REVIEW:

MULTIPLE PATERNITY AND SPERM STORAGE IN TURTLES

DAVID A. GALBRAITH

The Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent CT2 7NX, UK

Present address: The Centre for Endangered Reptiles, 347 rue Bourget, Granby, Quebec J2G 1E8, Canada

ABSTRACT

Multiple paternity is the occurrence within a single clutch of offspring fathered by more than one male. This pattern may be an an adaptive feature of the mating system of turtles. Mating systems are the adaptive features of reproduction which contribute to variation in the probability of a particular egg being fertilized by a particular sperm. Turtle populations have rarely been studied specifically in terms of multiple paternity or mating systems. Five features related to multiple paternity are discussed: spacing behaviour prior to courtship, mate-seeking and mate choice, agonistic encounters between individuals, sperm storage, and sperm competition. Several studies have examined movements and spacing behaviours in turtles, and have drawn inferences about mate-seeking. At present, multiple paternity has been detected in clutches of loggerhead turtles (*Caretta caretta*), wood turtles (*Clemmys insculpta*), and snapping turtles (*Chelydra serpentina*). In wood turtles, a relationship between male dominance and paternity has been detected through DNA fingerprinting. Sperm storage has been demonstrated in several species, but studies of sperm competition are lacking. Directions for future research are considered.

INTRODUCTION

The reproductive biology and behaviour of turtles have rarely been considered from the perspective of mating systems: the "ensemble(s) of behaviours and physical adaptations specific to mating, as well as some of the social consequences of these behaviours" (p. 251, Vehrencamp & Bradbury, 1984). Mating systems consist of those factors influencing which pair of gametes fuse to form a zygote, ranging from social factors to the physiology of ovum/sperm interactions. In other words, a complete description of the mating system of a particular population would include all of the ways in which mate choice, copulation and fertilization differed from a random model of gamete assortment. As individuals may vary in the specifics of these factors, there is potential for both natural and sexual selection to produce adaptations. Some authors have approached adaptive explanations for specific features of reptilian life histories in terms of mating systems seen in other taxa (Kaufmann, 1992), or evolutionary expectations of features of the life histories, such as intense male-male competition for mating opportunities in species without significant paternal investment (Obbard, 1983, Trivers, 1972).

Within any mating system, conflicting strategies may evolve between males and females which result from differences in the costs of reproduction, either as differences in risks or in reproductive effort. The fundamental roles of male and female turtles are highly stereotyped. Pair-bonds are assumed not to form (but have they been looked for?), males contribute no parental care, and the investment of females ends with the completion and abandonment of the nest after egg laying.

One aspect of reproduction, the presence of multiple paternity within clutches, has recently been studied in many taxa using allozyme electrophoresis, and more recently DNA fingerprinting methods (Birkhead, 1989). It is possible that multiple paternity is a common feature of the reproductive biology of turtles. Only a few studies to date, however, have attempted to detect multiple paternity directly. These studies include those of nests of loggerhead turtles *(Caretta caretta)* from a beach in Australia (Harry & Briscoe, 1988); and nests of snapping turtles (*Chelydra serpentina*, Galbraith et al., 1993) and wood turtles (*Clemmys insculpta*) in North America (Galbraith, 1991).

Making use of limited genetic variation detected by allozyme electrophoresis, Harry & Briscoe (1988) were able to demonstrate significant deviations from expected Mendelian offspring genotype frequencies in clutches from eight of 21 female loggerhead turtles surveyed. These deviations were interpreted as evidence of multiple paternity. In addition, Harry & Briscoe (1988) found that in two cases, second nests from the same female in a single season appeared to have different paternal genome components, suggesting that the loggerheads mated between clutches but within the same year. This finding could also represent a case of sperm precedence in a species with very long-term sperm storage.

More recently, Galbraith et al. (1993) used DNA fingerprinting to indirectly detect multiple paternity in two of three clutches of snapping turtles examined, by detecting significant deviations from expected distributions of paternal minisatellite bands. In a study of wood turtles, Galbraith (1991) directly detected multiple paternity in two of six clutches by demonstrating that at least one offspring within each of the nests had a different father than the remaining offspring in that clutch.

Among other reptiles, multiple paternity has been demonstrated in four snake species. Snakes are relatively easy to breed in captivity, and several snake species exhibit interesting copulatory adaptations which may be related to sperm competition (see below). Multiple paternity has been demonstrated in natural nests of garter snakes (*Thamnophis sirtalis*)

using ratios of colour morphs (Gibson & Falls, 1975), and allozyme electrophoresis (Schwartz *et al.*, 1989). Multiple paternity has been demonstrated in three other species of snakes in captive breeding settings: copperheads (*Agkistrodon contortrix*) by the use of pigment patterns (Schuett & Gillingham, 1986), and in kingsnakes (*Lampropeltis getulus*, Zweifel & Dessauer, 1983), and adders (*Vipera berus*, Stille *et al.*, 1986) by protein electrophoresis.

In addition to the specific cases of multiple paternity detected in reptiles, it should be noted that the recent application of paternity analysis in populations of birds has revealed multiple paternity in many cases (Quinn *et al.*, 1987, Burke *et al.*, 1989, Gibbs *et al.*, 1990, and others).

The objective of this review is to provide a framework for the discussion of multiple paternity and sperm storage in turtles. Mating systems in turtles are therefore discussed, with occasional reference to other reptiles.

FACTORS AFFECTING MULTIPLE PATERNITY

Five groups of factors may be of particular relevance in explaining multiple paternity, and sperm storage, in turtles. The individual aspects of any mating system are, by definition, a suite of characters which are highly interdependent. As is the case with other biological systems, the mating system is composed of features whose state may be shared among the individual species or populations under study, and therefore assumed to be ancestral or 'primitive', or which may differ among populations or species ('derived', and usually assumed to be adaptive). Characters in the ancestral state are sometimes assumed to be limited by phylogenetic 'constraints', in which the species or populations under study do not vary in that character because natural selection has insufficient heritable variation upon which to operate.

First, turtles exhibit behaviour prior to courtship which will have a subsequent bearing on territoriality, spacing, or access to mates. In addition to such behaviour, population structure and sex ratios will influence how many males a female encounters.

Second, movements and activities by either sex may be directly associated with courtship and mate choice, and are of obvious importance to the number of times a female may be inseminated prior to clutch fertilization. As most publications concerning courtship and mate choice in turtles have concentrated on descriptions of mating behaviours this aspect of the mating system will not be discussed here in detail.

Third, aggressive encounters between individuals of the same sex, or between the sexes, may be very important for mate choice, the setting-up of dominance hierarchies, and mate access, and have been reported in some turtle species.

Fourth, the ability of females to store viable sperm for years (and perhaps the longevity of spermatozoa) will promote multiple paternity and sperm competition.

Finally, sperm competition, in which spermatozoa from different males present at the same time within a single female may compete for fertilization, and sperm precedence,

in which the order of insemination determines the order in which sperm from each male encounters ova, must be discussed relative to multiple paternity.

Specific characteristics, such as sexual size dimorphisms, may also have significant roles in several of these areas. Each of the five factors identified above are discussed below for their relevance to explaining multiple paternity in turtle clutches.

MOVEMENTS AND BEHAVIOURS PRIOR TO COURTSHIP

The social behaviours of turtles are complex and subtle, but few studies have investigated any of them in a systematic fashion (Harless, 1980). Movement patterns and spacing behaviours have received the most attention, largely from studies in which radiotelemetry has been used to follow individuals over periods of months or years (e.g. Obbard & Brooks, 1981, Morreale *et al.*, 1984, Galbraith *et al.*, 1987).

Home ranges may be a function of individual size, age, or experience, if the holding of home range is related to male-male or male-female agonistic encounters (Kaufmann, 1992). In the present context, home ranges are potentially important for mate acquisition in that home ranges may define areas in which males locate females, either during the course of daily activities or during the annual nesting migrations that females of some species exhibit (Obbard & Brooks, 1980). In yellow-bellied slider turtles (*Pseudemys scripta*), Morreale *et al.*, (1984) found that the movements of male turtles were earlier in the season, and of longer duration and distance than those of females. This suggests that males in this species may move in order to increase their chances of encountering potential mates. Such movements may therefore mean that females may encounter several males throughout the course of a season.

Movement patterns and home ranges have also been shown to be sexually dimorphic in snapping turtles (*Chelydra serpentina*; Obbard & Brooks, 1981), but follow a different pattern. In snapping turtles, a species in which males are larger than females (Obbard, 1983), male movements and home ranges were found to be smaller than those of females in a population in central Ontario, Canada. In addition, adult female snapping turtles in the same population undergo an annual nesting migration which may expose them to several of the more sessile males (Obbard & Brooks, 1980, see below).

AGONISTIC BEHAVIOURS

Another important component of the mating system in some turtle species is the behaviour which establishes dominance hierarchies (Harless, 1970, Schafer & Krekorian, 1983, Kaufmann, 1992). Among both wood turtles (*Clemmys insculpta*) and Galapagos tortoises (*Geochelone elephantopus*), dominance rank among adult individuals has been associated with physical attributes. Among adult wood turtles, dominant males tend to be larger, and older, than subordinate males (Harless, 1970, Kaufmann, 1992). Among Galapagos tortoises Schafer & Krekorian (1983) found that rank relationships varied between tortoises with different shell shapes. In tortoises with dome-shaped shells rank appeared to be correlated with the number of physical contacts between individuals. In those with saddle-shaped shells, however, rank was correlated with the height to which the neck could be extended.

To date a single study has demonstrated a relationship between male agonistic behaviour and subsequent reproductive success in a turtle population. In a population of wood turtles in central Pennsylvania, USA, dominance rank was shown to be significantly correlated with body mass and also with frequency of copulatory behaviour (Kaufmann, 1992). In order to test whether there was a relationship between observed dominance rank and reproductive success, DNA fingerprinting (Jeffreys et al., 1985a, 1985b) was used to carry out paternity analyses in the same population. Galbraith (1991) found that the males which were fathers of offspring from 10 nests laid in 1989 were significantly higher in the dominance hierarchy than expected by chance if there was no association between rank and paternity. Such hierarchies may be important in establishing access to females, or in influencing the chances of specific males completing copulations (Kaufmann, 1992).

COURTSHIP BEHAVIOURS AND COPULATION

Reproductive behaviour has been most often described in turtles from the point of view of courtship or mating behaviour as stereotypical acts (see an extensive review by Carpenter & Ferguson, 1977). Courtship displays and behaviour vary immensely among species of turtles. Some species exhibit a complex series of elaborate displays by the male, which includes "fanning" the foreclaws in front of and above the female's head, or while facing the female (Kramer & Fritz, 1989). Courtship of this sort has been documented from highly aquatic pond turtles in the family Emydidae (Berry & Shine, 1980). In contrast, some "bottom-walking" turtles such as snapping turtles appear to have a system of forced insemination (Obbard, 1983). Still other patterns of courtship have been demonstrated among tortoises, which include protracted periods of butting with the carapace, biting, and attempted mountings (Auffenberg, 1977). Among wood turtles, recent studies by Kaufmann (1992) have demonstrated complex courtship and mating sequences which include long periods of time in which males remain mounted on the females but do not initiate copulation.

The evolution of courtship behaviour and sexual dimorphisms in turtles are clearly related. Species in which males perform elaborate courtship displays also tend to be species with small males relative to females (Berry & Shine, 1980), and some species in which males are larger than females appear to have little or no courtship behaviour prior to insemination (Obbard, 1983).

Sexual dimorphism in adult size has been shown to vary between species and among populations in turtles (Iverson, 1985). Two broad patterns of sexual size dimorphism have been reported among turtles (Berry & Shine, 1980). Turtles in which locomotion is usually by swimming in open water generally display males smaller than females. Larger aquatic species which "bottom-walk", or large species such as tortoises, which are primarily terrestrial, display males which are the same size or more likely larger than females (Berry & Shine, 1980).

Several hypotheses have been proposed to account for the adaptive nature of sexual size dimorphisms in turtles. One theory is that the mating system in species with males much larger than females is a "forcible insemination" system, in which males must be above a certain size to subdue a female and achieve mating opportunities (Berry & Shine, 1980, Obbard, 1983). Whether a male turtle can inseminate a female which is making all efforts to resist remains to be tested, but such a system is highly unlikely in those species which can close the carapace (e.g., the box turtle, Terrapene carolina). Although female mate choice has not been investigated in turtles, it is possible that females could use the force exerted by males prior to copulation as an indication of male fitness.

Intrasexual competition is another possible explanation for large males, if male size is advantageous in the acquisition of home ranges or in agonistic behaviours (Kaufmann, 1992). In addition, as intersexual agonistic behaviour and dominance hierarchies may also exist in turtle populations (Schafer & Krekorian, 1983), size-related dominance could establish a mating system based on the dimorphism in which forcible insemination was not necessary.

It is also possible that sexual differences in adult size are not related to sexual selection. Alternative hypotheses include ecological niche partitioning (Shine, 1980), in which intraspecific competition is reduced by each sex using a different resource base. It is also possible that a sexual size dimorphism is an emergent feature derived through energetic differences between males and females (Fitch, 1981): as one sex begins to divert energy from growth to reproduction, a disparity in size could result if the other sex continues to grow (Fitch, 1981). However, growth requires the investment of energy which could otherwise be diverted into reproductive activities, suggesting that such differences should be seen as a description of the mechanism, rather than the explanation of the phenomenon of a sexual size dimorphism.

The study of sexual size dimorphisms is difficult in long-lived species with indeterminant growth because body size varies with age. It is necessary to specify ages being compared, or to compare growth curves between the sexes. Unless differences due to age and experience are controlled for in the analyses, any differences observed between the sexes could be spurious.

Sexual dimorphisms other than size have been found in some turtle species. Among some pond turtles, for example, elongated claws on the forelimbs are used by the males to "titillate" the females during courtship (Kramer & Fritz, 1989). Perhaps the most spectacular sexual dimorphism in any turtle species, rivalling the colourful sexual displays of some lizards (Ferguson, 1977), are the seasonal colour changes in male painted terrapins (Callagur borneoensis), and related large Asian river turtles. Adult male painted terrapins change from a dark phase to a light phase through a complex series of changes in the characteristics of the epithelium, which can be triggered by testosterone administration (Moll et al., 1981). A reproductive function for this colour change has been suggested but not directly demonstrated (Moll et al., 1981). It is possible that the seasonal colour changes are behavioural status displays used by other males or by females, or possible as species-recognition features. Moll et al. (1981) observed that the species which display such colour changes are river-dwellers, for which visual signals would be more effective than olfactory signals, as olfactory cues would be swept away from individuals by flowing water.

The acquisition of mates by males is not a function of male behaviour alone, but is an interaction between males and fe-

males, and therefore female mate choice must be considered as well. No published research has yet been directed towards a quantitative assessment of female mate choice in a natural population of turtles.

SPERM STORAGE AND MULTIPLE INSEMINATIONS

Although relatively few studies have actually demonstrated multiple paternity in reptile populations, it is likely that multiple paternity is common (Saint-Girons, 1975, Devine, 1984). Several studies have demonstrated the storage of sperm within the reproductive tracts of female turtles which had been sequestered from males for periods longer than a year (reviewed by Saint-Girons, 1975, and Devine, 1984; see also Gist & Jones, 1987, 1989), and others have demonstrated the production of fertile eggs months or years after last contact with males (Schuett, 1982, Schuett & Gillingham, 1986).

Recently, Gist & Jones (1987, 1989) have undertaken detailed examinations of the reproductive tracts of female turtles, and have demonstrated the presence of sperm within tubules of the proximal oviducts, in representatives of seven taxonomic families of North American turtles. The sperm are stored within narrow tubules in the albumin-secreting region of the oviduct, which appear to be specialized for that function (Gist & Jones, 1989).

The storage of sperm within the oviducts of the females may present three reproductive advantages. First, as the first eggs which travel down the oviduct in each clutch will tend to "sweep" any contents of the oviduct downwards, sperm storage provides a reservoir of sperm for fertilization of subsequent eggs (Gist & Jones, 1989). Secondly, as many turtle species display asynchrony in the gonadal cycles of males and females, storage of viable sperm by the female may be required for successful fertilization (Gist & Jones, 1989). Thirdly, long term sperm storage may be an adaptive feature of the life-history of females in which individuals are very long-lived (Galbraith & Brooks, 1987), and hence may not have any contact with males in some years.

An important prediction arising from the demonstration of long-term sperm storage by female turtles is that mate-guarding behaviours by males may not be highly effective (Kaufmann, 1992). It would be informative to test for seasonal variation in the ability of the females to receive and retain sperm, but no studies of this, or of sperm precedence, have been attempted in turtles.

Among laboratory-mated adders (*Vipera berus*), females may mate with more than one male and produce bipaternal clutches (Stille et al.,' 1986, 1987). Although specialized sperm storage structures have not been found in female vipers (Andren & Nilson, 1987), sperm storage for a year is possible (Stille et al., 1986). A secretion from the male adder which induces contraction of a sphincter in the uterus of the female forms a copulatory plug (Nilson & Andren, 1982). In the case of the adder, the copulatory plug appears to retain sperm rather than to categorically prevent multiple insemination (Stille et al., 1986, Stille & Niklasson, 1987, but see Andren

& Nilson, 1987, for an opposing view).

Evolutionary theory suggests that there is a fundamental conflict between males and females in the distribution of paternity within clutches. An individual male would maximize his reproductive success if he could father many or all of the offspring within the clutch of each female he mates with. In contrast, distributing paternity among more than one male within individual clutches may increase the reproductive success of individual females. If there are no advantages to having a particular male as sole father of a clutch, multiple paternity will decrease the expected relatedness among the offspring while retaining the expected relatedness of 0.5 between the female and each offspring. There is also direct evidence that multiple mating by female snakes may increase female reproductive success, possibly though sperm competition (Madsen et al., 1992).

SPERM COMPETITION AND SPERM PRECEDENCE

Once copulation has been effected, there are additional opportunities for variation in male reproductive success in turtles. Prior to oviposition, sperm competition may take place if sperm from two or more males are present within the reproductive tract of a female simultaneously (Parker, 1970). Elegant mechanisms have been described which can evolve under conditions of sperm competition (reviewed in Smith, 1984, see also Birkhead et al., 1987). In some taxa, copulatory plugs are deposited in the reproductive tract of the female by a male after insemination, apparently to thwart mating attempts by subsequent males (Devine, 1975). Some authors have even suggested that a proportion of the sperm in mammalian ejaculates has a "kamikaze" function, in that it may block or entangle sperm from subsequent inseminations (Baker & Bellis, 1988).

If polygynous species of birds are taken as a model for sperm competition in turtles, then males may be expected to attempt to copulate with many females, rather than concentrate on only a few females (Birkhead et al., 1987). As male turtles provide no parental care, competition among males for mating opportunities is expected to be intense (Trivers, 1972).

Sperm competition has been inferred from the presence of multiple paternity. Two methods have been used to detect multiple paternity within clutches, or litters, of vertebrates. In the direct method, multiple paternity is demonstrated by paternity analysis for each offspring by which more than one male is assigned within the clutch (Zweifel & Dessauer, 1983, Stille et al., 1986). Direct assignment is the most satisfactory method for detecting multiple paternity, and is required for the assessment of male reproductive success. However, if the males cannot be compared to the offspring, multiple paternity can be inferred from the distribution of paternal elements within the genotypes of the offspring sampled (Gibson & Falls, 1975, Schwartz et al., 1989, Harry & Briscoe, 1988). A null hypothesis is constructed using the expected distribution of segregating genetic markers given a single father, and if the null hypothesis can be rejected on the basis of the observed distribution of the offspring's paternal markers, then more than one father is assumed to have contributed to the clutch (Westneat et al., 1987).

Although Devine (1984) and others have predicted that sperm competition should take place in reptiles, no demonstration of relative competitive abilities of ejaculates of individual males has been made. Under conditions of sperm precedence, for example, mating order affects the success of males which sequentially inseminate females (Sims *et al.*, 1987). It is possible that the first male which achieves copulation with a given female in a receptive period would father her offspring, and perhaps have sperm stored as well. However, in some bird species, multiple layers of stored sperm result in a "first in-last out" pattern of sperm precedence (Compton *et al.*, 1978, Sims *et al.*, 1987). It is unlikely that a large volume of semen could remain within the uterus of a female turtle after the first few eggs have descended, and so sperm stored within the folds and glandular recesses of the oviduct may be important in fertilizing every clutch (Gist & Jones, 1989).

Recently, the demonstration that female adders which copulate more frequently than others also have a higher mean number of live offspring has led to the suggestion that the increase in viability of fertilized eggs is due to sperm competition, in which the 'best' sperm compete for the chance to effect fertilization (Madsen *et al.*, 1992). If this interpretation is correct, the study of vipers represents the first direct demonstration of a fitness advantage to females of sperm competition. The findings of Madsen *et al.* (1992) further supports the view that the copulatory plug does not prevent multiple insemination in adders.

PROSPECT

Although systematic research into the mating systems of turtles has been relatively sparse, several empirical studies have pointed to hypotheses which should be rigorously tested. Further research on the social behaviours of turtles in natural populations will fill out our understanding of the distribution of dominance hierarchies and agonistic behaviour. However, until genetic markers are used for determination of male reproductive success, quantitative assessment of the adaptive significance of turtle social behaviour, and the role of sexual selection, will remain untested.

The opportunities which are now available in this field are immense. The methodological limits of parentage analysis using allozymes (Hayasaka *et al.*, 1986, Westneat *et al.*, 1987, Wrege & Emlen, 1987) have receded as DNA fingerprinting has developed. DNA fingerprinting (Jeffreys *et al.*, 1985a, 1985b) and related methods (for example see Tautz, 1989) have been demonstrated in turtles (Galbraith, 1991) and in crocodilians (Demas & Wachtel, 1991), and have been used extensively for studies of behavioural ecology in birds (e.g. Quinn *et al.*, 1987, Wetton *et al.*, 1987, Burke *et al.*, 1989, Gibbs *et al.*, 1990).

We are therefore not faced with a lack of appropriate genetic markers for unambiguously determining parentage in reptiles. However, there remain few studies in which individual animals have been observed in both same-sex and intersexual behaviours in which the power of DNA profiling methods could then be used to demonstrate a connection between behaviour and male reproductive success, or between multiple paternity and the factors discussed above. Furthermore, relatively few studies of turtles have attempted to identify characteristics by which individual reproductive success may vary in field populations.

Why is sperm stored at all in mobile, polygynous, long-lived species like turtles? Several adaptive hypotheses for sperm storage can be put forward at this time. Sperm storage is a feature of both the female and male reproductive systems. However, it may be argued that females stand to gain more than males from sperm storage.

First, storing sperm allows the male and female reproductive cycles in many turtle species to function asynchronously. Females must lay their eggs in the spring in temperate regions in order to allow for complete incubation. On the other hand, males inseminate females in the fall in some species, at the height of agonistic interactions and when the dominance hierarchy is well established. Perhaps the asynchrony in sexual cycles is an example of conflicting sexual strategies, and sperm storage is the evolved compromise (Gist & Jones, 1989).

Second, stored sperm provides a ready supply for fertilization in case the female is not inseminated in a particular year. Thus, stored sperm allows individual females to reproduce, and in some senses pre-adapts individual females to be colonizers (hence the propensity for tortoises to colonize oceanic islands) in situations of low population density.

Third, storing sperm will promote multiple paternity and sperm competition. Multiple paternity may be an advantage from the point of view of the female because it will lower genetic relatedness among offspring (Loman *et al.*, 1988). Thus, females can bring reduce the risk of inbred offspring by storing sperm from several males. If the female had to depend upon fresh sperm alone then multiple paternity would probably be much rarer. Interestingly, multiple paternity presents a conflict between male and female reproductive interests: males which fertilize entire clutches clearly would be at an advantage. Sperm competition may also be a feature of multiple paternity which presents an adaptive advantage to females, as suggested recently by Madsen *et al.* (1992), through the selection of most active sperm. This question of the consequences of multiple insemination on the rate of infertility among eggs within clutches should be reviewed and further investigated, as this may represent an important aspect of sperm competition.

Finally, there may be geometric constraints in the fertilization of a clutch of turtle eggs. If a female is inseminated after one clutch is shelled and before oviposition, the eggs will form an effective barrier to sperm reaching the storage sites for subsequent clutches, and the eggs may act to flush sperm out of the uterus upon oviposition. Perhaps females must store sperm so that later eggs in each clutch are fertilized: failure to fertilize the whole clutch would be a severe evolutionary penalty for females.

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