Effects of ontogenetic processes and rearing conditions

Chapter · January 1995

DOI: 10.1007/978-94-011-1222-2_8

CITATIONS
12

READS
294

2 authors, including:

Gordon Burghardt
University of Tennessee
320 PUBLICATIONS **7,548** CITATIONS

SEE PROFILE

Health and Welfare of Captive Reptiles

Edited by

Clifford Warwick
Director of the Institute of Herpetology
Worcester, UK

Fredric L. Frye
Director of the Fund for Clinical Research
Davis, California
USA

and

James B. Murphy
Curator of the Department of Herpetology
Dallas Zoo
Texas, USA

CHAPMAN & HALL
London · Glasgow · Weinheim · New York · Tokyo · Melbourne · Madras

1995

7 Effects of ontogenetic processes and rearing conditions

Gordon M. Burghardt and Donna G. Layne

7.1 INTRODUCTION

Captive breeding of reptiles at institutions and by private individuals is often considered a major part of reptile conservation efforts. Captive-bred reptiles are also becoming a significant source for the 'pet' store trade. They are also used in behavioural, physiological and biomedical research, because there is some control over the rearing and breeding history and because the use of captive-reared animals potentially reduces the impact of collection on wild populations. There are now many publications by professionals in reptile behaviour outlining husbandry procedures and behavioural factors (for example Schaeffer *et al.*, 1992; Warwick, 1990a,b). However, it may not be enough to raise captive-bred animals to be seemingly healthy adults. Even though reptiles are highly precocious as neonates, early rearing conditions and short-term interventions may have long-lasting effects on later behaviour. These effects may not be immediately apparent but they can influence the health and well-being of the animal in captivity, as well as determine how well (or poorly) they could survive if they were to be released into the wild.

In this chapter we outline the major life history stages and classes of events that may affect the subsequent behavioural repertoire and perceptual responses of reptiles. Due to limits of space and the nature of our own

Health and Welfare of Captive Reptiles. Edited by Clifford Warwick, Fredric L. Frye and James B. Murphy. Published in 1995 by Chapman & Hall, London. ISBN 0 412 55080 6

experience we will concentrate mainly on squamate reptiles and, to a lesser extent, turtles and crocodilians. Behavioural aspects of development and their consequences for behavioural competence will be emphasized. It cannot be sufficiently stressed that, to be complete, the study of development must also consider neural, endocrine, reproductive, metabolic, psychological, phylogenetic and ecological factors (Burghardt, 1988; Chiszar, Smith and Carpenter, in press). Even the study of the mental experiences of reptiles may be necessary to add to the predictive power of various captive regimes in terms of breeding, showing species-typical behaviour and ability to adapt to various settings. Individual differences are a prime area for further study as both genetic and experiential variation may play a part in the physical and psychological well-being of reptiles in captivity. Early work on reptile learning and behavioural development is reviewed elsewhere (for instance Burghardt, 1977, 1978); selected studies will be reviewed here to illustrate phenomena and concepts that we see as currently relevant to captive management.

7.2 THE PRENATAL PERIOD

The earliest condition that all animals experience is that of the prenatal environment. The behavioural consequences of interventions in this period have been little studied, although progress is being made with laboratory rodents (for example, Smotherman and Robinson, 1988). A few pioneering descriptive studies are available for reptiles, such as Decker (1967) in common snapping turtles (*Chelydra serpentina*) and Holtzman and Halpern (1989) in common garter snakes (*Thamnophis sirtalis*).

Prenatal hormones are important in sexual differentiation, as is well known. However, recently it has been shown that embryos are influenced by hormone production in adjacent embryos, with post-natal effects on behaviour and morphology (review in Yahr, 1988). Although sexually dimorphic behaviour in neonate reptiles has been studied, it is possible that delayed effects from chance, non-genetic uterine position may lead to feminized or masculinized behaviour in males and females, respectively, in viviparous species. This possibility is ripe for study.

A documented influential factor during ectotherm development is temperature. Being readily manipulated, temperature is one factor for which prenatal manipulation has been carried out. Atypical incubation temperatures (oviparous species) or exposure of pregnant females to temperature extremes (viviparous species) can prevent embryos from developing, produce developed but stillborn neonates, or result in physical abnormalities (Vinegar, 1973, 1974; Burger, Zappalorti and Gochfeld, 1987; pers. obs. on *Thamnophis sirtalis*). In our laboratory Jim Schwartz and Hal Herzog held pregnant wild-caught *T. sirtalis* females at a constant

20, 25 or 30 °C for the final weeks of gestation, where 25 °C is the typical successful temperature for maintaining females. Five litters at the 25 °C temperature were born in early August with no deformities. Of 13 litters born at a constant 20 °C, 20 animals out of 245 were clearly deformed with kinked bodies, flat heads, no skull or abnormally large eyes. In eight litters, all neonates were born dead; in the other five litters only 37 of 100 neonates were alive at birth. Parturition was delayed until September or October. Of the 12 litters held at the 30 °C temperature, all litters contained live animals at a rate indistinguishable from the normal temperature. Gestation was accelerated, with births occurring in June and July. However, seven litters contained deformed snakes, with mostly kinked bodies, but also including a neonate with a foreshortened snout and one without a lower jaw.

Even moderate deviations from a proven successful temperature can thus have deleterious consequences. Of course, in the field (and usually in our laboratory) females have the opportunity to select their own body temperatures to some extent. Still, adverse effects of temperature during development may have limited the geographical range of many species.

The role of temperature is more complicated than being a neutral factor setting a delimited range in which a given species of reptile normally develops and is born without incident. The temperature of incubating eggs has been found to determine sex in some lizards, primarily geckos, agamids and lacertids (Gutzke and Crews, 1988), several kinds of turtles (Morreale *et al.*, 1982) and crocodilians (Ferguson and Joanen, 1982; Lang, 1987). These species lack sex chromosomes entirely (Bull, 1980). In many crocodilians and lizards higher temperatures frequently lead to males, lower temperatures to females, and intermediate temperatures to a mix of both sexes. In many turtles females are produced at higher temperatures, males at lower ones; other variants also exist (Janzen and Paukstis, 1991). Animals from the top of the nest cavity may be proportionally biased to one sex and those lower in the cavity to another if a temperature gradient exists. There are also time periods during incubation which are more sensitive to temperature effects for sex determination than others; in alligators, for example, the critical period lies between 7 and 21 days of incubation (Ferguson and Joanen, 1982). This phenomenon of temperature-dependent sex determination apparently eluded scientists and breeders for many years because of the difficulty and apparent irrelevance of ascertaining and recording the sex of hatchling turtles and crocodilians, groups in which the phenomenon is nearly ubiquitous.

There is little information on potential long-term effects on behaviour due to the temperature experienced prenatally independent of sex, but there are some intriguing findings. Temperature during incubation has been linked to hatchling thermoregulatory behaviour in crocodiles

(*Crocodylus palustris*) (Lang, 1985, 1987) and to hatchling size and sprint speed in lizards (*Podarcis muralis*) (van Damme *et al.*, 1992).

Detailed studies of the effects of egg incubation temperature on hatchling behaviour have been conducted on snakes (Burger, 1989, 1990, 1991). Drinking speed, righting response, locomotion, incline, tube crawl, ability to bridge a gap and antipredator responses were examined to measure the responses of hatchlings in situations similar to those they might encounter in their natural environment (Burger, 1989). Black racers, *Coluber constrictor,* incubated at 22 °C and 28 °C showed no difference in locomotor speed, but those from the 28 °C group exhibited greater manoeuvrability. In a species that relies on speed and agility in capturing prey and avoiding predators, incubation temperature probably impacts its survival capabilities. Kingsnakes, *Lampropeltis getula,* incubated at these same temperatures and at 32 °C, also had better hatchling performance at the intermediate temperature, 28 °C. Those snakes born from the high-temperature group, though longer in snout-vent length, were less agile and not defensive. The low-temperature group did not hatch at all (Burger, 1990). Long-term effects on behaviour (up to six months) have been found in hatchling pine snakes, *Pituophis melanoleucus*. Again, hatchlings from the low (21–23 °C) and the high (30–32 °C) temperature condition did not perform the tasks as well as those from the intermediate (26–28 °C) temperature groups (Burger, 1989).

The incubation temperatures of eggs and the extremes that gravid females are exposed to can be somewhat controlled in captivity. The effects of temperature on the sex, size, physical condition and behaviour of animals are important considerations in preserving a captive population of reptiles. For example, Gutzke and Crews (1988) have shown that those few female leopard geckos born at high temperatures (which usually produce males) are morphologically normal but more aggressive than typical females and never breed. These results are probably dependent on hormonal changes, which are very important in courtship, dominance and intraspecific aggression (Alberts, Pratt and Phillips, 1992; Greenberg, 1992; Phillips, Alberts and Pratt, 1993).

7.3 PARENTAL CARE

Once a neonate is born or hatched, it is confronted with a whole new set of situations. For mammals and birds, the first associations are with an adult, usually one or both parents. The general consensus appears to be that parental rearing is better for the animal than hand-raising by humans. This is especially important in a captive breeding programme because early rearing experience has been shown to affect adult sexual behaviour in many mammals (Mellen, 1992 and references therein) and birds (Hess,

1973). For example, Mellen (1992) found that maternal-reared domestic cats, *Felis catus*, copulated more readily than those raised by humans alone.

Reptiles, however, with a few exceptions do not provide parental care (Shine, 1988; Somma, 1990). To date, parental care has not been observed in turtles and in snakes the association is with brooding pythons, cobras defending a nest, and finding newborns with or in the vicinity of the mother after birth (reviewed in Shine, 1988). Parental care has been observed in lizards, especially the skinks (*Eumeces* spp., Noble and Mason, 1933; Evans, 1959; Somma and Fawcett, 1989; and *Corucia zebrata*, Pough, 1991). The former protects the eggs from predators, and keeps the eggs from moulding and drying out by turning and moving them. The prehensile-tailed skink (*Corucia zebrata*) usually produces only one large neonate at a time, which remains with the female for some time. Honnegger (1985) reported that a female and her young reacted aggressively toward a keeper trying to separate them. Because coprophagy does occur in this species (Honnegger, 1985), it is possible that during this association the young receive the species-specific gut microflora necessary for digestion. Neonatal iguanas may also need to eat inoculated faeces in order to digest food properly. It has been shown that, for a period after hatching, green iguanas are highly motivated to eat faeces (Troyer, 1982, 1984). Although this acquisition of microflora by the neonate from the adult may not entail any active social relationship between the generations, it does have implications for laboratory-bred animals.

The best documented examples of reptilian parental behaviour occur in crocodilians. Crocodilians build and guard nests and patrol the shallow pool nearby where the hatchlings will swim. When the eggs pip, the calls of the hatchlings bring in the mother and sometimes the father (Hunt, 1980; Herzog, 1975; Lang, 1987) to dig out the hatchlings and carry them to water. The hatchlings of some species remain with their parents and other adults for up to two years (Garrick and Lang, 1977; Lang, 1987). According to Lang (1987), these social interactions involve animals of different age classes and 'directly affect' how an individual feeds, defends itself, and reproduces. The health and behaviour of animals raised in captivity without benefit of such social interactions may therefore be compromised. Another effect of captivity, even with naturalistic outdoor enclosures, is that young crocodilians may habituate to, or become positively attracted to, humans. This has advantages in that such captives are less disturbed by maintenance. If they are also more tolerant of their penmates (Lang, 1987), then aggression in somewhat crowded conditions may be reduced. However, learning to associate certain cues with humans can be a disadvantage as with the young *Crocodylus moreleti* described by Hunt (1980). Because they associated the keepers and the sound of metal

trays with food, the crocodiles 'lunged at a human figure every time one passed'.

Although food imprinting has been identified in turtles (see below), the filial and sexual imprinting seen in mammals and birds has not been investigated in reptiles, nor are there any convincing anecdotes. However, some such attachment process could be present in crocodilians due to the prolonged association of mother and offspring. An experiment of exposing hatchling alligators to humans or models and then checking for bonding at a later time is worthwhile and should be explored in a zoo or other captive breeding facility. Similarly, studies should be made of skinks that brood their eggs and may then stay with their young for a few days.

7.4 HANDLING AND NOVEL ENVIRONMENTS

The next condition a captive neonate experiences is handling and introduction to some sort of enclosure. Even if the adults in a collection are housed in semi-natural enclosures, the neonates are usually maintained in smaller containers with relatively simple cage furnishings. This arrangement allows for easier cleaning and more individual care when housing several litters. There are no specified space requirements for reptiles as there are for many mammals and birds housed in a laboratory environment. Individual aquaria, glass jars and assorted plastic boxes are chosen to provide enough space for the animal and a water dish (Murphy and Campbell, 1987). As the neonates grow they are transferred to larger containers whenever it appears that they are too big for the one they are in.

For at least two litters of captive-born rattlesnakes, *Crotalus enyo*, raising them in cages normally used to house adults did not significantly affect their performance on tests of locomotive ability or their investigation of a novel environment (Marmie, Kuhn and Chiszar, 1990). Both litters were also compared with wild-caught adults on their ability to strike and trail prey. The captive-born animals did not search as intensely, perhaps because they had never had to search very far in order to find their food (but see Chiszar *et al.*, 1985, discussed below). Individual variability in the performance on these tests was not compromised by the rearing conditions. Herzog and Burghardt (1988), working with garter snakes, found individual and litter differences in defensive temperament that remained stable for up to a year. However, different housing, handling and feeding procedures could lead to marked differences in subsequent responses to a standard antipredator behaviour test (Herzog, Bowers and Burghardt, 1989; Bowers and Burghardt, 1992), with more positive contact leading to calmer snakes.

7.5 CAGE SIZE AND STRUCTURE

Clearly reptiles in relatively large enclosures can engage in more behaviour than those in smaller quarters. Many snakes are housed in cages in which they cannot even stretch out unencumbered. This is obviously very restrictive (see also Chapter 9) but the size of the container may not be as important as what is in it. The type of substrate used does not appear to affect behaviour unless it interferes with, or even prevents, the animal from doing something that it would normally do, such as burrow or defecate. Thigmotactic (tactile) stimuli may be needed by some species (for instance snakes), so clear shelters may be used to provide the animal with a sense of security while it is still visible for observation. However, spitting cobras, *Naja mossambica pallida*, if given a choice, prefer an opaque shelter (Radcliffe and Chiszar, 1983; Chiszar *et al.*, 1987). Thus transparent shelters may not be suitable for well-lit enclosures. They may be very useful for observation in dimly lit or red-light displays.

The position of objects in the cage is also important for the maintenance of naturalistic behaviours. Reptiles are ectotherms and control their body temperature (metabolic rate, activity level) by behavioural thermoregulation. All containers should be provided with a thermal gradient within the range known for that species, although young animals may have different preferred temperatures than adults (cf. Lang, 1987, for crocodilians). The quality and intensity of light provided may also be important in behavioural ontogeny (for example, Moehn, 1974; Sievert and Hutchison, 1991). The sources of heat and light, or the placement of shelters and other furnishings should not force the animal to choose between security and maintaining temperature (Pough, 1991). Other behaviours may be affected by the arrangement of cage furnishings. For example, Roger Avery (in Pough, 1991) notes that for the lizard *Lacerta vivipara* not only thermoregulation but also feeding behaviour is compromised by the lack of complexity in the cage environment. Some objects may be necessary to facilitate skin-shedding or the escape of subordinates from more dominant individuals.

The possible long-term effects of environmental enrichment on the lives of captive reptiles, so often demonstrated in mammals from rodents to primates, is a wide-open area needing urgent study. Providing 'play' objects to a Nile soft-shelled turtle (*Trionyx triunguis*) has reduced self-injurious behaviour in a long-term captive animal (Marcellini, pers. comm.; Burghardt, Ward and Roscoe, in preparation). Such habitat enrichment may also be developmentally important. For example, do burrowing or sand-dwelling lizards benefit in demonstrable ways if they have appropriate substrates, even if providing them precludes study or public viewing?

7.6 SOCIAL ARRANGEMENTS

The next decision that must be made is whether or not to house neonates together. While many reptiles seem to live solitary lives outside mating seasons, social aggregations may be more common than expected even in snakes (Gillingham, 1987). This may be especially true of neonates. Keeping more animals per enclosure reduces the number of containers to be maintained, the amount of building space used and, more importantly, the amount of individual attention each animal receives. In group situations care must be taken to ensure that all individuals have access to food, water, heat and shelter, as dominant–subordinate relationships can greatly affect growth, colour and behaviour (for example green iguanas, pers. obs.; Phillips, Alberts and Pratt, 1993). Sufficient space along with the proper distribution of food, water, perches and retreats can help to ensure that all individuals have relatively equal access to these necessities with as little stress as possible. Group housing is probably not the best choice for delicate and socially aggressive species that require intensive maintenance such as many chamaeleons (*Chamaeleo* spp.). At the Oklahoma City Zoo the keepers found that neonates ideally should be housed individually. If lizards were housed in groups of six to ten, the amount of horizontal space was more important than the vertical because the neonates could space themselves on 'equal planes'. This prevented smaller individuals from being forced to the floor of the cage, where they did not feed or drink as well as the others (Castle, 1990).

In some of the more social species, like crocodilians and iguanas, isolation from their peers may be stressful in their first year. For example, hatchling crocodiles are quite gregarious and tend to pile on top of one another in group enclosures (Lang, 1987). If aggressive interactions develop that may limit the feeding and growth of smaller individuals, then animals should be sorted by size and put into new groups. Juvenile green iguanas will do similar piling on or maintain tactile contact at night (Burghardt and Rand, 1985). There is evidence that neonate green iguanas may recognize siblings (Werner *et al.*, 1987) and this may influence both current grouping patterns and subsequent social interactions involving food.

Group housing has other effects on feeding. In young turtles, *Pseudemys nelsoni*, the amount of food eaten was significantly greater for those animals housed together than for solitary individuals (Bjorndal, 1986). In this case the competition for food may have encouraged feeding. Social facilitation of feeding has been described in iguanid lizards (Greenberg, 1976). In other cases, such as the hatchling chameleons and crocodiles mentioned above and snapping turtles, *Chelydra serpentina* (Froese and Burghardt, 1974), a dominance relationship may develop that discourages some individuals from feeding and even limits access to the food. Young

garter snakes, *Thamnophis radix*, will also compete for food and they appear to recognize their competitors because they avoid them in non-feeding encounters (Yeager and Burghardt, 1991). Group-housed garter snakes fed separately grew faster than those kept and fed in isolation or those kept and fed in groups (Burghardt, 1990).

Are there long-lasting effects of social experience? As pointed out above, no evidence of filial, sexual or parental imprinting has been demonstrated. This does not mean that some kinds of bonds do not occur, nor that interactions with conspecifics are not useful or faciliatory, even if not essential. Perhaps some difficulties associated with breeding reptiles in captivity are a consequence of the animals bonding with heterospecifics (Bowers and Burghardt, 1992). It may be, however, that too much human contact is itself disruptive of natural social behaviour. Chiszar, Smith and Carpenter (in press) note that many successful reptile breeders urge minimal handling of snakes meant to be bred later. As in the area of enriching environments physically, the risks and benefits of social manipulation have been much more systematically addressed in primates (for example, Visalberghi and Anderson, 1993).

7.7 FEEDING

Inducing reptiles to feed is often one of the most difficult aspects of maintaining them in captivity. Yolk storage may mean that food will not be accepted or even needed right after birth or hatching. With exotic or rare species, we often do not know what their diet is in the wild. With neonates the problem is confounded by the fact that what they can or will eat is often very different from what the adults will eat. There may be a change in what is accepted as the individual grows (Mushinsky, Hebrard and Vodopich, 1982). Young racers might eat crickets, for example, while adults may prefer rodents (Herzog and Burghardt, 1974). Most often what is offered is what is most readily available. For example, species that specialize in eating amphibians or lizards can be tricked into accepting laboratory mice. Such mice are usually readily available and have the advantage of being relatively parasite-free. They can be disguised with the skins or rubbings from the natural or preferred prey items and eventually the disguise will not even be needed. Once, we had a large wild-caught black rat snake in the laboratory that would not eat mice or other appropriate prey, such as baby chicks. However, after putting an abandoned bird nest in its cage with a mouse neonate, the snake fed readily; after that it ate mice regularly. Weldon, Walsh and Kleister (in press) review the many ways in which chemoreception can be used to induce reptiles to eat.

Laboratory mice and other prey items like fish are often presented to reptiles pre-killed for health, safety, ethical or aesthetic reasons. In the

previously mentioned study on captive-born rattlesnakes, the animals struck at and trailed a mouse even though it was presented to them already dead (Marmie, Kuhn and Chiszar, 1990). That the snakes struck and trailed regardless of their experience in a captive environment reflects their innate abilities. They did not, however, pursue the trail as 'vigorously' as the wild-caught group, which probably reflects their not having to search very far in actual distance and also their having learned that the dead mouse would always be there at the end of the trail. Yet Chiszar *et al.* (1985 and 1993) found that long-term captives fed dead mice did not have reduced trailing times in strike-induced chemosensory searching studies. How does the fact that captive reptiles do not have to forage actively for their next meal, or that the offered food may not be something they would eat or have access to in their natural environment, affect them later in life?

While prior experience with one prey versus another can have consequences on food choice even of an imprinting nature (Burghardt and Hess, 1966; Fuchs and Burghardt, 1971; Arnold, 1978; Lyman, 1990; Burghardt, 1992; Grassman, 1993; see reviews in Burghardt, 1978, 1990), such altered preferences may be short-lived. In addition, individual differences in prey preferences may not be as suppressed or obliterated as once thought (Burghardt, 1975). When tested, after three years on single-prey diets, *Thamnophis* spp. still showed subtle effects of their chemosensory preferences at birth (Yeager, Lyman-Henly and Burghardt, unpublished data). Periodic variation in prey offered may be sufficient to keep even old animals willing to eat a variety of prey types.

Even so, the choice of prey items accepted by neonates such as juvenile garter snakes can be influenced by prior exposure to prey chemicals even though they are not allowed to come into physical contact with the prey items (Burghardt, 1992). In this context we want to emphasize the nature of the differences between individuals and among related taxa. These differences may be more pronounced in generalist species that feed on a variety of prey types, each demanding somewhat different perceptual, prey capture and handling, and learning abilities. Closely related *Thamnophis* vary in their ability to capture and ingest fish and in their ability to profit from experience (Halloy and Burghardt, 1990).

For years we have raised litters of several species of *Thamnophis* on diets of fish, earthworms or free choice of either and have monitored growth, ingestion rates, prey preference and chemosensory responses. Some sample data are included here because they show the kind of useful information that can be gathered fairly simply by systematic feeding and record keeping. Growth data for two litters of *Thamnophis sirtalis* neonates born to two wild-caught females from the same area in Michigan are shown in Figure 7.1. The snakes were raised on equivalent amounts of vitamin and mineral fortified earthworms (*Lumbricus terrestris*) or mosquito fish (*Gambusia affinis*) for over 8 months under controlled

conditions. The litters of 28 and 31 neonates were divided equally into earthworm and fish diet groups, balanced by sex as closely as possible. There were significant litter, sex and dietary effects on body mass, although the details varied between the second and third weighings (Lyman-Henley, 1991).

7.8 DEFENSIVE BEHAVIOUR

The antipredator and defensive responses of reptiles constitute a major problem for captive maintenance unless these responses are thoroughly understood and accommodated. Next to feeding reliably, defensive temperament is probably the most troublesome problem in captivity. This is especially true with highly venomous snakes, particularly fast-moving ones such as mambas, and large potentially dangerous species such as pythons and anacondas, monitors, a few large turtles (*Macroclemys*, *Trionyx*) and crocodilians (*Crocodylus*). But flighty and defensive species, even 'harmless' ones, may themselves be at risk, even if their care-givers are not. Currently we are studying young habu (Okinawan pit vipers, *Trimeresurus flavoviridis*), which are the source of most venomous snakes bites on Okinawa. Their extraordinary 'short fuse' and alertness make them both dangerous and difficult to maintain, perhaps due to stress.

Ontogenetic considerations certainly can play a role. One indication of this is the common experience that wild-caught adults of many species are often ill-suited for captivity, while captive-reared individuals become much more docile, readily feed, tolerate human viewing during normal activities and so on. Thus captive-reared animals are not only desirable from a conservation standpoint (i.e. do not directly deplete natural populations) but also from a captive management perspective.

Mortality in captive reptiles is usually the result of birth defects, failure to feed, stress, disease and euthanasia of 'surplus' stock, not predation. So why worry about the competence of an animal's defensive response where there are no predators (except perhaps uneaten rodent 'prey')? It is necessary to determine if captive rearing conditions are affecting biologically relevant responses to a threat. We may, for example, use these observations to draw conclusions about how a species responds in nature, or to find out if a component necessary for their survival, if released into their natural habitat, has been compromised.

The absence of parental or non-parental adult associations early in the life of a young crocodilian could be fatal in the wild because its main line of defence (after sharp teeth, tail thrashing, swimming away, going limp when held in jaws) is to vocalize and alert conspecifics that it is in trouble. If raised in captivity in the presence of conspecifics a young crocodile may at least be able to compete more successfully for a territory, nest site or a

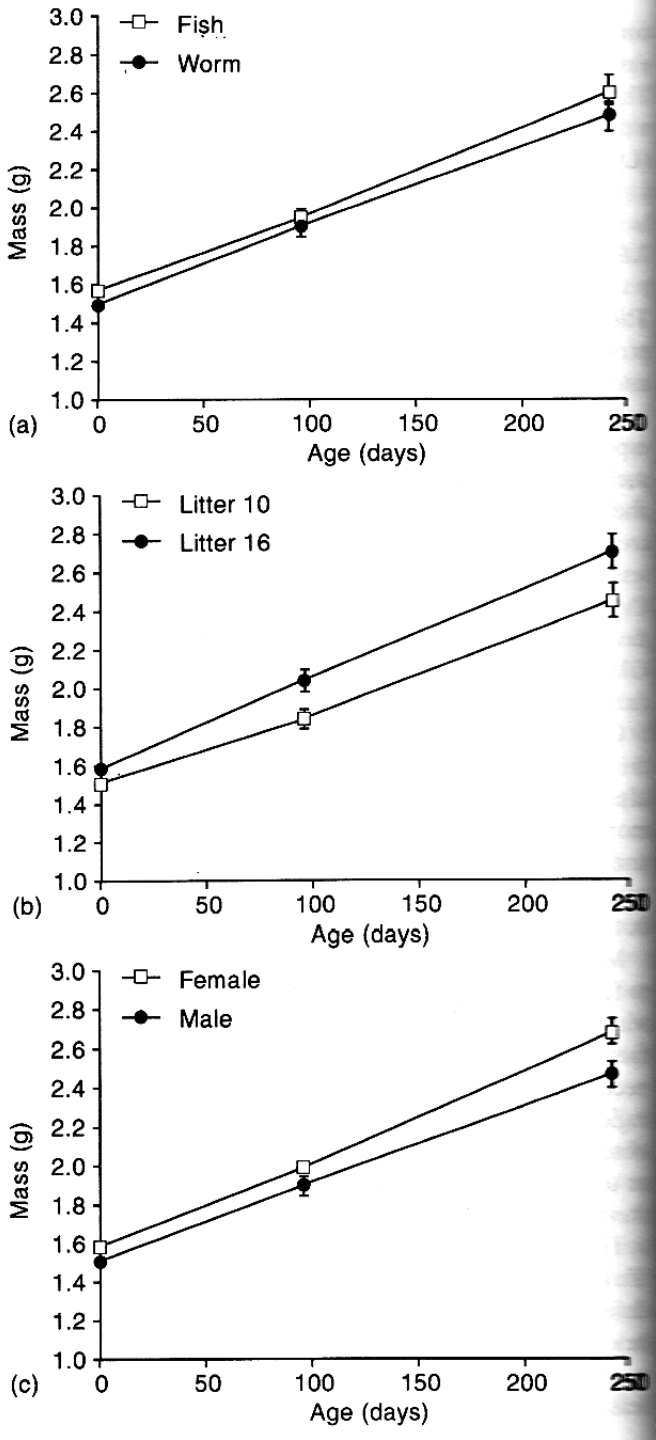

Figure 7.1 Growth of two litters of *Thamnophis sirtalis* (n = 28 and n = 31) divided into diet groups balanced by litter and sex and reared on either fish or earthworm diets under controlled conditions. Mass in grams ± standard error over time (a) diet; (b) litter, (c) sex. (From Lyman-Henley, 1991.)

mate because, if released when mature, crocodilians have few enemies except some large carnivores and humans.

Many young reptiles have been observed performing species-typical defensive behaviours without prior experience (Greene, 1988). Neonates of some garter snake species, *Thamnophis*, will coil and strike at a human hand when first removed from the mother's cage (pers. obs.). When tested in standardized trials, neonates may strike at a human finger when they are one day old (Herzog and Burghardt, 1986). It appears that snakes are the most studied group of reptiles when it comes to describing and quantifying antipredator responses in the laboratory. Within the garter snakes alone there are species, population, litter and individual differences in their responses (Arnold and Bennett, 1984; Herzog and Burghardt, 1986, 1988; Herzog, Bowers and Burghardt, 1989; Herzog and Schwartz, 1990).

Captivity and handling have been reported to reduce the defensiveness of some turtles, lizards, and snakes (reviewed in Greene, 1988 – most articles, expectedly, referred to recent captives, not captive-raised). Most reptiles whose cage environments are provided with hiding places and or visual barriers do not appear to be disturbed by activity outside of their cage (Chapter 8). They may become habituated to activity that is not biologically relevant or directly affecting them at that time (Hediger, 1950). Wild-caught water snakes, *Nerodia*, may become more tractable when they do not have a place to hide – when they can see what is going on about them all the time (P. Andreadis, pers. comm.). It does seem, however, that for many species captive-reared animals reach levels of desensitization to captive regimes that wild-caught adults never do. This may be related to ecology, body size and especially species-characteristic defensive behaviours that become established during ontogeny and then become resistant to modification. For example, wild-caught adult green iguanas (*Iguana* sp.) and white throated monitors (*Varanus* sp.) are much shyer, more difficult to get to feed or observe feeding, more likely to stay in retreats and are more readily stressed and defensive to human intrusion than captive-reared animals from the same population maintained in comparable settings (pers. obs.; J.A. Phillips, pers. comm.).

Responses that may be considered defensive displays may also be a sign of stress. For example, a snake that strikes at the glass or a lizard that runs into the wall every time someone walks by may endure injury or be so stressed that it does not feed or thermoregulate properly, thus affecting its health (Warwick 1990a, b). Handling beyond that required for normal maintenance did not necessarily have a calming effect on young *Thamnophis sirtalis* (Herzog, 1990). Those that were handled prior to presentation of a model predator had higher strike scores than the controls but not as high as those who had previously been harassed by the same model predator. The effect of disturbance on snake behaviour is documented in Chapter 8.

Habituation to the captive environment may cause neonate bushmasters, *Lachesis muta*, to stop vibrating their tails and striking at about one month of age (Greene and Santana, unpubl. obs. in Green, 1988). Hampton and Gillingham (1989) showed that neonate eastern garter snakes, *Thamnophis sirtalis*, that became habituated to a visual stimulus in a test situation did not become habituated to the observer who approached and handled the snakes after the test. Extensive comparative studies of habituation of defensive responses in four species of naïve *Thamnophis* have found major species and individual differences in several measures, including striking, coiling and fleeing (Herzog, Bowers and Burghardt, 1989; Bowers, 1992). This indicates that temperaments differ even among individuals from the same litter and reinforces the imperative for keepers of captive reptiles to view each animal as an individual with its own distinct personality that may colour its reactions to a variety of contexts.

Body pattern and colour may indeed be important. Many neonate reptiles, especially numerous snakes and freshwater turtles, have distinctive and vivid colours and patterns not found in adults. What should we make of these differences and how are they related to behavioural differences between juveniles and adults? One hypothesis worth exploring is that such differences are related to avoiding predation rather than serving to enhance food procurement or conspecific sociality. The colours are often too vivid to be merely cryptic. The pattern of stripes may be related to responses to predators: striped individuals (and species) are more prone to flight than fight than are banded, blotched or patternless animals (for example, Brodie, 1989). However, more may be going on here. Although neonate reptiles may be much more vulnerable to predation than adults, they may also be less tasty and thus colour and pattern variants could be aposematic (warning). Britson and Gutzke (1993) have demonstrated that neonate turtles are avoided by potential fish predators and that this seems to be due to their behaviour (bites, scratching) rather than any toxic or noxious chemicals. The bright colours and patterns in juveniles could then be viewed as warnings to the relatively small predators who normally eat prey weighing only a few grams.

It is possible that the rings on the neck of several colubrid snakes (for example *Diadophis punctatus*, *Natrix natrix*, *Storeria dekayi*) may be related to aposematic colouring because they are usually white, yellow or orange against a black or dark brown background. If only the head is noticed by a predator, or the head/neck (nuchal) region is in the process of being attacked, the view of the nuchal area as an aposematic signal could cause confusion or hesitation by the predator and give the victim a little more time to escape. That there may be a developmental component is shown by the Japanese tiger snake, *Rhabdophis tigrinis tigrinis*, in which the bright neonatal yellow or white neck band is lost in the adults.

Similarly, *Thamnophis melanogaster* neonates are much more brightly coloured than adults, often with contrasting ventral areas that can be flashed in the vigorous defensive responses of this species (Herzog and Burghardt, 1986). In the future, we may be able to make predictive statements about the temperament of species and individuals, and thus how they might initially be approached in captivity, by considering their colour and markings and the developmental changes that may occur.

7.9 LONG-TERM INFLUENCE OF CAPTIVE REGIMES

As ethical, legal and perceived conservation imperatives foster increasing interest in captive breeding, we can expect to see marked changes in the behaviour of reptiles in captivity. Over several generations it is likely that, given the great amount of variability seen in reptiles, selection will favour certain genotypes that seem to do well in captivity in terms of feeding, growth, readiness to mate and production of viable offspring. It may be that within a few generations of such artificial selection important behavioural and physiological changes will occur that are to varying degrees incompatible with survival in the wild. These may have important consequences for animal welfare, as well as species and habitat status and any recovery efforts. For this reason, environmental means of encouraging behaviour that is inadvertently selected against or relaxed in captivity, such as feeding and antipredator responses, may need to be fostered through deliberately developed procedures to assess behavioural competence (Chiszar, Smith and Radcliffe, 1993) and to develop any necessary rehabilitation procedures.

At the moment this may not seem to be a critical issue, but we are convinced that it will be for some species in a very short time. It is particularly unfortunate that amateur and professional reptile breeders are actually proud of producing and selling hybrids and aberrantly patterned mutants such as albino pythons (for example Barker, 1991). This is as ethically and biologically irresponsible as the marketing of white tigers in zoos. Neither the species not the freak individuals benefit, as the genetic changes may, and do, alter aspects of the phenotype other than the novel colour or pattern.

But lest those who do not breed for freaks become too outraged, it is necessary to remember that Darwin also noted 'unwitting' selection for certain traits. And our often sparsely furnished, cramped and unnatural housing arrangements in zoos, laboratories, breeding and 'headstarting' facilities may be creating behaviourally distorted animals that can thwart recovery, restoration and genetic integrity schemes.

7.10 CONCLUSIONS

Reptiles, as is being discovered for so many animals, are dependent in many and varying ways on environmental factors and experience. The life events experienced by reptiles from the moment of conception may be critical to their later behavioural capabilities, preferences, temperament, growth and reproduction. The developmental trajectory of any animal is also constrained, buffered, channelled and even shaped by its specific genetic heritage. This heritage is not only species-characteristic but, more importantly, individualized. Thus any guidelines and procedures for keeping and rearing, for example, 'the' copperhead or 'the' green iguana must recognize the great effects that both ontogeny and individual differences can play in the behavioural phenotype of any given representative. As captive breeding and rearing of reptiles becomes more common and is perceived as necessary for conservation and education, the effects of artificial selection for captive survival will manifest themselves in many and diverse ways. Thus for a long time to come our knowledge will be in a continual state of flux, even with common species. Our attention to patterns and processes of development must enter into every captive management programme. The pioneering papers of Chiszar and his colleagues (for example, Chiszar, Murphy and Iliff, 1990; Chiszar, Smith and Radcliffe, 1993; Chapter 8) merit close attention for their cautionary wisdom.

Undoubtedly, there are many twists and complications that we will encounter while endeavouring to improve the management and rearing in captivity of reptile species. Accumulating the necessary detailed data is a daunting task. What we need to cultivate is a questioning ethological attitude that examines a reptile's life from the animal's point of view, while realizing that it is ultimately our own point of view tempered with current scientific knowledge.

ACKNOWLEDGEMENTS

Preparation of this chapter and collation of unpublished data were supported by NSF research grants BNS-8709629 and BNS-9111387. We thank the many undergraduates and graduate students who over the years have contributed to the well-being and scientific understanding of our laboratory colony. We also thank Lani Lyman-Hanley for permission to reproduce Fig. 7.1 and Paul Andreadis, Dan Cunningham, Monique Halloy and many more reviewers for helpful comments on an earlier version.

REFERENCES

Alberts, A.C., Pratt, N.C. and Phillips, J.A. (1992) Seasonal productivity of lizard femoral glands: relationship to social dominance and androgen levels. *Physiology and Behavior*, **51**, 729–33.

Arnold, S.J. (1978) Some effects of early experience on feeding responses in the common garter snake *Thamnophis sirtalis*. *Animal Behaviour*, **26**, 455–62.

Arnold, S.J. and Bennett, A.F. (1984) Behavioral variation in natural populations, III. Antipredator displays in the garter snake, *Thamnophis radix*. *Animal Behaviour*, **32**, 1108–18.

Barker, D. (1991) One of a kind. *Vivarium*, **2** (6), 32–3.

Bjorndal, K.A. (1986) Effect of solitary vs. group feeding on intake in *Pseudemys nelsoni*. *Copeia*, **1986**, 234–5.

Bowers, B.B. (1992) Habituation of antipredator behaviors and responses to chemical prey extracts in four species of garter snakes, *Thamnophis* (Serpentes: Colubridae). PhD Dissertation, University of Tennessee, Knoxville.

Bowers, B.B. and Burghardt, G.M. (1992) The scientist and the snake: relationships with reptiles, in *The Inevitable Bond*, (eds H. Davis and D. Balfour), Cambridge University Press, Cambridge, pp. 250–63.

Britson, C.A. and Gutzke, W.H.N. (1993) Antipredator mechanisms of hatchling freshwater turtles. *Copeia*, **1993**, 435–40.

Brodie, E.D. III (1989) Genetic correlations between morphology and antipredator behavior in natural populations of the garter snake *Thamnophis ordinoides*. *Nature*, **342**, 542–43.

Bull, J.J. (1980) Sex determination in reptiles. *Quarterly Review of Biology*, **55**, 3–21.

Burger, J. (1989) Incubation temperature has long-term effects on behavior of young pine snakes (*Pituophis melanoleucus*). *Behavioral Ecology and Sociobiology*, **24**, 201–7.

Burger, J. (1990) Effects of incubation temperature on behavior of young black racers (*Coluber constrictor*) and kingsnakes (*Lampropeltis getulus*). *Journal of Herpetology*, **24**, 158–63.

Burger, J. (1991) Effects of incubation temperature on behavior of hatchling pine snakes: implications for reptilian distribution. *Behavioral Ecology and Sociobiology*, **28**, 297–303.

Burger, J., Zappalorti, R.T. and Gochfeld, M. (1987) Developmental effects of incubation temperature on hatchling pine snakes *Pituophis melanoleucus*. *Comparative Biochemistry and Physiology*, **87A**, 727–32.

Burghardt, G.M. (1975) Chemical prey preference polymorphism in newborn garter snakes *Thamnophis sirtalis*. *Behaviour*, **52**, 202–25.

Burghardt, G.M. (1977) Of iguanas and dinosaurs: social behavior and communication in neonate reptiles. *American Zoologist*, **17**, 177–90.

Burghardt, G.M. (1978) Behavioral ontogeny in reptiles: whence, whither, and why?, in *The Development of Behavior: Comparative and Evolutionary Aspects*, (eds G. Burghardt and M. Bekoff), Garland, New York, pp. 149–74.

Burghardt, G.M. (1988) Precocity, play, and the ectotherm–endotherm transition: profound reorganization or superficial adaptation, in *Handbook of Behavioral Neurobiology, Vol 9, Developmental Psychobiology and Behavioral Ecology*, (ed. E.M. Blass), Plenum, New York, pp. 107–48.

Burghardt, G.M. (1990) Chemically mediated predation in vertebrates: diversity, ontogeny, and information, in *Chemical Signals in Vertebrates, Vol 5*, (eds D.W. McDonald, D. Müller-Schwartz and S.E. Natynczuk), Oxford University Press, Oxford, pp. 475–99.

Burghardt, G.M. (1992) Prior exposure to prey cues influences chemical prey preferences and prey choice in neonatal garter snakes. *Animal Behaviour*, **44**, 787–89.

Burghardt, G.M. and Hess, E.H. (1966) Food imprinting in the snapping turtle, *Chelydra serpentina*. *Science*, **151**, 108–9.

Burghardt, G.M. and Rand, A.S. (1985) Group size and growth rate in hatchling green iguanas (*Iguana iguana*). *Behavioral Ecology and Sociobiology*, **18**, 101–4.

Castle, E. (1990) Husbandry and breeding of chameleons, *Chamaeleo* spp. at Oklahoma City Zoo. *International Zoo Yearbook*, **29**, 74–84.

Chiszar, D., Murphy, J. and Iliff, W. (1990) For zoos. *Psychological Record*, **40**, 3–13.

Chiszar, D., O'Connell, B., Greenlee, R. *et al.* (1985) Duration of strike induced chemosensory searching in long-term captive rattlesnakes at National Zoo, Audubon Zoo, and San Diego Zoo. *Zoo Biology*, **4**, 291–4.

Chiszar, D., Radcliffe, C.W., Boyer, T. and Behler, J.L. (1987) Cover seeking behavior in red spitting cobras (*Naja mossambica pallida*): effects of tactile cues and darkness. *Zoo Biology*, **6**, 161–7.

Chiszar, D., Smith, H.M. and Carpenter, C.C. (in press) An ethological approach to reproductive success in reptiles, in *Captive Management and Conservation of Amphibians and Reptiles*, (eds J.B. Murphy, K. Adler and J.T. Collins), SSAR Contributions in Herpetology.

Chiszar, D., Smith, H.M. and Radcliffe, C.W. (1993) Zoo and laboratory experiments on the behavior of snakes: assessments of competence in captive-reared animals. *American Zoologist*, **33**, 109–16.

Decker, J.D. (1967) Motility of the turtle embryo, *Chelydra serpentina*. *Science*, **157**, 952–4.

Evans, L.T. (1959) A motion picture study of maternal behavior of the lizard, *Eumeces obsoletus* Baird and Girard. *Copeia*, **1959**, 103–10.

Ferguson, M.W.J. and Joanen, T. (1982) Temperature of egg incubation determines sex in *Alligator mississippiensis*. *Nature*, **296**, 850–3.

Froese, A.D. and Burghardt, G.M. (1974) Food competition in captive juvenile snapping turtles, *Chelydra serpentina*. *Animal Behaviour*, **22**, 743–9.

Fuchs, J. and Burghardt, G.M. (1971) Effects of early feeding experience on the responses of garter snakes to food chemicals. *Learning and Motivation*, **2**, 271–9.

Garrick, L.D. and Lang, J.W. (1977) Social signals and behaviors of adult alligators and crocodiles. *American Zoologist*, **17**, 225–39.

Gillingham, J.C. (1987) Social behavior, in *Snakes: Ecology and Evolutionary Biology*, (eds R.A. Seigel, J.T. Collins and S.S. Novak), Macmillan, New York, pp. 184–209.

Grassman, M. (1993) Chemosensory orientation behavior in juvenile sea turtles. *Brain, Behavior and Evolution*, **41**, 224–8.

Greenberg, N. (1976) Observations of social feeding in lizards. *Herpetologica*, **32**, 348–52.

Greenberg, N. (1992) The saurian psyche revisited: lizards in research, in *The Care and Use of Amphibians, Reptiles, and Fish in Research*, (eds D.O. Schaeffer, K.M. Kleinow and L. Krulisch), Scientists Center for Animal Welfare, Bethesda, Maryland, pp. 75–91.

Greene, H.W. (1988) Antipredator mechanisms in reptiles, in *Biology of the Reptilia, Vol 16* (eds C. Gans and R.B. Huey), Wiley, New York, pp. 1–152.

Gutzke, W.H.N. and Crews, D. (1988) Embryonic temperature determines adult sexuality in a reptile. *Nature*, **332**, 832–4.

Halloy, M. and Burghardt, G.M. (1990) Ontogeny of fish capture and ingestion in four species of garter snakes (*Thamnophis*). *Behaviour*, **112**, 299–318.

Hampton, R.E. and Gillingham, J.C. (1989) Habituation of the alarm reaction in neonatal eastern garter snakes, *Thamnophis sirtalis*. *Journal of Herpetology*, **23**, 433–5.

Hediger, H. (1950) *Wild Animals in Captivity*, Butterworth, London.

Herzog, H.A. (1975) An observation of nest opening by an American alligator, *Alligator mississippiensis*. *Herpetologica*, **31**, 446–7.

Herzog, H.A., Jr (1990) Experiential modification of defensive behaviors in garter snakes. *Journal of Comparative Psychology*, **104**, 334–9.

Herzog, H.A., Jr and Burghardt, G.M. (1974) Prey movement and predatory behavior of juvenile western yellow-bellied racers, *Coluber constrictor mormon*. *Herpetologica*, **30**, 285–9.

Herzog, H.A., Jr and Burghardt, G.M. (1986) Development of antipredator responses in snakes I: Defensive and open-field behaviors in newborns and adults of three species of garter snakes (*Thamnophis melanogaster*, *T. sirtalis*, *T. butleri*). *Journal of Comparative Psychology*, **100**, 372–9.

Herzog, H.A., Jr and Burghardt, G.M. (1988) Development of antipredator responses in snakes III: Stability of individual and litter differences over the first year of life. *Ethology*, **77**, 250–8.

Herzog, H.A., Jr, Bowers, B.B. and Burghardt, G.M. (1989) Development of antipredator responses in snakes IV: Interspecific and intraspecific differences in habituation of defensive behavior. *Developmental Psychobiology*, **22**, 489–508.

Herzog, H.A., Jr and Schwartz, J.M. (1990) Geographical variation in the antipredator behavior of neonate garter snakes, *Thamnophis sirtalis*. *Animal Behaviour*, **40**, 597–8.

Hess, E.H. (1973) *Imprinting*, D. Van Nostrand, New York.

Holtzman, D.A. and Halpern, M. (1989) In vitro technique for studying garter snake (*Thamnophis* sp.) development. *Journal of Experimental Zoology*, **250**, 283–8.

Honnegger, R.E. (1985) Additional notes on the breeding and captive management of the prehensile-tailed skink (*Corucia zebrata*). *Herpetological Review*, **16**, 21–3.

Hunt, R.H. (1980) Propagation of Morelet's crocodile, in *Reproductive Biology and Diseases of Captive Reptiles*, (eds J.B. Murphy and J.T. Collins), SSAR Contributions to Herpetology Number 1, pp. 161–5.

Janzen, F.J. and Paukstis, G.L. (1991) Environmental sex determination in reptiles: ecology, evolution, and experimental design. *Quarterly Review of Biology*, **66**, 149–79.

Lang, J.W. (1985) Incubation temperature affects thermal selection of hatchling crocodiles. *American Zoologist*, **25**, 16.

Lang, J.W. (1987) Crocodilian behaviour: implications for management, in *Wildlife Management: Crocodiles and Alligators* (eds G.J.W. Webb, S.C. Manoles and P.J. Whitehead), Surrey Beatty and Sons, Australia, pp. 273–94.

Lyman, L.P. (1990) The effects of dietary and social experience on the development of behavior in Butler's garter snake, *Thamnophis butleri*. Unpublished Masters Thesis, University of Tennessee, Knoxville.

Lyman-Henley, L.P. (1991) Effects of social and dietary experience on chemosensory response, aggregation behavior, and kin recognition in the eastern garter snake, *Thamnophis sirtalis sirtalis*. PhD Dissertation, University of Tennessee, Knoxville.

Marmie, W., Kuhn, S. and Chiszar, D. (1990) Behavior of captive-raised rattlesnakes (*Crotalus enyo*) as a function of rearing conditions. *Zoo Biology*, **9**, 241–6.

Mellen, J.D. (1992) Effects of early rearing experience on subsequent adult sexual behavior using domestic cats (*Felis catus*) as a model for exotic small felids. *Zoo Biology*, **11**, 17–32.

Moehn, L.D. (1974) The effect of quality of light on agonistic behavior of iguanid and agamid lizards. *Journal of Herpetology*, **8**, 175–83.

Morreale, S.J., Ruiz, G.J., Spotila, J.R. and Standora, E.A. (1982) Temperature-dependent sex-determination: current practices threaten conservation of sea turtles. *Science*, **216**, 1245–7.

Murphy, J.B. and Campbell, J. A. (1987) Captive maintenance, in *Snakes: Ecology and Evolutionary Biology*, (eds R.A. Seigel, J.T. Collins and S.S. Novak), Macmillan, New York, pp. 165–82.

Mushinsky, H.R., Hebrard, J.J. and Vodopich, D.S. (1982) Ontogeny of water snake foraging ecology *Ecology*, **63**, 1624–9.

Noble, G.K. and Mason, E.R. (1933) Experiments of the brooding habits of the lizards *Eumeces* and *Ophisaurus*. *American Museum Novitates*, **619**, 1–29.

Phillips, J.A., Alberts, A.C. and Pratt, N.C. (1993) Differential resource use, growth, and the ontogeny of social relationships in the green iguana. *Physiology and Behavior*, **53**, 81–8.

Pough, F.H. (1991) Recommendations for the care of amphibians and reptiles in academic institutions. *I.L.A.R. News* Fall 1991, **33** (4), 1–21.

Radcliffe, C.W. and Chiszar, D. (1983) Clear plastic hiding boxes as a husbandry device for nervous snakes. *Herpetological Review*, **14**, 18.

Schaeffer, D.O., Kleinow, K.M. and Krulisch, L. (eds) (1992) *The Care and Use of Amphibians, Reptiles, and Fish in Research*, Scientists Center for Animal Welfare, Bethesda, Maryland.

Shine, R. (1988) Parental care in reptiles, in *Biology of the Reptilia, Vol 16, Ecology B: Defence and Life History*, (eds C. Gans and R.B. Huey), Alan R. Liss, New York, pp. 275–330.

Sievert, L.M. and Hutchison, V.H. (1991) The influence of photoperiod and position of a light source on behavioral thermoregulation in *Crotaphytus collaris* (Squamata: Iguanidae). *Copeia*, **1991**, 105–10.

Smotherman, W.P. and Robinson, S.R. (1988) The uterus as environment: the ecology of fetal behavior, in *Handbook of Behavioral Neurobiology Vol 9*, (ed. E.M. Blass), Plenum Press, New York, pp 149–96.

Somma, L.A. (1990) A categorization and bibliographic survey of parental behavior in lepidosaurian reptiles. *Smithsonian Herpetological Information Service*, No. 81, 53 pp.

Somma, L.A. and Fawcett, J.D. (1989) Brooding behavior of the prairie skink,

Eumeces septentrionalis, and its relationship to the hydric environment. *Zoological Journal of the Linnean Society*, **95**, 245–58.

Troyer, K.E. (1982) Transfer of fermentative microbes between generations in a herbivorous lizard. *Science*, **216**, 540–2.

Troyer, K.E. (1984) Behavioral acquisition of the hindgut fermentation system by hatchling *Iguana iguana*. *Behavioral Ecology and Sociobiology*, **14**, 189–93.

van Damme, R., Bawens, D., Brana, F. and Verheyen, R. (1992) Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizard *Podarcis muralis*. *Herpetologica*, **48**, 220–8.

Vinegar, A. (1973) The effects of temperature on the growth and development of embryos of the Indian python, *Python molurus* (Reptilia: Serpentes: Boidae). *Copeia*, **1973**, 171–3.

Vinegar, A. (1974) Evolutionary implications of temperature induced anomalies of development in snake embryos. *Herpetologica*, **30**, 72–4.

Visalberghi, E. and Anderson, J.R. (1993) Reasons and risks associated with manipulating captive primates' social environments. *Animal Welfare*, **2**, 3–15.

Warwick, C. (1990a) Reptilian ethology in captivity: observations of some problems and an evaluation of their aetiology. *Applied Animal Behaviour Science*, **26**, 1–13.

Warwick, C. (1990b) Important ethological and other considerations of the study and maintenance of reptiles in captivity. *Applied Animal Behaviour Science*, **27**, 363–6.

Weldon, P.J., Walsh, T.S. and Kleister, J.S.E. (in press) Chemoreception in the feeding behavior of reptiles: relevance to captive maintenance and management, in *Captive Management and Conservation of Amphibians and Reptiles*, (eds J.B. Murphy, K. Adler and J.T. Collins), SSAR Contributions in Herpetology.

Werner, D.I., Baker, E.M., Gonzalez, E.C., and Soza, I.R. (1987) Kinship recognition and grouping in hatchling green iguanas. *Behavioral Ecology and Sociobiology*, **21**, 83–9.

Yahr, P. (1988) Sexual differentiation of behavior in the context of developmental psychobiology, in *Handbook of Behavioral Neurobiology, Vol 9*, (ed. E.M. Blass), Plenum Press, New York, pp. 197–243.

Yeager, C.P. and Burghardt, G.M. (1991) The effect of food competition on aggregation: evidence of social recognition in the plains garter snake *Thamnophis radix*. *Journal of Comparative Psychology*, **105**, 380–6.