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Natural History of the Gecko *Hemidactylus prashadi*: Demography, Spatial Partitioning, Diet, and Reproduction in a Human-altered Habitat

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Abstract.—**Human-induced alterations have had a profound impact on the environment affecting several species. Many lizards, however, especially members of the gecko genus *Hemidactylus,* are cosmopolitan and are found living on buildings in urban areas. Nevertheless, how some reptiles colonize and thrive in human-altered habitats remain relatively less explored, partly due to the lack of adequate natural history on different species. Here, we study the natural history of Prashad's Gecko (*Hemidactylus prashadi*), a poorly studied, large-bodied gecko, which is believed to have recently colonized houses in the study region. We report new populations of this species extending the range further south to Kerala, India. We also studied the demographic structure, spatial partitioning, diet, and reproduction of the lizard in a residential building in Kozhikode district, Kerala. We found the population in the building was dominated by adult females and juveniles, while adult males and sub-adults were few. Perch height and non-lethal injuries of individuals on the building suggest intense intraspecific competition and spatial partitioning between juveniles and adults. Diet was mostly arthropods but showed low frequency of light-attracted insects. Reproduction extended from November to May with a clutch size of two eggs, but we also observed an instance of possible communal nesting. Overall, our study provides detailed natural history of a population of *H. prashadi*, which has recently started occupying human-altered habitats.**

Key Words.—Prashad's Gecko; demography; diet; ecology; human-modified habitats; lizards; niche partitioning; reproduction

Introduction

Human-induced alterations to nature have been one of the most prominent environmental changes on the planet within the last two centuries (Zhou et al. 2015), negatively affecting the survival of many species (McKinney 2006; McDonald et al. 2008; Aronson et al. 2014). Many lizards, particularly members of the family Gekkonidae, however, are considered cosmopolitan species and are well adapted to living in urbanized environments (French et al. 2018). Among gekkonids, the genus *Hemidactylus*, with over 173 recognized species, is one of the most speciose and widely distributed groups globally (Uetz, P., P. Freed. and J. Hošek [Eds.]. 2021. The Reptile Database. Peter Uetz. Available at http://www.reptile-database.org. [Accessed 29 March 2021]). Several species of this genus are common in human habitations and have successfully colonized new areas by human-mediated translocations (Vences et al. 2004). How reptiles respond to anthropogenic disturbances may vary with species, habitat, and life histories (French et al. 2018); however, a broader understanding of what traits allow these geckos to colonize and adapt to urban environments is lacking due to inadequate natural history information on many species.

In India, the genus *Hemidactylus* is represented by approximately 45 species (Uetz et al. 2021, *op cit*.), yet almost nothing is known about the ecology and natural history of most species. Among the few studies that describe their natural history, most only provide notes on the distribution and a qualitative assessments of microhabitat use (e.g., Giri et al. 2003; Giri and Bauer 2006; Gaikwad et al. 2009; Pal et al. 2013). Natural history, however, is broad and encompasses every aspect of the life of an animal including distribution, demography, inter and intraspecific interactions, and life history based on direct observations (Greene 1986, 2005). While the field of natural history has not been well appreciated by some scientists in recent years (Noss 1996; Futuyma 1998), there is growing concern regarding the general lack and incompleteness of natural history data and its importance in conservation (Greene and Losos 1988; Bury 2006; Greene 2005). There is also a need to revitalize the practice of natural history through improving the technology and quality of empirical data collected in the field (Greene 1986; Tewksbury et al. 2014). Here, we try to bridge this gap in the natural history of Indian lizards by providing preliminary information on the demographic structure, diet, and life history of the Prashad's Gecko (*Hemidactylus prashadi*) in a human-altered habitat.

Materials and Methods

Study organism.—*Hemidactylus prashadi* is a large-bodied gecko endemic to the Western Ghats of India (Giri and Bauer 2006). The species was first described from the neighborhood of Jog in North Kanara district, Karnataka (Smith 1935), and has subsequently been reported from several localities in the Western Ghats of Karnataka, Goa, and Maharashtra (Giri and Bauer 2006; Naniwadekar and Deepak 2010; Tikader and Sharma 1992; Jadhav et al. 1991; Srinivasulu et al. 2014). Although primarily rupicolous (dwelling among the crevices of rocks in deep forests; Jadhav et al. 1991), some studies have observed this species living on trees and on the walls of houses in villages (Giri and Bauer 2006; Naniwadekar and Deepak 2010). Our surveys in the midland hillocks of Kerala, India, have found populations of this species in Madaippara in Kannur District and Karingad, Chengodumala, and Thuruthamala in Kozhikode District, extending the range of this species further south into Kerala (Fig. 1). Recent phylogenetic analyses based on the ND2 gene have confirmed that these populations are indeed *H. prashadi* (Ishan Agarwal, pers. comm.). We focus our observations on two of these populations in Kerala.

Study site.—We carried out our observation on *H. prashadi* in two midland hillocks in Kozhikode District:

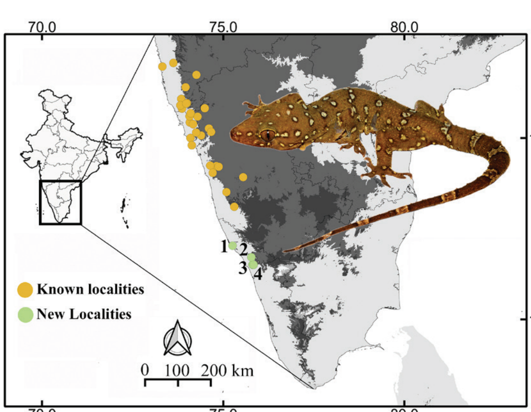

Figure 1. Photograph of the Prashad's Gecko (*Hemidactylus prashadi*) showing the spot pattern used for individual identification of geckos along with a distribution map. Points on the map show localities from previous studies (orange; see Srinivasulu et al. 2014 for list of localities) and the current study (green). The new localities are 1 - Madaipara, 2 - Karingad, 3 - Chengodumala, and 4 - Thuruthamala. (Photographed by Vivek P Cyriac).

Chengodumala and Thuruthamala. Chengodumala (11.50749N, 75.80667E) is an abandoned plantation that is now a heavily fragmented and degraded forest due to extensive illegal granite quarrying. Thuruthamala (11.50611N, 75.83944E) is more heterogeneous, with rubber and coconut plantations, several reed patches, large open rock structures, and moist deciduous to semi-evergreen forest patches. The hilltop has a small human settlement with six houses widely separated from each other. Our interactions with the residents of Thuruthamala indicated that the estate was established in 2000 and that *H. prashadi* had recently colonized the houses, arriving 2–3 y after construction. Our study focused on one of the residential buildings where the plantation workers resided. The residence was a single-story building on an approximately rectangular plot with a basal area of 56.16 m^2 with three rooms and tiled roofing.

Field sampling and individual identification.—We made opportunistic observations whenever possible on the population in Chengodumala and Thuruthamala during multiple visits between 2010 and 2013. We also carried out more systematic observations at the residence in Thuruthamala making 15 visits between July 2012 and August 2013. During each visit, we spotted geckos using a flashlight during the night between 1900 and 2100.

For each gecko that we successfully captured, we applied a temporary field identification number and photographed the dorsal spot pattern using a Cannon 1000D™ SLR camera (Cannon India Pvt. Ltd., Gurgoan, Haryana, India), which we found to be unique to individual geckos. We ensured that photographs were taken perpendicular to the geckos from an approximate distance of 30 cm to maintain consistency and increase individual identification accuracy. We used the software I3S Manta™ (Tienhoven et al. 2007), which facilitates individual identification based on comparing the natural markings of individuals from photographs. For each image, we marked three reference points, one on the tip of the snout and the other two on both the knees of the hindlimbs. Each spot present within these three reference points was then marked and added to the database supplemented with sex, age class, the snout-vent length (SVL), and tail length (TL). We determined the sex of adults by the presence or absence of femoral pores and hemipenal bulge, while we could not determine the sex of juveniles and sub-adult geckos. We categorized age classes by SVL: juvenile (35–59 mm SVL), sub-adult (60–84 mm SVL) and adult (≥ 85 mm SVL). We determined these categories based on approximate ages inferred from the time intervals between recaptured individuals, wherein size ranges corresponded to an approximate age of 1–6 mo for juveniles, 6–12 mo for sub-adults and greater than 12 mo for adults (pers. obs.). To further facilitate individual identification, we also noted the pattern and number of natural scars or injuries on each individual. Scars and injuries included any fresh or healed wounds on the integument and the loss of digits on the limbs.

Demographic structure.—We analyzed the demographic structure separately during two time periods to avoid placing the same individual in two separate age groups: between July and November 2012 during the non-breeding season and April to May 2013 towards the end of the breeding season (see reproductive ecology section of results). To estimate the population of *H. prashadi*, we carried out five capture-recapture sessions during April 2013. Capture-recapture was restricted to two weeks with a two-day gap between each of the five capture sessions. During each capture session, we caught individuals and photographed and identified them by comparing the spot pattern in I3S Manta. We analyzed the capture history using the program CAPTURE (White et al. 1982) implemented in Density v.5.0.3.1 (Efford et al. 2004). The site where we conducted the capture-recapture sessions was isolated and considerably far enough (about 300 m) from other residential buildings or natural rock boulders to have not included individuals from outside the building. Further, we restricted the capture sessions to a short duration compared to the expected life span of the gecko, which for tropical geckos is estimated to be 2–4 y (Bustard and Hughes 1966; Pancharatna and Kumbar 2005). Also, sampling was conducted at the end of the breeding season (see reproduction section of results), thereby reducing the chances of new individuals being added to the population. Thus, we assumed no death, birth, immigration, or emigration in the populations and considered the population to be a closed population. We compared the fit of five closed models, a null model (M0), a model accounting for temporal variation in capture probability (Mt), accounting for behavioral responses (Mb), heterogeneity in capture probability model (Mh) under a 2-point finite mixture distribution and a Beta-binomial distribution. We evaluated these models using the second derivative of Akaike's Information Criterion (AICc).

Perch height and non-lethal injuries.—To examine if geckos spatially segregated themselves, we recorded the perch height and age class before capturing each gecko during each visit. We recorded three categories for the perch height on the walls: 0–1 m, 1–2 m, and 2–3 m from the ground. To evaluate the level of intraspecific competition and/or predation within the population, we noted the number of scars or injuries on the body and the tail condition for each gecko. In cases where there were multiple missing digits on the limbs, we counted these injuries as one for each limb and did not count each missing digit as separate injuries. We recorded tail condition as being original or autotomized irrespective of the number of times a gecko may have had its tail autotomized.

Diet.—We determined the diet of *H. prashadi* between July 2012 and August 2013 by examining fecal pellets collected from the building in Thuruthamala. During each visit, we collected relatively fresh fecal pellets in individual plastic zip-lock bags. After each collection, we cleaned the surrounding area to ensure that we collected fresh fecal pellets defecated during that particular season. We examined each fecal pellet under a stereomicroscope by gently spreading out the contents using forceps in a petri dish containing water, and photographed the prey remains. We identified the prey items in each pellet to the level of order using taxonomic keys (Gullan and Cranston 2014). To evaluate temporal variations in the diet, we categorized the prey consumed during three seasons: summer, monsoon, and post-monsoon. We then calculated the Levin's Standardized Niche Breadth Index (*B*; Hurlbert 1978) for the three seasons using the formula

$$B = (1/\Sigma p_i^2) - 1/n-1$$

where p_i is the proportion of prey item i in the diet composition and n is the total number of prey items observed in the diet. Levin's index ranges from 0–1, where a value of 0 indicates a highly specialized diet where only one or few prey items are consumed, while a value of 1 indicates that all prey items are eaten in equal proportion.

Reproductive ecology.—Because we did not observe geckos mating, we determined the breeding season based on the number of months we observed gravid females (determined visually through the translucent abdomen) and eggs. When we found eggs, we noted the clutch size and nesting site characteristics, and we incubated them *ex-situ* at room temperature (24°–28° C) in plastic containers with sand as the substrate. Two of these eggs incubated *ex-situ* were laid by a gravid female captured from Thuruthamala in January 2013 while being maintained in captivity for a few days before being released. We measured and weighed eggs before incubation. We measured and photographed hatchlings and added them to the I3S Manta database. We later released hatchlings back to the capture site.

Statistical analyses.—We used R 3.3.2 (R Core Team 2016) for all statistical analyses. We tested for differences in the frequency of different prey types in the fecal pellets of *H. prashadi* using a Chi-square test. We then performed pairwise comparisons between the prey type categories using the R package RVAideMemoire v. 0.9–69 (Hervé 2014). To test for seasonal variation in the diet, we carried out pairwise comparisons of the four most prominent prey types across three seasons. The proportion of each prey type in the fecal pellets was compared between summer (April), monsoon (May-July) and post-monsoon (September) using a Fisher's Exact Test on the proportions.

To test for perch height preferences, we first carried out a Chi-square test on the number of individuals of each age class occupying the three perch height categories, after which we carried out pairwise comparisons of the groups using the RVAideMemoire v. 0.9–69 package (Hervé 2014). We also calculated the niche overlap in perch height use between the three age classes using Pianka's Niche Overlap Index (O_{jk}; Pianka 1973)

$$O_{jk} = \frac{\sum_i^n p_{ij}\, p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \, \sum_i^n p_{ik}^2}}$$

where p_{ij} is the proportion of resource *i* to the total resources used by age class *j*, p_{ik} is the proportion of resource *i* to the total resources used by age class *k*, and n is the total number of resource states. We calculated the Pianka's Niche Overlap Index using the EcoSimR v. 0.1.0 package (Gotelli et al. 2015). We tested for an association between the number of scars/injuries and SVL using a non-parametric Kendall's Rank Correlation test. We also tested whether the number of individuals with autotomized tails were significantly different from individuals with original tails using an Exact Binomial Test. For all tests, $\alpha = 0.05$.

Results

***Demographic structure*.**—We identified 21 individuals of *H. prashadi* using photo-identification between July 2012 to August 2013. These included eight adult females, five adult males, two sub-adults, and six juveniles. We recorded 11 individuals each during the non-breeding period (July-November 2012) and during the end of the breeding period (April-May 2013). During both periods, the demographic structure was similar with a greater number of adult females and juveniles than adult males and sub-adults (Fig. 2). Capture-recapture in April 2013 led to 21 captures of 10 individuals made over the five sampling sessions (Table 1). The number of unique individuals captured increased with each sampling but stabilized by the fourth sampling occasion (Table 1). The model selection indicated the null model (M0) as the best-fit model and was significantly better than all other models (ΔAICc > 3). We found a per occasion capture probability of 0.42 for the 10 individuals captured for the null model. The overall capture probability for the null model, i.e., the probability that an individual has been captured on at least one occasion, was 0.93. The estimated population size of *H. prashadi* in the building was 10.0 ± 1.0 (standard deviation), with a confidence interval of 10.0–14.1. Program CAPTURE provides only the upper bounds of the confidence interval and the total number of individuals captured as the minimum number of individuals in the population.

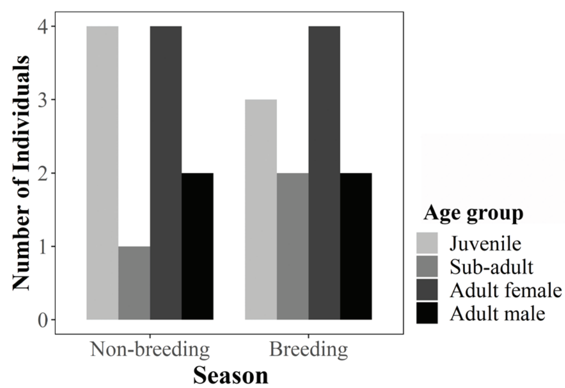

FIGURE 2. Demographic structure of the Prashad's Gecko (*Hemidactylus prashadi*) during the non-breeding season (July-November 2012) and breeding season (April-May 2013) from a building in Thuruthamala, India.

***Perch height and non-lethal injuries*.**—Perch height differed significantly among age classes ($X^2 = 17.65$, df = 4, $P = 0.001$). Adults occupied higher perches on the walls (2–3 m) significantly more than the 0–1 m ($P = 0.007$) and

TABLE 1. Capture history of individual Prashad's Gecko (*Hemidactylus prashadi*) for five capture sessions from a building in Thuruthamala, Kozhikode, India. Age class are juvenile (J), sub-adult (SA), and adult (A), sexes are female (F), male (M) and unknown (UN), and if the individual was captured (1) or not captured (0) during each particular session.

Gecko ID	Age class	Sex	Sessions 1	2	3	4	5
HP1	SA	UN	1	0	0	1	1
HP5	A	F	1	0	0	1	0
HP7	A	M	1	1	0	1	1
HP8	A	F	1	0	0	0	1
HP9	A	F	0	1	0	0	1
HP10	A	F	0	1	1	0	1
HP12	J	UN	0	0	1	0	0
HP13	A	F	0	0	1	0	0
HP14	SA	UN	0	0	1	0	1
HP15	A	M	0	0	0	1	0

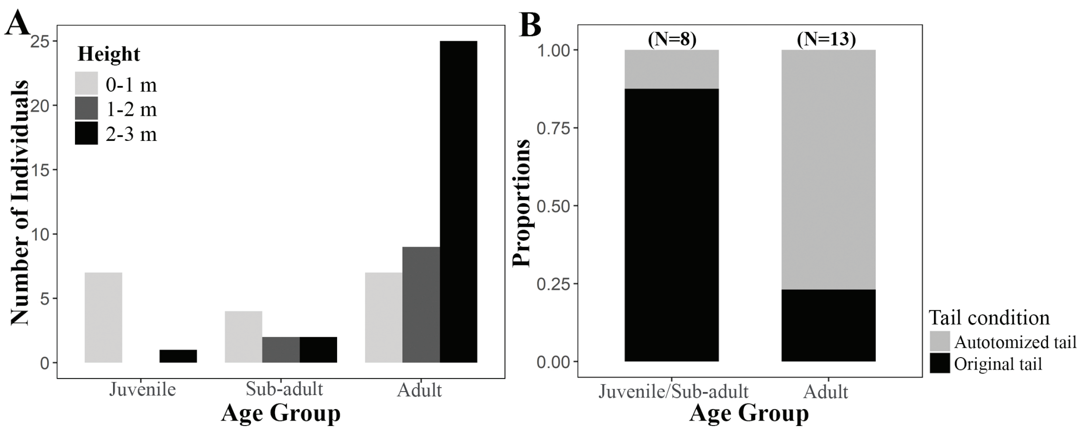

Figure 3. Perch height selection and non-lethal injuries in the Prashad's Gecko (*Hemidactylus prashadi*) from a building in Thuruthamala, India. (A) Number of individuals of *H. prashadi* of different age classes occupying different perch heights. (B) Proportion of individuals with autotomized/regenerated tails among juveniles/sub-adults and adults.

1–2 m (P = 0.024) perch height categories. Juveniles predominantly occupied the lowest perches (0–1 m) compared to higher perches (0–1 m) compared to the higher perches (1–2 m: P = 0.026; Fig. 3); however, there was no significant difference in the perch heights occupied by sub-adults (all $P > 0.05$). Sub-adults considerably overlapped perch heights with juveniles (O = 0.866) and adults (O = 0.713). Niche overlap was low between juveniles and adults (O = 0.381). There was a significant positive correlation between SVL and the number of body scars (τ = 0.264; Z = 2.80, P = 0.005). A significantly higher number of adults had autotomized tails (n = 13, P = 0.048), while a significantly higher number of juveniles and sub-adults had their original tails intact (n = 8, P = 0.039; Fig. 3).

Diet.—The diet of *H. prashadi* in Thuruthamala was mainly arthropods belonging to six orders of insects and one order of arachnid (Table 2). We found 76 prey items from 67 fecal samples. Cockroaches (Blattodea) were the dominant prey item comprising 39.47% of the total prey, followed by beetles (Coleoptera) with 23.68%, spiders (Araneae) with 11.84%, and grasshoppers and katydids (Orthoptera) with 10.52%. Earwigs (Dermaptera), wasps (Hymenoptera), and mantises (Mantodea) together accounted for < 8% of the diet, while 6.57% of the items remained unidentified (Fig. 4).

The mean number of prey items per fecal sample was 1.09 ± 0.30 (standard deviation) during summer, 1.08 ± 0.27 during monsoon, and 1.25 ± 0.44 during post-monsoon period. The number of prey types in fecal pellets differed significantly (X^2 = 72.211, df = 7, P < 0.001). Pairwise comparison indicated that cockroaches were significantly higher in representation compared to all other prey types (Fisher's Exact Test, P < 0.010) except beetles (Fisher's Exact Test, P = 0.130). The frequency of beetles was significantly higher compared

Table 2. Diet composition (sample size, n, and percentage of total) of Prashad's Gecko (*Hemidactylus prashadi*) from 76 fecal samples collected from a building in Thuruthamala, India, during summer (n = 23), monsoon (n = 28), and post-monsoon (n = 25) seasons.

	Summer		Monsoon		Post-monsoon	
Prey	n	%	n	%	n	%
Araneida	1	4.35	2	7.14	6	24.0
Blattoidea	11	47.8	12	42.9	7	28.0
Coleoptera	7	30.4	5	17.9	6	24.0
Dermaptera	1	4.35	1	3.57	1	4.00
Hymenoptera	1	4.35	0	0	1	4.00
Mantodea	0	0	1	3.57	0	0
Orthoptera	2	8.70	4	14.3	2	8.00
Unidentified	0	0	3	10.7	2	8.00
Niche Breadth Index *B*	0.28		0.42		0.54	

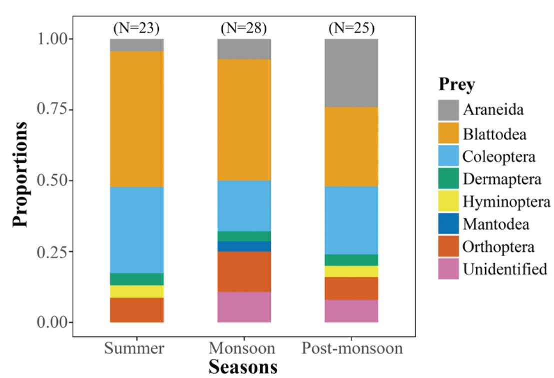

Figure 4. Diet composition of the Prashad's Gecko (*Hemidactylus prashadi*) from a building in Thuruthamala, India. Plot shows the proportion of different prey items found in the fecal pellets of *H. prashadi* during summer, monsoon, and post-monsoon. The abbreviation N represents the number of fecal pellets examined during each season.

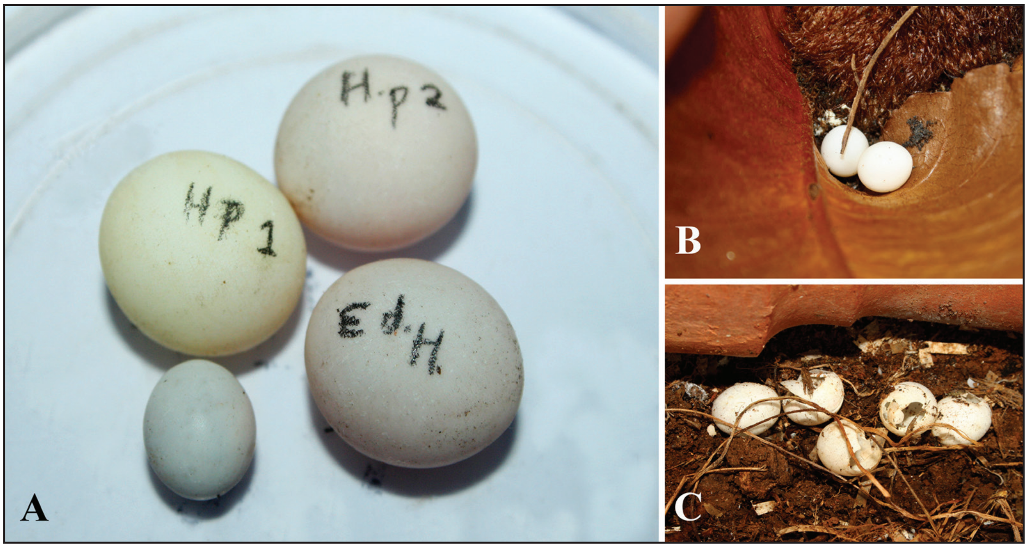

Figure 5. Eggs of the Prashad's Gecko (*Hemidactylus prashadi*) found in southern India. (A) Three eggs of *H. prashadi* along with an egg of the South Asian House Gecko (*H. frenatus*) for size comparison (Photographed by Vivek P Cyriac). (B) A clutch of two eggs of *H. prashadi* found in the center of a fern (*Dryneria.* sp.) growing on the side of a rock boulder in Chengodumala, Kozhikode, India (Photographed by P.K. Umesh). (C) Potential communal nesting in *H. prashadi* showing four hatched and one unhatched egg found under a roofing tile in Thuruthamala, Kozhikode, India (Photographed by P.K. Umesh).

to mantids, hymenopterans, dermapterans and unidentified prey types (Fisher's Exact Test, $P < 0.05$) but was not significantly different from spiders (Fisher's Exact Test, $P = 0.130$) and grasshoppers and katydids (Fisher's Exact Test, $P = 0.100$). The frequency of spiders, grasshoppers, and katydids was significantly higher compared to mantises (Araneae: Fisher's Exact Test, $P = 0.029$; Orthoptera: Fisher's Exact Test, $P = 0.046$). The proportion of the four main prey items in the diet did not differ seasonally (Fisher's Exact Test, all $P > 0.05$). Trophic niche breadth was lowest during summer ($B = 0.28$) but increased during monsoon ($B = 0.42$) and post-monsoon ($B = 0.54$) seasons.

Reproductive ecology.—We did not observe mating in *H. prashadi*; however, we found gravid females between November and May. In Chengodumala, where *H. prashadi* is found among rock boulders, we found two eggs 6 December 2010 laid in the center of a fern (*Dryneria* sp.) that was growing on the side of a rock boulder (Fig. 5). We also found eggs in the building in Thuruthamala between January and May in cracks in the walls, in cardboard boxes, and underneath plastic covers that were hung on the walls. The six eggs incubated *ex-situ* were large, white in color, and measured an average of 15.57 ± 0.432 (standard deviation) mm in length, 13.64 ± 0.287 mm in width, and weighted 1.68 ± 0.075 g (Fig. 5). Four of the eggs that we incubated *ex-situ* hatched 51–56 d from the date of collection, while the two eggs laid by the gravid female took 90 d. We also found four hatched and one unhatched egg behind a pile of tiles in Thuruthamala 6 May 2013 (Fig. 5). Neonates incubated *ex-situ* had an average SVL of 39.0 ± 1.72 mm and an average tail length of 43.9 ± 2.19 mm.

Discussion

Demography and intraspecific competition.—We estimated population size at our study site to be 10.0 geckos (95% confidence interval, 10.0–14.1) during our sampling sessions. Our observations also indicate that the demographic structure of *H. prashadi* in the building was similar during both sampling periods in 2012 and 2013. We found higher numbers of adult females and juveniles during both periods, while numbers of adult males and sub-adults were comparatively low. Although our evaluation of demographic structure is based on a small number of individuals ($n = 21$), our ability to individually identify geckos in the building adds confidence that the demographic structure likely reflected actual numbers in the focal sub-population during the study period. Studies on other lizards have indicated that sub-adult males generally disperse out of the population due to intense intraspecific competition with adults, and therefore are less represented in the population (Clobert et al. 1994; Locey and Stone 2008; Stabler et al. 2012).

Our analyses indicate that tail autotomy and injuries/scars were high in adult *H. prashadi*. Non-lethal injuries such as body scars and lost digits have long been used to quantify the level of inter and intraspecific interactions in natural populations (Schoener and Schoener 1980; Vervust et al. 2009; Donihue et al. 2015). Around 70%

of adults had scars or missing digits, which could have been from previous or recent aggressive encounters. The number of wounds on the geckos was positively correlated with SVL, suggesting that aggressive interactions were more intense in adult geckos. Around 77% of adults also had regenerated tails. Tail autotomy is a well-known antipredatory defense in many lizards and is a measure of predator inefficiency (Arnold 1984; Bateman and Flemming 2009), and thus expected to be higher in adults (Werner 2017). Recent studies, however, have indicated that tail autotomy can be driven by intraspecific competition rather than predation (Pafilis et al. 2009; Brock et al. 2014; Itescu et al. 2017). For example, in two species of geckos, tail autotomy rates decreased with different predation indices and increased with gecko abundance (Itescu et al. 2017). There are also direct observations of lizards biting off the tails of conspecifics (Deem and Headman 2014). Although the high tail loss in adult *H. prashadi* could be due to predation from Domestic Cats (*Felis catus*) or rats (*Rattus* spp.), it could also be indicative of high aggressive interactions with conspecifics competing for the same resources. Interestingly, on one occasion, we also observed kleptoparasitism in these geckos, where the larger among two geckos approached and snatched a katydid prey from a third smaller individual (Fig. 6). Kleptoparasitism is generally thought to increase with increased competition (Broom and Ruxton 1998; Hamilton 2002), and thus is further suggestive of high intraspecific competition among adult geckos.

Height selection among individuals indicated spatial partitioning between age classes. Juveniles mainly occupied lower perches near the ground while adults occupied higher perches. Giri and Bauer (2006) also observed similar niche partitioning in natural habitats where juveniles of *H. prashadi* were predominantly observed on trees while adults were more rupicolous (rock dwelling). We also found overlap in perch height between sub-adults and adults, suggesting that sub-adults may also move to higher perches at a tipping point of being too big for low perches and too small for high perches. As individuals grow, the intermediate-aged animals share much of their prey resource with juveniles and adults (Polis 1984). Such dietary requirements may force sub-adult *H. prashadi* to ascend to greater perch heights. On the other hand, moving to higher perches may expose them to aggressive encounters with adults forcing them to disperse into adjacent areas (Locey and Stone 2008). Studies have suggested that juveniles and sub-adults are the primary agents of diffusion dispersal in lizards (Clobert et al. 1994; Locey and Stone 2008; Stabler et al. 2011; Lange et al. 2013). Although we did not examine dispersal rates, our results suggest that sub-adults may experience more aggressive encounters with adult geckos as they grow older and thus disperse out of the population explaining the disproportionately

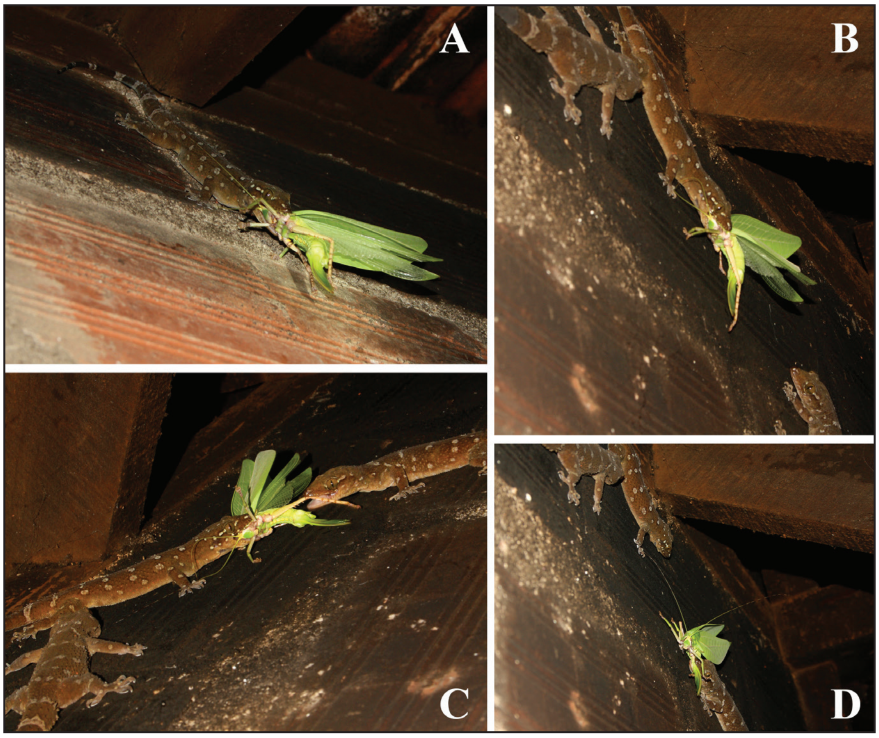

Figure 6. Kleptoparasitism in the Prashad's Gecko (*Hemidactylus prashadi*) from Thuruthamala, India (Photographed by P.K. Umesh). (A) An adult *H. prashadi* with a captured katydid. (B) Two conspecifics approaching the individual with the captured prey. (C) The larger of the two geckos snatching the prey from the smaller individual. (D) The larger gecko moving away with the stolen prey.

low numbers of sub-adult in the population.

Diet.—The diet of *H. prashadi* based on our fecal pellet analysis was essentially arthropods. We found that *H. prashadi* were not dietary specialists but foraged heavily on roaches and beetles. Some studies have questioned the reliability of fecal pellets in diet analyses due to the lower representation of soft-bodied prey in fecal pellets (Angelici et al. 1997; Pincheira-Donoso 2008). We found that soft-bodied prey such as spiders were comparatively well represented in fecal pellets suggesting that fecal pellets can be a reliable source of dietary information. Interestingly, we found very low or no representation of lepidopterans and dipterans that are generally attracted to artificial light. Dietary studies on geckos inhabiting urban areas have found high frequencies of lepidopterans and dipterans, thought to be due to artificial lighting (Powell et al. 1990; Saenz 1996; Tkaczenko et al. 2014; Barragán-Ramírez et al. 2015; Akintunde et al. 2020). Geckos found away from artificial lighting, however, have been found to have higher proportions of non-flying insects (Iturriaga and Marrero 2013). The low representation of light-attracted insects in the diet of *H. prashadi* could indicate the avoidance of artificial lights. Although we did not record lighting levels and sources, our general observation found these geckos to be more active on walls with dim or no artificial lighting. Similar avoidance of lighted areas or a preference for dim and dark areas has been observed in the Mediterranean Gecko (*H. turcicus*), a gecko well adapted to urban environments in the USA (Meshaka 2011).

While we found no significant seasonal dietary differences in *H. prashadi*, niche breadth was low during summer, indicating stronger preference to certain prey while diet was more generalized during monsoon and post-monsoon. Although we have not examined how prey diversity changes across seasons in Thuruthamala, studies have shown that arthropod diversity generally increases during the monsoons (Janzen and Schoener 1968; Pearson and Derr 1986; Frith and Frith 1990; Arun and Vijayan 2004). The change in dietary niche breadth of *H. prashadi* could reflect such seasonal changes in arthropod diversity.

Reproduction.—We captured gravid females between November and May, suggesting an extended breeding season similar to many other tropical and urban-adapted *Hemidactylus* (Sanyal and Prasad 1967; Selcer 1986; Shanbhag et al. 1998; Punzo 2001; Anjos and Rocha 2008). Shanbhag et al. (1998) found that the Brook's House Gecko (*H. brookii*) in south India (possibly Murray's House Gecko, *H. murrayi*, according to recent taxonomic revisions: Lajmi et al. 2016) have an acyclic extended breeding period from October to June unlike the Northern House Gecko (*H. flaviviridis*) found in north India, which had a cyclic reproduction (Sanyal and Prasad 1967). The breeding season we inferred for *H. prashadi* was consistent with those reported by Shanbhag et al. (1998), suggesting an asynchronous and prolonged breeding season. Giri and Bauer (2006) reported that juveniles of *H. prashadi* in wild populations were only seen during June to August, suggesting a restricted or peak in breeding activity. Although we are unsure if *H. prashadi* shows peaks in breading activity in the wild, our observations of juveniles throughout most of the year (April-November) and gravid females between November and May indicate extended breeding activity in human-associated populations in Thuruthamala.

Eggs incubated ex-situ hatched between 51–90 d, suggesting a gestation period of around three months. Interestingly, we also observed possible communal nesting in *H. prashadi*. Occasionally, geckos produce a single egg or rarely two mature eggs in a single ovary leading to three eggs being laid (Church 1962; Fitch 1970). Thus, a clutch of five eggs must be by at least two females. The five eggs we found in May 2013 were not observed during our earlier visits between July 2012 and January 2013, suggesting that these eggs were likely laid after our previous field visit during the same season. Communal nesting is rare among members of the genus *Hemidactylus* but has been recorded in the Moreau's Tropical House Gecko (*H. mabouia*) and *H. turcicus*, which are both invasive species of geckos associated with human habitations (Selcer 1986; Paulissen and Buchanan 1991; Locey and Stone 2007; De Sousa and Freire 2010). Communal nesting in lizards is generally a response to the relative scarcity of nesting sites or for predator protection or because of direct benefits from metabolic heating or regulated hydric exchange due to proximity to other eggs (Rand 1967; Radder and Shine 2007; Mateo and Cuadrado 2012). Being a rupicolous gecko, *H. prashadi* may prefer to lay eggs in rock crevices or among plants found on rock boulders; however, the lack of such microhabitats in human habitations may force these geckos to share available nest sites.

The ability to successfully establish populations and adapt to urban environments has been extensively studied in birds and mammals and are attributed to several factors (e.g., Kark et al. 2007; Santini et al. 2019). In comparison, little attention has been given to understand how reptiles adapt to urban environments and, in turn, how this may contribute to range expansion of some species (French et al. 2018). Several species of *Hemidactylus* have been considered cosmopolitan lizards and are known to have a wide distribution shaped by both natural transoceanic dispersals and human-mediated transport (Vences et al. 2004). Upon reaching new localities, many of these geckos have rapidly colonized human habitations and expanded their ranges (Case et al. 1994; Petren and Case 1996; Meshaka 2000; Meshaka et al. 2006; Locey and Stone 2006). Here, we present a natural history account of *H. prashadi*, a species that has recently occupied human habitations in Kerala and we shed some light on the population and life history of species colonizing human altered environments.

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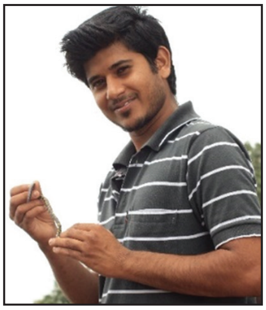

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