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RESEARCH PAPER

Mate Familiarity Affects Pairing Behaviour in a Long-Term Monogamous Lizard: Evidence from Detailed Bio-Logging and a 31-Year Field Study

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Abstract

Long-term monogamy is most prevalent in birds but is also found in lizards. We combined a 31-year field study of the long-lived, monogamous Australian sleepy lizard, *Tiliqua rugosa*, with continuous behavioural observations through GPS data logging, in 1 yr, to investigate the duration of pair bonds, rates of partner change and whether either the reproductive performance hypothesis or the mate familiarity hypothesis could explain this remarkable long-term monogamy. The reproductive performance hypothesis predicts higher reproductive success in more experienced parents, whereas the mate familiarity hypothesis suggests that effects of partner familiarity select for partner retention and long-term monogamy. Rates of partner change were below 34% over a 5-yr period and most sleepy lizards formed long-term pair bonds: 31 partnerships lasted for more than 15 yr, 110 for more than 10 yr, and the recorded maximum was 27 yr (ongoing). In the year when we conducted detailed observations, familiar pairs mated significantly earlier than unfamiliar pairs. Previous pairing experience (total number of years paired with previous partners) had no significant effect. Early mating often equates to higher reproductive success, and we infer that is the case in sleepy lizards. Early mating of familiar pairs was not due to better body condition. We propose two suggestions about the proximate mechanisms that may allow familiar pair partners to mate earlier than unfamiliar partners. First, they may have improved coordination of their reproductive sexual cycles to reach receptivity earlier and thereby maximise fertilisation success. Second, they may forage more efficiently, benefiting from effective information transfer and/or cooperative predator detection. Those ideas need empirical testing in the future. Regardless of the mechanism, our observations of sleepy lizard pairing behaviour support the mate familiarity hypothesis, but not the reproductive performance hypothesis, as an explanation for its long-term monogamous mating system.

Introduction

The evolution of monogamy within a single breeding season is often explained by obligate biparental care (Mock & Fujioka 1990) or an inability to reach the polygyny threshold and access multiple females (Emlen & Oring 1977; Lukas & Clutton-Brock 2013). Other possible explanations include enforced monogamy by males through mate guarding (Brotherton & Komers 2003) and territoriality (Mathews 2002), which both ensure exclusive access to either the mating partner or her home range. Similarly, females may also enforce monogamy through aggressive behaviour towards other females (Gowaty 1996) or through preventing the male partner from attracting additional females (Eggert & Sakaluk 1995). However, these mechanisms do not adequately explain long-term monogamy or pair fidelity – the persistence of pair bonds across more than one mating season (Black 1996).

Long-term monogamy is most prevalent in birds but is also found in other taxa, including lizards (Bull 2000; Reichard & Boesch 2003). For pair fidelity to evolve, fitness associated with retaining the same partner from 1 yr to the next must be higher than in pairs that have changed partners. Three main hypotheses have been developed to explain why pair fidelity is sustained across successive mating seasons. The resource-based hypothesis suggests that resources, including mates, are limited, and switching to alternative territories or mates from 1 yr to the next is too costly (Choudhury 1995). The reproductive performance hypothesis predicts higher reproductive success in older, more experienced parents and favours retaining partnerships rather than risking new and possibly less experienced partners (Forslund & Pärt 1995). The mate familiarity hypothesis suggests higher reproductive fitness in pairs that retain the same partners because their familiarity with each other makes them more efficient and more coordinated in reproductive behaviours. In birds, familiarity can improve the performance of reproductive behaviours such as nest building and offspring provisioning and ultimately increases fitness (Black 2001; Sánchez-Macouzet et al. 2014). For example, in the bearded reedling (*Panurus biarmicus*), familiar pair partners start contributing to building the nest more synchronously, breed earlier, and their offspring have higher hatching and fledging success (Griggio & Hoi 2011). In this paper, we do not measure reproductive fitness directly, but consider some parameters of reproductive performance that we argue indirectly indicate reproductive success.

Familiarity between partners may also improve reproductive fitness through coordination of sexual reproductive cycles. Greylag goose *(Anser anser)* pairs with higher synchronisation of seasonal testosterone cycles, for example have higher reproductive success (Hirschenhauser 2012). In some species, females need to be primed to reach sexual receptiveness, for example through sustained courtship (McComb 1987; Lea et al. 2001; Wilczynski & Lynch 2011). We hypothesise that such priming behaviour might be more efficient among familiar male and female pair partners, either because partners have stronger responses to familiar courtship signals, or because familiar partners are together earlier, longer or more frequently, providing more opportunity for priming.

Monogamous mating with the same partner across multiple breeding seasons has been reported in very few lizard species (Bull 2000). Our study species, the Australian sleepy lizard, *Tiliqua rugosa*, is one of those species and shows long-term monogamy (Bull 1988, 2000) in the absence of biparental care. The sleepy lizard has been estimated to live up to 50 yr (Bull 1995) and has previously been reported to retain monogamous partnerships, in some cases, for over 20 yr (Bull 1988). Within each spring and summer season, pairs remain close to each other, normally no more than 30 cm apart, for long periods during the 6–8 wk before mating, but then, after mating in late Oct. or early Nov., they become more loosely associated (Leu et al. 2011b). Although partners interact on a similar proportion of days before and after mating, the association strength, measured as the intensity and duration of interactions, is much reduced after mating (Leu et al. 2011b). Many of those partnerships reform in early Sep., the spring time of the following year (Bull 1988), although in each new spring season, there are some new partnerships that form. When previous partnerships do not reform in a subsequent year, displaced males are generally smaller (Bull 1990) or more heavily parasitised (Bull & Burzacott 2006) than males that are retained in partnerships.

Females produce litters that average two live young about 5 mo after mating, and near the end of the summer (Bull et al. 1993). Most litters are fathered by the male social partner although extra-pair paternity (EPP) occurs in 14% of the offspring (Bull et al. 1998). Parental care is rare in lizards and normally involves protection rather than provisioning of neonates (O'Connor & Shine 2004). For example, in some *Egernia* species that are closely related to the sleepy lizard, offspring typically remain with their parents, protected from predators and climatic extremes because the adults tolerate the juveniles sharing the same refuges (Chapple 2003). However, the sleepy lizard has no overt parental care, although offspring remain within the maternal home range during their first spring, but without direct social contact (Bull & Baghurst 1998). This could be argued to represent some low-level form of indirect maternal care. Nevertheless, parturition occurs at a time when the male partner is living separately from the female, and hence, biparental care is absent. It seems unlikely that improved mate coordination during biparental care can explain long-term monogamy in the sleepy lizard.

Here, we first provide new data on rates of partner change and report updated data on the duration of pair bonds in this species. We then investigate two hypotheses (reproductive performance and mate familiarity) to explain this long-term monogamy. Although we cannot discount the resource-based hypothesis, it seems unlikely that access to alternative mates is limited because sleepy lizards live in overlapping home ranges rather than defended territories, males can regularly contact alternative female partners, and males do not aggressively defend their female partners against rival males (Murray & Bull 2004). Although lizards with social partners establish exclusive core home range areas with their partner, there are extensive intersexual overlaps of the wider home range (Kerr & Bull 2006). Furthermore, social pair partners spend on average 30 per cent of their active time together and 70 per cent apart (Leu et al. 2011b). We suggest that alternative partners are available and switching to them would not be costly.

We then studied the behaviour of 14 pairs of lizards more intensively in 1 yr. We considered they were familiar pairs if they had been together in one or more previous years, and quantified their years of previous pairing experience with any partner based on pair records from previous years. We asked whether familiar partners or lizards with greater pairing experience showed greater reproductive fitness. Measuring reproductive success in the sleepy lizard is difficult because parturition normally occurs in deep, inaccessible refuges (Bull et al. 1993), and because capturing secretive neonates that quickly leave the proximity of their mother (Bull & Baghurst 1998) is extremely difficult. Instead, we used the time of mating and the intensity of pair interaction as indirect measures of reproductive fitness.

Specifically, we tested the predictions that experienced or familiar pair partners (1) mate earlier, and (2) engage more frequently in social contact, perhaps allowing possible acceleration of the development of sexual receptiveness, than do less experienced or less familiar partners. Mating early can have direct reproductive benefits if mating and parturition date are related, because offspring born earlier have higher survival in lizards (Wapstra et al. 2010; Le Henanff et al. 2013). Our aim was to develop a clearer understanding of long-term monogamy in the sleepy lizard and, more generally, to help clarify how monogamy might evolve in taxa such as lizards that lack biparental care.

Methods

Study Area

Our study site was a 10 × 15 km area of homogeneous chenopod scrubland, dominated by blue bush, *Maireana sedifolia*, and located near Bundey Bore Station in the mid-north of South Australia (33°54′16″S, 139°20′43″E). The site has an average annual rainfall of about 250 mm.

Pair Familiarity and Pairing Experience

From 1982 to 2012, we searched for lizards for 5–10 h/d, along about 120 km of tracks in the study area, usually on 5 d each week from early Sep. to mid-December. This is the spring and early summer period when these lizards are most active (Bull 1987; Firth & Belan 1998). On each survey day, a subset of tracks was slowly driven or walked along. Randomly encountered lizards were hand captured and individually marked by toe-clipping. Because these lizards move very slowly, almost every lizard that was seen was captured. Nevertheless, our random encounter survey was incomplete, in that we did not encounter and catch all resident lizards in each year, although we know they maintain stable home ranges (Bull & Freake 1999) and we deduced many uncaptured lizards were present because we found them at a similar location in a subsequent year. Nor did we always encounter adult lizards with their partners in the pairing period, because pairs are not always together (Bull 1994, 2000).

During the random encounter study, a male and female were considered to be paired if they were found within 30 cm of each other when captured (Bull 1988). Over the 31-yr study, we made 53 021 captures of 11 960 individual sleepy lizards. Paired lizards were commonly encountered with 5162 cases of male–female pairs, or 19.5% of all captured lizards in pairs. Based on those data, for each encountered pair we determined the first and the last year that they were found together without forming any other partnerships, and derived a frequency distribution for the duration of partnerships. Because some lizards were not encountered, or were not encountered in pairs in some years, and because some partnerships probably extended into years before and after the survey, our data are likely to underestimate the real duration of many of the partnerships. Following Bull (1988), we subsampled the data set and used a 5-yr period (2007–2011) to calculate the rate of partner change among pair partners that were encountered in at least two different years. We deduced the maximum length of time between captures and determined whether pair partners were found with the same or a new partner. We did this separately for males and females.

Pairing Behaviour

In Sep. and early Oct. 2012, we located 14 already established male–female pairs, with both male and female already encountered in the surveys from previous years. We classified each of the 14 lizard pairs as 'familiar' (n = 7) if each had been caught with the same partner during the random encounter surveys, in at least 1 yr before 2012, and 'unfamiliar' (n = 7) if they had not been caught in that pair combination in any previous year. We also quantified for each lizard its previous pairing experience with other partners as the number of years in the random encounter surveys before 2012 in which it had been caught paired with other opposite sex partners (males: $\tilde{x}$ 1.5 yr; range 0–11 yr; females: $\tilde{x}$ 2.0 yr; range 0–7 yr).

We attached a GPS data logger to the dorsal surface of the tail of each lizard using surgical tape. Mean body mass measured at the end of the season (to the nearest 5 g) was 644 g among the 14 males (SE = 25.3 g; range = 500–825 g) and 689 g among the 14 females (SE = 37.8 g; range = 510–910 g). Mean body size (snout-to-vent length) also measured at the end of the season (to the nearest 5 mm) was 314 mm (SE = 3.8 mm; range = 280–330 mm) and 311 mm (SE = 4.4 mm; range = 285–340 mm) among males and females, respectively. The loggers weighed 37 g, 5.6% of the mean body mass of the 28 lizards, 7.4% of the lightest and 4.1% of the heaviest lizard. GPS loggers were synchronised to record locations simultaneously. They recorded locations of each lizard, when the lizard was moving around, every 10 min for 6 wk from mid-October until late Nov. During this period, lizards maintain pair associations, mate and then separate. Every 12 d, we relocated each lizard to download GPS data and change batteries. We did not detect any adverse effects of the GPS loggers when lizards were relocated and caught. There was no unnatural decrease in body condition or behavioural lethargy. At the end of the study, we removed the GPS loggers and released all lizards. Lizards naturally shed their skin in the following months after their release which would rid the skin of any effect that was not visually detected.

We used GPS locations to derive interaction frequencies and pairing behaviour between partners, as previously described (Leu et al. 2011a,b), inferring social contacts based on spatial proximity. As before, with comparable GPS data, we considered partners to be in direct social contact if they were within 2 m of each other, and taking into account the precision of the GPS readings ($\tilde{x}$ 6 m), we inferred that two lizards were in contact if location records were within 14 m of each other (Leu et al. 2010). This might have overestimated the real frequency of lizard social contacts, but would not have affected relative comparisons, as the same bias applied to all pairs.

We split the 42-d observation period into 6 wk. In each week and for each pair, we calculated the simple ratio association index (SRI) as the number of observations when the two lizards were in social contact divided by the number of observations when both lizards were moving around (Leu et al. 2010). The SRI is a relative measure of contact frequency and allows direct comparison among pairs with different numbers of observations. We excluded one pair from the analyses because, although they were initially found in an apparent partnership, their overall SRI was below 0.1, a threshold previously used to identify monogamous pairing in this species (Leu et al. 2010, 2011b). We chose this threshold to define a social pair bond. Although it is arbitrary, it is consistent with the definition that social interactions are more frequent among members of the same social unit than among members of different units (Struhsaker 1969). We have previously shown a clear bimodality of interaction rates among all pairwise combinations of sleepy lizards in a larger study population, which separated male–female social pairs (SRI >0.1; average SRI = 0.3 before mating) from all other interactions (Leu et al. 2010, 2011b).

Frequency of social contact between partners increases during the mating season, peaks at the time of mating and then quickly decreases as pairs split up after mating (Bull et al. 1998). We chose two parameters as measures of reproductive behaviour of each pair: time of mating was the week when SRI peaked, and pairing intensity was the SRI value in that week (Fig. 1). We used separate one-way ANCOVAs to determine whether the two parameters, time of mating and pairing intensity, were influenced by either pairing experience or pair familiarity. In other lizards, female fecundity and male competitive ability have both been reported to increase with body size (Olsson 1992, 1993; Whiting & Bateman 1999). Therefore, we included a measure of body size, the snout-to-vent length of both male and female as additional covariates in the analyses. We then, separately for males and females, determined whether lizards with familiar pair partners differed in their body condition from lizards with unfamiliar partners. Lizards were weighed at the end of the study, and we used the standardised residuals from a linear regression of mass vs. snout-to-vent length as a measure of body condition. Data followed the assumptions of the test statistic, and analyses were performed in IBM SPSS 20.

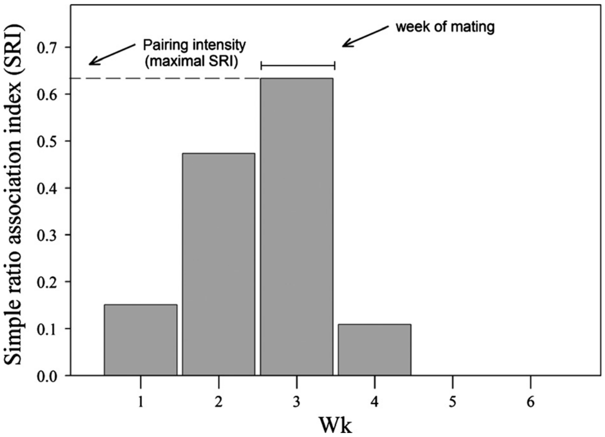

Fig. 1: Frequency of social contact (SRI) for pair 8743-1874 over 6 wk, beginning on 14 Oct. 2012. Parameters derived from these data were as follows: (1) the time of mating that was inferred to be in the week with the highest SRI and (2) the pairing intensity, the SRI value in that week.

Ethical Note

All procedures used were formally approved by the Flinders University Animal Welfare Committee (AWC reference numbers E377 and E305 for the road survey and GPS tracking study, respectively). The studies were conducted in compliance with the Australian Code of Practice for the Use of Animals for Scientific Purposes and under a South Australian Department of Environment, Water and Natural Resources Permit to Undertake Scientific Research.

The longitudinal study, starting in 1982, required permanent marking of nearly 12 000 different individual lizards, to allow continuous identification across years. We used a toe-clip numbering code, analogous to the technique used by Sinn et al. (2008). We removed the distal portion (i.e. up to the nearest joint from the toe-nail) of a maximum of two toes per foot. We could not mark this many different individuals with one toe per foot. Toe-clipping in reptiles and amphibians causes relatively low stress responses (Perry et al. 2011). Furthermore, Langkilde & Shine (2006) showed that toe-clipping did not induce a significantly higher corticosterone level in the lizard *Eulamprus heatwolei* than induced by handling lizards for measuring. In contrast, they reported that microchipping, an alternative technique for long-term marking of individuals, induced significantly higher corticosterone levels than toe-clipping. We used surgical grade scissors, which were disinfected between lizards. Toe-clipping was quick (less than one minute in total) and never resulted in more than a single drop of blood. Bleeding stopped within seconds, and lizards were only released after bleeding had stopped. We never observed subsequent infections over more than 30 yr of recapturing individual lizards. Most sleepy lizards quickly enter a calm state after being caught by hand. We marked lizards without physically restraining them in a bag or applying a sedative, anaesthetic or analgesic. Our aim was to minimise handling time, because extended handling can stress lizards more than toe-clipping (Langkilde & Shine 2006). We believe that removing lizards from their home range to observe recovery from an anaesthetic, for instance, would greatly increase their stress levels.

Results

The frequency distribution of pairing duration (Fig. 2), derived from observations over 31 yr, showed one partnership that has been retained for 27 yr (and is ongoing), 31 partnerships that have lasted for more than 15 yr and 110 that have lasted for more than 10 yr. The random nature of the survey and the incomplete monitoring of many partnerships mean that these values probably underestimate actual partnership durations. During the 5-yr period 2007–2011, 102 males and females were found in pairs in multiple years. Of these, the partner in 1 yr was the same on a subsequent year in 66.1% of 105 cases in males and 67.6% of 115 cases in females. Pair fidelity remained similar across time and did not decrease with greater time between captures (Table 1).

In 2012, body size had no effect on either of the two parameters of pairing behaviour that we considered,

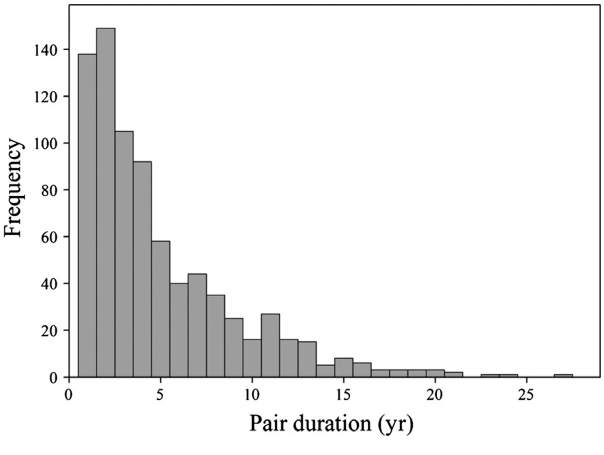

Fig. 2: Frequency distribution of the duration of pair fidelity for partnerships detected in the 31-yr random encounter survey. Duration was calculated as the difference between the earliest and latest year when a pair was encountered together.

Table 1: Pair fidelity and partnership exchange rates among lizard pairs captured in two different years

	Years between captures									
	1		2		3		4		Total	
	Same	Diff	Same	Diff	Same	Diff	Same	Diff	Same	Diff
Males	38	19	21	10	12	9	5	1	76	39
%	0.67	0.33	0.68	0.32	0.57	0.43	0.83	0.17	0.66	0.34
Females	33	15	15	14	16	3	7	2	71	34
%	0.69	0.31	0.52	0.48	0.84	0.16	0.78	0.22	0.68	0.32

Table 2: Influence of pair familiarity on timing of mating and pairing intensity. Male and female snout-to-vent length (SVL) and previous pairing experience with other partners were included as covariates in each one-way ANCOVA

Pair behaviour	$F_{1,7}$	p
Time of mating		
Pair familiarity	8.91	0.02
Male pairing experience	0.45	0.53
Female pairing experience	1.00	0.35
Male SVL	0.15	0.71
Female SVL	0.00	0.98
Pairing intensity		
Pair familiarity	0.16	0.70
Male pairing experience	4.78	0.07
Female pairing experience	0.05	0.83
Male SVL	0.53	0.49
Female SVL	0.37	0.56

either for males or for females (Table 2). Similarly, previous pairing experience of either the male or female partner did not have a significant effect on the timing of mating or the intensity of the pairing interaction (Table 2). Males that had gained more previous pairing experience tended to associate less intensely with their current female partner, although this trend was not significant (p = 0.07). However, familiarity with the partner did have a significant effect on the timing of mating, but not on the intensity of pairing. The seven familiar pairs mated significantly earlier (by a mean of 1.8 wk) than the six unfamiliar pairs included in the analyses (Table 2, Fig. 3). Lizards with familiar partners did not differ in their body condition from those with unfamiliar partners (females with familiar partners: $\bar{x} = -0.15$, SE = 0.34, N = 7 and unfamiliar partners: $\bar{x} = 0.17$ SE = 0.44, N = 6; $t_{11} = 0.59$, p = 0.57; males with familiar partners: $\bar{x} = 0.20$, SE = 0.35, N = 7 and unfamiliar partners: $\bar{x} = -0.23$, SE = 0.42, N = 6; $t_{11} = -0.81$, p = 0.44).

Discussion

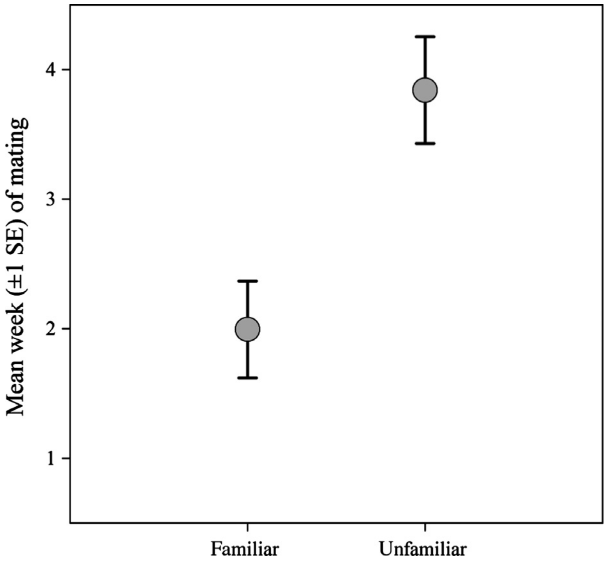

Fig. 3: $\bar{x}$ (±1 SE) week of mating of familiar (N = 7) and unfamiliar (N = 6) pair partners in 2012. Mating was assumed to occur during the week of maximal social contact. Week 1 was the week starting 14 Oct. Means are estimated marginal means from the ANCOVA model.

We recorded long-term pair bonds in the sleepy lizard that frequently exceeded 10 yr, with a detected maximum of 27 yr (this pair bond is still active). This confirms and extends our previous report on the long-term pair bond of the sleepy lizard (Bull 1988). These are remarkable pair bond durations for any vertebrate and suggest strong selection for pair fidelity. Nevertheless, not all pair bonds were retained over the years. On average, one-third of partnerships changed over the course of 5 yr. These partner exchange rates are similar to those reported from the same population 25 yr ago (Bull 1988). It suggests that partnership exchange rates are stable over time. Male sleepy lizards that were separated from their female partners were generally smaller (Bull 1990) or more heavily parasitised (Bull & Burzacott 2006) than males that were retained in partnerships, perhaps indicating that partner exchange allows females to re-pair with higher quality males. Nevertheless, many individuals form remarkable long-term pair bonds, implying that the relative benefits of long-term mate fidelity are usually higher than the benefits of partnership change.

What are the drivers of this remarkable mating system? Of three possible explanations that we considered, one, the resource-based hypothesis, particularly relating to the availability of alternative mating partner, seems unlikely. Between the other two, our study found stronger support for the mate familiarity hypothesis than for the reproductive performance hypothesis. The reproductive performance hypothesis predicts higher reproductive fitness in more experienced individuals. Neither male nor female pairing experiences significantly influenced pairing behaviour, although there was a tendency for experienced males to associate less frequently with their pair partner. Males initiate temporary separation more frequently than females, but also initiate reunions more often (Leu et al. 2011b). This is consistent with the view that monogamous mating systems often result from, or promote, intense sexual conflict (Hosken et al. 2009), but does not strongly suggest that long-term partnerships are sustained by the advantage of remaining with an experienced partner.

We suggest the mate familiarity hypothesis is the most likely explanation for long-term pairing in sleepy lizards. We found that pairs that were familiar with each other from previous seasons mated significantly earlier than unfamiliar pairs. Due to the incomplete nature of the random encounter survey, pairs that we classified as unfamiliar could have included previously undetected male and female combinations, although the likelihood of this error decreased with the duration of the pair bond. This potential source of error, the possible inclusion of familiar partners in the unfamiliar category, means that our tests were conservative.

The pattern of earlier matings of familiar pairs of lizards is consistent with findings in birds, where familiarity allows the early onset of reproductive activities, such as nest building and initiation of the clutch (Adkins-Regan & Tomaszycki 2007; Griggio & Hoi 2011; Sánchez-Macouzet et al. 2014). Ultimately, it will be necessary to link the distinct behavioural differences between familiar and unfamiliar partners in the sleepy lizard to reproductive success, to further cement the mate familiarity hypothesis. However, measuring reproductive output in the sleepy lizard is logistically very difficult, and quantifying the adaptive advantage of early mating was beyond the scope of this study. Nevertheless, other studies have shown that early mating can translate into higher reproductive success. For instance, in the socially monogamous bird, the blue-footed booby, *Sula nebouxii*, familiar pairs establish their clutch earlier and are able to produce more fledglings (Sánchez-Macouzet et al. 2014). Similarly, in the lizard *Niveoscincus ocellatus* early born offspring have higher survival rates (Wapstra et al. 2010). Hence, if there is a similar relationship in the sleepy lizard, and mating early leads to early parturition and higher survival of offspring, this could increase fitness in familiar pairs compared to non-familiar pairs. Selection that favours early mating in this way could lead to advantages for individuals that retain familiar partners over multiple years.

Two possible explanations for why familiar pairs mate earlier both assume that information transfer is more efficient among familiar than unfamiliar individuals (Swaney et al. 2001). First, we have previously suggested a female sleepy lizard only becomes receptive after prolonged male attention, priming her to reach mating readiness (Bull 2000). Now, we suggest that females may be more receptive to priming from familiar males, thereby accelerating the reproductive cycle. Second, we have previously reported that a female is alerted to and responds to an approaching threat more rapidly when a male partner is present (Bull & Pamula 1998). Lizards react to a threat by running away, and individuals within pairs may be alerted more quickly to subtle behavioural changes if they are with a familiar partner. In particular, if a female sleepy lizard is more confident in the capacity of a familiar male partner to alert her to approaching threats, she may devote more time to foraging and less time to vigilance herself.

Increased foraging efficiency may then allow earlier mating and breeding, because many lizard species are capital breeders that gather energy reserves over prolonged periods prior to the expenditure during reproduction (Bonnet et al. 1998). In contrast, income breeders simultaneously acquire and expend the required energy for reproduction (Bonnet et al. 1998). However, a recent study has shown that both capital and income energy allocation strategies may play a role in lizard reproductive physiology (Warner et al. 2008). Nevertheless, sleepy lizard females with familiar partners may be able to acquire the capital to breed more quickly if they can spend more time foraging, and less time on vigilance activities. However, if this was the case, females with familiar partners should be in better body condition than females with unfamiliar partners and this was not the case. Body condition did not differ between lizards with familiar and unfamiliar partners. Hence, early mating of familiar pairs was not due to better body condition. Neither did body condition influence whether pair partners were retained or not.

In summary, familiar pairs mated earlier than unfamiliar pairs, suggesting that the mate familiarity hypotheses are the most likely explanations for long-term monogamy in the sleepy lizard. We hypothesise that the primary mechanism driving the early mating could be an efficient social coordination between familiar partners before mating, in activities including sexual priming, or through enhanced reliability of information transfer during foraging and joint vigilance. However, these hypotheses need empirical testing and further research will help us understand these proposed mechanisms and their relative importance as well as the adaptive advantage of early mating in the sleepy lizard.

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