Foraging Ecology, Genetic Diversity and Spatial Behaviour of Caucasian lynx in Anatolia

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CHAPTER 1: General Introduction

Large carnivore research and conservation in Turkey

Biodiversity conservation is often linked to the conservation of flagship or umbrella species. Protecting such species should in turn result in the conservation of a wider array of biological diversity (Walpole & Leader-Williams, 2002). Conservation of wildlife species often requires highly demanding practices such as habitat preservation and restoration, animal protection, animal relocation, captive breeding and reintroductions (IUCN/SSC, 2008). However, for data deficient animal populations it is difficult to design efficient conservation measures because there is insufficient information on their population, demographic and genetic status (IUCN/SSC, 2008). Turkey has many species of large mammals that at a global level are considered to be at risk such the leopard *Panthera pardus*, the striped hyena *Hyaena hyaena* and the mountain gazelle *Gazella gazella*. Some are considered, at the national level, to be endangered or decline in population size, including the leopard, the striped hyena, the brown bear *Ursus arctos*, chamois *Rupicapra rupicapra* and fallow deer *Dama dama*. Several subspecies of widely distributed carnivores, including the Asiatic lion *Panthera leo persica*, the Caspian tiger *Panthera tigris tigris* and the Asiatic cheetah *Acinonyx jubatus venaticus* have been extirpated in Turkey in the last two centuries (Sekercioglu et al., 2011). Captive breeding, wildlife reserves and reintroduction efforts of the Wildlife Department at the Ministry of Agriculture and Forestry in Turkey are focused on ungulate species such as the autochthonous fallow deer, red deer *Cervus elaphus*, Anatolian wild sheep *Ovis gmelinii anatolica*, goitered gazelle *Gazella subgutturosa* and mountain gazelle. Considering large carnivores, there is only one wildlife development reserve allocated to protect the local striped hyena population. Despite of its extinct and extant large mammal diversity, species specific conservation research in the country is still in the developing stage. Most studies employ camera trapping in order to establish inventories of medium and large mammal communities (Can and Togan, 2010; Ilemin and Gürkan, 2010; Akbaba and Ayas, 2010).

Turkey is a very large country that harbours a wide variety of ecosystems and climatic zones, region specific anthropogenic activities and different compositions of wild and domestic ungulates (Sekercioglu et al., 2011). Therefore, in order to understand the ecology and behaviour of large carnivores and the level of the human-carnivore conflict in the country, species-specific multi-region studies are a necessity to propose appropriate evidence based conservation solutions. Such research has been conducted by several groups on a limited number of species and is often restricted to single populations. For instance, the large mammal with the highest number of published research articles in Turkey is the brown bear. All studies focused on a single population in northeastern Turkey (Ambarli

and Bilgin, 2008; Ambarli, 2016a, 2016b; Cozzi et al., 2016; Ambarli et al., 2018), yet being a widely distributed large carnivore in Turkey, diet, population dynamics and genetics and level of conflict with humans are expected to vary across the country. Conflict might take place with bee keepers and orchard owners in northern Turkey (the largest brown bear population in the country), shepherds in Eastern Turkey and bee keepers in southwestern Turkey (a critically endangered bear population numbering probably less than 30 individuals) depending on the main human activity and available food base (Ambarli et al., 2016). As the carnivore responsible for most conflicts, the gray wolf *Canis lupus* is still very little studied and the contribution of livestock and wild prey to wolf diet in different regions of the country is still unknown. Until today, there is one published study that focused on local wolf diet, where livestock farming is the main human activity and wild prey is very scarce (Capitani et al., 2016). An interview-based, unpublished study focused on wolf-shepherd conflict in central Anatolia where wild prey was almost absent (Tug 2005). With these two studies, a misperception of wolves in Turkey focussing on domestic livestock as food might be likely, possibly exacerbating the perception of woves as a source of livestock damage even in regions of Turkey where wild prey is common and livestock depredation low or absent. Such a misperception or a negative reputation also holds true for the striped hyena; this species has been almost totally extirpated in its range in western Turkey (AbiSaid and Dloniak, 2015). The establishment of the striped hyena protection reserve did not improve protection for the local hyena population as much as was expected, and interviews with locals (Mengüllüoğlu unpublished data) revealed that poaching of striped hyenas continues. People often confuse this cryptic and shy species with the spotted hyena *Crocuta crocuta* which does not occur in Turkey but nevertheless incites fear and hence an aggressive attitude. In southeastern Turkey, where a low density population still thrives, there are few records of conflict with livestock farmers or attack on humans.

Turkey is home to five felid taxa, the wildcat *Felis silvestris,* the jungle cat *Felis chaus*, the caracal *Caracal caracal*, the Caucasian lynx *Lynx lynx dinniki* and the Persian leopard *Panthera pardus saxicolor*. Latter went extinct in the western part of the country in the 1980s, it is under heavy poaching pressure, and with the on-going armed conflict in this region, field based research and conservation is currently not possible (Avgan et al., 2016). The Caucasian lynx is relatively widespread in the country and occurs in most mountain ranges (Breitenmoser et al., 2017). Although it is currently considered to be one of two widely distributed felid species in Turkey (Turan, 1984), the other being the wildcat, information about the status, ecology and genetics of the lynx in the country is still scarce. Highway collisions and habitat fragmentation by hydroelectric dam constructions are considered to be the main anthropogenic activities threatening the large lynx populations in Turkey (Mengüllüoğlu, unpublished data). Poaching also takes placeas there are media reports of five to ten individuals being

poached in various parts of the country every year. During the most recent period, there were 5 cases reported in the national media between January 2018 and March 2019. Unlike for the other large carnivores which also have large populations in neighbouring countries (Lortkipanidze, 2010; Jacobson et al., 2016), Turkey probably holds the largest Caucasian lynx population and therefore is key to the viability and genetic diversity of this subspecies of Eurasian lynx. Therefore, in order to set up efficient conservation measures and prevent a population decline of Caucasian lynx similar to those of other large felids in Turkey, a conservation action plan is urgently needed. Such conservation action plan requires baseline ecological, behavioural and genetic data.

Eurasian lynx research and conservation

The Eurasian lynx is a Palearctic species and one of several felids with a wide distribution. Its historical distribution once covered all of Europe except for the Iberian Peninsula and ranged all the way to the Middle East, the Himalayas and Tibet as well as far eastern Asia (Breitenmoser et al., 2017). Populations occur in a wide variety of habitats including European deciduous forests, boreal mixed and coniferous forests, tundra, central Asian rocky mountain steppes and alpine zones in Asia and Europe.

Most studies on the ecology, behaviour and genetics of Eurasian lynx have been conducted on populations in central and eastern Europe (e.g., Jedrzejewski et al., 1993; Okarma et al., 1997; Jobin-Molinari et al., 2000; Sunde et al., 2000; Rueness et al., 2014) and few elsewhere (Sedalischev et al., 2014; Weidong, 2010). Whereas mtDNA diversity has been characterized for several populations of Eurasian lynx across its range and different subspecies, nuclear genetic data are only available for European lynx populations, several of which are considered 'endangered' or 'vulnerable' (Rueness et al., 2014; Bull et al., 2016). The two subspecies of Eurasian lynx in Asia, *L. l. dinniki* and *L. l. isabellinus*, are still understudied in terms of their local ecological and behavioural requirements and adaptations, genetic diversity and evolutionary genetics. The presence of more charismatic felid species in their distribution range, such as snow leopard *Uncia uncia,* tiger and leopard in southern-central Asia and leopard in Caucasus and Iran may have contributed to their neglect in terms of scientific field studies. Most publications on the Asian subspecies of lynx are anecdotal, obtained while collecting data on larger felids or other carnivores, and providing limited ecological information or distribution records.

The Caucasian lynx has one of the southernmost distributions of the various Eurasian lynx subspecies, stretching from the Anatolian part of Turkey to the Caucasus and Iran. Compared with its north and central European conspecifics, it displays some ecological, behavioural and morphological differences.

It mostly occurs in fairly dry and open coniferous and open hilly and mountain habitats. In Turkey, it is a protected species under Turkish law. No hunting quotas are issued by the Department of Hunting. However, anthropogenic factors mentioned above threatening extant lynx populations and probably limiting their connectivity. Only recently did researchers collect some actual evidence for the occurrence of the species in different parts of the country and realized that it is fairly common (Ambarlı et al., 2010; Chynoweth et al. 2015) and can occur in high densities (Mengüllüoğlu, 2010; Avgan et al., 2014). Perhaps unexpectedly, lynx distribution in Turkey does not overlap much with roe deer, the main prey species in Europe, it has much higher densities in suitable habitats than known from European populations, and its presence highly overlaps with the distribution of the brown hare *Lepus europaeus* rather than that of ungulates (Soyumert et al., 2018). Hence, it seems that prey requirements, habitat use, high densities and space use of lynx in Turkey might be very different from lynx populations in Europe. Designing conservation actions built upon expectations derived from populations studied in Europe therefore might not be an appropriate approach. A Caucasian lynx conservation action plan should instead be built upon robust baseline information collected from Caucasian lynx populations.

To meet this challenge, the present dissertation was designed in collaboration with Wildlife Department of General Directorate of Nature Conservation and National Parks, Turkish Ministry of Agriculture and Forestry. The plan was to collect baseline ecological, behavioural and genetic data on Caucasian lynx populations in Turkey. The work reproted in this dissertation focused on three large Caucasian lynx populations in order to reveal their feeding requirements, and a study area in northwestern Turkey to reveal spatial tactics, population genetics and social organization of Caucasian lynx, making use of, benefitting from the insights gained by and expanding the results from long-term monitoring of the same population.

Study areas

Turkey is a large country and home to three of the world's 34 biodiversity hotspots: Mediterranean, Irano-Anatolian and Caucasus (Conservation International 2005). It is also at the junction of three of 37 phytogeographical regions: Mediterranean, Irano-Turanian and Euro-Siberian. It therefore has a substantial biological diversity, a high degree of endemism and different plant and associated animal communities in different parts of the country. Except for the wide spread wild boar *Sus scrofa*, all ungulate species have localised distributions or are limited in their occurrence to specific parts of the country (Turan, 1984). Wild boar and brown hare are the only two common potential prey species occurring almost anywhere in Turkey, their ranges therefore completely overlap with extant lynx

populations. Wild goat *Capra aegagrus* coincides with half of the lynx distribution in southern and eastern Turkey, and red deer *Cervus elaphus* in northwestern Turkey overlaps with one third of the lynx distribution in Turkey. Roe deer distribution has a very limited overlap with lynx distribution in Turkey because of their different habitat preferences. Therefore, based on Eurasian lynx foraging ecology in European populations, which are known to specialise on ungulates, lynx in Turkey are likely to choose different prey species than European populations, and prey choice possibly depending on the specific locality in Turkey.

Therefore, lynx foraging ecology and prey preferences was studied in three lynx populations occupying different ecosystems, where lynx are sympatric with at least two ungulate species in each case. In a high Mediterranean ecosystem in southern Turkey, the lynx study population overlapped with wild goat and wild boar. In a forest-steppe mixed ecosystem in northwestern Turkey, the overlap was with red deer and wild boar, and in a subalpine Caucasian ecosystem in northeastern Turkey the lynx study population overlapped with wild goat and wild boar. Population genetics and spatial organization were studied in a forest-steppe mosaic ecosystem in nothwestern Turkey, as this population has been long-term monitored since 2009. The insights gained from such long-term monitoring were expected to instruct the period of intensive study available for this dissertation.

Figure 1. Locations of the three study areas (colored in orange) in Turkey

South: Mediterranean ecosystem

According to the IUCN Mediterranean Biodiversity Assessment from 2010, the Mediterranean population of Eurasian lynx is listed as endangered. In Europe there is one indigenous Mediterranean lynx population with an estimated number of 50 individuals occurring in several Balkan countries, Albania, Kosovo, Macedonia and Montenegro (Melovski et al., 2012). A reintroduced Carpathian lynx population is distributed across Bosnia, Croatia and Slovenia and experiences serious levels of inbreeding (Sindicic et al., 2013; Bull et al., 2016). The lynx population in southern Turkey is therefore a potentially important stronghold for Mediterranean lynx if its population size is sufficiently large.

The study area in southern Turkey was in Antalya Çığlıkara Nature Reserve and Cedar Research Forest in Antalya province. It is mostly covered by evergreen Lebanon cedar trees *Cedrus libani* and junipers *Juniperus excelsa* and otherwise sparse vegetation. The study area covered 180 km^2 at elevations between 1,290 and 3,000 m. Lynx distribution in this region starts at an altitude of around 1000 m and thus overlaps with the distribution of local wild goats. The reserve is close to settlements but also surrounded by high mountains and its access by people is limited. Human activities are not allowed in the park area; there is no free road access. The area is known to have a high density of lynx (Avgan et al., 2014). Potential prey species in this study area are wild goat, wild boar and brown hare.

North-west central: Forest-steppe mosaic ecosystem (long-term monitoring)

Long-term population monitoring through camera trapping, GPS tracking and genetic sampling were started in Nallıhan Mountains, northwestern Anaolia, in 2009 (Figure 1). Altitude varied between 500 m and 1,550 m. The study area was located in the transition zone between the dry western Black Sea (xero-euxine) and central Anatolian (Iran-Turan) floristic zones. This region is also influenced by the Mediterranean floristic zone (western Aegean), through the catchment area of the Sakarya River (Aksoy, 2009). Vegetation composition and structure depended on altitude and historical human use. The lower areas (500–1,000 m) were covered by Turkish pine *Pinus brutia*. Above this belt, a temperate coniferous forest reached up to 1500 m and was composed of black pine *Pinus nigra*, junipers *J. excelsa* and *J. oxycedrus* with an understorey of oak *Quercus pubescens* dominated scrub, other key species including the oleaster-leafed pear *Pyrus elaeagnifolia* and several species of hawthorn *Crataegus spp.* (Aksoy, 2009). The human population in this area is at a low density and restricted to several villages in the surrounding lowland and valleys. The potential prey species for lynx are red deer, wild boar and brown hare. The area is home to several other large carnivores, including brown bear and gray wolf and meso-carnivores such as golden jackal *Canis aureus*, red fox and jungle cat (Mengüllüoğlu, 2010).

Northeast: subalpine ecosystem (Artvin, Lesser Caucasus)

Fecal samples were collected in the Kaçkar Mountains of Artvin Province, in north eastern Turkey, in an area of 400 km^2 (Figure 1). Our survey area covered elevation zones between 700 and 2,500 m. The vegetation changes from oak woodlands at 700–1,600 m to alpine meadows above 2,200 m with mixed dense forest, dominated by fir *Abies nordmanniana* and spruce *Picea orientalis* on northern slopes, and Scots pine *Pinus sylvestris* woodland on southern slopes (Ambarlı and Bilgin, 2013). Deciduous shrubland occurred mostly on the southern slopes of the mountains at drier lower elevations, mixed forests were present in more humid parts. Wild goat, chamois, wild boar and brown hare are potential prey of lynx in this area. Brown bear, gray wolf, golden jackal and red fox are other carnivore species in sympatry with lynx in this area (Ambarlı and Bilgin, 2013).

Structure of this dissertation

The results of this study are presented in the form of three manuscripts in chapters 2 to 4:

Chapter 2. Prey base is one of the main factors influencing success in carnivore conservation actions and maintaining healthy carnivore populations. It is also one of the major drivers of carnivore ecology such as daily movements, home ranges and demography, including adult and juvenile survival, population turnover and longevity. In Chapter 1 ("Foraging ecology of Eurasian lynx populations in southwest Asia: Conservation implications for a diet specialist"), I investigated the foraging ecology of Caucasian lynx populations in three major ecosystems of Turkey based on collected faeces and estimated prey abundances. I quantified ecosystem-specific prey preferences and the functional response of the lynx and compared them with central and eastern European lynx populations.

Chapter 3. As in this study, many population monitoring and conservation studies of data deficient carnivore populations start in small study areas and are confined to a limited number of resident individual ranges. In Chapter 2 ("Non-invasive faecal sampling reveals spatial organization and improves measures of genetic diversity for the conservation assessment of territorial species: Caucasian lynx as a case species"), I investigated the genetic variability, relatedness and spatial organization of the northwest Anatolian lynx population and investigated the influence of sampling type (invasive vs. non-invasive) on genetic diversity measures of territorial (and philopatric) species. This study was based on lynx genotypes obtained from non-invasive faeces and from tissue and hair samples collected from lynx being caught in box traps for the purpose of collaring them with GPS telemetry devices. By applying a genotype subsampling analysis, I investigated how sampling type

might influence the genetic diversity measures of the same lynx population as a result of spatial organization of adult lynx and philopatry in females.

Chapter 4. Caucasian lynx has one of the southernmost distributions within the range of the Eurasian lynx. Earlier studies showed that Eurasian lynx home range sizes decreased and density increased from northern to southern latitudes. In Chapter 3 ("Female and male Caucasian lynx have distinct spatial tactics at different life-history stages in a high density population"), I investigated the population density and home range sizes of female and male adult lynx in northwestern Anatolia and compared them with central and eastern European lynx populations. Here I applied spatially explicit capture-recapture models to estimate lynx density and conventional home range methods to estimate the home range size of different lynx age classes in the main study area. In this chapter, I also discuss the possible influence of prey base and hunting on density and home range size of different Eurasian lynx populations in Europe and Turkey.

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CHAPTER 2: Foraging ecology of Eurasian lynx populations in Anatolia

Foraging ecology of Eurasian lynx populations in southwest Asia: Conservation implications for a diet specialist

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DM, HA, AB, and HH designed the study. HA and DM conducted field works. DM and HA performed laboratory analysis and calculations. DM and HA wrote the drafted manuscript. HH and AB provided input to the writing of the manuscript. HA, DM, HH, and AB revised the final manuscript. HA is the corresponding author.

Abstract

Intraspecific variation in key traits of widespread species can be hard to predict, if populations have been very little studied in most of the distribution range. Asian populations of the Eurasian lynx (*Lynx lynx*), one of the most widespread felids worldwide, are such a case in point. We investigated the diet of Eurasian lynx from feces collected Mediterranean, mixed forest-steppe, and subalpine ecosystems of Turkey. We studied prey preferences and functional responses using prey densities obtained from Random Encounter Modelling. Our analysis revealed that the main prey was brown hare (*Lepus europaeus*) in all three areas (78%-99% of biomass consumed) and lynx showed a strong preference for brown hare (Chesson's selectivity index, α = 0.90-0.99). Cannibalism contributed at least 5% in two study areas. The type II functional response of lynx populations in Turkey was similar to the Canada lynx (*Lynx canadensis*) and daily food intake in grams per lynx matched that of Canada lynx and Iberian lynx (*Lynx pardinus*), both lagomorph specialists, rather than those of Eurasian lynx from Europe. Therefore, lynx in Turkey may be better described as a lagomorph specialist even though it coexists with ungulate prey. We suggest that ungulate-based foraging ecology of Eurasian lynx in Europe may be a recent adjustment to the availability of high densities of ungulates and cannot be representative for other regions like Turkey. The status of lagomorphs should become an essential component of conservation activities targeted at Eurasian lynx or when using this species as a flagship species for landscape preservation.

Keywords: brown hare, cannibalism, feeding behaviour, functional response, prey preferences, Turkey

Introduction

Assigning a certain trait to a particular population and generalising it towards the species can cause over-simplification errors, especially in case of widespread species which experience substantial variation in environmental conditions and habitats (Putman and Flueck, 2011). Such generalizations may miss relevant variability in behaviour, physiology and ecology between populations, particularly in taxa such as carnivores that show considerable interspecific and intraspecific variation (Lott 1991, Moehlman and Hofer, 1997). These generalizations may become of practical relevance if conservation actions are built upon expectations derived from populations studied elsewhere, with the potential to fail if the biology of the local population is different, for instance because it is adapted to local and historical environmental conditions.

The Eurasian lynx (*Lynx lynx* Linnaeus, 1758) is a Palearctic species and one of several felids that have very wide distributions. Although European populations have suffered a tremendous decline, the species still covers a vast range from central Europe to central, north and far eastern Asia. Most studies on the ecology and behaviour of lynx have been conducted on populations in central and eastern Europe (e.g. Jedrzejewski et al., 1993; Okarma et al., 1997; Jobin et al., 2000; Sunde et al., 2000; Odden et al., 2006), with very few exceptions (Weidong, 2010; Sedalischev, 2014), and concluded that Eurasian lynx is a specialist predator of medium-sized and large-sized ungulates, and hunts smaller mammals when ungulates are not available (Jedrzejewski et al., 1993; Breitenmoser et al., 2000; Odden et al., 2006). If this general hypothesis is correct, then other lynx populations, for instance in Asia, should show the same foraging ecology and feeding preferences as the central European populations. From a comparative perspective, it is noteworthy that other lynx species rarely hunt medium-sized or large-sized ungulates and prefer to hunt lagomorphs instead. For instance, although it is known to kill other prey species (Bergerud, 1983) the Canada lynx (*Lynx canadensis*) is considered to have specialised on hunting snowshoe hare (*Lepus americanus*), the only available medium-sized mammal in North America present during the evolution of this lynx species (Werdelin, 1981). Similarly, the Iberian lynx (*Lynx pardinus*) is a specialist hunter of rabbits (*Oryctolagus cunniculus*). Since Eurasian lynx first evolved in Asia (Werdelin, 1981), an alternative hypothesis suggests that we should expect Eurasian lynx in Asia to be a lagomorph specialist like Canada and Iberian lynx and differ in its foraging ecology from Eurasian lynx populations in central and eastern Europe where the lynx diet is based on ungulates.

In this study, we tested both hypotheses by studying the foraging ecology and diet of Eurasian lynx (*Lynx lynx*) populations in three geographic regions of Anatolia, the Asian part of Turkey. We also compared the foraging ecology of lynx in Turkey, other Eurasian lynx populations, Canada and Iberian

lynx. Our three study areas represent major ecosystems in much of southern Europe and southwestern Asia: a Mediterranean ecosystem in the south, a mixed forest-steppe ecosystem in the central part and a subalpine ecosystem (Lesser Caucasus) in northeastern Anatolia. We collected faecal samples of lynx in those ecosystems where lynx is in sympatry with at least two ungulate species known to be preyed by Eurasian lynx elsewhere. Additionally, we used camera trap data to estimate prey densities and biomass to quantify prey preferences of lynx subpopulations in Turkey and compare them to European conspecifics and other lynx species. We discuss implications of these results for the design of appropriate conservation initiatives for lynx in Turkey.

Material and Methods

Study areas

South: Mediterranean ecosystem (Antalya)

Faecal samples from the Mediterranean ecosystem were obtained from Antalya Çığlıkara Nature Reserve and Sedir Research Forest in Antalya (Figure 1). The study area was mostly covered by evergreen Lebanon cedar trees (*Cedrus libani*) and otherwise sparse vegetation. The study area covered 180 km^2 at elevations between 1290 m and 3000 m. It was close to settlements but also surrounded by high mountains and had limited access. Human activities were not allowed in the park area; there is no free road access. The area is known to have a high density of lynx (Avgan et al. 2014). Potential prey species in this study area were wild goat (*Capra aegagrus*), wild boar (*Sus scrofa*) and brown hare (*Lepus europaeus*). Gray wolf (*Canis lupus*) and red fox (*Vulpes vulpes*) were two intra-guild carnivores in sympatry with lynx in this area (Avgan et al., 2014).

Central-west: Steppe-forest mosaic ecosystem (Ankara)

Here, faeces of lynx were collected in an area of 400 km^2 in the Nallıhan Mountains (Figure 1). The elevation varied between 500 m to 1550 m and the study area was located in the transition zone between the dry western Black Sea (xero-euxine) and central Anatolian (Iran-Turan) floristic zones. This region is also influenced by the Mediterranean floristic zone (western Aegean), through the catchment area of the Sakarya River (Aksoy, 2009). Vegetation composition and structure depended on altitude and historical human use. The lower areas (500 to 1000 m) were covered by Turkish pine (*Pinus brutia*). Above this belt, temperate coniferous forest reached up to 1500 m and was composed of black pine (*Pinus nigra*), junipers (*Juniperus excelsa* and *J. oxycedrus*) with an understory of oak-

dominated scrub (*Quercus pubescens*, *Pyrus elaeagnifolia*, *Crataegus* spp., Aksoy 2009). The human population in this area is at a low density and restricted to several villages in the surrounding lowland and valleys. The potential prey species for lynx are red deer (*Cervus elaphus*), wild boar and brown hare. The area is home to several other large carnivores, including brown bear (*Ursus arctos)*, gray wolf, golden jackal (*Canis aureus*), red fox and jungle cat (*Felis chaus*) (Mengüllüoğlu, 2010).

Northeast: subalpine ecosystem (Artvin, Lesser Caucasus)

Faecal samples were collected in the Kaçkar Mountains of Artvin Province, in north eastern Turkey, in an area of 400 km^2 (Figure 1). Our survey area covered elevation zones between 700 m to 2500 m. The vegetation changes from oak woodlands at 700–1600 m to alpine meadows above 2200 m with mixed dense forest, dominated by fir (*Abies nordmanniana)* and spruce (*Picea orientalis)* on northern aspects, and Scots pine (*Pinus sylvestris*) woodland on southern aspects (Ambarlı and Bilgin 2013). Deciduous shrubland occurred mostly on the southern aspect of the mountains at drier lower elevations whereas mixed forests were present in more humid parts. Wild goat, chamois (*Rupicapra rupicapra*), wild boar and brown hare are potential prey of lynx in this area. Brown bear, gray wolf, golden jackal and red fox are other carnivore species in sympatry with lynx at this area (Ambarlı and Bilgin, 2013).

Figure 1. Locations of the three study areas (colored in orange) in Turkey

Faeces collection and diet analysis

Relatively fresh samples (n = 27) were opportunistically collected in the southern study area while walking on dirt roads between December 2013 and April 2014. We identified them to be of lynx origin by size, shape and distinct odour. The only faeces which could be misidentified in this area were those of red foxes. We excluded two faeces because they failed the lynx scat identification criteria (Kaczensky et al., 2009), namely their segmentation and shape patterns, and had smaller diameters (1.4 and 1.5cm).

Faeces (n = 101) from the central-western study area were collected by walking on active wildlife trails, dirt roads and ridgelines in the Nallıhan Mountains between November 2013 and March 2015. In order to reduce the chance of falsely designating faeces from other wild carnivores and dogs as lynx faeces, a Labrador breed dog was trained to find and identify lynx faeces (Smith et al., 2001) in this study area, since this area is more frequently visited by domestic hunting dogs than the other two study areas.

The samples (n = 69) from the subalpine study area were collected randomly between 2010 and 2014 on 10 predetermined transects along trails below the tree line. They were chosen because of the long distance from settlements and human interference, lack of road access and the absence of red foxes. The length of transects varied between 1.5 km to 8.0 km (mean distance = 3.8 ±0.7 km). They were checked on foot every year.

In addition to visual and olfactory identification, all samples collected from forest-steppe study area (n = 101) and fresh samples from Mediterranean (n = 16) and subalpine study areas (n = 20) were genetically analysed for microsatellites and confirmed to belong to lynx. Although, old samples were not genetically analysed, they matched in size and appearance the genetically identified 137 lynx samples. Lynx faeces were oven-dried and washed following the protocols of Wagner et al. (2012). Prey remains such as hair, bones, teeth, nails and feathers were separated and weighed. Hairs were classified according to their microstructure and identified with the help of reference books (Teerink 1991) or by comparing them with local wildlife and livestock reference collections taken from the Berlin Natural History Museum (Supplementary Material, Table A1). After classification of faecal material, the frequency of occurrence (FO) of each species in the diet was noted and compared with the diets of lynx populations in Europe (Klare et al., 2011). For the purpose of estimating the consumed biomass per prey species, we used the lynx regression model of Wachter et al. (2012), which was applied to the results of European lynx feeding experiments conducted by Rühe et al. (2007). We calculated the consumed mass of each prey species per faeces and then multiplied this value with the total ingested volumes. For the species that were not included in Rühe et al.'s (2007) experiment we

directly applied the model on average body weight of prey species and obtained consumed biomass per faeces.

Prey preferences

Population densities and mean biomass of the prey species in the study areas have to be known in order to assess prey preferences. For the prey species where individuals cannot be individually distinguished in camera-trap photos, density estimation in forest habitats is difficult and generally gives biased results as the actual population numbers are underestimated (Jobin et al. 2000). We therefore used the Random Encounter Model (REM; Rowcliffe et al., 2008) to estimate the density *D* of mid-sized and large herbivore prey as $D = \frac{y}{t} * \frac{\pi}{Vr(2+\theta)}$, where *y* is the number of independent photographic events, *t* is camera trap days (ctd), *V* is average speed of animal movement, *r* and ϑ are the camera trap detection distance (in kilometre) and angle (in radian). Animal movement speeds were taken from published literature with GPS fix frequencies of 15 minutes for red deer (Pepin et al. 2004) and wild boar (Spitz et al., 1990) and one hour for brown hare (Schai-Braun, 2012). Since there is no published data for movement speed of wild goat, we used movement speed of a wild goat collared in our subalpine study area with GPS fix frequency of two hours (Ambarlı, unpublished data).

In the model, we used the numbers of captures and camera trap days from the recent camera trapping studies in the southern and subalpine study areas (Avgan et al., 2014 and Ambarlı and Bilgin, 2013, respectively). The former one placed camera traps for 1093 camera trap days on dirt roads, and in the latter one camera traps were set up on trails in extremely rugged montane habitats for 620 camera trap days. Camera trapping data for the forest-steppe mosaic ecosystem were gathered from a 684 camera-trap-days survey, implemented by us while doing faeces surveys in the spring of 2014. In this survey, 12 camera trapping stations (two Cuddeback Attack, WI, USA, camera traps per station) were installed covering a minimum convex polygon of 148 km^2. Traps were installed on forest trails and, where there was no access to interior forest due to steepness, we installed them on dirt roads. We set a minimum interval of 30 minutes to assign two pictures of the same species as independent captures. Camera trap detection distance and angles where obtained from Meek et al. (2012). The camera trap surveys conducted in the three different ecosystems were designed to photograph lynx, but they also photographed other carnivores and prey species. Soofi et al. (2017) showed that red deer density estimates by distance sampling and REM did not differ significantly from each other although the camera traps were installed on leopard trails. Therefore, we assume that placements were random with respect to the movements of the three ungulate species and brown hare. We used

delta method (Seber, 1982) to calculate 95% of confidence intervals for the estimated densities (Table 1).

Table 1. Body weights (¾ adult female live body weights for ungulates) and camera-trap parameters used to calculate Random Encounter Model (REM) densities and prey biomass in three study areas in Turkey. a) Demirbaş et al. 2013, b) Turan 1984, c) Avgan et al. 2014, d) This study, e) Ambarlı and Bilgin 2013, f) Schai-Braun et al. 2012, g) Spitz et al. 1990, h) Ambarlı unpub.data, i) Pepin et al. 2004, j) Meek et al. 2012

Ecosystem	Herbivore prey	Body weight (kg)	Captures	Trap days	Travel speed (*v*)	Radius (*r*)	Angle (*ϑ, in radians*)	REM density (km^{-2}); 95% Confidence intervals	Number of stations
Mediterranean	brown hare	3.17[a]	343[c]	1029[c]	0.890 ± 0.163[f]	0.011[j]	0.70[j]	36.15 ± 7.46; [26.69 - 55.52]	17[c]
	wild boar	60[b]	26[c]		6.591 ± 3.157[g]			0.41 ± 8.56; [0.19 - 2.31]	
	wild goat	30[b]	1[c]		1.580 ± 0.027[h]			0.07 ± 0.00; [0.06-0.07]	
Forest-steppe	brown hare	3.17[a]	508[d]	684[d]	0.890 ± 0.163[f]	0.011[j]	0.70[j]	88.27 ± 18.77; [64.94 - 134.92]	12[d]
	red deer	75[b]	41[d]		3.988 ± 1.788[i]			1.59 ± 8.98; [0.80 -7.98]	
	wild boar	60[b]	57[d]		6.591 ± 3.157[g]			1.34 ± 11.55; [0.61 - 7.34]	
Subalpine	brown hare	3.17[a]	7[e]	620[e]	0.890 ± 0.163[f]	0.011[j]	0.73[j]	1.33 ± 0.28; [0.98 - 2.04]	8[e]
	wild boar	60[b]	12[e]		6.591 ± 3.157[g]			0.31 ± 4.07; [0.14 -1.68]	
	wild goat	30[b]	21[e]		1.580 ± 0.027[h]			2.24 ± 0.04; [2.16 - 2.33]	

On the basis of the estimated densities, available mean prey biomass was calculated by using an average adult live body weight of 3.17 kg for brown hare (Demirbaş et al., 2013) and three fourth of female adult live body weights of 75 kg for red deer, 30 kg for wild goat and 60 kg for wild boar to account for juveniles (Turan, 1984).

Chesson's selectivity index α (Chesson, 1978) was then used to assess lynx prey preferences. Chesson's α is defined as the proportion of prey species in the scat divided by the proportion of prey species *i* in the environment, p_i, normalized in such a way that the sum of the alpha values over all *k* prey species equals one (Chesson, 1978).

Functional response

We assessed the functional response and daily food intake rates of three species of lynx preying on their favourite prey species using Holling's disc equation (Holling, 1965). These included our three lynx populations in Turkey preying on brown hare (Mediterranean, An1; Forest-steppe, An2; Sub-alpine, An3), two European lynx populations preying on mountain hare (*Lepus timidus*) in Finland (Fin1, Fin2), seven Eurasian lynx populations in central and eastern Europe preying on roe deer (Eu1-Eu7), and compared them with the lagomorph specialists Canada lynx, CL (preying on snowshoe hare) and Iberian lynx, IL (preying on rabbits). Prey intake (Ψ, prey intake per lynx per day) was calculated as $(\Psi) = \frac{aN}{1+a(h1+h2)N}$, where *a* is the area of effective search per unit time, *N* is the prey density, h_1 is the time per attack multiplied by attacks per successful capture and h_2 prey handling time which is the time period needed to consume and digest a killed prey item (Holling, 1965). Calculated prey intakes were multiplied with available carcass masses of prey to get food intake rates in grams per lynx per day (please see the Supplementary Material, Table A2 for references of all population specific parameters used in these calculations).

We used two different average daily moved distances (DMD) for Eurasian lynx in Turkey and other areas of Eurasian lynx range because of the differences in habitats and body sizes. DMD for lynx populations in Turkey was calculated from 5 radio-collared lynx individuals and 15,421 GPS locations (24 fixes per day) to be 5.12 km/day (Mengüllüoğlu, unpublished data), whereas an average DMD of 7.2 km/day (Jedrzejewski et al., 2002) was used for the European populations. Densities for roe deer, mountain hare, snowshoe hare and European rabbits were obtained from previous published work (Supplementary Material, Table A2). Success of attack was assumed to be the same for brown hare, and mountain hare as 35% (Pulliainen, 1995) and for roe deer as 66% (Pulliainen, 1995). Since hares and rabbits are completely consumed by lynx, total adult mass was used for the calculation of biomass

consumed. For roe deer, 70% of roe deer body mass was assumed to be ingested by lynx as indicated in the previous feeding studies (Okarma et al., 1997; Sunde et al., 2000; Rühe et al., 2007).

Time per attack on hares was assumed to be the same as the attack time of Canada lynx on snowshoe hare, i.e. 33 seconds (Pulliainen, 1981), and 30 seconds for Iberian lynx on European rabbit (Supplementary Material, Table A2). Time per digestion for brown hare was estimated from cluster data for 5 lynx individuals from Anatolia to be 3 days on average (Mengüllüoğlu et al., unpublished data) and 2 days of digestion for Finnish lynx populations (Pulliainen, 1981), 2 days for Canada lynx and one day for Iberian lynx (Supplementary Material, Table A2). An average number of 6 days was used for European lynx populations consuming roe deer (Jobin et al., 2000). A sensitivity analysis (Burgman et al., 1993) was carried out to assess which parameters in Holling's disc equation had a strong influence on Ψ, by applying Beck's Rule (Beck, 1983). Ψ was regarded as highly sensitive to a given input parameter if a 10% change in the value of the input parameter led to a change in Ψ which exceeded 10%, and showed low sensitivity if the change in Ψ was less than 10%.

Results

Diet of lynx populations in Turkey

A total of 22 different prey species were identified from 256 food remains in 195 faeces (Table 2). Eurasian lynx in the Mediterranean ecosystem had five prey items (Table 2). The most diverse diets belonged to Eurasian lynx in forest-steppe and subalpine ecosystems, with 16 and 15 different prey items, respectively, including unidentified birds and rodents as two items (< 5%). The number of prey items was higher in the two northern ecosystems (forest-steppe and subalpine) as here the faecal samples contained small mammals, birds and several carnivore species. The main prey of lynx was the brown hare in all ecosystems (Figure 2). Relative frequencies of occurrence of brown hare expressed as percentages were very high and quite similar: 100 % for the Mediterranean study area, 86% for the forest-steppe study area and 89% for the subalpine study area (Table 2). In terms of relative total biomass consumed, brown hare constituted 99% of the diet in the Mediterranean study area, 85% in the forest-steppe study area and 78% in the subalpine study area (Figure 3).

Table 2. Diet from faeces of Anatolian lynx in three different study areas in Turkey, expressed as frequency of occurrences (FO), relative frequency of occurrences (%FO), relative volume (% Vol) and relative biomass (% Bio). Bold percentages indicate Bio > 5%.

		Mediterranean (n=25)				Forest-Steppe Mosaic (n=101)				Subalpine (n=69)			
Wild prey	**Kg consumed per faeces**	**FO**	**% FO**	**% Vol**	**% Bio**	**FO**	**%FO**	**% Vol**	**% Bio**	**FO**	**% FO**	**% Vol**	**% Bio**
Capra aegagrus	1.03									4	6.2	5.9	**8.2**
Sus scrofa	0.49*/0.78	1	4	1.6	1.0*	3	3	2.7	2.8	1	1.5	1.4	1.5
Lepus europaeus	0.77	25	100	96.9	**98.5**	86	86	81.4	**84.8**	58	89.2	74.5	**77.6**
Lynx lynx	0.8					10	10	8.2	**8.9**	6	9.2	5.4	**5.8**
Canis aureus	0.8					1	1	0.7	0.7				
Vulpes vulpes	0.61									1	1.5	0.1	0.1
Martes foina	0.2									1	1.5	0.1	0
Sciurus anomalus	0.2	1	4	1	0.3	2	2	0.3	0.1				
Sciurus vulgaris	0.2									5	7.7	1.5	0.5
Glis glis	0.2									1	1.5	0.8	0.2
Dryomys nitedula	0.2					1	1	0	0				
Muscardinius avellanarius	0.2					1	1	0.3	0.1	2	3.1	0.6	0.2
Apodemus sp.	0.2	2	8	0.3	0.1	2	2	0.4	0.1	1	1.5	0	0
Microtus sp.	0.2					7	7	1.7	0.5	5	7.7	0.8	0.2
Myodes glareolus	0.2					1	1	0.1	0				
Crocidura sp.	0.2					1	1	0.2	0.1				
Unidentified rodent	0.2	1	4	0.2	0.1	1	1	0	0	7	10.8	0.6	0.2
Tetraogallus caspius	0.46									3	4.6	2.2	0.8
Unidentified bird	0.07					3	3	2	0.2	3	4.6	2.7	0.3
Testudo gracea	0.14					1	1	0.2	0				
Domestic prey													
Canis familiaris	0.93					1	1	1	1.2				
Felis catus	0.37					1	1	1	0.5				
Capra hircus	1.03									2	3.1	3.1	4.4

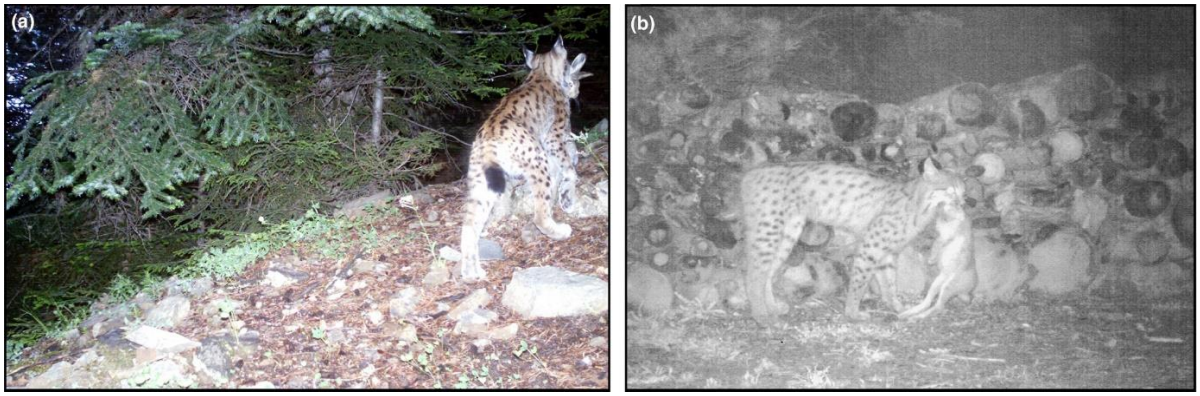

Figure 2. Camera trap photographs of lynx with killed brown hare in (a) subalpine study area in northeastern Turkey and (b) forest-steppe study area in central-west Turkey

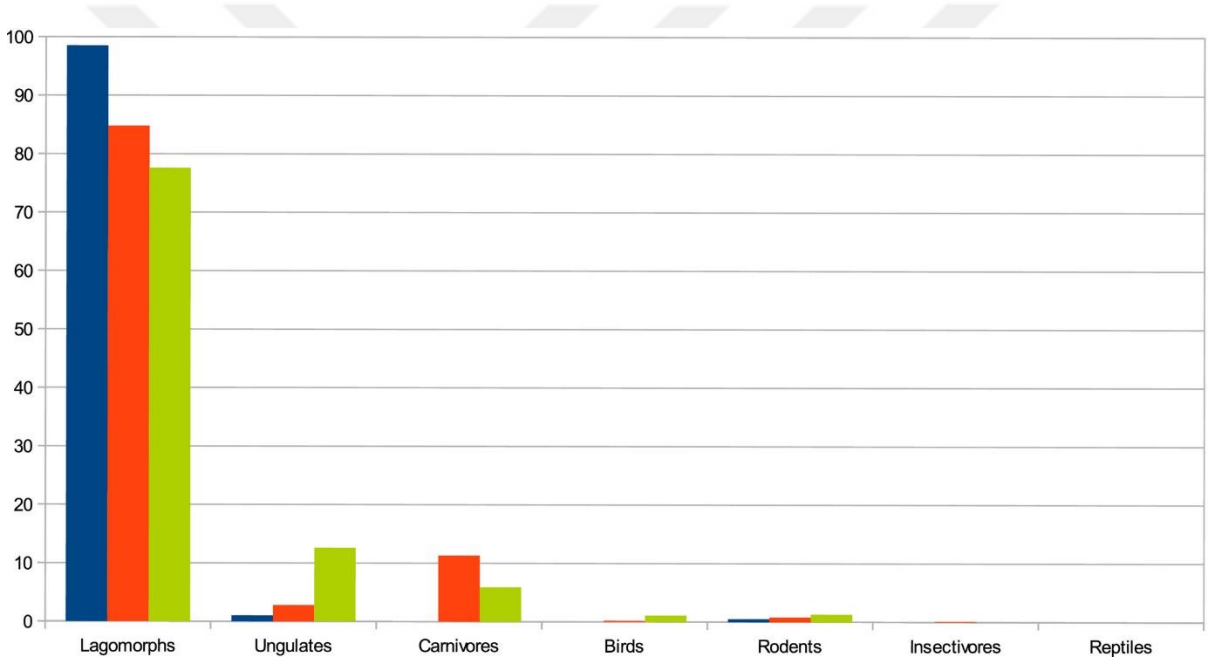

Figure 3. Percentages of consumed biomass in three lynx diets. Blue - Mediterranean, red - forest-steppe, and green - subalpine study areas.

Cannibalism

Eight samples (8.0%) from the forest-steppe study area and 5 samples (7.2%) from the subalpine study area (Table 2) presented lynx remnants, including hair, bones and claws, suggesting consumption of lynx carcasses rather than just documenting self-grooming. In the forest steppe study area, one sample was collected in autumn 2013 and seven in spring 2014, and the samples in the subalpine

study area were collected in spring and autumn of 2010-2014. No such evidence was found in the Mediterranean study area. This is a conservative assessment of the contribution of cannibalism to the diet as we considered that the faeces with lynx hair making <50% of contents could be attributed to self-grooming.

Prey preferences

In all three study areas, brown hare was the single dominant preferred prey among several other prey species (Table 3). Even in the presence of high available biomass of ungulates, as in the forest-steppe study area with red deer (24.9% of prey biomass) and in the subalpine study area with wild goat (74.6% of prey biomass), Chesson's α for lagomorphs was 0.90 and 0.99 respectively. In the forest-steppe study area, red deer was avoided even though it constituted the second highest available biomass amongst the three most common prey species (Table 3). Moreover, in the subalpine study area, brown hare biomass was available at only 4.22 kg/km^2 (5.6%), but comprised 77.6% of the diet of lynx in this study area. Hence, Chesson's resource selection index showed strong avoidance of wild goat and red deer where they occurred. Wild boar was avoided as prey species in all three study areas (Table 3).

Table 3. Herbivore prey biomass and selectivity, in lynx diet in Turkey. Notes: n.p. -not present, n.a. -not applicable)

	Prey species	Mediterranean	Forest-steppe	Subalpine
biomass in diet (%)	brown hare	**98.52**	**84.76**	**77.58**
	wild goat	0.0	n.p.	8.2
	wild boar	1.04	2.84	1.48
	red deer	n.p.	0.0	n.p.
biomass available (kg/km²)	brown hare	**114.70**	**280.08**	4.22
	wild goat	2.10	n.p.	**67.20**
	wild boar	24.60	80.40	18.60
	red deer	n.p.	119.25	n.p.
biomass available (%)	brown hare	**81.12**	**58.38**	4.69
	wild goat	1.49	n.p.	**74.65**
	wild boar	17.40	16.76	20.66
	red deer	n.p.	24.86	n.p.
Chesson's α	brown hare	**0.95**	**0.90**	**0.99**
	wild goat	0.00	n.a.	0.01
	wild boar	0.05	0.10	0.00
	red deer	n.a.	0.00	n.a.

Functional response of Eurasian lynx, Canada lynx and Iberian lynx populations to prey

Ψ was not highly sensitive to any parameter. The most influential parameter was prey mass and digestion time (parameter h_2), with the 10% change in input indicating a 10% change in output (*Ψ*). Lynx in Turkey, Canada lynx and Iberian lynx exhibited a largely similar functional response pattern (similar to type II) and reached close values of asymptotic food intake (900-1000 g/day, 700-800 g/day, 800-900 g/day respectively) at high prey densities whereas Eurasian lynx populations in Europe showed a different pattern (Figure 4). Here, asymptotic prey intake was already reached at relatively low roe deer densities (at 3 individuals km^2), substantially earlier than in other functional responses. Food intake of Finnish populations of Eurasian lynx consuming mountain hare (1400-1500 g/day) were above these three, but below the seven Eurasian lynx populations which preferentially consume roe deer in central and eastern Europe, where asymptotic prey intake was at its highest level (1900-2000 g/day).

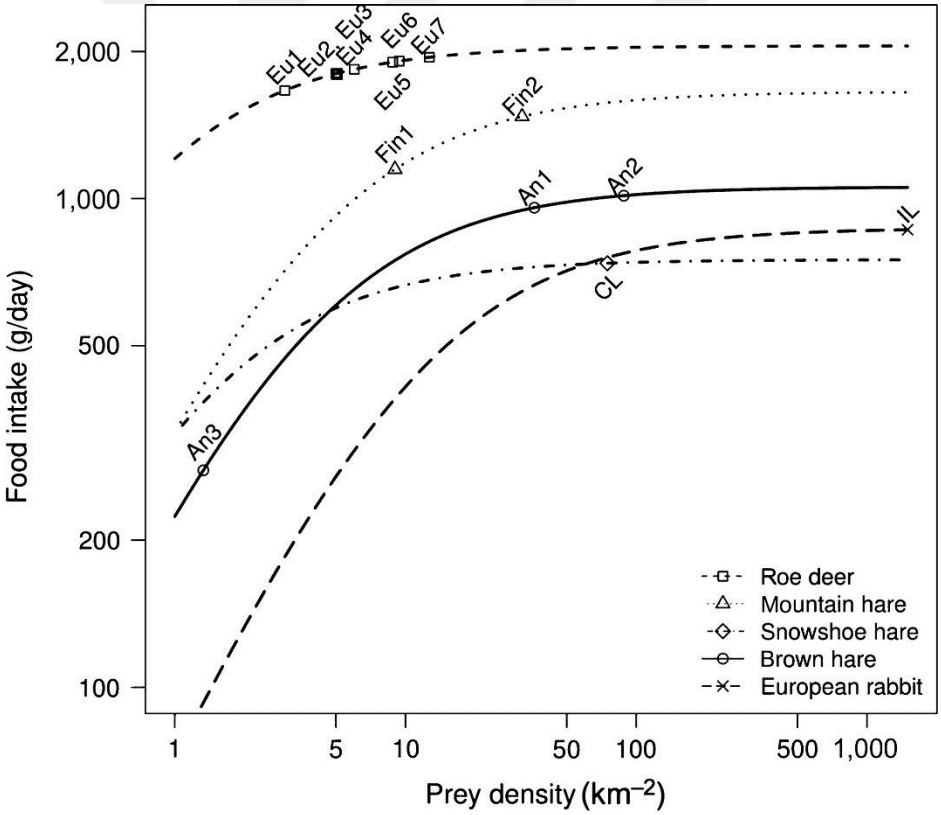

Figure 4. Functional response of Eurasian lynx in Turkey (An1-An3), Eurasian lynx in central and eastern Europe (Eu1-Eu7) and in Finland (Fin1, Fin2), Canada lynx (CL) and Iberian lynx (IL) to their preferred prey.

DISCUSSION

The results of this study allowed us to document and understand the importance of high variability in feeding adaptations of a widespread felid species, the Eurasian lynx. Considering the entire distribution of this species, populations in Turkey are geographically closer to European than to Asian populations, yet they show very different dietary patterns.

Mammals are the most important prey category in the diet of lynx in three study areas in Turkey, comprising more than 90% of the diet in average. This result was in accordance with other Eurasian lynx populations throughout its distribution range except for east Siberian populations where birds also contributed significantly (Sedalischev et al., 2014). In contrast to most Eurasian lynx populations in Europe, lynx populations in Turkey strictly relied on brown hare, which formed in average 87% of prey biomass in their diet, even in the presence of mid-sized or large herbivores such as wild goat, chamois, red deer and wild boar. In forest-steppe and subalpine study areas, high biomass of wild goat and red deer did not affect dietary preferences of lynx in Turkey. In these areas, wild goat contributed only 8.2% of prey biomass and red deer was absent in the diet, and thus both species seemed to be avoided. The only ungulate species which contributed to the diet in all three study areas was wild boar, but it did not exceed 3% in any area. Together with cannibalised lynx, other carnivore species were the second most important food category in the diet of lynx in Turkey. Livestock (domestic goats) were consumed by lynx only in the subalpine area in amounts of 4.4% of prey biomass. However, our data do not allow us to determine whether this contribution resulted from depredation or scavenging.

A similar focus on lagomorph prey preferences was described in six lynx populations in Yakutia, Siberia, with mountain hare making 70% of frequency of occurrence in lynx faeces in three areas where hare densities were high (Sedalischev et al., 2014). Sedalischev (2014) suggested that in the areas where mountain hare densities were low, musk and roe deer, young of red deer, moose and reindeer together with birds contributed more to the diet (20 % and 25% of frequencies of occurrences for total deer and birds respectively). Also, in two other populations in northern Asia and northwest Russia, lagomorphs substantially contributed to the diet, with more than 35% of frequency of occurrence (Sedalischev et al., 2014). In none of those three study areas did wild ungulates occur in more than 10% of faecal samples, with the exception of semi-domestic reindeer **(***Rangifer tarandus*) which occurred at 17% in the northern Asia study area (Sedalischev et al., 2014). Similarly, diet of lynx populations in Tibet (53% frequency of occurrence) and north China (81% frequency of occurrence) are mainly composed of lagomorphs (Weidong 2010), although in Tibet lynx lived in sympatry with Tibetan gazelles (*Procapra picticaudata*), Tibetan antelope (*Pantholops hodgsonii*) and blue sheep (*Pseudois nayaur*) and in China lynx lived in sympatry with red deer and roe deer. Ungulates only

formed 20% and 11% of frequencies of occurrence in Tibet and north China respectively (Weidong, 2010).

Foraging preferences and phylogeography of Eurasian lynx

Anatolia was a refuge for many species during the last glacial periods, including brown hare and the Eurasian lynx (Rueness et al., 2014; Stamatis et al., 2008). Cold and dry climatic conditions supported the expansion of steppes rather than forests (Atalay, 1998) and, in turn, encouraged the range expansion of brown hare which is still present in most Turkish habitats except for the northern deciduous forests. Other steppe dwelling animals such as Anatolian souslik (*Spermophilus xanthoprymnus*) have also expanded their ranges during these periods (Gür, 2012). We therefore suggest that the high preference of lynx in Turkey for lagomorph prey rather than mid-sized ungulates regardless of their densities and distributions, and its presence in drier habitats but not in humid deciduous forests (Soyumert, 2011), was a result of a joint biogeographical history which may have resulted in an evolutionary adaptation in terms of foraging specialisation.

Lynx populations in Europe have a decreasing trend of available lagomorph biomass in diet from north to south, most probably due to habitat changes and competition between different lagomorph species occupying these habitats (Jedrzejewski et al., 1993). In contrast to the co-occurrence of mountain hares and lynx in boreal forests of northeastern Europe, in central and southern Europe brown hare occurs mostly in farming areas, open habitats and forests with many openings, and thus are absent in most lynx habitats (Jedrzejewski et al., 1993). The restriction of Eurasian lynx to densely forested habitats in central and southern Europe may have been a consequence of anthropogenic influence, which forced lynx populations out of more open habitats and made the lynx a “refuge species” of forests here as in the case of European bison (*Bison bosanus*) (Kerley et al., 2011). Jedrzejewski et al. (1993) pointed out that density of hare and its contribution to lynx diet was higher where there were more forest openings than when there was dense pristine deciduous forest. On the other hand, in the same study they suggested that lagomorph contribution to lynx diet decreases from northern to southern latitudes. This might be true for Europe, but does not apply to lynx populations elsewhere. Our study and other studies elsewhere in Asia (e.g. Weidong, 2010; Sedalichev, 2014) showed that further south and east, in Turkey, Tibet, northeast China and Siberia, lynx diet was mainly composed of lagomorphs. Therefore, it is likely that the very low contribution of brown hare to lynx diet in central and southern Europe is a consequence of different habitat use by these two species forced by anthropogenic pressures. High densities of forest ungulates and very low densities of lagomorphs in

central and southern Europe might be the main cause of dietary specialisation of local lynx populations on ungulates.

Cannibalism and intraguild predation

Most of the faecal samples which consisted of lynx remains in the forest-steppe study area were collected during the mating and spring (March-May) seasons and in the subalpine study area in spring and early autumn. This time period is crucial for survival of juvenile lynx, as it is when they separate from their mother and begin their own solitary life looking for a new place to live (Schmidt 1998) and when adult male lynx become aggressively defensive of their territory during mating season (Mattisson et al., 2013). In a high-density lynx population where many floaters meet many territorial individuals, the chance of encountering a superior conspecific and hence of death is higher (Avgan et al. 2014). Death can take place due to direct killing or injuries resulting from aggressive encounters. Although intraspecific killing can take place in Eurasian lynx behaviour (Andrèn et al., 2006; Mattisson et al., 2013), only two cannibalism events in the wild were previously recorded in Eurasian lynx, in Finland (Pulliainen, 1995) and the Kostroma region in Russia (Zaitsev, 2009).

Our data suggest that intraspecific killing and cannibalism might be a regular occurrence in lynx populations in Turkey for several reasons: First, we encountered this behaviour in two different ecosystems independently (n = 13). Second, the lynx faeces that included lynx remains in forest-steppe study area (n = 8) were coming from three male and four female individual territories (GPS tracking, Mengüllüoglu, unpublished data). Third, six of these samples were genetically (12 microsatellites) identified to originate from five different male and one female individuals. And finally, we encountered high numbers of lynx (27 individuals identified with the help of 12 microsatellites, Mengüllüoğlu, unpublished data) in an area of 400 km^2 during a period of 3 months when those samples were collected. Therefore, the evidence we obtained does not suggest this to be a rare behaviour from very few individuals. It may be that cannibalism here was likely to originate from a high lynx density and probable resource and space competition. However, we are not sure whether cannibalism was a result of killing conspecifics for the purpose of feeding or killers made the best out of a bad situation.

Interspecific consumption of other carnivore species by lynx was also recorded in the diet of the central-western and subalpine study areas, which included golden jackal, domestic dog and domestic cat in the forest-steppe study area and red fox and stone marten (*Martes foina*) in the subalpine study area. This is the first report of Eurasian lynx consuming a golden jackal. Our method of dietary analysis

using faecal samples does not allow us to distinguish whether these carnivores were scavenged or depredated. However, the lynx is unlikely to be limited to scavenging golden jackals or red foxes, because lynx are known to kill and eat red foxes (Odden et al., 2006**),** racoon dogs and domestic dogs (Okarma et al. 1997) as mesopredator prey or kill and leave the dead bodies (Jobin et al., 2000). If it is correct to assume that Eurasian lynx not only kill red foxes but also golden jackals, then there is the possibility that they may influence the population dynamics of more than one mesopredator. In case of the red fox, Eurasian lynx have the capacity to influence its population dynamics (Sunde et al., 1999). It is at least conceivable that this may also apply to golden jackals where they are sympatric. Perhaps the recent expansion of golden jackals from southeastern Europe into central Europe might have been encouraged not only by the absence (or reduced presence) of grey wolves (Krofel et al., 2017) but also the absence of Eurasian lynx across many central European ecosystems and the restriction of Eurasian lynx to forested habitats in this region.

Prey preferences

Our data from three different lynx habitats, where lynx is in sympatry with at least two ungulate species, showed that even when the biomass of brown hare was lower than the biomass of mid-sized and large ungulate species, lynx selectively preyed on brown hare (Table 3). This contrasts with the foraging ecology of Eurasian lynx in central and eastern Europe where even juvenile lynx (~12 kg body size) prey on fully-grown medium-sized ungulates, such as roe deer and also on fawns, yearlings and females of red deer (Okarma et al., 1997). Red deer was totally avoided in the forest-steppe study area where neither adult and juvenile deer nor calves were consumed by the lynx population. Wild boar was part of the diet in all three study areas, but was clearly avoided in relation to its abundance as demonstrated by low values of Chesson's α (Table 3). The wild boar remains in the analysed samples were probably scavenged after the "drive hunts" by local hunters for population control, when carcasses are generally left untouched since the meat is not eaten due to religious beliefs. In two cases, Eurasian lynx were reported to feed on wild boar carrions killed by hunters in winter time (Radikal, 2012). Wild goat was the only ungulate species which contributed more than 5% of consumed biomass in lynx diet in the subalpine study area. However, considering the available biomass of this species as a prey source, its percentage in the diet did not indicate any preference by lynx.

Functional response

As suggested by the type II functional response curve, lynx in Turkey had approximately half of the asymptotic prey intake rate of European lynx populations which feed on roe deer (~950 g/day and ~1800 g/day respectively). This lower intake rate is in concordance with the smaller body size of lynx in Turkey. The only lynx population which had a very low main prey intake (220 g/day) was the subalpine lynx population (An3). The low prey intake of lynx in subalpine area might originate either from low capture rates, or from low density of hares. We think that the low capture rate of brown hare in here was most likely a result of very slow trigger speed (4 seconds) of the camera trap model used in that study. In case of a really low population density of hares, lynx diet in the sub-alpine ecosystem would hardly be composed of 78% brown hare in biomass and lynx here would shift to alternative prey sources with higher available biomass (such as wild goat, Table 3), unless this predator population is strictly a lagomorph specialist. Indeed, subalpine lynx population had a higher share of ungulate, bird and rodents in their diet than the two other lynx populations in Turkey, but still selectively preyed on brown hare like a typical lagomorph specialist (Elton and Nicholson, 1942; Stenseth et al., 1997).

As reported by previous studies on Eurasian lynx populations in central and eastern Europe, the asymptotic intake level was reached quickly even at low roe deer densities and lynx consumed around 1800 g (mean = 1836 ± 94 g) of meat per day (Okarma et al., 1997; Nilsen et al., 2009). Eurasian lynx populations in central and eastern Europe have larger home range sizes (Herfindal et al., 2005) than lynx populations in Turkey (Avgan et al., 2014; Mengüllüoğlu, unpublished data), consistent with the idea that there is a negative correlation between the size of a home range and the density of the major prey (Herfindal et al., 2005). Although the search time might increase at lower prey densities, this seemed to matter little as roe deer killing rates in different populations were similar (5 to 6 days per roe deer), resulting in little differences in food intake rates (Figure 4, Supplementary Material Table A2).

As shown by the similarity of the type II functional response curves of lynx in Turkey, Canada lynx and Iberian lynx, we suggest that lynx in Turkey has specialized on a lagomorph diet. This foraging preference may be facilitated by adaptations to hunting brown hares, such as a smaller lynx body size of 9-16 kg in Turkey (Mengüllüoglu et al., unpublished data), and higher population densities at 4.2 individuals/100 km^2 (Avgan et al., 2014) than elsewhere in Europe – where densities are more like 0.4 individuals/100 km^2 in Germany (Weingarth et al., 2012) or 3.4 individuals/100 km^2 in Poland (Okarma et al., 1997). If this is the case, then we would expect the present distribution of lynx in Turkey to show a considerable overlap with that of brown hare, and a little overlap between lynx and roe deer. Pine forests, forest-steppe ecosystems and alpine regions in Turkey appear to provide good habitats to maintain brown hare populations at high densities. These are the areas where lynx are present and

live in sympatry with the brown hare in Turkey (Ambarlı et al., 2010; Avgan et al., 2014; Capitani et al., 2016). On the other hand, despite thousands of trap-days of camera trapping (Soyumert, 2011; Özkazanç et al., 2017) not a single photograph of a lynx has ever been registered in temperate deciduous ecosystems where roe deer is present at high densities and brown hare is very rare, such as the central Black Sea forests 100 km to forest-steppe study area. Such a match in predator-prey distributions, specialized diet and prey preferences in three major ecosystems of Turkey suggest that in Turkey the lynx is a lagomorph specialist felid.

Peculiarities of a specialist diet

Eurasian lynx populations in central and eastern Europe are adapted to their main prey, roe deer, by having larger body size and low population density in comparison with lagomorph specialist populations of this species. Therefore, these populations may have a lower chance of encountering prey, have an increased search time and radius, may have to defend larger territories, face a potentially dangerous opponent prior to a successful kill and then may have to defend kills from kleptoparasitism by other carnivores. Kleptoparasitism is a common phenomenon in Eurasian lynx populations in central and Eastern Europe where lynx kills are regularly scavenged or stolen by other predators such as red foxes, martens, brown bears and even people (Haglund, 1996; Krofel et al., 2012). Given all this time and effort, efficacy of food acquisition is also reduced as lynx consumes only flesh making up to 70% of carcass mass (Okarma et al., 1997; Sunde et al., 2000; Rühe et al. 2007).

Previous studies have shown that lagomorph specialist lynx species can experience high population fluctuations following fluctuations in prey densities (Canada lynx: Elton and Nicholson, 1942; Stenseth et al. 1997) or reach the brink of extinction due to prey shortage (Iberian lynx: Ferrer and Negro, 2004). Yet, lagomorph populations can reach very high densities and then reward specialist predators with a rich supply of food. Also, kleptoparasitism is irrelevant since lagomorph specialist lynx can immediately take their kill away from a kill site and consume it within a short period of time. Lynx carrying killed hares in a mouth are not uncommon on camera trap photographs and personal observations in Turkey (Figure 2).

Conservation implications

Our results demonstrated that the diet of the Eurasian lynx in Turkey consists mostly of brown hares and that its foraging ecology fulfils expectations for a lagomorph specialist, similar to Iberian and Canada lynx, regardless of ecosystem. This result is in sharp contrast to what would be expected from

the generalization of feeding ecology of lynx in Europe over larger scales. Our studies are also consistent with previous results of Asian populations of the Eurasian lynx, which also strongly rely on lagomorphs (Weidong, 2010; Sedalichev, 2014).

To become efficient, lynx conservation programs in southwest Asia should be implemented in areas with moderate to high densities of lagomorphs and clearly address the status, threats and factors related to these species. Any rewilding projects undertaken in southwest Asia should consider using individuals from lynx populations from Turkey rather than from Europe where lynx rely on ungulate prey. First, this will ensure that the lynx will adequately cope with the local prey base. Second, this will increase public acceptance and minimize the potential for conflict with farmers because predation on domestic livestock by lynx in Turkey is very rare in contrast to predation on domestic livestock by lynx in central and eastern Europe (Odden et al., 2006).

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CHAPTER 3: Genetic variability in northwest Anatolian lynx

Non-invasive faecal sampling reveals spatial organization and improves measures of genetic diversity for the conservation assessment of territorial species: Caucasian lynx as a case species

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Authour contributions:

DM, JF, and DWF conceptualized the study. DM conducted field works, laboratory and formal analyses. DM wrote the drafted manuscript. DM, JF, DWF and HH provided input to the editing and review of the manuscript. DM is the corresponding author.

Abstract

The Caucasian lynx, *Lynx lynx dinniki,* has one of the southernmost distributions in the Eurasian lynx range, covering Anatolian Turkey, the Caucasus and Iran. Little is known about the biology and the genetic status of this subspecies. To collect baseline genetic, ecological and behavioural data and benefit future conservation of *L. l. dinniki,* we monitored 11 lynx territories (396 km^2) in northwestern Anatolia. We assessed genetic diversity of this population by non-invasively collecting 171 faecal samples and trapped and sampled 12 lynx individuals using box traps. We observed high allelic variation at 11 nuclear microsatellite markers, and found no signs of inbreeding despite the potential isolation of this population. We obtained similar numbers of distinct genotypes from the two sampling sources. Our results indicated that first order female relatives occupy neighbouring territories (female philopatry) and that territorial male lynx were highly unrelated to each other and to female territorial lynx, suggesting long distance male dispersal. Particular male and female resident territorial lynx and their offspring (kittens and subadults) were more likely to be trapped than resident floaters or dispersing (unrelated) lynx. Conversely, we obtained more data for unrelated lynx and higher numbers of territorials using non-invasive sampling (faeces). When invasive and non-invasive samples were analysed separately, the spatial organisation of lynx (in terms of female philopatry and females and males occupying permanent ranges) affected measures of genetic diversity in such a way that estimates of genetic diversity were reduced if only invasive samples were considered. It appears that, at small spatial scales, invasive sampling using box traps may underestimate the genetic diversity in carnivores with permanent ranges and philopatry such as the Eurasian lynx. As non-invasive sampling can also provide additional data on diet and spatial organisation, we advocate the use of such samples for conservation genetic studies of vulnerable, endangered or data deficient territorial species.

Keywords: *Lynx lynx dinniki*, Anatolia, microsatellites, philopatry, territoriality, non-invasive faecal sampling, carnivore conservation

Introduction

Conservation of wildlife species often requires highly demanding practices such as habitat preservation and restoration, animal protection, animal relocation, captive breeding and reintroductions [1]. For data deficient animal populations it is difficult to devise efficient conservation measures because there is insufficient information on their ecological, demographic and genetic status [1]. Non-invasive sampling strategies such as collecting faecal samples can provide crucial information about diet, allostatic load, reproduction, genetic diversity, and the dynamics in animal populations [2-4]. Once samples have been collected, genetic markers such as mtDNA and microsatellites can be used to assess genetic variability [5], estimate levels of inbreeding and relatedness [6, 7] and quantify total and effective population sizes [8]. Data acquired from such conservation genetic studies provide important information for efficient conservation actions [9, 10].

Among lynx species, the Eurasian lynx *Lynx lynx* has the widest geographic distribution. Populations occur in a wide variety of habitats, ranging in the Palearctic region from Scandinavia and central Europe to far eastern Russia, and can also be found south of the 20th degree of latitude [e.g., in southwest Asia and Tibet; 11]. Whereas mtDNA diversity has been characterized for some populations of this species [12], nuclear genetic data are only available for European populations of the Eurasian lynx, several of which are considered 'endangered' or 'vulnerable' [11, 13, 14].

The two subspecies of *Lynx lynx* in Asia, *L. l. dinniki* and *L. l. isabellinus*, are still little known in terms of their ecological requirements, spatial and genetic population structure and their genetic diversity. The Caucasian lynx *L. l. dinniki* (Satunin 1915) has one of the southernmost distributions of Eurasian lynx [11], stretching from the Anatolian side of Turkey to the Caucasus and Iran. Compared with their north and central European conspecifics, Caucasian lynx display some behavioural and morphological differences. They are lagomorph specialists (similar to the Iberian lynx *Lynx pardinus*), have a smaller body size [15] and smaller home range sizes, and thus occur in suitable habitats at higher population densities [16] than European subspecies. They live in dry open, rocky and coniferous habitats and scrape mark [15, 17], a marking behaviour that in the genus *Lynx* is otherwise only observed in bobcats [*Lynx rufus*; 18]. Highway collisions, habitat fragmentation and poaching are the main factors threatening the Caucasian lynx across its range [19].

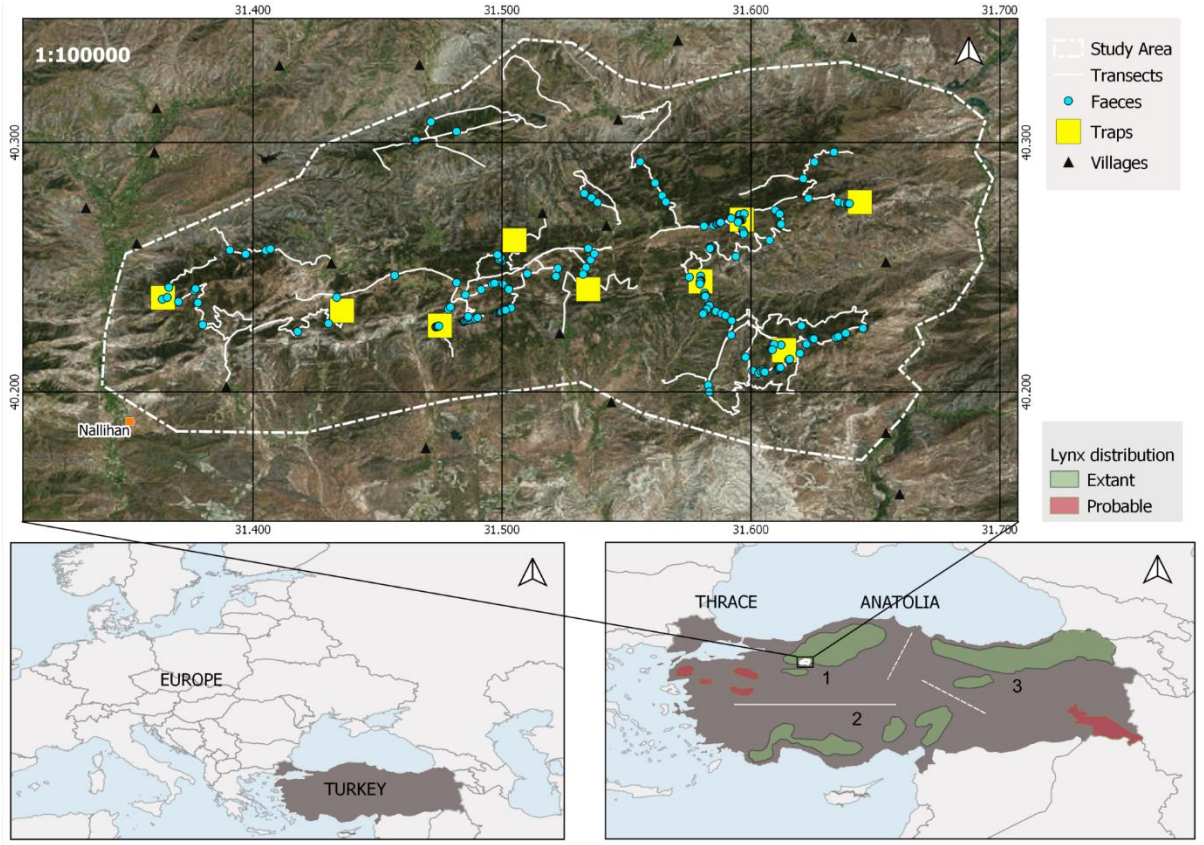

Fig 1. Location of the study area in north-west Anatolia and distribution of the three big extant lynx populations. 1: Northwestern, 2: southern, 3: northeastern lynx populations [11]. The continuous line indicates complete and dashed lines indicate potential isolation.

Previously, two phylogeographic studies included Caucasian lynx among sampled subspecies of the Eurasian lynx [12, 20]. Both reported high mtDNA haplotype diversity and both suggested the presence of a glacial refugium for Eurasian lynx in this region. They did neither assess genetic variability at nuclear loci, nor did they assess the potential effect of recent anthropogenic activities and environmental changes on this variability. Such information is valuable to plan and carry out efficient lynx conservation measures [14].

Three large Caucasian lynx populations occur in Turkey [11]. The northwestern Anatolian lynx population is isolated from the southern and northeastern populations by a series of natural and human constructed barriers (Fig 1). The inner Anatolian plateau with its agricultural landscape separates the northwestern lynx population from the southern population (Fig 1, continuous line), and a series of big dams (e.g. Seydim dam, Gökcedogan dam, Altinkaya dam) and human settlements separate it from the northeastern population (Fig 1, dashed line between 1 and 3). The southern population is isolated from the northeastern population by a series of rivers and dams situated in the

deep valleys of the Anatolian diagonal mountain series (Fig 1, dashed line between 2 and 3). It is neither known whether there is gene flow between these populations, nor whether they are isolated and at risk from becoming genetically impoverished.

Non-invasive sampling enables researchers to collect samples in the field without disturbing the animals or putting them at health risk, and potentially represents a means to obtain genetic material from many individuals. For example, it may be feasible to collect faecal samples from a large area at a reasonable cost and effort. Genotyping success of non-invasively collected samples depends on several factors such as duration of exposure of the faeces to sun and humidity, as they affect the speed of DNA degradation, presence of PCR inhibitors [21], the amount of DNA in the sample originating from the study species [22], and the length of the DNA fragment (allele) to be amplified. Some of these factors are difficult to control for, such as the amount of inhibitors or the exposure to environmental conditions and aging of samples before collection, unless defecation is observed. Other factors such as collection procedure, storage and handling of the samples [23] are under the control of the investigator.

The collection of invasive samples can also be challenging. Its success depends on the population density of the study species and the trapping methodology used. The study design needs to take animal welfare into account and may be costly in terms of time and the resources required [24, 25]. Moreover, trapping success may depend on field experience with the study species, prior monitoring of the population to localise good trapping sites and the behavioural response of individuals to traps. In the case of many species with permanent ranges such as lynx, invasive sampling using boxes or cage trapping systems may require so much effort that inevitably the number of trapping locations will be locally restricted and confined to a small number of ranges or territories.

Some authors [26] have stressed the importance of a proper sampling scheme for the assessment of the genetic diversity in populations of philopatric animal species. They concluded that sampling at small spatial scales ("clumped sampling") can produce results of apparently low genetic diversity and high relatedness among individuals. Considering that territoriality and female philopatry are common in many large carnivores, including the Eurasian lynx [27, 28], it is possible that genetic diversity measured at small spatial scales would be affected by spatial organization. However, populations of lynx (or other species) do not consist of territorial individuals only. Male lynx disperse long distances [27, 29] and females will also disperse if all the areas adjacent to the natal range are occupied [26]. In addition, there can be animals with large home ranges that are 'resident' and waiting to take over a local territory, often termed 'floaters' – a recent example amongst felids is that of the cheetah

(*Acinonyx jubatus*) where both territorial animals and floaters were identified as constituting the population of residents [30].

To our knowledge, no study has followed up on this idea and actually compared how sampling source (invasive vs. non-invasive) might influence the assessment of genetic diversity measures in philopatric animal populations where adults occupy permanent ranges and thus are not randomly distributed. Since stationary trapping systems such as box traps are more likely to capture territorial residents as these are habituated to the presence of traps, we hypothesise that non-invasively collected faecal samples are more likely to provide evidence of other classes of residents such as floaters as well as dispersing or nomadic lynx, none of which are likely to habituate to traps, and thus increase the measurement of genetic diversity. These animals are part of the same population – therefore measures which include these lynx would more accurately reflect the genetic diversity of the entire population.

In this study we conducted the first assessment of the spatial organisation (female philopatry, male dispersal and relatedness) and genetic variability of the northwest Anatolian *L. l. dinniki* population using nuclear microsatellite markers with the help of non-invasively and invasively sampled material. We examined the genetic variability of this potentially isolated Eurasian lynx population and evaluated it in the context of similar data for Eurasian lynx populations from central and Eastern Europe. In addition, we tested the predictions from our hypothesis and compared measures of genetic diversity obtained from different sample sources (invasive vs. non-invasive) to provide insights into the effect of different sampling methods on estimates of genetic diversity in a territorial carnivore at a small spatial scale.

Materials and Methods

Study Area

All samples were collected in an area of 396 km^2 in the Nallıhan Mountains (40º11'- 31º21'; Fig 1), which is a mountain chain that lies in the transition zone between the dry western Black Sea (xero-euxine) and central Anatolian (Iran-Turan) floristic zones. The area does not hold any form of protection status, and is part of the state forests management system. This region is also influenced by the Mediterranean floristic zone (western Aegean), through the catchment area of the Sakarya River [31]. Vegetation and landscape have been shaped by altitude and historical human use. The lower areas (500 to 1000 m) are covered by steppe in the south, which is gradually replaced by Turkish pine (*Pinus brutia*). Above this belt, temperate coniferous forest reaches up to 1500 m and is

composed of black pine (*Pinus nigra*) and junipers (*Juniperus excelsa* and *J. oxycedrus*) with an understory of oak-dominated scrub (*Quercus pubescens*, *Pyrus elaeagnifolia*, *Crataegus* spp., 29) with frequent forest openings. The mean annual temperature is 9.6º Celsius and the mean annual total precipitation is 543 mm [32]. The human population in this area is at a low density and restricted to several villages in the surrounding lowland and valleys. Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are the common large herbivores, and brown hare (*Lepus europaeus*) is the main lynx prey species here [15]. The area is home to several other large and medium-sized carnivores, at higher elevations brown bear (*Ursus arctos*) and grey wolf (*Canis lupus*) are sympatric with lynx, and at lower elevations golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*) and jungle cat (*Felis chaus*) occur, which rarely occur in lynx and wolf habitat [33].

Sample collection

In total, 183 samples were collected between November 2013 and March 2017. Swab samples taken from the outer layer of lynx faeces (N = 171; [34]) were collected by walking on active lynx trails, dirt roads and ridgelines at altitudes ranging from 1000 to 1500 meters above sea level (asl), in the Nallıhan Mountains (Fig 1). In order to reduce the chance of falsely identifying faeces from other wild carnivores and domestic dogs as lynx faeces, we used a scat detection dog [35] trained on Caucasian lynx faeces collected at Ankara Zoo. Additionally, we also applied identification criteria to correctly assign lynx faeces based on shape, segmentation (i.e. well-defined tapered segments [36]) and diameter [37]. Lynx faeces were also collected for the purpose of diet analysis [15]. Based on visual inspection, faeces varied considerably in age. We collected the samples in an area (396 km^2 in total) that covered the territories of individually recognised male (n = 5) and female (n = 6) lynx that had previously been repeatedly identified over several years by camera trapping (S3 Table). By repeatedly searching the study area, we collected 171 faecal samples on 52 survey days (Table 1).

Table 1. Summary of parameters for invasively and non-invasively collected samples

	non-invasively collected	invasively collected
effort (days*)	52	961
number of territories covered	11	10
number of territories sampled**	9	9
samples collected	171	12
samples collected per day	3.28	0.01
	11 loci / 8 loci	11 loci / 8 loci
genotyped samples	27 / 45	11 / 12
distinct genotypes	10 / 14	11 / 12
territorial lynx	7 / 8	6 / 6
kittens	1 / 2	3 / 4
dispersers and floaters***	2 / 4	2 / 2

*search days for non-invasive sampling, trapping days multiplied by active traps

**successful genotyping

***dispersers are subadult dispersing and floaters are adult non-territorial resident lynx that use much larger home ranges than territorials [29]

Capture of lynx and field work were performed in collaboration with the Wildlife Department of the Turkish Ministry of Agriculture and Forestry (WDT) under protocol and permit number 30057506-030-1867 issued by the department. Five cage traps constructed by the WDT (length: 2 m, height: 1.5 m, width: 1 m) were used for capturing lynx. Captured lynx individuals were anaesthetised and sampled by the authorised wildlife veterinarian of the WDT following national ethical legislation. No specific permit was required for anaesthesia and lynx treatment as it was conducted by the WDT. Traps were placed on lynx trails at nine trapping stations in the territories of four male and six female lynx (Table 1). We monitored the traps by GPRS camera traps (Keepguard KG860, Keeptime industrial (Asia) Co., LTD, Hong Kong, CHINA) and VHF transmitters. Each trap was visited and checked every second day. Over the course of three trapping seasons (= 961 active trap days between December and April during the years 2015-2017), we obtained "invasive" samples from 12 lynx caught in traps at five trapping stations, three in 2015, five in 2016 and four in 2017. "Invasive" samples (n = 12) were collected as small ear tissues (n = 9), a mouth swab (n = 1) and plucked hair from kittens (n = 2). For the anaesthesia of 9 lynx, 5mg/kg ketamine and 0.2mg/kg medetomidine were used. They were fitted with 185 g GPS collars (e-obs GmbH, Grünwald, Germany). One old adult male captured in 2015 and two kittens

captured in 2016 were neither anesthetised nor collared because of unsuitable age and ethical concerns.

DNA extraction and genotyping

DNA was extracted from all sample types using a commercially available forensic DNA extraction kit (GEN-IAL GmbH, Troisdorf, Germany) following the manufacturer's instructions. As no other felid species was present in the lynx habitat (1000 m to 1500 m asl) and golden jackals and red fox were distributed at lower elevations close to human settlements due to interference competition by wolves and lynx [32], we did not apply genetic species identification. PCR cycling conditions were the same as in Bull et al. [14]. All samples were genotyped at fourteen microsatellite loci originally derived from the domestic cat (*Felis* c*atus*) [38, 39] and the Canada lynx (*Lynx canadensis*) [40]: FCA006, FCA008, FCA082, FCA097, FCA105, FCA229, FCA441, FCA478, FCA506, FCA718, FCA1023, F115, LCA109 and LCA110. We also genotyped samples at two sexing loci: amelogenin and zinkfinger (F-AMEL and Z-Zf). One of each primer pair was labeled with a fluorescent dye (6-FAM, HEX) and loci were amplified in 5 multiplexes of 10 µL final reaction volume, applying the recommended conditions by the multiplex PCR kit manufacturer (Qiagen Multiplex PCR Kit, Qiagen, Hilden, Germany).

As genotypes determined from non-invasive samples may be incomplete or suffer from errors (e.g. allele dropout, false alleles), we applied a maximum likelihood approach [41] to ensure that genotypes were reliably identified. We genotyped each faecal sample in duplicates and only retained samples that had consistent allele calls in both amplifications. If a mismatch was observed, a new DNA extraction of the same sample was carried out and the procedure was repeated (parallel genotyping). Thus, every sample was genotyped two or four times. If there was no further material left for a second extraction round, or if the second round of duplicate genotyping also showed mismatches, the respective sample was discarded. We retained genotypes that included consistent amplifications at 12 or more loci (but see below).

Given the large number of samples taken in the field and the size of the area surveyed, multiple sampling of some individuals was expected. Applying the option 'alleleMismatch=2' of the software *Allelematch* version 2.5 [42], we compared genotypes and assigned multiple samples to the same genotype (i.e. individual). This included genotypes that did not match because of size shift in one allele (N = 3) and/or missing data (N = 3). To quantify the discriminatory ability of our loci, we estimated the cumulative values of the unbiased probability of identity (P_{IDunb}) and probability of identity given siblings (P_{IDsib}) using the software GIMLET version 1.3.3 [43].

Genetic analyses

The probability for the presence of null alleles at the fourteen microsatellite loci was estimated using the software MICROCHECKER version 2.2.3 [44]. Potential deviations from Hardy-Weinberg equilibrium (HWE) and presence of linkage disequilibrium (LD) were both tested using GENEPOP version 3.4 [45]. We used FSTAT version 2.9.3.2 [46] to estimate the inbreeding coefficient (F_{IS}) and expected (H_E) and observed heterozygosities (H_O). Allelic richness (A_R) and Kosman and Leonard's measure of genetic dissimilarity versus geographic distance [47] were determined using the R package *PopGenReport* version 2.1 [48]. A_R was estimated using rarefaction of eight genotypes per population (except for Slovakian lynx, N = 6). Kosman and Leonard's measure of genetic dissimilarity was applied to visualize the spatial organisation and pairwise relatedness among territorial lynx (i.e. excluding the kittens and other individuals without territories) in the study area. This required a spatial coordinate to represent the individuals included in the analysis. The procedure to allocate the appropriate spatial coordinate is explained below. Additionally, we conducted a spatial autocorrelation analysis using GenAlEx version 6.502 [49, 50]. To obtain equal numbers of comparisons per distance class, we used the "even sample classes" option. Intra-population pairwise relatedness (M_{xy} [51]) values were estimated using the R package *Demerelate* version 0.9-3 [52].

We also used our microsatellite data and reanalysed them in combination with the data of Bull et al. [14] using the ten microsatellite loci shared in these studies (FCA006, FCA008, FCA082, FCA097, FCA105, FCA229, FCA506, FCA718, FCA1023, and LCA110). This enabled us to compare northwest Anatolian lynx and autochthonous and reintroduced Eurasian lynx populations in central and Eastern Europe in terms of genetic diversity and intra-population relatedness.

DNA sampling method and diversity measures

In order to evaluate whether the two sampling methods ("invasive" vs. "non-invasive") affected estimates of population genetic diversity, we needed more samples with complete genotypes. Therefore, we removed three microsatellite loci that had generated missing data for numerous samples. The eight loci for which additional samples had a complete genotype were FCA008, FCA082, FCA097, FCA105, FCA229, FCA1023, LCA109 and LCA110. For this aforementioned comparison, we considered the mean number of alleles ($\bar{N}$) and the expected heterozygosity (H_E) as measures for genetic variability, estimated using the function 'subsample.gen' of the R package *Resampledivers*ity version 1.0 [53]. This function allowed us to consider various sizes of subsamples of our genotypes

(separately for the invasive and non-invasive samples, as well as for the combined sample set), with sizes ranging from 2 to 22, with 100 iterations per number of genotypes. In this manner, we tracked how an increase in sample size changed the estimates of $\bar{N}$ and H_E. We then used Tukey's test to examine whether $\bar{N}$ and H_E values differed significantly between sample types. The test was conducted for the range of genotypes from 2 to 12, the latter being the maximum number of genotypes among invasive samples. Bonferroni's inequality method [54, 55] was used to adjust the significance threshold by the number of comparisons, resulting in an adjusted significance threshold of $\alpha = 0.0015$.

Lynx population monitoring

Along with 'non-invasive' and 'invasive' genetic sampling, the lynx population had also been monitored by camera traps at 54 different stations since autumn 2009 (S3 Table) and by recording the movements of nine individual lynxes had been tracked using GPS transmitters since 2015. We matched lynx genotypes from non-invasively collected samples to individuals (morphology) if the sample from a particular individual had been collected from a camera-trapping station with evidence of a picture having been taken during defecation, or when the faeces were found in very close proximity (maximum distance of 5 m) of a camera trap station in the following two days after the picture had been taken. Faeces (and their corresponding genotypes) were categorized as belonging to a kitten, when the faeces diameter was smaller than the diameter of adult lynx faeces [37], there was no picture of the defecating individual and the faeces was found in the territory of a female lynx to which the pairwise relatedness of the genotype was higher than 50%.

One spatial coordinate per individual was used in the analysis of the spatial organisation of territorial lynx in our study area for the genetic dissimilarity vs. distance analysis. If the territorial resident individual was collared (n = 5), we used the home range centroid estimated from GPS data as the spatial coordinate. For the remaining territorial residents (n = 5), we used the spatial coordinates of the centroid of the minimum convex polygon established from locations where faecal samples had been collected with this genotype and the locations of camera traps where pictures of that particular individual had been taken.

Results

Except for the monomorphic locus FCA478, which was excluded from further analyses, all other microsatellite loci were polymorphic, with the number of alleles (N_A) ranging from three to seven (Table 2). No combination of microsatellite loci was in linkage disequilibrium (LD) but two loci (F115, FCA441) had a significant probability for the presence of null alleles. These two loci also showed signs of inbreeding (as measured by F_{IS}) and deviated significantly from Hardy-Weinberg equilibrium (HWE, Table 2). Therefore, these two loci were omitted in subsequent analyses.

Table 2. Summary of genotyping results at 14 microsatellite loci for north-western Anatolian lynx

Locus	N_A	H_E	H_O	p_{HWE}	F_{IS}	f_{null}
FCA006	3	0.68	0.76	n.s.	-0.130	-0.07
FCA008	3	0.62	0.87	n.s.	-0.405	-0.17
FCA082	7	0.80	0.82	n.s.	-0.032	-0.03
FCA097	5	0.64	0.72	n.s.	-0.122	-0.06
FCA105	4	0.74	0.61	n.s.	0.176	0.08
FCA229	3	0.52	0.61	n.s.	-0.176	-0.09
FCA441†	7	0.83	0.35	<0.01	0.571*	0.37*
FCA478†	1	0	0	n.a.	n.a.	0
FCA506	5	0.44	0.35	n.s.	0.200	0.09
FCA718	5	0.72	0.87	n.s.	-0.201	-0.1
FCA1023	5	0.76	0.65	n.s.	0.150	0.06
F115†	3	0.62	0.08	<0.01	0.866*	0.74*
LCA109	3	0.67	0.67	n.s.	0.012	-0.01
LCA110	5	0.59	0.61	n.s.	-0.078	-0.05
Average across 11 loci	4.45	0.65	0.69		-0.050	

* $p < 0.05$

† microsatellite loci removed from subsequent analyses

Number of alleles (N_A), expected (H_E) and observed (H_O) heterozygosity, probability of deviation from Hardy-Weinberg equilibrium (p_{HWE}), inbreeding coefficient (F_{IS}), estimated frequency of null alleles (f_{null}, [56]).

Relatedness and spatial organization

The analysis of pairwise relatedness of lynx in the study area revealed that territorial females had a wide range of relatedness within the study area, including three female-female pairs that were highly related (consisting of two different groups of mother-daughter pairs; Fig 2A). Territorial male-male pairs generally showed lower relatedness, including two highly unrelated pairs (Fig 2A). The mean genetic dissimilarity among territorial lynx (n = 10) varied by distance. We found a moderate increase in dissimilarity over shorter distances of up to 17 km, after which it declined (Fig 2B). When the sexes were considered separately, neighbouring territorial female lynx displayed high similarity, and dissimilarity peaked at 17 km (Fig 2C), corresponding to a distance of three female territories in the study area. Neighbouring males showed high dissimilarity and none of the territorial males were close relatives (Fig 2D). The results of the spatial autocorrelation analysis were broadly consistent with these finding. There was a significant positive correlation ($r \geq 0.12$) at distance classes up to 7 km ($P \leq 0.05$) and a significant negative correlation ($r \leq -0.11$) at distance classes of 13 km and 16 km ($P \leq 0.05$) (S2 Figure). In order to conduct the spatial autocorrelation analysis with a sufficient number of samples we had to include all genotypes (including kittens, dispersers and floaters); sample deficiency was the reason why the analysis could not be separately performed for females and males.

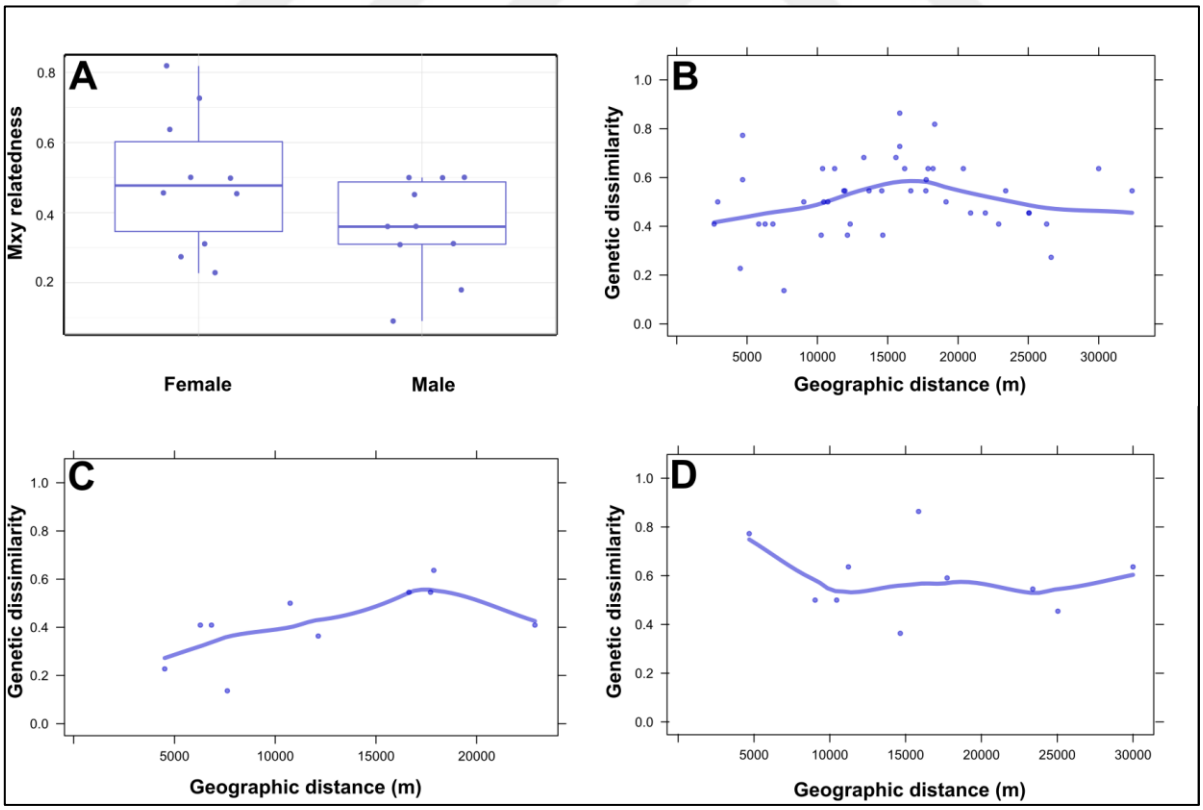

Fig 2. Relatedness and spatial organization of territorial lynx in northwestern Anatolia. M_{xy} relatedness values (A) of female and male territorial lynx in northwestern Anatolia. Plots of genetic

dissimilarity (Kosman and Leonard, 2005; n_{loci} = 11) versus geographic distance, for (B) all territorial lynx ($n_{genotypes}$ = 10), (C) for territorial females ($n_{genotypes}$ = 5) and (D) territorial resident males ($n_{genotypes}$ = 5).

Genotyping success and genetic diversity measures

Amplification success of the 11 loci across all samples was 66 %. Among the 171 'non-invasive' samples, 27 (15.8%) were successfully genotyped twice at nine to eleven microsatellite loci (i.e. with consistent allele calls). Among the 'invasive' samples, all 9 tissue samples, the mouth swab and one out of two plucked hair samples generated data for the same number of loci (91.7 %). Among the 27 non-invasive and 11 invasive samples (n = 38), we detected 18 unique lynx genotypes (7 females and 11 males), 10 from non-invasive and 11 from invasive samples; three genotypes were detected using both sources. The cumulative estimates of probability of identity were: $P_{IDunb} = 1.02 \times 10^{-9}$ and $P_{IDsib} = 3.12 \times 10^{-4}$. The mean A_R was 3.96, mean H_E and H_O were 0.65 and 0.69, respectively, and mean F_{IS} was -0.055.

When one locus was removed from the dataset and measures of genetic diversity were re-estimated from the 10 microsatellite loci matching the ones previously employed by Bull et al. [14], the mean diversity measures of lynx in Anatolia were not affected (Tables 1 and 2). Re-analysis of our dataset and data from Bull et al. [14] showed that genotypes from Anatolia ($n_{genotypes}$ = 18, n_{loci} = 10) had the second highest A_R and H_O values after the lynx population from Russia and the second lowest F_{IS} value after the lynx population from Slovakia (Table 3). Among the autochthonous *L. lynx* populations, Anatolian, Latvian and Russian lynx had the lowest mean relatedness, followed by Estonian lynx (Fig 3). Two autochthonous lynx populations (Poland and Slovakia) displayed a higher relatedness, with values closer to that of reintroduced European lynx populations. Among reintroduced European lynx populations, the lynx populations from the Bohemia-Bavarian and Vosges-Palatinian areas had the highest relatedness values (Fig 3). Using the same reduced dataset ($n_{genotypes}$ = 18, n_{loci} = 10), an analysis of pairwise relatedness (M_{xy}) revealed 14 full-sibling/parent-offspring pairs (M_{xy} threshold = 0.59), 37 half-sibling pairs (M_{xy} threshold = 0.43), and 102 pairs of unrelated individuals for lynx in northwest Anatolia.

Table 3. Comparison between the northwestern Anatolian lynx population and other autochthonous and reintroduced European lynx populations [14], based on reanalysis of 10 shared microsatellite loci

Population	*N*	A_R	H_E	H_O	F_{IS}
NW Anatolia	18	3.62	0.65	0.69	-0.055
Other autochthonous populations					
Estonia	34	3.57	0.67	0.67	0.004
Latvia	29	3.52	0.70	0.66	0.064
Poland	18	3.17	0.60	0.59	0.014
Russia	10	3.74	0.73	0.71	0.033
Slovakia	6	2.90	0.57	0.63	-0.121
Reintroduced populations					
Bohemia-Bavaria	12	2.61	0.46	0.44	0.044
Vosges-Palatinian	23	2.57	0.49	0.47	0.042
Croatia	8	2.91	0.53	0.46	0.132
Slovenia	12	2.81	0.54	0.51	0.059

Numbers of genotypes (*N*), allelic richness (A_R), observed (H_O) and expected (H_E) heterozygosity, inbreeding coefficient (F_{IS}).

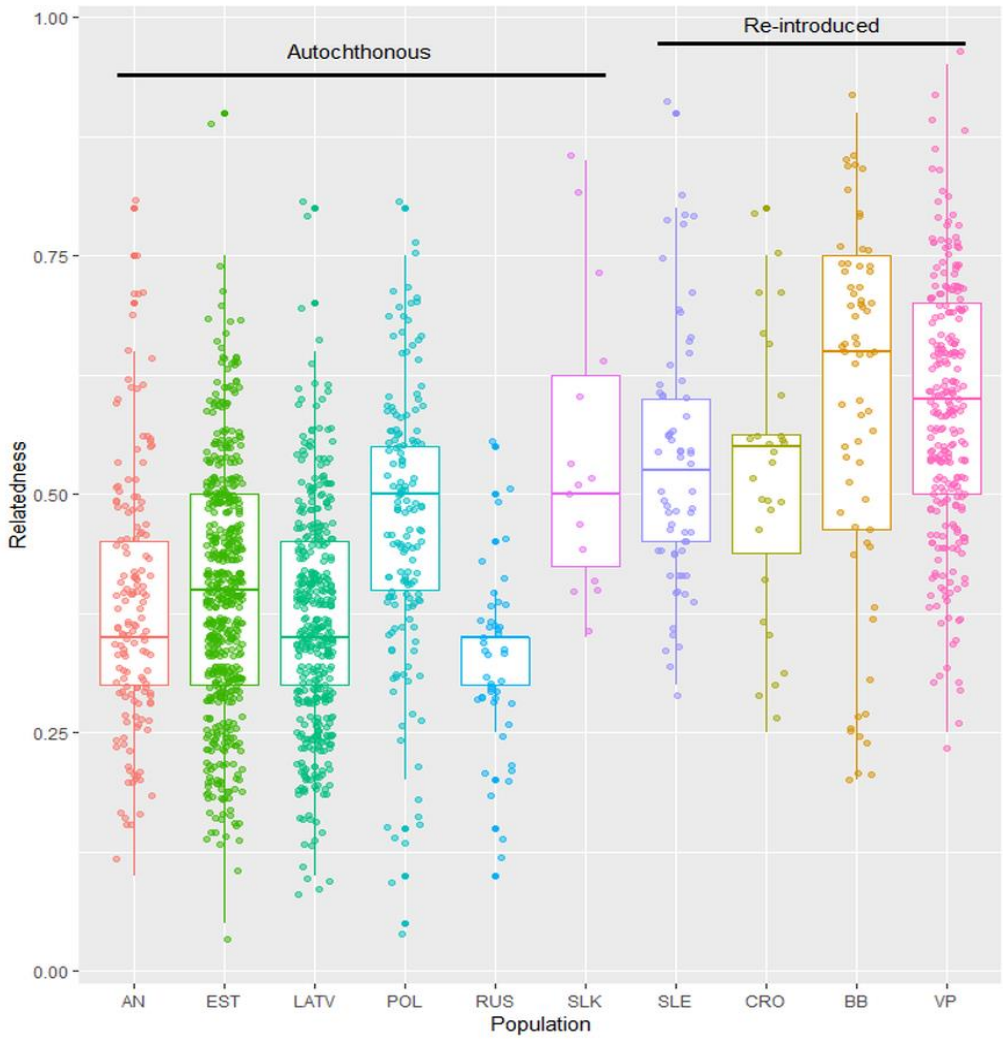

Fig 3. Relatedness (M_{xy}) among individuals in Eurasian lynx populations, including northwestern Anatolia and autochthonous and re-introduced lynx populations of central and eastern Europe (based on reanalysis of 10 shared microsatellite loci [14])

Sampling method and diversity measures

Over 52 survey days we collected 171 faecal samples (mean: 3.3 samples/ day) with the help of a scat detection dog (Table 1). In 961 trapping days we trapped and sampled 12 lynx (mean: 0.01 samples or animals/ day), visiting each trap every other day and renewing lures (i.e. lynx urine). We obtained a similar number of genotypes from both sampling approaches (Table 1), but needed a 19-fold higher effort in the 'invasive' sampling approach.

A reduction of the number of loci to eight microsatellites (see Methods) increased the number of unique genotypes to 22 among 57 samples. This larger dataset included one additional genotype that was detected using the two sample types and increased the number of overlapping genotypes to four.

We identified 14 unique genotypes among 45 non-invasively collected samples and 12 unique genotypes from the 12 invasively collected samples (Table 1). Cumulative estimates of probability of identity using the eight microsatellite loci were $P_{IDunb} = 3.79 \times 10^{-7}$ and $P_{IDsib} = 2.67 \times 10^{-3}$.

When we applied the subsampling analysis, the curves depicting the accumulation of mean number of alleles ($\bar{N}$) and expected heterozygosity (H_E) differed between the two sampling methods (Fig. 4). For both measures, genotypes from invasively collected samples were significantly less diverse than those from non-invasively collected samples (after subsamples of 6 or 7 genotypes; Tukey's test, $p\bar{N} < 0.0015$, $pH_E < 0.0015$) or if all samples were combined (after subsamples of 5 genotypes; Tukey's test, $p\bar{N} < 0.0015$, $pH_E < 0.0015$). The diversity observed among genotypes from non-invasively collected samples did not significantly differ from the diversity measured among all genotypes (for all subsample comparisons; Tukey's test, $p\bar{N} > 0.0015$, $pH_E > 0.0015$).

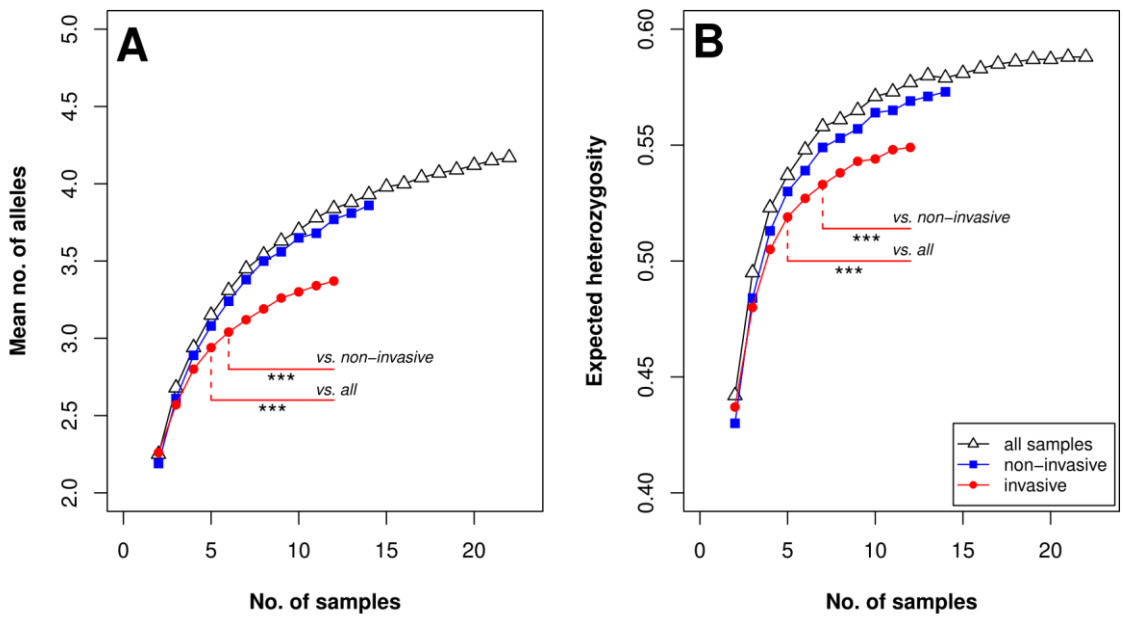

Fig 4. Accumulation rates of diversity measures with increasing sample numbers per sample type. A) Mean numbers of alleles ($\bar{N}$), and B) expected heterozygosity (H_E) values for genotypes sampled non-invasively (N=14), invasively (N=12) and for all genotypes (N=22), using 8 microsatellite loci.

Lynx population monitoring

Along with camera trapping and GPS collaring of lynx, genotyping enabled us to monitor 18 lynx individuals for periods from 6 months to 8 years (S3 Table). Nine lynx individuals were monitored by means of camera trapping, genetic monitoring and GPS tracking, and the remaining nine lynx by camera trapping and genetic monitoring but without GPS tracking. We matched seven of the unique

lynx genotypes with known lynx morphologies from lynx visits and defecation in front of or very close to camera trap stations. Except for one subadult (monitored for 6 months) these lynx were territorial residents monitored over several years. Three of the individuals caught in the cage traps were genetically sampled (hair from two kittens and tissue from an old male) but not GPS tracked. We monitored the 18 lynx over a mean of 3.1 ± 2.2 years using the combination of camera trapping, genotyping (non-invasive and invasive sample sources) and GPS tracking. The remaining four individuals were only identified by faecal genotypes. Unfortunately, these lynx could not be matched to camera trap pictures because defecation had not occurred in proximity to a camera trap.

Discussion

In this study, we report the first population genetic diversity measures for Caucasian lynx *L. l. dinniki*, focusing on the potentially isolated northwestern Anatolian population. We consider the diversity of *L. l. dinniki* in the context of previously published data for autochthonous and reintroduced Eurasian lynx populations in Europe (subspecies *L. l. lynx* and *L. l. carpathicus*), and consider the consequences of using invasive sampling versus non-invasive sampling for measures of genetic diversity of this territorial felid.

Genotyping

Genotyping is a valuable tool for assessing population genetic status and viability of endangered or data deficient animal populations [8, 57]. Planned and applied conservation activities such as captive breeding or re-introduction projects of endangered species use population genetics as a tool to measure genetic diversity in wild populations (e.g. *Lynx pardinus* [58]). Most preliminary conservation activities and conservation genetics studies of wild populations start in small survey areas, or are locally restricted because of restricted distribution of the target populations (e.g. *L. pardinus* [57]; *L.l. balcanicus* [59]; *Panthera pardus orientalis* [60]; *Panthera pardus melas* [61]). Small survey areas might in turn result in lower genetic diversity estimates.

Two sampling strategies are common: 'invasive' and 'non-invasive'. As our study is the first one on the *L. l. dinniki* population in northwestern Turkey, and because we were interested in generating baseline information on population genetics, we used both approaches. The 'invasive' sampling strategy was applied to ensure reliability of genotyping results, the 'non-invasive' sampling strategy was applied because it would increase the number of samples available for the study. The method was even improved by employing a scat detection dog. Having samples from both sampling approaches also provided an opportunity for a comparison of the results obtained in both approaches. Future surveys

of the northwestern population and other populations of Caucasian lynx in Turkey, Caucasus and Iran could then potentially rely on data from 'non-invasive' sampling.

As described in other studies, genotyping success in faecal samples can be a relatively low in relation to sampling effort and this can vary among species [62, 63]. In our study we attribute the low amplification success of non-invasive samples to the unknown and highly varying time lengths for which the faeces were exposed to environmental influences. We did not restrict ourselves to collecting fresh faecal samples only, because older faeces would also be useful for the purpose of diet analysis [15]. Long exposure time may not just influence genotyping success per se, but may also cause genotyping errors that need to be accounted for and which may also vary across species [5, 64-66]. Our genotyping results suggest that studies focused on genetic analyses should emphasize the collection of samples from freshly defecated faeces.

Spatial organisation

The spatial genetic analysis of the territorial members of northwestern Anatolian lynx population (combined sampling sources) revealed a unimodal genetic dissimilarity pattern, with a peak at 17 km (line in Fig 2B). Pairwise comparisons revealed that territorial females were most similar to each other at distances of up to 8 km, indicating that mothers and their daughters held neighbouring territories. The most dissimilar female pairs were observed at distances of 17 km (Fig 2C). No closely related males occupied neighbouring territories, indicating that male offspring of territorial males establish territories at larger distances from the territory they were born in. In our study area, the mean distance (MD) between the territory centres of territorial males was 12.1 km ± 3.1 km and 7.1 km ± 2.5 km for territorial female lynx (DM unpublished data). The results of the spatial autocorrelation analysis among lynx in our study area is consistent with this finding, indicating the highest negative correlations (i.e. most dissimilar genotypes) at distance classes of 13 km and 16 km (S2 Figure). Therefore, to overcome the negative influence of sampling at small spatial scales (i.e., clumped sampling) on genetic diversity, sampling of female lynx neighbouring territories should be avoided as these females will very likely be closely related. A sampling design that places live traps at every second female territory would most probably capture a higher genetic diversity, while reducing the relatedness among genotypes at the same time. In our study area, this would correspond to a minimum distance of 15 km between traps and would need to be specified for other Eurasian lynx or philopatric carnivore populations, and depend on their respective densities.

Impact of spatial organisation on measured genetic diversity

We observed substantial differences between measures of genetic diversity of a single lynx population derived from two sampling approaches (Fig 3), for which we identified four reasons: First, systematic 'non-invasive' sampling (in our study with a scat-detection dog) is more likely to sample the population evenly, both due to the larger number of samples to be collected and the much higher number of locations covered. Second, the chance of non-invasively sampling a resident floater or dispersing individual is much higher than the chance of cage-trapping a member of this segment of the population. Whereas resident floaters or dispersing animals remain in a particular area only for a few days, it is likely that they will leave traces such as one to two faeces/day [67] during a visit, which can be detected during non-invasive sample collection for some time after these individuals left the area again. Because box or cage traps stay in their locations for long periods of time, (often over months or even years; including inactive non-trapping periods), territorial lynx become accustomed to them. The chance of trapping territorial lynx and their kittens is therefore higher (S4 Figure and S5 Video) than the chance of trapping visiting lynx individuals such as resident floaters or dispersing individuals, which are less likely to be habituated to the traps. Third, to increase the chance of trapping territorial resident lynx, trap stations are placed in locations that are frequently visited by residents, such as lynx marking sites or on frequently used trails. These locations are often determined by prior camera trapping and are generally either in the core areas of lynx territories or are located in the overlapping ranges of several adult lynx. Fourth, female philopatry can further enhance the effect of sampling protocol on diversity measures if samples are collected in neighbouring female territories, thereby increasing the chance of collecting samples from related territorial individuals (e.g., mothers and their daughters).

If we had only used invasive samples for genetic monitoring, as was done for many preliminary conservation projects for endangered species [60, 68, 69], we would have underestimated the genetic variability in our study population. Therefore, our results emphasize the importance and usefulness of non-invasive sampling for conservation genetics studies of endangered and data deficient territorial carnivore populations, particularly at small spatial scales.

Genetic diversity

Within Anatolia. Considering its substantial diversity (H_E = 0.65, H_O = 0.69) and lack of inbreeding (F_{IS} = -0.05), the northwestern Anatolian lynx population currently does not appear to require any management to bolster its genetic diversity. In order to conserve its current genetic diversity, we

highly recommend identification and maintenance of primary lynx habitats and corridors in northwest Anatolia. As there is no other study on Anatolian lynx we could compare our findings with, our data provide a 'genetic baseline' of a seemingly healthy lynx population, available to future studies to measure anthropogenic and other impacts on this population (e.g., along a time line). Similar work is also needed for the other two Turkish populations of *L. l. dinniki* in order to determine whether the three big populations in Anatolia (Fig 1) are currently connected by gene flow.

Comparison with other populations. Compared with other autochthonous and re-introduced lynx populations in central and Eastern Europe (Table 3, Fig 2), only the (presumably much larger) Russian lynx population had higher values for its genetic diversity indices (e.g. A_R and H_O) than the north-western Anatolian population. We observed a low mean relatedness in the northwestern Anatolian population, similar to that observed for autochthonous populations sampled over much larger geographic areas (e.g. Latvia, Russia; Fig. 3).

Lynx population monitoring

Non-invasive genetic monitoring of carnivore populations is being increasingly used in wildlife studies. When combined with invasive sampling and camera trapping, this technique can provide valuable information on space use, marking behaviour and survival, and reveal interactions between individuals or groups [70]. By genotyping and re-sampling lynx individuals in this study, we obtained data on population dynamics, genetic relatedness, space use and other issues such as marking behaviour and spatial interactions [17] of a Caucasian lynx population for the first time. Genotyping revealed some dynamics between neighbouring territorial individuals such as male lynx intruding into territories of neighbours during mating time [17]. Although this population had been monitored since 2009 using camera traps, the relatedness among territorial lynx was still unclear but could be solved within our study. Besides revealing female philopatry genotyping also highlighted that shared pelage patterns (light background colour/ small dots) and thus has been assumed to be relatives, were actually unrelated, whereas others with very different pelage patterns (light background colour/ small dots vs. dark background colour/ big spots) turned out to be either a mother-offspring pair or a pair of full siblings (Fig. 5). As in other species too [71, 72], these phenotypes appear to have a complex inheritance in lynx (e.g. dominance, pleiotropy), and cannot be used to infer relatedness.

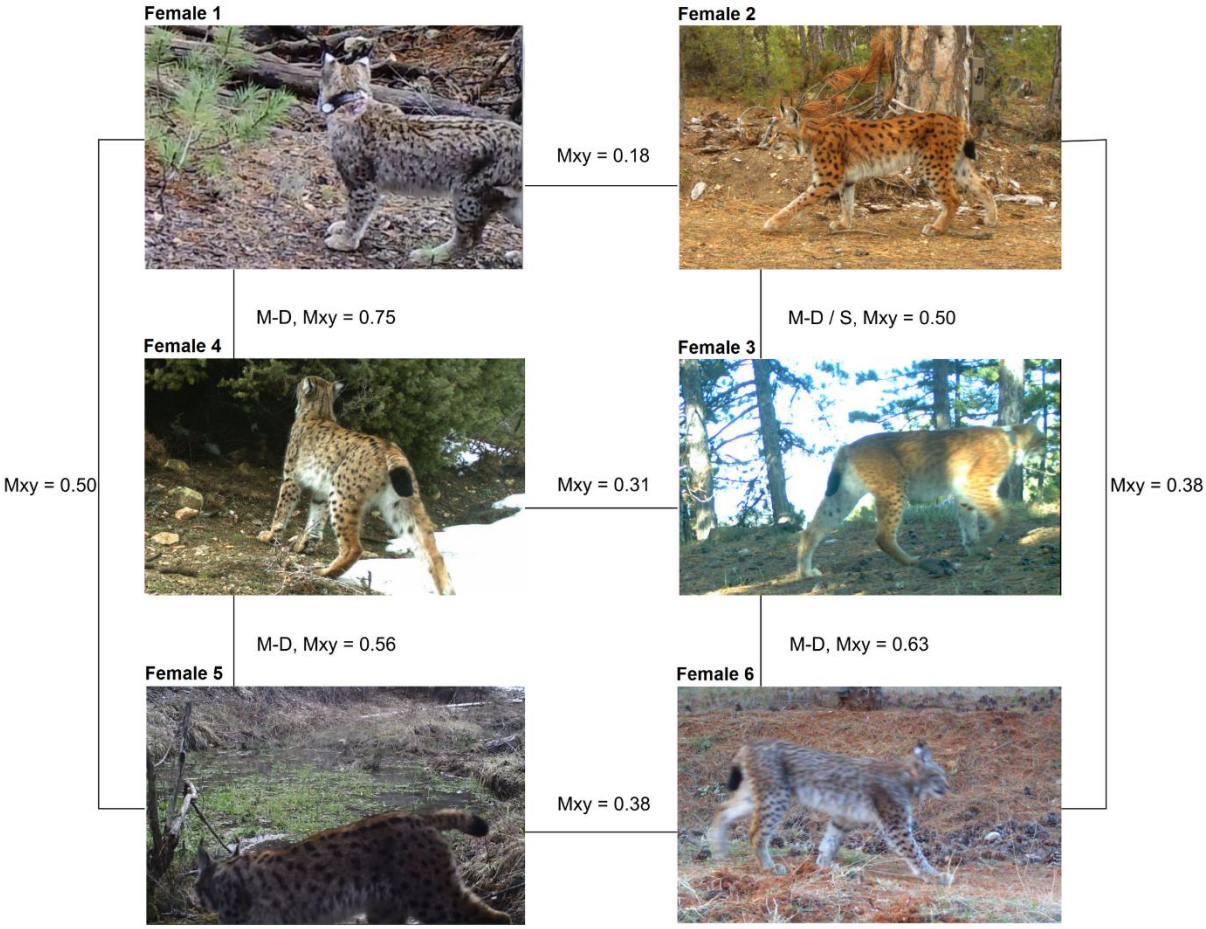

Fig 5. Coat patterns and M_{xy} relatedness values of territorial (No 1 – 5) and subadult (No 6) female lynx in NW Anatolia. Mother – Daughter (M-D), Mother – Daughter or Siblings (M-D / S)

Even if it is not combined with 'invasive' sampling and GPS tracking, in long-term studies, 'non-invasive' sampling along with camera trapping will serve as an important tool to monitor populations of individually recognizable animals [73]. If territorial individuals can be identified both phenotypically (e.g.by camera traps) and genotypically (via the genotyping of faeces), then linking this information will allow obtaining a much more comprehensive picture of behavioural and reproductive dynamics of the population in focus. The employment of a wildlife scat detection dog will even help to increase the success rate of such an approach.

Conclusions

Caucasian lynx (*L.l. dinniki*) in northwestern Anatolia displayed high genetic diversity. Assessment of other Caucasian lynx populations in Anatolia and elsewhere is required to evaluate the conservation

status of this subspecies. Our results show that sampling approach, territoriality and female philopatry can influence measures of genetic diversity, which may be relevant to conservation management decisions. 'Non-invasive' faecal sampling reduces the impact of female philopatry and territoriality on diversity measures and provides information on other important aspects of the biology and ecology of the species, which in turn can help to inform conservation management decisions.

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Supporting Information

S1 Table. Eighteen lynx genotyped at fourteen autosomal and two sexing loci (F-Amel and Z-Zf).

Data used to estimate genetic diversity measures and pairwise-relatedness among genotypes of northwestern Anatolian lynx population (Tables 2 and 3 and Fig 2 and S2 Figure). Orange color indicates the three microsatellite loci that were removed, and grey the two sexing loci.

			Multiplex A						Multipilex B						Multiplex C						Multiplex D								Multiplex E					
Genotype	Individual ID	Sample source	LCA110	LCA110	FCA506	FCA506	F115	F115	FCA008	FCA008	FCA006	FCA006	FCA082	FCA082	FCA097	FCA097	FCA478	FCA478	FCA718	FCA718	FCA229	FCA229	FCA105	FCA105	F-AMEL	F-AMEL	FCA1023	FCA1023	FCA441	FCA441	Z-Zf	Z-Zf	LCA109	LCA109
1	Female 1	invasive + non-invasive	97	97	196	196	240	240	137	137	182	182	241	247	142	142	193	193	218	222	156	160	189	189	216	216	223	231	127	127	166	166	179	181
2	Female 2	non-invasive	99	99	196	196	232	240	131	133	180	182	247	249	138	142	193	193			156	156	189	191	216	216	225	231			166	166	177	177
3	Female 3	invasive	97	99	194	196	236	236	133	137	180	180	243	247	136	142	193	193	218	222	156	156	189	191	196	216	225	231	119	119	166	166	177	179
4	Female 4	non-invasive	97	97	196	196			133	137			241	247	142	142	193	193	218	222	156	160	189	189	216	216	229	231			166	166	179	181
5	Female 5	invasive + non-invasive	97	99	196	196	236	236	133	137	178	180	241	247	142	144	193	193	222	222	156	160	187	189	216	216	229	231	139	139	166	166	179	181
6	Female 7	invasive	99	99	194	196			133	137	180	182	243	243	136	138	193	193	214	222	156	160	191	191	216	216			119	119	166	166	177	179
7	Female 9	non-invasive	97	97	180	196					180	182			142	142	193	193	218	222	156	160	189	189	216	216	231	231	113	113	166	166	179	181
8	Male 1	invasive + non-invasive	97	99	196	196	236	236	133	133	178	182	241	247	142	144	193	193	222	230	160	160	187	187	196	196	223	231	127	127	163	166	179	179
9	Male 2	non-invasive	99	105	194	194			133	137	178	180	239	243	136	142	193	193			156	158	189	193	196	216	225	227	127	131	163	166	177	177
10	Male 4	invasive	99	101	196	196			133	137	178	180	232	243	138	142	193	193	222	230	156	160	187	193	196	196	225	225	139	139	166	166	177	181
11	Male 5	non-invasive	97	97	196	198	232	232	131	133	182	182	232	245	142	142	193	193	214	230	156	160	191	191	196	196	225	225	119	127	163	166	177	181
12	Male 6	invasive	97	99	196	196			133	137	178	182	241	247	142	142	193	193	222	222	156	160	187	189	196	196	223	223	131	135	163	166	179	181
13	Male 8	invasive	97	99	196	196	236	236	133	137	180	182	232	243	140	142	193	193	214	222	156	156	189	191	196	196	225	225	119	127	166	166	177	179
14	Male 9	invasive	99	99	194	196	232	232	131	137	178	180	239	247	136	138	193	193	214	226	156	156	191	193	196	196	227	231	135	135	163	166	177	177
15	Male 10	invasive	97	99	196	196	236	236	131	133	180	182	243	247	136	138	193	193	222	230	156	160	187	193	196	216	223	227	119	127	166	166	181	181
16	Male 11	invasive	97	99	196	196	240	240	133	137	180	182	241	243	138	142	193	193	218	222	156	156	187	191	196	216	223	225	135	143	163	166	177	179
17	Male 12	non-invasive	97	99	196	196	236	236			178	178	241	241	142	144	193	193			160	160	187	187	196	216	223	231	119	119	166	166	179	179
18	Male 13	non-invasive	97	99			236	236			178	180	243	243	136	142	193	193	218	226	156	160	189	191	196	216	225	225			166	166	177	179

S1 Table 2. Twenty-two lynx genotyped at eight autosomal and two sexing loci. Data used to examine the influence of sampling methods on genetic diversity and relatedness (Figs 4-6) in NW anatolian lynx population.

			Multiplex A		Multiplex B				Multiplex C		Multiplex D						Multiplex E					
Genotype	Individual	Sample Source	LCA110	LCA110	FCA008	FCA008	FCA082	FCA082	FCA097	FCA097	FCA229	FCA229	FCA105	FCA105	F-AMEL	F-AMEL	FCA1023	FCA1023	Z-Zf	Z-Zf	LCA109	LCA109
1	Female 1	invasive + non-invasive	97	97	137	137	241	247	142	142	156	160	189	189	216	216	223	231	166	166	179	181
2	Female 2	non-invasive	99	99	131	133	247	249	138	142	156	156	189	191	216	216	225	231	166	166	177	177
3	Female 3	invasive + non-invasive	97	99	133	137	243	247	136	142	156	156	189	191	196	216	225	231	166	166	177	179
4	Female 4	non-invasive	97	97	133	137	241	247	142	142	156	160	189	189	216	216	229	231	166	166	179	181
5	Female 5	invasive + non-invasive	97	99	133	137	241	247	142	144	156	160	187	189	216	216	229	231	166	166	179	181
6	Female 6	non-invasive	97	99	133	137			136	142	156	156	187	191	216	216			166	166	177	179
7	Female 7	invasive	99	99	133	137	243	243	136	138	156	160	191	191	216	216			166	166	177	179
8	Female 8	non-invasive			133	133	239	247	136	142	156	158	189	191	216	216	225	231	166	166		
9	Female 9	non-invasive	97	97					142	142	156	160	189	189	216	216	231	231	166	166	179	181
10	Male 1	invasive + non-invasive	97	99	133	133	241	247	142	144	160	160	187	187	196	196	223	231	163	166	179	179
11	Male 2	non-invasive	99	105	133	137	239	243	136	142	156	158	189	193	196	216	225	227	163	166	177	177
12	Male 3	non-invasive	97	99	133	137			138	142	156	160	191	191	196	216	223	231	163	166	177	177
13	Male 4	invasive	99	101	133	137	232	243	138	142	156	160	187	193	196	196	225	225	166	166	177	181
14	Male 5	non-invasive	97	97	131	133	232	245	142	142	156	160	191	191	196	196	225	225	163	166	177	181
15	Male 6	invasive	97	99	133	137	241	247	142	142	156	160	187	189	196	196	223	223	163	166	179	181
16	Male 7	invasive	97	97	133	133	245	247	138	142	156	156	191	191	196	196	231	231	163	166	177	177
17	Male 8	invasive	97	99	133	137	232	243	140	142	156	156	189	191	196	196	225	225	166	166	177	179
18	Male 9	invasive	99	99	131	137	239	247	136	138	156	156	191	193	196	196	227	231	163	166	177	177
19	Male 10	invasive	97	99	131	133	243	247	136	138	156	160	187	193	196	216	223	227	166	166	181	181
20	Male 11	invasive	97	99	133	137	241	243	138	142	156	156	187	191	196	216	223	225	163	166	177	179
21	Male 12	non-invasive	97	99			241	241	142	144	160	160	187	187	196	216	223	231	166	166	179	179
22	Male 13	non-invasive	97	99			243	243	136	142	156	160	189	191	196	216	225	225	166	166	177	179

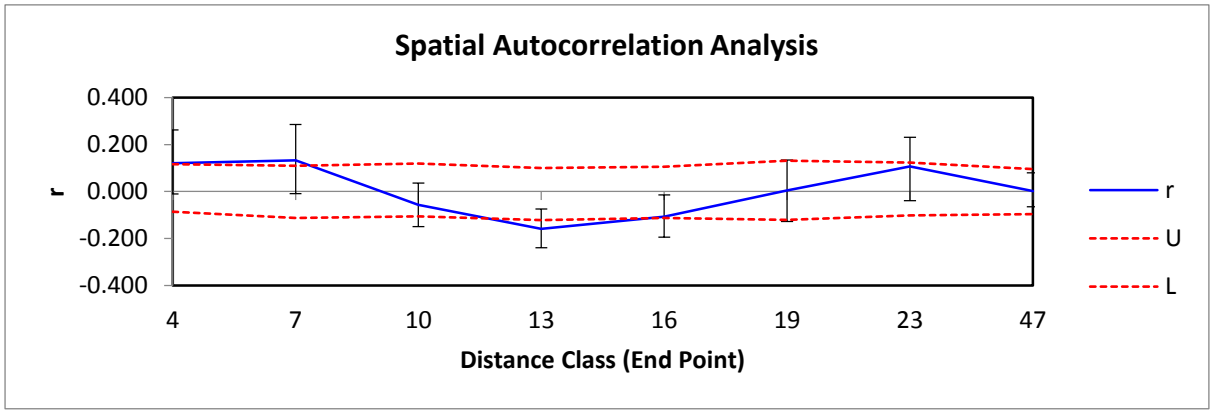
S3 Table. Lynx individuals monitored in between 2009 and 2017.

Camera trapping (CT), Genotyping (G), GPS telemetry (T). Bold values indicate total amount of genotypes obtained using 11 and 8 microsatellite loci.

	Individual	Name	No. of times genotype detected	Genotypes per year (11 loci/8 loci)				Social status at first sampling time	Modes of tracking	Tracking period	Years	Status in 2017
	Males		11 loci/8 loci	2013-2014	2014-2015	2015-2016	2016-2017					
1	M1	Turbo	9/12	5/6	3/4	1/2		Territorial	CT + G	2009-2016	7	Dead.
2	M2	Başgan	4/8	4/8				Territorial	CT + G	2012-2015	4	Dead.
3	M3	Özgür	0/3	0/1		0/2		Territorial	CT + G	2012-continued	5	Shifted to territory of M1. Alive and resident.
4	M4	Kısakuyruk	1/1		1/1			Territorial	CT + G + T	2012-2017	5	Alive and resident.
5	M5	Ardıç	4/7		3/6		1/1	Territorial	CT + G	2015-2017	3	Replaced M2. Alive and resident.
6	M6	Uluhan	1/1		1/1			Non-territorial	CT + G + T	2015-2017	3	Dispersed.
7	M7	Kardeş 2	0/1			0/1		Non-territorial	CT + G	2016-2017	1.5	Dispersed.
8	M8	Kırıkdiş	1/1			1/1		Non-territorial	CT + G + T	2016-2017	2	Was a floater. Established a territory outside of study area.
9	M9	Evrim	1/1			1/1		Non-territorial	CT + G + T	2016-2017	1.5	Dispersed.
10	M10	Ruffy	1/1				1/1	Non-territorial	CT + G + T	2017-continued	0.5	Floater.
11	M11	Finger	1/1				1/1	Non-territorial	CT + G + T	2017-continued	0.25	Floater.
12	M12	195	1/1				1/1	Non-territorial	G	2017	-	Unknown.
13	M13	199	1/1				1/1	Non-territorial	G	2017	-	Unknown.
	Females											
14	F1	İpek	3/5	1/2	1/2		1/1	Territorial	CT + G + T	2009-continued	8	Alive and resident.
15	F2	Eylül	2/2	2/2				Territorial	CT + G	2014-continued	4	Alive and resident.
16	F3	Frida	2/2				2/2	Territorial	CT + G + T	2015-continued	3	Alive and resident.
17	F4	Asi	3/3			2/2	1/1	Territorial	CT + G	2015-continued	3	Alive and resident.
18	F5	Xena	1/2				1/2	Territorial	CT + G + T	2016-continued	2	Alive and resident.
19	F6	İncebenek	0/1	0/1				Non-territorial	CT + G	2014	0.5	Probably died after a serious fight with F1 in Spring 2014 (DM unpublished camera trapping data).

20	F7	Kardeş 1	1/1			1/1		Non-territorial	CT + G	2016-2017	2	Dispersed.
21	F8	104	0/1			0/1		Non-territorial	G	2015	-	Unknown.
22	F9	194	1/1				1/1	Non-territorial	G	2017	-	Unknown.
		Total	**38/57**	**12/20**	**9/14**	**6/11**	**11/12**					

S2 Figure. Results of spatial autocorrelation analysis for all lynx individuals genotyped at 11 microsatellite loci.



S4 Figure. Female 1 trapped with 11 months old male kitten. Father of this male kitten was also captured in the same trap at another occasion.

S5 Video. Female 4 (daughter of Female 1) is checking an inactive trap with her two kittens. One of the kittens in the video is Female 5, which was captured and collared next trapping season (14 months later) in the same trap. (**Not embeddable to the printed version of the thesis**)

CHAPTER 4: Spatial ecology and density of northwest Anatolian lynx

Female and male Caucasian lynx have distinct spatial tactics at different life-history stages in a high density population

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Manuscript in preparation

DM conceptualized the study. DM conducted field work. DM, SE and AB conducted the formal analyses. DM wrote the drafted manuscript. DM, AB, and HH provided input to the writing and editing of the manuscript.

Abstract

The Caucasian lynx *Lynx lynx dinniki* is a subspecies of Eurasian lynx that occupies the Anatolian part of Turkey, Caucasus and Iran. So far little is known about its spatial behaviour, population dynamics or individual interactions, a prerequisite to appropriate conservation actions. We used GPS telemetry to record the behaviour of seven individuals in northwestern Anatolia for less than a year and of two individuals for less than two years, thereby obtaining eleven lynx home ranges. Analyses of 95% kernel utilization distribution (KUD) and 100% minimum convex polygons (MCP) revealed the smallest mean adult female (n = 4) home range sizes at 46 ± 8 km^2 (95% KUD) and 49 ± 16 km^2 (100% MCP) ever reported for Eurasian lynx. Adult males of the Caucasian lynx population in northwest Anatolia displayed two different spatial tactics. Male territorial residents defended and occupied permanent territories with a mean (n = 2) of 176 ± 3 km^2 (95% KUD) and 183 ± 5 km^2 (100% MCP), three to four times the size of female home ranges. Resident floaters (n = 2) roamed within strikingly large, permanent home ranges of a size of 2419 ± 2208 km^2 (95% KUD) and 2114 ± 2004 km^2 (100% MCP), comparable to home range sizes of Scandinavian lynx populations. With 4.9 individuals per 100km^2, population density was high, suggesting that the presence of adult male floaters (eight to ten years old) was a consequence of a fully occupied landscape by territorial residents and revealing a flexibility of spatial behaviour of Eurasian lynx previously not recognised. We suggest that such a high population density and behavioural flexibility may have been aided by the legal protection of and apparent low levels of poaching of this population. The observed spatial tactics are unlikely to be seen in most of the previously studied European populations of the Eurasian lynx either because they suffer high levels of anthropogenic killing, or – if reintroduced – were unlikely to be at carrying capacity. Predicting spatial behaviour from studies conducted on exploited or reintroduced lynx populations are therefore unlikely to reveal the full breadth of lynx responses to specific environments. For effective and appropriate conservation planning, data from lynx populations in a reasonably natural state such as ours where space, individual interactions, prey and pathogens are likely to be the key drivers are therefore essential.

Keywords: Caucasian lynx; GPS-collar; spatial tactics; territoriality; floaters; home range; population density; spatial capture-recapture

Introduction

The general observation that many carnivores have simple social organizations, with males and females living a solitary lifestyle and independent home ranges (Gittleman, 1989). This is also largely the case in felids, where only two species, the lion (*Panthera leo*) and the domestic cat (*Felis catus*) have been recognised to be social (McDonald et al., 2000; Schaller, 1972). Detailed recent studies of cheetahs (*Acinonyx jubatus*) have demonstrated that even in felids with a simple social organisation, complex male spatial tactics can be observed which include both territorial residents and resident floaters (Caro, 1994; Melzheimer et al., 2018). This spatial tactic has been described as a unique form of social organisation in mammals (Melzheimer et al., 2018). In the cheetah populations in the Serengeti and in Namibia where such complex male spatial tactics were observed it was clear that sites for male territories were limited and floaters usually waited for a vacancy to arise. Such a queueing system is a form of organisation whose importance is only being gradually recognised and which poses interesting evolutionary questions (e.g. Maynard Smith 1982). Few queues have been described from mammals; examples are male mating queues in thirteen-lined ground squirrels (Schwagmeyer and Parker, 1987), male social queues for dominance rank in the spotted hyena *Crocuta crocuta*, (East and Hofer, 2001), and offspring queuing to inherit parental territories in the red fox *Vulpes vulpes* (Lindström, 1986). The cheetah studies suggest that populations of other solitary felids with comparatively minor anthropogenic interference close to or at carrying capacity could show a queueing system amongst males similar to the floaters observed in cheetahs, thereby representing different life history stages of adult males.

The spatial ecology and organization of Eurasian lynx *Lynx lynx* through radio-telemetry has been studied only for the two subspecies of Eurasian lynx (*L.l. lynx* and *L.l. carpathicus*) occupying Europe. Some of these studies reported largest mean territorial home ranges for felidae (Linnell et al. 2001; Herfindal et al., 2005). Home range size of Eurasian lynx populations in central and eastern Europe generally decreases from northern to southern latitudes (Herfindal et al. 2005; but: Schmidt et al. 1997). Herfindal et al. (2005) suggested that the latitude reflected environmental productivity in terms of prey density and that this was the main driver of home range size in Eurasian lynx populations.

The spatial ecology of Caucasian lynx *L.l. dinniki* populations has never been studied before. This subspecies of Eurasian lynx is a lagomorph prey specialist (Mengüllüoğlu et al. 2018) and can occur at high densities in suitable habitats (Avgan et al., 2014). The northwest Anatolian Caucasian lynx population was previously reported to display high genetic diversity and no signs of inbreeding, suggesting that this lynx population did not suffer a recent bottleneck (Mengüllüoğlu et al. 2019). All lynx populations in Anatolia are autochthonous, legally protected, no hunting quotas issued and

apparently little poached, although poaching is known to take place in various parts of Anatolia (Şekercioglu et al., 2011). Therefore, the Caucasian lynx population in northwest Anatolia is an example of a non-exploited population likely to display behaviour in terms of spatial tactics and individual interactions and associated population dynamics typical for natural populations close to or at carrying capacity.

Caucasian lynx occur in Anatolia in xeric temperate coniferous forests, open steppe habitats with scattered trees, and open rocky habitats distributed over the Anatolian mountains and plateaus. Brown hare (*Lepus europaeus*) is the main prey of lynx in Turkey as shown in three main ecosystems (Mediterranean, forest-steppe mixed and subalpine; Mengüllüoğlu et al. 2018). These ecosystems generally exhibit lower primary production than north Anatolian (Black Sea coast) or central European humid and temperate mixed and dedicuous forests (Evrendilek et al., 2007). A recent study of ten study sites in northern Anatolia reported that lynx presence was significantly positively correlated with brown and presence of coniferous woodland rather than the presence of roe deer (*Capreolus capreolus*) and the type of humid deciduous habitat which roe deer occupy in Turkey (Soyumert et al. 2019). Therefore, based on primary production hypothesis (Herfindal et al. 2005) we should predict low lynx densities and large home range sizes in Anatolian lynx population due to their habitat preference patterns. An alternative hypothesis can also suggest that because of its lagomorph specialist diet lynx populations in Anatolia should display high density and smaller home range sizes as in other lagomorph specialist lynx species (i.e. *L. Canadensis,* Burdett et al. 2007; *L. pardinus*, Ferreras et al. 1997).

In order to test the predictions from these three hypotheses we studied lynx in northwestern Anatolia at a site where lynx have been monitored through camera trapping since 2009. We used camera trap data to assess lynx density and used GPS telemetry to observe the behaviour of male and female adult lynx and record their movements and the location and sizes of their home ranges.

Methodology

Study area

The study was conducted in the Nallıhan Mountains (40°11’- 31°21’; Fig 1), a mountain chain in the transition zone between the dry western Black Sea (xero-euxine) and central Anatolian (Iran-Turan) floristic zones. The area does not hold any form of protection status, and is part of the state forests management system. This region is also influenced by the Mediterranean floristic zone (western Aegean), through the catchment area of the Sakarya River (Aksoy 2009). Vegetation and landscape

have been shaped by altitude and historical human use. The lower areas (500 to 1000 m) are covered by steppe in the south, which is gradually replaced by Turkish pine (*Pinus brutia*). Above this belt, temperate coniferous forest reaches up to 1500 m and is composed of black pine (*Pinus nigra*) and junipers (*Juniperus excelsa* and *J. oxycedrus*) with an understory of oak-dominated (*Quercus pubescens, Pyrus elaeagnifolia, Crataegus spp.*) scrub with frequent forest openings. Mean annual temperature is 9.6º C, mean annual total precipitation 543 mm (ClimateData.org). The area does not hold any form of protection status, and is part of the state forests management system. The human population in this area is at a low density and restricted to several villages in the surrounding lowland and valleys. Red deer (Cervus elaphus) and wild boar (Sus scrofa) are the common large herbivores, and brown hare (Lepus europaeus) is the main lynx prey species (Mengüllüoğlu et al. 2018). The area is home to several other large and medium-sized carnivores. At higher elevations brown bear (Ursus arctos) and grey wolf (Canis lupus) are sympatric with lynx. At lower elevations golden jackal (Canis aureus), red fox (Vulpes vulpes) and jungle cat (Felis chaus) occur rarely in habitat occupied by lynx and wolves (Mengüllüoğlu 2010).

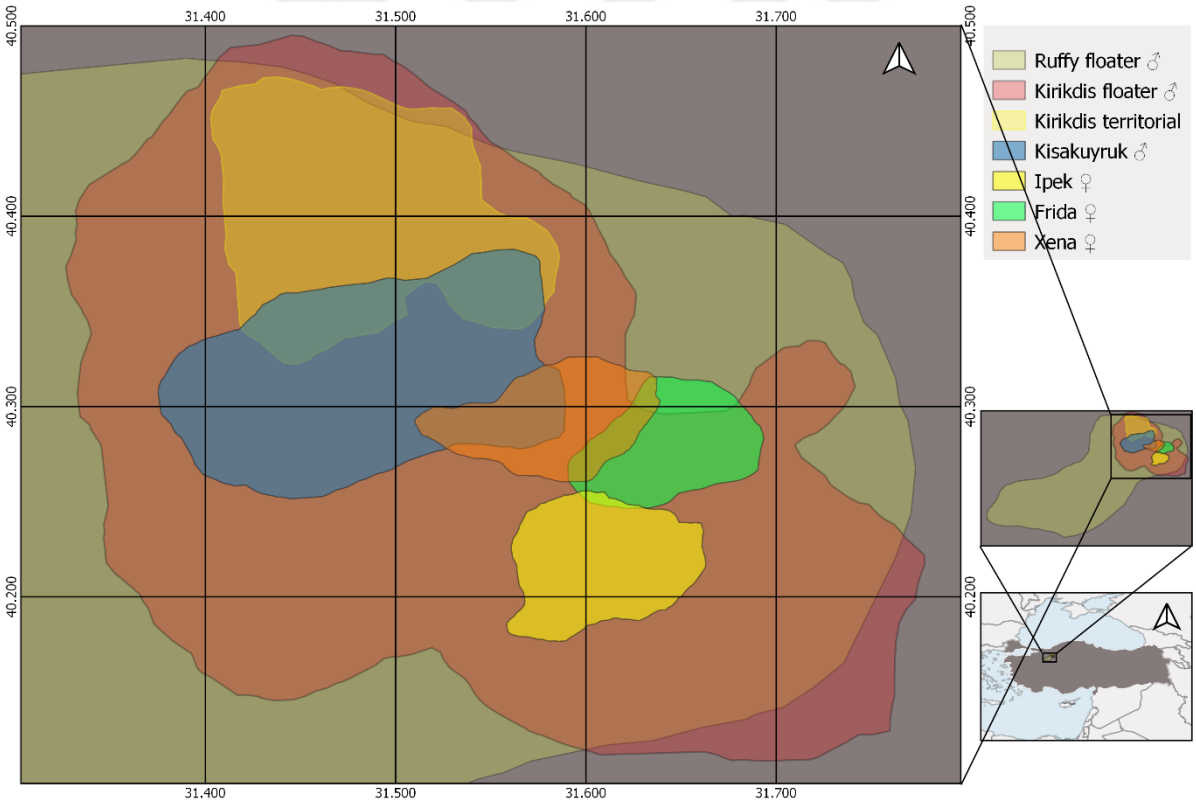

Figure 1. Location of the study area in the Nallıhan Mountains in Turkey and 95% kernel utilisation distribution home ranges of resident adult lynx. The home ranges of one individual male, Kirikdis are presented separately for the floater and territorial stage. Produced using Quantum GIS (2015).

Live trapping and tracking

Live trapping and capture of lynx was performed in collaboration with the Wildlife Department of the Turkish Ministry of Agriculture and Forestry (WDT) under protocol and permit number 30057506-030-1867 issued by the department. We used five cage traps produced by the WDT (length: 2 m, height: 1.5 m, width: 1 m). Traps were placed on lynx trails at nine live trapping stations, monitored by GPRS camera traps (Keepguard KG860, Keeptime industrial (Asia) Co., Hong Kong, China) and VHF transmitters continiously, and visited and checked every second day. Over the course of three live trapping seasons (n = 961 active trap days) during the winters of 2014, 2015 and 2016 from December until April in the following spring, 16 lynx (five females and 11 males) were captured. Age was estimated on the basis of tooth wear (Table 2 in Marti and Ryser-Degiorgis, 2018). Nine lynx were fitted with 185 g GPS collars (e-obs GmbH, Grünwald, Germany) after anaesthesia with the help of 5mg/kg ketamine and 0.2mg/kg metedomidine. Anaesthesia was carried out by the authorised wildlife veterinarian of the WDT according to national ethical legislation. No specific permit was required for anaesthesia and handling of lynx as it was conducted by the WDT. One old adult male captured in 2015 and two kittens captured in 2016 were neither anesthetised nor collared due to unsuitable age and ethical concerns. Four other adult lynx, three males and one female, were trapped during the first two live trapping periods but escaped, as the traps produced by the WDT were still under development and had some weak sides subsequently strengthened. Rate of live capture was 1 lynx per 60 trap days for 16 captured lynx and 1 lynx per 107 trap days for the collared lynx.

GPS collars recorded between 12 and 48 locations per day. We tracked the lynx on a mean of 250 ± 224 days (S.D., range 19-612) and obtained on average 4154 ± 3926 GPS locations (S.D., range 285-11,173, Table 1). We downloaded GPS data via handheld UHF antennas from hill tops. One 11 month old male, one 2 year old male and one 4 year old resident female could be tracked an average of 20 days whence the GPS collar failed. Locating GPS collared lynx was difficult because of the rugged montane topography of the study area cut by many valleys and series of heights.

Home range analysis

We estimated home ranges with the help of 95% kernel utilization distributions (KUD) and 100% minimum convex polygons (MCP) using the R (R Development Core Team, 2014) package *'adehabitatHR'* version 0.4.16 (Calenge 2011) . Lynx were classified into adult males, adult females, subadult males based on body size, tooth wear and camera trap monitoring since 2009. If an individual was frequently camera trap pictured and breeding in the study area (i.e. breeding females) prior to live capture and collaring, it was classified as resident territorial. All results are presented as means ± standard deviations.

For individuals with data for more than one year (one male and one female) we calculated separate home ranges for each year. We estimated the number of tracking days required for reliably estimating the home range size for an adult female using the 95% KUD as follows. We compared first 35 days 95% KUD HR of a long term monitored adult female lynx with its annual 95% KUD HR. In the comparison, breeding period was exluded from annual HR of long term monitored fmelae, as 21 days HR of short term monitored female lynx did not overlap with this period (i.e. during breeding and denning female HR is smaller than the HR at other seasons; Schmidt, 1998)). Hence, 5th, 8th, 10th, 15th, 20th, 25th, 30th, 35th days' 95% KUD HR were compared to mean 95% KUD HR of mating, autumn and winter seasons). We did not implement this method for the other two young male lynx (one 11 months juvenile and one 23 months old subadult) with short term tracking data as they did not have stable territories. To compare body mass northwest Anatolian lynx with those from other studies we applied the nonparametrtic Mann-Whitney U-test (Hollander et al., 2014). Statistical tests were performed in PAST software (Hammer et al., 2001).

We also calculated seasonal home ranges. Dependent neo-natal kittens and denning is known to influence adult female home range size during summer, winter might change local prey abundance because of snow cover and limit lynx movements in montane areas, and during the mating season male lynx may search over larger areas to find mates. For this purpose we defined a summer season as 15 April to 14 September (i.e. reproduction, denning of female lynx and dependent stationary kittens; Schmidt, 1998), a winter season as 15 December to 14 February (i.e. low prey availability; Demirbas and Albayrak, 2015) and a mating season as 15 February-14 April (Brietenmoser-Wuersten et al., 2007).The annual lynx cycle was completed by an autumn season defined as 15 September to 14 December (i.e. when female with kittens start to roam total home range).

Capture-mark-recapture (CMR) survey

Camera trapping was conducted at 17 camera trap stations using Reconyx HC600 and Bushnell Trophy Cam 119678 HD MAX camera traps, using between two and four cameras per location. Cameras were active 24 hours a day and set to continuous record with no delay between consecutive images or videos. Some cameras were set near live trapping stations as the live traps were placed along active lynx trails recognised from long-term population monitoring. Camera trapping was part of long-term lynx monitoring and therefore cameras were active throughout the year. We chose the period from 24.12.2015 to 02.04.2016 (100 days) to estimate lynx population density in order to capture high lynx activity before and during mating season (Breitenmoser et al. 2006). We also tested a longer survey period to increase the number óf photographic recaptures as some lynx individuals had been trapped in the area already (7 lynx in winters 2014-2015 and 2015-2016) and might have been wary of camera

traps. Therefore, we increased the twelve 5-days occasions generally used in Eurasian lynx CMR studies to 20 5-days occasions, hoping that population closure was not statistically violated.

With the beginning of the long-term study in 2009, we applied a camera trapping study design similar to other Eurasian lynx camera trapping surveys. This meant that the mean nearest neighbour distance between camera traps was 2.2 ± 0.8 km (range 1.2 km to 3.9 km). We did not use a grid system, as camera trapping was designed to serve other purposes as well as the CMR survey.

Population density estimation

Spatial capture-mark-recapture (SCR) models are a newly developed class of models which estimate density whilst allowing for individual movement outside the camera trapping grid, thereby overcoming the problem of defining the survey area as with traditional, non-spatial capture-mark-recapture models (Royle et al., 2014). SCR models work on the assumption that each individual i has a permanent (albeit) unobserved activity centre s_i. The probability of observing an individual is a monotonically decreasing function of the distance y_{ij} from the activity centre to any given camera trap (detector) j (Sollmann et al., 2011). The models combine a state model, representing the geographic distribution of individual home ranges and treating them as a homogeneous Poisson point process, with an observation model which estimates the probability of encountering an individual at a given detector, e.g. a camera trap, as a function of the distance of the detector from the individual's activity centre (Borchers and Efford, 2008).

The R (R Development Core Team, 2014) package '*secr*' version 3.2.0 (Efford, 2012) was used to estimate density using a maximum likelihood framework. The package requires three input files, the first, the 'capture history' file, was created by individually identifying lynx using unique pelage pattern and assigning sex using the presence or absence of the external scrotum with the testes and the presence of associated kittens. Individual capture histories were then constructed for individuals using twenty 5-day occasions (Avgan et al., 2014). The second input file, the 'trap deployment' file, details the UTM GPS locations of camera traps, along with a binary string to represent when a particular detector was active ('1'), or inactive ('0') during a sampling occasion. The third input file, the habitat mask, represents the habitat in the vicinity of the detectors potentially occupied by the species of interest, and can delineate habitat and non-habitat sites within the outer limit (Efford, 2019). The habitat mask was constructed by placing a 15.44 km buffer around the camera trap minimum convex polygon (MCP) in QGIS 3.6.0 (2015), and overlaying a shape file layer containing areas of non-habitat within the buffer area to create a shapefile of the suitable habitat around the camera traps. A buffer of 15.44 km was used as this was the mean maximum distance moved (MMDM) by six GPS-collared male lynx in the study area. Unsuitable habitat was defined as open agricultural fields and villages in

the Nallihan district that were not used by the collared lynx individuals (n = 9). After removal of the unsuitable habitat, the 15.44 km buffer resulted in a sampling area of 1048 km^2.

SCR density models were ran to select the most appropriate detection (observational) process, either half-normal or negative exponential, using Akaike's Information Criterion adjusted for small sample size (AICc) for either model. The hazard rate detection process was not considered, as this is only recommended in situations in which the survey area is fully surrounded by a natural or artificial boundary, given that density estimates from it do not reach a plateau fairly promptly with an increasing buffer width (Efford, 2017). Three density models were ran, using the most appropriate detection process, in which $g_0(\lambda_0)$, the capture probability at the centre of an individual's home range, and б, a function of the scale of animal movement were affected by various factors: (1) the null model in which both g_0 and б were constant (λ_0 ~ 1, б ~ 1), (2) the behaviour b_1 model in which g_0 was affected by the response of individuals to camera traps (λ_0 ~ b, б ~ 1), (3) a second behaviour model, the learned response b_2, in which both g_0 and б were affected by the response of individuals to camera traps (λ_0 ~ b, б ~ b). Due to small sample sizes, sex specific models were not considered. All models were ranked using AIC_c values. Population closure was tested by performing the closure test (Otis et al., 1978) within the secr package.

Latitude, female home range size and population density

We tried to understand the relationship between latitude, female home range size and lynx population density. Nonparametric partial correlations were run using the R package ppcor version 1.1 (Kim, 2015), choosing Kendall's τ as calculation option. Kendall's τ was chosen rather than Spearman's ρ because it affords less weight to extreme data values than does Spearman's ρ and hence is conservative approach.

Results

Tracked lynx

We captured and collared two breeding adult (Ipek and Frida) and one non-breeding adult female lynx (Xena), and three adult (Kisakuyruk, Kirikdis and Ruffy), one young adult (Finger) and two juvenile male lynx (Uluhan and Evrim, Table 1). Both young adult lynx (Xena and Finger) were 23 months old and both juveniles were 11 months old at capture time. The other five collared lynx were older than four years (Table 1). Mean body mass of adult lynx from both sexes were smaller than masses of adult Eurasian lynx in European populations: Mean body mass of adult female lynx in our study area (13.1 ± 0.4 kg, n = 3) was significantly smaller than the mean body mass of female Swiss lynx (17.6 ± 1.9 kg,

n = 4; Mann Whitney U test, U = 0, p = 0.05; data from Breitenmoser et al. 1993). Mean body mass of adult male Caucasian lynx in our study area (16.6 ± 0.9 kg, n = 4) and Swiss male lynx (22.0 ± 1.5 kg; U = 0, p = 0.05). Mean body mass of Caucasian juvenile lynx from our study area (10.0 ± 0.6 kg, n = 2) did not differ from the mean body mass of Swiss juvenile lynx (11.2 ± 1.6 kg; U = 4.5, p = 0.28).

All three collared females held territories, whereas only one adult male lynx (Kisakuyruk) held a territory at the time of capture and collaring. This male individual have repeatedly camera trap pictured in the same area since 2012 and stayed in the same area after capture and collaring. Even after battery of his collar failed camera traps continued to repeatedly capture this individual until July 2018. Two other adult males (Kirikdis and Ruffy) that were not known prior of capture and collaring, were resident but apparently floater non-territorial adults and moved across a large home ranges. At the second year of GPS tracking Kirikdis shrank his home range to one fifth the size of his home range at the first year.

Home range size

The home range size of adult female lynx Ipek reached the asymptotic value of 66.0 ± 8.0 km^2 (excluding summer season when she gave birth and used half of her 2015 HR) within 10 days. After this date, the home range size fluctuated within one standard deviation at 68.0 ± 2.6km^2 during the following 25 days (Fig. 2). Therefore 10 to 15 tracking days were sufficient to estimate the 95% KUD home range of adult females (Fig. 2) which allowed us to use home range data from adult female territorial lynx Frida with 21 days of tracking data to calculate a mean home range size for adult female lynx.

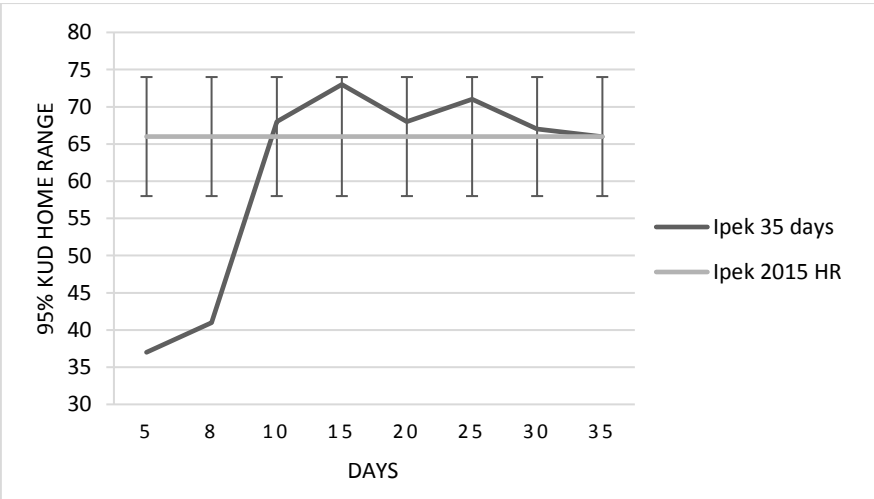

Figure 2. Home range size of adult female territorial lynx Ipek during the first 35 days after capture and collaring in comparison to its mean home range size in 2015 (66.0 km^2) excluding the summer season. Error bars indicate standard deviation for seasonal home range size (8.0 km^2) excluding the summer of 2015.

Females had small home ranges (n = 4, 95% KUD = 46.2 ± 7.5 km^2, 100% MCP = 49.4 ± 16.0 km^2, Fig. 1, Table 1). Mean home range size of territorial males (n = 2, 95% KUD = 176.0 ± 2.9 km^2, 100% MCP = 182.9 ± 4.7 km^2) was almost four times larger than female home ranges (Fig. 3). Home ranges of two adult male lynx classified as floaters (Ruffy and Kirikdis) were enormously large (n = 2, 95% KUD = 2419.2 ± 2208.2 km^2, 100% MCP = 2113.9 ± 2004.2 km^2). Ruffy had KUD and MCP home range sizes corresponding to 86 and 72 female home ranges, respectively (Fig. 1). Kirikdis used a home range equivalent to 19 KUD and 14 MCP female home ranges, five times larger than his subsequent range as a territorial resident (95% KUD = 173.9 km^2, 100% MCP = 179.5 km^2) during the second year of tracking (Fig. 1). Floater adult males held larger home ranges than adult males with permanent territories (Fig. 3), at a mean of 14-fold territorial male KUD and 12-fold territorial male MCP home range sizes (Table 1).

	Date of capture	**Age at capture [years]**	**Body mass [kg]**	**Number of days tracked**	**Number of GPS fixes**	**95%KUD**	**100%MCP**
Territorial adult females							
İpek 2015	20.03.2015	9-10	12.8	332	6586	54.1	69.2
İpek 2016				231	4585	36.7	48.9
Xena	29.03.2017	23 months	13.0	242	4591	49.8	49.4
Frida	21.03.2017	4-5	13.6	21	276	44.1	30.2
Mean			13.3±0.4	206.5±131.7		46.2±7.5	49.4±15.9
Territorial adult males							
Kırıkdiş 2017				283	3693	174.0	179.5
Kısakuyruk	08.03.2016	7-8	15.6	161	2081	178.1	186.2
Mean				222±86.3		176±2.9	182.9±4.7
Non-territorial adult males (Floaters)							
Kırıkdiş 2016	24.03.2016	7-8	16.5	329	4294	857.7	696.7
Ruffy	08.03.2017	9-10	17.7	263	3459	3980.6	3531.1
Mean			*16.6±0.9	296±46.7		2419.2±2208.2	2113.9±2004.2
Non-territorial young males							
Uluhan	20.03.2015	11 months	10.6	346	7234	447.3	932.3
Finger	21.03.2017	23 months	16.5	21	284	103.9	71.4
Evrim	17.03.2016	11 months	9.4	19	300	57	41.7
Mean			**10±0.8	128.6±188.2		202.7±213.1	348.5±505.8

Table 1. Capture date, age and body mass at capture, total tracking days and number of GPS locations, individual and mean home range sizes of lynx tracked in our study. *calculated using body masses of Kirikdis, Kisakuyruk, Ruffy and Finger. **calculated using body masses of Uluhan and Evrim

We tracked one juvenile male lynx (Uluhan) for a long time period until he was 22 months old (346 days). Twenty days after being captured and collared together with his mother, Uluhan separated from his mother at 10th April 2015. During the following months he moved across larger areas than his natal home range (home range size of his mother, Ipek), covering up to 447.3 km^2 (95% KUD) or 932.3 km^2 (100% MCP).

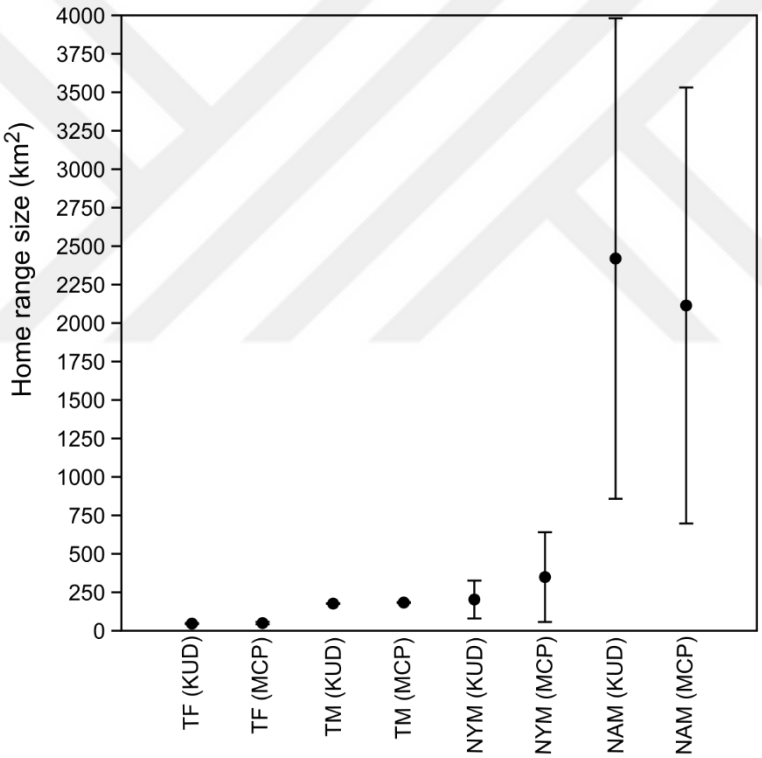

Figure 3. 95% KUD and 100% MCP home range sizes of territorial female (TF), territorial male (TM), non-territorial young male (NYM) and non-territorial adult male lynx (NAM). Dots and whiskers indicate mean and one standard deviation values of 95% KUD and 100% MCP home ranges, respectively.

Seasonal home range sizes

Analysis of seasonal tracking data showed that female lynx had their smallest mean KUD home range size during the summer season (n=3, 40.3 ± 9 km^2) and their largest home range size during winter

(n=1, 78.9 km^2). Female KUD home range sizes during the mating season (n = 4, 52.1 ± 14 km^2) and during autumn (n=3, 56.9 ± 15 km^2) were between both extremes. Seasonal male home ranges were similar across all seasons (Supplementary table).

Lynx density

The closure test (z = -0.003, p = 0.5) confirmed that data selection did not deviate from the expectation of a closed population. Camera traps were active during 1391 camera trap days (ctd), effective camera trapping effort was calculated as 81%. Twelve different adult individuals, seven males and five females, of Caucasian lynx were photographed 36 times at 11 camera trap stations. Seven of these lynx, three males and four females, were repeatedly photographed 24 times, five lynx were photographed once. We obtained 11 spatial recaptures (i.e. recaptures of same individual at additional camera trap stations) for three male and three female lynx. Females were spatially recaptured at most at one and males were spatially recaptured at four, three and one stations.

The exponential detection function was the best fit (AICc = 317.70, Log-likelihood = -154.53) Half-Normal) for the dataset when compared to half-normal (AICc = 329.20, Log-likelihood = -160.27) and therefore used to run the three density models. The hazard rate detection process was not considered, as this is only recommended in situations in which the survey area is fully surrounded by a natural or artificial boundary, given that density estimates from it do not reach a plateau fairly promptly with an increasing buffer width (Efford, 2017).

Examination of the AIC_c values identified the 'behaviour' b_1 model as the best fit, which produced a density estimate of 4.9 ± 1.6 (S.E.M.) lynx per 100 km^2 (95% confidence interval [CI] 2.7 – 9.1, Table 2). The capture probability at the centre of the home range, g_0, was estimated at 0.17 ± 0.06 (S.E.M., 95% CI 0.08 – 0.32), and б estimated at 986.6 ± 333.06 (S.E.M., 95% CI 517.4 – 1,880.2).

Table 2. Summary of model fit for SCR density models from package secr. AIC_c is adjusted for small samples sizes, AIC_c wt is the difference between the smallest AIC_c value and all the others, the model with the highest AIC_c wt is then the one with the highest support, K the number of parameters in the model.

Model	Notation	AIC_c	ΔAIC_c	AIC_c wt	log likelihood	K
Null	(λ_0 ~ 1, $б$ ~ 1)	306.81	1.69	0.29	-150.08	3
Behaviour	(λ_0 ~ b1, $б$ ~ 1)	305.12	0.00	0.68	-145.70	4
Learned response	(λ_0 ~ b2, $б$ ~ b)	311.05	5.93	0.03	-154.51	5

Comparing latitude, population density, home range size

Table 3 summarises data on mean female home range sizes and population density in relation to the latitude of eight Eurasian lynx study populations. The analysis of partial correlations indicated that there was a strong, negative relationship between female home range size and population density given the latitude (Kendall's partial τ = -0.946, p = 0.0029). There was no partial correlation between neither, female home range size and latitude given the population density (Kendall's partial τ = 0.332, p = 0.3), nor between population density and latitude given female home range size (Kendall's partial τ = 0.064, p = 0.8).

Table 3. Latitude, mean female 100% MCP home range sizes and lynx population density at eight study areas of different subspecies distributed along a north-south latitudinal gradient.

Supspecies	Population	Latitude	Home range	Density	Reference
L.l. dinniki	**NW Anatolia**	40	49	4.9	This study
L.l. carpathicus	**Jura**	46	168	1.19	Zimmermann and Breitenmoser, 2007; Molinari-Jobin et al., 2007
L.l. carpathicus	**Germany**	48	187	1.18	Magg et al., 2016
L.l. lynx	**Bialowieza**	52	133	3.2	Schmidt et al., 1997
L.l. lynx	**Akershus**	59	286	0.4	Gervasi et al., 2013
L.l. lynx	**Østafjells**	59	317	0.3	Gervasi et al., 2013
L.l. lynx	**Hedmark**	61	544	0.25	Gervasi et al., 2013
	Finnmark-Troms	69	1173	0.1	Gervasi et al., 2013

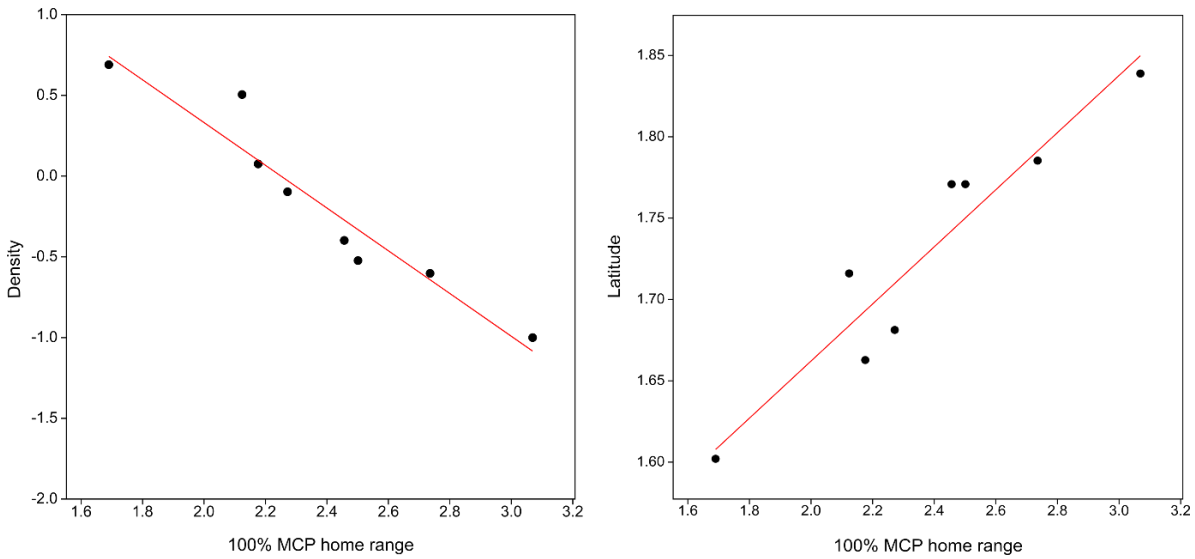

Figure 4. The bivariate linear relationship of log transformed lynx population densities and latitudes of eight Eurasian lynx populations with mean territorial female 100% MCP home ranges.

Discussion

In this study, we report for the first time home range size and spatial behaviour of Caucasian lynx *L. l. dinniki* using high frequency GPS tracking data, focusing on the potentially isolated yet unexploited northwest Anatolian population. We also consider the home range size and density of *L. l. dinniki* in the context of previously published data for autochthonous and reintroduced Eurasian lynx populations in Europe (subspecies *L. l. lynx* and *L. l. carpathicus*). Being an unexploited high density lynx population, where its dynamics are regulated by individual interactions and prey availability, our results provide crucial information on ecology and behaviour of Eurasian and Caucasian lynx within a natural state.

Home range

Our study revealed the smallest adult female mean home range size has ever reported for Eurasian lynx which is comparable to home range size of another lynx species, the Canadian lynx *L. Canadensis* (Burdett et al., 2007). Whereas, mean adult territorial male home range was comparable to some of the Central and east European lynx populations such as populations in Jura Mountains (Zimmermann and Breitenmoser 2007) and Bialowieza Primeval Forests (Schmidt et al. 1997). In general, male territories are known to overlap with one to two female home ranges in Eurasian lynx populations (Schmidt et al. 1997). However, in our study area it seems that territorial male home ranges can

overlap with three to four female home ranges and adult floater males' home ranges overlap with strikingly high numbers of female territories.

Seasonal female home range size revealed to be smaller during summer season from data of two females one having two years and the other one year tracking data. The adult breeding female Ipek, had very small summer home ranges as this female gave birth to three kittens in summer 2015 and two kittens in summer 2016. In both years she enlarged her home range size towards the autumn season and she used the largest home range at winter 2015-2016 (78.9km^2; supplementary table). The increasing trend in female home ranges from summer towards winter season have been reported by many studies to be related with having dependent kittens in denning period. However, we also think that, in the case of Caucasian lynx, this trend might also be highly related with lower availability of prey towards the end of autumn as the main prey (Mengüllüoğlu et al., 2018) in the study area deceases reproduction during this time of the year. Brown hare reproduction in our study area and in many habitats in Turkey starts much earlier (February) than ungulate reproductions and it continues until mid- (October) or late autumn depending on the annual weather conditions (Demirbas and Albayrak, 2015). Therefore, there is a continuous food supply for lynx almost all year round with a probable exception of winter months as hares fall prey to high density lynx and human hunters. As male home ranges are much larger than female home ranges, prey availability might not influence the size of male home ranges.

Besides the very small territorial female home ranges revealed, our study also revealed non-territorial adult male lynx with strikingly large home ranges. These 'floater' lynx were both 8 to 10 years old, therefore they weren't young dispersers. They had very large home ranges in Eurasian lynx standards, one of them having a home range size comparable to male lynx home range sizes those live in far northern latitudes such as Scandinavia. The other floater, however, had such a large home range size (almost 4000km^2) that might be record for an adult Eurasian lynx. Disperser young male individuals are known to range over larger areas than territorial adult male lynx. However, adult floater males we tracked, had stable home ranges and always roaming the same large home range visiting the same places repeatedly. Floater adult Eurasian lynx older than an age of four and with such large stable home ranges, has never been mentioned by any of the previous studies conducted on spatial ecology of Eurasian lynx. We think that the high lynx density in our study area and a landscape fully occupied by adult male territorial lynx, thus, competition for territories might be a reason for the presence of adult floater males queuing for territories (Melzheimer et al., 2018). This was also confirmed in our study as one of these adult floater males shrank his floater home range to its one fifth and apperantly established a small permanent territory at the second year of tracking.

Floaters in our study might have been territorials before or waiting for a long time to establish a territory since their separation from mothers. Our data does not allow us to elaborate on previous state of these lynx as they were not encountered since 2009 even with the camera traps before their capture and collaring. However, the only adult male that was territorial during his capture (Kisakuyruk), has been monitored by camera traps since 2012 and was continuing to defend his territory in summer 2018 (continuous camera trap recaptures) even after battery of his collar was failed. Moreover, other adult territorial male lynx, some of which escaped the live traps during our live capture survey, also held long term territories and camera trapped frequently since the start of our monitoring study in 2009 (8, 6 and 3 years). All of these four territorial males, displayed defensive marking behaviour such as frequent cheek rubbing, claw marking and faecal scrape marking, genetically identified belonging to them (long term monitored male territorial lynx in Mengüllüoğlu et al., 2015 and 2019).

Interestingly, the floater with a striking home range size (Ruffy), after his capture and collaring did not leave the close proximity of the live trapping location and stayed in the study area almost one month during the mating season visiting three adult female territories. Therefore, while large home range strategy of floater males might be highly related with searching for vacated territories, it can also be related with covering maximum numbers of female home ranges, so that annual mating is guaranteed. This way even if a floater male would never become a territorial at his lifetime, it is very likely that he would contribute to the genetic variability among the members of the local population. Hence, a high density lynx population in this sense does not only keep a large number of individuals but also maintains its high genetic diversity (Mengüllüoğlu et al., 2019) by floater individuals that roam tremendous home range sizes and use opportunity of mating unguarded receptive female lynx when it is possible.

Density

Secr density estimation revealed one of the highest independent lynx densities has ever reported for Eurasian lynx (4.9 lynx/100km^2) followed by a density of 4.2 independent lynx/100km^2 for lynx population in southern Turkey (Avgan et al., 2014). Behaviour model was determined to be the best fit for our data and it also reflects the reality in our study as camera trapping was simultaneously running together with live trapping where camera traps were also used to monitor lynx activity at live trap stations. Eight out of 12 lynx individuals captured by camera traps during the CMR survey were also caught in live traps in 2014-2015 and 2015-2016 live trapping seasons and four of these eight individuals were collared. Therefore, there is a high possibility that these lynx might have associated camera traps with live traps and developed camera trap shyness as every live trap was also monitored

by at least two camera traps visible to caught individuals. This pattern was also confirmed by decrease at camera trap visitation rates of territorial lynx and GPS data that showed occasions of close presence to camera traps that were not confirmed with pictures and videos (DM unpublished data).

Lynx populations in our study area and in southern Turkey occur at high densities, are lagomorph hunters and live in sympatry with high density lagomorph prey (Mengüllüoğlu et al., 2018). Our study revealed significantly smaller body size for adult lynx than lynx in Europe and Anatolian lynx consumes around half of the daily food intake of lynx populations in Europe (Mengüllüoğlu et al., 2018). Therefore, it is very likely that the hare densities in northwestern and southern Anatolia are high enough to sustain high density lynx populations. However, the relationship between hare population dynamics and lynx numbers should appropriately be investigated in order to drive robust conclusions. To achieve this, lynx and hare populations should be monitored for long terms at major ecosystem types of Anatolia (Mengüllüoğlu et al., 2018). An additional reason for high lynx density in Anatolia might be the absence of quota hunting and low level of poaching at major lynx habitats.

Home range and density of Eurasian lynx populations

Previous studies mentioned the significant relations between latitude and lynx home range sizes (Herfindal et al., 2005). The relations were attributed to increasing primary production from north to south. However, we couldn't find any strong patial correlation of latitude neither with home range size nor population density. Partial correlation analyses only revealed a strong negative correlation between density and home range size, given latitude. As in our study area (543mm; CLIMATEDATA.ORG), mixed dry coniferous and steppe ecosystem in Anatolia receives much lower mean annual precipitation, experiences dry and hot summers and is not as productive as deciduous and mixed temperate forest ecosystems in Europe and in black sea coast of Turkey (Evrendilek et al. 2007). However, lynx still occur at Anatolian ecosystems at high densities (this study and Avgan et al., 2014). Therefore, other dynamics are likely to influence lynx home range size here. Brown hare as a dry and open habitat specialist main prey, which can reproduce up to nine times a year with a mean litter size of 3.1± 0.7 (Demirbas and Albayrak, 2015) and with its high density in our study area, (Mengüllüoğlu et al., 2018) might be the main supporter of a high density lynx population. Continuously reproducing high density lagomorph prey base can also support high lynx density and smaller female home ranges as it decreases prey searching area and time. Very low rate of human caused lynx mortality (one lynx have been reported to be killed in a car crash in last 5 years in our study area) might be another important factor.

Perhaps the very low density and large home range size of lynx in Scandinavian Peninsula might also be a result of by anthropogenic factors such as large amount of lynx and prey harvesting and poaching

(Nilsen et al., 2012). This pattern is also observed in Bavarian lynx population where illegal poaching is a serious threat for reintroduced lynx population (48th latitude; Heurich et al., 2018) and prey base (roe deer) and individuals here occupy large home ranges (Magg et al., 2016) although primary production in the Bavarian ecosystem is much higher than in ecosystem type in our study area. Further north, BPF lynx population however display very high densities and hence much smaller home range sizes in European standards, where lynx and prey harvesting is not allowed inside the national park (Schmidt et al., 1997). Therefore, in the context of central European lynx populations, human caused lynx and prey mortality might be the major drivers of lynx densities and home range sizes as these two are highly negatively correlated.

It is noteworthy that adult floater males in our study area have very large home ranges that can cover up to 72 female home ranges. It is obvious that these large home ranges are not caused by environmental factors or prey availability but rather searching for territories continuously. Therefore, home range size might rather be a direct result of densities and social interactions among individuals of carnivore populations as long as the prey density and biomass is above the thresholds to feed the observed carnivore densities.

Conservation implications

Our study revealed a very high density lynx population where females occupied smallest mean home range size has ever reported for Eurasian lynx. Different prey type, an unexploited lynx population and very high density are likely the reasons for the observed small home ranges. High rate of cannibalism and aggressive defensive marking behaviour such as scraping were previously also reported for this lynx population and these behaviour are most likely a result of high lynx density. A landscape fully occupied by adult territorial individuals causes late territory establishment in male lynx and adult floater individuals roam very large home ranges queuing to take over occupied or vacated territories (Melzheimer et al., 2018).

Results of our study provide crucial information for Eurasian and Caucasian lynx ecology and behaviour as this research was conducted on a natural state, unexploited, high density lynx population. Individual interactions (i.e. competition for territories and intraspecific killing; Mengüllüoğlu et al., 2018) and space were likely the limiting factors. Our population constitutes as a good model for understanding the evolutionary behaviour and dynamics in Eurasian lynx populations. Lynx populations in central and eastern Europe often suffer high rate of anthropogenic killing with a few exceptions. It seems that regardless of ecosystem productivity, lynx populations can occur at high densities as long as locally

adapted prey base can be maintained. Perhaps the well protected lynx and prey populations in Bialowieza Primeval Forest are a good example of this, as the lynx population there occurs at highest densities in Europe. Therefore, we recommend the use of data from lynx populations at natural states (i.e. BPF or northwest Anatolia) while modelling reintroduction scenarios and carrying capacities for Eurasian lynx in Europe. Conclusions driven from exploited or reintroduced lynx populations might not be reflecting evolutionary behaviour of Eurasian lynx populations and result in misleading assumptions. We also recommend preservation of the current lynx habitats and long term lynx and prey population monitoring in northwest Anatolia for understanding the long term dynamics and interactions in this valuable lynx population.

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Supplementary table. 95% KUD and 100% MCP seasonal home range sizes of territorial female (*TF*), territorial male (*TM*), non-territorial sub-adult male (*NSM*), non-territorial adult male (*NAM*) and juvenile lynx (*J*) in northwest Anatolia.

	Mating		**Summer**		**Autumn**		**Winter**	
TF	KUD	MCP	KUD	MCP	KUD	MCP	KUD	MCP
İpek 2015	69.4	60.9	41.2	53.2	74.3	83.3		
İpek 2016	57.6	60.1	30.9	43.8	47	42.9	78.9	79.3

Xena	37.2	30.7	48.8	61.5	49.4	56.1		
Frida	44.1	30.2						
Mean	52.1±14.3	45.5±17.4	40.3±9	52.8±8.9	56.9±15.1	60.7±20.6		
TM								
Kırıkdiş 2017	861	198.1	175.7	193	172.2	166.1		
Kısakuyruk	174.2	122.3	172.1	169				
Mean	517.6±485.6	160.2±53.6	173.9±2.5	181±16.9				
NAM								
Kırıkdiş 2016	359.1	562.4	748	741	1123	959.9		
Kırıkdiş 2017							1197.5	887.8
Ruffy	660.4	396	3559.3	2902.9	3279.2	2285.8		
Mean	509.7±213.1	479.2±117.7	2153.6±1987.9	1822±1528.7	2201.1±1524.7	1622.9±937.6		
NSM								
Uluhan 2015			101.4	189.4	323.6	400.5	405.7	377.3
Uluhan 2016	252.5	73.6						
Finger	103.9	71.4						
Mean	178.2±105.1	72.5±1.6						
J								
Uluhan 2015	47	50.8						
Evrim	57	41.7						
Mean	52±7.1	46.3±6.4						

CHAPTER 5: General discussion

The purpose of this study was to collect baseline ecological, genetic and behavioural information that is urgently needed to set up an efficient conservation action plan for Caucasian lynx *L.l. dinniki* in Turkey. This included a study on diet and foraging ecology of the three largest Caucasian lynx populations occupying three major lynx habitat types in Anatolia, the Asian part of Turkey. It also included a study on the spatial organisation, genetic variation and interactions between individuals in a study area in northwestern Anatolia which started as a long-term monitoring effort in 2009. The results of this study indicated substantial differences between foraging ecology and dietary requirements, spatial behaviour and organization and life history traits between the European subspecies of the Eurasian lynx studied in Europe and the lynx populations of the Caucasian subspecies which occur in Anatolia. The results demonstrate that it would not be appropriate to draw conclusions from or base conservation action upon the results from the European subspecies when the purpose is to improve the conservation status of Caucasian lynx. With the baseline information contained in this study, the design of conservation plans and subsequent studies on Caucasian lynx, their prey base and their habitats in Anatolia will be facilitated.

Contrary to the general notion that the Eurasian lynx is a predator of mid-sized ungulates (Werdelin, 1981) **Chapter 2** provides information that the diet of the Eurasian lynx in Anatolia consists mostly of brown hares *Lepus europaeus* (78 % - 99 % of prey biomass consumed) and that its foraging ecology fulfils expectations for a lagomorph specialist, similar to Iberian *Lynx pardinus* and Canada lynx *Lynx canadensis* in very different ecosystems. All three Caucasian lynx populations studied in this respect live in sympatry with mid-sized and large ungulates such as wild goat *Capra aegagrus*, chamois *Rupicapra rupicapra*, wild boar *Sus scrofa* and red deer *Cervus elaphus* in Anatolia, prefer brown hare over ungulates. Caucasian lynx in Anatolia display comparable body size and physiological requirements to individuals of other lagomorph specialist lynx species and consume no more than half the daily food required to sustain a European Eurasian lynx individual. Legal protection of lynx and absence of hunting quotas, high lynx densities in suitable lynx habitats and the presence of resident adult floaters in the male population suggest that the dynamics of lynx populations in Anatolia are primarily determined by prey availability and access to territories. A curious result was the observation of a high incidence of cannibalism, an aggressive behaviour rarely observed in low density European lynx populations, in two ecosystems in Anatolia. A second major food category of lynx in Anatolia were meso-carnivores such as red fox *Vulpes vulpes*, golden jackal *Canis aureus*, domestic cat *Felis catus* and domestic dog *Canis familiaris*. These results suggest that lynx may affect the population dynamics of other carnivore species, as has been previously discussed for Euasian lynx (Sunde et al., 1999;

Helldin et al., 2006). A bachelor thesis that analysed my long term camera trapping data (2009-2015) from the study area in the forest-steppe mix ecosystem in northwest Anatolia revealed that red fox density declined with increasing altitude, whereas the chance of camera trapping increased (Oltmann, 2017). At lower altitudes, red foxes may have been sustained by a close association with human settlements. The observed cases of intraspecific and interspecific killing of carnivores are akin to interference competition. If such interference competition affects population dynamics and foraging rates, then brown hare populations would also benefit and could continue to sustain high lynx densities. This chapter only focused on lynx foraging ecology in Anatolia. Lynx-hare and lynx-fox numerical dynamics have yet to be investigated.

Estimated genetic diversity measures of wild animal populations can significantly differ from real population genetic diversity if sampling methodology does not adequately account for species specific spatial organisation and behaviour. In **Chapter 3**, I used nuclear molecular markers to investigate how sampling methodology ('invasive' vs. 'non-invasive') can affect the measures of genetic diversity within one Caucasian lynx population. The results indicated that samples collected from lynx caught in stationary box traps ('invasive' sampling) was biased to sample particular territorial individuals and their offspring because of lynx habituated well to the presence of these to traps inside their territories. Female philopatry further increased this effect, as the prominent representation of neighbouring mother-daughter territorial female individuals and their kittens in the 'invasive' sample reduced the apparent genetic variability in the population. 'Non-invasive' faecal sampling produced a better representation of all residence classes, improved the measures of genetic diversity and resulted in a significantly higher genetic diversity measure as additional unrelated territorial and floater individuals were also sampled. The results also indicated a high genetic diversity and no sign of inbreeding for northwest Anatolian lynx. Non-invasive faecal sampling not only provides more reliable genetic diversity measures but also additional information on other important aspects of the biology and ecology of the same population such as diet, spatial organisation and the preence of female philopatry, which in turn can help to inform conservation management planning. This chapter provides list of molecular markers and first genetic diversity measures of a Caucasian lynx population. Any research planned throughout the range of Caucasian lynx in Turkey, Caucasus and Iran is highly recommended to use the same list of successful markers and follow the methodological suggestions of this chapter, in order to produce comparable and reliable information. Future conservation management planning of Caucasian lynx populations would highly benefit from comparable information.

Population densities, spatial organisation and behaviour are key compomnents for conservation planning. Whereas density estimates can provide indirect information on population status and

habitat quality, spatial behaviour can provide clues on carrying capacities in terms of the maximum number of territories if the species displays a territorial system, population specific dispersal abilities, gene flow and re-colonization of unoccupied habitats by individuals of populations of conservation concern. In **Chapter 4**, I investigated the spatial behaviour and density of northwest Anatolian lynx population through GPS tracking of nine lynx individuals and camera trapping. The results yielded the smallest mean territorial female and male home range sizes ever reported for Eurasian lynx, and a high density comparable to that of Caucasian lynx populations in southern Anatolia (Avgan et al. 2014). A different prey type, a high prey density and the lack of exploitation are likely to contribute to the high density observed. The discovery of adult male resident floaters in a high density population which queue for access to territories is striking. This type of male spatial organisation resembles the male spatial organisation in high density cheetah populations in eastern and southern Africa. A landscape fully occupied by adult territorial individuals is likely the cause of late territory establishment in male lynx and very large home ranges of floaters queuing to take over occupied or vacated territories (Melzheimer et al. 2018). It is unclear at present to what extent access to females and mating opportunities are shared or divided between floaters and territorial residents. It is interesting that in my Caucasian lynx study areas, not only did territorial residents hold small territories, they also employed of scent marking known as scraping (personal observations). This is a behaviour not observed in low density Eurasian lynx populations (Mengüllüoğlu et al., 2015) but known from other lynx species, principally bobcat (Allen et al., 2015). To what extent the observed high incidence of cannibalism in two study areas is a consequence of high lynx density, lack of adequate prey, or associated with specific mating tactics is unclear at present.

The results of this chapter provide crucial information for Eurasian and Caucasian lynx ecology and behaviour, as this research was conducted on an unexploited, high density lynx population where individual interactions, prey base and space were likely the limiting factors. The northwest Anatolian lynx population probably constitutes a good model to understand the evolution and full phenotypic plasticity of spatial behaviour in Eurasian lynx populations. Lynx populations in central and eastern Europe often suffer a high incidence of anthropogenic killing (Andren et al., 2006; Sindičić et al., 2016; Heurich et al., 2018). It seems that regardless of ecosystem productivity, lynx populations can occur at high densities as long as there is a locally adapted prey base, as in the Białowieza Primeval forest (Jedrzejewski et al., 1996) and northwest Anatolia. Therefore, the use of data from unexploited lynx populations is highly recommended for modelling reintroduction scenarios and carrying capacities for Eurasian lynx in Europe. Conclusions derived from exploited or reintroduced lynx populations are likely to apply only to such disturbed populations, do not cover the full breadth of phenotypic plasticity and thus are likely to underestimate the adaptability of lynx, thereby misleading conservation planning.

This thesis sheds light on foraging ecology, diet, spatial organization and behaviour and genetic variability of Caucasian lynx in Anatolia. It also provides baseline information required to set up a conservation action plan of Caucasian lynx in Anatolia. The methods applied and explored in this study, particularly the non-invasive techniques for estimating genetic variability and population density, should be also applied to other Caucasian lynx populations to gather information on their status. Studying spatial behaviour and social organisation through GPS tracking and camera trapping of a higher number of individuals and at a larger scale in the study area in northwest Anatolia should also be continued to confirm and extend the results of this study and reveal long-term dynamics in this high density lynx population and its prey. Information from long-term monitoring of this particular population which was started in 2009 would not only benefit Caucasian lynx conservation but would also be helpful for a better understanding of the full scale of adaptability of the Eurasian lynx, and thus for its conservation and research elsewhere, by providing information on evolutionary ecology and behaviour of Eurasian lynx. The results of this study suggest that the Eurasian lynx, just like the other lynx species, might have first evolved as a lagomorph specialist (Werdelin, 1981). The implications would be profound and thus this question is an important one that remains to be investigated by studying in greater detail the life history traits and evolutionary genetics of Anatolian and Asian Eurasian lynx populations.

Conservation implications for Caucasian lynx in Anatolia

Only a small part of the range of Caucasian lynx occurs in Anatolia in protected areas (Sekercioglu et al., 2011; Breitenmoser et al., 2017). This subspecies of Eurasian lynx almost completely occurs in the mountain ranges of Anatolia, Caucasus and Iran, so mountains and associated montane habitats play the most important role for the lynx. In contrast to European populations of the Eurasian lynx, forest cover might not be a good indicator of lynx habitat quality, since lynx in Anatolia and its main prey brown hare mostly occur in dry and fairly open forested or montane rocky steppe habitats. Considering the low lynx densities in Iran (Moqanaki et al., 2010) and the limited range of Caucasian lynx in the Caucasus (Breitenmoser et al., 2017), Turkey probably holds the largest population of Cauacasian lynx and therefore plays a very important role in ensuring its future viability.

In the last two decades, Turkey's mountains witnessed the planning and construction of massive hydroelectric power (HEP) plants, currently a total of 4000 dams planned until 2023 (Sekercioglu et al., 2011). These dams will decrease connectivity of suitable lynx habitats and increase fragmentation. Highways across major lynx habitats may become another major threat to lynx populations. Every year at least five lynx individuals are hit by vehicles when trying to cross highways. At current high densities

and the wide distribution of lynx in Anatolia, road kills might not cause a significant impact on lynx numbers at this point in time. However, together with HEP constructions and reduced habitat connectivity, every lynx individual crossing between fragmented populations becomes increasingly important for maintaining gene flow among subpopulations. Such detrimental effects could be prevented, if the construction of highways includes the building of green bridges, thereby maintaining habitat connectivity.

As the lynx in Anatolia are almost completely nocturnal, as is its main prey (Soyumert et al., 2019), and lynx depredation on domestic livestock is almost absent, encounters with humans and lynx-human conflict might be considered to be moderate or minimal. The specialist lagomorph diet of lynx in Anatolia can prevent the kind of negative attitude that arises elsewhere from lynx predation on wild ungulates, the most common conflict type between lynx and hunters in Europe. As far as I am aware, there is currently no poaching of lynx in Anatolia that arises from such conflict. Poaching is rare but still occurs, probably a consequence of lack of knowledge about this species. Poachers may even kill lynx out of curiosity to closely examine a species unknown to them, as dead bodies are left untouched at the site of poaching.

In summary, maintaining connectivity of lynx habitats through green bridges and raising awareness about lynx, its ecology and behaviour by providing easily accessible information through Turkish media would be essential steps for lynx conservation in Anatolia.

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EDUCATION

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2008-2010 — **M.Sc. Biology** | Middle East Technical University, Turkey

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2002-2008 — **B.Sc. Biology** | Middle East Technical University, Turkey

1999-2002 — **High school graduate** | Toros High School | Turkey

PROFESSIONAL ACTIVITIES

2008-2012 — **Freelance researcher, field team coordinator and wildlife expert** | Turkey

- Biodiversity Focused Forestry Project in Forests of Gümüşhane (2012:P21-SGP), **Nature Conservation Centre**. Determination of status and distribution of Brown bear (*Ursus arctos*) and Roe deer (*Capreolus capreolus*) populations by noninvsive methods and interviewing foresters and locals.
- Wildlife Development Reserves Management Plans. **Yeşerim Forestry Industry Trade Consultancy Limited Company.** Konya Bozdağ, Kütahya Türkmenbaba, İzmir Bayındır Ovacık, Muğla Köyceğiz
- Determination of distribution, Behavior, population size and structure, breeding capacity of White-breasted Kingfisher (*Halcyon smyrnensis*) and colonial breeding bird species and finding out the threats on this local population. **DAD- Turkish Nature Research Society.**
- Kackar Mountains Sustainable Forest Use and Conservation Project (EU funded). Wildlife Assistant. **TEMA**.

- Tuzla, Akyatan Lagoons Management Planning Project. Wildlife surveying, big mammal tracking by non-invasive methods (camera-trapping), preparation of mammal lists and production of wildlife report. **DAD- Turkish Nature Research Society.**
- Göksu Delta Special Environmental Protection Area, Purple Gallinule Conservation and Monitoring Project. **DAD- Turkish Nature Research Society.**

March – May 2012 **Field techniques training** | SCANDLYNX, Scandinavian Lynx Project, NINA, Norway. Eurasian lynx and roe deer live capture and treatment procedures.

2004 – 2007 **Field techniques training** | Kence Lab of Ecology and Genetics, Middle East Technical University, Turkey. Improvement of conservation approaches to reintroduced Anatolian Mouflon (*Ovis gmelinii anatolica*) populations by aid of data obtained by radiotelemetry and genetic sampling. Radio-telemetry and monitoring.

TEACHING

June 2017 **METU Archeology Project funded by TÜBİTAK (Elementary school level)** | Middle East Technical University

- Bioarcheology lecturer and student guide

Advanced Field Techniques course (MSc level) | Middle East Technical University

- Application of camera trapping and radio-telemetry techniques

LANGUAGES

Turkish	Native
English	Fluent, written and spoken
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PEER-REVIEWED JOURNAL ARTICLES

Published or accepted articles	**Mengüllüoğlu D**, Ilaslan E, Emir H, Berger A (2019). Diet and wild ungulate preferences of wolves in north-west Anatolia during winter. PeerJ 7:e7446 https://doi.org/10.7717/peerj.7446 **Mengüllüoğlu D,** Ambarli H (2019). Assesing caracal-prey interactions by spatial and temporal analyses. European Journal of Wildlife Research 65: 54 https://doi.org/10.1007/s10344-019-1294-2

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PRESENTATIONS

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ZUSAMMENFASSUNG

Grundlegende ökologische, genetische und verhaltensbezogene Informationen für den Kaukasischen Luchs *Lynx lynx dinniki* in der Türkei sind bisher nur lückenhaft vorhanden. Um einen effizienten Erhaltungsplan aufzustellen sind diese aber von dringender Erfoderlichkeit. Diese Dissertation soll diese Lücke schließen und untersucht die Ernährung und Nahrungssuche der drei größten kaukasischen Luchspopulationen in Anatolien, dem asiatischen Teil der Türkei. Des Weiteren wurde die räumliche Organisation und genetische Variation sowie die Interaktionen zwischen Individuen in einem Untersuchungsgebiet im Nordwesten von Anatolien von mir untersucht in welche Langzeitbeobachtungen seit 2009 einflossen.

In **Kapitel 2** quantifizierte ich die Ernährung, die Beutevorlieben und Ernährungsweise von drei kaukasischen Luchsbeständen in Anatolien im Vergleich zu europäischen Luchsbestände. Die Nahrung des eurasischen Luchses in Anatolien besteht hauptsächlich aus braunen Hasen (78% - 99% der Beute-Biomasse). Seine Nahrungsökologie entsprach der Erwartung eines Lagomorph-Spezialisten, ähnlich dem iberischen Luchs *Lynx pardinus* und dem kanadischen Luchs *Lynx canadensis* in anderen Ökosystemen. Kaukasische Luchse in Anatolien weisen vergleichbare Körpergrößen und physiologische Voraussetzungen zu den anderen auf Lagomorphe spezialisierten Luchsarten auf und verbrauchen so nur circa die Hälfte der täglichen Nahrung, die typischerweise vom europäischen Eurasischen Luchs (*L. l. lynx, L. l. carpathicus*) benötigt wird. Es gab auch regelmäßige Fälle von Kannibalismus in zwei der anatolischen Populationen, das sehr nur selten bei anderen europäischen Luchsbeständen mit geringer Dichte beobachtet wurde.

In **Kapitel 3** habe ich mit molekularen Markern untersucht, wie die Methode der Probennahme, Indices für genetische Diversität beeinflussen kann, wenn die Population aus ortsansässigen und andere Männchen und phylopatrischen Weibchen besteht. Ich habe die "invasiven" Probenahme, durch Gewebeentnahme von gefangenen Luchsen mit der "nicht-invasiven" Probenahme durch Kotproben verglichen. Dazu wurden Kotproben mithilfe von einem speziell trainierten Spürhund gesucht und gefunden. Es zeigt sich das, die „invasive“ Probenahme nicht geeignet ist um die generelle genetische Diversität festzustellen da nur einige wenige territoriale Individuen und ihre Nachkommen gefangen werden, und die echte genetische Variation dadurch systematisch unterschätzt wird. Die „nicht-invasive“ Probenahme von Kotproben führte zu einer weniger selektiven Auswahl der Proben. Die Population wurde über alle Altersgruppen und die Geschlechter besser beprobt und sorge für eine höhere und vor allem verläßlichere Einschätzung der Diversität. Die Ergebnisse für die untersuchte Population im nordwestlichen Teil Anatolien zeigen eine hohe genetische Vielfalt und keine Anzeichen von Inzucht. Die nicht-invasive Probenahme liefert nicht nur zuverlässigere genetische

Diversitätsmessungen, sondern liefert auch zusätzliche Informationen zu anderen wichtigen Aspekten der Biologie und Ökologie der in dem Gebiet lebenden Luchse, einschließlich Ernährung, räumlicher Organisation und der Präsenz von Standorttreue weiblicher Individuen. All diese Informationen können in die Entwicklung des Naturschutzmanagements einfließen.

In **Kapitel 4** untersuchte ich das räumliche Verhalten und die Dichte einer nordwestanatolischen kaukasischen Luchspopulation. Dazu sammelte ich GPS-Daten von neun Luchsen und zusätzlich Bilder mit Kamerafallen. Die Ergebnisse zeigten, dass der Kaukasische Luchs in diesem Untersuchungsgebiet im Mittel die kleinsten Territorien haben (Weibchen: 95% KUD = 46 ± 8, 100% MCP = 49 ± 16 Männchen: 95% KUD = 176 ± 3, 100% MCP = 183 ± 5), die je für eurasischen Luchse berechnet wurden. Gleichzeitig wurden hohe Dichten ähnlich zu Populationen im Süden Anatoliens gefunden (4,9 Luchse / 100 km2). Die Beutespezialisierung bei gleichzeitig hohen Beständen der präferierten Beutetierartsowie das Fehlen der Wilderei führen zu den kleinen Streifgebiete. Im Detail zeigten die Ergebnisse zwei räumliche Taktiken für männliche Tiere, die mit unterschiedlichen Lebensphasen verbunden waren – erwachsene Tiere beginnen Leben zunächst als “floaters” mit etablierten und stabilen Sreifgebieten. Auf der Suche nach eigenen Territorien streifen sie durch riesige gebiete (95% KUD = 2419 ± 2208, 100% MCP = 2114 ± 2004), wahrscheinlich teilweise über Jahre. Inhaber von Territorien verteidigen diese gegen diese „Floater“. Es ist derzeit unklar, ob Gebietsansässige und / oder Floater Väter der ansässigen philopatrischen weiblichen Tiere sind. Durch die hohen Dichten ist es wahrscheinlich üblich, dass alle Gebiete von erwachsenen territorialen Individuen besetzt sind und Floater weite Strecken zurücklegen müssen. In dieser Hinsicht ähnelt der kaukasische Luchs der räumlichen Organisation der Geparden *Acinonyx jubatus*, bei denen auch diese zwei Taktiken in dicht besiedelten Populationen im östlichen und südlichen Afrika dokumentiert wurden.

Diese Arbeit bedeutet ein grossen Wissenszuwachs über die Nahrungssuche, die Ernährung, die räumliche Organisation, das Verhalten sowie die genetische Variabilität des kaukasischen Luchses in Anatolien. Außerdem enthält sie grundlegende Informationen, die zur Erstellung eines Aktionsplans für den Schutz von kaukasischen Luchsen in Anatolien erforderlich sind. Damit ein derartiger Aktionsplan umgesetzt werden kann, sind die hier angewendeten und präsentierten nicht invasiven Methoden zur Populationsgenetik und Dichteabschätzung essentiell für die Erforschung von andern kaukasischen Luchs Populationen in Anatolien und anderswo.

SUMMARY

Baseline ecological, genetic and behavioural information is still lacking and is urgently needed to set up an efficient conservation action plan for Caucasian lynx *Lynx lynx dinniki* in Turkey. This dissertation investigated the diet and foraging ecology of the three largest Caucasian lynx populations occupying three major lynx habitat types in Anatolia, the Asian part of Turkey. I also studied the spatial organisation and genetic variation as well as interactions between individuals of Caucasian lynx in a study area in northwestern Anatolia where I benefitted from long-term monitoring efforts started in 2009.

In **Chapter 2,** I quantified the diet, prey preferences and functional response of three Caucasian lynx populations in Anatolia from a comparative perspective of European Eurasian lynx populations. The diet of the Eurasian lynx in Anatolia consists mostly of brown hares (78 % - 99 % of prey biomass consumed). Its foraging ecology fulfils expectations for a lagomorph specialist, similar to Iberian lynx *Lynx pardinus* and Canadian lynx *Lynx canadensis* in other ecosystems. Caucasian lynx in Anatolia display comparable body sizes and physiological requirements to individuals of other lagomorph specialist lynx species and consume half the daily food required to sustain a European Eurasian lynx (*L. l. Lynx or L. l. carpathicus*) individual. There was a high incidence of cannibalism, an aggressive behaviour that has very rarely observed in low density European lynx populations, observed in two ecosystems in Anatolia.

In **Chapter 3**, I used nuclear molecular markers to investigate how sampling methodology can affect measures of genetic diversity if the population contains male territorial residents, other male residents and females are philopatric. I contrasted 'invasive' sampling, where tissue samples are obtained from individuals caught in box traps, with 'non-invasive' sampling, which requires the search and collection of faecal samples (in my case optimised through the training and use of a domestic dog trained to find lynx faeces) and the use of camera trapping. The results demonstrated that 'invasive' sampling was an inefficient technique and biased in favour of sampling particular territorial individuals and their offspring, thereby underestimating the true genetic variation in the population. 'Non-invasive' faecal sampling resulted in a less biased sampling of all sexes and classes of residents, an improved estimate of genetic diversity measures and a significantly higher level of genetic diversity obtained. The results indicate a high genetic diversity and no signs of inbreeding for northwest Anatolian lynx. Non-invasive faecal sampling not only provides more reliable genetic diversity measures but also delivers additional information on other important aspects of the biology and

ecology of the same population, including diet, spatial organization and the presence of female philopatry, which in turn can help to inform conservation management planning.

In **Chapter 4**, I investigated the spatial behaviour and population density of a northwest Anatolian Caucasian lynx population through GPS tracking of nine lynx individuals and camera trapping. The results indicated that Caucasian lynx in this study area have the smallest mean territorial female and male kernel utilisation distribution (KUD) and minimum convex polygon (MCP) home ranges (females: 95% KUD = 46±8, 100% MCP = 49±16; males: 95% KUD = 176±3, 100% MCP = 183±5) ever reported for Eurasian lynx and a high density (4.9 lynx/100km^2), on a level comparable to southern Anatolia. A different prey type, a high prey density and the absence of exploitation of this lynx population are likely drivers of the observed small home ranges. The detailed results revealed two male spatial tactics associated with separate life history stages – adult males start their residency in a population as resident floaters, ranging across huge home ranges (95% KUD = 2419 ± 2208, 100% MCP = 2114 ± 2004) and queuing for a territory, probably for several years. Territorial residents defend small territories. It is at present unclear whether territorial residents and / or floaters are candidate males to father the offspring of the resident philopatric females. A landscape fully occupied by adult territorial individuals is likely the cause of late territory establishment in male lynx and the large home range sizes of floaters. In this respect, Caucasian lynx resemble the spatial organisation of cheetahs Acinonyx jubatus, where the existence of floaters queuing for territories has also been documented in high density populations in eastern and southern Africa.

This thesis sheds light on foraging ecology, diet, spatial organization and behaviour and genetic variability of Caucasian lynx in Anatolia. It also provides baseline information required to set up a conservation action plan of Caucasian lynx in Anatolia. For such an action plan to become effective, the non-invasive population genetics and density estimate methods applied in this study will be an essential tool for the assessment of the status of other Caucasian lynx populations in Anatolia and elsewhere.

Selbständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit selbständig und ohne unzulässige Hilfe oder Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe.

I hereby confirm that I have made this work autonomously. I assure that I have read and only used the specified sources claimed in this work.

Berlin, April 28 2019

Deniz Mengüllüoğlu