Clutch Size in the Tropical Scincid Lizard *Emoia sanfordi*, a Species Endemic to the Vanuatu Archipelago

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The majority of species in the scincid genus *Emoia* (Squamata: Scincidae) have a fixed clutch size of two eggs per clutch and produce between two and four clutches per year. One lineage within *Emoia*, the *Emoia samoensis* species group, consists of 13 species occurring in Melanesia and the islands of the southwestern Pacific Ocean, and exhibits variation in clutch size, with previously reported clutch sizes of two to five eggs. Little is known about reproduction in several members of this lineage including *Emoia sanfordi*, a large-bodied lizard endemic to the archipelago of Vanuatu in the South Pacific. We analyzed reproduction and clutch size in *E. sanfordi* females and discovered that there is a substantial amount of intraspecific variation, with clutch size ranging from two to seven eggs, with a modal clutch size of five eggs. Females were reproductively active throughout the study period of June through October and appear to be laying multiple clutches. The variation in clutch size seen in *E. sanfordi* is congruent with the variation previously reported within other closely related species.

Key words: *Emoia samoensis* group, eggs, lygosomine skink, Melanesian fauna, Oceania, reproductive cycle, reproduction, Scincidae, Southwest Pacific Ocean

INTRODUCTION

Reptiles are highly variable with respect to reproduction, as mode of reproduction, reproductive output, and even mechanism of sex determination vary greatly across and within lineages (Pianka and Vitt, 2003). Number of eggs per clutch, egg or offspring size, frequency of reproduction, and age at first reproduction all vary within squamates as do the life history characteristics that determine reproductive output. Some traits reflect strong phylogenetic conservatism, whereas other traits appear to be more evolutionarily labile, with many independent origins and transitions. One trait that has received considerable attention is clutch size, which is the number of eggs or live offspring produced by a female at a given time.

Some squamate lineages have a fixed clutch size, with all females producing the same number of eggs for every clutch. For example, all anoline lizards (>350 species) have a fixed clutch size of a single egg (Pough et al., 2004; Smith et al., 1972; Zug et al., 2001). In contrast, other squamate lineages exhibit a large degree of variation in reproductive traits. Within the family Scincidae (>1,360 species) there is

considerable variation in both reproductive mode and clutch size, with the evolutionary transition from oviparity (egg-laying) to viviparity (live-bearing) evolving independently more than 100 times (Shine, 1985; Smith et al., 2001).

Clutch size affects a suite of traits associated with offspring fitness, and it is therefore expected that clutch size would be evolutionary labile in order to balance various selective forces that optimize parent and offspring fitness. It has been suggested that female lizards delay reproduction until they have stored enough energy to produce the largest clutch their body cavity can accommodate (Vitt and Congdon, 1978) and that there is some optimal relationship between body cavity size and clutch size (Qualls and Shine, 1995). Multiple factors have been suggested to influence clutch size, including adult body size. Larger lizards have a larger body cavity, and thus have the potential to hold more eggs, and species that have greater variation in adult body size might be expected to have greater variation in clutch size (Fitch, 1970).

The lizard genus *Emoia* is a diverse skink lineage with more than 70 currently recognized species distributed in the South Pacific and Southeast Asia (Brown, 1991). This ecologically diverse genus has been subdivided into eight species groups that represent putative evolutionary lineages (Brown, 1991). Limited data on clutch size and mode of reproduction have been reported in 51 species; all examined species are oviparous, and seven of the eight lineages have

a fixed clutch size of two eggs (Brown, 1991; Cree, 1994; Greer, 1968). The remaining lineage within *Emoia*, the *samoensis* species group, exhibits variation in clutch size.

The variation in clutch size within the *E. samoensis* group is unique within this species-rich and ecologically diverse genus (Brown, 1991; Cree, 1994; Greer, 1968). The *samoensis* species group includes 13 species that are all relatively large in size (SVL 45–122 mm; only a single species has a SVL less than 52 mm at maturity) and occur throughout the islands of Melanesia and the southwestern Pacific Ocean, with the highest diversity in the island groups of Vanuatu, Fiji, Tonga, and Samoa (Brown, 1991; Zug and Ineich, 1995). Previously recorded clutch sizes within this lineage range from two to five (Table 1) (Baker, 1947; Brown, 1991; McCoy, 2006). Greer (1968) observed a relationship between body size (snout-vent length) and clutch size in female *Emoia nigra*, a member of the *E. samoensis* species group. It is unknown, however, if this relationship exists in other species in this species group. Given the limited number of specimens examined, clutch size may be more variable within this lineage than presently estimated

Table 1. Available data on clutch size for the species within the *Emoia samoensis* group lineage. Data are from lizards examined as part of this study and previously published work (Brown, 1991; Schwaner, 1980). Clutch size data represent the minimum and maximum values reported for female specimens with eggs. Sample sizes indicate the number of female specimens examined for body size. The snout-vent length (SVL) data are presented as the range in body size of female specimens examined. If we could not find published data for clutch size, we report this as no data.

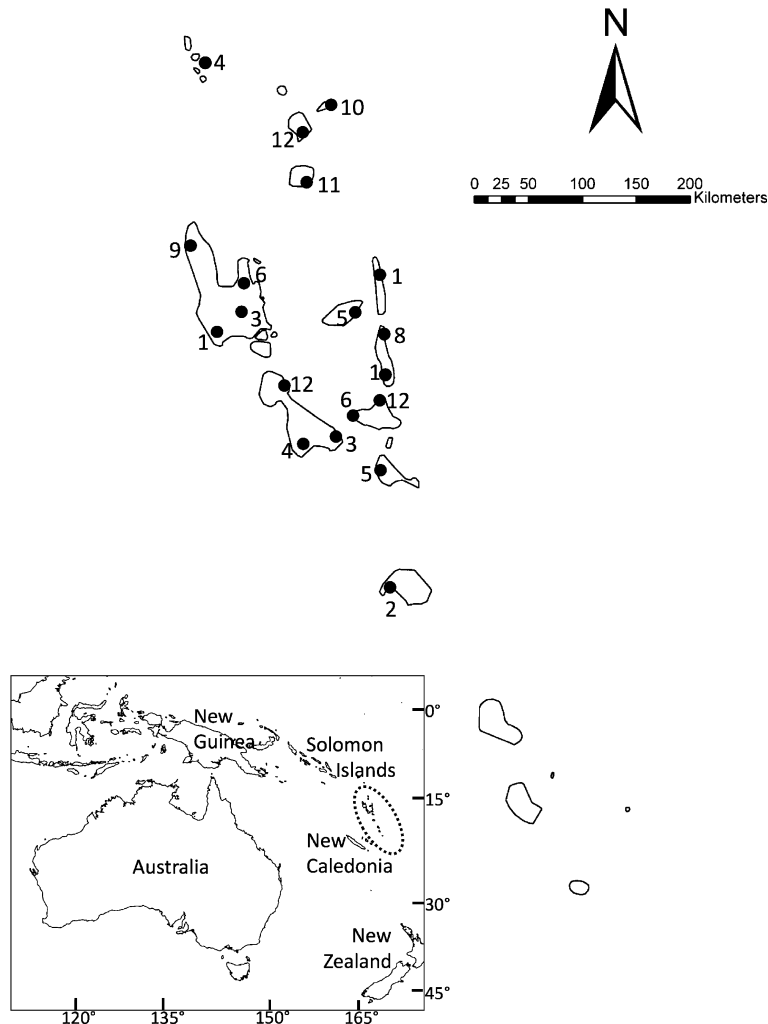| Species	Clutch size	Female SVL (mm)
Emoia aneityumensis	4 to 5	71.0–88.0 ($n=2$)
Emoia campbelli	No data	68.9–92.7 ($n=5$)
Emoia concolor	2	52.8–73.5 ($n=7$)
Emoia erronan	No data	73.7 ($n=1$)
Emoia flavigularis	No data	58.9–75.5 ($n=10$)
Emoia loyaltiensis	No data	60.0–73.0 ($n=2$)
Emoia nigra	2 to 4	85 −114 ($n>100$)
Emoia nigromarginata	2 to 3	59.8–73.4 ($n=12$)
Emoia parkeri	2	45.5–53.8 ($n=10$)
Emoia samoensis	4 to 7	84 −114 ($n=65$)
Emoia sanfordi	3 to 7	68.3–114 ($n=115$)
Emoia tongana	2	52.2–67.0 ($n=10$)
Emoia trossula	2 to 5	67.9–107.8 ($n=15$)

Fig. 1. Vanuatu Archipelago, with sampling localities indicated with black circles. The number next to each circle is the number of females examined from that locality. *Emoia sanfordi* does not occur on the five southernmost islands (Erromango, Tanna, Aneityum, Aniwa, and Futuna). Sampling for this study encompasses the geographic distribution of this species, which is endemic to the Vanuatu Archipelago.

(Brown, 1991; Greer, 1968). Examination of additional specimens and species will increase understanding of the variation in clutch size that occurs in this lineage and the evolution of clutch size in *Emoia*.

One of the 13 *E. samoensis*-group species, *E. sanfordi* is a large, arboreal skink endemic to the central and northern islands of the Vanuatu Archipelago (Brown, 1991), a group of oceanic islands in the southwest Pacific Ocean (Fig. 1). Little is known about reproduction in this species, including basic life history data such as size at sexual maturity and seasonality of reproductive cycles. Based on examination of 17 specimens, clutch sizes of three and four eggs have been reported (Brown, 1991), but due to low sample numbers there may be more variation in clutch size within this species than previously identified.

In this study we present preliminary data on reproduction and clutch size in *E. sanfordi* in the Vanuatu archipelago. The natural history of this endemic lizard has been largely unexplored, and these data provide a broader foundation for understanding the reproductive biology of *E. sanfordi*, and the genus *Emoia* in general, and provide insight into the evolution of variation in clutch size.

MATERIALS AND METHODS

Emoia sanfordi were collected during four field seasons from June to October 2001, 2002, 2004, and 2005. We collected and preserved 115 females by hand and other methods (Hamilton et al., 2007) from 19 sampling localities on 12 islands that spanned the entirety of the species range (Fig. 1). In the laboratory we recorded snout-vent length (SVL), reproductive condition, and clutch size. We defined reproductively active females as a range of conditions from individuals exhibiting early follicular development up to females with shelled eggs. All specimens are deposited in the Louisiana State University Museum of Natural Science (Appendix 1).

In order to determine the relationship between female body size (SVL) and clutch size, a regression was performed with SVL as the independent variable and clutch size as the dependent variable. To evaluate the influence of timing of deposition on clutch size, we used an ANOVA in which month captured was the independent variable and clutch size the dependent variable. We evaluated the roles of island area and latitude on clutch size using regressions; latitude and island area were each used as an independent variable in an analysis in which mean clutch size was the dependent variable. Data were examined for normality prior to analysis, and all statistical analyses were conducted with SYSTAT 10.2.01 (Systat Software, Point Richmond, CA). The significance level was set at 0.05 for all tests.

RESULTS

Of the 115 females examined, 55 were reproductively active (as defined by presence of follicular development). Of these individuals, 40 had shelled or yolking eggs. The smallest female with follicular development had a SVL of 90.3 mm, whereas the smallest female with developed eggs was 89.5 mm SVL. There was a high degree of variation in clutch size, with clutch size ranging from two to seven eggs. The mean clutch size for the 40 females with eggs in our sample was 5.00 eggs and modal clutch size was 5 eggs. Clutch sizes of 3–6 eggs were common; clutch sizes of 2 eggs and 7 eggs were each observed in single individuals.

There was no obvious relationship between egg placement within the oviduct and the number of eggs in the oviduct. Individuals with an even number of eggs had the same number of eggs in each oviduct, and for those females with an odd number of eggs neither the left nor the right oviduct was observed to have a higher probability of having the greater number of eggs.

There was a significant, positive relationship between clutch size and female body size (Fig. 2; y=0.115x–6.58). Female body size is a relatively good predictor of clutch size, explaining 46.4% of the variation in egg number (F=31.175; $p<0.01$; $r^2=0.464$). Clutch size also varied over time, as the relationship between month and clutch size approached statistical significance ($p=0.059$).

Mean clutch size was not explained by island size ($p=0.307$; $r^2=0.104$). Latitude was positively correlated with mean clutch size ($p=0.0019$; $r^2=0.637$). Mean clutch size increased with distance from the equator (Fig. 3).
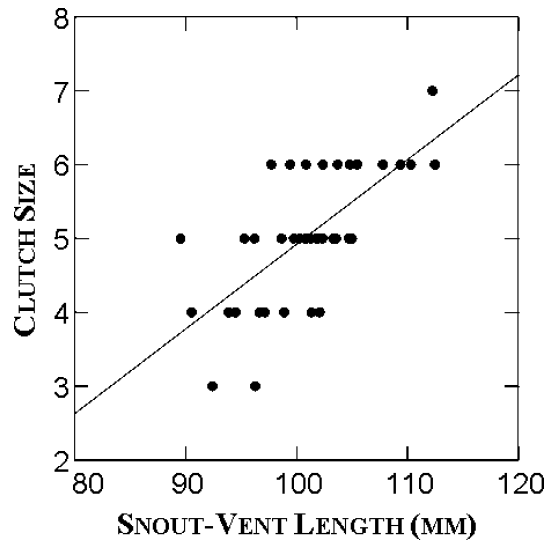

Fig. 2. Relationship between female body size (SVL in mm) and the number of eggs per clutch (clutch size) in *Emoia sanfordi*. There is a positive correlation (slope=0.115) between clutch size and snout-vent length ($p<0.01$, $r^2=0.464$).
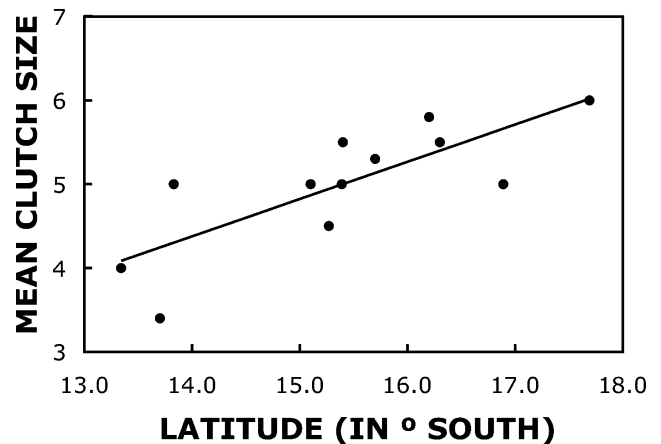

Fig. 3. Positive relationship between mean clutch size and latitude ($p=0.0019$; $r^2=0.637$).

Table 2. Reproductive data for female *Emoia sanfordi*. Early follicular females ("EF") are described as those in the early stages of follicular development, while gravid females ("Gravid") are those with shelled or yolking eggs. Reproductively active females ("RAF") include all females that were either in early follicular development or gravid. The percent of females that were reproductively active ("% RAF"), the percent of females that were gravid ("% Gravid"), and the percent of females in the early stages of follicular development ("% EF") are shown in relation to both the total number of females examined each month ("Total F"), as well as the number of females that were found to be reproductively active each month ("RAF").

Month	Total F	RAF	% RAF	% RAF EF	% EF	% RAF Gravid	% All F Gravid
June	9	5	55.56	0.00	0.00	100.00	55.55
July	26	10	38.46	50.00	19.20	50.00	19.20
August	40	20	50.00	30.00	15.00	70.00	35.00
September	6	2	33.33	0.00	0.00	100.00	33.00
October	34	18	52.94	22.22	11.76	77.78	41.18

DISCUSSION

There appears to be some seasonal influence on *E. sanfordi* reproduction, indicated by the alternating frequency of females gravid with eggs and females with early follicular development (Table 2). Our data suggest that females produce more than one clutch during June to October. However, the total number of clutches each female can produce per season and per year is still unknown because of the limited collections of *Emoia sanfordi* and a lack of data during the wet season (November to May). Limited data are available for other species of *Emoia*: *E. atrocostata* and *E. cyanura* (fixed clutch size of two eggs) produce at least two clutches each year and, on average, 4 and 3.9 eggs per female per year, respectively (Alcala and Brown, 1967; Cree, 1994). *Emoia nigra* (variable clutch size 2–4 eggs) is the closest relative of *E. sanfordi* for which data on average annual reproductive output are available. Production of two or more clutches and an average of 4.6 eggs per female per year, was reported for *E. nigra* (Schwaner, 1980). To evaluate the seasonality of reproduction in *E. sanfordi* and the annual reproductive output additional data are needed from November to May.

We excluded the single individual with two eggs in the left oviduct and none in the right oviduct from statistical analyses because the majority of lizard lineages, with the exception of anoline lizards, ovulate one or more eggs simultaneously from each oviduct (Jones et al., 1979). There are four possibilities for the absence of eggs in this oviduct: the oviduct might be non-functional, the egg(s) may not have been fertilized, the egg(s) may have been aborted, or the female may have deposited part of her clutch and retained some eggs. As the oviduct appeared functional, and the eggs in the oviduct were very large, partial deposition is the most likely cause as lizards lay eggs from one oviduct at a time. In any case, the lack of eggs in the right oviduct suggests this individual represents an anomaly.

Variable clutch size is the ancestral condition for reptiles (Kratochvil and Kubicka, 2007); variable clutch sizes occur in crocodiles, tuataras, most species of turtle, and the majority of squamate reptiles. Assuming that variable clutch size is also the ancestral condition for lizards, a fixed clutch size has evolved independently more than 20 times in lizards (Shine and Greer, 1991). Some families of squamate reptiles, such as Scincidae, contain species with the ancestral condition of variable clutch size and species that have evolved a fixed clutch size.

The number of eggs increases with female body size in *E. sanfordi*, as in the closely related *E. nigra* (Greer, 1968). These data suggest that clutch size in *Emoia* is positively correlated with female size, at least for the members of the *Emoia samoensis* species group. Lizard species with a larger mean female body size produce larger clutch sizes (Seigel and Ford, 1987). The species within this evolutionary lineage are among the largest species of *Emoia* (Brown, 1991), and this is the only lineage that has variation in clutch size. Perhaps the smaller body size of many species within the other lineages in this genus has selected for a smaller, two-egg clutch.

Clutch size of squamates varies between congeners in tropical regions vs. temperate zones (Huang, 2006a; James and Shine, 1988; Shine and Greer, 1991), as well as island vs. mainland species (Huang, 2007; Ji and Wang, 2005). Environmental (temperature and other climatic variables associated with latitude) and ecological (resource availability, predator density) hypotheses have been suggested to explain general trends seen in clutch sizes. Comparison of clutch size of *Emoia sanfordi* from mainland and insular populations was not possible, as this species is endemic to the islands of Vanuatu, but we did examine the relationship between island size and mean clutch size. In contrast to the findings of Knapp et al. (2006) that *Cyclura cychlura* females from a larger island produced significantly larger and heavier clutches than conspecific females from a smaller island, there was no relationship between island size and clutch size in *E. sanfordi*.

Clutch size in *E. sanfordi* was correlated with latitude (Fig. 3). A positive relationship between clutch size and latitude has also been reported for the lacertid lizard *Takydromas* and within the agamid lizard genus *Japalura* (Huang, 2006a; Huang, 2007), but variation in clutch size was not correlated with latitude in the scincid lizard genus *Mabuya* (Huang, 2006b). What is driving the significant relationship between clutch size and latitude in *E. sanfordi* is unclear. Ecological factors have been suggested to influence clutch size and to explain the latitudinal clutch size gradient, especially in birds. Increased predator densities have been shown to reduce clutch sizes in birds (Kleindorfer, 2007), and food and resource availability has been shown repeatedly to positively influence clutch size for squamates (Ballinger, 1977; Seigel and Fitch, 1985; Seigel and Ford, 1991; Seigel and Ford, 2001). It has also been suggested that the relationship between clutch size and latitude is driven by climatic factors such as amount of rainfall, seasonality in rainfall, or temper-

ature (Lepage and Lloyd, 2004).

Despite the positive relationship between female body size and clutch size observed in *E. nigra* and now *E. sanfordi*, variation in clutch size within the *Emoia samoensis* group may be driven by factors other than the overall larger body size of this species group. Clutch size (and mass) was found to be smaller in many actively foraging lizard species, perhaps to reduce predation risk (Huey and Pianka, 1981; Vitt and Congdon, 1978). Many members of the other evolutionary lineages within *Emoia* are active foragers, either in the forest floor leaf litter, along thin branches and vines, or on beach or intertidal areas, whereas many species within the *Emoia samoensis* group appear to utilize a foraging strategy that more closely approximates that of a sit-and-wait predator. These different foraging modes, and associated different levels of predation risk, may also be responsible for the maintenance of a variable, and larger, clutch size, a trait suggested to be ancestral for lizards (Kratochvil and Kubicka, 2007). Other life history traits have been shown to influence clutch size in lizards. Fossorial lizards have small clutch sizes with relatively large individual offspring (Ashton, 2005; Dunham et al., 1988), whereas arboreal lizards tend to have larger clutches (Dunham et al., 1988). The *Emoia samoensis* group contains lizards that are predominantly arboreal, and this species group as a whole has a greater propensity to arboreality than other lineages within *Emoia*. The least arboreal member of the *E. samoensis* species group is *E. nigra*. Despite being one of the largest species in the *E. samoensis* group (SVL 85–114 mm), *E. nigra* has a relatively small clutch size (2–4 eggs). The other two *E. samoensis* species group members that are as large as *E. nigra* are capable of producing much larger clutches: *E. sanfordi* (68–114 mm) produces clutches of 3–7 eggs, and *E. samoensis* (84–114 mm) produces clutches of 4–7 eggs (Table 1).

The difference in clutch size among evolutionary lineages within *Emoia* is not necessarily the result of a single selective force. Reduction in clutch size to a fixed clutch of one or two eggs in all gekkonid lizards has been suggested to result from selection for larger offspring (Kratochvil and Kubicka, 2007), as a decrease in clutch size leads to an increase in offspring size (Sinervo and Licht, 1991), whereas this same trend of decreasing clutch size in all species of *Anolis* results from selective pressure to reduce the burden placed on females by larger clutches (Kratochvil and Kubicka, 2007). Multiple selective pressures including foraging mode, habitat associations, and female body size may be responsible for the reduction in clutch size seen in most lineages of *Emoia*.

ACKNOWLEDGMENTS

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Appendix 1. *Emoia sanfordi* specimens examined from the Vanuatu Archipelago. Specimens are housed in the Louisiana State University Museum of Natural Science in the Collection of Reptiles and Amphibians.

Ambae Island: LSUMZ 90193, 90199, 90200, 90204, 90207
Ambrym Island: LSUMZ 90155, 90156, 90160, 90162–90164, 90167, 90169–90174, 90176–90178, 90181, 90183
Efate Island: LSUMZ 89879, 89885
Epi Island: LSUMZ 89889, 89891, 89892, 89894, 89895
Gaua Island: LSUMZ 89936–89938, 89940–89946, 89948
Maewo Island: LSUMZ 90210
Malakula Island: LSUMZ 90116–90118, 90121, 90122, 90124, 90129–90132, 90134, 90138, 90140–90143, 90146, 90148, 90149
Mota Lava Island: LSUMZ 89899, 89904–89906, 89908, 89911–89913, 89915, 89916
Pentecost Island: LSUMZ 90211, 90215, 90216, 90218, 90220, 90226, 90229, 90231, 90233
Espiritu Santo Island: LSUMZ 90884–87, 90889–92, 90898–99, 90902, 90905, 90908–09, 90911, 90913–14, 90917
Loh Island: LSUMZ 90917, 90921, 90924–25
Vanua Lava Island: LSUMZ 89918, 89920–89921, 89924–89926, 89928, 89929, 89932, 89933, 89935