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Resource dispersion and relatedness interact to explain space use in a solitary predator

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Resource dispersion or kin selection are commonly used to explain animal spatial and social organization. Despite this, studies examining how these factors interact in wild populations of solitary animals are rare. We used 16 years of individual-level spatial and genetic data to disentangle how resources and relatedness influence spatial organization of a solitary predator, the Eurasian lynx *Lynx lynx*. As expected, space-use overlap between neighbouring individuals increased when food resources were heterogeneous and unpredictably distributed (as predicted from resource dispersion) or when neighbours were closely related (as predicted from kin selection). However, these patterns were highly dependent on each other. Increased spatial overlap was restricted to mother–daughter dyads, with this effect only occurring in areas and during seasons when prey was clumped and irregularly distributed in the landscape. Additionally, full-siblings with similar levels of genetic relatedness did not show these patterns, suggesting that kin selection is mediated through mother–daughter recognition, and is only beneficial under specific resource dispersion circumstances. Our results provide key insights into the flexibility of spatial organization of solitary animals, and clearly show the importance of considering the interaction between resources and kinship when assessing animal space use patterns.

Keywords: individual-based studies, *Lynx lynx*, relatedness, space use, territoriality

Introduction

Animal spatial organization results from a combination of resource utilization patterns and cost–benefit decisions governing individual interactions (Maher and Lott 2000). Because resources are often heterogeneous in space and time, their dispersion and predictability are important factors influencing territoriality, such as the degree of space-use overlap (Maher and Lott 2000, Johnson et al. 2002). Furthermore, the cost of competition can be offset by inclusive fitness benefits of sharing resources with close kin (Hamilton 1964, Reyer 1984, Parker et al. 2002). However, while both resource dispersion and kin selection have been used extensively to explain population structure and spatial dynamics in animals (Hamilton 1964, Macdonald 1983, Pen and Weissing 2000, Johnson et al. 2002, Bourke 2014, Macdonald and Johnson 2015), studies have

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generally not examined how these two major drivers of spatial organization interact in wild populations (but see Griesser and Nystrand 2009, Banks et al. 2011). This is particularly true in non-cooperative, solitary species where explanations of the within- and between-population covariation of different spatial organizations are largely missing (Maher and Lott 2000, Hatchwell 2010, Kappeler, et al. 2013), but see Brown and Brown (1993). With increasing evidence that also solitary species share resources with related conspecifics (Kitchen et al. 2005, Støen et al. 2005, Maher 2009, Innes et al. 2012), we may expect that the spatial and temporal variation in their social organization may not only be explained by resource dispersion but also from intrinsic benefits from sharing resources with kin. Since these benefits can be environmentally mediated (Banks et al. 2011), resource dispersion and relatedness should be examined together in order to account for possible interactive effects.

Resource predictability influences the degree to which an animal can depend on its environment over time, with larger home ranges needed to account for higher spatiotemporal resource variability (Johnson et al. 2002, Eide et al. 2004, Newsome et al. 2013). Hence, the range required to sustain an individual's resource demand during periods of low resource availability may be large enough to support additional individuals during periods of high resource availability (Johnson et al. 2002). According to the resource dispersion hypothesis (Macdonald 1983), heterogeneously distributed, highly clumped and unpredictable resources should thus result in increased spatial overlap between individuals (Johnson et al. 2002, Eide et al. 2004, Newsome et al. 2013, Elbroch et al. 2016). However, presence of additional animals may inflict high competition when resources are scarce, making strong year-round territoriality and constant overlap beneficial, independent of resource fluctuations (von Schantz 1984).

Spatial proximity of closely-related individuals as well as the ability to recognize kin is needed for kin selection to influence resource sharing and spatial organization (Hamilton 1964, Hatchwell 2010). Hamilton's rule predicts that behaviours, such as resource sharing, should be favoured when $rb > c$; where r is the relatedness of the individuals sharing the resource, b is the benefit to the recipient and c is the cost to the provider (Hamilton 1964). Since costs and benefits of sharing resources via home range overlap will depend on the distribution of resources in the environment, resource dispersion should influence cost–benefit calculations and determine under what environmental conditions kin selection is favoured. Non-cooperative solitary species live within a complex social context of direct and indirect conspecific interactions (Hofmann et al. 2014), with recent studies demonstrating the importance of relatedness for these interactions (Kitchen et al. 2005, Støen et al. 2005, McEachern et al. 2007, Maher 2009, Meshriy et al. 2011, Innes et al. 2012, Quaglietta et al. 2014). However, spatial proximity and interactions between related individuals might not always result in fitness benefits, e.g. due to costs of increased competition (Griffin and West 2002, West et al. 2002, Stockley and Bro-Jørgensen 2011, Smith 2014). Fitness cost–benefits from resource sharing may also vary greatly for different genealogical relationships (e.g. due to parent–offspring conflict and sibling competition (Parker et al. 2002, Hudson and Trillmich 2008).

The Eurasian lynx *Lynx lynx* is a solitary, territorial felid, with a polygamous mating system where female home ranges are primarily determined by access to food and male home ranges by access to females (Herfindal et al. 2005, Mattisson et al. 2011a, Aronsson et al. 2016). In this study, we assess how the interaction between resource dispersion (i.e. prey) and genetic relatedness influence space-use overlap for lynx by using long-term (1994–2010) individual-level spatial and genetic data from two separate study areas within the Scandinavian lynx population (Fig. 1a). In the southern study area, main prey for lynx is roe deer *Capreolus capreolus* (Andrén and Liberg 2015). In south-central Sweden, roe deer are stationary within 1–2 km^2 home ranges and living solitary or in small groups (Cagnacci et al. 2011, Morellet et al. 2013). In the northern study area, main prey for lynx is herd-living, migratory reindeer *Rangifer tarandus* (Mattisson et al. 2011b), managed by indigenous Sámi herders. The northern study area is located within reindeer summer grazing area and, in the autumn, the reindeer herds move to winter grazing areas east of the study area (Danell et al. 2006). Consequently, at the lynx home range scale, in the southern study area the main prey is relatively homogenous and predictable distributed in time and space as compared to in the northern study area where the main prey is clumped, unpredictable and highly seasonal (Fig. 1b, for more information see 'Study system' below). In both areas, lynx space use (e.g. home range size and habitat selection) is highly influenced by prey availability (Mattisson et al. 2011a, Rauset et al. 2012, Aronsson et al. 2016) and lynx in the north have both lower reproductive rates and higher age at first reproduction compared to in the southern area (Nilsen et al. 2012). Lynx exhibit a male-biased dispersal pattern where approximately one third of subadult females establish in the vicinity of their natal territory (Samelius et al. 2012). Consequently, spatial relatedness structures may be formed by philopatric females (Holmala et al. 2018) creating an opportunity to examine the impact of both genetic relatedness and prey dispersion on space-use patterns.

Here, by simultaneously considering the influence of both relatedness and resource dispersion on lynx space-use overlap, we aim to disentangle how these different factors influence spatial organization of solitary predators. We assess three main questions. First, does intrasexual space use overlap depend on sex in the two study areas? Second, does relatedness affect intrasexual space use overlap, and to what extent is this effect influenced by variation in resource dispersion? Third, is space use overlap different for parent–offspring dyads compared to full-sibling dyads that are equally related but may differ in terms of kin competition or recognition?

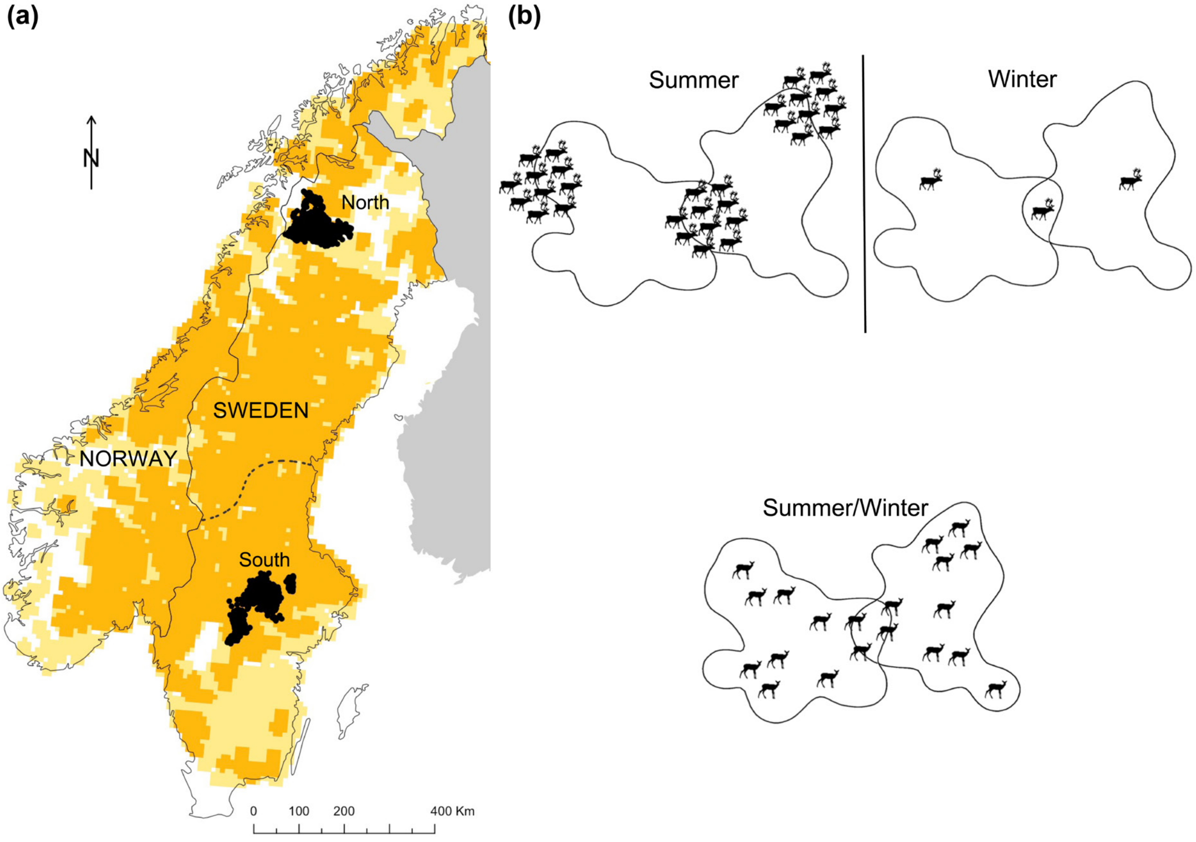

Figure 1. Locations from 49 lynx monitored in the southern and northern study area (a). Dashed line marks the southern boundary of the reindeer husbandry area. The distribution of lynx in Scandinavia is shown in yellow (dark cells indicated areas of permanent occurrence, light cells indicate areas of sporadic occurrence, from Chapron et al. (2014)). At the lynx home range scale (b), the study areas represent differences in prey dispersion and predictability. The northern study area is within the summer grazing areas for herd living and migratory reindeer, resulting in clumped and seasonal food resource. In the southern study area lynx primarily prey on roe deer, which are stationary year-round and solitary or living in small groups, resulting in an evenly dispersed and predictable food resource.

Methods

Study system

The southern study area ranges from 30 to 500 m a.s.l, and is dominated by intensively managed coniferous (*Pinus sylvestris* and *Picea abies*) and deciduous forests (mainly *Betula pubescens* and *B. pendula*) creating a mosaic of even-aged forest stands interspersed with agricultural land, mires and lakes (proportion of agricultural land increasing from 1 to 20% north to south). The northern study area is characterized by deep valleys starting at 300 m a.s.l and high alpine plateaus with peaks ≤ 2000 m a.s.l. Lower elevations are dominated by coniferous forest interspersed by mires and lakes, followed by hillsides and high elevation downy birch forest (*B. pubescens*), forming the tree line at 600–700 m a.s.l., followed by shrubs and heaths leading up to bare rock. Lynx primarily inhabit the valleys from the coniferous forest to alpine heath (Rauset et al. 2012).

In the southern study area, roe deer density range between 2 and 4 roe deer km^{-2} (Andrén and Liberg 2015) and 81% of lynx prey is roe deer. Lynx predation is the main cause of roe deer mortality (Samelius et al. 2013), killing approximately 3–6 roe deer/30 days and lynx kill rate is not influenced by roe deer density (Andrén and Liberg 2015). Roe deer are solitary or living in small groups and in south-central Sweden roe deer are stationary within 1–2 km^2 home ranges (Cagnacci et al. 2011, Morellet et al. 2013). Consequently, roe deer space use are much more restricted than lynx (lynx home ranges 300–1000 km^2, Aronsson et al. 2016). Each lynx home range consists of a matrix of forest stands, agricultural fields and pastures (Hemmingmoore et al. 2020), ensuring patches of good roe deer habitat. The northern half of Sweden is designated reindeer husbandry area used by indigenous Sámi reindeer herding communities (Fig. 1a), and the northern study area is located within the summer grazing areas for four reindeer herding districts (Supplementary material Appendix 1 Fig. A1). The number of reindeer within these herding districts fluctuated between 20 000 and 30 000 during the study period (Sámi Parliament, Kiruna, Sweden). Reindeer migrate between summer and winter grazing areas, reaching the study area in late spring for calving (Danell et al. 2006). Within the summer grazing areas of each district reindeer move in large herds over vast areas (> lynx home ranges 700–1700 km^2, Mattisson et al. 2011a), their movement influenced by forage availability, weather and insect harassment (Skarin et al. 2008). During summer, reindeer is the main prey for lynx (i.e. > 60% of lynx prey is reindeer in the study area, kill rate 3–5 reindeer/30 days for female lynx and 8–11 reindeer/30 days for males, Mattisson et al. 2011b). In autumn, each district move their herds to winter grazing areas 100–300 km to the east of the study area (Supplementary material Appendix 1 Fig. A1). Lynx do not follow the reindeer migration in winter (Danell et al. 2006), instead they feed on the few remaining reindeer scattered across the landscape and small prey such as mountain hare *Lepus timidus*, grouse *Tetrao* spp., ptarmigan *Lagopus* spp. and rodents (*Rodentia*) (Mattisson et al. 2011b). In both study areas, a majority of adult lynx mortalities were human-caused, and although the specific causes differed between the areas (i.e. traffic, legal hunting and poaching in the south, versus poaching in the north), the sex-specific survival rates were similar (males: 0.77 and 0.79, females: 0.83 and 0.85, in northern and southern study areas, respectively) (Andrén et al. 2006).

Lynx capture

We used location data from 1997 to 2010 (south) and 1994 to 2010 (north). Lynx were captured and immobilized following ethically approved handling protocols (Arnemo et al. 2012), and fitted with VHF-transmitters (1996–2008: MOD335, MOD400NH, IMP/150/L and IMP/400/L Telonics, USA) or GPS-collars (2003–2014; GPS plus mini, Vectronics Aerospace, Germany; Televilt Posrec 300 and Tellus 1C, Followit, Sweden). When immobilized, a small tissue biopsy, a blood sample and a hair sample were taken from each captured lynx for genetic analysis.

Spatial analysis

We only included resident animals ≥ 20 months old, as most subadult lynx had established in their own home range by 18 months of age (Samelius et al. 2012). We estimated annual lynx home ranges (i.e. 1 February year t to 31 January year t + 1) using the bivariate normal kernel in the 'adehabitatHR' package (Calenge 2006) in the R software ver. 3.4.4. (<www.r-project.org>). We defined home ranges as the 90% probability contour of each kernel utilization distribution. For smoothing parameter, we used the 'reference bandwidth' multiplied by 0.8 to avoid over-smoothing (i.e. we visually reviewed contours created by the reference bandwidth multiplied by 0.5–1, with 0.05 increments, Aronsson et al. 2016). To reduce biases from different sampling frequencies between animals and years we randomly sampled 1 location/day/individual, also using this procedure we have previously shown that annual lynx home range size estimations for the same dataset is not influenced by collar type (Aronsson et al. 2016). We used a minimum of 25 locations for annual home range estimates (following Aronsson et al. 2016), average annual locations per individual included was 93 ± 9 SE. All individuals were monitored ≥7 months per year, to ensure that neighbouring individuals were monitored simultaneously. Neighbours were defined as lynx with overlapping home ranges or with home range borders within the sex- and area-specific minimum home range diameter and an area in between that could not hold a resident lynx individual (assessed using lynx locations, landscape and habitat information in ArcGIS). We found 83 unique neighbouring dyads made up by 49 individuals (Table 1). To quantify space use overlap between neighbouring individuals we used two measurements: overlap index (OI; Ginsberg and Young 1992) and volume of intersection (VI; Millspaugh et al. 2004). Both measurements range from 0 (no overlap) to 1 (identical). Because individual lynx were monitored during multiple years we obtained a total of 246 annual overlap estimates (Table 1) of which 40 home ranges were not overlapping (south: 16 females, 12 males; north: 12 females). Our results were robust with respect to overlap measurements, we present OI in the following text (see Supplementary materials Appendix 2 for results using VI).

To assess seasonal variation in the interactions between females in the northern study area we calculated the distance between simultaneous GPS locations (≤ 3 min apart) for neighbouring female pairs and years (n = 24) and randomly selected 1 distance day^{-1} pair^{-1} (n = 5047). We divided the year into three seasons based on reindeer abundance and herding practices: summer (May–July; high reindeer abundance, large herds), autumn (August–November; generally high reindeer abundance although yearly variations due to weather-dependent herding practices and migration) and

Table 1. Number of neighbouring female and male lynx pairs monitored in the northern and southern study areas. Average with associated 95% CRIs (), min and max for relatedness values and overlap index, as well as number of pairs and number of overlap estimates [ ] for each genealogical relationship category (i.e. parent–offspring, full siblings, half siblings and unrelated) for each sex and study area.

		Relatedness value			Overlap index			Most likely genealogical relationship			
	Pairs	Mean (CRI)	Min	Max	Mean (CRI)	Min	Max	PO	FS	HS	U
North											
Female	26 [82]	0.20 (0.12–0.28)	0.0	0.5	0.19 (0.14–0.26)	0.0	0.84	7 [32]	1 [6]	7 [18]	11 [26]
Male	10 [24]	0.08 (0.007–0.16)	0.0	0.3	0.28 (0.18–0.39)	0.0	0.81	0 [0]	0 [0]	3 [8]	7 [16]
South											
Female	22 [72]	0.25 (0.15–0.36)	0.0	0.8	0.08 (0.05–0.12)	0.0	0.49	5 [20]	2 [4]	5 [16]	10 [32]
Male	25 [68]	0.09 (0.02–0.16)	0.0	0.7	0.17 (0.11–0.24)	0.0	0.20	1 [4]	1 [4]	3 [8]	20 [52]

winter (December–April; low and scattered reindeer abundance) (Bjärvall et al. 1990, Danell et al. 2006, Skarin et al. 2008). Distances were categorized based on whether at least one individual in the pair was located within the home range overlap area or not. To assess the interaction between neighbouring females we compared the distance between simultaneous locations with random locations simulated within corresponding overlapping areas (see Supplementary materials Appendix 3 for full details). In the southern study area, none of the highly related pairs were simultaneously monitored with GPS collars, consequently we could not assess seasonal differences in interactions between neighbours.

Genetic analysis

Genomic DNA from blood, tissue and hair were genotyped on 17 microsatellite loci located on the autosomal genome (see Supplementary material Appendix 4 for full details). We used ML-Relate (Kalinowski et al. 2006) to calculate relatedness values (r) and the most likely genealogical relationship categories. The existence of close genealogical relationships (i.e. half siblings (HS), full siblings (FS) or parent–offspring (PO) was tested by likelihood ratio tests using the maximum likelihood estimates, based on 10 000 randomizations and the 95% confidence interval. Among the 33 females included in the analysis, 14 of 48 neighbouring pairs were known to be close kin, consisting of 12 mother–daughters (MD), where the daughter was caught as a kitten in the lair of a collared mother, and two sib pairs that was first caught as juveniles in the same litter. Based on the most likely relationship from ML-RELATE, 10 of 12 known MD pairs (83%) and both of the two known FS dyads were classified accordingly. The remaining two MD dyads were classified as FS in ML-RELATE, with a likelihood difference of 0.79 and 0.48 from MD. Since FS relations were not possible, due to difference in age, in these two cases they were categorized as MD for this study.

Statistical analysis

We modelled annual space use overlap for each sex and study area as a Bayesian zero-inflated beta regression (Ospina and Ferrari 2012), that incorporates a two-step process to account for 1) non-overlapping neighbours (Eq. 1–2) and 2) the degree of overlap when overlap >0 (Eq. 3–6).

$$\gamma_i = \alpha_{j[i]} + a_k X_{ik} \tag{1}$$

$$\begin{aligned}\left[\alpha, \boldsymbol{a}, \mu_\alpha, \sigma_\alpha \mid \mathrm{y}_a, \mathrm{X}\right] \propto & \prod_{i=1}^{N} \mathrm{Bernoulli}\left(\mathrm{logit}\left(\mathrm{y}_i\right) \mid \gamma_i\right) \\ & \times \prod_{j=1}^{J} \mathrm{normal}\left(\alpha_j \mid \mu_\alpha, \frac{1}{\sigma_\alpha}\right) \times \prod_{k=1}^{K} \mathrm{normal}\left(a_k \mid 0, 0.0001\right) \\ & \times \mathrm{uniform}\left(\sigma_\alpha \mid 0,3\right)\end{aligned} \tag{2}$$

and

$$\mu_i = \beta_{j[i]} + b_k X_{ik} \tag{3}$$

$$\begin{aligned}\left[\beta, \boldsymbol{b}, \mu_\beta, \sigma_\beta, \sigma \mid \mathrm{y}_b, \mathrm{X}\right] \propto & \prod_{i=1}^{n} \mathrm{beta}\left(\mathrm{logit}\left(\mathrm{y}_i\right) \mid p_i, q_i\right) \times \prod_{j=1}^{J} \mathrm{normal}\left(\beta_j \mid \mu_\beta, \frac{1}{\sigma_\beta}\right) \\ & \times \prod_{k=1}^{k} \mathrm{normal}\left(b_k \mid 0, 0.0001\right) \times \mathrm{uniform}\left(\sigma_\beta \mid 0,3\right) \\ & \times \mathrm{uniform}\left(\sigma \mid 0,1\right)\end{aligned} \tag{4}$$

$$p_i = \frac{\mu_i^2 - \mu_i^3 - \mu_i \sigma^2}{\sigma^2} \tag{5}$$

$$q_k = \frac{\mu_i - 2\mu_i^2 + \mu_i^3 - \sigma^2 + \mu_i \sigma^2}{\sigma^2} \tag{6}$$

where γ_i is the deterministic predictions of the probability of no overlap, $\mathbf{y}_a$ is a vector of binary overlap values (i.e. 1 for not overlapping neighbours and for overlapping neighbours, $n = 246$), μ_i is the deterministic predictions for amount of overlap, $\mathbf{y}_b$ is a vector non-zero overlap measurements ($n = 206$), $\boldsymbol{a}$ and $\boldsymbol{b}$ is vectors of model parameters and $\mathbf{X}$ is explanatory variables (i.e. continuous relatedness values (linear and quadratic) or the 4-level genealogical relationships categories). The subscript k in both models indexes the number of covariates. To account for the same individual being present in multiple neighbouring pairings we included the focal individual for each overlap measurement as a group level effect on the intercept in each model (α and β), indexed by the subscript j. Lastly, we combined the two models to generate predictions for overlap using $(1 - \gamma) \times \mu$.

We used JAGS (Plummer 2003) called from R using the 'rjags' package (Plummer 2016) and for each model we ran two independent chains with different starting values and after discarding the first 100 000 iterations we accumulated 900 000 samples from each chain. Convergence was assessed by visual inspection of trace plots and the Gelman and Rubin diagnostic (< 1.1; Gelman and Rubin 1992).

For model comparisons we used the Watanabe–Akaike information criterion (WAIC). The WAIC was based on the posterior predictive distribution generated within the JAGS model structure (Hooten and Hobbs 2015). We present posterior means with associated 95% credible intervals (CRIs) for estimated model parameters and predictions unless otherwise stated. To make probability statement on differences between groups we subtracted their posterior distributions within the JAGS model structure (i.e. A-B). The proportion of the resulting probability distribution that is above zero is then the probability (*Pr*) that group A > group B (presented in results as *Pr*(A > B) = X%). A probability of 50% indicates the mean estimate for the difference is 0 and has no predictive value.

Results

Difference between sexes and study areas

For both females (F) and males (M), home range overlaps were larger in the northern study area (N) compared to in the southern study area (S) (Table 1; $Pr(M_N > M_S) = 96\%$, estimated difference = 0.11 (−0.01 to 0.23); $Pr(F_N > F_S) = 100\%$, difference = 0.11 (0.05–0.18)). Neighbouring males overlapped more than neighbouring females in the south ($Pr(M_S > F_S) = 100\%$, difference = 0.09 (0.02–0.16)), while the probability that males overlap more than females decreased in the north ($Pr(M_N > F_N) = 93\%$, difference = 0.08 (−0.03 to 0.21)).

Relatedness and overlap between neighbours

Relatedness of neighbouring females ranged from unrelated ($r = 0.0$) to closely related ($r \geq 0.5$) in both study areas, with all relationship categories occurring in both areas (Table 1). Among males, highly-related neighbours were uncommon in the south and did not occur in the north (Table 1). Thus, neighbouring females had higher relatedness values than neighbouring males in both study areas ($Pr(r_F > r_M) = 98\%$ and 99% for northern and southern study area, respectively; Table 1). However, there was no evidence that the average relatedness varied between the study areas for males nor females ($Pr(r_S > r_N) = 79\%$ and 56% for females and males, respectively).

Space use overlap between neighbouring females increased linearly with increasing relatedness in the north (Fig. 2; ΔWAIC 3.2 and 9.3 for quadratic and intercept only models, respectively), whereas there was no effect of relatedness on female overlap in the south (Fig. 2; ΔWAIC was 1.7 and 5.9 for linear and quadratic models, respectively). Based on predictions from the linear model in the north there was a 100% probability of higher overlap for highly related neighbours ($r = 0.5$) compared to unrelated individuals ($r = 0.0$). By categorizing relatedness into the most likely genealogical relationship it was evident that the positive effect of relatedness on female space-use overlap in the north was restricted to mother–daughter dyads (MD), and did not include full-siblings (FS) (Fig. 2). There was higher overlap for MD in the north when compared to other types of relationships ($Pr = 96–100\%$, Table 2a). There was little or no evidence of a difference in overlap between the other relationships in the north, nor between any relationships in the south (Table 2a). Furthermore, MD had larger space use overlap in the north compared to south ($Pr = 100\%$; Table 2b), while there was a small study area difference for FS and half-sibling (HS) overlap and no overlap difference for unrelated (U) neighbours (Table 2b). Males were not included in the analysis of the effect of relatedness on space-use overlap due to the low sample size for highly-related neighbouring males (Table 1).

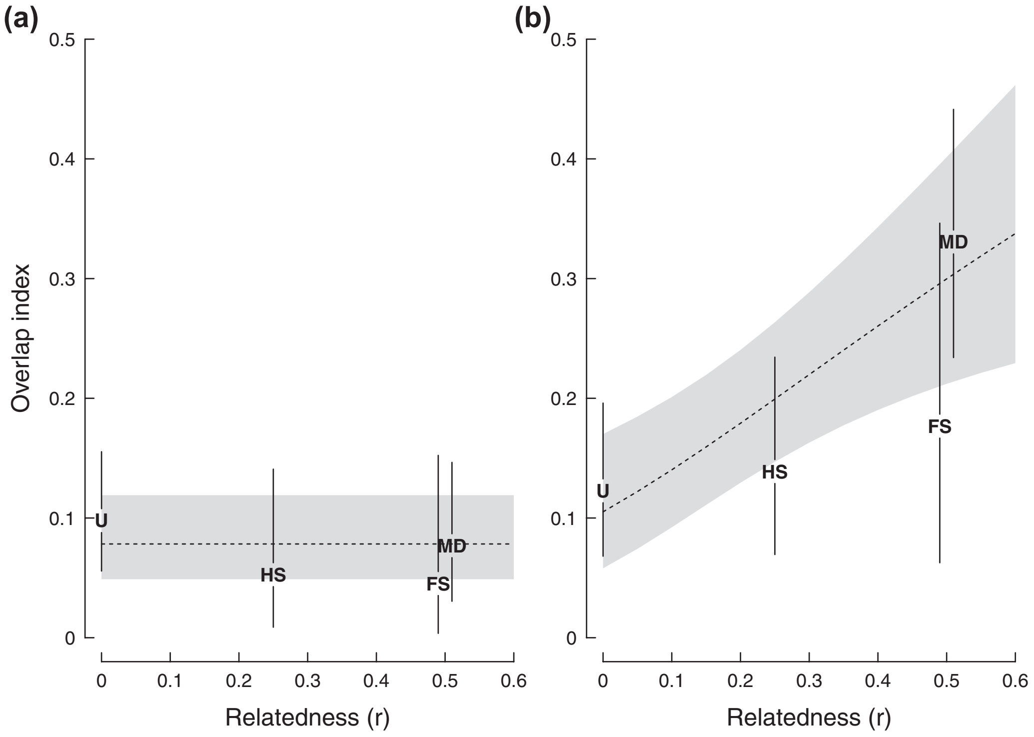

Figure 2. Model predictions with associated 95% CRIs for the effect of genetic relatedness on female home range overlap in the southern (a) and northern (b) study areas (see Supplementary material Appendix 1 Fig. A2, A3 for separate model parameters and predictions). Additionally, the predicted overlap values for each genealogical relationship category is included at corresponding relatedness values (unrelated, $r = 0$; half-siblings, $r = 0.25$; full-siblings and mother–daughter, $r = 0.5$) with associated 95% CRIs (vertical lines).

Table 2. Within (a) and between (b) study area comparison of overlap index (OI) for female lynx home range. In (a) probability (*Pr*) of higher OI for each genealogical relationship category compared to all less or equally related categories and the estimated difference (OI diff) with 95% credible intervals. In (b) probability of higher overlap index in the northern compared to the southern study area (*Pr*(N > S)) for each genealogical relationship category, and the estimated difference with 95% CRIs. Genealogical relationship categories are; mother–daughter (MD), full siblings (FS), half siblings (HS) and unrelated (U).

(a) Within study area comparison					(b) Between study area comparison		
	North		South				
	Pr	OI diff (CRI)	*Pr*	OI diff (CRI)		*Pr*(N > S)	OI diff (CRI)
Category					Category		
MD > FS	96%	0.15 (−0.02 to 0.30)	75%	0.03 (−0.08 to 0.11)	MD	100%	0.25 (0.13–0.37)
MD > HS	100%	0.2 (0.07–0.31)	75%	0.02 (−0.06 to 0.10)	FS	94%	0.13 (−0.02 to 0.31)
MD > U	100%	0.2 (0.10–0.32)	23%	−0.02 (−0.08 to 0.04)	HS	93%	0.08 (−0.03 to 0.19)
FS > HS	68%	0.04 (−0.11 to 0.22)	45%	−0.007 (−0.1 to 0.1)	U	64%	0.02 (−0.05 to 0.11)
FS > U	77%	0.05 (−0.08 to 0.22)	13%	−0.05 (−0.12 to 0.05)			
HS > U	63%	0.02 (−0.07 to 0.12)	12%	−0.04 (−0.11 to 0.04)			

Proximity between neighbouring individuals and seasonal variation

Because there was no difference in space use overlap among FS, HS and U we pooled all their distances between simultaneous GPS-locations (n = 1890) for comparison with MD (n = 3157) in the northern study area. At the yearly scale, lynx mothers and daughters were located closer to each other compared to other neighbouring pairs (Fig. 3, proportion of distances ≤ 1, 5 and 10 km was 1, 6 and 18% for MD, and 0, 0.7 and 8% for other dyads). Furthermore, for 68% of the distances within 10 km for MD (n = 567) at least one individual in the pair was within the overlap zone (Fig. 3b.1), whereas the corresponding proportion for other dyads (n = 154) was 20% (Fig. 3b.2). MD neighbours were more often than expected within ≤ 10 km of each other during the summer, when prey abundance is high but unpredictable, compared to during autumn and winter (Fig. 4a). Other

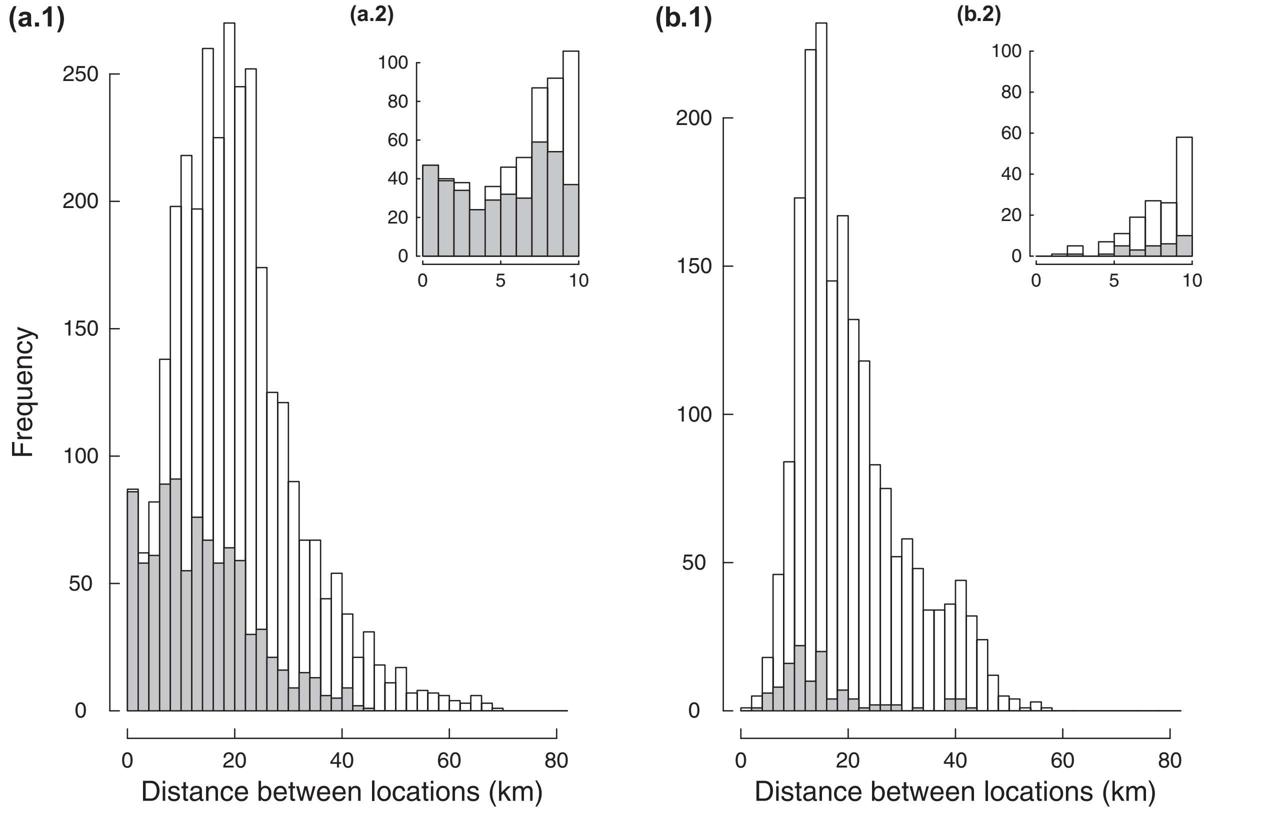

Figure 3. Distances between simultaneous GPS-locations for neighbouring mother–offspring (a.1) and non-mother–offspring (b.1) females in the northern study area. Grey shading indicates distances where at least one individual in the pair was within the home range overlap area. The insets in the upper right corner of each figure (a.2 and b.2) shows histograms of all distances ≤ 10 km in 1 km intervals. See Supplementary material Appendix 1 Fig. A4 for seasonal histograms.

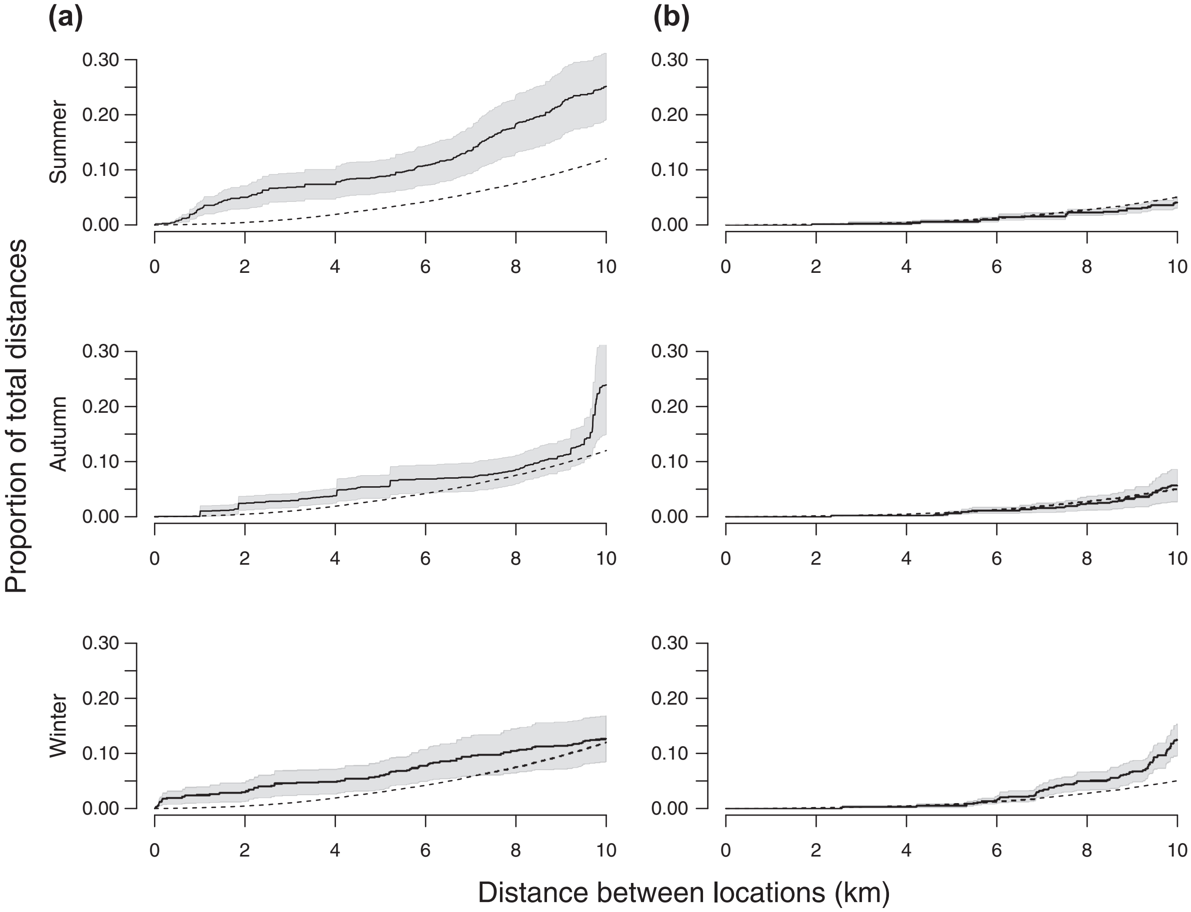

Figure 4. Lower left section of the cumulative distributions of seasonal distances (≤ 10 km from Supplementary material Appendix 1 Fig. A5) between simultaneous locations and random locations for mother–offspring (a) and non-mother–offspring (b) lynx in the northern study area during summer, autumn and winter. Solid lines represent the mean cumulative distance for all pairs, grey areas the standard error and dashed lines show distances between random locations.

dyads were further apart compered to MD and the distances between individuals were not different from random locations (Fig. 4b).

Discussion

By simultaneously considering the influence of both prey resources and relatedness, we were able to show that their interaction influence lynx spatial organization. We found that both space-use overlap and interaction between mothers and daughters increased when prey resources were unpredictable and highly clumped in time and space. When including relatedness in our analysis, we could see that that a higher female overlap in the north compared to south was not solely due to differences in prey dispersion (Maher and Lott 2000, Eide et al. 2004, Newsome et al. 2013, Macdonald and Johnson 2015), but due to resource sharing among relatives when prey resources were unpredictable and highly clumped (Fig. 2).

Intrasexual space-use overlap was larger for males than for females in both study areas (Table 1). In solitary carnivores, males maximize their space use to increase mating opportunities, whereas female home ranges should include enough resources for survival and offspring provisioning (Sandell 1989, Aronsson et al. 2016). Male lynx have larger home ranges than females, which are expected to be more difficult to keep exclusive (Mattisson et al. 2013) and consequently overlap more than female home ranges. Furthermore, intrasexual overlap was larger in the north compared to the south for both males and females (Table 1). In the north, females increase their home range size to account for seasonal variation in prey abundance, while male home ranges increase to access females (Mattisson et al. 2011a, Aronsson et al. 2016). However, if the larger female space-use overlap in the northern study area is solely due to higher variation in prey abundance and predictability (i.e. decreased territoriality during periods with an excess of prey (Maher and Lott 2000, Johnson et al. 2002), or that the larger home ranges are harder to defend (Mattisson et al. 2013)), we would expect the variation in overlap to be independent of relatedness. On the contrary, we found that relatedness had an important positive effect on female overlap in the north, but not in the south (Fig. 2, Table 2a). This difference between study areas was not simply because of a difference in the number of related neighbours, because there were many female close kin neighbours in both areas (Table 1) and the average relatedness between females was similar ($P(r_S > r_N) = 79\%$). The average relatedness among males was very low, and only eight of 35 pairs were close kin (Table 1), as expected from male-biased dispersal (Samelius et al. 2012). Furthermore, yearly survival estimates were similar in both areas, and mortality rates due to hunting and poaching combined are almost identical (15.5% and 15.2% in the northern and southern study area, respectively) (Andrén et al. 2006).

We suggest that the observed effect of relatedness on female space use in the north is explained by the large seasonal variation in prey dispersion (i.e. regularly re-occurring season with low prey abundance, winter) in combination with the low predictability during the re-occurring season with high prey abundance (i.e. herd-living and highly movable prey in summer). Female lynx home range size is set to meet the needs during seasons with the lowest resource abundance, and home ranges do not contract when food is abundant (Aronsson et al. 2016). The inclusive fitness benefits of sharing space with kin may increase under resource-limiting conditions, given that the benefit to the receiver is high during this time (Banks et al. 2011). This can be predicted from Hamilton's rule (i.e. sharing should occur when relatedness (*r*) times benefit to the recipient (*b*) is higher than the cost for the giver (*c*); Hamilton 1964). Of course, costs of the giver should also increase under resource-limiting conditions; however, where territorial space is being shared by adult, resident individuals, the role of giver and recipient is also shared. This means that both the costs and benefits in Hamilton's rule apply to both individuals, with space sharing likely involving an ongoing reversal of roles. That there was an effect of relatedness on female space-use overlap in the northern but not in the southern study area supports the idea that the effect of relatedness on space-use overlap is mediated by resource dispersion (Fig. 2, Table 2a). Consequently, where prey resources are seasonal, heterogeneous and unpredictable (north), the benefit of reduced territoriality between highly related neighbours during seasons with high but unpredictable resource abundance is higher than the cost during seasons with low resource abundance. Where resources are predictable and homogeneously distributed (south), the cost is always relatively high compared to the benefit, independent of relatedness (i.e. c is always $> rb$). The benefit of sharing space when resources are highly clumped and unpredictable is presumably because the probability of gaining 'access' to prey increases with area (i.e. by reduced territoriality both individuals have access to the herd currently present in any of the two neighbouring home ranges) and reduces costs of territorial defence between close kin (Brown and Brown 1993). Furthermore, a smaller proportion of 2-year old females breed in the northern compared to the southern study area (22% versus 74%; Nilsen et al. 2012), and in Norway, lynx with seasonal access to reindeer have a decreased probability of reproducing compared to lynx with reindeer available year around (Walton et al. 2017). Consequently, mother and daughter sharing access to prey resources may increase both individual's chances of reproducing.

Our analyses of annual space-use overlap do not assess whether the observed pattern in the northern study area is a consequence of seasonal differences in individual interactions (i.e. mother–daughter sharing prey resources during the summer). For this, we used detailed location data from neighbouring pairs simultaneously monitored with GPS transmitters. We show that mother–daughter dyads were generally in closer proximity to each other than dyads of all other relationship categories (Fig. 3), especially during summer (Supplementary material Appendix 1 Fig. A4). Furthermore, mother–daughter neighbours were closer to each other than expected from random locations during summer, compared to autumn and winter, and we did not observe this for the other relatedness categories (Fig. 4). This further supports the idea that the increased annual space-use overlap in the northern study area was primarily explained by reduced territoriality between mothers–daughters during periods with high prey abundance (c.f. Newsome et al. 2013).

A prerequisite for differential territorial behaviour as a function of relatedness is that lynx are able to recognize kin or discriminate between genetically related and genetically unrelated individuals (Smith 2014). The two major mechanisms of kin discrimination found in mammals are based on either familiarity, i.e. learnt recognition of relatives, or phenotypic matching (Tang-Martinez 2001). Both mechanisms suggest that the ability to discriminate between kin and non-kin decreases with decreasing relatedness and thus tolerance towards neighbouring intruders is not expected to be linearly associated with relatedness (Smith 2014). By comparing overlap for the different relationship categories, we show that the effect of relatedness was primarily caused by an increased overlap between mother–daughter dyads and not the similarly related full-siblings. We could not assess if the effect of relatedness was due to learnt recognition (i.e. mother offspring, littermates) or phenotypic matching (i.e. non-littermate full-siblings) because of the small sample size of full-siblings. However, there was an 87% probability that the half-sibling relationship category had a lower overlap than predicted for the corresponding relatedness of 0.25, assuming a linear effect of relatedness on overlap (Fig. 2). This supports that space-use overlap is primarily driven by a nepotistic tolerance among mothers and adult daughters.

The tolerance of sharing space with related neighbours indicates that kin selection (Hamilton 1964) may play an important role in the spatial organization of Eurasian lynx, a solitary and territorial species. Similarly, several other solitary species share resources with kin to a larger extent than non-related individuals (Bailey 1993, Smith 1993, Poole 1995, Janečka et al. 2006, Innes et al. 2012, Rodgers et al. 2015). However, there are also studies that showed no effect of relatedness on resource sharing (Nicholson et al. 2011, Elbroch et al. 2016, Schmidt et al. 2016) or even contradictory results within the same species (Schenk et al. 1998, Moyer et al. 2006). We found that neither resource dispersion nor kin selection alone could explain lynx spatial organization, in fact, had we only considered relatedness or resource dispersion, important effects would have been overlooked. Consequently, between-study contradictions and species-specific 'special cases' may be the result of failing to account for how these general ecological drivers interact. To understand the flexibility of animal spatial organization, our study highlight the need to take into account both environmental factors and genetic relationships (Maher and Lott 2000, Kappeler et al. 2013, Hofmann et al. 2014) and that there are likely to be large knowledge gains when these interactions are examined.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.mcvdncjxk> (Aronsson et al. 2020).

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Author contributions – This study was conducted within long term research projects led by HA and JP. MA, ML, JP and HA designed the study. MA performed spatial analysis. MÅ performed genetic analysis. MA and ML performed statistical analysis. MA wrote the manuscript with support from JP, MÅ and all other co-authors. All authors approved submission of the manuscript. JP and HA were shared senior authors and project leaders.

Permits – All animal-handling procedures were approved by the Swedish Animal Ethics Committee and fulfils their ethical requirements for research on wild animals, protocol number C239/12.

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Supplementary material (available online as Appendix oik-07258 at <www.oikosjournal.org/appendix/oik-07258>). Appendix 1.