

CALOTES VERSICOLOR (Oriental Garden Lizard). DIET. *Calotes versicolor* is among the most geographically widespread members of the genus (Uetz and Hošek 2014. The Reptile Database. <http://reptile-database.reptarium.cz>, accessed 29 Apr 2014) naturally occurring in Afghanistan, Bangladesh, Bhutan, Cambodia, India, Indonesia (Sumatra), Myanmar, Nepal, Pakistan, Peninsular Malaysia, South East Iran, Singapore, South China, Sri Lanka, Thailand, and Vietnam, and additional introduced populations in Sulawesi, Malaysian Borneo, Maldives, Mauritius, Oman, Seychelles, and USA (Florida) (Enge and Krysko 2004. Florida Sci. 67:226–230; Matyot 2004. Phelsuma 12:35–47; Radder 2006. Curr. Sci. 91:1354–1363). It is a very adaptable, prolific species and is commonly found in human-altered environments including highly urbanized areas (Erdelen 1988. J. Herpetol. 22:42–52). Although it is generally considered an insectivore, field records suggest that it is more an opportunistic omnivore with a wide range of prey. However, such records are often scattered in gray literature and in this review we collate published records and observations of our own and those of our colleagues, and subsequently discuss the possible reasons for dietary breadth.

Our review revealed records of *Calotes versicolor* feeding on members of nine broad faunal groups (annelids, mollusks, insects, myriapods, arachnids, crustaceans, amphibians, reptiles, birds, and mammals) as well as plant matter (Table 1). Insects comprise most of the diet of *C. versicolor*. One of us (HS) observed an adult lizard feeding on a swarm of ants on the ground at a rate of one ant in every five to six seconds for ca. 30 seconds. Sit-and-wait foraging patterns have also been used to catch wasps visiting a puddle of water (Supun Wellappuliarachchi, pers. comm.). *Calotes versicolor* even preys upon large species like the Atlas Moth (*Attacus taprobanis*) (HS, pers. obs.). Additionally, orthopterans, mantodeans, dipterans, odonates, blattodeans, hemipterans, and dermapterans constitute a lesser content in the diet (Rao 1975. Brit. J. Herpetol. 5:467–470; Indurkar and Sabnis 1976. Comp. Physiol. Ecol. 1: 9–12; Sharma and Vazirani 1977. Rec. Zool. Surv. India 73:77–93; Chandra 1983. Plant Protection Bulletin 35:35; Qiu et al. 2001. Zool. Res. 22:367–374). Annelids are a constituent of the diet of *C. versicolor*, but are represented in a low volume in gut contents (Rao 1975, *op. cit.*) which could be due to high digestion rate of soft-bodied prey (Verheyen 1991. Funct. Ecol. 5:507–517; Qu et al. 2011. Curr. Zool. 57: 684–700). RS observed an adult male feeding on a small annelid, *Megascolex coeruleus*, that emerged on the surface soon after a rain. This lizard generally forages on the surface (tree trunks or on ground), but can opportunistically unearth fossorial prey like annelids (Sharma 2002. Cobra 48:14–15). RS observed a sub-adult lizard preying on an asparassid *Heteropoda venatoria* and a failed attempt of an adult female to catch a sub-adult theraphosid *Poecilotheria pedersoni* (before it escaped to a tree hollow) in Sri Lanka.

Several groups of herpetofauna, including amphibians, agamids, geckos, skinks, and snakes are known prey items of *C. versicolor*. Records of feeding on juveniles of other agamids are common. S. Wellappuliarachchi (pers. comm.) observed an adult *C. versicolor* preying upon an injured *C. calotes* (SVL ca. 80–100 mm) after the latter was attacked by a cat. Holding its prey by the belly, the lizard hit the *C. calotes* on a brick wall vigorously several times and then carried it onto the top of a coconut tree. Senanayake (1980. Tiger Paper 7:26–28) reported

TABLE 1. Records of prey items of *Catolotes versicolor* (AH: Anthropogenic Habitat; DO: Direct Observation; N/A: Not Available; SC: Stomach Contents).

Prey taxon	Location	Habitat	Evidence	Citations	Notes
ANNELIDS					
Earthworm	¹ Orissa, India; ² Rajasthan, India	¹ AH; ² Forest nursery	¹ SC; ² DO	¹ Rao 1975; ² Sharma 2002	¹ size of prey: 65 mm; SVL of lizard: 106 mm
<i>Megascolex coeruleus</i>	Kithulgala, Sri Lanka	Lowland rainforest	DO	Somaweera, pers. obs.	size of prey: ~250 mm; SVL of lizard: > 400 mm
MOLLUSCANS					
Gastropods	¹ Orissa, India; ² Tongshi, China	¹ AH; ² N/A	¹ SC; ² SC	¹ Rao 1975; ² Qiu et al. 2001	
INSECTS					
<i>Aritacus taprobantis</i> (Sri Lankan Atlas Moth)	Peradeniya, Sri Lanka	AH	DO	Sudasinghe, pers. obs.	size of prey: 220 mm wingspan
Caterpillar of a moth	India	AH	SC	Sharma and Vazirani 1977	
Butterflies	¹ Amarvati, India; ² India; ³ Tongshi, China	¹ N/A; ² AH; ³ N/A	¹ SC; ² SC; ³ SC	¹ Indurkar and Sabnis 1976; ² Sharma and Vazirani 1977; ³ Qiu, et al. 2001	
Lepidoptera larvae	Orissa, India	AH	SC	Rao 1975	
Beetle (Coleopterans)	¹ Yagirala, Sri Lanka; ² Amarvati, India; ³ India; ⁴ Orissa, India; ⁵ Tongshi, China	¹ AH; ² N/A; ³ AH; ⁴ AH; ⁵ N/A	¹ DO; ² SC; ³ SC; ⁴ SC; ⁵ SC	¹ Sudasinghe, pers. obs.; ² Indurkar and Sabnis 1976; ³ Sharma and Vazirani 1977; ⁴ Rao 1975; ⁵ Qiu et al. 2001	
Hemipterans	Tongshi, China	N/A	SC	Qiu, et al. 2001	
Cicadas	Tongshi, China	N/A	SC	Qiu, et al. 2001	
Ants	¹ Weerapokuna, Sri Lanka; ² Amarvati, India; ³ India; ⁴ India; ⁵ Orissa, India; ⁶ Tongshi, China	¹ AH; ² N/A; ³ AH; ⁴ N/A; ⁵ AH; ⁶ N/A	¹ DO; ² SC; ³ SC; ⁴ N/A; ⁵ SC; ⁶ SC	¹ Sudasinghe, pers. obs.; ² Indurkar and Sabnis 1976; ³ Sharma and Vazirani 1977; ⁴ Daniel 1983; ⁵ Rao 1975; ⁶ Qiu et al. 2001	
Bees	Tongshi, China	N/A	SC	Qiu et al. 2001	
Wasps	¹ Mihintale, Sri Lanka; ² India; ³ Tongshi, China	¹ Wild; ² N/A; ³ N/A	¹ DO; ² SC; ³ SC	¹ S. Wellappuliarachchi, pers. comm.; ² Bhatti 1988; ³ Qiu et al. 2001	¹ SVL of lizard: ca. 100–120 mm
Termites	¹ Tamilnadu, India; ² India	¹ Wild; ² N/A	¹ DO; ² DO	¹ Manakadan 1993; ² Parihar 1978	
Grasshoppers	¹ Amarvati, India; ² Orissa, India; ³ Tongshi, China	¹ N/A; ² AH; ³ N/A	¹ SC; ² SC; ³ SC	¹ Indurkar and Sabnis 1976; ² Rao 1975; ³ Qiu et al. 2001	
<i>Chirotopogon</i> sp. (Grasshopper sp.)	India	N/A	DO	Chandra 1983	
Cockroaches	¹ Amarvati, India; ² Arugambay, Sri Lanka	¹ N/A; ² Wild	¹ SC; ² DO	¹ Indurkar and Sabnis 1976; ² Naalin Perera, pers. comm.	
Dragonflies	¹ Orissa, India; ² India; ³ India; ⁴ Tongshi, China	¹ AH; ² AH; ³ N/A; ⁴ N/A	¹ SC; ² SC; ³ DO; ⁴ SC	¹ Rao 1975; ² Sharma and Vazirani 1977; ³ Mitra 1996; ⁴ Qiu et al. 2001	
Earwigs	¹ Orissa, India; ² Amarvati, India	¹ AH; ² N/A	¹ SC; ² SC	¹ Rao 1975; ² Indurkar and Sabnis 1976	
Mantises	Tongshi, China	N/A	SC	Qiu et al. 2001	
Dipterans	Tongshi, China	N/A	SC	Qiu et al. 2001	

TABLE 1. Continued.

Prey taxon	Location	Habitat	Evidence	Citations	Notes
MYRIAPODS					
Millipedes and centipedes	'Amaravati, India; ² Orissa, India	'N/A; ² AH	¹ SC; ² SC	¹ Indurkar and Sabnis 1976; ² Rao 1975	
<i>Scolopendra</i> sp. (centipede)	Assam, India	AH	DO	Kalra 2000	
<i>Rhysida</i> sp. (centipede)	West Bengal, India	N/A	SC	Ahmed 1984	
<i>Proterosperphormage</i> sp. (millipede)	West Bengal, India	N/A	SC	Ahmed 1984	
Siphonophorids	Tongshi, China	N/A	SC	Qiu, et al. 2001	
ARACHNIDS					
Spiders	'India; ² Orissa, India; ³ Tongshi, China	'AH; ² AH; ³ N/A	¹ SC; ² SC; ³ SC	¹ Sharma and Vazirani 1977; ² Rao 1975; ³ Qiu et al. 2001	
<i>Heteropoda venatoria</i>	Kandy, Sri Lanka	Home garden	DO	Somaweera, pers. obs.	size of prey: ca. 30 mm; SVL of lizard: ca. 70 mm
<i>Poecilotheria pedersoni</i>	Bundala, Sri Lanka	Dry scrubland	DO	Somaweera, pers. obs.	size of prey: ca. 70 mm; SVL of lizard: > 300 mm
CRUSTACEANS					
Isopods	Tongshi, China	N/A	SC	Qiu et al. 2001	
AMPHIBIANS					
Frogs	India	N/A	N/A	Daniel 1983	
REPTILES					
Sub-adult <i>Calotes versicolor</i>	Jaipur, India	Forestry arboretum	DO	Sharma 1992	TotL of lizard: ca. 330 mm
Juvenile <i>Calotes versicolor</i>	Singapore	Urban park	SC	Diong 1994	size of prey: 35 & 45 mm; SVL of lizard: 104 & 110 mm
<i>Calotes calotes</i> (Green Garden Lizard)	Matara, Sri Lanka	AH	DO	S. Wellappuliarachchi, pers. comm.	size of prey: ca. 80–100 mm; SVL of lizard: > 150 mm
Juvenile <i>Ceratophora stoddarti</i> (Rhino Horned Lizard)	Sri Lanka	N/A	DO	Senanayake 1980	
<i>Sitana ponticeriana</i> (Fan-throated Lizard)	Sri Lanka	N/A	DO	de Silva 2006	
Hatchlings of <i>Draco volans</i> (Flying dragons)	Singapore	N/A	SC	Diong et al. 1994	
Lizard (unidentified)	Orissa, India	AH	SC	Rao 1975	size of prey: 21 mm; SVL of lizard: 92 mm
<i>Hemidactylus brooki</i> (Brook's House Gecko)	Jaipur, India	Forestry arboretum	DO	Sharma 1992	
<i>Hemidactylus</i> sp. (possibly <i>H. frenatus</i>)	Mihintale, Sri Lanka	AH	DO	S. Wellappuliarachchi, pers. comm.	size of prey: 100 mm (TotL); SVL of lizard: 150 mm
<i>Hemidactylus leschenaultii</i> (Bark Gecko)	Naula, Sri Lanka	Home garden (on a shed wall)	DO	Somaweera, pers. obs.	size of prey: 120 mm (TotL); TotL of lizard: ca. 350 mm

TABLE 1. Continued.

Prey taxon	Location	Habitat	Evidence	Citations	Notes
<i>Lankascincus fallax</i> (Common Lanka Skink)	Mihintale, Sri Lanka	AH	DO	S.Wellappuliarachchi, pers. comm.	size of prey: 80–100 mm TotL; SVL of lizard: ca. 140 mm
<i>Xenochropis piscator</i> (Checked Keelback)	Pune, India	Abandoned quarry	DO	Thite and Nerlekar 2012	size of prey: ca. 80–200 mm (TotL); SVL of lizard: 120 mm
<i>Amphiesma stotatum</i>	Chennai Snake Park, India	wild	DO	Kalaiarasan and Rajarathnam 2005	size of prey: 130–170 mm (TotL)
<i>Lycodon aulicus</i> (Common Wolf Snake)	Rajasthan, India	Forest nursery	DO	Sharma 1998	size of prey: 250 mm (TotL)
BIRDS					
Eggs of <i>Ploceus philippinus</i> (Baya Weaver)	Punjab, India	AH	DO	Dhindsa and Toor 1983	
<i>P. benghalensis</i> (Black Throated Weaver)					
<i>P. manyar</i> (Streaked Weaver)					
<i>Passer domesticus</i> (House sparrow)	Bombay, India	N/A	DO	Paralkar 1995	
Small birds, nestlings	India	N/A	N/A	Daniel 1983	
MAMMALS					
<i>Mus</i> sp. (Field Mouse)	Sigiriya, Sri Lanka	AH	DO	S.Wellappuliarachchi, pers. comm.	size of prey: 40–50 mm (head and body)
ANIMAL EXCRETA					
Excreta of <i>Iguana iguana</i> (Green Iguana)	India	AH	Captivity	Rajarathnam and Kalaiarasan 1999	
PLANT MATTER					
buds of <i>Tabernaemontana</i> sp.	Bombay, India	National Park	DO	Sekar 1987	
Plant matter of <i>Dalbergia sissoo</i> , <i>Rosa indica</i> , <i>Gossypium</i> sp., <i>Saccharum onujfo</i> , <i>Sorghum</i> , <i>Morus alba</i> , <i>Cyanodon</i> sp., <i>Kochia</i> sp., <i>Acacia</i> sp., <i>Sesstrum nocturnum</i> , <i>Sesstrum alba</i> , and flower parts of <i>Calotropis procera</i> .	Hansi and Bulandshar, India	N/A	SC	Bhatti et al. 1988	
<i>Solanum nigrum</i> , <i>Solanum melanogena</i> , <i>Rosa indica</i> , <i>Althea rosea</i> , <i>Malvestrum</i> sp.					
fallen dry leaf of <i>Magnifera indica</i>	Deola forest range, India	Forest nursery	DO	Sharma 1998	
fallen flowers of <i>Morinda tinctoria</i> and flowers of <i>Cassia marginata</i>	Chennai snake park, India	AH	DO	Aengals 2000	
Germinating seeds of <i>Feronia limonia</i>	Rajasthan, India	Forest nursery	DO	Sharma 1993	
Shoots of <i>Vigna sinensis</i> (Cowpea)	Calicut, India	AH	DO	Devasahayam and Devasahayam 1989	
Grass, leaves, twigs	Amarvati, India	N/A	SC	Indurkar and Sabnis 1976	
Grasses, leaves, seeds, twigs	Orissa, India	AH	SC	Rao 1975	
Stones	¹ Amarvati, India; ² Orissa, India	¹ N/A; AH	¹ SC; SC	¹ Indurkar and Sabnis 1976; ² Rao 1975	

the Sri Lankan montane agamid *Ceratophora stoddarti* as a prey item of *C. versicolor*. However, currently *Ceratophora stoddarti* and *C. versicolor* are largely allopatric and thus this report seems questionable. Several species of geckos including *Hemidactylus frenatus* (S. Wellappuliarachchi, pers. comm.) and *H. leschenaultii* (RS, pers. obs.) are also taken. Several incidents of these lizards taking small snakes as prey are known from India (Sharma 1998. J. Bombay Nat. Hist. Soc. 96:146–147; Kalaiarasan and Rajarathinam 2005. Cobra 61:16–20; Thite and Nerlekar 2012. Herpetol. Notes 5:518–518). Endotherms are arguably rare in the diet of *C. versicolor*, but they do feed on bird eggs, nestlings, and adult birds (Daniel 1983. The Book of Indian Reptiles. Bombay Natural History Society, Bombay, India; Dhindsa and Toor 1983. J. Bombay Nat. Hist. Soc. 80:221–222; Paralkar 1995. J. Bombay Nat. Hist. Soc. 92:426). S. Wellappuliarachchi (pers. comm.) observed an adult lizard (total length ca. 180–200 mm) feeding on a *Mus* sp. (Field Mouse) in Sri Lanka, taking more than 20 minutes to completely swallow it, during which the lizard frequently squashed the mouse by hitting it on a rock. However, it is uncertain whether the lizard actively caught the live mouse or if the mouse was scavenged.

Plant material is also a known component of the diet. The reason for feeding on plant matter is not clear, but could be for obtaining moisture (Devasahayam and Devasahayam 1989. J. Bombay Nat. Hist. Soc. 86:253) as well as nutrients (Indukar and Sabnis 1976, *op. cit.*), or could reflect secondary or accidental ingestion (Rao 1975, *op. cit.*; Bhatti et al. 1988. J. Bombay Nat. Hist. Soc. 84:692–693). However, active feeding on plant matter has been observed (Sekar 1987. J. Bombay Nat. Hist. Soc. 85:199; Devasahayam and Devasahayam 1989, *op. cit.*; Sharma 1994. J. Bombay Nat. Hist. Soc. 91:150; Sharma 1998. Cobra 34:21–22; Aengals 2000. Cobra 40:18).

Several factors may influence the wide spectrum of food habits known for this species. 1) *Calotes versicolor* is among the most widespread non-gekkonid lizards in the world (Enge and Krysko 2004, *op. cit.*; Matyot 2004, *op. cit.*; Radder 2006, *op. cit.*), thus would encounter and hence could potentially prey on a large range of prey items within its range. 2) It is a relatively large lizard where males may attain 140 mm (SVL) and a total length over 450 mm (Radder et al. 2001. J. Herpetol. 35:156–160). Adults also have large heads with a relatively wide gape. Body size is known to greatly influence many aspects of the morphology, physiology, and ecology of organisms (Meiri 2008. Global Ecol. Biogeog. 17:724–734.), thus prey size as well prey spectrum could vary linearly with the size of the predator allowing them to consume a larger range of prey items. Arguably, this could help them displace populations of smaller competitors (e.g., *Bronchocela cristatella* in Singapore: Diong et al. 1994. Nature Malaysiana 19:46–54). 3) *Calotes versicolor* is commonly observed in anthropogenic habitats including home gardens, parks, plantations, and cities (Somaweera and Somaweera 2009. Lizards of Sri Lanka: A Colour Guide with Field Keys. Chimaira Buchhandelsgesellschaft mbH, Frankfurt am Main. 304 pp.). Individuals often forage on ground, foliage, and on man-made structures, and males often display from fences and other conspicuous perches. Hence the species is more commonly seen, increasing the likelihood of observing foraging behavior. This explains why most feeding observations are anecdotal and opportunistic in man-made environments.

Diet breadth and foraging success are of great importance in understanding the distribution of a predator and to understand its population dynamics and inter-specific interactions (Pitt and

Ritchie 2002. Oikos 96:157–163). Coupled with its wide thermal tolerance limits (Qiu et al. 2009. Acta Ecol. Sinica 29:1738–1744) and habitat generalism (Radder 2006, *op. cit.*), a broad diet may have assisted the colonizing success of this species.

We thank I. Agarwal, T. Amarasinghe, B. Dayananda, M. Elphick, S. R. Ganesh, M. Greenlees, M. Gunawardena, S. Karunaratna, B. Kekulandala, K. Maduwage, U. Manthey, Chandra Mouli, N. Perera, G. Vogel, and S. Wellappuliarachchi for providing literature and personal observations.

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