



Short communication

Does human infrastructure shape scent marking in a solitary felid?

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ABSTRACT

Human development, such as construction of roads and trails, can affect several animal behaviour traits and is increasing worldwide. Despite the importance of scent marking for communication and social organization in many mammals, it is not clearly understood how scent marking is affected by human habitat modification. We used snow tracking data collected across six winters to study the effects of road infrastructure on the marking behaviour of Eurasian lynx (*Lynx lynx*) in a human-dominated landscape. We found that lynx marked at higher rates (11.2 urine sprays/km) on human routes (forest roads and logging trails) than when walking in natural habitat (5.8 sprays/km). This pattern was noted in both sexes, although males walked on human routes more frequently and scent marked more often than females. Compared to previous studies the mean marking rates we observed were the highest documented so far for wild felids. This may mainly be due to regular use of human routes (42% of all lynx movement) and the high scent marking rates found thereon. Human routes channelize lynx movement, and scent marking on these routes likely increases the probability of the chemical message being received by a conspecific; therefore human routes might enable more effective communication in territorial felids. Since most of the landscapes worldwide are covered by road networks and various human objects, the marking behaviour of wild mammals may be profoundly changed due to human-caused habitat modifications.

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Human infrastructure, such as roads and trails, is an increasingly widespread feature of most landscapes worldwide and can produce strong effects on animal communities (Trombulak and Frissell, 2000). These effects have been studied extensively for several animal behaviour traits, such as movement, home range size and distribution, selection of breeding sites, and feeding behaviour (e.g., Ciuti et al., 2012; Jerina, 2012; Sazatornil et al., 2016; Trombulak and Frissell, 2000). Wildlife is well known for having adverse reactions to human activity and scent (Bates et al., 2007; Wilmers et al., 2013; Tablado and Jenni, 2015), but studies focusing on determining how interspecific dynamics with humans, including linear infrastructure, activity and development, affect the scent-marking behaviour of wild animals is not well understood. There are synanthropic species that are sometimes attracted to developed areas regardless of scent, while results for species that tend to avoid humans are mixed. For example, puma (*Puma concolor*) scent-marking areas are located away from highly developed areas (Wilmers et al., 2013), while wolves (*Canis lupus*) regularly use roads, but evidence of selection of this human infrastructure for

scent marking has been equivocal (Peters and Mech, 1975; Zub et al., 2003).

Scent marking is an important aspect of communication and social organization for many mammals, and it is the predominant form of communication among most solitary felid species (Allen et al., 2016; Bailey, 1974; Smith et al., 1989; Vogt et al., 2014). Scent marking has many functions, including marking territories (Bailey, 1974; Smith et al., 1989; Gosling and Roberts, 2001) and advertising for mates (Vogt et al., 2014; Allen et al., 2015). Many species return to specific areas located in their home ranges to scent mark; these areas are conceptually referred to as 'chemical bulletin boards', as they are repeatedly used for indirect communication through scent marking (Ferkin and Pierce, 2007; Wolff et al., 2002). Individuals scent mark throughout their home ranges rather than just on borders, and are likely to select scent-marking locations that are conspicuous and have a high probability of success of being found by conspecifics (Ahlbom and Jackson, 1986; Bothma and le Riche, 1995; Gosling and Roberts, 2001; Piñeiro and Barja 2012).

To study the potential effects of road infrastructure on the scent-marking behaviour in solitary felids, we used snow tracking data collected across six winters to measure scent-marking rates of Eurasian lynx (*Lynx lynx*) in a human-dominated landscape. Eurasian lynx is a solitary apex carnivore that is found across Europe

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and Asia. As is typical for solitary felids, Eurasian lynx have large home ranges (Linnell et al., 2001), display intrasexual territoriality (Breitenmoser and Breitenmoser-Würsten, 2008; Schmidt et al., 1997), and scent mark (via urine spraying) throughout their home range (Vogt et al., 2014). In general lynx avoid areas of intensive human land use (Schadt et al., 2002), but regularly use forest roads and similar habitats with less human use (Vogt et al., 2016). Lynx sometimes scent mark more frequently in the periphery of their home ranges (Sæbø, 2007), and also when walking on or close to trails, roads, forest edges, ravines, and small watercourses throughout their home range (Vogt et al., 2016).

The objectives of our study were: (1) Determine whether lynx scent mark more frequently on human routes (gravel forest roads and dirt trails used for logging) compared to natural (off-road) habitats. We predicted higher marking frequency on human routes, because such linear infrastructure might channelize lynx movement and thus increase their utility as chemical bulletin boards. (2) Compare scent-marking rates between male and female lynx. According to previous studies (Sæbø, 2007; Allen, 2014) we predicted that males would exhibit higher overall rates of scent marking than females. (3) Perform a review of each study that reported marking rates of felids and compare them with results of our study.

Our study was conducted in the forest landscape of Dinaric Mountain Range in Slovenia (45°25'–45°47'N, 14°15'–14°50'E) where a dense network of regularly maintained human routes is established (primarily for logging activities) with an average density of approximately 2 km of forest roads and 10 km of dirt trails per km² of forest. Eurasian lynx in Slovenia are part of the Dinaric lynx population, one of the most threatened populations in Europe (Krofel and Jerina, 2016).

We used intensive snow tracking to document the scent-marking behaviours in Eurasian lynx. In total we followed 20 lynx tracks, but for our analyses used the 18 tracks which were >1 km in length ($n_{\text{male}} = 13$, $n_{\text{female}} = 3$, $n_{\text{unknown}} = 2$). These tracks were sampled during six winters in the course of twelve years from 2005 to 2017 ($n_{05-06} = 2$, $n_{06-07} = 5$, $n_{07-08} = 3$, $n_{14-15} = 1$, $n_{15-16} = 5$, $n_{16-17} = 2$); on five occasions we followed the track across multiple days. Most (94%) of the lynx tracks alternated several times between human routes and natural habitat. We noted the sex of the lynx when possible ($n = 16$) either through genetic analyses from non-invasive samples collected on the tracks ($n = 8$; scats, urine and hairs were used for genetic analysis performed on 20 polymorphic microsatellite loci and one sex-specific locus; for details see Polanc et al., 2012 and Sindičić et al., 2013), the tracking of radio-collared individual sexed during capture ($n = 1$; Krofel et al., 2013), or the characteristics of tracks ($n = 7$; size of the foot print and presence/absence of kitten tracks). Because it was not possible to always individually identify the lynx ($n = 10$), we could not determine the number of different individuals sampled and the same individuals were likely tracked multiple times during the study period.

We focused on urine spraying, because cheek rubbing was difficult to detect, Eurasian lynx generally do not use scrapes or faeces for marking (Breitenmoser and Breitenmoser-Würsten, 2008), and claw marking was infrequent ($n = 2$). When urine marking, lynx typically create an easily recognizable track pattern in the snow by making a short detour from their direction of travel and turning their hindquarters towards an object in order to spray urine upon it (Vogt et al., 2016; see also Appendix A). After new snowfall we located a fresh lynx track and followed it while documenting the location of each occurrence of urine spraying. We used a handheld GPS to record the course and length of the lynx path, and noted the coordinates for each instance of urine spraying. We also documented whether the sprayed urine occurred on a human route (i.e., gravel road or logging dirt trail) or in natural habitat (i.e. off-road).

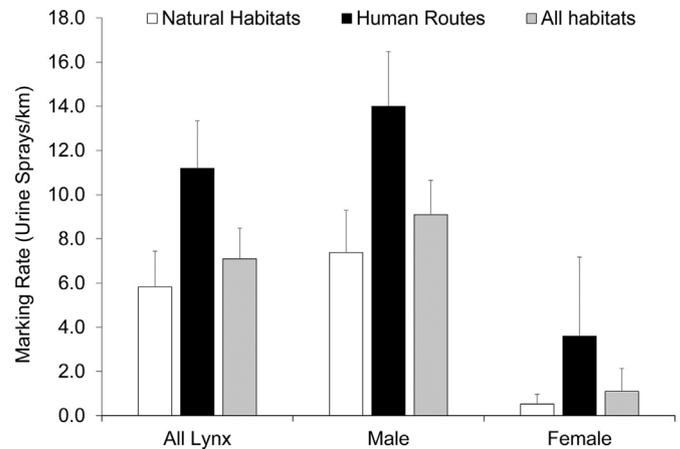


Fig. 1. The mean scent-marking rates of Eurasian lynx, split by all lynx, males, and females, and shown among natural habitats (white), human routes (black), and mean for all areas (grey), with error bars representing the standard error.

We used program R version 3.2.2 (R Core Team 2015) for all of our statistical analyses, and in each analysis we considered $p < 0.05$ to be statistically significant. We first calculated summary statistics for our data, calculated marking rates as number of urine sprays/km of lynx track, and then tested our predictions. We calculated scent-marking rates by dividing the number of recorded urine sprays by the length of lynx path for each track and separately for each sex and habitat type. We used non-parametric tests due to small sample sizes. We first used a Wilcoxon Signed Rank Test to determine whether lynx differ in their rate of urine spraying between human routes and natural habitats. Second, we used a Mann-Whitney U Test to determine whether male and female lynx differ in their rate of urine spraying. Third, we used Wilcoxon Signed Rank Tests to determine whether either male or female lynx differ in their rate of urine spraying between human routes and natural habitats.

We followed the 18 Eurasian lynx tracks a total of 94.1 km and recorded 619 urine marking events. Lynx walked 54.2 km in natural habitat (58%), and 39.9 km on human routes (42%; 30.2 km on gravel forest roads and 9.7 km on logging dirt trails). We followed male lynx for a total of 61.6 km, with 27.1 km walking in natural habitat (46%) and 33.4 km on human routes (54%). We followed female lynx a total of 27.6 km, with 23.3 km walking in natural habitat (85%) and 4.2 km on human routes (15%).

Overall, we documented a mean urine marking rate of 7.1 (± 1.4 SE, range: 0.0–20.0) sprays/km. We found that lynx marked with higher rate on human routes (11.2 sprays/km, ± 2.1 SE) than when walking in natural habitat (5.8 sprays/km, ± 1.6 SE) ($V = 116$, $p = 0.014$) (Fig. 1). We also found that males sprayed urine significantly more frequently (9.1 sprays/km, ± 1.6 SE) than females (1.1 sprays/km, ± 1.0 SE) ($W = 1$, $p = 0.007$) (Fig. 1). Both sexes exhibited an increased frequency of scent marking on human routes (male = 14.0 sprays/km, ± 2.5 SE; female = 3.6 sprays/km, ± 3.6 SE) when compared to natural habitats (male = 7.4 sprays/km, ± 1.9 SE; female = 0.5 sprays/km, ± 0.5 SE) (Fig. 1), but only males were significantly different between types ($V = 77$, $p = 0.027$).

Compared to previous studies of scent-marking rates of felids, the overall mean urine spraying rates for Eurasian lynx in Slovenia were the highest marking rates reported so far, with the exception of studies that only reported the maximum rates found (Table 1). The scent-marking rates we recorded in natural habitats were similar to previous studies of lynx and other felids, but marking rates we recorded on human routes were over 3-times as high as other documented marking rates, and resulted in our overall lynx marking rates being twice as high as any other previous study. Our review of reported scent-marking rates for felids also highlights the need

Table 1
The scent-marking rates (scent marks/km) for felids noted in the scientific literature. When possible, for each study we provide the rates for all individuals, males, and females, the rates for each type of scent marking, and notes on where and when they occurred and the samples sizes.

Species	Rate (scent marks/km)		Female	Type of Marking	Subset	Season	Sample size (number of animals/total track length)	Source
	All	Male						
<i>Lynx lynx</i>	7.10	9.09	1.10	Urine Spraying	All	Winter	n.a./94 km	This Study
<i>Lynx lynx</i>	5.83	7.38	0.52	Urine Spraying	Natural Habitats	Winter	n.a./94 km	This Study
<i>Lynx lynx</i>	11.19	14.00	3.59	Urine Spraying	Human Routes	Winter	n.a./94 km	This Study
<i>Lynx lynx</i>	1.35	1.81	0.94	Urine Spraying	All	Winter	n.a./ca. 800 km	Sæbø (2007)
<i>Lynx lynx</i>	3.40	n.a.	n.a.	Urine Spraying	All	Winter	15/185 km	Vogt et al. (2016)
<i>Lynx lynx</i>	1.03	n.a.	n.a.	Urine Spraying	All	Winter	2/105 km	Hücht-Ciorga (1988)
<i>Lynx lynx</i>	0.02	n.a.	n.a.	Claw Marking	All	Winter	n.a./94 km	This Study
<i>Lynx canadensis</i>	10.6–11.8 ^a	n.a.	n.a.	Urine Spraying	All	Winter	n.a./n.a.	Saunders, 1963
<i>Lynx rufus</i>	3.00 ¹	n.a.	n.a.	Urine Spraying	All	n.a.	2/2 km	Bailey (1974)
<i>Panthera pardus</i>	0.12	0.13	0.09	Claw Marking	All	All year	n.a./2665 km	Bothma and le Riche (1995)
<i>Panthera pardus</i>	0.08	0.10	0.01	Urine Spraying	All	All year	n.a./2665 km	Bothma and le Riche (1995)
<i>Panthera pardus</i>	0.06	0.07	0.04	Body Rubbing	All	All year	n.a./2665 km	Bothma and le Riche (1995)
<i>Panthera uncia</i>	n.a.	0.30 ¹	n.a.	Scraping	All	n.a.	2/10 km	Schaller (1977)
<i>Panthera tigris</i>	2.11	2.40	1.80	Urine Spraying	Animal trail	All year	2/303 km	Smith et al. (1989)
<i>Panthera leo</i>	n.a.	3.68 ²	n.a.	Urine Spraying	Road	n.a.	1/2 km	Schaller (1972)
<i>Felis nigripes</i>	n.a.	n.a.	64.6 ³	Urine Spraying	All	June/July	1/1 km	Molteno et al. (1998)

^a only maximum rates reported.

¹ only 2 observations.

² only 1 observation.

for future studies that focus on marking rates in different types of habitat and among types of scent marking other than urine spraying (Table 1).

Since many of the previous studies of lynx and of other felid species were conducted in regions with lower road density compared to our study area, we suggest that the intensity of human habitat modification could be a factor in anthropogenic perturbations of the scent-marking behaviour of solitary felids. At the same time, we assume that the low intensity of human use of this infrastructure plays an important role, as felids are known to avoid areas with frequent human presence (Schadt et al., 2002; Wilmers et al., 2013). Therefore the combination of a dense network of human infrastructure that has low human use might present the situation with pronounced effects on felid marking behaviour.

The high overall marking rates we observed are primarily due to male lynx, which more frequently walked on human routes and also scent marked more frequently than females. This difference among sexes is similar to other felids (Allen et al., 2015; Bothma and le Riche, 1995), and supports similar findings for Eurasian lynx where males are more frequent visitors to scent-marking sites, and also scent mark more frequently than females (Vogt et al., 2014, 2016). Human routes do not delineate the home range boundaries recorded in the study area (Krofel, 2012), and lynx are using human routes throughout their home ranges, likely for ease of movement and to patrol their territories. Therefore, the more frequent use of human routes by males would be expected given their larger home range size compared to females (Breitenmoser and Breitenmoser-Würsten, 2008; Linnell et al., 2001). Scent marking by lynx shows seasonal variation (Schmidt and Kowalczyk, 2006; Vogt et al., 2014, 2016), with a peak during the late winter breeding season and the least frequent marking in summer when mothers are denning and raising young (Vogt et al., 2014). Because this study was conducted during winter, some of our tracking days were likely to correspond with the breeding season and the higher scent-marking rates that occur for both sexes during this period could be a confounding factor when comparing with other studies.

Besides providing a means of easier and faster travel, the linear human infrastructure could also increase the efficiency of scent marking. A recent study from Switzerland showed that lynx scent mark more intensively when walking in a straight line (Vogt et al., 2014). In a landscape with rugged terrain, which is characteristic for most of the range of the Dinaric lynx population, the possibility of walking in a straight line is notably more likely on human routes than in natural habitat. Additionally, the frequent use of human routes channelizes movement, and may provide structure for 'chemical bulletin boards' used by the mammal populations throughout their home ranges (e.g., Ferkin and Pierce, 2007; Vogt et al., 2014; Wolff et al., 2002). Scent marking on human routes therefore likely increases the probability of a chemical message being received by a conspecific, and we suggest that human modification of the landscape may enable territorial felids to communicate more effectively. Given the fact that most of the landscapes in the modern world are now covered by road networks (Trombulak and Frissell, 2000) the scent-marking behaviour of species such as lynx that selectively use human routes for indirect communication may have been profoundly changed due to human-caused habitat modification.

Besides creating linear infrastructure, humans could also affect felid marking behaviour through the construction of cabins, fences, poles, and other conspicuous objects. Like many other carnivores, lynx often use conspicuous objects in their environment for scent marking, and human objects often stand out in natural habitats and likely serve as attractive objects for scent marking (for example see video file showing Eurasian lynx scent marking forest cabin in Appendix A). Indeed, a study in Poland revealed that human objects were the most frequently used objects by Eurasian lynx for scent

marking by cheek rubbing (Schmidt and Kowalczyk, 2006). Since such objects are often located along human routes, linear infrastructure likely promotes their use as marking objects.

Among solitary felids, scent marking is essential to territoriality (Bailey, 1974; Gosling and Roberts, 2001; Smith et al., 1989) and mate selection (Allen et al., 2015; Vogt et al., 2014). Our findings suggest that Eurasian lynx possibly adapted their scent-marking behaviour to human co-existence over the last thousands of years as human infrastructure has developed and increased across the Eurasian landscape. This highlights the need for more studies to better understand anthropogenic effects on scent marking of carnivores in human-dominated landscapes. Roads and other linear human infrastructure can have strong negative effects on carnivores, including collisions with vehicles, habitat fragmentation, limiting dispersal and gene flow, as well as increasing the access of people to remote areas which might increase legal and illegal hunting (see Trombulak and Frissell, 2000 for review). Our results suggest that human routes with low use by people might improve effectiveness of indirect communication in solitary felids. However, it remains to be seen whether this could have beneficial impacts on important traits at the population level, such as increased breeding success and stability of the social system, and whether these effects are large enough to counteract the negative effects of human routes and other development. Studies to determine scent-marking rates are labour-intensive, but can provide information on the function and mechanisms of scent marking, and we encourage future studies of this kind, especially of species and marking behaviours for which marking rates are poorly known.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2017.05.003>.

References

- Ahlbom, G.G., Jackson, R.M., 1986. Marking in free-ranging snow leopards in west Nepal: a preliminary assessment. *Proceedings of the 5th International Snow Leopard Symposium*, 25–49.
- Allen, M.L., Wittmer, H.U., Houghtaling, P., Smith, J., Elbroch, L.M., Wilmsers, C.C., 2015. The role of scent marking in mate selection by female pumas (*Puma concolor*). *PLoS One* 10, e0139087.
- Allen, M.L., Wittmer, H.U., Setiawan, E., Jaffe, S., Marshall, A.J., 2016. Scent marking in Sunda clouded leopards (*Neofelis diardi*): novel observations close a key gap in understanding felid communication behaviours. *Sci. Rep.* 6, 35433.
- Bailey, T.N., 1974. Social-organization in a bobcat population. *J. Wildlife Manage.* 38, 435–446.
- Bates, L.A., Sayialel, K.N., Njiraini, N.W., Moss, C.J., Poole, J.H., Byrne, R.W., 2007. Elephants classify human ethnic groups by odor and garment color. *Curr. Biol.* 17, 1938–1942.
- Bothma, J.D., le Riche, E.A.N., 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 and Bern.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS One* 7, e50611.
- Ferkin, M.H., Pierce, A.A., 2007. Perspectives on over-marking: is it good to be on top. *J. Ethol.* 25, 107–116.
- Gosling, L.M., Roberts, S.C., 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Adv. Study Behav.* 30, 169–217.
- Hücht-Ciorga, I., 1988. Studien zur Biologie des Luchses: Jagdverhalten, Beuteausnutzung, innerartliche Kommunikation und an den Spuren fassbare Körpermerkmale. Ferdinand Enke Verlag, Stuttgart.
- Jerina, K., 2012. Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. *J. Mammal.* 93, 1139–1148.
- 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., Skrbinišek, 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.
- Krofel, M., 2012. *Predation-Related Interspecific Interactions in Eurasian Lynx (Lynx lynx) in Northern Dinaric Mountains*. Doctorate Thesis. University of Ljubljana, Ljubljana.
- Linnell, J.D.C., Andersen, R., Kvam, T., Andren, H., Liberg, O., Odden, J., Moa, P.F., 2001. Home range size and choice of management strategy for lynx in Scandinavia. *Environ. Manage.* 27, 869–879.
- Molteno, A.J., Sliwa, A., Richardson, P.R.K., 1998. The role of scent marking in a free-ranging, female black-footed cat (*Felis nigripes*). *J. Zool.* 245, 35–41.
- Peters, R.P., Mech, L.D., 1975. Scent-marking in wolves. *Am. Sci.* 63, 628–637.
- Piñeiro, A., Barja, J., 2012. The plant physical features selected by wildcats as signal posts: an economic approach to fecal marking. *Naturwissenschaften* 99, 801–809.
- Polanc, P., Sindičič, M., Jelenčič, M., Gomerčič, T., Kos, I., Huber, Đ., 2012. Genotyping success of historical Eurasian lynx (*Lynx lynx* L.) samples. *Mol. Ecol. Resour.* 12, 293–298.
- R Core Team, 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Sæbø, H.S., 2007. Scent marking behaviour in the Eurasian lynx, *Lynx lynx*. Master thesis. Norwegian University of Life Sciences (Ås).
- Saunders, J.K., 1963. Movements and activities of the lynx in Newfoundland. *J. Wildl. Manage.* 27, 390–400.
- Sazatornil, V., Rodríguez, A., Klaczek, M., Ahmadi, M., Álvares, F., Arthur, S., Blanco, J.C., Borg, B.L., Cluff, D., Cortés, Y., García, E.J., Geffen, E., Habib, B., Iliopoulos, Y., Kaboli, M., Krofel, M., Llaneza, L., Marucco, F., Oakleaf, J.K., Person, D.K., Potočnik, H., Ražen, N., Rio-Maior, H., Sand, H., Unger, D., Wabakken, P., López-Bao, J.V., 2016. The role of human-related risk in breeding site selection by wolves. *Biol. Conserv.* 201, 103–110.
- Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Cerveny, J., Koubek, P., Huber, T., Stanisa, C., Trepl, L., 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *J. Appl. Ecol.* 39, 189–203.
- Schaller, G.B., 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. The University of Chicago Press, Chicago and London.
- Schaller, G.B., 1977. *Mountain Monarchs: Wild Sheep and Goats of the Himalaya*. The University of Chicago Press, Chicago and London.
- Schmidt, K., Kowalczyk, R., 2006. Using scent-marking stations to collect hair samples to monitor Eurasian lynx populations. *Wildl. Soc. B* 34, 462–466.
- Schmidt, K., Jedrzejewski, W., Okarma, H., 1997. Spatial organization and social relations in the Eurasian lynx population in Białowieża Primeval Forest, Poland. *Acta Theriol.* 42, 289–312.
- Sindičič, M., Gomerčič, T., Polanc, P., Krofel, M., Slijepčević, V., Gembarovski, N., Đurčević, M., Huber, Đ., 2013. Kinship analysis of dinaric lynx (*Lynx lynx*) population. *Sumar List* 137, 43–49.
- Smith, J.L.D., Mcdougal, C., Miquelle, D., 1989. Scent marking in free-ranging tigers, *Panthera tigris*. *Anim. Behav.* 37, 1–10.
- Tablado, Z., Jenni, L., 2015. Determinants of uncertainty in wildlife responses to human disturbance. *Biol. Rev.* (online), <http://dx.doi.org/10.1111/brv.12224>.
- Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv. Biol.* 14, 18–30.
- Vogt, K., Zimmermann, F., Kolliker, M., Breitenmoser, U., 2014. Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. *Behav. Process.* 106, 98–106.
- Vogt, K., Hofer, E., Ryser, A., Kolliker, 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.
- Wilmsers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V., Williams, T., 2013. Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS One* 8, e60590.
- Wolff, J.O., Mech, S.G., Thomas, S.A., 2002. Scent marking in female prairie voles: a test of alternative hypotheses. *Ethology* 108, 483–494.
- Zub, K., Theuerkauf, J., Jedrzejewski, W., Jedrzejewska, B., Schmidt, K., Kowalczyk, R., 2003. Wolf pack territory marking in the Białowieża primeval forest (Poland). *Behaviour* 140, 635–648.