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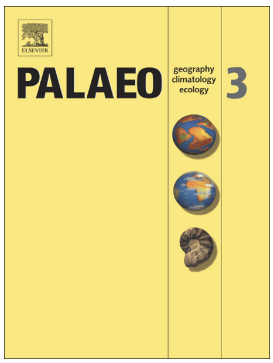

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A taphonomic investigation of small vertebrate accumulations produced by the snowy owl (*Bubo scandiacus*) and its implications for fossil studies

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Abstract

The action of predators, such as diurnal raptors, owls, mammals or humans, influence the nature of small vertebrate fossil assemblages but currently their taphonomic features are still poorly understood. In this study, we investigate the taphonomic signature of the snowy owl (*Bubo scandiacus*) based on an analysis of pellets collected at breeding sites located in Greenland and the Canadian Arctic. This taxon is widely distributed through the North Hemisphere and was an important predator in Pleistocene times. Taphonomic parameters suggest that, contrary to previous assumptions, *B. scandiacus* produces, on average, moderate digestion of incisors, molars and post-cranial elements, and should be classed as a Category 3 or Category 3/4 predator according to the terminology established by Andrews. Significant inter-site variability was observed for some of the damage considered (in particular, digestion on incisors), and a key finding is that variability and the associated statistical confidence intervals are crucial notions that should be taken into account when assessing taphonomical features, in order to reliably identify the potential predator(s) responsible for small vertebrate fossil accumulations.

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Keywords: Paleoenvironmental reconstruction, taphonomy, modern owl pellets, predation, digestion, lemming, birds

1. Introduction

Small vertebrate remains (i.e. fish, herpetofauna, birds, insectivores and rodents weighing < 1 kg) are frequently fossilized, preserved and collected in palaeontological and archaeological sites in association with human artefacts. They have been recognized for many decades for their potential use in biochronological, palaeoecological, palaoenvironmental and palaeoclimatological reconstructions (e.g. Chaline, 1972; Brothwell and Jones, 1978; Chaline and Mein, 1979; Jeannet, 1981; Marquet, 1993; Tchernov, 1996; Montuire, 1999; Kowalski, 2001; Montuire and Marcolini, 2002; Hernández Fernández, 2006; Cuenca-Bescós et al., 2010; Rofes et al., 2015; Royer et al., 2016).

As for large mammals, many different scenarios can explain the accumulation of their bone remains (e.g. Korth, 1979; Andrews, 1990; Denys, 1994; Stahl, 1996), such as attritional death (natural traps or natural death in burrows – i.e. Pelletier et al., 2016), bone-collecting species (e.g. Shipman and Walker, 1980) and human consumption (e.g. Stahl, 1982; Fiedler, 1990; Simonetti and Cornejo, 1991; Henshilwood, 1997; Armstrong, 2016; Mallye and Laroulandie, in press). Among these scenarios, many consider predation by non-human predators to be the main factor in the accumulation of small vertebrate remains (e.g. Dodson and Wexlar, 1979; Kowalski, 1990; Kusmer, 1990; Denys et al. 2017). Indeed small mammals and other small vertebrates are an important food source for a large number of non-human predators, including terrestrial carnivores, diurnal and nocturnal birds of prey.

However, predator diets, not only, depend on prey abundance in the surrounding environment, but are also related to the biological, ecological and behavioral characteristics of each predator (Frochot, 1967; Glue, 1970; Chaline, 1977; Andrews, 1990; Kowalski, 1990).

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Consequently, each agent or process (i.e. birds of prey, small carnivores, and attritional death) could generate specific small vertebrate accumulations that are distinct both in terms of species abundance and composition. Qualitative and quantitative variations observed in fossil material throughout a stratigraphy could therefore not only be the result of local environmental changes, but also changes in small vertebrate accumulators. Failing to distinguish such cases could potentially lead to biases in the reconstruction of past climate and environmental conditions (e.g. Mellet, 1974; Andrews 1990; Kowalski, 1990; Stoetzel et al., 2011). Deciphering the agent(s) and/or mechanism(s) responsible for accumulations of remains could thus offer us the opportunity to both control and correct such biases.

Identifying the agent(s) responsible for assemblage deposition and accumulation is, however, a real challenge for zooarchaeologists and palaeontologists. Biological observations have shown that the preservation of small vertebrate skeletal remains within pellets and scats varies from predator to predator (Short and Drew, 1962; Raczyński and Ruprecht, 1974; Lowe, 1980). These observations have been the basis of pioneering works (Mellet, 1974; Mayhew, 1977; Dodson and Wexlar, 1979; Korth, 1979; Andrews and Nesbit Evans, 1983; Denys, 1985) and have become common in taphonomic studies ever since.

In this regard, the work of Andrews (1990) became an undeniable landmark in taphonomy. This author used a systematic approach to investigate many small rodent consumers in order to suggest criteria for distinguishing different categories of predators. Since then, many neotaphonomic reference frameworks have been produced to describe and explore, in the greatest depth possible, any potential agents responsible for small vertebrate accumulations (i.e. amphibians, rabbits, birds and small mammals (e.g. Denys et al., 1996; Bailon, 2011; Denys, 2011; Denys and Cochard, 2017; Laudet and Selva, 2005; Laroulandie, 2002; Bocheński, 2005; Montalvo et al., 2007; De Cupere et al., 2009; Lloveras et al., 2012; Souttou et al., 2012; Lloveras et al., 2014; Fernández et al., 2017). In investigating

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palaeontological and archaeological contexts, many studies have relied on these reference frameworks to identify agents, with greater or lesser accuracy depending on the level of confidence placed on the criteria used (e.g. Fernández Yalvo and Andrews, 1992; Fernández Yalvo et al., 1998; Denys et al., 1987; Vigne, 1994; Vigne et al., 1994; Sanchez et al., 1997; Stoetzel et al., 2011; Demirel et al., 2011; Belmaker and Hovers, 2011; Desclaux et al., 2011).

Many neotaphonomic studies have focused on definitive descriptions of the bone modification patterns produced by several modern predators. However, most of these experiments and reference frameworks did not take into account the variability (Denys, 1985; Denys et al., 1996; Denys et al., 1997; Saavedra and Simonetti, 1998; Cochard, 2008; Denys, 2011; Rudzik et al., 2015) that can be observed at an inter-individual level, depending, for instance, on the individual's identity, age (Kowalski, 1990; Andrews, 1990; Williams, 2001) or degree of hunger (Raczynski and Ruprecht, 1974). This variability can also occur at a population scale, influenced by the surrounding environment, such as prey assemblage composition and relative abundance, prey size or season of capture (Andrew, 1990; Bocheński et al., 1993; Bocheński, 1997; Saavedra and Simonetti, 1998; Andrews and Fernández-Jalvo, 2018).

To distinguish between agents responsible for accumulations, several criteria are generally used, such as digestion and breakage patterns. Nonetheless, different predators can be produced these marks, and generally only mean values of the criteria are used. However, variability is a crucial factor that is regularly underestimated and not usually included in the criteria considered. To establish variability, extensive sampling is required (Denys, 2011). Consequently, reference frameworks based on limited samples or describing particular cases must be questioned and used with caution when considering past faunal assemblages (Williams, 2001; Denys, 2002; 2011).

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Among the predators responsible for small vertebrate accumulations, the snowy owl (*Bubo scandiacus*) is a bird of prey that has been widely identified in bone remains from the Late Pleistocene from the Russian plains to southwestern France (Mourer-Chauviré, 1975; Tyrberg, 1998; Potapova, 2001; Laroulandie, 2016). This predator is able to hunt many different small vertebrates, although lemmings constitute one of their preferred prey (Watson, 1957; Gilg et al, 2006; Holt et al., 2015; Therrien et al., 2015). The question therefore arises as to whether this owl may have been responsible for fossil bone accumulations. However, the taphonomic features of small vertebrate accumulations produced by the snowy owl have barely been investigated, with only two existing modern reference frameworks, each based on less than fifteen individuals. The first concerns rodents from a pellet sample collected from several roost sites on Bathurst Island in northern Canada (Andrews, 1990, p. 35), while the second concerns birds, adult quails (*Coturnix coturnix)*, that were fed to a couple of snowy owls during experimental feeding (Bocheński, 1997). This paper aims to re-evaluate snowy owl accumulations by investigating the variability in the taphonomic signatures of different accumulations from three nest sites.

2. Materials and methods

2.1 Study localities

Vertebrate remains were collected from snowy owl pellets (*Bubo scandiacus*) taken from three distinct breeding sites located on two Arctic Canadian Islands (Bylot Island and Victoria Island; Fig. 1) and in Greenland (Hochstetter). The pellets were collected during the summers of 2000, 1999 and 2013, respectively. At all these three sites, pellets were collected over more than 20 km², some of them being collected on roots other on nest sites. The pellets from Bylot (number of pellets unknown) and Victoria (number of pellets = 20) islands were collected initially whole, but were not packed individually and were subsequently

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disaggregated when our study begins. Those from Hochstetter were still more or less intact (number of pellets = 27). The climatic and environmental conditions of these three sites are typical of high latitude, circumpolar regions.

The site of Bylot is located on the southwestern plains of Bylot Island off the northern tip of Baffin Island (Latitude 73.15^{o}N; Longitude 79.90^{o}W). The island is a Migratory Bird Sanctuary and is part of Sirmilik National Park (Lepage et al., 1998). The vegetation is composed of a mixture of wetlands and mesic tundra, the uplands being largely dominated by mesic tundra. The annual average air temperature on Bylot Island is -14.5°C (mean winter = -32.8°C; mean summer = 4.5°C - Cadieux et al., 2008). Snowy owls only nest on Bylot Island during peak lemming years, which occur every 3–4 years on this island, including the year of 2007 (Gruyer et al., 2008).

The pellets from Victoria were collected in the southeastern part of the island, near Cambridge Bay (Latitude 69.13°N; Longitude -104.84°W). This region is mainly composed of a tundra vegetation enduring harsh climatic conditions, with mean January and July temperatures close to -30 and 8 °C, respectively (Schaefer and Messier, 1994).

Hochstetter Forland is situated in northeastern Greenland (Latitude 75.16°N; Longitude -19.70°W) and has a typical, relatively dry climate, with short, cool summers and very cold, long winters. Continuous frost prevails from early September to late May most years, and temperatures below -40 °C are recorded during most winters. Mean summer temperatures are around 3.5°C (Meltofte, 1981).

The three study sites have relatively similar communities of small (less than 5 kg) terrestrial vertebrates (although with more diversity of species in Canada) composed of: northern collared lemming (*Dicrostonyx groenlandicus)*, American brown lemming (*Lemmus trimucronatus*; in Canada only), arctic hare (*Lepus arcticus*), stoat (*Mustela erminea*), arctic fox (*Vulpes lagopus)* and red fox (*Vulpes vulpes;* in Canada only), passerines (various species**,**

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including *Corvus corax*), shorebirds (various species), ducks (various species), geese (various species), divers (various species), skuas (various species), gulls (various species), arctic tern (*Sterna arctica*), rock ptarmigan (*Lagopus mutus)* and willow ptarmigan (*Lagopus lagopus;* on Victoria only), rough-legged hawk (Buteo lagopus; in Canada only), falcons (*Falco peregrinus* and *Falco rusticolus*) and snowy owl (*Bubo scandiacus*) (Parmelee et al., 1967; Banfield, 1974; Boertmann, 1994; Lepage et al., 1998).

2.2 Taxonomic identification

To develop a multi-taxa, taxonomical approach covering the entire diet of the predator as explored by Denys et al. (2017), the taxonomic identification of bone remains was carried out on the three vertebrate categories for which bones were observed: birds, rodents and small carnivores. The specific identification of bone remains was carried out through comparisons with modern vertebrate collections curated at the PACEA (De la Préhistoire à l'Actuel : Culture, Environnement et Anthropologie) laboratory of Bordeaux University, France.. Species identification between the two lemmings was carried out on cranial and tooth remains.

2.3 Analysis of the rodent remains

Rodent population structure was investigated using the length of the femur, which was divided into eight size classes, ranging from 8 to 24 mm, the full length of this long bone being reached within a few weeks of birth. Complete or incomplete ossification of the femoral heads was noted, as well as the distal epiphysis of the humerus. In the absence of any more reliable information on lemmings, data regarding epiphysis fusion from two other rodents, the mouse and the rat, was used to estimate the relative age of the prey: the distal epiphysis of the

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humerus merges at around 3–4 weeks, whereas the fusion of the proximal femur begins between 13 and 15 weeks (Zoetis et al., 2003).

To investigate the origin(s) of the rodent remains, three data sources were generally used: skeletal-part representation, bone breakage patterns and bone surface modifications with the digestion degree.

Concerning the skeletal part representation, we chose to focus mainly on the principal long bones (the humerus (HUM) and ulna (ULN) for the fore limb and the femur (FEM) and tibia (TIB) for the hind limb), as well as the hemi-mandibles (MAND), maxillary (MAX) and vertebrae (VERT). The numbers of these identified skeletal elements (NISP) were counted, while any radial, carpal, metacarpal, tarsal, metatarsal, phalange and rib fragments were discarded to simplify the approach and gain time. On one side, these latter bones could be subjected to a more important loss or destruction during the digestion process. On the other side, these smaller elements are also subject to screening methods used, leading if not adapted to significant under-representation in archaeological sites. As a consequence the confidence we can have in this material is thus relatively weak. The relative abundance (Dodson and Wexlar, 1979; Andrews, 1990) was calculated using the following formula:

$$Ri = MNEi / (MNI \times E) \times 100 \quad (1)$$

in which Ri is the relative abundance of element *i*, MNEi is the minimum number of skeletal element *i*, MNI is the minimum number of individuals based on the highest number of any single element in the assemblage (for Hochstetter, the MNI by pellets was not calculated), and E is the number of element *i* in the prey skeleton.

In addition, the proportions of skeletal elements were evaluated using the three ratios originally proposed by Andrews (1990). They were, however, slightly modified in order to ensure statistical rigor in calculating confidence intervals, so that they could be applied despite the discarded bone elements, as follows:

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- **AN/PO%** = (HUM + ULNA) / (HUM + ULNA + FEM + TIB) x 100 (2)

in which **AN** represented the number of bones from the anterior part and **PO** the number of bones from the posterior part;

- **CRA/POSTCRA%** = MAND x 2 / (MAND x 2 + HUM + FEM) x 100 (3)

in which **CRA** referred to the cranial elements and **POSTCRA** to the postcranial elements;

- **Z/E%** = (TIB + ULNA) / (TIB + ULNA + FEM + HUM) x 100 (4)

in which **Z** referred to the zygopodia (tibiae and ulnae) and **E** to the stylopodia (femora and humeri).

All these calculations lay within the interval [0-100]. For instance, the absence of cranial or postcranial elements would lead the CRA/POSTCRA% proportion to be 0 or 100, respectively, whereas the CRA/POSTCRA% would be around 50 when a similar number of these different elements was observed. The degree of breakage was investigated on the humerus, ulna, femur and tibia in order to calculate the degree of completeness with the following formula: (NISPi complete long bones) / (total NISPi long bones) x100, in which NISPi referred to the Number of Identified SPecimens of element *i*. Bones are counted as complete if they include the shaft and significant portions of the proximal and of the distal part, as established by Andrews (1990).

Digestion features were recorded on the lower and upper incisors, first lower molars, proximal femur and distal humerus. Degrees of digestion of the teeth were based on the categories described by Andrews (1990), Fernández-Jalvo and Andrews (1992) and Fernández-Jalvo et al. (2016). Five digestion degrees were established: null (0), light (1), moderate (2), heavy (3) and extreme (4). Isolated molars and incisors were not analyzed separately from those *in situ* in the mandible or maxillary, because the proportion of *in situ* teeth is highly dependent on the methods used to recover remains in an archaeological context

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(i.e. water sieving, with baths or continuous water flow). For the two long bones selected—the humerus and the femur—we only separated digested versus non-digested bones.

Since Andrews (1990) provided all the raw data for the sample from the roost sites on Bathurst Island (northern Canada), we were able to recalculate the above proportions in order to calculate confidence intervals and compare them with our own data.

2.4 Analysis of the bird remains

Although a large quantity of bones was collected, only a few of them belonged to birds. The taphonomical study of these remains was therefore more descriptive than for the rodent remains.

The porosity of the bone was observed in order to evaluate the presence of "adult" or "juvenile" individuals, depending on bone maturity (Serjeantson, 2009). The wing to leg proportions (Ericson, 1987) were calculated for small and large birds: NISP wing / (NISP wing + NISP leg) x 100, based on the humerus, ulna and carpometacarpus for the wing, and the femur, tibioatarsus and tarsometatarsus for the leg. The proportion of complete elongated bones (scapula, coracoid, humerus, ulna, radius, carpometacarpus, femur, tibiotarsus and tarsometatarsus) was calculated as a whole as follows:
(NISP complete long bones) / (total NISP long bones) x 100. To investigate the impact of prey size on fragmentation patterns, the main length of the bird remains was measured and the results were classified into two categories: smaller or larger than the Common blackbird, *Turdus merula*. Despite the small sample size, absolute numbers were also recorded for the main long bones, in order to establish whether the different degrees of fragmentation observed by Bocheński (1997) were also observed in our sample.

The presence and quantity of mechanic damage (notches and punctures) caused by beak pressure during the reduction of the prey (Laroulandie, 2002) was also recorded.

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Digestion marks were observed on all the bones that were anatomically identified. For the long bones, we observed and described the digestion of each of the extremities, namely the articulations or the edge of the breakage when they were fragmented. Given their low number, it was not pertinent to explore the potential differential damage according to the proximal or distal ends of each long bone. For the other bones, the observation was global. The intensity of the digestion damage was recorded according to five degree categories as with the rodent teeth.

2.5 Statistical calculations

The 95% confidence intervals were calculated as a binomial proportion based on the Wilson score method with a continuity correction (e.g. Vollset, 1993). Average values calculated for the four sites (Victoria, Bylot, Hochstetter and pellets from Bathurst Island studied by Andrews, 1990) were weighted according to the minimum number of individuals. We used the Cumulative Link Models (clm) function from "ordinal" package (Christensen, 2015) in R statistical software (R Development Core Team, 2017) to evaluate difference of digestion degrees (defined as ordered factor).

3. Results

3.1 Prey diversity

More than four hundred different prey were collected in the three samples (Table 1). They belonged to at least 3 mammal and 5 bird taxa. Rodentia dominated the corpus, representing almost 97% of the prey. Bird remains were observed in the pellets from two of the sites: Hochstetter and Bylot Island. In both cases, they constituted the snowy owl's largest prey. Indeed, the weight of the prey ranged from a few dozen grams to 1.5 or 2.0 kg for the largest prey identified, a king eider (*Somateria spectabilis*).

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The largest quantity of bone remains was documented at the site of Bylot with 261 bones collected. Four birds of small size belong to the Passeriformes order, two of them being immature individuals. Six birds of large size, identified as five immatures (but not chicks) and one adult belong to Anatidae. Inside this latter family, two taxa have been identified, one being a king eider, *Somateria* cf. *spectabilis* (the adult), and the other being an Anserini (one immature). The bird MNI represented less than 5% of the total prey. One adult small carnivore individual (stoat, *Mustela erminea*) was identified from two bone remains (tibia and fibula). Two species of rodents were identified: the northern collared lemming (*Dicrostonyx groenlandicus*) and the North American brown lemming (*Lemmus trimunocranus)*, with a minimum number of individuals of 130 and 131, respectively (obtained from the relative abundance of first upper molars). In this sample, 44 humeri showing no attached distal epiphyses came from very young individuals (i.e. 12% of the bone remains), which were most likely less than 4 weeks old. In 27.8% [22.7 – 33.5%] of cases, the femoral heads were not fused, probably corresponding to individuals younger than 3 months (Zoetis et al., 2013). Adult lemmings thus constituted the majority of Bylot snowy owl prey.

The Victoria site mainly delivered Northern Collared lemming remains (*D. groenlandicus)*, together with a few North American brown lemming (*L. trimunocranus)* bones. The MNI was 50 (estimated from the ulna) with at least 43 *D. groenlandicus* and 2 *L. trimunocranus*. Sixteen percent of the humeri had an unfused distal epiphysis and 37.0% [27.3 – 47.7%] of the femurs presented no merged femoral head (Fig. 2; supplementary material).

A total of 27 pellets from the Hochstetter site were dissected. They have mean length of 65 mm (SD = 17) and diameter of 34 mm (SD = 4) and a mean value of 3 individuals per pellet (range between 1 and 7 individuals), which was similar to other studies (e.g. Berg and Pedersen, 2011). The bone remains were attributed to two birds (an adult rock ptarmigan,

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Lagopus cf. *muta* and a sub-adult small scolopacidae, *Calidris alpina/alba*) and to the northern collared lemming (Table 1). The 3,165 rodent remains analyzed gave an MNI of 78 based on the first upper molars. In the Hochstetter sample, we identified 25 humeri without their distal epiphysis (i.e. 21% of these bone remains) and 32 femurs with unfused proximal heads (i.e. 31.1% of the femurs [22.5 – 41.1%]). These proportions were relatively close to that observed for the two other sites (Fig. 2).

These results of prey diversity are quite similar to those from other studies (e.g. Boxall and Lein, 1982; Patterson, 2007; Detienne et al., 2008). As noted by previous authors, this prey diversity is relatively representative of local environment, although the prey capture varied significantly with biotic (e.g. sex and ages of predator, lemming density and rodent cycles) and abiotic (e.g. season, habitat quality and climate) conditions (e.g. Chamberlin, 1980; Boxall and Lein, 1982; Therrien et al., 2014). Globally, birds constitute a minor part of these samples, the success of *B. scandiacus* being weaker in capturing these preys (Chamberlin, 1980; Gilg et al., 2006).

3.2 Taphonomical observation of the bird bones

Given the low number of bird remains, we did not investigate the skeletal survivorship profile in detail. However, it should be noted that in the Bylot sample, the remains came from all the main parts of the skeleton. The axial skeleton was for instance represented by head fragments (premaxillar, mandible and quadrate), cervical, thoracic and caudal vertebrae, and the synsacrum. Bones from the scapular and pelvic girdles, wings and legs were present for both the small and large birds. However, neither the distal bones of the wing nor the coracoid were identified for the large birds. The wing to leg proportion was 50.0% [32.2–67.8%] for the small birds and 30.6 % [16.9–48.3%] for the large birds. These values did not differ from each other, nor from the experimental snowy owl feeding conducted by Bocheński (1997), or

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from the expected 1/1 ratio. In this sample of pellets, the size of the bird bones varied from 3 to 49 mm (Fig. 3) with an average length of 15.4 and a median of 13.0 mm (S.D. = 9.3 mm). The fragmentation of bird long bones was relatively low for the small birds and high for the large ones (Table 2). This difference was highly statistically significant ($Z = 3.4$ for $p < 0.01$). For the large birds, the humerus, tibiotarsus and, to a lesser degree, the femur, were more fragmented than the tarsometatarsus, a pattern already observed by Bocheński (1997) for quails. Beak impacts were observed on six large bird remains, 5 thoracic vertebrae from adults and a distal humerus fragment from an immature bird. A single notch was observed on two of the vertebrae, while the three others were damaged by two perforations and one or two notches (Fig. 4f). The humerus presented a single puncture. Two-thirds of the bird remains from Bylot presented digestion damage (Table 3; Fig. 4a, b, d). Given the small number of remains, the result does not appear different if we considered only the articular ends of the long bones or all the observed zones (articular ends, breakage of long bones, and global for the other bones). The digestion damage was light in most cases, with less than 10% of the observed zones presenting heavy or extreme damage (Table 3).

In the Hochstetter sample, bird remains were observed in 7 pellets out of the 27 pellets analyzed. One of them contained two-thirds of the bird remains discovered in the sample (NISP = 20/33). These bones belonged to the head (premaxillar, right hemi-mandible and quadrate) and to the right members and scapular girdle of a *Calidris alpina/alba*. Only a femur, a scapula and an ulna shaft fragment were observed from the left side of this prey. Another pellet contained only a proximal left ulna fragment that could be from the same individual. In this case, these two pellets might have constituted a singular example of multirejection (Laudet et al., 2002). Five other pellets contained very partial prey, most of them of large size. The size of the remains varied from 3 to 37 mm (Fig. 3), with an average length of 12.5 mm and a median of 12.0 mm (S.D. = 7.1 mm). Of the 17 long bones

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identified, 6 were complete, all from the *Calidris*. Mechanic damage was observed on 8 remains, all long bones. This consisted of single (NISP = 5) and bilateral notches (NISP = 2) located on the fracture edges and, in one case, a puncture (Fig. 4c, e). Three quarters of the bird bones had been digested, which was not different from Bylot. Considering only the articular ends of the long bones, the percentage appeared lower, but the small sample size prevented accurate comparison. Once again, the intensity of digestive damage was light for the majority of observed zones (Table 3).

3.3 Taphonomical observation of the rodent remains

All the skeletal elements of rodents were represented in the snowy owl pellets. Globally, there was a good relative abundance of the bones studied, above 50%, except for the vertebrae (Fig. 5). However, sizeable inter-site variations could be seen in terms of the relative abundance of some bones. For instance, the mean value for the relative abundance of femurs from Victoria was close to 98% whereas at Hochstetter and Bylot it was 81% and 68%, respectively. For the ulna, mean values ranged from 67% in Bylot to 78% in Hochstetter, while once again Victoria showed the highest mean value of relative abundance with 100%. As a global pattern for the long bones, the Bylot site tended to present the lowest values and Victoria the highest ones. This pattern was, however, not observed for the cranial and tooth elements. Furthermore, the site of Hochstetter showed a relative abundance of maxillaries 15% higher than for the two other sites, although the mean values of the other elements were between that of the two other sites. Finally, the most abundant element was not the same on each site, namely the ulna (followed by the femur) for Victoria, the maxillary for Hochstetter, and the molars for Bylot.

The AN/PO% index, used to evaluate differential preservation of the anterior and posterior limbs, was close to 50% for the three sites suggesting no imbalance in the signature

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of snowy owl pellets. The CRA/POSTCRA% index, reflecting differential preservation of the postcranial and cranial elements was also close to 50%, as was the Z/E% index concerning the zygopodia and stylopodia elements (Fig. 6; supplementary material).

The four long bones (humerus, ulna, femur and tibia) presented relatively high mean values of completeness, ranging from 70 to 95% (Fig. 7; supplementary material). Inter-site variations reached a 17% difference in femur completeness between Bylot and Victoria, with Victoria presenting a higher bone completeness than the other two sites.

Skeletal elements with evidence of rounding and corrosion due to digestion were frequently observed. For the post-cranial elements, proportions of digested long bones ranged from 19 to 57% (Fig. 8). Sizeable differences were observed between the sites, especially between the samples from Victoria, which showed the lowest percentages, and those from Bylot, which showed the largest percentages. The Hochstetter sample showed percentages of digested long bones close to that of Bylot. The incisors also presented large ranges of inter-site variation, with different proportions of digested elements between the lower and upper teeth. The latter presented the highest level of digested elements in the three samples. Except for the molars, Bylot had the highest proportion of digested elements in comparison with the two other sites. Indeed, the three sites presented very close proportions of digested first lower molars, varying only between 30 and 40%.

Concerning the degree of digestion, the first lower molars and the lower and upper incisors showed Level 1 digestion degrees close to 21, 19.5 and 35%, respectively (Fig. 9; supplementary material). Few elements presented strong or extreme digestion degrees, and those observed mainly came from the Bylot samples, with for instance upper incisor proportions reaching up to 10% for strong digestion and 5% for extreme digestion. By analyzing digestion degrees, significant difference could be observed in digestion pattern obtained between sites and remains analyzed (Table 4, $p<0.0001$). Bylot presents different

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patterns in comparison with the two other sites that are especially noticeable on both lower and upper incisors (Fig. 9). These three elements (first lower molars, upper and lower incisors) show also distinct digestion degree patterns. It suggests that incisors should not be pooled together, and that the distinction in digestion degree between molars and incisors could potentially be an indicator to differentiate some predators.

4. Discussion

Based on bone and tooth damage (i.e. breakage, digestion, and skeletal element proportions) due to the consumption of modern small vertebrates by predators, these predators have been classified in several categories according to damage levels.

Two main classification systems have been established. The one from Andrew (1990) was based on damages observed on modern rodent samples consumed by avian and mammalian predators, sorting them into five categories. The snowy owl was mainly ranked within predator Category 1, which signified little modification (such as incisor and postcranial digestion or skeletal element proportions), and secondly within Category 2 due to the more extensive breakage of postcranial elements and molar digestion. Only the ratio between the cranial and post-cranial elements fell into Category 4 (Andrews, 1990).

The second classification system (Bocheński, 2005) is based on bird remains modified by various raptors. Bocheński (2005) used the percentage of digested bones to distinguish 3 categories of predators. Categories 1 and 2, which include nocturnal raptors, are characterized by a percentage of digestion at or below 50%. The third category, which is characterized by almost 100% digested bones, includes the diurnal raptors. According to the material analyzed by Bocheński (1997), the snowy owl falls into Category 1, the one for which digestion damage is the lowest. These two systems are not exactly equivalent, but their use is complementary according types of prey, their abundances and the studied skeletal elements.

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A crucial point here is that the results of these classification systems for the snowy owl were based on restricted samples. In the case of Andrews' study, there were only 14 rodent individuals from pellets of wild snowy owl(s) (Andrews, 1990) and the reference set analyzed by Bocheński was based on eight adult quails, which were fed to a couple of snowy owls (Bocheński, 1997). Yet, a wild predator does not produce a fixed bone pattern that remains invariable through time and space. On the contrary, predators generate variable patterns of bone deposits (Saavedra and Simonetti, 1998) with average trends under similar conditions. As a consequence, reference frameworks must be based, as far as possible, on extensive sampling. Such an approach could thus ensure that variability is taken into account as well as the associated confidence intervals in order to avoid any over-interpretation (Denys, 2002, 2011). This work appraises bone and tooth damage created by snowy owls in three new samples in order to review the classical parameters used to investigate accumulator agents.

4.1 The effects of prey size

The size of prey is regularly assumed to be an important variable (e.g. Bocheński et al., 1993; Laudet and Hamdine, 2001; Cochard, 2008; Mallye et al., 2008). Undoubtedly, this parameter could explain the difference in completeness between the long bones of the small and large birds from the Bylot sample. According to the natural history observations (Scherzinger, 1974; Chamberlin, 1980), when the prey size is too large, snowy owls dissect it instead of swallowing it whole. This could explain the damage observed on the bones (i.e notches and punctures) and the incompleteness of the skeletons that were found in the pellets. These last observations are complementary with the ones made during Bocheński's experiment (1997), in which the snowy owl segmented medium-sized prey before partially swallowing it. Completeness of bones and proportions of notches or punctures must thus be

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carefully considered and combined with prey size in order to avoid any misinterpretation with other raptors.

4.2 Inter-site variability

In our samples, similarities were observed between the sites, even though they did not all present entirely comparable prey assemblages. Bird remains were globally rare: they were absent at one site (Victoria) and accounted for less than 5% of the MNI at both the other sites (Hochstetter and Bylot). Lemmings dominated each assemblage (Table 1), but the species were not found in the same proportions. In each of the samples, adults dominated the prey population, however, it should be noted that very young lemmings were present in a significant proportion, as shown by the unfused humeri. In our experience, this is an uncommon pattern in the archaeological record.

By taking into account the confidence intervals related to the sample size in order to interpret the variability of proportions and indexes, inter-site differences were observed, in a few cases, outside of the statistical ranges. For instance, the long bones from Victoria were more proportionally numerous than those from Bylot (Fig. 5). In contrast, except for the molars, digested elements were more numerous from Bylot than from Victoria (Fig. 8 and 9). When we look at the global trend for the three sites, the Bylot sample is clearly distinguished by a greater abundance of digested elements associated with higher digestion degrees. This higher digestion may explain the globally lower preservation rate of skeletal elements from the Bylot sample. Conversely, the Victoria sample was constituted by longer and better preserved bone remains, with greater completeness and less digestion damage. As previously mentioned, these inter-site differences could be due to many variables, and it is difficult to define here which factor(s) best explain this variability.

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4.3 Inter-study variability

The small number of bird bones found in our new samples has limited the scope of our observations. However, results concerning wing/leg proportions and long-bone completeness are similar to those noted by Bocheński. In contrast, differences seem to exist in terms of digestion damage. At Bylot, digestion of the articular ends of the bird long bones was around 63.4%, which is higher than that calculated from Bocheński's data (1997, table VIII p. 287; 43.4% [35.5–52.0%]). At the same time, this percentage is closer to the higher values observed for the rodents from this sample (Fig. 8). This difference could be due to individual raptor characteristics and the way in which they regurgitated the pellets: on the one hand, there is a single male in a zoo, whereas on the other hand, there are undoubtedly several different wild owls from different nest sites, including unfledged youths. Other parameters could be responsible for these differences, such as the age of the prey, and the difference in bony structures and porosity between young and adult prey. The anatomical composition of the sample could also play a substantial role, if we hypothesize that digestion could have different effects on the articular parts of the long bones. Yet, in our case, this latter factor does not seem to have been particularly significant as the least digested bones in the Bocheński sample (the long bone from the leg and the carpometacarpus) were observed in similar proportions in the Bylot sample. In any case, the reference frameworks on birds remain too scarce for the potential variables to be clearly understood.

To provide a comparison with Andrews' study (1990), we have documented Andrews' results from snowy owl samples in Figures 5, 6, 7 and 8 along with our own results. When only the mean values of Andrews' data are compared with ours, several dissimilarities can be observed. However, many of them are only due to the small MNI analyzed by this author. When confidence intervals are taken into account, many of these differences are not statistically robust, as illustrated by the completeness of the long bones (Fig. 7). The three

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indexes AN/PO%, Z/E% and CRA/POSTCRA% for Andrews' values were recalculated from the raw data. The values of our samples were relatively similar to those of Andrews (1990; Fig. 6). Concerning the index between postcranial and cranial elements (CRA/POSTCRA%), there were no significant differences (Fig. 6). The values were close to 50%, indicating a proportional preservation. The relative abundance of maxillaries and mandibles from Bathurst Island tends to be relatively low compared to our data (Fig. 5), thus slightly impacting the CRA/POSTCRA% index. Although Andrews (1990) ranked the snowy owl as a Category 4 predator for this modification, it seems most likely to be due to the small sample size. Nonetheless, a few discrepancies with Andrews' data should be noted regarding the digestion proportions previously observed on bird bones. In terms of digestion damage, the snowy owl was mainly assumed to be a Category 1 predator for incisor and postcranial elements and to be a Category 2 predator for molars (Andrews, 1990). These observations differ greatly, however, from the digestion proportions observed for the three sites with higher proportions of digested elements (Fig. 8). Indeed, by comparing our results with that of other predators, the recorded digestion patterns are on average closer to that of a Category 3/4 predator for incisors (Fig. 10), Category 3/4 for molars (Fig. 11), and Category 3 for postcranial digestion (Fig. 12). It should be noted that many of these differences could only be related to the restricted sample size as demonstrated by the large confidence intervals (Fig. 10, 11, and 12).

These differences with Andrews' results could also be related to biological and ecological factors, notably such as types of site (nest *vs* roost) in which the pellets from each represent only a part of the diet (Korth, 1979). Indeed, Andrews' sample (1990) came from roost sites on Bathurst Island, whereas the samples from this study were collected from the nests of snowy owls. As noted, differences in digestion have been observed for barn owls (*Tyto alba*) between pellets from the nest site and those from the roost site (Bruderer and Denys, 1999; William, 2001; De Cupere et al., 2009). In such cases, these differences are

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most likely related to the digestion by young individuals, which is stronger than that of adults. Nonetheless, in the case of fossil accumulations, the distinction between these two types of site is still challenging (De Cupere et al., 2009).

4.4 Toward modern reference frameworks?

The results of this study give rise to questions about upcoming taphonomical investigations. Indeed, one major problem is that taphonomical features are not unique to only one or two predators. They are shared by almost all predators, and the only difference that could be used is their relative proportions. Surprisingly, few studies have been performed to complete Andrews' undertaking (e.g. Denys, 2011), although many studies on fossil materials have used the data from modern reference sets to identify the potential predators of fossil accumulations. Furthermore, for most of the predators, a single study is available, performed on non-statistical samples (Denys, 2002, 2011). Until now, taphonomical features were barely investigated by taking into account confidence intervals due to restricted sample sizes. In the current state of research, considering biological variability, one particular taphonomical feature, or an average pattern calculated from different raptor populations, seems to be an inadequate tool, especially when confidence intervals are not included in the analyses. Obviously, a better knowledge of the actual variability of predator signatures is of crucial importance. For instance in case of snowy owl accumulation, its differentiation from other predators from category 3 and 3/4 (as European Eagle owl) still remains difficult, although consequences in terms of palaeoecological and palaeoenvironmental reconstructions are different. Molar digestion features could help in such approaches, but should be explored with supplementary referential. Nonetheless transferring such data to the fossil record is a much harder challenge. Such approaches are indeed based on the weighty working hypothesis that a single predator accumulated the bone remains. In a single fossil assemblage, bones could,

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however, have been accumulated by several predators, especially in cave contexts in which many trogloxene predators can have inhabited the site through time.

A further issue arises when we consider that modern reference sets, such as this one, record only a taphocenosis (e.g. Kowalski, 1990). They do not record the complex fossilization processes associated with potential post-depositional effects that can greatly modify bone elements and bias investigations such as the skeletal representation of individuals by eliminating the smallest elements. Furthermore, the fragmentation of long bones could be increased, rendering these ratios only useful to a limited degree: high levels of completeness could be related to predators that do not break bones, whereas high fragmentation could be the result of many variables.

Finally, the need for modern reference sets has led us toward three propositions:

1) The first is to generate more modern, statistically confident reference sets. Simplifying and optimizing the approach by focusing on a small number of specific bones and variables that are applicable and informative for studies on fossil materials could be prioritized. By completing Andrews' undertaking, classifications of predators would also be improved and the discontinuous ranking currently observed in digestion degrees could thus be avoided (Fig. 10, 11 and 12).
2) The second proposition is to include, as far as is possible, all the prey hunted in the analysis by considering the diversity of prey, its sizes and its preferential behaviors (Denys et al., 2017). For instance, this study shows that very different sizes of prey were consumed by snowy owls, from young lemmings to large ducks and geese. Today, according to biological studies, snowy owls are highly dependent on their lemming prey and it seems that a significant relationship exists between the number of lemmings in their diet and the local density of lemmings (Gilg et al, 2006; Therrien et al., 2014). On the other hand, the absence of lemmings in pellet

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remains is not a sufficient criteria to attribute other predators as the producers of these pellets. For instance, at Hochstetter, many of the snowy owl pellets produced in winter, when lemmings are living under a deep layer of snow, consist exclusively of rock ptarmigan and arctic hare remains (Gilg, unpublished). The question thus also arises for fossil bone accumulations, the snowy owl having been, for instance, present in southwestern France during the Late Glacial, when no lemmings are known to have inhabited this region (e.g. Laroulandie, 2016; Royer et al., 2016). This point also suggests that the modern relationship between prey and predators should always be taken with caution.

3) The final proposition is to look at major changes in bone accumulations and taphonomic features throughout a stratigraphy in order to establish the integrity of a particular deposit level in comparison with others (e.g. Stoetzel et al., 2011; Royer et al., 2013), and to exclude it if any doubt exists.

5. Conclusions

Snowy owl remains have been widely collected at many fossiliferous sites and the species could be a likely predator of many small vertebrate bone accumulations. This study has investigated the taphonomical features that were documented on bones from three modern accumulations. A moderate inter-site variability was observed for some variables. This study shows differing results from those obtained previously, in particular higher digestion patterns and degrees. It is noteworthy that previous studies were based on restricted sample sizes, limiting full investigation into variability due to biological or ecological factors. As already emphasized by previous authors, variability and the associated statistical confidence intervals are thus crucial notions that must be fully considered when interpreting taphonomical features and attempting to identify the predator(s) responsible for accumulations.

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Figure captions

Figure 1: Map of the Arctic region showing the three sites at Hochstetter, and on Bylot, Victoria and HOC islands, sampled in this study. The breeding grounds of *Bubo scandiacus* is based on data from http://www.iucnredlist.org/

Figure 2: Histograms of lemming population structure obtained in relation to the length of the femur (mm) distinguishing figured individuals with a fused femoral head (grey), and those with unfused femoral heads (white). NISP refers to the Number of Identified Specimens.

Figure 3. Histogram obtained from the length (mm) of Bylot bird remains. NISP refers to the Number of Identified Specimens.

Figure 4. Examples of damage to bird bones collected from snowy owl pellets. A, Bylot, humerus of a small bird (Passeriformes) showing digestion on the proximal and distal articulations (1: moderate digestion on the proximal articulation; heavy digestion on the distal articulation); B., Bylot, heavy digestion on a pedal phalange from a large bird; C., Hochstetter, beak notch on a small bird (*Calidris*); D., Bylot, ulna of a small bird (Passeriformes) showing heavy digestion of the proximal articulation; E., Hochstetter,

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moderate digestion damage and beak notches on the proximal humerus of a large bird (*Lagopus*); F., Bylot, punctures and notches on a thoraxic vertebra from a large bird.

Figure 5. Relative abundance (%) of the different skeletal elements of lemmings, documented according to the location.

Figure 6. Indexes between anterior and posterior limbs (AN/PO%), between postcranial and cranial elements (CRA/POSTCRA%), and between zygopodia and stylopodia elements (Z/E%) shown with their confidence intervals according to the sample. See the text for calculation of these indexes. The dotted line shows the 50% value. Andrew (1990)'s index values have been recalculated from the raw data (see supplementary material).

Figure 7. Completeness (%) of long bones documented per site. Raw data have been detailed in Supplementary material.

Figure 8. Proportion (%) of digested elements per site. Raw data have been detailed in Supplementary material.

Figure 9. Proportion of digested elements (First lower molar, upper incisor and lower incisor) per site according to degree of digestion. Digestion categories: none (0), light (1), moderate (2), heavy (3) and extreme (4).

Figure 10. Proportion (%) of digested incisors ordered by the predator type. Colors represent the five categories of predators as defined by Andrews (1990) and refined by Fernández-Jalvo et al. (2016). Data are from Andrews (1990) and this study. Star shows percentage of arvicoline incisors digested by tawny owls (Andrews and Fernández-Jalvo, 2018).

Figure 11. Proportion (%) of digested molars ordered by the predator type. Colors represent the five categories of predators as defined by Andrews (1990) and by Fernández-Jalvo et al. (2016). Data are from Andrews (1990) and this study. Star shows percentage of arvicoline molars digested by tawny owls (Andrews and Fernández-Jalvo, 2018).

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Figure 12. Proportion (%) of digested femur ordered by the predator type. Colors represent the five categories of predators as defined by Andrews (1990). Data are from Andrews (1990) and this study. Star shows data of tawny owls from Andrews and Fernández-Jalvo (2018).

Table captions

Table 1. Minimum Number of Individuals (MNI) reported for each species at each location. NISP (in brackets) refers to the Number of Identified Specimens. * = large sized birds; ** = small sized birds in comparison with the size of the Common blackbird, *Turdus merula*.

Table 2. Long bone completeness (raw data and percentage) for small and large birds from Bylot snowy owl pellets. The interval limits (% min and %max of completeness) calculated with 95% of confidence are given in the brackets. * data used to calculate the statistical test Z.

Table 3. Percentage and intensity of digestion observed on bird remains from Bylot and Hochstetter snowy owl pellets. NISP refers to the Number of Identified Specimens. The interval limits (% min and %max of proportions) calculated with 95% of confidence are given in the brackets.

Table 4. Results from Cumulative Link Models (clm) function showing differences calculated from digestion degree between the three site (Victoria, Bylot and Hoc) and between the thre e elements (Lower incisors, Upper incisors and Molars). The condition number of the Hessia n is 113.9, AIC is 4691.11 and number of observations is 1986. Asterisk (∗∗∗) denotes the si gnificance less than 0.001 levels.

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MNI (NISP)	Bylot 2000	Victoria 1999	Hochstetter 2010
Lemmus trimunocranus	131	2	-
Dicrostonyx groenlandicus	130	43	78
Rodentia indet.	-	5	-
Mustela erminea	1 (2)	-	-
Anatidae*	6 (44)	-	-
Lagopus cf. *muta**	-	-	1 (3)
*Calidris alpina/alba***	-	-	1 (21)
Passeriformes**	4 (51)	-	-
Aves indet. (large size*)	(166)	-	(7)
Aves indet. (small size**)	-	-	(2)

Table 1

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		Who le bone	Fragmente d bone	otal	% completeness [%min - %max]
		Small birds			
	Coracoid	2	1		_
	Scapula	0	1		_
	Humerus	3	2		60.0 [17.0 – 92.7]
	Ulna	4	3		57.1 [20.2 – 88.2]
	Radius	0	2		_
carpus	Carpometa	4	0		_
	Femur	5	0		100.0 [46.3 – 98.1]
	Tibiotarsus	2	3		40.0 [7.3 – 83.0]
tarsus	Tarsometa	5	1		83.3 [36.5 – 99.1]
	Total	**25***	**13**	**8***	**65.8**
		Large birds			
	Scapula	0	2		_
	Humerus	0	9		0.0 [1.0 – 37.1]
	Ulna	1	1		_
	Radius	2	0		_
	Femur	1	5		16.7 [0.9 – 63.5]
	Tibiotarsus	0	10	0	0.0 [0.9 – 34.5]

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tarsus	Tarsometatarsus	7	2		77.8 [40.2 – 96.1]
	Total	**11***	**29**	**0***	**27.5**

Table 2

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		Bylot		Hochstetter	
			% [binomial proportion]		% [binomial proportion]
	NISP observed	56		2	
	NISP digested	76	68.8 [62.7-74.3]	5	78.1 [59.6-90.1]
	NISP non digested	0	31.3 [25.7-37.4]		21.9 [9.9-40.4]
	Observed zones	35		8	
	Digested zones	16	64.5 [59.1-69.6]	8	58.3 [43.3-72.1]
	Light	42	65.7 [58.9-71.9]	3	82.1 [59.9-94.0]
	Moderate	3	24.5 [19.0-30.9]		17.9 [6.0-40.1]
	Heavy	4	6.5 [3.7-10.9]		_
	Extreme		3.2 [1.4-6.8]		_
ends	Observed long bone articular	01		0	
ends	Digested long bone articular	4	63.4 [53.2-72.6]	9	45.0 [23.8-68.0]

Table 3

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	Estimate	Standard Error	Z value	Pr(>|z|)	
Site - Bylot	0.6767	0.136	4.977	6.45E-07	**
Site - Hochstetter	-0.1464	0.1618	-0.905	0.365668	
Element – Upper incisor	0.4344	0.105	4.137	3.52E-05	**
Element – Molar	-0.3981	0.1073	-3.712	0.000206	**

Table 4

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Highlights

- Taphonomical features of *Bubo scandiacus* were investigated from three nest sites

- Inter-site and inter-study variabilities were observed on taphonomical features

- Snowy owl produces moderate digestion of incisors, molars and postcranial elements

- This predator must be classed as a Category 3 or Category 3/4

- Variability and associated statistical confidence intervals are crucial notions

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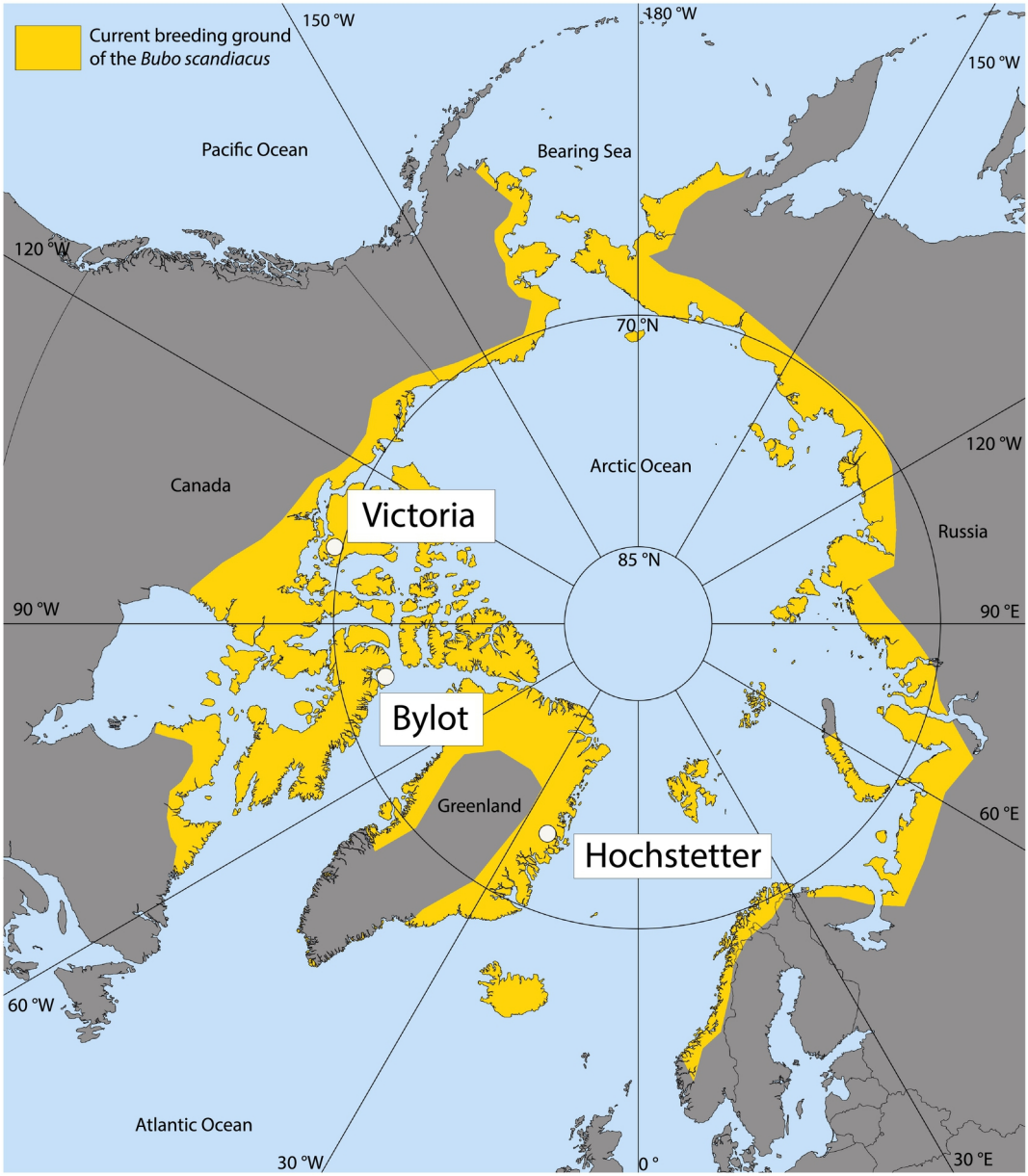
Current breeding ground of the *Bubo scandiacus*
150 °W
180 °W
150 °W
Pacific Ocean
Bearing Sea
120 °W
70 °N
120 °W
Canada
Arctic Ocean
Victoria
Russia
85 °N
90 °W
90 °E
Bylot
Greenland
60 °E
Hochstetter
60 °W
Atlantic Ocean
30 °W
0 °
30 °E

Figure 1

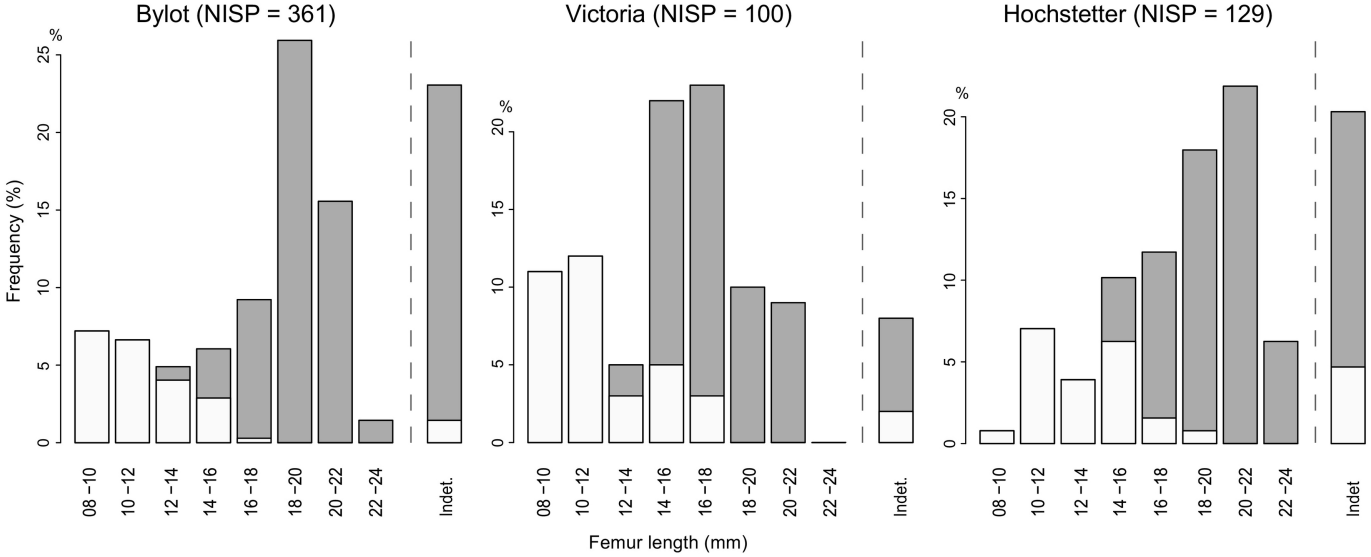
Bylot (NISP = 361)
Victoria (NISP = 100)
Hochstetter (NISP = 129)
Frequency (%)
%
0
5
10
15
20
25
08 –10
10 –12
12 –14
14 –16
16 –18
18 –20
20 –22
22 –24
Indet.
Femur length (mm)

Figure 2

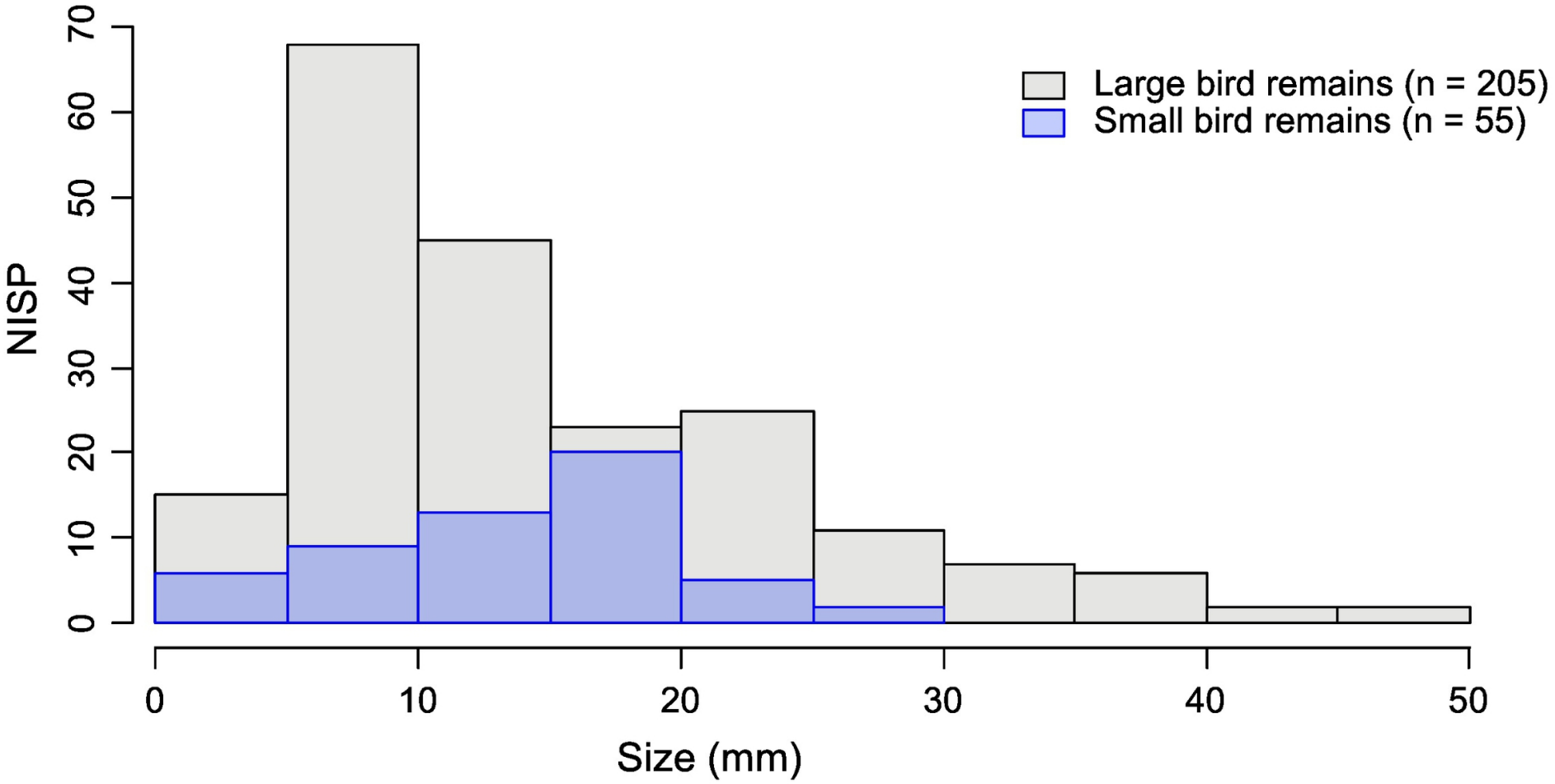
Large bird remains (n = 205)
Small bird remains (n = 55)
NISP
0
10
20
30
40
50
60
70
0
10
20
30
40
50
Size (mm)

Figure 3

Figure 4

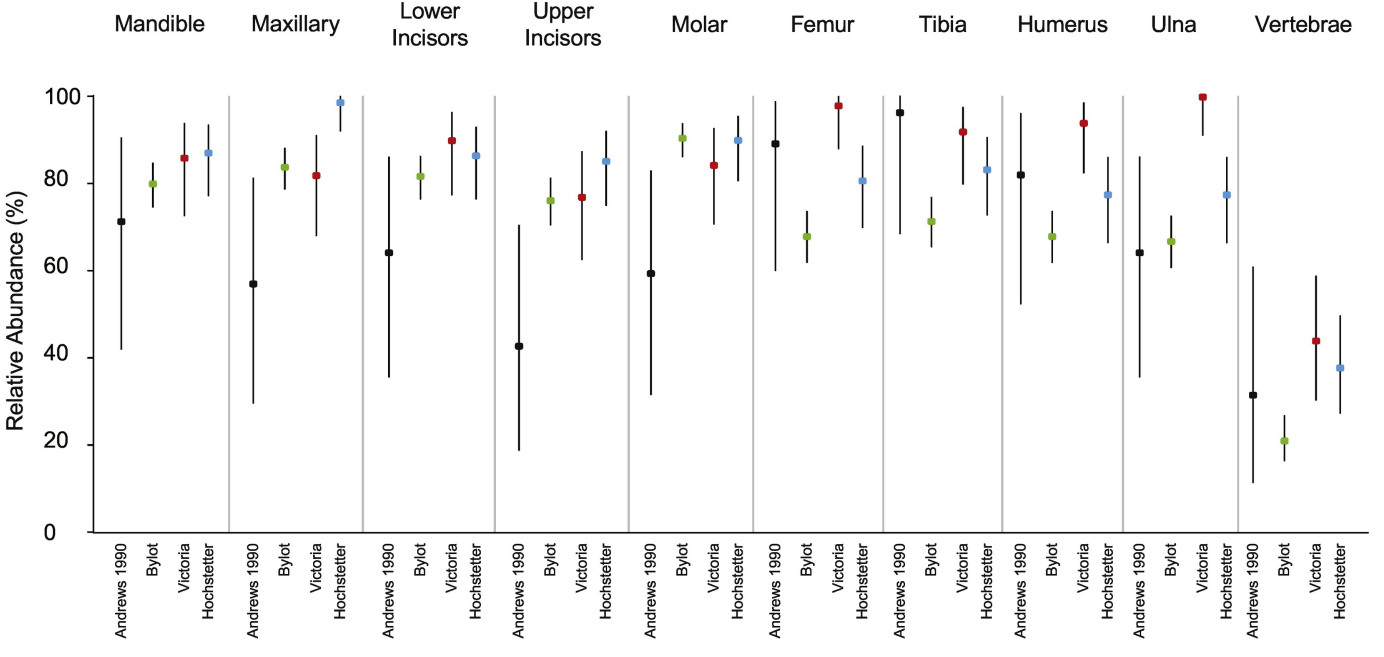
Mandible
Maxillary
Lower Incisors
Upper Incisors
Molar
Femur
Tibia
Humerus
Ulna
Vertebrae
Relative Abundance (%)
100
80
60
40
20
0
Andrews 1990
Bylot
Victoria
Hochstetter

Figure 5

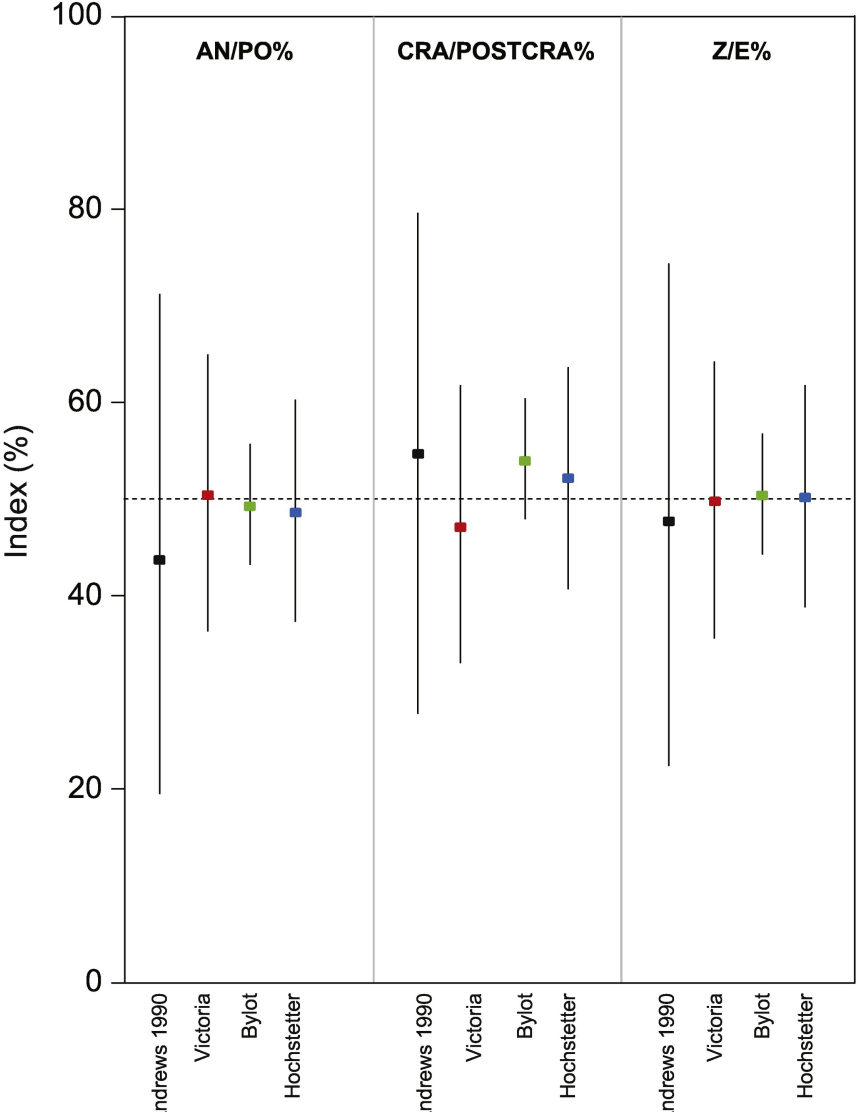
AN/PO%
CRA/POSTCRA%
Z/E%
Index (%)
100
80
60
40
20
0
Andrews 1990
Victoria
Bylot
Hochstetter
Andrews 1990
Victoria
Bylot
Hochstetter
Andrews 1990
Victoria
Bylot
Hochstetter

Figure 6

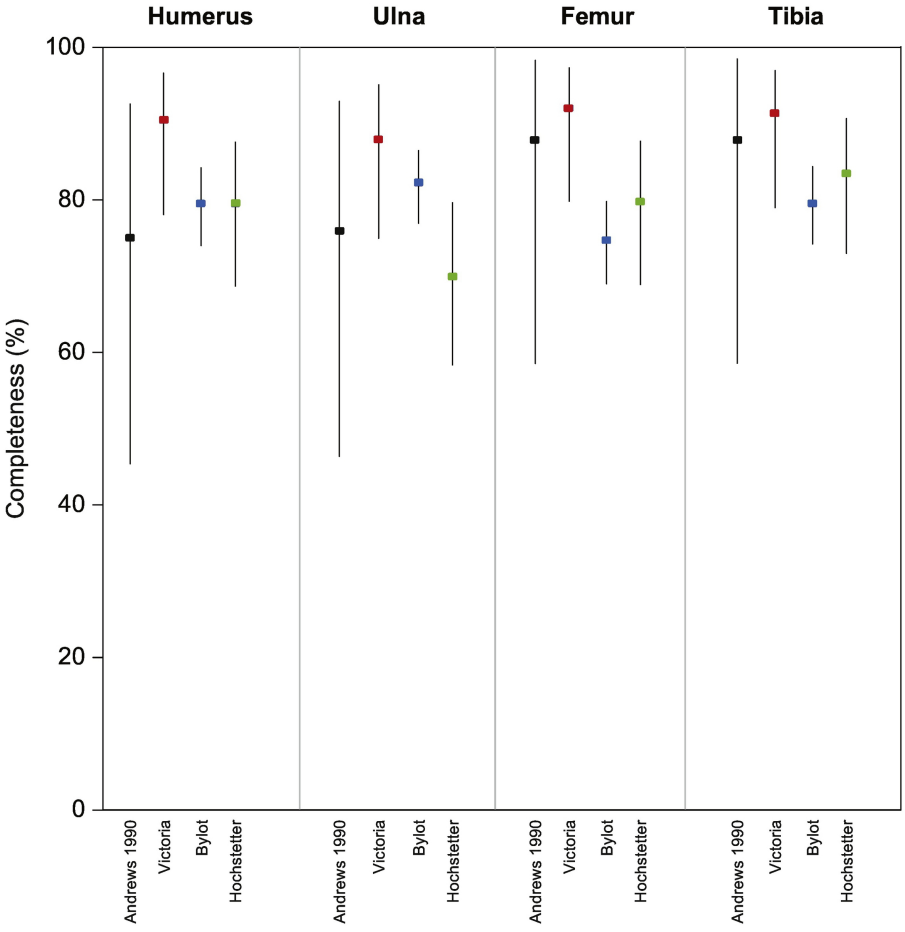
Humerus
Ulna
Femur
Tibia
Completeness (%)
100
80
60
40
20
0
Andrews 1990
Victoria
Bylot
Hochstetter

Figure 7

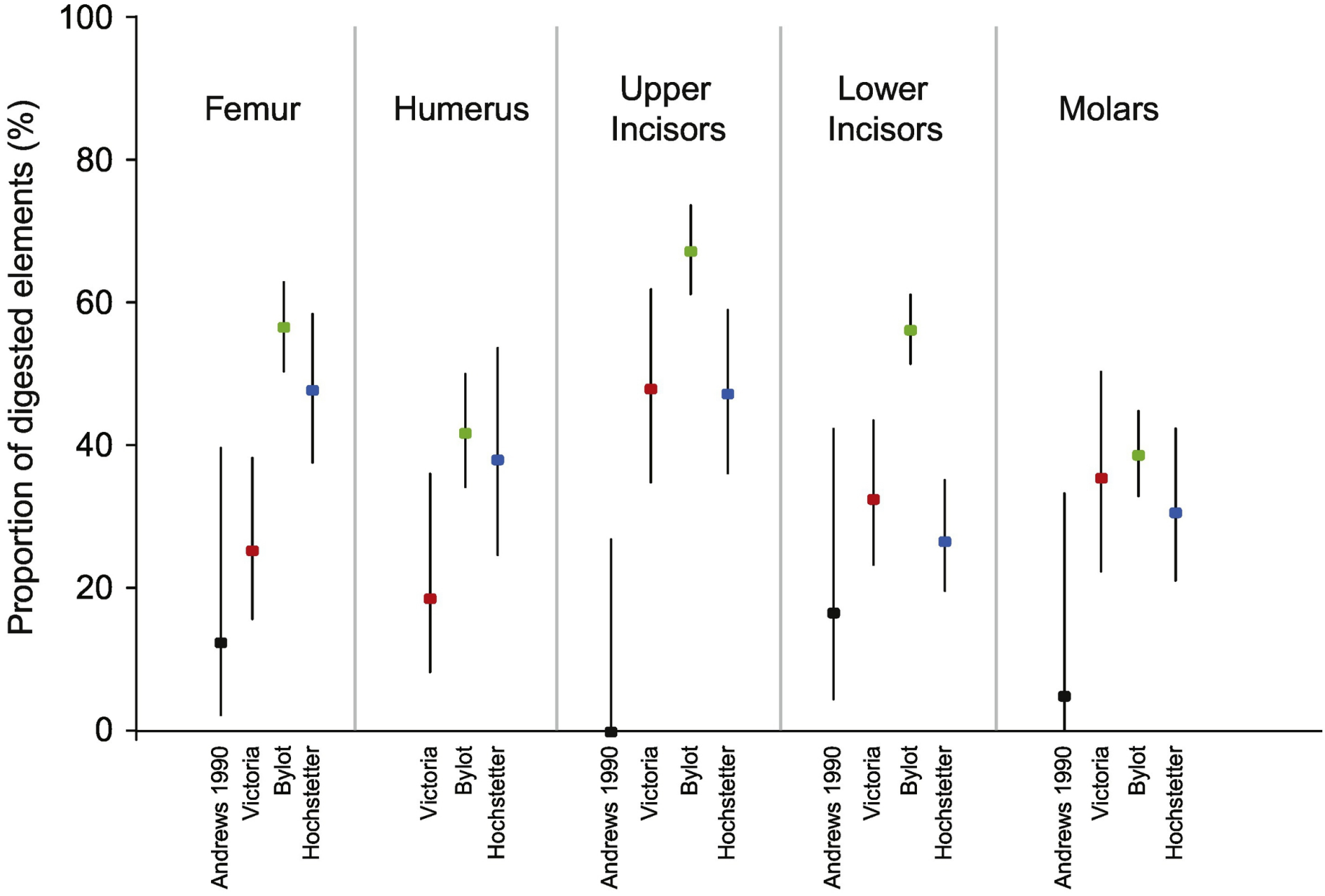
Proportion of digested elements (%)
100
80
60
40
20
0
Femur
Humerus
Upper Incisors
Lower Incisors
Molars
Andrews 1990
Victoria
Bylot
Hochstetter

Figure 8

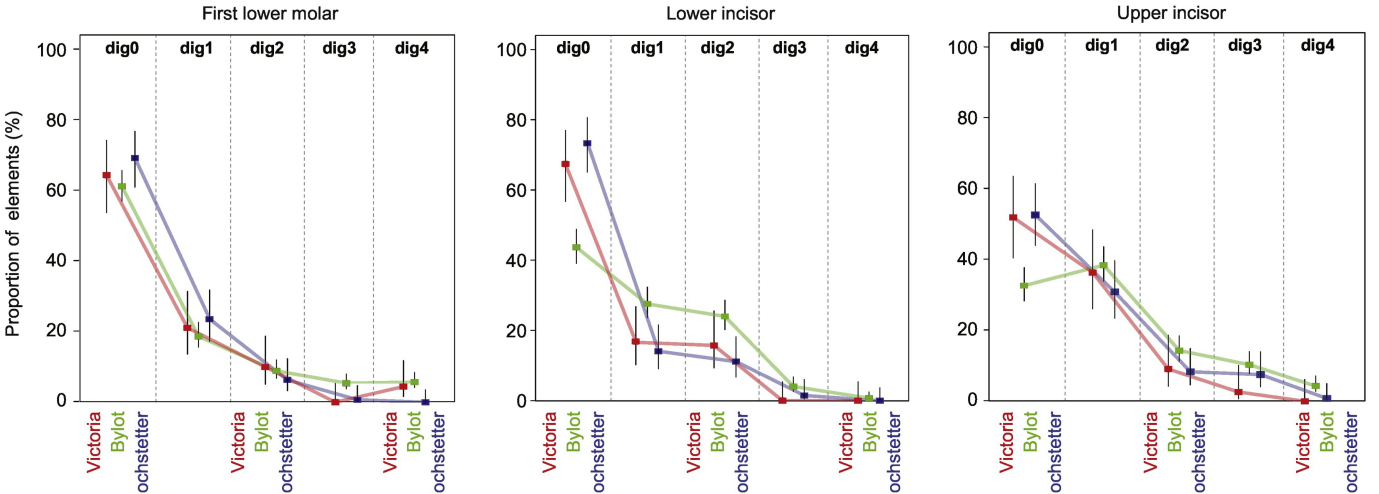
First lower molar
Lower incisor
Upper incisor
Proportion of elements (%)
100
80
60
40
20
0
dig0
dig1
dig2
dig3
dig4
Victoria
Bylot
Hochstetter

Figure 9

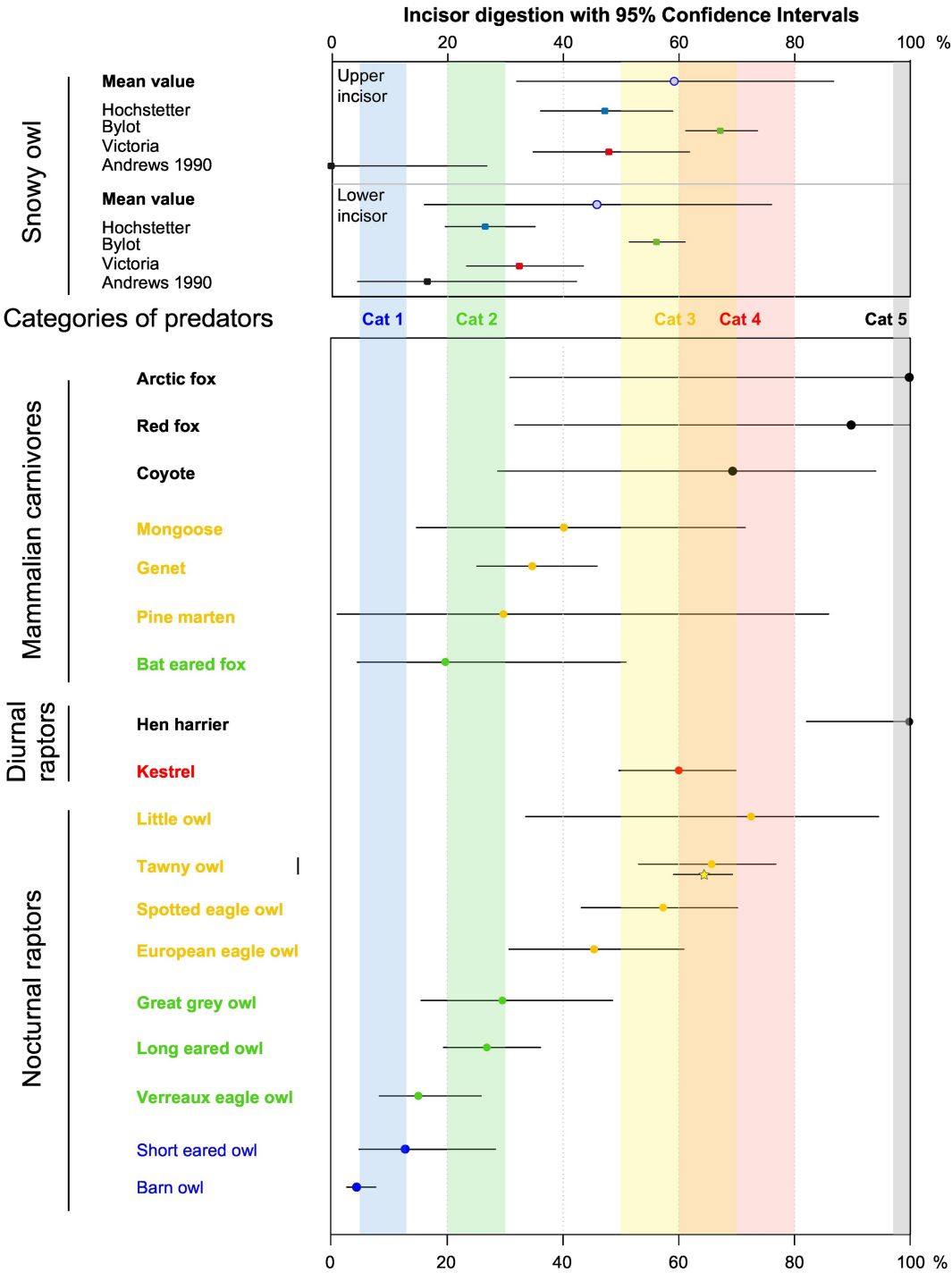
Incisor digestion with 95% Confidence Intervals
0
20
40
60
80
100 %
Snowy owl
Mean value
Hochstetter
Bylot
Victoria
Andrews 1990
Upper incisor
Mean value
Hochstetter
Bylot
Victoria
Andrews 1990
Lower incisor
Categories of predators
Cat 1
Cat 2
Cat 3
Cat 4
Cat 5
Mammalian carnivores
Arctic fox
Red fox
Coyote
Mongoose
Genet
Pine marten
Bat eared fox
Diurnal raptors
Hen harrier
Kestrel
Nocturnal raptors
Little owl
Tawny owl
Spotted eagle owl
European eagle owl
Great grey owl
Long eared owl
Verreaux eagle owl
Short eared owl
Barn owl
0
20
40
60
80
100 %

Figure 10

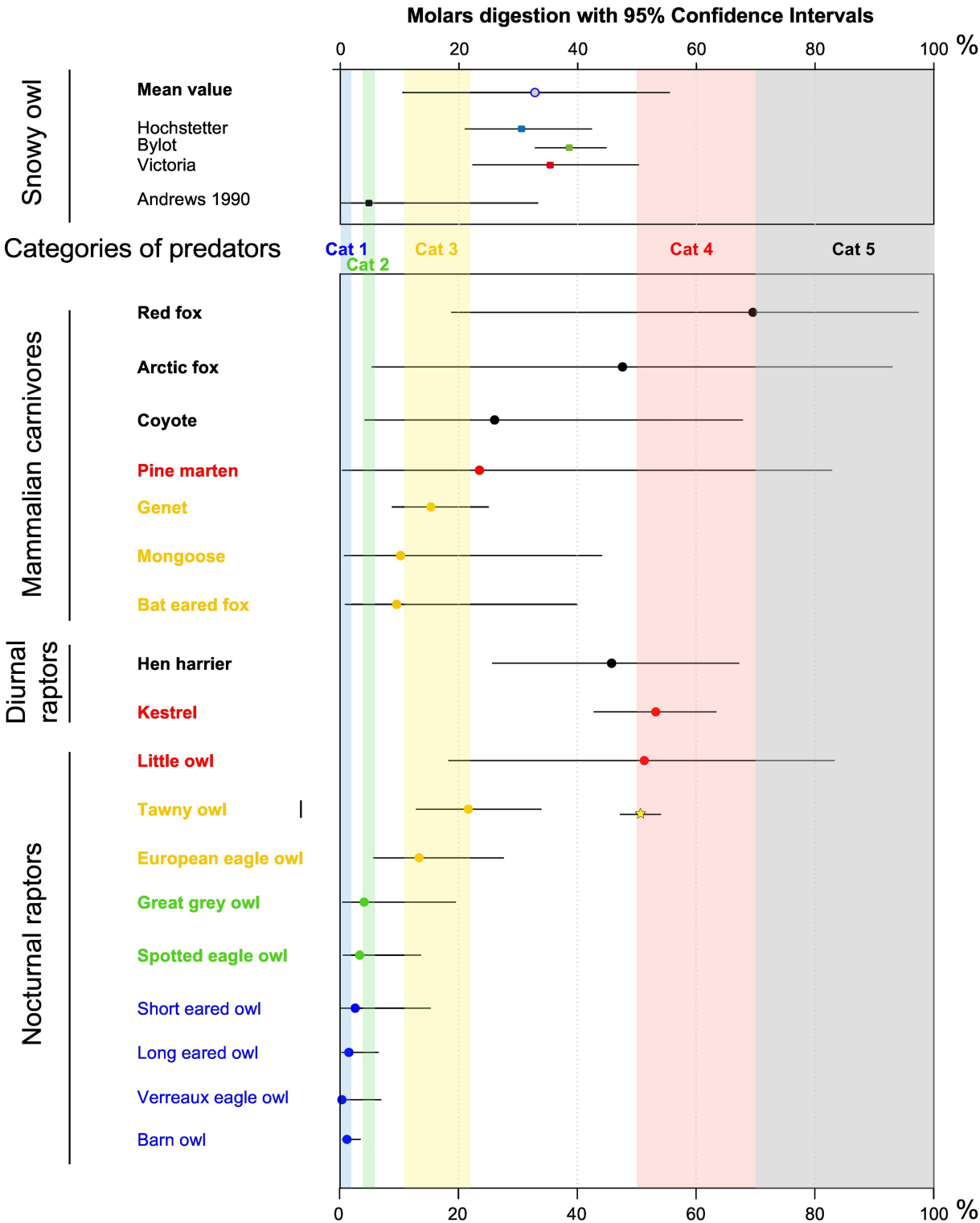
Molars digestion with 95% Confidence Intervals
0
20
40
60
80
100
%
Snowy owl
Mean value
Hochstetter
Bylot
Victoria
Andrews 1990
Categories of predators
Cat 1
Cat 2
Cat 3
Cat 4
Cat 5
Mammalian carnivores
Red fox
Arctic fox
Coyote
Pine marten
Genet
Mongoose
Bat eared fox
Diurnal raptors
Hen harrier
Kestrel
Nocturnal raptors
Little owl
Tawny owl
European eagle owl
Great grey owl
Spotted eagle owl
Short eared owl
Long eared owl
Verreaux eagle owl
Barn owl

Figure 11

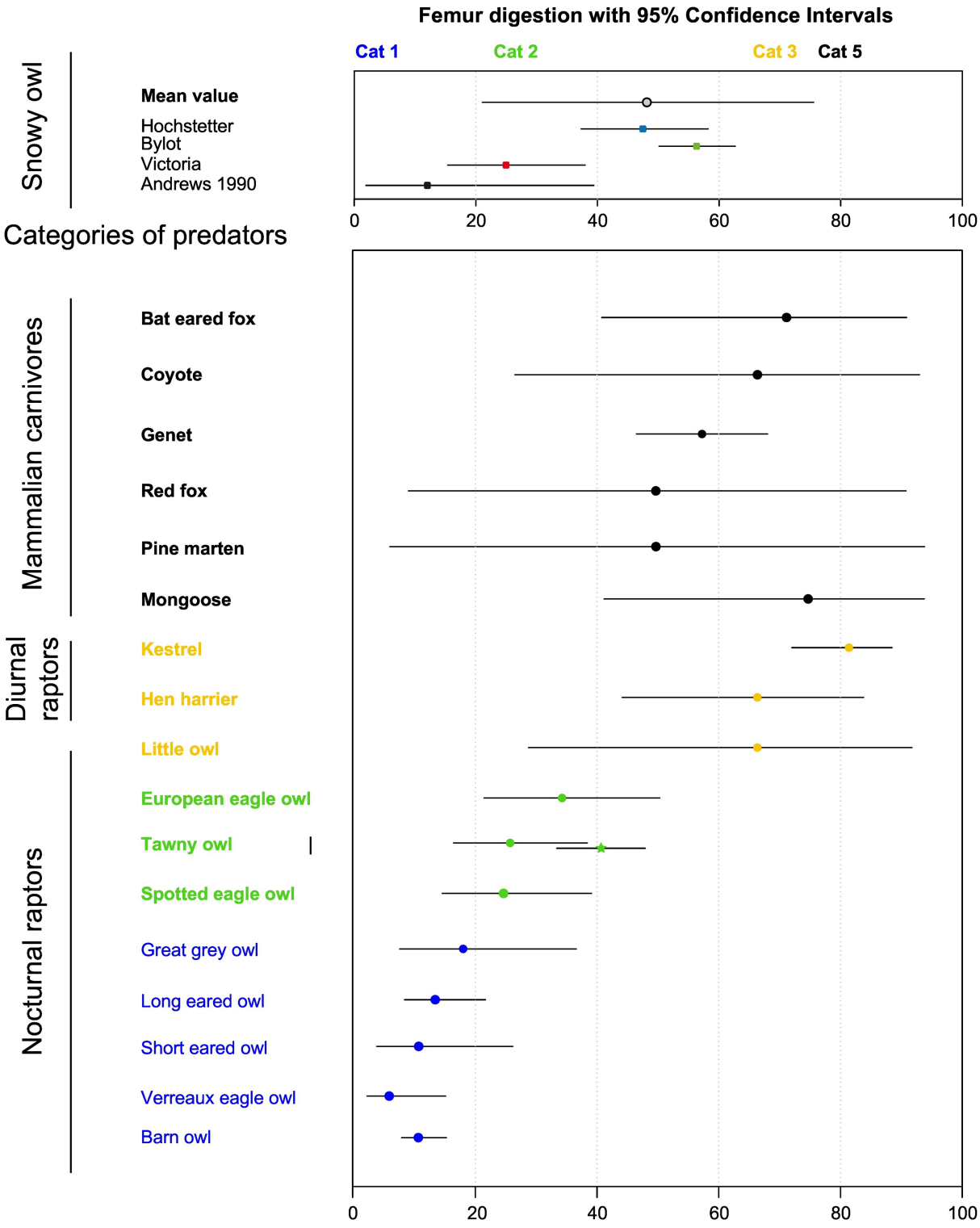
Femur digestion with 95% Confidence Intervals
Cat 1
Cat 2
Cat 3
Cat 5
Snowy owl
Mean value
Hochstetter
Bylot
Victoria
Andrews 1990
0
20
40
60
80
100
Categories of predators
Mammalian carnivores
Bat eared fox
Coyote
Genet
Red fox
Pine marten
Mongoose
Diurnal raptors
Kestrel
Hen harrier
Little owl
Nocturnal raptors
European eagle owl
Tawny owl
Spotted eagle owl
Great grey owl
Long eared owl
Short eared owl
Verreaux eagle owl
Barn owl
0
20
40
60
80
100

Figure 12