

Growth patterns and reproductive strategies in the lizard, *Calotes versicolor* raised in captivity

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Abstract. The paper describes the growth patterns and breeding strategies in the lizard, *Calotes versicolor* in captivity. The lizards were raised in laboratory from hatching. It was observed that these lizards attain sexual maturity at 7.42 ± 0.5 months of age. Growth rate in males is always higher than in females and sexual size dimorphism in *C. versicolor* is due to the difference in growth rate between the sexes. The study revealed that some females reproduce in the first year at smaller body size (snout-vent length-SVL ~ 8 cm) with small clutch size while some skip reproduction in the first year, grow larger (SVL ~ 11.5 cm) and reproduce in second year with larger clutch size, yet others reproduce in first year, skip reproduction in second year and reproduce in the third year and some skip reproduction in the first 2 years of life and reproduce in third year attaining larger body size (SVL >13.6 cm) with greater clutch size. Thus, females exhibit different strategies of trade-off between growth and reproduction. In addition, the study showed that *C. versicolor* may lay as many as 3 clutches of eggs in a breeding season. Thus, the study provides information on growth, age at sexual maturity, relationship between growth and reproduction and reproductive strategies exhibited by the lizard in captivity.

Keywords. Growth, breeding, reproductive episodes, *Calotes versicolor*.

INTRODUCTION

Growth pattern is a key aspect in the life history of any species (Andrews, 1982; Sinervo and Aldoph, 1989; Roff, 1992; Arendt, 1997) and reproduction is the most costly event in an animal's life. Body size and growth rate are particularly important life history traits because of their relation to reproductive output, longevity, age at first reproduction, and so on (Andrews, 1982; Bauwens and Verheyen, 1985; Ferguson and Talent, 1993; Clobert et al., 1998; Lorenzon et al, 1999; Bronikowski, 2000). Knowledge of growth rates can also help in determining the size at sexual maturity and the maximum size attained (Andrews, 1982; Bronikowski, 2000; Seminoff et al., 2002).

Most studies on growth rates in lizards are mainly based on mark and recapture surveys (Bellairs, 1969; Jenssen and Andrews, 1984; Shine, 1988; James, 1991; Sugg et al., 1995; Allan et al., 2006) or on frequency distribution of individuals in a population collected at different points of time in a year (Andrews, 1976; Ferguson and Brockman, 1980; Bishop and Echternacht, 2003). Surprisingly, a few studies are devoted to understand the relationship between investments in somatic growth and reproduction in reptiles (Townes, 1975). Studies on captive breeding of the giant day gecko (Demeter and Birchard, 1994), snakes (Shiryayev et al., 2007), turtles (Wood and Wood, 1980; Perez et al., 2004), crocodiles and gharial in India (Whitaker and Basu, 1983), do not touch upon the relationship between growth and reproduction. The studies on growth patterns in captive lizards (e.g., *Phrynosoma ditmarsii* - Montanucci, 1988; *P. madagascariensis* - Demeter and Birchard, 1994; *Sceloporus undulatus* - Haenel and John-Alder, 2002) report the growth up to sexual maturity and in relation with reproductive events like clutch size frequency of clutches in a single breeding season, etc. Thus, the relationship between investments in somatic growth versus reproduction in lizards is poorly understood.

Calotes versicolor is a seasonal breeder. The dorsal body color of the lizard is light-brown greyish, transverse spots on back and sides (Tikader and Sharma, 1992). Both the sexes develop red color on antero-dorsal region during breeding season (Pandav et al., 2007). It has an extended breeding season in Southern India (May to October). The adult female lizard measures from 8–14.5 cm in snout vent length (SVL). It is a multi-clutched lizard with clutch size varying from 7–33 eggs (Shanbhag et al., 2000). Hence, it forms a good model to study the energy allocation (trade-off) between growth and reproduction. The present study deals with growth pattern in relation to sex, age at first maturity, and reproductive strategies in *C. versicolor* raised in captivity from hatching.

MATERIALS AND METHODS

We collected *C. versicolor* from Dharwad city (15°17'N, 75°3'E), Karnataka, India in May-June 2003. Six females in early gestation were identified by the presence of eggs that felt soft during palpation of abdomen and these were maintained in outdoor terraria at Department of Zoology, Karnatak University, Dharwad. Upon appearance of a single crease on the lateral side of the abdominal wall close to the hind limbs, the oviductal eggs in these lizards were deemed to have reached stage 27–28 embryos (Shanbhag et al., 2003). The eggs with oviductal embryos at stage 27–28 were stripped from these lizards, since the oviposition in *C. versicolor* takes place at embryonic stage 27–28 (Muthukarruppan et al., 1970) and were incubated in the laboratory. Each gravid lizard yielded 20 ± 3 eggs (range 17–22, $n = 6$) and a total of 124 eggs were collected. The eggs were incubated in laboratory (at ambient temperature 27.71 ± 0.29 °C and moisture 40–45%) and hatchlings were obtained.

As soon as hatchlings emerged from the eggs ($n = 114$), they were placed in the glass terraria (30×30×25 cm) with wire mesh at the top for ventilation. Up to 10 hatchlings were reared per terrarium and 12 terraria were used for rearing hatchlings. When lizards attained two months, they were maintained in terraria (90×90×60 cm) made up of wire mesh on all sides except bottom. The lizards were kept in 1:2 male/female ratio in captivity as the males are generally seen with more than one female in the wild during breeding season. The sex of the lizards was identified at hatching by protrusion of hemipenis (Harlow, 1996). Thus, each terrarium housed 6 individuals (2 males, 4

females) and was exposed to natural sunlight. When lizards grew six months old, they were maintained in outdoor terraria of size 150×120×120 cm with wire mesh on top and two sides, and other two sides of transparent acrylic plates. They were provided with soil-sand mixed bed, large dried twigs for climbing, the potted plants, hiding places with broken earthen pots, and a water bowl. The newborn hatchlings were fed daily with termites and early instar silkworm larvae. Juveniles and sub-adults were fed with the silkworms, small cockroaches and grasshoppers on alternate day. Adult lizards were likewise fed on alternate day with silkworms, silk-moths, cockroaches, and grasshoppers and other insects caught in swapping of insect nets.

A total of 122 hatchlings (10 hatchlings obtained from wild caught lizards, that survived for more than 5 months, and 112 hatchlings obtained from 9 clutches of 7 captive born lizards) were used to study the growth patterns in this species. The snout-vent length (SVL), head length (HL), head width (HW), and head depth (HD) to the nearest mm were recorded at hatching. The hatchlings were marked by thermocol beads tied loosely on the posterior part of the trunk. Subsequently when hatchlings were one month old they were permanently marked by unique toe clipping. SVL and head size (HL, HW, and HD) of these lizards were recorded at monthly intervals.

Statistical analysis

In order to assess the variation in growth, the slopes for SVL of individual lizard were derived by taking observations of SVL in 5 consecutive months at a time moving from hatching to 4th month (H to 4), from 1 to 5, from 2 to 6, and so on till one year (12th month) by using time as the independent variable. The slopes obtained were compared by global *F* test to know the fluctuations in the growth pattern with respect to month and age (Rohatgi, 1976). Significance level was checked at 0.05. The lizards that survived for one year or more ($n = 14$) were considered for statistical analysis to have longitudinal data though 46% ($n = 50$) lizards born in captivity survived up to 7 months. To know whether there is a monthly variation in SVL and growth rate of male and female lizards (within a sex), if any, the data were analyzed by Friedman rank analysis. Variations in monthly growth in SVL, and head size (length, width, and depth) at a given age between the sexes were analyzed by Mann-Whitney U test. Data are represented as mean \pm SE. To know the relationship between growth patterns and temperature, if any, the data was analyzed by linear regression.

RESULTS

The eggs from natural nests hatched on 80 ± 2 days. All eggs in a clutch hatched within three days. The hatching success was higher than 95% in a clutch and 88% of these hatchlings survived at the end of the first month, while 63% of them survived at the end of the 3rd month. Out of these 46% lizards survived up to the 7th month. Seven females and seven male lizards survived for 1 year and 2 females survived for 2 years and 8 months. Overall, survival rate at the end of the first year was 13%.

When lizards were 6 months old, both the sexes developed black patches ventro-laterally in the neck region, a sign of onset of sexual maturity (Pandav et al., 2007). The males exhibited red colored hues on the head and gular area. The lizards began exhibiting courtship behavior when they were between 7–8 months. SVL of these males was 9.4 ± 0.02 cm ($n = 17$) and that of females was 8.3 ± 0.13 cm ($n = 33$). The mated females were soon gravid and laid eggs in captivity (Fig. 1).

Among the captive born lizards that survived for a year or more, 6 of them (L₁ to L₅ and L₈) bred in the 1st year between the age of 7-8 months (first breeding season after their hatching), 1 lizard (L₆) skipped breeding in the 1st year and bred in the 2nd year at an age of 21 months and another lizard (L₇) skipped breeding in the first two years and



Fig. 1. *Calotes versicolor* laying eggs in captivity.

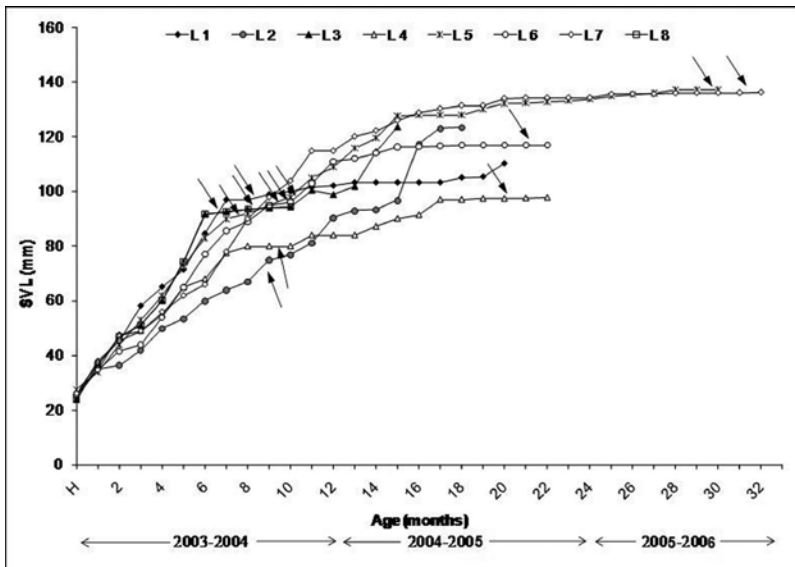


Fig. 2. Changes in the snout to vent length (SVL) in female *C. versicolor* that bred in first year and those that skipped breeding in the first or/and second year. Arrowheads indicate the month when the lizard oviposited. Note that the variations in growth pattern of lizards reflect a trade-off between growth and reproduction. H = month at hatching (October).

bred in the 3rd year at the age of 32 months. Two lizards laid 2 clutches in first breeding season, the interval between two clutches was 25 days for one lizard and 45 days for the other. Lizard (L₈) laid 3 clutches in first year (Fig. 2), not included in analysis as it died at the age of 10 months), laid second clutch of eggs after 25 days after ovipositing first clutch and third after 51 days of ovipositing second clutch not included in analysis as it died at the age of 10 months. This lizard died while ovipositing the third clutch. The lizards that bred and laid eggs within the first year, the clutch size ranged from 11–15. However, the lizards that skipped the breeding in the first year or two years the clutch size was 20–21.

Pattern of growth

Changes in SVL of male and female *C. versicolor* for a period of one year is shown in Table 1. SVL of both the sexes was comparable up to 4 months. However, the males grew larger than the females from 5th month onwards (Table 1, 2).

The female SVL increased by 5–7 mm/month during the initial 4 months. The growth in SVL increased rapidly by 8–9 mm/month in the next 3 months (March to May), prior to onset of breeding season ($F_7 = 83.83, P = 0.000$). The growth in SVL was significantly low during 8 to 12 months of age (June to October) (Table 1, 3).

In males, SVL increased by 3–12 mm/month during the first 4 months. The SVL increased rapidly (12–13 mm) in the 5th month to attain a size of 73.14 mm ± 0.9 in the 6th (April) month (Table 1). The growth in SVL of males was low when the lizards were 8 to 9 months (June to July) coinciding with the breeding activity ($F_7 = 22.39, P = 0.021$). An increase in SVL was seen in 10th to 12th (August to October) months (Table 1).

Table 1. Shows the snout-vent length (SVL), head length (HL), head width (HW), and head depth (HD) in *C. versicolor* from hatching up to one year of age H = month at hatching (October); n = 14 (females n = 7; males n = 7).

Months	SVL (mm ± SE)		HL (mm ± SE)		HW (mm ± SE)		HD (mm ± SE)	
	Female	Male	Female	Male	Female	Male	Female	Male
H	26.87 ± 0.7	25.53 ± 0.7	9.54 ± 0.4	9.27 ± 0.1	5.97 ± 0.1	5.81 ± 0.1	5.23 ± 0.2	5.07 ± 0.1
1	33.02 ± 1.2	37.36 ± 0.6	10.98 ± 0.3	11.36 ± 0.3	6.77 ± 0.1	6.9 ± 0.1	5.76 ± 0.15	6.02 ± 0.1
2	38.38 ± 1.1	40.52 ± 0.6	13.16 ± 0.4	12.86 ± 0.2	7.45 ± 0.1	7.56 ± 0.1	6.75 ± 0.07	6.8 ± 0.1
3	42.97 ± 0.5	43.77 ± 0.8	14.62 ± 0.4	14.35 ± 0.6	8.09 ± 0.2	8.49 ± 0.2	7.28 ± 0.1	7.35 ± 0.2
4	48.96 ± 0.7	48.18 ± 1.4	15.63 ± 0.3	18.38 ± 1.2	8.64 ± 0.1	10.61 ± 0.7	7.75 ± 0.2	9.13 ± 0.6
5	52.85 ± 0.3	60.88 ± 2	18.06 ± 0.4	22.91 ± 0.8	9.58 ± 0.1	12.25 ± 0.5	8.57 ± 0.2	10.71 ± 0.4
6	60.49 ± 1.2	73.14 ± 0.9	20.01 ± 0.7	25.6 ± 0.8	10.49 ± 0.2	13.57 ± 0.3	9.61 ± 0.3	11.91 ± 0.2
7	69.87 ± 3	90.59 ± 1.4	22.33 ± 0.5	27.7 ± 0.4	11.91 ± 0.3	15.39 ± 0.3	10.57 ± 0.3	12.99 ± 0.2
8	81.48 ± 2.8	92.79 ± 1.3	23.89 ± 0.2	30.52 ± 0.6	13.54 ± 0.2	17.99 ± 0.8	12.3 ± 0.4	14.29 ± 0.2
9	86.98 ± 2.7	94.89 ± 1.6	25.39 ± 0.6	32.66 ± 0.8	15.57 ± 0.8	19.46 ± 0.9	12.99 ± 0.5	16 ± 0.4
10	90.72 ± 3	105.2 ± 2.0	27.88 ± 1.2	33.65 ± 1.4	16.31 ± 0.5	21.37 ± 0.9	13.98 ± 0.6	16.7 ± 0.5
11	102.95 ± 2.2	113.02 ± 2.9	27.96 ± 0.9	37.5 ± 1.04	16.72 ± 0.8	23.5 ± 0.5	14.7 ± 0.5	18.5 ± 0.5
12	108.25 ± 2.2	120.32 ± 2.8	32.13 ± 0.8	40 ± 0	21.17 ± 1.2	27.2 ± 0.9	16.04 ± 0.4	20.1 ± 0.5

There was no significant difference in HL and HW between the sexes during the first 3 months. However, HL and HW were significantly larger in males than in females from 4th month onwards (Table 1, 2). Also, a significant difference in the HD was observed in lizards of 5 months or older, the head depth being greater in males than females (Table 1, 2).

Linear regression analysis revealed that ambient temperature does not have any influence of temperature on growth patterns ($r^2 = 0.070$, $P = 0.696$).

Growth, age at first reproduction and reproductive strategies exhibited by female

Individual growth in SVL of 7 female lizards that were born, bred and survived for a year or more in captivity is depicted in Fig. 2. The lizards L₁ to L₅ attained sexual maturity at the age of 7.42 ± 0.5 months and reproduced in the first breeding season (June-August, 2004) at 7.5–9.8 cm SVL (Fig. 2). The clutch size these lizards ranged from 11 to 15. Among these 4 individuals, L₄ lizard also bred in the second year (June-July, 2005) at the age of 20 months (clutch size 20). However, this lizard died due to oviductal infection. SVL of L₁ to L₃ was more than that of L₄ at the onset of subsequent breeding season (Fig. 2).

The lizard (L₅) laid 2 clutches of eggs at an interval of 45 days between June-August (2004) at 9.2 cm SVL, and clutch size was 11 and 15. This lizard attained the size of 10.9 cm at the end of the first year. It skipped reproduction in the second year and attained a size of 13.3 cm at the end of second year of age (June, 2005) (Fig. 2). It bred in the 3rd year at the age of 30 months.

Table 2. Shows *U* and *P*-values from Mann Whitney U test for monthly variations in snout vent length (SVL), head length (HL), head width (HW), and head depth (HD) between male and female *C. versicolor* from hatchling until one year of age (n = 14).

Months	SVL		HL		HW		HD	
	U	<i>P</i>	U	<i>P</i>	U	<i>P</i>	U	<i>P</i>
H	15	0.224	15	0.224	19	0.482	19	0.482
1	7	0.025	17	0.337	20	0.565	16	0.276
2	17	0.337	21	0.654	19	0.482	22.5	0.798
3	20	0.565	21	0.654	16	0.276	22	0.749
4	17	0.338	9	0.048	8	0.035	13	0.141
5	1	0.003	1	0.003	2	0.004	2	0.004
6	0	0.002	0	0.002	0	0.002	1	0.003
7	0	0.002	0	0.002	0	0.002	0	0.002
8	0.5	0.002	0	0.002	0	0.002	4	0.008
9	7	0.025	0	0.004	0	0.027	2	0.01
10	0	0.002	3	0.038	0	0.008	3	0.038
11	5.5	0.015	0	0.014	0	0.013	0	0.013
12	5.5	0.015	0	0.007	0.5	0.019	0	0.013

H = month at hatching (October). Significant values are given in bold.

Table 3. Shows *F* and *P*- values from global *F* test for changes in growth in snout vent length (SVL) in *C. versicolor* from hatching until a period of one year (*n* = 14).

Months	<i>F</i> - value		<i>P</i> - value	
	Males (<i>n</i> = 7)	Females (<i>n</i> = 7)	Males	Females
H to 4	0.35	1.00	>0.05	>0.05
1 to 5	0.66	1.25	>0.05	>0.05
2 to 6	0.32	0.28	>0.05	>0.05
3 to 7	0.22	0.90	>0.05	>0.05
4 to 8	0.28	0.68	>0.05	>0.05
5 to 9	0.74	0.02	>0.05	>0.05
6 to 10	1.62	0.91	>0.05	>0.05
7 to 11	3.19	5.87	<0.05	<0.05
8 to 12	1.34	6.55	>0.05	<0.05

H = month at hatching (October)

The lizard L_6 did not breed in the first year (2004) and grew up to 11.1 cm. This lizard reproduced for the first time at age of 21 months (June 2005) at SVL of 11.7 cm and laid 20 eggs (Fig. 2).

The lizard (L_7) that did not breed in the first year attained a size of 11.5 cm and was the largest among the females at the end of the first year. This lizard did not show any breeding activity in the 2nd year also. The lizard showed 3–5 mm/month growth throughout the second year and attained the size 13.4 cm at the end of the 2nd year. It reproduced in the 3rd year, at the age of 32 months (June, 2006) and at size of 13.7 cm and developed a clutch of 21 eggs. However, it died before oviposition due to some infection in the digestive tract.

The lizards (L_1 to L_5) that bred in the first year showed almost negligible growth in SVL during reproductive period and attained SVL of 9.15 ± 0.84 cm at the age of one year. In contrast, the lizards (L_6 and L_7) that did not reproduce in the first year grew in their SVL and attained size of 10.3 and 11.5 cm at the age of one year. The lizards (L_5 and L_7) that did not reproduce in the second year also showed growth in their SVL and attained size of >13 cm at the age of 2 years. In general, growth in SVL was low during the breeding and also in the 2nd and 3rd year of their life when compared to that in the first year (Fig. 2).

DISCUSSION

The present study provides the first information on the age at maturity, growth, and breeding frequency in captivity in an arboreal agamid lizard the *C. versicolor* from the tropical region of South India. The earlier reports suggested that *C. versicolor* attains maturity in 9–12 months (Asana, 1931) and lays more than one clutch (Shanbhag, 2002). The present findings showed that some members in a population of *C. versicolor* may attain sexual maturity as early as seven months of age and breed in first year while others may breed in 2nd or

3rd year. The earlier assumption that *C. versicolor* is a multi-clutched lizard (Shanbhag, 2002) is confirmed by the present study. One of the lizards developed three clutches of eggs during the same breeding season. Thus, the present study showed that if food supply is uninterrupted, *C. versicolor* may produce as many as 3 clutches in the first year itself.

It is well known that the growth rate in herpets changes between cool and warm seasons in temperate habitats (Bjorndal et al., 1998; Wapstra et al., 2001), with arrest of growth during cooler seasons. However, present study revealed that growth is low, but not arrested in *C. versicolor* during winter. Statistical analysis also showed that temperature per se has no significant influence on growth rate. It may be because winter is not so severe in tropical part of India unlike in temperate areas. Further, the growth rate though low continues even after attaining sexual maturity in *C. versicolor* as in *Crotalus horridus atricaudatus*, *Leiolopisma suteri* and *S. undulatus* (Towns, 1975; Shine and Iverson, 1995; Haenel and John-Alder, 2002).

There are several reports comparing growth rates between the sexes in lizards based on the wild populations and mark-recapture studies (Bellairs, 1969; Jenssen and Andrews, 1984; Shine, 1988; James, 1991; Sugg et al., 1995; Allan et al., 2006). The males of *Agama agama*, *Phrynocephalus interscapularis*, *Anolis opalinus* and *Cophosaurus texanus scitulus* grow larger than the females. The females exhibit slow growth rate as they invest more energy in reproduction (Bellairs, 1969; Jenssen and Andrews, 1984; Shine, 1988; Sugg et al., 1995). The study by James (1991) showed that the female of the genus *Ctenotus* grows slower than the male but reaches the larger asymptotic body size than its male counterparts in most species. Males and females of common wall lizard, *Podarcis muralis* reach similar snout-vent lengths, but males have relatively longer tails and heavier in body mass (Allan et al., 2006). A study involving demographic analysis of growth rate in field and also in controlled laboratory condition on eastern fence lizard, *Sceloporus undulatus* reported that in natural environment females grow faster than their male counterparts before the end of the first year (before sexual maturity) while in laboratory there was no sex specific difference in growth until maturity (Haenel and John-Alder, 2002). The present study shows that SVL growth is more pronounced in males than in females before attaining sexual maturity in captive *C. versicolor*. Hence, males attain slightly larger size than the females at first maturity. Further, males are also larger than females at one year of age. These observations suggest that males are larger in size than the females at comparable age.

Sexual size dimorphism (SSD) has been reported in several reptiles by either collecting data on wild caught species or by mark – recapture studies (Berry and Shine, 1980; Gibbons and Lovich, 1990; Forsman and Shine, 1995; Brana, 1996; Huang, 1996; Fernandez and Rivera, 2001; Webb et al., 2002; Pinto et al., 2005). However, studies on SSD in reptiles by long term growth studies in laboratory are scarce (Haenel and John-Alder, 2002). The differential growth rate between the sexes prior to sexual maturity seems to lead to SSD in *Tropidurus torquatus* (Pinto et al., 2005). An earlier study by Radder et al (2001) reported that SVL biased SSD does not occur in *C. versicolor*. Conclusions of Radder et al (2001) were based on wild caught lizards and they did not consider the age of the lizards. But the present study showed a significant difference in SVL between the sexes from 5 months of age and also after maturity in the same age group suggesting SSD in SVL. However, SSD observed in relative head size in the present study is in conform-

ity with the findings of Radder et al (2001). The larger body and head sizes in males may help to overpower its rival and get access to the female similar to reported in *Eumeces laticeps*, *Niveoscincus microlepidotus*, and *Lacerta vivipara* (Cooper and Vitt, 1993; Olsson et al., 2002; Hofmann and Henle, 2006). During breeding season, male-male combat is often seen in *C. versicolor* possibly over a female. During such combats we have seen that males virtually stand on their hind legs and tail and blow each other with heads.

Two important life history traits in lizards are the size at first maturity and fecundity. A trade-off between the body size and age at reproduction is reported in *S. undulatus* (Ferguson and Talent, 1993) and *Microlophus delaninis* (Jordan and Snell, 2002). Also, the clutch size is reported to be positively correlated to the body size in lizard species (Ferguson and Talent, 1993; Blanckenhorn, 2000; Shanbhag et al., 2000; Radder and Shanbhag, 2003, 2004). Thus, larger body size is related to the fecundity/fitness of the female. However, attainment of a larger body size delays reproduction and is often accompanied by a lower probability of survival to the next breeding season. The present study revealed a plasticity in size and age at maturity operating among a population of *C. versicolor*. Some females may mature at smaller size with small clutch size as early as at seven months of age like the lizard L₃ in the present study while others may skip reproduction at first breeding season after their birth, grow larger in size, reproduce in second year and thus increase fecundity with greater clutch size (Lizard L₆). Yet, others (Lizard L₅) reproduce in the first year and skip reproduction in the second year and reproduce in the third year with even greater clutch size. Also, some females do not reproduce in first two years, grow in size and reproduce in the third year with highest fecundity (Lizard L₇). Thus, a trade-off is seen between age at sexual maturity, body size, and fecundity in *C. versicolor*.

The present study shows that differential growth patterns in female *C. versicolor* lead to the variations in key life history traits such as age at maturity, body size and annual and lifetime reproductive output of individuals in a population. Though our sample size of lizards beyond one year was small, the data highlight different adaptive strategies (growth and reproduction) operating in a population of *C. versicolor*.

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