

Review Paper

Reproductive strategies in snakes

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Snakes of both sexes display remarkable flexibility and diversity in their reproductive tactics. Many features of reproduction in female snakes (such as reproductive mode and frequency, seasonality and multiple mating) allow flexible maternal control. For example, females can manipulate not only the genotypes of their offspring (through mate choice or enhanced sperm competition) but also the phenotypes of their offspring (through allocation 'decisions', behavioural and physiological thermoregulation, and nest-site selection). Reliance on stored energy ('capital') to fuel breeding results in low frequencies of female reproduction and, in extreme cases, semelparity. A sophisticated vomeronasal system not only allows male snakes to locate reproductive females by following scent trails, but also facilitates pheromonally mediated mate choice by males. Male–male rivalry takes diverse forms, including female mimicry and mate guarding; combat bouts impose strong selection for large body size in males of some species. Intraspecific (geographical) variation and phenotypic plasticity in a wide array of reproductive traits (offspring size and number; reproductive frequency; incidence of multiple mating; male tactics such as mate guarding and combat; mate choice criteria) provide exceptional opportunities for future studies.

Keywords: life history; reproduction; reptile; Serpentes; sexual selection

1. INTRODUCTION

Neglected in ecological and behavioural research for many years, snakes have recently begun to attract intense interest from many researchers (Shine & Bonnet 2000). This renaissance in snake research has encompassed many conceptual approaches, with reproductive tactics among the most popular topics. Evolutionary interpretations of snake reproductive strategies have proliferated, reflecting three major features of reproductive biology in snakes: diversity, plasticity and covariation with other traits. First, these animals encompass massive diversity in reproductive traits. Second, many of these traits vary, either through local adaptation or direct responses to proximate cues. Third, reproductive tactics are clearly linked to features of the environment or of the species' morphology and ecology. For example, viviparity (live-bearing) has evolved from oviparity (egg laying) in at least 30 independent lineages of snakes, usually in association with the invasion of cold climates (Blackburn 1985; Shine 1985). Similarly, male–male interactions range from mutual tolerance to overt physical battles, and are closely linked to patterns of sexual dimorphism in body size (Shine 1994). Such correlations between reproductive tactics and other environmental and biological traits encourage researchers seeking adaptive explanations for reproductive diversity. Many of these traits vary intraspecifically as well as interspecifically (table 1), facilitating tightly controlled comparisons between taxa that differ in the characteristic of interest. This close phylogenetic focus enables powerful tests of adaptationist hypotheses.

This review will briefly summarize some of the recent work on snake reproductive strategies, focusing on developments since earlier reviews (Devine 1984; Seigel & Ford 1987; Olsson & Madsen 1998). I will, of necessity, be highly selective. I have, for example, ignored general issues of life-history evolution such as ages and body sizes at

maturation (Parker & Plummer 1987; Ford & Seigel 1994; Bronikowski & Arnold 1999; Bronikowski 2000), or the interplay between natural selection and sexual selection in generating diversity in 'reproductive' traits (Pearson *et al.* 2002). I have emphasized empirical findings, and the ideas generated by them, rather than broad conceptual schemes (e.g. Duvall *et al.* 1992, 1993; Arnold & Duvall 1994). I have ignored the physiological mechanisms that provide functional linkages between genotypes and phenotypes by controlling reproductive activities (Gans & Crews 1992). Finally, I have emphasized questions within my own fields of research, and thus, have tended to focus on my own studies and those of my collaborators.

2. FEMALES

Reproduction involves both costs and benefits to an organism's fitness. The benefits are obvious (production of offspring) but costs also drive the evolution of reproductive tactics (Bonnet *et al.* 1999b, 2002). Reproduction may increase a female snake's risk of death (through starvation or predation; Plummer 1997; Gregory *et al.* 1999) or disease (via sexual transmission or physiological stress). Similarly, reproduction may severely impact upon her energy balance through increased metabolic expenditure (due to energy allocation to the clutch, and to maintenance of high body temperatures during pregnancy) or foregone feeding opportunities (Madsen & Shine 1993c; Gregory *et al.* 1999; Lourdais *et al.* 2002a). Such energy costs may reduce her future growth rate and thus, probable fecundity (Bell 1980; Shine 1980). Mortality costs are so high for females in some snake species that many produce only a single litter in their lifetimes (Madsen & Shine 1992a, 1994; Luiselli *et al.* 1996, 1997; Brown & Weatherhead 1997; Bonnet *et al.* 2002). Such costs impose strong selection to adjust reproductive tactics to local conditions of food supply and predator densities,

Table 1. Intraspecific geographical variation in major reproductive traits within snake species. (These cases are examples only; for many traits, additional cases are known.)

intraspecifically variable trait	species	authority
sexual differences		
in mean adult body size	<i>Natrix natrix</i>	Madsen & Shine (1993b)
in relative head size	<i>Thamnophis sirtalis</i>	Shine & Crews (1988)
in home range size	<i>Pseudechis porphyriacus</i>	Shine (1987)
reproductive output		
clutch size	<i>Nerodia rhombifera</i>	Aldridge <i>et al.</i> (1995)
reproductive frequency	<i>Drysdalia coronoides</i>	Shine (1981)
offspring size	<i>Storeria occipitomaculata</i>	Semlitsch & Moran (1984)
relative clutch mass	<i>Thamnophis sirtalis</i>	Seigel <i>et al.</i> (1986)
mode of reproduction	<i>Psammophylax variabilis</i>	Broadley (1977)
seasonality of reproduction		
females	<i>Thamnophis marcianus</i>	Seigel <i>et al.</i> (2000)
males	<i>Boiga irregularis</i>	Bull <i>et al.</i> (1997)
female parental care		
nest attendance	<i>Liasis fuscus</i>	Madsen & Shine (1999b)
shivering thermogenesis	<i>Python sebae</i>	Shine (1988b)
male mating tactics		
criteria for mate choice	<i>Thamnophis sirtalis</i>	LeMaster & Mason (2002)
mate guarding	<i>Vipera berus</i>	Luiselli (1995)
male–male combat	<i>Morelia spilota</i>	Shine & Fitzgerald (1995)
multiple mating	<i>Thamnophis sirtalis</i>	Garner <i>et al.</i> (2002)
seasonality of mating	<i>Python reticulatus</i>	Shine <i>et al.</i> (1999a)
mate-searching tactics	<i>Nerodia sipedon</i>	Brown & Weatherhead (1999)
male courtship behaviour	<i>Thamnophis radix</i>	Ford (1996)

thus generating interspecific and intraspecific divergence in reproductive tactics.

The obvious fitness benefit of reproduction is the production of viable offspring. Female snakes can control (and thus, potentially, selection can optimize) the following components.

(a) *Seasonal timing of reproduction*

Even in the tropics, most snakes reproduce seasonally (Fitch 1982; Vitt & Vangilder 1983; Shine *et al.* 1999a), perhaps reflecting underlying seasonal variation in resource levels, hatchling survival rates and/or the costs of reproduction. In cold climates, thermal requirements for embryogenesis limit reproduction to the warmer months, imposing a strong seasonality (Vitt & Vangilder 1983). Substantial variation in reproductive timing can occur even within a single population, and may generate important fitness variation (Farrell *et al.* 1995; Madsen & Shine 1999b).

(b) *Total energy allocation to reproduction*

Total litter mass (and thus, energy content) is highly linked to maternal body size in many snake species (Seigel & Ford 1987), presumably reflecting physical constraints on clutch volume (Vitt & Congdon 1978; Shine 1992). However, female body size will determine litter mass only if females delay reproduction until they have enough energy to fill their body cavity with eggs or embryos. A long-term field study on vipers (*Vipera aspis*) reported this situation in only 1 of 9 years, with reproductive allocation below the level at which it was constrained by (and thus, correlated with) maternal body size in the other 8 years (Lourdais *et al.* 2002b). Within the constraints set by maternal body volume, selection fine-tunes reproductive investment to match costs. For

example, relative clutch masses may be atypically high for snake populations with few predators and abundant food (e.g. *Gloydus shedaoensis*; Sun *et al.* 2002) and unusually low if pregnancy severely impairs maternal locomotion (e.g. aquatic species; Shine 1988a). Laboratory experiments demonstrate that local resource levels can substantially modify reproductive output in female snakes (Ford & Seigel 1989; Seigel & Ford 1991).

(c) *Frequency of reproduction*

If reproduction requires 'risky' behaviour (e.g. frequent basking) regardless of clutch size, selection should favour females to delay reproduction until they can produce a large clutch (Bull & Shine 1979). Such fecundity-independent costs are widespread, especially in viviparous species that must carry the litter for a long period (Naulleau & Bonnet 1996). Thus, many female snakes do not initiate reproduction until their body reserves exceed a threshold value (Bonnet *et al.* 2002). This threshold value is relatively invariant within some species (e.g. *Vipera aspis*; Bonnet *et al.* 2001, 2002) but fluctuates through time in populations exploiting highly stochastic resources (e.g. *Acrochordus arafurae*, *Liasis fuscus*; Shine & Madsen 1997; Madsen & Shine 1999a, 2000b). Some snakes rely on 'capital' (stored energy) for reproduction, thus temporally dissociating energy acquisition from expenditure. Others rely on 'income' (energy obtained through current feeding), and modify reproductive expenditure according to current resource levels (Shine & Madsen 1997; Brown & Shine 2002). The balance of reliance upon capital versus income also shifts among years within a single population (Bonnet *et al.* 2001). Paradoxically, one of the most important aspects of female reproduction in snakes may be that in many populations,

most females do not breed in most years. Inevitably, frustrated researchers have tended to study the atypical systems with high reproductive frequencies; we do not know how this bias has affected our overall view of snake reproduction. Long-term studies are critical for this as well as other reasons (Fitch 1999).

(d) *Offspring size*

Offspring sizes vary enormously, and (unsurprisingly) are linked to mean adult body size. Neonates of larger species are larger in absolute terms, but smaller relative to adult body size, than in smaller species (Shine 1978). Offspring size is also affected by selection (for example, larger prey sizes favour increased neonatal size; Sun *et al.* 2002) and by allocation trade-offs (larger clutches are composed of smaller offspring; King 1993). Maternal body size has less effect on offspring size than on litter size, but some taxa show either positive or negative correlations between maternal and offspring sizes (Shine 1981; Stewart 1989). In one viviparous natricine snake, facultative placental nutrient transfer generates such a correlation (Stewart 1989).

(e) *Offspring quality*

Although offspring size and number obviously influence maternal fitness, and have been the primary foci of analysis, viability of offspring may vary considerably, and hence be a critical source of among-female variation in fitness. The survival rates of neonatal pythons, for example, were influenced more by inter-clutch variation than by body sizes (Madsen & Shine 1998). Females of some snake species show consistency in offspring phenotypes among successive clutches (Madsen & Shine 1992a), whereas others do not after the influence of maternal body size is removed (Luiselli *et al.* 1996). Maternal (clutch) effects are very widespread in snakes as in other animals and are generated by genetics, maternal allocation and direct environmental effects both on the female and on her developing offspring; statistical analyses of offspring traits should not ignore this source of variation (King 1997). Female snakes can exert some control over at least three aspects.

- (i) *Maternal investment.* Offspring viability is affected not simply by the absolute amount of nutrients allocated to each ovum (Sinervo *et al.* 1992), but also by subtle variations in egg composition. For example, hormone levels in the yolk can modify developmental trajectories (Bowden *et al.* 2000).
- (ii) *Genetic quality of the offspring.* The mother's own genotype obviously influences her offspring. More interesting is the paternal contribution, in all taxa except the parthenogenetic *Ramphotyphlops braminus* (Kamosawa & Ota 1996). Females could influence the genetic constitution of their offspring by mate choice, but there is little evidence of female snakes exerting an active choice for one male over another (Olsson & Madsen 1998). Female copperheads (*Agkistrodon contortrix*) may evaluate the vigour of prospective mates by mimicking male challenge postures for combat (Schuett & Duvall 1996). More generally, a male's vigour influences his ability to obtain copulations (Shine *et al.* 2000a) and, a female

that resisted ineffective courtship might thus mate with more-than-usually vigorous males. If this dimension in male behaviour has a genetic underpinning, females that resist ineffective courtiers might thereby enhance the genetic quality of their offspring. Cryptic post-copulatory mate choice via sperm competition may be more important. In a small inbred population of adders (*Vipera berus*), females that mated with multiple males enhanced the viability of their offspring (Madsen *et al.* 1992), probably via rejection of sperm from males with genotypes too similar to their own (Olsson *et al.* 1996). However, multiple mating did not affect offspring viability in another (outbred) adder population (Luiselli 1993).

- (iii) *Incubation environment.* In egg-laying squamates, thermal and hydric conditions during incubation can substantially modify developmental rates (and thus, the timing of hatching) and also phenotypic traits of the offspring (Burger 1989, 1990, 1991, 1998; Burger *et al.* 1987; Burger & Zappalorti 1988). Thus, reproducing females directly influence the phenotypes of their offspring by selecting nest-sites with specific incubation conditions (Shine & Harlow 1996). Seasonal or geographical variation in weather conditions generates significant variation in hatchling phenotypes (Webb *et al.* 2001). Because much of embryogenesis occurs before oviposition (Shine 1983; Blackburn 1995), maternal thermoregulation can also modify hatchling phenotypes (at least in lizards; Shine 1995). Most dramatically, the shift from oviparity to viviparity considerably changes both the mean and variance of thermal and hydric conditions under which the embryos develop (Shine 1995; Arnold & Peterson 2002). The evolution of maternal brooding, especially in pythons that regulate nest temperatures by shivering thermogenesis, similarly modifies hatchling characteristics (Shine *et al.* 1996). Female pythons (*Liasis fuscus*) demonstrate remarkable flexibility by nest brooding only when benefits to the offspring exceed costs to the mother (Madsen & Shine 1999b).

Although no snakes are known to show temperature-dependent sex determination (TSD), incubation temperature can influence hatchling sex ratios via a higher mortality of sons at lower temperatures (Burger & Zappalorti 1988). Similarly, maternal body temperatures during pregnancy affected scalation traits of sons more than daughters in a viviparous snake species (Arnold & Peterson 2002). Such sex differences in responses to incubation temperature may favour the evolution of TSD (Charnov & Bull 1977), and facilitate maternal control over offspring sex ratios by nest-site selection or maternal thermoregulation. Intriguingly, offspring sex ratios in viviparous snakes have been reported to shift with maternal age (Madsen & Shine 1992c), body size (Dunlap & Lang 1990; Weatherhead *et al.* 1998) and reproductive output (Luiselli *et al.* 1996). Studies on lizards confirm that TSD can occur in viviparous species (Robert & Thompson 2001) and that incubation temperature can override genetic sex determination even in species with heteromorphic sex chromo-

somes (Shine *et al.* 2002a). The potential for further work in this area is clear.

(f) *Overview for females*

Because reproduction is very energy-expensive for female snakes, the acquisition, storage and expenditure of energy are fundamental themes of their reproductive adaptations. This emphasis has many implications. Female snakes, for example, often grow larger than conspecific males (thus increasing fecundity; Shine 1994), have larger heads relative to body length (thus eating larger prey; Houston & Shine 1993), are more heavy-bodied (reflecting energy storage; Scott *et al.* 1995; Madsen & Shine 2002), and coordinate their reproductive decisions with temporal fluctuations in energy availability (Madsen & Shine 2000b; Bonnet *et al.* 2001). Because many macrostomate snakes rely on infrequent ingestion of large prey items (Greene 1983), food intake may be low relative to maternal body size. Thus, female reproduction is infrequent, and is often fuelled by long-term energy stores (capital breeding; Bonnet *et al.* 1998). The critical importance of energy has also favoured adaptations to reduce energy expenditure, including sedentary behaviour, low basal metabolic rates, and the ability to downregulate organs (such as the digestive tract) during quiescent periods (Pough 1980; Secor & Diamond 1995). Logistically, the scarcity of post-hatching parental care in snakes (Shine 1988b) simplifies measures of resource allocation to reproduction, and reliance on a few large meals allows experimenters to manipulate the food intake of free-ranging animals to examine plasticity in traits such as thermoregulation, reproduction and habitat use (Blouin-Demers & Weatherhead 2001).

3. MALES

As in females, reproduction for male snakes imposes costs as well as benefits. Energy allocation is less important than it is for females, but may still be significant (Olsson *et al.* 1997). Male snakes frequently forgo feeding during the mating season thus also experiencing 'opportunity costs' (Madsen & Shine 2000a). In many snake species, for males, the major cost of reproduction may be the risk of mortality due to extensive movements during the mating season (Aldridge & Brown 1995; Bonnet *et al.* 1999a). Differing movement patterns at this time of year may impose selection for sex differences in colour (Shine & Madsen 1994; Forsman 1995).

The reproductive tactics under selection in male snakes differ in important respects from those for females, albeit with many points of commonality.

(a) *Seasonal timing of reproduction*

The extensive interspecific variation in the seasonality of sperm production has stimulated classificatory schemes (e.g. prenuptial versus postnuptial; Saint Girons 1982) but remains puzzling. In many species, males produce sperm shortly before mating and mate shortly before females ovulate. However, there may also be substantial time lags between these components, sometimes reflecting winter inactivity (i.e. sperm produced in autumn, mating in spring; e.g. Saint Girons 1982). In some snake species, males mate long after the sperm has been produced and while their circulating androgen levels are low (Saint

Girons 1982; Crews 1984; Crews *et al.* 1984). Sperm storage in either males or females is thus an essential part of the reproductive cycle in many snake species (e.g. Almeida-Santo & Salomo 1997; Bull *et al.* 1997); as for many aspects of snake reproduction, it confers great flexibility (in this case, it decouples the timing of mating from ovulation). Sperm may remain viable inside the female reproductive tract for up to several years (Seigel & Ford 1987).

(b) *Total energy allocation to reproduction*

Male snakes, unlike females, do not require any threshold level of energy stores to initiate reproduction (Bonnet & Naulleau 1996; Aubret *et al.* 2002). We might expect relative testis mass to vary among snake species in accord with mating opportunities; for example, larger testes are expected in taxa with frequent multiple mating and, hence, a high potential for sperm competition (Olsson & Madsen 1998). This prediction remains untested. In garter snakes (*Thamnophis*), limits on a male's ability to produce gelatinous mating plugs may constrain the total number of copulations per male per season and hence, select for male mate choice (Shine *et al.* 2001a).

(c) *Frequency of reproduction*

The often-low reproductive frequencies of female snakes do not apply to males, which typically reproduce every year after maturation (based on testis development; Saint Girons 1982). Males also often mature earlier than females (Parker & Plummer 1987) and thus, operational sex ratios (OSRs; Emlen & Oring 1977) typically are male-biased. OSRs vary among years and populations in response to local resource availability (and thus, the proportion of adult females reproducing). In turn, shifts in OSR modify determinants of male reproductive success. In male adders, for example, selection on body size is more intense in years when fewer females reproduce and hence, most matings are preceded by male-male combat (Madsen & Shine 1992d). Intriguingly, some adult-size males may not engage in reproductive activities in some years (e.g. in *Nerodia sipedon*; Weatherhead *et al.* 1995), suggesting an unexplained temporal complexity in male tactics.

(d) *Number of matings*

Variation in mating success constitutes the major raw material for sexual selection in males of most snake populations, and operates to optimize male performance at a variety of tasks.

- (i) *Mate location.* If reproductive females are difficult to find, mate-searching tactics will be under strong selection. During the mating season, males move around in ways that maximize their probability of encountering a receptive female (i.e. move more, and often in straight lines or in specific habitats where females are concentrated; Duvall *et al.* 1985, 1990). They detect females using subtle cues such as pheromonal trails deposited on the substrate, and follow these trails to locate the female (Mason 1992, 1993; Mason *et al.* 1989; Greene *et al.* 2001; LeMaster *et al.* 2001). We do not know the extent of variation in trail-detection and trail-following

abilities among male snakes, nor its importance for male mating success (but see Madsen *et al.* 1993).

- (ii) *Male–male rivalry.* Males may vanquish rivals by excluding them from a prime habitat; although rarely reported, this behaviour may nonetheless be common (e.g. Carpenter 1984; Webb & Shine 1997). Perhaps more often, males defeat rivals by defending areas around the female rather than any fixed territory. Males of many snake species engage in highly ritualized physical struggles during the mating season, typically involving intertwining wrestling matches; biting may sometimes be involved (Gillingham 1987). Losing males may be severely stressed, and postpone further reproductive activities (Schuett 1996). Even in species in which males do not show overt physical rivalry, such as natricine colubrids and boids in ‘mating balls’ of many males plus a female, more subtle physical struggles may influence reproductive success (Rivas & Burghardt 2001). For example, males may push aside the tails of their rivals, such that larger males obtain more matings than do smaller conspecifics (Madsen & Shine 1993a; Weatherhead *et al.* 1995; Luiselli 1996; Shine *et al.* 2000e).
- (iii) *Alternative male mating tactics within a single population.* In European adders (*Vipera berus*), some males guard females after mating and thereby reduce the probability of subsequent insemination (Madsen *et al.* 1993; Luiselli 1995). Small males may avoid battles with larger males, but instead wait nearby and court the female after their larger rival has departed (Madsen *et al.* 1993). Ontogenetic shifts in the pheromonal cues that stimulate courtship in garter snakes (*Thamnophis sirtalis*) mean that much of the courtship by smaller males is directed towards females too small to attract attention from larger males (Shine *et al.* 2001a). Although originally described as an alternative mating tactic based on confusing other males within a ‘mating ball’ (Mason & Crews 1985), female mimicry in the same species seems more likely to reflect advantages unrelated to mating. Courted ‘she-males’ are warned by the attention of other males, and protected from attack by predatory crows (Shine *et al.* 2000b, 2001b).
- (iv) *Courtship effectiveness.* Despite detailed descriptive studies on snake courtship, we still do not understand the process by which a courting male snake induces receptivity in his partner. This interaction has generally been interpreted as ritualized persuasion (e.g. Devine 1984), but recent studies suggest intense conflict between the sexes, including the possibility of forcible insemination (Shine *et al.* 2000c). In captivity, male presence may accelerate female reproductive cycling (*Python curtus*; DeNardo & Autumn 2001).

Sexual struggles in male snakes generate diverse correlations between male phenotypic traits and mating success. The most obvious involve body size, with larger males obtaining more matings, not only in species with male–male combat (e.g. *Vipera berus*; Madsen *et al.* 1993; *Agkistrodon contortrix*; Schuett 1997), but also in species with less

vigorous physical battles (tail-wrestling; Madsen & Shine 1993a; Luiselli 1996; Shine *et al.* 2000e). However, larger size might be a disadvantage if other males use body size as a cue to elicit courtship (*Eunectes murinus*; Rivas & Burghardt 2001). One unusual study documented the appearance of a novel gene in an adder population, influencing colour pattern as well as sexual-size dimorphism. This gene rapidly spread through the population, as predicted by measures of mating ability (Madsen & Shine 1992b). Success may also go to heavier-bodied and/or more vigorous males (Shine *et al.* 2000a,e), those with longer tails relative to body length (Shine *et al.* 1999b) or those with ‘average-length’ tails (Shine & Shetty 2001). Mating systems of some snake species may genuinely be ‘scrambles’, with no reproductive advantage to larger body size in males (*Acrochordus arafurae*; Shine 1986; *Laticauda colubrina*; Shetty & Shine 2002). Even in species with male combat (where we might expect larger males to obtain more matings), variance in male mating success may be driven by mate-searching ability rather than fighting ability and hence, larger size may be irrelevant to reproductive success (Duvall & Schuett 1997). However, phylogenetic analyses reveal that the degree of sexual-size dimorphism is influenced by the mating system: the evolution of male–male combat has been accompanied by shifts in male growth patterns and hence, in the direction and degree of sexual dimorphism in mean adult body size (Shine 1994).

(e) *Sperm competition*

Mating success may bear little relationship to male fitness, if paternity is strongly influenced by competition among sperm from rival males, within the female’s reproductive tract (Olsson & Madsen 1998). The opportunity for sperm competition is high in snakes; females of many species mate with multiple partners and show multiple paternity of the resulting clutches (Schwartz *et al.* 1989; Hoggren 1995; Garner *et al.* 2002; see Olsson & Madsen (1998) for a review). Mate guarding, mating plugs and prolongation of copulation may be evolutionary responses to this phenomenon (Andersson 1994; Olsson & Madsen 1998; Shine *et al.* 2000d). Molecular analyses of paternity will doubtless clarify these issues in coming years.

(f) *Mate quality*

Males of at least two distantly related snake species allocate more courtship to larger females (*Thamnophis sirtalis*; Aleksuik & Gregory 1974; *Laticauda colubrina*; Shetty & Shine 2002). Male garter snakes also court heavy-bodied females more actively than thin females (Gartska *et al.* 1982). A female’s size and body shape predict her reproductive output (see above) and hence, courtship to larger fatter animals may enhance male fitness. Pheromones (skin lipids) may offer the most important cues for such discrimination both among females within a single population, and as species-isolating mechanisms to maintain separation between sympatric taxa (Mason 1992; Shine *et al.* 2002b).

(g) *Overview for males*

Two dominant themes in the reproductive tactics of male snakes are the central role of mate location as a determinant of reproductive success, and the presence of a remarkable chemosensory apparatus that facilitates this

task. Low female reproductive frequencies in many snakes may also have favoured male ability to discriminate between reproductive and non-reproductive females, in order to direct courtship to the former rather than the latter. Indeed, sexual selection may well have driven much of the evolution of the snake vomeronasal system, although it has also been co-opted for other tasks such as foraging and predator detection (Greene 1997). In turn, the dependence on pheromonal trail following may reflect the locomotor mode of snakes, which usually results in continuous deposition of substrate trails. Animals that walk, hop, swim or fly do not deposit such continuous trails and hence, may best be located using other sensory modalities. One consequence of the sophisticated vomeronasal system of snakes is that pheromonally based male mate choice may be more important in this lineage than in most other vertebrate groups.

4. DIRECTIONS FOR STUDY

The spectacular recent increase in the volume of research on reproductive tactics in snakes has been accompanied by a massive expansion of the ecological, geographical and phylogenetic systems under study. Until the late 1970s, studies in this field were firmly based around a few 'model organisms': notably natricine colubrids in North America (*Thamnophis*) and northern Europe (*Natrix*), and viperids from the same two areas (*Crotalus*, *Vipera*). These organisms continue to be the focus of disproportionate attention, but studies in other parts of the world and on other snake lineages are providing a broader view of the diversity in snake reproduction. A major challenge for the field continues to be the development of new 'models', preferably from lineages (such as scolecophidians) that are phylogenetically and ecologically very different from previously studied organisms.

The conceptual focus of snake reproductive studies has also broadened. Earlier paradigms of snakes as primitive inflexible organisms have been replaced by an increasing appreciation of the subtlety, complexity and, above all, plasticity of snake biology. Topics such as social organization and sex allocation may become major fields of enquiry in their own right. Increasingly, experimental approaches take advantage of the high levels of phenotypic plasticity in snakes to explore direct environmental effects on morphology and behaviour.

This phenotypic plasticity has generated substantial intraspecific variation in many reproductive traits. Nearby populations of the same species often display remarkable differences (table 1). Island populations offer some of the most extreme examples, with spatial variation in prey resources generating massive divergence in snake morphology and behaviour (e.g. Schwaner & Sarre 1988; Forsman 1991; Pearson *et al.* 2002). Much of this variation is directly induced by prey availability influencing growth trajectories of individual animals, but other examples of this variation may have a genetic underpinning (e.g. Seigel & Ford 1991; Madsen & Shine 1993*b*). Thermal heterogeneity in the environment may also induce substantial shifts in life-history traits (Madsen & Shine 1999*b*).

These sources of variation mean that only rarely are major reproductive traits common to all members within major lineages (*contra* Schuett *et al.* 2001). To examine

evolutionary shifts in traits of interest, we need robust phylogenetic hypotheses within as well as among lineages. The increasing availability of such phylogenetic information provides exceptional opportunities to explore the fine-grained heterogeneity in ecological, behavioural and reproductive traits among snakes within an evolutionary perspective. In turn, this rapid expansion of phylogenetic and ecological data provides powerful opportunities to pose and test hypotheses inaccessible for study in many other kinds of organisms.

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