

Maximizing male reproductive success in the broad-headed skink (*Eumeces laticeps*): preliminary evidence for mate guarding, size-assortative pairing, and opportunistic extra-pair mating

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Abstract. Several lines of evidence suggest that male *Eumeces laticeps* may increase reproductive success by 1) mating with larger females to increase clutch size, 2) mate guarding to be present during the female's receptive period and/or prevent sperm competition, and 3) engaging in extra-pair copulations. Clutch size increases with female body size, establishing a potential advantage of male preference for large female mates. Mate association lasts up to 8 days and possibly longer, with a mean of nearly 5 days. Males may remain with females during a major portion of the mating season, which preliminary data suggest lasts about two weeks, suggesting that mate-guarding may reduce the level of polygyny. Tethered introductions of intruder males to consort pairs showed that consort males use aggressive behavior to exclude other males from the vicinity of females. *Eumeces laticeps* exhibits strong positive size-assortative pairing, suggesting the possible importance of male choice of large mates. Female preference for large males could account for this relationship, but only if large females prefer the largest possible males within the acceptable size range and aggressively exclude other females from preferred males. Females are sometimes aggressive to each other, especially near nest sites, but aggression is suppressed by males, as shown by tethered introduction of females to consort pairs. Size-assortative pairing may be based in part on male preference if males can prevent larger females from aggressively excluding smaller ones. In addition to preferentially guarding large females, males not currently guarding mate with any females not large enough to deter them aggressively. A field observation of an extra-pair copulation, responses by consort males to introduced females, and the lack of size preference in the absence of consorts suggest that males may engage opportunistically in extra-pair copulations to increase reproductive success and are not then choosy about female size.

Introduction

Mate choice by males traditionally was considered unimportant (Bateman, 1948; Wade, 1979) because males may have opportunities for multiple matings at low cost. When males invest only their genes in offspring, their fitness should be maximized by fertilizing

as many eggs as possible (Halliday, 1983; Trivers, 1972). Males should maximize lifetime reproductive success (RS, here number of offspring) by all available means. In polygynous species males achieve this primarily by fertilizing multiple females, but could also enhance reproductive success by mating with the most fecund females. To prevent reductions in eggs fertilized per female mated due to sperm competition, males may guard their mates, blocking access by other males. When costs of and opportunities for mating preclude or limit multiple mating, males theoretically should select mates for traits related to fecundity, such as body size and correlates of the quality of female parental care (reviewed by Andersson, 1994).

In many vertebrates, including lizards that have variable clutch size (Dunham et al., 1988; Fitch, 1970), the number of offspring produced per episode increases with female body size. Male fitness in these species could be increased if males select large female mates. In some mammals (Berger, 1989) males also potentially benefit from any size(age)-related gain in female parental skills. Among lower quadrupeds, males of some salamander species (Verrell, 1985, 1986, 1989) and a few lizard species have been reported to choose large females as mates (Fitzgerald, 1982; Rostker, 1983; Olsson, 1993).

The lizard data are very meager. The most convincing evidence for male choice is that for the lacertid *Lacerta agilis* (Olsson, 1993). In *L. agilis* there is positive size-assortative mate association in the field and males court the larger of two females more frequently than the smaller in simultaneous choice tests (Olsson, 1993). In the field large males of the crotaphytid lizard *Crotaphytus collaris* are consorts of large females of high fecundity (Rostker, 1983). It has not been demonstrated that large male collared lizards select large females as mates, but this seems likely due to the sequence of territorial establishment. Females establish small territories before males do. Males then appear to establish territories that overlap maximally with those of females (Fitch, 1956; Rostker, 1983; Ruby, 1986). A similar situation occurs in *Sceloporus jarrovi* (Ruby, 1978, 1981, 1986), in which males selected large female mates in the laboratory (Fitzgerald, 1982). Male choice of large females also was reported in other species of *Sceloporus* (Fitzgerald, 1982).

We present field and laboratory information bearing on male choice and mate guarding in the broad-headed skink *Eumeces laticeps*. Males might increase their own fitness by choosing large mates for two reasons. First, in *Eumeces* clutch size increases with female body size as indicated by the significant increase in number of vitellogenic follicles and/or eggs brooded with female snout-vent length (SVL) (Hasegawa, 1990, 1994; Vitt and Cooper, 1985a). However, the evidence regarding oviductal eggs and number of eggs laid is not as conclusive (Vitt and Cooper, 1985a, 1986a). We discuss published information on the relationship between clutch size and SVL in *E. laticeps* and its close relatives. Second, because female *Eumeces* remain with the eggs until they hatch and may remain briefly with the juveniles (Somma, 1985; Vitt and Cooper, 1989), larger females might provide greater protection against predators. Such protection might operate

through selection by large females of nest sites having physical characteristics enhancing survival of eggs or juveniles or through ability to hold optimal sites against intrasexual competitors.

Male *E. laticeps* guard females during the breeding season (Vitt and Cooper, 1985b), and prevent access to females by other males. Mate guarding may reduce the likelihood of sperm competition in *E. laticeps*, but it is not known whether females mate multiply. If not, mate guarding may assure exclusive access to the female during a brief period of sexual receptivity. Although previous observations showed that males and females were associated for at least several hours, longer-lasting association was unknown (Vitt and Cooper, 1985b). Only limited anecdotal evidence showed that males associated with females defended them against other males (Cooper and Vitt, 1986; Vitt and Cooper, 1985b). In this study, we present data extending the known duration of association between pairs and demonstrating that males associated with females consistently defend them against other males.

Male *E. laticeps* attain larger maximum size than females (Vitt and Cooper, 1985b), which prefer large males (Cooper and Vitt, 1993). We predicted that a male preference for large female mates would be reflected by positive size-assortative association in pairs observed in the field. Males associated with females in the field are larger than males not associated with females (Cooper and Vitt, 1993), which might be explained solely by the female preference for large males. If males also prefer large females, females observed with the large, guarding males should be larger than the mean adult female size if small females are not guarded or are guarded briefly. Our impression from years of field observations is that large females are much more likely to be observed with males than are small females. Size-assortative mating would occur if, in addition, the largest guarding males are associated with the largest females.

Aggression between females might produce a positive size-assortative association between members of consort pairs if larger females drive smaller ones away from large, preferred males. Such female aggression could account for size-assortative association even in the absence of a male preference for large females. To test this female aggression hypothesis, we placed unfamiliar females in close proximity with mated pairs in the field.

Because female *E. laticeps* aggressively reject courtship by smaller males (Cooper and Vitt, 1993), sometimes biting much smaller males even when they do not court, attempts to mate with larger females or even approaching them could be maladaptive for smaller males. Not only might small males be injured by the female or attacked by larger males, they might suffer increased risk of predation due to the greater conspicuousness entailed by courtship and female aggression. Therefore we predicted that adult males that were too small to have any chance of success would not court and that the percentage of males courting would rise as male size increased relative to female size.

We further examined male mating behavior in laboratory tests. Even if males prefer large females, they might increase fitness by copulating with smaller ones either if individual matings are not very costly or larger females are unavailable. To assess potential

flexible male response to females of suboptimal size in the absence of larger females and for extrapair copulation with small, unguarded females, we presented single females to single males.

Materials and methods

Subjects and maintenance, and significance levels

Field observations were made on reproductive behavior and related phenomena during the years 1982-1985, 1987, 1992, and 1994 on barrier islands near Charleston and in Aiken and Barnwell Counties, South Carolina. For the laboratory studies lizards were collected on Kiawah Island and Seabrook Island, Charleston County, South Carolina in April, May and June, 1987. They were transported to the Savannah River Ecology Laboratory, where they were maintained in a building having translucent walls and a roof that was retracted on fair days. Lizards were exposed to the photothermal cycle of the laboratory's vicinity except that afternoon temperatures were often a few degrees higher inside the building than outside.

Each lizard was housed individually in a glass terrarium ($49 \times 49 \times 32$ or $30 \times 30 \times 26$) having a wire screen top and containing a sand substrate, a water bowl, and a shelter site. The lizards were fed approximately 10 adult crickets, sometimes dusted with vitamin and mineral supplements, three times per week. This diet was occasionally supplemented with neonatal mice and assorted invertebrates. Water was available *ad libitum*.

Laboratory observations were conducted during the summer of 1987. For laboratory studies done during the nonbreeding season (after early June), males were given subcutaneous implants of testosterone in Silastic capsules several weeks before being tested. Such treatment restores the bright orange head coloration typical of breeding males and activates sexual and aggressive behavior (Cooper et al., 1987). Females, in tests for which sexual receptivity and pheromone production were important, were injected subcutaneously with doses of estradiol known to induce receptivity reliably (Cooper et al., 1986).

All laboratory tests were conducted at ambient temperatures from 29 to the mid-30s°C between 10:30 and 15:30 h when the lizards were fully active. To begin each trial, the experimenter placed a lizard or lizards in a cage, usually the home cage of one lizard (specified below), and withdrew to a blind to observe and record social behaviors. If no courtship or aggression occurred within 30 min, the trial was terminated. Reported significance levels of all statistical tests for both laboratory and field data are one-tailed because the predictions were directional.

Clutch size

The correlation between number of eggs and female snout-vent length was determined for the congeneric *E. obsoletus* from data in Hall (1971). The data are comparable to our

data (Vitt and Cooper, 1985a) in being based on counts of oviductal eggs and deposited clutches. They exclude counts of vitellogenic follicles.

Mate guarding

Duration of mate guarding was assessed by observing pairs of lizards found less than 0.3 m from each other on consecutive days during the breeding season (10-20 May 1994) on Seabrook Island. Individuals were recognized by differences in size, color patterns, regenerated tails, and damage to scales, particularly head wounds caused by aggression between males (Cooper and Vitt, 1987, 1991; Vitt and Cooper, 1985b, 1986b). Individual recognition was further facilitated by site fidelity and low population density.

To determine the extent to which males associated with females attempt to exclude other males from females, we introduced tethered unfamiliar adult males to male-female pairs on Seabrook Island on 15-17 May 1994. Males were tethered by wrapping the trunk at midbody with strapping tape tied to string connected to a fishing pole. To introduce a tethered male, an investigator slowly approached the pair and lowered the male to the ground about 1 m from the pair. In preliminary tests with unpaired males and females, this method elicited normal social responses. Each consort male was tested only once and each tethered male was introduced only once. Responses by consort males to tethered males recorded were attacks and snout-down displays. The snout-down display, in which the neck is elevated and the snout pointed down, is typically performed as a threat to other males from some distance before any actual fighting begins.

Size-assortative pairing

SVLs of adult lizards ($SVL \geq 85$ mm, Vitt and Cooper, 1985a) captured in the field during mate-guarding or while basking together (within 0.3 m) were measured to the nearest mm. These data allow comparison of relative sizes of females associated with males and other females by a Mann-Whitney *U*-test and calculation of the regression and correlation between sizes of males and females found together. These data were collected on Kiawah Island and Seabrook Island in May 1984 (Vitt and Cooper, 1985b) and 1987.

Female aggression

Because females sometimes exhibit aggression to conspecific females in the vicinity of nest sites (Cooper and Vitt, unpublished field and laboratory data), it is possible that female aggression toward other females coupled with female preference for large male mates might account for any positive size-assortative mating. To examine this possibility, we tested responses of females in consort pairs to other females tethered and introduced by the same method in the same vicinity on the same dates.

Effect of females size on male courtship and copulation frequency

A single female was placed in a male's home cage. Each male was tested once with a female smaller than the male by more than 10 mm SVL ($n = 18$) or with a female larger than the male by more than 10 mm ($n = 5$). Because male SVL was 98-135 mm, 10 mm constituted 0.07-0.10 of male SVL. Trials were conducted between 2 June and 27 July. To examine possible changes in probability of mating success in a range of relative sizes in which success of courtship and probability of female aggression were uncertain, additional trials were done with lesser size differences (males 6-10 mm larger, $n = 1$; 0-5 mm difference, $n = 6$; and females 6-10 mm larger; $n = 6$). Comparisons were made by Fisher exact probability tests (Siegel, 1956).

Results

Clutch size

In the Great Plains skink *E. obsoletus*, female SVL and number of eggs were positively correlated ($r_s = 0.49$, $n = 27$, $P < 0.01$). As for *E. laticeps*, a few relatively large females had smaller than expected clutches.

Mate guarding

Fourteen distinguishable pairs were observed. Typically they could be found together throughout the day. While at rest they were often in bodily contact or nearly so. When the female of a pair moved, the male usually followed closely, but the members of a pair were sometimes separated briefly by over 2 m during foraging. The number of separate days on which a particular consort pair was observed ranged from one to eight, with four pairs being observed on only one day, one on two days, two on three days, one on four days, two on five days, one on six days, two on seven days, and one on eight days.

These data are minimal estimates of the true duration of association. Of the four pairs recorded on only one day, two pairs were collected on that day and a third was in a site visited only once. In addition, one of the pairs observed on three days was captured on the third day. Among pairs that could possibly have been observed together for more than one day, 10 of 11 were. The number of days observed per pair for pairs that could have been observed together longer was 4.8 ± 0.7 (SE), $n = 10$.

In ten introduction of tethered males to consort pairs, nine consort males attacked tethered males. Eight consorts attacked without preliminary signalling, presumably because the tethered lizards were placed so close to them. Only one consort male performed snout-down aggressive displays prior to attacking. The remaining consort male fled from the introduced male, which was larger by 10 mm SVL. Three of the consort males that attacked and drove away the tethered male were smaller than the tethered male by less than 5 mm SVL; another was the same size as the tethered male. Consort males

were larger in the remaining trials. In two trials the consort male chased the nonresident away from the female and then returned quickly to her side. In all 10 trials, the female remained still initially. Only the female whose consort fled from the larger introduced male moved away, and only when approached by the tethered male.

Size-assortative mating

Females found with males were larger than other adult females (table 1). Of 26 females collected in 1987 (24 on 12-13 May, 2 on 27 May), six were found with males. These six were significantly larger than the remaining females ($U = 14$; $n = 6, 20$; $P = 0.003$). Both members of nine pairs of consorts were measured, two in 1984 and seven in 1987. For these pairs, male size increased significantly with female size (fig. 1). The Pearson correlation coefficient is 0.83 ($df = 7$, $P < 0.01$). The differences in snout-vent-length were considerable, males being larger by 17.8 ± 2.2 mm (range = 8-25).

Table 1. Body sizes of females (snout-vent length in mm) were greater for individuals found with males than for individuals found alone.

	<i>n</i>	Mean	<i>s_x</i>	Range
Female with male	6	110.5	2.0	101-115
Female alone	20	99.8	1.9	86-111

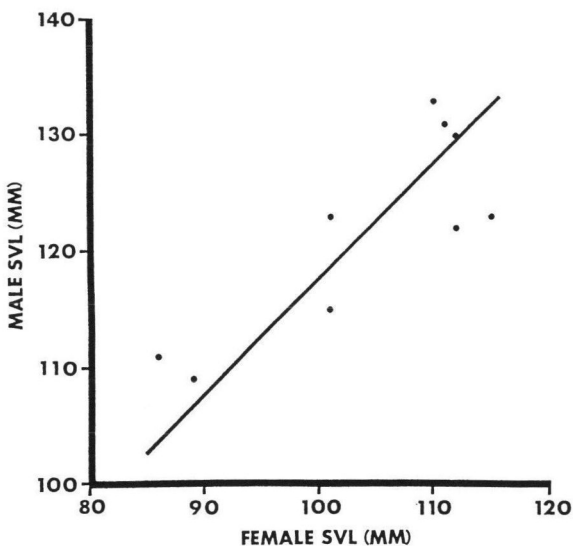


Figure 1. In consort pairs of *Eumeces laticeps*, male body size (snout-vent length = SVL) increases with female body size according to the regression equation (male SVL) = 1.01 (female SVL) + 16.4 ($F = 15.73$; $df = 1, 7$; $P < 0.005$).

Female aggression

In nine of 11 trials the consort female exhibited no aggressive responses. In another trial the consort female directed an aggressive display (snout-down) to the tethered female and approached, but ignored the intruder after preliminary tongue-flicking. In the remaining trial, the consort female approached the tethered female aggressively, but was chased away from her by the male. In one trial, consort female began to approach the tethered female, but stopped when the male approached the tethered female. There was no indication that consort females prevent access to males by other females.

Effect of female size on male courtship and copulation frequency

When the data are cast in three categories of relative size, the percentage of males courting and copulating decreases as the relative size of the female increases (table 2). Males frequently courted females that were much smaller than the males and females that were relatively small compared to other adult females (table 3, which presents data on size differences between the sexes and females SVLs for data from table 2 in which sizes differed by at least 15 mm). The data were not tested statistically in the forms presented in tables 2 and 3 due to small sample sizes, but the effect of relative size was

Table 2. The proportion of males courting females increases with male size relative to female size. Size is given as SVL in mm.

	Female smaller by ≥ 6 mm	Sizes similar	Female larger by ≥ 6
Courted	14	4	2
Did not court	4	2	6
Copulated	13	1	1
Did not copulate	5	5	7

Table 3. Males courted females of all sizes between 15 and 30 mm shorter than themselves. Size differences between the sexes (A) and female SVLs (B) are in mm.

A.	Size difference			
	Number	Mean	$s_{\bar{x}}$	Range
Courted	12	22.08	1.35	17-30
Not courted	4	23.25	3.33	15-30
B.	Female SVL			
	Number	Mean	$s_{\bar{x}}$	Range
Courted	12	103.5	1.94	99-112
Not courted	4	101.0	2.48	95-106

assessed statistically by pooling data to form two size categories (next paragraph). The raw data and the statistical tests suggest that success in copulating may decline more rapidly than frequency of courtship as male size relative to female size decreases and that small female size does not decrease the likelihood of courtship by males.

Males courted substantially smaller females in 14 or 18 trial, but courted only two of eight substantially larger females (table 2), showing a higher frequency of courtship to smaller females ($P = 0.017$). They also copulated with a higher frequency of smaller (13 of 18) than larger (1 of 7) females ($P = 0.007$). Adding data from the additional trials in which size differences were usually smaller, males that courted copulated with 14 of 15 females smaller by ≥ 6 mm and with 2 of 6 females of lengths at least as great as their own. Males had a significantly higher success rate when courting smaller females ($P = 0.002$).

Discussion

Clutch size

Several significant correlations show that fecundity increases with female body size in congeners reproductively similar to *E. laticeps*. Female size is positively correlated with 1) number of oviductal eggs and brooded eggs in *E. obsoletus* (Hall, 1971), 2) number of brooded eggs in *E. okadae* (Hasegawa, 1985), 3) numbers of vitellogenic follicles, oviductal eggs, and brooded eggs in *E. okadae* (Hasegawa, 1990), and 4) numbers of vitellogenic follicles, oviductal eggs, brooded eggs and corpora lutea in *E. okadae* (Hasegawa, 1994). Values for these correlations are about 0.50, indicating much scatter. Deviation from the predicted relationship may result from poor nutritional status, disease, or senescence resulting in follicular atresia. Post-ovipositional mortality, notably from predation and ingestion by females, may reduce the realized clutch size from its potential maximum. Female *Eumeces* may eat their own eggs (Hasegawa, 1985; Noble and Mason, 1933), usually those that have died (Groves, 1982; Cooper and Vitt, personal observations).

We (Vitt and Cooper, 1985a) reported a significant relationship between female size and number of vitellogenic follicles in *E. laticeps*, but not for those data combined with number of oviductal and brooded eggs (Vitt and Cooper, 1985a). However, given the many sources of variation in clutch estimates, small sample sizes may account for the few cases in which no significant relationship was observed between clutch size and female size in *Eumeces* (Vitt and Cooper, 1985a, 1986a). Data for all *Eumeces* species examined with sufficient sample sizes reveal increases in clutch size with female body size.

In our data for *E. laticeps* the number of vitellogenic follicles increased significantly with body size (Vitt and Cooper, 1985a), but the evidence for follicles plus oviductal and brooded eggs was unclear. Three large females had relatively small clutches. If the

data for those clutches were anomalous due to losses specific to individuals rather than to large body size, the combined clutch size data for number of eggs brooded and oviductal eggs would be positively related to female body size by Spearman rank correlation ($r_s = 0.503$, $n = 16$, $P < 0.05$). The positive correlation between female body size and number of vitellogenic follicles and the existence of large clutches in some large females indicates that larger females can produce larger clutches when healthy and well nourished. Follicular atresia in the field may be responsible for relatively small clutches by some large females.

The totality of available evidence suggests that there may be a real increase in clutch size at the time of deposition with female body size over most of the adult female size range. The fundamental relationship between female size and number of vitellogenic follicles presumably translates into an important, although imperfect, long-term relationship between female size and clutch size. If so, males can increase the number of offspring per copulation by mating with the largest females. Other potential factors favoring a male preference for large females would be greater success of large females in obtaining superior nest sites and in defending their eggs against predators. These abilities have not been studied, but might compensate for some loss in deposited clutch size among large females.

Mate guarding

Mate association lasts much longer than previously known. Previous data based on short-term field observations and observations of caged males in physical contact with females had suggested that mate guarding might not last much longer than one day (Cooper and Vitt, 1987; Vitt and Cooper, 1985b). However, the caged animals were in such close enforced proximity that mate guarding of longer duration may have gone undetected. The present data indicate that mate guarding sometimes lasts at least eight days and typically lasts at least several days. Mate guarding thus lasts through a major portion of the mating season, which appears to be limited to about two weeks (Cooper and Vitt, unpublished observations), and might in some instances last the entire season. It is not known whether mate-guarding sometimes persists until oviposition, but males are not associated with brooding females (Cooper and Vitt, unpublished observations).

Aggressive behavior by guarding males toward introduced males coupled with their return to their females after chasing the introduced males indicates that males not only associate with females, but guard them. Attacks by consort males on slightly larger tethered males suggest that the expected selective payoff from mate guarding is sufficient to justify considerable risk of injury. As mate guarding is presumably a mechanism of paternity assurance, males may remain with females either to copulate with them when they become sexually receptive for a limited time or to prevent sperm competition, which has been demonstrated in the lacertid lizard, *Lacerta agilis* (Olsson, 1993).

Guarding mates is presumably costly because males spend considerable time with females, suffer frequent injuries during fights (Cooper and Vitt, 1987; Vitt and Cooper,

1985b), and are conspicuous due to their behavior. In the phrynosomatid lizard *Sceloporus jarrovi*, territorial aggression causes increased male mortality (Marler and Moore, 1988). Similar decreases in survival or expected future reproductive success in *E. laticeps* might account for the delay in attempts at mate guarding until large size has been attained.

Size-assortative mating and female aggression

Although the mean size of females in consort pairs was larger than that of other females, even some very small females had male consorts. The smallest guarded female was 86 mm, very close to the minimum SVL at maturity of about 85 mm. Presumably all females in breeding condition can produce viable offspring. Although large males may guard large females for intervals longer than a week (Cooper, unpublished data), they sometimes leave these females to mate with other, smaller females (Cooper, single unpublished observation).

If males do not prefer large females, can a combination of female choice of large males with aggressive behavior among females or among males account for the large size of paired females? Females exhibit some aggressive behavior toward other females, especially in the vicinity of nest sites before and after depositing eggs (Cooper, unpublished data). However, their lack of aggressive behavior to tethered nonresident females in the presence of consort males, the absence of any observations of aggression between females in the presence of males despite many years of field observations, and the rarity of observed aggression between females make it highly unlikely that female aggression can account for the large size of female consorts.

If females can choose among potential mates in the acceptable size range, the female preference for large males might be responsible for the large size of males in consort pairs. Such males would aggressively drive away smaller males. However, if males do not also prefer large females, the sizes of females in consort pairs should be a random sample from the adult female size range in the absence of aggressive interactions among females. Thus, the most likely explanation for the larger than average size of females in consort pairs is male choice favoring large females.

The smallest adult males may be entirely excluded from mating by female preference for large mates (Cooper and Vitt, 1993). Nevertheless, even the smallest males among those are large enough by their second breeding season to be acceptable mates to all but the very largest females (Cooper and Vitt, 1987, 1993; Vitt and Cooper, 1985b). Thus, the strong size-assortative pairing in *E. laticeps* cannot be explained by female aggression to males.

Small adult males, which mature at the same length as females, were absent in the consort pairs (Cooper and Vitt, 1993). To reduce the risk of injury or death by fighting larger males, small adult males defer agonistic encounters until they grow larger (Cooper and Vitt, 1987). Up to nearly 100 mm SVL, they are excluded from mating, except possibly at low population densities. Many males that might be acceptable mates for

females do not mate. As a result of aggression by both females and large males toward smaller males, pairing in *E. laticeps* is positively size-assortative with a truncated male size distribution.

Male choice of large female mates to maximize reproductive success accounts readily for positive assortative pairing in broad-headed skinks. Because large males exclude smaller males from the presence of females (Cooper and Vitt, 1987; Vitt and Cooper, 1985b), males largely determine size relationships of consort pairs. Except at low population densities, female choice is likely limited to rejection of males below the acceptable size threshold. Positive size-assortative mating would exist even if females did not prefer large males.

Effect of female size on male courtship and copulation frequency

The prediction that the probability of courtship rises as males become larger relative to females was confirmed, suggesting that males are sensitive to risk and/or probability of success. In the field, guarding males are typically much larger than the minimal acceptable mate size for their consort females (Cooper and Vitt, 1993). Effects of avoidance of injury due to female aggression and of low probability of copulation on the probability that a male courts are confounded in the present data. Both factors have deleterious consequences that increase progressively below threshold size for male acceptability to females.

Males substantially smaller than females could be least likely to court solely because they have virtually no chance of copulating. Males engaging in such fruitless courtship may not only waste time and energy, but attract the attention of predators, or, even more likely, larger conspecific males capable of injuring or killing them. Although we cannot separate the effects of risk of predation, injury due to aggression by larger males, and injury due to aggression by females with the present data, we believe that female aggression *per se* deters courtship by smaller males. Female aggressive behavior clearly caused smaller males to stop courting in some instances. Nevertheless, when males are large enough relative to females to have even a low, but nonzero, chance of success, courtship may be predicted because the potential payoff is high. Such occasional success is illustrated by the single male that copulated despite being smaller than the female by 6 mm.

Despite their exclusion from females by larger males (Cooper and Vitt, 1987) and rejection by larger females (Cooper and Vitt, 1993), small males may sometimes copulate, as in *Iguana iguana* (Dugan, 1982) and *Cnemidophorus tigris* (Anderson and Vitt, 1990), as well as *E. laticeps*. Small male *E. laticeps* presumably may enhance their lifetime reproductive success by courting females not much larger than themselves. Males in their first reproductive season as adults have not been observed guarding females in the field. Slightly older, larger males having some probability of being accepted as mates, occasionally follow large females guarded by large males (Cooper and Vitt,

1987, 1993). This anecdotal evidence provides another hint that males assess risks and payoffs of courtship.

Male mating tactics

Both sexes prefer large mates, but for different reasons, males gaining more offspring and females genetic quality (Cooper and Vitt, 1993) as mate size increases. Even if multiple mating opportunities reduce the relative importance of variance in fecundity of individual females, males should prefer to guard large females due to the potentially large number of offspring. Given the long duration of mate guarding and the short mating season in *E. laticeps*, the advantage gained by mating with a large female may contribute importantly to variance in male reproductive success.

The only two experimental studies of male mate choice based on female size in lizards have detected male preferences for large mates. Males of four species of the phrynosomatid lizard genus *Sceloporus* chose large females as mates after being allowed to view both females (Fitzgerald, 1982). When allowed to choose between two females initially placed in separate compartments, male lacertid lizards (*Lacerta agilis*) consistently courted the larger female and made more investigatory visits before courting when the size difference between females was small (Olsson, 1993). Simultaneous choice tests are needed to test the hypothesized male preference for large female mates in *E. laticeps*.

It is very likely that males not only guard the largest females possible to maximize offspring sired, but also take any opportunities to mate with additional females. Only anecdotal field evidence is available, but it supports this possibility. During the breeding season the largest males guard females for periods sometimes lasting more than a week. A male can only guard one female by following her closely throughout the daily activity period. However, a 115 mm male that had been observed with a female for seven days briefly left her to copulate with a smaller female (85 mm) at the end of the daily activity period (Cooper, personal observation).

If such opportunistic mating is widespread, variance in male reproductive success may be greater than suggested by the observation of apparently monogamous relationships between consorts. Preliminary tests in the laboratory indicate that large unpaired males court adult females of all sizes. Males, in addition to guarding large females, may flexibly mate with females of any size not subject to prevention by female aggressive behavior. This could be tested by longer-term tethered introductions of females to consort pairs and to males temporarily away from their guarded females or by removal studies. In the present study, several males closely investigated introduced females in the presence of their consort females, tongue-flicking and following them, suggesting that mating attempts might occur. However, the tethered females were removed before any mounting attempts occurred.

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References

- Anderson, R.A., Vitt, L.J. (1990): Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* **84**: 145-157.
- Andersson, M. (1994): Sexual selection. Princeton, New Jersey, Princeton University Press.
- Bateman, A.J. (1948): Intra-sexual selection in *Drosophila*. *Heredity* **2**: 349-368.
- Berger, J. (1989): Female reproductive potential and its apparent evaluation by male mammals. *J. Mammal.* **70**: 347-358.
- Cooper, W.E., Jr., Vitt, L.J. (1986): Tracking of female conspecific odor trails by male broad-headed skinks (*Eumeces laticeps*). *Ethology* **71**: 242-248.
- Cooper, W.E., Jr., Vitt, L.J. (1987): Deferred agonistic behavior in a long-lived scincid lizard *Eumeces laticeps*: Field and laboratory data on the roles of body size and residence in agonistic strategy. *Oecologia* **72**: 321-326.
- Cooper, W.E., Jr., Vitt, L.J. (1991): Influence of detectability and ability to escape on natural selection of conspicuous autotomous defenses. *Canad. J. Zool.* **69**: 757-764.
- Cooper, W.E., Jr., Vitt, L.J. (1993): Female mate choice of large male broad-headed skinks. *Anim. Behav.* **45**: 683-693.
- Cooper, W.E., Jr., Mendonca, M.T., Vitt, L.J. (1986): Induction of sexual receptivity in the female broad-headed skink, *Eumeces laticeps*, by estradiol 17β . *Horm. Behav.* **20**: 235-242.
- Cooper, W.E., Jr., Mendonca, M.T., Vitt, L.J. (1987): Induction of orange head coloration and activation of courtship and aggression testosterone in the male broad-headed skink (*Eumeces laticeps*). *J. Herpetol.* **21**: 96-101.
- Dugan, B. (1982): The mating behavior of the green iguana, *Iguana iguana*. In: Iguanas of the world, p. 320-341. Burghardt, G.M., Rand, A.S., Eds. Park Ridge, New Jersey, Noyes Publications.
- Dunham, A.E., Miles, D.B., Reznick, D.N. (1988): Life history patterns in squamate reptiles. In: Biology of the reptilia, Vol. 16, ecology B, defense and life history, p. 441-552. Gans, C., Huey, R.B., Eds, New York, Alan R. Liss.
- Fitch, H.S. (1956): An ecological study of the collared lizard, *Crotaphytus collaris*. *Univ. Kans. Publ. Nat. Hist.* **8**: 213-274.
- Fitch, H.S. (1970): Reproductive cycles of lizards and snakes. *Misc. Publ. Univ. Kans. Mus. Nat. Hist.* **52**: 1-247.
- Fitzgerald, K.T. (1982): Mate selection as a function of female body size and male choice in several lizard species. Doctoral dissertation, Univ. Colorado, Boulder.
- Groves, J.D. (1982): Egg-eating behavior of brooding five-lined skinks, *Eumeces fuscatus*. *Copeia* **1982**: 969-971.
- Hall, R.J. (1971): Ecology of a population of the Great Plains skink (*Eumeces obsoletus*). *Univ. Kans. Sci. Bull.* **49**: 357-388.
- Halliday, T.R. (1983): The study of mate choice. In: Mate choice, p. 3-32. Bateson, P., Ed., Cambridge, Cambridge University Press.
- Hasegawa, M. (1984): Biennial reproduction in the lizard *Eumeces okadae* on Miyake-jima, Japan. *Herpetologica* **40**: 194-199.
- Hasegawa, M. (1985): Effect of brooding on egg mortality in the lizard *Eumeces okadae* on Miyake-jima, Izu Islands. *Copeia* **1985**: 497-500.
- Hasegawa, M. (1990): Demography of an island population of the lizard *Eumeces okadae* on Miyake-jima, Izu Islands. *Res. Pop. Ecol.* **32**: 119-133.

- Hasegawa, M. (1994): Insular radiation in life history of the lizard *Eumeces okadae* in the Izu Islands, Japan. *Copeia* **1994**: 732-747.
- Marler, C.A., Moore, M.C. (1988): Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behav. Ecol. Sociobiol.* **23**: 21-26.
- Noble, G.K., Mason, E.R. (1933): Experiments on the brooding habits of the lizards *Eumeces* and *Ophisaurus*. *Am. Mus. Novit.* **619**: 1-29.
- Olsson, M. (1993): Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). *Behav. Ecol. Sociobiol.* **32**: 337-341.
- Rostker, M.A. (1983): An experimental study of collared lizards: effects of habitat and male quality on fitness. Doctoral dissertation, Oklahoma State University, Stillwater.
- Ruby, D.E. (1978): Seasonal changes in the territorial behavior of the iguanid lizard *Sceloporus jarrovi*. *Copeia* **1978**: 430-438.
- Ruby, D.E. (1981): Phenotypic correlates of male reproductive success in the lizard, *Sceloporus jarrovi*. In: Natural selection and social behavior: recent research and new theory, p. 96-107. Alexander, R.D., Tinkle, D.W., Eds, New York, Chiron Press.
- Ruby, D.E. (1986): Selection of home range site by females of the lizard, *Sceloporus jarrovi*. *J. Herpetol.* **20**: 466-469.
- Siegel, S. (1956): Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.
- Somma, L.A. (1985): Notes on material behavior and post-brooding aggression (sic) in the prairie skink *Eumeces septentrionalis*. *Nebraska Herpetol. Newsl.* **6**: 9-12.
- Trivers, R.L. (1972): Parental investment and sexual selection. In: Sexual selection and the descent of man, p. 136-179. Campbell, B., Ed., Chicago, Aldine-Atherton.
- Verrell, P.A. (1985): Male mate choice for large, fecund females in the red-spotted newt, *Notophthalmus viridescens*: How is size assessed? *Herpetologica* **41**: 382-386.
- Verrell, P.A. (1986): Male discrimination of larger, more females in the smooth newt, *Triturus vulgaris*. *J. Herpetol.* **20**: 416-422.
- Verrell, P.A. (1989): Male mate choice for fecund females in a plethodontid salamander. *Anim. Behav.* **38**: 1086-1088.
- Vitt, L.J., Cooper, W.E., Jr. (1985a): The relationship between reproduction and lipid cycling in the skink *Eumeces laticeps* with comments on brooding ecology. *Herpetologica* **41**: 419-432.
- Vitt, L.J., Cooper, W.E., Jr. (1985b): The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Canad. J. Zool.* **63**: 995-1002.
- Vitt, L.J., Cooper, W.E., Jr. (1986a): Skink reproduction and sexual dimorphism: *Eumeces fasciatus* in the southeastern United States, with notes on *Eumeces inexpectatus*. *J. Herpetol.* **20**, 65-76.
- Vitt, L.J., Cooper, W.E., Jr. (1986b): Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): age-specific differences in costs and benefits. *Can. J. Zool.* **64**: 583-592.
- Vitt, L.J., Cooper, W.E., Jr. (1989): Maternal care in skinks. *J. Herpetol.* **23**: 29-34.
- Wade, M.J. (1979): Sexual selection and variance in reproductive success. *Am. Nat.* **114**: 742-747.

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