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Modeling potential effects of brown bear kleptoparasitism on the predation rate of Eurasian lynx

Modeliranje možnih vplivov kleptoparazitizma s strani medveda na stopnjo plenjenja pri evrazijskem risu

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Abstract: Kleptoparasitism is a frequent phenomenon when consumption of prey by predator continues for a relatively long period. This is common when prey is larger or of a similar size as the predator. We built a simple model to study the potential effects of the kleptoparasitism by the brown bears (*Ursus arctos*) on the predation rate of the Eurasian lynx (*Lynx lynx*) in the northern Dinaric Mountains, where the two species coexist. When using data from literature and preliminary studies in the study area, the model suggests substantial increase in the predation rate of the lynx due to the scavenging activity of bears. However, additional data from the field on the frequency, time course and seasonal variation of the bear's visits to carcasses are needed, as well as an evaluation of the lynx' possibilities to increase the predation rate. We suggest that the effects of kleptoparasitism should be considered when evaluating the impact of predation on populations of wild game and during conservation efforts for conservation of endangered carnivore species.

Key words: Eurasian lynx, *Lynx lynx*, brown bear, *Ursus arctos*, kleptoparasitism, interspecific competition, predation, kill rate, Dinaric Mountains

Izvleček
Kleptoparazitizem je reden pojav pri vrstah, kjer potek hranjenja plenilca s plenom poteka dolgo časa. To je pogosteje, kadar je plen večje ali podobne velikosti kot plenilec. V prispevku predstavljava preprost model, ki sva ga pripravila, da bi bolje spoznala možne vpliva kleptoprazitizma s strani rjavega medveda (*Ursus arctos*) na stopnjo plenjenja pri evrazijskem risu (*Lynx lynx*) na območju Severnih Dinaridov, kjer obe vrsti sobivata. Ob uporabi podatkov iz tuje literature in naših preliminarnih raziskav iz raziskovanega območja model predpostavlja bistveno povečanje stopnje plenjenja pri risu zaradi medvedjega prehranjevanja z ostanki plena. Za boljše ovrednotenje vplivov kleptoparazitizma bodo potrebni dodatni podatki o frekvenci, časovnem poteku in sezonskih razlikah pri obiskovanja ostankov risovega plena s strani medvedov ter ocena sposobnosti risa, da kompenzira izgube zaradi kleptoparazitizma s povečanjem stopnje plenjenja. V splošnem priporočava, da bi se morali vplivi kleptoparazitizma upoštevati pri ocenjevanju vplivov plenjenja plenilcev na populacije divjadi in pri prizadevanjih za ohranitev ogroženih vrst plenilcev.

Ključne besede: evrazijski ris, *Lynx lynx*, rjavi medved, *Ursus arctos*, kleptoparazitizem, medvrstna kompeticija, plenjenje, stopnja plenjenja, Dinaridi running title: Effects of bear kleptoparasitism on lynx predation rate

Introduction

The Dinaric Mountains represent one of a few regions in central Europe where three species of large carnivores still coexist. The consequence of this sympatric occurrence of the brown bear (*Ursus arctos*), gray wolf (*Canis lupus*), and Eurasian lynx (*Lynx lynx*) are unique interspecific interactions (Kos et al. 2005). It has been shown that both exploitation and interference competition can have important effects on the distribution and demography of carnivores (Fedriani et al. 2000, Linnell and Strand 2000). However, the interactions among these three endangered species in Europe are still mostly unstudied and poorly understood.

An important part of the interactions between large carnivores may take place at prey remains (Hunter et al. 2007). Lynx and wolves in the Dinaric Mountains hunt mainly ungulates (Krofel 2006, Krofel and Kos 2010), and due to the large size of prey the process of consumption by predator can take a considerable amount of time, especially by the solitary living lynx (Krofel et al. 2006). A prolonged time of consumption increases the possibility of kleptoparasitism by scavenging species. Although obligate scavengers among vertebrates in temperate regions of the Northern Hemisphere are rare, there are numerous species that are facultative scavengers, as almost all predators are scavengers to some extent (Selva et al. 2003). Since these scavengers also use carrion from prey remains, they represent food competitors to the predators. It has been noted that kleptoparasites can have an important impact on the predator (Carbone et al. 1997) and it has even been suggested that prey selection in some carnivores is adapted as to minimize the losses due to scavenging (Jędrzejewski et al. 1993; however, see Hayward et al., 2006). Predators also exhibit different other behaviours to decrease the probability of scavengers finding their prey, such as covering the prey remains with various materials or caching in trees (Bothma and le Riche 1984, Červený and Okarma 2002).

Up to 13 species of scavengers have been reported to be feeding at lynx kills in different regions in Europe and according to present data the red fox (*Vulpes vulpes*), wild boar (*Sus scrofa*), and raven (*Corvus corax*) are the most frequent visitors at the prey remains (Hucht-Ciorga 1988, Jędrzejewska and Jędrzejewski 1998, Jobin et al. 2000, Červený and Okarma 2002). However, all of these studies were made in areas where brown bears are already extinct. Until present, practically no data are available on the effects of interactions between the Eurasian lynx and brown bears.

Due to their large size, brown bears can displace the predators from their kills and also consume most of the eatable remains of a carcass when they find prey remains. In this way, they differ from other, smaller facultative scavengers. Because of their good olfactory abilities bears are efficient at locating carcasses in the forest (Herrero 1985). Thus they might influence the process of prey consumption by the lynx and consequently also its predation rate. We built a simple model to study the potential effects of the presence of brown bears on the predation rate of the Eurasian lynx in the northern Dinaric Mountains.

Methods and study area

The study was conducted in the northern part of the Dinaric mountain range. The Dinaric Mountains extend along the Adriatic coast from the Friuli plain in Italy in the north-west to the Albanian mountains in the south-east. The study area (46˚10'-45˚20'N and 13˚33'-15˚13'E) is located in the High Karst region of Slovenia and Gorski Kotar in Croatia. Limestone and dolomite prevail in the area, and the relief shows numerous karst phenomena, such as dolines, collapse dolines, uvalas, horizontal caves, vertical shafts, steep canyons, poljes etc. Surface water is rare as water run off is largely underground. The climate is a mix of influences from the Alps, the Mediterranean sea and the Pannonian basin with annual temperatures averaging 5-8 ˚C, ranging from an average maximum of 32 ˚C to a minimum of -20 ˚C, and average annual precipitation of 1400-3500 mm. Most of the area is covered by the fir-beech associations (*Omphalodo-Fagetum*), with four dominant tree species: the common beech (*Fagus sylvatica*), silver fir (*Abies alba*), Norway spruce (*Picea abies*), and sycamore maple (*Acer pseudoplatanus*) (Kordiš 1993).

The lynx in the northern Dinaric Mountains hunt mainly roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fat dormouse (*Glis glis*) and to a lesser extent other rodents, chamois (*Rupicapra rupicapra*), red fox (*Vulpes vulpes*), and birds (Rajković 1999, Krofel 2006). The average density of brown bears in southern Slovenia was estimated to approximately 10 bears / 100 km^2 of forest (Kaczensky and Knauer, 2000, Skrbinšek et al. 2008)

For modeling we used data from literature on the daily food requirements and consumption process of lynx from Poland and Switzerland (Jędrzejewska and Jędrzejewski 1998, Jobin et al. 2000, Molinari-Jobin et al. 2002). Preliminary results obtained from the northern Dinaric Mountains, correspond to values reported in these studies (Krofel et al. unpublished data).

We searched for lynx kills with the use of VHF telemetry and the area was searched, when two or more consecutive locations were obtained in a radius of 200 m at intervals of at least six hours during the night or on consecutive nights. We also searched for prey remains during snow-tracking of lynx and inspected prey remains found by chance during field work or those reported by hunters, foresters etc. The presence of scavengers at kills was determined on the basis of footprints and scats around the carcass, feeding signs and/or via direct observations during visits to the carcasses.

When constructing the model, we presumed that lynx in a given area hunt only adult ungulates. In order to further simplify the relationships, we assumed that lynx never use two carcasses at the same time (i.e. lynx kill their next prey only after they have finished with the consumption of the previous one and never return to eat the old prey remains) and that the amount of ingested meat is constant regardless of the sex or age of the lynx. Therefore the predation rate depends on the amount of meat consumed by the lynx per year and the amount of meat gained per prey:

$$N_p = \frac{365 * R}{CM_{av.}} \quad \ldots(1)$$

where N_p is the number of animals killed by the lynx per one year, $CM_{av.}$ the average biomass consumed by the lynx per animal killed, and R the average daily requirement of food for lynx (including the days when the lynx is not eating).

Next, we presumed that the area is inhabited by brown bears, which occasionally feed on the lynx kill remains. We also assumed that when finding a carcass, bears consumed or removed all the remaining parts of the carcass that could be eatable for the lynx. We can now express the lynx predation rate as follows:

$$N_p = \frac{(1-\varphi_b) * N_p * CM_w + \varphi_b * N_p * CM_b}{CM_{av.}} \quad \ldots(2)$$

where φ_b is the percentage of cases when bears find lynx kills before the lynx has finished with its consumption, CM_w the average biomass consumed by the lynx per animal killed when the bear does not find the prey, and CM_b the average biomass consumed by the lynx per animal killed when the bear finds the prey.

CM_w also depends on the average biomass consumed per day by the lynx per animal killed when it is feeding (CM_f) and the average time, during which the lynx is feeding on the kill, if the bear does not find the prey remains (t_w):

$$CM_w = CM_f * t_w \quad \ldots(3)$$

Similarly, CM_b depends on the CM_f and the average time, during which the lynx is feeding on the kill, before the bear finds the prey remains (t_b):

$$CM_b = CM_f * t_b \quad \ldots(4)$$

When we combine these equations we can express the lynx predation rate as:

$$N_p = \frac{365 * R}{CM_f\,(t_w - t_w * \varphi_b + t_b * \varphi_b)} \quad \ldots(5)$$

Results

When data on lynx consumption from the literature (R = 2 kg; CM_f = 3 kg; t_w = 4 days) are incorporated into the model and if we assume that bears are not present in the area, the model predicts the predation rate of 60.8 adult ungulates killed per year or approximately one animal every 6 days. This values are comparable with the predation rates reported for Eurasian lynx from regions where bears are absent – 43 to 76 deer per year in Białowieża, Poland (Jędrzejewska and Jędrzejewski 1998) and 58.6 to 79.4 ungulates per year in the Swiss Jura Mountains (Molinari-Jobin et al. 2002).

If we now assume that bears are present in the area and that they feed on the remains of lynx prey, the model predicts that the predation rate would increase. In this way, lynx would compensate the losses from scavenging by bears, in order to retain the same amount of food ingested. The degree of the increase of the lynx predation rate would depend on: 1.) the percentage of cases when bears find lynx prey, before the lynx has finished consuming it, and 2.) the time after the killing, when bears find the prey (Figs. 1-2).

In our preliminary study, bears found three out of 11 ungulates killed by the lynx in the northern Dinaric Mts. It should be noted, however, that these data are limited to winter time. If we insert this amount (φ_b = 0.27) into the model and assume that on average bears find lynx prey on the second day after the killing (i. e. after lynx has had two meals), the model predicts a kill rate of 70.3 ungulates per year, which corresponds to the increase of 15.6 %. If the calculation is made under the assumption of the bears finding the lynx prey on the third day after the killing, the model predicts a kill rate of 65.2 ungulates per year (7.2 % increase).

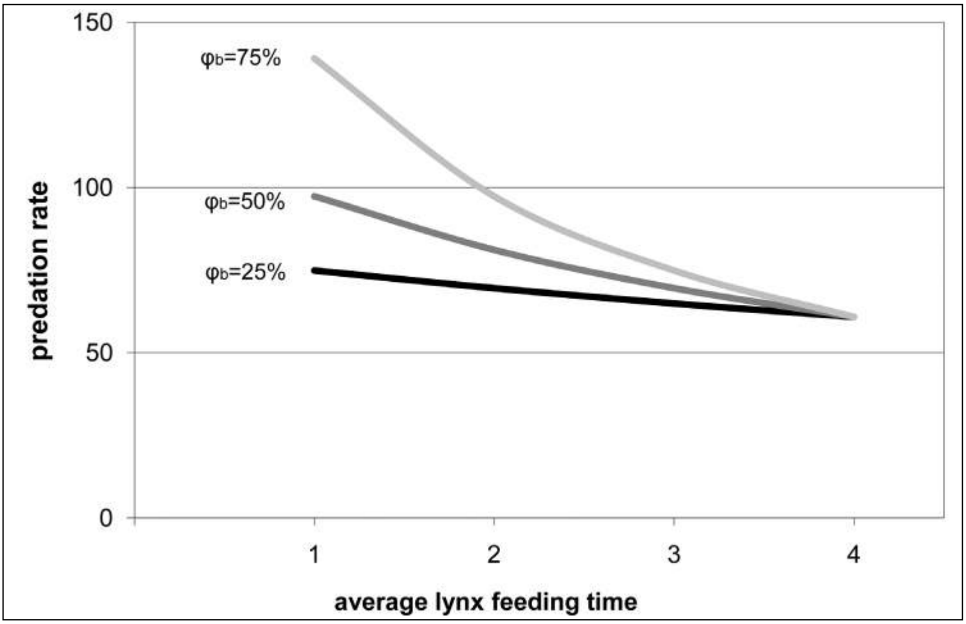

Figure 1: Model of the effects of scavenging activity of brown bears (*Ursus arctos*) on the predation rate of the Eurasian lynx (*Lynx lynx*). The graph shows the change in lynx predation rate (number of animals killed by lynx per year) as the function of the average time, during which the lynx feeds on its kill before the bear finds the prey remains, for three different percentages of cases, when bears find the lynx kill before the lynx has finished with consumption (φ_b), if t_w = 4 days, CM_f = 3 kg, and R = 2 kg (see text for the meaning of abbreviations).

Slika 1: Model vpliva hranjenja rjavega medveda (*Ursus arctos*) z ostanki plena na stopnjo plenjenja evrazijskega risa (*Lynx lynx*). Graf prikazuje spremembe v stopnji plenjenja risa (število živali, ki jih ris upleni na leto) v odvisnosti od povprečnega časa, ko se ris hrani s svojim plenom, preden ga najde medved. Rezultati so podani za tri različne vrednosti deleža primerov, v katerih medvedi najdejo ostanke plena še preden je ris končal s hranjenjem (φ_b), ob predpostavki, da velja t_w = 4 dni, CM_f = 3 kg in R = 2 kg (glej tekst za razlago kratic).

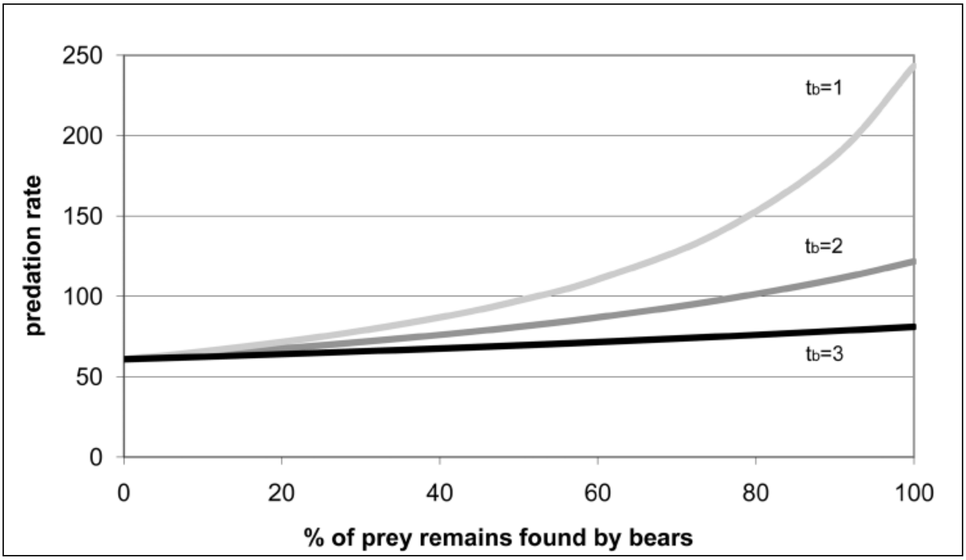

Figure 2: Model of the effects of scavenging activity of brown bears (*Ursus arctos*) on the predation rate of the Eurasian lynx (*Lynx lynx*). The graph shows the change in lynx predation rate (number of animals killed by the lynx per year) as the function of the percentage of cases, when bears find the lynx kill before the lynx has finished with consumption for three different values of the average time during which the lynx has fed on the kill before the bear finds the prey remains (t_b), if t_w = 4 days, CM_f = 3 kg, and R = 2 kg (see text for the meaning of abbreviations).

Slika 2: Model vpliva hranjenja rjavega medveda (*Ursus arctos*) z ostanki plena na stopnjo plenjenja evrazijskega risa (*Lynx lynx*). Graf prikazuje spremembe v stopnji plenjenja risa (število živali, ki jih ris upleni na leto) v odvisnosti od deleža primerov, v katerih medvedi najdejo ostanke plena še preden je ris končal s hranjenjem. Rezultati so podani za tri različne vrednosti povprečnega časa, ko se ris hrani s svojim plenom, preden ga najde medved, ob predpostavki, da velja t_w = 4 dni, CM_f = 3 kg in R = 2 kg (glej tekst za razlago kratic).

Discussion

As in other regions where similar studies have been conducted (Hucht-Ciorga 1988, Jędrzejewska and Jędrzejewski 1998, Jobin et al. 2000, Červený and Okarma 2002), vertebrate facultative scavengers frequently feed on lynx prey remains in the northern Dinaric Mountains (Krofel 2006). However, this area distinguishes itself from other regions in the presence of high density of brown bears, which may have important influences on the predation rate of the lynx, as is suggested by the model presented here. This could be compared to the results reported from North America, where brown and black bears (*Ursus americanus*) visited 25 % of ungulates killed by cougars (*Puma concolor*) (Murphy et al. 1998).

When estimating the effect of kleptoparasitism by bears on lynx predation rate from our results, it should be noted, that most of the data come from the winter period, when bears are generally less active (Huber and Roth 1993) and their influence might thus be underestimated. Also, the carrion is more difficult to find in the winter for the bears which rely mainly on their sense of smell, due to the slower decomposition processes in lower temperatures. On the other hand, in snowy conditions bears can follow the lynx trail more easily (Krofel and Kos 2007) and the results from diet analysis of bears in Slovenia showed that bears consume more meat in the winter and spring than in other seasons (Grosse et al. 2003, Krofel et al. 2008a). Also, the consumption of prey remains by the lynx is slower in winter (Krofel et al. 2006;

however, see Okarma et al. 1997), therefore the possibility of bears finding the carcass before the lynx has finished eating is greater in winter.

More data from the field are needed to obtain more accurate parameters for the model and validate the predictions of the effects of bear kleptoparasitism on lynx predation rate. In the future studies, the lynx' possibilities to increase the predation rate under different prey densities should also be evaluated. Studies from Poland suggest that lynx increase their hunting effort in response to lower availability of prey with increasing daily movements (Schmidt 2008). However, it is not known what is the success and upper limit of such increased hunting effort and if it at all appears in response to losses of prey to scavengers. More data are needed also on the effects of different seasons on lynx-bear interactions, due to seasonal differences in lynx and bear diet, as well as bear activity.

According to the currently available data and the model presented here, the effects of kleptoparasitism by the brown bear may have substantial effect on the predation rate of the Eurasian lynx. We expect similar effects, although probably to a lesser degree, also from scavenging activity of other large scavengers (e.g. gray wolf and wild boar) and due to prey removal by humans (Krofel et al. 2008b). We suggest that effects of kleptoparasitism should be considered when evaluating the impact of predation on populations of wild game and during efforts for conservation of endangered carnivore species.

Povzetek

Kleptoparazitizem je reden pojav pri vrstah, kjer potek hranjenja plenilca s plenom poteka dolgo časa. To je pogosteje, kadar je plen večje ali podobne velikosti kot plenilec, kot na primer pri evrazijskem risu (*Lynx lynx*). Do sedaj je so avtorji iz različnih območjih po Evropi opisali, da so se z ostanki risovega plena hranili mnogi vretenčarski fakultativni kleptoparaziti (Hucht-Ciorga 1988, Jędrzejewska in Jędrzejewski 1998, Jobin in sod. 2000, Červený in Okarma 2002). Vendar pa nobena od teh raziskav ni bila opravljena na območju, kjer še živi tudi rjavi medved (*Ursus arctos*), ki bi zaradi svoje velikosti in dobrega voha lahko predstavljal pomembnega kleptoparazita za evrazijskega risa in vplival na njegovo stopnjo plenjenja. Zato sva izdelala preprost model, s katerim željva bolje spoznati možne vpliva kleptoprazitizma s strani rjavega medveda na stopnjo plenjenja pri evrazijskem risu na območju Severnih Dinaridov, kjer obe vrsti sobivata. Ob uporabi podatkov iz tuje literature in naših preliminarnih raziskav iz raziskovanega območja model predpostavlja bistveno povečanje stopnje plenjenja pri risu zaradi medvedjega prehranjevanja z ostanki plena. Ob predpostavki, da medvedi v povprečju najdejo risov plen drugi po uplenitvi (povprečje velja samo za primere, ko medved najde plen še pred koncem risovega hranjenja s tem plenom), se stopnja plenjenja poveča iz 60.8 na 70.3 kopitarjev na leto (porast za 15.6 %), v primeru, da medvedi najdejo plen v povprečju tretji dan, pa se stopnja plenjenja poveča za 7.2 %. Model je pokazal tudi, da je stopnja plenjenja precej odvisna tako od deleža ostankov plena, ki jih medved najde, kot od povprečnega časa od uplenitve do trenutka, ko medved najde plen (Sl. 1-2). Za boljše ovrednotenje vplivov kleptoparazitizma s strani rjavega medveda na stopnjo plenjenja evrazijskega risa bodo potrebni dodatni podatki o frekvenci, časovnem poteku in sezonskih razlikah pri obiskovanja ostankov risovega plena s strani medvedov. Upoštevati bo potrebno tudi sezonske razlike v prehrani risa in medveda ter oceniti sposobnosti risa, da kompenzira izgube zaradi kleptoparazitizma s povečanjem stopnje plenjenja. Podoben učinek kot pri kleptoparazitizmu s strani medveda lahko, verjetno sicer v manjši meri, pričakujemo tudi pri izgubah plena zaradi drugih večjih mrhovinarjev, kot npr. volka (*Canis lupus*) in divjega prašiča (*Sus scrofa*), ter zaradi odstranjevanja ostankov plena s strani človeka (Krofel in sod. 2008b). V splošnem priporočava, da bi se morali vplivi kleptoparazitizma upoštevati pri ocenjevanju vplivov plenjenja plenilcev na populacije divjadi in pri prizadevanjih za ohranitev ogroženih vrst plenilcev.

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