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## Social organization of Red foxes (Vulpes vulpes) in the Swiss Jura Mountains

By J.-S. MEIA and J.-M. WEBER

Institute of Zoology, University of Neuchâtel, Neuchâtel, Switzerland LIBRARIES

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## Abstract

We studied the social organization of red foxes *Vulpes vulpes* for four years (September 1989–August 1993) in a 30-km<sup>2</sup> area in northwest Switzerland. We caught and tagged 64 foxes, fitted 25 of them with radio-collars, and established a total of 18 641 locations. We made 1470 direct observations of foxes, including 234 intra-specific encounters. There were five main findings: (1) Foxes formed spatial groups in mountainous areas; (2) in addition to the alpha pair and the helpers, the groups also included at least one additional non-helping female (old female that has lost its alpha rank); (3) although we usually observed only one litter in each group, mating was not limited to the dominant pair; (4) there were very few encounters between individuals. When conspecific foxes meet, they ignore each other in more than half the cases. Even at the resting sites, which were shared, foxes usually did not meet; (5) the social organization of foxes appeared more stable than expected. We observed no change in social organization, despite a large decrease in the density of the fox's main prey, the water vole *Arvicola terrestris scherman*. The Resource Dispersion Hypothesis (R.D.H.) is the best existing model on group formation in solitary carnivores to explain the observed situation.

## Introduction

Until recent years red foxes (*Vulpes vulpes* L.) were considered to be typical solitary carnivores. Then the radio-tracking studies of NIEWOLD (1976, 1980), MACDONALD (1979, 1980, 1981) HARRIS (1980), LINDSTRÖM (1980) and VON SCHANTZ (1981) showed that foxes can live in "spatial groups" (MACDONALD 1983) in different habitats (e.g. urban areas). In such situations, more than one pair of adults share the same area. Although individuals of a group show overlapping home ranges, encounters are rare (MACDONALD 1981; WHITE and HARRIS 1994). The social organization of foxes in certain areas and/or habitats remains unclear, and relations between members of a group need further investigation (WHITE and HARRIS 1994). In central Europe, the social organization of foxes has not been studied, except by POULLE et al. (1994). It has been suggested that foxes could be more solitary there because of particular conditions such as hunting and rabies (ARTOIS 1989; ARTOIS et al. 1990).

Several hypotheses have been proposed to explain why solitary foragers, such as foxes or European badgers (*Meles meles* L.), share their home range with conspecifics. They were recently summarized and discussed by WOODROFFE and MACDONALD (1993). According to these hypotheses, group formation is governed by food quantity and/or distribution. Most of these hypotheses were based on observations in one type of habitat and need to be tested and discussed in relation to other conditions.

In this context, we studied a fox population in the Swiss Jura Mountains in an area characterized by a fluctuating prey, the water vole *Arvicola terrestris scherman* Shaw (WEBER and AUBRY 1993). Three questions were addressed: 1. What was the social organization of foxes in this area?; 2. Was the social structure affected by changes in food availability, i.e. the fluctuations of water voles?; and 3. Which hypotheses could best explain the observed social structure?

## Material and methods

#### Study area

The 30-km<sup>2</sup> study area is in the northwestern part of Switzerland, 20 km north of Neuchâtel (47° 09' N, 6° 56' E). The altitude ranges from 900 to 1 290 m. Average annual rainfall is 1 329 mm and average annual temperature 6.8 °C. Snow cover is present sporadically from November to March (up to 1 m). Pastures and meadows cover 55% of the surface, pastures 25%, and spruce, *Picea abies* dominated forests to 20%. Most of the soil cover is thin and therefore the number of dens is low (see MEIA and WEBER 1992).

Cattle breeding is the main agricultural activity. About 80 farms are evenly distributed over the area linked by a network of small roads. Fox hunting is traditional and is still carried out in some winters, e.g. the number of families in the study area was reduced from eight to two in winter 1887–88 (A. PARATTE, pers. comm.). Throughout northern Switzerland, including the study area, foxes have been vaccinated against rabies (Steck et al. 1982; WANDELER et al.1988). Only one case of a rabid fox was reported in the area during our study (A. HENNET, pers. comm.)

In the study area, foxes are mainly nocturnal (WEBER et al. 1994) and rest by day either in a den or above ground according to the amount of cover available (MEIA and WEBER 1993). Home range sizes are small (seasonal estimates: 0.48–3.06 km<sup>2</sup>) and they are not affected by changes in food availability (MEIA and WEBER 1995).

#### Social organization

Foxes were caught using stopped-neck snares, foot snares, or by placing a net around a den into which we introduced a terrier dog. They were then tranquillized and individually tagged with one or two coloured eartags (Dalton Supplies Ltd, Henley-on-Thames, UK). We fitted adult-sized foxes with activity-monitoring transmitters (Wildlife Materials Inc., Carbondale Ill, USA), and subadults with expanding radio-collars (AVM Instrument Co., Livermore Ca, USA). The collared foxes were monitored weekly during continuous tracking sessions of 24 hours, or of six hours during the night, and located during the diurnal period each day. A portable spotlight was used to confirm the radiolocation and to observe the behaviour of the individual. The presence of another fox ( $\leq 100$  m, POULLE et al. 1994) and possible interactions were also recorded. We also observed foxes: 1. during night lighting sessions, along a standard circuit (see below), and 2. during den-watching. All observations were made with 10×40 binoculars. Foxes were considered juvenile up to 31 August, subadult between 1 September and 31 December of their first year.

We calculated range overlap between Minimum Convex Polygons (MCP, MOHR 1947) including all locations established in one season, excepting some scarce excursions (ZIMEN 1984). The overlap between two home ranges is presented as the mean of their percentage overlaps (GEFFEN and MACDONALD 1992). We also recorded the number of unmarked foxes seen during tracking sessions or night lighting in the home ranges of the collared foxes. The sex of the individuals could be sometimes determined by the posture when marking (LABHARDT 1990) or the size and shape of the individual.

When two foxes met, we considered that an interaction occurred when the behaviour of one individual influenced in a perceptible way the behaviour of the second one (McFarland 1990). The attitudes during encounters were interpreted using the indications of MECH (1970), ARTOIS (1989), and LABHARDT (1990).

## Density, reproduction, mortality

We estimated the density of foxes in two ways. First, we counted the individuals observed during night lighting sessions once a month on three successive nights along a 30-km representative circuit. Since the

number of foxes seen fluctuated (see WEBER et al. 1991; MEIA et al. 1993 for previous discussions), we have chosen to use seasonal data. The possible changes in the density were calculated using seasonal means, whereas the real density was estimated using the higher number of foxes observed per session in each season: we divided this number by the surface of the study area to obtain a minimal estimate, and by the surface lit up with a spotlight to obtain a maximal estimate. Second, we counted the number of families, i. e. the number of breeding dens used each year (see MEIA and WEBER 1992 for more details).

To estimate annual reproduction, we counted the number of cubs at each breeding den. We evaluated mortality by collecting dead foxes. We also used the body weight of the cubs caught as an indication of their life expectancy.

## Food

Fox scats were collected every month to analyse the diet composition (for detailed methods, see WEBER and AUBRY 1993; FERRARI and WEBER 1995). The density of water voles was estimated in spring, summer and autumn (PASCAL and MEYLAN 1986; WEBER and AUBRY 1993). No trapping occurred in winter because of frozen ground and snow cover. Other food resources (small mammals, domestic stock, earthworms, wild fruits, and exploitable scraps) were measured and their abundance estimated in fixed plots (FERRARI and WEBER 1995).

## Results

## Number of captures, number of observations

Between September 1989 and August 1993, we made 79 captures, corresponding to 64 foxes. We caught 35 females and 29 males; the difference was not significant (Fisher test, p > 0.05). All subadults/adults (15 individuals: four males and 11 females) and 10 juveniles were fitted with a radio-collar; they were monitored between one and 45 weeks. Altogether, we established 18 641 locations during 143 24-hour tracking sessions, 84 6-hour tracking sessions, and 2 670 daily diurnal locations. We have described 1 470 direct observations of foxes including 234 intra-specific encounters.

#### Social organization

## a) Overlap between home ranges

An adult female (F 11) showing a nomadic range use (ZIMEN 1984; MULDER 1985; MEIA and WEBER 1995) has been separated from resident foxes; its range overlapped widely with those of two resident females (Tab. 1). Overlap in resident foxes varied from 0.1 to 58.2% (Tab. 1). The overlap was large ( $\bar{x} = 45.3\%$ , Tab. 1) between foxes with home ranges containing the same breeding den, and small ( $\bar{x} = 3.9\%$ , Tab. 1) between foxes with ranges containing two breeding dens. There was no significant difference (Mann-Whitney U-test, p > 0.05).

Groups	N*	Overlap between home ranges [%]			
		x	sd	min	max
a) Resident-nomadic	4	27.7	6.6	22.1	35.5
b) Resident-resident	9	13.1	19.6	0.1	58.2
same breeding den	2	45.3	18.3	32.3	58.2
different breeding den	7	3.9	3.9	0.1	12.1

Table 1. Overlap between seasonal home ranges (MCP) of subadult/adult foxes.

\* Number of observations

Tracking and night lighting sessions confirmed that several individuals shared the same areas. Results from autumn and winter have not been used to estimate the number of foxes sharing the same areas because these seasons correspond to the dispersal period, which included movements of subadults that could not be morphologically distinguished from adults. We observed up to six additional adults in the home range of the collared foxes, but more frequently between one and three (Tab. 2). No trend of increase/decrease was observed during the study period. We noticed that the same foxes were not seen in two different ranges, unless a favourable feeding patch was present near the boundary (e.g. F25 or M21 groups in spring 1993, when an innkeeper provided food in the small overlapping part of both ranges, Tab. 2).

Individual	Season	Nightlighting		Tracking-sessions			
		N*	individuals	N*	individuals		
F8	spring 92 summer 92	1 -	i	2 2	f, m f, m		
F12	spring 91 summer 91	4 3	F10, F11, i, i F11, f, i	5 4	F10, F11, m, f, i F10, F11, m, f		
F19	summer 91 spring 92	-		3 2	m, f, i m, f		
F24	summer 93	2	F10, i	3	F10, m, f		
F25	spring 93 summer 93	2	i, i	5 3	M21, m "short tail", m, f, i "one-eyed" i "one-eyed", i, i		
F27	spring 93 summer 93	3 2	i, i, i m "scar", i	3 2	m, i, i i, i		
M21	spring 93 summer 93	2 3	i, i F22, i, i	6 3	F25, M11, M12, f, i, i F15, m, f		

 Table. 2. Adult individuals (f, females; m, males; i, not known) observed in the home ranges of the radio-tracked foxes (spring and summer).

\* Number of individuals

## b) Encounters

Although several subadult/adult foxes shared the same area, they were rarely seen together. Collared individuals were observed with another fox in less than 15% of the observations (Table 3). There was no difference in this proportion at den sites (23.1%) and other sites (13.5%) (Fisher test, p > 0.05, Tab. 3). Few differences were noticed between seasons (Fisher test, p > 0.05, Tab. 3). Encounters between more than two individuals were scarce (two foxes: 88.4%, three: 9.3%, four: 2.3%).

Resting sites (especially den sites) were often shared by several foxes which usually went in and out at different times and did not meet. Of the 1282 observations of foxes away from the den site, only 11.8% concerned individuals seen together, and then the foxes ignored each other in more than half the cases (Fig. 1). In those cases, the foxes, up to four, were mainly observed foraging in the same area (47 cases/82) or resting close to each other (12/82). These observations without interaction were more usual in autumn (62.2%), when several subadults still shared the parental range; they were less frequent in winter (30.0%) (Fisher test, p < 0.05).

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Season		Den	Elsewhere		
	alone	with conspecific(s)	alone	with conspecific(s)	
Winter Spring Summer Autumn	6 (85.7%) 14 (66.7%) 0 20 (83.3%)	1 (14.3%) 7 (33.3%) 0 4 (16.7%)	182 (84.3%) 314 (87.2%) 276 (88.5%) 404 (85.8%)	34 (15.7%) 46 (12.8%) 36 (11.5%) 67 (14.2%)	
Total	40 (76.9%)	12 (23.1%)	1176 (86.5%)	183 (13.5%)	





Fig. 1. Observations of foxes (without the observations at a den and the observations with juvenile foxes). Percentages of foxes observed with conspecific(s), percentages of interactions, and percentages of sensu stricto interactions (see text).

There was an interaction between individuals in only 69 cases, between two foxes. As shown in figure 1, we defined two categories. First, we distinguished the "synchronized activities" that concerned situations with two foxes doing the same activity at the same time, often at a very short distance (< 5 m) from each other. In all these cases, the behaviour of one individual seemed clearly to influence the behaviour of the other one: one fox followed the other (11 cases/28), both were foraging side by side (11/28), or fled together (6/28). Second, we recognized several interactions with a succession of attitudes taken alternatively by the two foxes; they were called "sensu stricto (s. s.) interactions" and were aggressive and non-aggressive encounters (24/41), play (9/41), or mating (2/41). The encounters were usually brief and, in most of the cases (20/24), we did not notice any aggressive attitude. In four cases, the encounters indicated the social status of tagged animals.

#### c) Cooperation

We observed adult foxes taking care of the young at 15 breeding dens. In most cases (11/ 15), only one adult (usually a female) was observed rearing the pups. In one case, they were two adults (one female and one indeterminate). In two cases, they were three adults (two females and one male) and in one case five adults (three females, one male, and one indeterminate). Our observations at dens with adults and juveniles (N = 30) showed that one or two adults could rest in the den with the pups (N = 9), but, more frequently, the adults were observed reaching the den site in late afternoon (N = 17). Then they suckled, provided food or guarded the area while the cubs were playing. Only one adult fox was usually observed with cubs (N = 30), even if several adults were seen at the den during the rearing period; in eight cases, we noted that the adults came one after the other. We very rarely observed several adults rearing the cubs at the same time (N = 2). The mother dominated the other vixens at the den (N = 5), other vixens showed typical subordinate attitudes; in three cases they were fightened away by the mother. In three cases, the subordinate vixens were young animals of previous years; they took care of the young, and one of them was observed suckling. No evidence was collected on the relative status of the mother and the father of the pups. The males that we observed at dens played with the cubs, provided food or guarded the area (N = 5). In two cases, radio-tracking showed that an old vixen that had reared young in the past could live in the area of the breeding den without taking part in the rearing process. These females appeared to dominate the other foxes of the area, even though they had lost their breeding status. One of these old vixens was seen mating with the dog of the area, although she did not rear cubs the following spring. Other observations suggested that mating was not limited to one pair of foxes in each group: for example, we saw one male trying to mate with a subordinate female, and we radio-tracked young females that had cubs but lost them in the first weeks after the birth.

#### Food abundance and characteristics of the fox population

## a) Food availability

Water voles were very abundant at the beginning of the study but decreased strongly between 1989 and 1993 (Fig. 2a). Scat analysis showed that the abundance of water voles was correlated with their consumption by foxes (WEBER and AUBRY 1993; FERRARI and WEBER 1995). The decrease in importance of water voles in the fox's diet was accompanied by an increase in the frequency of occurrence of all other food resources, but especially wild fruits and scavengeable items (FERRARI and WEBER 1995).

#### b) Density of foxes

The seasonal means of the number of foxes counted during the night lighting sessions varied between four (winter 91–92) and 19 (autumn 92). We observed some seasonal differences: there were fewer observations in winter than in other seasons due to snow cover in

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winter limiting movements and foraging. The arrival of cubs in spring, moving increasingly until autumn, led to more observations. Overall, no significant changes in density occurred ( $r_s = 0.27$ , p > 0.05, Fig. 2 b). This stability appeared also when counting the number of families each year (1990: 11 families, 1991: 10, 1992: 13, 1993: 11;  $\chi^2$  goodness-of-fit, p > 0.05). The estimates of density (based on night lighting sessions and number of families) lay between 0.4 (minimum estimate) and 3.2 (maximum estimate) individuals per km<sup>2</sup>.

## c) Number of young

Reproduction was stable. The total number of cubs in each year was, respectively, 46, 30, 43, and 43 cubs (Tab. 4). We counted between one and seven cubs/family ( $\bar{x} = 3.98$ , sd = 1.54); there was no difference between years (Kruskal-Wallis one-way ANOVA, p > 0.05, Tab. 4).

Year	N cub*	N fam**	Number of cubs per family			
		-	x	sd	min	max
1990	46	11	4.60	1.51	2	7
1991	30	10	3.75	1.39	2	6
1992	43	13	3.58	1.38	2	7
1993	43	11	3.91	1.81	1	7

Table 4. Number of cubs per family.

\* Total number of cubs

\*\* Total number of families

## d) Mortality

Mortality was difficult to estimate. A few foxes were found killed by traffic or mowing, especially juveniles when the breeding den was close to a road or meadow. The mortality of subadult/adult foxes remained uniform during the whole study period, because hunting pressure remained low. On the other hand, juvenile mortality seemed to increase: body weight of the juveniles caught decreased from year to year, although cubs were captured in the same period ( $r_s = -0.4$ , p < 0.01, N = 51, Fig. 2 c). Our observations showed that the adults had difficulties in providing food for the young when there were fewer water voles. In 1993 we noticed at least two cubs dying of starvation. Dead cubs were usually eaten by siblings.

## Discussion

#### Social organization

In the groups of foxes observed during our study, the home ranges of the individuals did not overlap totally as described by NIEWOLD (1980), HERSTEINSSON and MACDONALD (1982), or MULDER (1985) but corresponded more closely to the situations observed by HARRIS (1980), VON SCHANTZ (1981) and POULLE et al. (1994) who noted that subordinate individuals use only a small part of the group range. There was no (or only a very small) overlap between the ranges of adjacent groups, as most frequently described (SARGEANT 1972; NIEWOLD 1980; HERSTEINSSON and MACDONALD 1982; MULDER 1985; PHILLIPS and CATLING 1991), but it appeared that foxes entered the range of adjacent groups to reach a rich feeding patch (e.g. human food supply), as observed in other areas (HARRIS 1980). Our observations of the relations between group members agree with the descriptions of

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**Fig. 2.** Food abundance and characteristics of the fox population during the study period. a) density of water voles (no trapping occurred during winter); b) number of foxes estimated from night lighting sessions; c) weight of the juvenile foxes.

MACDONALD (1979, 1980, 1981) who noted, as POULLE et al. (1994) and WHITE and HARRIS (1994), that individuals met only rarely. In our area, the relations between group members were less intense than those observed by MACDONALD (1979, 1980, 1981), because the members of a group usually did not meet in the feeding patches, but used them serially. Such behaviour seems advantageous if food resources are homogeneously distributed and quickly renewed (GEFFEN and MACDONALD 1993). This was probably the most frequent situation in our area (voles when abundant, earthworms during favourable nights). It was also indicated by patterns of movement and core areas (MEIA and WEBER 1995). In the few observations of foxes foraging together, we noted that the resources were clumped (group of berry trees, meadow after mowing), as they are in urban areas where several foxes visit a garden at the same time (HARRIS 1980; MACDONALD 1981). Even when rearing the young, or in the resting sites which corresponded to important meeting points (POULLE et al. 1994), foxes did not meet. POULLE et al. (1994) supposed that sharing of resting sites provided the opportunity of direct contacts between group members and thus

played a role in the maintenance of social cohesion within the group. This was probably not so in our area. Resting sites and feeding patches were used in a similar way: foxes shared them if necessary or profitable, even with individuals of adjacent groups, but showed usually no interactions.

Mating was not limited to the dominant pair. This differs noticeably from the descriptions of spatial groups (MACDONALD 1979, 1980, 1981) but agrees with observations on other species, like the European badger (CRESSWELL et al. 1992). Admitting that the simple presence of the dominant leads to "stress" and a decrease of the mating ability of the subordinates (MECH 1970; MACDONALD 1980), explains why all foxes mated when encounters were scarce in the study area. Red fox polygyny was already observed by ZABEL and TAGGART (1989) and suggested by other authors, e.g. VON SCHANTZ (1981). Loss after mating (VON SCHANTZ 1981) probably explains why only one litter per group was seen. Another reason could be a low ovulation rate in subordinate females when food is scarce (CARR and MACDONALD 1986; LINDSTRÖM and LINDSTRÖM 1991). Subordinate females obtain less of the food in the group range than dominant individuals.

Earlier studies of red foxes in mountainous areas (JONES and THEBERGE 1982; BOITANI et al. 1984; BLANCO 1986) did not examine social behaviour in detail, although the situation appears similar to the present study. The social structure of foxes in mountainous habitats has probably remained unclear because of the difficulty in studying it.

#### Stability of the social structure: explaining models

There was no change in the social structure of the fox population, despite a large decrease in the water vole population, although it has been shown that the number of families, the number of juveniles, and/or the number of individuals in groups depend on the quantity of available food (ENGLUND 1980a; KOLB and HEWSON 1980; VON SCHANTZ 1984 b; LINDSTRÖM and LINDSTRÖM 1991).

The Resource Dispersion Hypothesis R.D.H. (MACDONALD 1983; CARR and MACDO-NALD 1986) predicts that the distribution of food patches determines the size of home ranges, whereas the richness of patches determines the number of individuals in the groups. According to this model, there is enough food to have more than one pair of individuals in each range even when water voles are scarce. Thus, ARTOIS (1989) assumes that the habitats of central Europe are very favourable for foxes and contain enough food even when rodents are scarce. Assuming the distribution of food patches in the study area did not change between 1989 and 1993, and that the total quantity of food did not decrease substantially (since excluding some group members was not necessary), this model could explain group formation in our area.

The Constant Territory Size Hypothesis C.T.S.H. (LINDSTRÖM 1980; VON SCHANTZ 1984 a) was proposed for areas with fluctuating resources. In such habitats, the animals chose their territory when resources were scarce and maintained it, accepting conspecifics, when resources became abundant. This model supposes that the fluctuation period of prey is shorter than the life of the predator. As the cycles of water voles are pluriannual (4–8 years), whereas most of the foxes probably do not reach an age of four years, this hypothesis does not work well in our study area. Moreover, there was no change in group size with the decreasing quantity of food. However, there is a delay between prey decrease and effects on predators (ENGLUND 1980 b; LINDSTRÖM et al. 1994) and the effect of food shortage in the study area may not yet have become apparent. We consider, like ARTOIS (1989), this model inappropriate for central Europe, because it focusses on one food resource only, without taking in account the many other resources.

The Territory Inheritance Hypothesis T.I.H. (LINDSTRÖM 1986) predicts that groups form when subadults have difficulty in dispersing because all territories are occupied, and then remain in their parent range without breeding initially, but eventually acquiring re-

productive status. This model could be applied in our study, since we observed subadult females that did not disperse and were helpers in the following years. Later observations (S. MEYER, pers. comm.) showed that these females could finally reach a high rank in the hierarchy and rear their own cubs. Nevertheless, we believe, like ARTOIS (1989) and WOODROFFE and MACDONALD (1993), that this model explains how groups form and are maintained, rather than why groups form or not.

The Prey Renewal Hypothesis P.R.H. (WASER 1981) suggests that when prey is renewed quickly, being territorial is not necessary, and then home ranges can be shared with conspecifics. Our observations are consistent with this hypothesis: we observed that foxes formed groups and we consider that the main prey (water voles, earthworms and exploitable scraps) renews quickly. However, this hypothesis supposes that other criteria ("food patches" or dens) determine the territory, as already emphasized by WOODROFFE and MAC-DONALD (1993), and in this way it should be used in association with R.D.H.

There are two problems in explaining fox social organization. First, social life in foxes is inconspicuous. Second, social life in foxes is very flexible and the hypotheses to explain why foxes can form groups appear to be too limited. Even if the R.D.H. seems to be the best model, the dispersion of resources is probably not the only influencing factor. Environmental and behavioural factors also influence the social life (SAUNDERS et al. 1993). Our work, like other recent studies in carnivore social life (e. g. HOFER and EAST 1993; THURBER and PETERSON 1993), reveals a situation that partially differs from classical descriptions.

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## Zusammenfassung

#### Sozialstruktur des Rotfuchses (Vulpes vulpes) im Schweizer Jura

Von September 1989 bis August 1993 wurde im Schweizer Jura eine Rotfuchspopulation untersucht. Es wurden 64 Füchse markiert und 25 davon mit Radiosendern ausgerüstet. Insgesamt wurden 18500 Peilungen durchgeführt und 1470 Beobachtungen, mit 234 intraspezifischen Begegnungen, beschrieben. Wir haben die folgenden Resultate erhalten: (1) In gebirgigen Habitaten können Füchse in Gruppen leben; (2) Die Gruppen bestehen aus einem Alpha-Paar und einigen Helfern und einer Fähe, die nicht als Helferin auftritt (alte Fähe, die nicht mehr als Mutterfähe wirkt); (3) Obwohl sich die Paarungen nicht nur auf das Alpha-Paar beschränken, wird immer nur ein Wurf pro Gruppe beobachtet; (4) Füchse begegnen anderen Füchsen selten. Wenn sie sich trotzdem treffen, nehmen sie keinerlei Notiz voneinander. Kontakte werden vermieden; (5) Die Sozialstruktur ist viel stabiler als wir angenommen haben. Wir können trotz einer starken Verminderung der Schermaus Arvicola terrestris scherman, die die Hauptbeute des Fuchses in diesem Gebiet bildet, keine Veränderung beobachten. Die "Resource Dispersion Hypothesis (R.D.H.)" ist das beste Modell, um unsere Beobachtungen zu erklären.

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Authors' addresses: Dr. J.-S. MEIA, Rue de la Tour 4, CH-2520 La Neuveville, Switzerland and Dr. J.-M. WEBER, Institut de Zoologie, Université de Neuchâtel, Emile-Argand 11, CH-2007 Neuchâtel, Switzerland.

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