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Quantifying group size in the red fox: impacts of definition, season, and intrusion by non-residents

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Short title

Defining red fox social groups

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Abstract

Determining group membership is fundamental to studies of social behaviour and monitoring population changes. However, this can be challenging for ecologically-important solitary-foraging carnivores such as red foxes, which have flexible social systems. We used camera-traps to quantify seasonal changes in rates of territory intrusion by non-residents and compared group definitions based on shared space use (spatial overlap) and social encounters (spatiotemporal overlap). Group sizes based on spatial overlap were overestimated but incorporating a minimum number of sightings (sighting threshold) improved accuracy. Groups defined by spatiotemporal overlap were similar in size to those based on spatial overlap with a sighting threshold but included different individuals, highlighting the challenges of determining group membership. Groups were smallest in spring and summer and largest in autumn and winter because all definitions failed to exclude non-residents during the mating and dispersal seasons. However, non-residents were recorded year-round: over half were known or probable neighbours, and so may be relatives of territory residents. Strangers were most common in winter, when non-residents were more likely to be males in search of extra-group copulations. We conclude that groups of territorial, solitary foragers may be defined more accurately by combining patterns of space use, sighting frequency and social connectivity rather than considering these measures in isolation. When social information is not available, spatial overlap measures should include a sighting threshold. Surveying several adjacent territories concurrently helps identify the origins, and motivations, of non-resident visitors.

Introduction

Group size is the most obvious feature of sociality and a key measure of social complexity (Whitehead, 2008). It is also a fundamental parameter in many population studies (e.g. Harris, 1981; lossa *et al.*, 2009). For obligate social species, groups are usually spatially isolated and can be defined using shared space use and/or social behaviour (Gese, Rongstad & Mytton, 1988; Hennessy, 2007; le Roux *et al.*, 2009). While similar techniques have been used to define groups of facultative social species, the meaning of a 'group' varies widely. For instance, terms such as 'spatial group' have been applied when individuals with overlapping home ranges, and hence shared space use, spend little time socialising (Wagner, Frank & Creel, 2008; Martin *et al.*, 2013).

Red foxes *Vulpes vulpes* are solitary foragers, but form groups of \geq ten adults at high population densities because there are limited opportunities for dispersers to establish their own territory (Baker *et al.*, 1998; lossa *et al.*, 2009). This social flexibility makes it difficult to determine the membership of fox social groups, and is further complicated because neighbouring territories overlap as population density increases (Trehwella, Harris & McAllister, 1988; Baker *et al.*, 2000; Potts *et al.*, 2013). However, despite the challenges, it is essential to be able to quantify red fox group size and inter- and intra-group movements to improve management strategies for such a widespread (Schipper *et al.*, 2008) and economically- and ecologically-important species (Webbon, Baker & Harris, 2004; Saunders, Gentle & Dickman, 2010; Fleming *et al.*, 2017; Radford *et al.*, 2018).

Although social relationships are an obvious consideration, hitherto red fox group size estimates have been based on capture and/or space use data (Harris, 1981; Harris & Rayner, 1986; Poulle, Artois & Roeder, 1994; Baker *et al.*, 1998, 2000; lossa *et al.*, 2009).

These techniques limit the accuracy of group-size estimates because low capture rates and infrequent recaptures make it difficult to identify all the members of a social group, and to monitor the rates of territorial intrusion by non-group members (Baker *et al.*, 2001; Soulsbury *et al.*, 2011), which can lead to population density being overestimated (Sutherland, Elston & Lambin, 2013). While camera traps have great potential to compile individual sighting histories, thus far they have not been used to define red fox group sizes and composition (Sarmiento *et al.*, 2009; Bengsen, 2014; Ramsey, Caley & Robley, 2015).

To further our understanding of the social structure of red foxes, we used camera traps to compare three commonly-used methods of defining social group size in mammals. In particular, we quantified seasonal variation in fox group size, and patterns of territory intrusion by non-residents. We addressed the following hypotheses: (i) group size is largest when based on space use alone due to non-residents making extraterritorial movements (Baker *et al.*, 2001; Soulsbury *et al.*, 2011); (ii) group size estimates are smallest, and most realistic, when based on social connections because foxes avoid encounters with non-group members (White & Harris, 1994); (iii) groups are largest in autumn prior to the onset of dispersal (Baker *et al.*, 2007; Soulsbury *et al.*, 2008); (iv) territory intrusion is highest in winter when males seek extra-group copulations (Soulsbury *et al.*, 2011); and (v) non-resident visitors are usually neighbours from surrounding territories as home ranges often overlap in *Vulpes* species (Baker *et al.*, 2000; Eide, Jepsen & Prestrud, 2004; Kitchen *et al.*, 2006; Darden, Steffensen & Dabelsteen, 2008).

Methods

Study area and data collection

Data were collected from July 2013 to May 2015 in seven urban fox territories (groups) in 1.5 km² of northwest Bristol, UK (Table S1). It is the site of an intensive study covering four decades and there is a long-term record of population density and social group structure based on radio-tracking, capture-mark-recapture (CMR) and sighting data (Baker, Newman & Harris, 2001; Baker *et al.*, 1998, 2000, 2001, 2004; Iossa *et al.*, 2009). In each territory we conducted four to six camera trap surveys for 40 consecutive days in each of four seasons in gardens (food patches) where householders already provisioned the foxes \geq twice weekly (Table S1), usually with household scraps and/or dog food. To avoid influencing fox behaviour, we only used gardens where the householders had an established history of provisioning the foxes and, if their feeding practices changed during the study, that garden was eliminated in subsequent seasons. Hence the number of camera traps varied between seasons in some territories (Table S1, Fig. S1); for full details see Dorning & Harris (2017).

Seasons were spring (March-May: birth, early cub-rearing), summer (June-August: late cub rearing, onset of juvenile independence), autumn (September-November: onset of dispersal), winter (December-February: peak dispersal, mating). In each territory, camera trap surveys covered ~44 % of each season.

We used one camera trap (ScoutGuard SG565F-8M, Boly Media Communications, Inc., USA) per garden set 40-70 cm above ground overlooking the provisioning area. Cameras were active continuously and recorded a burst of 1-3 photos per motion-triggered event. Batteries and memory cards were changed weekly. Despite repeated exposure, we found no evidence that foxes were adversely affected by the flash or noise of the camera traps

e.g. changes in time spent at the feeding point, removing food to eat elsewhere, or changes in behaviour over the course of the 40-day trapping period.

To ensure consistency and accuracy, foxes were identified by one person (JD) using a combination of physical features on various parts of the body; the types and locations of identifying features varied between foxes. We compiled individual identification sheets for each season showing key features under different lighting conditions to aid identification and account for temporal changes in appearance. Morphological features were combined with spatiotemporal information: we grouped photos by territory and viewed them in chronological order, and recorded each fox as either new, a known animal, or unidentifiable. JD was able to identify the individual fox in 99 % of photographs; the remainder could not be identified due to poor image quality or because key identifying feature(s) were not visible. In blind tests, JD achieved 99% agreement between fox identifications (Dorning, 2016; Dorning & Harris, 2017). Data were managed in Camera Base v. 1.6 (Tobler, 2013). Since foxes are primarily crepuscular/nocturnal (Saunders *et al.*, 1993; Caravaggi *et al.*, 2018), 'days' started and ended at noon to ensure independent sampling.

Determining group size

We compared spatial overlap (SO), spatial overlap with a minimum number of sightings (hereafter sighting threshold; SOST) and spatiotemporal overlap (STO) as three potential methods to determine group size for each season; see Table 1 for details and the rationale for each method. We only included foxes > 5 months old because the movements of younger animals were restricted to limited parts of their natal range (Robertson, Baker & Harris, 2000). For SOST, we selected a sighting threshold of 20 survey days rather than the

number of patch visits to exclude individuals that made multiple visits on a few nights. This sighting threshold marked a discontinuity in sighting frequency (Fig. S1) and we considered individuals to be non-residents if they were sighted in a territory on fewer than 20 days in a 40-day survey period.

Social networks can be constructed using either interactions or associations (Whitehead, 2008); photographs are instantaneous records of associations and can be more informative if interactions are rare or difficult to observe (Farine, 2015). According to the 'gambit of the group' approach (Whitehead & Dufault, 1999), animals are associated in situations where interactions could occur. In our study, most gardens were < 25 x 25 m (White & Harris, 1994), and their open nature (predominantly lawns, ornamental flowerbeds) would ensure physical, visual, olfactory and/or auditory interactions between co-occurring visitors.

Photographs of individuals visiting a patch were first grouped into independent visits based on a time interval threshold of 15 mins i.e. a gap of more than 15 mins between photographs of an individual was considered to indicate separate visits by that fox (Dorning & Harris, 2017). This threshold was derived by plotting the time interval between consecutive photographs of each individual in each season; see Fig. S2 for an example. The times of the first and last photo in each visit were used to determine spatiotemporal associations between dyads. Unlike the 'chain rule' method (Mann *et al.*, 2012; Best, Blomberg & Goldizen, 2015), this ensured that all associations were real rather than assumed. We recorded solitary visits as 'self-associations'. The date-time of each association was half-way between the start and end time of a visit for a self-association and half-way between the start and end time of dyadic overlaps. Association data from each territory and season were converted into matrices in SOCPROG v.2.6 (Whitehead, 2009).

Data were input in dyadic format so, if an individual associated with > 1 conspecific during a patch visit, each dyadic association was recorded on a separate row.

We used the simple ratio index (SRI) to estimate the proportion of time each dyad spent associated, scaled from 0 (never observed together) to 1 (always observed together):-

$$SRI_{AB} = \frac{x}{x + Y_{AB} + Y_A + Y_B}$$

where x is the number of sampling periods in which individuals A and B were associated, Y_{AB} is the number of sampling periods in which A and B were identified but not associated, and Y_A and Y_B are the number of sampling periods in which only A or B was identified (Ginsberg & Young, 1992). The SRI is statistically unbiased if, as here, all associates and individuals were equally likely to be identified whether associated or alone (Ginsberg & Young, 1992; Whitehead, 2008).

Association matrices were exported to Netdraw (Borgatti, 2002): nodes (foxes) were connected by edges (lines) with edge weight (thickness) proportional to the SRI. Spring-embedding from random start positions was used to determine optimal node arrangement; this places nodes with strong SRIs closer together.

Statistical analyses

Data were analysed using mixed models fitted by maximum likelihood in R version 3.2.4 using *lme4* version 1.1-11 (Bates *et al.*, 2015). We selected the best model error structure based on AICc i.e. corrected for small sample size (Burnham & Anderson, 2002). We used a Poisson generalized linear mixed model (GLMM) with a log link function to compare group

sizes between seasons: territory ID was included as a random effect to account for repeated measures. The data were under-dispersed (deviance/residual degrees of freedom = 0.58), but negative binomial models run using *glmmADMB* version 0.8.3.3 (Fournier *et al.*, 2012; Skaug *et al.*, 2016) did not fit the data better (Poisson $AIC_{C13} = 422.3$, negative binomial type 1 (quasi-Poisson parameterisation) $AIC_{C14} = 425.3$, negative binomial type 2 (standard negative binomial parameterisation) $AIC_{C14} = 426.0$). So we considered Poisson a suitable error structure and used likelihood ratio tests for stepwise model refinement to identify the minimal model that contained only significant fixed effects: the associated chi-squared values are reported.

Individuals that did not meet the criteria for group membership by SOST and STO were considered to be non-residents. We used SOST to identify the non-residents in each territory each season, and photographic records from this study and any historical data to classify the origin of non-residents, where 'neighbours' were from an adjacent territory; 'previous group members' had dispersed from the focal territory; and 'strangers' may have been previous group members or neighbours but were not recognised as such, or were known to be from non-adjacent territories. We used a Poisson GLMM to investigate whether the number of non-residents was influenced by season, their origin, and the interaction between the two, with territory as a random effect. These data were over-dispersed (deviance/residual d.f. = 1.33), but negative binomial models in package *glmmADMB* did not fit the data better (Poisson $AIC_{C13} = 313.4$, negative binomial type 1 $AIC_{C14} = 314.7$, negative binomial type 2 $AIC_{C14} = 315.1$), so the *lme4* Poisson model is reported. We used Wilcoxon rank sum tests to determine whether non-residents were more often male than female in each season.

Residual plots confirmed that both models were an acceptable fit to the data. *Post hoc* Tukey tests to correct for multiple comparisons were run in package *lsmeans* version 2.23 (Lenth, 2016) and the means back-transformed from the log scale for inference. Interactions were analysed with the package *phia* version 0.2-1 (De Rosario-Martinez, 2015), with resulting *P* values adjusted for multiple comparisons (Holm, 1979). All tests were considered significant at $P < 0.05$.

Ethical statement

This study was observational, and no animals were caught or handled. However, some animals had been ear-tagged during earlier studies. All the capture and handling techniques conformed to the guidelines of the American Society of Mammalogists (Sikes *et al.*, 2016), were approved by the University of Bristol Animal Welfare and Ethics Committee, and licensed under the Animals (Scientific Procedures) Act 1986.

Results

We analysed 124,808 photos of 175 foxes > 5 months old (101♂, 42♀, 32 unknown sex) during 38,520 independent patch visits (Table S2). Network diagrams used for STO revealed between-season and between-territory variation in group size and connectivity (Fig. S3). Some foxes (mostly non-residents) were always observed alone: these 'isolates' were particularly common in autumn and winter and least common in summer, although they were abundant throughout the year in territories 5 and 6. Plots of estimated group sizes plotted in order of data collection showed seasonal variation; in territories 1 and 6 group size increased sharply following the initial summer survey (Fig. S4). Both definition method and season had a significant influence on estimated group size (Fig. S5). The effect of definition was consistent across all seasons, as indicated by the non-significant

interaction (Table S3); the intercept of this relationship varied between territories (SD = 0.291, 95% CI = 0.17-0.57).

Pairwise Tukey tests showed that groups defined by SOST and STO were similar in size (z-ratio = 1.13, $P = 0.497$), whereas groups defined by SO were significantly larger (SO-SOST: z-ratio = 9.53, $P < 0.001$; SO-STO: z-ratio = 8.56, $P < 0.001$; Fig. 1). When averaged across definitions, group size was similar in spring and summer (z-ratio = 2.16, $P = 0.133$) and autumn and winter (z-ratio = 1.62, $P = 0.367$), but significantly different between these two pairs of seasons (SP-AU: z-ratio = 2.789, $P = 0.027$; SU-AU: z-ratio = 4.879, $P < 0.001$; SP-WI: z-ratio = 4.371, $P < 0.001$; SU-WI: z-ratio = 6.390, $P < 0.001$). In spring and summer mean group size \pm SE defined by SO was 11.0 ± 1.4 (95% CI = 8.9-14.2) and 5.0 ± 0.7 (95% CI = 3.9-6.5) by SOST and STO. Comparable figures in autumn and winter were 17.7 ± 2.2 (95% CI = 13.9-22.6) and 8.0 ± 1.0 (95% CI = 6.3-10.3).

In winter, groups defined by SO contained almost three times more males than females (Table 2). Groups defined by SOST and STO had approximately equal sex ratios in every season but did not always include the same individuals. On each territory, up to five foxes per season (mean = 0.9) changed from resident to non-resident or *vice versa*, depending on whether groups were defined by SOST or STO (Table S4). This discrepancy between definitions was most common in winter but also varied between territories, being greatest in territory 6.

Non-resident visitors

Most non-residents were recorded in winter (mean \pm SD = 14.1 ± 3.4) and fewest in summer (3.3 ± 3.2 ; Table S5). Over half of non-residents were known or probable

neighbours (Table 3). Non-residents were more often males than females in winter (Wilcoxon rank sum test: $W = 0$, $P = 0.022$, $r = -0.824$), but there was no significant sex difference in any other season (spring: $W = 19$, $P = 0.518$, $r = -0.173$; summer: $W = 25$, $P = 0.281$, $r = -0.288$; autumn: $W = 17$, $P = 0.363$, $r = -0.243$).

Numbers of neighbours and strangers were similar in all seasons apart from winter when strangers were more abundant (t -ratio = 2.659, $P = 0.021$; Fig. 2). Non-residents were least often previous group members, which were significantly less common than neighbours in all seasons (Tukey contrasts, spring: t -ratio = 3.330, $P = 0.003$; summer: t -ratio = 2.786, $P = 0.015$; autumn: t -ratio = 4.156, $P < 0.001$; winter: t -ratio = 4.022, $P < 0.001$), and significantly less common than strangers in spring (t -ratio = 3.263, $P = 0.003$), autumn (t -ratio = 3.940, $P < 0.001$) and winter (t -ratio = 5.365, $P < 0.001$).

The number of non-residents varied with season (GLMM: $\chi^2(9) = 69.860$, $P < 0.001$) and origin ($\chi^2(8) = 130.270$, $P < 0.001$); the effect of season depended on origin ($\chi^2(6) = 13.864$, $P = 0.031$; Table S6). The intercept of this relationship varied widely between territories (SD = 0.395, 95% CI = 0.21-0.80). There was significant seasonal variation in the number of non-residents that were neighbours ($\chi^2(3) = 9.507$, $P = 0.047$) and strangers ($\chi^2(3) = 41.008$, $P < 0.001$) but not previous group members ($\chi^2(3) = 1.909$, $P = 0.592$; Fig. 2). The effect of season differed between neighbours and strangers ($\chi^2(3) = 11.988$, $P = 0.022$): there was a far greater difference between summer and winter in the number of strangers compared to the number of neighbours (estimated difference = 5.647, $\chi^2(1) = 9.809$, $P = 0.031$). Specific contrasts revealed that strangers were most common in winter (Tukey contrasts, WI-SP: t -ratio = 4.046, $P < 0.001$; WI-SU: t -ratio = 5.365, $P < 0.001$; WI-AU: t -ratio = 2.886, $P = 0.020$) and least so in summer (Tukey contrasts, SU-SP: t -ratio = 3.005,

$P = 0.014$; SU-AU: t -ratio = 3.879, $P = 0.001$; Fig. 2). Similar numbers of strangers were observed in spring and autumn. More neighbours were recorded in autumn than summer (Tukey contrast: t -ratio = 2.712, $P = 0.034$).

Discussion

While group size is a key measure for behavioural, ecological and management studies, it was difficult to define in red foxes using any one of the methods we explored. In particular, territory boundaries were more permeable to non-residents than previously thought, emphasising the complexity of inter- and intra-group dynamics in canids, and the difficulty of estimating group size and membership in group-living solitary foragers generally. This flexibility in their social systems is also likely to be a key factor leading to the wide distribution of red foxes (Schipper *et al.*, 2008) and their ability to resist lethal approaches to population management (Baker & Harris, 2006).

Red fox groups were significantly larger when just defined by SO. While SOST and STO provided similar estimates of group size, the individuals assigned to each group varied: during each seasonal survey, up to five foxes were assigned a different group membership (resident or non-resident) based on the definition. One contributory factor may have been the sighting threshold we used to define SOST groups: although we set a minimum requirement of sighting an individual on 50% of days (20 in each 40-day survey period), we may still have included neighbours that visited patches regularly but were not socially integrated into the resident group. This is also likely to be an issue in habitats other than urban areas, since red foxes travel long distances to share productive food patches (Tsukada, 1997).

Similarly, groups defined by STO may have included chance encounters between foragers from different groups that were attracted to the same food patch, especially since the majority of non-residents were known or probable neighbours, and so may have been related to group residents (Baker *et al.*, 2004). A more robust definition of resident group membership should incorporate sighting frequency and both previous and current social connections. However, such long-term data are rarely available: when spatiotemporal associations are not recorded and group size, rather than membership, is required, the most robust measure of group size (and hence most easily compared between studies) is spatial overlap, so long as it includes an appropriate sighting threshold, although this is likely to vary between studies.

Groups were smallest in spring and summer (5-11 adults, depending on the definition used) and largest in autumn and winter (8-18 adults, depending on definition). Previous spring group size estimates during periods of high population density in Bristol were: mean 4.6 adults, maximum 8, $n = 13$, 1990-1994 (Iossa *et al.*, 2009); mean 4.8 adults, maximum 7, $n = 26$, 2005-2011 (Whiteside, 2012). However, our group size estimates are not directly comparable to these earlier studies, which were minimum figures due to the difficulties of catching and/or recognising every animal. Furthermore, the earlier estimates only included adult animals (> 1 year old). Camera trap photographs limit the ability to age foxes once they near full size, and so we were unable to exclude sub-adults (animals 6 – 12 months old) from our analyses. An inability to age animals accurately is a potential limitation of camera trapping studies. They also risk overestimating group size if individuals are misidentified (Yoshizaki *et al.*, 2009) and camera sites attract non-residents (Larrucea *et al.*, 2007), although these were not issues in our study. The large number of records and identification protocols minimised the risk of errors (Dorning, 2016), and the long history of

provisioning in the gardens selected for camera sites ensured that we did not influence fox behaviour during our study.

Hitherto, foxes that are not obviously members of a social group have variously been described as 'transients' or 'floaters' e.g. Cavallini (1996). These terms have never been properly defined but imply that these animals are not connected to a particular area or social group. This lack of precision reflects the quality of information that can be collected using radio-tracking, CMR and observational studies. While it is clear that more information is needed to understand the role of non-residents in red fox social systems, our data suggest that the large numbers of non-residents we recorded were part of the social system, may play a key role in the spread of information and/or diseases, and may help explain the resistance of fox populations to perturbation.

Groups defined by SO were male-biased in winter and included twice as many non-residents as residents, mostly males from nearby territories seeking extra-group copulations. Dispersing males generally move along territory boundaries (Soulsbury *et al.*, 2011), and so were less likely to be recorded by our camera traps, which were set at food patches within territories. However, although they were most common in winter, non-residents occurred year round, and this may explain why vacancies in fox territories are filled within 3.5-5 days, regardless of season (Potts, Harris & Giuggioli, 2013). Non-residents were mostly visitors from adjacent territories, suggesting that they maintain information year-round about surrounding territories. This is probably particularly advantageous at higher population densities due to the increased levels of inter- and intra-group competition, and so foxes (predominantly males) are more likely to attain dominance through dispersal than philopatry (Baker *et al.*, 2000).

Seasonal variation in group size differed between territories, particularly territories 1 and 6. Group size in territory 1 increased from summer 2013 to spring 2014: during this period the residents were starting to use different halves of their territory, probably as a prelude to division, which is a route to dominance for philopatric offspring (Baker *et al.*, 1998, 2004). In territory 6, the dominant male's death after the first camera trap survey led to an influx of non-residents throughout autumn and winter, and group size only stabilised in spring once a new dominant male had become established. During the period of instability, non-residents spent an unusually large amount of time at the territory's food patches and several foxes resident in other territories, such as the dominant pair from territory 4, were also defined as territory 6 residents based on the 20-day sighting threshold. Spending more time on the territory also increased the possibility of spatiotemporal association with resident foxes, and hence the inclusion of non-residents in the social network. This highlights the difficulty of using one group-size definition to cover all social situations, the impact of breeder loss on canid group stability (Brainerd *et al.*, 2008; Borg *et al.*, 2014), and how culling may be counter-productive because of the ensuing social disturbance (Doherty & Ritchie, 2017).

While over half of non-residents were known or probable neighbours, this is almost certainly an underestimate. We were not able to study all adjacent territories, and so some animals listed as strangers were probably neighbours from territories adjacent to the study area. Previous group members were also difficult to identify because we did not have historical data on all the animals prior to the onset of this study. Most red foxes do not disperse far from their natal territory (Harris & Trehwella, 1988), so neighbouring foxes are often related (Iossa *et al.*, 2009), and residents may be amenable to visits from relatives (Kitchen *et al.*,

2005). The number of visiting neighbours was relatively constant throughout most of the year but was significantly higher in autumn; since most foxes disperse to nearby territories, this was consistent with an increase in exploratory movements at the onset of dispersal (Woollard & Harris, 1990).

Strangers were least common in summer, which was the only season when residents outnumbered non-residents. As isolates were also least common in summer, this may be the best time to quantify group size. Strangers were most common in winter, when male foxes travel up to 2.7 territory diameters in search of extra-group copulations (Baker *et al.*, 2004). As reproductive movements are directed (Soulsbury *et al.*, 2011), they are probably based on knowledge of potential mating opportunities obtained from reconnaissance movements in earlier seasons. So many of the strangers we recorded throughout the year may have been trying to locate potential mating partners in preparation for the winter breeding season.

Conclusions

While this is the first detailed study of what constitutes a social group for a solitary-foraging canid, of necessity our analyses were based on a limited number of social groups. Red fox group size and membership varied with definition method, and the relatively high rate of extraterritorial movements could contribute to the overestimation of group size. Group size was also influenced by the specific social environment on a territory. As a consequence, there was no hard-and-fast rule for determining whether a fox was a resident or non-resident. Summer may be the best time to quantify red fox group size since groups were smallest, and it was the only season when residents outnumbered non-residents and isolates were least common. Fox social groups should be defined using a combination of

space use, sighting frequency and social connections to account for the frequency of extraterritorial movements, which make territorial boundaries difficult to define and increase intergroup contact rates. Our data also highlight the shortcomings of using ill-defined measures of group size (Scott *et al.*, 2018).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Details of camera trap surveys conducted in each territory and season. Note that not all surveys were used in the analyses. E (early) indicates that the survey was in the first half of the season, L (late) that it was in the second half of the season.

Table S2 Number of photos and independent patch visits by foxes aged > 5 months in each season used in the analyses.

Table S3 Poisson GLMM investigating the effect of season and definition method on estimated group size. Coefficients (β) are on the log scale and significant *P* values for fixed effects included in the minimal model are shown in bold. Unit of analysis = number of individuals. Sample size = 84 observations.

Table S4 Numbers of individuals that were assigned a different group membership, i.e. changed from resident to non-resident or *vice versa*, depending on whether groups were defined by spatial overlap with a sighting threshold (SOST) or spatiotemporal overlap (STO).

Table S5 Seasonal variation in the number of non-resident foxes recorded in each territory in different seasons.

Table S6 Poisson GLMM investigating the effect of season, origin (neighbour, previous group member (PGM) and stranger) and their interaction on the number of non-resident

visitors observed in territories. Coefficients (β) are on the log scale and significant P values are shown in bold. Unit of analysis = number of individuals. Sample size = 84 observations.

Figure S1 Distributions of sighting frequencies (days observed out of 40) for foxes > 5 months old. Distributions are plotted separately for each season and for all data pooled.

Figure S2 Ascending inter-record time intervals in each season for the dominant male fox in territory 1. Arrows indicate the threshold time interval, the point at which the rate of increase changed, as selected by eye.

Figure S3 Unfiltered network diagrams used to determine group size by spatiotemporal overlap. Diagrams include foxes > 5 months old. Males are shown in black, females in white and foxes of unknown sex in grey. Node shapes represent dominant foxes (■), subordinates (●) and individuals of unknown social status (▲). Edge weight is proportional to the simple ratio association index but scales differ between diagrams. All isolates are shown on the left of each network.

Figure S4 Seasonal changes in group size defined by three different methods: SO - spatial overlap, SOST - spatial overlap with a sighting threshold, STO - spatiotemporal overlap. Group size is plotted separately for each territory in the order of data collection; not all territories were surveyed concurrently.

Figure S5 Regression estimates with standard errors from a Poisson GLMM investigating the effect of season and definition on group size. Estimates are on the log scale.

Table 1 Definitions of resident group membership.

Method	Definition	Rationale
Spatial overlap (SO)	Resident group members were all individuals captured (photographed) at any patch on a given territory during each 40-day survey	To enable comparisons with previous studies
Spatial overlap with a sighting threshold (SOST)	Resident group members were foxes resident on a territory, inferred from sighting frequency. Foxes captured at any patch on more than 50% of the total survey days (≥ 20 out of 40) were considered to be residents and foxes captured on < 20 days non-residents	To avoid overestimation due to captures of foxes making extraterritorial movements
Spatiotemporal overlap (STO)	Resident group members were individuals connected to the main component of a social network, i.e. excluding isolated individuals and pairs with no other social connections. Networks were constructed based on dyadic associations at patches in each territory	To consider social behaviour in addition to space use

Table 2 Group size in each territory and season defined by spatial overlap (SO), spatial overlap with a sighting threshold (SOST) and spatiotemporal overlap (STO). Groups only include foxes > 5 months old. SD = standard deviation. Sex ratios (male:female:unknown) show the number of different animals seen in the year.

Definition	Territory	Spring	Summer	Autumn	Winter	Mean \pm SD	Sex ratio
SO	T1	15	8	15	21	14.8 \pm 5.3	9:6:1
	T2	11	6	8	20	11.3 \pm 6.2	7:4:1
	T3	12	8	17	20	14.3 \pm 5.3	8:5:2
	T4	9	4	16	17	11.5 \pm 6.1	6:4:1
	T5	20	13	24	25	20.5 \pm 5.4	12:7:2
	T6	16	14	32	30	23.0 \pm 9.3	13:9:1
	T7	5	6	11	17	9.8 \pm 5.5	5:4:2
	Mean \pm SD	12.6 \pm 4.9	8.4 \pm 3.7	17.6 \pm 8.1	21.4 \pm 4.6	15.0 \pm 7.3	
	Sex ratio	6:5:2	3:5:1	9:7:2	14:5:2		8:5:1
SOST	T1	13	7	11	13	11.0 \pm 2.8	6:5:0
	T2	5	5	4	5	4.8 \pm 0.5	2:3:0
	T3	5	5	5	4	4.8 \pm 0.5	3:2:0
	T4	4	4	6	5	4.8 \pm 1.0	2:3:0
	T5	5	4	8	8	6.3 \pm 2.1	4:3:0
	T6	5	8	14	12	9.8 \pm 4.0	4:6:0
	T7	4	3	4	4	3.8 \pm 0.5	1:3:0
	Mean \pm SD	5.9 \pm 3.2	5.1 \pm 1.8	7.4 \pm 3.8	7.3 \pm 3.8	6.4 \pm 3.2	
	Sex ratio	3:3:0	2:3:0	4:4:0	3:4:0		3:3:0
STO	T1	11	7	10	13	10.3 \pm 2.5	6:4:0
	T2	7	6	5	7	6.3 \pm 1.0	3:4:0
	T3	6	5	6	6	5.8 \pm 0.5	3:3:0
	T4	4	4	7	6	5.3 \pm 1.5	3:2:0
	T5	6	5	9	10	7.5 \pm 2.4	5:3:0
	T6	6	9	13	17	11.3 \pm 4.8	6:6:0
	T7	4	4	4	5	4.3 \pm 0.5	1:3:0
	Mean \pm SD	6.3 \pm 2.4	5.7 \pm 1.8	7.7 \pm 3.1	9.1 \pm 4.5	7.2 \pm 3.2	
	Sex ratio	3:3:0	3:3:0	4:4:0	5:4:0		4:3:0

Table 3 Total counts, sex ratios and origins of non-resident foxes recorded in each season across all territories ($n = 7$). Sex ratios (male:female:unknown) show the number of different animals seen in the year.

Season	Neighbours		Previous group members		Strangers		Total
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Spring	23 (13:10)	48.9	2 (0:2)	4.3	22 (10:4:8)	46.8	47 (23:16:8)
Summer	16 (6:10)	69.6	2 (1:1)	8.7	5 (1:2:2)	21.7	23 (8:13:2)
Autumn	36 (21:15)	50.7	3 (3:0)	4.2	32 (16:4:12)	45.1	71 (40:19:12)
Winter	34 (26:8)	34.3	5 (4:1)	5.1	60 (46:2:12)	60.6	99 (76:11:12)
Mean %		50.9		5.6		43.6	

Figure 1 Mean group size (\pm 95% confidence intervals) defined by different methods in different seasons, based on a Poisson GLMM. Definition methods were spatial overlap (SO), spatial overlap with a sighting threshold (SOST) and spatiotemporal overlap (STO).

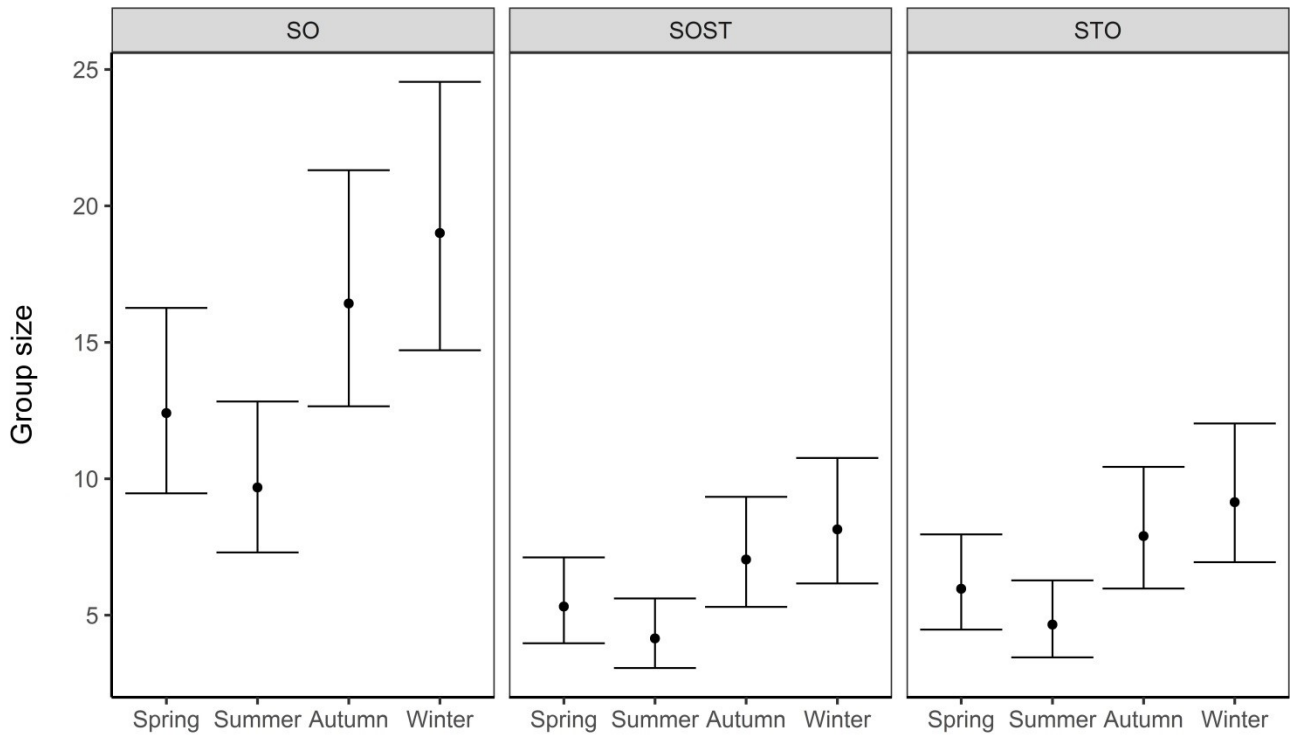
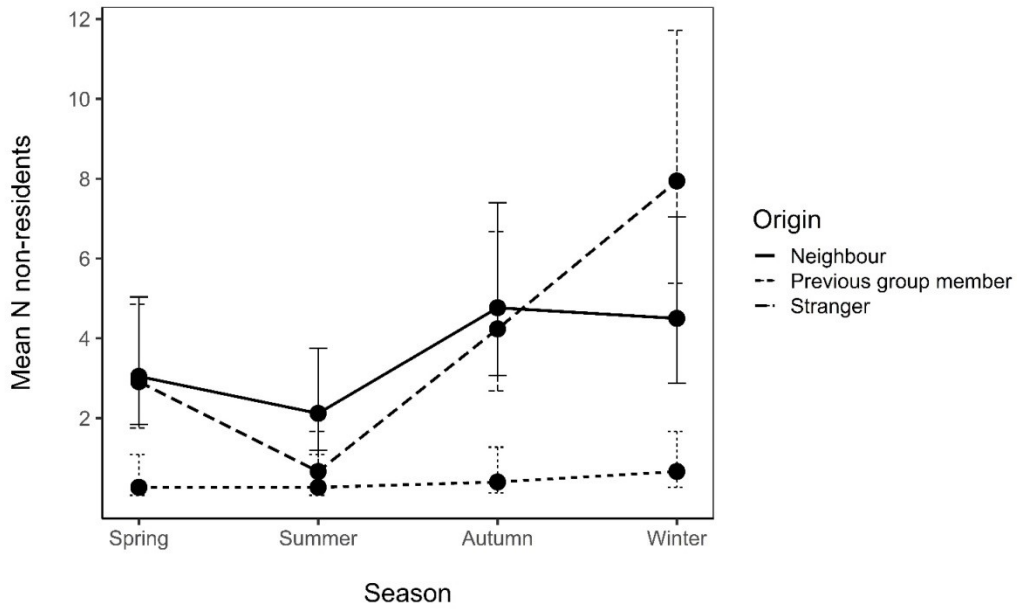


Figure 2 Mean number of non-residents of different origins (neighbour, previous group member or stranger) expected to visit an average territory in each season. Estimates are based on a Poisson GLMM and error bars show 95% confidence intervals.



1 **Supporting information**

2 **Table S1** Details of camera trap surveys conducted in each territory and season. Note that
 3 not all surveys were used in the analyses. E (early) indicates that the survey was in the first
 4 half of the season, L (late) that it was in the second half of the season.

Territory	Season	Early or late	Start date	End date	Survey length (days)	No. of cameras active	Total no. camera days	Mean days active per camera	Used for analysis
T1	Summer	L	18/07/13	27/08/13	40	6	236	39	Y
	Autumn	L	29/10/13	08/12/13	40	4	160	40	Y
	Winter	L	26/01/14	07/03/14	40	4	160	40	Y
	Spring	L	18/04/14	28/05/14	40	5	200	40	Y
T2	Summer	L	24/07/13	02/09/13	40	3	115	38	N
	Autumn	L	23/10/13	02/12/13	40	4	160	40	Y
	Winter	L	20/01/14	01/03/14	40	4	160	40	Y
	Spring	L	16/04/14	26/05/14	40	4	160	40	Y
	Summer	L	16/07/14	25/08/14	40	5	200	40	Y
T3	Summer	L	29/07/13	07/09/13	40	3	106	35	N
	Autumn	L	23/10/13	02/12/13	40	4	160	40	Y
	Winter	L	14/01/14	23/02/14	40	4	160	40	Y
	Spring	L	16/04/14	26/05/14	40	4	160	40	Y
	Summer	L	16/07/14	25/08/14	40	4	160	40	Y
T4	Autumn	E	13/09/13	23/10/13	40	4	160	40	Y
	Winter	E	10/12/13	19/01/14	40	4	160	40	Y
	Spring	E	06/03/14	15/04/14	40	5	200	40	Y
	Summer	E	02/06/14	12/07/14	40	4	160	40	Y
T5	Autumn	E	10/09/13	20/10/13	40	3	120	40	N
	Winter	E	03/12/13	12/01/14	40	5	200	40	Y
	Spring	E	04/03/14	13/04/14	40	5	200	40	Y
	Summer	E	02/06/14	12/07/14	40	5	197	39	Y
	Autumn	E	03/09/14	13/10/14	40	5	193	39	Y
T6	Autumn	E	10/09/13	20/10/13	40	3	120	40	N
	Winter	E	17/12/13	26/01/14	40	4	160	40	N
	Spring	E	07/03/14	16/04/14	40	3	120	40	N
	Summer	E	10/06/14	20/07/14	40	4	160	40	Y
	Autumn	E	08/09/14	18/10/14	40	5	200	40	Y
	Winter	E	03/12/14	12/01/15	40	5	200	40	Y
	Spring	E	03/03/15	12/04/15	40	5	200	40	Y
T7	Summer	L	23/07/14	01/09/14	40	4	159	40	Y
	Autumn	L	15/10/14	24/11/14	40	4	159	40	Y
	Winter	L	16/01/15	25/02/15	40	4	160	40	Y
	Spring	L	19/04/15	29/05/15	40	4	160	40	Y

6 **Table S2** Number of photos and independent patch visits by foxes aged > 5 months in each
 7 season used in the analyses.

Territory	Spring		Summer		Autumn		Winter		Total	
	Photos	Visits	Photos	Visits	Photos	Visits	Photos	Visits	Photos	Visits
T1	8603	2020	3390	1270	6253	1915	5568	1987	23,814	7192
T2	7215	1577	3741	1189	3608	1347	3258	1283	17,822	5396
T3	6168	1559	4531	1073	3350	1282	2666	1238	16,715	5152
T4	3811	1367	5387	1180	5129	1811	2716	1098	17,043	5456
T5	4265	1093	5079	1057	5510	1915	4345	1512	19,199	5577
T6	2775	930	5203	1695	3667	1324	3944	1674	15,589	5623
T7	5344	1385	2856	776	2936	955	3490	1008	14,626	4124

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12 **Table S3** Poisson GLMM investigating the effects of season and definition method on
 13 estimated group size. Coefficients (β) are on the log scale and significant P values for fixed
 14 effects included in the minimal model are shown in bold. Unit of analysis = number of
 15 individuals. Sample size = 84 observations.

Model parameter	β	SE	z	χ^2	d.f.	P
<i>Fixed effects</i>						
Intercept	2.518	0.138	18.237			
Definition				123.870	2	< 0.001
Definition (SOST)	-0.847	0.089	-9.528			
Definition (STO)	-0.732	0.085	-8.564			
Season				50.860	3	< 0.001
Season (summer)	-0.248	0.115	-2.164			
Season (autumn)	0.280	0.101	2.789			
Season (winter)	0.426	0.098	4.371			
<i>Non-significant fixed effects</i>						
Season * definition				6.856	6	0.3344
<i>Random effects</i>						
	Variance	SD				
Territory ($n = 7$)	0.084	0.291				

16 Reference categories were definition = SO and season = spring.

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20 **Table S4** Numbers of individuals that were assigned a different group membership, i.e.
21 changed from resident to non-resident or *vice versa*, depending on whether groups were
22 defined by spatial overlap with a sighting threshold (SOST) or spatiotemporal overlap
23 (STO).

Territory	Spring	Summer	Autumn	Winter
T1	2	1	1	0
T2	0	0	0	1
T3	0	0	0	2
T4	0	0	2	1
T5	1	1	0	3
T6	2	2	5	1
T7	0	0	0	0

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27 **Table S5** Seasonal variation in the number of non-resident foxes recorded in each territory
28 in different seasons.

Territory	Spring	Summer	Autumn	Winter	Mean \pm SD
T1	2	1	4	8	3.8 \pm 3.1
T2	6	1	4	15	6.5 \pm 6.0
T3	7	3	12	16	9.5 \pm 5.7
T4	5	0	10	12	6.8 \pm 5.4
T5	15	9	16	17	14.3 \pm 3.6
T6	11	6	18	18	13.3 \pm 5.9
T7	1	3	7	13	6.0 \pm 5.3
Mean \pm SD	6.7 \pm 4.9	3.3 \pm 3.2	10.1 \pm 5.6	14.1 \pm 3.4	

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33 **Table S6** Poisson GLMM investigating the effects of season, origin (neighbour, previous
 34 group member (PGM) and stranger) and their interaction on the number of non-resident
 35 visitors observed in territories. Coefficients (β) are on the log scale and significant P values
 36 are shown in bold. Unit of analysis = number of individuals. Sample size = 84 observations.

Model parameter	β	SE	z	χ^2	d.f.	P
<i>Fixed effects</i>						
Intercept	1.113	0.257	4.331			
Origin				130.270	8	< 0.001
Origin (PGM)	-2.442	0.734	-3.330			
Origin (stranger)	-0.044	0.297	-0.150			
Season				69.860	9	< 0.001
Season (summer)	-0.363	0.324	-1.120			
Season (autumn)	0.448	0.266	1.687			
Season (winter)	0.391	0.269	1.455			
Origin * season				13.864	6	0.031
Season (summer) : origin (PGM)	0.363	1.046	0.347			
Season (autumn) : origin (PGM)	-0.043	0.946	-0.045			
Season (winter) : origin (PGM)	0.525	0.875	0.601			
Season (summer) : origin (stranger)	-1.119	0.590	-1.897			
Season (autumn) : origin (stranger)	-0.073	0.383	-0.192			
Season (winter) : origin (stranger)	0.612	0.366	1.675			
<i>Random effects</i>						
	Variance	SD				
Territory ($n = 7$)	0.156	0.395				

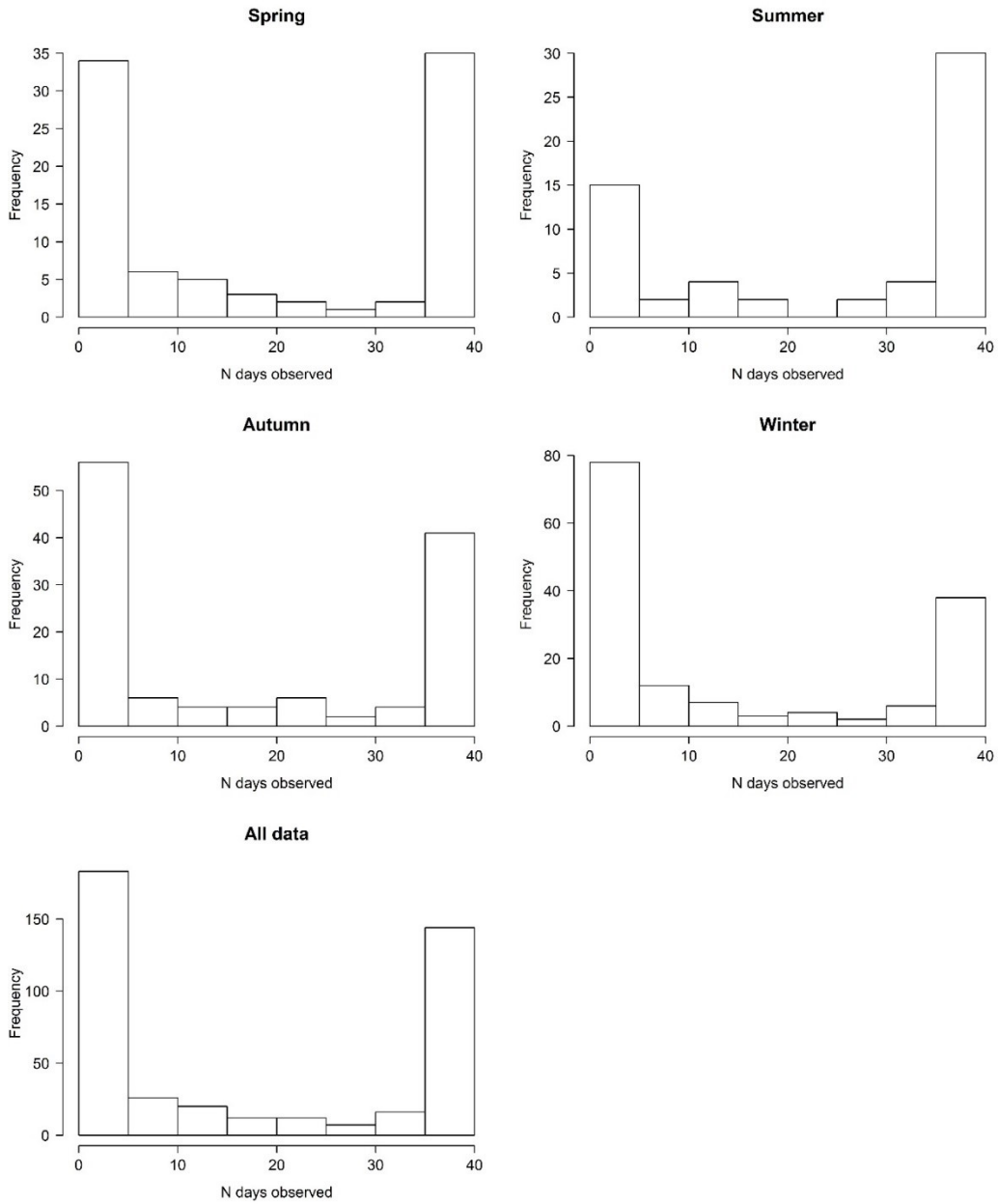
37 Reference categories were season = spring and origin = neighbour.

38

39

40 **Figure S1** Distributions of sighting frequencies (days observed out of 40) for foxes >
41 5 months old. Distributions are plotted separately for each season and for all data
42 pooled.

43



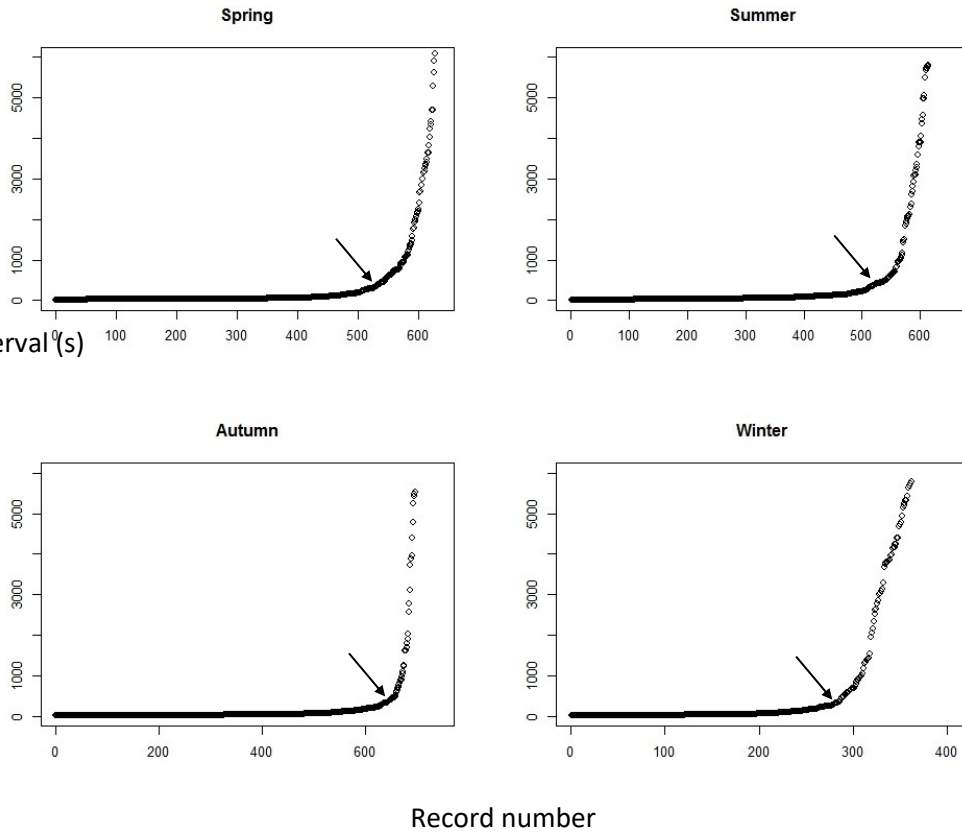
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47 **Figure S2** Ascending inter-record time intervals in each season for the dominant
48 male fox in territory 1. Arrows indicate the threshold time interval, the point at which
49 the rate of increase changed, as selected by eye.

50

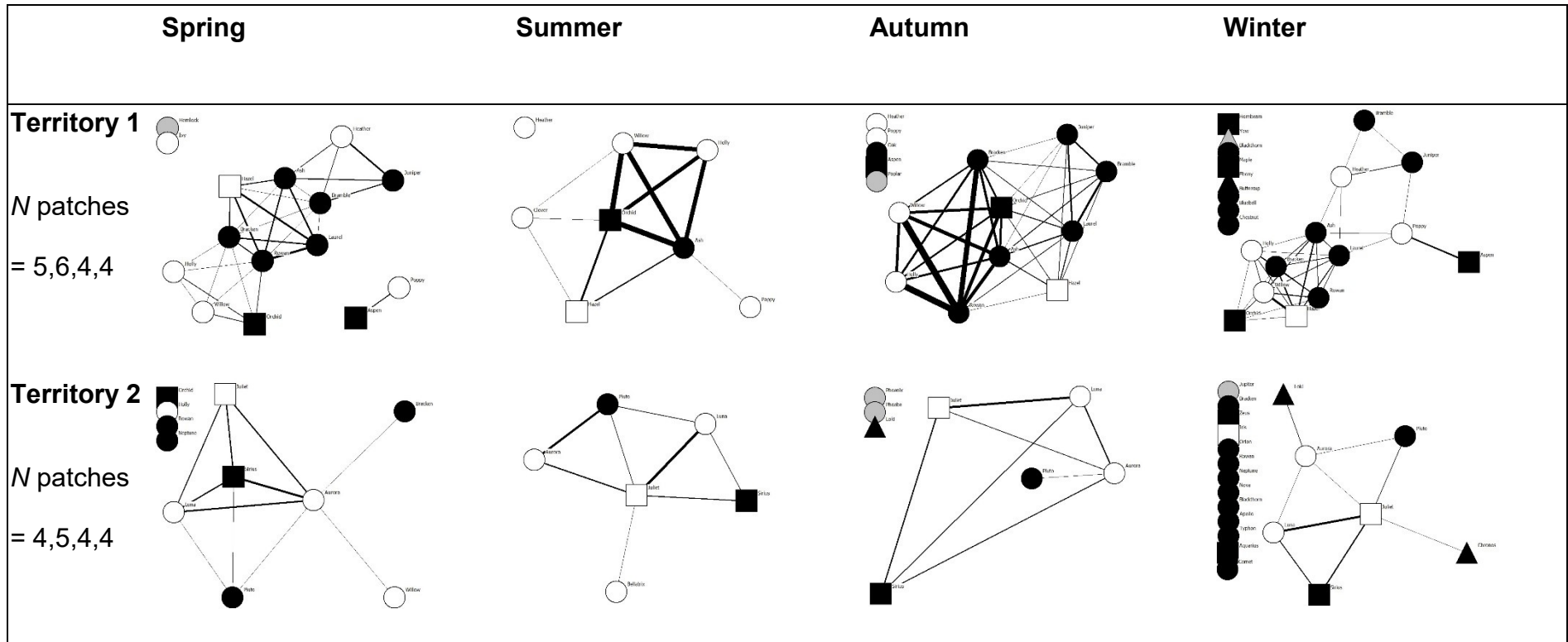


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54 **Figure S3** Unfiltered network diagrams used to determine group size by spatiotemporal overlap. Diagrams include foxes > 5
 55 months old. Males are shown in black, females in white and foxes of unknown sex in grey. Node shapes represent dominant foxes (■),
 56 subordinates (●) and individuals of unknown social status (▲). Edge weight is proportional to the simple ratio association index
 57 but scales differ between diagrams. All isolates are shown on the left of each network.
 58



Spring

Summer

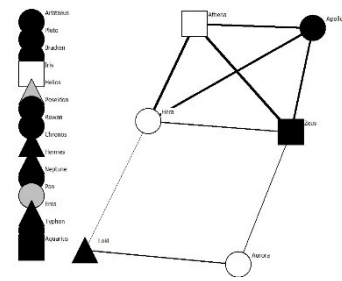
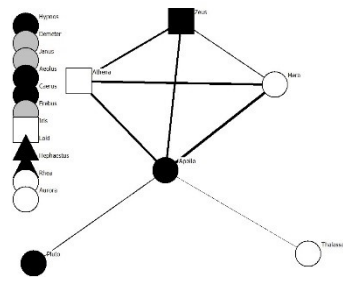
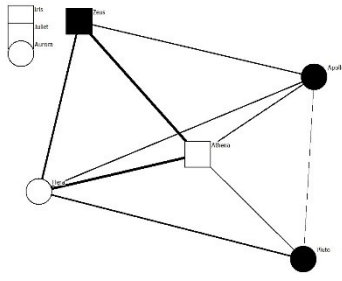
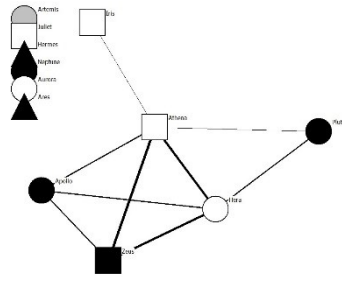
Autumn

Winter

Territory 3

N patches

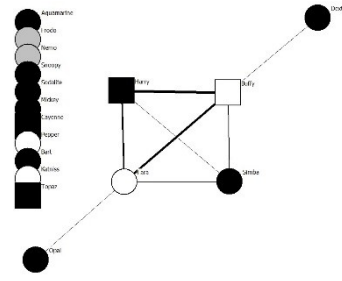
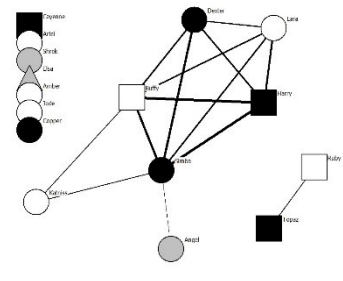
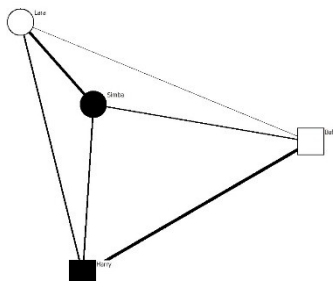
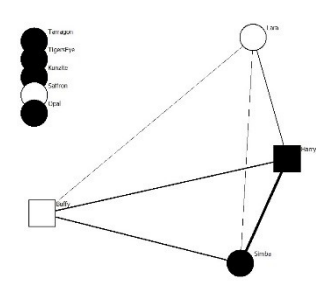
= 4,4,4,4



Territory 4

N patches

= 5,4,4,4



Territory 5

N patches

= 5,5,5,5

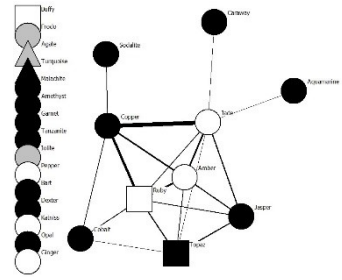
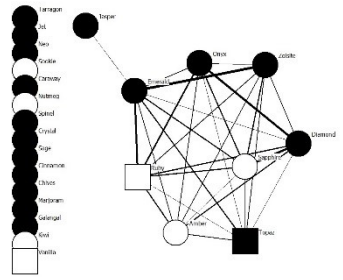
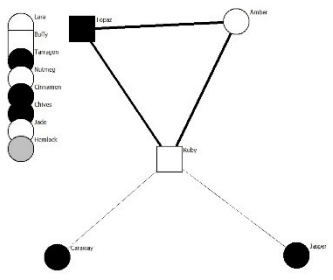
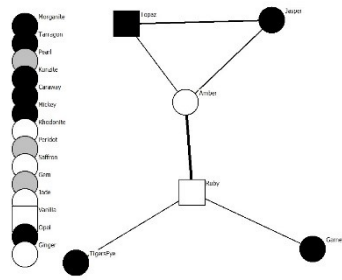


Figure S4 Seasonal changes in group size defined by three different methods: SO - spatial overlap, SOST - spatial overlap with a sighting threshold, STO - spatiotemporal overlap. Group size is plotted separately for each territory in the order of data collection; not all territories were surveyed concurrently.

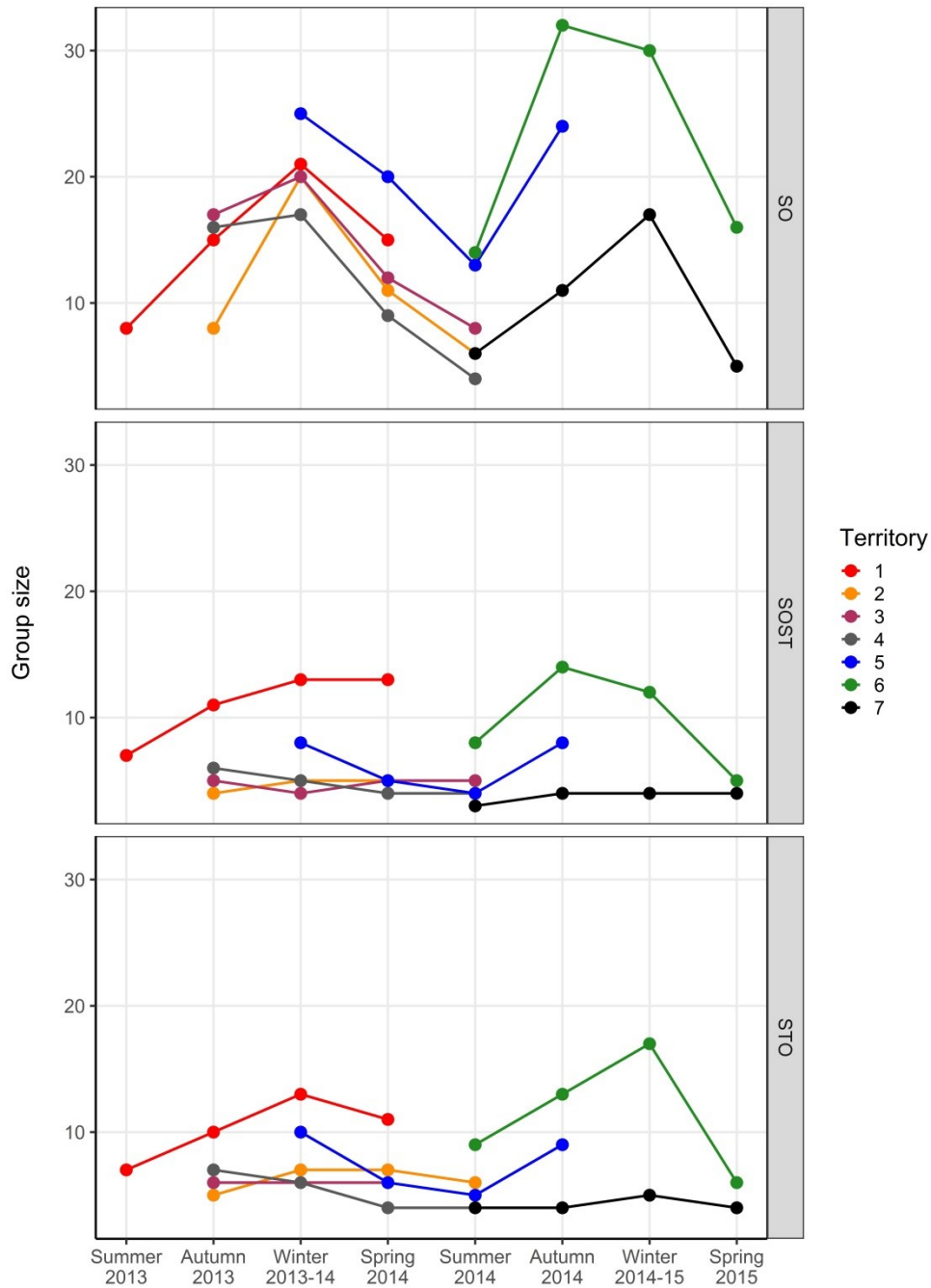


Figure S5 Regression estimates with standard errors from a Poisson GLMM investigating the effect of season and definition on group size. Estimates are on the log scale.

