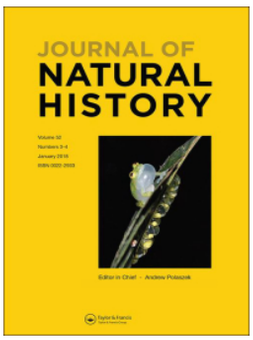

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Observations on natural diet and reproductive behaviour of an endemic snail *Indrella ampulla* (Benson 1850) (Gastropoda: Ariophantidae) from the Western Ghats, India

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ABSTRACT

This study investigates the natural diet and breeding behaviour of *Indrella* (Ariophantidae), a monotypic snail genus endemic to the Western Ghats in India. Our observations show that the only *Indrella* species, *I. ampulla*, is a generalist in its dietary preference. Its diet consists predominantly of a variety of plants and plant materials, occasionally interspersed with fungi and dead conspecifics. Its breeding season overlaps with the monsoon in the Western Ghats – May through September. During mating, copulating pairs display 'face-to-face' mating and 20 to 30 eggs are laid. Hatching success in the field could not be assessed. Low hatching success under artificial conditions and the difficulty of locating and monitoring the egg clutches in the field warrant further exploration with a greater effort to ascertain their reproductive success. This study reports the first natural history observations of this common yet relatively unknown snail species *Indrella ampulla*.

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KEYWORDS
breeding; conservation; food preference; terrestrial snail; Western Ghats

Introduction

Indrella ampulla (Benson 1850) is a large terrestrial stylommatophoran gastropod belonging to the family Ariophantidae. The genus is endemic to India's Western Ghats and is monotypic, originally described from 'Koorda Ghat', Nilgiri Hills, in south-western India (Benson 1850; Blandford and Godwin-Austen 1908). *Indrella ampulla*, based on current understanding, is a widespread and locally abundant species distributed in the wet evergreen forests of the central and southern Western Ghats (between 9.00 and 13.25° N; Aravind unpublished). *Indrella ampulla* has four colour morphs: yellow, red, orange and bi-coloured (Raheem et al. 2014; Chakraborty and Aravind 2020). The red morph occurs below 10°N, whereas the yellow and orange morphs are sympatric and occur between 10 and 13°N in the Western Ghats (Chakraborty and Aravind 2020). Henry H. Godwin-Austen (1901) provided the first detailed report on the anatomy (including the reproductive anatomy) of *I. ampulla* based on specimens collected from the Nilgiris district in Tamil Nadu State of southern India (now Nilgiri district). Similar to many other terrestrial

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gastropods from the tropics, this species, despite its large body size and bright colouration, has not enjoyed much attention in research, leaving a dearth of information in terms of its ecology, natural history and phylogeography since its original description.

Many natural history studies across the globe have shed light on terrestrial mollusc feeding preferences and reproductive strategies (Mason 1970; Chatfield 1976; Jennings and Barkham 1979; Seifert and Shutov 1979; Raut and Ghose 1983; Chang 1991; Oli 1996; Gupta and Oli 1997; Parkyn et al. 2015). Food preference is influenced by their habitat, the abundance and distribution of food resources, competition, predation risk, and the season and time of day (Williamson and Cameron 1976; Chang 1991; Iglesias and Castillejo 1999; Gillete et al. 2000; Scott et al. 2005).

On the other hand, a compilation of reproductive behaviour of stylommatophoran snails and slugs by Davison and Mordan (2007) reports on only four of the 30 genera within the family Ariophantidae (Mitra et al. 2005). To the best of our knowledge, there exists no new report or update to this information, reiterating the lack of information about the natural history of tropical land snail species. Furthermore, most of the studies mentioned above represent species from the temperate regions, and are lacking in information on molluscs from the tropical regions. India is home to at least 1140 species of land snails (Sajan et al. 2021) with high diversity in the two biodiversity hotspots, viz. the Western Ghats and Northeast India (a part of Indo-Burma hotspot; Aravind, unpublished). Only a handful of studies discuss the feeding ecology of the Indian snails, based on laboratory research as well as field conditions (Senthilkumar and Thirunavukarasu 1989; Oli 1996; Oli and Gupta 1997; Valarmathi 2017; Barman et al. 2021; Yadav et al. 2021). In the present communication, we provide the first comprehensive field-based natural history observations on feeding, reproductive behaviour and colour shift during ontogeny in *I. ampulla* from multiple locations across the Western Ghats.

Materials and methods

All observations related to feeding and breeding behaviour of *I. ampulla* are based on opportunistic sightings during fieldwork, carried out between April 2017 and June 2020. Observations were carried out at Lakkidi (11.5127°N, 76.0356°E, 827 m asl) and Meppadi (11.5627°N, 76.1593°E, 866 m asl) in Wayanad district of Kerala, and in the Anamalais (10.3166°N, 76.8733°E, 962 m asl), in Southern India. Mid-elevation wet-evergreen forests characterise both study areas, with a similar rainfall regime of 3000–4500 mm, received mainly during the south-west monsoon between June and October. Temperature ranges from 8°C during the coldest months (December to February) to 35°C during the warmest months (April and May). The study areas have plantations, predominantly coffee (*Coffea arabica* and *C. robusta*) in the Wayanad regions and tea (*Camellia sinensis*) in the Anamalai regions. Apart from the above-mentioned sites, some feeding observations by the senior author from other parts of the Western Ghats are also included where necessary.

Observations of feeding activity and diet were carried out in both study areas. For every observation made in the field, information on the feeding activity and duration was manually noted and the activity was photographed wherever possible. Reproductive behaviour and development were studied only for the individuals of the yellow morph (the type morph of *I. ampulla*) from Lakkidi, Wayanad, in the Western Ghats. The temperature during the observation period was between 25 and 27°C, with humidity over

90%. The sites had a 100% canopy cover of large evergreen trees, and the forest floor was covered with a thick layer of litter and fallen branches and logs. The soil was generally wet due to heavy rains. A total of six pairs of live individuals of two colour morphs (three pairs each of yellow and bicoloured) were kept captive in a glass terrarium (24 × 12 inches) for 15 days to observe reproductive behaviour in captivity concurrently with mating pairs that were observed in wild. Since none of the pairs showed any mating behaviour in captivity, only the observations from the field are reported here. Hatchling success in captivity was observed by carefully relocating the eggs from the wild to a 10 × 10 × 5 inch terrarium, replicating the substrate and water levels observed at the collection site (ovipositional site). Shell size was measured using a Mitutoyo™ digital calliper to the nearest 0.1 mm.

Results

In both study areas, *I. ampulla* appears to be a fairly common species, found in a wide variety of habitats such as wet evergreen forests, coffee and cardamom plantations, and even human habitations close to the natural forests. The average species encounter ratio is approximately six individuals per 200 m^2 in all regions studied. It is generally found on branches of small shrubs, on fallen and decaying logs, and occasionally on the forest floor. The activity period of *I. ampulla* is limited to late summer after initial monsoon showers (late April to May) and during the south-west monsoon season (June to October), during which the average temperature is around 18 to 25°C. Although there was no evidence of aestivation, *I. ampulla* was observed to be dormant inside rock crevices and tree holes, underneath leaves and occasionally in building and crevices within, during the other times of the year.

Feeding

Indrella ampulla is an opportunistic feeder and was observed feeding on a wide range of flora (fresh plant matter of angiosperms, mushrooms and lichens) and scavenging on dead plant and animal matter in all sampling locations during the study period (Figure 1). Juveniles were always seen feeding on the surface of trees, rotten logs or litter on the forest floor, and no scavenging behaviour was observed among them. A list of feeding observations from areas across the Western Ghats is provided in Table 1. In one instance, the red morph of *I. ampulla* was found feeding on human faeces at Valparai in Anamalai forest region in Southern India.

Breeding

Mating pairs were observed during April in Wayanad, after the first showers, generally along streams where the moisture is high and the climate is cooler. While most mating pairs were sighted during the night (after 18.00 hrs; n = 16), few sightings were also made during the day (n = 6), mostly early in the mornings (06.00–09.00 hrs) when the humidity was high and the temperature was low. All mating pairs were sighted on the forest floor or on rocks close to water bodies, or very rarely on trees (we made one observation of a mating pair on a tree trunk at about 2 m from the ground). However, many individuals

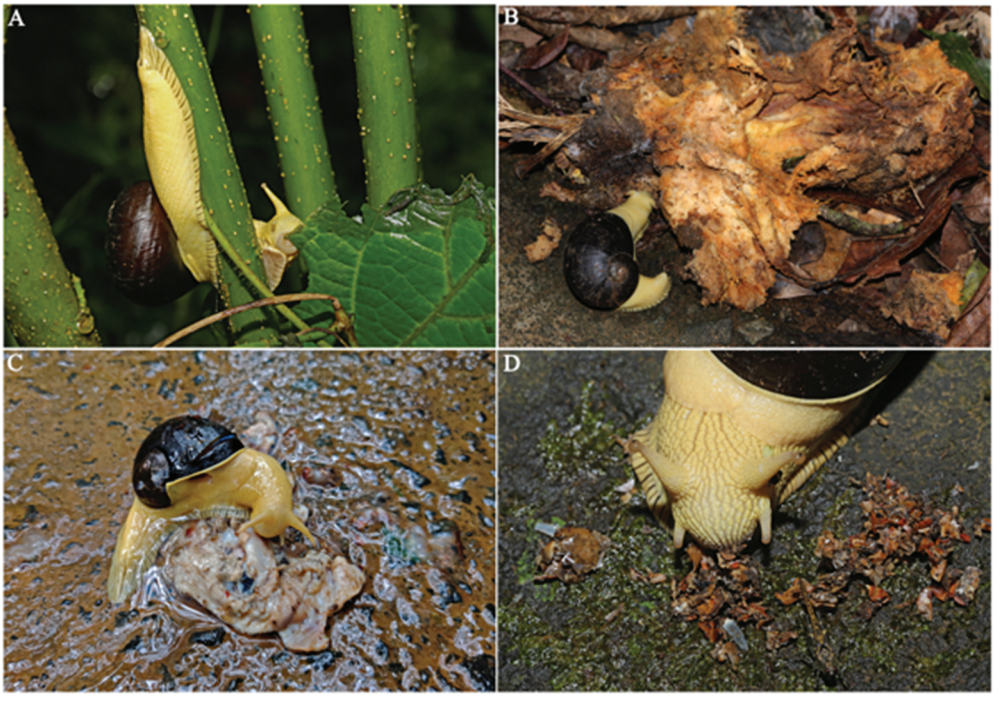

Figure 1. *Indrella ampulla* (from Wayanad) feeding on different food items. (a) *Burmansia* sp., (b) decaying *Artocarpus heterophyllus* fruit, (c) road-crushed *I. ampulla*, (d) unknown droppings. Images not to scale.

were seen in the forest canopies (10 m and above); therefore, mating in the treetops is considered possible but has not been observed. The copulation position in mating pairs was 'face-to-face simultaneous reciprocal' (see Davison and Mordan 2007), with the head of one individual curled towards the lower lateral side of the other's mantle (Figure 2(a)). The posterior part of the foot was curled towards the left side of the anterior part of the other individual, reaching close to the posterior left dorsal lobe. The phallus everts from the right side of the anterior portion of the head and curls along the opposite individual's phallus, passing through its right lateral surface to reach the female organ in both individuals simultaneously. The pointed distal end of the amatorial organ reaches the mating partner's lower surface, just below the buccal cavity (Figure 2(d)), and both individuals remain motionless or nearly motionless for about 15 minutes. The phalluses are reverted for a brief gap of about 1 minute and then the process repeats, for 6–8 consecutive cycles. However, of the two observations of mating pairs (n = 2), each lasting approximately 2.5–3 hours, both times we failed to observe the eversion of the penis and transfer of sperm. A basic ethogram is provided in Table 2. Since most molluscan reproductive observations are based on captive individuals, we attempted the same with *I. ampulla*. But none of the six pairs kept in captivity for 3 weeks attempted to mate.

We found one clutch of 20–30 smooth, spherical (5–6 mm) thin-layered eggs inside a mud crevice in the forest floor at about 07.30 hrs on 15 May 2018 at Wayanad. Eggs were initially unidentified, as there are no previous reports of the eggs of *I. ampulla*. We collected 8–10 eggs from this clutch and placed them in the aforementioned terrarium.

Table 1. Summary of food sources for *Indrella ampulla* from the Western Ghats.

Locality	Food	Parts	Colour morph	No. of Individuals	Source
	Plants and fruits				
Wayanad	*Strobilanthes* sp.	Leaf	Yellow	20	This study
Wayanad	Angel's trumpet (*Brugmansia* sp.)	Leaf	Yellow	4	This study
Wayanad	Mango (*Mangifera indica*)	Fruits	Yellow	30	This study
Wayanad	Coffee fruits (*Coffea cenophora* and *C. arabica*)	Fruits	Yellow	10	This study
Wayanad	Areca nut (*Areca catechu*)	Fruits and leaves	Yellow	3	This study
Wayanad	Jackfruit (*Artocarpus hetrophylus*)	Fruits	Yellow	15	This study; Kinloch 1921
Wayanad	Jackfruit (*Artocarpus hirustus*)	Fruits	Yellow	4	This study
Idukki	Cardamom fruit (*Ellettaria cardamomum*)	Flowers and fruits	Red	15	Sen et al. 2016 This study
Coorg	Hibiscus (*Hibiscus rosa-sinesnsis*)	Flowers	Orange	5	This study
Nylliampathy	Fungus	Thallus	??	??	Kinloch 1921
Coorg, Idukki	White mushroom (unidentified species)	Full	Orange, ???, red	2 ?? 1	This study Blanford and Godwin-Austen 1908 www.jungledragon.com/image/65070/indrella_ampulla.html
Coorg, Idukki Wayanad	Lichens (unidentified species)	Thallus	Orange, red, yellow	5 each	This study
Anamalais	Moss		Orange	1	www.youtube.com/watch?v=gCnkoQ6nRJg
			Red	1	www.flickr.com/photos/65624062@N08/23865356425/
	Animals (roadkill and carcase) and others				
Wayanad	Elliot's forest lizard (*Monilesaurus ellioti*)		Yellow	1	This study
Wayanad	Leaping frog (*Indirana* sp.)		Yellow	1	This study
Wayanad	Yellow treefrog (*Polypedates pseudocruciger*)		Yellow	1	This study
Wayanad	Bicoloured frog (*Clinotarsus curtipes*)		Yellow	2	This study
Wayanad	*Indrella ampulla* (road-killed individual)		Yellow	2	This study
Valparai	Human faeces		Red	4	This study

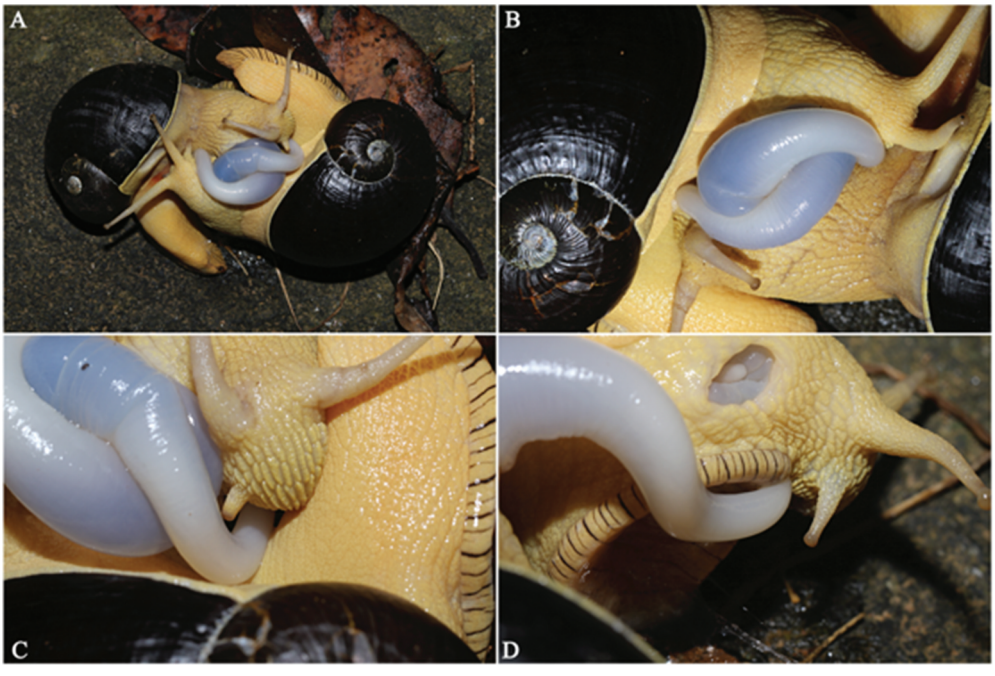

Figure 2. Reproductive behaviour of *Indrella ampulla*. (c and d) showing closeups of mating and phallus organs. Images not to scale.

Table 2. Tentative ethogram of reproductive behaviour of *Indrella ampulla*.

Behaviour	Description
Coming close	Two individuals come close to each other
Circling of the mating individuals	The two individuals circle each other simultaneously for almost 15 minutes in the curved body position
Face-to-face position	After circling, they remain motionless for a few minutes
Simultaneous reciprocal	Both individuals are involved in mating, by fertilising each other
Eversion of amatorial organ	Amatorial organs of the two individuals evert at the same time and pierce each other near head
Eversion of penis	Penis everts towards the end of the mating and happens simultaneously for the two individuals
Sperm exchange	Not seen during our observation
Separation of individuals	After about 2.5–3 hours, the two individuals separate from each other
Egg laying	Lay eggs in the crevice under the rock, on the fallen tree or in a similar secluded place. We have seen eggs in the crevices but have not observed any individual laying eggs during our field observation. We presume egg laying happens in the night even though mating may occur in the morning.

Of these, six eggs hatched within 8 days from the date of collection and were confirmed as *I. ampulla*, after observing the hatchlings. A second clutch of 24 eggs (5–6 mm) was found inside a crevice of a fallen tree alongside a stream with soil substrate and partially filled with water, at about 21.30 hrs on 25 June 2019. Fourteen eggs were collected from this clutch to compare the hatchling success between the ovipositional site and in captivity. Unfortunately, all the eggs in the ovipositional site were washed out following torrential rains. Only three out of 14 eggs hatched in

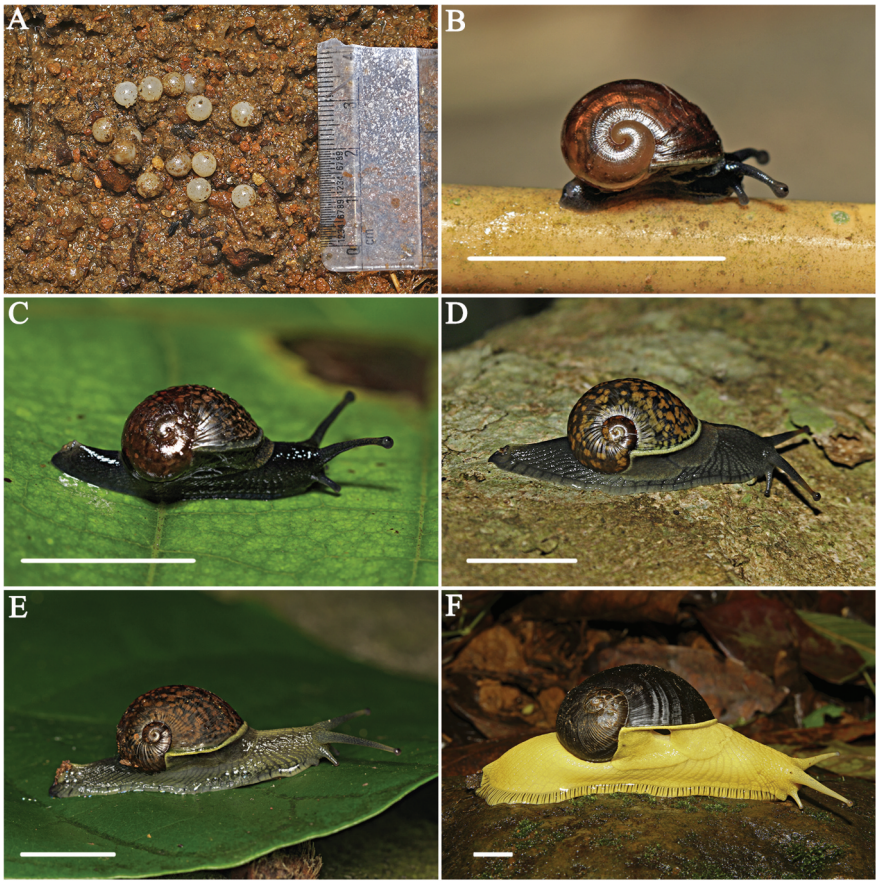

Figure 3. Eggs (in terrarium) and colour change in different developmental stages of *Indrella ampulla*. Scale (b–f) = 1 cm.

captivity. Hence, with the limited available information, it is rather difficult to ascertain the incubation period of the eggs and hatching success, as the information on when the eggs were laid is uncertain.

Hatchlings measured 4–5 mm on average, with a very soft shell that was brown in colour with slight black patches (Figure 3(c)). During this stage of ontogeny, the mantle could be completely reverted inside the shell. Interestingly, the soft body of the hatchlings of the yellow morphs was all black, and they acquired the yellow colour as they matured. In all observations (~200 individuals) of juveniles and hatchlings of *I. ampulla* during the study period, the soft body parts of all individuals were black in colour. As juveniles matured (to 9–10 mm in shell size), the thin, delicate layer in the lower lateral side of the shell first changed in colour to yellow along with the eye retractor muscle and the shell simultaneously becoming more bright-brownish with irregular black patches (Figure 3(c)). As the individuals matured and grew, the mantle and parts of the soft body then changed in colour to yellow along with the foot region, while the shell remained brown with black patches (Figure 3(d)). Later in ontogeny, the body's yellow colour became more prominent, with feeble black markings on the foot, while the shell remained slightly brownish (Figure 3(e)). Individuals

with a shell size of 45–50 mm were always observed to be fully yellow in body colour with a pale blackish shell (Figure 3(f)). Apart from this, there have been a few sporadic observations of juvenile *I. ampulla* from Idukki, Kerala, and these were also found with the blackish soft body parts. It is expected that the red morphs of *I. ampulla* have a similar ontogenic colour shift since all the reports and observations of *I. ampulla* from this region are of the red morph, but complete developmental stages have not yet been observed for this population.

Discussion

Our results from the observations of feeding behaviour show that *I. ampulla* is a generalist omnivore with a relatively wide food range. The isodont radula consists of 100 rows of teeth with a 145 + 17 + 1 + 17 + 145 configuration (see Blandford and Godwin-Austen 1908). The radular morphology indicates that they have wide food preferences. Apart from vegetation, *I. ampulla* also scavenges on dead snails, which could be an additional source of dietary calcium (Ozgo and Bogucki 2006). They are also voracious feeders on mushrooms (Blandford and Godwin-Austen 1908; Kinloch 1922; Aravind, pers. observation). In parts of their range, they are considered a pest in cardamom plantations as they are known to feed on the flowers and young fruits (Sen et al. 2016). However, our subsequent visits and interaction with the plantation workers in the same location indicated that such mass feeding activity has not reoccurred, suggesting the previous incident to be a sporadic event. Further research on feeding behaviour, in the lab as well as in the field, is necessary to obtain information on their dietary breadth. Also, dietary analysis using modern tools such as DNA metabarcoding of faecal samples and gut content will help us understand the species' dietary breadth (Ruppert et al. 2019). Gupta and Oli (1997) and Oli (1999) studied food preference under laboratory conditions for several land snail species in the Himalayan region. Although such studies are important for understanding the quantity of food intake and assimilation pattern, they do not give any information on the natural dietary breadth of the species.

The pulmonate land snails have complex reproductive organs and breeding biology. In general, most of the globular to flat-shelled (low-spired) hermaphroditic species show face-to-face mating behaviour (Asami et al. 1998; Koene 2006; Davison and Mordan 2007; Jordaens et al. 2009; Soldatenko and Petrov 2012). However, there are certain exceptions, like the long-shelled species *Pontophaedusa funiculum* (Mousson 1856) (Clausiliidae) (Pall-Gergely and Németh 2008), which is known to mate by 'shell-mounting'. Almost 50% (19 out of 40 families) of the families reviewed by Davison and Mordan (2007) show face-to-face mating (see also Asami et al. 1998). *I. ampulla* has a globose shell and the current observations on its mating behaviour are congruent with the findings reported for other genera in Ariophantidae (superfamily Limnocoidea) using the 'face-to-face simultaneous reciprocal' method of copulation (Davison and Mordan 2007). The present observation adds to a growing list of species with face-to-face mating behaviour and is one of the few such reports from this part of the world. Raut and Ghose (1984) have provided a detailed report on the reproductive behaviour of *Macrochlamys indica* (Ariophantidae). This species also shows face-to-face mating (Raut and Ghose 1984; Aravind, pers. observation). *Microcystina* sp. (Ariophantidae) also shows face-to-face mating behaviour (Aravind, pers. observation).

Oli and Gupta (1997) report cross-fertilisation behaviour for several land snail species (*Bensonia monticola*, *Euaustenia monticola*, *E. cassida*, *Macrochlamys glauca*, *M. nuda*, *M. veiscula*) from the Himalayan region but failed to provide more information on the copulation and mating process. According to Heller (1993), self-fertilisation (= selfing) is more common in freshwater molluscs than in marine and terrestrial species. In our work, however, we did not see any individual 'selfing' during the study period. Also, our observations on mating behaviour are not complete since we did not observe the exchange of spermatophore or sperm, and hence a detailed comparison on the mating behaviour with other stylommatophorans in general and ariophantids in particular is difficult. Several of our attempts to rear the species in captivity, isolated within the field, or in the terrarium in the lab were not successful, probably due to differences in temperature, humidity and microclimatic conditions, which we failed to replicate exactly. The current study also reports the eggs clutch size of *I. ampulla* for the first time from the field, as well as preliminary information on ovipositional behaviour, ovipositional site selection, and reproductive success. As reported for many other ariophantids in India (Oli and Gupta 1997) the life cycle appears to be annual and breeding occurs only during the early monsoon (end April) and late monsoon (end September).

Shell plasticity and the ontogenic colour shifts in molluscs have always focused more on the shell structure than the soft body parts (Byers 1989; Lindberg and Pearse 1990; Manríquez et al. 2009; Johannesson and Butlin 2017). However, in *I. ampulla*, it appears that the soft body undergoes a more drastic colour change than the shell. The hatchlings are darker and become brighter and more conspicuous (yellow, orange and red) as they mature. Previous studies in many groups have shown that conspicuous colour patterns are often adapted to keep the predation pressure low (Aronsson and Gamberale-Stille 2012; Cyriac and Kodandaramaiah 2019) and also as aposematic signals (Ruxton et al. 2004; Dreher et al. 2015). It is possible that the adults of *I. ampulla* use the conspicuous colours to decrease the predator pressure, but further study with experimental models to understand this colour shift and polymorphism is highly warranted.

Understanding the natural history of any species is very important to elucidate the interconnections among species, habitats, and ecosystems and the interactions between abiotic and biotic elements, which in turn helps in devising conservation measures (McCallum and McCallum 2006; Barrows et al. 2016; Anderson 2017). Importantly, *I. ampulla*, despite being an endemic species, is considered a pest in cardamom plantations as they are known to feed on the flowers and young fruits (Sen et al. 2016). In a recent study, the invasion of *I. ampulla* is predicted to spread in future and they are considered a threat to the cardamom plantations in the Western Ghats (Sen et al. 2016). This makes it even more important to understand the ecology and natural history of this species. Although current observations provide new insights into aspects of the natural history of *I. ampulla* that were previously unknown, more observations and data are required to understand the species better from an ecological perspective. For example, knowledge of the natural history characteristics, e.g. of reproductive behaviour and colour change, are based on only six observations from a single location and morph (yellow). It is likely that the red morph has a similar ontogenic shift, but more samples of other colour morphs from different locations are needed to confirm this.

The observations provided herein, on feeding and breeding behaviour, fill a gap in the basic natural history knowledge of *I. ampulla*, a charismatic land snail of the Western Ghats. This study will also help future researchers to develop and test hypotheses on the feeding and breeding ecology of this species. Standardisation of laboratory rearing protocols and laboratory-based observations of breeding behaviour and growth patterns need to be undertaken in future to shed light on those aspects that are difficult to study under field conditions. Furthermore, developing an understanding of the natural history of the endemic snail *I. ampulla* not only helps in its conservation and management, but also provides data and knowledge for comparative studies on the feeding and reproductive behaviour of other terrestrial snails that are poorly known from the tropical regions of the world.

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Disclosure statement

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References

Anderson JGT. 2017. Why ecology needs natural history. Am Sci. 105(5):290. doi:10.1511/2017.105.5.290

Aronsson M, Gamberale-Stille G. 2012. Evidence of signalling benefits to contrasting internal color boundaries in warning coloration. Behav Ecol. 24(2):349–354. doi:10.1093/beheco/ars170

Asami T, Cowie RH, Ohbayashi K. 1998. Evolution of mirror images by sexually asymmetric mating behavior in Hermaphroditic snails. Am Nat. 152(2):225–236. doi:10.1086/286163

Barman H, Paul P, Aditya G. 2021. The arboreal microsnail *Pupisoma dioscoricola* (C. B. Adams, 1845) from West Bengal, India: morphology, plant preferences and distribution. Zool Ecol. 31(2):148–157. doi:10.35513/21658005.2021.2.8

Barrows CV, Murphy-Mariscal ML, Hernandez RR. 2016. At a crossroads: the nature of natural history in the twenty-first century. BioSci. 66(7):592–599. doi:10.1093/biosci/biw043

Benson WH. 1850. Characters of several new East Indian and South African Helices, with remarks on some other species of the genus occurring at the Cape of Good Hope. Ann Mag Nat Hist Series. 2 (5):213–217. doi:10.1080/03745486009494916
Blandford WT, Godwin-Austen HA. 1908. Fauna of British India, Mollusca (Testacellidle and Zonitidae). London: Taylor and Francis.
Byers BA. 1989. Habitat-choice polymorphism associated cryptic with shell-color polymorphism in the limpet *Lottia digitalis*. Veliger. 32:394–402.
Chakraborty S, Aravind NA. 2020. Colourful giants of the Western Ghats: *Indrella ampulla* (Gastropoda: Ariophantidae). Tentacle. 28:4–6.
Chang H. 1991. Food preference of the land snail *Cepaea nemoralis* in a North American population. Malacol Rev. 24:107–114.
Chatfield JE. 1976. Studies on food and feeding in some European land molluscs. J Conchol. 29:5–20.
Cyriac VP, and Kodandaramaiah U. 2019. Conspicuous colours reduce predation rates in fossorial uropeltid snakes. PeerJ 7:e7508. doi:10.7717/peerj.7508
Davison A, Mordan P. 2007. A literature database on the mating behaviour of stylommatophoran land snails and slugs. Am Malacol Bull. 23:173–181. doi:10.4003/0740-2783-23.1.173
Dreher CE, Cummings ME, Pröhl H. 2015. An analysis of predator selection to affect aposematic coloration in a poison frog species. PLoS ONE. 10(6):e0130571. doi:10.1371/journal.pone.0130571
Gillete R, Huang RC, Hatcher N, Moroz LL. 2000. Cost-benefit analysis potential in feeding behaviour of a predatory snail by integration of hunger, taste and pain. PNAS. 97:3585–3590. doi:10.1073/pnas.97.7.3585
Godwin-Austen HA. 1901. On the anatomy of the *Helix ampulla* of Benson, and its generic position in the Ariophantinae. J Molluscan Stud. 4(5):187–190. doi:10.1093/oxfordjournals.mollus.a065812
Gupta PK, Oli BP. 1997. Food preference of some species of terrestrial molluscs in Kumaon Himalayan forests. Vasundhara. 2:27–39.
Heller J. 1993. Hermaphroditism in molluscs. Biol J Linn Soc. 48:19–42. doi:10.1111/j.1095-8312.1993.tb00874.x
Iglesias J, and Castillejo J. 1999. Field observations on feeding of the land snail Helixx aspersa Muller, J Molluscan Stud. 65(4): Pages 411–423. doi:10.1093/mollus/65.4.411
Jennings TJ, Barkham JP. 1979. Litter decomposition by slug in mixed deciduous woodland, Holarctic. Ecology. 2:21–29.
Johannesson K, Butlin R. 2017. What explains rare and conspicuous colours in a snail? A test of time-series data against models of drift, migration or selection. Heredity. 118:21–30. doi:10.1038/hdy.2016.77
Jordaens K, Dillen L, and Backeljau T. 2009. Shell shape and mating behaviour in pulmonate gastropods (Mollusca). Biol J Linn Soc. 96(2): 306–321. doi:10.1111/j.1095-8312.2008.01122.x
Kinloch AP. 1922. Food of the Snail (*Indrella ampulla*). JBNHS. 28:557–558.
Koene JM. 2006. Tales of two snails: sexual selection and sexual conflict in Lymnaea stagnalis and Helix aspersa. Integr Comp Biol. 46:419–429. doi:10.1093/icb/icj040.
Lindberg DR, Pearse JS. 1990. Experimental manipulation of shell color and morphology of the limpets *Lottia asmi* (Middendorff) and *Lottia digitalis* (Rathke) (Mollusca: Patellogastropoda). J Exp Mar Biol Ecol. 10:173–185. doi:10.1016/0022-0981(90)90125-V.
Manríquez PH, Lagos NA, Jara MA, Castilla JC. 2009. Adaptive shell colour plasticity during the early ontogeny of an intertidal keystone snail. PNAS. 106(38):16298–16303. doi:10.1073/pnas.0908655106
Mason CF. 1970. Food, feeding rates and assimilation in woodland snails. Oecologia. 4:358–373. doi:10.1007/BF00393394
McCallum ML, McCallum J. 2006. Publication trends of natural history and field studies in herpetology Herpetological. Conserv Biol. 1:62–67.
Mitra SC, Dey A, Ramakrishna. 2005. Pictorial guide to land snails. Kolkata: Zoological Survey of India.
Oli BP. 1996. Ecology of terrestrial molluscs in Kumaon kumaun Himalayan forest [Ph.D. Thesis]. Nainital (India): Kumaun University.

Oli BP. 1999. Feeding in some species of terrestrial molluscs from Kumaon Himalayan forests. Zoos' Print. 14:40–43.
Oli BP, Gupta PK. 1997. A report on land mollusc fauna of Kumaon Himalayan forests. Zoos' Print. 5:1–6.
Ozgo M, Bogucki Z. 2006. Shell predation and cannibalism in land snails living on acid and calcium-deficient soils. Folia Malacol. 14(4):217–220. doi:10.12657/folmal.014.019
Pall-Gergely B, Németh L. 2008. Observations on the breeding habits, shell development, decollation, and reproductive anatomy of Pontophaedusa funiculum (Mousson 1856) (Gastropoda, Pulmonata, Clausiliidae, Phaedusinae). Malacol Bohemoslov. 7:11–14. doi:10.5817/MaB2008-7-11
Parkyn J, Challisthianagara A, Brooks L, Specht A, McMullan-Fisher S, Newell D. 2015. The natural diet of the endangered camaenid land snail *Thersites mitchellae* (Cox, 1864) in northern New South Wales, Australia. Aust Zool. 37:343–349. doi:10.7882/AZ.2014.042
Raheem DC, Taylor H, Ablett J, Preece R, Aravind NA, Naggs F. 2014. A systematic revision of the land snails of the Western Ghats of India. Trop Nat Hist. 4:1–298.
Raut SK, Ghose KC. 1983. Food preference and feeding behaviour of two pestiferous snails *Achatina fulica* (Bowdich) and *Macrochlamys indica*. Rec Zol Surv Ind. 80:421–440.
Raut SK, Ghose KC. 1984. Pestiferous land snails of India. Zoological Survey of India. Technical monograph No. 11; 177.
Ruppert KM, Md Kline RJ, Rahman S. 2019. Past, present, and future perspectives of environmental DNA (eDNA) metabarcoding: a systematic review in methods, monitoring, and applications of global eDNA. Glob Ecol Conserv. 17:e00547. doi:10.1016/j.gecco.2019.e00547.
Ruxton GD, Sherratt TN, Speed MP. 2004. Avoiding attack. The evolutionary ecology of crypsis, warning signals and mimicry. Oxford (UK): Oxford University Press.
Sajan SK, Das S, Tripathy B, and Biswas T. 2021. Malacofaunal inventory in Chintamoni Kar Bird Sanctuary, West Bengal, India. J Threat Taxa 13(2): 17807–17826. doi:10.11609/jot.4456.13.2.17807–17826
Scott JD, Dawson-Scully K, and Sokolowski MB. 2005. The neurogenetics and evolution of food-related behaviour. Trends Neurosci. 28: 644–652.
Seifert DV, Shutov SV. 1979. Role of certain terrestrial molluscs in the transformation of leaf litter. Ekologiya. 5:58–61.
Sen S, Shivaprakash KN, Aravind NA, Ravikanth G, Dayanandan S. 2016. Ecological niche modelling for conservation planning of an endemic snail in the verge of becoming a pest in cardamom plantations in the Western Ghats biodiversity hotspot. Ecol Evol. 6:6510–6523. doi:10.1002/ece3.2368.
Senthilkumar T, and Thirunavukkarasu. 1989. Ecological significance of the land snail Cryptozona bistrialis (Beck) (Mollusca: Gastropoda). Paper presented at the National Symposium on Natural Resources and their Conservation. A.V.C. College, Mayilathurai
Soldatenko E, Petrov A. 2012. Mating behaviour and copulatory mechanics in six species of Planorbidae (Gastropoda: Pulmonata). J Molluscan Stud. 78:185–196. doi:10.1093/mollus/eyr056.
Valarmathi V. 2017. Food preference and feeding behaviour of the land snail Cryptozona bistrialis in Nagapattinam, Tamil Nadu India. Int. J. zool. Appl. Biosci. 2(2): 90–94
Williamson P, and Cameron RAD. 1976. Natural diet of land snail Capaea neomoralis. Oikos. 27: 493–500.
Yadav O, Jadhav M, Kininge S, Bajantri P, Bhosale A. 2021. Land snails feeding on dead frogs. Reptile Amphib. 28(3):546–547. doi:10.17161/randa.v28i3.15817