remains unclear to what extent and how the global lizard population will be affected by this phenomenon on a geographical scale. Furthermore, there is a need to establish a connection between extinction risk and the prioritization of conservation efforts. In this context, we aim to address concerns related to geographically isolated and critically small lizard populations, highlighting why they face an exceptionally high risk of extinction. We also explore the potential for entire populations to vanish without notice. A comprehensive understanding of these factors is essential to inform the prioritization of conservation initiatives aimed at safeguarding lizard populations in tropical countries under future climate change scenarios.

Keywords: climate change; communal nesting; conservation; lizards; maternal plasticity; philopatry
Introduction

Climate change has profound and far-reaching consequences for global biodiversity and ecosystems across numerous biomes and taxa [1, 2]. These impacts are evident across all biological scales, encompassing genes, species, communities, and ecosystems. Behavioral and morphological changes, species extinctions, shifts in phenology and geographic ranges, alterations in ecosystem-level productivity and stability, modifications in species interactions and emergent properties, and an increase in the frequency and severity of extreme events will continue to be observed worldwide as the pace of climate change accelerates alarmingly [3–15]. As a primary driver of global environmental change, climate change will exacerbate the adverse effects of pre-existing human stressors such as land-use change, biological invasions, and environmental pollution [14, 16–18].

Lizards can be particularly vulnerable to climate-induced extinctions due to their dependence on environmental temperature to regulate their metabolism [19]. On the other hand, growth and development, reproductive physiology, spatial distribution, activity patterns, and species interactions of lizards are directly influenced by temperature and precipitation [16]. While substantial local population extinctions have been documented worldwide in recent decades (4% of local populations since 1975), this issue is expected to worsen in the future, with local population extinctions projected to reach 40% worldwide, while one-fifth of global lizard species are predicted to become extinct by 2080 [20]. The increasing magnitude of warming during lizards' reproductive seasons prolongs the time they spend in refuge, reduces foraging time, and decreases net energy gains, leading to energy deficits for reproduction [21]. Heat stress can also induce physiological and metabolic abnormalities, resulting in direct mortality. Repeated subthermal warming has led to elevated embryonic mortality and reduced hatching sizes, as well as poor body condition among hatchlings and slower post-hatching growth [22]. Even a slight increase in temperature can have significant impacts on lizards' behavior, metabolism, and population growth [23]. Among oviparous lizards with temperature-dependent sex determination, exposure to elevated temperatures can result in skewed sex ratios unless compensated for by evolutionary adaptations or behavioral plasticity [24].

Tropical biomes are among the warmest ecosystems on the planet, with the lowest inter-annual as well as intra-annual variability in atmospheric temperatures. In these biomes, the biota are either near their physiological thermal tolerance limits and lack trait plasticity or evolutionary adaptations to cope with climate adversities [25]. Climate-induced changes in habitat structure, such as tree mortality, alterations in vegetation stratification, variations in stem density, and canopy thinning, can also result in population declines, and even local extirpation, of tropical lizards [26, 27]. Consequently, tropical regions are likely to experience considerably hotter climates or other climate anomalies that do not have a modern-day equivalent [25]. Climate-induced degradation of habitat quality, such as reductions in the quality of forest-floor leaf litter, has also been implicated in the puzzling decline in lizard population density in neotropical montane protected areas, including primary forests [28]. Indeed, the adverse effects of climate change on tropical lizards are significant and are becoming increasingly evident. Tropical lizards inhabiting low elevations experience warm climates throughout the year. However, some forest-dwelling thermoconformers are active at lower body temperatures and are therefore intolerant of elevated atmospheric temperatures [29]. Apart from decreased physiological performance, ongoing warming trends may favor warm-adapted, open-habitat competitors and predators, which can displace thermally sensitive forest-specialist lizards. Tropical lizards inhabiting montane habitats, such as tropical rainforests, are physiologically specialized to narrow environmental temperature ranges and are unlikely to acclimate to warming trends. Therefore, they are disproportionately affected by even minor shifts in temperature [30].

Climate change vulnerabilities vary across geographies for lizards and other taxa [7, 31, 32]. Although the risk of climate-induced extinctions among tropical lizards is indisputable, the extent and mechanisms of species loss at smaller geographical scales within the tropical realm remain unclear. In particular, oviparous species from tropical regions are the most susceptible group to climate warming [33–35]. Evidence suggests that egg incubation temperatures influence embryo survival, offspring sex, hatching size, behavior, and hatching performance [22, 24, 36]. However, some oviparous reptiles adjust their oviposition behavior by laying eggs earlier or later in the season and selecting cooler nesting sites (e.g., deep crevices or excavating deeper nests, shaded sites) to mitigate the effects of rising temperatures [24, 37].

Evidence has emerged regarding maternal behavioral plasticity in seeking alternative oviposition sites that provide a microclimate suitable for embryonic development and offspring survival [38, 39]. Nevertheless, counterevidence from latitudinal intraspecific comparisons suggests that nest-site selection is a highly conservative trait that remains consistent throughout the species' ranges [37]. Similarly, in some reptile species, oviposition site choice is “monotypic” and females exhibit philopatry by returning to their natal nests or hatching sites. One consequence of philopatry is communal nesting, which exposes multiple nests to climate warming, resulting in impaired hatching survival and an increased risk of long-term extinction [34]. Furthermore, philopatry leads to smaller, fragmented, independent breeding colonies, reducing the co-adapted gene complexes within local populations and accelerating a significant decrease in population size due to the lack of adaptive potential (e.g., increased temperatures) within the population [40]. This highlights concerns about geographically isolated, extremely small reptile populations with low maternal plasticity and why they are at a very high risk of extinction, with the entire population potentially disappearing unnoticed.

Methods and mat

To investigate this phenomenon, we chose the tropical island nation of Sri Lanka. Sri Lanka is recognized as one of the world's reptile hotspots, boasting 244 reptile species, of which 67% are endemic [41]. Currently, it remains unclear how vulnerable Sri Lankan reptiles are to climate warming, and they have been underrepresented in climate change literature [42].

We conducted a comprehensive review using published literature and our own survey data to identify reptile species that exhibit communal nesting and philopatry. In our literature review, we initially searched the Web of Science using the following combination of keywords in article titles, abstracts, and keywords: “reptile” OR “lizard” OR “Sauria” AND “Sri Lanka”. We supplemented this systematic review by searching Google Scholar to gather any additional relevant articles. Subsequently, we manually reviewed the articles to select those that included oviparous philopatric lizard species. Through the combined efforts of Web of Science and Google Scholar searches and after manual screening, we identified a total of 12 articles, comprising 6 research manuscripts, 2 reviews, and 4 opinion articles or similar brief communications.

Our field data originated from in-situ observations conducted by us and other field biologists. These field observations took place in Sri Lanka, covering various geographical regions and multiple habitat types over a 10-year period (2012–2022). We conducted opportunistic surveys to study different lizard species during this time frame.

Results and discussion

We discovered that 23 reptile species (previously described) exhibit philopatry and engage in communal nesting. All of these species belong to the family Gekkonidae, which is endemic to Sri Lanka, and can be categorized into two genera: Calodactylodes (golden gecko; one species) and Cnemaspis (day geckos; 22 species) (refer to Supplementary Materials 1). The golden gecko, known as
Calodactylodes illingworthorum, inhabits the eastern and south-eastern regions within dry-mixed evergreen forests [43, 44]. Females from these species lay their eggs inside communal nests located in vertical rock crevices situated on isolated and unexposed granite rock outcrops (please refer to Supplementary Materials 2).

Although these outcrops have dense vegetation growth, they are situated within forests. In general, clutch sizes for golden geckos ranged from 276 to 185 eggs, with each egg measuring 11.2 mm × 12.6 mm. The equivalent figures for all day gecko species were 14 to 112 eggs, with egg sizes ranging from 4.7 mm to 5.2 mm. In both species, the eggs were white and spherical in shape (refer to Supplementary Materials 2), but the eggshells of golden geckos were notably more robust than those of day geckos. Information on variations in oviposition-site choice for these species was largely unknown and undocumented. However, careful observations of oviposition sites revealed that relatively few nesting sites were available, and there was limited flexibility in their nesting behavior. Furthermore, these nesting sites had relatively high canopy cover (65%), which reduced solar exposure. Consequently, the eggs would be subjected to higher environmental temperatures due to climate warming [34].

These species exclusively use rock cavities and crevices as nests, with very rare instances of utilizing wattle and daub houses attached to rocks. There is no evidence to suggest any ground digging or any other manipulation of nesting substrates, making the transition to novel nesting substrates such as soil or leaf-litter implausible. The biogeographical zones where these lizards inhabit either have consistent temperatures throughout the year or minimal temperature variations between seasons (rainy vs. dry), making temporal shifts in oviposition ineffective. Therefore, the most viable option for females is likely to seek alternative nesting sites with cooler substrate temperatures. These alternative thermally favorable microclimates can be found by moving into shaded outcrops with canopy protection or selecting rock outcrops with different orientations to the sun. Erosion caves of varying geological origins may also offer alternative nesting sites, although their usefulness for diurnally active geckos remains questionable due to poor illumination.

These communal nesting gecko species are exclusively rupicolous. Most other Day gecko species in Sri Lanka are also predominantly rupicolous, with only a few being arboreal or ground-dwelling. Therefore, rupicolous oviposition is evidently a conservative trait across the lineage. Given the morphological and biomechanical constraints, the evolution of novel traits, such as digging into the forest floor or manipulating substrates, is highly unlikely. Nevertheless, no research has been conducted to explore their reproductive and pre-rational plasticity or their evolutionary adaptive traits to compensate for climate warming.

Moreover, Sri Lanka’s communal nesting gecko species are geographically isolated, have small range sizes (area of occupancy 1 km² and extent of occurrence 2 km²), and are limited to small localities and habitat patches [41, 45]. The forest patches inhabited by these species are approximately 50–100 ha in size, ranging between 10–1800 m in altitude. Their habitats are isolated by anthropogenic landscapes or rivers and streams, while they mostly inhabit forested and woodland landscapes outside the protected area networks. Across this wide elevation gradient, despite thermalclines and variations in orographic precipitation, all communal-nesting geckos consistently use rock outcrops and caves for oviposition. Similarly, their nesting sites remain unchanged, regardless of the varying sizes of the forest patches. However, more eggs and egg clutches can be observed in larger forests and fewer in smaller ones. These observations imply that nesting-site selection is a highly conservative and less flexible trait.

All of these species are microhabitat specialists with narrow fundamental and realized niches, limited to moist, cool rock outcrops embedded in forests and farmland. These observations indicate that cool and damp environments are essential for the survival of these species, highlighting the narrow ecological niches they occupy [27]. This could be one of the key drivers of speciation in these geckos, where narrow ecological niches likely served as an isolating mechanism. Most importantly, this also underscores the fact that these species are at very high risk of extinction because this point endemism contributes to the entire population unknowingly facing extinction due to climate warming. In addition to direct physiological stress, rising temperatures, reduced precipitation, and other climate extremes can lead to reduced forest growth and increased forest mortality [26]. Drought-affected forests may not effectively protect the rock outcrops from other environmental stressors. Furthermore, the habitats of these species are constantly disrupted by anthropogenic activities such as the explosion of granite boulders, illegal legging, and man-made forest fires [44]. These human-induced insults can exacerbate the climate-change predicament for these geckos. Species movements in search of alternative oviposition sites can be stressful for these limited dispersal species [46].

This information helps identify the taxa most vulnerable to climate warming, aiming to reduce the likelihood of their extinction in tropical and subtropical countries. Furthermore, the biogeographic patterns of these species, distributed across remote localities or existing in extremely small populations, remain poorly studied, resulting in a lack of information for their conservation efforts [45]. They face a high risk of extinction due to climate warming, which is exacerbated by habitat loss, geographical isolation, long-term neglect, a poor understanding of their genetic resources, relationships with each other, and their area of origin. Therefore, local conservation action plans are necessary to prioritize the extinction risks of these species before the entire population unknowingly faces extinction due to climate warming.

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http://doi.org/10.1073/pnas.1800425115


