

Use of space and social organization of female mountain gazelles (*Gazella gazella gazella*) in Ramat HaNadiv, Israel

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Abstract

The social organization of female mountain gazelles was studied on Mount Carmel, Israel. The behaviour of distinctly recognized individuals was studied by year-round observations. Female gazelles lived in groups whose composition remained constant throughout the year, and new females did not freely enter the established groups. Group home ranges overlapped, but various groups replaced each other in the same area at different times of the day. Different groups tended to use different parts of the overlapping home range. In general, but especially in summer, the different groups largely avoided being synchronously together in the same area. The occurrence of two groups in the same area at the same time was a rare event and when it occurred, a high rate of agonistic interaction was observed between the groups. Hence, groups of female mountain gazelles hold and defend temporal territories against other female groups. Mean seasonal group size ranged between 3.4 and 6.4 and was largest during winter, when groups of females joined together occasionally and little agonistic interaction was observed between the groups. It is suggested that group size is affected by food availability and predation pressure.

Key words: Mountain gazelle, *Gazella gazella*, ungulates, territory, Israel

INTRODUCTION

Most terrestrial mammals confine their activities to a limited area, often termed 'home range'. Home range may be defined as 'the area over which the animal normally travels in pursuit of its routine activities' (Leuthold, 1977), and exclusive home range is often referred to as 'territory'. A territory has been defined in many ways: for example, 'a spatially fixed area within which a given animal consistently prevents certain other individuals from engaging in certain activities' (Leuthold, 1977), or 'a fixed, exclusive area with presence of defense that keeps out rivals' (Brown & Orians, 1970). Both definitions stress the fixation of territory in space and its exclusiveness. However, in some circumstances territory size and configuration may change in relation to distribution and abundance of limiting resources (Kruuk & Macdonald, 1985).

Ungulates use space in a variety of ways, ranging from non-exclusive home range through exclusive home range to an arena. Leuthold (1977) summarized this

variety for African ungulates, while emphasizing that his division represents a continuum rather than a clear cut division between the various types. Among ungulates, territories are generally held and defended by males, and their main function is for mating. However, in the impala *Aepyceros melampus* territorial males occupy the best portion of the habitat, and territoriality may bring about a differential distribution of available resources such as food from which other males are excluded, but it is available for females and young (Jarman & Jarman, 1973; type B of Jarman, 1974). In forest dwelling species (e.g. water chevrotain *Hyemoschus aquaticus*, *Cephalophus* spp., *Sylvicapra* spp. and Kirk's dikdik *Madoqua kirki*) home ranges of females overlap those of the males, or they live in monogamous pairs within the male territory, but do not take an active role in its defence (class A of Jarman, 1974) or social organization (type 3 of Leuthold, 1977). In this situation the territory is functioning both for mating and for defence of resources, mainly food. Following Emlen & Oring (1977), monogamy of solitary ungulates was termed as 'resource defence monogamy' (Kishimoto & Kawamichi, 1996). In non-monogamous species the female may live in a 'harem' whose home range overlaps a male home range, or she may move

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freely between male territories. Otherwise the animals may form large herds (eland *Taurotragus oryx*, warthog *Phacochoerus aethiopicus*) or smaller groups (gerenuk *Litocranius walleri*, reedbeek *Redunca redunca*), which can be stable (elephant *Loxodonta africana*, zebra *Equus grevyi*) or 'open' groups, that females join for relatively short periods of time (gerenuk, reedbeek) (references in Jarman, 1974 and Leuthold, 1977). Among ungulates, female territories are rarely reported, but in the serow *Capricornis crispus*, females defend their territories against other females (Kishimoto & Kawamichi, 1996).

The size of a home range is a compromise between various environmental conditions and selection pressures such as primary production, resource dispersion, individual metabolic requirements, predation and social pressures, and thus no simple functional link between body size and home range can be expected (Damuth, 1981). The size of the area occupied by an animal must be large enough to provide an adequate supply of resources (Grant, Chapman & Richardson, 1992). Thus, female roe deer *Capreolus capreolus* adjust the size of their home range in response to decreasing food supply (Tufto, Andersen & Linnel, 1996). Home range is related to body size or metabolic requirements in a wide variety of taxa (e.g. McNab, 1963; Clutton-Brock & Harvey, 1977; Gittleman & Harvey, 1982). Owen-Smith (1988) showed that home range of large female herbivores in Africa is linearly related to body mass, and Grant *et al.* (1992) showed that among various groups of mammals, including ungulates, undefended home ranges are larger than defended ones. This was explained by the fact that an undefended home range can be used by other individuals, thus reducing the availability of resources from it (Grant *et al.*, 1992).

Several studies have been conducted on the social structure of gazelles in East Africa (Estes, 1967; Walther, 1969, 1973; Grau & Walther, 1973; Sinclair, 1985) and on the mountain gazelle *Gazella gazella gazella* in Israel (Grau, 1974; Baharav, 1974, 1981, 1983a, 1983b). These studies were carried out in an all-inclusive manner, without identifying the individuals. The results of these studies indicate that among gazelles, as in several other ungulates, female groups constitute open units with individuals moving freely between the groups at any time, including among and in the male territories (Grau, 1974; Mendelsohn & Yom-Tov, 1987). In contrast, adult males occupy territories delineated by 'odour stations', which they maintain by frequent urination and defecation (Grau & Walther, 1976). Female groups move freely within male territories, and no adverse relations were reported between female groups. The aim of this work is to study the social organization of individually identified, free-ranging female mountain gazelles.

METHODS

The study area

The study was conducted at Ramat HaNadiv, Southern Mount Carmel, Israel (32° 31' N, 34° 55' E) in an area of

4.5 km², surrounded by human habitation and agricultural fields. The climate in this region is Mediterranean with relatively cool, wet winters (average monthly temperature in January 11.9°C) and hot, dry summers (average monthly temperature in August 24.9°C). Rainfall averages 600 mm annually, and occurs mainly from November to March. The plant communities are dominated by several trees, such as *Ceratonia siliqua* and *Quercus calliprinos*, and shrubs *Pistacia lentiscus*, *Calycotome vilosa*, *Sarcopoterium spinosum*, *Phillyrea media* and *Rhamnus palestinus*. The vegetation types are batha (dwarf shrubs of up to 0.5 m and herbs), garrigue (a higher stage of shrubs, 1–2 m high, and small trees), and scrub forest ('maquis', of medium-sized trees up to 12 m (Zohary, 1962)). One part of the study area (termed 'bathtub') is a wide valley, where the primary vegetation type is an open batha, dominated by herbs with scattered bushes and few trees.

Animals

The mountain gazelle is the most abundant bovine species in Israel, numbering up to 10 000 individuals during the 1980s. The gazelles occupy mainly open grassland and batha, but also inhabit other habitats apart from dense forest. This species is a grazer and browser. In northern Israel during winter gazelles feed mainly on grasses, and later in spring on dicotyledons. During summer when green food is scarce, they browse on the leaves and fruit of *Ziziphus lotus*, a common low spiny shrub; during autumn, before the rains, they feed on *Cynodon dactylon*, a common weed, and on acorns *Quercus* spp. when available. Only a few plants are rejected altogether, and even plants that are known to be poisonous are often consumed (Mendelsohn & Yom-Tov, 1987).

Behavioural observations

A small population of about 50 mountain gazelles inhabits the area (Getraide & Perevolotzky, 1990). Eleven females were individually identified and observed regularly throughout the entire period. In each field observation we recorded the distance between females, and the following behaviour patterns noted: walking, eating, lying down and agonistic interaction. Agonistic behaviours included (1) chasing, in which a female chases away another female by tilting its head and threatening it with the horns; (2) approaching and lowering the head slightly, to which the approached female reacts by moving away from the approaching gazelle; and (3) passive chasing, in which one female approaches another female at a moderate pace, or while eating, and the second female calmly gives up its place. In the present analysis, no distinction was made between the above types of agonistic behaviours, but the number of agonistic interactions between females was recorded.

The only predators of gazelles (mainly fawns) in the

study area are golden jackals *Canis aureus* and feral dogs. A herd of about 180 cattle are introduced to the study area every late winter and early spring, which decreases the availability of herbs considerably.

The study area was mapped and marked by a grid of prominent markers placed 50 m apart. In order to check whether the female groups occupied the same area at the same time, the study area was divided into 6 sub-units, which were distinguished by topography and roads. We recorded entry and exit times for each group from each area. Observations were logged from vehicle and fixed observation points, during daytime, throughout the year, from April 1992 to November 1993. There were at least 6 full observation days (from sunrise to sunset) for each season (autumn: October–November; winter: December–February; spring: March–May; summer: June–September), with a total of 1080 observation hours throughout the study. During the study, the gazelles became used to our presence, and flight distance shrank to 15–20 m from the vehicle, with no apparent effect on their behaviour. The short flight distances enabled us to distinguish between and identify individual females by irregularities in their horns (Grau, 1974). The observations were made employing the focal animal method, which focuses on the behaviour and movement track of a single individual throughout the entire observation period of the day. Location points were recorded, with the location point expressing the presence of the female in a designated area at the time of observation. The locations of nearby gazelles were recorded concurrently.

Analysis

The home range size and configuration were analysed using the program 'Wildtrak' for the Macintosh computer (Todd, 1993) and calculated by 2 separate methods:

1. 90% minimum convex polygon of total range. This method is based on connecting each extreme location point obtained during that season and calculating the size of the enclosed area. The advantage of this method is that the home range is based on real location points in which a particular individual was observed. However, the spread of the location points is not normally distributed and the very extreme points, whose frequency is low, considerably expand the home range area. For this reason we adjusted the configuration of the range. The 90% value was selected because plots of cumulative percentage of fixes vs home range size revealed a moderate slope at 90% and a sharp increase thereafter. To calculate the 90% ranges, fixes were first ranked according to distance from an arithmetic mean centre of activity, and the most peripheral point was dismissed before successive recalculations of the mean arithmetic centre of the remaining points until the most peripheral 10% had been discarded (Ford & Krumme, 1979; Kenward, 1987).

2. Summed area of utilized grid cells. In this method, the area is divided into squares of equal size. For each

square, the number of location points in which an animal has been observed is counted. This method provides information on the maximum exploitation of the home range. The advantage of this method is that the home range area is little affected by scattered and deviant points. In the study area the grid measured 50 × 50 m, with the location points noted with accuracy of 25 × 25 m. Since the deviation can thus be ± 12.5 m, a 10 m grid was chosen for analysis.

We selected the home range analyses because both methods are non-parametric and require no dependence of fixes, as none of the methods calculates estimates based on probabilities. Both methods are most suitable for our study design. We collected fixes via observations at 1 min intervals, thus the autocorrelation in these data is probably considerable. Further, we see no reason that the fixes collected will be distributed normally because food resources for gazelles are distributed as patches and not in a homogeneous pattern.

Using 'Wildtrak', we calculated the overlap area between pairs of females, and overlap percentage in respect to each female. The percentage overlap between each 2 female ranges was calculated as the percentage of the common area of 2 home ranges (Todd, 1993).

The composition of female groups was determined by two methods: overlap in area used, and the proportion of time the gazelles spent together. The size and composition of the female groups was recorded upon each entry into the area being checked. The number of individuals in a group includes fawns, but not adult males. A female observed with a fawn older than 2–3 months (the age at which the fawns begin to join the female groups together with their mothers) was counted as a group consisting of 2 individuals, but a female moving with a fawn younger than the above age was not counted as a group.

We used multi-dimensional scaling (MDS) to summarize the frequencies of co-occurrence of females. Monotonic Kruskal's MDS was used because it effectively summarizes frequency variation on 2 dimensions and makes minimal assumptions about the distribution of the data (Borg, 1981). Euclidean distance matrices, calculated from the frequencies or overlap matrices, were used as the initial input data. The fit of the data to the model was estimated through a Shepard diagram (Shepard, 1962), and by the stress factor. The stress factor is a measure of the fit of the data into 2 dimensions and it varies between 0 and 1, with values near zero indicating a better fit. In our analysis, the stress factors were considerably lower than 0.1. The program SYSTAT for the Apple Macintosh (Wilkinson, 1992) was used for these calculations.

RESULTS

Home range

The average number of observation days (±SD) per female was 41 ± 12.6, range 18–58), and an average of

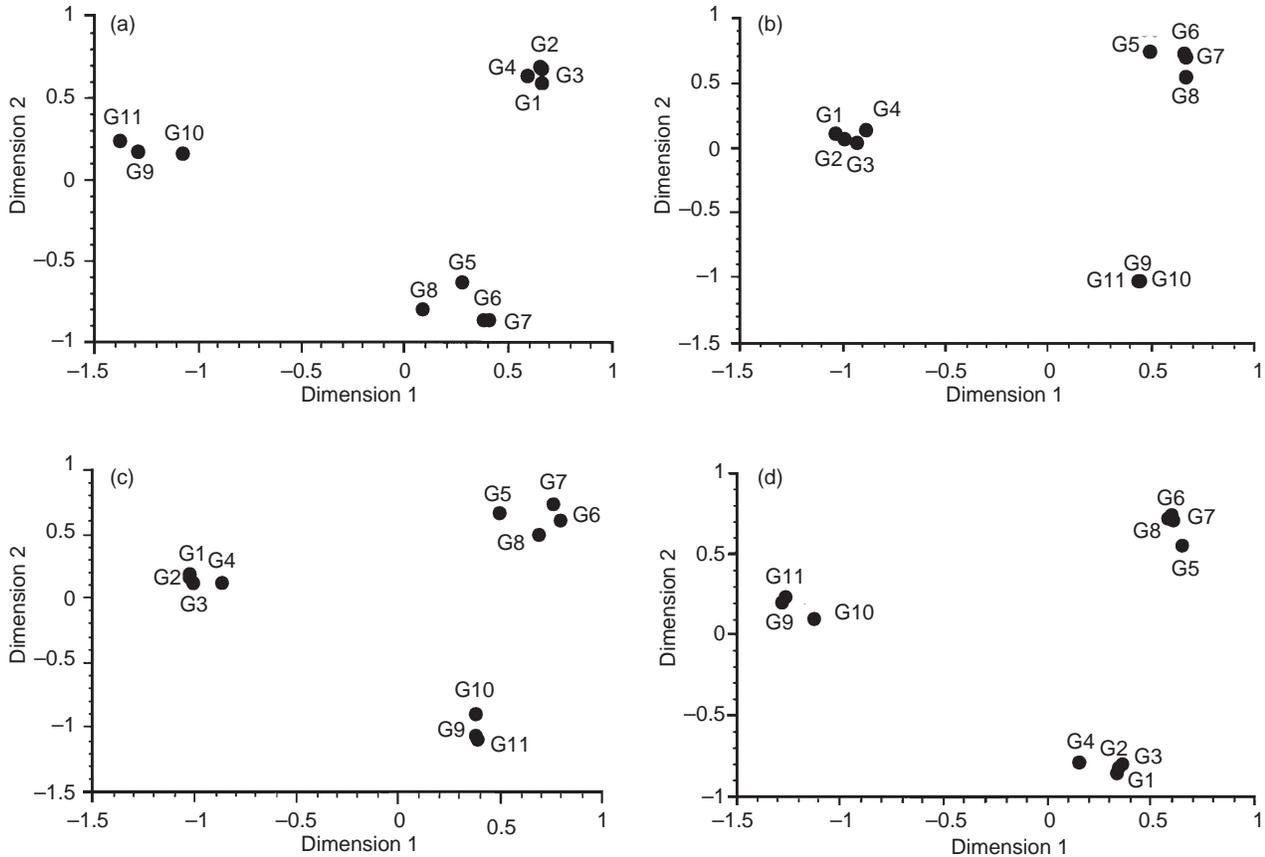


Fig. 1. (a) Kruskal's monotonic multidimensional scaling of percentage home range overlap between all observed female gazelles during the whole study period (Stress factor = 0.001, number of observation days for females ranged 18–58). (b) Kruskal's monotonic multidimensional scaling of percentage time females lying down together during summer (Stress factor = 0.005, number of observation days for females ranged 9–19). (c) Kruskal's monotonic multidimensional scaling of percentage time spent together of female pairs in summer (Stress factor = 0.011, number of observation days for females ranged 8–16). (d) Kruskal's monotonic multidimensional scaling of percentage time spent together of female pairs in winter (Stress factor = 0.002, number of observation days for females ranged 8–26). Proportion of variance explained by the two-dimensionality fit was 0.999 in all four cases.

657 location points (± 176.6 , range 275–785) was obtained for each female.

The size of the home range obtained by both methods (minimum convex polygon and grid cell) was significantly correlated ($r^2 = 0.89$, $F_{1,9} = 64.6$, $P = 0.0001$), thus confirming the reliability of the results. Because a large sample size of location points is required for the grid cell method, we used the 90% minimum convex polygon method for further analysis. According to this method, the mean home range size of female gazelles was 16.5 ± 0.51 ha ($n = 11$, range 10.9–24.3), and there was no significant difference in the size of the home range between the seasons (Friedman test: $F_{10} = 6.6$, $P = 0.08$).

Group size

Mean seasonal group size was 6.40 ± 2.16 ($n = 35$), 3.94 ± 1.39 ($n = 38$), 3.42 ± 0.94 ($n = 56$) and 3.83 ± 1.24 ($n = 30$) in winter, spring, summer and autumn, respec-

tively, and differed significantly between the seasons (square root transformed data, $F_{3,155} = 31.55$, $P = 0.00001$), being significantly larger in winter than in the other seasons (LSD *a posteriori* test, $t = 1.975$, $P < 0.05$). No differences in group size were discerned between the remaining seasons.

Determining composition of female groups

Female group composition was determined using multidimensional scaling which presents the relationships among all individuals in a two-dimensional space. Individuals were clustered based on home range overlap, time spent together during summer and winter and time spent at rest (Fig. 1a–d).

MDS clustering based on home range overlap showed three distinct groups numbering four (females 1, 2, 3, 4), four (females 5, 6, 7, 8), and three (females 9, 10, 11) females (Fig. 1a). These group compositions were stable and were maintained throughout the year.

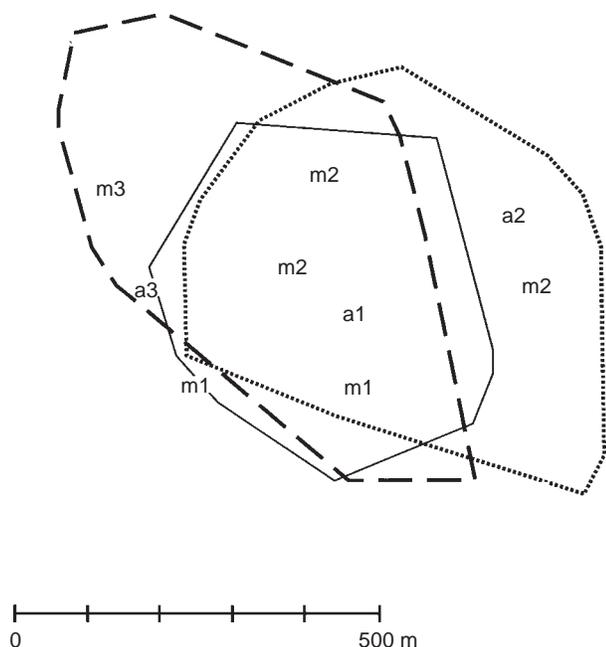


Fig. 2. Home ranges (90% minimum convex polygon) and the most frequently used resting areas of the three female gazelle groups in Ramat HaNadiv during summer and autumn. Home range boundary for group 1 is indicated by a solid line, for group 2 by a dotted line, and for group 3 by a broken line. Morning and afternoon resting sites are presented as 'm' and 'a', respectively, plus a group designation number.

The distribution of females occurring together in summer and winter is presented in Fig. 1c & d. These plots indicate that some females tended to spend time together much more than with others. In general, females that were observed together in more than 55% of the observations were the same individuals that clustered together by the MDS.

Group cohesiveness is further illustrated by the resting behaviour of female groups (Fig. 1b). All females rested twice daily, in late morning and late afternoon, and each of the three groups had preferred resting places for each period. During summer and autumn, most morning rests of group 1 occurred in two places, in which 72.9% and 18.9% of the observed rests ($n=37$) took place; group 2 had three morning resting places in which 72%, 20% and 8% of all rests ($n=25$) took place; and in group 3, 86.6% of all the observed morning rests ($n=15$) occurred in one place. For afternoon rests, each group preferred one locality, in which 89.6% ($n=29$), 88.8% ($n=18$) and 83.3% ($n=18$) of all the observed rests took place for groups 1, 2 and 3, respectively. Group composition in these resting places was similar to that observed in other activities (Figs 1b & 2).

In summary, independent analyses based on home range overlap and time spent together clearly show that the same individuals are systematically involved with each group, and group members never interchange.

Overlapping of home range and time avoidance between the groups

The home range area of the three groups was 11.35, 22.22 and 15.12 ha in groups 1, 2 and 3, respectively (Fig. 2). The overlapping area of the home ranges consisted of 81.2%, 44.0% and 62.4% of the total home ranges of groups 1, 2 and 3, respectively.

Presence of more than one group (of the three) at the same time and in the same area (overlaps) was observed in only 3.8% of the observations (13 out of the 342 possible interactions: 19 observation days in summer and autumn, in which all three groups were observed \times 6 sub-units \times 3 groups), indicating mutual avoidance (Sign-test, $P=0.01$ between group 1 and 2 and between group 1 and 3; $P=0.001$ between group 2 and 3). Two of the above 13 overlaps were due to a group being chased out of its area by feral dogs.

The mean (\pm SD) rate of agonistic interactions between the females in the various seasons was 9.28 ± 2.24 ($n=14$), 8.90 ± 2.21 , ($n=10$), 12.35 ± 3.62 ($n=17$) and 11.57 ± 1.59 , ($n=7$) during winter, spring, summer and autumn, respectively. There was a significant difference in the rate of interactions between the seasons (square root transformed data, one way ANOVA, $F_{3,44} = 3.88$, $P=0.01$). The amount of agonistic interaction within a group was higher in summer than in winter and spring (LSD *a posteriori* test, $t=2.015$, $P<0.05$). The rate of agonistic interactions was higher in autumn than winter and spring, but the differences were not significant.

During the study there were eight occasions in which two female groups were observed approaching each other. The mean rate of agonistic interactions between alien and local females (20.75 ± 3.45) was significantly higher than were agonistic interactions within groups in all seasons (t -test: $t=7.92$, $P=0.0001$ in winter; $t=7.90$, $P=0.0001$ in spring; $t=5.28$, $P=0.0001$ in summer; $t=6.29$, $P=0.0001$ in autumn). When an alien group intruded into the home range of a known group, all agonistic interactions were directed at the intruding females, and not within the known group.

DISCUSSION

The main finding of this study is that female mountain gazelles live in permanent groups which occupy temporal territories, and various groups replace each other in the same area at different times of the day. The preferred food of the mountain gazelle in Israel is herbaceous plants (Mendelssohn & Yom-Tov, 1987), but most of our study area is covered by bushes and trees, and herbs are plentiful in only one part of it (the 'bathtub'). In this area female groups replace each other during the day. Group composition remains constant throughout the year, and new females do not freely enter the established groups as had been previously thought (Grau, 1974). However, in winter when food is

plentiful, groups of females occasionally joined together apparently because there is less need to protect this resource, and few agonistic interactions were observed between the groups. While group home ranges overlap, in the summer the different groups largely avoided being together in the same area at the same time. During the rest of the year, the simultaneous occurrence of two groups in the same area was a rare event, and when it occurred, a high rate of agonistic interaction was observed between the groups. It thus appears that female mountain gazelles maintain temporal territories in the summer, as do males when courting females. As far as we are aware, this is the first report of bovine females holding intra-sexual territories, whose function is apparently to ensure an undisturbed access to favourable grazing areas.

Traditionally, territories are defined as 'fixed, exclusive area with presence of defence that keeps out rivals' (Brown & Orians, 1970). In other words, an exclusive area is defended continuously for a certain time. Doncaster & Macdonald (1991) reported another type of territoriality, 'drifting territoriality', where territories of urban red foxes *Vulpes vulpes* move in time across an area. Our results show that female mountain gazelles form a type of territoriality where the same area is defended by more than one group, but at different times of the day. This type of territory may be termed 'confined drifting territory', and describes a situation where an area, defended by a group of individuals, is drifting spatially only within the boundaries of a larger, non-exclusive range.

Group size

For gazelles, the principal advantages of living in groups are defence against predation and reduced vigilance, which in turn increases feeding efficiency (Fitzgibbon & Lazarus, 1995). The disadvantages are higher visibility of individuals to predators and greater competition for resources (Wilson, 1975). The size of the group in which animals live is a compromise between the various advantages and disadvantages. In our study group size was significantly larger in winter, as could be expected when food is plentiful and small groups merge into larger ones, apparently as protection against predation and other disturbances. However, in dry seasons, as food becomes scarcer due to cattle grazing and later by lack of rain and green herbs, groups tend to break up. We also found that the number of agonistic interactions within groups was higher in summer, implying possible competition for a limiting resource (i.e. food). In spring, also a season when food is plentiful, group size was small, but this was apparently due to the fact that most foaling takes place then. Females leave their group before giving birth and remain separated from their group for about 4 weeks until joining it again with the fawn.

Home range

The size of home range is a compromise between various environmental conditions and selection pressures (Damuth, 1981). Nonetheless, in many mammals home range is positively related to body size (McNab, 1963; Damuth, 1981). For example, the home range area (HR, ha) of large female herbivores in Africa increases linearly with body mass (BM, kg) and is described in the equation (Owen-Smith, 1988):

$$HR = 1.35 BM^{1.25}$$

Thus, the expected home range area of an 18 kg female mountain gazelle would be about 50 ha, but the data from which the equation was calculated vary greatly. Our observations show that the average home range area of female gazelle groups in Ramat HaNadiv is smaller than the calculated value (16.5 ha). There may be two reasons for this: the regression line was calculated for herbivores in drier areas of Africa in comparison to our study area, where the climate is cooler and wetter and the carrying capacity is larger, thus requiring a smaller home range for each individual. It is also possible that a limiting factor exists in Africa, such as an irregular water supply which would require a larger home area, while at Ramat HaNadiv water is available throughout the year. In addition, the fact that the area of Ramat HaNadiv is small and surrounded by extensive human habitation, may cause the gazelles to reduce their home range.

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REFERENCES

- Baharav, D. (1974). Notes on the population structure and biomass of the mountain gazelle, *Gazella gazella gazella*. *Israel J. Zool.* **23**: 39–44.
- Baharav, D. (1981). Food habits of the mountain gazelle in semi arid habitats of the eastern Lower Galilee, Israel. *J. Arid Environm.* **4**: 63–69.

- Baharav, D. (1983a). Observation on ecology of the mountain gazelle in the Upper Galilee, Israel. *Mammalia* **47**: 59–69.
- Baharav, D. (1983b). Reproductive strategies in female mountain and dorcas gazelles (*Gazella gazella* and *Gazella dorcas*). *J. Zool. (Lond.)* **200**: 445–453.
- Borg, I. (1981). *Multidimensional data representations: when and why?* Ann Arbor, Mich.: Mathesis.
- Brown, J. L. & Orians, G. H. (1970). Spacing patterns in mobile animals. *Annu. Rev. Ecol. Syst.* **1**: 239–262.
- Clutton-Brock, T. H. & Harvey, P. H. (1977). Primate ecology and social organization. *J. Zool. (Lond.)* **183**: 1–39.
- Damuth, J. (1981). Population density and body size in mammals. *Nature* **290**: 699–700.
- Doncaster, P. C. & Macdonald, D. W. (1991). Drifting territoriality in the red fox *Vulpes vulpes*. *J. Anim. Ecol.* **60**: 423–439.
- Doncaster, P. C. & Macdonald, D. W. (1996). Intraspecific variation in movement behaviour of foxes (*Vulpes vulpes*), a reply to White, Saunders and Harris. *J. Anim. Ecol.* **65**: 126–127.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223.
- Estes, R. D. (1967). The comparative behavior of Grant's and Thomson's gazelles. *J. Mamm.* **48**: 189–209.
- Estes, R. D. (1974). Social organization of the African Bovidae. In *The behavior of ungulates and its relation to management*: 166–205. Geist, W. & Walther, F. (Eds). Morges, Switzerland: IUCN.
- Fitzgibbon, C. D. & Lazarus, J. (1995). Antipredator behaviour of Serengeti ungulates: individual differences and population consequences. In *Serengeti II*. Sinclair, A. R. E. & Arcese, P. (Eds). Cambridge: Cambridge University Press.
- Ford, G. & Krumme, D. W. (1979) The analysis of space use patterns. *J. Theor. Biol.* **76**: 125–155.
- Getraide, S. & Perevolotzky, A. (1990). *The ecology of the mountain gazelle (Gazella g. gazella) in Ramat HaNadiv*. Society for the Protection of Nature in Israel and Yad Hanadiv (In Hebrew).
- Gittleman, J. L. & Harvey, P. H. (1982). Carnivore home range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* **10**: 57–63.
- Grant, J. A. W., Chapman, C. A. & Richardson, K. S. (1992). Defended versus undefended home range size in carnivores, ungulates and primates. *Behav. Ecol. Sociobiol.* **31**: 149–161.
- Grau, G. A. (1974). *Behaviour of mountain gazelle in Israel*. PhD thesis, Texas A & M University.
- Grau, G. A. & Walther, F. R. (1976). Mountain gazelle agonistic behaviour. *Anim. Behav.* **24**: 626–636.
- Jarman, P. J. (1974). The social organization of antelope in relation to their ecology. *Behaviour* **48**: 215–267.
- Jarman, P. J. & Jarman, M. V. (1973). Social behaviour population structure and reproductive potential in impala. *East Afr. Wildl. J.* **11**: 329–338.
- Kenward, R. (1987). *Wildlife radio tagging: equipment, field techniques and data analysis*. London: Academic Press.
- Kishimoto, R. & Kawamichi, T. (1996). Territoriality and monogamous pairs in a solitary ungulate, the Japanese serow, *Capricornis crispus*. *Anim. Behav.* **52**: 673–682.
- Kruuk, H. & Macdonald, D. W. (1985). Group territories of carnivores: empires and enclaves. In *Behavioural ecology: ecological consequences of adaptive behaviour*. 521–536. Sibley, R. M. & Smith, R. H. (Eds). Oxford: Blackwell Scientific Publications.
- Leuthold, W. (1977). *African ungulates*. Berlin: Springer-Verlag.
- McNab, B. K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.* **97**: 133–140.
- Mendelsohn, H. & Yom-Tov, Y. (1987). *Mammals of Israel*. Tel Aviv: Ministry of Defense Publ. House (In Hebrew).
- Owen-Smith, R. N. (1988). *Megaherbivores. The influence of very large body size on ecology*. Cambridge: Cambridge University Press.
- Shepard, R. (1962). The analysis of proximities: multidimensional scaling with an unknown distance function. *I. Psychometrika* **27**: 125–139.
- Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the African ungulate community? *J. Anim. Ecol.* **54**: 899–918.
- Todd, I. A. (1993). *Wildtrak: non-parametric home range analysis for the Macintosh*. Oxford: ISIS Innovation Ltd.
- Tufto, J., Andersen, R. & Linnel, J. (1996). Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *J. Anim. Ecol.* **65**: 715–724.
- Walther, F. R. (1976). Flight behavior and avoidance of predator in Thomson gazelles. *Behaviour* **34**: 184–221.
- Wilkinson, L. (1986). *SYSTAT: the system for statistics*. Evanston, Illinois: SYSTAT Inc.
- Wilson, E. O. (1975). *Sociobiology*. Cambridge, Mass.: Harvard University Press.