

Chapter 2

Dominance

Abstract

The highveld mole-rat, *Cryptomys hottentotus pretoriae*, is a group-living bathyergid. Species of the Bathyergidae exhibit varying degrees of sociality; from solitary to eusocial species. Bathyergid sociality and dominance has commonly been assessed using ordinal procedures. Using these procedures, the highveld mole-rat is classified as being loosely social. These methods are often subjective and can not deal with ties in rank and other complications. This study uses an objective and more robust cardinal assessment method in order to assign dominance ranks to individuals of specific colonies. It was found that the highveld mole-rat is indeed loosely social with no correlations being observed between individual dominance rank and sex, mass or reproductive status respectively. It is proposed that this method of dominance assessment be used in future dominance related assessments, especially within the Bathyergidae.

Introduction

There have been various attempts in the literature to define dominance relationships amongst individuals as well as many attempts to measure it. The concept of dominance is notoriously inadequately defined (Richards 1974). Attempts to measure dominance include the assessment of priority to incentives, agonistic behaviour, approach/retreat and avoiding behaviour, mating success, display behaviour, grooming behaviour, posture and gait, distance from the alpha male, general spacing and associative attention (physical contact, grooming and play) (Richards 1974). Historically, it has proven difficult to rank individuals reliably on a single measure or to correlate between ranks when using several measures (Richards 1974). For example, Bernstein (1970) failed to establish correlations between behaviours and suggested that social responses were not derived from a "single social mechanism". Contradictions abound in the literature and confused statements are reported where data has been obtained that does not fit traditional theories of social dominance (Richards 1974). Circular arguments are also common where, for example, priority of access to resources leads to dominance but where it is also stated that dominance leads to priority of access to resources (Chance 1956). Lack of correlations may be due to methodological problems or because of other behavioural (including social) or physiological factors (Richards 1974).

The most inclusive and representative definition of dominance relationships amongst individuals has been proposed by Boyd & Silk (1983). These authors suggest that dominance relationships are characterised by three structural properties, namely; stability, transitivity and linearity. Stability in a group of individuals exists as long as individual A always beats individual B in an encounter. Richards (1974) defines group stability as when a group has lived together for a relatively long period of time and no changes are evident in the group composition and that there is no sign of a decline in the health of any individual. Chase (1974) associates increasing group stability with a decreasing frequency and intensity of interactions. It is suggested that this is dependent upon the time that the group has been together. Transitivity exists in a group of individuals when individual A is dominant over individual B and individual B is dominant over individual

C while individual A is dominant over individual C (Richards 1974, Chase 1974). In order for a linear dominance hierarchy to exist, all triads must be transitive. If these three properties are present in a group of animals then unambiguous ordinal dominance ranks can be assigned to each individual in the group and the rank will correspond to the number of individuals in the group that each individual dominates. All three of these properties must be present in a group of individuals in order for ordinal dominance ranks to be assigned. This is unlikely to be the case in mole-rat colonies. Assessing dominance in groups where individuals interact infrequently also proves to be a difficult task (Richards 1974).

The process of assessing dominance relationships involves several steps in order to construct a dominance matrix. These steps include: (i) identifying a behaviour or set of behaviours that are clearly associated with dominance, (ii) establishing a set of criteria to determine the unambiguous identification of winners and losers of dyadic interactions and (iii) collecting observations and assessing the temporal consistency of outcomes (Boyd & Silk 1983). If these steps can be done without deviation then the resulting matrix would allow the individuals in the group to be assigned ordinal dominance ranks (Boyd & Silk 1983). However, it is only very occasionally that these steps are followed without deviation and/or further assumptions. It is sometimes very difficult to determine which behaviour(s) should be used to assess dominance. Hierarchies based on different behaviours do not always agree (Boyd & Silk 1983). Ties in dominance rank are sometimes encountered and further problems are encountered when all individuals in the group do not interact with each other (Boyd & Silk 1983). Dominance relationships between pairs of individuals may be ambiguous such that individual A sometimes dominates individual B but individual B sometimes dominates individual A. If a single pair of individuals in the group show ambiguity in their dominance relationship, individuals cannot be ordered in a linear hierarchy (Boyd & Silk 1983).

Ordinal measures of dominance fail to include the level of ambiguity between pairs of individuals (Boyd & Silk 1983). Using this technique it is also difficult to assess the significance of temporal or contextual fluctuations in the dominance relationship of two

individuals (Boyd & Silk 1983). The use of ordinal measures may distort or obscure the actual relationship between dominance and other variables of interest (Boyd & Silk 1983).

Two types of ranks are evident from the literature. A basic rank is one in which a dominant-subordinate relationship exists between two individuals, not interfered with by the group to which they belong (Richards 1974). The construction of a linear social dominance hierarchy is not possible between dyads tested in this way. A dependant rank is a dominant-subordinate relationship between two individuals that is modified by other individuals or by group dynamics (Richards 1974). As Carpenter (1954) and Hinde (1971) state “dominance relationships have a pervasive effect on group organisation”. Thus, for social dominance hierarchies to be used in studies of social behaviour and for social interactions to be predicted accurately, the concept and definition of dominance needs to be adequate (Richards 1974).

Another branch of dominance measures has been debated in the literature and is used in this study. This method of assigning ranks to individuals in a social group is a method that involves using cardinal indices and not ordinal dominance ranks. Unlike the ordinal method, wins, losses as well as ties can be dealt with (Boyd & Silk 1983). This method is based on the method of pairwise comparisons (Boyd & Silk 1983). Cardinal methods express the amount of dominance rather than its order (Boyd & Silk 1983) allowing a measure to be calculated which shows by how much an individual is dominant over another for each behavioural act used. This is possible as the method assigns individuals to a straight line so that the distance between points for each individual represents the amount by which one individual dominates another. The amount that one individual (i) dominates another (j) is defined in terms of the probability that i beats j in any given encounter (P_{ij}). This definition relies on the assumptions that probabilities are constant during observations and that the outcome of an encounter is probabilistically independent of outcomes of previous encounters (Boyd & Silk 1983). Independence means that the probability that i wins any number of consecutive encounters = P_{ij}^n (Boyd & Silk 1983).

The assumptions of the cardinal method of dominance assessment formalize the notion that the outcome of any encounter has a deterministic and random component (Boyd & Silk 1983). This assumes that a deterministic component is stable during the observation period and that random effects on different contests are independent (Boyd & Silk 1983). The assumptions are likely to be violated when dominance relationships are being established or challenged and are likely to be valid when group dynamics are stable (Boyd & Silk 1983).

The use of the cardinal dominance index (CDI) method of assessment does not rely on subjective weightings of different behavioural acts as the method results in an index of dominance and not a rank. This index of dominance can then be ordered, resulting in a dominance rank for each individual in the colony.

The aim of this study was to re-evaluate the dominance hierarchy of the highveld mole-rat using an alternative dominance assessment method to that previously undertaken by Moolman *et al.* (1998) and to determine whether animal mass, sex or reproductive status was correlated to individual dominance position in the colony. It is hypothesised that colonies of the highveld mole-rat would be loosely social and that neither reproductive status, animal mass nor sex would provide reliable correlates to dominance.

Methods and Materials

Behavioural sampling was conducted on each of two colonies (consisting of seven and eight individuals respectively) of the highveld mole-rat. Behavioural sampling for each colony consisted of scan sampling of dyadic interactions for each individual in each colony, each minute. Each colony was observed for a period of 50 hours giving a possible 3000 observations for each individual, although each individual was not always observed to be undergoing a dyadic interaction. The 50 hours of observations for each colony were conducted over a 2 month period between 1999-2000 allowing 30 minutes – 3 hours of behavioural sampling per day (depending on the level of activity in the colony). Animals were only observed when at least half of the individuals were active. Data therefore consisted of counts, for each individual, for each type of interactive behaviour commonly observed.

Ten dyadic interactive behaviours were identified as being common to both colonies and in sufficient frequency to allow individual calculation (each individual had to have at least one interaction per behaviour type). The ten behaviours are listed in Table 1, along with the assumption as to whether they were considered to be dominant or submissive behaviours. An ethogram of the common behaviour types as well as most other behaviours is given in the Appendix.

Table 1: Behaviours used in the analysis of dominance and whether each behaviour was assumed to be dominant or submissive.

Dominant Behaviour	Submissive Behaviour
Clash	Hop
Pass Over	Pass Under
Push	Paw
Tail Bite	Retreat
	Squeak
	Tail Lift

Data Collection

Data was recorded solely by the author by hand on custom made data sheets which made it possible to record data at the rate referred to above. In all cases, individual observations of behaviour were recorded. No winners or losers were identified due to the subjective nature of these decisions. A series of examples follow which illustrate how the behaviour was recorded:

If two individuals clash, then the antagonist and the other individual are recorded with a clash. If the clash continues into the next minute, a further clash is recorded for each animal. This continues until the clashing activity stops.

If an individual lifts its tail while being passed over by another animal, the passing animal is recorded with a pass over while the animal that lifts its tail is recorded with a tail lift.

Using ordinal dominance methods, this interaction would have been recorded as a win for the passing animal.

Data was analysed in order to determine whether dominance rank and sex, mass or reproductive status were significantly correlated. Results were compared to that of Moolman *et al.* (1998) whose study was based on a single colony using factor analysis (ordinal dominance methods).

Cardinal Dominance Indices (CDIs) were calculated instead of other ordinal dominance ranks (using factor analysis). The methods for calculating the CDIs were written in SASS by M. van der Linde (Statistics Dept., University of Pretoria). The programming follows the methods laid out by Boyd & Silk (1983).

Using 50 hours of observations for each colony, matrices were constructed for each of the behaviours listed above. The matrices consisted of the total number of observations of behaviour for each individual and its partner as only dyadic interactions were recorded.

For each behaviour and colony a CDI was calculated for each individual (using the constructed matrices and programming by M. van der Linde). An associated probability value was also determined during this procedure. CDI's were recorded when the associated probability values had become constant. In most cases, less than 100 iterations were necessary to achieve constant associated probability. For those behaviours where probability values still varied at 100 iterations, the CDI was taken at the 101 iterations stage.

The CDI's were then ranked for each individual (per colony and behaviour) where the highest index was given the highest rank (one) and considered to be the most dominant individual in the colony, for that behaviour; and the lowest index was given the lowest rank (seven or eight, depending on the number of individuals in the colony) and was considered to be the least dominant individual for that behaviour.

In order to combine behaviours so that a single dominance hierarchy could be constructed, rank frequencies were determined for all behaviours so that the individual

with the highest frequency for each rank was assigned that rank in the colony. Using an ANOVA procedure, it was possible to analyse mass vs rank.

Results

Individuals within each colony were ranked by ordering rank frequencies obtained from the cardinal dominance index for each behaviour. A resulting dominance hierarchy was constructed together with individual mass, sex and reproductive status (Table 2). As individual 6 from colony 2 occupied both position 5 and 6 in the rank frequency analysis, her rank was assigned midway between the two rank values (5.5).

Table 2: Final dominance hierarchies resulting from behaviour matrix and rank frequency analysis using the cardinal dominance index (CDI) method.

COL	RANK	SEX	STATUS*	MASS (g)	COL	RANK	SEX	STATUS*	MASS (g)
1	1	F	NR	111	2	1	M	R	115
1	2	F	NR	81	2	2	M	NR	93
1	3	F	NR	52	2	3	M	NR	109
1	4	F	R	102	2	4	F	R	91
1	5	M	NR	161	2	5.5	F	NR	89
1	6	F	NR	52	2	7	F	NR	85
1	7	M	R	165	2	8	M	NR	82

*: NR = non-reproductive individuals, R = reproductive individuals.

The dominance hierarchy was analysed using an ANOVA procure (for each colony) for correlations between individual rank and mass (Figure 1 and 2). No correlation was evident in the linear regression analyses for colony 1 ($R^2=0.13$, $p=0.44$), while there was a statistically significant correlation for colony 2 ($R^2=0.68$, $p=0.02$).

Visually assessing the dominance matrix, it appears that no relationship exists between individual rank and reproductive status or sex. Although in colony 2 the heaviest male (assumed to be the reproductive male) is the most dominant individual, this does not seem to be the case across the two colonies, since colony 1 does not show that the heaviest male is the most dominant individual in the colony.

It is evident that the individual that was determined to be the reproductive female in each colony exhibits an intermediate rank – not being overtly dominant but not being overtly submissive either. The relative ranks of the two reproductive females in each colony is intermediate; at position 4. Although both reproductive females are occupying this position in the dominance hierarchy, it is probable that the equal relative ranking of these females occurred by chance.

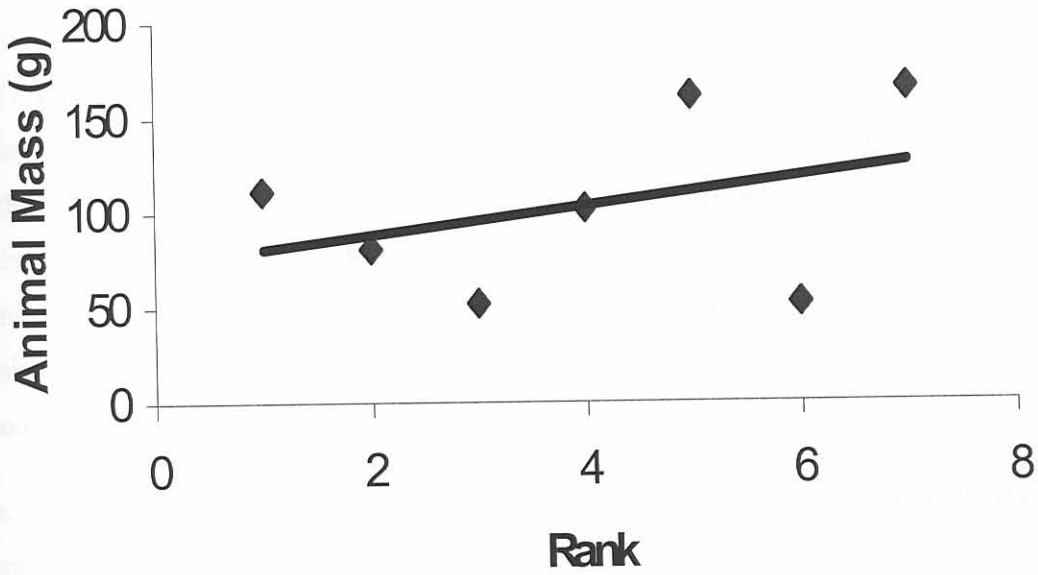


Figure 1: The resulting straight line from a regression analysis of individual rank vs mass (g) for individuals belonging to colony 1. The regression coefficient was calculated to be 0.13 and $p=0.44$.

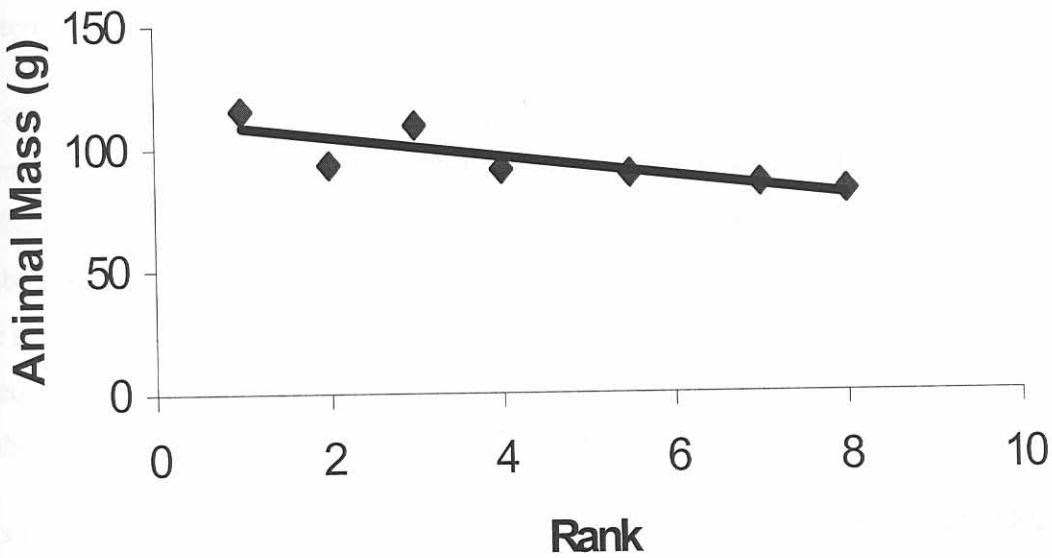


Figure 2: The resulting straight line from a regression analysis of individual rank vs mass (g) for individuals belonging to colony 2. The regression coefficient was calculated to be 0.68 and $p=0.02$.

Discussion

The highveld mole-rat (*Cryptomys hottentotus pretoriae*) is a social bathyergid that lives in familial groups. Although social, the highveld mole-rat does not appear to have a predictable social colonial dominance hierarchy. From graphical as well as visual analyses, it is evident that individuals do not show any predictable relationship between dominance rank and individual mass, sex or reproductive status. Although there was a significant correlation between mass and rank for colony 2, this was not evident for colony 1 and this result can therefore not be used to reach any broad conclusions.

The dominance hierarchy that results from the Cardinal Dominance Index method of hierarchy determination uses available behavioural data to determine the relative dominance index of each individual in each colony. The behavioural data that was used comprised the most common behaviours in each colony (see Table 1). The assumptions that were made using these behavioural acts were whether the behaviour could be considered to be an act of dominance or an act of submissiveness. These assumptions were thought to be valid as logic (from preliminary observations) played a role in the determination.

A second important assumption made was that an inverse relationship existed between dominance and submissiveness. Hence the most submissive individual (for a particular submissive behaviour) could also be thought of as the least dominant individual (for that submissive behaviour). It was therefore possible to use behaviours that were assumed to be submissive in the study. The individuals were arranged, before the final rank frequency analysis, so that the results were in terms of dominance and not submissiveness.

As Richards (1974) states, it is sometimes difficult to assess which behaviour(s) to use in order to assess dominance in a social group. Using different behaviours ultimately leads to different resulting dominance hierarchies (Boyd & Silk 1983). It was therefore decided, in this study, to incorporate as many behavioural acts (whether assumed to be submissive or dominant) as was possible depending on individual and colony activity.

In the early stages of a study of dominance, it is important to state, categorically, what behaviour is considered to represent a win and which behaviour is considered to be a loss, to an individual (Boyd & Silk 1983). As removing subjectivity was a part of the goal of this study, wins and losses were not identified and individuals were not scored in this way. Individuals were observed on their absolute dyadic interactions and the data was therefore representative of counts of behaviour types between individuals within a colony. Although the assumption of whether a behavioural act is dominant or submissive could be seen to be subjective, it is believed that these assumptions hold - especially after preliminary observations were undertaken.

Boyd and Silk (1983) suggest that three structural properties characterize dominance relationships; stability, transitivity and linearity. Group stability in their view exists as long as individual A always (without exception) beats individual B (Boyd & Silk 1983). However, as wins and losses were not determined in this study (as “beats” is a loaded term – representing something positive to the individual) this definition of group stability was not appropriate. Richards’ (1974) definition of group stability is not as subjective, and states that group stability is achieved when the group has been together for a relatively long period of time with no changes evident in group composition or individual’s health. The definition of Chase (1974) was also used in this study where increasing group stability was associated with decreasing interaction frequency and intensity. Individuals were only observed after a period of three weeks of being placed in the artificial tunnel system and interactions had become relatively infrequent.

It is likely that mole-rat colonies do not meet the requirements for the ordinal method of dominance assessment since group transitivity is unlikely. For a group to be transitive, with individual A dominating B, and B dominating C – A would have to dominate C (Richards 1974). As this situation is unlikely group linearity is also thought not to exist in colonies of the highveld mole-rat, as linearity only exists where all triads are transitive (Chase 1974). Thus, colonies of *C. h. pretoriae* do not fit the generally accepted models of social dominance hierarchy assessment, except for the fact that they can become stable, and ordinal methods were therefore not used.

The studies carried out on other social bathyergids to date have all used ordinal dominance methods to assess dominance hierarchies (and resulting social structure) of colonies. This study therefore takes a unique standpoint on the social structure of social bathyergids in terms of the above considerations. It also, unfortunately, makes detailed comparisons of results difficult. In what follows, I will discuss other bathyergid species whose social structure has been studied but one must bear in mind that they were carried out using an ordinal ranking technique.

The Bathyergidae exhibit a broad spectrum of sociality (Jarvis & Bennett 1991) – the genus *Cryptomys* is not only the most specious but also exhibits a continuum of sociality from social to a eusocial species (Jarvis & Bennett 1991). Of the cryptomid species that have been studied to date, all are social and include *C. hottentotus hottentotus* (Bennett 1989), *C. darlingi* (Gabathuler *et al.* 1996) and *C. mechowi* (Wallace & Bennett 1998). Most colonies consist of a single reproductive pair that are generally the largest and most dominant colony members (*Cryptomys hottentotus hottentotus*; Bennett 1989, *Cryptomys darlingi*; Bennett *et al.* 1994 and *Cryptomys mechowi*; Wallace & Bennett 1998). In the case of the eusocial Damaraland mole-rat (*Cryptomys damarensis*), it is thought that up to two reproductively active males could inhabit a single colony (Jarvis & Bennett 1993). Colonies of the common mole-rat, *C. hottentotus hottentotus*, exhibit a loose social structure (Rosenthal *et al.* 1992.) and are thought to have frequent dispersal events (Rosenthal *et al.* 1992). Dominance in the Damaraland mole-rat (*C. damarensis*) was shown to be positively correlated to body mass but not related to sex (Gaylard *et al.* 1998).

Colonies of the highveld mole-rat (*C. h. pretoriae*) are thought to consist of a single reproductive pair. This was determined by histological examination (Moolman *et al.* 1998). The species is thought to be transiently social (Moolman *et al.* 1998). Moolman *et al.* (1998) also showed that the highveld mole-rat lacks a distinct dominance hierarchy, colonies are short-lived and colony fragmentation frequently occurs. Similar conclusions can be made from the results of this study. It was found that the highveld mole-rat was loosely social as predictable dominance hierarchies could not be constructed on the basis

of sex, mass or reproductive status. The strongest dominance hierarchies and social structures are found in the eusocial bathyergids; the naked mole-rat (*Heterocephalus glaber*) and the Damaraland mole-rat (*Cryptomys damarensis*). In colonies of these species, strong dominance hierarchies are evident with the reproductive individuals of both sexes appearing to show dominance over the rest of the colony.

The highveld mole-rat appears to be a very loosely social bathyergid, fitting into the cryptomid social continuum at the lower end of the social scale. This is verified by the fact that lone animals as well as pairs of animals are frequently caught following good rains. The aridity food distribution hypothesis (Jarvis *et al.* 1994) predicts that soil aridity (and, covariantly, food distribution) are important factors favouring the evolution of sociality. For most bathyergid species, this theory holds true with solitary species being found in areas with more predictable precipitation and the eusocial species occurring in areas with unpredictable, and low, annual precipitation (Jarvis *et al.* 1994). The highveld mole-rat is interesting as the species is found in a summer rainfall region with relatively high and predictable levels of annual precipitation. This habitat would, according to the hypothesis, select for a more solitary existence since soil hardness (an important factor to foraging and individual dispersal) would not be limiting in a region with sufficient, seasonal rainfall.

It is thus an important finding that the highveld mole-rat is a loosely social bathyergid, also being captured individually as well as in pairs. Pairs and lone animals are usually common in the early part of the year (Janse van Rensburg 2000, G. Malherbe pers. obs.) that coincides with the summer rainfall months. It is perhaps an interesting question; is eusociality the culmination of evolutionary forces or is eusociality an early part of a diverging family's history? In more mesic regions with more predictable and higher precipitation, could a solitary existence not be selected for in place of sociality? In this species it appears as though colonies break up frequently and that being social is not selected for as in eusocial species which occur in less predictable environments.

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Appendix

In the ethogram that follows, a description is given of those behaviours used in the analysis of dominance for this study as well as other behaviours that were observed.

Dominant Behaviours

Pass Over

One animal passes another animal by walking over it from its anterior or posterior region. This behaviour can occur even when both animals are very large; the passing mole-rat seems to force itself over the other animal. The passing mole-rat usually uses all its limbs in the process. The receiver may also lift its tail. The receiving animal may try and inhibit the passing animal by bracing itself with its limbs on the sides of the tunnel or by lifting itself so the tunnel is effectively blocked. The event is only recorded if the passing animal is successful.

Push

One animal pushes another animal by a backwards sweeping action of its hind limbs. The action is similar to that used when the animal is cleaning the burrow or moving food and other debris from one chamber to another. The receiving animal can either be facing the pusher or with its anterior towards the pusher. The receiver occasionally locks itself in position in the burrow system by bracing itself on the sides of the tunnel or simply allows itself to be pushed along the tunnel. The antagonist may also brace itself on the sides of the tunnel while pushing. The action is usually followed by the pusher moving (walking or running) forward again (away from the receiver).

Tail Bite

The antagonist approaches the receiver from the receiver's posterior and bites or nips at the receiver's tail. Occasionally the receiver lifts its tail in response at which time the antagonist either nips or bites at the tail again or does not. Occasionally, the receiver would turn around in the tunnel to face the antagonist. A nip was defined as a short bite at the tail while a bite was defined as an extended hold on the receiver's tail. A tail bite could also be followed by a passing behaviour.

Clash

The antagonist usually comes into contact with another animal's anterior, retreats slightly, and then pushes the other animal with its buccal cavity open so that the extrabuccal incisors are agape. The animals then lock extrabuccal incisors gently while both animals gain and lose ground (move forward or backward from their original positions). The clash usually ends with one of the animals moving away. A clash between two individuals can last for several minutes, by far the longest dyadic interaction amongst colony members. Retreats can occur between clashing bouts.

Submissive Behaviours

Pass Under

One animal passes another animal by walking under the other animal from its anterior or posterior region. This behaviour can occur even when both animals are very large; the passing mole-rat seems to force itself under the other animal. The passing mole-rat usually uses all its limbs in the process. The receiver may also lift its tail. The receiving animal may try and inhibit the passing animal by bracing itself with its limbs on the sides of the tunnel. The receiving animal may also allow easier passage by lifting itself so the tunnel is effectively open. The event is only recorded if the passing animal is successful.

Retreat

An animal that retreats usually does so quickly in response to meeting another individual in the tunnel or chamber. The action is usually associated with a fast backward running motion followed by the animal turning around (if in a tunnel) and then moving forward more slowly than the initial retreat.

Tail Lift

An animal usually lifts its tail from a horizontal to a vertical position in response to an approach to the animal's posterior by another individual. An animal may also lift its tail in response to any of the dominant behaviours listed above or during a pass under event.

Squeak

This type of vocalisation is defined as being a relatively prolonged sound of lower pitch and longer duration than another type of vocalisation (the chirp). The squeak is more common than the chirp. Squeaking can be from any animal and is usually heard in response to another animal's action(s). Squeaking can be in response to any of the dominant behaviours listed above or during a pass under event. Squeaking is done by very young individuals (birth to a few days old) if the mother is not present, they are left alone or they are attempting to attach to a teat.

Hop

This behaviour is characterised by a series of vertical jumping movements by the animal. The animal can be on all fours or can be in a submissive posture on its back with its limbs in the air. The animal can be approaching another or can be the animal being approached. Occasionally, the hopping motion is simultaneously carried out with a series of chirps (which are high pitched and short duration vocalisations).

Paw

An animal paws another at the receiver's posterior region above the tail. Pawing occurs using either or both forelimbs and can last for a relatively long period of time. The receiving animal may respond with a tail lift action. The pawing action may precede a pass over or pass under action.

Description of other behaviours observed.

Sniff

An animal investigates another individual's posterior. The receiving animal usually lifts its tail in response.

Urine Lapping

This behaviour can be done by the urinating animal or the urine of another animal is lapped. Unusually, during this behaviour, the tongue of the individual is visible external to the buccal cavity. This behaviour has been very rarely observed (three times in the entire experimental period).

Copulation

An individual mounts another individual from behind and exhibits pelvic thrusting activity. This behaviour has been observed between reproductive animals (of different sexes) as well as between two males and two females, although rarely. Normal copulation is also rarely witnessed.

Table 3: Biostatistics of the individuals belonging to each of the colonies used in this study.

Colony 1	Sex	Assumed Reproductive Status*	Mass (g)	Colony 2	Sex	Assumed Reproductive Status*	Mass (g)
42S	F	R	108	RP	F	R	87
	F	NR	92		F	NR	87
	F	NR	89		F	NR	85
	F	NR	86		F	NR	83
	F	NR	65		F	NR	74
	M	R	137		M	R	115
	M	NR	150		M	NR	94
					M	NR	52

*R=reproductive, NR=non-reproductive