



Spacing behaviour and its implications for the mating system of a precocial small mammal: an almost asocial cavy *Cavia magna*?

CORNELIA KRAUS, JOACHIM KÜNKELE & FRITZ TRILLMICH

Department of Animal Behaviour, University of Bielefeld

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Socioecological models for small mammals attempt to explain the causal relations between the spatiotemporal distributions of food resources, females and males. We tested their predictions for a wild population of *Cavia magna*, a grazing, precocial rodent, by analysing spacing behaviour in relation to various demographic features. Between May 1999 and January 2001 we collected capture–recapture data on 309 individuals and monitored 55 females and 49 males by radiotelemetry in periodically inundated wetland in Uruguay. Cavies showed a nonstationary use of space: monthly home ranges drifted over the whole study site. Female home ranges overlapped with those of several others. Females were randomly distributed and we found no evidence for socially mediated reproductive synchrony. Males ranged over larger areas than females, showing even less site fidelity, and also overlapped with several rivals. This basic spacing system remained stable over a wide range of densities and sex ratios. Independent of sex, animals used overlap zones randomly with respect to each other. Significant dynamic (spatiotemporal) interaction was most frequent between males and females. However, interaction analyses revealed no evidence for stable social bonds between animals, regardless of sex. We suggest that unpredictable female locations prevent males monopolizing females spatially. Because females are solitary, males could monopolize only one female by maintaining close proximity, rendering a roaming mating tactic more successful. Our findings point to a solitary ‘social’ system and overlap promiscuity as the likely mating system for the *C. magna* population studied.

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Ecological factors such as predation risk and food availability play a central role in shaping the social organization and mating system in mammals (Emlen & Oring 1977; Clutton-Brock 1989). The reproductive success of female mammals is thought to be limited primarily by access to food resources, leading to lower potential reproductive rates, whereas for males the limiting resource is access to receptive females (Trivers 1972; Clutton-Brock & Parker 1992). These sex-specific selective forces determine the spatial and temporal distribution of females and males and thus contribute importantly to a species’ social and mating system (Clutton-Brock 1989; Davies 1991; Reynolds 1996).

Models for small mammals connecting spatial and social organization (Ostfeld 1985, 1990; Ims 1987) predict females of species relying on food resources with low abundance, patchy distribution and slow renewal rate, such as seeds, to be territorial (to show a high degree of intrasexual exclusiveness of home range, Kaufmann 1983), because the benefits of monopolizing

these resources outweigh the costs of defending them. Territoriality leads to an even female distribution, which in turn makes it costly for males to monopolize females spatially. Consequently, males in these species are usually nonterritorial. In contrast, in species with a diet of abundant, evenly distributed and rapidly renewed food sources, such as grasses, the ratio of benefits to costs for maintaining an exclusive home range would be low and therefore females show considerable home range overlap and are often spatially clumped. These clumped females represent a defensible resource, which males can monopolize within a territory leading to a spatially even male distribution (Ostfeld 1985, 1990).

Ims (1987, 1988a, 1990) emphasized the temporal aspect of female distribution as decisive for male mating tactics. Regardless of the spatial female distribution, males should search widely for mating opportunities if reproduction is asynchronous, resulting in large overlapping male home ranges and promiscuous mating. If reproduction is synchronous, males should try to monopolize females by defending territories comprising one to several female home ranges, thus leading to polygamy or, as a special case, monogamy if females are

Correspondence: C. Kraus, Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Postfach 100131, 33501 Bielefeld, Germany (email: Cornelia.Kraus@uni-bielefeld.de).

widely dispersed or have large home ranges. As Ostfeld (1990) pointed out, evidence for the 'females in space' and the 'females in space and time' hypotheses are difficult to separate because females are more likely to reproduce synchronously when spatially clumped and asynchronously when dispersed (Ims 1990).

Other ecological and social factors are known to influence the cost-benefit ratio of space monopolization and often lead to a shift in spatial and social organization (see Lott 1984 for intraspecific variation in social systems). High female density might lead to space sharing in females (e.g. *Microtus oeconomus*: Gliwicz 1997). Inclusive fitness benefits (kinship effects) through female philopatry or female grouping, for example caused by predation, can promote female spatial clustering (e.g. *M. townsendii*: Lambin & Krebs 1991; but see Agrell 1995 for *M. agrestis*). For males the decision to stay or to roam can depend on their resource-holding potential, that is, body mass (*Apodemus sylvaticus*: Tew & Macdonald 1994; *M. oeconomus*: Gliwicz 1997). The operational sex ratio correlates with the intruder pressure and thus potentially regulates the defensibility of clumped females (Ostfeld 1990). When female ranges become very large, monopolization of more than one female spatially might not be feasible and male roaming behaviour will be more successful (*Peromyscus leucopus*: Wolff & Cicirello 1990).

The models described have been developed mainly for microtine rodents, which show considerable inter- and intraspecific variation in spatial organization and mating system (reviewed in Madison 1990; Ostfeld 1990; Ostfeld & Klostermann 1990). To assess their general predictive value for small mammals, studies of nonvole rodent species are essential. The South American family Caviidae seems a promising candidate to test these theories, because their mating systems are also highly diverse: from the monogamous maras, *Dolichotis patagonum* (Taber & Macdonald 1992a, b) to polygynous wild cavies, *Cavia aperea* (Sachser 1998; Sachser et al. 1999; Asher & Sachser 2000; but see Rood 1972) and promiscuous cuis, *Galea musteloides*, with multiple paternity litters (Schwarz-Weig & Sachser 1996; Sachser 1998; Sachser et al. 1999) to the flexible societies of the capybara, *Hydrochoerus hydrochaeris* (Macdonald 1981; Herrera & Macdonald 1987, 1989). Nevertheless, detailed field data are available only for the larger family members, for which the relation between the spatial distribution of crucial resources and that of females is in accordance with the model (Ostfeld 1985, 1990): for example female maras are territorial when food resources are patchy, but their ranges overlap when they feed in rich patches (Taber & Macdonald 1992a), and similar correlations have been found for the group-living capybara (Macdonald 1981; Herrera & Macdonald 1987, 1989). The connection between female and male distributions seems less straightforward (Ims 1988b); male mating tactics are more likely to be the outcome of multiple factors (e.g. Sandell & Liberg 1992). For the smaller species few field studies exist, with partly contradictory results. Rood (1972) found overlapping home ranges for both sexes in *Microcavia australis* and *C. aperea* and suggested promiscuous mating, but Asher & Sachser (2000) found small territorial units of a few

females and a male in *C. aperea* and proposed resource defence polygyny as the mating system in their low-density population in Brazil.

We investigated the spacing behaviour of *Cavia magna*, a recently described but almost unstudied caviomorph species which superficially resembles the partially sympatric *C. aperea* (see Ximénez 1967, 1980 for morphological details). These cavies feed mainly on grasses and are adapted to the periodically inundated wetlands near the Atlantic coast of southern Brazil and Uruguay. Based on the models described above, we predicted that (1) females would have overlapping home ranges. This spacing behaviour should lead to (2) a spatially clumped distribution of females showing (3) a high degree of reproductive synchrony. (4) Males should occupy territories enclosing (5) several smaller female ranges. To interpret findings supporting or rejecting predictions 1–5, we measured several potentially modulating factors, that is, density, operational sex ratio, temporal breeding pattern and male body mass.

METHODS

Study Area and Study Population

The study site was near the Atlantic coast within the national park Refugio de Fauna Laguna de Castillos, in the department of Rocha, Uruguay. Cattle were excluded in 1997 and an extensive 'caraguatál' (ca. 3.3 ha), a typical wetland vegetation with the key species *Eryngium pandanifolium* (a tall spiny shrub), developed, surrounded by short and adjacent long grassland, providing protection and food for coexisting populations of *C. aperea* and *C. magna* (see Gambarotta et al. 1999 for a description of the reserve and its fauna). The cavies relied on the caraguatál and always returned to it for shelter; they thus formed a kind of 'island population'. Owing to the humid climate (ca. 1100 mm/year) and the altitude of 0 m above sea level, the area was characterized by marked seasonality with partial flooding during the winter (March/April to October/November; Fig. 1), the duration and extent varying strongly between years. We measured the water level in the area as water depth of a little creek at the edge of the study site. To facilitate fieldwork we established a grid system (250 × 200 m) with wooden stakes marking the intersections at 10-m distances.

Capture-Recapture

The systematic capture-recapture study lasted from May 1999 to January 2001 with 200 traps (Tomahawk Live trap, Tomahawk, U.S.A.) distributed on the grid system positioned within a 5-m radius around grid stakes. We trapped the complete caraguatál and parts of the grassland to ensure that we covered the whole cavy population. Twice monthly (in biweekly intervals), for two consecutive nights, traps were placed unbaited on the runways most heavily used. The cavies could feed on grass through the floor of the trap. Water was not provided because cavies in the wild do not usually drink

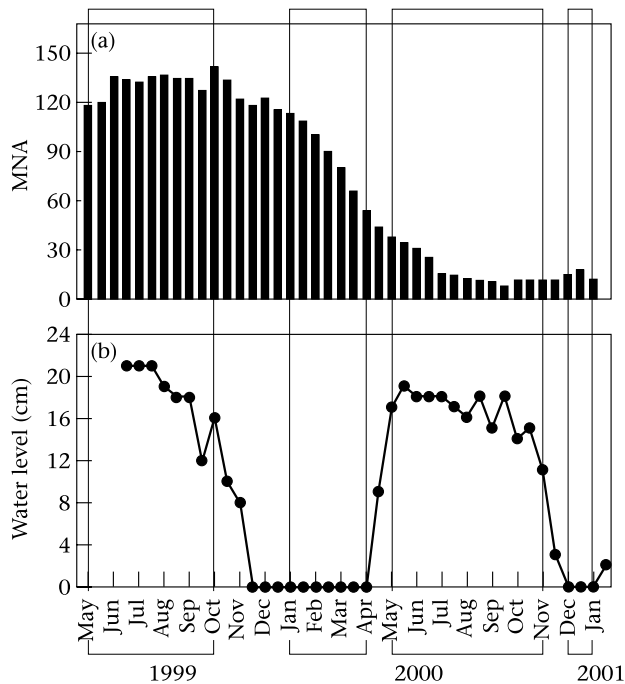


Figure 1. (a) Changes in population size, estimated as minimum numbers alive (MNA), and (b) changes in water level during the study period. Boxes indicate periods of high and low water levels and small and large population size, respectively, which were chosen for the analysis of home range size (Table 1).

additional water. Traps were set in the late afternoon, 2 h before sunset, and again at night 2 h before sunrise. Four to five hours after opening them, we checked the traps and left them closed for the rest of the night and day. Trapping was confined to these hours because twilight phases were identified as the caviés' main activity periods and because we wanted to avoid exposing them to heat stress during the day or to rain and cold at night. Caviés that were trapped repeatedly during one trapping session did not lose weight. Out of 2154 captures, seven *C. magna* died during the 29 months capture-recapture study. Between trapping sessions we left traps locked open to habituate the caviés to the traps and to prevent them from changing their preferred runways. Caviés caught for the first time were marked individually with a transponder (11.5 mm long and 2 mm in diameter; Trovan Euro I.D., Weilesdist, Germany) injected subdermally between the shoulders and with a numbered metal ear tag (6 mm long and 2 mm wide; National Band & Tag Co., Newport, U.S.A.). We sexed each individual, determined the reproductive state (females: closed or open vaginal membrane, lactating, pregnant; males: scrotal testes) and measured body mass and length before releasing them. Permission for trapping wild caviés in Uruguay was granted by the Ministerio de Gandería Agricultura y Pesca.

Radiotracking

Between May 1999 and January 2001 we fitted 55 female and 49 male adult *C. magna* with radiotransmitters

with an external antenna, tuned to separate frequencies of the 150-Mhz band and a life expectancy of 4 months (Sirtrack, Havelock North, New Zealand). Transmitters were attached with cable tie collars, sheathed in silicon tubing to minimize the risk of injury. The whole package weighed between 4 and 6 g (0.6–2.0% of the animal's body mass). Signals were picked up with a Telonics receiver and we used a hand-held three-element yagi aerial (Sirtrack) for tracking. Owing to their habit of 'freezing' in high vegetation the caviés could be located very accurately (even caught by hand). Tracking was stopped when we could receive the signal with the aerial disconnected (2–5 m distance, i.e. a tracking resolution of 5 m) and assign the animal's location to a 5×5 -m quadrat based on the grid system. The disadvantage of this method was that foraging areas within the home range covered only by short grass could not be identified, because the caviés would react to an approach by running to high vegetation for shelter. However, these small patches were surrounded by dense vegetation and by midwinter 2000 they had disappeared completely. All radiotagged animals were located up to six times a day with at least a 4-h interval between successive localizations. To minimize circadian effects on the record of space use by individuals, we distributed tracking sessions over all 24 h of the day. On average two such 24-h rounds were completed within 1 month. Mortality rates of collared and uncollared animals did not differ substantially (C. Kraus, unpublished data).

Data Analysis

Population size was estimated from capture-recapture data as 'minimum numbers known to be alive' (MNA, Krebs 1966). We marked caviés from November 1998 onwards and during the study period few unmarked adults, probably immigrants, were caught (eight adults in 24 capture sessions in 2000). As we know from the radiotracked individuals, emigration, at least of adults, was at best rare. Therefore, this estimator should accurately reflect the population dynamics, although during population decline numbers might be slightly underestimated. We calculated the population sex ratio as the proportion of females in the population from MNA. The operational sex ratio (OSR, Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996) was estimated as the percentage of oestrous females in relation to males over 400 g (approximate weight at maturity) for each trapping session: $\text{open F}/(\text{open F} + \text{adult M})$.

Because during most of the study period we tracked only a small proportion of the population, we used capture data to evaluate the spatial distribution of the sexes. We conducted an exemplary nearest-neighbour analysis (Clark & Evans 1954) for the first catch in August 1999, when about one-third of the females caught were in oestrus (open vagina). A Clark-Evans ratio R of 1 represents a random distribution of the animal class considered, falling towards 0 with an increased degree of clumping and rising to 2.15 for perfectly dispersed distributions. The area comprising all individuals caught was used as a reference area for the spatial distribution.

Usually analyses using the Clark–Evans ratio determine range centres to evaluate the spatial distribution. Therefore our results must be interpreted with caution because, with capture data, only discrete locations (trap stations) have a nonzero probability of occurrence and the current activity of the individuals caught (i.e. moving) will influence the spatial pattern. Nevertheless, because of the moderately high trap density, the dispersion patterns estimated should give a useful ‘snapshot’ of the spatial distribution of the classes of interest in the population.

Data for home range size and home range overlap were analysed with the Ranges V software (Kenward & Hodder 1996). We combined data from live trapping and radio-tracking because capture locations were usually included within the larger tracking ranges. As White & Garrott (1990) emphasized, tracking data are always three dimensional, that is, defined by their *X*, *Y* and time coordinates. In our study the latter became especially important because area observation curves in incremental area analyses (Odum & Kuenzler 1955; Kenward & Hodder 1996) never reached an asymptote, even for animals that were tracked for several months (up to 8), thus indicating that home ranges were not stable over time. Hence, we could not determine a minimum number of locations needed for home range description, nor a percentage of fixes needed to define a core area (the curve percentage range size on percentage fixes did not have an inflection point). To obtain comparable ‘range units’, we partitioned the study period into fixed monthly intervals yielding monthly home ranges, which contained on average 48 locations, that is, two 24-h rounds (see above). In total, we obtained 197 monthly ranges from 27 females and 27 males. For all other animals tracked, we could not collect enough consecutive locations, because of predation or transmitter failures.

Because the density distribution of the location data was not continuous, we used only nonprobabilistic estimators of home range size. For each monthly home range we selected as a measure of the home range size observed two parameters: (1) the size of the 100% minimum convex polygon (MCP; Mohr 1947) representing the area over which the individual ranged during the month considered; and (2) the sum of the areas of all grid cells containing locations of the individual (GC; Siniff & Tester 1965). Although the MCP is a useful measure of the total area an animal requires, it might include large parts where the animal was never found. In fact the MCP was on average 10 times larger than the GC. On the other hand, the GC method underestimates the area the animal actually used, but has the advantage of being a more accurate reflection of the raw data. Therefore, it represents a less biased basis for extended analyses, for example of range overlap between individuals (see White & Garrott 1990 for a review of the limitation of different home range estimators).

As a first step towards understanding individual space use we investigated the effects of sex, water level (WL) and population size (PS) on home range size (MCP and GC). Second, to describe home range shift, we analysed the percentage overlap of GCs of the same animal

between consecutive months. Interaction analysis was carried out on three levels. To test for home range exclusiveness we calculated the percentage overlap of GCs for all dyads (pairs of animals) that were tracked concurrently.

Some difficulties in testing hypotheses based on percentage overlap of dyads arise if only a more or less random and changing subsample of the population is tracked simultaneously. First, overlap values between dyads are usually used as independent data points, but dyads in which the same animal has a different partner are statistically not strictly independent (‘partly dependent dyads’). To assess whether partly dependent dyads can be treated as statistically independent ones, that is, show the same variability, we randomly selected pairs of partly dependent and pairs of independent dyads. Because overlap was known to change over the study period we chose 5 months distributed over the study period and performed Mann–Whitney *U* tests on the difference in percentage GC overlap between dyads of partly dependent and independent pairs. If partly dependent (DD) dyads were more similar, the difference between pairs should be on average smaller than for pairs of independent dyads (ID). We found no significant differences in the median or the variability, measured as the positive difference of the values to the median (Mann–Whitney *U* tests: for all months $N_{ID}=N_{DD}=10$; August 1999: $N_{animals}=7$; February 2000: $N_{animals}=10$; April 2000: $N_{animals}=11$; August 2000: $N_{animals}=8$; December 2000: $N_{animals}=8$; median: all $U>37$, all $P>0.35$; variability: all $U>39$, all $P>0.44$).

Second, if two animals had zero overlap, that might reflect an exclusive range use (based on mutual avoidance or territorial defence) or just indicate that they inhabited different parts of the study area and therefore had a zero probability of overlapping anyway. As the criterion for potential overlap in GCs we used the nonzero percentage overlap in MCPs, that is only dyad partners that had some chance of meeting during the given month were included in the analyses. Finally, a related problem concerns the dependence of the distribution of overlap values on the population size. For a given proportion of animals tracked simultaneously, the probability of choosing ‘true’ nearest neighbours with no animals ranging between them increases with decreasing population size. To assess the degree of home range exclusiveness for the different dyad classes, mainly the overlap values of such nearest neighbours (NN) are of interest. Therefore, for each dyad class we included only the five dyads showing the highest GC overlap values (‘top 5’ NN) in the analyses.

Static interaction analyses investigate the space use of dyad partners in the overlap zone. To assess whether the area of overlap of the home range was more, less or equally used compared to the nonoverlap zone, we performed a linear regression between the percentage of locations in the overlap zone and the percentage GC area overlap for each dyad class. For dyads with substantial area overlap ($\geq 15\%$) the degree of concordance in the use of the overlap areas was estimated with nonparametric grid cell analyses (Doncaster 1990). For this the Spearman rank correlation coefficient r_s is calculated between the

frequencies with which the dyad partners used the shared grid cells, thus indicating positive, negative or absent coordination of space use within the overlap zone. Because the frequency of locations for the 5×5 -m grid cells was relatively low, we instead used those based on the 10×10 -m grid cells for the calculation of these correlations.

Finally, to test for social associations, again for all dyads with 15% GC area overlap or more, we investigated the spatiotemporal correlation of space use or dynamic interaction. These analyses indicate whether a pair of animals is more (positive dynamic interaction) or less (negative dynamic interaction) likely to maintain specified distances given the configuration and use of their home ranges (Macdonald et al. 1980). The nonparametric approach developed by Doncaster (1990) compares the observed and theoretical distance distributions of simultaneous locations (here time interval <30 min). We used chi-square tests to determine whether separations up to a critical distance occurred more or less often than expected. We chose 7 m as the critical separation distance assuming that animals are aware of each other when located in adjacent grid cells. In addition, to evaluate the general pattern of distances the animals kept, we used Jacob's Index to compare observed and possible distances for given home range configurations (location distributions; Kenward et al. 1993). This measure assumes a value of 0 if observed and possible distances are the same, rises to +1 if observed distances are smaller than possible ones, reflecting attraction, and falls towards -1, if observed distances exceed possible ones, indicating that animals avoid each other.

Statistical analyses follow Sokal & Rohlf (1995) for parametric and Siegel & Castellan (1988) for non-parametric methods, respectively. All tests are two tailed.

RESULTS

Demographic Background

Population size varied considerably during the study period, from a peak of about 140 individuals in early October 1999 to the complete extinction of the population in January 2001 (Fig. 1a). Estimation of the minimum number of animals known to be alive (MNA) based on capture data showed a high, fairly stable population size until the austral summer of 2000, when numbers began to decline continuously because of high predation pressure: 92% of the radiotracked animals were killed by predators and we lost track of the remainder (C. Kraus, unpublished data). From August 2000 until the end of the study (and the population), numbers remained extremely low. Local density was modulated by seasonal changes in water level (Fig. 1b), with large parts of the habitat inundated for several months during the austral winter, forcing the animals to concentrate in the drier parts. Therefore, the effects of both population size and water level on spacing behaviour were basically density effects, with water level having an additional and independent effect on position within the study area.

There was no clear nonreproductive season in 1999, as single juveniles were found during winter months. Nevertheless, reproduction was seasonal; the temporal distribution of juveniles differed significantly from an even one over the whole study period (chi-square test: $\chi^2_{40}=407.71$, $P<0.001$) and was concentrated in spring and early summer (September 1999–December 1999), when 92% of all new juveniles of that year (August 1999–July 2000) were caught. Within these 4 months of peak reproduction the temporal distribution of juveniles differed from an even one (chi-square test: $\chi^2_7=57.11$, $P<0.001$) and the number of females in oestrus (with open vaginal membrane) correlated significantly with the number of new juveniles caught 2 months later ($r_s=0.81$, $N=10$, $P=0.005$). These findings suggest that initially reproduction was moderately synchronized: 50% of the juveniles of the first pulse of reproduction (first catch of September to first catch of November 1999) could be assigned to the first catch in October 1999. We identified three pulses of juveniles (always the first catch in October, December 1999 and February 2000) separated by the caviés' approximately 2-month gestation period, the degree of synchrony decreasing with the progressing breeding season.

The population sex ratio did not vary significantly from unity (0.5 ; $F/[F+M]$) during most of the study period. Nevertheless, it showed a seasonal pattern with a slight male bias during the peak birth season and a subsequent decline during the remainder of the year until it reached significantly female-biased values around 0.75 (minimum: 0.86) during winter 2000, characterized by low overall density. These findings point to a male-biased mortality or emigration. Because of the caviés' long gestation period (*C. magna*: 64 days, C. Kraus, unpublished data) the operational sex ratio (here defined as the proportion of receptive females in the adult population, excluding nonreceptive females) is likely to be far below 0.5 for most of the time. The highest, that is, less male-biased OSR values measured were 0.26 (first catch August 1999), 0.19 (first catch October 1999) and 0.23 (first catch February 2000) and finally 0.5 (second catch July 2000) during the period of low density and low overall sex ratio, but this latter value is likely to be imprecise because we caught only one female with an open vagina and one sexually active male. Nevertheless, these crude estimates show a temporally strongly variable OSR and thus the males' potential to monopolize females fluctuated.

Spatial Distribution

Figure 2 shows the spatial distribution of caviés caught during the first trapping session in August 1999. The spatial distribution of the classes considered did not deviate significantly from a random distribution (adult males: $R=1.08$, $t_{27}=0.77$, $N=28$, $P<0.50$; anoestrous (closed) females: $R=1.07$, $t_{27}=0.68$, $N=28$, $P>0.50$; oestrous (open) females: $R=0.98$, $t_9=0.09$, $N=10$, $P>0.50$). Furthermore, values of the Clark–Evans ratio R were close to 1.0 pointing to an almost perfectly random distribution.

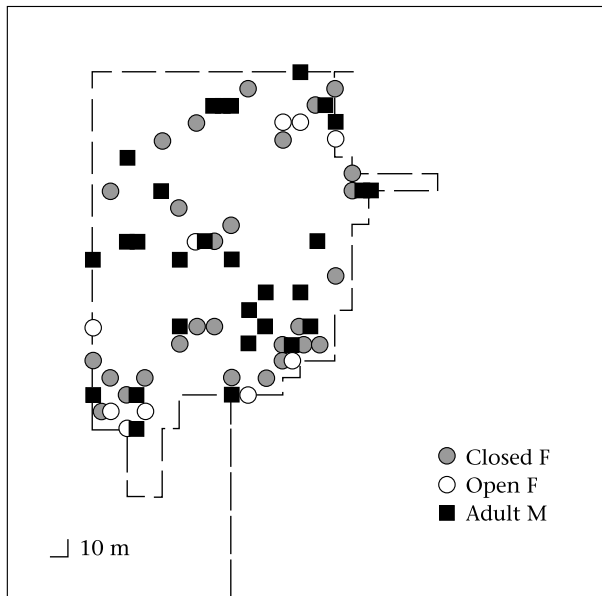


Figure 2. Spatial distribution of oestrous females (open F), anoestrous females (closed F) and adult males (adult M) in the first catch in August 1999. Dashed line: outline of the grid system.

Home Range Size

To investigate the effects of sex, water level (WL, high versus low) and population size (PS, large versus small) on home range size, we carried out a three-way ANOVA (Table 1). MCPs and GCs of males were slightly but significantly larger than those of females. Cavies used significantly larger MCPs during periods of high water level than during the dry summer months, but did not enlarge their GCs. MCPs tended to be larger when population size was large, although not significantly so, but again, we found no effect of population size on GCs. The sex versus water level interaction was significant with males showing an increase in GCs and females a decrease when water levels were high. We also found a significant interaction between sex and population size: females had larger GCs in small than large populations, whereas size of male GCs remained unchanged.

Male body mass and home range size (MCP) were correlated significantly only during periods of high water level (Pearson correlation: low: $r_{10} = -0.07$, $P = 0.83$; high: $r_{10} = 0.80$, $P = 0.002$). For females, no significant relation between body mass and home range size existed, regardless of water level (Pearson correlation: low: $r_9 = 0.35$, $P = 0.29$; high: $r_{10} = 0.37$, $P = 0.19$).

Home Range Shift

Rising water levels forced the cavies to withdraw to the drier, southeastern parts of the study area during winter (Fig. 3). Independently of the water level, the cavies showed little home range stability. Instead, they seemed to move their ranges from month to month following a nonrandom direction, as shown by the declining percentage of within-individual overlap in GCs between the first and successive months of animals tracked for at least 4

months (Friedman test: $F_2 = 16.0$, $N = 8$, $P < 0.001$; Fig. 4a). The overall ranging area (MCP = 3.46 ha) of one female tracked for 8 consecutive months included the whole grid system (3.25 ha). Home range fidelity was significantly lower in males than in females (Mann-Whitney U test: $U = 21$, $N_{\text{females}} = 17$, $N_{\text{males}} = 7$, $P = 0.014$; Fig. 4b).

Home Range Exclusiveness

Neither females nor males occupied exclusive ranging areas (MCPs); both sexes showed considerable intrasexual as well as intersexual overlap with several conspecifics (Fig. 3). In 77% of the dyads that shared parts of their MCPs we also observed overlapping GCs and 19% of the dyads showed more than 5% GC overlap when the area was dry (Fig. 5). With rising water levels, cavies simply 'moved closer', resulting in a significant shift in the distribution of overlap values (Kolmogorov-Smirnov two-sample test: $Z = 4.82$, $N_{\text{Low}} = 113$, $N_{\text{High}} = 61$, $P < 0.001$) with neighbouring animals sharing on average 15–20% (median) of their GCs.

Because of the strong impact of water level on population density, and the dependence of overlap on population size described above, we investigated the effect of dyad class (female–female dyads: FF; female–male dyads: FM; male–male dyads: MM) on GC overlap separately for high and low water levels and small and large population sizes, respectively (Fig. 6). Whenever a sample of five ('top 5' of nearest-neighbour dyads) would have represented more than one-third of all dyads in that dyad class for the period considered, we show only the two highest values to permit at least a descriptive comparison. Unfortunately, MM dyads could be included in the analysis only once. Overlap between males tended to exceed that between females, although not significantly so (Kruskal-Wallis test: PS large and WL low: $N = 5$ for all groups, $H_2 = 7.98$, $P = 0.02$; post hoc: $|R_{\text{FF}} - R_{\text{MM}}| = 6.66 < 6.77$, $P < 0.10$), but with the exception of the first period (PS large and WL high), when only a small proportion of the population was tracked, MM values lay between those of FF and FM dyads. GC overlap in FM dyads significantly exceeded that of FF dyads ($N = 5$ for all groups; PS large and WL low: Kruskal-Wallis test, post hoc: $|R_{\text{FF}} - R_{\text{FM}}| = 7.2 > 6.77$, $P < 0.05$; PS small and WL high, Mann-Whitney U test: $U = 3$, $P < 0.05$) or at least tended to do so (PS small and WL low, Mann-Whitney U test: $U = 4$, $P = 0.08$).

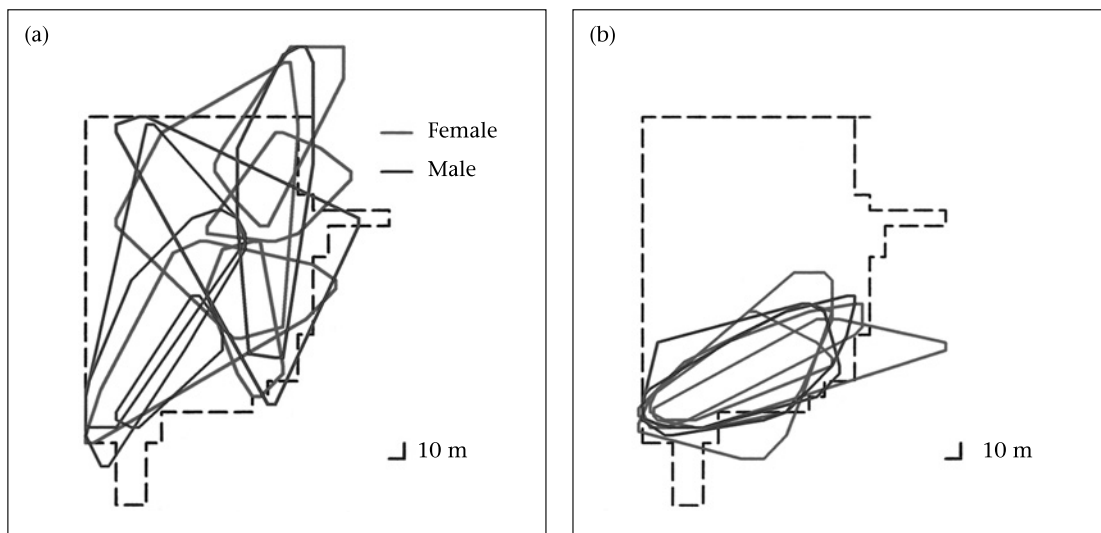
Static Interaction

Percentage area overlap was a highly significant predictor of the percentage of localizations of a cavy in the overlap zone (Fig. 7). For all dyad classes, 95% confidence intervals for the intercepts included zero, and the slope (b) was only slightly above 1.0, with 1.0 included in the 95% confidence intervals (CI_b) for FF and MM dyads or at the edge of this interval for FM dyads (linear regression: FF dyads: $r^2 = 0.70$, $t_{b,66} = 12.3$, $N = 67$, $b = 1.12$, 95% $CI_b = 0.94, 1.30$; FM dyads: $r^2 = 0.86$, $t_{b,90} = 23.1$, $N = 91$, $b = 1.10$, 95% $CI_b = 1.01, 1.20$; MM dyads: $r^2 = 0.87$,

Table 1. Effects of sex, water level (WL) and population size (PS) on home range size (minimum convex polygon, MCP; grid cells, GC)

Factor (N)	MCP			GC		
	Size (ha)	$F_{1,41}$	P	Size (ha)	$F_{1,41}$	P
Sex						
F (25)	0.767±0.397	13.65	0.001	0.073±0.013	6.53	0.01
M (24)	1.183±0.621			0.081±0.012		
Water level						
Low (23)	0.774±0.415	11.91	0.001	0.077±0.013	0.45	0.50
High (26)	1.145±0.609			0.077±0.012		
Population size						
Small (24)	0.931±0.495	3.13	0.08	0.078±0.011	0.00	0.95
Large (25)	1.009±0.614			0.076±0.014		
Sex×WL		1.15	0.29		5.70	0.02
Sex×PS		1.14	0.30		4.59	0.04
WL×PS		1.97	0.17		0.99	0.33
Sex×WL×PS		1.91	0.18		0.56	0.46

Means are given ±SD. F: Female; M: male. Univariate ANOVA: MCP: $F_{7,41}=3.65$, $P=0.004$, $R^2=0.38$; GC: $F_{7,41}=2.59$, $P<0.05$; $R^2=0.28$. The periods of high and low water levels and small and large population size, respectively, chosen for the analysis are highlighted in Fig. 1.

**Figure 3.** Minimum convex polygons (solid lines) of radiotracked cavies (a) during February 2000 (water level low), and (b) August 2000 (water level high). Dashed line: outline of the grid system.

$t_{b,23}=12.3$, $N=24$, $b=1.21$, 95% $CI_b=1.00,1.41$; all $P<0.001$). Divergence from a strict proportionality became more pronounced for higher percentages of area overlap. This might be explained by the cavies being confined to a small part of the study area during periods of high water levels and, therefore, they probably overlapped increasingly in more heavily used areas. When we pooled all dyad classes for dry periods (as their regression coefficients did not differ significantly), the slope approached 1.0 (WL low: $r^2=0.89$, $t_{b,61}=22.3$, $P<0.001$, $N=62$, $b=1.02$, 95% $CI_b=0.93,1.11$), whereas a slope of 1.0 was not included in the 95% confidence interval of the regression for high water levels ($r^2=0.78$, $t_{b,119}=20.6$, $P<0.001$, $N=120$, $b=1.14$, 95% $CI_b=1.03,1.25$). These

findings suggest that overlap areas were neither the most nor the least used parts of the range. Furthermore, there was no indication of an unbalanced use of the area of overlap (no disjunctive clouds of data above and below the regression line). The somewhat larger scatter for higher overlap values seems to reflect individual variation between dyads, independent of dyad class.

For 90 dyads with at least 15% overlap in GCs we calculated a Spearman rank correlation between the frequencies with which dyad partners used the shared grid cells for 129 dyad-months (Table 2). Significant static interaction was rare in all dyad classes (10.0%). For same-sex dyads the proportion of dyads with significant static interaction was about 5%, that is, at chance level,

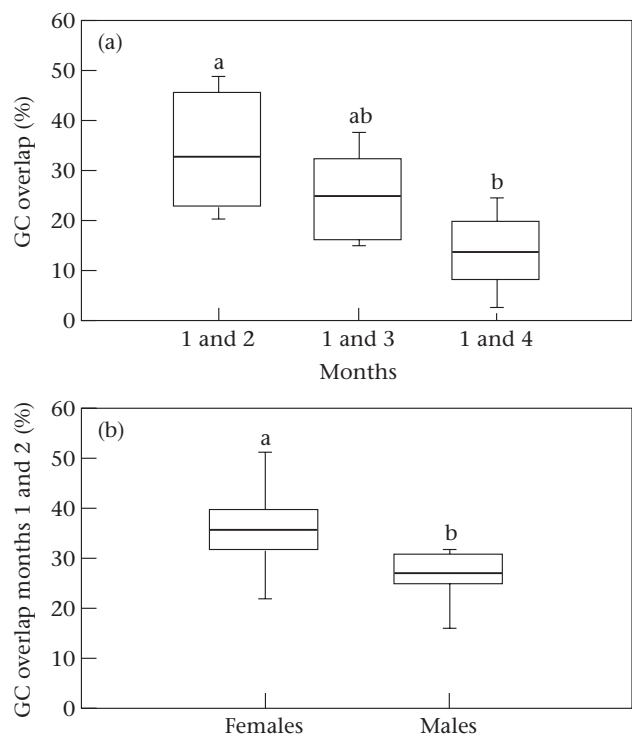


Figure 4. (a) Directional home range shift over 4 successive months, and (b) home range fidelity of the sexes. Values represent median, quartiles and range of percentage overlap between grid cells containing locations (GCs). Different letters above box plots denote significant differences between groups (post hoc tests follow Siegel & Castellan 1988).

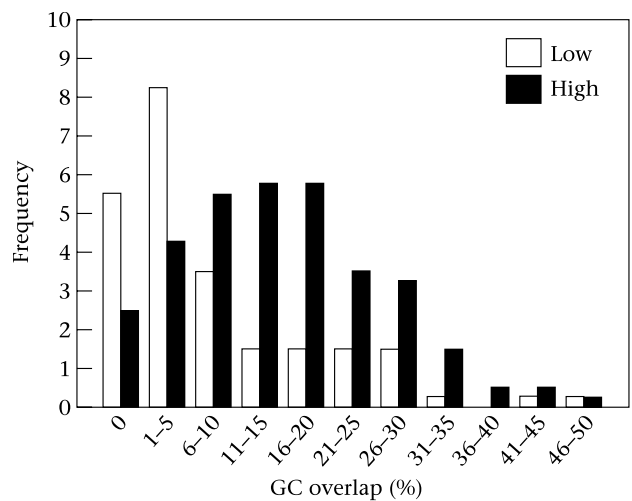


Figure 5. Frequency distribution of percentage overlap in grid cells containing locations (GCs) for periods of low and high water level. Included are all dyads with a nonzero overlap in minimum convex polygons.

assuming a random use distribution. Of the five dyads with significant static interaction that were tracked for more than 1 month, none showed consistent static interaction for even 2 consecutive months. Nevertheless, eight of the 10 significant interactions were positive (concordant range use), and only two were negative (discordant

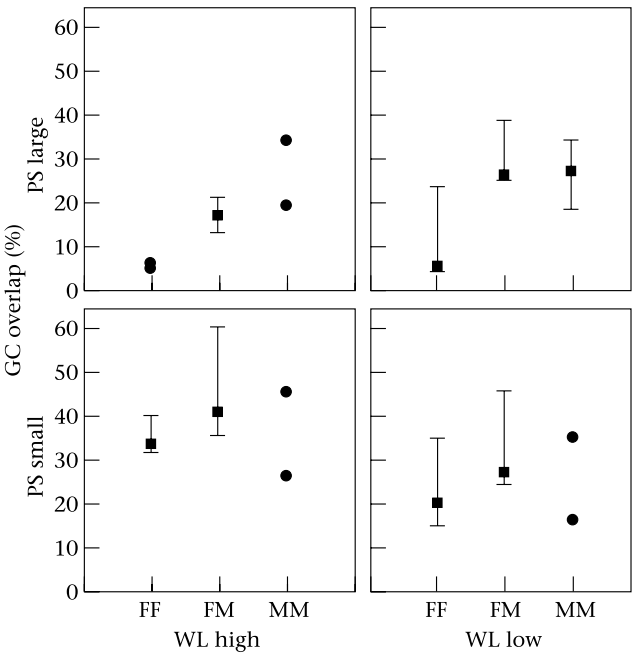


Figure 6. ‘Nearest neighbour top 5’ values of overlap in GCs (grid cells containing locations) for female–female (FF), female–male (FM) and male–male (MM) dyads at high versus low water level (WL), and large versus small population size (PS), respectively. Depicted are median values and range or the two highest values when not enough dyads were available (see text for further details).

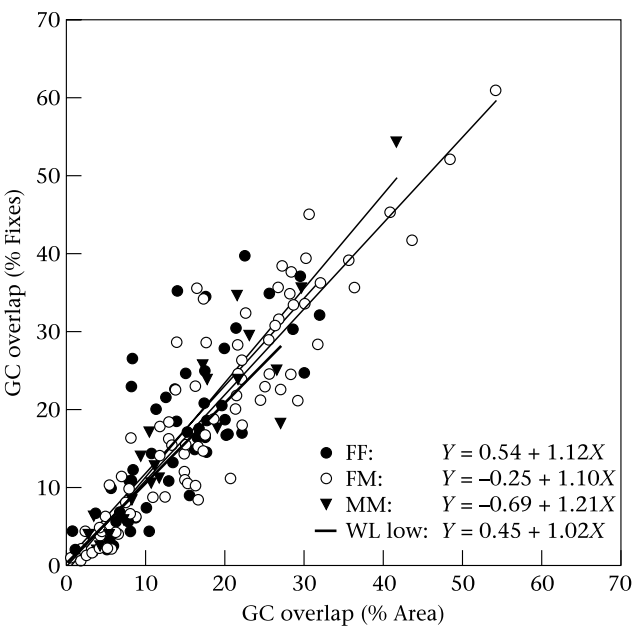


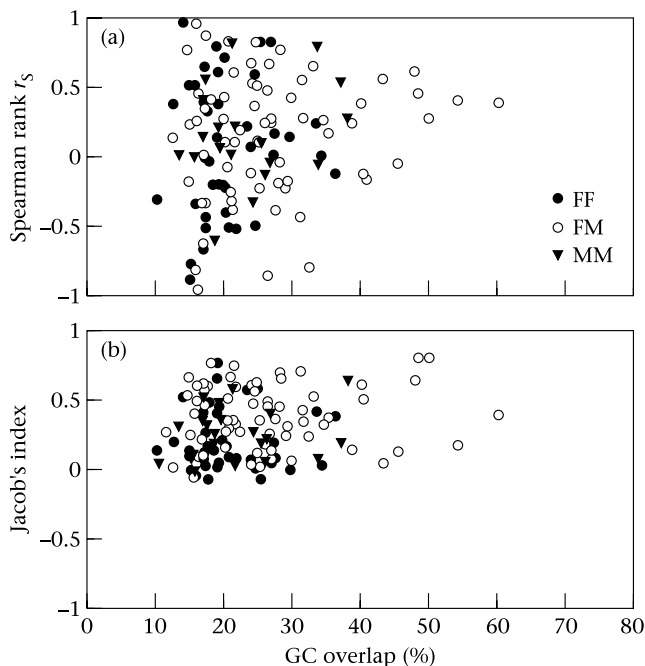
Figure 7. Linear regression of the percentage of localizations in the overlap zone (% Fixes) on percentage GC (grid cells) overlap (% Area). FF: female–female; FM: female–male; MM: male–male dyads (thin lines). If only periods of low water level (WL) are considered and all dyad classes are pooled, the slope of the regression line approaches 1.0 (thick line). See text for statistics.

range use). Only one (FM) of the 90 dyads showed significant static interaction during the dry season, suggesting that coordination of range use within overlap

Table 2. Significant static and dynamic interaction for dyads sharing at least 15% of their grid cells

Dyad class	Static interaction		Dynamic interaction	
	N	N _{sig} (% _{sig})	N	N _{sig} (% _{sig})
FF	26	1 (3.8)	28	10 (35.7)
FM	49	7 (14.3)	53	19 (35.8)
MM	15	1 (6.7)	17	2 (11.8)
Total	90	9 (10.0)	98	31 (31.6)

FF: Female–female; FM: female–male; MM: male–male. Significance of static interaction was determined by Spearman rank correlations between the frequencies with which dyad partners used the shared grid cells. N: number of different dyads analysed; N_{sig} (%_{sig}): the number (%) of dyads in which significant static interactions were found. Significance of dynamic interaction was determined with chi-square tests based on a critical distance of 7 m.

**Figure 8.** (a) Space use of dyad partners. Spearman rank correlation coefficients (r_s) between the frequencies with which dyad partners used the shared grid cells versus percentage grid cell (GC) overlap for the three dyad classes. (b) Jacob's Index versus GC overlap for the three dyad classes. FF: female–female; FM: female–male; MM: male–male. Depicted are all dyad-months.

zones is likely to be caused by external forces such as water level. The overall rarity of significant static interaction and its lack of consistency points to a random range use within the overlap zone, independent of dyad class.

Spearman rank correlation coefficients (Fig. 8a) revealed no differences in the degree of concordance in space use between dyad classes (ANCOVA, factor dyad class: $F_{2,86}=0.09$, $P=0.92$), but there was a significant increase in r_s values with larger overlap areas (ANCOVA, covariate overlap: $F_{1,86}=4.03$, $P<0.05$).

Dynamic Interaction

Evidence for dynamic interaction (spatiotemporal associations) was more frequent than that for static interaction (Table 2). Of 98 dyads (based on 134 dyad-months) about one-third (31.6%) showed significant dynamic interaction for at least 1 month. Interactions were positive in all instances. For a given month, dynamic interaction was significantly more likely in FM than in same-sex dyads (chi-square test: $\chi^2_1=4.54$, $P=0.03$). Like static interaction, dynamic interaction was not usually consistent: of the nine dyads (four FF, five MM) with dynamic interaction and tracked for at least 2 months, none of the FF dyads and only two of the FM dyads showed significant dynamic interaction for more than 1 month. In addition, for dyads showing significant dynamic interaction only an average percentage of 18.9% (range 7–34%) of the simultaneous locations yielded distances below the critical distance of 7 m, that is, for most of the time dyad partners did not maintain proximity. These findings suggest that although social interactions were not rare among caviés with strongly overlapping ranges, no stable social bonds between adult females or females and males existed.

Dyad partners did not actively avoid each other: for only a few cases did the Jacob's Index fall below zero (Fig. 8b). In relation to the distances expected, the observed distances maintained in pairs of females were significantly larger than those in FM dyads (ANCOVA, factor dyad class: $F_{2,94}=4.95$, $P=0.009$; post hoc Tukey's HSD test for unequal N: FF versus FM: $P=0.01$; FF versus MM: $P=0.86$; FM versus MM: $P=0.20$), independent of the amount of overlap (ANCOVA, covariate overlap: $F_{1,94}=1.09$, $P=0.30$) and consistent with the higher probability of significant dynamic interaction in the latter (Fig. 8b).

Static and dynamic interaction seemed to be independent: only four dyads had both significant static and dynamic interaction (number of expected cases: three). Furthermore, we found no significant correlation between r_s and Jacob's Index (Pearson correlation: $r_{88}=0.16$, $P=0.14$). To summarize, the caviés' spacing behaviour seemed to be hardly affected by conspecifics sharing their home ranges: animals of both sexes neither avoided nor attracted one another, apart from short-term associations between male–female pairs.

DISCUSSION

As predicted by current socioecological theories, (1) females of the grazing *C. magna* had overlapping home ranges. Their pattern of space use (2) led not to the expected aggregated but to a random female distribution. Reproduction (3) was only partly synchronous, with the degree of synchrony declining in the course of the year. In contrast to prediction (4), male *C. magna* were not territorial but overlapped with both other males and females. Male home ranges were slightly larger than those of females, but did not encompass even one female range (5). These findings are consistent with a mating system of scramble competition polygyny or overlap promiscuity

(Wittenberger 1979) but not with resource or female defence polygyny as expected from the models (Ostfeld 1985, 1990; Ims 1987).

General Spacing Behaviour: a Nomadic Small Mammal?

Spacing behaviour of *C. magna* was characterized by gradual home range shifts evading habitat deterioration such as rising water levels and following resources, probably fresh grass on recently dried-up areas. In the course of the year most parts of the study area were visited: the total ranging area of one female tracked for 8 months included the whole grid system. We are not aware of any other small mammal for which such a 'nomadic' use of space is documented (but see Lurz et al. 1997, 2000 for some nomadism in red squirrels, *Sciurus vulgaris*). Although in many small mammals males search large areas for mating opportunities (e.g. Schwagmeyer 1988; Michener & McLean 1996), females are usually rather sedentary. Nomadic behaviour of subadults (e.g. Myllymäki 1977) or breeding dispersal of females is generally completed before the next reproductive attempt is started (reviewed in Lambin 1997).

Because most small mammals produce altricial young, they depend on a nest site for the lactation period and thereby seem predisposed for a sedentary lifestyle. In contrast, caviés produce precocial young which are fully mobile within a few hours of birth (Rowlands & Weir 1974; Eisenberg 1981). This reproductive strategy could be partly an adaptation to the rather unpredictable habitat, to reduce juvenile mortality, for example caused by sudden changes in water levels, and to optimize resource exploitation in space and time. Even migration-like phenomena are documented for *C. aperea*: Bilenca et al. (1995) reported several instances of localized migration from overexploited to unused crop field borders (see also Rood 1972; Galante & Cassini 1994 for similar large-scale movements of *C. aperea*). Similarly, in May 1999 our study population experienced an influx of about 60 unmarked individuals (mostly adults) of *C. magna*, which coincided with rising water levels in the area. In their space use patterns these caviés seem more reminiscent of ungulate species, with which they also share other features of reproduction and ecology, than of small mammals (Jarman 1974; Derrickson 1992; see also Case 1978; Stahnke & Hendrichs 1988; Taber & Macdonald 1992a for analogous adaptation in caviomorphs and ungulates).

Spatial Organization and Mating Pattern

In most small mammals one of the sexes is territorial, with female spacing behaviour setting the frame for males (Ostfeld 1985, 1990; Lurz et al. 2000; but see Boellstroff & Owings 1995). In contrast, the spacing system of *C. magna* was characterized by considerable inter- as well as intrasexual home range overlap of both sexes. In combination with the larger male than female home ranges, this pattern renders a monogamous or polygynous system based on resource or female defence, respectively,

highly unlikely. Instead, these findings are consistent with a system of scramble competition polygyny (Thornhill & Alcock 1983), or overlap promiscuity (Wittenberger 1979). In this context we prefer the latter expression, because space use patterns alone do not allow a distinction between pure scramble and contest competition or a combination of both.

The greater overlap of female ranges by males than by females suggests that males actively search for mating opportunities. Hence, intrasexual competition in this species seems to contain elements of scramble competition. Nevertheless, the ratio of male to female home range size was low compared to species where scramble competition predominates (e.g. Schwagmeyer 1988; Tew & Macdonald 1994; Michener & McLean 1996). Because of the large, nonexclusive female ranges, males can share home ranges with many females by enlarging the area used only slightly. We also found circumstantial evidence for contest competition in male *C. magna*: body mass correlated with male home range size when water levels were high, that is, during peak mating periods, and the species shows sexual dimorphism (Ximenéz 1980). Nevertheless, most of the time the population sex ratio was approximately even and severe wounds inflicted by physical combat were rarely seen in males (*C. Kraus*, personal observation). The operational sex ratio was highly male biased most of the time. Even when it peaked, on average three males were available per oestrous female. Combined, these results suggest that both scramble and contest competition play a role in intrasexual competition among male *C. magna*.

Demography

Many studies on small mammals document the impact of demographic factors on the spacing system (Madison 1990; Ostfeld & Klostermann 1990; Nelson 1995). Animals may adjust for increased population density either by permitting increased home range overlap (Myllymäki 1977; Ostfeld et al. 1985; Ims 1987; Agrell 1995; Gliwicz 1997) or by restricting their movements to smaller ranges (Ostfeld 1985, 1986; Wolff 1985; Wolff & Cicirello 1990; Lambin & Krebs 1991). The latter effect should be more pronounced in territorial species, assuming that their costs of sharing space are higher. As therefore expected, the main effect of high density (via rising water level) in our study population was a strong increase in range overlap. Males used even larger home ranges during periods of high water levels, which included peak mating periods, and showed no change in their spacing behaviour with declining numbers. That males as well as females were truly nonterritorial became especially evident when population size was reduced to about 10 individuals (eight females, two males) and water levels were low: the caviés still showed extensive overlap leaving large parts of the study area unused. One could speculate that for females the costs of sharing resources with conspecifics are much lower than the combined benefits of exploiting resources of maximum quality and maybe of improving antipredator tactics (see below). For males, spatial monopolization of several females was

obviously not feasible, even under the favourable conditions of a high sex ratio and overlapping female ranges. Population density thus had modulating effects on spacing behaviour, but the basic space use patterns were stable over a wide range of densities.

The interaction between spacing system and demography might also operate in the opposite direction. Territoriality in particular may have density-limiting effects (Krebs & Myers 1974; Krebs 1979; Boonstra & Rodd 1983). Despite their low intrinsic rate of increase, a high degree of space sharing in populations of *C. magna* and other caviés (Rood 1972) might allow them to reach the high densities observed in this study and reported for many parts of South America where they are considered pests (Rood 1972; Galante & Cassini 1994; Bilenca et al. 1995).

Interactions: an Almost Asocial Cavy?

When animals show nonexclusive spacing behaviour, analyses of spatial and dynamic (spatiotemporal) interactions can provide information on the social system of a population. For *C. magna*, static interaction analyses for pairs of animals that shared considerable parts of their home range (at least 15%) revealed no evidence for 'local territoriality': overlap zones were not the least used parts of the ranges, the location frequency in the area shared was not skewed for the dyad partners, and finally, significantly discordant range use (negative static interaction) in the overlap area was extremely rare. Similarly, we found no indication of group memberships: overlap zones were not the most frequented parts of the ranges. In fact the percentage area overlap was an excellent predictor of the intensity with which caviés used the parts they shared. Significantly concordant use (positive static interaction) of overlap areas was also rare and not consistent. The tendency for a disproportionate use of overlap areas and the higher degree of concordance with rising range overlap can be attributed to an increased probability that shared parts include important patches. The sex of the dyad partner did not have a significant effect on the intensity or the degree of concordance with which caviés used the area shared. In short, caviés neither avoided nor preferred overlap zones and seemed to use them randomly with respect to each other.

Unlike static interaction, evidence for spatiotemporal (dynamic) interaction was more prevalent. Caviés did not actively avoid each other. Relative to expected distances, the observed distances between female-male dyads were significantly smaller than those between females. Males maintained mutual distances similar to those between females. Under the assumption that caviés are aware of each other when they are no further apart than a critical distance (here 7 m), we found significant positive dynamic interaction in roughly one-third of all dyads considered (criterion as above). Dynamic interaction was more likely to occur between females and males than between same-sexed dyad partners. Nevertheless, dynamic interaction was usually not consistent and the proportion of simultaneous locations with distances below the critical one was not high (19%). Furthermore,

the occurrence of significant static and dynamic interaction seemed to be independent. Therefore, we conclude that although social interactions among *C. magna* are not rare, no stable social bonds are formed either between females or between females and males, which probably form temporary consortships when females are receptive.

Most of the time, females as well as males led a solitary life, a result contradictory to the predominant perception that guinea pigs are social animals (Rowlands & Weir 1974; Sachser 1998). The social system inferred fits well with current socioecological theories. Whereas diurnal species often use the advantages of group living to minimize predation risk, nocturnal species usually rely on crypsis as the primary antipredator strategy (Taylor 1984, e.g. antelope: Jarman 1974; primates: van Schaik & van Hoof 1983). Wild caviés are subject to intense predation and rely on dense vegetation as shelter (Rood 1972; Cassini 1991; Asher & Sachser 2000; this study, unpublished data). Animals in our study population were mostly nocturnal, especially during summer, whereas in winter they were crepuscular and sometimes active by late afternoon. Apart from females with young or male-female 'pairs', we never saw cohesive groups outside the cover of vegetation, but because activity periods were synchronized the caviés foraged in loose aggregations. We suggest that they combine the advantages of a solitary lifestyle, being inconspicuous when hiding from predators in dense vegetation, with those of aggregating while foraging on exposed ground. This kind of social system resembles the sociality of group 2 in ground squirrels, *Marmotini* (sensu Armitage 1981), where 'individuals aggregate in favourable habitat, but all members of the colony live individually'.

Temporal Breeding Pattern

Reproductive synchrony might develop as a consequence of climatic seasonality or reflect a sexually selected reproductive strategy (Ims 1990). With increasing degrees of asynchrony the potential for multiple matings and thus for sexual selection in males rises (Ims 1988a). *Cavia magna* has no obligate nonreproductive season, as expected from the observed absence of strong effects of photoperiod and cold on female reproduction in *C. aperea* (Trillmich 2000). Nevertheless, the frequency of reproductive events changed over the year with most oestrous periods/births occurring between July/September and February/April, respectively. Pulses of oestrous females and recently born juveniles became less distinct in the course of the main breeding period and disappeared afterwards. Hence there is no indication of a socially mediated maintenance of synchrony (Ims 1987, 1990; Ims et al. 1988).

Another way of separating socially from environmentally induced reproductive synchrony is to test whether reproduction among neighbouring individuals is significantly more synchronized than among more widely spaced individuals (Ims et al. 1988; Ims 1990). We found no evidence for such social components of reproductive synchrony in *C. magna*: oestrous as well as anoestrous females were distributed almost perfectly randomly. This

fits well with the observation that under laboratory conditions not even females housed together synchronize their oestrous cycles (C. Kraus, unpublished data). In conclusion, the temporal breeding pattern observed in our study population is unlikely to reflect a female reproductive strategy but is probably the consequence of a seasonal environment.

Synthesis

Although some features of the spacing system of *C. magna* were in accordance with socioecological models for small mammals (Ostfeld 1985, 1990), the consequences predicted did not arise. As in most mammalian groups studied, the distribution of resources represented a reliable predictor of female spacing behaviour (ungulates: Jarman 1974; primates: Wrangham 1980; solitary carnivores: Sandell 1989; microtines: Ostfeld 1985, 1990). However, to us it is not clear why an evenly distributed food resource should lead to a clumped female distribution (Ostfeld 1985, 1990), rather than a random one, without any other factors favouring aggregation, such as certain antipredator defence strategies. Excluding conspecifics from homogeneously distributed grasses and abundant forbs does not seem to benefit female *C. magna*. Females neither coordinated space use in overlap zones nor avoided each other: they moved solitarily, probably an adaptation to crepuscular and nocturnal habits under high predation pressure. We suggest that this rather random spacing behaviour with respect to other individuals, in combination with the large ranging areas that were caused by the changing environment, led to the observed random distribution of females.

Male spacing behaviour was also not consistent with predictions derived from the models. Although conditions for male territoriality seemed favourable with overlapping female ranges (Ostfeld 1985, 1990) and at least partly synchronized reproduction (Ims 1987, 1990), males showed a transient, nonexclusive use of space. They did not change their spacing behaviour even when female density was low and sex ratio high, two factors identified by the formal model of Sandell & Liberg (1992) as promoting exclusive space use. The nonstationary, nomadic space use of randomly distributed females led to large female ranges and unpredictable female locations, rendering it impossible for males to monopolize several females within an economically defensible territory, independent of the degree of reproductive synchrony, population and operational sex ratio. Nevertheless, it would probably be feasible for a male to monopolize females by consistently maintaining proximity, but as females are solitary only one could be followed. It seems that under such circumstances the roaming tactic yields higher fitness benefits resulting in overlap promiscuity.

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