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Abstract. Recent technological developments in non-invasive methods facilitate study of the behaviour of elusive predators. We used two types of automatic digital video surveillance systems in combination with GPS telemetry to record feeding behaviour of wild Eurasian lynx (*Lynx lynx*), intraspecific prey sharing and scavenger activity at ungulate kill sites in the Dinaric Mountains. This approach proved an effective and mostly non-invasive way to obtain detailed data on the consumption of prey by lynx and kleptoparasites, especially when the advanced video system was used. Lynx spent a considerable amount of time in the vicinity of the kill site, but usually visited the carcass for feeding only once per night with a mean visit time of 35 min and most of the feeding occurred during the first half of the night. Lynx covered 83 % of prey remains, which seemed to be effective against avian scavengers that only found 17 % of the carcasses. We recorded six vertebrate species scavenging on lynx kills, with red fox (*Vulpes vulpes*) and brown bear (*Ursus arctos*) being the most frequent kleptoparasites. Based on our results, we provide recommendations for future research using this method, as well as outlining the pros and cons of advanced *vs.* simple video systems.

Key words: camera-trapping, prey sharing, scavengers, predation, *Lynx lynx*

Introduction

Recent technological developments in non-invasive animal monitoring methods have the potential to radically change and improve the way wildlife research is conducted (Long et al. 2008). This includes studies on the predation and feeding behaviour of elusive predators, as well as their intra- and inter-specific interactions. To study these aspects of predator ecology, researchers have traditionally used techniques such as direct observations from the ground or air (e.g. Molinari & Molinari-Jobin 2001, Hunter et al. 2007), animal tracking in snow or sand (e.g. Haglund 1966, Bothma & Le Riche 1986, Selva et al. 2005), and VHF telemetry (e.g. Okarma et al. 1997, Jobin et al. 2000, Krofel et al. 2006). While these techniques provide the desired results for some species in some regions, they are usually labour-intensive and costly. In addition, they cannot be used in all environments (e.g. areas with dense vegetation or with no suitable tracking substrate), or for all species (e.g. predominantly nocturnal species).

The development of global positioning system (GPS) telemetry has provided a tool to collect information on the foraging behaviour of carnivores, such as detecting kill sites and estimating searching and feeding times (see Merrill et al. 2010 for review). However, there are many aspects of the prey consumption process that are difficult to study with this method alone, including feeding and caching behaviour, detailed time course of feeding bouts, presence of kleptoparasites, and intra- and inter-specific interactions at prey remains.

Remote photography and automatic video surveillance has the potential to provide additional information difficult to obtain using GPS telemetry or traditional methods. Compared to direct observations, remote recording often substantially reduces research effort and costs, as well as researcher-related disturbance of animals (Cutler & Swann 1999, Bridges et al. 2004). Recently, this technique has been increasingly used in wildlife studies, especially for monitoring purposes, such as detecting the presence of individual species and estimating occupancy, relative and absolute abundances (Rovero & Zimmermann 2016). In addition to monitoring animal populations, this approach can be applied to study wildlife ecology and behaviour. For

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example, in the 1980s and 1990s analogue photography was used to study feeding bouts at predator kills (e.g. Hücht-Ciorga 1988, Pierce et al. 1998). The development of digital photography later improved the efficiency of this approach and nowadays the widespread use of automatic digital video surveillance (ADVS) enables the collection of detailed information on animal behaviour. ADVS is today being increasingly applied to behavioural and ecological studies, such as monitoring nesting behaviour and nest predation (Reif & Tornberg 2006, Gula et al. 2010), scavenger activity (Allen et al. 2016a), use of artificial feeding sites (Popova et al. 2017, Fležar et al. 2019), denning behaviour (Racheva et al. 2012), marking behaviour (Allen et al. 2016b), and intra- and inter-specific interactions (Lovich et al. 2014, Elbroch et al. 2017).

Here we applied ADVS techniques to study the feeding behaviour and intra- and inter-specific interactions of an elusive large carnivore, the Eurasian lynx (*Lynx lynx* (Linnaeus, 1758)) in a remote and inaccessible environment with dense vegetation in the northern Dinaric Mountains in Slovenia and Croatia. The Eurasian lynx is a mid-sized (12-35 kg) solitary predator, characterized by low population density, large home ranges, elusive behaviour, and crepuscular-nocturnal activity (Breitenmoser & Breitenmoser-Würsten 2008). Given the endangered status of many lynx populations, including the one in our study area (von Arx et al. 2004), there is a need for new cost-effective approaches to studying lynx ecology and behaviour.

The goals of our study were to test the applicability of two types of ADVS systems to provide data on the feeding behaviour of Eurasian lynx, potential intra-specific prey sharing among the lynx and kleptoparasitic interactions with scavenging species. Detailed information on Eurasian lynx feeding behaviour will improve our understanding of lynx' behaviour at kills and the potential effects of kleptoparasitism. This information can help improve the success of trapping at kill sites, which is often used to capture lynx for research purposes (i.e. telemetry studies). Furthermore, we compared data on prey use from video surveillance with data simultaneously obtained by GPS telemetry. This approach enabled us to test some of the assumptions currently used in telemetry studies without video surveillance (e.g. Belotti et al. 2018) to improve interpretation of telemetry data in future research.

We tested two types of ADVS system: 1) a sophisticated, custom-made video system with picture analyser (hereafter "advanced ADVS"), and 2) a simple,

low-cost commercial video system kit for wildlife surveillance (hereafter "simple ADVS"). Based on our findings, we provide a list of the advantages and deficiencies of both types of ADVS systems for behavioural and ecological studies of wildlife. We also provide recommendations that will help future studies of other mammals with similar behaviour that are difficult to study using traditional methods.

Study Area

The study was conducted in the northern part of the Dinaric Mountain Range (Central and south-east Europe), in the Snežnik-Javorniki and Kočevska regions of Slovenia and the Gorski Kotar region of Croatia (45°24′-45°47′ N and 14°15′-14°50′ E). Altitudes range from approximately 150 m above sea level to the peak of Mount Snežnik at 1796 m. Limestone and dolomites are the prevailing geological formations in the area, forming a characteristic rugged relief with numerous karst phenomena. The climate is a mix of influences from the Alps, the Mediterranean Sea and the Pannonian basin with an average annual temperature of 7 °C, ranging from an average monthly maximum of 18 °C to an average monthly minimum of –2 °C, and average annual precipitation of 1700 mm. Most of the area is covered by Dinaric fir and beech forests (*Omphalodo-Fagetum* s. lat.), with four dominant tree species: common beech (*Fagus sylvatica*), silver fir (*Abies alba*), Norway spruce (*Picea abies*), and sycamore (*Acer pseudoplatanus*). The area is mostly uninhabited by humans, with scattered villages dotting the valleys.

Eurasian lynx in this region belong to the Dinaric population, which is currently regarded as one of the most endangered populations in Europe (Krofel & Jerina 2016). Dinaric lynx mainly hunt wild ungulates, which together represent 88 % of the biomass consumed by lynx. Roe deer (*Capreolus capreolus*) are the main prey species (79 % of consumed biomass), and edible dormouse (*Glis glis*) and red deer (*Cervus elaphus*) the most important alternative prey, each representing approximately 7 % of consumed biomass (Krofel et al. 2011, 2014). The average size of home range of tracked lynx was 215 km^2 (Krofel 2012). Besides Eurasian lynx, brown bear (*Ursus arctos*) and grey wolf (*Canis lupus*) are present in the area, as well as several species of smaller carnivore.

Material and Methods

Video systems

We used two types of ADVS to monitor lynx kill sites, advanced and simple ADVS. The advanced

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ADVS we built ourselves. We used a motion-activated, infrared-sensitive IP camera system set (Mobotix M22M-Sec-Night; www.mobotix.com) with interchangeable lens, independent infrared light (840 nm), 2-3 external batteries (65-100 Ah), and external hard disk connected wirelessly to retain data in case of theft. Recording was activated through motion detection using image recognition, with two seconds prior to an event included in each recording. A single person usually needed approximately one hour to set up the video system. Most of this time was spent establishing the wireless connection between the camera and the hard disk, mounting all parts of the system, and programming the picture analyser for motion detection. Transport to remote areas without road access could be difficult for the advanced ADVS, as the system weighed around 60 kg, mainly due to the large batteries required.

Simple ADVS were commercial trail cameras (Scoutguard Sg580m and U-Way U150X) containing camera lens, pyroelectric infrared (PIR) sensors and infrared reflector. Unlike the advanced ADVS, this system did not permit capture of footage prior to each detected event (recording started with a delay of several seconds), changing camera lenses, using different infrared reflectors, establishing a wireless connection to the recording device, or defining only specific areas in the viewfinder where movement should be detected. It also had a limited range of adjustable settings; but it was easier to set up, usually taking less than 10 minutes. The total weight of the simple ADVS including batteries was 500-600 g.

To obtain an adequate overview of the area of interest and a balanced exposure, we placed the camera and an infrared light in a tree, usually about 2-4 meters above ground. Pilot studies showed that placing the camera and infrared light at this height caused less disturbance to the animals compared to cameras set at the eye level of the animal (M. Krofel, unpublished data). Although some animals (lynx and some of the scavengers) occasionally looked directly into the camera, they did not appear to be disturbed by it. The distance of the ADVS to prey remains was 5-10 meters.

Field work
In the period 2006-2012, we captured five lynx (three females and two males) and equipped them with GPS telemetry collars (TVP Positioning AB, Sweden and Vectronic Aerospace GmbH, Germany) using standard protocols (see Krofel et al. 2013 for details). All of the lynx were captured during winter and monitored for an average of 210 days. GPS collars were scheduled to attempt 7-8 GPS fixes per day. We used GPS location cluster analysis of lynx telemetry data to locate kill sites with prey remains of ungulates killed by lynx (see Krofel et al. 2013 for details). Kill sites were left undisturbed (except for deployment of the ADVS) and the carcasses were not fixed to the ground.

Video surveillance was conducted between February and August (one kill site in February, three in March, one in April, four in May, two in July, and one in August) on the kill sites of all five collared lynx (1-6 kill sites per lynx). Monitored carcasses were of nine adult roe deer, two roe deer calves (nine and 11 months old), and one red deer calf (nine months old). We estimated age based on the size of killed animals and after the video monitoring was completed collected lower jaw for precise aging (see Krofel et al. 2014 for details). ADVS (always one camera per kill site) was deployed at the kill sites on average 3.7 days (SD = 2.6) after the lynx killed their prey, therefore the first feeding bouts were usually missed. We usually revisited the kill site 2-4 days after deploying the video system to change batteries and move the camera if the position of the prey remains had changed. Prey remains were monitored until all soft tissue was consumed (either by lynx or scavengers).

To complement the range of scavenger species using lynx kill sites and examples of prey sharing among lynx we also included additional data obtained through snow tracking, direct observations and non-invasive genetic analyses (for details see Krofel 2012 and Sindičić et al. 2013). These data are reported separately from the video surveillance data.

Data processing and analysis
We manually checked all video recordings and noted (whenever possible) species recorded, time of arrival and departure, total time present at the kill site and the time spent feeding on prey remains. We calculated the duration of visits, return intervals (i.e. time between departure after one visit and arrival for the next), number of visits per night, arrival times in relation to sunset, and the proportion of time each species was recorded feeding on a carcass relative to the total time it was present at the kill site. When calculating duration of the visits, return intervals, and times from the first arrival to the last departure of the night, we considered only visits with known departure times (times of arrival were known for all visits). We used a Wilcoxon rank sum test to compare visit duration relative to number of visits per night. Data were
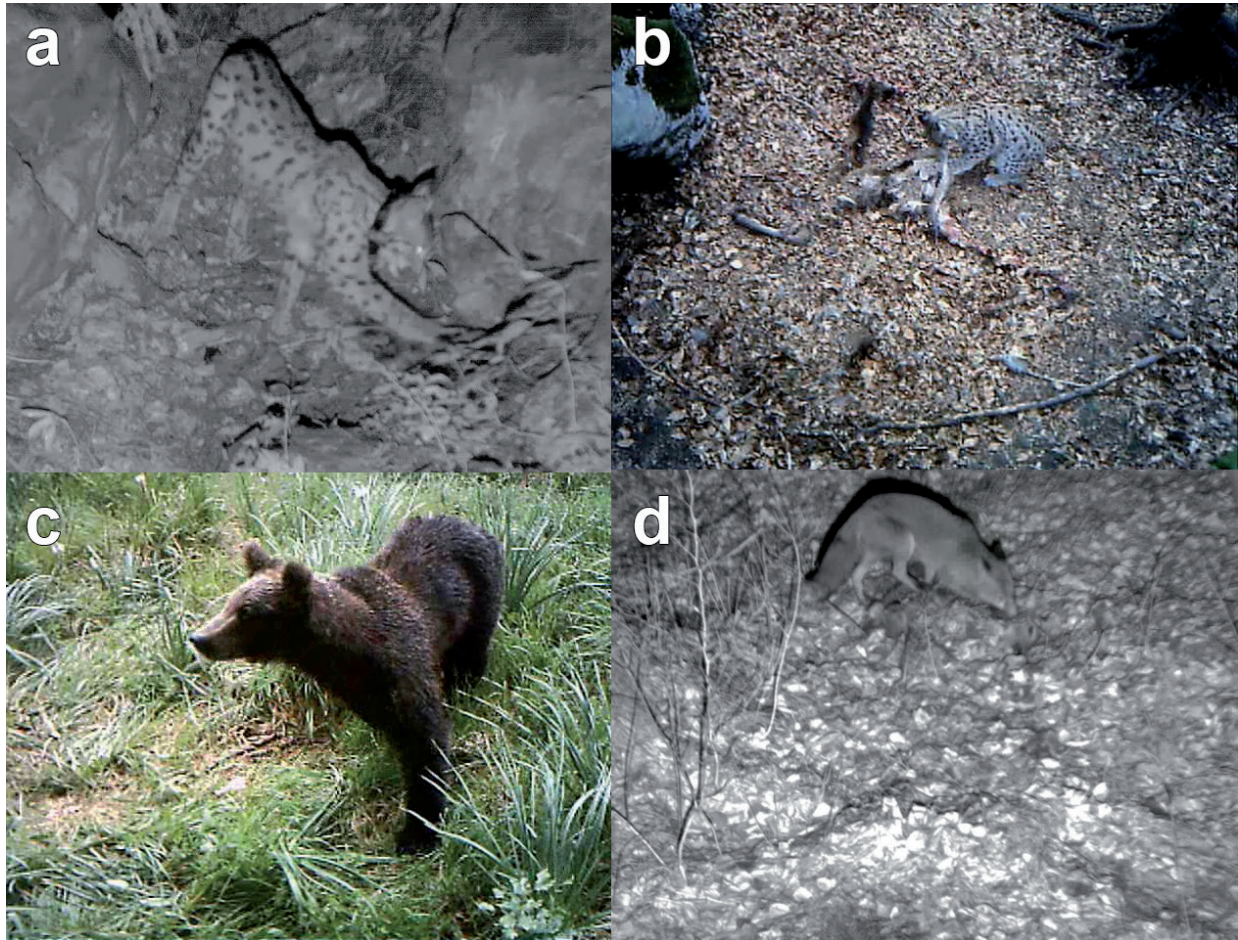
Fig. 1. Still photographs extracted from video recordings showing a collared female Eurasian lynx covering a roe deer carcass (a), uncollared male lynx feeding on a red deer calf (b), brown bear at a lynx kill site (c), and red fox eating prey remains (d). Images (a) and (d) were recorded with advanced (b) and (c) with simple automatic digital video system.

calculated for each adult lynx separately, even when a pair of adult lynx was feeding on the same prey remains. Females with kittens were considered as one (family) unit.

Coat patterns and other characteristics (e.g. presence of a GPS collar) were used to identify individual lynx. Unlike lynx, we were not able to distinguish between individuals of most scavenger species, so all results for video-recorded scavengers refer to species, not individuals. We defined each arrival of the same individual (assumed, in case of scavengers) that occurred more than 10 minutes after its previous departure as a separate visit. For scavenger species, we recorded the same data as for lynx and additionally also calculated the percentage of kill sites visited by each species, the percentage of time present at lynx kill sites (i.e. percentage of time a given species was recorded relative to the total time of all species present at kill sites), and the frequency of removing parts of the carcass (i.e. total number of recorded caching behaviours divided by total number of visits for each scavenger species). For lynx we also calculated how often they covered their prey. In this case we only used those visits with recorded departures since lynx typically cover their prey at the end of their visits.

According to the crepuscular-nocturnal activity pattern of lynx (Heurich et al. 2014) and many scavengers, we present visits to the kill site for each "night", which we defined as the 24-h period from noon (12:00) of one day until noon of the next. To distinguish between the visits in different light conditions, we defined "dark" as a period between the end of nautical twilight one day and the beginning of nautical twilight the next day, "twilight" as the period between sunset and the end of nautical twilight, and between the onset of nautical twilight and sunrise, and "day" as a period between sunrise and sunset (Krofel et al. 2013). Nautical twilight beginning and end times, and sunrise and sunset times in the study area were obtained from the online database of the US Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

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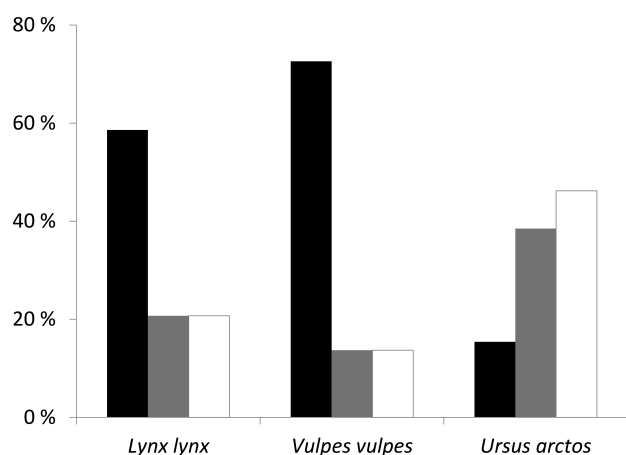
Fig. 2. Visits of Eurasian lynx (n = 29), red fox (n = 73) and brown bear (n = 13) at lynx kill sites in relation to temporal period (black = night, grey = twilight, white = day).

Finally, we measured the distances of each GPS location of collared lynx to the kill site (recorded in the field with a handheld GPS device) for time periods when kill sites were simultaneously monitored with the ADVS and calculated the proportion of GPS positions with lynx recorded at the carcass in relation to the distance between the kill site and GPS position of the lynx. Thus, on this basis we estimated how often lynx were actually feeding when they were located in the vicinity of a kill site according to the telemetry data.

Results

We deployed the ADVS at 12 lynx kill sites and monitored the consumption process over 54 nights for a total of 1263 hours. All of the surveyed kill sites were located in Dinaric fir and beech forests. We used the advanced ADVS at eight kill sites (25 nights) and simple ADVS at four kill sites (27 nights). In total we obtained 5 h 26 min of video recordings of lynx behaviour at kill sites (Fig. 1a-b), among which 4 h 52 min were recorded using advanced ADVS and 34 min using simple ADVS. Video recordings from both advanced and simple ADVS showed that lynx were actively feeding for 4 h 37 min (85 %). We also obtained 8 h 20 min of video recordings of other species present at the lynx kill sites (Fig. 1c-d), which included 5 h 3 min of recordings of their scavenging activity (feeding behaviour).

Lynx visits and consumption of prey remains
In 59 % of their visits, lynx arrived at the kill sites in the dark, 21 % during twilight, and 21 % during the day (n = 29; Fig. 2). On average, lynx arrived at the kill sites 71 ± 224 min (mean ± SD) after sunset (n = 29). When only the first arrivals of the night are considered, they arrived on average 47 ± 131 minutes after sunset (n = 20). The earliest arrival was at 12:56 or 352 minutes before sunset and the latest first arrival of the night at 22:32 or 201 minutes after sunset. On average, lynx visited prey remains 1.45 ± 0.69-times

Table 1. Vertebrate species recorded with automatic digital video surveillance at lynx kill sites in Slovenia and Croatia (n = 12 kills sites, 54 nights, 13 h 46 min of video recordings). Duration and number of visits are presented as mean ± SD with sample sizes in parentheses. Number of visits per night refers only to the nights when a given species was detected (number of these nights is presented in parentheses for each species). For the purposes of this study a "night" was defined as 24-h period from noon (12:00) of one day until noon of the next day.

	% kill sites visited	Total time present at kill sites (% of all species)	No. of visits	Visit duration (min)	% nights visited	Number of visits per night
Lynx lynx	75.0	39.5	29	35.4 ± 26.0 (17)	37.0	1.45 ± 0.69 (20)
Vulpes vulpes	58.3	47.2	73	8.5 ± 14.1 (73)	31.5	4.3 ± 3.0 (17)
Ursus arctos	33.3	6.6	13	6.9 ± 7.6 (10)	14.8	1.6 ± 0.5 (8)
Capreolus capreolus	16.7	0.1	2	10.3 (1)	3.7	1.0 ± 0.0 (2)
Strix uralensis	16.7	0.0	3	0.1 ± 0.0 (3)	3.7	1.5 ± 0.7 (2)
Rodentia	8.3	0.1	1	0.7 (1)	1.9	1.0 (1)
Glis glis	8.3	0.1	2	0.2 ± 0.1 (2)	3.7	1.0 ± 0.0 (2)
Salamandra atra	8.3	1.5	1	12.0 (1)	1.9	1.0 (1)
Erithacus rubecula	8.3	3.6	1	0.5 (1)	1.9	1.0 (1)
Turdus	8.3	0.1	1	0.0 (1)	1.9	1.0 (1)
Martes foina	8.3	0.3	1	2.4 (1)	1.9	1.0 (1)
Buteo buteo	8.3	0.2	1	1.9 (1)	1.9	1.0 (1)
Turdus merula	8.3	0.7	3	2.0 ± 1.5 (3)	1.9	3.0 (1)
Cervus elaphus	8.3	0.0	1	/	1.9	1.0 (1)
Sus scrofa	8.3	0.0	1	/	1.9	1.0 (1)

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Table 2. Visitation, feeding and caching behaviour of Eurasian lynx and scavenger species recorded with automatic digital video surveillance at lynx kill sites (n = 12, 54 nights) in Slovenia and Croatia. Time of arrival and return intervals are presented as mean ± SD with sample sizes in parentheses. Times of arrivals are presented relative to the time of sunset on a given day (negative values indicate hours before sunset, positive after sunset). First arrival refers to the first visit of the night. Return intervals for lynx refer to individual animals since we were able to identify individuals based on their coat patterns and presence of GPS collars. Individual identification was not possible for most scavenger species, therefore results presented for scavengers refer to species and not individuals.

	Total time feeding (min)	% time feeding	No. of cachings (per visit)	Time of arrival (h)	Time of first arrival (h)	Return intervals – all (min)	Return intervals – same night only (min)
Lynx lynx	276.8	84.9	0	1.2 ± 3.7 (29)	0.8 ± 2.2 (20)	363.5 ± 270.1 (10)	320.1 ± 283.6 (8)
Vulpes vulpes	267.1	68.5	0.2	3.4 ± 6.0 (73)	1.2 ± 2.0 (17)	231.5 ± 342.9 (66)	102.3 ± 122.4 (56)
Ursus arctos	33.7	61.6	0.5	−2.9 ± 8.0 (13)	−3.6 ± 7.8 (8)	865.6 ± 1411.9 (7)	48.2 ± 28.3 (4)
Martes foina	1.6	68.8	0	8.3 (1)	8.3 (1)	/	/
Rodentia	0.7	100.0	0	9.5 (1)	9.5 (1)	/	/
Buteo buteo	0.1	6.1	0	−1.3 (1)	−1.3 (1)	/	/
Sus scrofa	0.1	15.79	0	−4.3 (1)	−4.3 (1)	/	/

per night (mode: 1, max: 3; n = 20 nights, 29 visits). Mean return interval was 364 ± 270 min (min-max: 18.5-897 min; n = 10 pairs). When only visits during the same night are considered, mean return interval was 320 ± 284 min (min-max: 18.5-897 min, n = 8 pairs). The mean time from first arrival to last departure of the night was 286 ± 379 min (median: 89 min, min-max = 0.5-968 min, n = 8 pairs). The mean length of visit was 35.4 ± 26.0 min (n = 17) with the longest visit duration 83 minutes. When only

Table 3. Number of GPS lynx locations with confirmed lynx feeding among all recorded GPS locations during the video monitoring of kill sites with respect to the distance from the kill site.

Lynx distance to kill site (m)	GPS locations with confirmed feeding/all GPS locations
< 10	2/2
10-50	1/8
50-100	0/5
100-500	0/15

visits during which lynx were feeding are considered the mean visit lasted 40.0 ± 24.0 min (n = 15). We did not detect significant differences in visit duration when lynx visited prey remains once or several times per night (Wilcoxon rank sum test; all visits: W = 18, n = 17, p = 0.15; only first visits of the night: W = 22, n = 11, p = 0.25), nor between first and second visits of the night (W = 26, n = 17, p = 0.53).

Lynx departures from kill sites were recorded in 77 % and 44 % of visits monitored with advanced (n = 13) and simple ADVS (n = 16), respectively. In 53 % of recorded departures (n = 17) lynx covered prey remains before leaving. Ten of the 12 monitored prey remains (83 %) were covered at least once during the consumption process, which was indicated by the presence of a heap of material on or in the vicinity of the kill remains. When all field-checked lynx kill sites are considered (i.e. including those not recorded with ADVS; n = 57), lynx covered prey remains at least once during the consumption process at 75 % of the kill sites. Lynx usually started feeding on the hindquarters

Table 4. Pros and cons of advanced and simple automatic digital video surveillance (ADVS) systems.

	Advanced ADVS	Simple ADVS
Pros	- Reliable detection of larger animals present and continuous recording → arrivals, departures and feeding bouts are reliably recorded - Can be custom-built → enable adjustments to better fit the research goals	- Easy to use and set up → less disturbance of the kill site - Lower costs - Lower battery consumption - Easily obtainable
Cons	- High cost - More awkward and time-consuming to set up → more disturbance of the kill site and higher risk of causing lynx to abandon the kill - Appropriate knowledge required to build and operate the system - Higher battery consumption → need for heavier battery or frequent battery replacement	- Lower detection sensitivity → lower data reliability and more chance of data loss and bias towards detection of larger animals - Fewer adjustments possible

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and gradually proceeded towards the neck, removing and not eating intestines in the process.

We never recorded more than one lynx feeding on a carcass simultaneously, although in two cases two lynx took turns feeding on the same prey remains: once a female and her nine-month old kitten, and once an unknown male and a collared female.

Scavengers at lynx kill sites
From video recordings we recorded the presence of 14 vertebrate species at lynx kill sites, among which six species were recorded scavenging on lynx kills (Tables 1 and 2). In addition, we recorded five additional (i.e. not recorded with video surveillance) scavenger species at these and other lynx kill sites from tracks in snow and direct observations: grey wolf, mouse or vole (Muridae or Arvicollidae), raven (*Corvus corax*), jay (*Garrulus glandarius*), and coal tit (*Periparus ater*). Considering all species recorded at lynx kills sites using ADVS, scavengers spent 61 % of their time feeding at the kill sites.

Similarly to lynx, scavengers arrived to lynx kill sites primarily (58 %) during the dark and on average 96 ± 434 min after sunset (Table 2; n = 104). The exception was brown bears, which most often visited kill sites during the day (Fig. 2). We found notable differences in return intervals between different scavenger species. Red foxes (*Vulpes vulpes*) were the most common scavenger of lynx prey, both in terms of number of visits to kill sites (70 % of all scavenger visits; n = 104) and the proportion of kill sites where they were detected (58 %; Table 1). The second most common were brown bears, which was also the scavenger that most frequently removed parts of the carcasses from the kill sites (on average at every second visit; Table 2). In contrast to mammals, avian scavengers were only found at two (17 %) of the monitored carcasses.

Lynx use of prey remains in respect to telemetry data
We obtained 51 GPS lynx locations during ADVS monitoring of lynx kill sites. Among these, 30 were obtained < 500 m from the kill site, 15 < 100 m of the kill site and two within 10 m of the kill site. With ADVS we could confirm feeding by the lynx in both locations that were < 10 m from the kill site, 30 % of locations < 50 m from the kill site and none of the locations > 50 m from the kill site (Table 3).

Discussion
Video surveillance
Unlike some large carnivores that live in open habitats, the Eurasian lynx is difficult to observe in the wild.

Thus video surveillance of lynx kills presents a rare opportunity to observe their behaviour. The relatively long feeding time of this species (on average 3.2 days, range 0.5-6 days; Krofel et al. 2013) makes the combination of GPS telemetry, satellite or global system for mobile communications (GSM) data transfer and automatic video surveillance extremely valuable, as it enables fast detection of kill sites and monitoring of prey remains while consumption is still taking place. We were able to acquire data that would otherwise be almost impossible to obtain or would demand considerable effort. Video monitoring is also superior to direct observations due to lower disturbance to the animals, acquisition of more objective material, possible use of recordings for repeated analysis by several experts, potential use for future studies with different objectives or for educational purposes, monitoring during dark periods, and it is less time consuming for field personnel (Reif & Tornberg 2006). Video monitoring, however, also has some disadvantages compared to direct observations, such as limited area of observation and possible technical errors. Compared to photography, video monitoring gives more information, especially about behaviour (e.g. covering or moving the carcass and animal interactions). Compared to analogue equipment, digital video surveillance enables continuous monitoring even in poor light conditions, is less disturbing to the animals as IR light can be used, and it facilitates handling, analysis and storage of the collected material.

However, caution is needed when monitoring prey remains while the predator is still using the carcass as disturbance by humans can cause the lynx to abandon its kill (Krofel et al. 2008). In our study the lynx failed to return to the carcass to feed after deployment of ADVS in three cases (25 %). Lynx movements obtained through GPS telemetry suggest that in two of these cases the lynx had already abandoned the kill site before our arrival, while in one case (8 %) our disturbance probably caused the lynx to stop using the carcass. There might be considerable variation in individual tolerance to human presence at kill sites, and some animals can apparently become habituated to it, like the female lynx and its two kittens regularly observed directly from a tent by Molinari & Molinari-Jobin (2001). We advise that monitoring is terminated or the method changed if a given lynx is observed to abandon the kills in response to visits by the researcher. To reduce disturbance we also suggest that time spent at the kill site and the number of field personnel should be minimized. In addition,

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on-the-ground VHF telemetry can be used to determine lynx location before approaching the kill site. We assume that disturbance is lower when the lynx is further away from the kill site or when the researcher approaches the kill site from the opposite direction to where the lynx is located. However, this assumption still needs to be properly tested. During preparatory trials at other locations we found that the IR light source is best mounted a few meters above ground (e.g. on a tree), because the red glow of the 840 nm IR illuminator when set at the eye level of the animals can disturb them (M. Krofel et al., unpublished data). Location of light source is less important when illuminators with longer wave lengths are used (~940 nm, so called "black IR"), but these have considerably higher power consumption for the same illumination. According to our video recordings of animal behaviour, setting up ADVS a few meters above ground did not cause the lynx to abandon their kills. On the other hand, when our team was present at the kill site during attempts to recapture and sedate a lynx with a tranquilizing rifle, the lynx abandoned the prey in two out of three cases (M. Krofel et al., unpublished data).

Experience from using advanced and simple ADVS showed both systems have pros and cons (summarized in Table 4). Advanced ADVS enabled more reliable and less biased data detection (towards larger species), which makes this system superior for advanced behavioural studies and research requiring reliable detection of large and medium-sized animals. The advantages of simple ADVS include lower costs and fast deployment, which makes it more appropriate for studies requiring simultaneous monitoring of numerous sites and it reduces the disturbance to the kill site. Generally we found simple ADVS appropriate for documenting the presence and visitation rate of larger species, but calculating exact feeding times and especially recording times of departure was less reliable. Missing or moved carcasses between consecutive recordings also indicated that not all animal visits to the kill sites were recorded by the simple ADVS, something that did not happen with the advanced ADVS. Probably the main reason for this is a more sophisticated and precise motion detection with the advanced ADVS, which relied on a built-in picture analyser, where the user could precisely define areas in the recorded image where movement should be detected (e.g. on the carcass and main approach points to the kill site), as well as adjusting sensitivity. In contrast, the simple ADVS relied on less reliable PIR sensors and often stopped recording while lynx or scavengers were feeding and exhibiting limited movement. The simple ADVS also failed to record lynx leaving the kill site in more than half of the visits. This resulted in a lower amount of video footage obtained from the simple compared to the advanced ADVS despite a similar number of trap nights. The main drawback of the advanced ADVS was that considerably more effort was required to transport, deploy and maintain the system, as well as its higher cost. However, video surveillance technology is developing rapidly and newer systems with lighter batteries will be easier and faster to deploy, as well as more reasonably priced making the advanced ADVS systems an attractive option for future research.

Lynx behaviour

As the Dinaric lynx population is small and possibly heading towards extinction, our study included a relatively small number of animals. Nevertheless, we were able to obtain several hours of video footage of wild Eurasian lynx at the kill sites, which provided us with insights into the time course of their feeding behaviour. The duration of individual feeding bouts and total time spent at the kill sites we recorded was considerably shorter compared to the female with two kittens that were directly observed at the kill sites for several nights by Molinari & Molinari-Jobin (2001) in the Swiss Jura Mountains. At present it is difficult to ascertain whether the differences are related to the presence of kittens or whether they are the consequence of individual variability or possible effects of human presence. Due to the relatively small sample size of animals monitored, both our own and the Swiss observations may not be representative for all lynx and should be used with caution as there could be important differences among individuals or different sex or age categories. For example, monitoring of feeding bouts of cougars (*Puma concolor*) showed that females with kittens visited kill sites significantly earlier in the night compared to other social groups (Pierce et al. 1998).

In most cases, monitored lynx in the Dinaric Mountains visited prey only once per night, which is in contrast to observations from Poland, where lynx visited kill sites at least twice daily (Okarma et al. 1997). However, observations from Poland were made using only data from VHF telemetry, so it is possible that lynx sometimes came into the vicinity of the prey without actually approaching and feeding on the carcass. Researchers sometimes interpret telemetry

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data by assuming that predator presence in the vicinity of the kill site indicates feeding (e.g. when present within 100 m of the killing site; Belotti et al. 2018). However, our combined data from video surveillance and simultaneous GPS telemetry tracking showed that this assumption is not always correct, as lynx were actually present at the carcasses only in 20 % of the cases when GPS locations were located within 100 m from the kill sites (all of feeding bouts were recorded when GPS locations were < 50 m and even for this distance feeding was confirmed only in 30 % of cases; Table 3). Therefore, we urge researchers to use caution when using only telemetry to study feeding behaviour and we suggest the use of ADVS for this purpose.

During the consumption process following a successful hunt, lynx spend most of the nights close to the kill site based on GPS telemetry data (Krofel et al. 2013), but the video surveillance data presented here indicate that they are actually present at the carcasses and feeding for relatively short periods each night. We also noted that most of the feeding occurred in the early hours of the night. This finding is in accordance with the times of the first visits obtained from lynx capture times at kill sites (Breitenmoser & Breitenmoser-Würsten 2008; M. Krofel et al., unpublished data). The timing of feeding bouts in our study corresponded with the first peak in lynx nocturnal activity (Heurich et al. 2014), while the second peak in the second half of the night appears to be connected with other behaviours such as hunting and patrolling their territory. This observation fits with the times of the first GPS locations at the kill sites, which we assume indicate the approximate time of making the kill; we noted that 45 % of successful hunts took place in the second half of the night (M. Krofel et al., unpublished data).

Female lynx are known to share their kills with dependent offspring (Breitenmoser & Breitenmoser-Würsten 2008), which was also documented in our case. Less is known about prey sharing among independent lynx. We noted one such case using ADVS when a collared female and unknown male were alternately using the same kill. Through snow tracking we documented another such case of alternating feeding by an adult male and female. We established through non-invasive genetic analysis that the prey was killed by the male. Both cases of prey sharing among adult males and females occurred during the mating season (February-March) thus prey sharing was likely connected with the close proximity of the mating pair. We have not recorded prey sharing among independent individuals outside the mating season, which suggests that this behaviour is less frequent in Eurasian lynx compared to some other felids, such as cougars (Elbroch et al. 2017).

Scavengers using lynx kills
Scavenging is an important ecosystem process (Wilson & Wolkovich 2011) and scavengers can significantly affect the predation, reproduction, social system and evolution of predators (Cooper 1991, Iyengar 2008, Balme et al. 2017, Tallian et al. 2017), including Eurasian lynx (Mattisson et al. 2011, Krofel et al. 2012, Krofel & Jerina 2016). Video surveillance is probably the most reliable and cost-efficient method of monitoring scavenging activities and kleptoparasitic interactions, at least for larger vertebrates. It enables detailed timing of scavenger visits and their behaviour, as demonstrated in the present study. On average, scavengers in Dinaric Mountains spent a similar amount of time feeding on lynx prey remains as the lynx. This finding suggests that lynx may lose a considerable amount of their prey to kleptoparasites. Further research incorporating controlled feeding trials on various scavengers in captivity could be used to translate the feeding times recorded in this study into prey biomass consumed by individual species.

The video recordings analysed here indicate that red fox and brown bear are the most important kleptoparasites of Eurasian lynx in the Dinaric Mountains, in terms of the proportion of lynx kills found by a kleptoparasite, time spent feeding and frequency of caching behaviour. This result confirms previous research in the area based on snow tracking and other signs of evidence (Krofel 2012), which in combination with GPS telemetry showed that lynx lost 32 % of their kills and 15 % of all consumable biomass to scavenging bears, which managed to displace the lynx from their kill sites and reduced the number of days they were able to feed (Krofel et al. 2012). These values correspond well with data obtained in this study (33 % of lynx kill sites were found by bears; Table 1).

Both bears and foxes returned to the carcasses more often per night than the lynx. This result was likely related to longer visit duration in the case of lynx, which often became satiated for the whole night with a single meal. Bears and foxes on the other hand made several shorter visits and often removed parts of the carcasses to consume away from the kill site. In the case of foxes, this could be connected with risk of attack by lynx, since lynx are known to kill foxes and comprise 4 % of the diet of lynx in the study area (Krofel et

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al. 2011). Nevertheless, this effect was not sufficient to prevent foxes from using lynx prey remains, even during nights when lynx remained in the vicinity of the kill site. When comparing return intervals between scavengers and lynx it should be kept in mind that among scavengers we could not identify individuals (in contrast to lynx). Therefore, higher return rates for scavengers could also by the result of more than one individual visiting the kill site.

Among scavengers on lynx kills, mammals considerably outnumbered avian scavengers. This finding is in contrast to ungulate carcasses killed by grey wolves or found dead, which were monitored with video surveillance or photo-traps in forests in the same study area, where birds were considerably more frequent scavengers (Krofel 2011). We suggest that the reason for this difference could be in lynx' anti-kleptoparasitic behaviour of covering prey remains; avian scavengers in European forests locate carcasses primarily by vision (Hücht-Ciorga 1988) and could explain the high frequency of prey covering by lynx.

Conclusions and implications

We demonstrated that use of the ADVS, especially the advanced type, can provide detailed information and precise estimates of the timing of the consumption process of ungulate carcasses killed by Eurasian lynx. Especially when used in combination with GPS telemetry, this is an efficient and largely non-invasive method to study the ecology and behaviour of an elusive predator and several kleptoparasites that scavenge on the remains of its prey.

The data we present here can contribute to planning the capture of lynx at their kill sites for research purposes, and aid in interpretation of telemetry data regarding the use of prey remains. We believe that many of our findings can be applied to other felids, such as leopards (*Panthera pardus*), tigers (*P. tigris*), snow leopards (*P. uncia*), and cougars, as well as other predators that repeatedly return to their kill sites, such as grey wolves, wild dogs (*Lycaon pictus*), wolverines (*Gulo gulo*) and some hyenids. Similar approaches can be used for monitoring other kinds of frequently used feeding sites or dens (Long et al. 2008, Rovero & Zimmermann 2016). We believe that the rapid technological development of camera and storage systems, paired with increasingly cheaper and more efficient battery technology, will make these systems more efficient, cost-effective, and easier to deploy in the future. These developments will facilitate further advances in research and understanding wildlife behaviour and ecology.

Acknowledgements

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