



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



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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.

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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

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