Monitoring of facultative avian scavengers on large mammal carcasses in Dinaric forest of Slovenia

Spremljanje priložnostnih ptičjih mrhovinarjev na truplih velikih sesalcev v dinarskem gozdu Slovenije

Miha Krofel

Biotechnical Faculty, University of Ljubljana, Večna pot 83, SI-1000 Ljubljana, Slovenia, e-mail: miha.krofel@gmail.com

Facultative vertebrate scavengers have an important role in forest ecosystems, however, not much is known as to their use of carrion in temperate forests. Three carcasses of Red Deer Cervus elaphus and European Roe Deer Capreolus capreolus found dead or killed by Grey Wolf Canis lupus were monitored in March and April 2010 and 2011 on Menišija Plateau in northern Dinaric Mountains (central Slovenia) using photo-trapping and video surveillance. Carcasses were monitored for 26 days, during which 708 photos and 43 video recordings of scavengers were taken. In the 91% of all visits recorded, birds were the most frequent scavengers, with Common Buzzard Buteo buteo as the most frequent species present at 76% of all visits. On average, Buzzards returned to carcasses twice per day, with an average visit lasting 29 min. Common Buzzards used carcasses to a significantly higher degree on days with snow cover, which was due to the more frequent visits per day and not to longer visits. Recorded antagonistic interspecific interactions suggested that Common Buzzards were the dominant species in the observed avian scavenger guild, as they displaced Ravens Corvus corax and Goshawk Accipiter gentilis from the carcass. However, Ravens frequently mobbed Common Buzzards while scavenging. Once an Ural Owl Strix uralensis also visited prey remains of Grey Wolf, but feeding could not be confirmed. Observations suggested that carcasses of large mammals could be locally and temporarily an important food source for some facultative avian scavengers in Dinaric forests, especially in times when other food is scarce. Data from the two wolf kills also confirm the importance of predation by large carnivores in providing food for scavengers. Given the small amount of meat consumed, kleptoparasitism by solitary raptors did not bring significant losses to large carnivores, whereas gregarious avian scavengers like corvids can importantly affect the consumption process and consume large amount of biomass in a relatively short time.

Key words: scavenging, carrion consumption, feeding behaviour, kleptoparasitism, avian scavengers, forest, Dinaric Mountains **Ključne besede:** mrhovina, mrhovinarstvo, prehranjevanje, kleptoparazitizem, ptičji mrhovinarji, gozd, Dinaridi

1. Introduction

Scavenging by vertebrates has been recognized as one of the key ecological processes with widespread consequences for the structure and stability of food webs (DeVault *et al.* 2003, Wilson & Wolkovich 2011). Birds are often among the most frequent scavengers on large carcasses, especially in open habitats

(SELVA et al. 2005, HUNTER et al. 2006, MATTISSON 2011). Since obligatory vertebrate scavengers (e.g. vultures, Ruxton & Houston 2004) are usually rare in densely vegetated habitats, facultative scavengers play the major role in forest ecosystems. However, despite the prevalence and importance of scavenging, little is known about carcass use by facultative scavengers in temperate forests (SELVA et al. 2005).

This is partly due to the difficulties of detecting carrion use by traditional methods (SÁNCHEZ-ZAPATA et al. 2010). In Slovenia, too, published literature on scavenging is scarce and limited to theoretical models (Krofel & Kos 2011) and anecdotic records from direct observations of scavenging birds, e.g. Common Buzzard Buteo buteo (BORDJAN 2003, SKRBINŠEK & KROFEL 2008), Goshawk Accipiter gentilis, Ural Owl Strix uralensis (Krofel 2005), Griffon Vulture Gyps fulvus (Šere 1998, Vidmar 2007), Jays Garrulus glandarius (Krofel 2006), Hooded Crow Corvus cornix (BORDJAN 2003), and Raven Corvus corax (Krofel 2006, Vidmar 2007).

Using remote digital surveillance methods, I monitored scavenging activities at large mammal carcasses in Dinaric forests of Slovenia in order to improve our knowledge about carrion use by avian scavengers in this ecosystem and to test applicability of photo-trapping and video surveillance for monitoring scavenger activities in forest habitats. In addition, I tried to determine the dominance hierarchy within the avian scavenger guild in the Dinaric forest and the effects of presence of snow cover on the use of carrion by birds.

2. Study area and Methods

Carcasses were monitored on the Menišija Plateau, which is a high karst massif located in the northern Dinaric Mountains in central Slovenia (45°55'N, 14°20'E). Its altitude ranges from ca. 300 to 998 m a.s.l. Average annual temperature is 7 °C and average annual precipitation 1590 mm. During winter, average monthly temperatures reach a minimum in January of –2 °C, with snow cover lasting between 13 to 110 days. Most of the area is covered by fir-beech associations *Omphalodo-Fagetum* s. lat., with four dominant tree species: Common Beech *Fagus sylvatica*, Silver Fir *Abies alba*, Norway Spruce *Picea abies*, and Sycamore Maple *Acer pseudoplatanus* (Kordiš 1993).

To monitor scavenging activity, I used a self-constructed photo-trap made from a digital SLR camera (Canon 350D) with active infrared trail monitor (1st and 2nd carcass) and a video camera Scout Guard SG 550 M with built-in passive sensor (3rd carcass). Cameras and detection sensors were camouflaged. The photo-trap was set to take one photo every 0.5–5 min for as long as movement was detected, and the video camera to record for 12 s every minute when movement was detected. When only a single photo was made, I assigned 0.5-minute of presence to the visit. If more than one individual of the same species was recorded at the carcasses at the same

time, this was recorded as one visit. Carcasses were not weighed in order to minimize disturbance. In the study area, a yearling female Red Deer *Cervus elaphus* weighs, on average, 58 kg, a yearling Red Deer stag 63 kg, and an adult male European Roe Deer *Capreolus capreolous* 16 kg (values refer to the body weight without digestive tract, i.e. ca. 84% of total body weight) (SLOVENIA FOREST SERVICE AND SLOVENIAN HUNTING ASSOCIATION *unpubl.*). The amount of meat left on carcasses was estimated visually. I used Fisher's exact test and Wilcoxon rank-sum test (WILCOXON 1945) for testing differences of carrion use between days with and without snow cover.

3. Results

Three carcasses were monitored for a total of 26 days in late winter and early spring 2010 and 2011. The carcass of a yearling Red Deer stag (1st carcass) found dead was monitored from 1 to 3 Mar 2010. The carcass found was opened in the abdomen and the head was removed. The 2nd carcass was a yearling female Red Deer killed by Grey Wolf Canis lupus. The Wolf had eaten most of the hind legs, part of the internal organs and some meat from one shoulder. When I found the prey remains (on 7 Mar 2010), several Ravens flew away. Ravens had obviously eaten the eyes and some other soft parts. I deployed photo-trap in the evening on 12 Mar and then monitored the carcass until 2 Apr 2010. The 3rd carcass was an adult male European Roe Deer killed by two wolves on the night before a camera was deployed (4 Mar 2011); the kill site was monitored until 13 Mar. When the prey remains were found, most of the meat from the posterior half of the carcass and the majority of the internal organs had been eaten by the wolves and scavengers. Ravens and Common Buzzards were observed on the carcass when it was found. Snow cover was present from 8 Mar until 19 Mar 2010 and during the entire monitoring period in 2011. The aerial distance between the 1st and 2nd carcasses was 2.5 km and 4.5 km between the 2^{nd} and 3^{rd} carcasses. The 1^{st} and 2^{nd} carcasses were not yet completely consumed when monitoring was terminated and I estimated visually that a considerable amount of meat was still present on both carcasses. On the other hand, the 3^{rd} carcass was completely consumed and removed by scavengers on the third night (5-6 Mar), so only data from the first two days were included in the analysis.

In total, 708 photographs and 43 video recordings of scavengers present at the carcasses were recorded (Table 1). The most frequent scavenger was the Common Buzzard (76% of all visits, Figure 1). Ravens

Table 1: Records of scavenger presence on three large mammal carcasses in Dinaric forest on Menišija Plateau (central Slovenia) in late winter and early spring 2010 and 2011.

Tabela 1: Zabeleženo pojavljanje mrhovinarjev ob treh truplih velikih sesalcev v dinarskem gozdu na Menišiji (osrednja Slovenija) v pozni zimi in začetku pomladi v letih 2010 in 2011.

Carcass / Truplo	No. of monitoring days / Št. dni monitoringa	No. of recordings/ Št. posnetkov	No. of scavenger visits / Št. obiskov mrhovinarjev	No. and percentage (%) of visits by birds/ Št. in odstotek (%) obiskov ptic
1st carcass / 1. truplo	3	34 photos / fotografij	4	3 (75)
2 nd carcass / 2. truplo	21	674 photos / fotografij	23	22 (96)
3 rd carcass / 3. truplo	2	43 video clips / video posnetkov	15	13 (87)
Total / Skupaj	26	75I	42	38 (91)

(10% of all visits) were recorded only on the 3rd carcass. Several Ravens were observed flying from the carrion when the 2nd carcass was found. However, no more Ravens were detected during further monitoring of this carcass. No Ravens were recorded at the 1st carcass. Among other vertebrates, carcasses were visited by the Goshawk (3rd carcass), the Ural Owl (2nd carcass), the Wildcat Felis silvestris (1st carcass), the Red Fox Vulpes vulpes (3rd carcass), the Stone Marten Martes foina (3rd carcass), Mice Apodemus sp. (2nd carcass), and Domestic Dog (3rd carcass). It was observed, by tracks in the snow, that the Grey Wolf returned to its prey once again (2nd carcass), but did not approach the carcass close enough to trigger the photo-trap or to be able to consume any more meat. The Grey Wolf pair did not return to the 3rd carcass, perhaps also because the female was killed by a car three days after the predation event occurred (own data).

Common Buzzards and Ravens comprised the majority of recorded bird scavenger species. The former were detected on the carcasses on 15 days (58% of all days monitored). On days when present at the carcasses, an average (mean \pm SD) of 2.1 \pm 1.2 visits per day was recorded (range: 1-4 visits per day). Average return time between consecutive visits during the same day was 149 ± 100 min (range 21-310 min, n = 11). The average time spent at the carcass during each visit was 29 ± 27 min (range 0.5-118 min, n = 24). It appears that the presence of snow cover affected the use of carcasses, as Common Buzzards spent significantly more time at carcasses on days when snow cover was present than on days without snow, which was due to the more frequent visits and not longer visits (Table 2). During the two days of monitoring of the 3rd carcass, Ravens were present 18 and 125 min per day, with each visit lasting 36 min on average (range 0.5-125 min, n = 4).

According to the photographs and video recordings, Common Buzzards were eating mainly from the opened parts of the carcasses on the abdomen, rib cage, and neck, while Ravens were also eating from the head, especially through the eye orbits. Removing pieces of carcass and taking them away was observed only in Ravens. Common Buzzards and Ravens were feeding on carcasses under a range of weather conditions (sunny, overcast, rain) and throughout the day, including time after sunset (range from 7.31 to 18.44 hrs), although they were most frequent in the morning and midday.

Only the 3^{rd} carcass was visited by more than one individual of scavengers simultaneously. On 79% of recordings (n = 29), more than one Raven was present.



Figure 1: Common Buzzard *Buteo buteo* feeding on carcass of female Red Deer *Cervus elaphus* killed by Grey Wolf *Canis lupus* (referred to as 2nd carcass in the text) in northern Dinaric Mountains (central Slovenia), 12 March 2010 (photo: M. Krofel)

Slika1: Kanja *Buteo buteo* med prehranjevanjem na truplu košute *Cervus elaphus*, ki jo je uplenil volk *Canis lupus* (v tekstu navedeno kot 2. truplo), v dinarskem gozdu na Menišiji (osrednja Slovenija), 12.3.2010 (foto: M. Krofel)

Table 2: Presence of Common Buzzards *Buteo buteo* at large mammal carcasses in Dinaric forest on Menišija Plateau (central Slovenia) in the periods with (9 days) and without snow cover (17 days) in late winter and early spring 2010 and 2011.

Tabela 2: Pojavljanje kanj *Buteo buteo* ob truplih velikih sesalcev v dinarskem gozdu na Menišiji (osrednja Slovenija) v obdobju s snežno odejo (9 dni) in brez nje (17 dni) v pozni zimi in začetku pomladi v letih 2010 in 2011.

Presence / Pojavljanje	All days/ Vsi dnevi	Snow cover/ Snežna odeja	No snow/ Brez snega	Test results/ Rezultati testov
Percentage of days present at the carcasses / Odstotek dni z zabeleženim pojavljanjem ob truplih	58%	89%	41%	Fisher's exact test P = 0.04
Total time spent at the carcasses/ Celoten čas, porabljen ob truplih	938 min	602 min	336 min	Wilcoxon rank-sum test $W = 122, P = 0.01$
Mean time spent at the carcass per monitoring day / Povprečen čas ob truplu na dan spremljanja	36.0 min	66.8 min	19.7 min	
Mean time spent at the carcass per visit / Povprečen čas ob truplu na obisk	29.3 min	30.1 min	28.0 min	Wilcoxon rank-sum test $W = 118$, $P = 0.95$, n.s.
Mean number of visits per day/ Povprečno število obiskov na dan	1.23	2.22	0.71	Wilcoxon rank-sum test W = 122, P = 0.01

The average number of Ravens present was 4.2 ± 2.2 (range 1-7). On the 3rd carcass, two Common Buzzards were present simultaneously in 15% of the recordings (n = 33). I observed antagonistic intraspecific interactions in 47% of the recordings when several Ravens were simultaneously present at the carcass (n = 17), usually with one clearly dominant Raven chasing away the others. No antagonistic interactions were observed among Buzzards. I also observed several direct interspecific interactions among avian scavenger guild species. Common Buzzards appeared to be dominant among the recorded scavengers as they chased away Ravens (5 observations) and Goshawks (2 observations). However, three recordings also detected that the Ravens pecked the Common Buzzards in the wing or tail and then quickly flew away. Common Buzzards were never driven away by Ravens, even when outnumbered 1 to 7. On 55% of the recordings (n = 18) with both species, Ravens and Common Buzzards were simultaneously feeding without antagonistic interactions.

4. Discussion

The monitoring of deer carcasses in Dinaric forests supported previous observations that, when available, carcasses of large mammals are used regularly by raptors and Ravens, especially during winter (e.g. KACZENSKY *et al.* 2005, KROFEL 2005, SELVA *et al.* 2005, BLÁZQUEZ

et al. 2009). Feeding on carcasses has, on the other hand, only rarely been recorded among owls (KÖNIG et al. 1999, SELVA 2004, DÍAZ-RUIZ 2010). For the Ural Owl, only two records of presence at carcasses were found in the available literature (SAUROLA 1995, KROFEL 2005). However, for these cases, as well as for the observation on Grey Wolf prey from the present study, the possibility also exists that the owls were hunting rodents at the carcass and not necessarily feeding on the carrion. Similar to my observation, HEBBLEWHITE & SMITH (2010) reported presence of the Great Grey Owl Strix nebolusa at Grey Wolf prey in Canada.

The absence of Ravens among the photographed scavengers on the 1st and 2nd carcasses is interesting, although they found at least one of these monitored carcasses. Ravens in Slovenia regularly feed on mammal carcasses (Tome et al. 2009); they are frequently observed on Menišija Plateau in flocks of more than 100 individuals (Krofel 2010) and were observed on the 3rd carcass when it was found. Probably the most plausible explanation for their absence would be that they were afraid to approach the first two carcasses because of the disturbance I caused when visiting the carcasses (usually every 3-5 days), or they were able to see the camouflaged photo-trap and were scared by it. Similarly, during the monitoring of prey remains of Eurasian Lynx Lynx lynx, preliminary results indicated that Ravens were observed flying away several times from the carcass (Krofel 2006), but they were never recorded at any of the monitored deer carcasses when automatic video system was deployed (Skrbinšek & Krofel 2008, M. Krofel unpubl.). In general, Ravens are regarded as shy when approaching animal carcasses, especially when disturbed by humans (RATCLIFFE 1997). The anecdotic example from this study, when a predator returned to the vicinity of its prey, but was reluctant to approach the carcass to continue feeding, indicates that a similar behaviour may also hold true for Grey Wolves. Depending on the sensitivity of the video system, this method may also be less suitable for detecting smaller scavenger species. Although the presence of mice was detected, it is possible that some of the smaller avian scavengers, e.g. tits, which sometimes consume meat or collect hair from carcasses for nesting material (HUCHT-CIORGA 1988), have been missed. Therefore caution is needed when interpreting data of scavenging activity from photoor video-monitoring for some scavenger species. However, in general the method proved effective, as it enabled continuous and detailed monitoring of scavenging activity for a prolonged time. I believe that this method is also less disturbing to the feeding animals than direct observations, especially in forest habitats, where the observer has to be close to the carcass, because observations from large distances are usually impossible due to decreased visibility.

Size is often an important factor directing dominance in antagonistic interspecific interactions, although grouping is sometimes used by smaller species to counterbalance their disadvantage in size and to attain dominance in order to compete more successfully for resources (PALOMARES & CARO 1999). Common Buzzards, which were the largest bird species recorded, appeared to be dominant in the observed avian scavenger guild, even when outnumbered by Ravens. Nevertheless, Ravens frequently mobbed Common Buzzards while they were scavenging. Mobbing of larger raptors is often observed in Ravens, especially around nests and food sources (RATCLIFFE 1997).

Carrion usually comprises a relatively small proportion of the overall diet of Common Buzzards (Jedrzejewska & Jedrzejewski 1998). However, their frequent and long visits suggest that carcasses of large mammals can present a locally and temporarily important food source for some facultative avian scavengers, especially in times when other food is scarce, e.g. when ground is covered with snow. Data from the two Grey Wolf kills also confirm the importance of predation by large carnivores in subsidizing scavengers, as has been suggested in previous studies

(Wilmers et al. 2003, Selva et al. 2005). On the other hand, the effect of scavengers on the predator should not be neglected (Krofel & Kos 2010, Mattisson 2011). Given the long time of feeding and relatively small amount of meat removed by Common Buzzards from the Grey Wolf prey, kleptoparasitism by solitary raptors is unlikely to constitute a significant source of loss for predators of large mammals, which usually consume their prey in a few days (Peterson & Ciucci 2003, SKRBINŠEK & KROFEL 2007). In contrast to this, gregarious avian scavengers like corvids can remove considerable amounts of a carcass in a relatively short time, as was observed on the 3rd carcass. Similarly, observations on real and simulated Grey Wolf kills in North America revealed that Ravens can remove from 2 to 37 kg of meat per day and thus considerably influence the prey consumption process and perhaps also the kill rate and social behaviour of the predator (Peterson and Ciucci 2003, Vucetich et al. 2004, KACZENSKY et al. 2005).

Acknowledgements: I would like to thank G. Donati, P. Draškovič, C. Groff, R. Rizzoli, and A. Žagar for their help with the field-work. I am also grateful to L. Božič and an anonymous reviewer for their helpful suggestions to improve the manuscript.

5. Povzetek

Priložnostni vretenčarski mrhovinarji imajo ključno vlogo v gozdnih ekosistemih, vendar je o njihovi izrabi mrhovine v gozdovih zmernega pasu za zdaj še malo znanega. S pomočjo doma narejene foto-pasti in avtomatske video kamere je avtor marca in aprila 2010 ter 2011 spremljal aktivnost mrhovinarjev na dveh truplih jelena Cervus elaphus in enem truplu srnjaka Capreolus capreolus v dinarskem gozdu na Menišiji (osrednja Slovenija). Dve trupli (košuta in srnjak) sta bili plen volkov Canis lupus, mladi jelen pa je bil najden poginjen. Skupaj je bilo v 26 dneh spremljanja narejenih 708 fotografij in 43 video posnetkov z mrhovinarji ob truplih. Ptiči so bili z 91 % obiskov najpogostejši zabeleženi mrhovinarji. Najpogostejša vrsta je bila kanja Buteo buteo (76 % vseh zabeleženih obiskov). Kanje so se ob vsakem obisku povprečno zadrževale ob truplih 29 min in se vračale k mrhovini dvakrat dnevno. Kanje so se z mrhovino hranile v večjem obsegu v obdobju s snežno odejo, kar je bila posledica večjega števila obiskov in ne dolžine posameznega obiska. Posnetki agresivnih medvrstnih interakcij ob truplih kažejo, da so bile kanje dominantna vrsta med zabeleženim cehom ptičjih mrhovinarjev, saj so ne glede na številčno razmerje od trupla pregnale tako krokarje Corvus corax kot kragulja Accipiter gentilis. Kljub podrejenosti in manjši velikosti pa so krokarji večkrat nadlegovali kanje, ko so se le-te prehranjevale. Enega izmed volčjih plenov je obiskala tudi kozača Strix uralensis, vendar samega prehranjevanja z mrhovino ni bilo mogoče potrditi. Na podlagi opazovanj sklepam, da so lahko trupla velikih sesalcev lokalno in v omejenem časovnem obdobju pomemben vir hrane nekaterih vrst ptic dinarskih gozdov, ki se hranijo tudi z mrhovino, zlasti v obdobjih pomanjkanja hrane. Podatki iz spremljanja volčjih plenov so potrdili pomen plenjenja velikih zveri za zagotavljanje hrane mrhovinarjem. Glede na majhno količino požrtega mesa kleptoparazitizem s strani samotarskih vrst ujed očitno nima večjega vpliva na plenilce velikih sesalcev, nasprotno pa velja za bolj socialne vrste, kot so krokarji, ki lahko v razmeroma kratkem času odstranijo večje količine mrhovine in s tem pomembno vplivajo na proces konzumacije.

6. References

- BLÁZQUEZ, M., SÁNCHEZ-ZAPATA, J.A., BOTELLA, F., CARRETE, M. & EGUÍA, S. (2009): Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. Acta Oecologica 35: 645–650.
- Bordjan, D. (2003): Kanja *Buteo buteo*. Acrocephalus 24 (117): 75.
- DeVault, T.L., Rhodes Jr., O.E. & Shivik, J.A. (2003): Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. – Oikos 102: 225–234.
- DÍAZ-RUIZ, F., BUENESTADO, F., FERNÁNDEZ-DE-SIMÓN, J. & FERRERAS, P. (2010): First record of rabbit carrion consumption by Eurasian eagle-owl (*Bubo bubo*) on the Iberian peninsula. – Journal of Raptor Research 44: 78–79.
- Hebblewhite, M. & Smith, D.W. (2010): Wolf community ecology: ecosystem effects of recovering wolves in Banff and Yellowstone National Parks. pp. 69–120 In: Musiani, M., Boitani, L. & Paquet, P. C. (eds.): The world of wolves: new perspectives on ecology, behaviour and management. The University of Calgary Press, Calgary.
- Hucht-Ciorga, I. (1988): Studien zur Biologie des Luchses: Jagdverhalten, Beuteausnutzung, innerartliche Kommunikation und an den Spuren fassbare Körpermerkmale. – Ferdinand Enke Verlag, Stuttgart.
- HUNTER, J.S., DURANT, S.M. & CARO, T.M. (2006): Patterns of scavenger arrival at cheetah kills in Serengeti National Park Tanzania. – African Journal of Ecology 45: 275–281.
- ЈĘDRZEJEWSKA В. & JĘDRZEJEWSKI W. (1998): Predation in vertebrate communities: The Biłowieża Primeval Forest as a case study. – Springer, Heidelberg.
- KACZENSKY, P., HAYES, R.D. & PROMBERGER, C. (2005): Effect of raven *Corvus corax* scavenging on the kill rates of

- wolf *Canis lupus* packs. Wildlife Biology 11: 101–108. König, C., Weick, F. & Becking, J.H. (1999): Owls. A Guide to the Owls of the World. – Pica Press, Sussex.
- Kordiš, F. (1993): Dinarski jelovo bukovi gozdovi v Sloveniji. Strokovna in znanstvena dela 112. – Oddelek za gozdarstvo, Biotehniška fakulteta, Ljubljana.
- Krofel, M. (2005): Kragulj *Accipiter gentilis* & kozača *Strix uralensis.* Acrocephalus 26 (124): 49.
- KROFEL, M. (2006): Plenjenje in prehranjevanje evrazijskega risa (*Lynx lynx*) na območju Dinarskega krasa v Sloveniji.
 Diplomska naloga. Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za biologijo, Ljubljana.
- Krofel, M. (2010): Opažanja velikih jat krokarjev *Corvus corax* na Pokojiški planoti (osrednja Slovenija). Acrocephalus 32 (145/146): 147–149.
- KROFEL, M. & KOS, I. (2010): Modelling potential effects of brown bear kleptoparasitism on the predation rate of Eurasian lynx. – Acta Biologica Slovenica 53 (1): 47–54.
- MATTISSON, J. (2011): Interactions between Eurasian lynx and wolverines in the reindeer husbandry area. PhD thesis. – Swedish University of Agricultural Sciences, Uppsala.
- Palomares, F., & Caro T.M. (1999): Interspecific killing among mammalian carnivores. American Naturalist 153: 492–508.
- Peterson, R.O. & Ciucci, P. (2003): The wolf as a carnivore. pp. 104–130 In: Mech, L. D. & Boitani, L. (eds.): Wolves; Behavior, Ecology, and Conservation. The University of Chicago Press, Chicago.
- RATCLIFFE, D. (1997): The Raven. T & A D Poyser, London.
- Ruxton, G.D. & Houston, D.C. (2004): Obligate vertebrate scavengers must be large soaring fliers. Journal of Theoretical Biology 228: 431–436.
- SAUROLA P. (1995): [Finnish Owls.] Book Group Ltd., Helsinki. (in Finnish)
- SELVA, N. (2004): Life after death scavenging on ungulate carcasses. pp. 59–68 In: Jedrzejewska, B. & Wojcik J. M. (eds.): Essays on Mammals of Bialowieza Forest. Polish Academy of Sciences, Bialowieza.
- Selva, N., Jędrzejewska, B., Jędrzejewski, W. & Wajrak, A. (2005): Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology 83: 1590–1601.
- Skrbinšek, T. & Krofel, M. (2008): Analiza kvalitete habitata, hrana in kompeticija. Projekt DinaRis. Zaključno poročilo. – University of Ljubljana, Ljubljana.
- SÁNCHEZ-ZAPATA, J.A., EGUÍA, S., BLÁZQUEZ, M., MOLEÓN, M. & BOTELLA, F. (2010): Unexpected role of ungulate carcasses in the diet of Golden Eagles *Aquila chrysaetos* in Mediterranean mountains. Bird Study 57: 352–360.
- ŠERE, D. (1998): Beloglavi jastreb *Gyps fulvus.* Acrocephalus 19 (87/88): 67.
- Tome, D., Krofel, M. & Mihelič, T. (2009): The diet of the raven *Corvus corax* in south-west Slovenia. – Annales, Series Historia Naturalis 19: 161–166.
- VIDMAR, J. (2003): Beloglavi jastreb *Gyps fulvus*. Acrocephalus 28 (133): 80.
- Vucetich, J.A., Peterson, R.O. & Waite, T.A. (2004): Raven scavenging favours group foraging in wolves. – Animal Behaviour 67: 1117–1126.

WILMERS, C.C., CRABTREE, R.L., SMITH, D.W., MURPHY, K.M. & GETZ, W.M. (2003): Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. – Journal of Animal Ecology 72: 909 – 916.

Animal Ecology 72: 909 – 916.
WILCOXON, F. (1945): Individual comparisons by ranking methods. – Biometrics Bulletin 1 (6): 80–83.

WILSON, E.E. & WOLKOVICH, E.M. (2011): Scavenging: how carnivores and carrion structure communities. – Trends in Ecology and Evolution 26: 129–135.

Arrived / Prispelo: 10. 9. 2010 Accepted / Sprejeto: 19. 3. 2012