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

by

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running title: seasonal patterns of reproduction

INTRODUCTION

Tenebrionid beetles are prominent features of desert ecosystems. Considerable study of this group has taken place with interest directed toward habitat utilization (Tanner & Packham,1965, Calkins & Kirk,1975, Sheldon & Rogers,1984) and temporal patterns of activity, both on diel (Kramm & Kramm,1972, Holm & Edney,1973 Doyen & Tschinkel,1974, Hamilton, et al,1976, Smith & Whitford,1976, Kenagy & Stevenson,1982) and seasonal (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) has investigated the reproductive condition of active beetles. Her study of two Namib desert tenebrionids indicated that, like activity patterns, female gonadal development responded to rainfall patterns.

From the available data it would appear 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 two tenebrionid species, Eleodes hispilabris and Eusattus muricattus indicate 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 reproductive.

In addition, sexual differences in the timing of E. muricattus activity as well as sexual differences in reproductive effort represented by gonadal development for both species are presented.

METHODS

Beetles were collected from the Sevilletta sand dunes of central New Mexico on six sampling dates. Seasonal comparisons were made between beetles collected between 1600 and 1700 hours. 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. muricattus femur length was measured with an ocular micrometer). All masses were obtained using a Sartorius 2462 balance, to 0.1 mg.

Egg volumes were estimated by measuring the length and width of three eggs per female using an ocular micrometer and volume 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. Egg masses were obtained by weighing three eggs together and dividing by three.

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

RESULTS

Patterns of Reproductive Activity

Male E. hispilabris gonadal mass remained constant throughout the season whereas females yolk a batch of eggs until the summer rains arrive (Figure one). These eggs disappear from sampled beetles (presumably they have been oviposited) and no more vitellogenesis is evident during the balance of the season. This pattern is consistent with patterns observed by Seely (1973) in two species of Namib desert tenebrionids.

In sharp contrast to this pattern however, is E. muricattus. This species appears to have several reproductive bouts throughout the activity period (Figure one). Both male and female gonadal mass cycle throughout this period with three distinct reproductive bouts, only one of which coincides with the rainy season.

Comparison of morning and evening collections of E. muricattus indicate sexual differences in activity. Males are more evening active, with females more active during morning hours (Table one; $X = 10.37; p = .001$).

E. muricattus is a much smaller beetle than E. hispilabris (Table two). In spite of this E. muricattus produces larger eggs, both by volume and mass, than those of their larger counterpart.

Relative Reproductive Effort

Comparison of male and female reproductive effort indicate differences within and between species. E. hispilabris females expend a larger percentage of their biomass on reproduction than their male counterparts whereas in E. muricattus the reverse is true, with male expenditure exceeding those of females (Figure one; Table three).

DISCUSSION

Patterns of Seasonal Activity

Eleodes hispilabris reproduces on a seasonal schedule that is consistent with expectations of desert tenebrionid reproduction. They lay one batch of eggs per year and this oviposition bout occurs during the rainy season. Eusattus muricattus reproduction schedule is considerably different. At least three oviposition bouts occurred, only one of which corresponded to rainfall. I attribute this difference to the smaller size of E. muricattus.

E. muricattus, unlike larger desert tenebrionids, is a sand diver (Kenagy & Stevenson, 1982, personal observation), that is, it burrows into sand dunes. This behavior may limit the overall physical size of this species and thus limit the body cavity available for egg storage. Such a restriction directly limits E. muricattus clutch size. Vitt (1981) has shown a similar restriction on clutch size in crevice dwelling lizards.

Recently Stearns (1980, 1983a, 1983b, 1983c, 1984) has written that body size constraints on life history may result in the occurrence of life history characteristics that are inconsistent with present models of life history. Oviposition at times other than the optimum by E. muricattus may be a case in point. Egg size, another life history characteristic that has drawn much attention appears to have responded to

the oviposition strategy. Larger size of E. muricattus eggs may be an evolutionary response to oviposition at suboptimal times in an attempt to increase survivorship of those eggs under dry desert conditions.

Relative Reproductive Effort

Total reproductive effort by the sexes of a species should be equal (Fisher, 1958). This effort can be partitioned into either effort expended in finding a mate (ie. courtship, mate searching, including any risk involved in these processes) or maximization of fitness resulting from a mating (parental care, direct or indirect nutrient investment in gametes). This study attempts to measure the latter form of reproductive effort and I have found differences between the sexes within a species and differences between species. Typically females expend a greater proportion of their total reproductive effort in gametic effort than males with males expending energies in pursuit and courtship of females.

Eleodes hispilabris exhibits a pattern typical of many insect species in that females expend a larger percentage of their biomass on gamete production than do males. Though courtship and mating were not observed, it is assumed that males expend more effort in finding mate than females do and thus equalize their reproductive effort in this manner.

Eusattus muricattus however shows an atypical pattern in that

reproductive effort by males (measured by gonadal size) exceeds that of females. While no observations of courtship behavior have been made, this difference in the gametic/nutrient aspect of reproductive effort indicates the possibility of sex role reversal in this species. Such reversals have been documented in other insect groups (Gwynne, 1981, 1983, 1984; Smith, 1979).

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Revised

Figure one. Seasonal reproductive condition of Eleodes Hispliabris and Euasattus muricattus. Solid lines represent females. Males are represented by dotted lines. Vertical bars are standard errors.

Figure one. Seasonal reproductive condition of Eleodes Hispliabris and Euasattus muricattus. Solid line represents males. Females represented by dotted line. Vertical bars are standard errors.

Table one. Comparison of activity of male and female
Eusattus muricattus.

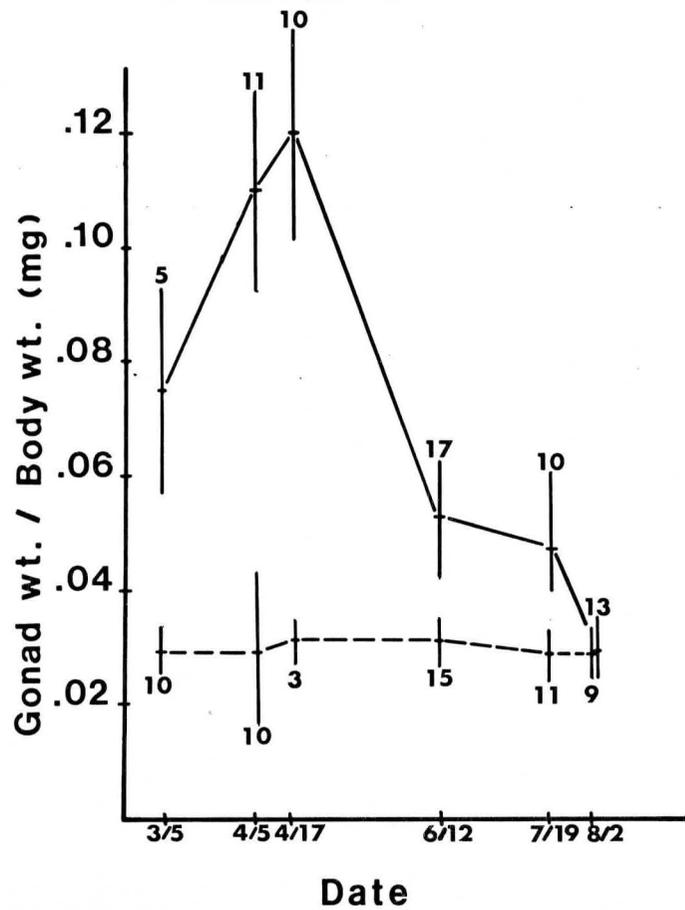
	morning	evening
male	11	19
female	22	6

$X = 10.37; p = .001$

Table two. Body and egg size parameters of *E. muricattus* and *E. hispilabris* beetles. Numbers in brackets are sample sizes.

	<i>E. muricattus</i>		<i>E. hispilabris</i>	
MALE	mean	SD	mean	SD
Body weight (mg)	111.1	26.81 (77)	404.2	95.23 (57)
Femur length (mm)	3.0	0.03 (77)	9.3	0.73 (57)
FEMALE				
Body weight (mg)	117.2	21.42 (45)	470.7	112.56 (66)
Femur length (mm)	3.1	0.36 (45)	9.2	0.77 (66)
<hr/>				
Egg weight (mg)	1.0	0.18 (7)	0.42	0.05 (6)
Egg volume (cu mm)	1.6	0.23 (7)	0.59	0.01 (6)

E. hispilabris



E. muricatus

