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EFFECTS OF CROWDING ON REPRODUCTIVE TRAITS OF WESTERN FENCE LIZARDS, *SCELOPORUS OCCIDENTALIS*

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***Abstract.*—Research on the natural history of lizards often involves attempting to identify sources of variation in life-history traits among different populations. Studying lizards under controlled laboratory conditions is a useful method for evaluating the relative effects of phenotypic plasticity and underlying genetic constraints on variable reproductive parameters. Therefore, there is a need to determine the best techniques for maintaining various species under laboratory conditions to avoid biasing data as much as possible. The purpose of our study was to determine if housing female Western Fence Lizards, *Sceloporus occidentalis*, in different sized breeding groups increased variability in reproductive parameters. We randomly assigned each of 96 healthy females to a control or one of three different sized groups, i.e. one female per cage (control), two females per cage, four females per cage, and eight females per cage. One male was randomly assigned to each cage. There were no statistical differences between the controls and females in the two-female groups for any parameter measured. Housing females in four- and eight-female groups decreased the mean number of clutches laid by females and decreased reproductive effort in terms of relative clutch mass (clutch mass divided by maternal body mass). Housing four or eight females together also increased the number of days before the first clutch was laid and increased the percentage of infertile eggs per clutch.**

Key Words.—crowding; phenotypic plasticity; reproductive variation; reptile

INTRODUCTION

Research on the natural history of lizards often involves comparing different populations and attempting to identify sources of variation in life-history variables among populations (Tinkle and Ballinger 1972; Niewiarowski 1994; Du et al. 2005). However, it is sometimes difficult to determine if observed differences are due primarily to phenotypic plasticity as a result of local conditions or due to underlying adaptive genetic differences (Ballinger 1983; Du et al. 2005). A useful research method for evaluating the sources of variation in life-history traits, particularly growth rates and reproductive parameters, is to raise offspring from different populations under similar conditions. This can be accomplished by reciprocal transplant studies in the field (Niewiarowski and Roosenburg 1993; Iraeta et al. 2008) and by conducting growth and reproduction studies for multiple populations under identical controlled laboratory conditions, i.e. common garden experiments (Ferguson and Talent 1993). Both techniques have advantages and disadvantages, depending on research goals. For example, an advantage of using reciprocal transplants for identifying sources of variation in life-history traits is that populations can be compared under natural conditions. A disadvantage of this method is that determining how a specific variable affects the lizards may be difficult. Conversely, an advantage of studying multiple populations under identical laboratory conditions is that specific environmental variables are more easily controlled and manipulated. However, interpreting the data relative to natural conditions may be difficult. Nevertheless, controlled laboratory experiments may help in determining the relative contributions of intrinsic and environmental factors to the variation of specific life-history traits.

The major obstacle to obtaining reliable reproductive data from laboratory breeding experiments is that the laboratory environment must be appropriate for the species so that lizards breed successfully. Due to limited space at most animal care facilities, information is needed on whether or not housing multiple females together is a proximate cause of variation in reproductive traits. Lizards of the genus *Sceloporus* occur throughout most of the United States and Mexico and are commonly used as model systems for evolutionary and ecological questions (Tinkle and Ballinger 1972; Ferguson et al. 1980; Smith et al. 2003; Villagran-Santa Cruz et al. 2009; Ramirez-Bautista et al. 2011). However, little is known about the effects of crowding on the reproductive traits of any species of *Sceloporus* under laboratory conditions (Talent et al. 2002). Therefore, the purpose of our study was to determine if housing different numbers of female Western Fence Lizards, *S. occidentalis*, in groups is a cause of variability in reproductive traits observed under controlled laboratory conditions.

FIGURE 1. Captive-reared adult male Western Fence Lizards, *Sceloporus occidentalis*, that originated from lizards captured in Fresno and Tulare counties, California, USA. (Photographed by Sean Ball)

METHODS

Rearing research animals.—We collected Western Fence Lizards (Fig. 1) from Tulare and Fresno Counties in the San Joaquin Valley of California, USA. Lizards at collection sites were almost entirely terrestrial. We used captured lizards to establish a laboratory colony of captive reared lizards. We incubated eggs obtained from the captive reared lizards at 32° C on moist vermiculite (1:1 ratio of vermiculite to water by weight).

We housed groups of 10–15 hatchlings in 74.2 L glass aquaria covered with a 3-mm steel mesh lid. A 30.0 (L) × 14.0 (W) × 3.8 (H) cm wooden board was placed flat on the bottom of the aquarium. The wooden board was large enough for all lizards to climb onto and bask simultaneously. A 3-cm layer of corncob substrate (particle size was approximately 3 mm in diameter) filled the remainder of the cage. No other cage furnishings were provided for retreat sites. However, most lizards burrowed into and slept under the substrate at night and occasionally hid under the substrate during the day. No visual barriers were present inside cages but we placed a cardboard barrier between all cages to prevent visual contact between lizards in adjacent cages. We provided heat and light by a 60-W incandescent light bulb that was positioned over one end of each cage to permit basking across a temperature gradient of approximately 26–40° C. We maintained ambient room temperature at approximately 22° C and a 14:10 h light:dark photoperiod was provided. We provided lizards with a water source and fed them *ad libitum* with House Crickets, *Acheta domesticus*, which had been fed with food consisting of a mixture of ground poultry laying pellets (see Rich and Talent 2008 for major ingredients) and vitamins. We placed a dish of Rep-Cal (Rep-Cal Research Labs, Los Gatos, California, USA) that contained calcium and vitamin D on the wooden board in all cages and both crickets and lizards occasionally consumed the Rep-Cal. In addition, we also gave lizards approximately 100 and 10 IUs of vitamins A and D, respectively, by oral gavage each month. Lizards were also periodically exposed to ultraviolet light to allow them to synthesize additional vitamin D.

We housed hatchlings in heterosexual groups for the first two months. At the end of the second month, we determined sex of lizards morphologically (males have enlarged post-anal scales whereas females do not) and we separated them into groups of 10–15 per cage with lizards of the same sex. We raised lizards for an additional three months, and then moved them into a temperature controlled room that was maintained at 10° C ambient temperature for four months of conditioning/brumation. We maintained lizards in the same type of cage in which they were reared. During the first month of the conditioning process, we placed a 40-

W incandescent light bulb above each cage for basking and we maintained lizards on a 12:12 h light:dark cycle each day. In addition, we provided lizards with food and water *ad libitum*. During the second month, we only turned on lights for 12 h once a week and we did not feed lizards, although water was always provided. During the third and fourth months, we maintained lizards in total darkness at 10 °C.

Breeding lizards.—After brumation, when lizards were nine months old, we removed both males and females from the controlled temperature room and allowed them to warm up to 22° C over a 24-h period. We weighed and measured 96 healthy females and randomly assigned them to four groups, which resulted in 24 females in each group. We placed the first group of females, one female per cage, into 24 cages. This group served as the control group for evaluating the effects of female group size on reproductive traits. For the second group, we placed two females per cage into 12 cages. We placed four females per cage into six cages for a third group, and eight females per cage into three cages for a fourth group. We randomly assigned one male to each of the 45 cages. Breeding lizards were housed on corncob substrate in 74.2 L glass aquaria with a visual barrier between cages under the same conditions as described for housing hatchlings.

To avoid bias due to cage position on three-shelf cage racks, we used a blocked design for cage placement. We placed the appropriate number of cages for housing one third of the females for the control and each of the three breeding groups on each of the three shelves of the cage racks. Furthermore, to limit stress to lizards, we maintained cages at the same position on a shelf throughout the study.

When gravid females appeared to be ready to lay their eggs as judged by their behavior of digging, we placed them in plastic laying chambers that contained approximately 8 cm of slightly moist sand. We collected eggs within 12 h following oviposition. For each female, we recorded the breeding group to which she belonged, her identification number, the oviposition date, and her mass and snout-vent length (SVL). The female was then placed back into her cage. We counted and weighed eggs of each clutch, and we determined egg fertility by visual examination and candling, which revealed a blastodisc in fertile eggs. Infertile eggs and possibly eggs with early embryonic death appeared collapsed, without fully formed eggshells, similar to infertile eggs described for other lizards (Olsson and Shine 1997; Uller and Olsson 2005). Hereafter, we refer to these eggs as infertile eggs. After a female laid a clutch of eggs, we calculated her reproductive effort by two methods. We calculated the relative clutch mass, which is defined as clutch mass divided by maternal body mass (Shine 1980). We used post-oviposition maternal mass and clutch mass for calculating relative clutch mass. We also calculated the relative egg number, which we define as the number of eggs in a clutch divided by maternal SVL. The breeding experiment continued until all females ceased laying eggs.

Statistical analyses.—Prior to statistical analyses, we tested the following data for normality and homogeneity of variance: the number of days females took to lay their first clutch, the length of time between the laying of subsequent clutches, post-oviposition body mass, post-oviposition SVL, clutch size, number of clutches laid, egg mass, the proportion of eggs that were fertile, relative clutch mass, and relative egg number. If the data passed both tests, we used analysis of variance (ANOVA) for data analyses followed by a Holm-Sidak post-hoc multiple comparisons test that compared the data of controls and different sized female groups. If data were not normal or were of unequal variance, they were analyzed with a Kruskal-Wallis nonparametric analysis of variance on the ranks followed by a Dunn's post-hoc test that compared the data of controls and different sized female groups. In addition, we used Chi-Square analyses to evaluate the effects of female group size on the proportion of females that laid eggs. All values in the text are expressed as mean ± standard error of the mean (SEM). A level of $P < 0.05$ was considered to be statistically significant. We conducted tests using SigmaStat® Version 3.1 (Systat, San Jose, California, USA).

RESULTS

The size distribution of female Western Fence Lizards in the different treatment groups was similar. There was no significant difference in mass ($H = 3.61$, df = 3, $P = 0.306$) or SVL ($H = 2.82$, df = 3, $P = 0.421$) among females in the different groups. In addition, there was no significant difference in the percentage of females that laid eggs among the groups ($X^2 = 6.64$, df = 3, $P = 0.084$). However, maintaining females in groups did have a negative effect on several other reproductive parameters (Table 1).

There was a significant difference in the mean number of days that it took females to lay their first clutch among treatment groups ($H = 20.50$, df = 3, $P < 0.001$). Control lizards laid their first clutch 44.43 ± 1.92 d after they were removed from brumation, whereas lizards in the eight-female group took significantly ($Q = 4.03$, $P < 0.05$) longer, 57.17 ± 4.32 d, to lay their first clutch (Fig. 2). However, the number of days between subsequent clutches was not significantly different ($H = 5.39$, df = 3, $P = 0.145$) among treatment groups.

The mean number of clutches of eggs laid per female was significantly affected by female group size

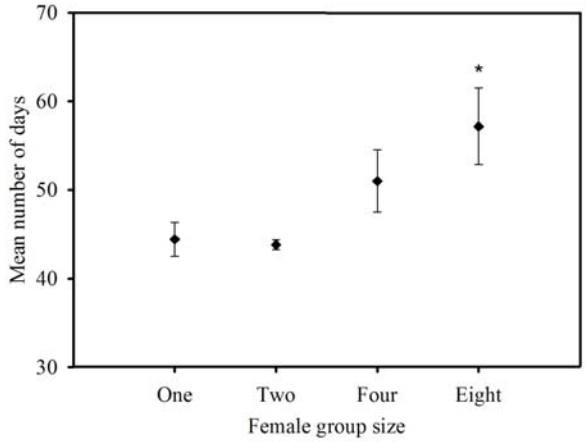

FIGURE 2. The effect of female group size of captive Western Fence Lizards, *Sceloporus occidentalis*, on the mean number of days before females laid their first clutch. For each group, n = 24 females. *Indicates a significant difference ($P < 0.05$) between the control mean and group size mean.

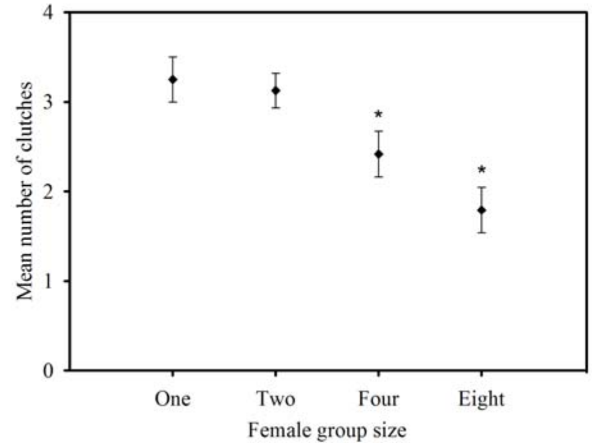

FIGURE 3. The effect of female group size of captive Western Fence Lizards, *Sceloporus occidentalis*, on the mean number of egg clutches produced. For each group, n = 24 females. *Indicates a significant difference ($P < 0.05$) between the control mean and group size mean.

regardless of whether the data were analyzed only for females that laid at least one clutch ($H = 17.28$, df = 3, $P < 0.001$) or for all females, including those that laid no eggs ($H = 22.68$, df = 3, $P < 0.001$; Fig. 3). Of the females that laid eggs, controls laid a mean of 3.39 ± 0.21 clutches, whereas lizards in the four- and eight-female groups laid significantly fewer clutches, 2.68 ± 0.19 ($Q = 2.42$, $P < 0.05$) and 2.26 ± 0.21 ($Q = 3.72$, $P < 0.05$) clutches, respectively.

Reproductive effort, in terms of relative clutch mass, was also significantly affected ($F_{3,246} = 4.88$, $P = 0.003$) by female group size. The relative clutch mass was significantly less, in the four- ($t = 2.59$, $P = 0.01$) and eight- ($t = 2.90$, $P = 0.004$) female groups compared to control lizards (Table 1). This reduced reproductive effort of the four- and eight-female groups was apparently due to smaller clutch masses that resulted from the cumulative effect of slightly fewer eggs per clutch and slightly smaller eggs (Table 1). However, when eggs per clutch and egg size were analyzed separately, neither clutch size ($F_{3,252} = 1.98$, $P = 0.117$) nor egg mass ($F_{3,161} = 0.66$, $P = 0.577$) was reduced enough in four- and eight-female groups to be significantly different. In addition, the relative egg number followed a similar trend with a decrease in the eight-female group but the difference was not statistically significant ($F_{3,251} = 2.53$, $P = 0.058$). Fertility of eggs laid was also significantly ($H = 32.41$, df = 3, $P < 0.001$) affected by female group size and the mean percentage of infertile eggs per clutch was significantly higher in females from four- ($Q = 3.17$, $P < 0.05$) and eight- ($Q = 3.25$, $P < 0.05$) female groups. The mean percentage of infertile eggs per clutch of control lizards was 11.08 ± 2.84, but was 31.40 ± 5.32 and 37.71 ± 6.68 for lizards in the four- and eight-female groups, respectively (Fig. 4).

TABLE 1. The effects of female group size on reproductive parameters (mean ± SEM) of Western Fence Lizards (*Sceloporus occidentalis*). Sample size for each female group is 24.

	Female group size			
Parameters measured	1 (Control)	2	4	8
Percentage of females that laid eggs	95.8	100	87.5	79.2
Female post-reproductive snout-vent length (mm)	72.24 ± 0.37	71.53 ± 0.34	72.03 ± 0.44	72.21 ± 0.53
Female post-reproductive mass (g)	12.17 ± 0.19	11.97 ± 0.18	12.57 ± 0.26	12.44 ± 0.28
Number of clutches (all females)	3.25 ± 0.25	3.13 ± 0.19	2.42 ± 0.25[b]	1.79 ± 0.26[b]
Number of clutches (laying females)	3.39 ± 0.21	3.13 ± 0.19	2.68 ± 0.19[b]	2.26 ± 0.21[b]
Days before first clutch laid	44.43 ± 1.92	43.83 ± 0.58	51.00 ± 3.51	57.17 ± 4.32[b]
Interclutch interval length (days)	27.15 ± 0.46	27.98 ± 0.79	29.30 ± 1.19	29.96 ± 1.05
Relative clutch mass	0.48 ± 0.01	0.48 ± 0.01	0.43 ± 0.01[b]	0.42 ± 0.02[b]
Clutch size	10.86 ± 0.25	10.23 ± 0.20	10.36 ± 0.27	10.05 ± 0.33
Egg mass (g)	0.53 ± 0.01	0.52 ± 0.02	0.50 ± 0.02	0.51 ± 0.02
Relative egg number	0.15 ± < 0.01	0.14 ± < 0.01	0.14 ± < 0.01	0.13 ± < 0.01
Percentage of infertile eggs / clutch	11.08 ± 2.85	10.58 ± 3.32	31.40 ± 5.32[b]	37.71 ± 6.68[b]

[b] Indicates value is significantly ($P < 0.05$) different from control

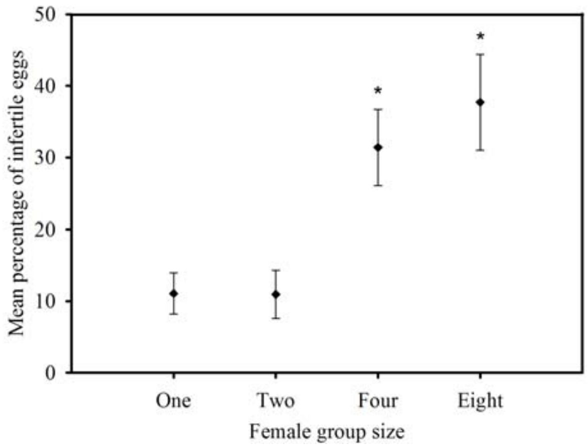

FIGURE 4. The effect of female group size of captive Western Fence Lizards, *Sceloporus occidentalis*, on the mean percentage of infertile eggs per clutch. n = 24 females for each group size. *Indicates a significant difference ($P < 0.05$) between the control mean and group size mean.

DISCUSSION

There were no statistical differences between the controls and females in the two-female groups for any parameter measured. However, housing lizards in four- or eight-female groups did result in increased variability in reproductive traits. The major effects of housing females in four- and eight-female groups were that they started laying eggs later than controls, laid significantly fewer clutches, laid significantly more infertile eggs per clutch, and had significantly smaller relative clutch masses.

Although housing four or eight Western Fence Lizard females together in 74.2 L glass aquaria was likely the proximate cause for variation in the reproductive traits exhibited by females in our study, the specific reasons why crowding affected reproduction are unclear. The females in the eight-female group started laying eggs significantly later than controls. Nevertheless, once females started laying eggs, the length of the interval between clutches was not affected by crowding. Furthermore, maintaining females in groups of four and eight individuals also significantly reduced the number of clutches of eggs laid by female Western Fence Lizards as well as their relative clutch masses. It is unlikely that competition for food was a factor related to the number of clutches laid because food was provided *ad libitum*. Therefore, it appears that interaction with other females or the male could be the direct cause of fewer clutches. Similar results were reported by Summers et al. (1995) who demonstrated that housing more than one female Green Anole lizard, *Anolis carolinensis*, with a male inhibited ovarian recrudescence in most females. However, it is also possible that housing a male Western Fence Lizard with four to eight females may have affected his courtship behavior or reproductive physiology in a way that inhibited the reproductive cycle of some females. It is known that ovarian growth is dependent on male stimuli in captive Painted Dragons, *Ctenophorus pictus* (Uller and Olsson 2005), and ovarian development is also affected by the amount of courtship behavior in Green Anoles (Crews 1974). However, to our knowledge, little is known about the specific effects of male courtship on the reproductive cycle of Western Fence Lizard females and research is needed in this area.

Egg fertility was significantly reduced in clutches laid by females in the four- and eight-female groups. The reasons for the reduced fertility are unknown because our study was not designed to determine whether the reduced fertility was due to altered physiology of the females or due to factors related to the male. Nevertheless, it seems likely that fertility was either related to females producing inviable ova possibly due to insufficient stimuli or stress, or males not fertilizing viable ova. If failure to fertilize ova was a factor, it could have been due to a reduction in the number of copulations per female compared to controls (Olsson and Shine 1997) or due to the production of an insufficient quantity of healthy sperm needed to fertilize all the eggs produced by multiple females (Takahashi and Parris 2009). To our knowledge, no information is available on the quantity of sperm produced by male Western Fence Lizards and further research is needed to determine if sperm quantity is sufficient to fertilize the eggs of multiple females.

Our data suggest that the variability in reproductive traits observed in our study was likely due to the effects of crowding and not to other proximate factors. Other proximate factors that could potentially affect the reproduction of lizards in captivity include incubation conditions, rearing conditions, age, size, food, infertile males, and density of lizards per unit area. However, with the possible exception of density, these factors probably did not affect the variability in reproductive traits observed in our study. For example, lizards were hatched from eggs that were incubated under identical conditions, hatchlings were reared under identical conditions, and lizards were conditioned for reproduction under identical conditions. Age was also not a proximate cause of the variability in reproductive traits observed during our study because all Western Fence Lizards were approximately nine months old when the breeding experiments were initiated and lizards were assigned to specific groups randomly. In addition, the size of females did not appear to be a cause of variability because there was no significant difference in the size of females assigned to the different groups. Another proximate factor that can cause variation in life-history traits of captive lizards is food availability (Mugabo et al. 2010, 2011). However, we fed lizards *ad* *libitum* and crowding did not affect the post-reproductive mass or SVL of females suggesting that social interaction did not reduce food consumption. Housing an infertile male with a group of females could also affect the results of a crowding study. In our study, only two of the male Western Fence Lizards in the 45 cages did not fertilize eggs. Both males were in the control group; one was housed with a female that did not lay a clutch and the other was with a female that produced a single infertile clutch. Therefore, our results were not biased by housing a sterile male with a group of females.

Our research on the effects of crowding used 74.2 L glass aquaria as cages for all female group sizes. Consequently, as the size of a group increased, the density of lizards in a cage increased. Our study was not designed to evaluate the relative effects of density versus group size on reproductive traits. Therefore, our results on the effects of maintaining Western Fence Lizards in groups may not apply to situations where similar group sizes of lizards are maintained in larger cages, because the density of lizards per unit area would be different. Furthermore, our study examined only one population of Western Fence Lizard and other populations may respond differently to crowding.

In summary, the overall purpose of our study was to obtain information that could be used to optimize the laboratory husbandry conditions of Western Fence Lizards so that life-history traits of different populations could be compared under identical laboratory conditions. Such studies may be helpful for evaluating the relative contributions of intrinsic and environmental factors to intraspecific variations in life-history traits that are observed in field studies. Our results indicate that housing female Western Fence Lizards in four- and eight-female groups was a proximate cause of variability in reproductive traits and is not a reliable breeding arrangement for comparing the reproductive traits among different populations, at least in the cage size used in our experiment. However, for the lizard population that we studied, housing lizards in heterosexual pairs or one male with two females appeared to work equally well as breeding arrangements to use in controlled laboratory experiments.

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Scott G. Talent is a student at Oklahoma State University in Stillwater, Oklahoma. He has a Bachelor’s degree in studio art and is currently working toward a B.S. in microbiology/cell and molecular biology. He plans to pursue his Ph.D. in biochemistry. Recently, he has been working with Dr. Larry G. Talent toward the development of the Western Fence Lizard as a laboratory reptile model for evaluating environmental stressors on life-history traits. He is currently evaluating the effects of endocrine disruptors on the cellular development of reproductive organs in *Sceloporus occidentalis*. (Photographed by Larry G. Talent)