UDK 630* 461
https://doi.org/10.31298/sl.145.5-6.6

Prethodno priopćenje – Preliminary communication
Šumarski list, 5–6 (2021): 269–278

STATE BORDER FENCES AS A THREAT TO HABITAT CONNECTIVITY: A CASE STUDY FROM SOUTH-EASTERN EUROPE

OGRADE NA DRŽAVNIM GRANICAMA KAO PRIJETNJA POVEZANOSTI STANIŠTA: STUDIJA SLUČAJA IZ JUGOISTOČNE EUROPE

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SUMMARY

The conservation value of transboundary management of wildlife populations in Europe, that marked end of the 20th and the beginning of the 21th century, has come under huge pressure since 2015 especially in the South-eastern Europe due to border fences construction in response to large influxes of refugees/migrants. The primary aim of this study was to present data on the direct impacts of the long fence on wildlife (e.g. fence-related mortality) across the Hungary–Croatia border. We collected data on fence-related animal mortality along 136 km of the fence in the first 28 months after its construction. In total, 64 ungulates (38 red deer, 23 roe deer, and three wild boar) were found entangled in or deceased due to the razor wire fence. In addition, we present direct (photographic) evidence of newly recorded behaviour of red deer, as they gather in huge herds attempting to cross the border fence between Hungary and Croatia. Short term effect of the border fence is reflected in direct animal mortality, and as obstruction to the movement and behaviour of animals. In the case that current fences will remain or continue to expand along the northern boundary of South-eastern Europe, it is likely that fragmented wildlife populations in the region will suffer from negative effects of genetic subdivision such as loss of alleles and reduced heterozygosity that can cause important long-term damage to their vitality.

KEY WORDS: Border fence, Wild ungulate mortality, Habitat fragmentation, Red deer, Roe deer, Wild boar, South-eastern Europe

INTRODUCTION
UVOD

The end of the 20th and the beginning of the 21st century were, in terms of biodiversity conservation, marked by the increased awareness of the large scale at which ecological processes occur and the realization that achieving collective goals would require international cooperation (Fonseca et al., 2014; Linnell et al., 2016a). This awareness was implemented in legislation accepted by the European Union, such as the

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Birds and Habitats Directives and Convention on Biological Diversity (Fleurke and Trouwborst, 2014), which resulted in the designation of the European Natura 2000 network. This is comprised of a network of ecologically important sites selected to ensure the long-term survival of Europe's most valuable and threatened species and habitats. Results of these actions are notable, with evidences of recovery of both large carnivore and herbivore populations (Apollonio et al., 2010; Chapron et al., 2014; Linnell et al., 2016b).

The South-eastern Europe is part of the Balkan Peninsula in Mediterranean basin, linking Central Europe with Asia Minor. It is one of the three European glacial refugia, and is a part of one of the world's 36 biodiversity hotspots (Zachos and Habel, 2011; Noss et al., 2015), with an area-adjusted mammal species richness significantly higher than in the rest of Europe (Kryštufek, 2004). However, the conservation value of transboundary management of wildlife populations in the South-eastern Europe has come under huge pressure since 2015 due to the border fence constructions in response to large influxes of refugees/migrants from Asia and Africa. In the wider region (Fig. 1), in the time when this study was done extensive fences existed between the state borders of Slovenia–Croatia (178 km), Hungary–Croatia (136 km), Hungary–Serbia (175 km), Greece–Turkey (182 km), North Macedonia–Greece (30 km), and Bulgaria–Turkey (233 km) respectively (Linnell et al., 2016b; Pokorny et al., 2017).

Fences that reduce movement over a range of spatial scales can be a threatening process for populations of large mammal species (Kowalczyk et al., 2012; Linnell et al., 2016a; 2016b; Pokorny et al., 2017). In the case of large mammals, such barriers can reduce the carrying capacity of habitats (Ben-Shahar, 1993; Forman et al., 2003) and threaten species by limiting access to resources, thereby leading to population decline (Olson et al., 2009; Ito et al., 2013; Olson, 2014). Fences that limit dispersal can alter gene flow, leading to genetic isolation of populations (Martinez et al., 2002; Epps et al., 2005; Daleszczyk and Bunevich, 2009), and compromise the ability of prey species to avoid predation (Davies-Mostert et al., 2013). Fencing also raises animal welfare concerns, as animals may become ensnared in the fence and die in agony (Harrington and Conover, 2006; Olson et al., 2009; Pokorny et al., 2017).

Border fences present a significant threat to wildlife due to their large continuous lengths, and the inability to mitigate their effect on wildlife populations without compromising their security (Linnell et al., 2016b). Several studies have investigated conservation issues associated with border fences: for example, earlier extinction is predicted for the ferruginous pygmy owl (*Glaucidium brasilianum*) population due to the United States–Mexico border fences (Doublet, 2011), gene flow in European bison (*Bison bonasus*) is impacted by the barrier between Belarus and Poland (Daleszczyk and Bunevich, 2009), and at the Mongolian–Chinese border, Mongolian wild asses (*Equus hemionus hemionus*) have restricted access to expansive plains of habitat (Kaczensky et al., 2011). Considering Croatia, Safner et al. (2019) did not detect any historical barrier effect of the river Kupa (which might act as a natural barrier along a part of Slovenia–Croatia border) on genetic structure of transboundary population of Northern chamois (*Rupicapra rupicapra*); however, as the state border along the river Kupa was fenced in 2015, which has caused important additional ungulate mortality (Pokorny et al., 2017), previous free transboundary gene flow may be seriously interrupted by the border fence.

At present, more investigation is required to identify threats of border fences to both animal mortality and population connectivity. As the Croatian border is in a large part fenced towards Hungary and Slovenia, and the existence of relevant databases on wildlife (particularly ungulates) mortality enables relevant insight into the issue, we used fences at the Hungary–Croatia border as a relevant case study of the influence of the border fencing on wildlife populations. However, as their construction is relatively recent (started in 2015), we emphasis the short-term impact, i.e. direct mortality of large mammals (ungulates) due to razor-wired fences, with predicting the possible long-term scenarios considering their barrier effect. In this paper, we present the first data on the direct effect of border fences constructed between Hungary and Croatia on wildlife populations.

MATERIALS AND METHODS
MATERIJALI I METODE

Study area – *Područje istraživanja*

Construction of the border fence between Hungary and Croatia began in September 2015 along approximately 136 km of the 355.5 km of the border (Fig. 1). This border fence is dual layered: towards Hungary a permanent 4 m high fence stands erect, whilst adjacent to this on the Croatian side is a razor-wired fence (Fig. 3A).

The fence along Hungary–Croatia border loosely follows the rivers Mura and Drava, in Pannonian region with elevations between 63 and 242 m above sea level. Land surrounding the border is largely agricultural, and forests are predominately composed of pedunculated oak (*Quercus robur*), different poplar (*Populus* sp.) and willow (*Salix* sp.) species, and narrow-leafed ash (*Fraxinus angustifolia*). Ungulates present in the area are red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), and wild boar (*Sus scrofa*). The Hungary–Croatia border fence is adjacent to the transboundary Regional park Mura–Drava protected area; nine Special Areas of Conservation

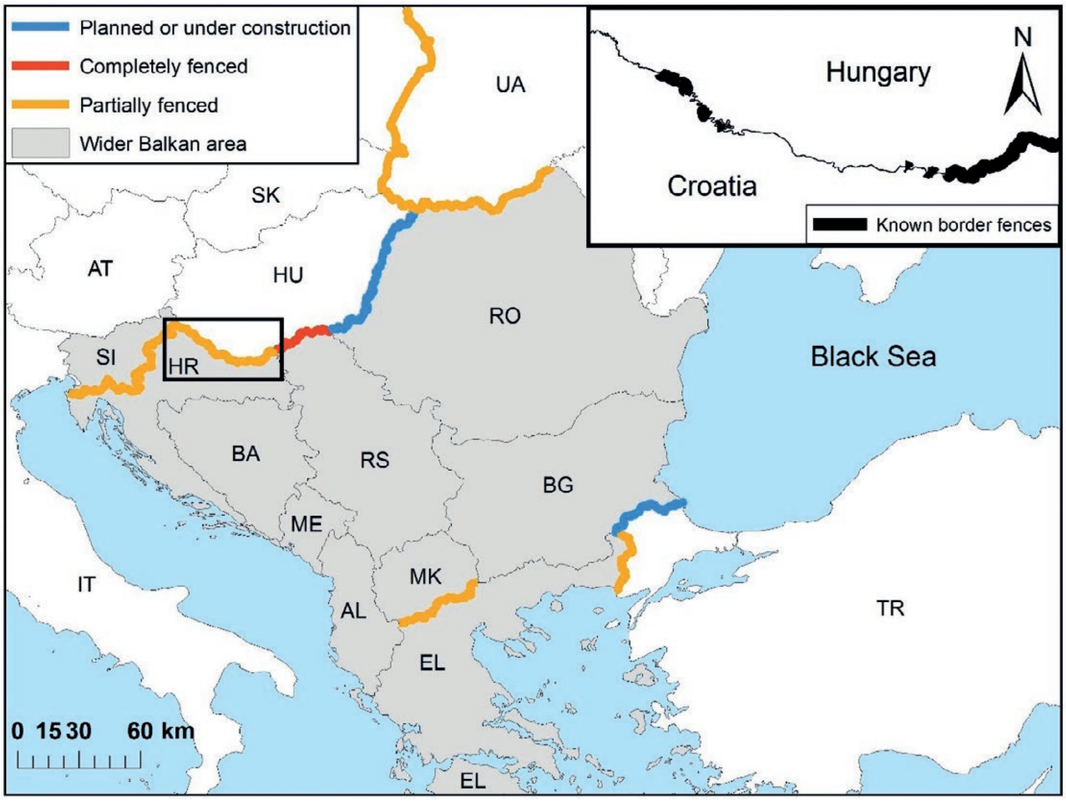

Figure 1. Map of existing and planned border fences in the South-eastern European region with detailed position of border fences at the Hungary-Croatia border (situation in 2017).

Slika 1. Karta postojećih i planiranih graničnih ograda na području jugoistočne Europe s detaljnim položajem graničnih ograda na granici između Mađarske i Hrvatske (stanje u 2017.).

(SAC) and four Special Protection Areas (SPA) of the Nature 2000 network are on Croatian side, whilst 15 SAC and two SPA are on the Hungarian side of the border.

Methods – *Metode rada*

Based on the Croatian hunting law (2018), all hunting organizations are required to record game animal mortality that occurs in their respective hunting grounds. This data, including data on fence-related mortality, was accessed from the official game management plans for the all 30 relevant hunting grounds that are located along the Hungary–Croatia border. However, to confirm available data and acquire additional information, we interviewed managers of these hunting grounds between September 2015 and December 2017.

The age of the dead animals was estimated by responsible hunting authorities in each hunting ground using macroscopic inspection of tooth eruption, replacement and patterns of tooth wear in mandibles (see for red deer: Lowe, 1967; Brown and Chapman, 1991; for roe deer: Aitken, 1975; Ratcliffe and Mayle, 1992; and for wild boar: Boitani and Mattei, 1992). All found animals were classified into three age groups as follows: juveniles (less than one-year-old), yearlings (between one and two years of age), and adults (older than two years), respectively.

RESULTS
REZULTATI

Out of 30 Croatian hunting grounds bordering Hungary, 13 had in the study period border fence within their area. Of these 13 hunting grounds, eight reported ungulate mortalities, whilst the remaining five recorded no mortalities. After the installation of fences at Hungary–Croatia border (in September 2015), 64 ungulates (38 red deer, 23 roe deer, and three wild boar) were found entangled in or deceased due to the razor-wired fence along the Croatian side of the border alone till the end of the study period, i.e. till December 2017 (Table 1; Supplementary Table S1). In addition, two large birds were also found dead in the fence: one whooper swan (*Cygnus cygnus*), and one white stork (*Ciconia ciconia*).

Overall, these figures equate to a mortality rate of 0.47 ungulates/km of fence in the 28-months period, made up of 0.28 red deer, 0.17 roe deer, and 0.02 wild boar, respectively.

The age structure of all fenced-killed ungulates found at the Hungary–Croatia border, regardless of the species, was as follows: six juveniles (fawns/calves/piglets), nine yearlings, and 48 adults; the age of one individual was undetermined (Supplementary Table S1). Age structure of red deer casualties found in the border fence indicates higher exposure

Table 1. Structure of ungulate mortality due to the Hungary–Croatia border fence (September 2015 – December 2017).
Tablica 1. Struktura papkara stradalih na graničnoj ogradi između Hrvatske i Mađarske (rujan 2015. – prosinac 2017.).

Species *Vrsta*	Sex *Spol*	Juveniles *Mladi*	Yearlings *Jednogodišnji*	Adults *Zreli*	**Total** ***Ukupno***
Red deer *Jelen obični*	**Total** ***Ukupno***	4	3	30	38*
	M / *M*	1	3	16	21*
	F / *Ž*	3	0	14	17
Roe deer *Srna obična*	**Total** ***Ukupno***	2	4	17	23
	M / *M*	1	1	5	7
	F / *Ž*	1	3	12	16
Wild boar *Divlja svinja*	**Total** ***Ukupno***	0	2	1	3
	M / *M*	0	0	1	1
	F / *Ž*	0	2	0	2

* For one individual, the age was not determined.
** Za jednu jedinku dob nije bila određena.*

of adults (>50%). Across all red deer mortalities in the Hungary–Croatia border fence, the sex ratio was in favour of males (21) over females (17). In the case of roe deer, seven male and 16 female mortalities were recorded (Table 1).

DISCUSSION
RASPRAVA

Overall ungulate mortality rate due to the Hungary–Croatia border fence (0.20 mortalities/km of fence per year) was 1.4-folds higher in a relative comparison (i.e., corrected for a time interval and the length of fences) with previously reported figures for Slovenia–Croatia border, where mortality of 0.12 ungulates per km of fence was registered in the 10-month period along 178 km of the border fence (Pokorny et al., 2017), corresponding to annual mortality of 0.14 individuals/km of fence. In the first 10 months after the construction, i.e. when the reported fence-related mortality at the Hungary–Croatia border was the highest (reaching 0.36 individuals/km of fence; see Fig. 2), ungulate mortality was even three-folds higher than at the Slovenia–Croatia border. Higher ungulate mortality rate in razor-wired fences along Hungary–Croatia border comparing to Slovenia–Croatia one corresponds well with the known extensive distribution and high abundances of red deer, roe deer, and wild boar in the entire transboundary area between Hungary and Croatia (Csányi and Lehoczki, 2010). However, also some other factors affecting spatial behaviour, i.e. increasing mobility of ungulates (particularly red deer) in this area, such as predominant plain open landscape, vicinity of several dispersed settlements, and frequent usage of dogs in drive hunts in the Hungary–Croatia transboundary zone could increase the fence-related mortality rate of ungulates in the study area. But it should be mentioned that our figures are comparable with other reported data on fence-related mortality, i.e. along roads in Colorado and Utah, USA, where average annual mortality of ungulates was estimated at 0.25 individuals/km of fence (Harrington and Conover, 2006).

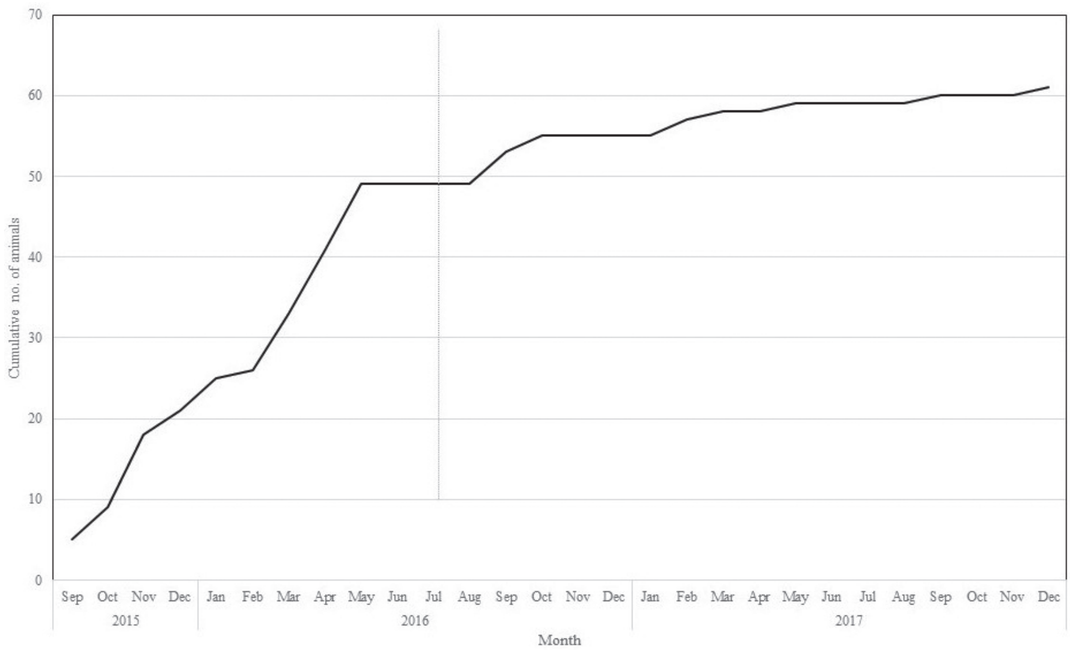

Figure 2. Cumulative monthly number of entangled animals found in the Hungary–Croatia border fence. Dotted line represents the end of the 10-month period since construction of the fence (enabling comparison with data for Slovenia–Croatia border fence; see Pokorny et al., 2017).
Slika 2. Kumulativni mjesečni broj zapletenih životinja pronađenih unutar ograde između Mađarske i Hrvatske. Točkasta linija predstavlja kraj 10-mjesečnog razdoblja od izgradnje ograde (za namjene komparacije sa rezultatima za ogradu na granici između Slovenije i Hrvatske; vidi Pokorny et al., 2017).

The age structure of all fence-killed ungulates was slightly biased towards adults which can be associated with their more intense spatial behaviour, i.e. higher mobility due to different social interactions that they face (i.e., red deer: Clutton-Brock et al., 2002; Loe et al., 2010; roe deer: Gaillard et al., 2008; Debeffe et al., 2012; wild boar: Keuling et al., 2010; Jerina et al., 2014).

In roe deer, the sex structure of victims (1:2.7 in favour of females) is consistent with the expected population sex structure of this moderate polygamous species (Orlowska and Rembacz, 2016), and is also in accordance with data for Slovenia–Croatia border (Pokorny et al., 2017). On the contrary, slight male-biased mortality of red deer in fences along Hungary–Croatia border (1.1:1 in favour of males) is completely unexpected and much different from the sex structure of red deer mortality at Slovenia–Croatia border (1:5.0 in favour of females; *ibid.*). This might be attributed to the specific demographic structure of intensively managed red deer populations in the Pannonian flatland (Rivrud et al., 2013), resulting in formation of large groups of adult stags which are almost unknown in hilly and mountain regions of the Dinaric zone. This indicates that the demographic structure of this otherwise very pronounced polygamous species is not so biased in favour of females. Moreover, red deer stags generally exhibit more intensive and variable non-migratory spatial behaviour (i.e., they have longer and more frequent roaming) and have larger home ranges than hinds (Clutton-Brock et al., 1982; Debeffe et al., 2019). In lowlands with no presence of large predators (as our study area is), the species tends to exhibit non-migratory behaviour (Kamler et al., 2008; Náhlik et al., 2009), resulting both in year-round presence of red deer in suitable habitats along the Hungary–Croatia border and in expressed differences in spatial behaviour between two

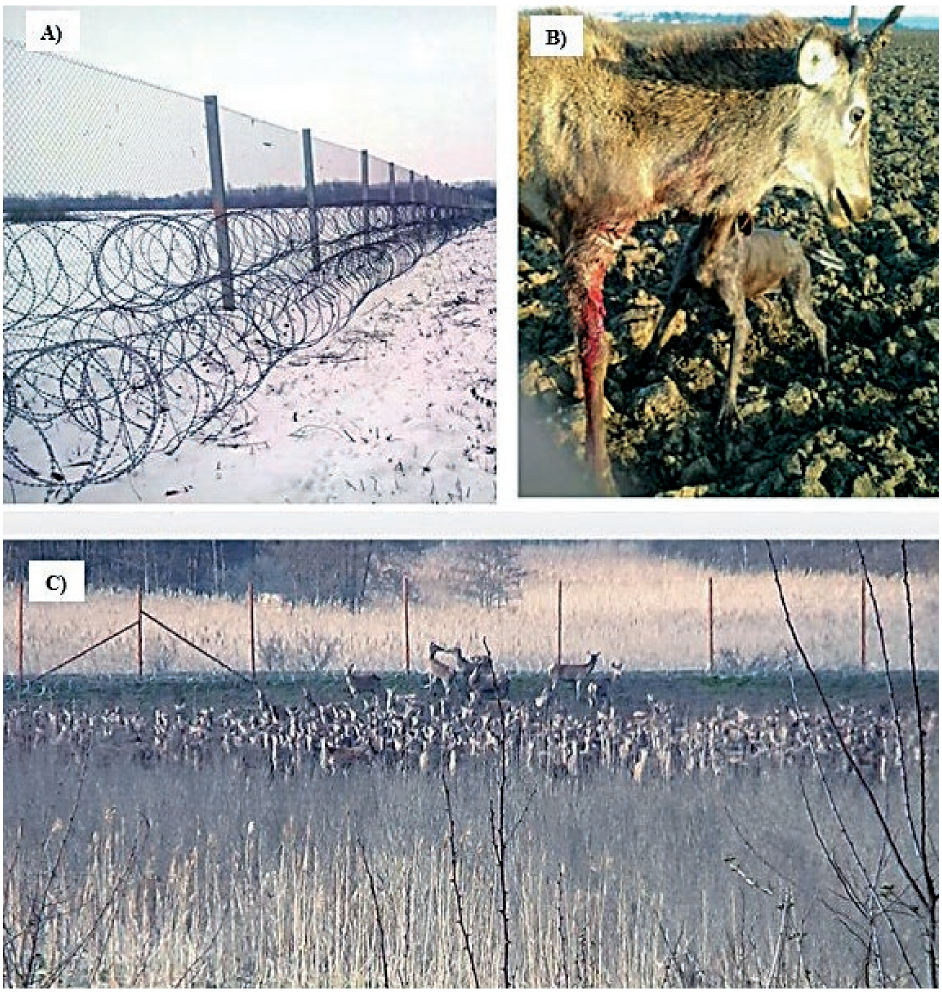

Figure 3. A) Border fence construction at the Hungary–Croatia border: the fence consists of three layers of razor wiring on the Croatian side, and a 4-metre high solid (mesh) fence towards the Hungarian side. B) Red deer (male yearling) with razor wiring injurie, found alive by bloodhound dog. C) Red deer gathering in a very huge herd attempting to cross the border fence between Hungary and Croatia. (Photos made by Damir Damjanov, Vlado Salonja, and Zlatko Anadrašević).

Figure 3. A) Izgradnja granične ograde na granici između Mađarske i Hrvatske: ograda se sastoji od tri sloja bodljikave žice na hrvatskoj strani i 4 metra visoke (čvrste) ograde prema mađarskoj strani. B) Jelen obični (mužjak jednogodišnji) – živ s ozljedama od bodljikave žice kojeg je pronašao krvosljednik. C) Jelenska divljač koja se okuplja u velika krda koja pokušavaju prijeći graničnu ogradu između Mađarske i Hrvatske. (Sve fotografije napravili Damir Damjanov, Vlado Salonja i Zlatko Anadrašević).

sexes. All these factors (presumably more males in the population as in hilly areas, absence of long-distance migrations, higher roaming rate and larger home ranges in males) may together explain a male-biased mortality of red deer due to border fences in the study area.

Records of fence-related ungulate mortalities at the Hungary–Croatia border were concentrated in the first nine months (Fig. 2) after the implementation of the fence (49 carcasses; 83%). This may indicate that the behaviour of ungulates has altered in response to the border fence, which is consistent with previous findings of Pokorny et al. (2017) who also reported the highest mortality rate of red deer in initial days after the construction of the fence as a new and previously unknown obstacle for animal movements at the Slovenia–Croatia border.

It should be noted, however, that the real rates of mortality may be underestimated by our data, as ungulates may escape wounded, and then die elsewhere on the Croatian side (Fig. 3B). Indeed, out of the eight hunting grounds with registered mortality due to border fence, seven contained evidence of injured animals escaping, indicated through blood and hair that remained on razor-wired fencing. In addition, large sections of the Hungary–Croatia border fence remained unobserved, as game managers from some hunting grounds could not reach the border fence due to several obstacles (i.e., river, ravines, or the remaining minefields from the 1990s).

While our results are limited to the Croatian side of the border fence, the mortality on the Hungarian side is expected to be minimal or even non-existent. Indeed, the additional four-metre high solid mesh fence on the Hungarian side presents no direct mortality risk, as the layer of razor wiring is out of reach for ungulates, i.e. it is constructed at the top of the fence, while on the Croatian side razor-wired fencing is on the ground level (Fig. 3A). However, due to such design the border fence is completely impermeable for large mammals which may be, in comparison to direct mortality of wildlife, much more serious ecological risk as it affects the connectivity of populations (see Linnell et al., 2016b).

Fence structure may be very important factor affecting the mortality rate of ungulates. For example, no wild boar mortality was registered in the Slovenia–Croatia border fence, instead they were observed several times managing to pass successfully through the razor-wired fence (Pokorny et al., 2017). In contrast, three mortalities of wild boar were recorded when animals attempted to cross from Croatia to Hungary. We believe this could be due to differences in fencing as there is a second, four-meter high solid mesh fence beyond the razor wires (Fig. 3A) blocking movement through to Hungary, and therefore trapping the animal in between the two fences. It is clear when considering comprehensive ecological effects of border fences, i.e. both the direct impact on wildlife mortality and their indirect impact as a barrier in the ecosystem, razor-wired fences *per se* are not as strong negative factor as when they are combined with solid mesh fences. The latter, although not directly contributing to wildlife mortality, may importantly increase this risk when constructed together with razor-wired fences. Alone, these impermeable fences may seriously diminish the connectivity of populations, without having any direct and obvious negative effects, i.e. without causing the direct mortality of individuals. It should be mentioned that Slovenia has, at several locations, begun changing the fence type from razor-wired fences into a panel design, which may even have more pronounced negative impacts on large mammal populations in the future.

Short-term consequences of the border fences along Croatian border with Hungary are clear in terms of direct mortality, and as an obstruction to the movement of animals in the case of the dual-layer fences and/or solid mesh fences alone, which are impermeable. Regarding the observed species, it must be considered that both red deer and roe deer are known to perform regular movement within their distribution range under specific environmental characteristics (see Georgii, 1980; Georgii et al., 1983; Luccarini et al., 2006; Mysterud et al., 2011 for red deer; and Wahlstrom and Lieberg, 1995; Mysterud, 1999; Cagnacci et al., 2011 for roe deer): the impacts of fencing can be obviously more severe in such circumstances. Therefore, possible long-term and cumulative consequences of border fencing must also be of a significant largescale concern.

There are documented evidences that ungulate species in the region often cross state boundaries freely. Feulner et al. (2004), for example, stated that there are no movement barriers for red deer within the Carpathian region, and movement is known to take place between western Romania and the Banat (Serbia) as well as between Bačka (Serbia), Hungary and Croatia. This is confirmed by the reports by some of the interviewed game managers, whom observed red deer gathering in huge herds as they attempt to cross the border fence between Hungary and Croatia (Fig. 3C). This kind of behaviour of red deer in the area had not been previously recorded, and game managers attributed it to the border fence effect.

CONCLUSION
ZAKLJUČAK

64 ungulates and two large birds deceased due to the razor-wired fence along the Croatia–Hungary border in 28-month study period are strong evidence that border fences present important new manmade threat to wildlife. Therefore, in the case that current fences will remain or continue to expand along the northern boundary of the South-eastern Europe, it is likely that wildlife populations will suffer much more than just short-term damage (e.g. mortality due to attempts to cross the fence) as the effects on the genetic structure will become more prominent with time.

In addition to the negative biological effects within population/species, border fences break the connectivity of the Natura 2000 network in Europe and violate several major wildlife treaties (Linnell et al., 2016a, 2016b), challenging the policies of European Union (e.g. EEC Habitats directive and Convention on Biological Diversity), and creating a dangerous precedent for other activities that affect the connectivity of ecosystems.

ACKNOWLEDGEMENTS
ZAHVALA

The authors would like to thank to all gamekeepers for great assistance in collecting data on ungulate mortality in fences along Hungary–Croatia border. Special thanks for the photos' provider: Damir Damjanov, Vlado Salonja, and Zlatko Anadrašević. This study was supported by the RESBIOS European Union's Horizon 2020 Research and Innovation Program (No. 872146). Both Slovene co-authors of the paper are members of the research program Forest biology, ecology and technology (P4–0107) which is financed by the Slovenian Research Agency. We would like to thank the Editor in chief, Prof. Josip Margaletić, the reviewer, Prof. Krešimir Krapinec, and the anonymous reviewer for their helpful comments on earlier draft of the manuscript.

REFERENCES
LITERATURA

- Aitken, R.J., 1975: Cementum layers and tooth wear as criteria for ageing roe deer (*Capreolus capreolus*). J Zool, 175: 15–28.
- Apollonio, M., Andersen, R., Putman, R., 2010: European ungulates and their management in the 21st century. Cambridge, Cambridge University Press, 618 pp.
- Ben-Shahar, R., 1993: Does fencing reduce the carrying capacity for populations of large herbivores? J Trop Ecol, 9: 249–253.
- Boitani, L., Mattei, L., 1992: Aging wild boar (*Sus scrofa*) by tooth eruption. In: Spitz, F., Janeu, G., Gonzales, G., Aulagnier, S. (Eds.). Ongules/Ungulates 91. Proceedings of the International Symposium. S.F.E.P.M.-I.R.G.M., Paris, Toulouse, France, 419–421.
- Brown, W.A.B., Chapman, N.G., 1991: The dentition of red deer (*Cervus elaphus*): a scoring scheme to assess age from wear of the permanent molariform teeth. J Zool, 224: 519–536.
- Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A.J.M., Morellet, N., Kjellander, P., Linnell, J.D.C., Mysterud, A., Neteler, M., Delucchi, L., Ossi, F., Urbano, F. 2011: Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos, 120: 1790–1802.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, Dj., Andrén, H., et al., 2014: Recovery of large carnivores in Europe's modern human-dominated landscape. Science, 346: 1517–1519.
- Clutton-Brock, T.H., Coulson, T.N., Milner-Gulland, E.J., Thomson, D., Armstrong, H.M., 2002: Sex differences in emigration and mortality affect optimal management of deer populations. Nature, 415: 633–637.
- Clutton-Brock, T.H., Guinness, F.E., Albon, S.D., 1982: Red deer: Behavior and ecology of two sexes. Chicago, University of Chicago Press, 378 pp.
- Csányi, S., Lehoczki, R., 2010: Ungulates and their management in Hungary. In: Apollonio, M., Andersen, R., Putman, R. (Eds). European ungulates and their management in the 21st century. Cambridge, Cambridge University Press, pp. 291–318.
- Daleszczyk, K., Bunevich, A.N., 2009: Population viability analysis of European bison populations in Polish and Belarusian parts of Białowieża Forest with and without gene exchange. Biol Conserv, 142: 3068–3075.
- Davies-Mostert, H.T., Mills, M.G.L., Macdonald, D.W., 2013: Hard boundaries influence African wild dogs' diet and prey selection. J Appl Ecol, 50: 1358–1366.
- Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Bon, R., Gaillard, J.M., Hewison, A.J.M., 2012: Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. J Anim Ecol, 81: 1327–1337.
- Debeffe, L., Rivrud, I.M., Meisingset, E.L., Mysterud, A., 2019: Sex-specific differences in spring and autumn migration in a northern large herbivore. Sci Rep, 9: 6137.
- Doublet, D., 2011: Effects of the United States-Mexico border fence on wildlife migration. Ge375 Final research Project.
- Epps, C.W., Palsbell, P.J., Wehausen, J.D., Roderick, G.K., Ramey II, R.R., McCullough, R., 2005: Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecol Lett, 8: 1029–1038.
- Feulner, P.G.D., Bielfeldt, W., Zachos, F.E., Bradvarovic, J., Eckert, I., Hartl, G.B., 2004: Mitochondrial DNA and microsatellite analyses of the genetic status of the presumed subspecies *Cervus elaphus montanus* (Carpathian red deer). Heredity, 93: 299–306.
- Fleurke, F.M., Trouwborst, A., 2014: European regional approaches to the transboundary conservation of biodiversity. In: Kotze, L., Marauhn, T. (Eds.). Transboundary Governance of Biodiversity. Martinus Nijhoff, pp 128–162.
- Fonseca, C., Torres, R., Santos, P.V.J., Vingada, J., Apollonio, M., 2014: Challenges in the management of cross-border populations of ungulate. In: Putman, R., Apollonio, M. (Eds.). Behaviour and management of European ungulates. Whittles Publishing, pp. 192–208.
- Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahring, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003: Road ecology: science and solutions. Washington, Covelo & London, Island Press.
- Gaillard, J.M., Hewison, A.J.M., Kjellander, P., Pettorelli, N., Bonenfant, C., Van Moorter, B., Liberg, O., Andren, H., Van Laere, G., Klein, F., Angibault, J.M., Coulon, A., Vanpé, C., 2008: Population density and sex do not influence fine-scale natal dispersal in roe deer. Proc Royal Soc B: Biol Sci, 275: 2025–2030.
- Georgii, B., 1980: Home range patterns of female red deer (*Cervus elaphus*) in the Alps. Oecologia, 47: 278–285.
- Georgii, B., Schröeder, W., 1983: Home range and activity patterns of male red deer (*Cervus elaphus*) in the Alps. Oecologia, 58: 238–248.
- Harrington, J.L., Conover, M.R., 2006: Characteristics of ungulate behaviour and mortality associated with wire fences. Wild Soc Bull, 34: 1295–1305.
- Ito, T.Y., Lhagvasuren, B., Tsunekawa, A., Shinoda, M., Takatsuki, S., Buuveibaatar B., et al., 2013: Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia. PLoS One 8: e56995.
- Jerina, K., Pokorny, B., Stergar, M., 2014: First evidence of long-distance dispersal of adult female wild boar (*Sus scrofa*) with piglets. Eur J Wild Res, 60: 367–370.

- Kaczensky, P., Kuehn, R., Lhagvasuren, B., Pietsch, S., Yang, W., Walzer, C., 2011: Connectivity of the Asiatic wild ass population in the Mongolian Gobi. Biol Conserv, 144: 920–929.
- Kamler, J.F., Jędrzejewski, W., Jędrzejewska, B., 2008: Home ranges of red deer in a European old growth forest. Am Midl Nat, 159: 75–82.
- Keuling, O., Lauterbach, K., Stier, N., Roth, M., 2010: Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany. Eur J Wild Res, 56: 159–167.
- Kowalczyk, R., Schmidt, K., Jedrzejewski, W., 2012: Do fences or humans inhibit the movements of large mammals in Białowieża Primeval Forest. In: Somers, M.J., Hayward, M.W. (Eds.). Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening process? New York, Dordrecht, Heidelberg & London, Springer, pp. 235–244.
- Kryštufek, B., 2004: A quantitative assessment of Balkan mammal diversity. In: Griffiths, H.I., Kryštufek, B., Reed, J.M. (Eds.) Balkan biodiversity. New York, Dordrecht, Heidelberg & London, Springer, pp. 79–108.
- Linnell, J.D.C., Huber, Dj., Trouwborst, A., Boitani, L., 2016a: Border controls: refugee fences fragment wildlife. Nature, 529: 156.
- Linnell, J.D.C., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, Dj., Reljić, S., Kusak, J., Majić, A., Skrbinšek, T., Potočnik, H., Hayward, W.M., Milner-Gulland, E.J., Buuveibaatar, B., Olson, A.K., Badamjav, L., Bischof, R., Zuther, S., Breitenmoser, U., 2016b: Border security fencing and wildlife: the end of the transboundary paradigm in Eurasia? PLoS Biology 14: e1002483.
- Loe, L.E., Mysterud, A., Veiberg, V., Langvatn, R., 2010: No evidence of juvenile body mass affecting dispersal in male red deer. J Zool, 280: 84–91.
- Lowe, V.P.W., 1967: Teeth as indicators of age with special reference to red deer (*Cervus elaphus*) of known age from Rhum. J Zool, 152: 137–153.
- Luccarini, S., Mauri, L., Ciuti, S., Lamberti, P., Apollonio, M., 2006: Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and effects of snow and winter feeding. Ethol Ecol Evol, 18: 127–145.
- Martinez, J.C., Carranza, J., Fernandez-Garcia, L., Sanchez-Prieto, C.B., 2002: Genetic variation in red deer population under hunting exploitation in South-Western Spain. J Wild Manage, 66: 1273–1282.
- Mysterud, A., 1999: Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. J Zool, 24: 479–486.
- Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V., Meisingset, E., 2011: Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos, 120: 1817–1825.
- Náhlik, A., Sandor, G., Tari, T., Kiraly, G., 2009: Space use and activity patterns of red deer in highly forested and in a patchy forest-agricultural habitat. Acta Silv Lign Hung, 5: 109–118.
- Noss, R. F., Platt, W.J., Sorrie, B.A., Weakley, A.S., Means, D.B., Costanza, J., Peet, R.K., 2015: How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. Diver Distrib, 21: 236–244.
- Olson, K.A., 2014: Saiga crossing options: guidelines and recommendations to mitigate barrier effects of border fencing and railroad corridors on Saiga antelope in Kazakhstan. Smithsonian Conservation Biology Institute.
- Olson, K.A., Mueller, T., Leimgruber, P., Nicolson, C., Fuller, T.K., Bolortsetseg, S. et al., 2009: Fences impede long-distance Mongolian gazelle (*Procapra gutturosa*) movements in drought-stricken landscapes. Mong J Biol Sci, 7: 45–50.
- Orlowska, L., Rembacz, W., 2016: Population dynamics and structure of roe deer (*Capreolus capreolus*) inhabiting small-size forests in north-western Poland. Fol Zool, 65: 52–58.
- Pokorny, B., Flajšman, K., Centore, L., Krope, F.S., Šprem, N., 2017: Border fence: a new ecological obstacle for wildlife in Southeast Europe. Eur J Wild Res, 63: 1.
- Ratcliffe, P.R., Mayle, B.A., 1992: Roe deer biology and management. For Comm Bull, 105: 28 pp.
- Rivrud, I.M., Sonkoly, K., Lehoczki, R., Csanyi, S., Storvik, G.O., Mysterud, A., 2013: Hunter selection and long-term trend (1881–2008) of red deer trophy sizes in Hungary. J App Ecol, 50: 168–180.
- Safner, T., Buzan, E., Rezić, A., Šprem, N., 2019: Small-scale spatial genetic structure of Alpine chamois (*Rupicapra rupicapra*) in Northern Dinarides. Eur J Wild Res, 65: 2.
- Wahlström, L.K., Liberg, O., 1995: Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*). J Zool, 235: 455–467.
- Zachos, F.E., Habel, J.C., 2011: Biodiversity hotspots: distribution and protection of conservation priority areas. Berlin, Springer.

SAŽETAK

Konzervatorska vrijednost prekograničnog gospodarenja populacijama divljih životinja u Europi, koja je obilježila kraj 20. i početak 21. stoljeća, našla se pod velikim pritiskom od 2015., posebice u jugoistočnoj Europi, zbog izgradnje graničnih ograda kao odgovor na velike prilive izbjeglica/migranata. Primarni je cilj ovoga rada predstaviti podatke o izravnim utjecajima ograde na divlje životinje (npr. smrtnost od ograde) preko mađarsko–hrvatske granice. Prikupili smo podatke o smrtnosti životinja vezanih uz granične ograde (ukupne dužine 136 km) u prvih 28 mjeseca poslije konstrukcije. Ukupno je pronađeno 64 dvopapkara (38 jelena običnog, 23 srne obične i tri divlje svinje) upleteno ili uginulo zbog bodljikave žice. Uz to, predstavljamo izravne (fotografske) dokaze o novo zabilježenom ponašanju jelenske divljači, okupljajući se u velika krda koja pokušavaju prijeći graničnu ogradu između Mađarske i Hrvatske. Kratkoročni učinak granične ograde ogleda se u obliku izravne smrtnosti životinja, a isto tako i kao opstrukcije kretanju i ponašanja životinja. Ako postojeće ograde ostanu ili se nastave širiti duž sjeverne granice jugoistočne Europe, vjerojatno je da će fragmentirane populacije divljih životinja u regiji patiti od negativnih učinaka genetske podjele, poput gubitka alela i smanjene heterozigotnosti, što može izazvati dugoročno značajnije štete u vitalnosti tih populacija.

KLJUČNE RIJEČI: granična ograda, uginuće divljih dvopapkara, fragmentacija staništa, jelen obični, srna obična, divlja svinja, jugoistočna Europa

Table S1: Registered ungulate mortality due to the Hungary–Croatia border fence, period September 2015 to December 2017.
Tablica S1: Registrirana smrtnost papkara zbog granične ograde između Mađarske i Hrvatske, u razdoblju od rujna 2015. do prosinca 2017. godine.

No.	Hunting Management District *Lovno područje*	Hunting ground *Lovište*	Species *Vrsta*	Sex *Spol*	Age (years)* Dob (godine)*	Date *Datum*
1	Koprivničko-križevačka	Gola Gotalovo	Roe deer	F	1	Sep 2015
2			Roe deer	F	3	Sep 2015
3			Roe deer	M	5	Oct 2015
4			Roe deer	F	6	Nov 2015
5			Roe deer	M	2	Nov 2015
6			Roe deer	M	3	Feb 2017
7			Red deer	M	2	Mar 2017
8	Koprivničko-križevačka	Repaš	Roe deer	F	2	Mar 2016
9			Roe deer	F	4	Mar 2016
10			Roe deer	F	1	Mar 2016
11			Red deer	M	3	Mar 2016
12			Red deer	M	4	Apr 2016
13			Red deer	F	6	Apr 2016
14			Red deer	F	2	Apr 2016
15			Red deer	F	5	May 2016
16			Red deer	M	2	May 2016
17			Wild boar	F	1	May 2016
18			Wild boar	F	1	May 2016
19			Red deer	M	<1	Sep 2016
20			Red deer	F	<1	Sep 2016
21			Red deer	F	3	Oct 2016
22			Wild boar	M	2	Oct2016
23			Red deer	M	5	Feb 2017
24	Koprivničko-križevačka	Peski	Red deer	M	1	Mar 2016
25			Red deer	F	4	Apr 2016
26			Red deer	M	3	Apr 2016
27	Osječko-baranjska	Podravlje	Red deer	F	3	Sep 2016
28			Red deer	F	5	Sep 2016
29	Osječko-baranjska	Baranjsko Petrovo selo	Roe deer	F	2	Oct 2015
30			Roe deer	F	4	Nov 2015
31			Roe deer	M	1	Nov 2015
32			Red deer	F	<1	Nov 2015
33			Red deer	M	2	Dec 2015
34			Red deer	M	6	Jan 2016
35			Red deer	M	4	Feb 2016
36			Roe deer	F	3	May 2016
37			Red deer	M	2	May 2016

No.	Hunting Management District *Lovno područje*	Hunting ground *Lovište*	Species *Vrsta*	Sex *Spol*	Age (years)* Dob (godine)*	Date *Datum*
38	Osječko-baranjska	Luč	Red deer	M	-	Sep 2015
39			Red deer	M	2	Sep 2015
40			Red deer	F	2	Sep 2015
41			Roe deer	M	<1	Oct 2015
42			Roe deer	F	3	Oct 2015
43			Roe deer	F	1	Nov 2015
44			Red deer	M	1	Nov 2015
45			Red deer	F	<1	Nov 2015
46			Roe deer	F	5	Nov 2015
47			Roe deer	M	3	Dec 2015
48			Red deer	M	3	Dec 2015
49			Red deer	M	2	Jan 2016
50			Red deer	F	5	Jan 2016
51			Roe deer	M	2	Jan 2016
52			Roe deer	F	2	Mar 2016
53			Roe deer	F	<1	Mar 2016
54			Roe deer	F	8	Apr 2016
55			Roe deer	F	6	May 2016
56	Osječko-baranjska	Duboševica	Red deer	M	1	Apr 2016
57			Red deer	F	3	Apr 2016
58			Red deer	F	6	May 2016
59			Red deer	F	10	-
60			Red deer	M	6	-
61			Red deer	M	10	Sep 2017
62	Osječko-baranjska	Topolje	Red deer	F	4	-
63			Red deer	F	5	May 2017
64			Red deer	M	4	Dec 2017

* Age was assessed on the basis of tooth eruption and wear; <1 means calf/fawn, 2+ means adult but precise age is unknown.

** Dob je procijenjena na temelju erupcije i istrošenosti zuba; <1 znači tele/lane, 2+ znači zrelu jedinku, ali nije poznata precizna dob.*