Behav Ecol Sociobiol (2017) 71:136
DOI 10.1007/s00265-017-2366-5

ORIGINAL ARTICLE

Where to leave a message? The selection and adaptive significance of scent-marking sites for Eurasian lynx

Maximilian L. Allen[1] · Lan Hočevar[2] · Maarten de Groot[3] · Miha Krofel[2]

Received: 21 December 2016 / Revised: 1 August 2017 / Accepted: 8 August 2017

Abstract
Scent marking is an important aspect of social organization and intraspecific communication for many mammals, including solitary felids. By selecting specific micro-locations for scent marking, an individual may increase its success in defending its territory and finding mates. Few studies, however, have reported the selection of scent-marking objects and sites by wild felids. To improve our understanding of this behavior and its adaptive significance, we developed and tested a set of mutually non-exclusive hypotheses explaining selection of scent-marking objects by Eurasian lynx (*Lynx lynx*). We used snow tracking to locate and determine the characteristics of objects lynx used and selected for urine spraying. Lynx did not mark objects according to their availability but selected juvenile conifers and often marked the surface that was sheltered from the elements ("persistence hypothesis"). Lynx also selected for objects similar in size to lynx and objects located on straight road sections and avoided the most frequently available object types. This selection may have both promoted detectability of the messages by the conspecifics ("detection hypothesis") and reduced energy expenditure of marking ("accessibility hypothesis"). Our study also indicated trade-offs faced by lynx, as the preferred marking objects were often not readily available. Therefore, suboptimal marking objects were sometimes used, most likely in order to maintain the high scent-marking frequency needed throughout their territory. We suggest that Eurasian lynx, and possibly other solitary felids, developed scent-marking behaviors that increase effectiveness and efficiency of their communication.

Significance statement
Scent marking is a form of communication that serves several purposes and allows the signals of the sender to reach a receiver indirectly. Persistence and detectability of these signals can have high adaptive value for solitary felids since the signals are essential for advertising territories for competitors and mates. Although both of these uses may depend on the micro-location where scent is deposited, the majority of studies have focused only on the marking sites used by felids and not on their availability or selection. By snow tracking Eurasian lynx, we showed that scent-marking sites most often *used* are not necessarily the same as the sites *selected*. We also provide insights into possible adaptive features of felid scent-marking and the possible mechanisms behind the selection of marking objects which likely serve to increase the effectiveness and efficiency of scent marking.

Keywords Eurasian lynx · *Lynx lynx* · Scent marking · Selection · Urine spraying · Communication

Maximilian L. Allen and Miha Krofel contributed equally to the manuscript.

Communicated by K. E. Ruckstuhl

Electronic supplementary material The online version of this article (doi:10.1007/s00265-017-2366-5) contains supplementary material, which is available to authorized users.

✉ Miha Krofel
miha.krofel@bf.uni-lj.si; miha.krofel@gmail.com

[1] Department of Forest and Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706, USA

[2] Wildlife Ecology Research Group, Department of Forestry, Biotechnical Faculty, University of Ljubljana, Večna pot 83, SI-1000 Ljubljana, Slovenia

[3] Department of Forest Protection, Slovenian Forestry Institute, Večna pot 2, SI-1000 Ljubljana, Slovenia

Published online: 19 August 2017

Introduction

Scent marking is an important aspect of social organization and the primary form of communication for many mammals, including solitary felids (Bailey 1974; Smith et al. 1989; Ghoddousi et al. 2008; Allen et al. 2016a). Scent marking is a form of communication that allows signals of the sender to indirectly reach a receiver (Gosling and Roberts 2001; Steiger et al. 2011) and is usually long-lasting (Alberts 1992; Jackson 1996; Vogt et al. 2014). Scent marking in felids serves several purposes (Vogt et al. 2014; Allen et al. 2016b), with the best understood uses being marking territories (Bailey 1974; Gosling and Roberts 2001) and advertising for mates (Mellen 1993; Vogt et al. 2014; Allen et al. 2015). Urine and feces are thought to be a relatively limited resource (Steiger et al. 2011), whose inexpensive nature outweighs the relative inefficiency of attempting to reach conspecifics indirectly through scent marking (Gosling 1990). An individual may therefore increase its success in defending its territory and finding mates by choosing scent-marking sites that have a high probability of being visited by conspecifics (e.g., Gosling and Roberts 2001) and by choosing micro-locations or plants which will increase the persistence of the organic volatile compounds in urine (Alberts 1992; Jackson 1996; Soler et al. 2009). Solitary felids occupy large home ranges, which they cannot constantly scent mark throughout. Therefore, they can be expected to focus on efficiency and persistence of scent marks, because persistent scent needs to be refreshed less frequently, and considerable effort might otherwise be required to regularly visit all parts of their large home ranges to ensure constant advertisement of their land tenure.

The majority of studies on scent marking by solitary felids focus on the form and function of scent marking (see review in Allen et al. 2016a), and relatively few have reported the use and/or selection of scent-marking objects and sites. European wildcats (*Felis silvestris*) choose plants that are visually conspicuous (e.g., large diameter and grouping of plants) and preferentially select certain plant species (Piñeiro and Barja 2012; Ruiz-Olmo et al. 2013). Similarly, leopards (*Panthera pardus*) select a particular acacia species over others for claw marking (Bothma and Le Riche 1995). However, Geoffroy's cats (*Leopardus geoffroyi*) vary in their selection of scent-marking objects based on habitat type (Soler et al. 2009). Snow leopards (*Panthera uncia*) regularly use protected (over-hanging) and northerly-oriented rocky surfaces, which is believed to enhance the longevity of scent marks by sheltering them from weather and other environmental factors (Ahlborn and Jackson 1986; Jackson 1996). The low number of studies focused on selection of scent-marking objects and sites (i.e., including information on availability, not only use) limits our ability to understand competing factors in selection, including the relative importance of ensuring persistence of scent marks, using conspicuous objects to promote detectability and the accessibility of objects for scent marking to reduce energy expenditure. To improve our understanding of object selection in scent marking by wild felids, we studied the scent-marking behavior of Eurasian lynx (*Lynx lynx*) from Dinaric population.

Eurasian lynx are solitary apex carnivores that occur across Europe and Asia in several isolated populations, many of which are small and considered threatened (Kaczensky et al. 2013). Eurasian lynx have large home ranges, typically measuring several hundred square kilometers and > 1000 km^2 in the northern populations (Linnell et al. 2001). Their social organization is similar to other solitary felids, displaying intrasexual territoriality with limited overlap on the periphery and overlapping home ranges between the sexes (Schmidt et al. 1997; Breitenmoser and Breitenmoser-Würsten 2008). Lynx are polygamous and monoestrous with peak of mating in late winter (Kvam 1990; Breitenmoser and Breitenmoser-Würsten 2008). During the breeding period, extra-territorial excursions of males have been recorded, sometimes with successful mating within the neighbor's territory (C. Breitenmoser-Würsten, unpublished results reported in Vogt et al. 2014). Aggressive intraspecific interactions are rare and usually occur between males during breeding season (Mattisson et al. 2013). The stability of land tenure system is believed to depend mainly on indirect communication, especially scent marking, which also plays a role in mate selection (Breitenmoser and Breitenmoser-Würsten 2008).

The typical scent-marking sequence by male and female lynx begins with olfaction, followed by cheek rubbing, and finally the spraying of urine (Online Resources 1 and 2). Male lynx are more frequent visitors to scent-marking sites and scent mark more frequently than females (Vogt et al. 2014, 2016; Krofel et al. 2017). Scent marking shows seasonal variation (Schmidt and Kowalczyk 2006; Vogt et al. 2016), with a peak during the late winter breeding season and the lowest frequency during summer when breeding females are denning and raising young (Vogt et al. 2014). Studies have shown differences in the objects scent marked by lynx, with Schmidt and Kowalczyk (2006) most frequently finding bridge railings, corners of sheds, fences, and tree trunks used for cheek rubbing, while Vogt et al. (2016) most frequently noted urine spraying on rocks and juvenile conifers. However, these studies were based only on objects used by the lynx, without knowing the availability of these objects in the environment, and it remains unknown whether lynx actively select certain objects or use them according to their availability. It also remains to be seen which characteristics are most important if the selection of scent-marking objects does occur. Such knowledge is essential for designing further studies and developing effective monitoring programs, which often rely on the use of hair snares or photo traps (Schmidt and Kowalczyk 2006; Zimmermann et al. 2013).

We used snow tracking across six winters over a period of 13 years to study Eurasian lynx scent marking in the Dinaric Mountains, Slovenia. Our objectives were as follows: (1) to determine the use and selection of objects for urine spraying and (2) to test which additional characteristics of the marked objects lynx were selecting for when urine spraying in respect to their assumed adaptive significance (Table 1). Based on previous studies on felid marking behavior (Ahlborn and Jackson 1986; Bothma and Le Riche 1995; Jackson 1996; Breitenmoser and Breitenmoser-Würsten 2008; Piñeiro and Barja 2012; Ruiz-Olmo et al. 2013; Vogt et al. 2014) and characteristics of different objects to retain smell (Alberts 1992; Nie et al. 2012), we developed a set of predictions, which we summarized into three mutually non-exclusive hypotheses (Table 2). According to the first hypothesis, the lynx would select for objects and characteristics that increase the persistence of scent marks ("persistence hypothesis"). Alternatively, lynx might select for objects and micro-locations that increase the probability of being detected by other lynx ("detection hypothesis") or those that decrease the amount of energy needed to mark them ("accessibility hypothesis").

Materials and methods

Study area

Our study was conducted in the Northern Dinaric Mountain Range in Slovenia (45°25′–45°47′N, 14°15′–14°50′E), where the altitudes range from 200 m to the peak of Mount Snežnik

Table 1 The variables, descriptions, and possible values of the documented objects scent marked during snow tracking of lynx. We provide reasoning behind our predictions of what objects and characteristics would be selected by lynx in conjunction with our hypothesis presented in Table 2

Variable	Description	Possible values	Reasoning behind the prediction
Object type	Type of the object used for marking	Rocks, juvenile conifers, tree stumps, tree trunks, other vegetation	To prolong longevity of the scent lynx would use and select for vegetation, which has higher surface-to-volume ratio and captures more urine. Also, the probability of inspecting object increases for more conspicuous (i.e., rarer) objects.
Height	The height of the object	< 0.5 m, 0.5–1 m, 1–2 m, > 2 m	Larger objects are more visible and therefore more visually conspicuous, and smaller objects (< 0.5 m) are below the nose level of potential receivers and level of urinating; therefore they are less accessible for marking and receiving the signal.
Slope	The direction the marked side of the object is facing according to the slope of the surrounding (20 m) terrain	Upwards, downwards, flat	The objects surrounded by flat ground are easier to access for marking and receiving the message. Objects on flat ground are also visually more conspicuous.
Road curvature	The side of the road curvature where the object is located	Inner side of the curve, outer side of the curve, straight road	Objects on the outer curve of the road are on the other side of the road from where lynx normally walk (pers. observation) and using them would increase the energy expenditure and lower the chances of being detected.
Direction	The cardinal/intercardinal direction the marked side of the object is facing	N, NE, E, SE, S, SW, W, NW	Objects facing the northern directions (NW, N, NE) are more sheltered from exposure to sun and other environmental factors.
Orientation	The orientation the marked side of the object is facing in respect to the direction of lynx travel	Towards, away, or parallel to the direction of departure	Detectability for lynx is higher for the sides of the objects that are parallel to their direction of movement, while accessibility for the sender is easier on sides parallel or towards direction of departure from the object.
Moss[a]	Presence of moss	With or without moss	Presence of moss increases the surface of the object, captures more urine, and could prolong longevity of the scent.
Tilt[a]	Tilt of the rock	Vertical, over-hanging, sloping backwards	Over-hanging rocks and vertical rocks better shelter scent from precipitation and are more accessible to mark and receive signal from close distances because lynx can step closer to the rock face.

[a] For rocks only

Table 2 Predictions and results of the scent-marking objects and their characteristics selected or used by the Eurasian lynx in the Dinaric Mountains, Slovenia, according to the three hypotheses separating persistence, detection, and accessibility (see Table 1 for description of the variables and reasoning behind the predictions). Selected characteristics are given among the results unless stated otherwise. For direction and orientation, we assumed that use reflects selection, given that most objects were possible to mark from several sides

Variable	Predictions according to the three hypotheses:			Results
	Persistence	Detection	Accessibility	
Object type	Vegetation	Object types with lower availability	Use according to the availability	Juvenile conifers
Height	–	Larger objects	> 0.5 m	0.5–1.0 m
Slope	–	Flat	Flat	Downwards facing rocks avoided
Road curvature	–	Straight road or inner curve	Straight road or inner curve	Straight road
Direction	NW, N, NE	–	–	SW, E, W
Orientation	–	Parallel	Parallel or away	Parallel
Moss	With	–	–	With[a]
Tilt	Over-hanging or vertical	–	Over-hanging or vertical	Sloping rocks avoided

[a] Most frequent use, but not confirmed selection in respect to availability

at 1796 m. The climate is a mix of influences from the Alps, the Mediterranean Sea, and the Pannonia Basin with average annual temperature of 7 °C, ranging from an average monthly maximum of 18 °C to an average monthly minimum of − 2 °C, and average annual precipitation of 1700 mm. The area is covered with mixed temperate forests intermixed with agricultural fields and small settlements. The limestone and dolomite geology of the area results in a rugged karstic relief and abundant karstic structures, such as cliffs, dolines, caves, and rock shelters. Lynx in Slovenia (currently estimated to 10–20 adult animals) are part of the Dinaric lynx population, one of the most threatened populations in Europe (Krofel and Jerina 2016).

Field methods

We used intensive snow tracking to document scent marking in Eurasian lynx. After a fresh snowfall that had continuous ground coverage, we searched for a fresh lynx trail and then followed it while documenting the location of each event of urine spraying, cheek rubbing, and claw marking. We used a handheld GPS to record the course and length of the lynx path and the coordinates for each occurrence of scent marking. When urine marking, lynx typically make a short detour from their direction of travel and turn their hindquarters towards visually conspicuous objects in order to spray urine, which creates easily recognizable track pattern in the snow (Vogt et al. 2016; Krofel et al. 2017). We used this movement pattern in combination with the visual or olfactory detection of urine to confirm each urine-marking event and locate the exact location of the scent mark. We also occasionally noted cheek rubbing and claw marking by inspecting objects approached by lynx for hair and/or claw marks. We noted the sex of the lynx when possible through genetic analyses from samples on the trail (Sindičić et al. 2013), the tracking of radio-collared individuals of known sex (Krofel et al. 2013), or the presence of kittens for females. Because it was not possible to always identify the lynx, we could not determine the exact number of different individuals sampled, and the same individuals were likely tracked multiple times during the study period. We assumed that a track belonged to the same individual if it occurred in the same area (taking into account lynx home range size), same time period (<7 years apart), and was of the same sex (when information of sex was available). We also took into account known life histories of some individuals (e.g., detected mortalities). The minimum number of different individuals sampled was eight.

We focused predominantly on urine spraying because we found cheek rubbing difficult to detect and Eurasian lynx generally do not use scrapes or feces for marking (Breitenmoser and Breitenmoser-Würsten 2008). When urine spraying occurred, we documented the type of the object used for marking (rock, juvenile conifer, tree stump, tree trunk, other vegetation, snow heap, human object, or other) and the height of the object. We also documented four variables of the microlocation on the object that was marked: curvature of the road (inner or outer side of the road curve, or straight road), cardinal/intercardinal direction of the side of the object marked, and orientation of the marked side of the object in respect to the travel path and slope of the surrounding landscape (see Table 1 for details). In our last years of monitoring (the winters of 2015–2016 and 2016–2017) when urine spraying occurred on rocks, we also noted whether the rock was covered with moss or not and the tilt of the rock.

On a subsample of lynx tracks on the forest roads (5 tracks, 12,381 m in total), we recorded data on the objects available for scent marking to compare the availability and use of objects for urine spraying. When walking on the forest roads, lynx almost exclusively marked the objects located on the sides of the road and did not leave the roads. Therefore, when sampling for availability of objects, we only sampled objects present on the side of roads. For each 10-m road section ($n = 1238$), we marked which potential marking objects were available along the edge of the road and noted which objects were marked by the lynx ($n = 106$). We used 10-m sections as our sample because we found that lynx would frequently mark at 20-m intervals on roads.

It was not possible to record the data blind because our study involved focal wild animals in the field.

Statistical analyses

We used program R version 3.3.1 (R Core Team 2016) and the *nlme* package (Pinheiro et al. 2016) for all of our statistical analyses, and in each analysis, we considered $P \leq 0.05$ to be statistically significant. We first calculated summary statistics for our data and then tested our series of predictions.

For all forthcoming analyses, we used generalized linear mixed models (GLMMs) using a Gaussian error distribution. In each model, the individual ID with the transect ID nested within it was included as a random effect, and because the transects were not of equal length, we used the log transformation of the transect length as an offset.

To determine if lynx marked certain types of objects more often than others when spraying urine, we used the percentage of each object type (human object, juvenile conifers, other vegetation, snow heap, rocks, tree stump, tree trunk) per transect as our independent variable. First, the model was checked with snow heaps (the least used object type) as a control. Then, the model was repeated with rocks, juvenile conifers, and tree stumps, which occurred most frequently as the control type.

To determine if lynx marked objects with certain characteristics more often than others when spraying urine, we used the percentage of the characteristic type used on each transect as the independent variable in the GLMMs. We tested each characteristic we recorded (Table 1), first overall for all objects, then for each object type. For rocks, we also tested for lynx use of rocks with or without moss and among different tilts of rocks.

To determine if lynx selected for certain types of objects and characteristics (i.e., used more often than available) when spraying urine, we compared the percentage of object type or characteristic used per transect to the percentage of objects or characteristics available per the same transect for the object types for which we had enough samples (rocks, juvenile conifers, other vegetation, and tree stumps) in the GLMMs. Therefore, the number of object types for our selection analyses was lower than in our use analyses. The analysis was done for every object type separately; the selection of characteristics was tested per characteristic per object type and all object types together.

Results

Overview

We followed 17 Eurasian lynx tracks ($n_{\text{male}} = 11$, $n_{\text{female}} = 4$, $n_{\text{unknown}} = 2$) during six winters over a span of 13 years ($n_{04\text{–}05} = 2$, $n_{06\text{–}07} = 5$, $n_{07\text{–}08} = 3$, $n_{14\text{–}15} = 1$, $n_{15\text{–}16} = 5$, $n_{16\text{–}17} = 1$) for a total of 91 km. On five occasions, we were able to follow the track across multiple days. We documented urine marking (97.9%) more frequently than cheek rubbing (1.9%) or claw marking (0.2%) ($n = 620$).

Types of objects sprayed with urine

Eurasian lynx sprayed urine significantly more often on rocks ($t = 7.62$, $P < 0.0001$), juvenile conifers ($t = 5.32$, $P < 0.0001$), and tree stumps ($t = 2.90$, $P = 0.0047$) than other types of objects (Fig. 1). Rocks were used significantly more than all other objects, and juvenile conifers were used significantly more than all objects other than rocks. Tree stumps were used significantly more often than snow mounds, tree trunks, and human objects.

Characteristics of objects sprayed with urine

In our series of 27 analyses, 25 of the variables exhibited a significant pattern (Table 3). Among all objects, characteristics that were used most include those that were 0.5–1 m in height, facing up slope, on straight roads, oriented towards

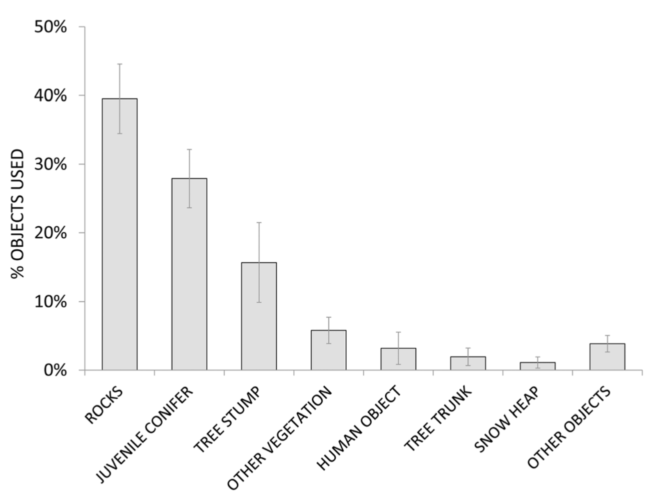

Fig. 1 Types of objects used by Eurasian lynx for scent marking with urine spraying in the Dinaric Mountains, Slovenia ($n = 607$). Error bars represent the standard error

Table 3 The characteristics of objects that Eurasian lynx sprayed with urine, reported for all objects and the four most frequently used object types. We report the variable name (see Table 1 for description of the variables) and the results as a *t* value, *P* value, the characteristic that was used most often, and the percent of times it was used compared to other characteristics used in the given object type

Variable	*t*	*P*	Characteristic	Use
All objects				
Height	3.39	0.0014	0.5–1 m	41.7%
Slope	4.88	< 0.0001	Up	57.9%
Road curvature	9.53	< 0.0001	Straight	69.1%
Direction	2.60	0.0104	Southwest	20.5%
Orientation	5.94	< 0.0001	Parallel	64.1%
Rocks				
Height	6.95	< 0.0001	0.5–1 m	57.4%
Slope	5.14	< 0.0001	Up	63.2%
Road curvature	6.38	< 0.0001	Straight	63.6%
Direction	2.36	0.0204	East	21.4%
Orientation	4.61	0.0001	Parallel	66.1%
Moss	4.56	0.0026	Moss	75.4%
Tilt	5.02	0.0002	Vertical	71.8%
Juvenile conifers				
Height	2.64	0.0119	1–2 m	36.2%
Slope	4.92	< 0.0001	Up	67.8%
Road curvature	5.89	< 0.0002	Straight	71.0%
Direction	2.32	0.0227	West	24.1%
Orientation	5.76	< 0.0001	Parallel	67.1%
Tree stumps				
Height	3.64	0.0009	0.5–1 m	40.9%
Slope	–	–	–	–
Road curvature	4.06	0.0006	Straight	65.0%
Direction	2.6	0.0112	Southwest	26.9%
Orientation	3.02	0.0068	Parallel	49.2%
Other vegetation				
Height	–	–	–	–
Slope	6.86	< 0.0001	Up	88.3%
Road curvature	2.80	0.0019	Straight	61.7%
Direction	2.93	0.0049	West	36.0%
Orientation	4.43	0.0004	Parallel	74.1%

southwest, and parallel to direction of lynx travel (Table 3). Among objects of different types, these patterns held true except for direction in many cases, and juvenile conifers of 1–2 m being used most often (Table 3). Among rocks, objects with moss and vertical tilts were used most often (Table 3).

Objects selected (use versus availability)

When comparing the selection (use versus availability) of object types that were sprayed with urine (Fig. 2), we found that juvenile conifers were the only object selected significantly

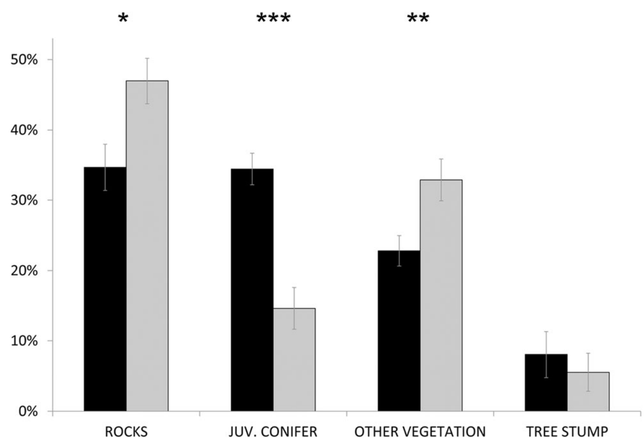

Fig. 2 The pattern in selection of objects sprayed with urine by Eurasian lynx on forest roads, shown as a comparison of the percent of objects used (black; $n = 106$) and their availability (gray; $n = 1417$). Asterisks indicate significant selection ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$), and error bars represent the standard error

more often than available ($t = 8.82$, $P = 0.0009$). In contrast, both rocks ($t = -3.72$, $P = 0.0205$) and other vegetation ($t = -4.63$, $P = 0.0098$) showed significant selection against being used.

Among the characteristics of all objects selected (Table 4), the height class 0.5–1 m was the only characteristic positively selected for ($t = 5.50$, $P = 0.0053$), while the height class > 2 m was selected against ($t = -2.98$, $P = 0.0408$). Among rocks, those with a height of 0.5 to 1 m were selected for ($t = 2.89$, $P = 0.0446$); while rocks with a height of > 2 m ($t = -3.07$, $P = 0.0371$), those facing downslope ($t = -3.00$, $P = 0.0400$), and those with a sloping tilt were selected against ($t = -4.76$, $P = 0.0089$) (Table 4). Among juvenile conifers, those on

Table 4 The selection of objects that Eurasian lynx sprayed with urine, as measured by the selection of characteristics compared to their availability. We report the variable name (see Table 1 for description of the variables) and the results as a t-value and *P*-value, followed by the characteristic with the highest selection (shown as a percent increased or decreased from expected use based on availability)

Variable	Characteristic	*t*	*P*	Selection
All objects				
Height	0.5 to 1 m	5.50	0.0053	12.2%
	> 2 m	− 2.98	0.0408	− 8.2%
Rocks				
Height	0.5–1 m	2.89	0.0446	40.1%
	> 2 m	− 3.07	0.0371	− 13.5%
Slope	Downslope	− 3.00	0.0400	− 2.8%
Tilt	Sloping	− 4.76	0.0089	− 19.7%
Juvenile conifers				
Road curvature	Straight	3.49	0.0252	13.5%
Other vegetation				
Height	1.0 to 2.0	− 3.42	0.0268	− 29.9%
	> 2 m	− 2.90	0.0439	− 15.0%

straight curvatures of roads were selected for (t = 3.49, P = 0.0252). Among other vegetation, those with height 1–2 m ($t = -3.42$, $P = 0.0268$) and > 2 m ($t = -2.90$, $P = 0.0439$) were selected against.

Discussion

The efficiency of scent marking, by creating marks with a high probability of detection by conspecifics due to their conspicuousness and persistence, is likely an important aspect of the selection of objects scent marked by animals, including solitary felids. Our analyses found general support for all three of our proposed hypotheses (Table 2). Lynx selected for objects that are expected to better retain smell (juvenile conifers) and avoided sloping rocks which are more exposed to precipitation ("persistence hypothesis"). Lynx also selected for objects of similar size as lynx, objects on straight road sections, and most often marked sides parallel to their travel routes and vertical rocks covered with moss. According to our predictions (Table 1), such marking placement promotes detectability of the messages ("detection hypothesis") and/or reduces the energy expenditure needed for marking ("accessibility hypothesis"). Our study thus provides insight into the adaptive significance of scent-marking behavior in the Eurasian lynx and possible mechanisms behind the selection of marking objects to increase the effectiveness of scent marking.

We found that Eurasian lynx most often sprayed urine on rocks, followed by juvenile conifers (Fig. 1), confirming observations from Switzerland where lynx also most often marked these objects (Vogt et al. 2016). However, by comparing the use of objects with their availability (Fig. 2), we showed that lynx actually selected only for juvenile conifers, while they selected against rocks. This could be explained by our "persistence hypothesis," as wildcats also showed preferential selection of conifer species (in that case *Juniperus communis*) (Ruiz-Olmo et al. 2013), which may be connected with the chemicals within the conifer slowing the release of volatile organic compounds in the urine. Our observations on object selection also correspond to scent marking by other carnivores, such as gray wolf (*Canis lupus*) (Barja 2003), red fox (*Vulpes vulpes*) (Miguel et al. 2009), and giant panda (*Ailuropoda melanoleuca*) (Nie et al. 2012). In addition, the shape and the larger surface-to-volume ratio of conifers compared to rocks likely better retain scent as it increases the adsorption of chemicals in urine (more urine staying on the surface instead of falling to the ground, which frequently occurs in urine spraying by lynx on smooth surfaces; pers. observation, see also video in supplementary data of Krofel et al. 2017) and better protects it from the elements (Alberts 1992; Nie et al. 2012). Prolonged persistence of scent marks on juvenile conifers would allow conspecifics to be able to receive chemical message for longer periods, which would decrease the need to frequently refresh the scent marks, therefore increasing the efficiency of scent marking by lynx.

The frequent use but not selection for rocks as scent-marking sites could also be explained by our "detection hypothesis." Given the large relative availability of rocks in our study area, this may make rocks that are lacking any other distinction less conspicuous and thus less attractive for scent marking. Piñeiro and Barja (2012) found that wildcats preferentially selected for more visually conspicuous objects, which likely increased the probability of detection for scent marks, and similar studies have shown that detection appears to be also important for other felids (Bothma and Le Riche 1995; Ruiz-Olmo et al. 2013; Allen et al. 2014) and other carnivores (Barja 2009; Miguel et al. 2009; Nie et al. 2012).

While we observed avoidance of rocks more exposed to precipitation according to the tilt of the marked face, there was no clear selection for northward-facing faces. This contrasts with observations of marking behavior of snow leopards (Ahlborn and Jackson 1986; Jackson 1996) and may be because the lynx habitats in Dinaric Mountains are less exposed to weather than the snow leopard range in the Himalayas, or because snow leopards frequently use scraping while scent marking (Jackson 1996) and shelter is therefore also needed to preserve the visual cues of the scrape (e.g., Allen et al. 2014).

When we analyzed characteristics of sites used for marking, we observed that lynx most often sprayed urine on rocks and juvenile conifers, the side of the object facing up the slope, objects that were 0.5–1 m high and located on straight road sections, and among rocks those covered with moss and with a vertical face. When taking into account the availability, we noted that lynx also selected for objects 0.5–1 m high and objects on straight road sections, but avoided rocks, objects on downward slopes and sloping sides of the rocks. Although there was some overlap in use and selection, this suggests that focusing research only on object use oversimplifies scent marking, stressing the importance of measuring object availability and thus selection of objects when conducting scent-marking behavior studies.

Our use of snow tracking informs our understanding of scent marking by Eurasian lynx and complements the previous studies that have been conducted with this (Vogt et al. 2016; Krofel et al. 2017) and other methods (e.g., Schmidt and Kowalczyk 2006; Vogt et al. 2014). One limitation of the snow tracking method was our difficulty in documenting behaviors other than urine spraying, such as cheek rubbing, which camera trap studies have shown often occurs in conjunction with urine spraying (Vogt et al. 2014; LH and MK, unpublished data; Online Resources 1 and 2). Another limitation is that because our study focused on winter (to use snow tracking), our data is limited to this season, and selection may be different in summer when leaves on young deciduous trees and other objects are available. Our study also focused on lynx marking behavior in the wild and did not measure persistence and detectability of scent marks or accessibility of marking sites directly. Future studies using an experimental framework could help to determine more precisely how different objects and variables affect the persistence of felid scent marks (e.g., comparison of scent persistence among plants, rocks and other objects, and among different aspects and tilt of the marked side of the object), how this affects the selection of objects for scent marking by mammals and efficiency of scent marking, and whether these characteristics increase investigation by conspecifics.

We found that lynx used and selected objects and microlocations for urine spraying in a way that likely contributed towards prolonging longevity of the scent message, increasing detectability of the chemical message by conspecifics, and promoting energy-efficient marking behavior. The efficiency and success of scent marking is generally difficult to study in the wild but has important implications for the fitness of individuals and populations. Our study also highlights the trade-offs faced by the lynx in object selection, as the preferred marking objects are often not readily available (juvenile conifers were available at only 17% of road sections). Lynx therefore need to use suboptimal marking objects to maintain the high scent-marking frequency throughout their territory that was reported for this species and is likely required for effective intraspecific communication (mean scent-marking rate 7.1 urine sprays/km; Krofel et al. 2017). Understanding use and selection of marking objects also has implications beyond behavioral ecology, with applied aspects including designing effective research and population monitoring schemes. These often depend on the successful selection of sites for live captures, photo-trapping, and hair-snaring (Schmidt and Kowalczyk 2006; Heurich et al. 2012; Krofel et al. 2013; Zimmermann et al. 2013), which are further important for successful conservation and management of endangered populations of Eurasian lynx and other felids.

Acknowledgments This study was partly financed by the Slovenian Research Agency (grant no. P4-0059) and by the European Union through INTERREG IIIA Neighborhood Program Slovenia/Hungary/Croatia 2004–2006 (project "DinaRis"). We are grateful to P. Apps, U. Fležar, L. Garamszegi, J. Javornik, A. Žagar, and an anonymous reviewer for reviewing drafts of the manuscript and providing several useful suggestions that importantly improved the manuscript.

Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed, and the work conforms to the legal requirements of the country in which it was carried out.

Conflict of interest The authors declare that they have no conflict of interest. All sources of funding are acknowledged, and the authors do not expect any direct financial benefits that could result from this publication.

Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

References

Ahlborn GG, Jackson RM (1986) Marking in free-ranging snow leopards in west Nepal: a preliminary assessment. In: Freeman H (ed) Proceedings of the 5th International Snow Leopard Symposium. International Snow Leopard Trust and Wildlife Institute of India, Seattle, Washington, pp 25–49

Alberts AC (1992) Constraints on the design of chemical communication systems in terrestrial vertebrates. Am Nat 139:62–89

Allen ML, Wallace CF, Wilmers CC (2015) Patterns in bobcat (*Lynx rufus*) scent marking and communication behaviors. J Ethol 33:9–14

Allen ML, Wittmer HU, Setiawan E, Jaffe S, Marshall AJ (2016a) Scent marking in Sunda clouded leopards (*Neofelis diardi*): novel observations close a key gap in understanding felid communication behaviours. Sci Rep 6:35433

Allen ML, Wittmer HU, Wilmers CC (2014) Puma communication behaviors: understanding functional use and variation by sex and age. Behaviour 151:819–840

Allen ML, Yovovich V, Wilmers CC (2016b) Evaluating the responses of a territorial solitary carnivore to potential mates and competitors. Sci Rep 6:27257

Bailey TN (1974) Social organization in a bobcat population. J Wildlife Manage 38:435–446

Barja I (2003) Marking patterns with faeces in the Iberian wolf. Etología 11:1–7

Barja I (2009) Decision making in plant selection during the faecal-marking behaviour of wild wolves. Anim Behav 77:489–493

Bothma JDP, le Riche EAN (1995) Evidence of the use of rubbing, scent-marking and scratching-posts by Kalahari leopards. J Arid Environ 29:511–517

Breitenmoser U, Breitenmoser-Würsten C (2008) Der Luchs: Ein Grossraubtier in der Kulturlandschaft. Salm Verlag, Wohlen/Bern, CH

Ghoddousi A, Hamidi AK, Ghadirian T, Ashayeri D, Hamzehpour M, Moshiri H, Zohrabi H, Julayi L (2008) Territorial marking by the Persian leopard (*Panthera pardus saxicolor* Pocock, 1927) in Bamu National Park, Iran. Zool Middle East 44:101–103

Gosling LM (1990) Scent marking by resource holders: alternative mechanisms for advertising the costs of competition. In: Macdonald DW, Müller-Schwarze D, Natynczuk SE (eds) Chemical signals in vertebrates, vol 5. Oxford University Press, Oxford, pp 315–328

Gosling LM, Roberts SC (2001) Scent-marking by male mammals: cheat-proof signals to competitors and mates. Adv Stud Behav 30: 169–217

Heurich M, Müller J, Burg M (2012) Comparison of the effectivity of different snare types for collecting and retaining hair from Eurasian lynx (*Lynx lynx*). Eur J Wildlife Res 58:579–587

Jackson RM (1996) Home range, movements and habitat use of snow leopard (*Uncia uncia*) in Nepal. University of London, PhD Dissertation

Kaczensky P, Chapron G, Von Arx M, Huber D, Andrén H, Linnell J (eds) (2013) Status, management and distribution of large carnivores—bear, lynx, wolf and wolverine—in Europe, part 1. IUCN/SSC Large Carnivore Initiative for Europe, Rome, Italy

Krofel M, Hočevar L, Allen ML (2017) Does human infrastructure shape scent marking in a solitary felid? Mamm Biol 87:36–39

Krofel M, Jerina K (2016) Mind the cat: conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. Biol Conserv 197:40–46

Krofel M, Skrbinšek T, Kos I (2013) Use of GPS location clusters analysis to study predation, feeding, and maternal behavior of the Eurasian lynx. Ecol Res 28:103–116

Kvam T (1990) Ovulation rates in European lynx, *Lynx lynx* (L.), from Norway. Mamm Biol 55:315–320

Linnell JD, Andersen R, Kvam T, Andrén H, Liberg O, Odden J, Moa PF (2001) Home range size and choice of management strategy for lynx in Scandinavia. Environ Manag 27:869–879

Mattisson J, Segerström P, Persson J, Aronsson M, Rauset GR, Samelius G, Andrén H (2013) Lethal male–male interactions in Eurasian lynx. Mamm Biol 78:304–308

Mellen JD (1993) A comparative analysis of scent–marking, social and reproductive behavior in 20 species of small cats. Am Zool 33:151–166

Miguel FJ, Valencia A, Arroyo M, Monclús R (2009) Spatial distribution of scent marks in the red fox (*Vulpes vulpes* L.): do red foxes select certain plants as signal posts? Pol J Ecol 57:605–609

Nie Y, Swaisgood RR, Zhang Z, Hu Y, Ma Y, Wei F (2012) Giant panda scent-marking strategies in the wild: role of season, sex and marking surface. Anim Behav 84:39–44

Piñeiro A, Barja I (2012) The plant physical features selected by wildcats as signal posts: an economic approach to fecal marking. Naturwissenschaften 99:801–809

Pinheiro J, Bates D, DebRoy S, Sarkar D (2016) nlme: linear and nonlinear mixed effects models. R package version 3:1–128 http://CRAN.R-project.org/package=nlme

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna http://www.R-project.org

Ruiz-Olmo J, Such-Sanz A, Piñol C (2013) Substrate selection for urine spraying in captive wildcats. J Zool 290:143–150

Schmidt K, Jedrzejewski W, Okarma H (1997) Spatial organization and social relations in the Eurasian lynx population in Bialowieza Primeval Forest, Poland. Acta Theriol 42:289–312

Schmidt K, Kowalczyk R (2006) Using scent-marking stations to collect hair samples to monitor Eurasian lynx populations. Wildlife Soc B 34:462–466

Sindičić M, Gomerčić T, Polanc P, Krofel M, Slijepčević V, Gembarovski N, Đurčević M, Huber Đ (2013) Kinship analysis of Dinaric lynx (*Lynx lynx*) population. Šumarski List 137:43–49

Smith JLD, McDougal C, Miquelle D (1989) Scent marking in free-ranging tigers, *Panthera tigris*. Anim Behav 37:1–10

Soler L, Lucherini M, Manfredi C, Ciuccio M, Casanave EB (2009) Characteristics of defecation sites of the Geoffroy's cat *Leopardus geoffroyi*. Mastozoologia Neotropica 16:485–489

Steiger S, Schmitt T, Schaefer HM (2011) The origin and dynamic evolution of chemical information transfer. Proc R Soc Lond B 278:970–979

Vogt K, Hofer E, Ryser A, Kölliker M, Breitenmoser U (2016) Is there a trade-off between scent marking and hunting behaviour in a stalking predator, the Eurasian lynx, *Lynx lynx*? Anim Behav 117:59–68

Vogt K, Zimmerman F, Kölliker M, Breitenmoser U (2014) Scent marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. Behav Process 106:98–106

Zimmermann F, Breitenmoser-Würsten C, Molinari-Jobin A, Breitenmoser U (2013) Optimizing the size of the area surveyed for monitoring a Eurasian lynx (*Lynx lynx*) population in the Swiss Alps by means of photographic capture–recapture. Integr Zool 8:232–243