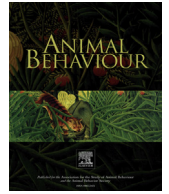


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**Abstract:** The costs of signalling are often expressed in terms of increased predation risk to the signaller; however, whether signalling predators also incur costs due to eavesdropping by prey and may attempt to reduce these costs is less well studied. In this study, we investigated whether there is a trade-off between intraspecific communication through scent marking and the risk of alerting prey in a wild population of a stalking predator, the Eurasian lynx. We followed lynx tracks in the snow and recorded scent marks and evidence of hunting behaviour along these tracks. Lynx preferred conspicuous objects for marking and increased scent marking rate when walking along linear structures, such as forest roads. This association was strongest when lynx were hunting, while there was only a weak correlation when no evidence of hunting could be detected. On tracks with evidence of hunting behaviour, lynx engaged less in scent marking. The relationship was most evident during the mating season, when lynx increased scent marking rates while they were not hunting. We further expected lynx to mark most in areas where they had recently hunted successfully, but time and distance to the last kill were not associated with scent marking rate. Our study supports the hypothesis that lynx face a trade-off between enhancing the detection probability of scent marks by conspecifics and avoiding eavesdropping by prey, and indicates that scent marking rate is influenced by several factors.



## Is there a trade-off between scent marking and hunting behaviour in a stalking predator, the Eurasian lynx, *Lynx lynx*?



Kristina Vogt<sup>a, b, \*</sup>, Elizabeth Hofer<sup>a, 1</sup>, Andreas Ryser<sup>a, 1</sup>, Mathias Kölliker<sup>b, 2</sup>,  
Urs Breitenmoser<sup>a, c, 1</sup>

<sup>a</sup> KORA, Carnivore Ecology and Wildlife Management, Muri, Switzerland

<sup>b</sup> Department of Environmental Sciences, Zoology and Evolution, University of Basel, Basel, Switzerland

<sup>c</sup> Institute of Veterinary Virology, University of Bern, Bern, Switzerland

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The costs of signalling are often expressed in terms of increased predation risk to the signaller; however, whether signalling predators also incur costs due to eavesdropping by prey and may attempt to reduce these costs is less well studied. In this study, we investigated whether there is a trade-off between intraspecific communication through scent marking and the risk of alerting prey in a wild population of a stalking predator, the Eurasian lynx. We followed lynx tracks in the snow and recorded scent marks and evidence of hunting behaviour along these tracks. Lynx preferred conspicuous objects for marking and increased scent marking rate when walking along linear structures, such as forest roads. This association was strongest when lynx were hunting, while there was only a weak correlation when no evidence of hunting could be detected. On tracks with evidence of hunting behaviour, lynx engaged less in scent marking. The relationship was most evident during the mating season, when lynx increased scent marking rates while they were not hunting. We further expected lynx to mark most in areas where they had recently hunted successfully, but time and distance to the last kill were not associated with scent marking rate. Our study supports the hypothesis that lynx face a trade-off between enhancing the detection probability of scent marks by conspecifics and avoiding eavesdropping by prey, and indicates that scent marking rate is influenced by several factors.

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Communication by means of visual, acoustic or chemical signalling is the key to most social interactions in animals. However, signals are often not only perceived by the intended receivers but can be intercepted and exploited by competing conspecifics or even by other species for their own benefit. This phenomenon is known as 'eavesdropping' and has been described in both intra- and interspecific contexts (Hughes, Korpimäki, & Banks, 2010; Hughes, Price, & Banks, 2010; McGregor & Dabelsteen, 1996; Peake, Terry, McGregor, & Dabelsteen, 2001; Steinberg et al., 2014; Zuk & Kolluru, 1998). The role of eavesdropping has been studied extensively in the context of predator–prey interactions (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005; Conover, 2007). Most of these studies have focused on the prey animal's perspective and have described either the costs of signalling in terms of

increased predation risk (Hughes, Kelley, & Banks, 2012; Hughes, Korpimäki, et al., 2010; Hughes, Price, et al., 2010; Koivula & Korpimäki, 2001) or the reaction of prey animals to predator cues (Apfelbach et al., 2005; Kats & Dill, 1998). The question of whether a signalling predator may incur costs due to interspecific eavesdropping by prey is less well understood. Several studies on echolocating predators have investigated how eavesdropping on ultrasound by prey may influence the predators' hunting strategies and their communication (e.g. several European bat species, Rydell, Jones, & Waters, 1995; killer whales *Orcinus orca*, Deecke, Ford, & Slater, 2005). Furthermore, it has been proposed that *Amblyseius swirskii* predatory mites 'chemically disguise' themselves to improve attack success on *Frankliniella occidentalis* thrips larvae (Van Maanen et al., 2015). These studies provide evidence that predators can prevent detection by their prey by modifying their hunting or communication behaviour, but we are not aware of any study investigating how mammalian predators may modulate chemical signalling in order to reduce the risk of interspecific eavesdropping.

\* Correspondence: K. Vogt, KORA, Thunstrasse 31, CH-3074 Muri, Switzerland.  
E-mail address: [k.vogt@kora.ch](mailto:k.vogt@kora.ch) (K. Vogt).

<sup>1</sup> Present address: KORA, Thunstrasse 31, CH-3074 Muri, Switzerland.

<sup>2</sup> Present address: Isenbachweg 2, CH-4226 Breitenbach, Switzerland.

Many mammalian predator species use scent marks for communication with neighbouring territory holders, mates or group members (i.e. wolves, *Canis lupus*, Peters & Mech, 1975; several felid species, Mellen, 1993; spotted hyaena, *Crocuta crocuta*, Burgener, East, Hofer, & Dehnhard, 2008; banded mongoose, *Mungos mungo*, Jordan et al., 2011). In wild felid species, scent marking is assumed to play an important role in territoriality, in reproductive behaviour, and in competition among same-sex individuals (several felid species, Sunquist & Sunquist, 2002; Eurasian lynx, Vogt, Zimmermann, Kölliker, & Breitenmoser, 2014; bobcat, *Lynx rufus*, Allen, Wallace, & Wilmers, 2015). Wide-ranging predators such as large felids or canids are limited in the amount of scent marks they can produce and the time they can invest in scent marking behaviour (Wyatt, 2014). In order to optimize scent marking efficiency, they should leave scent marks where they are most likely to be detected by conspecifics, e.g. along guiding topographic features such as paths or rivers (Wyatt, 2014). Scent marks are also more likely to be encountered when they are placed along a straight path (since a strongly winding path of the same length passes through a much smaller area; Conover, 2007). It is conceivable that optimizing detection probability by conspecifics may also facilitate eavesdropping by other species. In fact, a variety of studies has provided evidence that prey animals react to predator scent marks (Apfelbach et al., 2005). The observed responses range from changes in habitat use (e.g. avoidance of scent marks, Forsman, Monkkonen, Korpimäki, & Thomson, 2013; Swihart, Pignatello, & Mattina, 1991) to behavioural adjustments (e.g. decreased movement rates, Borowski, 1998) and physiological changes (e.g. delayed ovulation, Apfelbach, Wiest, & Vasilieva, 2001). Wild ungulates are known to show antipredator behaviours in response to predator scent marks: Kuijper et al. (2014) found that red deer, *Cervus elaphus*, showed a more than two-fold increase of vigilance level when presented with olfactory cues of a predator (wolf scats). Roe deer, *Capreolus capreolus*, increased vigilance levels when presented with Eurasian lynx urine (Eccard, Meißner, & Heurich, 2015) and reduced visit duration of sites where lynx scats were presented (Wikenros, Kuijper, Behnke, & Schmidt, 2015). Such eavesdropping responses by prey are of particular relevance for ambush predators, as they have to remain undetected by their prey for successful hunting. At the same time, they have a need for social communication and marking of their territory and, thus, may face a trade-off between intraspecific communication and the risk of alerting prey. In this study, we investigated whether there is evidence for such a trade-off in a wild population of the Eurasian lynx, a stalking and ambush predator for which scent marking has been formerly shown to play an important role in communication with competitors and mates (Vogt et al., 2014). To this end, we followed tracks of global positioning system (GPS)-collared lynx in the snow across the study area and identified scent marks along these tracks.

Eurasian lynx are specialized predators of medium-sized ungulates such as roe deer and chamois, *Rupicapra rupicapra*, which make up 84% of their diet in Switzerland on average. The remaining 16% consist of smaller prey species such as red foxes, *Vulpes vulpes*, European brown hares, *Lepus europaeus*, or marmots, *Marmotta marmotta* (Breitenmoser et al., 2010). The way lynx move throughout their large home ranges (males: 137 km<sup>2</sup>; females: 76 km<sup>2</sup> (mean Kernel 95%), Breitenmoser-Würsten et al., 2001) follows a characteristic pattern: stationary phases during which a lynx remains in the vicinity of a fresh kill for up to several days are interspersed with phases of increased movement, when it uses larger parts of its home range and presumably searches for prey in new areas. Excursions from unfinished kills occur mostly in males during the mating season (Breitenmoser & Breitenmoser-Würsten, 2008). During their movements, lynx of both sexes engage in scent

marking behaviour by means of urine marking at visually conspicuous objects such as rocks or young spruce trees (Vogt et al., 2014). Males mark generally more often than females; marking frequency increases during the mating season and there is evidence that marking sites may serve as 'chemical bulletin boards' for competitors and mates (Hucht-Ciorga, 1988; Vogt et al., 2014). Observations of prey animals investigating lynx marking sites have occasionally been made (roe deer, red deer, chamois, red fox; K. Vogt, personal observation). Lynx could avoid detection of fresh scent marks by potential prey by separating hunting from scent marking activity, either in space or in time. Under the hypothesis of a trade-off between lynx hunting and scent marking behaviour, we made the following nonmutually exclusive predictions: (1) lynx should leave their scent marks where there is a high chance of them being encountered by other lynx (e.g. along guiding topographical features or during long distance movements; Conover, 2007); (2) they should increase scent marking when the social benefits are high (e.g. during the mating season or when encountering other lynx); (3) they should spatially and/or temporally separate areas with high scent marking intensity from areas where the costs of being detected by potential prey are high (e.g. they should: (a) mark more in places where they have recently hunted successfully; and (b) avoid scent marking where they intend to hunt); (4) when the benefits gained from scent marking are high compared to the costs in terms of decreased hunting success (e.g. during the mating season), the separation between scent marking and hunting behaviour should be less pronounced.

## METHODS

### *Ethical Note*

From 2012 to 2014, we captured and radiotagged 15 Eurasian lynx (eight males, seven females) and recaptured four of them to change their collars. Lynx were captured following established standard protocols (described in Breitenmoser & Haller, 1993; Ryser et al., 2005; Ryser-Degiorgis et al., 2002; Zimmermann, Breitenmoser-Würsten, & Breitenmoser, 2005) and with all permits required according to Swiss legislation for capturing, immobilizing, and radiotagging lynx (capture permits from the Federal Office for the Environment: Bewilligung\_KORA\_Luchsfang\_BE\_2010/2011/2006-03219/02/05/03, Bewilligung\_KOR-A\_Luchsfang\_Kompartimente I, III und IV\_2011–2015; animal experimentation permit from the Animal Welfare Commission of the Office for Agriculture and Nature of the Canton of Bern: 109/10 and 111/13). The capture methods included foot snares (14 captures), solid wooden box traps (three captures) and a remote-controlled teleinjection system (one capture). Most captures took place from November to April, in order to avoid capturing pregnant or lactating females or small kittens. Three single animals (two males, one nonreproductive female) were captured between July and October, after the absence of kittens had been confirmed by camera traps set for one night at the kills where they were captured with foot snares the following night (see below).

Foot snares made from light aluminium hoops (20.5 cm diameter) and 3 mm wire cables were placed around fresh kills and connected to an alarm system. The cables were passed through aluminium tubes equipped with long springs to avoid leg injuries. The capture team, consisting of several experienced field biologists and a trained wildlife veterinarian, was always able to reach the capture site within 15 min of an alarm at most. Since foot snares were placed only at known lynx kills, the only bycatch were two dogs, *Canis familiaris*, which were released immediately. All animals were thoroughly checked for injuries during handling and all results were documented. The only injuries reported were two cases

with minor skin abrasions or swelling on one leg and two cases where lynx had bitten their own lips (no stitching needed). We tightly monitored the movements of all lynx after release and searched GPS location clusters until we could confirm that they were hunting successfully. Throughout this study, we regularly checked the movement patterns of all lynx and searched for prey remains. All lynx found dead in Switzerland are submitted to the Fish and Wildlife Health Centre at the University of Bern for examination (including histology). No capture-related injury (e.g. myopathy) has been detected during our study.

Unbaited double-door box traps made from solid wood ( $2 \times 0.75$  m and 0.8 m high) were placed on forest roads used by lynx. They were equipped with a global system for mobile communications (GSM)-based alarm system allowing for 24 h monitoring. We checked the functioning of the alarm daily and controlled box traps physically every 4 to 5 days to ensure proper functioning. When an alarm went off, the box trap was checked within 30 min to 1 h by one capture team member or by local game wardens. Any nontarget species were directly released and the rest of the capture team was alerted if a lynx was in the trap. Box traps were only operated during winter, when the outside temperature was low. Lynx did not spend more than 4 h in the box trap before immobilization; hence providing food and water was not necessary. Since the traps were dark and closed at all sides, animals were safe from weather conditions and predators and generally behaved calmly. All lynx caught were examined by a veterinarian and the only injuries reported were in some cases several split or broken claws, which lynx regrow. Sixteen nontarget animals were captured (four red foxes, two dogs, nine badgers, *Meles meles*, one stone marten, *Martes foina*), all of which were released without any visible injuries.

For one lynx capture, a minimally invasive capture system (MICS; Ryser et al., 2005) was used. The device consists of a blowgun remotely controlled by means of a built-in camera and a swivelling two-way pan-tilt head. The MICS is a highly selective system and allows for relatively stress-free captures of lynx. However, its use is restricted in our study area, since it can only be used in safe terrain (with no main roads, cliffs or white water nearby) as the darted animal is not physically restrained.

Lynx were immobilized with 0.1–0.15 mg/kg medetomidine hydrochloride (Domitor, Orion Corporation, Espoo, Finland) and 3.2–5.5 mg/kg ketamine hydrochloride (Ketasol, Graeb, Switzerland). Atipamezole hydrochloride (0.56–0.77 mg/kg; Antisedan, Orion Corporation, Espoo, Finland) was used as an antagonist for medetomidine and was injected at least 1 h after the last ketamine injection in order to ensure that ketamine had been fully metabolized (Ryser-Degiorgis et al., 2002). The anaesthesia protocol is well established and no adverse long-term effects have been recorded during our study or in previous studies using the same protocol (Molinari-Jobin, Molinari, Breitenmoser-Würsten, & Breitenmoser, 2002; Ryser et al., 2005; Ryser-Degiorgis et al., 2002; Zimmermann et al., 2005; Zimmermann, Pesenti, Mini, et al., 2012). Vital parameters of anaesthetized animals were closely monitored by a wildlife veterinarian. Our capture kit included blankets and hot-water bottles to prevent hypothermia as well as medications to counter the possible adverse effects described for the anaesthetics. The use of an antagonist for medetomidine further enabled us to interrupt anaesthesia in case of complications. However, this was never necessary during this study. Drugs were administered using a blow dart (box trap, foot snare and MICS captures), or lynx were held down with a net and given a direct intramuscular injection (foot snare captures). To reduce stress, animals were left undisturbed after drug injection until they were unconscious. During the process of waking up, animals were observed from a distance.

Lynx were equipped with GPS/GSM tracking units (GPS Plus Mini-1 C collars, Vectronic Aerospace GmbH, Berlin, Germany; Wild Cell SL/SD GPS-GSM collars, LoTek wireless, Ontario, Canada) weighing 250–300 g (mean 1.5% of lynx body weight, ranging from 1.25 to 2% for largest and smallest lynx, respectively). GPS collars were secured with blunt screw nuts provided by the manufacturer. Each collar contained a break-off device, allowing the unit to drop off after 1–2 years. The dropping of the unit has been documented for three of these individuals using camera traps. None of the captured lynx died due to capture procedures or problems with the collar or showed any skin abrasions caused by the collar. From earlier telemetry studies conducted in our study area using the same methods, radiotagged lynx are known to reproduce normally and live to an old age (Zimmermann et al., 2005; Zimmermann, Pesenti, Mini, et al., 2012).

### Study Area

The study area is situated in the northwestern Swiss Alps, expands over approximately 1500 km<sup>2</sup> and includes parts of the Bernese Oberland and the pre-Alps of the cantons Vaud and Fribourg (Vogt et al., 2014; Zimmermann, Pesenti, & Breitenmoser, 2012). Altitudes range up to more than 2000 m above sea level. The forested area covers 30% but is fragmented by human settlements and pastures. Human density is about 42/km<sup>2</sup> on average (Swiss Federal Statistical Office, 2015) and the area is intensively used for recreation, both in summer and in winter (hiking, skiing). The most common ungulate species are chamois and roe deer (Breitenmoser & Breitenmoser-Würsten, 2008; Breitenmoser & Haller, 1993). Red deer, Alpine ibex, *Capra ibex*, and wild boar, *Sus scrofa*, occur only locally and in low numbers. During a camera trapping census in winter 2013/2014, lynx density in the study area was estimated at 2.05 (1.50–2.60, 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., 2014).

### Snow Tracking

We followed the tracks of 15 GPS/GSM-collared lynx (eight males, seven females) from November to April 2012/2013 and 2013/2014. Eleven lynx were resident adults, two were subadults (year of birth known, 1.5–2 years of age) and two were either subadults or young adults (estimated by weight and tooth wear). Three of the subadult and young adult lynx had already become residents; the collar of the fourth stopped working after less than 1 year, so we could not determine its status. GPS/GSM collars were set to take seven locations per day and collars attempted to send GPS locations via SMS to a ground station at the office once per night. Locations were downloaded from the ground station every morning and one to two focal lynx were chosen from all successfully downloaded collars according to accessibility and snow conditions. We attempted to record a similar number of tracks per month for each lynx and a similar number of tracks corresponding to different movement patterns. Movement patterns were classified using GPS data (long distance = lynx moved >1000 m in a straight line within 6 h; explorative = lynx moved 100–1000 m straight line within 6 h, stationary = lynx moved <100 m in a straight line within 6 h). Since GSM coverage of our study area was not continuous and not all GPS collars were functioning during the whole study period, effective number of tracks for each lynx ranged from one to 17 tracks/individual (median = six tracks/individual). Moreover, snow cover during our study periods was not always continuous and some areas were inaccessible due to risk of avalanches, which resulted in our sample consisting of 20 stationary tracks, 33 explorative tracks and 64 long distance tracks.

We started tracking at a chosen GPS location of a collared lynx in order to ensure proper assignment to the individual. The mean accuracy calculated from a subsample of 46 GPS locations from four collars was  $8.8 \pm 1.3$  m SE in our study area. Tracks were 6–48 h old and were generally followed backwards. If lynx were known to have left the immediate area, we could also track forwards without disturbing the animal. We attempted to track for a minimum of 1000 m for long distance and explorative movements and 150 m for stationary movements. Tracking was interrupted either when the tracks were lost or when they led into inaccessible areas. All tracks were logged using a handheld GPS (Etrex vista HCx, Garmin, Olathe, KS, U.S.A.) with a mean accuracy  $\pm$  SE of  $1.9 \pm 0.4$  m in our study area (calculated from 71 test points). We recorded date and time of the snow tracking event, date and time of track formation, track length, time since last snowfall, snow conditions, number of marking sites, number of scats, presence of other lynx and evidence of hunting behaviour (see below). Track formation was derived from the GPS collar fix at the starting point. If the track passed several GPS locations taken by the collar, the median time point was calculated unless time since last snowfall provided additional information on track age. We used a trained dog on 97 tracks and 20 tracks were followed by an experienced tracker without a dog. When scent marking, lynx typically make a short detour from their direction of travel and turn their rear towards visually conspicuous objects in order to spray urine (Breitenmoser & Breitenmoser-Würsten, 2008), thereby creating an easily recognizable track pattern in the snow that precludes misidentification. For each track, snow conditions were described as follows: 1 = continuous snow cover; 2 = patchy (<50% of track); 3 = very patchy (>50% of track); 4 = no snow. Snow cover was coded as 1 or 2 for 93% of the tracks (89 with dog, 20 without dog). For the remaining 7% of tracks, we relied on the dog to hold the lynx track and show marking sites in snow-free patches. Of the marking sites, 92% could be identified by the track pattern; 8% were detected by the trained dog and were then confirmed by their typical smell by the tracker. All marking sites and scats were logged with the handheld GPS, and we recorded which objects were marked and whether scats were covered with snow, earth or plant material. Presence of other lynx was confirmed if the track of the focal lynx was crossing or following the track of another individual. Evidence of hunting was confirmed if prey remains were found or tracks showed that lynx were pursuing a prey animal unsuccessfully. We considered only cases where tracks of lynx and prey matched the following criteria: strides lengthened to full-out gallop, tracks parallel or overlapping, signs of a fast start, direct line of sight between starting point of chase and starting point of flight.

For each track, we searched the previous kill the focal lynx had made. In order to find kills, we searched GPS location clusters (GLCs), using methods similar to those in Krofel, Skrbinek, and Kos (2012) and in Svoboda, Belant, Beyer, Duquette, and Martin (2013). A GLC was defined as a set of at least two GPS locations within 100 m and a maximum time span of 72 h between consecutive fixes in the same GLC. Within each GLC, we searched a radius of 30 m around each fix for at least 1 h using a trained dog whenever possible. We searched all accessible GLCs preceding the track of the focal lynx until we found prey remains. Inaccessible GLCs were not searched but were included in the analysis as potential kills, if the time the lynx spent in the GLC was  $\geq 9$  h. Analysis of all searched GLCs in our study area during the two winter seasons 2012/2013 and 2013/2014 shows that kills were found in 72% of GLCs with a duration of  $\geq 9$  h ( $N = 259$ ), while we could find kills in only 17% of the shorter GLCs ( $N = 70$ ). We also found kills by chance on six tracks of uncollared lynx in the study area and included these tracks into our analysis.

### Statistical Analysis

To test for a possible relationship between lynx scent marking rate and hunting behaviour we quantified the following parameters from the tracking data: time since last kill was calculated as the time difference in days between the last GPS location in the GLC containing the previous (potential) kill and the time of track formation. Distance to last kill (in km) was calculated as the median of the distances of all track points from the previous kill site (true kills) or from the geometric centre of the GLC (potential kills) and was log-transformed to fit a normal distribution. GLCs were identified using the cluster generator script in R (version 3.1.0, R Development Core Team, 2013) kindly provided by N.J. Svoboda (Svoboda et al., 2013) and adapted by K. Vogt. Evidence of hunting was classified as 0 (no hunting detected), 1 (lynx attempted to hunt or made a kill during this tracking event) and 2 (lynx was still using a kill it had made before track formation).

To test for the relationship between social factors, lynx movement patterns and scent marking rate we investigated the following parameters. Reproductive season was defined by the date of track formation lying either before or during the mating season of Eurasian lynx (15 February–15 April; Breitenmoser & Breitenmoser-Würsten, 2008). Presence of other lynx was classified as 1 = detected or 0 = not detected. We assigned a structuredness index to each track, which was calculated as the proportion of a track's length intersecting with a 10 m buffer laid around linear structures (i.e. forest edges, primary and secondary roads, hiking trails, and small watercourses or ravines) to account for GPS error. If a large portion of the track follows linear structures the index lies close to 1; tracks with only a small portion following linear structures give values close to 0. Linear structures were extracted as vector data from the SwissTLM3D geodatabase of the Swiss Federal Office of Topography (ESRI File Geodatabase 10.1, <http://www.swisstopo.admin.ch>). This database has an accuracy of 1–3 m. To describe the movement patterns of lynx, we assigned a simple straightness index to each track. The index was calculated as the total track length divided by the distance between start and end point as described in Benhamou (2004). The index lies between 0 and 1, with values close to 1 representing very straight tracks and values close to 0 representing very curved or circular tracks.

We analysed factors influencing scent marking rate using generalized linear mixed models (GLMMs) with Poisson error distributions and log-link functions fitted by Laplace approximation (function `glmer()` of the R package `lme4`; Bates et al., 2015). We first constructed a full model representing our hypothesis of a trade-off between scent marking and hunting and including all factors that we believed to be relevant for the system and that were related to our predictions from the main hypothesis. The number of marking sites was set as the response variable and track length (log) was set as offset to take into account different track lengths. In the full model, evidence of hunting, time since last kill, distance to last kill, structuredness index, straightness index, mating season and presence of other lynx were included as fixed factors. We further added the interactions between evidence of hunting and mating season and between evidence of hunting and structuredness index. Sample size was too small to analyse tracks of male and female lynx separately or include sex and its interactions with other factors in the full model. Graphical visualization showed that correlations among factors were similar for both sexes and, therefore, data from males and females were pooled. We included lynx identity as a random factor to account for repeated measures (several tracks per individual) and for variation between individuals.

To test for the robustness of the full model, we also ran three simpler models representing subhypotheses: (1) hunting behaviour is not relevant for changes in scent marking rates (the factors

evidence of hunting, time since last kill, distance to last kill and all their interactions were excluded); (2) lynx movement patterns are not relevant for changes in scent marking rates (the factors structuredness index and straightness index and all their interactions were excluded); (3) presence of other lynx is not relevant for changes in scent marking rates (the factor presence of other lynx was excluded). These simpler models were then compared to the results of the full model by means of the Watanabe-Akaike information criterion (AIC) and Bayesian information criterion (BIC). We left mating season included in all models because its relevance for changes in scent marking rates is well known for many cat species (Mellen, 1993) and has previously been shown for Eurasian lynx (Vogt et al., 2014). To test for overdispersion, we also calculated a scaling parameter for each model using the function recommended by D. Bates (<https://stat.ethz.ch/pipermail/r-sig-mixed-models/2011q1/015392.html>).

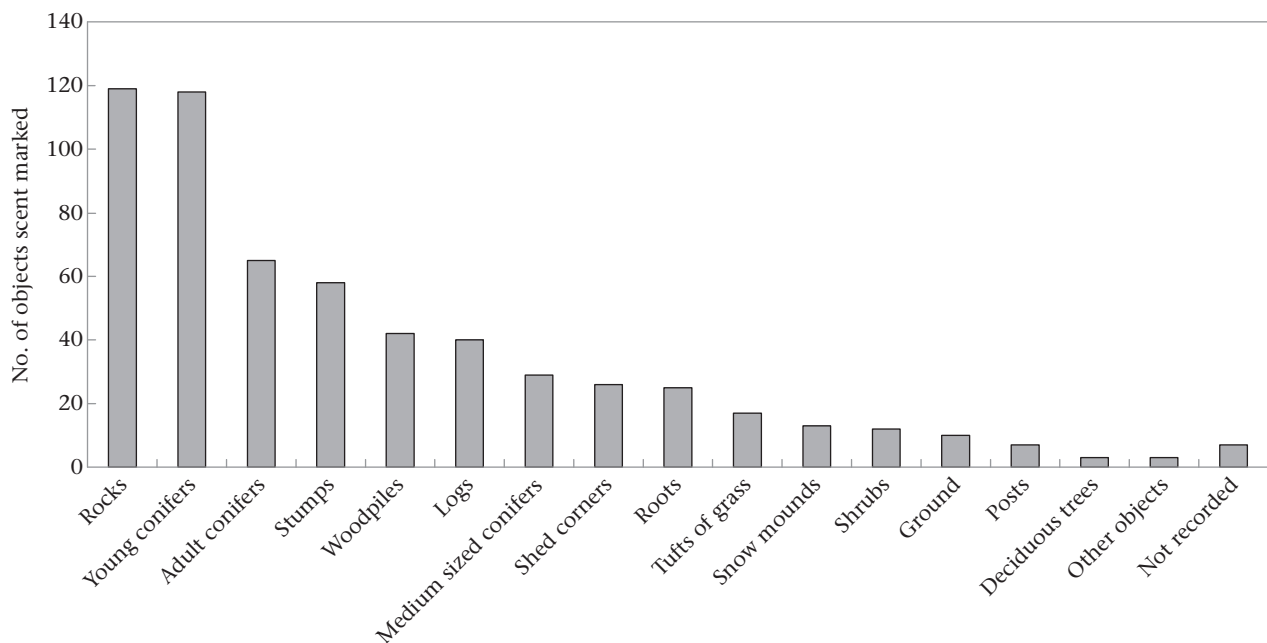
We present the model results as parameter estimates with standard errors (multiplied by the scaling parameter to account for overdispersion) and use Bayesian approaches to compute credible intervals (CrI) and draw inference from the full GLMM. This procedure has been described in Bolker et al. (2008) and has been implemented, for example, by Gruebler, Korner-Nievergelt, and von Hirschheydt (2010). For calculation of fitted values and CrI, we used the function `sim()` of the R package `arm` applying improper prior distributions (Gelman & Hill, 2007). We obtained posterior distributions of fitted values by directly simulating 5000 values from the joint posterior distributions of the model parameters. The means and the 2.5% and 97.5% quantiles of these fitted values were used as point estimates with their lower and upper 95% CrI boundaries, respectively. The strengths and uncertainties of correlations were evaluated based on estimates and CrIs of model parameters. All statistical analyses were conducted in R (version 3.1.0, R Development Core Team 2013) and ArcGIS (ArcGIS 10.1 SP for Desktop, Esri Inc., Redlands, CA, U.S.A.).

## RESULTS

We followed 111 tracks of 15 radiocollared lynx (1–17 tracks/individual) and six tracks of uncollared individuals over a total distance of 185 km (mean  $\pm$  SE =  $1.6 \pm 0.1$  km, range 0.2–5.6 km). The mean straightness value among all tracks was 0.447 ( $\pm 0.018$  SE) and the mean structuredness index was 0.466 ( $\pm 0.021$  SE). Sixty-four tracks were followed outside and 53 during the mating season. Tracks of other lynx were encountered in 22 cases. We found evidence of hunting during 28 tracking events, in 65 cases no hunting behaviour was detected and during 24 tracking events lynx were still using a kill made before track formation. We were able to retrieve the last kill for 71% of the tracks; potential kills were assumed for 29%. Marking rate varied widely between tracks and individual lynx (mean  $\pm$  SE =  $3.4 \pm 0.3$  marks/km track, range 0–18 marks/km track,  $N = 117$ ) but was similar between tracks with continuous snow cover (mean  $\pm$  SE =  $3.5 \pm 0.4$  marks/km track,  $N = 78$ ) and without continuous snow cover (mean  $\pm$  SE =  $3.3 \pm 0.5$  marks/km track,  $N = 39$ ). We recorded a total of 594 marking sites. The different objects used by lynx for scent marking with urine, and the frequency with which they were used, are shown in Fig. 1. The most common objects were rocks and young conifer trees, which are very abundant features in the alpine habitat of our study area.

### Factors Influencing Scent Marking Rate

We compared the full model to the three submodels by means of BIC and Watanabe-AIC (Table 1). Submodel 3 (excluding presence of other lynx) had the lowest information criteria values, and overdispersion was not higher than in the full model. While the parameter estimates of submodel 3 were very similar to those of the full model, the factor presence of other lynx did not seem to be



**Figure 1.** Objects used by lynx for scent marking with urine. Bars show the occurrence of different object types in a total of 594 marking sites found during snow tracking. Rocks = vertical faces of rocky structures; young conifers = conifers up to 1 m in height; medium-sized conifers = conifers up to 2 m in height, adult conifers/deciduous trees = higher than 2 m (trunk or lower branches marked); stumps = cut or broken tree trunks; logs = cut or broken trunks lying on the ground; roots = root plates of uprooted trees; tufts of grass/snow mounds = clearly elevated from ground; shrubs = bushes and young deciduous trees up to 2 m in height; ground = not elevated. Human-made structures include woodpiles, shed corners, fence or power line posts and other objects. Not recorded = object type not recorded.

**Table 1**  
Parameter estimates of the generalized linear mixed models (GLMMs) for scent marking rate

Fixed factors (Factor levels)	Full model		Submodel 1		Submodel 2		Submodel 3	
	disp=1.514	VarID=0.529	disp=1.609	VarID=0.560	disp=1.586	VarID=0.647	disp=1.514	VarID=0.527
	BIC=686.7	wAIC=1040.1	BIC=684.0	wAIC=1034.2	BIC=696.7	wAIC=1055.8	BIC=682.1	wAIC=1033.0
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	0.511	0.406	0.155	0.391	0.852	0.362	0.493	0.397
Structuredness index, SI	0.266	0.446	0.855	0.406			0.266	0.446
Straightness	0.553	0.455	0.498	0.463			0.568	0.450
Mating season	0.277	0.191	0.132	0.160	0.365	0.197	0.276	0.191
Presence of other lynx	-0.040	0.177	-0.130	0.174	-0.069	0.184		
Hunting								
Hunting=1	-0.850	0.441			-0.183	0.239	-0.846	0.441
Hunting=2	-1.132	0.752			-0.553	0.450	-1.139	0.752
Time since last kill	-0.009	0.041			-0.014	0.043	-0.008	0.041
Log(distance to last kill)	-0.056	0.070			-0.002	0.068	-0.057	0.069
Hunting * mating season								
Hunting=1 * mating season	-0.691	0.347			-0.592	0.352	-0.704	0.342
Hunting=2 * mating season	0.225	0.484			0.166	0.500	0.242	0.479
Hunting * SI								
Hunting=1 * SI	1.778	0.813					1.776	0.814
Hunting=2 * SI	0.913	1.362					0.913	1.362

The full model includes all factors (movement, social behaviour, hunting behaviour), submodel 1 only factors related to social behaviour and movement, submodel 2 only factors related to hunting behaviour and social behaviour and submodel 3 only factors related to hunting behaviour and movement (excluding the presence of other lynx). Mating season is known to influence scent marking rates (Vogt et al. 2014) and is included in all models. BIC: Bayesian information criterion; disp: scaling parameter for overdispersion; SE: standard error (corrected for overdispersion by multiplication with the scaling factor); VarID: estimated variance components due to lynx identity (random effect); wAIC: Watanabe-Akaike information criterion. Levels of the factor hunting (1 = evidence of hunting found along track, 2 = lynx is using a kill made before track formation) are compared to 0 = no evidence of hunting. The analysis was conducted on data from 117 snow tracking events.

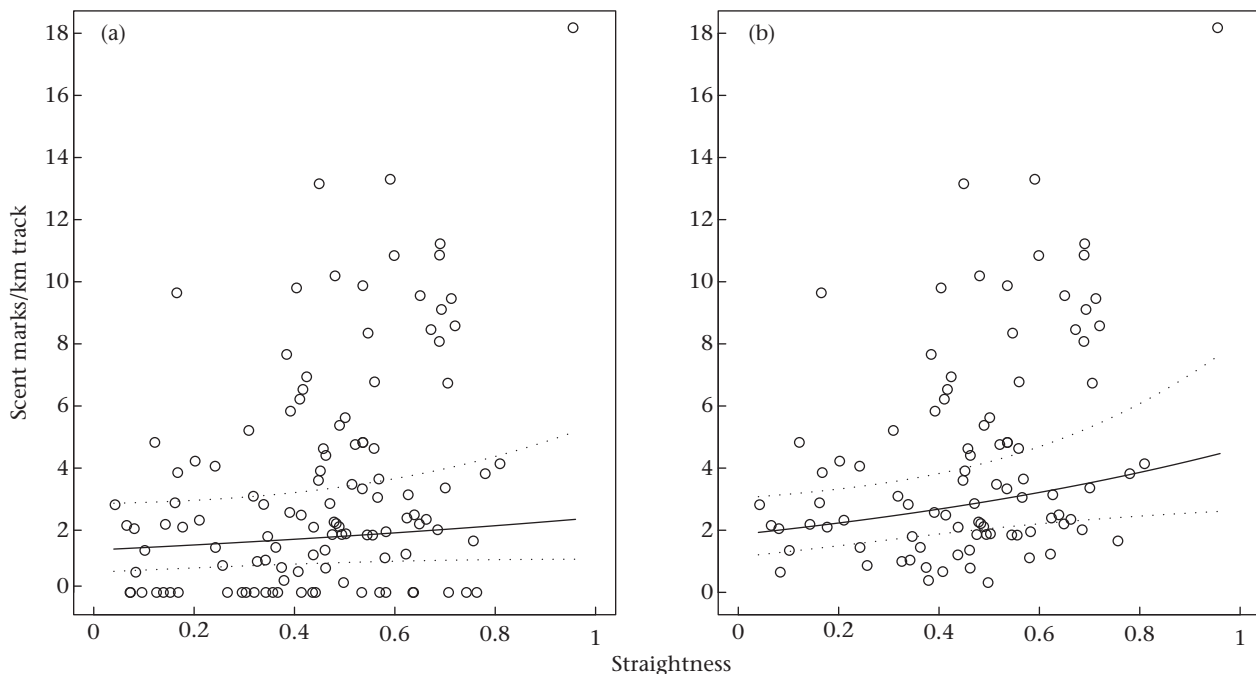
relevant for explaining the data (Table 1). We therefore chose submodel 3 for all further interpretation of our data.

According to this model, the correlations between structuredness index and scent marking rate and between straightness of the track and scent marking rate were weak and subject to a high level of uncertainty (Table 1).

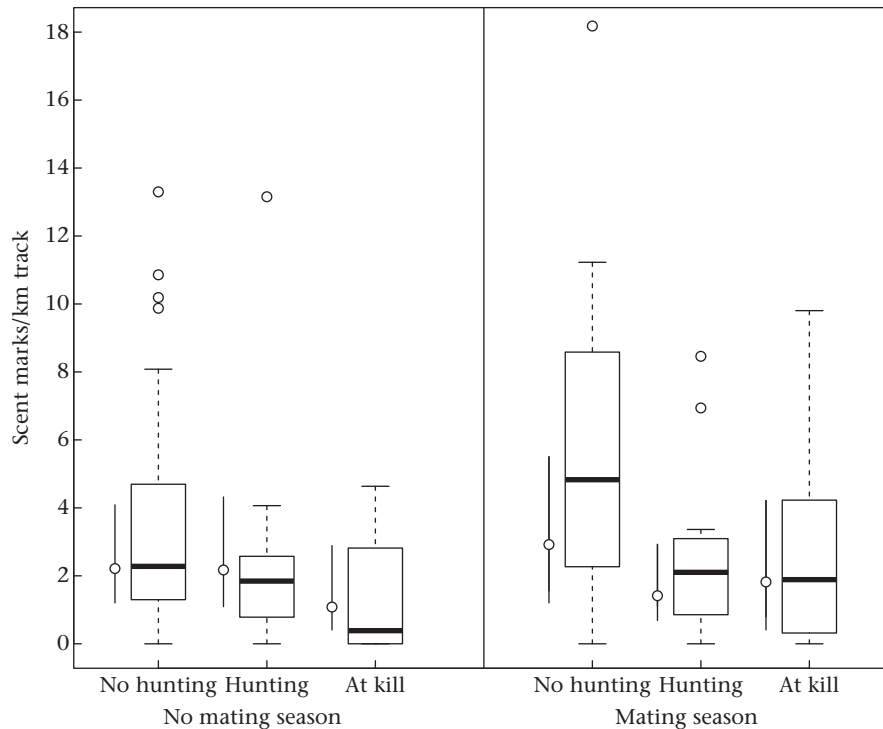
Tracks where no marking occurred at all were found among strongly winding paths as well as among straight ones, thereby lowering the estimate and increasing the variance (Fig. 2a). When only tracks with scent marking were considered in the GLMM ( $N = 92$ ), the association between straightness and scent marking

rate was stronger (estimate  $\pm$  SE =  $0.913 \pm 0.382$ ; Fig. 2b). According to this model, an increase in straightness index of 0.5 led to an increase in marking rate of 1.0 mark/km track (95% CrI 0.8–1.1 marks/km track).

Consistent with the result from the model selection, scent marking rates on tracks where other lynx were encountered (mean  $\pm$  SE =  $3.3 \pm 0.7$  marks/km track) were not higher than on tracks where we found no signs of presence of other lynx (mean  $\pm$  SE =  $3.5 \pm 0.4$  marks/km track). However, when averaging over all tracks, lynx marked more often during the mating season (mean  $\pm$  SE =  $4.2 \pm 0.5$  marks/km track) than outside the mating



**Figure 2.** Partial correlation of straightness of the track with scent marking rate. (a) All tracks ( $N = 117$ ); (b) only tracks with scent marking ( $N = 92$ ). Open circles = raw data; solid line = fitted values from the GLMM; dotted lines = 95% credible intervals. Evidence of hunting is set constant at 1; all other factors in the GLMM are set constant at their mean.



**Figure 3.** Partial correlation of the interaction between evidence of hunting and mating season with scent marking rate. Box plot = raw data. Each box encompasses the 25th to 75th percentiles, with the median represented by an interior line. Whiskers denote maximum values or, in case of outliers, 1.5 times the interquartile range. Circles denote outliers. Open circles with line segments = fitted values from the GLMM with 95% credible intervals. Hunting = evidence of hunting found along the track (kill or hunting attempt). No hunting = no evidence of hunting found along the track. At kill = lynx was feeding on a kill made before formation of the followed track. All other factors in the GLMM are set constant at their mean.

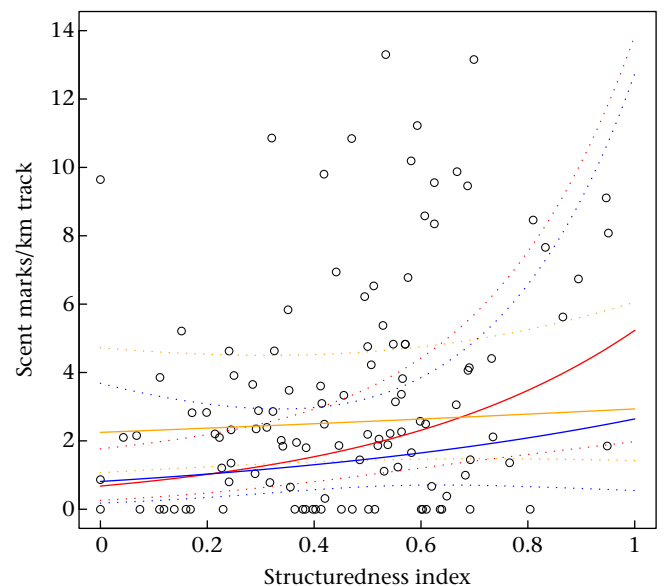
season (mean  $\pm$  SE =  $2.8 \pm 0.4$  marks/km track), although this difference was not significant (Table 1). Scent marking rate showed no correlation with time since last kill and distance to last kill (Table 1), but there was a stronger negative association between scent marking rate and evidence of hunting behaviour (Table 1). The difference between hunting and no hunting was most pronounced during the mating season, when lynx left  $2.6 \pm 0.8$  marks/km track (mean  $\pm$  SE) while hunting, compared with  $5.3 \pm 0.8$  marks/km track (mean  $\pm$  SE) when we found no evidence of hunting behaviour. Outside the mating season, this difference was less pronounced (Fig. 3). Conversely, the difference between the marking rate when using a kill compared to when lynx were hunting was highest outside the mating season, when lynx left  $2.3 \pm 0.7$  marks/km track (mean  $\pm$  SE) while hunting, compared with  $1.3 \pm 0.5$  marks/km track (mean  $\pm$  SE) when using a kill (Fig. 3).

The proportion of track following linear structures showed only a very weak correlation with scent marking rate for those tracks where no evidence of hunting could be detected (Fig. 4). However, scent marking rate increased with structuredness index when lynx were hunting (Table 1), i.e. an increase in structuredness index from 0.1 to 0.6 led to an increase in marking rate of 1.5 marks/km track (95% CrI 0.8–2.5 marks/km track). There was also a weaker correlation between scent marking rate and structuredness index for those tracks where lynx were using a kill (Table 1), although the uncertainty of this association was high (Fig. 4).

#### Caching of Scats

We also found 36 scats during snow tracking and recorded whether they were covered with snow, earth or plant material. Scats were more often covered when lynx were using a kill (six of

nine scats) or hunting (four of 10 scats). When lynx were not hunting, only five of 17 scats were covered.



**Figure 4.** Partial correlation of the interaction between evidence of hunting and structuredness index with scent marking rate. Open circles = raw data; solid lines = fitted values from the GLMM; dotted lines = 95% credible intervals; red = evidence of hunting found along the track (kill or hunting attempt); orange = no evidence of hunting found along the track; blue = lynx was feeding on a kill made before formation of the followed track. All other factors in the GLMM are set constant at their mean.



## DISCUSSION

Our study is based on detailed observations of scent marking and hunting activity of Eurasian lynx. We investigated whether there was a trade-off between lynx hunting and scent marking behaviour and predicted that: (1) lynx should leave their scent marks where there is a high chance of them being encountered by other lynx; (2) they should increase scent marking when the social benefits are high; (3) they should spatially and/or temporally separate areas with high scent marking intensity from areas where the costs of being detected by potential prey are high; (4) the separation between scent marking and hunting behaviour should be less pronounced when the benefits gained from scent marking are high compared to the costs in terms of decreased hunting success. The results are consistent with our hypothesis of a trade-off between chemical communication and hunting behaviour, while also showing that scent marking rates are influenced by a complex interplay of different factors.

Consistent with our first prediction, we found evidence that lynx try to increase detection probability of their marks by conspecifics. During their movements, lynx chose visually conspicuous objects for urine marking in almost all cases. We hardly ever recorded elimination of urine on the ground (Fig. 1). The visual component of the marked object enhances detection probability. This may be especially important for long-lasting scent marks with low volatility, such as those of lynx (Vogt et al., 2014; Wyatt, 2014). Furthermore, scent marking rate was correlated with track straightness when we excluded those tracks from the analysis where lynx did not mark at all. Conover (2007) argued that straight paths have a higher chance of being intercepted than strongly winding paths of the same length. It could be that track straightness is associated with the effort a lynx invests in scent marking, but is unrelated to the decision of whether it will engage in scent marking activity at all. In our study area, straight paths often coincided with lynx following forest roads, and straightness was therefore partly correlated with structuredness of the track. Lynx use forest roads for long distance movements. Especially during winter time, they can save energy by walking on ploughed roads or in snow shoe tracks (Zimmermann, Fattebert, Breitenmoser-Würsten, & Breitenmoser, 2007). It would therefore pay to increase scent marking rate during such movements, as forest roads are commonly used by conspecifics and allow for covering a large area at comparatively low costs. Moreover, forest roads, trails, forest edges, etc. channel the movements of animals and make it more likely that another lynx passes close enough to a scent mark to detect it.

Our second prediction was that lynx should increase scent marking when the social benefits are high. We found that lynx generally increased scent marking rate during mating season (mid-February to mid-April), which was also found during previous observations (Breitenmoser & Breitenmoser-Würsten, 2008; Vogt et al., 2014) and is well known from other felid species (Allen et al., 2015; Mellen, 1993; Smith, McDougal, & Miquelle, 1989; Sunquist & Sunquist, 2002). During this time, scent marking can be expected to play an important role in communication between the sexes as well as in intrasexual competition (Vogt et al., 2014). We also expected that the presence of another lynx would increase scent marking rate. However, this factor was not relevant for explaining the data. Whether it is beneficial for a lynx to increase scent marking rate upon encountering signs of presence of another lynx may strongly depend on the individual and pairing. An adult male encountering a female may have a stronger interest in advertising his presence than a subadult male encountering an adult male. Since individual variation in scent marking rate was high in our study and our sample size of encounters was small

( $N = 22$ ), we were not able to further subdivide the sample to test for the influence of pairing. Further studies including lynx of different social categories (e.g. resident adults versus dispersing subadults) would shed more light on how the trade-off between communication and hunting is influenced by social status.

Our third prediction was that lynx should spatially and/or temporally separate areas with high marking intensity from areas where the costs of being detected by potential prey are high. Vigilance of prey increases when a predator has been detected and decreases again in the absence of the predator due to the costs of high vigilance levels (Lima & Bednekoff, 1999). Thus, a lynx attacking a prey animal and then staying in the area for several days to feed on the kill presumably has a higher chance of being detected by potential prey than a lynx entering an area it has not used for some time. We therefore expected lynx to mark most often in areas where they had already hunted successfully and decrease scent marking rate as they moved further away, towards new hunting areas. However, neither time nor distance to the last kill was associated with scent marking rate. This may be because home ranges of lynx are much larger than those of any of their prey species (Baumann, Baboutai, & Struch, 2000; Boschi & Nievergelt, 2003; Hewison, Vincent, & Reby, 1998) and lynx are able to cover large distances in a short time. In our mountainous study area, the absolute distance moved by a lynx may be less informative than whether valleys or ridges are crossed. A lynx may, in fact, not have to move very far in order to enter a new topographic compartment, where prey animals are not yet alerted to its presence.

In contrast to time or distance to the last kill, the occurrence of hunting behaviour was associated with scent marking rate. Indeed, we found that lynx engaged less in scent marking on tracks with evidence of hunting behaviour. In 16 of 20 incidents where we could reconstruct from tracks how prey was pursued or killed by lynx, we observed that lynx did not wait for passing prey in an ambush, but encountered it while they were exploring their habitat. The sequences of stalking and attacking prey were very brief: after ca. 5 to 170 m, lynx would either catch their prey or abandon a chase. This suggests that stalking and killing prey is not very time consuming, and if lynx engage in scent marking less frequently at times when they are hunting, this does not solely reflect time constraints. Our findings also match field observations of Zheltukhin (1984), who found that Eurasian lynx in the upper Volga region were scent marking more frequently after hunting events than before. Similar evidence for a trade-off between hunting and communication was also found in killer whales, whose vocal activity increases after successful attacks on marine mammals or during surface-active behaviour, which is not hunting related (Deecke et al., 2005). Conversely, Monclús, Arroyo, Valencia, and Miguel (2009) stated that foxes in Spain defend their food resources by increasing scent marking rate and detectability of marks in places of high rabbit density and by placing their marks near rabbit latrines and scrapes. However, this study did not provide information on whether foxes had left their marks before or after successful hunting events, and the findings potentially reflected higher fox densities rather than elevated marking rates. We found no evidence of lynx increasing their scent marking rate around food resources. While using a kill, lynx marked less often than on tracks where no hunting behaviour was detected. When feeding on a kill for up to several days, lynx usually remain close by and often cover their kills with plant material or snow (Breitenmoser & Breitenmoser-Würsten, 2008). A low scent marking rate could further help to avoid drawing the attention of scavengers or conspecifics towards kills. This would match our observation that scats were more often covered around kills, although there may also be hygienic reasons for covering scats in places where an animal remains for several days. Other lynx species

are known to use latrines (e.g. Iberian lynx, *Lynx pardinus*, Gil-Sánchez, Ballesteros-Duperón, & Bueno-Segura, 2006; bobcat, López-Vidal et al., 2014), which could play a role in communication as has been reported for several carnivores (swift fox, *Vulpes velox*, Darden, Steffensen, & Dabelsteen, 2008; badger, Roper et al., 1993). The use of latrines has not been observed in Eurasian lynx (Breitenmoser & Breitenmoser-Würsten, 2008), but openly deposited scats could potentially convey information to conspecifics or prey.

Finally, we tested the prediction that the separation of scent marking from hunting behaviour should be less pronounced if the benefits gained from scent marking are high compared to the costs in terms of decreased hunting success. We observed that lynx increased scent marking rate during the mating season mostly at times when they were not hunting or when they were using a kill. When evidence of hunting could be detected, scent marking rates remained similar outside and during the mating season. Thus, the necessity of avoiding detection by prey animals seems to override the importance of communication during the mating season. The opposite seems to be the case for the effect of linear structures: scent marking rate increased with structuredness index when lynx were hunting, while there was no effect when no evidence of hunting could be detected. Although the credible intervals of our estimates were inflated at structuredness index values close to 1 due to a low number of observations, the interaction was still evident at structuredness index values below 0.6 (Fig. 4). While forest edges are the preferred habitat of roe deer, forest roads are usually avoided (Coulon et al., 2008). Pyrenean chamois, *Rupicapra pyrenaica*, were found to feed further away from forest edges and walking trails than expected by chance (Pépin, Lamerenx, Chadelaud, & Recarte, 1996). This suggests that forest roads are places where detection probability of scent marks by other lynx is high and the risk of eavesdropping by ungulate prey is low.

To conclude, the patterns of lynx scent marking activity observed during this study were consistent with the hypothesis of a trade-off between the benefits of social communication and the costs of detection by prey in this stalking predator: overall scent marking rate was lower when lynx were hunting, but hunting lynx increased scent marking rates in favourable places (along forest roads). Lynx also increased scent marking rates during the mating season but only when they were not hunting. Our study contributes to a better understanding of the costs of chemical signalling due to interspecific eavesdropping by approaching the topic from the so far neglected predator's perspective.

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