

Pup Shoving by Adult Naked Mole-Rats

Theodore Stankowich & Paul W. Sherman

Department of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, NY, USA

Abstract

Adult naked mole-rats (*Heterocephalus glaber*) characteristically perform an unusual behavior toward young: they shove small pups frequently and vigorously around the nest. We studied 15 litters in five captive colonies to quantify which adults shove pups, changes in shoving frequencies as pups develop, how external disturbances affect pup-shoving frequencies, and behavior of juveniles that were not shoved as pups. In all litters and colonies the breeding female shoved pups significantly more often than any other individual. Breeding females also shoved adult colony mates, but at far lower rates than they shoved pups. Breeding males shoved pups about half as often as did breeding females. Together, the parents shoved pups ten times more often than did nonbreeders. Frequencies of pup shoving peaked when pups were 3–4 wk old, roughly coincident with weaning. When colonies were disturbed experimentally, frequencies of pup shoving increased dramatically, whereas rates at which nonbreeding adults were shoved decreased sharply. We separated four newly-weaned litters and raised half the pups apart from their colony. When these litters were reunited 4–9 wk later, the unshoved (experimental) pups were the same size as the frequently shoved (control) pups, but the unshoved pups were significantly less likely to flee from a disturbance. Shoving of small pups encourages them to flee from danger, and also may enforce weaning.

Corresponding author: Paul W. Sherman, Department of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, NY 14853, USA. E-mail: pws6@cornell.edu

Introduction

Naked mole-rats (*Heterocephalus glaber*) are bathyergid rodents that inhabit arid regions of north-eastern Africa (Honeycutt et al. 1991a; Jarvis and Sherman, 2002). They live in subterranean colonies that typically contain 75–80 individuals, but sometimes exceed 250 individuals (Brett 1991; Lacey and Sherman 1997;

Braude 2000). Naked mole-rats are notorious because their social system fulfills the three criteria that define eusociality in insects (Jarvis 1981; Alexander et al. 1991; Sherman et al. 1995): namely (1) colonies are extended family groups, with overlapping generations; (2) reproduction is usually restricted to one female and one to three males per colony; and (3) nonbreeders cooperate to excavate and maintain the colony's burrow system, to forage, and to feed, care for, and defend the breeding female and her young (Sherman et al. 1991, 1992).

Cooperation in naked mole-rat colonies has been studied extensively (e.g. Lacey and Sherman 1991, 1997; Jarvis and Sherman 2002); however, colony life is not always harmonious. Conflicts occur frequently, often instigated by the breeding female, who is the largest, most active and aggressive individual. As she moves through the tunnels, the breeding female often shoves nonbreeders and then passes over (steps on) them (Clarke and Faulkes 1997). Breeding females rarely shove their male mate(s), but they shove nonbreeders (both sexes) at 12 times the hourly rate at which breeding males shove nonbreeders and almost 400 times the rate at which nonbreeders shove each other (Reeve and Sherman 1991). Larger, older nonbreeders are the primary targets of the breeding female's aggression (Reeve and Sherman 1991; Reeve 1992; Jacobs and Jarvis 1996). These are the least likely individuals to spontaneously engage in colony maintenance activities and the most likely to attempt supersedure of the breeding female. Occasionally shoving matches between the breeding female and large nonbreeders escalate into deadly fights for reproductive dominance (Lacey and Sherman 1991; Jarvis 1991; Clarke and Faulkes 1997, 2001).

Adult naked mole-rats usually are gentle with small pups. This makes sense because maltreatment of pups could reduce both the colony's future work force and individuals' inclusive fitnesses, as colonies are extended families of close relatives (Faulkes et al. 1990, 1997; Reeve et al. 1990; Honeycutt et al. 1991b). Moreover, young pups are neither a threat to breeders' dominance nor competitors for food or digging opportunities. Surprisingly, therefore, adult naked mole-rats often perform an unusual, seemingly aggressive behavior toward young: they shove the pups frequently and vigorously in and around the nest. As described by Lacey et al. (1991, p. 231) the behavior involves

'an adult shoving the blunt, anterior end of its muzzle (with the mouth closed) against the body of a pup. The adult's head vibrates rapidly side to side, and its body jerks forward with each push. As a result of contact with the adult's muzzle, the pup is knocked several centimeters away from the adult, sometimes with such force that the pup is lifted into the air. Pushes are usually repeated in rapid succession such that the pup is often moved 15–20 cm.'

Shoving of pups has been observed at least occasionally in every colony and litter that has been studied in captivity, implying that it is a normal aspect of juvenile development (Jarvis 1991; Lacey and Sherman 1991; O'Riain 1996). The behavior is directed specifically at pups — it does not simply result from young accidentally wandering into a shoving match between adults. Adults do occasionally kick pups sharply while sweeping the tunnels clear of debris, but

in those cases pups happen to wander up behind an active sweeper, and the adults' contact with the pups appears to be inadvertent.

In contrast to the many studies of shoving among adult naked mole-rats, shoving of pups has not been systematically investigated. We therefore set out to quantify details of pup-shoving behavior by directly observing and videotaping colonies. Data were analyzed to address four specific questions: (1) Which individual colony members and subgroups (breeders, nonbreeders, males, or females) shove pups most often? (2) How does the frequency of shoving change as pups develop? (3) Does pup-shoving frequency change when disturbances occur? (4) Does being shoved affect the subsequent behavior of juveniles? Answers to these questions enabled us to infer the likely functions of this unusual behavior.

Methods

Study Animals and Husbandry

Between Oct. 1990 and June 2001 we studied behaviors of 15 litters that were born in five captive *H. glaber* colonies at Cornell University (Tables 1 and 2). Founders of these colonies had initially been captured during 1980–1990 in south-eastern Kenya, near Mtito Andei (Colonies K and TT), and north-central Kenya, near Lerata (Colonies 100, 1200, and 1200C) (see Honeycutt et al. 1991a). Each colony had only one breeding female and one breeding male during our observations. Breeders and large nonbreeders were tattooed for visual identification; smaller nonbreeders and pups were marked with indelible ink.

Colonies were housed individually in artificial tunnel systems, ca. 7–10 m long and made of transparent Plexiglas tubing (4.5 cm inside diameter) interspersed with three Plexiglas boxes (20 × 20 × 12 cm) used as food, nesting, and toilet chambers. Wood shavings (untreated aspen) were provided as nesting material. Toilet boxes were scrubbed daily with a dilute bleach solution and shavings were

Table 1: Litters monitored for shoving behavior in this study

Colony	Date of birth	Pups (n)	Adults (n)	Observations
1200C	3 Jan. 1999	6	3	D, V
	22 Mar. 1999	10	9	D, V
	26 Nov. 1999	11	19	D, V
1200	26 Feb. 1996	4	27	D
	28 May 1999	7	4	D
	6 Jan. 1999	9	10	D
100	10 Oct. 1996	5	24	V
	27 Dec. 1996	6	29	D
K	26 Oct. 1990	6	19	V
	17 Feb. 1998	5	15	D
TT	5 Feb. 1991	5	28	V

D = Disturbance trials; V = Videotaped trials.

Table 2: Litters studied in the split-litter experiments (2000-01)

Litter	Colony	Date of Birth	Control n	Experimental n	Age isolated	Age returned	Duration (d)
1	1200	16 Jan. 2000	2	2	28	91	63
2	1200C	15 Feb. 2000	5	4	24	51	27
3	100	28 Feb. 2001	4	4	58	110	52
4	1200	12 Apr. 2001	5	4	23	65	42

replaced. The animals were fed ad libitum amounts of various tubers (e.g. sweet potatoes, carrots, jicama), supplemented with fruit (apples, pears, bananas), vegetables (lettuce, beans, corn), and baby cereal laced with vitamins. To simulate the subterranean environment, the rooms containing the tunnel systems were maintained at 30–32°C and 40–60% relative humidity. A few lamps equipped with 25-W red bulbs provided additional heat and dim illumination.

Behavioral Observations

Initial descriptions of pup shoving (e.g. Lacey et al. 1991; Lacey and Sherman 1991) were based on direct observations (i.e. an observer was present continuously in the colony room). Naked mole-rats are sensitive to foreign scents, sounds, and substrate vibrations (Jarvis and Bennett 1991; Francescoli 2000), so it is conceivable that the human presence affected shoving behavior. To find out, we remotely videotaped behaviors of adults toward five litters of pups in four colonies (two from Colony 1200C and one each from Colonies 100, K, and TT).

Videotapes were made using a Javelin CCTV black-and-white camera (Javelin Electronics, Torrance, CA) with an 8.5 mm, 1:1.5 lens. The camera was mounted on a tripod with the lens 45 cm above the transparent lid of the primary nestbox; the VCR was located in another room. The camera's field of view included the entire base of the nestbox and 4–6 cm of connecting tunnels. The camera was activated ≥ 2 h before taping began, and there was no further human contact with the mole-rats until the session was over. At the appointed time the VCR was turned on and the videotape was allowed to record until it stopped about 2 h later. Occasionally an unexpected disturbance occurred (e.g. a loud noise from an adjacent room) that caused the mole-rats to scramble out of the nest and run around excitedly. If a disturbance occurred during the first hour of taping the trial was aborted, and if it occurred in the second hour only behaviors prior to the disturbance were analyzed.

Videotapes were made when pups were 10–59 d old. Pup mortality prevented us from videotaping all five litters for the same length of time, but different litters were monitored for overlapping time periods. In total, 47.8 h of usable videotapes of pups were available from Colony 1200C, 25.3 h from Colony K, 22.9 h from Colony TT, and 19.8 h from Colony 100. We also analyzed shoving among adults, using 9.4 h of videotapes from Colony 1200 and 4.6 h from Colony 1200C.

Disturbance Trials

Preliminary scoring of the first few videotapes revealed that pup shoving frequencies indeed were substantially different (lower) when no observer was present than when a person was in the colony room. Human presence often coincides with disruption to captive colonies, such as cleaning toilets and tunnels, adding nesting material, or feeding the animals. To quantify effects of the observer's presence, from Oct. 1996 to Feb. 2000 we directly observed shoving in eight litters from four colonies (three each from Colonies 1200 and 1200C, and one each from Colonies 100 and K) when pups were 10–59 d old. We also recorded shoving of nonbreeders by the breeding male and female.

We started observations 2 h after the last human contact with a colony. An individual quietly entered the room and sat in a chair positioned <60 cm from the nest box. For the next 20 min, the time, initiator, and location of every shove seen anywhere in the colony was recorded. To standardize the observer's smell and behavior, the same individual participated in all trials, wore the same shirt (which remained in the lab and was used solely for these experiments), and used the same unscented hair products and soaps. At the end of the 20-min observation, the person tapped five times on the lid of the nestbox. This caused adults to flee the nest and mill around in the tunnels. Subsequently, the observer usually cleaned the toilet box, which caused additional disruption.

We do not know how often direct disruptions of a colony's nest occur in nature. Few mammalian predators could excavate nest chambers, which are located deep underground (Brett 1991b). However, rufous-beaked snakes (*Rhamphiophis oxyrhynchus*) and sand boas (*Eryx colubrinus*), which are important mole-rat predators (Hill et al. 1957; Braude 1991, 2000; Brett 1991a), enter colonies through open volcano holes and might move quickly enough to gain access to nests before being attacked and repelled by the mole-rats. The fact that the mole-rats typically excavate 'bolt holes' blind-ended tunnels that descend steeply from within nest chambers (Brett 1991b), implies that emergency escapes from the nest sometimes are necessary. If so, naked mole-rats' responses to disturbances of their nest in the lab may simulate what occurs in the wild.

Split-Litter Experiment

To assess the effects of being shoved on subsequent behavior of juvenile mole-rats, we randomly divided four litters approximately in half (Table 2) before high rates of shoving occurred. One randomly chosen sub-group from each litter (the 'experimental' pups) was removed from its natal colony and placed into a holding apparatus consisting of two Plexiglas boxes connected by a short tunnel. The apparatus was set up <1 m from the natal nestbox. Pups in the other sub-group ('control' pups) were handled briefly and returned home.

Experimental and control pups were treated identically and fed the same foods. To ensure that the experimental pups maintained physical and chemical contact with their colony, soiled nesting material from the natal colony was

placed in the experimental apparatus daily along with one juvenile sibling (a member of the previous litter). We chose juveniles as 'babysitters' because they rarely shove pups, although they readily flee from disturbances. Babysitters were exchanged daily so that experimental pups contacted multiple members of their natal colony.

To confirm that experimental pups were shoved less than controls, we observed both sets of pups every few days. The observer entered the room and sat quietly near (<60 cm) both the source colony's nestbox and the isolation apparatus for 10 min, recording all shoves observed in both. Then the toilets were cleaned, the bedding replaced, the animals were fed, and babysitters were exchanged, which together greatly disturbed the animals. Thereafter, both groups were again observed for 10 min and all shoves were recorded. Experimental and control pups in three litters were weighed weekly.

When rates of pup shoving in the source colony had diminished to <0.05 shoves/pup/min (4–9 wk after the experiment began: Table 2), experimental pups were marked with permanent ink and returned to their natal colony. Reunited litters were observed every other day for the next 2 wk. An observer entered the room, sat <60 cm from the nestbox, and for 20 min recorded numbers of experimental and control pups that were in and outside of the nestbox every minute. Then the observer tapped five times on the nestbox lid, and continued recording all shoves and pup locations every minute for the next 20 min. For two litters, the rates at which adults shoved each other before and after the disturbance also were recorded.

Analyses

In analyzing videotapes or direct observations, a 'shove' was defined as a single lunge toward a recipient (pup or adult), followed by contact between the shover's muzzle and the recipient's body. Usually the shover stood facing the recipient, and then lunged forward, keeping its neck and spine rigid until its muzzle made contact (Lacey et al. 1991). When pups were being shoved, the shover's forward movement was approximately perpendicular to the pup's midline. Often the shover retracted its muzzle straight back a few millimeters and repeated the motion several times in succession. These 'bouts' consisted of up to 20 shoves. For every shove that occurred we recorded the time, identity of the initiator, and location (nest or tunnel).

Because litters differed in size and videotaped trials occasionally varied in length, it was necessary to calculate a standardized per-capita shoving rate (shoves/min/pup) for each individual trial. To assess the time-course of shoving, for each trial we calculated shoving frequencies for all adult colony members combined and, separately, for the breeding female, breeding male, and nonbreeders as a group (i.e. a single datum is the per capita shoving rate exhibited by a particular individual or group of individuals on a particular day). As data were not normal, we transformed per-capita shoving rates using: $\sqrt{\text{rate} + \sqrt{\text{rate} + 1}}$.

Transformed daily shoving rates were grouped into consecutive 10-d pup ages and a mean (\pm SE) rate was calculated. We calculated pup-shoving rates (\pm SE) for all colonies combined, for each colony separately, for all adult shovers combined, and for individual classes of shovers (breeding female, breeding male, and nonbreeders as a group). Per-capita shoving rates by the breeding female and breeding male on adult nonbreeders were compared with the corresponding shoving rates on pups. Effects on shoving rate of colony (i: random factor), shover identity (i: random factor), type of shovee (i: random factor), trial type (i: random factor), and/or pup age (j: fixed factor) were tested with ANOVAs [General Linear Models: e.g. $Y_{ij} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \epsilon_{ij}$].

To analyze the split-litter study, we compared mean numbers of shoves received by experimental and control pups in each litter during (semi-) isolation and after reintroduction. For reunited litters we compared transformed (arcsine square root) mean proportions of experimental and control pups that were out of the nestbox before and after the disturbance with reverse stepwise ANCOVA (General Linear Model) using litter (i), pup group (j: control vs. experimental), and treatment (k: before tapping vs. after tapping) as random factors and time (l: number of days after reintroduction to natal colony) and time² (for a quadratic fit) after reintroduction as fixed factors. The final reduced model used was:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + (\beta\gamma)_{jk} + a_1 t_{ijkl} + a_2 t_{ijkl}^2 + \alpha_i t_{ijkl} + \alpha_i t_{ijkl}^2 + \beta_j t_{ijkl} + \beta_j t_{ijkl}^2 + \gamma_k t_{ijkl} + \gamma_k t_{ijkl}^2 + \epsilon_{ijkl}$$

To determine if treatment had differential effects on pup behavior we compared the two halves of each litter using ANOVA. All analyses were performed using SPSS 10.0 (SPSS Inc., Chicago, IL, USA).

Results

Which Colony Members Shove Pups?

Videotapes of four colonies revealed that of 2022 shoves on 10–59-d-old pups, 1345 (0.66) were performed by the breeding female, 482 (0.24) by the breeding male, and 195 (0.10) by all nonbreeders combined (Fig. 1). Most shoves of pups occurred in the nest box ($1780/2022 = 0.88$). Pups responded to shoves by fleeing, either within the nest box (young pups) or out into adjacent tunnels. Pups never retaliated to being shoved by shoving an adult back.

In each of the four colonies, the breeding female shoved pups significantly more often than the breeding male (G-tests: all $p < 0.0001$) and all nonbreeders combined (G-tests: all $p < 0.0001$); the breeding male shoved pups significantly more often than all the nonbreeders combined (G-tests: all $p < 0.0001$); and the two breeders together shoved pups significantly more often than all the nonbreeders combined (G-tests: all $p < 0.0001$). When data from all colonies

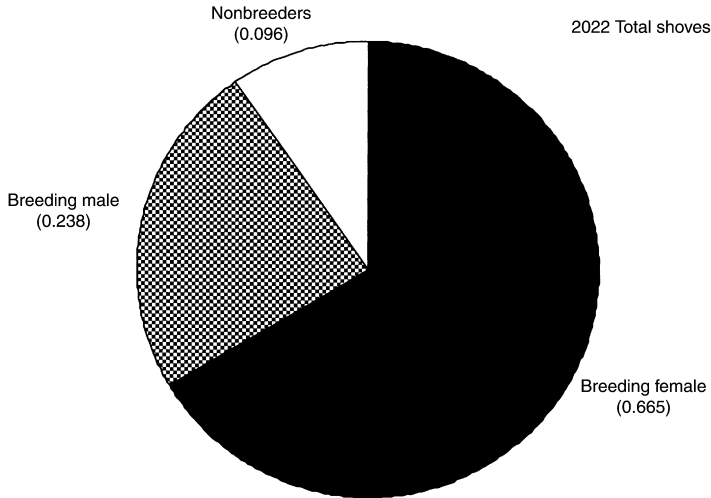


Fig. 1: Proportions of all 2022 shoves of naked mole-rat pups performed by breeding females ($n = 4$), breeding males ($n = 4$), and all nonbreeders ($n = 1-27$) during videotaped observations in four captive colonies

were combined, proportions of shoves on pups differed significantly between breeders and nonbreeders (G-test: $G = 1520.378$, $df = 1$, $p < 0.0001$) and between breeding females, breeding males, and all nonbreeders (G-test: $G = 1051.662$, $df = 1$, $p < 0.0001$).

When Are Pups Shoved?

Videotapes of four undisturbed colonies revealed that rates of shoving varied significantly with the ages of the young (ANOVA: $F_{4,13.6} = 15.378$, $p < 0.001$; Fig. 2a). Pups were shoved at the highest rates during days 20–29 (0.141 ± 0.041 shoves/min/pup), and there were significant differences in mean rates between days 10–19 and 20–29 (0.031 ± 0.004 vs. 0.141 ± 0.041 ; ANOVA: $F_{1,120} = 38.037$, $p < 0.001$), and 30–39 and 40–49 (0.049 ± 0.002 vs. 0.034 ± 0.004 ; ANOVA: $F_{1,95} = 21.931$, $p < 0.001$). There were no significant differences in rates of pup shoving between days 20–29 and 30–39 (0.141 ± 0.041 vs. 0.049 ± 0.002) and between days 40–49 and 50–59 (0.034 ± 0.004 vs. 0.032 ± 0.007) (ANOVA: both $p > 0.05$).

There were no differences in pup-shoving frequencies between colonies (ANOVA: $F_{3,14.0} = 0.446$, $p = 0.724$). The breeding female shoved pups at the highest rate in all time periods (Fig. 2b), followed by the breeding male, and the nonbreeders (ANOVA: $F_{2,8.1} = 27.370$, $p < 0.001$). When 10-d time periods were examined individually, the breeding female shoved pups significantly more often than the breeding male and the nonbreeders in all five time periods (Fig. 2b; ANOVA: all $p < 0.001$).

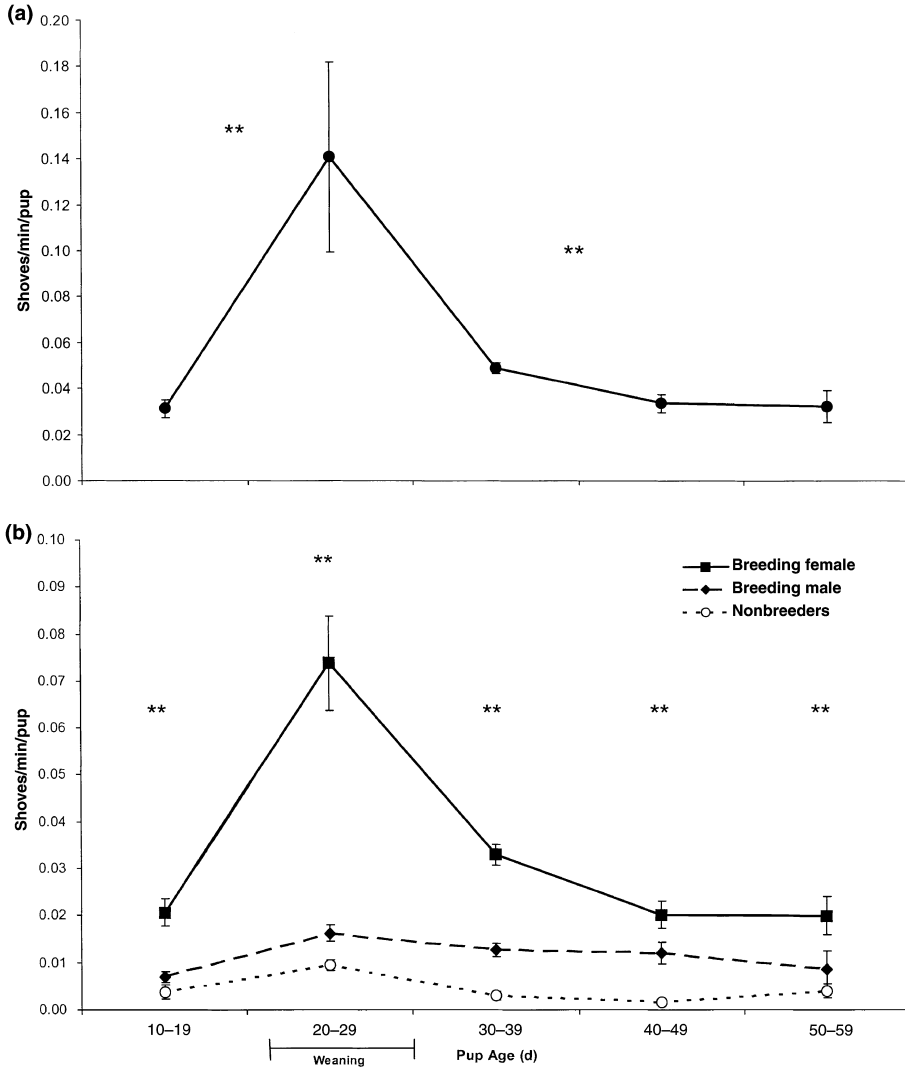


Fig. 2: Mean (\pm SE) rates at which pups were shoved throughout early development during undisturbed (videotaped) observations of four naked mole-rat colonies, averaged over 10-d time blocks. (a) Pup-shoving rates by all adults combined. Asterisks indicate results of ANOVAs for differences in mean shoving rates between consecutive time intervals (** $p < 0.001$). (b) Pup-shoving rates plotted separately for breeding females, males, and nonbreeders. Asterisks indicate results of ANOVAs for differences in the mean shoving rates of the breeding females, breeding males, and all nonbreeders in each time interval (** $p < 0.001$)

Effects of Disturbances on Pup Shoving

When the observer entered the colony room quietly, adults rarely fled the nest box. However, the animals never completely habituated, because they sniffed

the air frequently throughout trials. We noticed, as had Jarvis (1991), that when a colony containing newborn pups was disturbed adults often carried the young through the tunnels in their mouths. As weaning approached and pups grew larger and more mobile, they were carried less often and shoved more often in response to disturbances.

There were no differences in mean pup-shoving frequencies between colonies (ANOVA: $F_{3,13.8} = 1.390$, $p = 0.288$), but pups' ages again significantly affected frequencies of being shoved (ANOVA: $F_{4,13.9} = 7.84$, $p = 0.002$). Pup shoving increased in all five, 10-d intervals when an observer was present compared with undisturbed (videotaped) conditions (Fig. 3; ANOVA: $F_{1,4} = 10.120$, $p = 0.033$) and ages of the pups had a significant effect on the difference between disturbed and undisturbed conditions (ANOVA: $F_{4,260} = 4.213$, $p = 0.003$). Both parents significantly increased their shoving rates on pups when an observer was present (Fig. 4; for breeding females, ANOVAs: $F_{1,277} = 24.168$, $p < 0.001$; for breeding males, $F_{1,277} = 21.400$, $p < 0.001$).

Shoving of Adults

In undisturbed (videotaped) conditions, breeding females shoved adult nonbreeders 0.004 ± 0.003 times/min/recipient during days 10–59 (Fig. 4), an order of magnitude less often than they shoved pups (0.031 ± 0.003 shoves/min/pup) during the same time period (ANOVA: $F_{1,123} = 32.132$, $p < 0.001$). Breeding males shoved adult nonbreeders at about the same (low) rate as they shoved pups (0.009 ± 0.004 and 0.011 ± 0.001 shoves/min/recipient, respectively; ANOVA: $F_{1,123} = 2.143$, $p = 0.146$).

When an observer was present, shoving of adult nonbreeders decreased dramatically (ANOVAs: for males, $F_{1,26} = 4.786$, $p = 0.038$; for females, $F_{1,26} = 2.502$, $p = 0.126$). Indeed, breeding females never shoved nonbreeders in any disturbance trial ($n = 14$), and breeding males shoved nonbreeders only 0.001 ± 0.001 times/min/recipient during these trials (Fig. 4). Thus, breeders shoved nonbreeders significantly less often than they shoved pups (Fig. 4; ANOVAs: for females, 0.000 ± 0.000 vs. 0.081 ± 0.007 shoves/min/recipient, $F_{1,180} = 25.598$, $p < 0.001$; for males, 0.001 ± 0.001 vs. 0.033 ± 0.004 shoves/min/recipient, $F_{1,180} = 16.074$, $p < 0.001$).

Shoving and Behavioral Ontogeny

In our split-litter experiment (Table 2), semi-isolated pups (experimentals) in all four litters were shoved significantly less often by their elder sibling than pups that remained in their natal colony (controls) (Wilcoxon Signed-Ranks tests: all $p < 0.05$). Nonetheless, control and experimental pups matured at similar rates: there were no systematic differences in mean body weights between groups from the three litters that were weighed weekly (Mann–Whitney U-tests: all $p > 0.05$), and no differences in mean weights between experimental and control pups in any litter when they were reunited after 4–9 wk of separation (Mann–Whitney U-tests: all

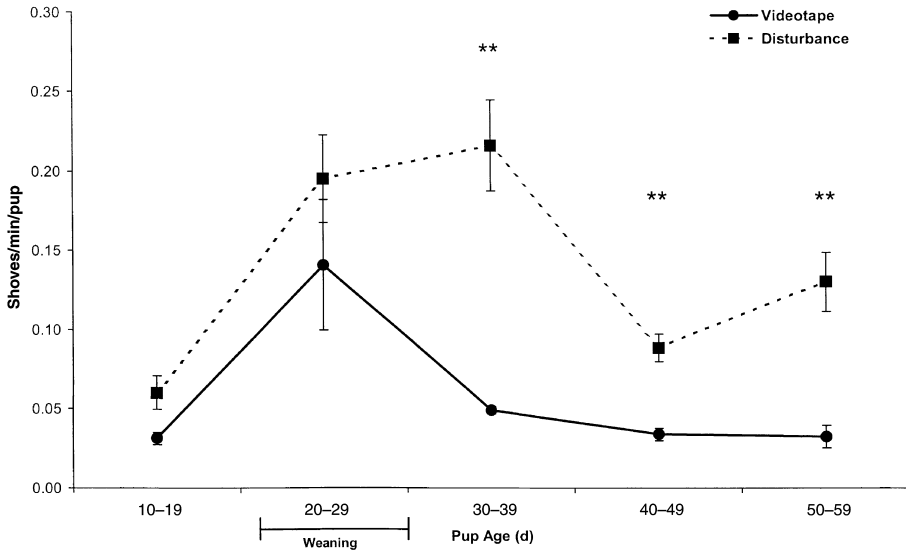


Fig. 3: Mean (\pm SE) rates at which 10–59-d-old pups in four colonies were shoved by adult naked mole-rats (breeders and nonbreeders combined) when undisturbed (videotaped) or in the presence of an observer (indicative of an impending disturbance). The approximate timing of weaning is indicated. Asterisks indicate results of ANOVAs of differences between disturbance and control conditions (** $p < 0.001$)

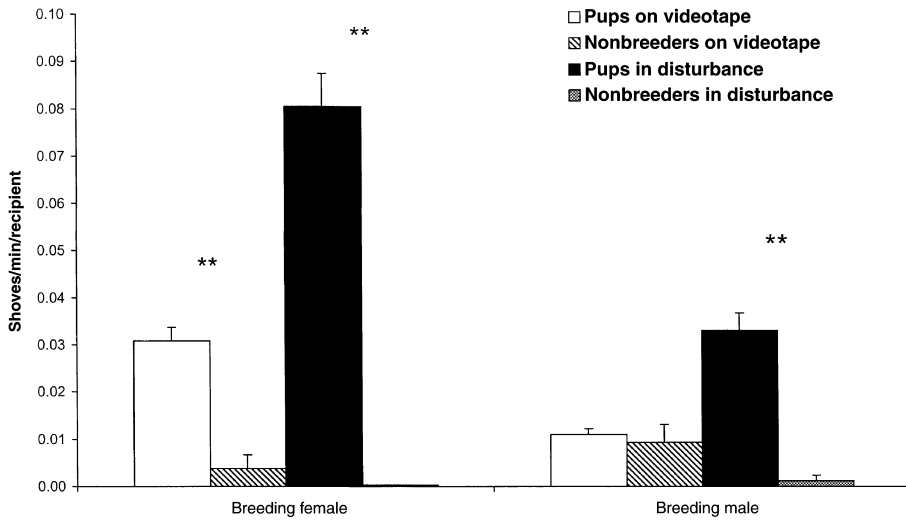


Fig. 4: Mean (\pm SE) rates at which breeding female and male naked mole-rats in four colonies shoved 10–59-d-old pups and adult nonbreeders, either when undisturbed (videotaped) or in the presence of an observer. Asterisks indicate results of ANOVAs of between-group differences (** $p < 0.001$)

$p > 0.05$). Once litters were reunited there were no differences in rates at which control and experimental pups were shoved (0.039 ± 0.016 and 0.030 ± 0.010 shoves/min/pup, respectively; Wilcoxon Signed-Ranks test: $Z = 0.359$, $p = 0.719$).

Reverse stepwise ANCOVA revealed that both isolating pups and tapping on the nest box had significant effects on the proportion of pups that ran out of the nest (Fig. 5; for isolation, $F_{1,138} = 6.04$, $p = 0.015$, for tapping, $F_{1,138} = 4.68$, $p = 0.032$). Additionally, the four litters responded differently to the presence of an observer ($F_{3,138} = 5.70$, $p = 0.001$) and to semi-isolation ($F_{3,138} = 6.89$, $p < 0.001$). Control (shoved) pups were significantly more likely to flee the nestbox in response to our disturbance than were experimental (unshoved) pups (Fig. 5; $F_{1,138} = 5.72$, $p = 0.018$). When tested separately, proportions of control pups that ran out of the nestbox increased significantly in response to tapping (0.333 ± 0.037 to 0.473 ± 0.046 ; ANOVA: $F_{1,5.8} = 8.345$, $p = 0.029$), whereas proportions of experimental pups that ran out did not vary significantly (0.235 ± 0.026 to 0.276 ± 0.027 ; ANOVA: $F_{1,1.1} = 8.261$, $p = 0.194$).

Numbers of days after litters were reunited ('time' and 'time²') also had a significant effect on pup flight behavior (for 'days after reintroduction', $F_{1,138} = 7.04$, $p = 0.009$). Time interacted significantly with several of the factors: litters responded differently over time (for litter \times time, $F_{3,138} = 5.25$, $p = 0.002$, for litter \times time², $F_{3,138} = 4.08$, $p = 0.008$); control pups were significantly more likely to flee the nestbox over time² than were experimental pups (Fig. 5; $F_{1,138} = 11.43$, $p = 0.001$); and pups were significantly more likely to flee the

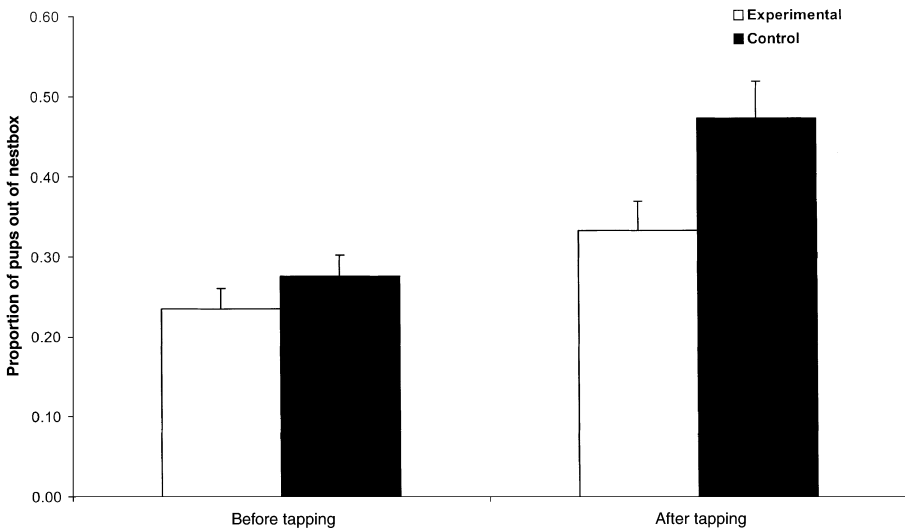


Fig. 5: Results of the split-litter experiment. Bars show mean (\pm SE) proportions of pups in four litters that remained outside the nestbox depending on whether they had been reared in their natal colony, where they were frequently shoved (control), or in semi-isolation (experimental), where they were seldom shoved. The first 20 min of observations occurred 'before tapping' then the nestbox lid was rapped sharply and behavior 'after tapping' was observed for another 20 min

nestbox over time² after tapping than they were before tapping (Fig. 5; $F_{1,138} = 8.02$, $p = 0.005$).

Discussion

Various forms of physical aggression, especially shoving, regularly occur among adult naked mole-rats. It has been hypothesized that shoving of adults incites lazy nonbreeders to begin working (Reeve and Sherman 1991; Reeve 1992), reinforces the reproductive dominance hierarchy (Jacobs and Jarvis 1996; Faulkes and Abbott 1997), or both (Clarke and Faulkes 2001). Shoving of pups is, superficially, a similar behavior. Does it therefore function in the same two contexts?

We think it does not, because the circumstances and timing of pup shoving differed so markedly from shoving of adults. First, shoving of pups began shortly after birth and peaked 3–4 wk later, long before pups were large enough to enter the colony's work force or become reproductive competitors. Secondly, shoving of pups increased dramatically when an observer was present compared with undisturbed (videotaped) conditions, whereas shoving of adult nonbreeders decreased sharply when an observer was present compared with undisturbed (videotaped) conditions (Figs 3 and 4). Thirdly, pups never retaliated after being shoved whereas adults often shoved back. Fourthly, rates at which the breeding female and male shoved their young were an order of magnitude higher than rates at which breeders shoved nonbreeders (Fig. 3). The latter results are consistent with those of Lacey and Sherman (1991) who also observed that pups are shoved more often by their parents than by nonbreeders, and more often by their mother than their father.

Maternal care obviously is essential for survival of mammalian young, yet multiple examples of mother–offspring aggression have been described (e.g. by Clutton-Brock 1991). These can be grouped into two general categories:

(1) Weaning conflict: Maternal aggression frequently accompanies weaning, for example in bison (*Bison bison*: Green et al. 1993), rhesus macaques (*Macaca multatta*: Gomendio 1989), peccaries (*Tayassu tajacu*: Babbitt and Packard 1990), white-tailed and fallow deer (*Odocoileus virginianus* and *Cervus dama*: Gauthier and Barrette 1985), and several baboon species (*Papio*: DeVore 1963). Such aggression is a manifestation of an evolutionary conflict between females and their offspring over the amount of maternal investment (e.g. milk) that she should provide (Trivers 1974).

(2) Natal dispersal: Maternal aggression frequently is a prelude to dispersal from the natal home range or territory, for example in pikas (*Ochotona princeps*: Smith 1974; Whitworth 1984), golden hamsters (*Mesocricetus auratus*: Rowell 1961; Schoenfeld and Leonard 1985), woodchucks (*Marmota monax*: Barash 1974), and Mediterranean blind mole-rats (*Spalax ehrenbergi*: Zuri and Terkel 1998). Such aggression is a manifestation of an evolutionary conflict between females and their offspring over how long young should remain near home when their presence reduces the mother's ability to rear future offspring.

Based on this information we initially hypothesized that pup shoving by naked mole-rats might represent mother–offspring conflict over weaning or dispersal. Indeed, natal dispersal is enforced by maternal aggression in several solitary-living bathyergid mole-rats (e.g. *Bathyergus suillus*, *B. janetta*, and *Georychus capensis*: Bennett and Faulkes 2000). However, mark-recapture studies (S. H. Braude, unpubl. data, Braude 2000) and genetic analyses of wild *H. glaber* colonies (Faulkes et al. 1990, 1997; Reeve et al. 1990; Honeycutt et al. 1991b) reveal that they are usually family groups, which result from natal philopatry (i.e. nondispersal of juveniles). Although a ‘disperser morph’ has been described (O’Riain et al. 1996), putative dispersers are never numerous, and they are always large, fat-laden, and reproductively mature. Most importantly, apparent dispersers that have been captured in the field are all adults, and no dispersing juveniles have ever been reported (Braude 2000). We conclude that pup shoving does not result from mother–offspring conflict over dispersal.

Weaning conflict is a more likely possibility because the most frequent shover was the pups’ mother (Figs 1 and 2b), and she was responsible for the significant increase in shoving during days 20–39, which roughly coincides with the termination of lactation (Jarvis 1991; Lacey and Sherman 1991). However, pups also were shoved spontaneously before, during, and after weaning (Fig. 2a), and not only by their mother, but also by their father and other colony members (Figs 1 and 2b). Moreover, pups were not shoved in response to approaching their mother and attempting to suckle, as typically occurs in weaning conflict. Rather, the breeding female sought out her young to shove them, especially when a disturbance was imminent. Apparently enforcing weaning is not the primary function of pup shoving.

Jacobs and Jarvis (1996) and Clarke and Faulkes (1997) argued that shoving of subordinates by breeders reinforces the colony’s social dominance hierarchy: the breeding female primarily shoves large colony mates (especially females) because they represent the greatest potential threats to supercede her. If ‘threat reduction’ is the function of pup shoving, the breeding female should begin shoving her offspring when they are old enough to insinuate themselves into the colony’s dominance hierarchy. Consistent with threat reduction, our data show that breeding females did shove pups most frequently when the young were beginning to spontaneously leave the nest (20–39 d of age: Fig. 2b). However, they were still too young to join the colony’s dominance hierarchy. Moreover, increased shoving in the presence of an observer (Figs 3 and 4) is not predicted by threat reduction — there is no reason why dominance should be more strongly enforced just prior to or during disturbances. In fact, breeders shoved adult nonbreeders less often when an observer was present (Fig. 4), and adult nonbreeders undoubtedly represent a greater reproductive threat to breeders than do small pups.

Alternatively, Reeve and Sherman (1991) and Reeve (1992) argued that breeders shove subordinates to incite them to perform colony maintenance tasks. These authors also observed that breeders shoved large males and females most often, and large individuals typically performed the fewest colony

maintenance activities (i.e. they are 'lazy'). Under this 'activity incitation' hypothesis, the breeding female shoves most frequently because she has the most at stake in keeping her colony well maintained and defended. If activity incitation is the function of pup shoving, the breeding female should begin shoving her offspring when they are old enough to begin working. Consistent with this, breeding females did shove pups most frequently just before they normally would begin performing colony maintenance tasks (Fig. 2b). However, pups did not begin working immediately after having been shoved. Moreover, there is no reason why work incitation should be more strongly enforced when an observer was present, and breeders shoved adult nonbreeders (the primary workers) less often when a disturbance occurred. In sum, although we cannot exclude the possibility that activity incitation or threat reduction may underlie some shoving of pups, neither adequately explains the patterns of shoving we observed (Figs 2–4).

Lacey et al. (1991) proposed two other hypotheses to explain pup shoving: enhancing the pups' peristaltic gut action and preventing pups from being trampled by moving them to the periphery of the nest. The former seems unlikely because there is no reason that digestion would require enhancement just prior to or during disturbances. However, shoving pups may move them out of the way of other fleeing colony members.

Results of the split-litter experiment suggest another possibility. After a disturbance, frequently shoved (control) pups were more likely to flee the nest box and stay away from the site of the disturbance than were unshoved (experimental) pups (Fig. 5). Either being shoved or observing colony-mates fleeing sensitizes pups to warning signs of danger (e.g., sounds, smells, vibrations) and encourages them to remain away from the area. In support of the former, the juvenile babysitter that was housed with the experimental pups always fled the nest box when the observer tapped on the lid or cleaned it, as did adults in the natal colony. Thus, both experimental and control pups frequently experienced older individuals fleeing from disturbances, but once litters were reunited the pups' behavior differed in response to disturbances, depending on whether or not they had actually been shoved.

O'Riain and Jarvis (1998) noticed that litters born when a colony was small grew more rapidly and attained greater body mass than litters born later in larger colonies. They suggested that later litters were developmentally retarded by being shoved more frequently by larger numbers of colony mates. However, most pup shoving was done by the two breeders (Fig. 1) and numbers of breeders do not change with colony size. Moreover, in our split-litter experiment, pups that were not shoved for 4–9 wk were not physically larger, heavier, or more developmentally advanced than pups that had been shoved the entire time. Thus, differences in behavior of our experimental and control pups were not because of differences in size or development.

Results of the split-litter experiment do suggest that pups responses to disturbances change over time. That control pups spent significantly more time out of the nestbox in response to repeated trials over time than did experimental pups

implies that shoving could sensitize pups to dangerous situations at an early age, and that shoved pups learn more quickly which stimuli are dangerous and how to respond to them. Also, all pups made this association faster when the stimuli were more apparent and significant (i.e. human scent vs. tapping + human scent). Thus, pups seem to learn to avoid dangerous stimuli with increasing experience, and shoved pups seemed to make this association faster than unshoved pups.

Our observations and experiments imply that although pup shoving by adult naked mole-rats looks aggressive, it is actually a special form of parental solicitude, not maltreatment. Although we cannot exclude the possibility that shoving helps enforce weaning, we believe shoving primarily encourages pups to flee from physical threats and to avoid them subsequently. Pup shoving by naked mole-rats thus illustrates Rheingold's (1963) point that maternal behavior is 'the chief agent in modifying the behavior of the young, the chief agent responsible for its learning.'

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