

Of rodents and foxes: Faunal activity and scavenging at carcasses in a Central European (Swiss) forest

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Abstract

Vertebrate activity can significantly affect forensic investigations. Trauma interpretation is impaired when vertebrates scavenge on injuries and inflict damage, and scavengers can hinder the recovery of human remains through dispersal. However, forensic scavenging research is scarce in Europe and lacking for Switzerland.

We conducted a 2-month baseline study followed by a 5-month experiment with six domestic pig (*Sus scrofa domestica*) carcasses in a Swiss forest during summer through fall. We monitored each three caged and uncaged carcasses with camera traps and documented vertebrate activities and taphonomic signatures on the remains, and calculated the scavenging rate.

Rodents (*Apodemus sylvaticus*, *A. flavicollis*, and *Myodes glareolus*) and red fox (*Vulpes vulpes*) scavenged and dispersed the remains. All carcasses and ca. 4 % of the recovered bones exhibited scavenging marks, including wet bone scavenging (rodents) mainly on small bones and protruding features, and scoring (red fox) on a rib. The presence of a carcass, decomposition stage, sun exposure and use of cages significantly influenced the number of vertebrate visits at the plots. Rodents preferentially scavenged caged, skeletonized remains at tree-covered plots and modified perimortem wounds beyond recognition. The few carnivore sightings focused on uncaged specimens.

The generally low scavenger participation was likely season-related, due to the rapid maggot infestation, or human presence. Future studies should evaluate the influence of these variables, including sun exposure. Our study informs forensic casework by highlighting the importance of rodents and to a lesser degree foxes as vertebrate scavengers and dispersal agents in central European temperate forests.

Keywords

forensic anthropology, taphonomy, scavenging, rodents, red fox (*Vulpes vulpes*), dispersal

Highlights

- Red fox and particularly rodents scavenged and dispersed pig bones and desiccated soft tissue
- All carcasses and 4 % of the recovered bones exhibited scavenging damage
- Scavenging damage included scores (by foxes) and wet-bone gnawing (by rodents)
- Rodent scavenging altered a perimortem wound beyond recognition
- Scavenger, sun exposure, cages and decomposition stage influenced the number of vertebrate visits

1. Introduction

In forensic investigations of human remains, the evaluation of any extrinsic factor capable of affecting a cadaver, e.g., in its decomposition rate or disarticulation pattern, is of primary relevance. One such factor is vertebrate scavenging, a frequent occurrence in forensic casework that can severely affect trauma interpretation and other analyses [1-5].

A common challenge when analyzing trauma is equifinality, e.g., taphonomic processes leading to body or skeletal damage resembling damage caused by interpersonal violence [6-11]. The distinction between perimortem trauma and postmortem damage is not always straightforward, and misinterpretations can have serious legal consequences. Furthermore, many scavengers are interested in the internal tissues of cadavers but are often unable to access the inner cavities. Therefore, they may start feeding at available entry points such as blunt impact and gunshot wounds [12, 13]. While doing so, the scavengers unavoidably modify these lesions or even entirely remove them, causing a loss of crucial information [12-14]. Carnivores typically leave tooth pits, punctures, scores and furrows on bones, and canids especially target the trabecula-rich ends of long bones to access the bone marrow [15]. Rodents, on the other hand, often create parallel or fan-shaped striations at exposed bone parts or cause a deep gouging into cancellous bones, called wet-bone gnawing [15, 16].

Both the recovery and subsequent analysis of human remains, including establishing a biological profile, and the interpretation of the scene are often impaired due to faunal-induced dispersal [3, 5, 17-20]. This is true especially in forensic anthropological cases, which often involve extended postmortem intervals (PMI) and outdoor exposed contexts [3]. Vertebrate scavengers are among the main taphonomic agents for dispersal. They predominantly disperse bones in the course of feeding on the remains, by moving around at the scene, or by deliberately removing body parts and bones to feed in isolation or cache them [14, 15, 21]. The latter behavior is known for many vertebrate taxa, including canids [18, 22], mustelids [12, 18], rodents [23, 24] and birds [25].

Many mammal and avian species engage in scavenging, and their scavenging activity and patterns depend on species, season, food availability, microclimate and interactions with other taxa [26-28]. The knowledge about species-specific scavenging patterns can help to interpret evidence more accurately and adjust search strategies [15, 19, 29]. For instance, Young et al. [29] found that police searchers who were briefed on red fox (*Vulpes vulpes*) scavenging and dispersal behavior recovered significantly more bones than those without previous knowledge.

Previous forensic experiments focusing on outdoor scavenging and dispersal were mainly conducted in North America [30-33], South Africa [34-37], and Australia [38-41]. Similar forensically-oriented studies from Europe, although scarce [42, 43], are limited to the UK [13, 18] and Spain [44]. Conversely, no systematic research on vertebrate scavenging of human remains or human proxies is available for Switzerland, despite empirical evidence of its presence in casework [5, 45]. This lack of data hampers regional investigations and it is therefore important to investigate vertebrate scavenging further, e.g., the taxa that are involved and their associated damage – specifically focused on species abundant in Switzerland and throughout Europe.

Our study stems from the above considerations and aims at enhancing the current knowledge about vertebrate scavenging activity in a specific, poorly investigated ecological setting. By studying the postmortem changes on six pig (*Sus scrofa domesticus*) carcasses in a temperate forest environment of Central Europe (Switzerland) for five months, we addressed the following questions:

- a) Which vertebrate scavengers are likely to access and modify these porcine remains?
- b) What damage on soft tissue and skeletal remains results from vertebrate scavengers?
- c) Which and how many skeletal elements can be expected to be scavenged?

2. Material and Methods

Our research design considers recently published recommendations on forensic scavenging experiments [43], including, whenever applicable, the ARRIVE guidelines (Animal Research: Reporting of *In Vivo* Experiments) [46].

Location and specimens

The location of our experiments is the forest habitat of Geissmont (Bern region, Switzerland: 46°59'37.0" N; 7°33'58.9" E, altitude ca. 750 m). We selected this specific location because human remains in Europe are frequently recovered in (suburban) forests [5, 47, 48]. Ecological features include a hilly mixed flora, dominated by common beech (*Fagus sylvatica*) and silver fir (*Abies alba*) trees and located within the Köppen-Geiger climate zone Cfb [49]. The average annual temperature is 9.3 °C (15.1 °C for the study interval), and the annual rainfall is 1021 mm (454 mm for the study interval) [50, 51]. Occasional forestry work, such as tree felling, and passers-by were present in the area before and during the study period. The nearest settlement was ca. 1.5 km away from the experimental site.

We studied six unclothed domestic pig carcasses of ca. 6 months age and 49-51 kg mass, following recommendations for cadaver weights in taphonomy experiments [52], bought dead from a local meat production farmer. The pigs were numbed (head) and killed (heart) by electric shocks in compliance with the Swiss national Animal Protection Ordinance (SR 455.1, Kap.8 TSchV of April 23, 2008) and under supervision of the veterinary office. The electric shocks caused burn lesions on the skin, henceforth addressed as perimortem wounds. The pig carcasses were deployed within four hours of death and without any treatment (e.g., no artificial cooling). The experiment was approved by the veterinary office of the Canton of Bern, and further ethical clearances were not applicable due to the specimens under study being dead.

Study design

We defined nine plots separated by at least 50 m distance in between to ensure minimal independent decomposition processes [43]. The maximum extent of the study area was ca. 300 x 200 m. Before the

experiment, we carried out a baseline study without carcasses to document the local wildlife at each plot. This was done for two months (April-June 2021) using two motion-activated infrared wildlife cameras (Braun Scouting Camera Black 1300 and Crenova Trail Camera 4K) per plot, one being at the same position as during the experiment and the other observing the wider area of the plot. Following this preliminary study, we positioned the pig carcasses and ran the experiment for five months (June 18th to November 14th in 2021). We chose the summer/fall season because human remains with longer postmortem intervals (PMI) are often discovered during this period due to increased outdoor activities and lack of snow cover [5]. Spatially, the nine plots (six pigs and three negative controls without pigs, each plot measuring 2 x 2 m staked off with bamboo sticks) formed three triangles, each containing one caged pig, one uncaged pig and one control plot (Figure 1). The control plots served to evaluate the influence of carcasses on the faunal activity. All pigs were placed on a metal grid for easier soil sampling beneath the carcasses for concurrent research, and three pigs were caged to exclude large scavengers (zinc-plated wire cage of 5 x 5 cm mesh size), as suggested previously [31, 43, 53, 54]. One of the triangles was located in a clearing with partly direct sunlight and a lack of tree cover, the two others beneath tree canopy were mostly shaded. During the experiment, plots were monitored by three (pig plots) or one (control plots) camera traps, with the main camera placed at the ventral side of the carcasses, one camera covering either head or tail side and the third camera a bit further away to oversee a larger area. The main cameras were used for analyses, and backup cameras were used in cases where the main camera failed temporarily, e.g., due to SD card errors. However, all recordings were screened in case a vertebrate was captured by the backup but not by the main cameras. Camera traps recorded date and time and were set to the highest sensitivity and to record three consecutive photographs plus a 10-second-video once triggered, with a 12-second interval in-between activations. After the experiment began (deposition day), duration is given in post-depositional days (PDD). On-site visits were conducted daily (PDD 1-10), every second day (PDD 10-20), every third day (PDD 20-38), weekly (PDD 38-66) and biweekly (PDD 66-149). Visits lasted less than one hour per plot and comprised non-invasive (documentation, SD-card changes), less invasive (collection of entomological

samples) and in total five more invasive interventions (soil sampling) throughout the entire study period. Soil was sampled while the ground grid beneath the carcass was lifted.

Data collection

Details on decomposition observed in our specimens can be found in a previous publication [55]. We documented the carcasses photographically during site visits. Directly after site visits, we correlated potential damage temporally with the camera trap recordings. Likewise, we identified vertebrates from the camera trap footage to the lowest possible taxonomic level using standard works [56, 57]. When the remains were completely skeletonized apart from isolated desiccated skin flaps after ca. five months, two anthropologists (first author and a helper) recovered the pig bones by manually filtering through the leaf litter of the plot areas (2 x 2 m), working from the center outwards. We collected bones from outside the plots if spotted readily, but did not search the periphery systematically. We calculated the recovery rate as percentage from an estimated total of 394 bones per pig, counting epiphyses as separate bones. The detailed bone count is documented in the supplementary document (Table S1). After recovery, we cleaned the bones with tap water and analyzed the scavenging defects macroscopically by visual inspection with the help of magnifying lenses, naming the detected damage according to Pokines [15]. All damaged bones were photographed and the damage was assessed qualitatively from photographs by two authors, who assigned the observed damage to the inflicting scavenger species by comparing them with descriptions from the literature [15, 42, 58], and by consulting our camera trap images that show the potential scavenger in action with the region of the carcass scavenged. The size of the damages was measured using the scales in the photographs. We calculated the scavenging rate as percentage of bones with scavenging marks out of the total of recovered bones.

The images and videos were processed using the software Timelapse2 (V2.3.0.6) [59]. One trigger resulted in three photographs and one video. When two triggers by the same species occurred five minutes or less apart, we counted the triggers as one single visit, assuming it is the same individual

[54]. Every visit was then assigned an activity (Figure 2): "background" (vertebrate outside of plot square), "interacting" (vertebrate within plot square, whether during the baseline study or the experiment), "feeding other" (feeding on non-porcine material, e.g., maggots), "scavenging" (feeding on pig material), or "transporting" (moving pig material at least 10 cm from original location). If the vertebrate performed two or more of these activities, the activity with the highest level of pig interaction was noted, starting from background (low level), interacting, feeding other, scavenging to transporting (high level).

Statistical analysis

We conducted statistical analyses on the subset of data points resulting from the experiment (without the baseline study). First, we performed a multiple correspondence analysis (MCA) with all variables expressing differences in: visiting taxon, decomposition stage (only of pig plots), presence/absence of cage, plot exposition to /protection from sunlight, as well as the activity. We then plotted the first two dimensions and performed a hierarchical cluster analysis (Ward method) on the complete set of dimensions (100 % of inertia). Subsequently, we applied a generalized linear model (GLM) to test for the statistical significance of the observed associations between variables and the total sum of visits, applying a Poisson distribution and a log link function. Decomposition stage 4 (skeletonization) lasted longer than the other stages, likely biasing the results (e.g., a higher number of visits simply due to a longer exposure of the pig to potential visitors). Therefore, we included an additional variable in the model that expresses the number of observation days by stage. To check if the presence of a carcass actually influences the number of vertebrate visits, we converted the number of visits-variable to a binomial one (plot visited vs. not visited) and then performed a logistic model with pig carcass presence and vertebrate taxon as factors. We performed all analyses with JMP®, Version 17.0.0. SAS Institute Inc., Cary, NC, 1989–2023, and setting alpha at 0.05.

All data supporting this study are included within the article and/or supporting materials.

3. Results

During the experiment, daily mean temperatures ranged between 1.9 – 23.7 °C (mean of 14.4 ± 5.4 °C) and rainfall varied between 0 – 48.3 mm per day (total 577.9 mm, mean of 3.9 ± 8.3 mm).

Vertebrate presence and activity

From a total of 3013 faunal vertebrate visits, 33 taxa were captured by the camera traps with 13 images showing undetermined vertebrates (Table 1). Undetermined vertebrates resulted from blurred or incomplete images of the animals, for instance. We classified all mammals and birds into five groups: birds, carnivores, deer, rodents, and wild boar. We excluded amphibian visits from further analyses due to their limited forensic relevance and poikilothermic nature, making camera-trap detection more unreliable. During the 2-month baseline study, the average number of total visits per plot was 105.7 for control and 131.5 for pig plots (1.9 and 2.4 per day, respectively). During the 5-month experiment, there was an average of 47.7 visits per control plot and 270.2 per pig plot (0.3 and 1.8 per day, respectively). Figures 3 and 4 show an averaged overview of presence and activity levels of the included groups. The control plots show a decrease of visits for all taxa ca. two weeks after the experiment started until the end. At the pig plots, deer and wild boars were present during the baseline study but not during the experiment. Carnivores were absent during the early experimental phase but present after ca. eight weeks, while avian visits highly increased in the advanced decomposition and early skeletonization phases. Rodent activity was high overall, with a peak at the beginning of the baseline study and again at the beginning of the skeletonization phase. Towards the end of the experiment, rodent visits became fewer overall. Apart from the pre-defined activities, we also found rodents occasionally to climb the cages or bamboo sticks. The data gap in the baseline study (May 3 to 5, 2021) is due to collective camera failure because of incompatible SD-cards.

The results of the multiple correspondence analysis (MCA) and the hierarchical cluster analysis showed a close proximity between rodents and scavenging, transporting, the skeletonized decomposition stage, shaded and to a lesser extend caged plots (Figure 5a and b). Carnivores were mainly in the

background of uncaged pigs in the early decomposition stage. Birds were associated with the advanced decomposition stage and sun-exposed plots but also interacted and fed on non-porcine material. Deer were captured during early decomposition and in the background.

We further illustrate these trends by plotting the relative frequency of each activity for each taxon and decomposition stage (Figure 6). These results show that the skeletonized stage was most diverse in terms of activities, with scavenging occurring during the advanced decomposition (rodents) and skeletonized (rodents, carnivores) phases. For deer and carnivores, background activity predominated.

The effect of each variable in the two generalized linear model (GLM) analyses is shown in Table 2. All variables are significantly associated with the number of visits per plot, including taxon, sun-exposed or shaded plots, presence or absence of a cage, and decomposition stage. Furthermore, plots with caged pigs are significantly more likely to be visited by vertebrates than plots with uncaged carcasses, and sun-exposed plots received significantly more visits than shaded plots.

The logistic model showed that carcass presence and taxon significantly influenced whether a plot was visited or not (Table 3a). Furthermore, the related odd ratios indicate that a plot with a carcass is 8.3 times more likely to be visited than a control plot (Table 3b). The output of the logistic model also confirms the differences in visits between taxa, with rodents being 9.9 times more likely to visit a plot compared to carnivores, and 90.3 times more likely compared to deer.

Based on the camera trap footage, two taxa scavenged the pig remains; carnivores (red fox) and rodents (bank vole, *Myodes glareolus*, wood mouse *Apodemus sylvaticus*, and yellow-necked mouse *A. flavicollis*). A red fox was captured feeding on soft tissue remnants and bones of Pig 1 on PDD 64 and transporting them on PDD 120. Rodent scavenging happened between PDD 8-141, with a nocturnal (8 p.m. to 7 a.m.) scavenging rate of 94.8 % (201/212) for *Apodemus* spp. and 66.0 % (99/150) for bank voles. On camera, we captured *Apodemus* spp. scavenging on pigs P2 (n=27), P3 (n=95), P5 (n=1) and P6 (n=89), and bank vole scavenging on P2 (n=150). We did not observe rodent scavenging at P1 and P4 on the camera footage.

Scavenging damage

We recovered 1704 bones in total, resulting in a recovery rate of 72.1 % (1704/2364), with mainly smaller bones such as vertebrae, carpals and tarsals, metacarpals and metatarsals, and phalanges missing (Table 4). Of the recovered bones, 3.8 % (65/1704) presented with traces of scavenging. We noted scoring (n=1), wet bone gnawing (n=64), and notches along the margin (n=1), but no tooth pits and punctures. The following recovered skeletal elements did not exhibit any scavenging traces: cranium, mandible, ulna, coxal bones, fibula, distal phalanges, sesamoids and hyoids.

Based on the camera trap footage, rodent gnawing was targeted particularly at soft tissue (64.6 %, 234/362) and less intensively on bone (14.4 %, 52/362). Whether the feeding was aimed at soft tissue or bone remained unclear in several cases (21.0 %, 76/362). We further recorded nine incidents where small rodents transported bones belonging to P3 (n=6) and P6 (n=3) between PDD 20-143. We did not observe rodent scavenging at P1 and P4 on the camera footage, but despite that, both pigs exhibited rodent-typical scavenging traces on the bones and soft tissue. Therefore, although scavenging by small rodents was frequent they were not always photographically captured, possibly due to their size.

The bone damage resulting from fox scavenging (Figure 7a) comprised several parallel, ca. 1-1.5 mm wide scores perpendicular to the shaft axis on a rib of P1 (Figure 7b), but no other scavenging damage types. We attributed the fox as the responsible scavenger because of video footage (a fox displaced this rib) and because of the damage morphology (not consistent with scavenging by the other animals captured at the time). The fox also removed a large patch of desiccated skin with adhering bones (PDD 64) and left it ca. eight meters away. A fox later marked it with urine (PDD 120) and carried the skin away entirely, as captured by the camera traps.

We attributed the remaining scavenging damage to rodents based on footage of the scavenging, the exclusion of other taxa via camera trap footage, and based on literature descriptions. Rodents caused soft tissue damage in the form of parallel striations along the margins of perimortem skin wounds, obscuring the shape and size of them (Figure 8a). We further noted parallel striations on a rib cartilage

(Figure 8b) and lacerated skin borders with irregular margins of brighter color than the rest of the skin (Figure 8c). Bones were especially susceptible to rodent scavenging at protruding features such as margins and processes (Figure 9a-d) and showed wet-bone gnawing ranging from single scrapings to larger-area (ca. 5 x 5 cm) destructions (Figure 9e). The rodent gnawing mainly affected cortical bone and usually did not penetrate deep into the underlying trabecular material. In some cases, we found semilunar notches along the cortical bone margins (Figure 9b). We noted bone flakes lying on the ground around some of the gnawed bones (Figure 9f). Based on the camera trap footage and the bone examination alone, we were not able to distinguish between the damage caused by bank voles and *Apodemus* spp.. We observed no pits, punctures or scores resulting from rodent scavenging.

4. Discussion

Our study aimed at identifying vertebrate taphonomic agents in a Central European (Swiss) temperate forest, to explore their scavenging activity and to document their inflicted damage on pig carcasses.

Vertebrate presence and activity

The observed range of vertebrate taxa and particularly scavengers is consistent with what would be expected in a central European forest in this location. However, large carnivores (apart from lynx) were absent and wild boar only present during the baseline study. The decrease in daily number of vertebrate visits during the experiment compared to the baseline study is more eminent and present for all taxa at control plots, while at pig plots, the decrease is mainly apparent for deer, carnivores and wild boar. Although humans already frequented our study area before the experiment, the researcher presence was high during the study. This entailed an increased amount of human scent in the area, potentially disturbing vertebrates [60-62]. Therefore, our frequent sampling visits (including soil sampling) are a possible explanation for the decrease in vertebrate abundance, specifically of deer and carnivores [60, 63].

At the control plots, the number of visits shortly increase for rodents and birds when the experiment started and then decreased for the rest of the study. In terms of activities at the control plots, the shift

from mainly background during the baseline study to mainly interacting activity during the experiment could be associated with the animals exploring the research material such as bamboo sticks or info tags. At the pig plots, the opposite trend was observed with mainly interacting during the baseline study, then mainly background until one week after the experiments start, and after that mainly interacting again. This could either be due to initial skepticism towards the pig carcasses or the human presence, which was daily in the first few days and then decreased, giving the vertebrates longer undisturbed intervals. The comparison shows that control plot data differs from baseline study data. This can either point to the 50 m not being enough distance between plots to assure independence of the control plots from carcass plots, to human presence negatively affecting the animal presence, or to differences in vertebrate behavior due to time of the year (baseline study April to June, experiment June to November). The latter two options are discussed further below.

A previous study suggested an association between decomposition stage and visits by foxes, with foxes showing a preference for remains in early decomposition [18]. In our case, visits and scavenging by foxes was observed only at skeletonized remains. This may be partly due to the rather short intervals for the early and advanced decomposition stage in our experiments (mean: seven and 13 days, respectively), counterbalanced by a more extended skeletonized phase (mean: 129 days).

Previous research highlighted an influence of cages on vertebrate scavenger behavior, especially a decrease of scavenging efficiency when larger scavengers were excluded [53, 54]. This could not be observed in our study because the large vertebrate scavenging rate was low overall. However, the cages did influence the number of visits by rodents. In our study, rodents preferred caged specimens in the shade, possibly due to the wire and tree canopy serving as protection from predators. Furthermore, the metal grid beneath the carcasses could have worked as a deterrent for the vertebrates. However, it did not seem to affect the rodents, and when foxes were captured in the plot area, they were standing on the grid. Therefore, we do not think that the grid deterred the vertebrates.

The avian visits and their feeding on non-porcine material increased in our experiment during the advanced decomposition, with blow fly larval masses serving as a food source for the birds. This has

been previously observed in multiple studies [13, 32, 34, 64, 65]. The increase of birds at sun-exposed plots may possibly be due to the facilitated spotting of food from above or of predators while feeding on the ground. On the other hand, a study from the Netherlands found that tree cover does not influence the carcass detection time by avian and mammal facultative scavengers [66].

Studies that mention scavenging rates calculated from the number of bones with gnawing marks are rare. However, 100 % of our porcine specimens were scavenged and this is consistent with what most studies report [18, 36]. We observed relatively few vertebrate scavengers: red fox (*V. vulpes*), wood mice (*Apodemus* spp.) and bank voles (*M. glareolus*). In previous experiments conducted in comparable environments, researchers noted a greater diversity of species scavenging, e.g., lynx (*Lynx lynx*), wolf (*Canis lupus*), domestic dog (*Canis lupus familiaris*) and cat (*Felis catus*), raccoon dog (*Nyctereutes procyonoides*), Eurasian badger (*Meles meles*), various small mustelids (*Mustelidae*), wild boar (*Sus scrofa*), squirrels (*Sciurus* sp.), hedgehog (*Erinaceus* sp.), as well as birds of prey and passerines [13, 53, 66-73]. We also recorded many of these species, as summarized in Table 1, but we do not have evidence for them scavenging. For instance, a lynx, badgers and martens walked a few meters past a fresh pig without interacting, even though they occasionally scavenge [53, 67, 74]. We further noted a striking absence of avian scavenging. Multi-season forest experiments in the UK and Germany report scavenging by buzzard (*Buteo buteo*), carrion crow (*Corvus corone*), common raven (*Corvus corax*), red kite (*Milvus milvus*) and magpie (*Pica pica*) [13, 68]. All of these species occur in our area as well. Despite their absence in our experiment, these birds should not be generally excluded as potential scavengers in Europe, especially in non-forest environments [42]. Similar accounts for other vertebrates that have been reported to gnaw dry bone exist, e.g., squirrels [13, 16, 24] and deer [75, 76]. However, remnants of soft tissue were still attached to many bones until the end of our experiment, and some of these species possibly would have scavenged at later stages.

The only large vertebrate scavengers we recorded feeding on the remains were red foxes. They transported, secondarily deposited consumed and once urine-marked carcass parts in our study, as did foxes in previous experiments [18, 32]. However, despite foxes being among the most common

and frequent scavengers in Europe, we only recorded them scavenging twice, and only after over two months. Another study from a German forest reported more frequent and intense fox activity at carcasses, with, e.g., 51 % of all visits [68], and 96 % of the overall scavenging [73]. A Canadian study in open as well as forest sites found that ca. 5 % of all scavenging was by red foxes [77]. In addition, Bassi et al. [73] documented an average of 2.6 days for the first red fox to start scavenging in Italian forests, Young et al. [18] reported an average of about 15 days in a UK woodland, and Morton and Lord [32] noted six weeks in a forest near Virginia, USA.

We recorded high levels of small rodent scavenging. Scavenging by these is a neglected aspect in most decomposition experiments, since they concentrate on larger vertebrates. For instance, several comparable studies report no small rodents [67, 68, 73, 78], which is possibly due to the difficulty of capturing their activities on camera [79]. Forbes and colleagues [77] recorded small rodents, but these only fed on maggots. On the other hand, Young et al. [13] reported wood mice scavenging during early and skeletonized stages of decomposition, accounting for about 8 % of the overall scavenging events. In addition, Synstelien [79] observed white-footed mice (*Peromyscus leucopus*) feeding on human soft tissue and bone throughout decomposition stages. Furthermore, small rodents and their potentially severe effects on human remains are often mentioned in forensic case reports [79-82].

We captured rodents and foxes transporting bones away from carcass sites several times and both were previously reported to disperse bones [10, 23]. It is therefore likely that these taxa account for at least some of the missing bones and affected our recovery rate, which was ca. 72 %. On the other hand, our search was limited to the 2 x 2 m plots. The soggy ground covered with leaf-litter was challenging for the recovery and could have likewise contributed to a lower recovery rate.

Compared to previous research, as discussed above, our study showed a relatively low facultative scavenger diversity and scavenging rate. There are several potential reasons for this. For instance, our carcasses were rapidly monopolized by invertebrate larvae, which can outcompete vertebrates by quick consumption of the tissues limiting the available nutritional resources, and the larval excretions

can make carrion inedible for vertebrates, especially in warmer temperatures [67, 83]. Several studies mention a late onset of vertebrate scavenging when there is severe insect colonization right after deposition [18, 32, 84]. For instance, fox scavenging has been shown to increase when decomposition proceeds slower and microbial and insect activity is less intense [85].

Furthermore, our experiment took place during summer and fall. However, for larger facultative scavengers it is also a period with easy access to alternative nutritional resources [86]. Vertebrate carrion consumption seems to increase in winter [67]. For instance, red fox scavenging accounts for up to 30 % of the food intake as opposed to sometimes 0 % in summer [68, 77, 87-91]. However, some studies note higher scavenging frequencies in summer compared to winter, e.g., for wolf, red fox, common buzzard, wild boar, hibernating bears, and migrating turkey vultures [67, 73, 84].

The perimortem wounds on our pig specimens were caused through electric burning and the smell of burned flesh may have had a repelling influence on scavengers. An anecdote of a hunter from our study area tells that when hunters cannot transport their shot game right away, they use to leave their fired cartridge cases on the carcasses over night to repel scavengers from feeding. However, red foxes were reported to scavenge on post-fire burned animal carcasses in Australia, although, the scavenging frequency was relatively low [93]. Magpies in the USA were observed to prefer burned over unburned pig carcasses, almost completely stripping off soft tissue [94]. The burn wounds in our study were relatively small and not well-expressed, which is why we do not think that there was a strong repelling influence on scavengers.

Scavenging damage

We were able to associate the bone damage with the responsible scavenger based on camera trap footage and visual examination of the bones, mainly because there were only two taxa involved (red fox and small rodents) and because fox scavenging was very rare. Most often, we could not distinguish the small rodent species from the footage, and we were also not able to assign scavenging patterns or damage to any of the three rodent species.

The bone damage resulting from red fox interaction with the pig carcasses were minor, and besides the one rib with scores, did not include any typical canid-alterations such as tooth pits or punctures [15, 42]. Scores alone are too unspecific and insufficient to identify the red fox as the scavenger. Ribs are frequently scavenged by foxes, but additional bones such as bones of the limbs and the scapulae are scavenged, too – which was not the case in our study [18, 95]. Our research demonstrates that foxes can affect cadavers, and despite that, our research is based on pig carcasses, humans may well be affected, too. In particular, the scavenger's ability to disperse body parts should be considered in casework and more details on their taphonomic signatures, the direction and distance of dispersal are required.

The rodents in our experiment altered perimortem wounds, as evidenced, for example, in a previous study with gunshot wounds [13]. We observed rodents preferring smaller bones or exposed features of larger bones to scavenge on. However, we did not observe pedestalling which is a common modification with wet-bone gnawing but mainly described for rat scavenging [15, 24]. This is likely due to the smaller body and jaw size and therefore less destructive force of mice and voles compared to rats. Despite the high abundance of small rodents and their potential to interact with carcasses, there are few experimental studies in the forensic literature on their various impacts, the dispersal patterns of bones, or the damage-based distinction between rodent species [16, 24, 81]. One reason for this might be that camera traps in decomposition studies are set too high or are not sensitive enough to capture these small vertebrates on the ground [79], or that the research focus lies on larger species. Our study stresses the importance of taphonomic changes caused by rodents for the interpretation of soft tissue trauma, because they can alter the size and morphology of a wound, but also completely remove it through consumption. On the bones, we mainly found rodent-inflicted wet-bone gnawing. The typical parallel striations on the cortical bone were absent, probably because the bones still being well enough collagenized for the rodents to easily penetrate through the cortical surface. Literature on the distinction of scavenging damage by species is scarce and concentrated on larger animals, where shape and depth of pits, punctures and scores can be measured. On the other hand, Pokines

and colleagues (2017) examined rodent and lagomorph gnawing characteristics, concluding that species identification based on the marks is generally impossible [81]. Furthermore, wet bone gnawing – the main rodent-inflicted damage type that we found – is only little specific. Therefore, the scavenging damage by bank voles and *Apodemus* spp. in our study were too similar, and we could not distinguish between them.

Limitations and future studies

There are some limitations to our study. For instance, we studied pig carcasses instead of human cadavers. Although studies have shown differences in decomposition and scavenging between these species, e.g., [31, 96], porcine carcasses are frequently employed as human proxies in forensic actualistic experiments because of similarities in anatomy, body composition and gut microbiota [52]. In Central Europe, there is currently no possibility to conduct experimental taphonomic research on surface-deposited human cadavers, and because of that, proxies are required. Future studies could evaluate our findings on a retrospective forensic case sample.

An interesting finding was that both detection modalities, camera traps and visual inspection in the field, recorded scavenging evidence that was missed by the other modality, respectively. Camera traps might miss scavenging due to camera failure, unfavorable angles of observation or the camera being too insensitive to capture small animals [79]. On the other hand, scavenging damage might not always be immediately detected because of the light or weather conditions, the covering of bones with plant material or the complete absence of bones due to removal by animals. The detection of small vertebrate scavenging would benefit from a combination of both modalities like in our study, or a better camera coverage of the scene.

In general, future research should consider some aspects regarding study design. For instance, sun exposure should be taken into account, and caged specimens should only be used in addition to uncaged carcasses or for baseline studies where, e.g., isolated small scavengers are the focus [43, 97]. Moreover, sampling activity is known to disturb scavengers [63, 98], and further experiments should

limit intrusions and possibly implement automated data collection [99]. A better understanding of how and to which extent human presence affects the scavenger behavior would be beneficial. Our study covered summer and early fall months. The seasonal behavior of facultative scavengers requires a control trial in colder seasons. This could help, e.g., to delineate the PMI in a forensic case.

5. Conclusions

Our study presents vertebrate activity and scavenging characteristics at and around pig carcasses in a temperate forest in Central Europe (Switzerland) during summer/fall. Avian and large vertebrate scavengers were conspicuously rare in our experiment, a valuable finding for forensic practice. We identified some potential causes for this low vertebrate activity that now require more investigations with a focus on seasonality, insect colonization and reduced human presence at the study site. In contrast to literature-based expectations, small rodents were our main scavengers; they altered perimortem wounds and damaged and dispersed numerous skeletal elements. Considering our findings, we believe it expedient to reinforce discussing the importance of small rodents as taphonomic agents. This is particularly directed towards field research where small rodents may go undetected due to the study design.

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TABLE 1: Vertebrate species visiting plots during the baseline study and the experiment, separated by plot type (C: control, P: pig).

			Baseline study				Experiment			
			(total visits)				(total visits)			
			C1-C3		P1-P6		C1-C3		P1-P6	
Group	Taxon	Scientific name	n	%	n	%	n	%	n	%
Birds	Bird (unidentified)	<i>Aves</i>	0	0.0	0	0.0	0	0.0	7	0.4
	Blackbird	<i>Turdus merula</i>	13	4.1	15	1.9	7	2.4	70	4.3
	Black woodpecker	<i>Dryocopus martius</i>	0	0.0	1	0.1	0	0.0	2	0.1
	Eurasian Bullfinch	<i>Pyrrhula pyrrhula</i>	0	0.0	1	0.1	0	0.0	1	0.1
	Chaffinch	<i>Fringilla coelebs</i>	0	0.0	2	0.3	0	0.0	5	0.3
	Gr. spotted woodpecker	<i>Dendrocopos major</i>	1	0.3	2	0.3	1	0.3	1	0.1
	Great tit	<i>Parus major</i>	0	0.0	1	0.1	0	0.0	5	0.3
	Hawfinch	<i>Coccothraustes coccothraustes</i>	0	0.0	1	0.1	0	0.0	0	0.0
	Eurasian jay	<i>Garrulus glandarius</i>	0	0.0	5	0.6	2	0.7	11	0.7
	Mistle thrush	<i>Turdus viscivorus</i>	0	0.0	2	0.3	0	0.0	131	8.1
	European robin	<i>Erithacus rubecula</i>	0	0.0	2	0.3	2	0.7	115	7.1
	Song thrush	<i>Turdus philomelos</i>	13	4.1	24	3.0	3	1.0	11	0.7
	Tawny owl	<i>Strix aluco</i>	0	0.0	1	0.1	0	0.0	2	0.1
	Eurasian wren	<i>Troglodytes troglodytes</i>	0	0.0	1	0.1	0	0.0	71	4.4
	Wood pidgeon	<i>Columba palumbus</i>	2	0.6	1	0.1	0	0.0	0	0.0
Carnivores	Badger	<i>Meles meles</i>	2	0.6	27	3.4	1	0.3	2	0.1
	Dog	<i>Canis familiaris</i>	0	0.0	0	0.0	3	1.0	7	0.4
	Domestic cat	<i>Felis catus</i>	0	0.0	0	0.0	0	0.0	1	0.1
	Lynx	<i>Lynx lynx</i>	0	0.0	0	0.0	1	0.3	1	0.1
	Pine marten	<i>Martes martes</i>	18	5.7	24	3.0	12	4.2	17	1.0
	European polecat	<i>Mustela putorius</i>	1	0.3	1	0.1	2	0.7	1	0.1
	Red fox	<i>Vulpes vulpes</i>	3	0.9	9	1.1	0	0.0	12	0.7
Deer	Deer (unidentified)	<i>Cervidae</i>	0	0.0	3	0.4	0	0.0	0	0.0
	Chamois	<i>Rupicapra rupicapra</i>	1	0.3	3	0.4	1	0.3	0	0.0
	Red deer	<i>Cervus elaphus</i>	0	0.0	18	2.3	0	0.0	0	0.0
	Roe deer	<i>Capreolus capreolus</i>	12	3.8	49	6.2	1	0.3	5	0.3
Rodents	<i>Apodemus</i> spp.	<i>Apodemus</i> spp.	224	70.7	543	68.8	235	82.2	912	56.3
	Bank vole	<i>Myodes glareolus</i>	8	2.5	16	2.0	0	0.0	201	12.4
	Muroidea	<i>Apodemus, Myodes</i>	0	0.0	0	0.0	0	0.0	6	0.4
	Squirrel	<i>Sciurus vulgaris</i>	17	5.4	23	2.9	14	4.9	23	1.4
Wild boar	Wild boar	<i>Sus scrofa</i>	0	0.0	3	0.4	0	0.0	0	0.0
Other	Common toad	<i>Bufo bufo</i>	0	0.0	0	0.0	1	0.3	0	0.0
	Common frog	<i>Rana temporaria</i>	0	0.0	0	0.0	0	0.0	1	0.1

Unclear	Vertebrata unidentified		2	0.6	11	1.4	0	0.0	0	0.0
Total			317	100	789	100	286	100	1621	100

TABLE 2: Results of the generalized linear model (dependent variable: number of visits). DF: degrees of freedom; L-R ChiSquare: likelihood ratio Chi squared value; p: significance of the chi squared test. Statistically significant results highlighted in bold.

Variables Run 1	DF	L-R ChiSquare	p
Taxon	3	2174.2874	< .0001
Sun / shade	1	73.353952	< .0001
Caged/ uncaged	1	339.29444	< .0001

Variable Rund 2

Decomposition stage	3	147.76441	< .0001
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TABLE 3: (a) Results of the logistic model (dependent variable: plot visited/not visited), and Wald Chi-Squared tests and odd ratios (b). DF: degrees of freedom; L-R ChiSquare: likelihood ratio Chi-squared; p: significance of the chi squared test. OR: odd ratio.

a)	No. of parameters	DF	L-R ChiSquare	p
Carcass Presence	1	1	76.240526	< .0001
Taxon	3	3	764.597111	< .0001

b)		OR	p (Wald)
Carcass present vs.	Carcass absent	8.3	< .0001
Rodents vs.	Carnivores	9.94	< .0001
Rodents vs.	Birds	2.26	< .0001
Rodents vs.	Deer	90.29	< .0001
Birds vs.	Carnivores	4.4	< .0001
Birds vs.	Deer	39.91	< .0001
Carnivores vs.	Deer	9.08	< .0001

TABLE 4: Data for the six pigs (P1 – P6), including number of recovered bones (from a maximum of 394), recovery rates, number of scavenged bones, scavenging rates, skeletal elements with scavenging signs and responsible scavengers based on camera recordings. In addition, the first scavenger event is given in post-depositional days (PDD). *Damage observed on remains without according footage, **scavenging activity observed on camera before damage observation on remain. MT/MC = metatarsals/metacarpals, T/C = tarsals/carpals.

Pig	Bones recovered (n)	Recovery rate (%)	Bones scavenged (n)	Scavenging rate (%)	Bones scavenged	Scavenger	First scavenging event (PDD)
P1	282	71.6	3	1.1	MT/MC, rib, scapula	Rodent, red fox	80 * rodent 64 * red fox
P2	276	70.1	16	5.8	Femur, humerus, MT/MC, patella, radius, sternum, T/C	Rodent (<i>Apodemus</i> spp., bank vole)	25 **
P3	308	78.2	10	3.2	Femur, humerus, MT/MC, T/C, tibia,	Rodent (<i>Apodemus</i> spp.)	38 *
P4	271	68.8	18	6.6	Femur, humerus, MT/MC, patella, phalanges, rib, T/C, vertebra	Rodent	59 *
P5	271	68.8	11	4.1	Femur, MT/MC, radius, rib, scapula, T/C	Rodent (<i>Apodemus</i> spp., bank vole?)	33 **
P6	293	74.4	7	2.4	MT/MC, T/C, tibia, vertebra	Rodent (<i>Apodemus</i> spp.)	8 **
Total	1701	72.0	65	3.8			

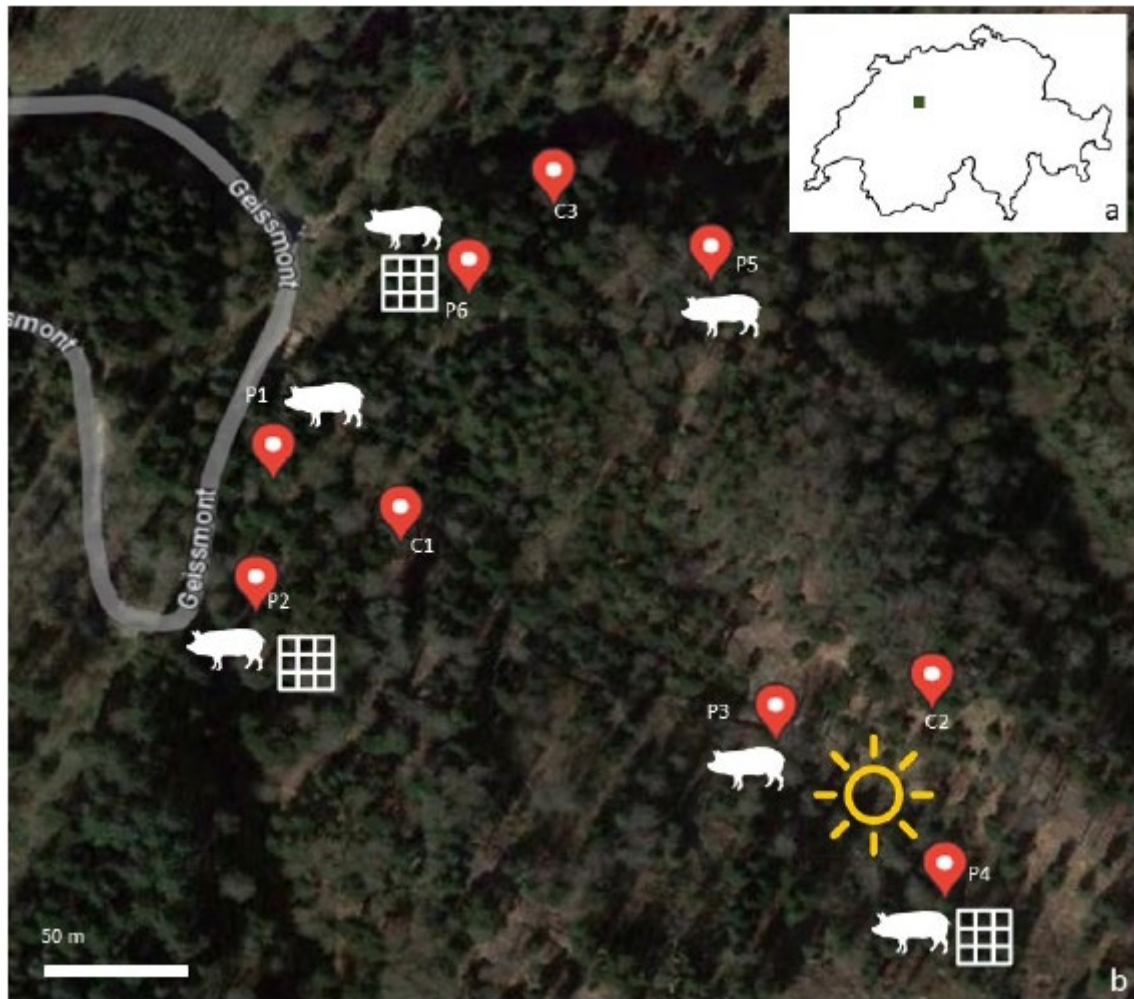


FIG. 1 Location of the experiment at the Geissmont site in Switzerland (a) including positions and variables of the nine plots (b). P indicating pig plots, C control plots, the grids denote caged specimens, the sun indicates the three sun-exposed plots. The Geissmont forest road is gravelled and closed for public vehicles.

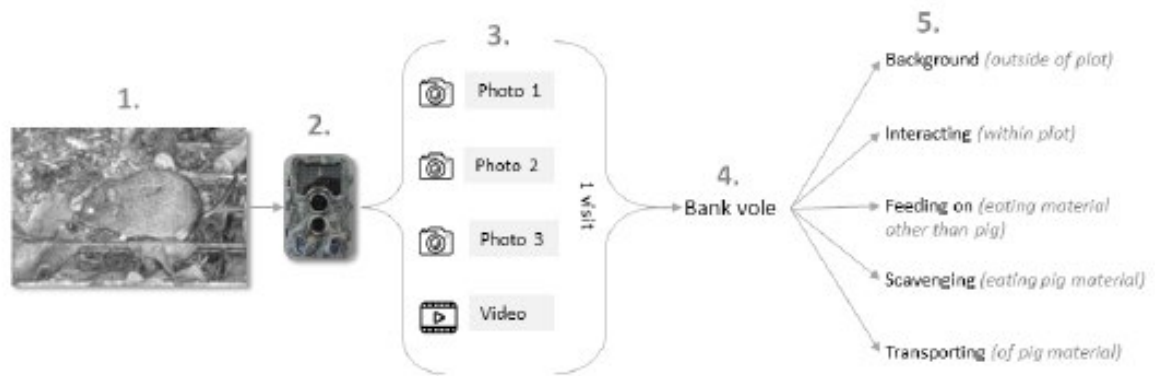


FIG. 2 Workflow for labelling the camera trap photos and videos: An animal (1.) triggers the camera trap (2.), which creates three photos plus a video in a row (3.), equaling one visit. Identification on the footage to the lowest taxonomic level possible (4.) and assignment of the activity (5.).

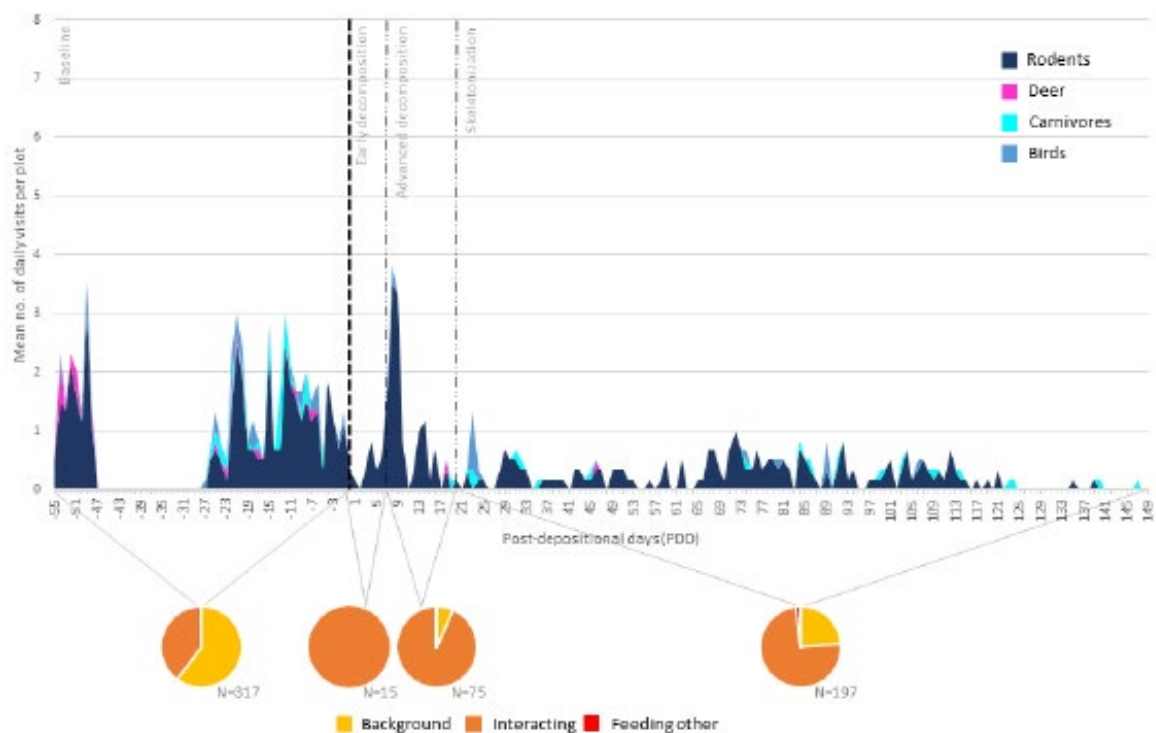


FIG. 3 Number of detected visits by vertebrates, averaged per day for the three control plots combined. The pie charts show the activities of all vertebrates together, separated by decomposition stage. Camera failure caused the data gap in the baseline study.

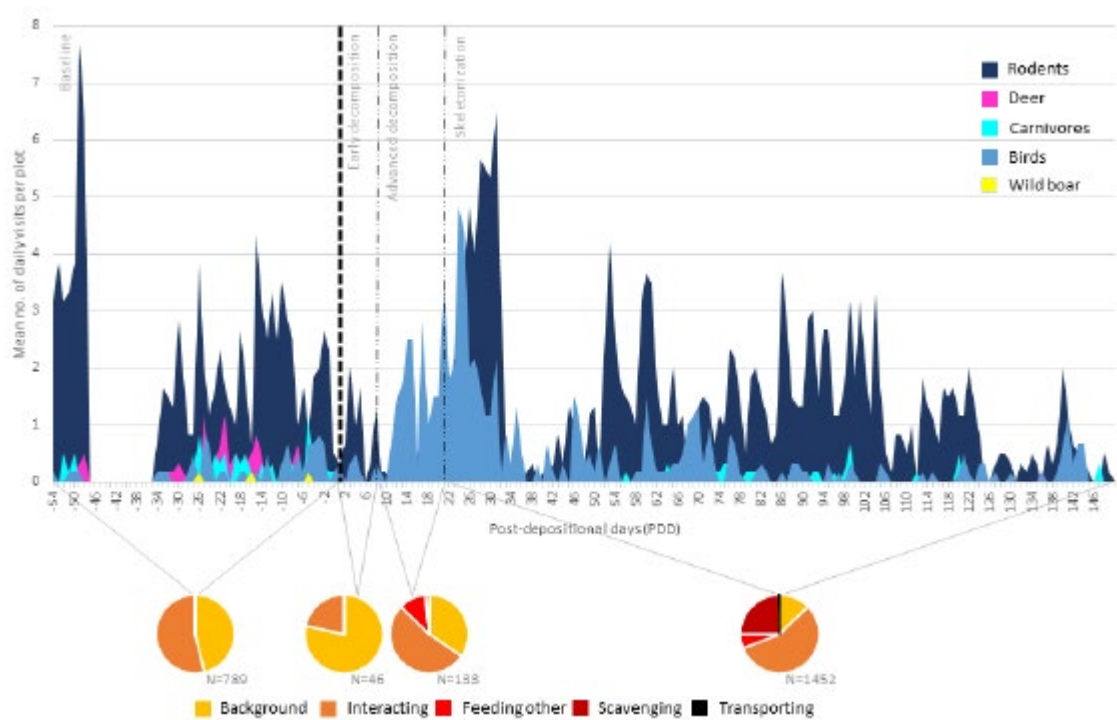


FIG. 4 Number of detected visits by vertebrates, averaged per day for the six pig plots combined. The pie charts show the activities of all vertebrates together, separated by decomposition stage. Camera failure caused the data gap in the baseline study.

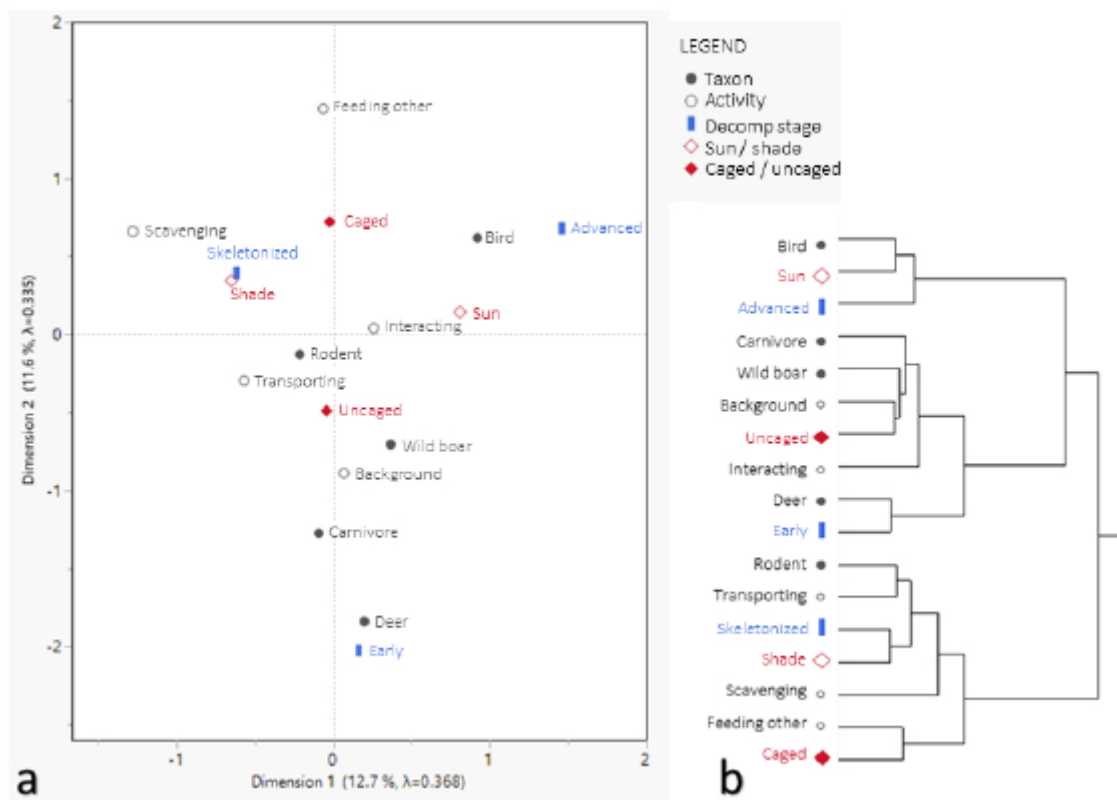


FIG. 5 (a) Plot of variables along the first two dimensions from the multiple correspondence analysis (MCA). The Euclidean distance between variables indicates their relative association. (b) Output of the cluster analysis computed on all dimensions from the MCA. The distance between branches indicates the strength of association between the relative variables.

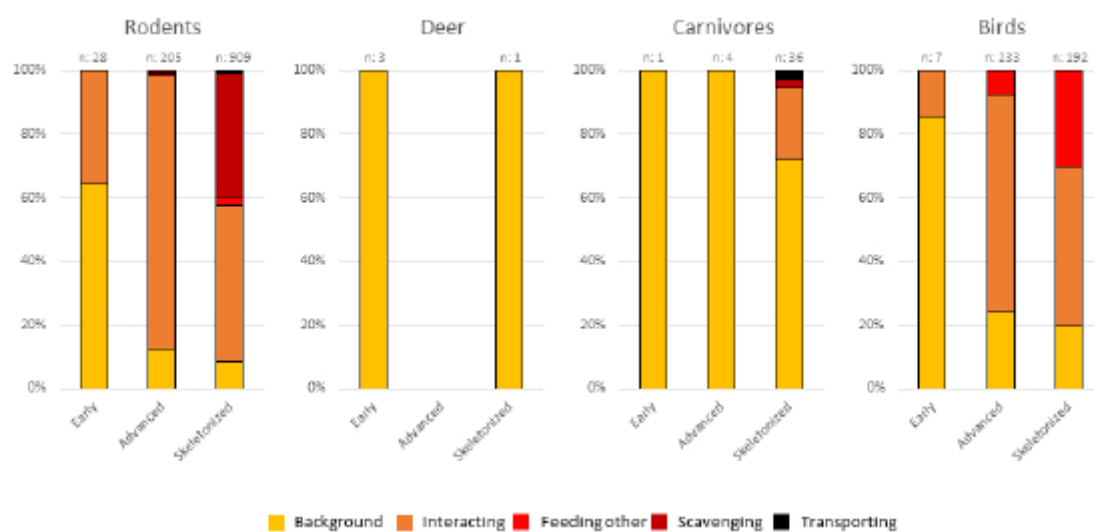


FIG. 6 Relative frequency of vertebrate activity on the total number of visits by decomposition stage for pig plots.

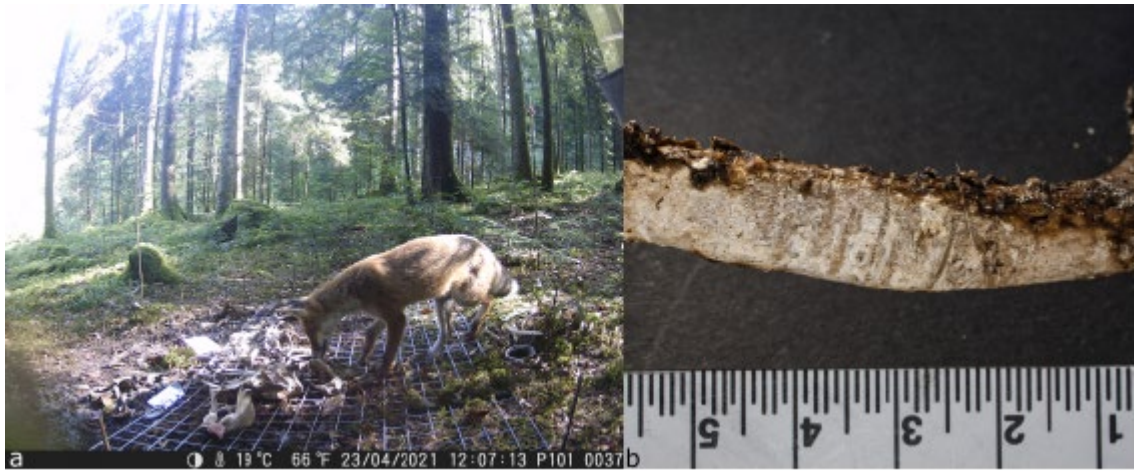


FIG. 7 A red fox inspecting the remains of pig P1 (a) and tooth marks on a rib of P1 caused by red fox teeth (b).



FIG. 8 Porcine soft tissue damage by rodents: a) inside of pig skin with an irregular oval-shaped hole and small, parallel striations towards the opening. b) Rib cartilage with perpendicular gnawing damage. c) Desiccated skin margin with indentations. Note the brighter color of the damaged margins.

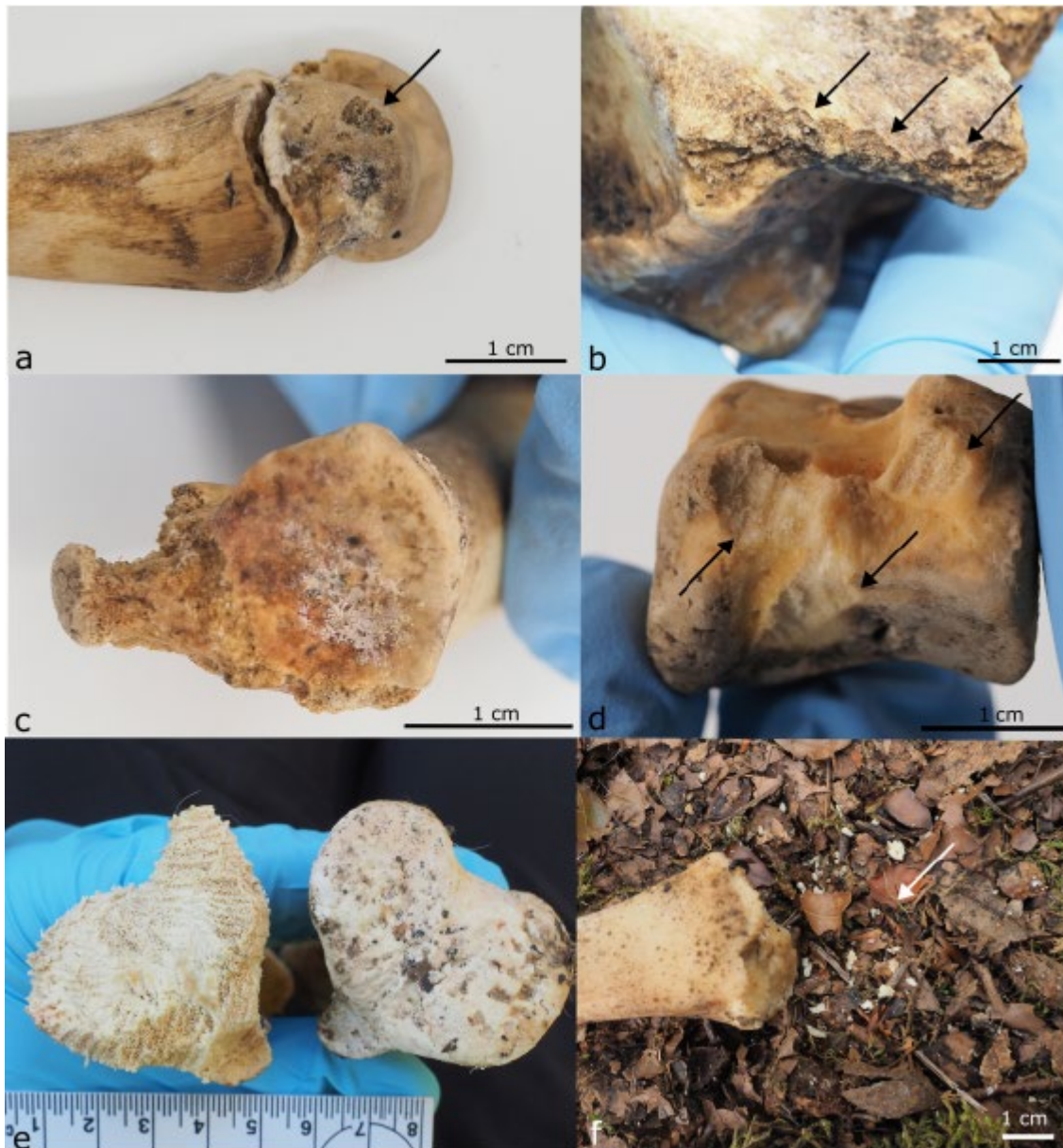


FIG. 9 Rodent-inflicted damage on porcine bones: a) small gnawing defects on the distal epiphysis of a metacarpal/metatarsal. b) Semilunar notches along a distal femur shaft end. c) Damage around the stylus of a metacarpal/metatarsal. d) Parallel striations on the margins of a carpal/tarsal bone. e) Larger-area surface destruction of a tibia plateau (left) compared to an undamaged bone (right). f) Bone flakes lying around a long bone.



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Of rodents and foxes: faunal activity and scavenging at carcasses in a Central European (Swiss) forest

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