

such as the brown shouldered lizard *Uta stansburiana*, additional internal shields (14, 15) intercept even more solar radiation. Without these shields, small lizards in their light phase would probably receive damage, immediate or long-term, to internal organs from radiation. Reflectivity change and its associated component of thermoregulation, in small to medium-sized diurnal desert lizards, may be possible only because of the presence of one or more underlying radiation shields.

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16. The amount of transmitted energy shown in Table 1 was computed as follows. Declination of the sun for each hour of the day on 22 June at 35°N was obtained from (19). Solar declination was converted to air mass using Table 1 in Gates (20). The energy available in the visible and ultraviolet as a function of air mass, that is, time of day, was determined by integration of the appropriate portions of Fig. 2 in Gates (20). The ultraviolet and visible energies available at each hour were plotted on separate graphs as a function of time of day. These graphs were then integrated over the time interval 9 a.m. to 4 p.m. to give the total energy available. This available energy was multiplied by the percentage of transmission of the body wall for ultraviolet and visible light, respectively, to give the values in Table 1. These values are conservative because the spectral curves in Gates (20) are for direct sunlight only and do not include scattered skylight. Visible light available from 9 a.m. to 4 p.m. on 22 June at 35°N latitude = 6.9×10^9 erg cm⁻². Ultraviolet light available from 9 a.m. to 4 p.m. is 1.09×10^9 erg cm⁻².
17. Because of the pronounced ultraviolet scattering by the atmosphere (18), shade seeking and posture changes will not reduce the radiation intensity as much. An estimated reduction of one-third for ultraviolet light instead of one-fourth for visible light seems reasonable.
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Mole Rat *Spalax ehrenbergi*: Mating Behavior and Its Evolutionary Significance

Abstract. *Mating behavior of the subterranean mole rat, Spalax ehrenbergi, consists of three distinct stages—agonistic, courtship, and copulation. Spalax sexual behavior reflects certain cricetid affinities, some features general in rodents, and others presumably related to its subterranean, territorial life. Within four groups of Spalax ehrenbergi, each with different numbers of chromosomes, recently found in Israel, mating behavior seems to provide partial reproductive barriers. Selective matings between chromosome forms may complement a cytologic isolating mechanism to prevent widespread natural hybridization.*

The mole rats, genus *Spalax*, are subterranean rodents comprising the monotypic family Spalacidae. Little has been reported on the biology of natural populations of *Spalax* (1), nor is its classification satisfactory (2). The currently accepted taxonomy (3) recognizes three species, *Spalax microphthalmus*, *S. leucodon*, and *S. ehrenbergi*, distributed from southeast Europe through the Middle East to North Africa.

Phenotypic variation in *Spalax* is relatively small, in contrast to its considerable genetic variation. Chromosome variation in *S. leucodon* (4) and *S. ehrenbergi* (5) is remarkable. Four forms of *S. ehrenbergi* occur in Israel and neighboring areas having diploid numbers (2n) 52, 54, 58, and 60, respectively (5). These mole rats are distributed clinally and parapatrically from north to south, along biogeographic regions of increasing aridity, probably reflecting adaptive systems. The 2n = 52 form ranges in the Upper Galilee Mountains; 2n = 54 form is found in the Golan Heights and Mount Hermon; 2n = 58 form is found in central Israel; and 2n = 60 form is found in Samaria, Judea, and northern Negev.

The relative rarity of natural hybrids, karyotypic homozygosity, and the mating trials reported here suggest that the four forms are probably sibling species. If this hypothesis is substantiated, Pleistocene speciation of *Spalax*, masked by convergent morphological adapta-

tions to subterranean life, might have been operating on a larger scale than hitherto assumed. We now report mating behavior of *Spalax* which suggests taxonomic affinities and the operation of ethologic barriers to reproduction between chromosome forms.

Mating experiments were conducted with adult animals of all chromosome forms, collected across Israel from August through November 1967. Each mole rat was kept in a separate cage to prevent casualties. Experiments were conducted in aquaria (70 by 35 cm) with a 5-cm layer of sawdust. For tests, animals were transferred to each other's cage, male to female and vice versa. Observations were recorded on movies, color slides, and tape recorder. When copulation occurred it was usually interrupted before ejaculation to save females for further tests. Description of copulation is based on three matings which were allowed to proceed to termination. Of the three females, one became pregnant but died several days later; the other two were not pregnant.

Seventy-seven mating trials were conducted on 17 females and 13 males, including animals of different chromosome forms. Only nine females were receptive. Receptivity was determined on the basis of behavioral, not vaginal, estrus. Copulation was achieved in 15 trials, involving 8 of 20 homogametic and 7 of 45 heterogametic tests. Homogametic tests involved partners of the same chromosome forms, whereas

heterogametic tests involved different chromosome forms.

Three distinct stages characterize the mating of *Spalax*: (i) agonistic (hostile), involving both attacks and fleerings; (ii) courtship; and (iii) copulation.

When a male and a female met, an initial characteristic defensive posture was assumed by each (Fig. 1A). This was followed by a series of attacks and fleerings. Confrontation involved exposure of incisors ready to bite. The male usually leaped and bit first, frequently in his partner's nasal region. Sometimes the male growled in a low-pitched voice, while the female cried in a high-pitched voice similar to that of the young. Receptive females did not attack but posed in a defensive posture. Nonreceptive females sometimes kept attacking and fleeing, calling vigorously and biting the male severely if he kept chasing them. Pregnant females uttered a low-pitched, trembling call, like ringing bells, which may be an avoidance signal. Between defensive displays either sex, but particularly males, roamed around, digging, eating, scratching, teeth-chattering, and climbing the walls of the cage.

The agonistic stage was usually prominent, yet it varied widely in pattern, intensity, and duration; rarely was it omitted. Bitings were significantly more frequent in heterogametic than in homogametic matings ($\chi^2_{(1)} = 8.85$; $.01 > P > .001$) (Table 1). The agonistic stage lasted from 0 to 15 minutes, averaging 8.3 minutes in 12 trials that achieved copulation. When either sex was not ready to mate, it lasted for hours, sometimes ending in casualties. When both were ready to mate, a dramatic switchover took place and courtship ensued.

Courtship was usually initiated by the male, though sometimes a female in full estrus was the initiator. Courtship started with partners facing each other with withdrawn incisors. They nuzzled each other gently, uttering a series of barely audible, trembling calls; vociferous cries were uttered only by females. The male caressed the female's head, sides, and entire body. The female remained sometimes passive while the male pulled her skin or pushed her body. Sometimes, the female kept crying, licked the male, and turned sideways to him; she then presented her back so he could sniff and lick her genitalia (Fig. 1B). Sexually vigorous males actively licked, caressed, pulled, pushed,

Table 1. Mating behavior of *Spalax ehrenbergi* in homogametic and heterogametic matings.

Type of mating	Tests (No.)	Matings with agonistic behavior		Copulations (No.)
		Bitings	No bitings	
Homogametic	20	4	15	8
Heterogametic	45	25	15	7

bit gently, and stepped over the female's head. Frequently the male shivered and called tremblingly in front of the female. Copulation did not ensue unless both partners were ready to mate.

The courtship stage was not continuous; partners parted and met time and again. During pauses, both sexes sometimes licked their own genitalia. Upon reencounter, feeble fights sometimes occurred, but courting soon resumed with increased efforts. Receptive females reacted promptly by licking the male and crying in a high-pitched voice.

In seven heterogametic matings, receptive females solicited courtship, but males did not respond.

The courtship stage varied in pattern, intensity, and duration both within and between chromosome forms. Within the latter, individual variation was remarkable. Some males tried to mate hastily before the female was fully receptive. Others displayed remarkable courting abilities and patience. Most males fell in the middle range, performing the male routine adequately to induce females to copulate. Courtship lasted from 8 to 55 minutes, averaging 21.5 minutes in 12 trials that achieved copulation.

Mounting, which starts the copulation stage, is attempted infrequently at first to test the female's receptivity. Some sexually excited males tried to copulate with the female's head. Normally, however, mounting started once the female presented her back to the male. She may have sniffed his genitalia before accepting him. Sometimes she moved away soliciting more courtship. Active courtship was resumed between the first mounting attempts. A high-pitched cry emitted by the female, as in courtship, continued frequently throughout the copulation stage.

First mounts were usually unsuccessful with no attempted intromission. The male mounted the female from behind, clasping her lumbar region with his front limbs (Fig 1C). He then exercised a series of rapid probing pelvic thrusts mostly without intromission. A fully receptive female raised her hindquarters and maintained this posture until the male dismounted, thus permitting intromission to take place. Frequently both sexes licked their genitalia thoroughly after the male dismounted, particularly after intromission. Between mountings a female often lay on her back while the male palpated her. Frequency of mountings increased with time. Rate of thrusting was reduced as the male achieved intromission, but each thrust was deeper and more energetic. Intromissions were brief but repeated. Copulation lasted 20, 45, and 90 minutes in three tests, the last one involving more than 60 mounts. This male kept copulating with a thoroughly exhausted female, and when she lowered her pelvis to prevent further intromission he "copulated" with her head and sides. An average mount lasted 10 seconds (range, 3 seconds to several minutes). Sometimes the female crawled during copu-

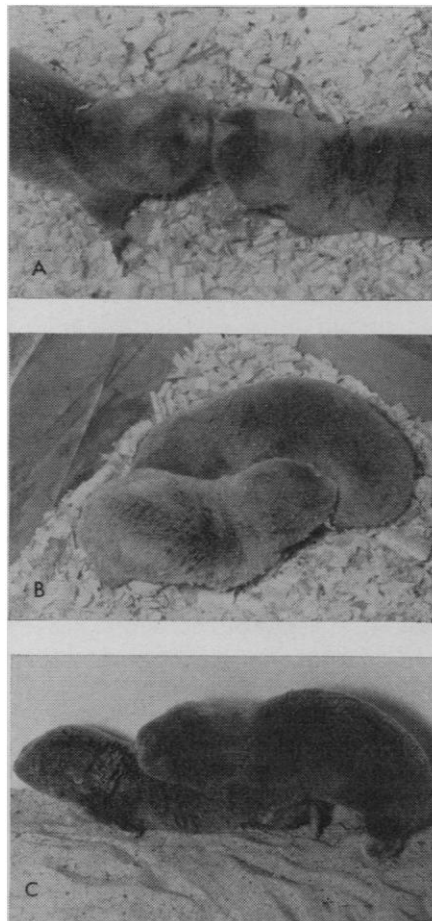


Fig. 1. Mating behavior of *Spalax ehrenbergi*. (A) Agonistic display; (B) courtship; and (C) copulation.

lation carrying the male on her back. After a varied number of intromissions the male gripped the female strongly, inserted his penis deeply, ejaculated, and then left her. He paid no attention to her after ejaculation. Usually he started eating eagerly, being indifferent to her even if she continued to solicit courtship. Yet no further agonistic behavior ensued. Additional copulations were observed sometimes within several hours.

Copulation was highly stereotyped in each sex and was the least variable stage. Nevertheless, individual variation was apparent in the intensity and subtle copulatory activities. The percentage of trials terminating in copulation was significantly higher in homogametic than in heterogametic matings ($\chi^2_{(1)} = 4.66$, $.05 > P > .025$) (Table 1).

Certain aspects of the mating behavior of *Spalax* reflect cricetid affinities, whereas others are common to several unrelated rodents (6). The copulatory behavior of *Spalax* recalls that of *Mesocricetus auratus* in the rear mounting, long duration, repeated mounts, and preejaculatory intromissions. Similar agonistic precopulatory behavior has been reported in *Microtus californicus* and other microtines. A prolonged courtship also occurs in *Microtus californicus* and *Cricetus cricetus*. Finally, remarkable individual variation characterizes also the mating behavior of *Microtus californicus*. Varied vocalizations function in sexual behavior of many unrelated species. Yet, despite cricetid affinities the complex of activities comprising the mating ritual of *Spalax* exhibits specializations presumably linked to its subterranean, highly territorial habits.

Elaborate breeding mounds are built by females in nature during the breeding season of *Spalax* from December to April (7). Encounters between the territorial males and females of *Spalax* elicit aggressive behavior in the laboratory, and presumably also in nature, regardless of sex or season. The sexes are found together in breeding mounds only during the winter reproductive season. Otherwise, males have separate, much simpler mounds than the breeding mounds of females. Copulation in nature is presumably effected within the breeding mounds. It is suggested that the elaborate courtship of *Spalax* may have evolved in order to overcome hostility which characterizes the encounter of the sexes and to induce females to copulate.

Mating behavior is of cardinal importance as an ethologic isolating mechanism (8), and may have played an important role in speciation of *Spalax*, concomitant with cytologic mechanisms (5). First, aggression is much more pronounced in the agonistic stage of heterogametic than homogametic matings, when frequency of bitings is used as an index of aggression. Second, copulations proved significantly more frequent in homogametic than in heterogametic matings (Table 1). If these trends are substantiated on a larger scale by assaying all possible combinations, they may indicate selective matings between chromosome forms. The ethologic barriers to reproduction may prove greater the larger the difference in chromosome numbers. They may complement a cytologic isolating mechanism operating to prevent widespread natural hybridization.

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Mimicry of Hymenoptera by Beetles with Unconventional Flight

Abstract. *Flower-visiting beetles of the genus Acmaeodera (Buprestidae) bear a striking resemblance to Hymenoptera in flight. Unlike most other beetles, they fly with their membranous hindwings only, and their forewings, which are inseparably coupled and permanently held over the abdomen, bear color markings commonly found on the abdomens of bees and wasps.*

In Arizona and in Florida, we have noticed certain flying insects that appeared to be bees or wasps, but which on close inspection turned out to be harmless beetles of the genus *Acmaeodera* (Buprestidae) (1).

Ordinarily, when beetles fly, they spread apart their hard front wings (elytra) and hold them out to the sides, relying for propulsion on the rapid beat of their hindwings (2). Buprestids, as a group, conform to the rule (Fig. 1A). But in *Acmaeodera*, the front wings are inseparably coupled along their middorsal junction (through a tight-fitting tongue and groove joint), and they are permanently restricted to their resting position over the back of the abdomen. *Acmaeodera* fly with their membranous hindwings only, without the usual pair of spread elytra projecting conspicuously from the sides (Fig. 1B). Bees, wasps, and other Hymenoptera, also fly with what ap-

pears to be a single pair of membranous wings (actually, they use all four wings, but the two of each side are hooked together and beat as a unit). Thus, through the simple expedient of retaining the elytra over the back, *Acmaeodera* achieve the image of hymenopterans in flight. For aerodynamic and other reasons, the expedient may not have been so simple to evolve. It called for special modifications, of which one—emarginate elytra (Fig. 1C) that permit the hindwings free motion at their bases during flight—is readily apparent.

An obvious diagnostic character of many bees and wasps, and one of the few reliable ones for when they are flying, is the conspicuous pattern of transverse colored bands (usually yellow, red, or white) that adorns their abdomen. *Acmaeodera* appear to imitate this pattern, although in their case the markings are on the elytra which