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SEASONAL PATTERNS OF REPRODUCTION IN TWO SPECIES OF DESERT BEETLES (COLEOPTERA: TENEBRIONIDAE)

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ABSTRACT

Current literature on desert beetle activity infers that seasonality of beetle activity is temperature and rainfall dependent, reflecting reproductive activity. In this study 2 desert tenebrionid beetles were compared. *Eleodes hispilabris* Say fits the expectations for reproduction, gaving 1 reproductive bout coincident with rainfall. *Eusattus muricatus* LeConte, however, has at least 3 reproductive bouts during the activity period, only 1 of which coincides with rainfall.

E. muricatus, although smaller, lays larger eggs than does *E. hispilabris*. Larger eggs may increase egg survivorship during suboptimal timing of oviposition by decreasing egg surface to volume ratios and thus minimizing desiccation. Larger nutrient reserves may increase survivorship of newly hatched juveniles.

Gonadal effort by *E. hispilabris* was typical, i.e., females expended greater amounts of energy than did males. In *E. muricatus*, however, male gonadal effort exceeded that of females. This is discussed with respect to reproductive effort theory.

RESUMEN

La literatura actual sobre las actividades de escarabajos del desierto, infieren que la actividad estacional de los escarabajos depende de la temperatura y precipitación, reflejando la actividad reproductiva. Se compararon en este ensayo 2 escarabajos tenbriónidos del desierto. *Eleodes hispilabris* (Say) se ajusta a las expectaciones de reproducción, teniendo un turno reproductivo coincidente con la precipitación. Sin embargo, *Eusattus muricatus* LeConte, ha tenido por lo menos 3 turnos reproductivos durante el período de actividad, de los cuales solo uno coincide con la precipitación.

Aunque más pequeno, *E. muricatus* pone huevos más grande que *E. hispilabris*. Los huevos más grande pudieran aumentar su sobreviviencia durante períodos subóptimos de la puesta de huevos por la reducción de la relación de la superficie de los huevos hacia su volumen, de aquí disminuyendo su desecación. Largas reservas de nutrientes pudieran aumentar la sobreviviencia de juveniles recién nacidos.

El esfuerzo gonadal por *E. hispilabris* fue típico, las hembras usando mas energía que los machos. Sin embargo, el esfuerzo gonadal de *E. muricatus* fue mayor en los machos que las hembras. Esto es tratado con respecto a la teoría de esfuerzo reproductivo.

Tenebrionid beetles are prominent features of desert ecosystems. Considerable study of this group has taken place with interest directed toward habitat utilization (Calkins & Kirk 1975, Sheldon & Rogers 1984) and temporal patterns of activity, both on diel time scales (Kramm & Kramm 1972, Holm & Edney 1973, Doyen & Tschinkel 1974, Hamilton et al. 1976, Smith & Whitford 1976, Kenagy & Stevenson 1982) and seasonal time scales (Rickard & Haverfield 1965, Rickard 1970, Ahearn 1971, Hinds & Rickard 1973, Rogers & Rickard 1975, Krehoff 1975, Thomas 1979, Wise 1981, Kenagy & Stevenson 1982, Sheldon & Rogers 1984) time scales. Explanations of these temporal activity patterns have related activity to temperature and rainfall patterns. Only Seely (1973) investigated the reproductive condition of active beetles. Her study of 2 Namib Desert tenebrionids indicated that, like activity patterns, female gonadal development responded to rainfall patterns.

From the published data it appears that beetle activity can be equated with reproductive activity. This interpretation, while not specifically stated by most, is implied by several authors in their discussions of the adaptive value of beetle activity patterns. Data presented here for 2 tenebrionid species, *Eleodes hispilabris* Say and *Eusattus muricatus* LeConte, indicate that reproductive cycles may, in some species, be independent of rainfall. These data also suggest that surface activity should not be assumed to mean that these beetles are in reproductive condition.

In addition, sexual differences in the timing of *E. muricatus* activity, and sexual differences in reproductive effort indicated by gonadal development, are presented for both species.

METHODS

Beetles were collected from the Sevilletta sand dunes of central New Mexico on 6 dates during 1981. Seasonal comparisons were made between beetles collected between 1600 and 1700 hours. One sample, made during the morning activity period, was compared to evening collections. Individuals were located visually. No attempt was made to standardize collection, though all observed beetles were collected. Following transport to the laboratory, the beetles were frozen. Measurements were made within 24 hours of capture using dial calipers (*E. muricatus* femur length was measured with an ocular micrometer). Body mass was measured and gonads were removed by dissection and weighed. All masses were obtained on a Sartorius 2462 balance, to 0.1 mg.

Egg volumes were estimated by length and width of 3 eggs per female, using an ocular micrometer, and volume was calculated on the assumption that the eggs were cylindrical. Mean values obtained by these procedures were used to represent egg volumes of the females from which they came. Individual egg mass was obtained by weighing 3 eggs together and dividing by 3.

To best represent the relative seasonal reproductive effort being made by beetles, seasonal data are presented as a ratio of gonadal mass to body mass. One-way analysis of variance was used to test for significance of apparent seasonal patterns. To test the possibility that body weight difference may be causing the seasonal patterns, analysis of covariance was also employed to remove the effect of body weight on seasonal patterns. In no case were results from these analyses inconsistent with those of one-way ANOVA.

RESULTS

Patterns of Reproductive Activity

Male *E. hispilabris* gonadal mass remained constant throughout the season (Fig. 1, $F=.66$; $p<.05$), whereas female gonadal mass increased until just prior to summer rains (Fig. 1, $F=24.4$; $p<.05$), after which eggs disappeared from sampled females (presumably they were oviposited). No vitellogenesis was evident during the balance of the season. This is consistent with patterns observed by Seely (1973) in 2 species of Namib Desert tenebrionids.

In sharp contrast however, *E. muricatus* appears to have several reproductive bouts during the activity period (Fig. 1; male, $F=5.8$; $p<.05$; female, $F=4.2$; $p<.05$). Both male and female gonadal mass cycle throughout this period, suggesting 3 distinct reproductive bouts, only 1 of which coincides with the rainy season.

Comparison of morning and evening *E. muricatus* collections of 2 August indicate sexual differences in activity. Males are active during both periods, while females are more active during morning hours (Table 1).

E. muricatus (although smaller) produces larger eggs than *E. hispilabris*, both by volume and mass (Table 2).

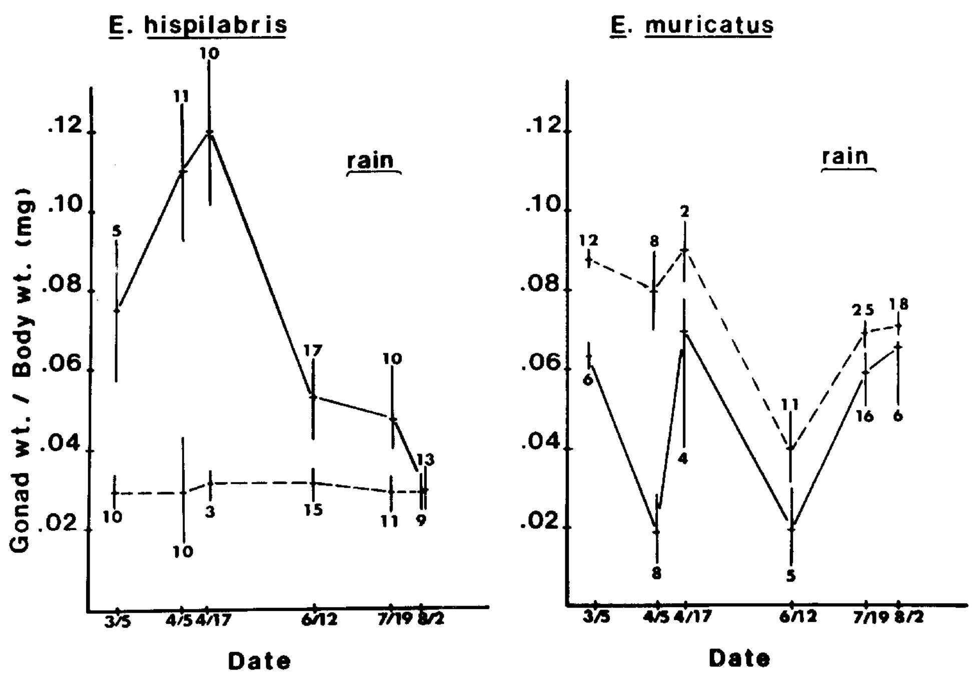

Fig. 1. Seasonal reproductive condition of *Eleodes hispilabris* and *Eusattus muricatus*. Solid lines represent females; Dotted lines represent males. Vertical bars are standard errors.

TABLE 1. COMPARISON OF ACTIVITY OF MALE AND FEMALE *Eusattus muricatus*.

	No individuals collected	
	morning	evening
male	11	19
female	22	6
	X^2=10.37; p=.001	

TABLE 2. BODY AND EGG SIZE PARAMETERS OF *E. Muricatus* AND *E. Hispilabris* BEETLES. NUMBERS IN PARENTHESES ARE SAMPLE SIZES.

	E. muricatus		*E. hispilabris*		
	MEAN	SD	MEAN	SD	
		MALE			
BODY WT. (mg)	111.1	26.81 (77)	404.2	95.23 (57)	*t = 22.58
FEMUR (mm)	3.0	0.03 (77)	9.3	0.73 (57)	*t = 6.48
		FEMALE			
BODY WT. (mg)	117.2	21.42 (45)	470.7	112.56 (66)	*t = 24.86
FEMUR (mm)	3.1	0.36 (45)	9.2	0.77 (66)	*t = 7.79
		EGG			
EGG WT. (mg)	1.0	0.18 (7)	0.42	0.05 (6)	*t = 7.86
EGG VOL. (cu mm)	1.6	0.23 (7)	0.59	0.01 (6)	*t = 10.14

*p < .001; unequal variance t-test

TABLE 3. RELATIVE GONADAL EFFORT IN 2 SPECIES OF TENEBRIONID BEETLES; (GONAD WEIGHT DIVIDED BY BODY WEIGHT).

	E. muricatus			*E. hispilabris*		
	MEAN	SE	N	MEAN	SE	N
MALE	0.07	.024	77	0.03	.008	56
FEMALE	0.05	.024	45	0.07	.054	66
		*t = 3.52			*t = 5.52	

*p < .001

Relative Gonadal Effort

Comparison of male and female gonadal effort (gonad wt./body wt.) indicate differences within and between species. *E. hispilabris* females expend a larger percentage of their biomass on this component of reproduction than their male counterparts, whereas in *E. muricatus* the reverse is true (Fig. 1; Table 3).

Discussion

Patterns of Seasonal Activity

Eleodes hispilabris reproduces on a seasonal schedule, i.e., consistent with expectations of desert tenebrionids reproduction. It lays 1 batch of eggs per year, in the rainy season. The reproduction schedule of *Eusattus muricatus* is considerably different. At least 3 oviposition bouts occur, only 1 of which corresponds to rainfall. I attribute this difference to the smaller physical size of *E. muricatus*. *E. muricatus*, unlike larger desert tenebrionids, is a sand diver (Kenagy and Stevenson 1982, personal observation), i.e., it burrows into sand dunes. This behavior may limit the overall physical size of this species and thus the body cavity available for egg storage. Such a restriction directly limits *E. muricatus* clutch size. Vitt (1981) found a similar restriction on clutch size in crevice dwelling lizards. Recently Stearns (1980, 1984) stated that body size constraints may result in the occurrence of life history characteristics that are inconsistent with present models. Oviposition, at times other than the optimum, by *E. muricatus* may be a case in point. Egg size appears to have responded to the oviposition strategy. Larger size of *E. muricatus* eggs may be an evolutionary response to oviposition at suboptimal times, increasing survival of eggs under dry desert conditions. Not only would developing larvae have more nutrients (presumably leading to greater size at hatching), but large eggs have the additional advantage of a smaller surface to volume ratio and are thus better able to resist desiccation.

Relative Gonadal Effort

Typically females expend a greater proportion of their total reproductive effort in gonadal effort than males. Males expend most reproductive energies in pursuit and courtship. *Eleodes hispilabris* exhibits such a pattern.

Eusattus muricatus however shows an atypical pattern of gonadal effort by males exceeding that of females. While no observations of courtship behavior have been made, this difference in the gametic/nutrient aspect of reproductive effort indicates that other parameters of the mating system may be different also. Sex role reversal has been documented in other insect groups (Gwynne 1981, 1983, 1984, Smith 1979). In Gwynne's studies, male katydids contributed to offspring production by depositing a spermatophore which, because it contained nutrients that increased egg production. Such spermatophores are formed from the contents of the male accessory glands (Leopold, 1976) which comprise the majority of male gonadal mass. Male *E. muricatus* gonadal mass may represent a large investment and thus may, as in the case of the katydids studied by Gwynne, result in sex role reversal in this species.

To propose that large gonadal mass represents a large paternal investment assumes that accessory glands are emptied during mating, which may not be the case. Large accessory glands may allow multiple mating within a short span of time. This study indicates a high degree of mating synchrony within *E. muricatus*. If males are "typical" (i.e., they do little to affect the number of eggs produced by a mate) their reproductive success is limited by the number of matings they attain (see Thornhill and Alcock (1983) who review the evolution of mating systems). If the female receptivity within the population is limited to a short time period, males able to mate repeatedly would be at a selective advantage.

More work on tenebrionid beetle reproduction would improve our general understanding of insect mating systems and clarify activity patterns of these beetles.

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PROLONGED COPULATION IN *PHOTINUS MACDERMOTTI* WITH COMPARATIVE NOTES ON *PHOTINUS COLLUSTRANS* (COLEOPTERA: LAMPYRIDAE)

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ABSTRACT

Photinus macdermotti Lloyd fireflies engage in copulations that are prolonged in comparison to those of *Photinus collustrans* LeConte. Coupling is prolonged to accommodate protracted ejaculate transfer and as a probable male adaptation to reduce sperm competition.

RESUMEN

Las copulaciones de la luciérnaga *Photinus macdermotti* Lloyd, son bastante prolongadas comparadas con las de la *Photinus collustrans* LeConte. Apareamiento es prolongado para acomodar la transferencia de la esperma y como una probable adaptación masculina para reducir la competencia de esperma.

INTRODUCTION

Previous studies of *Photinus macdermotti* Lloyd fireflies have mostly focused on flash communications (Lloyd 1966, 1979, 1981, 1984). This study begins at the behavioral point where those ended: with pair formation. Characteristics of *macdermotti* copulations are here documented and compared with those of *Photinus collustrans* LeConte matings. *P. collustrans* provide a base-line case for comparative studies of firefly sex, because almost all females are monogamous, and males typically invest minimal time and material in mating (Wing 1982, 1984). By contrast, *macdermotti* copulations are shown here to be prolonged. Explanations for this extended coupling are sought through studies of other *macdermotti* characteristics, including reproductive structures, the nature of the ejaculate, and female multiple mating.