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Organization of roe deer *(Capreolus capreolus)* in an open field habitat

By M. Stüwe and H. Hendrichs

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Abstract

The social organization of a roe deer *(Capreolus capreolus)* population was studied for 16 months in a cultivated field habitat which showed pronounced seasonal changes in availability of food and shelter. Foraging sites were influenced by the proximity of shelter. The location of resting sites was dependent on the proximity of shelter and foraging places. Multifamily groups were formed between November and April. Until onset of the territorial season they were joined by adult ♂♂, who developed a dominance hierarchy. Mean maximum group size was below two from May until October, increased to a maximum of 13 in January, and again declined below two in June. Proximate factors influencing or facilitating group formation in field habitats include: decrease of aggression between individuals after the territorial season; possibility for easy habituation of conspecifics to each other through the open habitat structure; increasing probability of meeting conspecifics at clustered attractive food resources in undisturbed areas; effects of a disturbance-gradient that 'pushes' the animals toward the quiet field centers.

Introduction

'Typical' roe deer habitat has been described as woodland areas with rather dense understory divided by small meadows and sometimes fields (Raesfeld 1905, 1978; Hennig 1962; Whitehead 1964; Bramley 1970; Delap 1970; Strandgaard 1972; Ellenberg 1978). Morphologically the roe deer seems to be well adapted to this type of habitat. The 'duiker' shape of its body points toward movements in dense understory, its circulatory system is more like a sprinter's than of a long-distance runner, and its digestive system is characteristic of a specialized browser (Raesfeld 1905, 1978; Krieg 1936; Flerov 1952; Hofmann and Geiger 1974; Büttner 1980).

In woodland areas, roe deer are widely distributed in spring and summer because of territorial behavior of ♂♂ and solitary behavior of ♀♀. After the late summer rut, these territories are no longer defended and home ranges then overlap. Thereafter groups of as many as five individuals are normal (Dzieciolowski 1979), usually containing only a single adult ♂. In severe winters, larger groups will associate at attractive feeding sites. (Raesfeld 1905, 1978; Hennig 1962; Kurt 1968; Strandgaard 1972; Ellenberg 1978; Bideau et al. 1983).

The occurrence of large, long-lasting roe deer groups in certain field habitats was only occasionally mentioned in early reports, as noted by Graczyk and Bereszynski (1978); Sokolov and Danilkin (1980). In 1960, Necas reported on the first study of roe deer inhabiting the open agricultural fields in southern Czechoslovakia. Kaluzinski (1974); Pielowski (1977, 1981); Zejda (1978); Reichholf (1980); Zejda and Homolka (1980); Bresinski (1982) later studied roe deer in similar habitats. The histories of all such populations are comparable: a few years after vast areas are cleared for agriculture, the new fields are inhabited by increasing numbers of roe deer. In large herds the deer use different fields in relation to attractiveness of the crop. Average herd size increases in autumn, reaches its maximum in late winter, and thereafter decreases until the last groups break up

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in late spring. Little is known about the behavior of these 'field' roe deer in summer, assumedly it then does not differ from that of roe deer in woodland habitats (Pielowski 1977).

The objective of this study was to investigate the utilization of an agricultural area by roe deer, their social organization under these conditions, and the proximate factors leading to the formation of large winter groups in such uncommon ecological situations.

Methods

The study was conducted near the town of Bielefeld in the north of the Federal Republic of Germany 52° N, 9° E). 370 hours of observation were made over a 180 day period between March 1981 and June 1982. On each of these days we censused approximately 180 ha of the total study area, recording group size, and its sex/age composition, location, and behavioral aspects of all animals encountered. Individuals who were not more than 50 m apart were considered to constitute a group. After a general survey, special observation sites were selected for recording intra- and intergroup behavior. Between June and August 1981, the standing height of agricultural crops drastically reduced deer visability and hence few data were obtained. Observations were made from cars, tree stands, or by stalking, using 8 × 56 and 8 × 20 ZEISS binoculars and a 30 × 75 OPTOLYTH spotting scope. The study area was used by about 25 deer. By the end of the study 18 individual deer could be identified by means of distinctive ear or body marks, or antler shapes. Sightings of 1586 deer in 597 groups were analysed for this study.

Study area

Approximately 96 % of the study area was flat open country subdivided into several agricultural fields of varying size (1–19 ha). The area was divided into two parts by a country road, which also bordered the fields on the east and west. A small river fringed by poplar woods bordered the study area on the north. On the northwest and east were small woodlots containing oak, beech, and alder trees with sparse undergrowth. A field of about 17 ha was cut off by a narrow hedge of willow and alder bushes (Fig. 1). The remaining area provided no cover after the crops were harvested. Adjacent fields were intersected by dirt roads which sometimes supplied some cover from deep ruts or tall grass and weeds. There were no trees or shrubs along the field borders. Intensive cultivation of these fields occurred in March and April, and again in late summer and fall when the crops were harvested. There was no human activity in the fields during winter, and only a slight amount in summer. Occasionally disturbances were caused by pedestrians and dogs. Hunting was very limited, with more animals killed by cars than by gun.

Food resources

Weeds and grasses grew unrestricted along the woods and field trails. Barley, wheat, and oats grew until about June, but then hardened. Sugar beet leaves were available from June until October. By early November all sugar beets had been harvested and piled along the field edges. During November most of these piles were removed, but at five sites some beets remained throughout the winter. Three sugar beet fields were not harvested well, and many broken beets remained on the surface. In October clover was sown in three fields. Shoots appeared in early November, and it was completely foraged by sheep on 21 Nov 1981. Winter wheat and winter barley was sown in many fields. However, due to a heavy frost period in November only one field had long and dense standing shoots in December. Nearly all winter grain then died during a second heavy frost period in January. Only one field near the beech wood started growing in March. All other fields had to be drilled again and had long shoots from mid April on. On a field near the hedge, sugar beets from the previous year were exposed when it was plowed on 8 March 1982.

Results

Foraging sites

Use of food resources in the fields by roe deer can be divided into four periods (Fig. 2). From June through October (period 1) deer foraged on grass and sugar beet leaves at sites scattered throughout the fields. During the first three weeks in November (period 2) 85 %

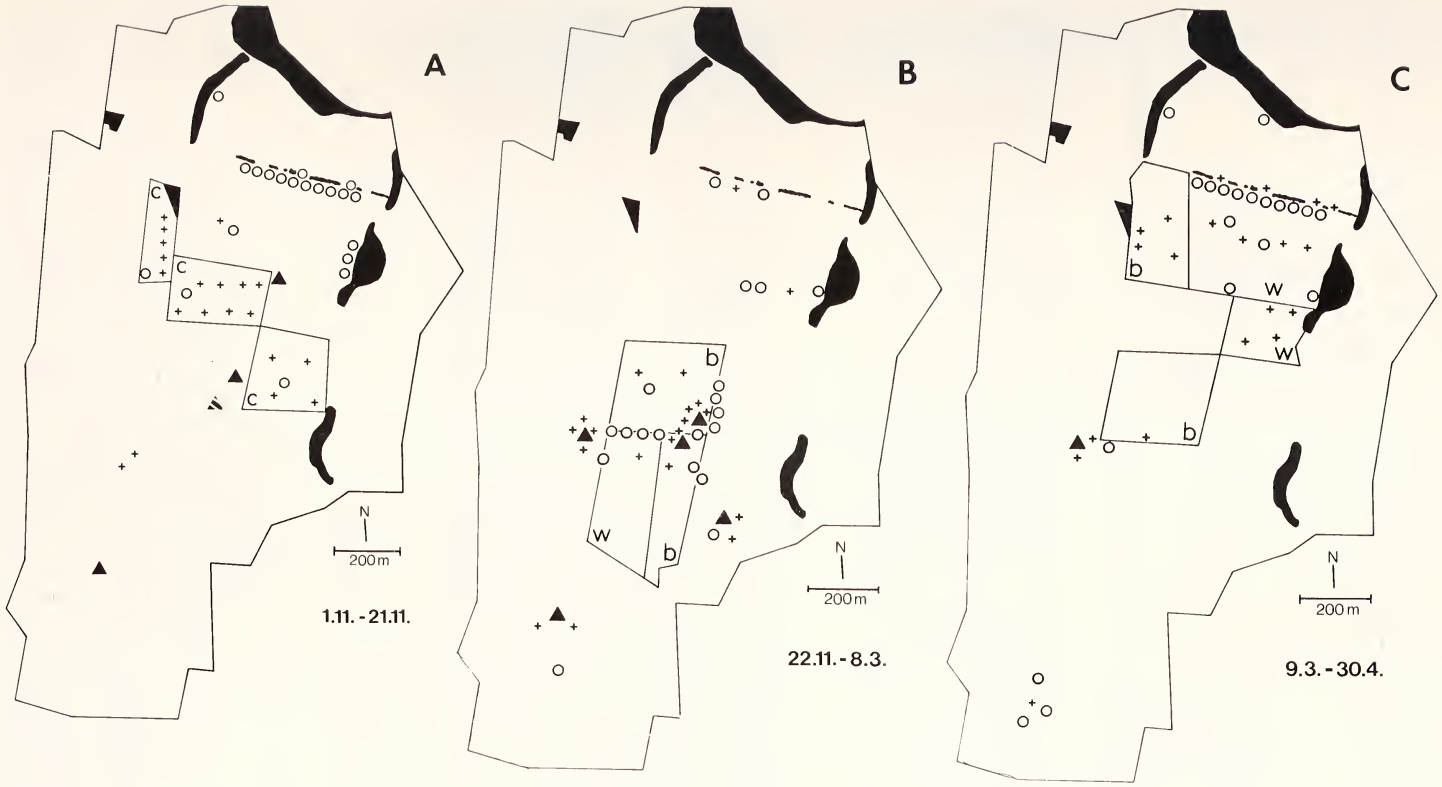

Fig. 1. Observed distribution of foraging (+) and resting (○) places of roe deer within the study area. Each symbol shows 5 % of the total number of animals found foraging or resting during each phase. Woodlots are shown in black. Important food items consisted of clover (c), wintergrain (w), fragments of harvested sugar beets (b), sugar beet piles (▲)

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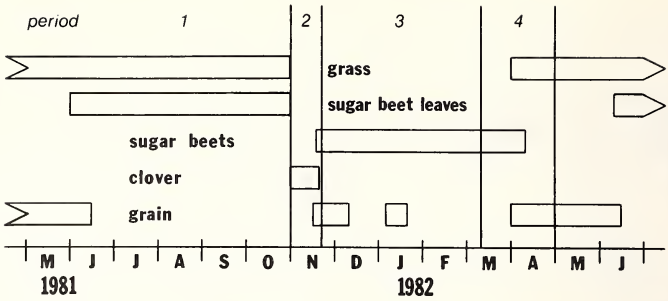

Fig. 2. Seasonal utilization of available food resources according to designated sampling periods (see text for criteria)

of all deer observed foraging were feeding on freshly growing clover, which covered 13 ha (7.2 %) of the study area (Fig. 1 A). When this plant was no longer available, deer started eating sprouted winter grain and unretrieved sugar beets in the center of the study area. Through early March (period 3) 70 % of all observed foraging took place on about 13 ha (7.2 %) of the study area (period 3) (Fig. 1 B). Foraging site again changed when the old sugar beets were exposed near the hedge, and deer immediately began eating them. Deer again foraged exclusively on grain crops when spring growth commenced (period 4) (Fig. 1 C).

Resting sites

Until November 1981, and after May 1982, all deer observed resting lay in tall grain, or sugar beet fields, or along woods (period 1). During November (period 2) (Fig. 1 A) and March/April (period 4) (Fig. 1 C), most resting sites were along woodland or the hedge. Between December and February (period 3) (Fig. 1 B), most resting sites were located in the center of fields next to foraging sites.

We distinguished between the numbers of deer resting up to 10 m beside woodland and those resting farther away from woodland. The ratio of such tallies differed between the November and March/April vs. December–February periods (see Table). Ratios for feeding sites did not differ, indicating that foraging in the vicinity of woodlands was minimal during all periods. Comparison of foraging and resting sites during periods 2, 3, and 4 shows that deer bedded near woodlands as long as food was available within 400 m (period 2 and 4), but that they bedded in the fields if food was farther away from an

Table

Roe deer foraging or resting inside or outside a range of 10 m along woodland
(N: number observed)

Period	2 (1 Nov–21 Nov) N	(%)	3 (22 Nov–8 Mar) N	(%)	4 (9 Mar–30 Apr) N	(%)
			Foraging			
Along woodland	1	(2)	56	(8)	52	(19)
Away from woodland	63	(98)	644	(92)	221	(81)
			Resting			
Along woodland	63	(78)	114	(15)	208	(74)
Away from woodland	18	(22)	666	(85)	72	(26)

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attractive woods edge (period 3). Deer were never seen resting in the southern woodlot, probably because there were two inhabited houses nearby.

Only foraging and resting sites used during the day are shown in Fig. 1, we did not observe deer at night.

Group size and composition

Deer frequently formed groups and then separated during our observations. To avoid repeatedly recording the same individuals, a mean maximum group size was computed which included only those animals in the largest group seen on each day of observation. Group size was below two until October 1981, reached a maximum of 12.9 in January, and again dropped below two in June 1982 (Fig. 3).

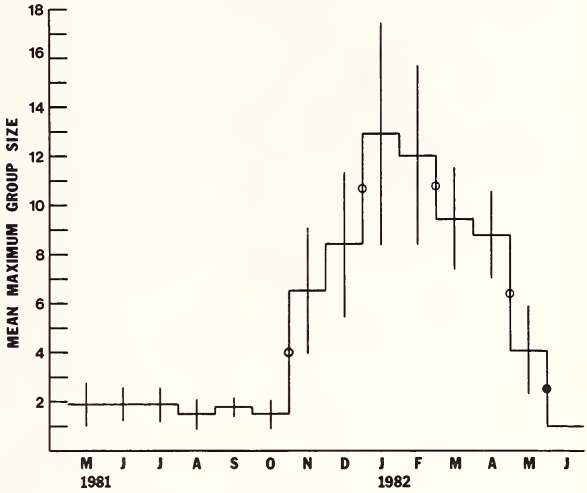

Fig. 3. Mean maximum group size of roe deer and extend of increases or decreases between study periods; open circles: $P < 0.01$, closed circles: $P < 0.05$ (Duncan's new multiple range test)

From May to October 1981 single ♂♂ and single ♀♀ with or without offspring (family units) were the rule. A family unit was sometimes accompanied by an adult ♂. In November several families commonly joined each other, and from mid-month on, such groups occasionally included more than one adult ♂. When these groups separated, however, the adult ♂♂ usually joined different subgroups. Group size stabilized in January and February. Individuals of family units sometimes joined different subgroups. Small groups could now include more than one adult ♂, all-♂♂ groups, however, were never observed. Group size started to decrease in March. Adult ♂♂ were no longer found together. One adult ♂ (M1), two yearling ♂♂ (M7, M8), four adult ♀♀, and three yearling ♀♀ comprised a single group until the end of April. In the alder wood adult ♂ M2 was frequently seen with one adult ♀. In the southern part of the observation area adult ♂ M3 was together with six ♀♀. In May, the two large groups started to separate, and the ♀♀ shifted to small groups of varying size and composition. Adult ♂♂ generally travelled alone or joined ♀♀-groups. By June only single deer were seen.

Social relationships

When group size started to increase in November, three adult ♂♂ (M1, M4, M6) and two young ♂♂ (M7, M8) were using the fields. In mid-month M1 and M6, members of the same group, fought severely. M6 lost the fight, but did not leave the group.

From December on, five adult ♂♂ (M1, M2, M4, M5, M6) could regularly be found in the fields. Normally they fed and bedded together in the same group without visible social interactions. However, when two groups came together, or when a group appeared to be disturbed, agonistic interactions were more likely to occur. ♂♂ who withdrew in such occasions from another ♂ were considered subordinate. Not all ♂♂ were observed

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interacting with each other. The information can, however, be summarized in three linear hierarchies:

M1 > M2 > M5 > M4 > M8 > M7 / M1 > M3 > M4 > M8 > M7 / M1 > M6 > M8 > M7

The combination of these hierarchies, at the points where information is missing, might not necessarily result in another linear hierarchy but could show a more complex picture.

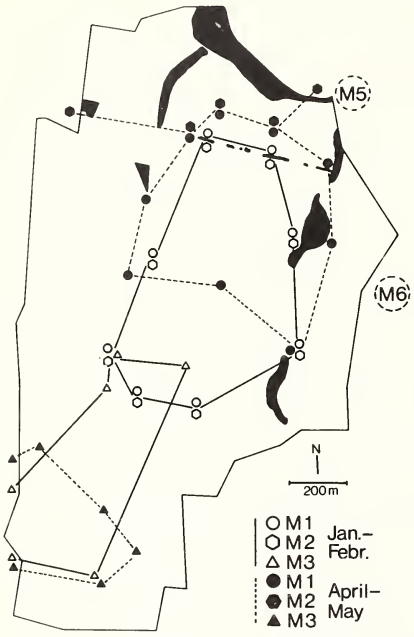

Fig. 4. Home ranges of adult male roe deer M1, M2, and M3 in January/February, and their respective territories in April/May 1982. Only their main locations are shown for M5 and M6

Agonistic interactions resulted in the dispersal of all but the dominant ♂ from the central fields by late February. On 28 Feb 1982 M1 chased M5 into the woods, and a few hours later provoked a severe fight with M3, who finally lost. The fresh carcass of M5 was found in the alder wood on 20 Mar 1982, in the same area he was twice seen before (Fig. 4). After their retreat from the central fields, M2 and M3 used parts of the north and south end of the observation area. Their home ranges expanded outside the observation area to an unknown extent. M1 shifted his home range to the north, so that it now included the whole length of the hedge (Fig. 4).

The two young ♂♂ (M7, M8) could be found in the same groups with M1 until May. One day before M8 shed his velvet he was repeatedly chased by M1 and one day after shedding he was seen alone more than 1 km away from the group. Later he was occasionally found in ♀♀-groups. The same happened two weeks later when M7 shed. He was chased by M1 and never seen together with him again.

Agonistic interactions between ♀♀ could be observed mainly in November and December, including five head-head fights in November. No hierarchy could be determined because not enough ♀♀ were identifiable at that time. However, two ♀♀ appeared to be dominant over all others. Only low intensity aggression was observed after December. At the end of April intense chasing between ♀♀ near the hedge became more frequent. At the same time ♀♀ started to separate from each other. They were found alone more often, at wood edges and along the hedge.

Discussion

Utilization of field resources

Roe deer are morphologically and behaviorally adapted to dense habitats and select a predominantly browsing diet. Agricultural fields do not offer any cover during several months of the year and only provide a limited variety of monocultural plants. Nevertheless they are inhabited by large numbers of roe deer (Zejda 1978; Reichholf 1980). In our study area deer first foraged solely on clover and later on sugar beets. When grain fields began to germinate again in April, deer immediately began feeding on the new shoots. They seemed to select the available plants according to their growing status. Zejda (1978) and Zejda and Homolka (1980) reported that deer in their field study area showed

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varying preferences for the different crops over the winter and completely left areas where they could not find preferred plants. Three characteristics of cultivated plants therefore are of importance: 1. They have a high nutritional value. 2. They are grown in amounts that cannot be overexploited. 3. Many of them are sown in fall and provide fresh growth in autumn when other plants terminate their growing season. 4. They do not offer much change or novelty.

To exploit food resources in fields, roe deer must leave protective woodland. Our deer showed changing strategies in the choice of foraging and resting sites in the fields. Utilization of food resources was influenced by its distance to adjacent cover. If food was present near woods, deer foraged there. When that food was no longer available, deer started feeding farther away from the woods. Choice of resting places depended upon the distance between foraging sites and adjacent cover. If deer foraged within 400 m of the woods, they rested there; if they fed farther away, they rested near their foraging sites. Reichholf (1980), however, reported that roe deer in his study area did not change strategies. Deer that foraged along wood edges were different animals from those that fed in open fields. Foraging and resting sites of roe deer in our fields also seemed to be influenced by human disturbances. Initially they fed on beets farthest from roads and trails used by man. When this food was consumed they sought beets closer to roads. However, deer still returned to the original foraging sites to bed.

Group formation

The special ecological situation of vast agricultural fields generally leads to the formation of larger deer groups (Necas 1960; Reichholf 1980) than found in woodland habitats (Dzieciolowski 1979; Bideau et al. 1983). Certain ecological and ethological factors might have proximately influenced the formation of winter groups in our field study area: 1. A decrease in aggression after the territorial season seemed to be a main precondition for the formation of large groups. It allowed animals to approach each other without the risk of an immediate agonistic interaction. 2. Open shelterless fields enabled deer to notice each other more often and over longer distances, and so probably facilitated an increasing habituation to strange or previously avoided conspecifics. 3. Clustered food resources attracted deer from distant areas and so increased the chance to meet other deer. 4. Lack of disturbances at some foraging places allowed deer to rest nearby and thus increased the probability to meet newly-arriving conspecifics there. 5. An increasing gradient of disturbance toward field edges (houses, roads, etc.) 'pushed' deer into the field center and thus effected higher concentrations there than at the periphery. 6. Single individuals or small groups sometimes seemed attracted to larger groups. Deer, fleeing perceived danger, often ran toward undisturbed groups, perhaps because these indicated an area of no immediate danger.

Separation of winter groups seemed to depend initially on the increase of aggression among ♂♂ at the onset of the territorial season, and later on conflicts among ♀♀ before the fawning season. Both times drastic ecological changes were not detectable in the fields. Deer were still feeding together on sugar beets in the center of fields when the subordinate ♂♂ left the groups in late February. When ♀♀-groups separated in May, the field crop had not yet grown tall enough to provide cover.

Social organization

During summer, the social organization of the roe deer in our field habitat was comparable to that of woodland populations. The onset and termination of the territorial season were independent of ecological factors such as the distribution of food and cover. Its timing was possibly related to endocrine (Sempéré 1978; Sempéré and Boisson 1981; Sempéré and

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Lacroix 1982), and behavioral changes (Ellenberg 1978), documented for roe deer in woodland habitats.

Roe deer in our study area, however, showed quantitative and qualitative differences in their social and spatial relations in winter, compared with most woodland populations. Large groups with several adult ♂♂ were formed. The composition of these groups might remain unchanged for several days, or could vary within hours. The rearrangements took place with little or no agonistic interactions; this perhaps was facilitated by the fact that most or all deer using the fields were familiar with one another. Dominance relationships structured the ♂♂, and probably the ♀♀ population. A dominant ♂ in a group became subdominant when a superior ♂ arrived, and became dominant again when he left. Hirth (1977) reports similar relationships for white-tailed deer that patroled different groups in search for estrous ♀♀, and gained access to ♀♀ when they dominated the resident ♂. Bresinski (1982) found that dominance hierarchies in field-living roe deer became far more distinct in severe winters. Older ♂♂ then drove subdominant individuals from food resources.

Large groupings of roe deer have been reported in a few instances. In some areas of the Soviet Union, herds of several hundred deer gather and migrate as far as 300 km to traditional wintering areas with shallower snow cover (Flerov 1952; Egorov 1965; Heptner et al. 1966). Also, in some agricultural areas of eastern Europe, herds of several dozen, and sometimes over 100 individuals, gather on fields to feed during winter (Necas 1960; Kaluzinski 1974; Pielowski 1977; Zejda 1978; Bresinski 1982). For none of these large herds social relationships above the mother-fawn unit have, however, been reported. They are considered to be anonymous aggregations as they are common in other cervids in temperate zones during the winter. In our study area the rather low population size and the clustered food resources lasting many weeks possibly facilitated the formation of individual social relations between all members of the population.

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Zusammenfassung

Zur sozialen Organisation einer Rehpopulation (Capreolus capreolus) in einem offenen Feldbiotop

Über 16 Monate wurde die soziale Organisation einer Reh-Population in einem landwirtschaftlich genutzten Gebiet studiert, das drastische saisonale Änderungen im Nahrungs- und Deckungsangebot aufwies. Nahrung wurde zunächst in der Nähe von Deckungsmöglichkeiten, im Verlauf des Winters immer weiter im offenen Feld gesucht. Die Rehe ruhten entlang von Deckungen, solange sie in deren Nähe ästen. Lagen die Nahrungsplätze weiter als 400 m von jeglicher Deckung, ruhten die Tiere im Feld. Mehr-Familien Gruppen wurden zwischen November und April gebildet. Bis zu Beginn der Territorialzeit konnten sie von adulten ♂♂ begleitet werden, die unter sich eine Rangordnung ausbildeten. Die durchschnittliche größte Gruppenzahl blieb unter zwei zwischen Mai und Oktober, stieg im Januar bis auf 13 an, und fiel im Juni wieder unter zwei. Proximative, die Gruppenbildung im Feld beeinflussende oder erleichternde Faktoren schließen ein: die Abnahme inter-individueller Aggression nach der Territorialzeit, die Möglichkeit, sich in dem offenen Habitat an Artgenossen leichter zu gewöhnen, die größere Wahrscheinlichkeit, Artgenossen an konzentrierten Nahrungsressourcen anzutreffen, die Auswirkungen eines Störungsgradienten, der die Tiere in die ruhigen Feldzentren drückt.

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Authors' addresses: Michael Stüwe, Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, VA 22630, USA; Priv. Doz. Dr. Hubert Hendrichs, Fakultät für Biologie, Universität Bielefeld, Morgenbreede 45, D-4800 Bielefeld 1, FRG

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