

**SOCIAL ORGANIZATION OF THE NAMIB DESERT  
TENEBRIONID BEETLE *ONYMACRIS RUGATIPENNIS***

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**Abstract**

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*Onymacris rugatipennis* is one of several diurnal adesmiine tenebrionid beetles living in various habitats near Gobabeb in the Namib Desert, South West Africa.

Late in the active part of the female daily cycle and before they dig into the ground, females are often persistently followed by one or more males. Intruding male challenges to followers are commonplace. Following occurs during the latter phase of the morning and especially during the afternoon activity cycle. Early in these activity cycles the principle male activity is feeding. Males emerge in the morning earlier than females, and late in their activity period most males are engaged in following or attempts to dislodge other followers. Of the five diurnal adesmiine species living near Gobabeb, only the males of *O. rugatipennis* fight with one another and defend space. Their space is maintained above the site where a female has dug into the ground at midday or in the evening. Defense involves exclusion of other males from the immediate vicinity of the female. Alien males are immediately evicted, but on some occasions there are serious challenges. Pairs of males may engage in vigorous wrestling matches involving head butting, shoving, throwing, biting, and kicking. Evenly matched individuals may wrestle for over 30 min and for more than 20 falls. The winner of such encounters remains over the buried female. The last individual to hold the space in the evening may mate with the resident female. The observed behavior is not territorial in the sense that there are no mutually recognized frontiers. There is, however, exclusive use of space and aggressive defense of that space.

Social order is re-established daily. There are no persistent inter-individual bonds between males and females. Males may return to the general area but not the exact place where they held space the previous day. Many individuals move long distances from the place where they were active on the preceding day.

Larger males tend to win wrestling matches. However, males are on the average smaller than females. Since larval males live in the habitats occupied by females, adult male body size is apparently not limited by larval energy limits. Hence we conclude that small adult male body size conveys advantages which may outweigh the disadvantage in wrestling matches. Some of the possible selection relationships countering large male size are discussed.

Females reject most mating attempts by males when they are active on the surface. They exercise no choice in mate selection following burrowing. Hence the mating system results in mating by the most persistent male followers and aggressive individuals able to hold the space above the place where the female burrows into the ground.

**Introduction**

Large black diurnal tenebrionid beetles of several species are a conspicuous feature of many terrestrial desert environments in the Namib Desert of South West Africa and Angola. There is a great diversity of such species, exceeding by a wide margin the tenebrionid diversity of any other desert (Koch 1961, 1962a, b). The environments occupied by these Namib tenebrionids range from vegetationless dune crests to well vegetated riparian areas along dry sandy washes of rivers (Fig. 1). This paper describes the social organization of one adesmiine tenebrionid beetle, *Onymacris rugatipennis*, living in a riparian habitat. Certain features of the social organization of this species can be related to the daily thermal cycle, to the time budget of each sex, and to sexual selection. The tactics of aggression are described and related to specific environmental variables.<sup>1</sup>

A considerable body of literature now supports the contention that certain features of animal social organization may be related to environmental variables. This conclusion has been developed especially in the case of birds and mammals (Crook 1965, 1970; Brown and Orians 1970; Eisenberg *et al.* 1972). Other studies have

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FIG. 1. *Eragrostis spinosa* grass clumps. This is a favored evening habitat of *Onymacris rugatipennis*. The seeds are a favored food of this species.

considered the mechanism relating social organization to resources (e.g., Smith 1968; Horn 1968; Hamilton *et al.* 1967; Hamilton and Watt 1970; Kaufmann 1974; Geist 1974). These investigations deal exclusively with vertebrates. This study emphasizes the behavior of a poikilothermic insect and the role of the thermal environment and thermal preferences in establishing certain features of social organization. Such parameters have not been considered previously in analyses of the environment relative to social organization.

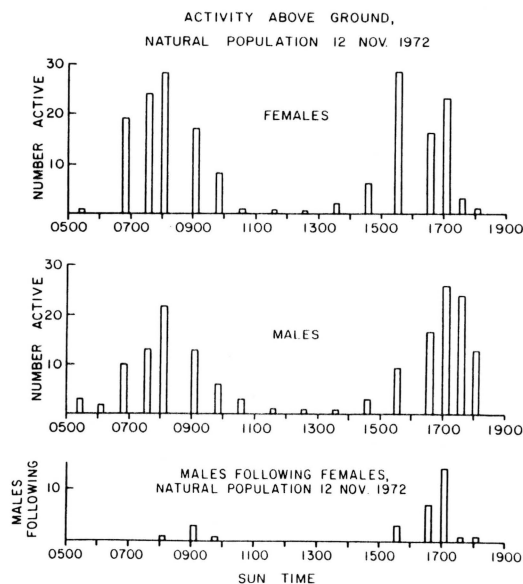


FIG. 2. Activity cycle of the tenebrionid beetle *Onymacris rugatipennis* under natural conditions in the environment shown in Fig. 1.

These observations can be related to the maxithermy hypothesis discussed in detail elsewhere (Hamilton 1973, 1975*b*). This hypothesis suggests that the activity cycle of certain animals is organized to maximize the time interval during which a body temperature of approximately 38°C can be maintained. As for most small desert poikilotherms at warm seasons this results in a bimodal activity cycle because the middle hours of the day are too hot to permit maintenance of optimal temperature levels. This is so for the diurnal adesmiine tenebrionid species living in (*Onymacris rugatipennis*, *Stenocara gracilipes*, and *Physosterna globosa*) or near (*Onymacris plana*, *O. laeviceps*) the desert riparian environment. All of these species occur within 1 km of the Namib Desert Research Station at Gobabeb, South West Africa, where these studies were conducted.

### Methods and Materials

The Kuiseb riverbottom at Gobabeb is heavily vegetated by comparison with the gravel plains to the north of the river and the almost barren sand sea to the south. Following the brief flowing of the river late in the southern hemisphere summer, forbs and grasses of diverse kinds produce heavy growth in the dry wash. Outside the wash the riverbottom is bordered by a dense *Acacia albida* forest further bracketed by an open *Acacia giraffae* woodland and scattered dense thickets of the shrub *Salvadora persica*. At various places in the dry wash there are large expanses of the grass *Eragrostis spinosa*. This perennial spiny leafless grass forms dense clumps which tend to collect sand (Fig. 1). The grass clumps are a favored habitat of *O. rugatipennis*, and most of the observations reported here were made in the vicinity of these clumps.

In addition to the systematic observation of particular behavioral activities in the field we made all day censuses of certain populations to determine the relationship of male and female activities to one another and to the environment. Censuses were made along a predetermined route at regular intervals, every hour or every half hour throughout the day. Beetle activity was noted with the aid of 10× binoculars. In the late afternoon when body temperatures are falling, beetles became less wary and they could be observed from less than a meter. Details of wrestling matches between males were concentrated at this time of day and were easily observed. The rapid sequences of behavior which comprise these interactions were recorded and subsequently analyzed.

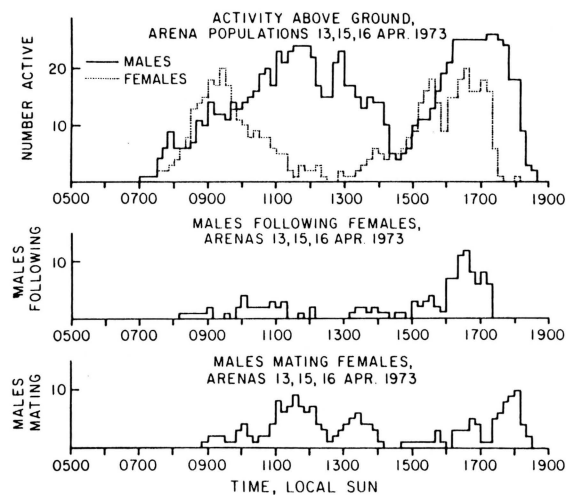


FIG. 3. Same as Fig. 2 except for a specified number of individuals placed in an arena in the natural environment.

To facilitate observation of identifiable individuals 700 adults were sexed and marked with small colored numbered discs glued to the thorax. These numbered discs are visible in several of the photographs accompanying this paper. Our marked beetles ranged widely. Over half of the marked individuals were never seen again. Many new individuals appeared in subsequent days. Sometimes we marked individuals with water colors with a small paint brush after an encounter began. On other occasions individuals could be identified for the duration of a fight by relative size, missing limbs, mud spots, and other individual characteristics.

A more detailed analysis of wrestling behavior was made by observing 300 marked individuals confined in a 10 by 4 m arena built around a small clump at *Salvadora* vegetation. This compound, near our living quarters, allowed us to habituate the inhabitants to our presence and to enhance the opportunity for close range observation.

Other observations were made in two arenas 3 m in diameter placed in the natural habitat of these insects. Both arenas were stocked with 18 numbered beetles, nine of each sex. Each group of nine beetles included three individuals each from the two size extremes and from the means for the natural population. Analysis of these observations and descriptions was enhanced by examination of 3000 ft of 16 mm film taken in the field (Hamilton 1975a).

### Results

*Onymacris rugatipennis* is, like other *Onymacris* species, a long lived beetle. Adults are active and reproduce throughout the year. There is a surge in abundance and reproductive rate following the irregular Namib rains (Seely 1973).

The daily cycle begins with all individuals buried in the dry riverbottom sands, beneath shrubs, or about the roots of *Eragrostis spinosa*. Following sunrise and the warming of surface sands the males emerge, on the average earlier than the females (Figs. 2, 3). Surface activity continues to increase as conditions for producing and maintaining body temperatures of 38°C develop (Hamilton 1973).

### Female-Male Interactions

Pursuit of females is a task which occupies considerable time (17.9% of 525 observations) for the males. Unattached males approach any moving individual, male or female. They often approach and pursue briefly males and females of another black tenebrionid, *Physosterna globosa*, common in the same environment (Hamilton and Penrith, in press). Species specific following may be interrupted for a variety of reasons, including, occasionally, successful copulation.

Following of females by males is concentrated at the end of the day (Figs. 2, 3). In the late afternoon throughout the year for the natural population the entire riverbottom is a flurry of females moving rapidly across the open sand, often well away from cover, on their way to places to burrow for the night. Males follow the same female for considerable intervals, maintaining about a body's length behind her (Fig. 4). When following, males rarely feed. Females may come upon especially favorable foods, e.g., dead nocturnal moths or other dead insects, and may linger to eat for many minutes while the male following remains in close attendance in the usual posterior position.

Males may discontinue following a female for many reasons (Table I). Persistence is more pronounced than the mean duration of following for free ranging individuals ( $\bar{X}$  = 158 sec for 28 observations, range 3 to 965 sec) might suggest. Of the 62 observations of males following females (Table I), 25 were terminated involuntarily by the male, either as a result of confusion or conflict with other males. We expect that when these studies are extended to include populations at various densities the degree of interference and confusion effects will be less and that following will be more persistent at low densities.

The temporal peak of male activity comes slightly later in the day than that for females (Fig. 2), and much later in the arena-type experiment (Fig. 3). For the field population the male activity surge is also later than that for females during the afternoon activity peak.

#### Male-Male Interactions

In this promiscuous society, relationships between a male and any particular female rarely last more than a few hours. While male "courtship" of females often seems to be chaotic and mixed with encounters between males, close and continuous observation reveals a social fabric based upon predictable and understandable behavior patterns.

#### Defense of Active Females

Males following females are frequently approached by other males. At high densities such challenges are nearly continuous. When approached, the following male moves closer to the female and may mount, grasping her with his forelegs (Fig. 5). The most frequent result is for intruding males to abandon the challenge. But sometimes intruders attempt to shove the initial follower away (see Fig. 5).

These actions, both following and challenging, have no courtship function in the sense of changing female willingness to accept or mate with a male but they do increase the possibility that a male will be with a female when she burrows into the sand.

#### Defense of Inactive Females

When females stop their surface activities for the morning or afternoon and burrow into the sand the opportunity for mating arises. A following male will continue to claim the surface immediately above the female and defend it against all conspecifics.

When focusing activities about a buried female the males do a considerable amount of excavating with their hind and middle legs; exposing the dorsal surface of the female may serve to confirm to the male the presence and location of the female. Later the sequence is reversed, and the male uses his forelegs to cover the female with sand. Once the female is covered, challenges from other males come less frequently and are less persistent. The male defense of the female may be extended to the defense of a space with weakly defined boundaries. This defense usually takes the form of radial movement from the site of the burrowed female to meet and butt approaching males, but it may also involve lateral movement. Defense of space develops only in and about the place where a female is buried, and may include nearly a square meter.

Table I. Reasons 62 male *Onymacris rugatipennis* discontinued following females in the arena situation described in the text

Reason for termination: Voluntary	Number of observations
Male voluntarily terminates, leaves female	22
Encounters another female and changes to follow her	10
Conflicts with another male	10
Encounters another pair, confusion arises	6
Male loses female	5
Male begins feeding	4
Encounters another male and changes to follow him	2
Frightened by observer	2
Copulation on sand surface	1

### *Butting*

The most frequent encounters between males involve head to head interactions in which the defending male approaches and head-butts the challenger, first pushing him, then withdrawing 2 or 3 mm to butt again (Fig. 6). Often butting suffices to induce the intruder to move on. These activities are so oriented that the head of the territorial male is directed away from the territory center, i.e., the point above the buried female. Challengers may also butt, especially if they are evenly matched in size or larger than the territory holder.

### *Overrunning*

If the intruder is persistent a more vigorous interaction may occur. In such cases, which usually follow a series of butting movements, the territorial male may make a vigorous run at the challenger, moving directly over the top of him. These charges often displace the challenger and, since the charge is invariably oriented away from the site of the buried female, it results in distal displacement of the challenger. Unlike butting, overrunning may also be made from the rear. Thus, after a male has been involved in a vigorous encounter and turns to move away he may be overrun by the resident male. Overrunning usually hastens the departure of the challenger from the vicinity of the defending male.

### *Wrestling*

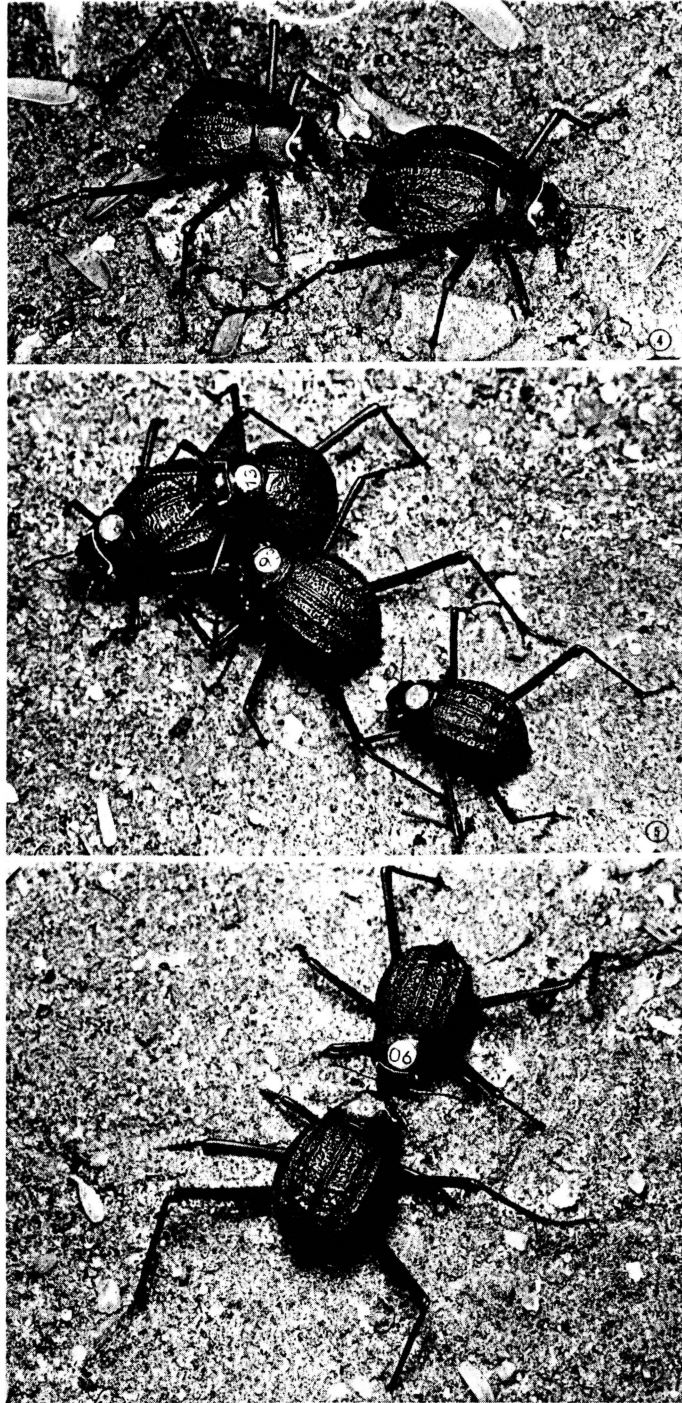
Wrestling between pairs of males initially attracted us to the question of the significance of the social behavior of *Onymacris rugatipennis*. It is more frequent and prolonged in the evening in the vicinity of vegetation clumps (Fig. 1) where males will eventually dig into the sand to spend the night. As males and females begin to concentrate in the vicinity of their roosts wrestling encounters break out. On most occasions encounters are limited to pairs of males but sometimes three or more individuals are involved. Wrestling cannot be described relative to any fixed point in space nor in terms of the directional orientation of either participant except that it begins in the vicinity of a female. Once wrestling begins, males wrestle just as vigorously regardless of where the contest may drift. Wrestling is essentially the same in all encounters. It begins with head to head butting, often causing one of the participants to be pushed backwards a few millimeters. Then one individual pushes under the other. The uppermost male seizes his opponent between the thorax and abdomen (Fig. 7). The upper male spreads his middle and hind legs well to the side. The lower male elevates his abdomen and places his head on the ground. He also takes a spread-legs position.

The object of the upper individual seems to be to topple the lower individual by pulling backwards (Fig. 8). Often just before toppling, the upper male will change the angle of his body, moving lower and pulling the end of the abdomen towards his opponent. The direction of the upset is in the direction of the uppermost individual so that in a successful throw he rolls onto his back. The usual result of an upset (93 of 112 cases) is for both participants to jump at once to their feet and immediately take a head to head position. This cycle is repeated, although the upper positions may be exchanged for the lower (Fig. 9).

Not all wrestling actions result in upsets. Often the uppermost individual is unable to throw his opponent. He may then slide over the top of his opponent or simply release his hold. Inability to throw usually results in loss of an encounter and desertion of the scene by the less effective wrestler. The winner becomes the territory holder.

### *Leg Kicking*

One common tactic by the lower male is to kick at the middle and hind legs of his opponent with his middle legs (as male 40 is doing in Fig. 9). Kicking is directed to the legs of opponent, and may be repeated many times during each bout. Kicking may serve



FIGS. 4-6. *Onymacris rugatipennis*. A male follows a female. This is the usual distance at which the male follows. 5, a female is pursued by three males. Large male 93 attempts to push away male 13, who has moved high onto the dorsal surface of female 15 and clings to her with his forelegs. Male 52 follows the action. 6, two males initiate an encounter over the spot where a female lies buried. They shove one another head to head. This behavior usually precedes wrestling.

to unbalance the upper individual so that he is unable to apply full force on the lower individual. When kicking is directed at only one side the action often comes from the back side of the leg of the uppermost individual and strikes that leg so as to move it forward.

### *Biting*

From a wrestling position in particular, one of the participants may seize a limb, antenna, or palp of his opponent. When a successful bite hold is established, it usually is not relinquished for a considerable interval, regardless of the positions of the participants. We observed one male remain with a hold on the hind leg while both participants remained on their backs for several minutes. Generally the bitten individual remains passive and it is the individual with the grasp that attempts to regain his feet while maintaining the bite hold. Although biting is seen less frequently than other aggressive behavior, it often plays a decisive role in determining the outcome of encounters.

In wrestling matches large males tend to win over small males (Table II). This insures either access to a female or in some cases the opportunity to fight with a new challenger. Hence in this context large body size and reproductive success are closely correlated.

When defeated, the loser turns to flee. The victor usually pursues the vanquished individual and may butt him on the hindmost point of his carapace. Or he may overrun his opponent and induce more rapid flight. Sometimes, especially in the late evening when both individuals have cooled and the pace of the retreat may be sluggish in spite of the greatest efforts of the victor, the victor may seize the losing male about the abdomen from above in the same position as in wrestling except that the mount is from the rear. This is essentially the same position that males take on females when other males attempt to usurp them while they are following females. Such actions spur the departure of the loser. The winning male then returns to the general vicinity of the combat and prances about high on his legs. Moments later he returns to the buried female and mates with her. He then digs into the ground for the night.

## Discussion

### *Sexual Size Dimorphism*

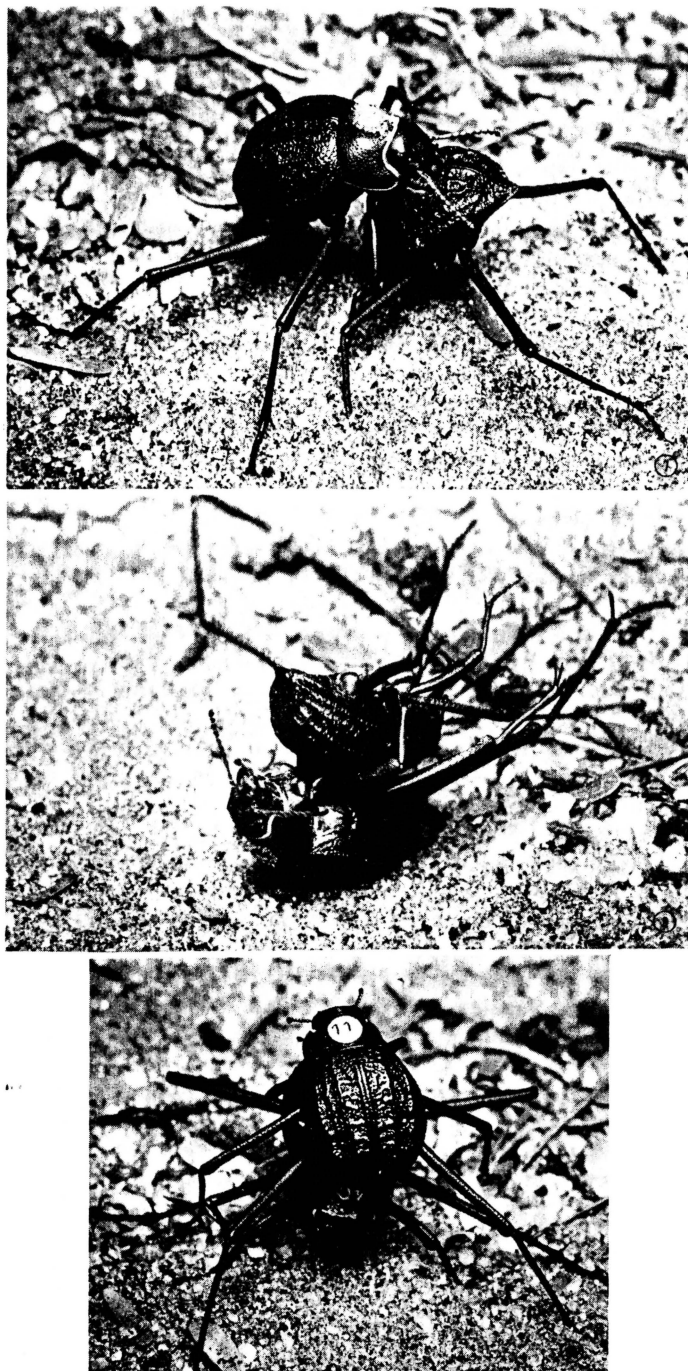
Elements of the social system of *Onymacris rugatipennis* are closely associated with the activity cycle of the two sexes. Females burrow into the sand earlier than males, both during the morning and the evening activity periods. There are several reasons why the timing of activity may be different for males and females.

Among vertebrates male-to-male competition for females has been a major factor promoting the evolution of sexual size dimorphism (Selander 1972). The degree of male

Table II. Sexual dimorphism of adult tenebrionid beetles *Onymacris rugatipennis* taken at random from the field near Gobabeb, South West Africa, and size of winners and losers in wrestling matches. All measurements were total body length to the nearest .01 mm

	Mean	Std. dev.	<i>n</i>
November 1972: Males	15.85	1.14	205
Females	17.69	1.04	155
April 1973: Males	16.19	1.13	250
Females	18.56	1.17	170
Wrestling males: Winners	17.14	1.16	33
Losers	16.27	1.13	33





FIGS. 7-9. *Onymacris rugatipennis*. Two males wrestle over the right to mate with a female buried nearby. In Fig. 7, male 40 is initiating the round from the upper position. He successfully throws male 11 (Fig. 8), who immediately takes the upper position in the next round. The time interval between Figs. 7 and 8 is 18 sec, and between 8 and 9 is 11 sec.

divergence from the female type is usually proportional to the degree to which effectiveness in active struggles between males enhances mating success (Orians 1969; Bartholomew 1970).

With the exception of certain primates, e.g., chimpanzees, macaque and rhesus monkeys, most animals fight in pairs, with larger individuals on the average dominating smaller ones. Among birds it has been argued that the usually larger body size of males insures dominance over females (Selander 1972). Most of these generalizations have been applied specifically to vertebrates.

Female beetles lay their eggs in the sand during periods of surface activity. Larvae spend their entire life below the surface. Pupation and emergence follow, establishing a fixed adult body size. There are significant seasonal changes in size for adult males and females (Table II), but the ratio of male to female size remains approximately constant. Since the environmental conditions leading to emergence as an adult are essentially the same for male and female larvae it follows that the resources to obtain the larger female body size are potentially available to males. The disadvantage of being small in wrestling encounters must thus be compensated for by some positive advantage to small male body size.

One advantage of being a relatively small male may be related to the daily activity cycle of males and females. Females are passive actors in sexual play during the surface phase of their activity cycle. Their actions focus on foraging for seeds, green vegetation, and dead insects. The males spend much time at other, courtship-related, activities such as locomotion, following, and defending females. Hence time available to them for acquiring food is limited. The daily activity cycle of this species is restricted to intervals when microclimatic conditions permit the maintenance of a narrow range of high body temperatures (Hamilton 1973). Thus male foraging time is limited by their activities for female acquisition. Small body size reduces maintenance energy requirements, thereby enhancing the opportunity to pursue females. Since males are active on the sand surface longer than females and at higher body temperatures (Hamilton 1975b), the metabolic cost per unit of weight to males relative to females is further increased.

Another hypothesis is that small body size for males is an adaptation to the more rigorous thermal environment they must encounter in the middle hours of the day. Male activity peaks later in the morning than for females and at this time body temperatures reach maximum tolerable levels (Hamilton 1973). Hence a relatively small body size might provide a thermal margin for activity at this critical time of day.

For small males to compete effectively reproductively with larger ones some males must acquire females without engaging in wrestling matches. Continuous observations of the beetles in the two 3-m arenas for 3 days showed that only 16% of the individuals engaged in wrestling matches on any given day. Only five of 49 observed matings in the arena followed wrestling encounters. While direct extrapolation to the field is not possible, the results of this experiment show that under some conditions access to females is not restricted to winners of wrestling matches.

Since the holder of the space above a buried female gains the right to mate with that female, there is probably no opportunity for a female to know the size nor identity of the male mating with her. Buried females did not refuse mating attempts. Therefore, female choice can be eliminated as a factor contributing to male body size.

### *Territoriality*

The observations reported here focus upon the general concept of territoriality. Female *Onymacris rugatipennis* defend nothing, not even the choicest morsels of food, although they may turn away or run from challengers, male and female, when they have a choice bit of fresh carrion in their mouth. Males defend against other males in a variety

Table III. Some characteristics of the *Onymacris rugatipennis* aggression system reported here (first two columns) compared with the territorial behavior of a songbird, the robin, *Erithacus rubecula* (Lack 1940), the herring gull, *Larus argentatus*, certain dragonflies (Jacobs 1955), and certain ants (Wilson 1971). Characteristics occurring sometimes but not always (in parentheses)

Characteristic	Animal					
	Male beetle, active female	Male beetle, inactive female	Robin	Herring gull	Dragonflies	Ants
Male only maintains space	+	+	+	-	+	-
Defends fixed space	-	(+)	+	+	+	+
Space secures:						
Food	-	-	+	(+)	-	+
Reproduction	(+)	+	+	+	+	+
Maintains space from day to day	-	-	+	+	(+)	+
Maintains mutual frontier with neighbor	-	-	+	+	+	-
Announces territorial space	-	-	+	+	-	-

of contexts, all related to access to females. These include following of females and seizure of the female when the following male is closely challenged, and defense of the space near buried females.

We have made a simple comparison (Table III) of the operation of the aggression system in the two alternative contexts for male *Onymacris rugatipennis*, for a songbird, the European Robin, *Erithacus rubecula* (Lack 1940), for certain ants (Wilson 1971), dragonflies (Jacobs 1955), and the herring gull, *Larus argentatus* (reviewed in Lack, 1968). *Onymacris rugatipennis* males have a relatively flexible social structure: that is, not all individuals show the same general social characteristics and the actual pattern expressed seems to be a function of the social and physical environment. The variable features of their social behavior are included in parentheses in Table III. For birds the features of territoriality vary from species to species, and the comparison to be most meaningful would have to be extended (see, e.g., Lack 1968; Brown and Orians 1970). What we wish to point out, however, is that the question: "Are these beetles territorial?" is not meaningful either for descriptive purposes or in making comparisons. These beetles share some behavioral characteristics with birds and other territorial animals. They diverge in other ways. The special nature of the aggressive system of these beetles apparently functions to enhance the probability that individual males will mate with a female, perhaps particular females. Defense of space is not involved in feeding activities. A scramble for food that is arranged in an indefensible way occurs instead of aggressive defense of food resources.

The behavior of other *Onymacris* species relative to their environment and social tactics may show why some of them make no attempt to defend space in any context.

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