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Journal Article

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Publication date:

2022-01

Permanent link:

<https://doi.org/10.3929/ethz-b-000520162>

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Originally published in:

Applied Animal Behaviour Science 246, <https://doi.org/10.1016/j.applanim.2021.105526>



Exploring the social network of European roe deer (*Capreolus capreolus*) in captivity

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ARTICLE INFO

Keywords:

Roe deer
Social flexibility
Captivity
Social network analysis
Affiliation
Social bonds

ABSTRACT

Socially flexible species might be at an advantage when facing environmental unpredictability, human-induced rapid environmental changes, or unnatural conditions such as encountered in captivity. The European roe deer (*Capreolus capreolus*) was originally described as solitarily living forest-dwelling species. In recent decades, it has expanded its range into urban and agricultural areas forming large aggregations in open habitats. Captive environments are thought to mimic some challenges encountered in rapidly changing habitats, however, to date no study has assessed how roe deer social structure changes in captive conditions. In this study, we explored the social network of a small group of captive and unrelated roe deer over the course of a ten-month period using camera traps. We found that the roe deer established a temporally stable and non-random social network with the buck as the most central and dominant individual. In addition, we analysed affiliative interactions, which have not been described in roe deer yet. We found that the affiliation network consisted not only of preferential associations between the buck and other females, but also between females, whereby a young female played a central role. The seasonal changes in roe deer' gregariousness observed in the wild were also observed in the captive population with an increase in association strength and social interactions in autumn. These results suggest that roe deer kept in a group setting in captivity seem to flexibly adjust their social behaviour; thus, supporting the assumption that roe deer show a high social flexibility that facilitates adaptations to various habitats.

1. Introduction

Living in groups has benefits, such as shared vigilance and dilution of predation risk (e.g. [Beauchamp, 2008](#); [Clark and Mangel, 1986](#); [Roberts, 1996](#)). However, costs are likewise involved (e.g. increased competition for resources, conspicuousness to predators, or disease transmission; [Beauchamp and Ruxton, 2003](#); [Ezenwa et al., 2016](#)). Benefits and costs are likely to vary, e.g. between habitats or seasons. Accordingly, also variation in social organisation is widespread amongst vertebrates ([Hirth, 1977](#)). For example, African striped mice flexibly change their social and reproductive behaviour in relation to environmental conditions ([Schradin et al., 2012](#)). However, some species seem to be very static in their social organisation and are, for example, exclusively found alone and never in pairs or groups, independent of the population density (e.g. chinese water deer: [Dubost et al., 2011](#)).

Social flexibility is defined as the ability to flexibly adjust social behaviours in response to environmental conditions ([Kappeler et al.,](#)

[2013](#); [Schradin et al., 2012](#)). This might lead to a change in the mating system (switch in mating partners), the social structure (increased/decreased social interactions), the social organisation (composition of the group), and may include the entire social system (e.g. pair-living to group-living). It has been hypothesised that social flexibility is an adaptation to unpredictable environments ([Schradin et al., 2012](#)) and might facilitate coping with captive conditions ([Mason et al., 2013](#)).

The European roe deer (*Capreolus capreolus*) is of special interest in the context of social flexibility. Roe deer are small-bodied browsers ([Linnell et al., 1998](#)) and the most abundant cervid species in Europe, despite being heavily hunted each year ([Lovari et al., 2016](#)). Over the course of the last decades, roe deer have successfully adapted to a variety of habitats (i.e. fields, urban areas, mountainous areas; [Ciach and Fröhlich, 2019](#); [Hewison et al., 2001](#); [Lamberti et al., 2004](#)) with varying degrees of predation pressure, suggesting a high behavioural and ecological flexibility in terms of social organisation ([Jepsen and Topping, 2004](#)), vigilance ([Benhaïem et al., 2008](#); [Sönnichsen et al.,](#)

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2013), and spatial behaviour (Bonnot et al., 2013). Furthermore, roe deer exhibit digestive plasticity and show difference in their digestive system depending on the habitat and food they can access (Serrano Ferron et al., 2012). This allows roe deer to flexibly adapt to digesting resources of varying quality while keeping the costs of digestion and rumination low.

Roe deer were originally described as solitary species that gather in small family groups during winter but otherwise avoid each other during the rest of the year (Hewison et al., 1998). Family groups consisting of does with their dependent offspring are the basic social unit (Bideau et al., 1983; Stubbe, 2008). In the last decades, a different social organisation has emerged in the so-called “field roe deer” (Hewison et al., 2001; Maublanc et al., 1987; Zejda, 1978). These roe deer inhabit large agricultural areas with an abundance of high-quality food but little possibilities to hide. They are found in large groups consisting of up to 70 animals (Bresinski, 1982), potentially compensating for a lack of shelter by collective antipredator vigilance (Hewison et al., 2001). These groups seem to form based on environmental conditions, such as population density, disturbances or resource availability (Cibien et al., 1989; Morellet et al., 2013; Villerette et al., 2006), but might also be driven by individual differences in risk assessment (Bonnot et al., 2015, 2018). A varying group composition is found over the course of seasons (Pays et al., 2007, 2012).

Roe deer show only little sexual size dimorphism (Lister et al., 1998) and exhibit a weakly polygynous mating system (Liberg et al., 1998; Vampé et al., 2008). Both sexes display differences in gregariousness across seasons. While mixed-sex groups are found during autumn and winter time, these gradually break up in spring (Maublanc et al., 1987; Villerette et al., 2006), when bucks start to establish their territories and females reduce their home range for giving birth (Hewison et al., 1998). Females do not establish territories but inhabit individual small home ranges, which can overlap with those of other, preferably related, females and several male territories (Biosa et al., 2015; Lovari et al., 2008; Vincent et al., 1983).

While roe deer have been kept in semi-wild enclosures within forests for hunting purposes for decades, they are only rarely encountered in captivity, e.g. in wildlife parks today (Werner, 2004). This is potentially due to their natural behaviour of hiding from visitors (see Morgan and Tromborg, 2007 for a review) and demanding needs in husbandry and enclosure design (i.e. provisioning of fresh browsing material and enclosure design with multiple hiding places; Werner, 2004). Furthermore, roe deer have been reported to occasionally show social intolerance leading to fatal attacks, which are likely a by-product of insufficient space and/or a lack of hiding possibilities to avoid another (Roviani, 2014; Wiesenthal, 1990). Although wildlife parks, research stations, as well as private persons, successfully keep groups of roe deer, there is limited knowledge on their social interactions, which might also be a reason why this species is generally considered as difficult to keep in captivity.

Especially for animals in captivity, which are bound to their given social environment, a functional social network is of immense importance (Morgan and Tromborg, 2007). Consequently, monitoring and understanding the social relationships within groups of captive animals has proven to be an important tool for maintaining social stability and hence the welfare of captive species (Rose and Croft, 2015). Understanding which individuals have preferred social relationships and are central to the cohesion of the group can provide valuable insights for management and husbandry decisions. These include removing or adding animals to a group (Lewton and Rose, 2020; Rose and Croft, 2018) or assigning certain individuals to a sub-group for e.g. breeding purposes.

By utilising social network analysis (Krause et al., 2007; Rose and Croft, 2015), we aimed at gaining an understanding of the social structure of a small group (n = 7) of unrelated roe deer kept at our research station in Switzerland. Camera traps, which have recently been validated for collecting social network data (McCarthy et al., 2019),

were employed to observe the roe deer from an initial introduction of all individuals during the breeding season in July up to spring of the following year. Social interactions as well as proximity between individuals were coded to construct a social network. Furthermore, we aimed at assessing the effect of seasons on changes in roe deer behaviour. Considering that roe deer are thought to be rather flexible in their social behaviour, we hypothesised that the roe deer would quickly adapt to the captive conditions by establishing a social group based on individualised relationships (dyads associating/exchanging social behaviours higher than mean of the group) rather than establishing individual small home ranges while avoiding each other. In addition, we predicted to find changes in social behaviour corresponding to the seasons, with an increase in overall interactions during the gregarious phase.

2. Methods

2.1. Subjects and housing conditions

Seven unrelated European roe deer (*Capreolus caperolus*; 1 male, 6 females) were kept at AgroVet-Strickhof Education and Research Center, site Frübüel, Canton Zug, Switzerland.

All individuals that participated in this study arrived at Frübüel at least 3 months prior to the start of the study and thus adapted to the novel living conditions. Two females were born in the wild, however, one was abandoned as a fawn and subsequently hand-raised while the other doe was found as an adult with injuries and cared for by humans in a wildlife park. All other roe deer were born in captivity. As these were raised in three different wildlife parks, all experienced humans on a daily basis, however, to a different degree (see Table 1 for details). At Frübüel, the roe deer were kept in four separate groups from February–July 2019, which were formed upon arrival of the roe deer (see Table 1). The roe deer were uniquely identified via coloured and numbered ear tags (size: 5×5 cm) and individually characterized via morphological features (i.e. body size, colour of fur, shape of head, antlers). None of the deer were with dependent offspring during the course of the study.

Ten separate enclosures (size: 2100 m² - 2500 m²; total: 20,500 m²), each possible to be combined with one another via gates (4 m width), were constructed at the research station; however, due to management reasons (i.e. haying and silage recovery, construction work within enclosures, limited camera coverage) not all enclosures were used simultaneously. All enclosures are connected via a central corridor (2 m width). A wooden fence of 1.60 m height prevents visual access between enclosures. Each enclosure is equipped with a feeding station (small roofed hut with an elevated feeding stand for pellet food and hay) and a semi-open hut with straw bedding. Natural vegetation is present in all

Table 1

Individual characteristics of roe deer participating in this study. ‘Origin’ denotes the place where the roe deer were born. The reaction to humans was subjectively assessed in their natal environment prior to the transport to the research station. ‘Previous group’ indicates the social group in which they were kept prior to the data collection of the study.

Individual roe deer	Ear Tag color	Sex	Year of Birth	Origin	Reaction to humans	Previous group
Lou/02	yellow	F	2017	A	Avoid	1
Mila/03	green	F	2018	B	Habituated	1
Judy/04	green	F	>2017 [#]	C ^x	Habituated	2
Rena/06	orange	F	2018	D*	Tame	1
Macchio/07	red	M	2018	E	Avoid	3
Frida/09	red	F	2018	B	Habituated	4
Lupita/10	orange	F	2018	B	Habituated	4

Reaction to humans: Tame = readily approach caretakers, allows petting; Habituated = coming close when food is provided; Avoid = very shy, immediate retreat when humans enter enclosure

[#] year of birth is unknown; status of teeth indicates she was born before 2017

^x cared for as adult following injury in the wild

* hand-raised in private home

enclosures (i.e. grass growing in the majority of the area, bushes, trees, shallow and elevated areas). During the course of the study, the roe deer were kept in one to four enclosures providing them with 2100 m² up to 6500 m² of space (see Table 2 for details). Mineralised pellets (GRANOVIT® Zoofeed: visitor pellets herbivores) were provided once a day, while water and hay were available ad libitum. In addition, fresh browse of various local trees was given several times a week, depending on seasonal availability. One of the three animal keepers entered the enclosures daily for providing food and checking on the animals.

2.2. Data collection

The roe deer were temporarily observed via video cameras installed within the enclosures from July 2019 until April 2020. Up to six motion-triggered cameras (Arlo Go, USA; Maginon WK3 HD, Germany) were installed, which recorded for 120 s when triggered. If the camera detected further motion following an event, it retriggered a recording within 10 s. From July–September, two additional cameras were used (Hikvision DS-2TD2615–7, China; Bosch FLEXIDOME IP ultra 8000i, Germany), which similarly recorded clips of 120 s after detecting a motion (see Table 2 for number of cameras per observation period). The cameras were positioned on top of the fence or in trees within the enclosure at a height of 1.5–2 m. On average, five cameras were installed per enclosure (range: 1–6 cameras per enclosure).

The video observations started in late July 2019, when all doors between the four enclosures (1–4) were opened simultaneously. After having opened the doors, the caretakers retracted, in order to avoid affecting the roe deer behaviour by their presence. The cameras were daily collected, and due to improved data management from September onwards on a weekly basis, for transferring the videos to a computer.

Over the course of the observation period, the composition of the roe deer group remained unchanged. Due to management reasons, the roe deer were relocated to different enclosures four times (see Table 2 for available space). This relocation was either done by leaving the doors to the central corridor open, so that the roe deer could explore the novel enclosure by themselves or by having an animal keeper lure the roe deer into a novel enclosure using food.

Videos under low-light conditions (i.e. dawn and night) were discarded as the roe deer could not be identified individually. Furthermore, if a human was inside the enclosures (i.e. experimenter, veterinarian, or animal keeper) or if the majority of roe deer could not be identified on a video (i.e. when being too far away from the camera or moving too quickly), the videos were neither included. If one or two individual roe deer could not be identified in the background, the video was still included, however, coding only the behaviour of the roe deer that could

Table 2

Overview of observation period, including space availability, number of cameras installed in enclosure(s), number of observation days per period and yielded video material.

Season	Period	Available space [m ²]	Cameras	Observation days	Video material [hrs]
Summer	July–August	6490	7	37	48.0
Autumn	September	6490	7	6	8.8
	November	4460	5	15	10.2
Winter	January–February	4210	4	35	25.9
	February	2120	4	9	17.1
	February	2230	4	5	7.3
Spring	March	2480	6	6	10.7
	March–April	4940	6	33	110.4
	April	2460	6	4	14.9
	Mean:	3987	5.4	Total: 150	Total: 253.2

unanimously be identified.

2.3. Ethogram

The proximity between the roe deer was coded undirected (i.e. in proximity or not), while social interactions were coded in a directed way (i.e. coding the sender and receiver per interaction; see Table 3). For the affiliative interactions, we coded how the recipient of the affiliative behaviour reacted (i.e. positive – mutual interest, neutral – no behavioural reaction, negative – avoidance or quick retreat without any agonistic behaviours). In case of agonistic interactions, also submissive behaviours without a previous threat were coded as an interaction (setting the submissive individual as receiver of the agonistic behaviour).

2.4. Analyses

The following behaviours were coded: identity of each visible roe deer, frequency of proximity (0/1), mating behaviours, and affiliative or agonistic interactions (sender, receiver). Furthermore, date, time and the duration of each roe deer being visible were noted.

For the social network analyses, we used SOCPROG (Whitehead, 2009, Version 2.9) and R (R Core Team, 2014, Version 3.5.2), including the packages ‘lme4’ (Bates et al., 2014) and ‘ggplot2’ (Wickham, 2009) for further analyses. Using the proximity data, we constructed an association network. The Half-Weight Index (HWI; Cairns and Schwager, 1987) was used to calculate association strength amongst individuals, as it was not possible to identify all individuals during each observation

Table 3

Ethogram of coded behaviours (see also Video S1).

Category	Behaviour	Description
Association	Proximity	Individuals within 5 m to one another.
	Nose contact	One individual approaches another one and makes nose contact, either to the head or torso region. The receiver of the nose contact either exhibits interest in the sender, shows no behavioural reaction or a negative reaction involving avoidance or retreat.
Affiliative interactions	Grooming	One individual is nibbling the fur of another one with its mouth, usually around the front part of the body (i.e. head and ears). The individual that is groomed either stands still passively (unilateral grooming) or actively grooms back (allogrooming).
	Threat	One individual approaches in slow movements, lowering the head, ears pointing backwards and fixating the other individual. The addressed roe deer quickly retracts in response to a threat (displacement).
Agonistic interactions	Head-butting	Quick forward movement towards another individual with a lowered head aiming at the torso or at the head. The addressed deer is either pushed away and retracts or quickly turns around and answers with a head-butt, resulting in a short pushing contest.
	Anogenital inspection	Buck sniffs and/or licks the genital area of a female. Often followed by flehmen. Can lead to chasing or mounting.
Mating behaviours	Chasing	Buck is directly following a female within 1–10 m distance in fast walk, trot or gallop. Female is running away from buck, sometimes in circles and might stop after some time. Can result in anogenital inspection or mounting.
	Mounting	Buck put his head of the rear end of a female and mounts her with his front legs; the hind legs remain on the ground. Can result in successful copulation or sudden termination if female starts running again.

Source: Adapted from Maublanc et al. (1987) and Espmark (1974).

(video recording). To assess the social differentiation of the group, we calculated the coefficient of variation (CV). A high CV value (~ 0.8) indicates that the probability of dyadic associations varies substantially between dyads, while a low CV indicates (~ 0.2) that dyadic associations are homogenous within the population (Whitehead, 2007). For quantifying preferred and avoided relationships, the observed association indices were compared with an estimated association index for a group of the same size with random associations based on likelihood ratio methods. Using these indices, we ran permutation tests within SOCPROG, increasing the number of permutations until the values stabilised.

Network characteristics, such as strength (sum of association indices of any individual within network), Eigenvector centrality (connectedness between individuals), and clustering coefficient (index for how well the associates are themselves associated), were generated for each individual roe deer. To test for the temporal stability of the association network, we calculated a Lagged and Null Association Rate across all observations. Based on a maximum likelihood estimation, we selected the model with the best fit to our data using the lowest Quasi Akaike Information Criterion (QAIC; Whitehead, 2007).

Two separate interaction networks were constructed, one based on agonistic and the other based on affiliative interactions. We tested for reciprocity in interactions within SOCPROG by using a Mantel Z-test (dyad compared to all others) and Hemelrijk Kr-test (Hemelrijk, 1990) to assess relative reciprocity (dyad compared to other dyads with same sender individual). The dominance structure was explored with de Vries' test for linearity (testing whether winners consistently win agonistic interactions, de Vries, 1995) and the rank of each roe deer within the dominance hierarchy was determined with the modified David's score (Gammell et al., 2003). Linear models (LM) were used for analysing the effect of season (summer, autumn, winter, spring) on associations and occurrence of social interactions. The response variable was corrected for differences in individual visibility by dividing the interaction rate by the observation time. To assess correlations between the association and interaction indices, we ran Mantel Z-tests (1000 permutations). To assess whether the association as well as the social interaction data was correlated with the occurrence of mating behaviours, we ran a Pearson correlation analysis.

3. Results

In total, the cameras recorded 7,609 video clips during daytime (253.2 h of video footage). Of these, we needed to exclude 143 videos due to the lacking identification of individuals. In total, we made 18,210 individual observations with an identification rate of 6.7 individuals per day and an average of 48.8 observations per day. Not all individuals elicited video caption equally often; the proportion of observations per individual ranged from 11.3% to 17.4% of all video recordings (see Supplementary Material for details). The individual observation time ranged from 72 to 116 h (mean \pm SD = 93 ± 18 hrs.; summer: range = 3.8 – 21.3 hrs., mean = 10.9 ± 5.7 hrs.; autumn: range = 3.2 – 5.2 hrs., mean = 4.2 ± 0.8 hrs.; winter: range = 12.4 – 26.7 hrs., mean = 20.0 ± 5.5 hrs.; spring: range = 46.7 – 67.0 hrs., mean = 58.0 ± 8.3 hrs.).

3.1. Association network

The roe deer exhibited individual differences in gregariousness, as some individuals were seen more often alone than others (proportion of observations without proximity to others: range = 0.20–0.37; mean \pm SD = 0.31 ± 0.06). The mean association rate was 0.27 ± 0.03 and the social differentiation of the roe deer population was rather low (CV = 0.388, $r_s = 0.993$; mean HWI: 0.16 ± 0.05 ; range: 0.09–0.29), indicating that dyadic association indices were not homogenous but only slightly differentiated (see Whitehead, 2007 for interpretation of social differentiation values). Females associated more often with the buck than with other females (mean association index \pm SD: M/F = 0.21, F/F =

0.14 ± 0.01). The network measures revealed that the buck was most often in proximity to other females (highest strength), highly connected within the social network (highest centrality), and also the individual with the highest indirect connection to others (reach; see Table 4 and Fig. 1). On the contrary, one female (Judy/04) had only weak direct associations, but was well associated with individuals that were highly connected throughout the group (highest clustering coefficient; see Table 4).

We found an effect of sex and season (Anova: $\chi^2 = 0.61$, $df = 3$, $p < 0.001$) on association strength, but no sex-season interaction (Anova: $\chi^2 = 0.12$, $df = 3$, $p = 0.109$). Accordingly, the buck exhibited a significantly higher association strength than females (LM: 0.38 ± 0.08 , $t = 5.06$, $p < 0.001$; see Fig. 2). Furthermore, the association strength was significantly higher during autumn compared to winter or summer (LM (autumn – winter): 0.24 ± 0.08 , $t = 3.19$, $p = 0.004$; LM (summer – autumn): 0.35 ± 0.08 , $t = 4.71$, $p < 0.001$; see Fig. 2). The association strength did not differ between winter and spring (LM: 0.13 ± 0.08 , $t = 1.73$, $p = 0.097$).

3.1.1. Preferential associations

Based on the association data, we detected preferred and avoided relationships, which differed significantly from the number of expected relationships within a random group of the same size (Permutation tests with 10,000 permutations with 1000 trials: observed/expected: 0.324/0.288, $p = 0.002$); expected number of significant dyads: 1.05; observed number of significant dyads: 12). Twelve out of the possible 21 dyads had significantly higher ($N = 5$ dyads) or lower association indices ($N = 7$ dyads) than expected (see Table 5).

3.1.2. Stability of associations

An analysis of the temporal stability revealed that the association network was not random, but rather based on rapid dispersal with two

Table 4

Network measures for associations (based on proximity), affiliative interactions (based on nose contact and grooming) and agonistic interactions (based on threats and head butts) for each individual roe deer, as well as mean and standard deviation (SD). The highest value per column and measurement is depicted in bold.

Individual roe deer	Strength	Eigenvector Centrality	Clustering Coefficient
Association			
Lou/02	0.81	0.33	0.57
Mila/03	0.95	0.38	0.56
Judy/04	0.90	0.38	0.59
Rena/06	0.91	0.37	0.58
Macchio/07	1.25	0.48	0.46
Frida/09	0.82	0.33	0.55
Lupita/10	0.92	0.36	0.53
Mean (\pm SD)	<i>0.94 \pm 0.15</i>	<i>0.38 \pm 0.05</i>	<i>0.55 \pm 0.04</i>
Affiliative interactions			
Lou/02	43.50	0.14	0.45
Mila/03	133.00	0.46	0.44
Judy/04	96.00	0.36	0.52
Rena/06	166.50	0.52	0.32
Macchio/07	153.50	0.51	0.37
Frida/09	45.50	0.14	0.37
Lupita/10	83.00	0.28	0.41
Mean (\pm SD)	<i>103.00 \pm 49.63</i>	<i>0.35 \pm 0.16</i>	<i>0.41 \pm 0.07</i>
Agonistic interactions			
Lou/02	110.50	0.33	0.52
Mila/03	139.50	0.41	0.47
Judy/04	130.00	0.37	0.46
Rena/06	113.00	0.34	0.52
Macchio/07	156.00	0.43	0.41
Frida/09	150.00	0.44	0.47
Lupita/10	95.00	0.29	0.57
Mean (\pm SD)	<i>127.71 \pm 22.45</i>	<i>0.37 \pm 0.06</i>	<i>0.49 \pm 0.05</i>

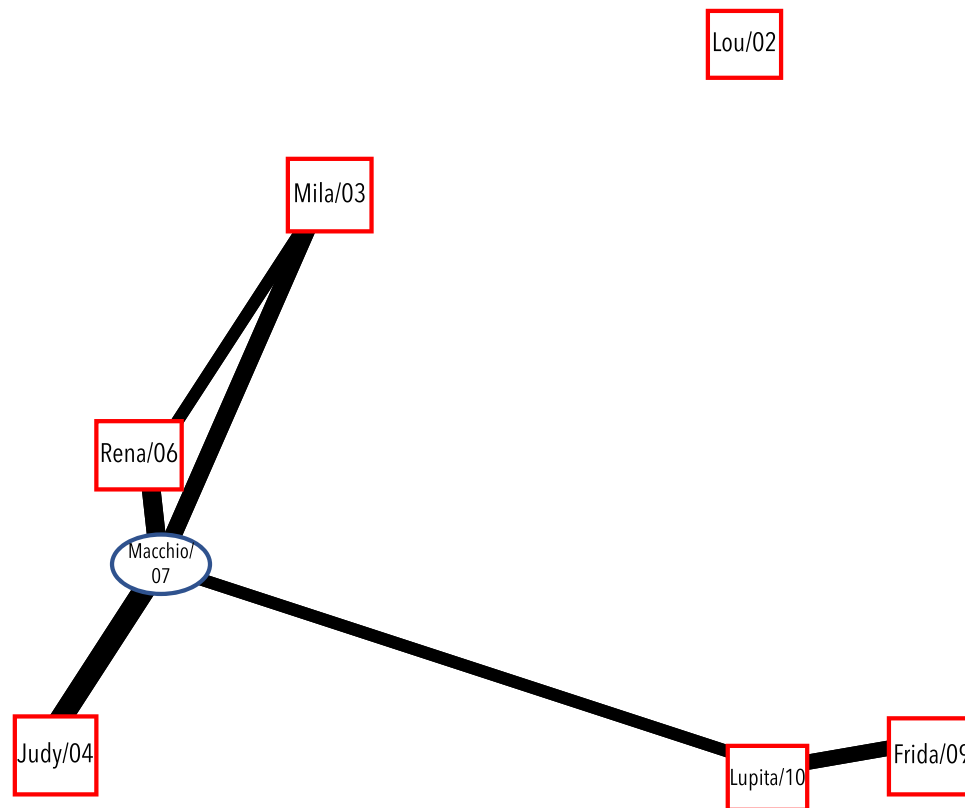


Fig. 1. Sociogram based on undirected proximity counts. Each node represents one roe deer. The shape of the nodes represents the sex (male = circle, female = rectangle). The thickness of lines connecting the nodes reflects the strength of associations (i.e. the more often they were seen together, the thicker the line). The distance between nodes is inversely proportional to the association rate. For simplicity, only association indices above the mean of the group (0.155) are depicted.

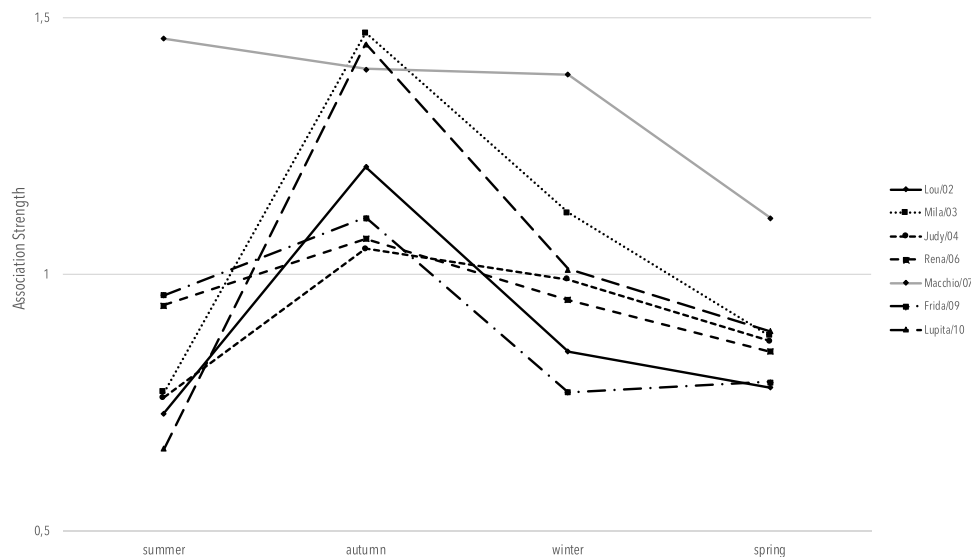


Fig. 2. Strength of associations per individual roe deer across seasons. The buck is plotted in grey, the females in black.

levels of casual acquaintances (see Fig. 3), as the model with $(a3 * \exp(-a1 * td) + a4 * \exp(-a2 * td))^2$ was the best fitting the data with the lowest QAIC value (see Supplementary Material for model selection).

² Parameters of the model are indicated as a1, a2, etc. The timelag is depicted as td (see Whitehead 2008).

3.2. Social interactions

We observed 1,615 social interactions during the course of the study. Of these 721 were affiliative interactions (44.6%) and 894 agonistic interactions (55.4%; see Video S1 for examples of agonistic and affiliative interactions). The majority of affiliative interactions were nose contacts (61.9%), while grooming was observed less often (38.1% of all affiliative interactions). Nose contact resulted in negative behavioural reactions (i.e. threat or retreat after initiating contact) in 24.7% of cases,

Table 5

Preferential associations based on Permutation tests. Association indices (based on Half-Weight index) are presented per dyad. Preferred associations are highlighted in light grey, avoided associations are highlighted in dark grey.

	Lou/ 02	Mila/ 03	Judy/ 04	Rena/ 06	Macchio/ 07	Frida/ 09
Mila/03	0.15					
Judy/04	0.10*	0.15				
Rena/06	0.11	0.16	0.14			
Macchio/ 07	0.15***	0.23	0.29***	0.25		
Frida/09	0.14***	0.13	0.10	0.09**	0.15***	
Lupita/10	0.15*	0.13**	0.12*	0.14**	0.17***	0.21***

*** $p < 0.001$,

** $p < 0.01$,

* $p < 0.05$

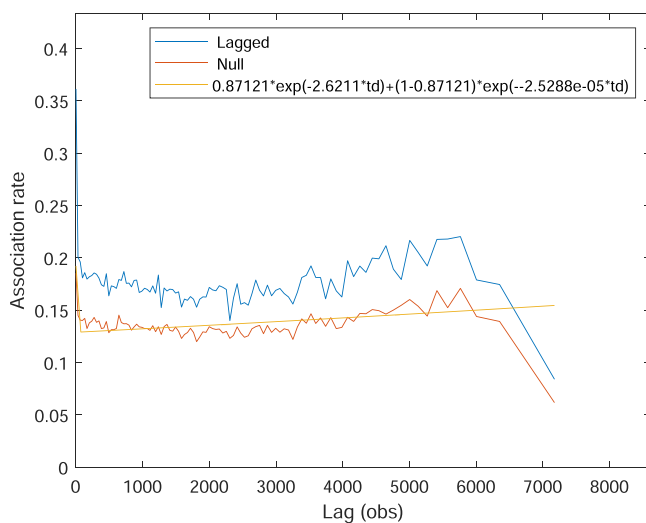


Fig. 3. Lagged (blue) and Null (red) association rates plotted over observations and compared to a fitted model (yellow). The lagged association rate is higher than the null association rate (based on random associations), thus, indicating that associations amongst roe deer were not random. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

in neutral reactions (no behavioural reaction from receiver) in 43.5%, and in positive reactions (i.e. mutual interest) in 31.8% of all observed nose contacts. More allogrooming was observed (61.5%) compared to unilateral grooming (38.5% of all grooming). Nose contact and grooming were positively correlated with each other (Pearson: $r_s = 0.42$, $p = 0.006$).

Supplementary material related to this article can be found online at [doi:10.1016/j.applanim.2021.105526](https://doi.org/10.1016/j.applanim.2021.105526).

3.2.1. Mating behaviours

In the time from 23rd of July to the 27th of August, mating-related behaviours between the buck and various females were observed. In total, 215 mating-related behaviours were recorded (182 chase, 25 inspect, 8 mounts, and 4 successful copulations). The buck displayed more mating-related behaviours towards certain females (i.e. Rena/06: 40.0%; Mila/03: 20.0%; Judy/04: 18.6% of all recorded mating-related behaviours) but showed interest in all of the females within the group, although with a lower frequency (e.g. Lupita/10: 3% of all mating behaviours). We found that association rate (HWI; Pearson: $r_s = 0.89$, $p = 0.016$) and rate of affiliative interactions ($r_s = 0.91$, $p = 0.012$) during summer season were positively correlated with the frequency of mating-related behaviours. The rate of agonistic interactions during summer season tended to be negatively correlated with the amount of

mating-related behaviours ($r_s = -0.80$, $p = 0.054$).

3.2.2. Interaction networks

The network based on agonistic interactions revealed that the buck emitted the most agonistic behaviours (highest strength; see Table 4). Frida/09 had the highest direct connection to other agonistic individuals within the group (highest Eigenvector centrality; see Table 4). Lupita/10 on the other end, barely emitted any agonistic behaviours (lowest strength), but was well connected to other individuals that frequently exchanged agonistic interactions with the rest of the group (highest clustering coefficient; see Table 4 and Fig. 4A). Agonistic interactions were most often directed from the buck towards other females (mean interaction rate: M-F: 51.33), while agonistic interactions occurred less often between females (mean interaction rate \pm SD: F-F = 19.40 ± 9.75). Almost no agonistic behaviours were directed towards the buck (mean interaction rate: F-M = 0.67).

In the affiliation network, we found that Rena/06 emitted the most affiliative behaviours towards others (strength) and had the highest direct and indirect connection to others within the group (Eigenvector centrality; see Table 4 and Fig. 4B). On the contrary, Judy/04 showed only little affiliative behaviours with others, but was well connected to highly affiliative individuals that had a high connection throughout the population (highest clustering coefficient; see Table 4). The least involved in affiliative interactions was Lou/02 indicated by the lowest strength. The majority of affiliative behaviours were directed towards the buck or elicited by the buck; less affiliation was observed amongst the females (mean interaction rate \pm SD: grooming: F-M = 11.67; M-F: 5.50; F-F = 5.73 ± 7.63 ; nose contact: F-M = 19.33, M-F = 14.67, F-F = 8.07 ± 1.99).

3.2.3. Effect of season on social interactions

We found a main effect of season on the occurrence of social interactions (Anova: $\chi^2 = 7.85$, $df = 3$, $F = 3.87$, $p = 0.014$). Accordingly, more social interactions occurred during the winter and spring time compared to summer season (LM: summer-autumn: 0.05 ± 0.31 , $t = 1.64$, $p = 0.108$; summer-winter: 0.71 ± 0.31 , $t = 2.33$, $p = 0.024$, summer-spring: 1.01 ± 0.31 , $t = 3.30$, $p = 0.002$; see Fig. 5). Both affiliative and agonistic interactions occurred equally often (LM: 0.31 ± 0.22 , $t = 1.41$, $p = 0.164$) and we could not detect a difference between types of interaction and season (Anova: $\chi^2 = 0.63$, $df = 3$, $F = 0.31$, $p = 0.819$).

3.2.4. Dominance hierarchy

The roe deer exhibited a significant linear hierarchy (de Vries h: 0.786 , $p = 0.034$ with 1000 permutations) with the buck being the most dominant individual (see Table 6 and Table S1 for David's scores across seasons).

3.2.5. Reciprocity of interactions

Affiliative interactions were reciprocated (Mantel Z-test (absolute reciprocity): $p < 0.001$); Hemelrijk Kr-test (relative reciprocity): $p < 0.001$); whereas agonistic interactions were not reciprocated (Mantel Z-test (absolute reciprocity): $p = 1.000$); Hemelrijk Kr-test (relative reciprocity): $p = 0.995$).

3.2.6. Correlations between network measurements

The association and affiliation rates were positively correlated with one another (Mantel Z-test: $p < 0.001$, $r_s = 0.68$), while the association rate and agonistic interactions were not correlated (Mantel Z-test: $p = 0.806$, $r_s = -0.03$). Accordingly, animals that spent more time in close proximity to each other also exchanged more affiliative interactions, while animals that had many agonistic interactions did not avoid each other's proximity. Also, the affiliation and agonistic networks were negatively correlated (Mantel Z-test: $p = 0.034$, $r_s = -0.24$), suggesting that animals that exchanged many affiliative interactions only rarely had agonistic encounters with each other.

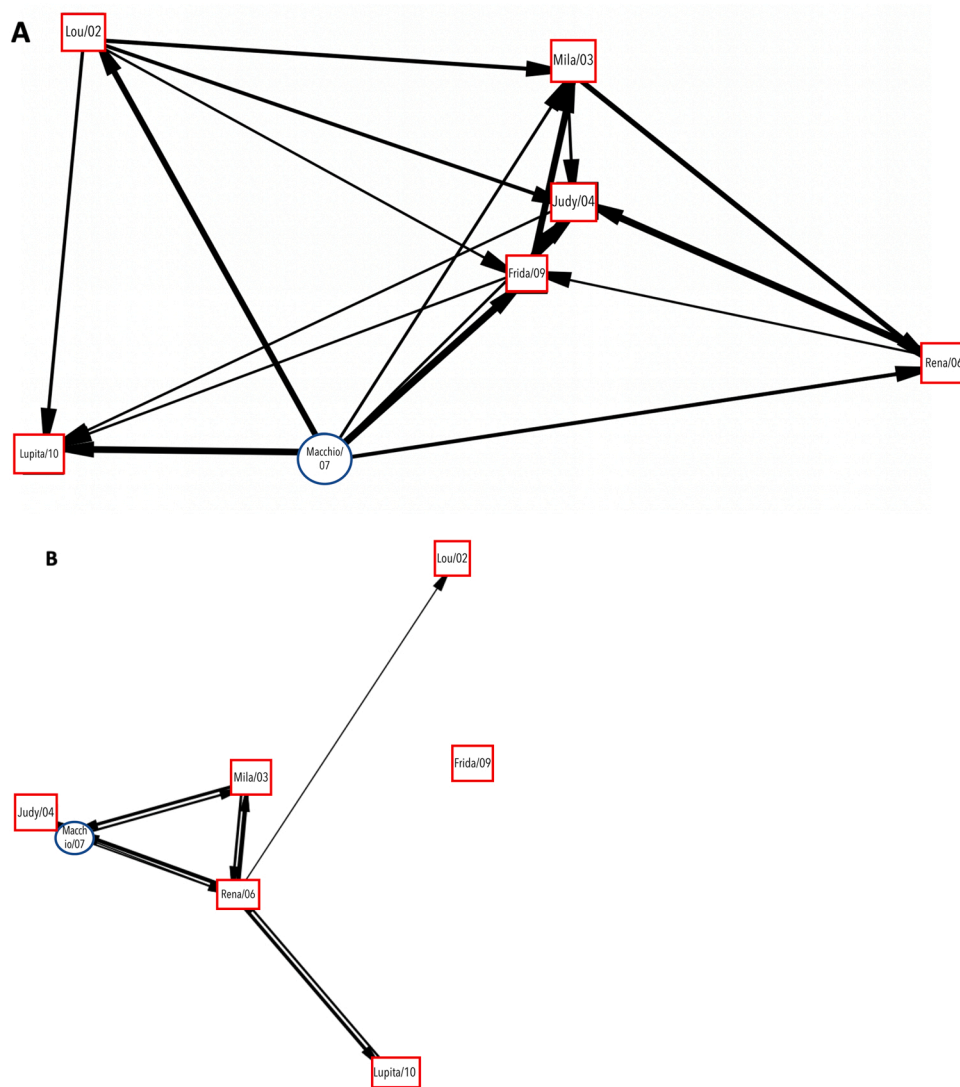


Fig. 4. Sociograms based on directed A) agonistic interactions and B) affiliative interactions. Each node represents one roe deer. The shape of the nodes represents the sex (male = circle, female = rectangle). The thickness of lines connecting the nodes indicates the strength of the interaction rate (i.e. the more often they were interacting, the thicker the line). The distance between nodes is inversely proportional to their interaction rate. Arrows point from the emitter of the behaviour towards the recipient. Only interaction rates above the mean of the group are depicted.

4. Discussion

Our observations of a small group of roe deer in captivity revealed that they formed a non-random social network with individualised relationships. The roe deer exhibited differences in individual gregariousness, and compared to other closely related deer species, such as the Chinese water deer, *Hydropotes inermis* (Dubost et al., 2011), and moose, *Alces alces* (Houston, 1974), which did not form individualised relationships in captivity, the roe deer established a stable social structure in the ten-month observation period. As expected for a seasonally gregarious species, the group cohesion was rather low. However, the social structure was different from a completely homogenous population. Furthermore, the lagged association analysis revealed that the social associations were stable across the ten-month observation period. Temporal association rates were based on two levels of casual acquaintances (Whitehead, 2007), suggesting that certain individuals preferentially associated for some time before breaking up and reuniting again later on, similar to the fission-fusion dynamics reported in field roe deer (Pays et al., 2012). The buck played a central role in the association network and almost all females (with the exception of Lou/02) were well connected with either the buck and/or the other females. Interestingly, avoided relationships were observed amongst the buck and individual females as well as between females. While the formation of close relationships between bucks and females has been observed earlier

(Maublanc et al., 1987), relationships amongst females have not been described yet. In general, it has been hypothesised that adult females are less sociable than adult males (i.e. from October to January) as they have dependent offspring with them (Villerette et al., 2006). This fact might lead to socio-spatial intolerance between females, in particular in spring and summer (Maublanc et al., 2012). Nonetheless, it needs to be noted that none of the available studies assessed affiliative interactions, but are rather based on agonistic interactions. In our group of roe deer, social preferences amongst the females were clearly present: out of the possible 42 dyads, five dyads exhibited a preferred relationship (4 F/F, 1 F/M) and seven dyads avoided relationships (4 F/F, 3 F/M). According to the *tend-and-befriend* hypothesis (Taylor, 2006), affiliation between animals (i.e. females) is an adaptive strategy to cope with stress (e.g. geese: Scheiber et al., 2009; baboons: Wittig et al., 2008). Other studies have likewise emphasised the importance of social bonds as a way to buffer stress (see Kikusui et al., 2006; Rault, 2012 for reviews on various species). While these studies were based on species that live in permanent social structures, in contrast to roe deer with its seasonal changes in sociality, they, nonetheless, suggest that the mechanisms involved in female associations might be similar across species. Consequently, the formation of social relationships and increased general social tolerance between the female roe deer might be an adaptive response to the restricted space associated with captivity and/or might have been facilitated by the fact that none of the females had offspring during the

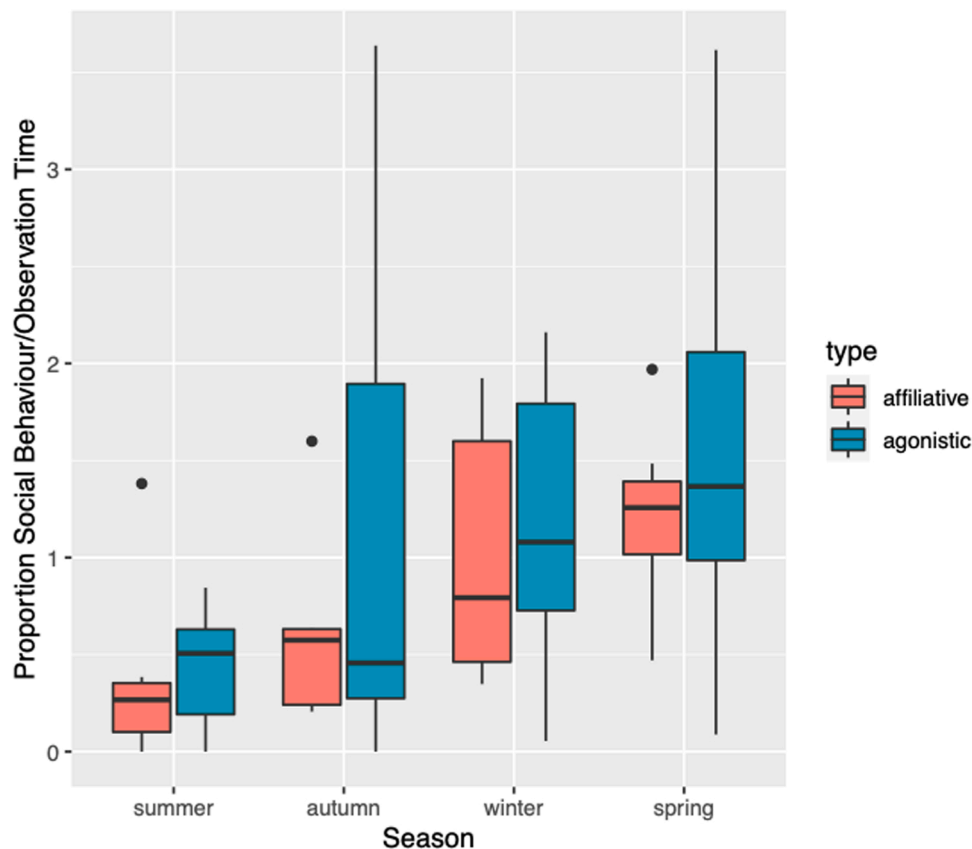


Fig. 5. Social behaviours (affiliative = red, agonistic = blue) corrected by individual observation time across seasons. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Table 6
Individual ranks within dominance hierarchy, based on modified David's score.

Rank	Individual roe deer	Sex	Modified David's score
1	Macchio/07	M	19.85
2	Lou/02	F	6.03
3	Rena/06	F	3.38
4	Mila/03	F	0.12
5	Frida/09	F	-4.87
6	Judy/04	F	-5.83
7	Lupita/10	F	-18.68

course of the study and that feeding competition was lacking as unlimited resources were provided. Contrary to a previous study on captive roe deer (Mertens and Turner, 1983), we found limited indication for an effect of familiarity on social preferences. One dyad consisting of familiar females (Frida/09 and Lupita/10) exhibited a preferred relationship with the highest association index found amongst female dyads; however, also unfamiliar females formed preferred associations, while other familiar females did only form non-preferred associations. Furthermore, we observed great inter-individual differences in social behaviour. While some females (i.e. Rena/06 and Mila/03) exchanged many social interactions, other females were either barely involved in social interactions and seemed to associate little (i.e. Lou/02) or were involved predominantly in agonistic interactions and associated only with specific deer but not the rest of the group (i.e. Frida/09). Unfortunately, with our dataset, we could not disentangle whether individual rearing histories influenced the roe deer' behaviour (e.g. Rena/06 was hand-raised, which might have affected her social behaviour) or rather personality differences in sociality exist in roe deer. Potentially, these individual differences in gregariousness and group composition (i.e. in terms of age, relatedness, sex) play an important role in the overall

behaviour of different captive groups (Maublanc et al., 2018; Mertens and Turner, 1983).

4.1. Seasonal changes in social behaviour

In the wild, roe deer form seasonal aggregations in winter consisting of one family unit, one adult buck, and sometimes a subadult male (Danilkin, 1995). In more open habitats these units aggregate into bigger groups, consisting of individuals of different sex and age classes (Villerette et al., 2006). During mating season in spring and summer, does and bucks mostly remain solitary. Interestingly, we likewise observed these seasonal changes in gregariousness in our captive group with an increase in association strength and social interactions during autumn and winter. During summer, the association strength was rather low, which might be explained by the re-grouping at the beginning of the observation period and/or by naturally reduced sociality during the mating season. The strength of associations began to peak in autumn, which also corresponds to the natural beginning of gregariousness in wild populations, but afterwards seemed to decrease again in winter and following spring. In particular, during the mating period in summer, the buck had a more central position while becoming less central during the rest of the observation period (autumn – spring). This observation is in line with the social behaviour of bucks in the wild, as they establish territories and engage in mating behaviours with various females, while joining groups of females during the gregarious phase in autumn and winter (Liberg et al., 1998). In addition, the number of social interactions increased during the roe deer' gregarious phase in autumn and winter, similar to reports of other wild and captive populations (Maublanc et al., 1987; Mertens, 1984). Again, this might be linked to the general increase in gregariousness during the winter period and the resulting potential for more social interactions (i.e. for the establishment

of social relationships across time). Our conclusions need to be taken cautiously, as we collected data only for one cycle of seasons and there was some variance in observation time per season.

4.2. Affiliation and agonistic interactions

Overall, we observed more agonistic than affiliative interactions. While the majority of agonistic interactions per individual were initiated by the buck (35%, mean females: 11%), affiliative interactions were initiated equally often by both sexes (buck: 17%, mean females: 14%) and directed towards same- and opposite-sex partners. Interestingly, this high rate of affiliative interactions observed amongst the females is not in line with previous findings, which reported that females are generally less sociable than males (Villerette et al., 2006). Furthermore, we found that the association network significantly correlated with the affiliation network, but not with the agonistic network. This might indicate that the roe deer maintained close spatial contact with those individuals with whom they exchange many affiliative interactions; consequently, suggesting that the observed affiliative interactions are indeed a form of socio-positive contact. In addition, these results are supported by the buck's differential investment into females during mating season in summer. We found that the buck directed more mating-related behaviours towards females that he was often seen associating with and that he exchanged many affiliative behaviours with outside the breeding season. Females that received more agonistic behaviours from the buck tended to also receive less mating-related behaviours. Nonetheless, given the current data, we cannot discern the causation of this correlation as affiliative interactions might be a by-product of close proximity or vice versa. The lack of a correlation between association network and agonistic network suggests that they did not actively avoid proximity to less preferred individuals, however, this might also be a by-product of the captive conditions (i.e. limited space to establish non-overlapping home ranges). The affiliation and agonistic networks were negatively correlated with another. Individuals that exchanged frequent affiliative behaviours were less involved in agonistic interactions with each other. Indeed, affiliative behaviours were reciprocated suggesting that a mutual exchange in affiliative behaviours results in building up a favourable relationship. Agonistic interactions, on the contrary, were not reciprocated, as expected in a linear dominance hierarchy (Espmark, 1974). These connections between network measurements indicate that the measurements of proximity, affiliation, and agonism, indeed are valid for describing the social structure of roe deer.

4.3. Captivity and behavioural flexibility

Recently, it has been hypothesised that species that are able to efficiently cope with captive conditions are also better in adapting to human-induced environmental changes (Mason et al., 2013). Roe deer populations are thriving in fragmented habitats (Jepsen and Topping, 2004) and seem to expand their habitat into urban areas as well (Ciach and Fröhlich, 2019). Furthermore, it has been described that roe deer flexibly adjust their vigilance behaviours and activity patterns to hunting pressure (Benhaïem et al., 2008; Bonnot et al., 2013); thus, suggesting that this species can effectively cope with human-induced changes. The roe deer in our study were not related with each other and of different age classes. Since they formed a temporally stable social network in the ten-month observation period, we propose the latter as a sign of behavioural flexibility towards captivity, indicating that roe deer can quickly adapt to novel situations (including i.e. limited space, artificial group composition, lack of offspring, food abundance) and adjust their social structure accordingly as long as only one adult buck is present within the group.

Future studies on other captive populations with more variable group structures (i.e. related females and different age classes) and across multiple seasons are required in order to validate our results. Furthermore, it will be very interesting to investigate the social network

of wild populations living in different habitats (i.e. field and forest roe deer), in order to find out whether the associations and relationships observed in this study are a way of coping with captivity.

5. Conclusions

Roe deer establish an individualised social structure in captivity, if the environmental factors are kept constant. The ability to cope with captivity, potentially by forming a social network and, thus, sharing vigilance behaviours or buffer stress, suggests that roe deer possess enhanced behavioural flexibility. Being able to quickly adapt to novel situations and circumstances likely facilitated the biological success of roe deer in modern agricultural and urban habitats.

Ethics statement

This study complies with the international guidelines of animal welfare and was approved by the Veterinary Office of the Canton Zug (ZG 104/20).

Author contributions

Désirée Brucks: Conceptualization, Methodology, Investigation, Analysis, Writing - original draft, review & editing; **Barbara Drews:** Conceptualisation, Writing - review & editing; **Susanne E. Ulbrich:** Conceptualization, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors have no competing interest to declare.

Acknowledgements

We are grateful to the AgroVet-Strickhof staff at Frübüel - Claudio Bowald, Dennis Fieber and Florian Kutzli - for taking care of the roe deer and providing technical support. Furthermore, we want to thank Louise Martin for ensuring the health of the roe deer by providing veterinary responsibility and support. And finally, we want to thank Sébastien Goumon for helpful discussions and feedback on the manuscript. The study was financed through core funding of the Animal Physiology Group at ETH Zurich.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.applanim.2021.105526](https://doi.org/10.1016/j.applanim.2021.105526).

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