



## Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*



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### ARTICLE INFO

#### Article history:

Received 8 March 2014

Received in revised form 24 March 2014

Accepted 28 April 2014

Available online 6 May 2014

#### Keywords:

Chemical communication

Competition

Scent-marking

Over-marking

Camera trapping

*Lynx lynx*

### ABSTRACT

Scent-marking is widespread among mammals and has been observed in many felid species. Although the behaviour is well-described, little is known about its function in wild felid populations. We investigated patterns of scent-marking and its role in intra- and intersexual communication among resident and non-resident Eurasian lynx *Lynx lynx* by observing interactions among wild lynx at natural marking sites by means of infrared camera traps. Marking activity of resident animals showed a peak during the mating season and was lowest during the time when females gave birth and lactated. Both sexes scent-marked, but male lynx visited marking sites much more often than females and marked relatively more often when visiting a site. Most visits to marking sites were by residents but we also observed scent-marking by non-residents. Juveniles were never observed marking. We found no evidence of lynx regularly renewing scent-marks after a certain 'expiry date' but the presence of a strange scent-mark triggered over-marking. Males responded similarly to the presence of another individual's scent-mark, irrespective of whether it was the top- or the underlying scent-mark in a mixture of scent-marks they encountered. Our results suggest that marking sites could serve as 'chemical bulletin boards', where male lynx advertise their presence and gain information on ownership relationships in a given area. Females placed their urine marks on top of the ones left by resident males, but further studies are needed to explain the functions of over-marking in females.

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Scent-marking with faeces, urine or glandular secretions is widespread among mammals (reviewed in Gosling and Roberts, 2001a,b). For instance, felids are well known to leave scent-marks (i.e. urine, faeces, saliva) at visually conspicuous sites (Macdonald, 1985) including a variety of distinct marking behaviours (Mellen, 1993): urine spraying, head or cheek rubbing, scraping, claw raking, sniffing, licking, or 'flehmení' (use of the vomeronasal organ; Doving and Trotter, 1998). When mammals encounter a scent-mark of another individual, they often place their own scent-mark on top of, touching, or adjacent to it. This phenomenon has been referred to as 'over-marking' by Ferkin and Pierce (2007) and has been observed in many different species (reviewed in Ferkin and Pierce, 2007). Over-marking occurs among breeding pairs (e.g. grey wolf, *Canis lupus*; Peters and Mech, 1975), same-sex competitors (e.g. house mice, *Mus domesticus*; Hurst, 1990a,b) and within social groups

(e.g. spotted hyena, *Crocuta crocuta*; Burgener et al., 2008; banded mongoose, *Mungos mungo*; Jordan et al., 2011a,b,c). The behaviour has also been observed in different felid species, most of which are solitary and territorial (i.e. tiger *Panthera tigris*; Smith et al., 1989; several small felid species; Mellen, 1993; cheetah, *Acinonyx jubatus*; Marnewick et al., 2006).

Several hypothesis for the behavioural function of over-marking have been proposed (reviewed in Ferkin and Pierce, 2007): Over-marking could create a mixture of odours ('scent blending'), such as a 'group odour' used for recognition in group-living species. Alternatively, over-marking could also cover the underlying odour of a conspecific ('scent masking'). Or finally, the information of both, the underlying and the overlying scent-mark, could remain available, thereby creating a 'chemical bulletin board' displaying information from multiple individuals. Several rodent species (e.g. golden hamster, *Mesocricetus auratus*; Johnston and Bhorade 1998; meadow vole, *Microtus pennsylvanicus*; Johnston et al., 1997; Ferkin, 1999) seem to be able to distinguish the donor of the top-scent-mark from the underlying scent-marks. Many studies have further investigated the possible functions of over-marking and the evidence

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provides support for several (not necessarily mutually exclusive) hypotheses. Ferkin and Pierce (2007) review 10 hypotheses related to over-marking and the supporting evidence. Here we focus on the first four, which are likely of high relevance for solitary and territorial carnivores such as felids: (1) Competition hypothesis: Over-marking animals gain an advantage over those individuals whose scent-marks they overlap, either by masking the underlying scent-mark or by demonstrating social dominance (Johnston et al., 1994; Rich and Hurst, 1999). Therefore, over-marking should occur most often among same-sex competitors (Ferkin and Pierce, 2007). (2) Chemical bulletin board hypothesis: Both the information from the bottom- and the top-scent-mark remains available, so that both donors can advertise their presence in an area (Wolff et al., 2002). Since scent-marks supposedly are costly and reliable signals of an animal's quality (Gosling and Roberts, 2001a), individuals could use information from 'chemical bulletin boards' to assess potential mates or same-sex competitors (Ferkin and Pierce, 2007). (3) Territoriality hypothesis: Scent-marking could play a role in competition between territory holders and potential intruders (Temeles, 1994; Sun and Müller-Schwarze, 1999; Sillero-Zubiri and Macdonald, 1998; Gosling and Roberts, 2001b). Under this hypothesis, only animals successfully defending an area can ensure that their own scent-marks predominate and are the ones most recently deposited. Thus, the consistent over-marking of scent-marks of rivals can potentially reflect the marker's resource-holding potential (Rich and Hurst, 1999). Resident individuals should most often over-mark the scent-marks of intruders, while intruders should be less likely to over-mark than residents. (4) Mate attraction hypothesis: Over-marking serves as a form of mate attraction and facilitates interactions between potential mates (Hurst, 1990c; Ferkin, 1999). It should therefore occur most often among conspecifics of opposite sex and during the time when females are receptive (Ferkin and Pierce, 2007).

Some studies on captive or domestic felids have provided the first insights on the information contained in scent-marks: Domestic cats (Natoli, 1985) and captive Eurasian lynx *Lynx lynx* (Sokolov et al., 1996) seem to distinguish different sexes, individuals and reproductive status from urine marks. In captivity, it has also been shown that males mark more often than females and marking frequency increases during the mating season (several small felid species: Mellen, 1993). However, only few studies have described scent-marking in the wild, e.g. leopard *Panthera pardus* (Bothma and Coertze, 2004), tiger (Smith et al., 1989), cheetah (Marnewick et al., 2006), Geoffroy's cat *Leopardus geoffroyi* (Soler et al., 2009) and Eurasian lynx (Hucht-Ciorga, 1988; Sokolov et al., 1995). These studies have focused mostly on describing the occurrence and frequency of scent-marking behaviour in few individuals, and not on observing interactions between different individuals. Here, we present the results from detailed observations on over-marking in a population of free-ranging felids. Eurasian lynx are solitary, territorial and occur at low densities (1–2 individuals per 100 km<sup>2</sup>, Zimmermann et al., 2012a,b). Resident male and female lynx in our study area occupy large home ranges (males: 137 km<sup>2</sup> (mean Kernel 95%,  $N = 11$ ), females: 76 km<sup>2</sup> (mean Kernel 95%,  $N = 12$ ); Breitenmoser-Würsten et al., 2001), with little home range overlap between neighbouring animals of the same sex (males: 4.8% (mean overlap of Kernel 95%,  $N = 5$ ), females: 12.8% (mean overlap of Kernel 95%,  $N = 12$ ); Breitenmoser-Würsten et al., 2001). Resident males almost entirely overlap the home ranges of one or two resident females, which they try to monopolise (Breitenmoser and Breitenmoser-Würsten, 2008). However, extra-territorial excursions of males occur during the mating season (Haller and Breitenmoser, 1986; Breitenmoser and Breitenmoser-Würsten, 2008) and we have documented one case where a resident male sired the offspring of a neighbour's female (Breitenmoser-Würsten, unpublished results). Eurasian lynx are

thought to be monoestrous (Kvam, 1990), although replacement litters are known to occur when the first litter is lost (Breitenmoser-Würsten et al., 2007). It is therefore crucial for the male to find and guard the female when she is ready to mate and this could be facilitated by scent-marking. Part of a lynx population consists of (mostly subadult) non-residents, which do not hold territories but move among the home ranges of established residents (Zimmermann et al., 2005). Since encounter rates of the wide ranging species lynx are low and aggressive conflicts among residents and non-residents have rarely been observed (Breitenmoser and Breitenmoser-Würsten, 2008), it is likely that indirect communication via scent-marking could play an important role in maintaining the social and spatial organisation of the lynx.

The first aim of this study was to describe the marking behaviour of Eurasian lynx at commonly used natural marking sites in a wild population. Since a communicative function of scent marking requires the repeated use of particular conspicuous structures and captive lynx of both sexes are known to scent-mark (Burmester, 2005), we predicted that both male and female adult lynx in the wild regularly head rub and spray urine to the same visually conspicuous structures (i.e. rocks, trees, woodpiles). Scent-marks of wide ranging mammals need to have a certain longevity in order to be picked up by conspecifics, which may not encounter them for several days or weeks. We therefore further expected that there would be an 'expiry date' to scent-marks in that resident lynx are more likely to refresh their own scent-marks as the marks become older.

The second aim of this study was to gain insight into whether over-marking at these sites has a function in communication among males and females and/or in competition among neighbouring residents and non-residents. We predicted that lynx marking activity increases before and during the mating season (mate attraction hypothesis), encountering the scent-mark of another individual triggers over-marking in resident lynx of both sexes (competition, chemical bulletin board or territoriality hypothesis), and non-resident lynx refrain from marking in order to avoid conflicts with residents (territoriality hypothesis).

## 1. Methods

This study was conducted in the north-western Swiss Alps, where spatial and social structure of the lynx population is well known from several previous radio telemetry studies (Haller and Breitenmoser, 1986; Breitenmoser and Haller, 1993; Breitenmoser-Würsten et al., 2001; Molinari-Jobin et al., 2007) and repeated camera trapping censuses (Laass 2001; Zimmermann et al., 2011, 2013; Pesenti and Zimmermann, 2013). The study area expands over 1424 km<sup>2</sup> and includes the Simmental, Diemtigtal and Saanenland in the Bernese Oberland, as well as the Pays d'Enhaut, the Haute Gruyère and the Jauntal in the pre-Alps of the cantons Vaud and Fribourg (Zimmermann et al., 2012a,b). During the camera trapping census in winter 2011/12, lynx density in the study area was estimated at 2.13 (1.73–2.53, 95% confidence interval) independent (subadult and adult) lynx/100 km<sup>2</sup> of suitable habitat (95.3% of total study area; Zimmermann et al., 2012a,b).

Marking sites were found along trails and forest roads frequently used by lynx and were identified either during snow tracking, radio tracking or while choosing sites for camera trapping censuses. Scent-marks are usually placed on visually conspicuous objects, where lynx hair can be found and urine marks can be smelled even by humans. The marked objects included wood piles, (cut) tree trunks, rocks, small spruce trees and the corner of a wooden shed. From December 2009 to July 2012, we observed a total of 22 marking sites by means of camera trapping (Fig. 1). Observation periods for different marking sites ranged from 4 months to 2.5

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