Why do female lizards lay their eggs in communal nests?

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Summary

1. In many reptile species, females oviposit communally (i.e. many clutches are laid within the same nest). This behaviour might result from constraint (scarcity of nest-sites offering suitable incubation conditions) or adaptation (direct fitness benefits accruing from the proximity of other eggs).

2. To test between these alternatives, we gathered field and laboratory data on montane scincid lizards *Bassiana duperreyi* from south-eastern Australia. Our data support the adaptationist hypothesis.

3. In the field, communal vs. solitary clutches were laid in similar sites, and the relative frequency of communal nesting was not predictable from nest-site availability. Thermal regimes for incubation did not differ between communal vs. solitary nests, nor between eggs at the core vs. periphery of a communal nest. In the laboratory, females selectively oviposited beside existing eggs rather than in otherwise identical potential nesting sites.

4. From cycling-temperature incubation in the laboratory, eggs incubated within a cluster of other eggs took up less water, but produced hatchlings that were larger and faster-running than were hatchlings from eggs incubated alone.

5. Hydric modifications of incubation conditions within a cluster of tightly packed eggs thus may provide a direct fitness benefit to communal oviposition.

Key-words: aggregation, *Bassiana duperreyi*, reproduction, Scincidae, sociality.

Introduction

Attempts to explain the causal mechanisms responsible for generating life-history diversity generally fall into one of two main categories: adaptation or constraint (Williams 1966; Uller 2003; Wilkinson & Gibbons 2005). The former type of explanation invokes selective advantages, and infers that the current distribution of a trait largely reflects fitness benefits. In contrast, the 'constraint' approach infers that phenotypic diversity is restricted by factors such as inflexible developmental trajectories, physical laws (e.g. allometry of surface area–volume relationships), or environmental conditions (e.g. small size due to food scarcity). Clarifying the roles of constraint vs. adaptation in the elaboration of specific traits remains a major challenge for evolutionary biology (Williams 1966; Congdon & Gibbons 1987; Arnold 1992; Leimar, Van Dooren & Hammerstein 2004).

Life-history variables have attracted particular interest in this respect, because of their tight linkage with repro-

ductive success and thus, organismal fitness (Roff 2002). That linkage facilitates empirical measurement of the fitness consequences of the trait in question (Endler 1986). In many cases, interspecific and/or intraspecific variation in life-history traits is best explained by a combination of adaptationist and constraint hypotheses. For example, the upper limit for total reproductive output of a female reptile may be set by the maternal abdominal volume available to hold the clutch (a constraint), but adaptation may regulate reproductive investment below this upper boundary because of selective forces relating to aquatic or arboreal locomotion (Vitt & Congdon 1978; Shine 1992; Pizzatto, Almeida-Santos & Shine 2007). Within the overall reproductive allocation, a trade-off between clutch size and offspring size makes it impossible to simultaneously optimize both variables; and thus, adaptation may optimize one (such as offspring size) such that variation in the other (in this case, clutch size) is driven largely by constraint (i.e. finite energy resources or maternal abdominal volume: Sinervo & Licht 1991; Brown & Shine 2007). Similarly, less-than-annual reproduction by female reptiles plausibly reflects a combination of adaptation (to delay reproduction until a large clutch can be produced) and environmental constraints (short summer seasons in

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cold climates: Bull & Shine 1979; Bonnet, Naulleau & Mauget 1992; Naulleau & Bonnet 1996).

The challenges of disentangling the roles of adaptation vs. constraint are even greater for simple behavioural variables. Functional correlates of complex morphological or physiological traits imply a fitness-driven process for their acquisition (Gans 1988; Blackburn 1992; Rose & Lauder 1996). In contrast, it is more difficult to support an adaptationist interpretation for behavioural traits that are flexible within the lifetime of a single individual. The obvious alternative is that organisms respond flexibly to local conditions – for example, to food availability or predator threat – and hence, observed patterns of diets or activity levels are driven by a mixture of adaptive (genetically coded, fitness-enhancing) factors and/or temporally or spatially variable local conditions (constraints).

In this paper, we explore the roles of adaptation and constraint with respect to a widespread but poorly understood behavioural trait: the tendency of female reptiles to aggregate for oviposition, such that a high proportion of eggs within a single population are laid within a few communal nests rather than many single ones (Graves & Duvall 1995; Bonfiglio, Balestrin & Cappellari 2004; Oda 2004; Doody 2006). The phylogenetic distribution of this trait suggests multiple evolutionary shifts both in the occurrence and the relative frequency of communal oviposition (Graves & Duvall 1995). Clearly, there are two different (but nonexclusive) potential reasons for females to oviposit communally: 'constraint' [nests providing optimal incubation (thermal, hydric, antipredator) conditions for eggs are scarce, so many females are forced to use the same site] or 'adaptation' (there is a fitness benefit to eggs laid within such large clusters, or to females that aggregate for this purpose: Blouin-Demers, Weatherhead & Row 2004; James & Henderson 2004).

We can test between these two hypotheses in several ways. For example, the 'constraint' hypothesis predicts that the frequency of communal oviposition depends upon nest-site availability; thus communal nests are expected to be more common in places and at times where potential nest-sites are scarce. In contrast, the 'adaptation' hypothesis predicts that (1) females will actively select oviposition sites containing previously laid eggs even if many empty sites are available, and (2) offspring somehow benefit from communal incubation (e.g. by metabolic heating from other eggs: Godley *et al.* 2001; Ewert & Nelson 2003; Zbinden, Margaritoulis & Arlettaz 2006). We have gathered extensive field and laboratory data on communally nesting montane lizards to test such predictions.

Methods

STUDY SPECIES AND AREA

Bassiana duperreyi (Dumeril & Bibron 1839) is a medium-sized (to 175 mm total length) scincid lizard that is widely distributed through cool-climate habitats in south-eastern Australia (Cogger 2000). In the Brindabella Range 40 km west of Canberra, in the Australian Capital Territory (148°50′ E, 35°21′ S), females of this species produce a single clutch of three to nine eggs each year during early summer (Shine, Elphick & Harlow 1997; Shine 1999; Shine & Elphick 2001). Oviposition is concentrated in sun-exposed sites, typically clearings within the eucalypt forest (Shine, Barrott & Elphick 2002). Both the developmental rates and phenotypic traits of hatchlings are influenced by incubation temperatures but are insensitive to substrate moisture content (Flatt *et al.* 2001). Eggs are laid beneath rocks and logs, facilitating the search for natural nests (Shine *et al.* 2002).

FIELD METHODS

Each year since 1994, we have searched clearings in the Brindabella Range for *Bassiana* nests, and recorded the number of eggs per nest, the depth of eggs beneath the soil surface, and the sizes of rocks and logs covering those nests. Miniature data-loggers (iButtons, Dallas Semiconductor, Dallas, TX, USA) within each nest have recorded thermal profiles of nests at Coree Flats (1050 m a.s.l.), Picadilly Circus (1240 m), and Mount Ginini (1615 m) (Shine 2002). For the present study, we also quantified thermal regimes at the top, bottom and middle section of each communal egg cluster, to explore the possibility of metabolic heating by eggs in clusters. For analysis, we classify all nests with less than 10 eggs as 'solitary' (i.e. representing a single clutch), although some of these presumably represent two small clutches. All nests with 10 or more eggs are definitely communal, because field-captured females never lay more than nine eggs.

COLLECTION AND INCUBATION OF EGGS

We collected eggs of *Bassiana duperreyi* from communal nests in the Brindabella Range (see above) in early December, when all nests were < 1 week post-laying. The eggs were packed in moist vermiculite (–200 kPa) and transported to the University of Sydney where they were weighed, marked with pencil on the shell and randomly distributed to experimental groups for incubation. Eggs were incubated in vermiculite (–200 kPa). To keep water availability constant across treatment groups, we used 7 g of vermiculite per egg for all incubations (e.g., 5 eggs × 7 = 35 g of vermiculite; 10 eggs × 7 = 70 g of vermiculite.

EXPERIMENTAL PROCEDURES TO EXAMINE EFFECTS OF COMMUNAL OVIPOSITION ON EGG HYDRIC EXCHANGE AND HATCHLING TRAITS

Eggs were obtained as described above, and randomly divided into five treatment groups (1, 5, 10, 15 or 25

eggs per group), each with at least two replicates. All treatment groups were placed in a cycling-temperature incubator with a mean temperature of 22 °C and a diel cycle ± 7·5 °C. We weighed eggs at 10-day intervals. As soon as hatchlings emerged, we measured and weighed them [snout-vent length (SVL), tail length, and body mass]. Each hatchling was then kept in an individual plastic box (22 × 13 × 7 cm) with a 12 h light : 12 h dark photoperiod. An underfloor heating element provided a thermal gradient from 20 to 35 °C within each cage for 8 h per day; ambient temperature fell to 20 °C overnight (see Shine & Harlow 1996 for details). Each box contained a shelter site and a water dish. The hatchlings were fed on live crickets three times a week. At 7 days post-hatching, we measured the young lizards' running speeds at 24 °C on a 1-m raceway containing infrared sensors to quantify elapsed times (see Shine & Harlow 1996 for details). Following these trials, the hatchlings were returned to the field for release.

EXPERIMENTAL PROCEDURES TO EXAMINE MATERNAL NEST-SITE SELECTION

To determine whether communal oviposition reflects an active preference by ovipositing females for sites already containing eggs (vs. a consequence of nest-site scarcity), we collected 26 gravid *B. duperreyi* from the Brindabella population in November, a few weeks prior to oviposition in the wild. These animals were transported to Sydney within 24 h of capture, and maintained thereafter in individual plastic bins (60 × 40 × 20 cm) containing moist sand (100 mm deep) and four potential nesting sites. Each such nesting site consisted of moist vermiculite 120 mm deep under an upside-down plastic box (12 × 12 × 2·5 cm), with a small doorway to allow ingress. We placed 25 dummy eggs (empty egg-shells from the previous year's egg incubation, cleaned and then filled with moist cotton-wool to resemble live eggs) in one of these four nesting sites (randomly selected); the others were empty. Ambient temperature was kept at 20 °C, but an underfloor heating element provided a substrate thermal gradient from 20 to 35 °C within the bin for 8 h per day. Gravid females were fed live crickets thrice weekly and water was provided *ad libitum*. Following oviposition, females were returned to the Brindabella Range and released.

Results

FIELD DATA ON FREQUENCY OF COMMUNAL NESTING

We obtained detailed data on 367 natural nests of *B. duperreyi* in the Brindabella Range over 11 years, containing a total of 5407 eggs (about 900 clutches). Of these 367 nests, at least 234 (64%) were communal (i.e. contained more than nine eggs; see Fig. 1). Mean number of eggs was 6·04 in solitary nests (range 1–9)
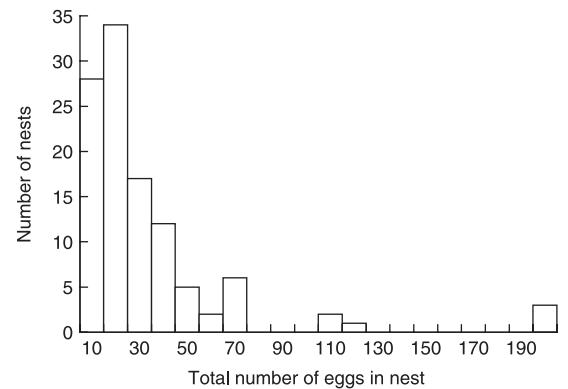

Fig. 1. Frequency distribution of numbers of eggs found in natural nests of scincid lizards *Bassiana duperreyi* in the Brindabella Range. Individual clutches never contain more than nine eggs (and rarely more than six), so that all nests with more than nine eggs must represent communal clutches.

vs. 18·06 (range 10–200) in communal nests; and thus, more than 80% of all eggs were found in communal nests.

The 'constraint' hypothesis predicts that changes in nest-site availability should generate changes in the frequency of communal nesting. Thus, we predict significant year-to-year variation if nest-site availability at a given site changes through time; and significant spatial heterogeneity if nesting areas differ in the numbers of suitable cover items. Our study sites in the Brindabella Range fulfil these conditions: some sites have many more exposed rocks than do others, and the number of such rocks has changed through time as a result of anthropogenic disturbance (e.g. vegetation clearing by hydroelectricity contractors removed > 90% of surface rocks at one site in 2001) and wildfire-induced shifts in vegetation cover and thus, degree of shading of rocks (critical for nest temperatures: Shine *et al*. 2002). Despite this variation, contingency-table tests reveal no significant spatial or temporal (annual) variation in the frequency of communal nesting [for tests across years within each of our three main sites, all $P > 0·05$; for comparisons among these sites in each of 11 years (1995–2005), all $P > 0·05$]. Detailed inspection of the data revealed no pattern for increased frequency of communal nesting following reduction in nest-site availability (e.g. decrease from 90% to 80% communal after anthropogenic rock removal at Coree Flats study area in 2001), nor for major decrease following increased nest-site availability (from 50% to 42% communal after reduction of shading due to wildfires at the Picadilly study site in 2003).

Another reason for nest-site availability to vary might be the numbers of other females laying eggs within a site, a parameter that varied over a 20-fold range across years within our study sites. However, the number of nests found within a site each year did not correlate with the proportion of those nests that were communal ($n = 28$ site × year samples, $r = 0·06$, $P = 0·75$). In summary, the proportion of nests that were communal was relatively stable despite temporal and spatial variation in factors that modify nest-site availability.

FIELD DATA ON PHYSICAL ATTRIBUTES OF NESTS

All nests were located beneath cover items (usually rocks, but sometimes logs) and we measured the dimensions of all such items. If nest-sites are scarce (as predicted by the 'constraint' hypothesis), we would expect females to utilize all opportunities and thus, larger cover items should attract more clutches (and thus, eggs). In practice, we found no significant correlation between the size of a cover item and the number of eggs beneath it [overall, $n = 284$ cover items, multiple logistic regression with single vs. communal clutch as the dependent variable, and independent variables cover-item length : likelihood ratio $\chi^2 = 1.84$, d.f. = 1, $P = 0.17$ (means 63·5 vs. 42·2 cm, respectively,); width, $\chi^2 = 1.05$, $P = 0.31$ (means 18·3 vs. 19·1 cm); depth, $\chi^2 = 0.17$, $P = 0.69$ (means 10·0 vs. 9·9 cm)]. Instead, communal clutches were fitted under even small rocks by extending deeper underground than did solitary nests (overall, comparing solitary vs. communal: mean depths below soil surface of uppermost egg, $\chi^2 = 0.96$, $P = 0.33$; of lowest egg, $\chi^2 = 26.2$, $P < 0.0001$).

FIELD DATA ON THERMAL ATTRIBUTES OF NESTS

Thermal regimes measured inside 110 natural nests were examined using mean nest temperatures as the independent variable, and 'communal vs. solitary' as the dependent variable. There was no significant difference in mean temperature between single vs. communal nests overall (20·31 vs. 20·09 °C; likelihood ratio from logistic regression $\chi^2 = 0.03$, d.f. = 1, $P = 0.87$) or separately within each of our three main sites (all $\chi^2 < 0.80$, $P > 0.39$).

Simultaneous measurements of temperatures at the top, middle and bottom of the egg cluster inside nine communal field nests were unaffected by probe placement (repeated-measures ANOVA with probe position as the factor and trimester of incubation as the repeated measure: probe position, $F_{2,12} = 0.29$, $P = 0.76$; interaction probe position vs. time, $F_{4,12} = 0.43$, $P = 0.79$). In summary, we found no consistent thermal differences among or within nests related to the number of eggs present.

EFFECTS OF COMMUNAL OVIPOSITION ON EGG HYDRIC EXCHANGE AND HATCHLING TRAITS

Eggs incubated in larger groups took up less water per egg during incubation (Fig. 2a; $F_{4,7} = 18.16$, $P < 0.001$) and thus weighed less immediately prior to hatching than did their singly incubated conspecifics (Fig. 2b; nested ANOVA, $F_{4,7} = 4.60$, $P < 0.04$). The communally incubated eggs none the less produced larger hatchlings (Fig. 2c; nested ANOVA for SVL, $F_{4,7} = 6.03$, $P < 0.02$; for mass, $F_{4,7} = 4.07$, $P < 0.05$) with significantly
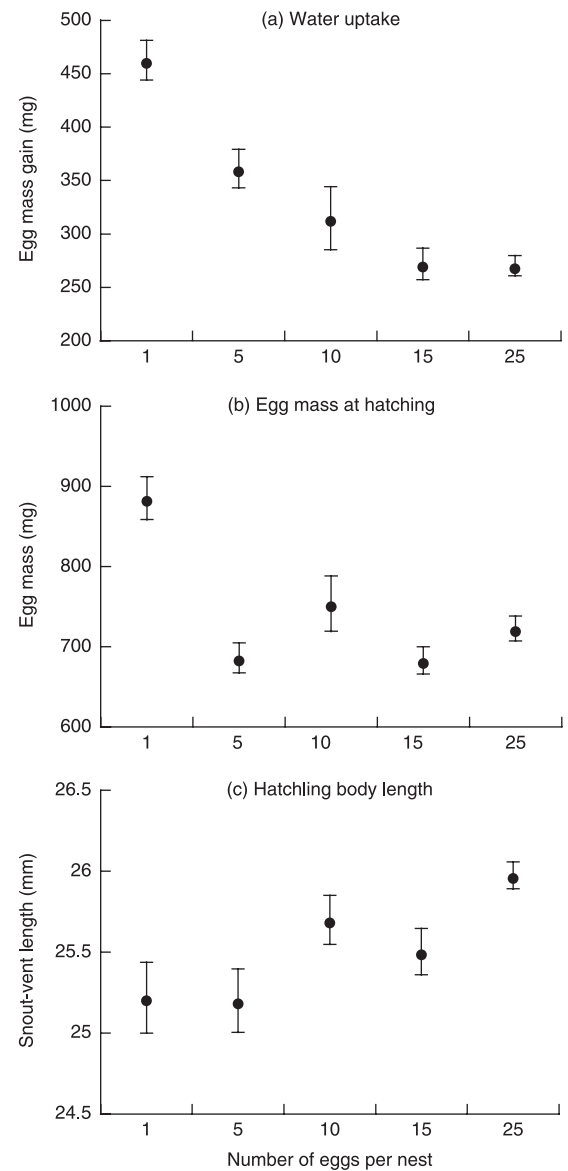

Fig. 2. Effects of communal incubation on water uptake by eggs and phenotypic traits of hatchling scincid lizards *Bassiana duperreyi*. Eggs were incubated either singly or within groups of five, 10, 15 or 25 eggs. The figure shows mean values and associated standard errors.

shorter tails relative to SVL (nested ANCOVA with SVL as covariate, $F_{4,7} = 4.26$, $P < 0.05$) that tended to run more rapidly along a 1 m raceway than did conspecifics from solitary incubation (nested ANOVA, $F_{4,7} = 4.07$, $P < 0.05$).

MATERNAL NEST-SITE SELECTION

Captive females laid 20 of 26 clutches in the nest-box containing dummy eggs, out of four nest-boxes available per cage (three of which did not contain such eggs). Thus, females oviposited beside dummy eggs far more often than would be expected based on the null hypothesis of equal probabilities of utilization of each box ($\chi^2 = 37.3$, d.f. = 1, $P < 0.0001$).

Discussion

More than 80% of eggs laid by *Bassiana duperreyi* in the Brindabella Range are deposited within communal clutches (probably more, because our criterion for recognizing communal nests was conservative). This high incidence reflects active maternal preference: in the laboratory, nesting females oviposited in sites that already contained cues from previously laid eggs. The alternative hypothesis – that communal oviposition results from a scarcity of suitable nest-sites – is not supported by our field data, because the frequency of communal oviposition was unaffected by spatial and temporal variation in nest-site availability. Our laboratory incubation studies suggest that oviposition beside an already-laid clutch may enhance maternal fitness by affecting the phenotypic traits of hatchlings, possibly mediated via effects of communal oviposition on water uptake by eggs.

Communal egg-laying occurs in a diverse array of reptile species, takes many forms, and has evolved and/ or been lost many times within reptile phylogeny (Graves & Duvall 1995). Thus, no single hypothesis is likely to explain the functional significance of such a diverse and labile trait. For example, metabolic heating by late-stage embryos may play a major role in species that produce large clutches of large eggs (e.g. some species of turtles: Ewert & Nelson 2003; Zbinden *et al.* 2006) but be trivial for the majority of squamates which (like *B. duperreyi*) produce such small eggs that metabolic heat production is insignificant. Similarly, the selective forces operating on communal oviposition may differ substantially between *B. duperreyi* (multiple clutches intermingled beneath existing cover items) compared with taxa in which many females nest within a small area, but in specially dug burrows rather than under an existing cover item, and with no direct physical contact between clutches (Graves & Duvall 1995).

Given this diversity, the relative importance of constraints vs. adaptive advantages must differ also. There are many situations in which suitable nest sites are limiting in space or time; for example, iguanas migrate long distances to areas that provide thermally optimal and predator-free nest-sites (Rand 1972; Bock, Rand & Burghardt 1985); and suitable hydric conditions may be scarce in arid or seasonally inundated habitats (Muth 1980; Brown & Shine 2004). Under such conditions, females of some squamate species delay oviposition until conditions are suitable (Andrews 1997) and hence, limited nest-site availability may enforce communal oviposition in time and space in reptiles (Blouin-Demers *et al.* 2004; Brown & Shine 2004) as well as in other types of animals (e.g. moorhens, McRae 1996).

However, simple nest-site scarcity cannot explain all cases of communal oviposition: nesting *B. duperreyi* seek out sites where eggs have been deposited previously. The same behaviour occurs in snakes [*Tropidonophis mairii* (Gray, 1841)] and may be widespread in communally ovipositing species (Brown & Shine 2005). The

selective forces for such maternal behaviour have attracted considerable speculation, involving putative fitness benefits such as easier nest excavation for mothers, predator satiation at the time of hatching, identification of suitable incubation conditions based on nest choice by more experienced conspecifics, and social facilitation of offspring development (Graves & Duvall 1995; Hayes 2000; Marco, Diaz-Paniagua & Hidalgo-Vila 2004; Branchi & Alleva 2006). Our data suggest a simpler alternative: communal incubation enhances the body size and locomotor speed of offspring that hatch from those eggs.

At first sight, the most likely reason for eggs to benefit from communal incubation would appear to be heating through the metabolic output of neighbouring eggs, because (1) some reptile eggs generate substantial heat during late embryogenesis (Godley *et al.* 2001; Ewert & Nelson 2003; Zbinden *et al.* 2006), and (2) in *B. duperreyi*, higher incubation temperatures accelerate embryonic development and produce larger faster hatchlings (Shine, Elphick & Harlow 1995). Heating due to the presence of conspecifics also has been identified as a probable force for communal nesting in frogs (Waldman 1982) and mammals (Rhind 2003). Our data militate against this explanation. First, measurements of nest temperatures failed to reveal the predicted shifts in thermal regimes (either in comparisons between communally incubated vs. solitary eggs, or between eggs in central vs. peripheral positions within the communal cluster). Although the proximity of other eggs increased mean temperature, the effect was trivial (< 0·25 °C). Also, hatching occurred at the same time in eggs from each of the incubation treatments (Radder and Shine, unpubl. data), a result inconsistent with thermal differentials (given the strong thermal dependence of incubation period: Shine *et al.* 1995).

Why, then, did communal incubation generate larger, faster hatchlings? Our data on water uptake show that close apposition to other eggs modifies hydric exchange between the egg and its environment, and thus the effects on hatchling traits might well be mediated by such hydric factors. Previous research has shown that dry incubation substrates reduce water intake by embryos, and reduce hatchling size as a result (e.g. Brown & Shine 2004; Deeming 2004). Remarkably, however, we found the opposite relationship between water uptake and offspring size: communally incubated eggs took up less water, but these smaller eggs yielded larger not smaller hatchlings. Phenotypic traits of hatchling *B. duperreyi* are relatively unaffected by hydric potential of the incubation substrate (Flatt *et al.* 2001), so the mechanisms by which proximity of other eggs influences water uptake and hatchling phenotypes warrants more detailed investigation. In the oviparous lacertid lizard *Lacerta schreiberi* (Bedriaga, 1878), eggs incubated within a cluster of other eggs take up less water than do solitarily incubated eggs, in some hydric conditions but not others (Marco *et al.* 2004). As in our

own study, the magnitude of this effect was great enough to affect hatchling phenotypes (Marco *et al.* 2004). In combination, these results suggest that communal oviposition often may affect hatchling viability, and hence impose selection on maternal nest-site preferences. The sensitivity of developmental processes to relatively minor modifications of incubation conditions thus may help to explain an otherwise puzzling phenomenon: the widespread occurrence of communal oviposition in squamate reptiles.

Acknowledgements

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Ecological Society,
Journal of Animal Ecology, **76**,
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