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Monogamy in lizards

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Abstract

Monogamy is relatively rarely reported in taxa other than birds. The reproductive system of many lizard species appears to involve multiple mating partners for both the male and the female. However, short-term monogamous relationships have been reported in some lizard species, either where the male defends a territory that is only occupied by a single adult female, or where males stay with females for a period of time after mating, apparently to guard against rival males. There are a few reported cases of more prolonged monogamous relationships in lizards, with the Australian sleepy lizard, *Tiliqua rugosa*, the best studied example. Adult males and females of this species form monogamous pairs for an extended period before mating each spring, and they select the same partner in successive years. The paper reviews possible functions of monogamy in this and other lizard species, and suggests that the additional perspective from studying lizards may enrich our overall understanding of monogamous behaviour.

Keywords: Lizard; Mating system; Monogamy

1. Introduction

Monogamy is where a single male and a single female form an exclusive association and cooperate in breeding activity (Wickler and Seibt, 1983; Gowaty, 1996). Black (1996) distinguished ''genetic monogamy'', where the partners are the sole parents of any offspring, from ''social monogamy'', where males and females are physically close for an extended period or share space or resources with each other. Social monogamy does not imply genetic monogamy. A high incidence of matings outside the pair bond has now been detected with DNA analysis, in many socially monogamous birds (Petrie et al., 1998). Social monogamy can be continuous over the whole year, or part-time, when partners only spend part of the year together, usually the breeding season.

Natural selection often favours characters that increase the number of offspring produced. For many species this leads to males mating promiscuously with as many females as possible. Females may also be advantaged by promiscuity if multiple paternity of their clutches results in higher offspring variability (Kempenaers et al., 1999), or if mating males provision females in some way.

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However, in many animal taxa, including frogs (Caldwell, 1997), some species show social monogamy. Three broad hypotheses are used to explain why monogamy, rather than promiscuity, is favoured in these species.

1. Males stay with their female partner to provide paternal care and to help raise the young, because their own reproductive success is reduced if the mother is left to raise the young alone (Emlen and Oring, 1977; Clutton-Brock, 1991).
2. Males guard single females, either because they cannot defend the home ranges of multiple females against rival males, or, in non-territorial species, to ensure their own paternity (Parker, 1974; Stamps, 1983).
3. Females adopt monogamy when they are advantaged by accompanying males. Females with more to lose from the withdrawal of male help are more likely to remain monogamous (Gowaty, 1996).

None of these hypotheses consistently explains monogamy over all cases (Black, 1996). The functions of monogamy are probably complex and may vary among species and among ecological conditions. As more monogamous species are studied a broader perspective will emerge. In this case it will be particularly useful to explore non-avian examples.

2. Polygyny in lizards

In reptiles, and lizards in particular, monogamy is rarely reported. The most commonly reported mating system is polygyny where a male mates with several females. Some species have "prolonged mate searching polygyny" (Aldridge and Brown, 1995) where males move about the habitat seeking to encounter and mate with females. Males of these species are more active than females and males are more often seen than females by investigators, as reported, for example, in the lizards *Anolis carolinensis* (Nunez et al., 1997) and *Psammodromus algirus* (Diaz, 1993).

In many lizard species males are also more active in the mating season because they are defending a territory. Dominant males can hold territories that contain the home ranges of several females (Jenssen et al., 1995; Heisig, 1993; Diaz, 1993; Panov and Zykova, 1993; Zykova and Panov, 1993; Johnston, 1997), leading to a territorial polygynous mating system. Territorial males of the lizard *Uta palmeri* get most of the observed matings with resident females (Hews, 1993), and DNA analysis of offspring from *Sceloporus virgatus* females suggests that males in close spatial proximity to the females father most of the young (Abell, 1997). Many lizard species are sexually dimorphic for size, particularly head size, or colour, and bigger or brighter males are better able to defend a territory (Thompson and Moore, 1992; Mouton and van Wyk, 1993; Johnston, 1997). Males of these species are often more aggressive than females towards conspecifics (Hauschild and Gassner, 1994) and aggressiveness is used to hold territories (Hews, 1993; Tokarz, 1995; Halloy, 1996).

3. Territorial behaviour and monogamy

Territorial behaviour in lizards can sometimes lead to monogamy. In some lizard species, some males defend an area occupied by a single female. This may be because one female home range is as large an area as the male can defend. Stamps (1983) suggested monogamy was more common in large than in small lizards. Males can defend the relatively small area occupied by several females in a small species, but not the larger areas occupied by several females of larger species. Alternatively, in lizard populations where there are polygynous males with high quality territories, some other males may become monogamous if their poorer territories attract fewer females. In two species of agamid lizards of the genus *Stellio*, some single males defend up to four females while others defend just one (Panov and Zykova, 1993; Zykova and Panov, 1993). *Sceloporus mucronotus* can occur in aggregations of one male with up to four females, but normally has monogamous associations of one adult male with one adult female (Lemos-Espinal et al., 1997). Similarly the Australian lizard *Egernia stokesii* has stable social groupings with one or more adult male and one

or more adult female (Duffield, pers. comm.). In all these cases populations contain both monogamous and polygynous individuals.

Monogamy in territorial lizards may involve more than just mate guarding. Halloy and Halloy (1997) suggested that a pair of *Liolaemus huacahuasicus* may be jointly defending their overlapping territories, and Cooper (1993) described pairs of *Eumeces laticeps* defending preferred oak trees with suitable tree holes. Territorial defense by a pair may be a form of indirect parental care if offspring are tolerated within the territory and benefit from its resources (Halloy and Halloy, 1997). In several lizard species, juveniles and subadults, assumed to be offspring of resident adult male and female lizards, are tolerated for extended periods within the territory. Examples include *Stellio*, (Panov and Zykova, 1993; Zykova and Panov, 1993) and *Egernia* (Duffield, pers. comm.). Thus stable group structure, including monogamy, may provide enhanced offspring success.

4. Multiple mating by female lizards

Territorial defence in lizards can reduce access to females by other males. For example, female *Anolis sagrei* were observed to have more than one mating partner in a season, but usually only when new males replaced previous territory holders, and rarely from a non-resident male entering the territory and mating (Tokarz, 1998). However, as in bird studies, observed mating frequencies may not reflect actual matings. In *Sceloporus virgatus*, DNA analysis of offspring showed some clutches with multiple paternity, and some males achieving matings without holding territories (Abell, 1997). In other non-territorial lizard species, females may mate with several males. Females of *Anolis valencienni* mate at least once a day over a six week mating period and have five or more different male partners (Hicks and Trivers, 1983). Females of *Niveoscincus microlepidotum* apparently mate several times in a season because they have multiple mating scars (Olsson and Shine, 1998), although these may have come from one or from several males.

Female *Lacerta agilis* can mate with several males in a season (Olsson and Madsen, 1995), and several males can fertilise each clutch (Olsson et al., 1994; Gullberg et al., 1997). In this species, multiply mated females can have higher reproductive success from enhanced genetic variabilty among their offspring, reduced inbreeding (Olsson and Madsen, 1995), or the opportunity for sperm competition (Olsson et al., 1996b). Males of *Lacerta agilis* cannot influence the number of offspring they fertilise, either by the order of mating or by the time lapse between successive male matings (Olsson et al., 1994). In fact the female has a greater role in sperm choice and selects preferentially the sperm from more distantly related males among those she has mated with (Olsson et al., 1996b). Thus where females will accept multiple mating, the primary mechanism available to males to ensure paternity is to guard the female from access by other males. This can lead to short term monogamous associations of one female guarded by one male.

5. Monogamy as mate guarding to inhibit multiple matings

In several non-territorial lizard species the male stays with the female for various lengths of time after successful mating. Males of the Australian southern bluetongue lizard, *Tiliqua nigrolutea*, retain their biting grip on the female shoulder for up to an hour after mating (A. Edwards, pers. comm.). Males of *Lacerta agilis* guard a female for hours to several days after mating (Olsson, 1993). Larger males of *Lacerta agilis* tend to guard females for longer periods than smaller males (Olsson et al., 1996a). *Ameiva plei* form "consort pairs" that mate several times over the two–four days during which the females are sexually receptive (Censky, 1995). Censky (1997) suggested that large males guard females from harassment by other males, defending against rival males, and providing females with more uninterrupted feeding time. This implies advantages to both male and female from the short partnership. In a two week mating season, males of the polygynous North American skink *Eumeces laticeps*

stay with females for five–eight days after mating (Cooper and Vitt, 1997).

These short term associations of male and female lizards after mating are usually considered to be mate guarding, a behaviour to reduce the opportunities for rival males. However, Olsson et al. (1996a) reported that, for *Lacerta agilis*, the time spent guarding a female had no influence on the number of young sired by other males. Thus mate guarding may not always be effective.

Some lizard species spend longer in monogamous pairs, particularly before mating. In *Niveoscincus microlepidotus* pairs form for an average of 29 days (and up to 84 days) during the mating season, males track females, and they appear to recognise their own partner from other females (Olsson and Shine, 1998). The reported explanation is that males guard females, in this case before mating, to ensure primary access to the female when she becomes receptive (Olsson and Shine, 1998). In African chameleons pair bonds last for at least 63 days in one species, 85 days in another, and can extend through successive reproductive cycles (Toxopeus et al., 1988).

In summary, two processes have been proposed to explain short term monogamous relationships in lizards. Both concern guarding females from the attention of rival males. In one the male defends a territory that contains a single female. In the other the male guards a single female for a prolonged period to prevent access for rival males. Few studies suggest any role for paternal care in monogamous relationships because it is virtually unknown in lizards. Few have considered monogamy from the perspective of a female lizard. These short monogamous interactions may be an evolutionary precursor to longer term behavioural associations between males and females in other lizard species. The rare examples where monogamy has been reported are scattered over a range of lizard families, and no phylogenetic pattern is yet apparent.

6. Long-term monogamy

Most research on long-term pair fidelity has been on birds. Black (1996) refers to "perennial monogamy" as partnerships that persist from one year to the next in at least 50% of the pairs. Ens et al. (1996) list over 120 monogamous bird species, but suggest monogamy is less common in other groups such as mammals (and lizards). Possible functions of monogamy within a breeding season cannot explain why individuals select the same partners in the next breeding season. One explanation is that if a pair establishes in one season, it may cost more to break out of the relationship than to remain with the same partner in a subsequent season, particularly for species where partnerships last all year. For example, the costs of locating a new partner and displacing a rival from that partner may exceed any benefits of the new partner over the old. And if there is little opportunity to improve mating performance by changing partners, the benefits of divorce may rarely exceed the benefits of fidelity. An individual trying to change partners may be disadvantaged, simply because most other individuals are monogamous, and opportunities for re-assortment of mating partners will be limited.

Three other explanations of long term pair fidelity have been developed from bird studies Black (1996). They are not necessarily exclusive. In each case both male and female partners potentially benefit from the monogamy.

First, long-term partners may be familiar with each other and more efficient in reproductive activities, such as shared parenting in birds (Clutton-Brock, 1991). In species with no parental care, familiarity may still improve premating collaboration, allowing earlier mating and perhaps resulting in earlier births, or larger or more vigorous offspring. Second, partners may stay together because they are more compatible than other local alternatives. The compatibility may be ecological or genetical. In the latter case, pairs may be retained because the partner is the most suitable available for producing outbred offspring. Third, pair retention may reduce opportunities for infection in populations susceptible to parasites or disease (Sheldon, 1993).

7. Long-term monogamy in lizards

There are few studies of lizards that report pair bonds persisting beyond a single mating season. *Chamaeleo hoehnelii* from Kenya probably stays with the same partner in the field over successive mating cycles, but this example is based on a few anecdotal observations (Toxopeus et al., 1988). A problem is that many non-territorial lizards do not have conspicuous displays, and are secretive and hard to observe in their normal social behaviour. Also population studies of lizards rarely continue for long enough to document long-term relationships.

An exception is the study of the Australian sleepy lizard, *Tiliqua rugosa*. This non-territorial lizard forms monogamous pair bonds for six–eight weeks before mating in late spring each year. The pairs split up after mating, but then reform, usually with the same partner, in the following year. This example of long-term pair fidelity in a lizard has been investigated with extensive observations and experimental manipulations. In the remainder of this paper, some of those studies will be reviewed. It is unlikely that this is the only lizard species with long- term fidelity to a single mating partner, but no other examples have enough detail to explore possible explanations for why monogamy has evolved in lizards.

8. The sleepy lizard

The scincid lizard *Tiliqua rugosa*, sometimes called the sleepy lizard, is widely distributed across southern and central Australia (Cogger, 1992). Sleepy lizards are mainly herbivorous, although opportunistically they will feed on invertebrates, bird eggs, nestling birds and vertebrate carrion (Dubas and Bull, 1991). Body size varies across the range. Most of our study has been near Mt Mary, a semi-arid site (average annual rainfall 250 mm) in the mid-north of South Australia, where both adult male and female lizards reach an average snout vent length of 30 cm (Bull and Pamula, 1996). At the start of spring, males and females near Mt Mary weigh an average 650 and 690 g respectively (Bull, 1990). During spring some females can grow to more than 900 g. They probably live for 20–50 years, and have low annual adult mortality (Bull, 1995).

Sleepy lizards are most active in spring and early summer (September–December) in southern Australia (Bull, 1987; Firth and Belan, 1998). It is too cold for lizard activity in winter, and by midsummer, when conditions become hot and dry, there is little plant food available and sleepy lizards have greatly reduced activity. They are not territorial, but occupy overlapping home ranges, with no size difference (3–9 ha) between males and females (Bull, 1994; Bull and Freake, 1999). Each lizard uses many refuge sites within its home range. The lizards maintain the same home range area in successive spring seasons (Bull and Freake, 1999) and can orient towards their home range when displaced (Freake, 1998).

Pairing is recorded when an adult male and female are within 30 cm, but usually they are much closer together. Paired lizards can be found in a refuge together, or walking, usually with the male a few centimetres behind the female, or feeding, although usually only the female in the pair feeds (Bull and Pamula, 1998). Pairs form from early September until mid-November and lizards in pairs can make up to 40% of all random encounter captures (Bull, 1988). Mating is infrequently observed during random encounters, but all observations have been in late October or early November, and pairing finishes soon after that (Bull, 1988). After a five month gestation, litters of one–three (average 2.09) live young are born in March or early April of the following year (Bull et al., 1993b; Pamula, 1997). The young stay within their mother's home range in their first year (Bull and Baghurst, 1998), but may disperse during the three–five years they take to reach adulthood (Bull, 1987, 1995). Monogamy is the normal social system in this species both within a season and across successive seasons.

9. Sleepy lizards: observations of monogamy within a season

During random encounter surveys near Mt Mary, and in a similar survey near Kadina (also

in South Australia), lizards were found in pairs up to seven times with the same partner in a season (Bull, 1987, 1988, 1990). There were up to 57 days, between September and November, separating the first and last capture of a lizard with the same partner. Similar patterns were observed with more regular locations of individual lizards using radio tracking over five field seasons at Mt Mary. In 96 cases, females that were located an average 49 days in a season, were located an average 11 days with a single male partner, and many females were with their partner on more than 20 days (Bull et al., 1998). The average duration from the first to last observation of pairing with a single partner was 34 days for radio-tagged lizards (Bull et al., 1998), but in 23 cases the duration of pairing in a season exceeded 50 days, and it lasted 94 days in one case.

During the main pairing period, September 15–November 15, individual radio-tagged pairs were found together on an average of 36% of observation days and apart on 64% of days (Bull et al., 1998). This average value conceals considerable variability. Some females in the population were found in pairs very infrequently if at all, while 17 radio-tagged females were found with male partners on more than 75% of observation days in the pairing period. The intensity of pairing increased over time in a season, and peaked in late October and early November (Bull et al., 1998). Our single snapshot records on each day may misrepresent whether or not a lizard paired on that day. We usually avoided more observations so that natural behaviour patterns were not disturbed (Bull et al., 1993a). However we know from some direct observations, from some cases of multiple locations in a day, and from cotton spool trailing records, that pairs spend some time on most days together and some time apart. The record of pairing for a day could depend on the time the lizard was located.

Individuals from a pair sometimes became separated, but then took deliberate paths to relocate the partner, apparently using chemical signals (Bull et al., 1993a). On three occasions, when a male re-established contact with its female partner, it was observed to nudge the female flank or back leg with its nose, and to tongue flick the female's flank (Bull et al., 1993a). In naturally and experimentally separated pairs, females as well as males were active in relocating their partners (Bull et al., 1993a). A case of necrophilia illustrates the strength of the pair bond (How and Bull, 1998). A female died in October 1997 after getting tangled in fencing wire. Two days later her male partner was tongue flicking and nudging the dead female, apparently still responding to partner specific cues. A similar observation of a male sleepy lizard showing courtship behaviour towards a dead female has been reported by Sharrad et al. (1995), although the pairing history was not known in that case.

While most individuals in the studied populations were monogamous within a season, both males and females have been observed with multiple partners. In the random encounter surveys, 12% of females were observed with more than one male during a season in the population near Kadina (Bull, 1987) and 10% were encountered with multiple partners in the Mt Mary population (Bull, 1988). One Mt Mary female was encountered paired on five occasions in one year, associated with four different males. Among the radio-tracked females near Mt Mary, 40% were seen with one to three other males besides their usual partner, but they were only with other males on an average of 1.0 days per female in a season (Bull et al., 1998). It is not known whether those additional males were just chance associations or attempted extra pair matings. Only two radio-tracked females were observed to change their main male partner during a season, spending most time with one male early in the season, and with another male later in the season (Bull et al., 1998).

We have used genetic data from polymorphic microsatellite DNA loci to supplement the observations of social monogamy in the Mt Mary population (Cooper et al., 1997; Bull et al., 1998). In four of 21 litters, at least one of the young had a genotype that did not match the main male partner of the mother. In three of those litters genetic evidence suggested that the litter had been fertilised by two males (Bull et al., 1998). Thus 19% of tested females had Extra-Pair Fertilization (EPF), despite the social monogamy. These results mirror those found for apparently monogamous birds.

Some males were also found with alternative partners. In the random encounter surveys, 28.4% of males that were found in pairs more than once in a season, were with different females, although no male was found with more than two females in a year (Bull, 1988). In that survey, males were significantly more likely to have alternative partners than females. Similarly, 18% of radio-tracked males were polygynous, attending two females during a season (Bull et al., 1998). One of those males was seen with the same two females in two successive years. The pattern of polygyny was sequential, in that the male spent a sequence of days with one female then another sequence of days with the other female, and so on. The genetic analysis suggested that polygyny did not advantage males in the Mt Mary population. Three of the four females with EPF were partners of polygynous males, and one polygynous male was the father of only two of the six young produced by his two partners (Bull et al., 1998). No radio-tracked male was found with more than two females in a season.

Despite these cases of multiple partners, most individuals in each sex remained effectively monogamous over the whole season, and they were the sole parents of offspring from the pair (Bull et al., 1998). Some hypotheses to explain why these prolonged monogamous partnerships are maintained each year are discussed below.

10. Functions of sleepy lizard monogamy within a season

Monogamous pairs could improve the survival of their young by cooperative assistance of the young. Direct parental care of young lizards is very rare (Somma, 1987, 1990), and paternal care of young lizards has not been reported. Maternal care can involve attending eggs (Noble and Mason, 1933; Hasegawa, 1985; Somma and Fawcett, 1989; Vitt and Cooper, 1989), and assisting young to hatch from their eggs or to emerge from vitellogenic membranes (Cowles, 1944). Lemos-Espinal et al. (1997) report that adult females of the Mexican knob-scaled lizard, *Xenosaurus newmanorum*, apparently guard neonates in rock cracks for several weeks to months after birth.

In sleepy lizards there is little evidence that females interact at all with their young after birth, although in laboratory trials they can significantly discriminate their own young from the young of other conspecific females (Bull et al., 1994; Main and Bull, 1996). In early spring, adults and new juveniles are infrequently observed refuging together. Juveniles are usually encountered alone. Radio-tagged juveniles and their mothers were never located together in the spring following birth, and their movements were independent, although the home ranges overlapped (Bull and Baghurst, 1998). There may be indirect maternal care in that the young lizard is tolerated within a home range, but there is no indication that this maternal care is enhanced in quality because the female was monogamous in the previous mating season. Indeed the monogamous partners separated five months before the young were born (Bull, 1988; Bull et al., 1991, 1998).

Males may adopt monogamy as a form of mate guarding. Substantial evidence for monogamous mate guarding in other lizards has already been discussed, and it may have a role for sleepy lizards. Males have larger heads than females and wider jaws that they use in male–male fights (Bull and Pamula, 1996), suggesting competition among males for access to mates. Also 24 males that were recorded as being displaced as partners during a season were significantly smaller than 122 males that were retained as partners (Bull, 1990), suggesting that larger males defend females better. Freake (1998) showed displaced males oriented towards their home ranges more successfully than displaced females in the mating season, and he suggested they were attempting to return quickly to defend female partners. Furthermore, the genetic analysis showed EPF was more common where the male spent less time with its female partner, or visited other females more frequently (Bull et al., 1998). Large size, wide jaws, and frequent attendance seem to improve the defence of a female. However, to put this in perspective, fights between males were rarely observed, despite many hours of field work over many years.

Mate guarding cannot be the whole explanation for prolonged monogamy, otherwise why should males stay with females over eight weeks when the

female only becomes receptive to mating at the end of that period. One explanation, supported by the observation that pairing is less intense early in the season, could be that the male simply contacts his female partner repeatedly to make regular checks on her sexual receptivity. That still does not explain why the male should spend so much time with the female during those contacts when she is not receptive. If pairing is for mate guarding, the frequent gaps during periods of separation, suggest the defence will not be particularly effective. Also, the females are not passive partners as would be expected under mate guarding, but actively re-establish contact if separated from their male partner (Bull et al., 1993a). Furthermore, after experimental divorces, unpaired females were not always attended or mated by any males (Bull, 1994), an unexpected result if males have to guard their mates from promiscuous rivals.

A third possible function of monogamy is that females may gain advantage from the prolonged association with a male. There are three possible advantages for females. One is enhanced vigilance. In the Mt Mary population, adult mortality is very low, and predation is rarely recorded (Bull, 1995). Juveniles are eaten by brown snakes, *Pseudonaja textilis*, and hawks (Bull, 1995; Bull and Baghurst, 1998), and sub-adults by feral cats and foxes (Main, 1998), but adults are usually too large to be threatened by these predators. In the past, however, adults may have been taken by human hunters or by pythons that were once endemic to the region. More recently, adult lizards that commonly feed on roadside flowering plants, are at risk from cars. Whether or not there now exist any predators of adult lizards, their evasive behaviour when approached, and their camouflaged dorsal colouration, suggest that predators have been an important selective agent.

In monogamous pairs of birds, one member of the pair will sometimes act as a sentinel for the other (Morton and Shalter, 1977; Wickler, 1985), usually with the male more vigilant than the female (Wittenberger, 1978). In those species, male vigilance increased with increased predator density (Artiss and Martin, 1995), and female foraging activity increased with increased male vigilance (Ashcroft, 1976; Gauthier, 1987; Ridley and Hill, 1987). In sleepy lizards, females were equally often encountered foraging whether alone or in a partnership, but males were significantly less often found foraging when in a pair than when alone (Bull and Pamula, 1998). When a foraging female had a male partner, it was significantly less often found actually eating, implying that the non-feeding male had alerted the foraging female to the approaching threat, and that she became aware of the danger earlier than if she had been alone (Bull and Pamula, 1998). Thus the presence of the male can improve the chance of a female detecting danger.

A second advantage to females in having a male partner may be through dilution of parasite infestation. Around Mt Mary, two tick species attach to lizards, mainly in their refuge sites. If a pair refuges together, then the ticks in that refuge may distribute themselves about the two lizards rather than just attaching to the female. Wikelski (1999) found a tick dilution effect for marine iguanas that lived in groups. For sleepy lizards, ticks have an adverse impact on sprint speed and endurance in the laboratory, and on activity in the field (Main and Bull, 1999). Also ticks transmit the haemogregarine parasite *Hemolivia mariae* to lizards at Mt Mary (Smallridge and Bull, 1999). We do not yet know the impact of the haemogregarine on sleepy lizards, but a related malarial parasite reduces fitness of other lizards (Schall and Houle, 1992).

A third advantage to females may be reduced attention from other males. There is a short period in spring when temperatures are warm enough for activity and when plant food is abundant. In that time females must lay down energy reserves to last until next spring, and to provision growing embryos. After mating, females rarely increase weight despite embryo development (Pamula, 1997), because by summer most of the food plants have become dry. Censky (1997) suggested pairing was advantageous to female *Ameiva plei*, because defending males reduced harassment from other males and allowed more time for females to forage. The same could be happening for sleepy lizards.

Even if females are advantaged in some way by a long monogamous partnership, why should males provide that partnership, and why does the monogamous pairing end as soon as mating has been completed? Presumably females would still gain advantages from the male presence after mating. One possibility is that females only become receptive for mating after some continual priming from male attention. This suggests that the function for males of the long pairing period is to raise female receptivity to mating initiatives. In some other animal species, female receptiveness increases following sustained male courtship (Crews, 1975; McComb, 1987). This hypothesis explains the lengthy pairing period before mating, and the rapid termination of pairing after mating. Males only get a mating if they have attended a female for some weeks to prime her. It also explains why females divorced during the season attract less male attention (Bull, 1994). The priming hypothesis is not exclusive of the mate guarding hypothesis. By the end of the pairing period males may need to guard the females they have primed from rival males.

Priming would probably involve the endocrine system. Endocrine control of reproductive function has been widely studied in lizards (Crews, 1979; Licht, 1984), including sleepy lizards (Bourne and Seamark, 1975; Bourne et al., 1985, 1986; Fergusson and Bradshaw, 1991). These studies have shown that various environmental cues, such as air temperature and day length can influence gonadal growth, and that exogenously administered sex steroids can stimulate aggression, reproductive behaviour and/or the development of secondary sexual characteristics. Additionally, the social environment of lizards has been shown to have an important role in stimulating reproductive development (Crews, 1974; Summers et al., 1995, 1997), such that female lizards raised in the presence of males have more advanced ovarian growth than if raised without males. We do not yet have evidence whether this is the case in sleepy lizards.

If the hypothesis is correct, it implies females need to be primed by males, rather than use alternative cues, such as day length, to bring on reproductive activity at the appropriate time in the season. Females may gain from prolonged male presence, and the level of male attention may also indicate environmental conditions to females. In poor years it may pay these long-lived females to skip reproduction. We know some females do not reproduce each year (Egan 1984), although the proportion of non-reproducers in a population has not yet been determined. If males are less attentive in poor conditions, females may not "turn on" reproductive functions. By ignoring day length cues, their reproductive strategy becomes more flexible.

These speculative ideas suggest inter-sexual conflict. The female "holds" the male for six–eight weeks. She benefits from increased protection from predators, parasites and the attention of other males, although she may lose some genetic opportunities for her offspring that would be available through multiple mating. The male must attend the female to prime her if he is to gain a mating, and loses time and opportunity for other matings.

In summary the functions of within season monogamy in lizards are still obscure. This more detailed study of monogamous sleepy lizards suggests that the simple explanation of mate guarding is inadequate to account for all of the behaviours observed.

11. Sleepy lizards: long-term monogamy

In the sample of sleepy lizards randomly encountered in a pair in successive years, 79% of the females were with the same male partner (Bull, 1988). One pair has remained together over ten consecutive years (Bull, 1994). Some of the 21% of cases where partners had changed could have resulted from the death or dispersal of a previous partner. However individuals displaced from pairs were as likely to be recaptured in the next year in random encounter surveys as were all other individuals of the same sex (Bull, 1990). A sample of 42 males that were in a pair in one year but had been replaced as partner in the next year, were significantly smaller than the 134 males that were retained in pairs over successive years (Bull, 1990). This suggests that younger, smaller males

may take some years to establish the more permanent mating partnerships of the larger, older males (Bull, 1990).

The five year radio-tracking study showed similar patterns. In 39 (76.5%) of 51 cases where females were observed in consecutive years, they were with the same main male partner. The females that changed partners had significantly less attention from their male partner in the year before the change than did females that retained their partner (Bull et al., 1998).

Many bird studies have relied on field comparisons of divorced and faithful individuals in the population to deduce the function of long-term pair fidelity (Ainley et al., 1990; Forslund and Larsson, 1991; Williams and Rodwell, 1992; Ens et al., 1993), but factors that may influence fidelity may also influence reproduction. For instance younger birds may be more likely to separate from their partners, and at the same time have lower reproductive success, so a correlation between divorce and lower reproduction does not necessarily imply that divorce has caused reduced reproductive output. Observations of trends can produce valuable clues, but appropriate field experiments provide a fuller understanding (Ens et al., 1996). This applies equally well to investigation of the functions of long-term pair fidelity in sleepy lizards. However, we have made little progress yet in understanding why lizards consistently choose the same partner each season.

12. Functions of long-term monogamy in sleepy lizards

We can speculate that there would be relatively low cost in locating and pairing with a new partner each year, because all lizards are effectively unpaired at the beginning of the season. Indeed there may be real reproductive benefits in swapping partners because not all females reproduce every year (Egan, 1984). Egan dissected field caught females. We have not yet found a non-destructive way to measure reliably the proportion of reproductive females in a population. Captured females that fail to produce young may either be non-gravid, or may have been gravid but stressed from captivity. As a result we have not yet determined whether the level of male attention is related to the offspring production of that year, although males continue to partner females even in years when the female does not reproduce. Since males leave females five months before the young are produced, they may have no way of determining reproductive success.

Familiarity with a partner may be an advantage of long-term pair fidelity. Familiar partners may be more efficient at feeding, or at detecting predators. They also may be reproductively more efficient. Young are born in autumn, and have little time to forage for their own food before the winter, when they must rely on stored energy reserves. Early next spring, six month old young weigh little more than at birth (Bull, 1995). Mortality of juveniles in their first winter is very high (Bull, 1995). If females could mate earlier, young could be born earlier, or larger, giving them a greater opportunity to survive the winter. Matings and births in the field are rarely observed, but our limited data from captured females showed no trend for more familiar partners to mate earlier or produce larger or earlier young. We have insufficient data yet to explore whether young of familiar partners are fitter than those of unfamiliar partners.

Another explanation for long-term fidelity may be that partners are more compatible to each other genetically than they are to other potential partners living nearby. We have determined relatedness values among 60 adult lizards using four polymorphic microsatellite DNA loci. Females in this sample were significantly less related to their male partners than they were to the other males that overlapped their home ranges (Bull and Cooper, 1999). The monogamous pair should produce offspring that are more outbred than if the pairing had been at random. An implication is that lizards in the population can recognise and discriminate against related individuals. We do not know the basis for that discrimination, but it suggests a function for the mother–offspring recognition that has been reported in sleepy lizards (Bull et al., 1994; Main and Bull, 1996). In a long lived population with low dispersal of offspring (Bull and Baghurst, 1998), parents could

contact their own sexually mature offspring as potential partners. Monogamy over time may result from selecting the least related partners each year.

Another possible function of long term monogamy could be to prevent the spread of parasites and diseases. It may be advantageous for an individual lizard to remain with the same partner if it did not get infected in the previous year, and if other potential partners may be more infectious. As discussed before, our study population has ectoparasitic ticks, which vector a haemogregarine blood parasite *Hemolivia mariae* (Smallridge and Bull, 1999). Both parasites could be transmitted between contacting individuals and both potentially reduce lizard fitness. Other parasites present now, or in the evolutionary past of the lizards, may also be transmitted through close contact during pairing. Long-term pair fidelity may originally have evolved in sleepy lizards in response to such parasites.

13. Summary

In the sleepy lizard, explanations of monogamy both within a season and across successive years, are complex and unresolved. If other monogamous lizard species were studied with comparable detail, equivalent complexities would probably arise. Similarly studies of monogamy in birds have required long and intense studies, and even then only empirical trends and some suggested explanations of those trends have been resolved (Black, 1996). To advance our understanding of the properties and functions of monogamous behaviour further, some more studies are needed with experimental manipulations. It may be that those can be carried out more easily with lizards than birds or mammals. Even though monogamy has been rarely reported in lizards up until now, they could provide important insights into understanding this rather difficult topic.

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