Reproductive strategies in the lizard, *Calotes versicolor*

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Animal species have evolved diverse reproductive strategies to maximize their reproductive success. Studies on the Indian garden lizard (*Calotes versicolor*) have recently revealed many fascinating reproductive strategies such as manipulation of clutch and egg size depending upon breeding timing, in spite of pelvic aperture constraint; switching from capital breeder to income breeder; female sperm storage as long as six months; oviductal egg retention for six months or even more under adverse conditions, by manifesting embryonic diapause and preventing oviposition. The findings on *C. versicolor* provide clues to the evolution of viviparity. In addition, perception of socio-sexual (tactile, visual and chemical) cues from conspecifics of opposite sex plays an important role in their own gonadal recrudescence and reproduction. The significance and mechanisms governing the evolution of diverse reproductive strategies in the lizard are discussed.

THE garden lizard, *Calotes versicolor* (family Agamidae) is widely distributed in India and it can be maintained with ease in captivity. It is a multi-clutched, seasonal breeder with long breeding season (May to October)[1,2]. It exhibits polyautochrony, i.e. ovulates many eggs simultaneously from both the ovaries[3,4]. Information on ovarian follicular kinetics[3], plasma sex steroid hormone profiles during gonadal cycles[4], fat body cycles[5,6], endocrine regulation of gonads[7–11] and accessory reproductive organs[12–14], and role of proximate factors in controlling gonadal cycles[2] is available for the species. In addition, gonadal sex differentiation[15,16] and mechanism controlling the phenomenon[17–20] are studied in this species. In recent years, the evolution of reproductive strategies of *C. versicolor* has been elucidated. This paper reviews reproductive strategies like manipulation of fecundity, switching from capital to income breeder, prolonged egg retention and embryonic diapause, female sperm-storage phenomenon, and role of socio-sexual factors in gonadal development in *C. versicolor*.

Manipulation of fecundity

The egg-laying pattern in squamates varies. Some species lay fixed number of eggs in a clutch (determinate clutch or fixed clutch). For example, most geckos have a clutch size of two eggs. In contrast, others lay variable number of eggs (e.g. *C. versicolor*, *Mabuya carinata*) in a clutch (variable clutch). In lizards with fixed as well as with variable clutch, especially from the tropical region, clutch frequency may vary with proximate climatic factors and food availability. On the other hand, in individuals with variate clutch pattern, both clutch size and frequency may vary in relation to proximate climatic factors, food availability, fat reserves of the body and maternal body size[21,22]. Several studies, especially on chelonians and squamates, describe how optimal reproductive fitness is achieved through manipulation of clutch and/or egg size[21–23]. There are species in which the egg size is optimized in a population irrespective of the body size of the female[24]. A fixity in pelvic aperture size leads to optimization of the egg size. However, in some species of turtles and lizards[24,25], the egg size is not optimized and therefore varies with the body size of the female. It has been shown in these species that an increase in the body size is accompanied by a corresponding increase in the pelvic aperture. Hence, in these cases optimization of egg size is not obligatory.

The recent studies by Shanbhag *et al.*[26] on fecundity manipulation by *C. versicolor* have revealed some interesting phenomena. They showed that the clutch size and clutch mass exhibit a positive correlation with body size (snout-vent length, SVL; Figure 1), indicating that reproductive investment is influenced by body size of the female. Further, the clutch and egg sizes are inversely related (Figure 2). Thus, a trade-off between clutch size and egg size (mass and volume) is obvious in *C. versicolor* and there is no optimization of egg size. More interestingly, the above study also showed that the total energy allocated for reproduction (clutch mass) remains the same in early, mid and late breeding individuals (Figure 3), even though the fecundity (clutch size) declines in late breeders. Apparently, the energy allocated for reproduction in each bout of egg production in *C. versicolor* is optimized by natural selection provided other conditions such as food availability, etc. are optimal, and predator pressure is minimal. Further, in this lizard SVL is the prime factor determining the clutch mass[26].

In *C. versicolor*, width of the pelvic aperture remains virtually constant over the entire range of body sizes after attainment of sexual maturity. Consequently, pelvic aperture size becomes a constraint and optimization of eggs become obligatory. If not, a female producing larger

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eggs may become egg-bound due to pelvic constraint and eventually die. In *C. versicolor*, late breeders produce large-sized eggs irrespective of their body size (Figure 3). Thus, producing larger eggs by late breeders could result in a setback. Yet, these lizards produce eggs of variable sizes. This intriguing problem was resolved by carefully analysing the data on egg dimensions[21]. The analysis showed that when the lizards produce larger eggs, they change the egg length rather than the width (Table 1) over the entire range of SVL to overcome pelvic constraint.

Like in most oviparous vertebrates, female lizards deposit extra yolk in the egg, beyond what is absolutely necessary for the development of embryo until the hatching stage. Interestingly, though there is a lot of variation in egg size with respect to early, mid and late breeding in the season, there is no appreciable difference in size (SVL) of hatchlings. However, larger eggs of the late breeding season produce heavier hatchlings and also possess more internalized yolk than those born early in the breeding season (May–June)[27]. Radder *et al.*[27] opine that producing heavier hatchlings with more internalized yolk at the end of the breeding season may enhance fitness of the hatchlings, since late born have to compete for

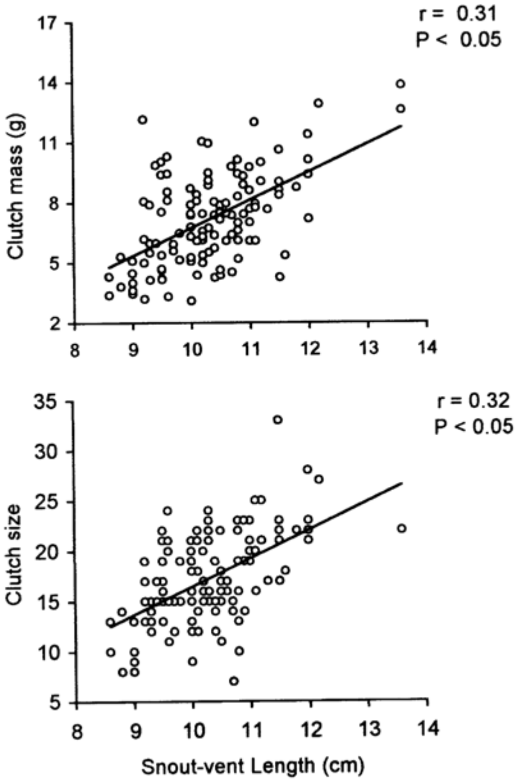

Figure 1. Positive relationship between body size (SVL) and clutch size and mass in *C. versicolor*.

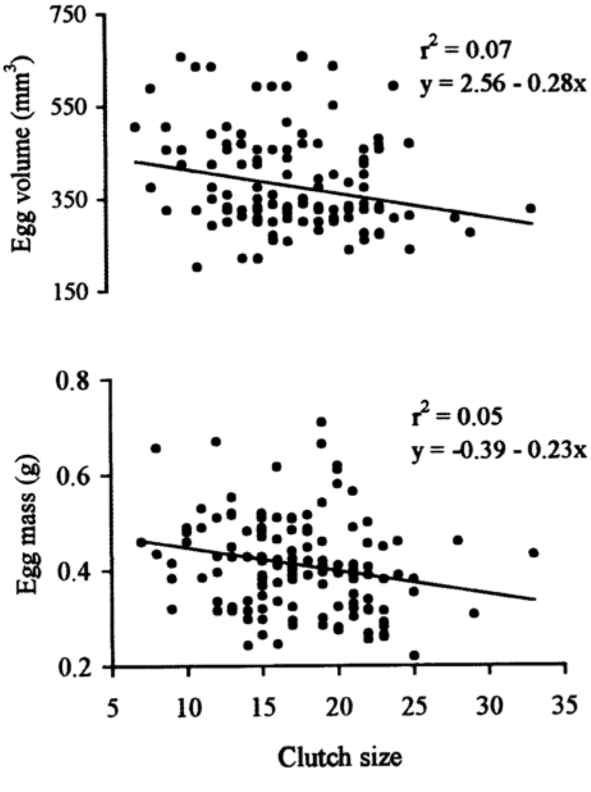

Figure 2. Clutch and egg sizes (mass and volume) and egg length and width in *C. versicolor*. Note that clutch size is negatively correlated with egg size and egg length.

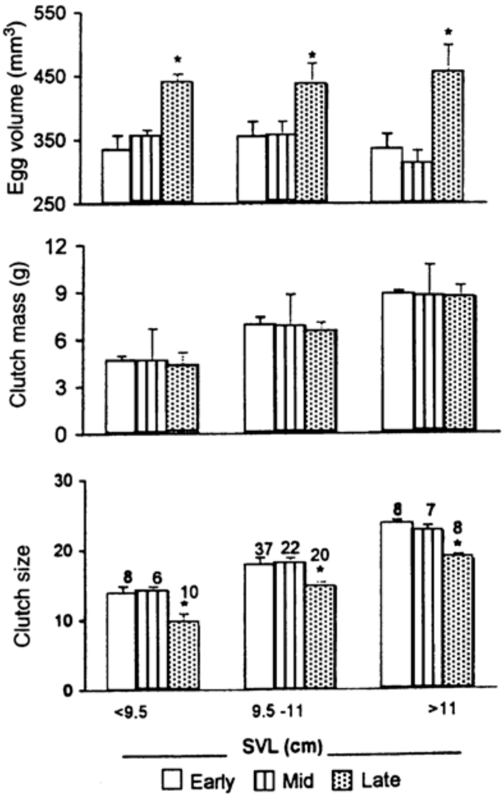

Figure 3. Change in clutch size, clutch mass and egg volume in *C. versicolor* of different SVL groups with respect to early, mid and late clutches. Asterisks above standard error bars indicate a significant difference within the same SVL group among early, mid and late clutches. Numbers above SE bars indicate sample size. (Adapted from Shanbhag *et al.*[26]).

Table 1. Length (*L*) and width (*W*) in mm of eggs in *Calotes versicolor* with respect to SVL

		Clutch		
SVL (cm)		Early (May–June)	Mid (July–August)	Late (September–October)
< 9.5	*L*	13.18 ± 0.13	12.66 ± 0.21	14.75 ± 0.53*
	W	7.18 ± 0.18	7.16 ± 0.30	7.60 ± 0.24
		(8)	(6)	(10)
9.5–11.0	*L*	12.98 ± 0.17	12.72 ± 0.18	13.75 ± 0.23*
	W	7.39 ± 0.10	7.22 ± 0.17	7.70 ± 0.16
		(37)	(22)	(20)
> 11.0	*L*	12.81 ± 0.33	12.93 ± 0.07	14.00 ± 0.42*
	W	7.31 ± 0.13	7.29 ± 0.38	7.81 ± 0.20
		(8)	(7)	(8)

*Significant difference within the same SVL group among early, mid and late clutches at $P < 0.05$ based on one-way ANOVA using log-transformed data. Numbers in parentheses indicate sample size. (Adapted from Shanbhag *et al.*[26]).

food and other resources with older individuals of early clutches.

Switching from capital to income breeding

All organisms must use their energy resources judicially to ensure growth, survival and reproduction. An organism may overcome increased demand of resources/energy for reproduction by increasing its food intake. The reproductive fitness could be achieved by two ways[28]. The so-called 'capital breeders' acquire food in advance and store it endogenously or exogenously until reproduction. Others, especially those living in a predictable environment with unlimited food resource, adjust their food intake concurrently with breeding activity (income breeders). Several species of squamates are known to store energy in the form of abdominal fat bodies or fat pads as reserve energy. The energy stores are mainly utilized as reserve food during hibernation in temperate species. Among tropical species, the fat bodies play a main supporting role in reproduction, especially during periods of unpredictable or fluctuating resource availability.

Shanbhag and Prasad[5] showed that in *C. versicolor*, the abdominal fat bodies have a supportive role in reproduction. An inverse relationship between the fat body mass and ovarian cycle is found in *C. versicolor* (Figure 4). They also demonstrated by experimental manipulations, such as fatectomy (FBX), ovariectomy (OvX) and E_2 treatment to the OvX lizards, that energy stores in the fat bodies are indeed used for growth of vitellogenic follicles. It is interesting to note that in *C. versicolor*, for the vitellogenic growth of the first clutch of eggs, the energy stores in the form of fat bodies are used up while the energy requirement for growth of vitellogenic follicles of subsequent clutches is met through intake of food. Thus, *C. versicolor* adopts a strategy of capital breeder for production of the first clutch of the season and later switches to income breeding by relying upon daily food intake for sustaining development of subsequent clutches of the season. Incidentally, food is generally abundant in the later part of the breeding season[5].

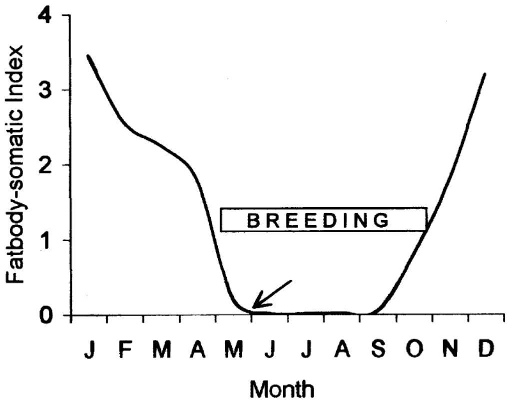

Figure 4. Fat body-somatic index (FBSI) during annual breeding cycle in *C. versicolor*. Note that FBSI drops at the formation of first clutch of the breeding season (arrow) and remains almost nil during the formation of subsequent clutches.

Sperm storage in females

Several species of reptiles are known to store sperm in the oviduct for variable length of time depending upon species[2]. This phenomenon is found among temperate species in which the gonadal cycles are temporally dissociated. For instance, the male skink (*Hemiergis peronii*) inhabiting the temperate region produces sperm in autumn and also mates with females prior to ovarian recrudescence[29]. The testes then regress. The females store sperm in the oviduct. After emergence from hibernation, females ovulate and use the stored sperm for fertilization. The young are born in early spring. Sperm storage in females is *obligatory* in such cases. The lizard, *C. versicolor* does not hibernate in south India. Also, the gonadal cycle in both the sexes is not temporally separated. Therefore, sperm storage by females is not obligatory in *C. versicolor*. Yet, they store sperms in sperm receptacles formed by the mucosal folds of the oviduct at the uterovaginal junction[30]. Survival of the sperm for as long as six months in the oviduct is an intriguing phenomenon. The physiological and biochemical factors responsible for sperm survival for such a long period are not fully understood. Sperms in the sperm receptacle are found with PAS-positive secretion, possibly derived from the secretion of male reproductive tract[31]. Also, secretions present in the sperm receptacle in *C. versicolor* exhibit elevated activity of acid phosphatase. This enzyme seems to be derived from the male and principally from the renal sexual segment, and may have a role in sperm sustenance in the female reproductive tract[31]. Shanbhag and Prasad[32] have experimentally shown the fertilizing ability of stored sperm in the species. Vitellogenic females reared in the laboratory in the absence of males were induced to ovulate by injecting PMSG. The eggs were not only fertilized using stored oviductal sperm, but they also successfully continued embryonic development. The oviductal sperm storage mechanism is also seen in *Psammophilus dorasalis* that lays more than one clutch per breeding season[33]. However, oviductal sperm storage is not observed in *M. carinata* that lays only one clutch during the breeding season[31]. This suggests that oviductal sperm storage strategy has been evolved in tropical lizards that lay eggs in multiple clutches possibly to eliminate repeated mating and reduce risk of predation. In *C. versicolor*, testicular regression commences earlier than that of the ovaries during a breeding season. In spite of early testicular regression in males, females produce eggs that seem to be fertilized by sperm stored in the oviduct.

Oviductal egg retention and embryonic diapause

Evolution of transition in reproductive mode from egg-laying to live-bearing is obvious in all classes of vertebrates, except in the aves. The reptiles are the first vertebrates to conquer life on land by evolving cleidoic eggs and internal fertilization. Retention of eggs in the oviduct for short duration (1–2 weeks) may help completion of early embryonic development. However, some species of lizards from temperate as well as tropical regions exhibit 'prolonged oviductal egg retention' phenomenon when oviposition sites or certain proximate factors (e.g. severe cold, lack of rains, etc.) are not congenial[34]. The egg retention phenomenon was systematically studied under laboratory condition in *C. versicolor* by Shanbhag and co-workers. Normally, the lizards retain eggs in the oviduct for about two weeks before oviposition, when embryos are around stage 27–28 of development[32,35]. Radder *et al.*[36] have shown that *C. versicolor* can retain eggs in the oviduct (Figure 5) for at least six months (maximum for any lizard species recorded so far), or even more in captive specimens. The eggs, if stripped from the oviduct, produce normal hatchlings following incubation at ambient temperature. Prolonged egg retention poses at least two problems to the mother. First, the growing embryos demand more oxygen and moisture. Secondly, the water imbibed through the parchment-like shells swells up the eggs and may cause difficulty in their exit through the pelvic aperture, the size of which is fixed in *C. versicolor*. Thus, the pelvic constraint must discourage any increase in egg width. However, *C. versicolor* has successfully overcome the problems associated with egg retention for prolonged period by evolving two mechanisms – arresting the embryonic development at stage 34 (embryonic diapause), and preventing oviductal contraction, *vis-à-vis* expulsion of eggs.

Control of embryonic diapause

Like in many other squamate species with flexible eggshell, eggs of *C. versicolor* increase in volume with embryonic growth following oviposition[37]. The increase in size of eggs is mainly due to imbibed moisture. Arresting embryonic growth at stage 34 limits the egg size such

Figure 5. *C. versicolor* with eggs retained in the oviduct for about 45 days. Arrows show bulges in the lateral abodominal wall due to presence of retained eggs.

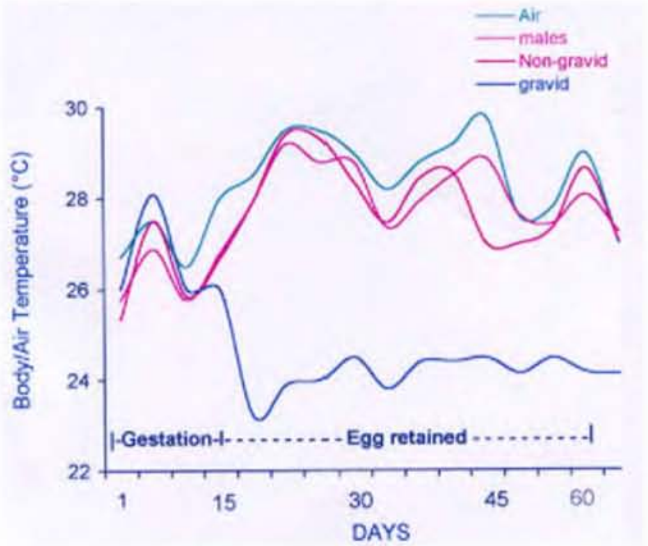

Figure 6. Ambient temperature and body temperature of males, non-gravid and gravid females. Note that there is a drastic drop in body temperature of gravid females with prolonged egg retention.

that it will facilitate their passage through the pelvic aperture. Further, arresting embryonic growth also reduces physiological demands of otherwise growing embryo for oxygen and moisture. Shanbhag *et al.*[38] have shown that the embryonic diapause is brought about in *C. versicolor* during prolonged egg retention by drastically lowering its body temperature by 3–5°C (Figure 6) throughout the period. Body temperature of the females with prolonged egg retention hovers around 23°C, and thereby brings about embryonic diapause. In conformity with this observation is the fact that *in vitro* embryonic growth in *C. versicolor* arrests around 23°C (ref. 37).

Endocrine control of prolonged egg retention

Like in other oviparous lizards[39,40], in *C. versicolor*, corpora lutea (CL) are the source of progesterone (P) in gravid individuals[41]. However, Shanbhag *et al.*[41] have shown that in *C. versicolor*, plasma P levels fall after mid-gestation, coinciding with trace 3β-hydroxysteroid dehydrogenase (3β-HSDH) enzyme activity in CL. These findings indicate that high levels of P are not essential after mid-gestation (i.e. after one week) in the lizard. Interestingly, in lizards with prolonged egg retention, i.e. beyond two weeks, the plasma P levels rise (Figure 7) despite the collapse of CL. Interestingly, a marked rise in 3β-HSDH activity is then observed in the adrenal glands, while CL continue to degenerate. Hence, in such lizards the source of elevated plasma P is the adrenal gland and not the ovaries[41]. Thus, in response to egg-retention stress, the adrenal glands (the main targets of stress) of gravid lizard secrete high amount of P. Shine and Guillette[42] had hypothesized that prolonged oviductal egg retention, one of the steps in the evolution of viviparity in reptiles, might have evolved under stressful ecological conditions, and hormones from adrenal glands might help in the process of egg retention. The findings on *C. versicolor*, besides showing that P secreted by the adrenal gland promotes oviductal egg retention (by its antimyometrial action), also provide experimental support to the 'stress-induced evolution of viviparity' hypothesis in reptiles.

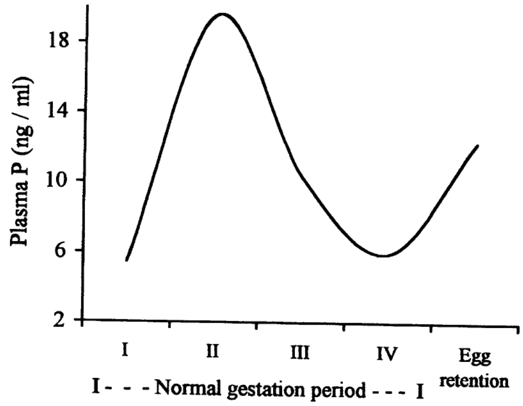

Figure 7. Plasma progesterone (P) levels in *C. versicolor* during normal gestation and prolonged egg retention period. I–IV represent stages during normal gestation: I, Following ovulation; II, During egg-shell formation; III, Embryo at stage 14–16; IV, Just before oviposition, stage 25–26 embryo. Note that plasma P levels drop and rise at stage II, drop to basal level prior to oviposition but rise again in lizards with retained eggs. (Adapted from Shanbhag *et al.*[41]).

Role of socio-sexual cues in reproduction

In seasonally breeding reptiles, a gonadal cycle typically involves recrudescence, breeding and post-breeding quiescence phases. Interaction between external (physical, climatic and social environment) and internal (neuroendocrine) factors is essential for successful reproduction. The control of gonadal cycles through endocrine mechanisms and proximate factors is reasonably well-understood for lizards[2,43]. Little is known about the role of social cues governing reproduction in lizards. Recent researches, however, show that social cues are also among important regulators of reptilian reproduction. The integration of social cues in lizards may be mediated through eyes, olfaction and vomeronasal systems with specific input to specific brain nuclei. In the brain, specific nuclei in the limbic system that concentrate steroid hormones receive input from these sensory areas, and these in turn project to the hypothalamus where both internal and external cues are integrated[43]. Studies dealing with the role of socio-sexual factors in reptilian reproduction are mostly carried out on the genus *Anolis*. These in general show that among lizards maintained in groups in the laboratory, the sexual composition of conspecifics of opposite sex, social experience and dominance–subordinance hierarchy through neuroendocrine mechanisms influence gonadal recrudescence and mating behaviour of the cagemates[44–46].

Through elegantly designed experiments, Shanbhag *et al.*[47] have demonstrated the importance of socio-sexual factors in gonadal recrudescence and plasma steroid hormone levels in *C. versicolor*. In this study, adult lizards were maintained in groups as (1) males and females, (2) males and females separated by a wire mesh, (3) same sex groups of males or females, (4) castrated males with intact females, and (5) OvX females with intact males from post-breeding to breeding phase. The study has shown that isolation of lizards from the opposite sex adversely affects gonadal recrudescence. In all-male groups, spermatogenetic recrudescence was not observed (Figure 8 *a*). The presence of females (intact or ovariectomized) is needed for initiation of spermatogenesis. Further, males that could view females with intact recrudescing ovaries through a wire mesh completed only one wave of spermatogenesis. But for sustenance of spermatogenesis, the presence of females with recrudescing ovaries producing estrogen is needed. Possibly, elevated E_2 levels are needed for production of pheromonal signals in the females. Therefore, perception of chemical, tactile and visual cues from the female by the male seems

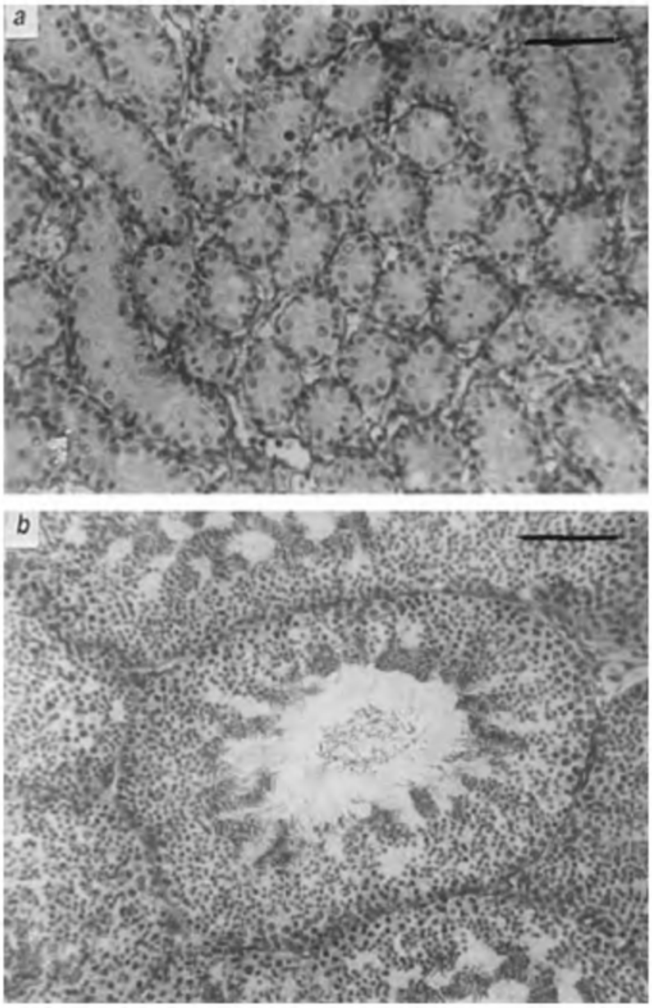

Figure 8. Transverse sections of the testes. ***a***, Small seminiferous tubules lined by a few spermatogonia and Sertoli cells in a male from an all-male group; ***b***, Enlarged seminiferous tubules and all stages of spermatogenesis, including sperm in lizards housed with intact females. Scale line indicates 50 μm.

to play an important role in sustaining qualitative and quantitative aspects of spermatogenetic activity (Figure 8 *b*) and high plasma T levels (Figure 9) in *C. versicolor*. Similarly, the presence of intact males with active spermatogenesis and elevated plasma T level facilitates recruitment and development of greater number of vitellogenic follicles (Table 2) and elevated plasma E_2 levels (Figure 9) in *C. versicolor*. The absence of males inhibits ovarian recrudescence. Females maintained with castrated males or receiving only visual/chemical cue from the males were unable to exhibit optimum ovarian activity. Thus, the perception of socio-sexual (tactile, visual and chemical) cues from the members of the opposite sex is important for regulating its own gonadal recrudescence *vis-à-vis* reproductive effort in *C. versicolor*. After all, the production of gametes is an expensive phenomenon and their production in the absence of mates in a seasonally breeding species would be a wasteful process.

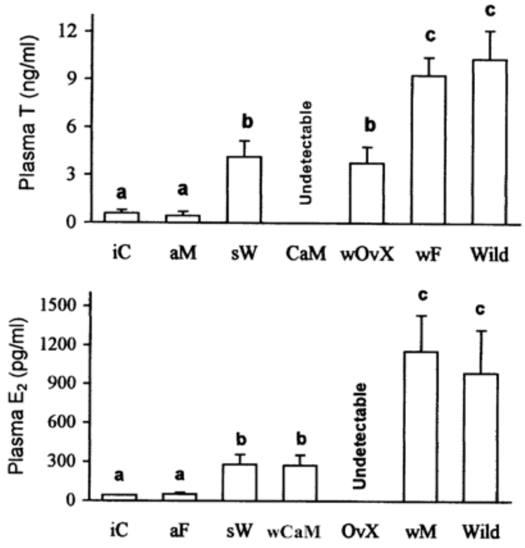

Figure 9. Plasma T (male) and E_2 (female) values in *C. versicolor* subjected to various socio-sexual situations. Values are mean ± SE ($n = 5$ for each group). iC, Initial control; aM, All males; aF, All females; sW, Separated from opposite sex by wire mesh; wCaM, Kept with castrated males; wOvX, Maintained with OvX females; wM/wF, Kept with intact males/females; OvX, Ovariectomized females; CaM, Castrated males; Wild, Wild caught male/female. Non-identical alphabets above the bar indicate significant difference among groups. (Adapted from Shanbhag *et al.*[47]).

Table 2. Effect of group composition on number of vitellogenic follicles and range of largest follicular diameter in female *C. versicolor*

Group	No. of vitellogenic follicles	Largest follicular diameter (mm)
Initial control	–	$0.59–0.80^a$
With intact male	12.20 ± 0.37^a	$3.80–7.96^b$
With castrated male	9.20 ± 0.58^b	$3.17–5.41^c$
Separated by wire mesh	6.80 ± 0.58^c	$2.78–3.92^c$
All females	–	$1.00–2.29^d$
Wild caught*	10.60 ± 0.93^a	$2.40–7.52^b$

Non-identical superscripts indicate a significant difference between groups at $P < 0.05$ analysed using one-way ANOVA. *Wild caught lizards at termination of the experiment.

Conclusions

Recent researches have shown that the garden lizard *C. versicolor* has evolved several strategies to optimize its reproductive fitness. For instance, plasticity to manipulate clutch and egg size depending upon the breeding timing is an interesting phenomenon exhibited by it. It would be interesting to know the pattern of clutch and egg-size modifications in other agamids and also in other sympatric lizards occupying different microhabitats. Female sperm storage and maintenance of viable sperm for over six months is another important strategy that seems to have co-evolved with multiple clutch pattern in *C. versicolor*. However, the mechanisms for survival of sperm in the oviduct for a long period are not yet fully understood and need investigation. DNA fingerprinting of stored sperm is needed to resolve whether *C. versicolor* follows monoandry or polyandry. Prolonged egg retention in the oviduct is a noteworthy strategy exhibited by *C. versicolor*. Whether lizards other than agamids found in India exhibit such a phenomenon, is unknown. Exhaustive studies involving more representative species are needed to generalize the mechanisms involved in prolonged oviductal egg retention in lizards. It should be noted that prolonged egg retention is a stage in the evolution of viviparity. Studies on *C. versicolor* show that such a phenomenon is related to stress (captivity, absence of suitable conditions for oviposition, and so on) and that adrenal glands, through secretion of P, promote egg retention. These findings provide experimental proof to the 'stress-induced evolution of viviparity' hypothesis. The most neglected area of research pertains to the role of social environment and interaction with conspecifics in the control of gonadal recrudescence in lizards. However, recent studies on *C. versicolor* show that conspecifics of opposite sex mutually regulate or affect gonadal recrudescence. Hence, social isolation leads to failure of gonadal recrudescence and thereby reproduction. Studies on *C. versicolor* have thus revealed conclusively the importance of cues (visual, olfactory and tactile) from conspecifics of the opposite sex in its own gonadal recrudescence.

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