Breeding phenology of *Psammophilus dorsalis*: patterns in time, space and morphology

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Since reproduction is costly, animals are expected to invest in reproduction when abiotic and biotic conditions are optimal. Although tropical ecosystems are not as starkly seasonal as temperate ecosystems, some tropical ecosystems may experience high seasonality in conditions that affect reproduction. Systematic studies of breeding phenology from tropical ecosystems are scarce. We describe the breeding phenology of *Psammophilus dorsalis*, a sexually dimorphic, diurnal, rupicolous lizard found in the tropical scrub forests of peninsular India. Regular census was conducted covering multiple habitat patches for three years, recording age and breeding status of lizards. Lizards were systematically caught, tagged, measured and released. We report clear breeding seasonality, with most males showing breeding colouration from May to September and juveniles emerging from September until April. Timing of breeding coincides with the annual peak in daily maximum temperatures, while juvenile emergence might be affected by the timing of the annual precipitation peak. We report that this is a predominantly annual species with a female-biased sex ratio and strong male-biased dimorphism in multiple morphological traits. In the face of climate change, detailed studies of breeding phenology of tropical animals are important, particularly for ectotherms, since these taxa are easily affected by changes in temperature and precipitation patterns.

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STUDIES on breeding phenology (i.e. the periodic changes in reproductive behaviour and physiology exhibited by animals within a year) indicate that not all animals reproduce throughout the year, tracking local conditions to time breeding activity[1,2]. The timing and length of breeding seasons are thought to result from cyclic annual variations in important biotic and abiotic conditions that influence offspring production, growth and survival[3]. Maximizing resource availability for offspring growth and survival is thought to be a primary influence on the timing of births[4], which, in turn, influences the timing of the breeding season. Temperate ecosystems witness large intra-annual variation in abiotic factors (mainly temperature and precipitation)[5], which cascades into variation in primary productivity[6], and hence resource availability. Breeding seasons are correspondingly typically short in these ecosystems[7,8]. In contrast, the tropics exhibit less seasonality and climatic variability and, hence, more consistent resource availability. Therefore, tropical animals are usually not expected to show the strikingly time-constrained patterns in breeding phenology of temperate animals.

Nonetheless, certain tropical and sub-tropical ecosystems may still show high seasonality because of local geographic and climatic factors (e.g. onset of monsoon). In such habitats, organisms are expected to show correspondingly seasonal breeding activity. Moreover, owing to physiological constraints, certain ectothermic taxa may require narrow ranges of temperature and precipitation for their reproduction[9,10], and thus, may show seasonality in breeding behaviour. However, there are relatively few systematic studies of breeding phenology on tropical animals. Studies on breeding phenology have been carried out mostly in temperate areas[11–13].

We examined the phenology of the reproductive behaviour of *Psammophilus dorsalis*, a tropical, diurnal lizard commonly found on rocky outcrops across peninsular India. The study site, Rishi Valley, Andhra Pradesh, shows high seasonality in rainfall and temperature. We expected that the reproductive behaviour of *P. dorsalis* would be strongly linked with the seasonal pattern in temperature and rainfall. By intensively monitoring an open population spread across multiple habitat-patches, we describe the annual cycles of rise and fall in the abundance of breeding adults and juveniles, which are indicators of the breeding season and of the period during which births occur respectively. Across these habitat patches, we compare patterns in adult densities and sex ratios observed during and outside the breeding peak. We also outline seasonal patterns in body-size (a proxy for age often used in reptile studies[14]) across the sexes over multiple years. We compare patterns seen in the breeding phenology of *P. dorsalis* with annual patterns in climatic variables (namely, air temperature and rainfall).

Methods

Study animal

Psammophilus dorsalis commonly occurs across peninsular India[15] (Supplementary Figure A). This lizard is rupicolous,

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diurnal and mostly insectivorous, though known to prey upon other smaller lizards[16,17]. The maximum lifespan reported in the wild is three years[18]. They are highly sexually dimorphic with males being much larger than females[19]. They are reported to breed during summer, with females typically laying 1–2 clutches of 5–7 eggs per clutch. Males show considerable variation in colouration, especially during breeding season (when they are jet black laterally and ventrally and bright yellow or orange dorsally), while the females maintain camouflaged colouration (Figure 1). Males lose their bright colours during non-breeding season. There are no systematic studies of the breeding phenology of *P. dorsalis*.

Study area

We studied *P. dorsalis* at Rishi Valley (13°32′N, 78°28′E; ca. 750 m elevation), Andhra Pradesh, India, between October 2009 and September 2013. The area receives rainfall from May to November. Even during this period, the amount received is low (annual average: 700 mm) and inconsistent, since it only occurs as flash-rains on relatively few days (Figure 2 *a*). Local temperatures are particularly high from March to May (annual range: 8–41°C). *P. dorsalis* is typically found on large boulders, and flat spans of granite strewn with rocks and mostly devoid of vegetation (sheet-rock henceforth). These sheet-rocks are found in a matrix of scrub and

Figure 1. Tagged male and female *Psammophilus dorsalis* in their habitat.

thorny vegetation, but lizards are typically not seen in the matrix. Based on reconnaissance visits, we selected 5 sheet-rocks, viz. Duranta Hill (DH), Boda Bunda 1, 2, 3 (BB1, BB2, BB3) and Gyadi Dona Bunda (GDB) that represented the observed natural variation in the sizes of sheet-rocks (Supplementary Table A). Each sheet-rock was mapped using a GPS (Garmin™ eTrexH), and their areas were calculated using QGIS (version 1.7.2 Wroclaw).

Daily measurements of maximum and minimum air temperature and rainfall were obtained from the weather station at Rishi Valley School.

Censuses

We defined fixed routes comprehensively covering each sheet-rock. As GDB was much larger than the other sheet-rocks, we defined multiple routes on it that were scanned in the same sequence for each census. One of the authors (S.D.) surveyed them by walking at a steady pace of 3–5 kmph and spotted lizards visually with the naked eye or with binoculars. Once a lizard was spotted, its location (sheet-rock), identity (if tagged), life-stage (juvenile if snout-vent length (SVL) less than ~6 cm and adult otherwise), sex (for adults only; juveniles could not be sexed) and reproductive status were recorded. Males were classified as breeding if they displayed breeding colouration. Females were classified as gravid if they showed a bulging abdomen. We collected data on reproductive status of adults from January 2011 to September 2013.

Initially, in a pilot study (October 2009 to June 2010), censuses were conducted during morning (0700–1200 h), afternoon (1200–1600 h) and evening (1600–1900 h). Based on the results of this study (Supplementary Figure B), further surveys for long-term monitoring were carried out only during the morning sessions, when lizard activity was highest. We surveyed each site once every two weeks during the breeding season (May–September) and at least once every month during rest of the year. Given the perching tendency of this species and the relatively small size of the focal sheet-rocks, most individuals on a sheet-rock are highly likely to be seen during a census. The lizard counts obtained using these censuses are a good index of the abundance of individuals, and are not used to estimate the total population present on the sheet-rock.

Morphometry

At the beginning of each breeding season (March) we captured, measured and tagged adult lizards intensively on the chosen sheet-rocks. The adult male population was sampled fully and a representative sample of females was obtained. As the breeding season progressed, any new adults arriving onto the focal sheet-rocks were also

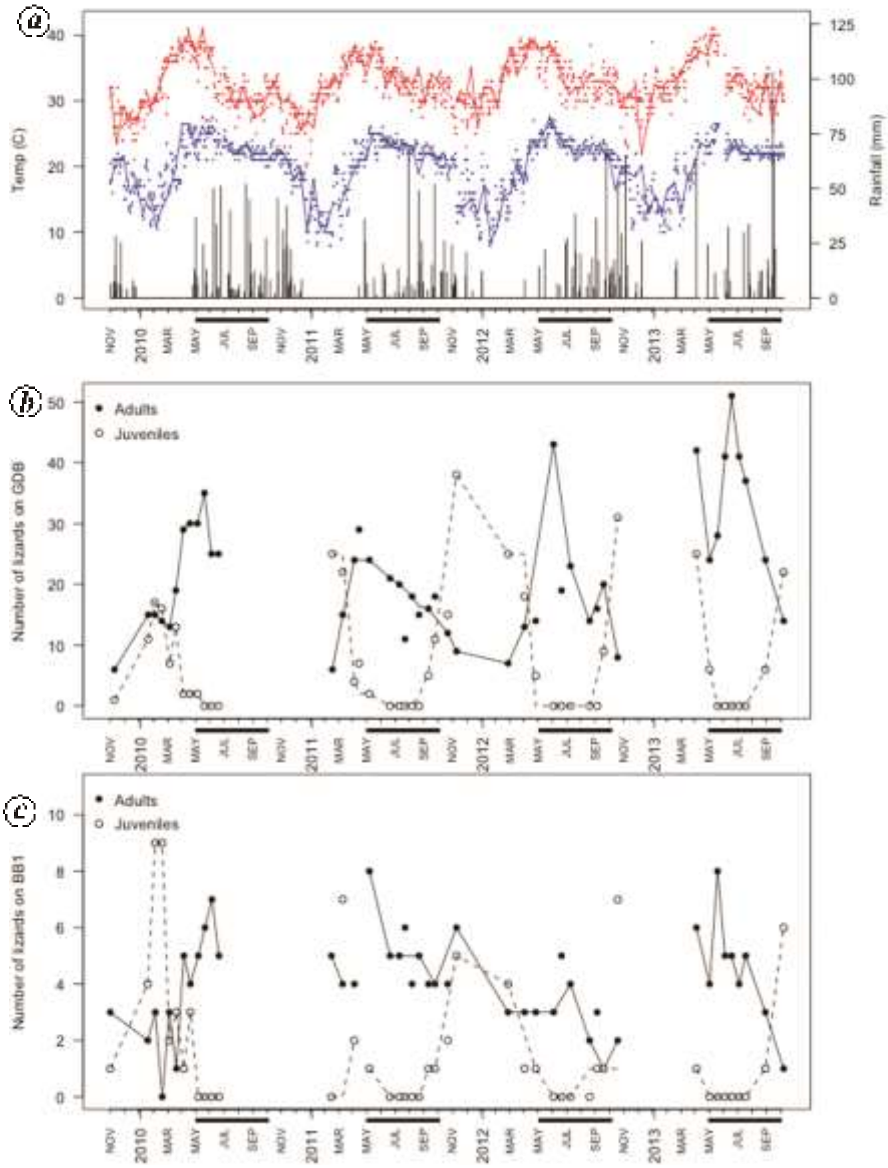

Figure 2. ***a***, Variation in temperature and rainfall at the study-site during the period of the study. Red and blue smoothing lines represent daily maximum and minimum temperatures respectively, while black bars indicate daily rainfall. ***b*** and ***c***, Total number of adults (solid dots) and juveniles (open circles) seen across 2 sites; GDB (***b***) harboured more lizards than other smaller sites like BB1 (***c***). Note difference in scales on y-axis. Refer to Supplementary Figure C, for details on the remaining small sheet-rocks. Solid lines above the month-labels depict the breeding season, May–September (see results).

tagged and measured. Lizards were caught by noosing. From 2009 to 2012, animals were tagged using a combination of temporary external markings (made on the dorsal surface of lizards using non-toxic ink) and permanent, injectable internal tags. Permanent tagging was carried out using PIT (passive integrated transponder) tags (Trovan™ ID-100B) in combination with a portable RFID (Radio Frequency Identification) reader (Trovan™ GR-250). For the year 2013, animals were tagged using colour-coded ceramic beads[20]. For each capture, we recorded weight, snout to vent length (SVL), tail length (TL), tail base width (TB), inter-limb length (IL), head width (HW), head height (HH) and head length (HL). Weight was measured to the closest gram using spring balances (Pesola™ Micro-line series). SVL and TL were measured using a ruler (least count 1 mm), while the rest of the measurements were carried out using vernier calipers (Mitutoyo™ Series 505) (least count 0.1 mm). We kept handling time to a maximum of 15 min, after which animals were released at their capture locations. All animal handling procedures were done in accordance with the animal-ethics guidelines of the Animal Ethics Committee of Indian Institute of Science, Bengaluru.

As part of an ongoing behavioural study, the sheet-rocks were visited at least three times a week during breeding season, and at least once a month during non-breeding season (apart from the censuses mentioned above). During these sampling sessions, tagged individuals were regularly re-sighted and recorded.

Analyses

Using smoothing (locally weighted polynomial regression), we graphically represent the annual patterns seen in juvenile and adult numbers, with a focus on the breeding status of adults. Unpaired *t*-tests and ANCOVA were used to compare SVLs and morphometric variation in HW respectively. All analyses were performed using R version 3.1.2 (ref. 21). We used the package lubridate to format and analyse data related to dates.

Results

Phenology

Peak maximum diurnal temperatures were observed from March to June (maximum: 41°C), while sporadic rainfall fell between May and November every year (Figure 2 *a*). The long-term morning census data revealed an annual pattern as well. Juveniles emerged onto the sheet-rocks starting from September until April (Figure 2 *b* and *c*). Relatively high numbers of adults were observed during the peak summer months (May–June) while relatively high juvenile numbers were seen in November–December, following the wet season. Out of the 205 lizards we tagged (138 males, 67 females), 194 (129 males, 65 females) were only seen during a single breeding season, while only 11 (9 males, 2 females) were seen in two consecutive seasons. The peaks in male and female numbers were temporally congruent (Figure 3 *a*). Within a year on any given sheet-rock, adult males were least abundant around January and most abundant around May–June. An annual cyclic pattern was observed in the data on mating activity of males, indexed by their display of breeding colouration. Most males displayed breeding colouration during May–September and non-breeding colouration during the rest of the year (Figure 3 *b*). A similar but weaker pattern was observed in the abundances of gravid versus non-gravid females. These patterns were more pronounced on the larger sheet-rock (GDB) (Figure 2 *b*) than on the small sheet-rocks like BB1, largely because lizard abundances were lower on the small sheet-rocks (Supplementary Figure C).

Behavioural observations (S.D., unpublished data) indicate that adults on a given sheet-rock maintained site-fidelity for months at a stretch. Out of the 208 individuals tagged in this study, there were only 6 instances of lizards moving between sheet-rocks. Lizards were most abundant on GDB (Supplementary Table B), the largest sheet-rock. Abundances were comparable at the rest of the sheet-rocks (DH, BB1, BB2 and BB3). Densities (lizards/ha) across sheet-rocks were similar (Supplementary Table B).

The sex ratio was typically female biased (GDB breeding season mean ± SD: 2.73 ± 0.27 females per male, non-breeding season: 1.61 ± 0.27, Supplementary Table B) and varied across sheet-rocks. Intensive observations made as part of an ongoing behavioural study indicated that the sex ratios seen during censuses were accurate and not biased by sex-differences in detectability, since additional females were not seen during these behavioural observations (unpublished data).

Morphometry

P. dorsalis adults showed a high degree of sexual size dimorphism. We used SVL as a measurement of body size. In general, males (mean ± SD = 10.15 ± 2.23 cm) were considerably larger than females (7.47 ± 3.12 cm) ($t = 9.84$, d$f = 225$, $P < 0.0001$), even when compared across large (GDB) and small (non-GDB) sheet-rocks. Male size was consistently larger during the breeding season (11.17 ± 1.12 cm) than during the non-breeding season (9.41 ± 2.40 cm) ($t = 5.19$, d$f = 148$, $P < 0.0001$). Females did not show any such seasonal pattern in their SVL (Supplementary Table A). Males also showed relatively larger heads (greater HW relative to SVL), when compared to females (Figure 4). HW seemed to increase faster relative to body size in males (slope >1) than in females (slope <1) (ANCOVA Interaction term Sex : log (SVL): $F_{1,198} = 82.68$, $P < 0.0001$). When compared to individuals larger than 8 cm SVL, the smaller individuals (6–8 cm SVL) showed rapid growth from February to June (Figure 5), with males growing faster than females.

Discussion

We report a strikingly predictable annual pattern in the breeding phenology of *Psammophilus dorsalis*. We also report large variation in adult abundances across space, and describe patterns in sexual dimorphism found in these lizards.

Breeding phenology

P. dorsalis showed clear seasonality in reproductive behaviour. The breeding season (courtship and mating activity) occurred from May to September, the time during which most adult males were in breeding colouration. Gravid females were seen from June until November, again indicating a restricted breeding season. Hatchlings started emerging from September (during the wet season) and continued till April. By May, very few juveniles occurred; most observed lizards were adults and the vast majority of adult males showed breeding colouration. These observations, taken together, indicate that juveniles show rapid growth and reach reproductive maturity by

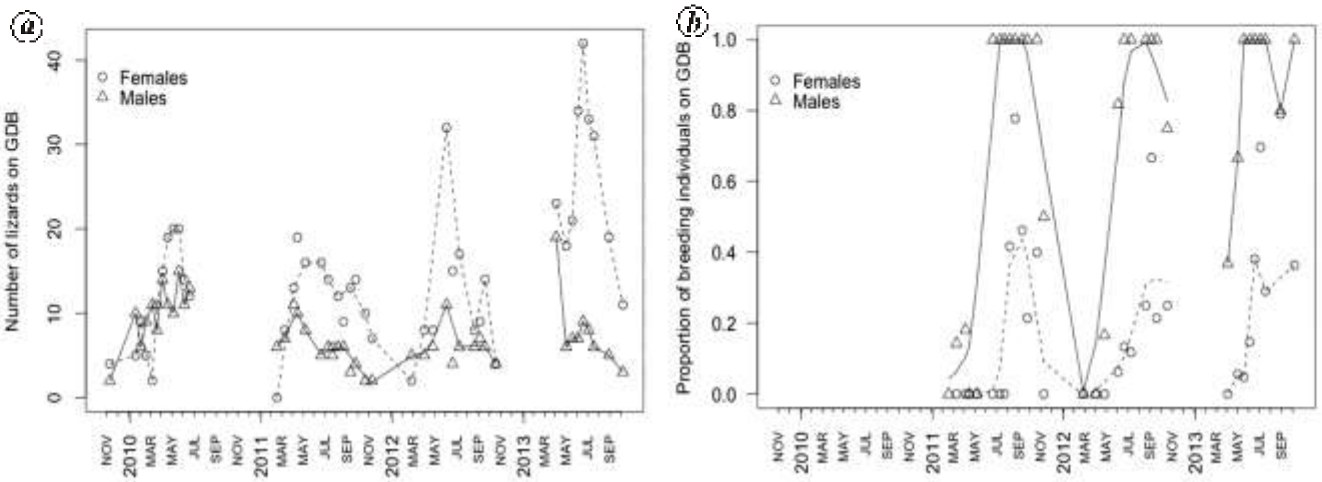

Figure 3. ***a***, Adult male and female abundances on GDB over the study period. ***b***, Proportion of adult males in breeding colouration (triangles) and females showing gravid status (circles) seen on GDB.

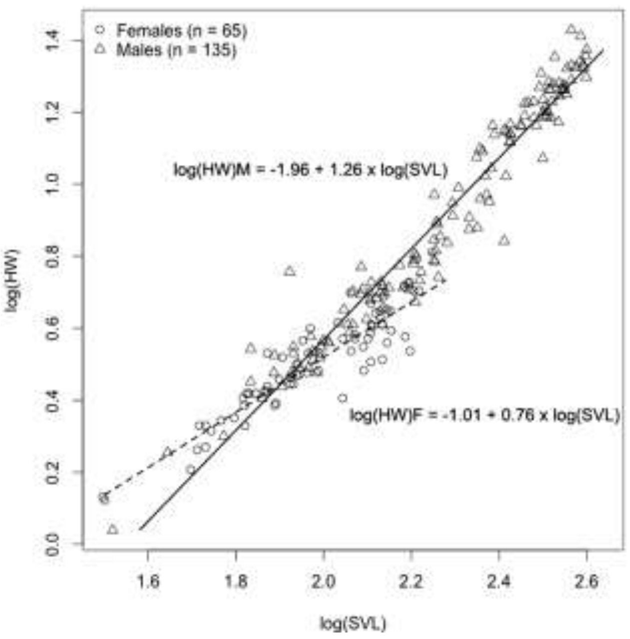

Figure 4. Relationship between head width (HW) and snout vent length (SVL) measured in cm and log-transformed. Controlling for body size, males have relatively larger HW than females. HW increases faster than SVL in males (slope >1, solid line) but slower than SVL in females (slope <1, dashed line).

the onset of the breeding season in May. A repeated measurement of size (SVL) over the lifetime of tagged individuals further confirms this inference (Figure 5). Adults continued to dominate the population during the breeding season until the next cohort appeared in August.

To the best of our knowledge, such clear seasonality with details of breeding phenology from a tropical lizard is being systematically documented for the first time. Our study site showed clear peaks in climatic variables, and the breeding status of lizards closely tracked these peaks. There are several possible reasons for this relationship. First, male mating behaviour and female egg-laying behaviour could be physiologically constrained by that year's climatic profiles. For example, the first monsoon rains could make the soil loose enough so that females are able to dig easily and initiate egg laying (S.D. personal observation). Second, the first hatchlings begin emerging on the sheet-rocks mid way through the monsoon season, when food resources for *P. dorsalis* (insects, juveniles of other smaller lizards) are likely to be most abundant. Similar patterns have been demonstrated in birds, where the time of hatching coincides with the wet season, when resources are most abundant[1]. Unlike males, which showed synchrony in their breeding status, we found that females were relatively less synchronous in their gravid status (Figure 3 *b*). This may be because: (a) females from this family are known to have multiple clutches in a given breeding season[22] and therefore mating activity may be temporally more restricted than egg-laying activity; (b) the gravid status of females was judged visually. This method may not always be accurate in assigning the gravid status of females.

An important finding from our study is that *P. dorsalis* appears to be predominantly an annual species. First, very few individuals (less than 5% of tagged individuals) were re-sighted across breeding seasons. Secondly, there has been no documented evidence of hibernation or aestivation in this species. Every year, hatchlings started emerging from August and were apparently able to reach reproductive maturity by May (the peak of the breeding season), inferred based on the temporal pattern in the size of the lizards caught, and supported by the repeated measurements made on a few individuals. Thirdly, behavioural observations made at focal and nearby sheet-rocks (unpublished data) and regular censuses indicate that

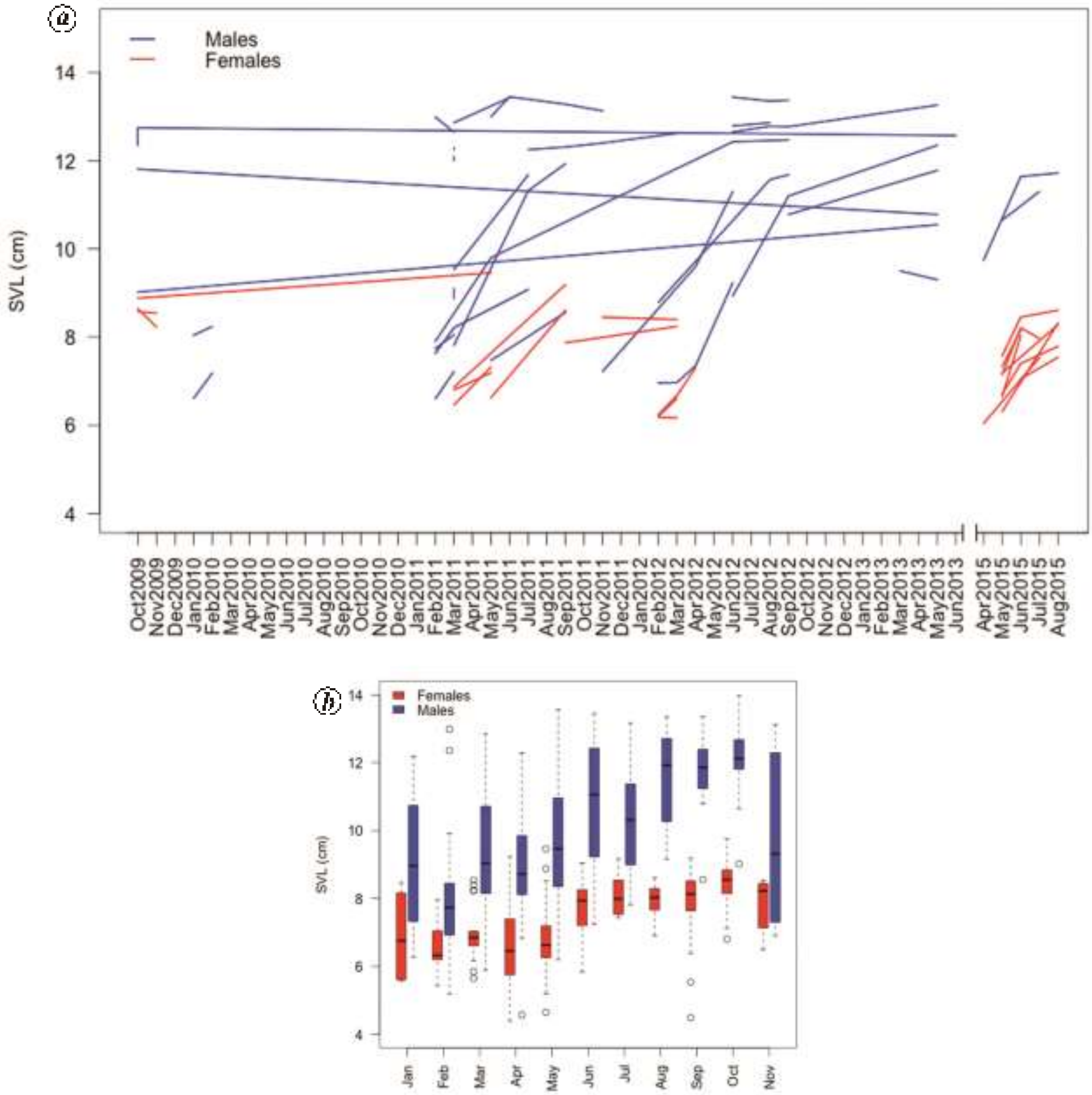

Figure 5. Repeated measurements of body size for tagged individuals recaptured once or more often during their lifetime. A line is an individual. ***a***, Parts of the timeline from our study period. Notice the high growth rates (steeper lines) of smaller individuals before and during first half of breeding season (February–June) compared to low/stagnant (shallow lines) growth of already matured larger individuals. ***b***, Size-composition of the population across months.

there is no large-scale movement of adults between habitat patches. Based on these findings, we conclude that most adults breed during only one breeding season and die at the end of it. Given the relatively large size of this lizard, this is a surprising finding. An alternative explanation for the disappearance of adults at the end of the first breeding season is that adults migrate to farther habitat patches at the end of their first breeding season. However, this is unlikely because, for non-migratory species like our study species, long-range movements are typically associated with dispersing juveniles rather than settled adults[23].

Sex ratios and sexual size dimorphism

We found clear patterns in adult sex ratio and sexual size dimorphism, suggesting that sexual selection is an important evolutionary process acting on male *P. dorsalis*. The sex ratio was generally female-biased (also documented in ref. 16); such a bias is generally thought to result from greater mortality on males due to behavioural and life history traits geared towards relatively high investment in mate competition when compared to females[24]. Together with the high level of spatial (across sheet-rock variation in abundances) and temporal clustering (Figure 3) of females and a strong female-biased sex ratio (Supplementary Table A), the strong male-biased size and colour dimorphism seen in *P. dorsalis* also indicates a high potential for sexual selection to act on males in this species. Using an extensive, multi-year data set, we substantiate the earlier reports of size dimorphism in *P. dorsalis*. Males, across seasons and habitat patches, were always larger than females. Adult males were larger during the breeding than during the non-breeding months; females did not show this pattern. This is possibly because males showed a steeper growth trajectory than females (Figure 5). Non-breeding males were largely the younger males. By the time the breeding season started (in May), most males showed substantial and rapid growth, unlike females that seemed to grow slowly. Male head width also increased rapidly unlike that of females suggesting that bite force is important in male–male competition.

Conclusions

We described prominent annual patterns in the breeding phenology of *P. dorsalis*. It was found that this is potentially an annual species with a female-biased sex ratio, and strong male-biased size-dimorphism. Dedicated studies monitoring the breeding phenology of non-charismatic taxa in general, and Indian reptiles even more so, are very rare. Ectotherms like reptiles and amphibians need such detailed studies, especially in the face of climate change, since these taxa are at a high risk from changes in temperature and precipitation patterns.

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