Social organization and mating system of the plains viscacha
(Lagostomus maximus)¹

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(With 4 figures in the text)

Plains viscachas live in communal burrow systems in groups containing one or more males, several females and immatures. Viscachas forage in groups at night and aggregate underground during the day. All members of a group use burrows throughout the communal burrow system and participate in digging at the burrows. Alarm calls are given primarily by adult males. Allogrooming occurs among all sex-age classes within a social group but not between members of different social groups. Agonistic interactions occur more often between members of different social groups than within a group.

The long-term social unit of the plains viscacha is the female group. Resident males disappear each year and new males join groups of females. Dominance is absent among females. Agonistic interactions are rare among adult males within a social group and dominance is not clearly evident.

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Introduction

The plains viscacha (Lagostomus maximus) belongs to one of three genera in the rodent family Chinchillidae. Descriptions of the natural history of the plains viscacha, mountain viscachas (Lagidium spp.) and chinchillas (Chinchilla spp.) suggest that all members of this family are colonial (Pearson, 1948; Llanos & Crespo, 1952; Jiménez, 1990). Mountain viscachas and chinchillas inhabit rocky outcrops and boulders in montane areas of Peru, Chile, Bolivia and Argentina, and the plains viscacha lives in communal burrow systems in grasslands and lowland desert scrub in Paraguay, Bolivia and Argentina.

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Although no detailed behavioural studies had been conducted on the plains viscacha or other members of the chinchilla family in a natural habitat prior to this study, earlier descriptive work suggested that the behaviour of the plains viscacha was extremely interesting for several reasons. Based on the extensive vocal repertoire and cooperative behaviours described by Hudson (1872), the social behaviour of this species appeared to be similar to that of the large Holarctic ground squirrels, thus placing it among the most social of rodents. This species is also one of the most sexually dimorphic rodents, which suggests that males and females use resources in different ways and/or that males have high variance in reproductive success as a result of female choice or male–male competition for mates (Selander, 1972; Demment, 1983; Rodman & Mitani, 1987). Also, plains vischas live in habitats where the temporal and spatial distribution of resources is relatively homogeneous and in environments where the availability of resources fluctuates greatly over time and space (Llanos & Crespo, 1952; Branch, 1989). Distribution of resources is proposed as one of the primary ecological factors influencing the evolution of sociality (Alexander, 1974). Comparative studies of vischas in different habitats could be used to test theoretical models relating social evolution to resources.

This paper describes the social organization and aspects of the mating system of the plains viscacha in desert scrub habitat in central Argentina. The degree of sociality of vischas and the strength of social bonds among sex–age classes are assessed from data on: (1) the length of tenure of individuals in social groups; (2) the size and composition of foraging groups; (3) the degree of overlap in use of space at burrow sites; and (4) the relative frequency among sex–age classes of aggressive versus cooperative behaviours. Male behaviour is also examined for evidence of dominance and female defence.

The study animal

The plains viscacha is the largest member of the chinchilla family. Adult females weigh 2.5–4.5 kg, and adult male vischas weigh up to 9 kg (Weir, 1974). Viscachas are active from dusk to dawn throughout the year and feed on a variety of grasses, forbs and low shrubs (Giulietti & Jackson, 1986). In central Argentina the primary breeding season extends from about mid-April to mid-June. Viscachas are polyovulators but usually only one or two young are born after a gestation period of about 154 days (Llanos & Crespo, 1952; Weir, 1971a,b; Jackson, 1989). Most young are born during a spring birth pulse in September and October. Young do not emerge from the burrows for several weeks after they are born.

Social groups are composed of 1–3 adult males, 2–5 times as many adult females, and immatures. Each group lives in a burrow system (viscachera) containing from 10 to over 100 burrows that connect to underground chambers (Llanos & Crespo, 1952). These principal burrow systems are occupied for many years. Viscachas drag sticks and other objects to the viscachera and temporarily or permanently plug some of the burrows. Scattered throughout the home range of each group of vischas are small satellite viscacheras containing a few burrows used for temporary cover (Llanos & Crespo, 1952; Jackson, 1986). Several principal viscacheras and associated satellite viscacheras are clumped together in a patch called a viscacheral.

Study area

Research was conducted in Lihue Calel National Park, La Pampa, Argentina (38° 00’ S, 65° 35’ W) from January 1985–August 1987. The park contains bare rock hills (589 m ASL)
surrounded by desert scrub (300 m ASL). Hot summers and cool winters with low, unpredictable annual rainfall (1983–1988, 567 mm ± 214 S.D.) are characteristic of this area. Vegetation is a fine-grained mosaic of open patches and shrubs (e.g. *Larrea cuneifolia*, *L. divaricata*, *L. nitida*, *Prosopis alpataco*, *P. caldenia*, *Condalia microfolia* and *Geoffroea decorticans*). A large variety of annual and perennial forbs and grasses occurs in the open areas and as the understorey of shrub patches.

Extensive behavioural observations were made on residents of 3 viscachas (V-41, V-101, V-107) within a single viscacheral at the base of the hills. The viscacheral covered about 13 ha and contained 8 principal viscachas and 93 satellite viscachas. When the study began the numbers of animals present were: 17 (V-41), 9 (V-101), 16 (V-107). Vegetation steadily declined because of low rainfall and heavy grazing by viscachas, and the viscacha population crashed with the decline in vegetation. By August 1987 all viscachas were inactive except V-101. Sex and age composition at each viscacheral for March 1985–August 1987 are given in Branch (1989).

Methods

*Trapping and marking*

Prior to initiating behavioural observations in late March 1985, most animals in the study area were captured in large corral traps baited with oats. Intermittent trapping was conducted throughout the study to catch immigrants and young. A total of 27 animals was captured at V-41, 30 at V-101, and 28 at V-107. Animals were weighed, measured, examined for scars, and marked with uniquely coloured ear tags.

*Age categories*

Males and females less than 1 year old were considered juveniles. Females give birth for the first time at about 1 year (Weir, 1971a; Branch, 1989; Jackson, 1989). Males do not reach reproductive maturity until 12–18 months and may not attain breeding status until much later (Llanos & Crespo, 1952; Branch, 1989; Jackson, 1989). Males do not breed in their natal viscachas and were categorized as subadults if they were at least 1 year old but still in their natal viscachas (Branch, 1989). For analyses with small sample sizes, all juveniles and subadults were lumped together as immatures.

*Collection of behavioural data*

Behavioural observations were conducted for 241 nights (978 h) between 1 June 1985–31 May 1986 and 1 September 1986–28 February 1987. Observations were made with a spotlight and binoculars from 6 platforms (1.5–2.5 m tall) that allowed complete coverage of the home ranges of animals from V-41, V-101 and V-107. Initially, observations were made with night goggles and ambient moonlight. Because animals had to be observed at a much closer range with this technique, it was necessary to follow them on foot. Animals never habituated to the movements of the observer. In contrast, viscachas quickly habituated to a stationary observer and the spotlight and fed within a few metres of the platforms. Observations began about 0.5 h prior to the emergence of animals from their burrows at dusk. Because the frequency of behavioural interactions was low, an attempt was made to observe for the maximum number of hours possible each night. Problems recharging batteries and frequent severe winds resulted in observation times actually ranging from 1–14 h per night (x = 4.1 ± 2.8 S.D.).

Every half hour the identity, behaviour, group and location of all animals were noted in scan samples (Altmann, 1974). A 20-m grid of flags formed a guide for estimating the location of animals. Animals were considered part of the same group if they moved together throughout the home range while foraging or were
present concurrently at the viscachera. All burrows were numbered with flags, and the nearest burrow opening and the distance from the burrow were noted for animals at viscacheras.

Fifteen minutes of continual behavioural observations were conducted between scan samples. Because animals were usually in a group, movements were not large, and the rates of occurrence of social behaviours were low, all animals could be observed simultaneously (focal group samples, Altmann, 1974; Wells & Bekoff, 1981). Data were collected on all bouts of digging and relocation of sticks, scent-marking, vocalizations, visits to viscacheras by adult males, and behavioural interactions, including identities and locations of the initiator and receiver of behaviours, identities of other animals present, and descriptions of behavioural sequences.

Ten males and 2 adult females were fitted with radio-collars (AVM, Livermore, CA) between 23 January and 1 June 1987. Animals were monitored at night to determine movement patterns and to locate individuals that were killed by predators. Between 5 March and 9 August 1987, the subterranean locations of 6 radio-collared animals were determined once during the day in V-101 for 4–21 days ($\bar{x} = 11.5 \pm 2.3$ S.D.) by walking over the viscachera with a radio receiver. The radio signal usually was strong and of about equal intensity within a 0.5-m circle. For each animal located underground, the centre of this circle was plotted on a map of the viscachera.

Statistical analyses

Chi-squared ($\chi^2$) goodness-of-fit was used to test for differences in frequencies of behaviours among seasons, sex and age classes, and individual males observed in focal group samples. Expected frequencies of behaviours for each test were based on the number of animals observed in scan samples in each category (e.g. during each season, in each sex and age class), or the number of times a particular male was observed. Expected frequencies based on the frequency of animals in scan samples take into account differences in levels of activity that influence the probability of observing behaviours, as well as differences in the number of animals in each category in the population. The frequency of dyadic interactions (agonistic encounters, allogrooming and cheek-rubbing) among members of different sex–age classes were also compared using $\chi^2$ goodness-of-fit tests. Expected rates of interaction were based on the number of dyads in scan samples (e.g. number of potentially interacting pairs of adult males, adult male–adult female pairs, immature–immature pairs, etc.; Michener, 1980; Ritchie & Belovsky, 1990). All other statistical tests followed standard parametric and non-parametric procedures (Siegel, 1956; Sokal & Rohlf, 1981). Summary data are given as means $\pm$ 1 standard deviation.

Results

Male and female tenure

Tenure of adult males ($4.7 \pm 3.4$ months, $N = 28$) within a viscachera was shorter than tenure of females ($9.0 \pm 7.3$ months, $N = 33$; $t = 2.81, 59$ d.f., $P < 0.006$; Fig. 1). No male was resident for more than one breeding season in any of the viscacheras in the viscacheral. Eleven of the 26 males that immigrated in spring and summer did not persist until the breeding season began in April. In 1985, all adult males disappeared within a few weeks of the appearance of new males (Fig. 1). Only one adult female disappeared during this time. Males may have emigrated or mortality may have been high because of injury during agonistic encounters with male immigrants or because of increased risk of predation during territorial displays (e.g. bouts of long distance vocalizations given only by males). During the second year, males and females were in poor condition and may have been particularly vulnerable to predation (Branch, 1989). Predation was confirmed for eight of ten males with radio-collars and both collared females (Fig. 1). One male was killed in a trap by a
Fig. 1. Tenure of adult males and females in viscacheras 41, 101 and 107. Asterisks mark animals that were killed by predators. Open bars indicate males that were of adult size but were probably still in their natal viscacheras. Um = Unmarked animals. The columns marked by the dotted lines indicate the breeding season.

mountain lion (Branch, 1989). No marked animals were found in periodic surveys of viscacheras within 1 km of the study area.

Because females remain in their natal viscachera and dispersal from the natal viscachera was delayed for some males for over two years, kinship was high among females and young males within a viscachera. Although several males appeared at viscacheras within a few days of each
other in the spring and summer, the fact that males did not arrive together and initially were antagonistic towards each other suggests that males were not related. The tenures of most males present during the breeding season in 1985 and male 130 in 1986 extended well beyond the breeding season, but few of the potential fathers were still in the viscachera when young were born in late September and October (Fig. 1). Only adult males 78 and 130 remained in the viscachera from the breeding season in the autumn until the young emerged from the burrows in December.

**Group size and composition**

Shortly before dusk viscachas emerge from their burrows, and as it becomes dark they leave the viscachera to feed. Females and immatures usually forage in groups, and males forage with female-immature groups or alone. All animals feed throughout the group home range and often move through a large part of the home range in a night. Groups return to the viscachera for brief periods between foraging bouts and coalesce, split, and change composition while foraging or at the viscachera.

Eighty-four percent of the animals recorded in scan samples were in groups. Mean group size was 2-7 ± 2.4 (range 1-17). Adult males were observed more often as singles (i.e., group size = 1) than other sex-age classes (percentage observed as singles—adult males, 35-4; subadult males, 24-6; adult females, 12-2; and juveniles, 8-6; χ² = 388.6, 3 d.f., P < 0.001). Data for June 1985-May 1986 indicated that males occurred as singles more often in summer (December–February) and autumn (March–May) than in winter (June–August) and spring (September–November) (χ² = 28.5, 3 d.f., P < 0.001, Fig. 2). The same pattern was evident for the second year of the study but the percentage of singles was lower (χ² = 9.0, 1 d.f., P < 0.003; September 1985–February 1986 vs. September 1986–February 1987). No seasonal or annual differences were found in the tendency of other sex and age classes to occur as singles or in groups.

**Space use at viscacheras**

Between foraging bouts animals from V-41 and V-101 frequently returned to their home viscachera and most social interactions occurred at the principal viscachera. Animals from V-107 remained in that viscachera during the day but frequented V-106, 116 m west of V-107, between foraging bouts at night. The harmonic mean centre of the home range of these animals was V-106 rather than V-107 (Branch, 1989). V-107 was in dense vegetation; V-41, V-101 and V-106 were in open areas which may have enhanced visual communication and predator detection.

The number of active and plugged burrows and approximate dimensions of the three viscacheras were as follows: V-41, 26 active, 28 plugged, 16 × 19 m; V-101, 17 active, one plugged, 6 × 11 m; V-106, 11 active, one plugged, 2.5 × 6 m. All open burrows were used at least occasionally. Animals often entered the viscachera by one burrow and left by another. The frequencies of sighting animals at each active burrow entrance in V-106 were random (Kolmogorov-Smirnov goodness-of-fit to a poisson distribution, z = 1.02, P = 0.25). In V-101 and V-41 some burrows were used much more frequently than expected, while others received little use (Kolmogorov-Smirnov goodness-of-fit test, V-41, z = 3.72, P < 0.0001; V-101, z = 3.01, P < 0.0001). There were no differences in use of burrow among sex and age classes at V-101 or V-106 (V-101, χ² = 7.34, 4 d.f., P = 0.11; V-106, χ² = 3.96, 6 d.f., P < 0.068). At V-41 differences in use of burrows among sex and age classes were significant (χ² = 21.5, 12 d.f., P < 0.05). Females and immatures generally emerged in the evening from one burrow, and females
were recorded at this burrow more frequently than expected. Immatures were recorded disproportionately at two burrows which they used during play near the periphery of the viscachera. However, all sex and age classes used these three burrows and all individuals used burrows throughout the viscachera.

Satellite viscacheras were used primarily by males (Fig. 3). During summer and autumn males spend more time sitting at burrow entrances of satellite and principal viscacheras (Fig. 2, $x^2 = 20.5$, 6 d.f., $P < 0.01$, data for June 1985–May 1986). This behaviour likely relates to defence of burrows from immigrant males, or the need for escape cover during territorial displays (Branch, 1989).

Telemetry data showed that animals concurrently resident in V-101 aggregated underground in the same area of the viscachera each day (Fig. 4). Adult males 179, 180 and 189 were together in V-101 in March–April 1987. All but one location of these animals fell within 2 m of the opening to burrow 10. Adult males 197 and 198 and female 164 were together during May–August. These animals resided in the north-west corner of the viscachera in a chamber several metres north of the nearest burrow opening. There was no evidence that resident males were less tolerant of each other during the breeding season, and inter-male distances within the viscachera did not change (mean between 197 and 198, 1.4 ± 1.4 m). Also, the mean distance between male 198 and female 164 (1.8 m ± 1.3, N = 3) was not significantly different from the distance between 197 and 164 (0.5 m ± 0.9, N = 9; $t = -2.03$, 10 d.f., $P > 0.06$), suggesting that one male did not exclude the other male from access to female 164. However, larger sample sizes may have produced significant differences.
Females may be guarded for only a few days during the breeding season while they are receptive and this behaviour could have been missed with telemetry data. During mid-July, males 197 and 198 moved together to V-41 for 2 days when the resident male there was killed by a mountain lion. Telemetry locations taken on 14 and 16 June at V-41 indicated that these animals were less than 1 m apart at V-41 and near the same burrow entrance. The overall picture obtained from telemetry data is clearly one of aggregation of individuals underground and high levels of behavioural tolerance and spatial overlap among males resident in the same viscachera.

Maintenance of the viscachera

Sixty-eight bouts of digging were observed at principal viscacheras (including 26 at V-106), and 10 bouts were observed at satellites. All sex-age classes participated equally in digging ($\chi^2 = 2.7, 2$ df, $P > 0.25$). Animals primarily enlarged and modified existing burrows rather than constructing new burrows.

Adult males ($N = 22$) were observed moving sticks around at the burrows more often than adult females ($N = 10$) and immatures ($N = 7$; $\chi^2 = 16.4, 2$ df, $P < 0.001$). Published conjectures on the function of sticks at the viscachera include deterring predators and raising the level of the viscachera to prevent flooding as soil is deposited over the sticks (Hudson, 1872; Llanos & Crespo, 1952). Sticks may prevent the grison (Galictis cuja) from entering burrows, but other predators are too large to enter burrows. Sticks are not likely important protection against flooding in Lihue.
Social organization of the Plains viscacha

Fig. 4. Locations of animals underground at V-101 and map of burrow entrances. All animals marked with filled symbols were resident at the same time, and animals marked with open symbols were resident together. Large circles with numbers indicate the location of burrow entrances. M = male, F = female.

Caeli because soil does not build up around sticks on viscacheras and rainfall is low. My data indicate that sticks serve as a substratum for scent-marking by males (Branch, 1989). Before and after moving sticks, males rubbed their cheeks on the sticks (N = 6) and marked sticks with urine (N = 7). Males moved sticks when they were alone at the viscachera and during agonistic encounters with other males. Twice females moved sticks during agonistic encounters with immigrant females.

Inter- and intra-group aggression

The frequencies of agonistic encounters between residents and non-residents were significantly higher than expected for adult males and adult females (Table I). Non-resident intruders were usually long-distance dispersers rather than neighbours (Branch, 1989). Most interactions (62 of 72) were chases, but violent fights involving biting, wrestling, kicking and rolling were observed among resident and intruding males. Females frequently bit intruding females on the hind quarters during chases.

Among residents, the level of aggression was lower or about equal to expected for all age classes except immatures (Table I). All animals tolerated close association of other animals (within a few centimetres), but occasionally interactions occurred when animals pushed against each other while feeding. Immatures frequently engaged in play wrestling that escalated into biting and rolling. This play-fight behaviour accounted for the higher frequency of interactions between immatures.
Table I

<table>
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<tr>
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<th>Non-residents</th>
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<th>Allogroom</th>
<th>Cheek-rub</th>
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<td></td>
<td>O</td>
<td>E</td>
<td>O</td>
<td>E</td>
</tr>
<tr>
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<td>13</td>
<td>4.8</td>
<td>3</td>
<td>1.6</td>
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<tr>
<td>I: I</td>
<td>12</td>
<td>10.4</td>
<td>20</td>
<td>9.0</td>
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\[ \chi^2 = 34.2, \quad \chi^2 = 21.1, \quad \chi^2 = 21.2 \]
\[ P < 0.0001, \quad P < 0.0001, \quad P < 0.0001 \]

In both sexes, adults had a greater number of scars than immatures (male, Mann-Whitney \( U = 408, P < 0.0001 \); females, \( U = 417, P < 0.001 \)). Between sexes there was no difference in immatures (\( U = 421, P = 0.11 \)), but the number of scars in adult males was significantly higher than in adult females (\( U = 864, P < 0.001 \)). The mean number of scars per animal by sex-age class was as follows: adult males, \( 3.16 \pm 2.52 \) (0–11), 44 animals; adult females, \( 1.63 \pm 1.56 \) (0–7), 63 animals; immature males, \( 1.07 \pm 1.3 \) (0–4), 41 animals; immature females, \( 0.46 \pm 0.58 \) (0–2), 26 animals.

Allogrooming, cheek-rubbing and dust bathing

Allogrooming and other amicable behaviours that may promote group cohesion (Steiner, 1973) occurred among all sex-age classes within a viscachera but were never observed between members of different viscacheras. During bouts of allogrooming, the primary contact behaviour between members of a viscachera, one animal nibbled on the neck and sometimes face and back of another animal. Animals occasionally touched noses and rubbed their cheeks together. All 66 bouts of allogrooming took place at viscacheras. Mutual grooming occurred in 52% of the bouts. Adult males were involved in 23% of the bouts of allogrooming, adult females in 77%, and immatures in

Table II

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<th>Initiators and recipients of allogrooming and cheek-rubs</th>
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<tr>
<td></td>
<td>Allogrooming</td>
</tr>
<tr>
<td></td>
<td>Male</td>
</tr>
<tr>
<td>Initiator</td>
<td>4</td>
</tr>
<tr>
<td>Receiver</td>
<td>8</td>
</tr>
</tbody>
</table>

1 Initiators and recipients are given for the beginning of each bout only. When roles were reversed within a bout, the new recipient and initiator of grooming were not included.
58%. Adult males were observed grooming other males twice outside behavioural sampling periods. All other sex-age classes groomed each other more frequently but allogrooming was much more common than expected between adult females (Table I). Adult females and immatures initiated grooming bouts about equally as often as they received grooming first (Table II). Adult males appeared to be receivers more often, but sample sizes were small. Because initiators and receivers are not independent, valid statistical comparisons cannot be made.

Yearling males and yearling females were observed approaching and touching noses with adult males and females 10 times. After three of these encounters, yearling males rubbed their cheeks on the adult male's cheek. Cheek-rubbing between members of a viscachera was observed on 25 other occasions and occurred primarily at viscacheras (21 of 28 bouts). Immature animals were the primary initiators of cheek-rubbing and adult males were the primary recipients. These patterns are quite distinct from patterns of initiators and receivers of allogrooming (Table I and II). Adult females participated in cheek-rubbing only occasionally but were observed initiating and receiving cheek-rubbing with adult males and immatures.

Juvenile viscachas, and sometimes adult females, gave short yelps while approaching an adult male for cheek-rubbing. Adult males stood with their tails arched and bristled, a posture often used in agonistic encounters. After rubbing cheeks with the male for several seconds on one or both sides, juveniles and occasionally females jumped back or straight up. Sometimes cheek-rubbing was reinitiated, or animals parted. The purpose of this behavioural sequence is unknown. This cheek-rubbing may be a scent-sharing behaviour, or it may serve some of the same functions suggested for 'kissing' among ground squirrels, such as appeasement, identification and group cohesion (Betts, 1976). The behaviour of immatures and females is suggestive of appeasement towards the male. This behaviour was observed when animals were foraging and milling around at the viscacheras but not in aggressive contexts. Betts (1976) notes that the dominant ground squirrel is the one that usually makes the first approach in greetings. This does not appear to be true for viscachas for this behavioural sequence.

Immediately upon leaving the burrows in the evening, viscachas frequently take a dust bath in a depression near the viscachera. The same depression is used repeatedly by all animals from the viscachera. Dust bathing may remove ectoparasites (e.g. fleas, lice and mites), which are common on viscachas (pers. obs.), and absorb oils in the fur. Dust bathing also functions in scent-marking in some species (Randall, 1987). Dust bathing and allogrooming, as well as cheek-rubbing, may be important for scent-sharing among members of the social group.

**Alarm vocalizations**

Viscachas give at least two alarm vocalizations which appear to signal 'differential urgency' as described for anti-predator calls of ground squirrels (Owings & Hennessy, 1984). When startled by a fox or my approach, adult females and immature animals gave one or two single syllable 'wank' calls. Infrequently the same call was given in response to the appearance of a mountain lion if the lion did not pose a serious threat (e.g. when the viscachas were very near the burrows and the lion was far away). This call could be heard for only a short distance, and probably was for communication with other members of the immediate group. When an individual gave a 'wank', the others looked around and sometimes immatures assumed a bipedal posture, but viscachas rarely ran indicating that this call communicates only mild alarm. During focal samples, one yearling male was observed giving a 'wank' call. The vocalizers were not determined for 31 other 'wank' calls.
While foxes prey on viscachas infrequently (Crespo, 1971), viscachas were the primary food of mountain lions in Lihue Calel during this study (Pessino, Villarreal & Branch, unpubl.). In response to mountain lions, dogs and sudden loud noises (e.g. gun shots), viscachas gave a two-syllable call similar to the 'pi-chung' vocalization given by males to advertise their occupancy of a home range (Branch, 1989). The second syllable of the anti-predator call was frequently higher pitched than in the 'pi-chung' call and calls were given more rapidly. All types of viscacha calls were highly variable. Some anti-predator calls were distinguishable only by context from calls used in male–male encounters. Unlike the 'wank' call, the two-syllable alarm call was audible for several hundred metres and often repeated. Viscachas from neighbouring viscacheras, as well as viscachas in the home range where the vocalizations occurred, frequently ran toward their principal viscachera in response to these calls. Calls were contagious among viscacheras.

Two-syllable calls were heard 168 times during behavioural observations when the calls clearly had an anti-predator function. The caller was known for 94 of these. Adult males gave 88 of the calls and females gave five. Adult males may detect predators prior to females because they are always alert for intruding males and spend more time sitting at the viscacheras than females.

While anti-predator vocalizations clearly warn other viscachas of potential danger, they may also influence the behaviour of predators. Mountain lions were sighted 41 times in the study area during behavioural observations. Ten chases of viscachas and one kill were observed. With the exception of one unsuccessful chase by a juvenile, lions never chased viscachas if animals gave any indication (e.g. vocalizations, alert postures, etc.) that they saw the lion before the chase began. Predators, as well as conspecifics, may be the target of anti-predator calls (Woodland, Jaafar & Knight, 1980; Owings & Hennessy, 1984).

Assessment of dominance

No behavioural interactions were observed that indicated dominance among adult females or among immatures. Twice an adult male was observed pushing females away from a pile of oats placed on the viscachera. In response, females arched and bristled their tails and ran but returned after a few seconds to feed beside the male. These observations suggest that males are able to dominate immatures and females, a likely case simply because of their large size. However, males rarely displayed dominance over other sex–age classes under more natural conditions.

Social dominance is usually determined by scoring the outcomes of dyadic, agonistic encounters (e.g. Paul & Kuester, 1987; Weatherhead & Teather, 1987; Roberts & Searcy, 1988). Dominance among males within a viscachera was difficult to detect. Only three aggressive encounters were observed among males that were established residents in the same viscachera. Low levels of aggression among males may have been because: 1) dominance was absent; 2) dominance was established by early aggressive encounters or some other factor such as size or prior residency when a new animal was incorporated into the viscachera; or 3) dominance was determined and/or maintained by nonagonistic behaviours (Francis, 1988).

Studies of mammals and birds have identified a variety of physical and behavioural traits, in addition to agonistic behaviour, which correlate with dominance status (Barlow & Ballin, 1976; Bell, 1981; Jackson & Winnegrad, 1988; Roberts & Searcy, 1988). I examined the following behaviours to determine if there were differences among males in frequencies of behaviours and consistent patterns for individual males across behaviours: 1) scent-marking; 2) bouts of vocalizations; and 3) access to principal viscacheras (Table III). Vocalizations included several calls that presumably function as threats to other males and advertise occupancy of a home range.
### Table III

Weights of males (kg) and frequencies of scent-marking, bouts of vocalizations, and sightings at the principal viscachera. *O* = observed frequency, *E* = expected frequency based on the relative frequency of sightings of each male in scan samples, and *χ²* = Chi-squared value from goodness-of-fit test.

<table>
<thead>
<tr>
<th>Male</th>
<th>Wt.</th>
<th>Scent-mark</th>
<th>Vocal bouts</th>
<th>Sightings</th>
</tr>
</thead>
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<tr>
<td></td>
<td></td>
<td>O</td>
<td>E</td>
<td>χ²</td>
</tr>
<tr>
<td>119</td>
<td>5.4</td>
<td>2</td>
<td>2.2</td>
<td>0.0</td>
</tr>
<tr>
<td>121</td>
<td>5.7</td>
<td>5</td>
<td>4.6</td>
<td>0.0</td>
</tr>
<tr>
<td>130</td>
<td>5.3</td>
<td>8</td>
<td>8.2</td>
<td>0.0</td>
</tr>
<tr>
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<td>15</td>
<td>0.05</td>
<td>315</td>
<td>Viscachera 41</td>
</tr>
<tr>
<td>Viscachera 101</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>129</td>
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<td>16</td>
<td>14.7</td>
<td>0.1</td>
</tr>
<tr>
<td>136</td>
<td>4.8</td>
<td>7</td>
<td>8.3</td>
<td>0.2</td>
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<tr>
<td>Total Rank 1</td>
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<td>0.3</td>
<td>82</td>
<td>Viscachera 101</td>
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<tr>
<td>Viscachera 107</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>104</td>
<td>5.3</td>
<td>8</td>
<td>4.3</td>
<td>3.2</td>
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<tr>
<td>118</td>
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<td>1</td>
<td>5.1</td>
<td>3.3</td>
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<td>139</td>
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<td>2.6</td>
<td>0.1</td>
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<td>Total Rank 1</td>
<td>12</td>
<td>0.6*</td>
<td>66</td>
<td>Viscachera 107</td>
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<td>118-104-139</td>
<td>14</td>
<td>1.9</td>
<td>58</td>
<td>118-104-139</td>
</tr>
</tbody>
</table>

* *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001

1 Ranks based on (O-E)

such as growls, snores, chucks and long distance ‘pi-chung’ calls (Eisenberg, 1974; Weir, 1974; Branch, 1989). I have no independent measure of dominance with which to correlate behaviours; therefore, the interpretation of these data is limited. However, consistent ranking in scores across behaviours may suggest differences in dominance status and provide useful insights given the paucity of evidence for dominance based on use of space and aggression. High levels of scent-marking are correlated with high dominance status in a variety of mammals, including rabbits, hamsters, gerbils and primates (Mykytowycz, 1968; Ralls, 1971; Bell, 1981, 1985; Zeller, 1987). Dominant males also vocalize more frequently than subordinates in some birds and mammals (Ficken, Weise & Reinartz, 1987; Whitehead, 1989). Access of males to principal viscacheras implies access to females and cover and thus also should correlate with dominance.

Males within viscacheras were ranked based on the difference between the observed frequency of behaviours and the expected frequency calculated from the number of times each animal was sighted in scan samples (Table III). In V-41 and V-101 the largest male had the highest ranking on all behaviours. In V-107 the largest male ranked first in vocalizations and access to the viscachera but exhibited the lowest frequency of scent-marking. Second and third place males were not consistent, but male 104 always had a higher ranking than male 139 at V-107. Rankings in V-101 and V-107 were consistent with other observations which may indicate dominance. Male 129 was observed chasing 136 at V-101. Three times male 139 left V-106 when male 104 approached. No
clear cases of avoidance or aggression were observed among resident males at V-41 during behavioural observations. Occasionally outside of observation periods, other encounters were observed that involved subtle avoidance of one male by another. These data suggest that dominance relationships exist among males. However, some animals simply may be more active than others. Likewise, lack of concordance among behavioural rankings for the same individual does not prove that dominance does not occur. If dominance does exist, it is subtle.

**Defence of females by males**

Adult females were present at only four of the 16 male-male agonistic encounters and 27 of the 133 bouts of scent-marking. Adult males scent-marked by rubbing their cheeks on sticks or urinating on sticks at the viscachera. Faeces were frequently found at burrow entrances and probably also functioned as scent-marks in a manner similar to the dung piles of European rabbits (Bell, 1985). However, faeces did not accumulate in dung piles and it was impossible to separate faeces which served as scent-marks from faeces simply resulting from elimination. Therefore, only scent-marking in the form of cheek-rubbing and urination on sticks was recorded. Chi-squared analyses were used to determine whether the presence of more than one male and the presence of females influenced the frequency of scent-marking. The number of times scent-marking occurred in four types of groups was tallied and compared to expected frequencies based on the number of groups of each type observed in scan samples (single adult males and no adult females, N of groups in scan samples = 294, 54.5% of total number of groups with males; multiple males and no females, N = 45, 8.3%; single males with females, N = 157, 29.1%; multiple males with females, N = 43, 7.9%). If the probability of scent-marking is constant and equal for all males, then the frequency of scent-marking will be a function of the number of males in the group. Based on this premise, expected frequencies were also calculated for each category by weighting groups by the number of males present (e.g. 2 groups · 3 males each = 6). In all cases, weighted and unweighted analyses produced the same results. Only the weighted analyses are presented here. Scent-marking occurred more frequently than expected in groups with multiple males as compared to single males, regardless of whether females were present (single male versus multimale groups with females, $\chi^2 = 22.8, 1 \text{ d.f.}, P < 0.001$; single male versus multimale groups without females, $\chi^2 = 71.82, 1 \text{ d.f.}, P < 0.001$). When groups with and without females were compared, scent-marking occurred less frequently than expected when females were present, regardless of whether one or several males were present (single male versus single male with females, $\chi^2 = 4.12, 1 \text{ d.f.}, P < 0.05$; multiple males only versus multiple males with females, $\chi^2 = 6.22, 1 \text{ d.f.}, P < 0.02$). This relationship appears because females and males were in the same group primarily during foraging, and scent-marking rarely occurs during foraging.

**Discussion**

Of the rodents whose social organization has been described, the social organization of the plains viscacha is most similar to that of the black-tailed prairie dog (*Cynomys ludovicianus*). Both species live in social groups composed of one or more males, several females and immatures (King, 1955; Hoogland, 1981a; Branch, 1989). Social groups occupy exclusive home ranges and are aggregated in patches called wards (prairie dogs) and viscacherales (viscachas). Females of both species remain in their natal social groups, and males move to other groups (Hoogland, 1981b; Branch, 1989). Cooperative behaviours such as allogrooming are common among members of a
social group but are rare between groups (Hoogland, 1981b, 1983). Dominance generally is absent except among males. In social groups of prairie dogs (coterie) with two males, one is dominant during the breeding season (King, 1955). Dominance also may occur among males within a viscachera, but data are not conclusive.

Viscachas and prairie dogs differ with respect to use of burrows, defence of home range boundaries, and alarm calling. Throughout the year each social group of viscachas lives in a single, interconnected burrow system (viscachera). All members have access to all burrows. Young are born within the viscachera and litters mix before coming above ground. Prairie dogs use burrows scattered throughout the home range of the coterie (King, 1955). Although prairie dogs frequently sleep communally, females defend nest burrows containing weaned young against other members of the coterie, as well as against strangers (Hoogland, 1981b). Female defence of burrows during pregnancy and lactation is common among many other species of marmots and ground squirrels and is important in protection of offspring from infanticide by females and males (Sherman, 1982; McLean, 1983; Hoogland, 1985; Armitage, 1986). Infanticide after invasion by a new male has been documented in ground squirrels and other social mammals (Sherman, 1982; Packer & Pusey, 1983; Hausfater & Hrdy, 1984). It is interesting to note that resident male viscachas disappeared and new males entered the viscachera about the time young were born. This suggests that the potential for infanticide should have been high.

Unlike prairie dogs, viscachas do not defend boundaries of the home range (Branch, 1989), but all animals defend the viscachera by chasing immigrants of the same sex-age class. Because viscachas use one central burrow system (the principal viscachera) as a refuge, the home ranges of viscachas may be defined by constraints on foraging away from the viscachera (e.g. increased risk of predation) rather than boundary defence. Differences in boundary defence also could be influenced by the nocturnal activity patterns of viscachas. Prairie dogs are diurnal. From a distance, it may be more difficult for viscachas to see intruders crossing boundaries. However, scent-marking also occurs primarily at viscacheras rather than home range boundaries (Branch, 1989). In other nocturnal species such as cats, wolves, and some primates, scent-marks frequently are used to advertise home range boundaries (Peters & Mech, 1975; Zeller, 1987; Smith, McDougal & Miquelle, 1989).

Studies of prairie dogs and other ground squirrels have shown that alarm calling and other cooperative behaviours occur most frequently among kin, and nepotism is important in the evolution of these behaviours (Sherman, 1977; Hoogland, 1983). If nepotism is important in the evolution of cooperative behaviour in viscachas, females should exhibit cooperative behaviours more frequently than males because they are more likely to have kin in the viscachera. Cooperative chases, allogrooming and group foraging did occur more frequently among females, but alarm calls were given most often by adult males. This suggests that non-nepotistic factors were important in the evolution of alarm calling. Calling may directly benefit males by discouraging pursuit by predators (Woodland et al., 1980), or alarm vocalizations could enhance male reproductive success by decreasing predation on females. Alternatively, under more favourable environmental conditions males may reside in a viscachera for more than one year and thus overlap with their offspring. Under these conditions, male alarm calls could be nepotistic.

The long-term social unit of viscachas is the female-bonded group. Females reside in the viscachera when no males were present and remained in the viscachera through a series of males. Though turnover of individuals was high, viscachas can live to be at least six years old (Jackson, 1986). Under more stable conditions, female groups may form closed matriarchal societies like the yellow-bellied marmot (Marmota flaviventris) and the black-tailed prairie dog (Armitage, 1986).
The mating system of the viscacha is similar to the harem polygyny model described for marmots and prairie dogs, but viscacha groups generally have more than one male and marmots and prairie dogs usually have one (Armitage, 1986). Male viscachas gain access to areas used by females through contest competition and attach themselves to female groups. Because a male cannot control more than one viscachera, the number of potential mates for a male is limited by the number of females in a viscachera which may be a function of female–female interactions or ecological factors unrelated to reproduction. Male viscachas rarely interact with neighbours except through vocalizations, but because of the close proximity of viscacheras, occasionally males may mate with females from other viscacheras.

Because up to three males are co-resident in each viscachera, the number of matings a male obtains within a viscachera may be determined by male–male interactions or female choice. Mate guarding has been reported for marmots and ground squirrels during the breeding season (Barash, 1981; Armitage, 1986; Sherman, 1989). I found no evidence that male viscachas guard females except by general vigilance of the area used by females. Males spend less time in groups with females prior to and during the breeding season than at other times of the year and spend more time in vigilance for intruding males. Females are often feeding in other parts of the home range when male–male encounters occur. Contests among male viscachas occur as much as six months before the breeding season and continue through the breeding season because of the high turnover of males and the arrival of dispersing males. Although guarding of oestrous females was not observed, it is possible that this behaviour and most copulations occurred underground. After mating, a vaginal plug forms which may prevent insemination by other males and thus alleviate the need for mate guarding (Weir, 1971a).

No behaviours were observed which suggested females had preferences for particular males. However, if female choice does occur, it probably occurs primarily among males within a viscachera. Because females are recruited into their natal viscachera, the choice of males for most females is limited to males resident in that viscachera. Emigration occurs in declining populations. When the number of animals in a viscachera becomes low, females and immatures move as a group to the nearest neighbouring viscachera (Branch, 1989). Thus, each female does not independently choose a viscachera-based on males. In this study, male turnover was so high that resident males sometimes changed between the time females immigrated into the viscachera and the breeding season. I suspect that male and female turnover was unusually high. However, if high turnover is typical, the availability of particular males as mates may not be predictable when females immigrate into a viscachera.

One of the most intriguing questions which remains to be answered is—Why do viscacheras contain more than one adult male? Though males do not cooperate in defence against intruding males (e.g. by cooperative chasing), all males in the viscachera defend it against non-resident males. The cost of defending the viscachera against all other males may be too high for a single male, but two or three males may be able to keep all other males out. Evidence for the high costs of defending a viscachera include the large number of scars in males, weight loss during spring and summer when males are interacting with intruding males (Branch, 1989), and the rapid turnover of males. Also, multiple males may be more effective in detection and warning against predators. Predation pressure has been suggested as one important selective factor in the evolution of multimale groups of primates, but data are not conclusive (Cheney & Wrangham, 1987). In order to understand fully the social relationships among males within a viscachera and the high turnover of males, it is essential to ascertain the degree to which matings are shared among males within a viscachera and measure life-time reproductive success of males in viscacheras with different
numbers of males and females. Also, genetic analyses should be conducted to confirm that males are not relatives.

Despite the extensive literature on the social behaviour of mammals, the relative importance of different selective pressures in the evolution of sociality is unknown for most species and often is the subject of considerable debate. Armitage (1981) suggests that the evolution of sociality in prairie dogs can be explained by direct reproductive benefits to females accruing from increased survivorship and reproductive success of young as a result of retention of young in the natal coterie. Similarly, philopatry may enhance survivorship of young female viscachas, and delayed dispersal of males results in larger body size at dispersal which may be important in gaining access to a new viscachera. The extensive use of warning calls by viscachas also suggests that predation is an important selective force for sociality in this species. Viscachas respond not only to warning calls from other members of their viscachera but also to calls made by animals from neighbouring viscacheras. Increased protection from predation is probably one advantage of the clumped distribution of viscacheras. In some species, localization of food resources or other key habitat features (e.g. burrow sites) also promotes sociality, and group foraging induces changes in the habitat which may be advantageous to members of the group (Hoogland, 1981a; Bell, 1983; Slobodchikoff, 1984). Viscachas form communal burrows in soils ranging from sandy to very rocky and are gregarious when unoccupied burrow systems are available (Llanos & Crespo, 1952; Branch, 1989). Burrow sites do not appear to be limiting for viscachas. However, the relationship between sociality and the distribution of food resources or other habitat features has not been examined in detail. Behavioural research on the plains viscacha in a variety of habitats and research on other members of the chinchilla family are needed to understand fully the evolution of sociality in this species.

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REFERENCES


SOCIAL ORGANIZATION OF THE PLAINS VISCACHA


