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## Article

# Multi-Taxa Neo-Taphonomic Analysis of Bone Remains from Barn Owl Pellets and Cross-Validation of Observations: A Case Study from Dominica (Lesser Antilles)

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**Abstract:** Paleo- and neo-taphonomic analyses of bone assemblages rarely consider all the occurring taxa in a single study and works concerning birds of prey as accumulators of microvertebrate bone remains mostly focus on small mammals such as rodents and soricomorphs. However, raptors often hunt and consume a large range of taxa, including vertebrates such as small mammals, fishes, amphibians, squamates and birds. Bone remains of all these taxonomic groups are numerous in many paleontological and archaeological records, especially in cave deposits. To better characterize the predators at the origin of fossil and sub-fossil microvertebrate accumulations and the taphonomic history of the deposit, it is thus mandatory to conduct global and multi-taxa taphonomic approaches. The aim of this study is to provide an example of such a global approach through the investigation of a modern bone assemblage from a sample of pellets produced by the Lesser Antillean Barn Owl (*Tyto insularis*) in the island of Dominica. We propose a new methodology that allows us to compare different taxa (rodents, bats, squamates and birds) and to experiment with a cross-validation process using two observers for each taxonomic group to test the reliability of the taphonomic observations.

**Keywords:** rodents; bats; lizards; birds; taphonomy; cross-validation; predation; *Tyto insularis*; Caribbean



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## 1. Introduction

The Lesser Antillean Barn Owl, *Tyto insularis* (Pelzeln, 1872), is an endemic Caribbean species characterized by a dark plumage and a small size, with a distribution restricted to the Lesser Antilles (Dominica, St Vincent, Grenadines islands and Grenada) [1–3] and whose taxonomic status as a species or subspecies is still discussed (e.g., [4,5]). Several studies have documented the food habits of the Barn Owl family (Tytonidae) in the Caribbean: *Tyto alba* (Scopoli, 1769) in the Greater Antilles [6–11], *T. insularis* on the island of Dominica [12] and *T. glaucops* (Kaup, 1852) in Hispaniola [2]. However, the taphonomy of the bone assemblages created by these predators in the insular Caribbean has never been investigated. This lack of scientific interest is not restricted to barn owls as this region currently suffers from an almost complete absence of neo-taphonomic investigation conducted on modern bone assemblages. As a result, although the role of barn owls is suspected in the accumulation of some of the known paleontological deposits in the Caribbean [13], the accumulation process of most subfossil bone accumulations has never been investigated. This generalized lack of taphonomic work in the Caribbean makes it difficult to interpret paleobiodiversity data, both for paleoenvironmental reconstructions (e.g., [14,15]) and for

the investigation of the evolution of faunal communities over time, under climatic and/or anthropogenic pressure. This is especially damaging as this situation can sometimes lead to a severe misinterpretation of the fossil records. To add to the lack of regional taphonomic comparison points, most available studies conducted in other geographic areas are mostly focused on small mammals such as rodents (e.g., [14,16]), which only account for a very limited part of the insular Caribbean paleobiodiversity. Indeed, native terrestrial small mammals are rare in the Caribbean islands, and commensal rodents (*Dasyprocta* spp., *Rattus* spp., *Mus musculus*) have mostly been introduced throughout the last few millennia by human populations during different waves of settlement [17–20]. Before these rodents arrived and their populations expanded, predators obviously had to exploit the locally available prey species (bats, birds, amphibians and squamates). In this context, it is therefore important to better characterize the taphonomic impact of raptors on the anatomical and faunal representation of the whole diversity of their available prey species. This is mandatory to better understand the history and representativeness of the Caribbean fossil and subfossil microvertebrate assemblages. More generally, multi-taxa taphonomic analyses remain rare [15,21–23] and deserve to be considerably developed.

The present study has several goals: (1) to provide new data on the taphonomic modifications caused by *Tyto insularis* on bone assemblage of Lesser Antillean prey species; (2) to test the effectiveness, reliability and reproducibility of the chosen taphonomic approach by involving several observers who specialize in different taxa (rodents, bats, squamates and birds); and (3) to propose a reliable and simplified methodology for multi-taxa neotaphonomic analyses that is potentially transposable to fossil and sub-fossil assemblages.

## 2. Materials and Methods

### 2.1. Owl Pellets Sampling

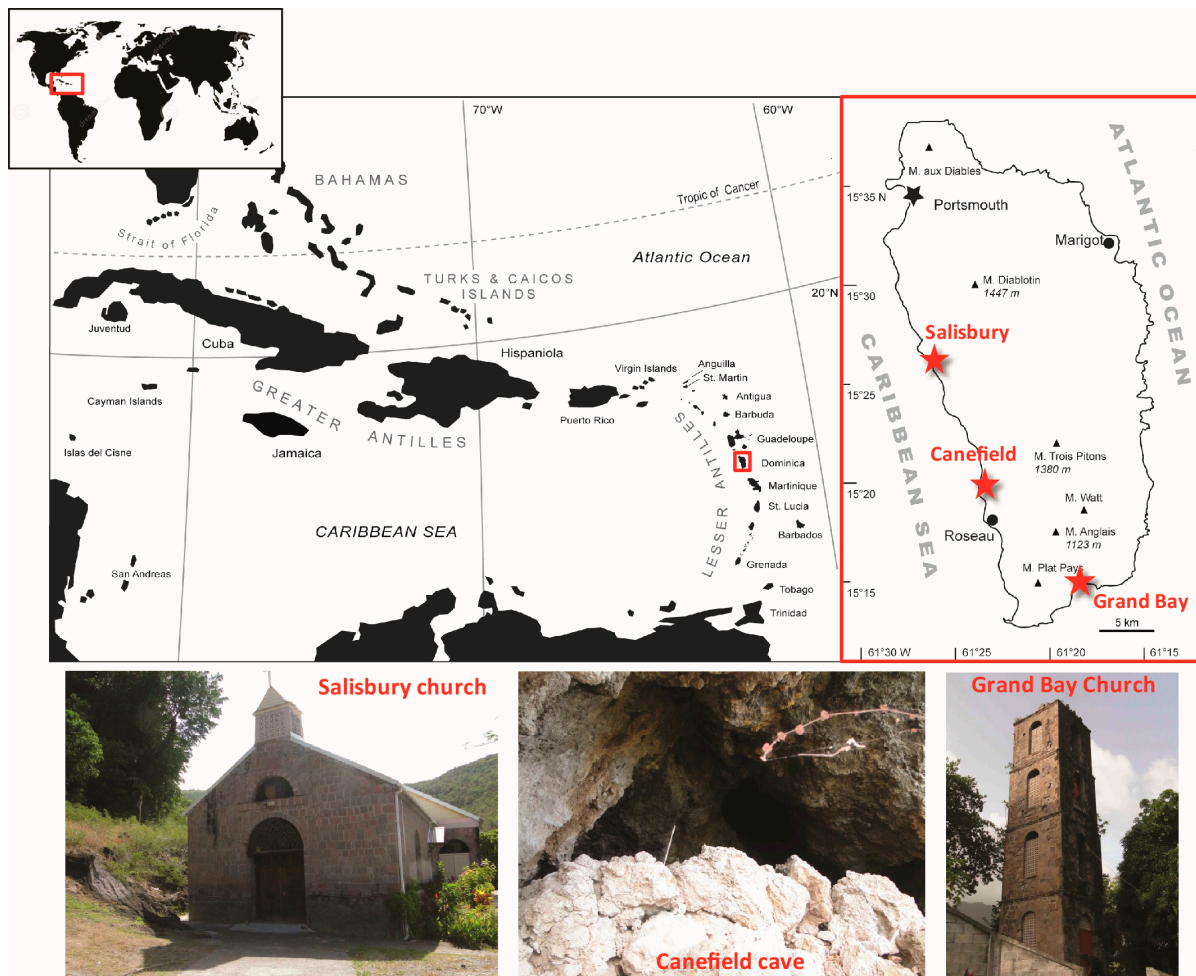
For this study, a total of 111 pellets produced by the Lesser Antillean Barn Owl (*Tyto insularis*) were collected in June 2014 (at the beginning of the rainy season) and January 2015 (at the beginning of the dry season) in three coastal localities on the island of Dominica (Figure 1): 34 pellets in a church tower at Salisbury (n = 5 in 2014; n = 29 in 2015), 50 pellets in a small cave near Canefield (n = 43 in 2014; n = 7 in 2015), and 27 pellets in a church tower at Grand Bay (n = 24 in 2014; n = 3 in 2015). Salisbury and Grand Bay are located in relatively rural areas, while Canefield is located in a more urban area.

Whole pellets and bulk material were collected on the ground in nests (Grand Bay, Canefield) or under roosts (Salisbury). Only pellets were considered in the present study. The whole pellets were isolated in a bag marked with a specific number. Each bag was then prepared individually: the pellets were soaked in water and the bones carefully extracted with fine pliers. The bones were then dried and packed in individually marked tubes so that each bone could be cross-referenced to the pellet from which it came.

### 2.2. Prey Identification

Bat and rodent species were identified through size and morphology of skulls, mandibles and post-cranial elements, thanks to data from the literature [13,24–27] and modern osteological collections (PACEA UMR 5199, Université de Bordeaux; Muséum national d'Histoire naturelle, Paris, France). The body mass was estimated according to [28].

Bird remains were not identified at the species level, mainly due to a lack of suitable reference collection, but also due to the unawareness of osteological characters allowing to identify small Passeriformes, particularly when the preservation state of the material prevents the observation of peculiar anatomical criteria. However, we observed that the majority of the birds belong to small Passeriformes, followed by rare hummingbirds and a single Common Ground Dove, *Columbina passerina*. Bird remains were assigned to size/weight classes (see infra) using some modern skeletons from the PACEA laboratory collection and following the data of body mass from [29].



**Figure 1.** Location of the three collection areas of the studied *Tyto insularis* pellets from the island of Dominica. Pictures: B. Angin.

The identification of squamate species is based on the morphology of both cranial and post-cranial elements. This approach was carried out using comparative skeletons from modern osteological collections (PACEA UMR 5199, Université de Bordeaux; Muséum national d'Histoire naturelle, Paris) and published osteological criteria [30,31].

For all taxa, the Number of Identified Specimens (NISP) was given, and the Minimum Number of Individuals (MNI) was calculated based on the most abundant element for each taxon and for each site (mainly mandibles/dentaries, but also long bones in some cases).

### 2.3. Taphonomic Analysis

The four faunal groups we considered (bats, rodents, birds and squamates) were well represented in the three studied samples, which allowed us to perform a multi-taxa taphonomic analysis. We tried to adapt the classical methods of analysis so that they were applicable to and comparable for all taxa (for example, we did not consider digestion on teeth, because this is not applicable to birds and because the digestion patterns are very different between mammals and squamates). Only pellets were studied, and the bulk material was not considered. The analyses were performed pellet by pellet, but in this study we present the results as a whole because this is closer to what is found in the fossil and sub-fossil record. To reach a sufficient sample size for the analysis to be relevant we had to pool together the data from the three sites, and we did not consider possible site-specific taphonomic characteristics.

### 2.3.1. Anatomical Representation

In order to propose a simplified methodology and maximize the analysis efficiency while obtaining informative data on the anatomical representation of the different skeleton parts in each assemblage, only some specific anatomical elements were quantified (Table 1). We considered the same number of bone elements for each taxon. From the skull, mandibles (mammals and birds) and dentaries (lizards) were counted. From the forelimbs, humerus (all taxa) and ulna (rodents and squamates), radius (bats) or carpometacarpus (birds) were studied. From the hindlimbs, femur and tibia were quantified for mammals and lizards, and femur and tarsometatarsus were considered for birds. The choice of these bones allows us to represent the proximal and distal parts of the limbs and concerns elements frequently recovered in the fossil record. Isolated epiphyses were put aside and not considered. We did not explore the presence of anatomical connection because similar observations are rarely transposable to fossil assemblages. To quantify anatomical distributions, several ratios were calculated: cranial/post-cranial, anterior/posterior and stylopodia/zeugopodia (Table 1).

**Table 1.** Elements considered for the anatomical representation and ratios.

	Anatomical Representation		Ratios		
	Cranial Elements	Post-Cranial Elements	Cranial /Post-Cranial *	Anterior /Posterior	Stylopodia /Zeugopodia
<b>Aves</b>	Mandible (Md)	Humerus (H), Carpometacarpus (Ca), Femur (F), Tarsometatarsus (Ta)	Md/(H + Ca + F + Ta)	(H + Ca)/(F + Ta)	(H + F)/(Ca + Ta)
<b>Squamata</b>	Dentary (D)	Humerus (H), Ulna (U), Femur (F), Tibia (Ti)	D/(H + U+F + Ti)	(H + U)/(F + Ti)	(H + F)/(U + Ti)
<b>Rodentia</b>	Mandible (Md)	Humerus (H), Ulna (U), Femur (F), Tibia (Ti)	Md/(H + U+F + Ti)	(H + U)/(F + Ti)	(H + F)/(U + Ti)
<b>Chiroptera</b>	Mandible (Md)	Humerus (H), Radius (R), Femur (F), Tibia (Ti)	Md/(H + R+F + Ti)	(H + R)/(F + Ti)	(H + F)/(R + Ti)

\* a correction of 8/2 was applied because there are two cranial elements and eight post-cranial elements.

The percentage of anatomical representation (PR) was calculated following the formula:  $PR = [Fobs / (Fth \times MNI)] \times 100$  (Fobs = observed frequency in the studied assemblage, Fth = theoretical frequency of the bone in an individual, MNI = minimum number of individuals). In rodents and squamates the hemi-mandibles/dentaries are separated, so the frequencies were divided by two for the calculation of the PR in a way that allows comparison with birds and bats for which hemi-mandibles are fused.

### 2.3.2. Fragmentation

The fragmentation of the remains was only recorded for the long bones considered in the anatomical distribution analyses. We followed the methodology of [14] and identified six fragmentation categories: (0) complete bone, (1) only proximal part, (2) proximal part + shaft, (3) only shaft, (4) distal part + shaft, (5) only distal part.

### 2.3.3. Surface Modifications

The study of surface alterations focused mainly on the observation of digestion traces on both extremities of long bones and on mandible/dentaries of adult individuals. We did not consider digestion on the distal extremity of rodent ulnae because this fragile part is rarely preserved in both modern and fossil assemblages. For every taxon, we used the following classification of the digestion grades (Figure S1):



- Not digested.
- Slight digestion. On long bones: polished/rounded articular surfaces, cortical bone slightly dissolved and substantia spongiosa slightly visible. On mandibles/dentaries: weak alteration of the anterior part of the bone, but the shape of the bone remains weakly or not modified.
- Moderate digestion. On long bones: substantia spongiosa much more exposed with holes in the cortical bone, but not necessarily on the whole articular surface; the global form of the extremity is preserved. On mandibles/dentaries: strong alteration and partial destruction of the anterior part and alteration of the surface of the *corpus* of the mandible, the shape of the bone and teeth (mammals, lizards) are modified.
- Strong to extreme digestion. On long bones: cortical bone totally dissolved and substantia spongiosa totally exposed or even dissolved; the extremity can be totally destroyed. On mandibles/dentaries: more than one third of the bone is destroyed, teeth (mammals, lizards) are altered.

We are aware that describing a continuous phenomenon by classes has its limits, but such an approach remains relevant to describe global alteration patterns, especially in large assemblages.

#### 2.3.4. Size/Weight Classes of Preys

In order to characterize the size of the exploited prey from different taxonomic groups, we created size/weight classes by taking into account the taxonomic attribution and maturity of bones. This avoids relying exclusively on the overall size of bones, which, depending on the investigated taxa, could be misleading. We created categories based on the weight of each taxon because this is the only variable that allows for comparisons between the different taxa:

- Size category 0: below 10 g (the gecko *Sphaerodactylus* sp.; birds such as small Passeriformes (Parulidae) and hummingbirds (Trochilidae)).
- Size category 1: 10 to 100 g (small lizards of *Anolis* genus; birds such as *Columbina passerina*, *Salinator albicollis*, *Mimus gilvus*; *Mus musculus*, young *Rattus* spp., all identified bat species).
- Size category 2: 100 to 300 g (lizards such as large *Anolis* spp., medium size *Pholidoscelis* spp., *Leiocephalus* sp. and newborn *Iguana* sp.; birds such as *Margarops fuscatus* and lagers; adult *Rattus rattus*, young *Rattus norvegicus*).

#### 2.4. Cross-Validation of Observations

Because two observers were involved for each taxonomic group, we decided to perform cross-validation of the taphonomic observations. Each observer is a specialist of a specific taxon: M.G. and V.L. for birds, S.B. and C.B. for squamates, D.C. and E.S. for small mammals. For Aves, the two observers made counts together, but taphonomic observations were made independently.

Such an approach remains rare, and, to our knowledge, only one other study has been conducted on observer bias in taphonomy—a blind-test evaluation of digestion on leporid bones [32].

In our approach, we compared the observations made by the two observers at the scale of the complete assemblages, but not bone by bone because this would have been too time consuming and complex to set up. Before starting the study of the material, the different observers met to discuss and agree on the methodology, the definition of digestion grades, etc. Thus, observers worked independently following a detailed methodology and filled in a similar results document that was created prior to the observations. The two resulting datasets for each taxonomic group (mammals, birds and squamates) were then combined and compared. Wherever necessary,  $\chi^2$  tests were performed to assess inter-observer differences (only statistically significant values are shown).

### 3. Results

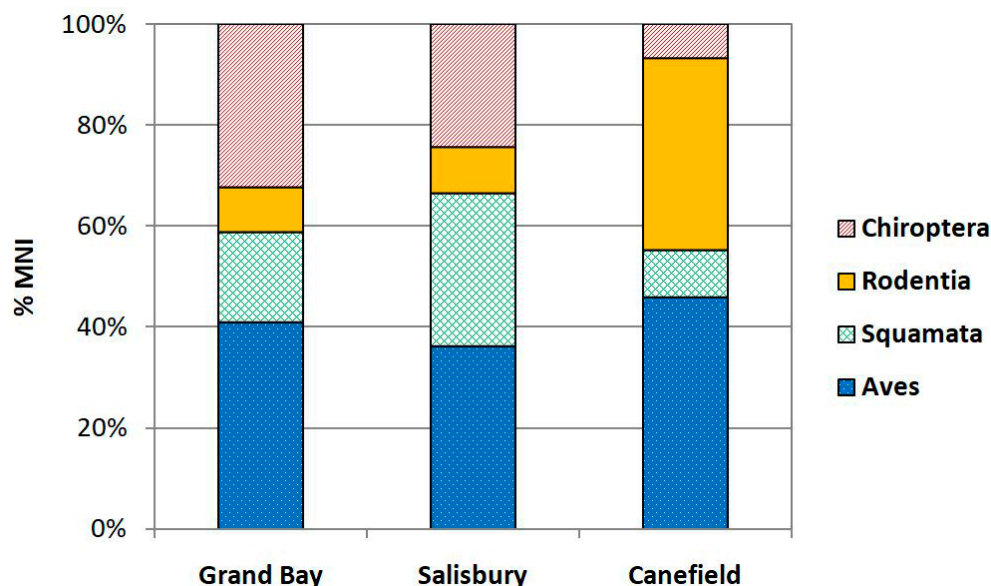
In this section, we present the observations made on the different variables used to define the taphonomic properties of bone assemblages. For each variable, we present both the overall results and the inter-observer differences.

#### 3.1. Faunal Spectrum

More than 1470 bone remains were studied, corresponding to around 194 prey individuals. The prey spectrum was large and diverse (Tables 2 and S1), dominated by birds of several sizes, but also included lizards (*Anolis* sp., *Thecadactylus rapicauda*), bats (*Ardops nicholsii*, *Artibeus jamaicensis*, *Artibeus schwartzi*, *Brachyphylla cavernarum*, *Monophyllus plethodon*, *Sturnira angelli*) and rodents (*Mus musculus*, *Rattus rattus*) (Table S1). At Canefield, we observed a larger proportion of rodents (corresponding to commensal mice and rats), which was consistent with the more urban location of this site (Figure 2). Most of the material was composed of prey less than 100 g (Tables 3 and S2), with larger preys at Canefield corresponding mainly to adult rats. These observations did not differ significantly between the observers.

**Table 2.** Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) of the prey taxa found in the three studied pellet samples from Dominica (mean values of the data from the two observers for each taxon; see detailed data in Table S1).

Prey Taxa	Grand Bay		Salisbury		Canefield		TOTAL	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
<b>Aves</b>	186.0	23.0	206.0	24.0	295.0	34.0	687.0	81.0
<b>Squamata</b>	75.5	9.5	159.0	20.0	36.5	7.3	271.0	36.0
<b>Rodentia</b>	27.0	5.0	39.0	5.5	207.5	27.5	273.5	38.0
<b>Chiroptera</b>	102.0	18.0	117.0	15.5	21.0	5.0	240.0	38.5
<b>TOTAL</b>	390.5	55.5	521.0	65.0	560.0	73.8	1471.5	193.5



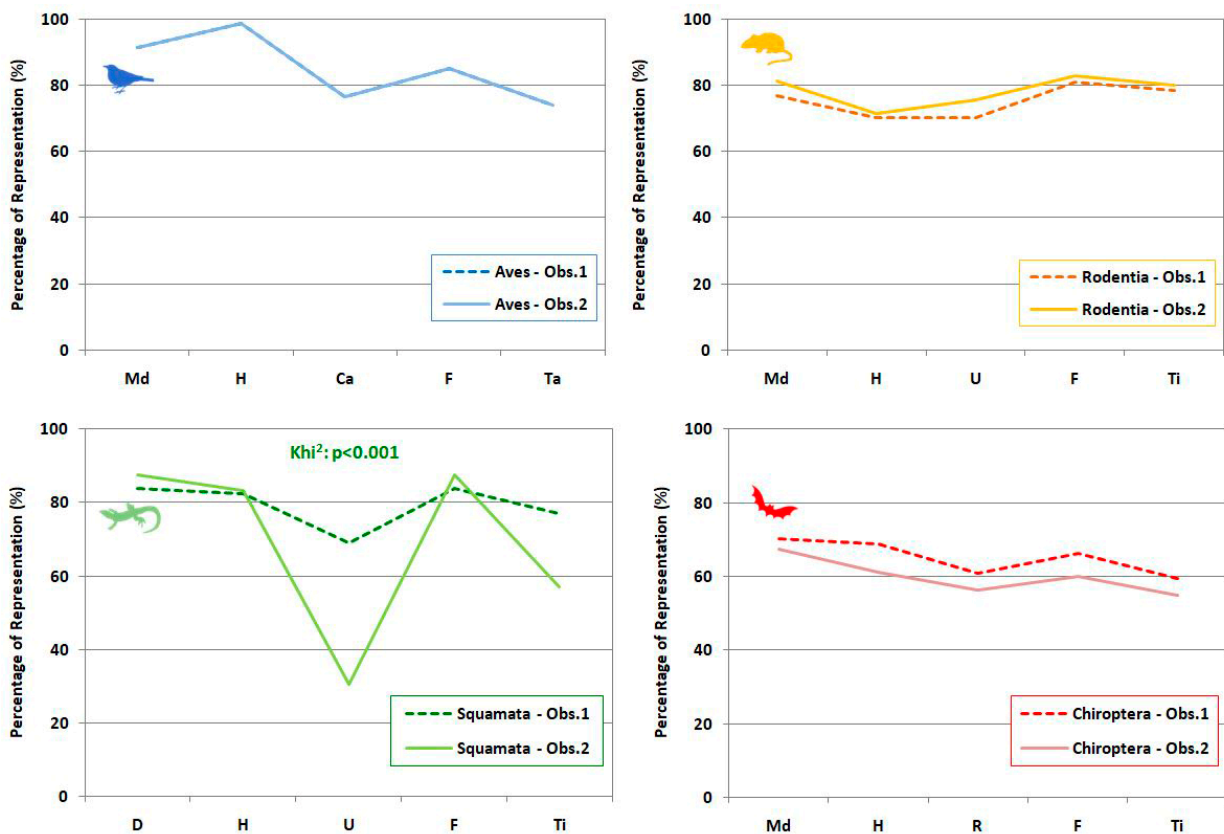
**Figure 2.** Relative proportions of the considered taxonomic groups in the three studied owl pellet samples.

**Table 3.** Size categories of the prey taxa found in the three studied pellet samples from Dominica (mean values of the data from the two observers for each taxon; see detailed data in Table S2).

Size Classes	Grand Bay		Salisbury		Canefield		TOTAL	
	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI
0 (<10 g)	107.0	13.0	71.5	9.0	119.0	14.0	297.5	36.0
1 (10–100 g)	275.5	40.5	447.5	55.0	431.0	57.0	1154.0	152.5
2 (100–300 g)	8.0	2.0	2.0	0.5	10.0	3.0	20.0	5.5
<b>TOTAL</b>	<b>390.5</b>	<b>55.5</b>	<b>521.0</b>	<b>64.5</b>	<b>560.0</b>	<b>74.0</b>	<b>1471.5</b>	<b>194.0</b>

3.2. Anatomical Representation

On average, the best represented elements among the considered anatomical parts were dentaries/mandibles for squamates and bats, humeri for birds and femora for rodents (Figure 3). In squamates, humeri and femora are well documented, while the radius and tibia are underrepresented compared to the other taxa; this is reflected in the stylopodia/zeugopodia ratio (Table 4). In small mammals, the studied elements are more or less equally found. Posterior elements are slightly more represented than anterior elements in “terrestrial taxa” (lizards, rodents), while the reverse is true in “flying taxa” (bats, birds) (Table 4).



**Figure 3.** Profiles of anatomical representation for each observer and for each faunal group, all sites combined (detailed data in Table S3). For birds, both curves are identical.



**Table 4.** Ratios calculated with the considered anatomical elements, all sites and observers combined (detailed data in Table S4). No significant difference was noticed between observers.

	Cranial/Post-Cranial	Anterior/Posterior	Stylopodia/Zeugopodia
<b>Aves</b>	1.09	1.10	1.22
<b>Squamata</b>	1.20	0.87	1.44
<b>Rodentia</b>	1.04	0.89	1.00
<b>Chiroptera</b>	1.13	1.03	1.11

Regarding the values obtained by the different observers for each group (Figure 3; Tables S3 and S4), in most cases there are only a few differences except for squamates, which show huge discrepancies for the ulna and tibia. This is probably due to the identification methodology adopted by both observers: one of them considered and identified smaller and more fragmented elements than the other. However, seeing intra-observer differences in their identification is not surprising since both of these elements are challenging to identify because of their lack of characteristic anatomical features.

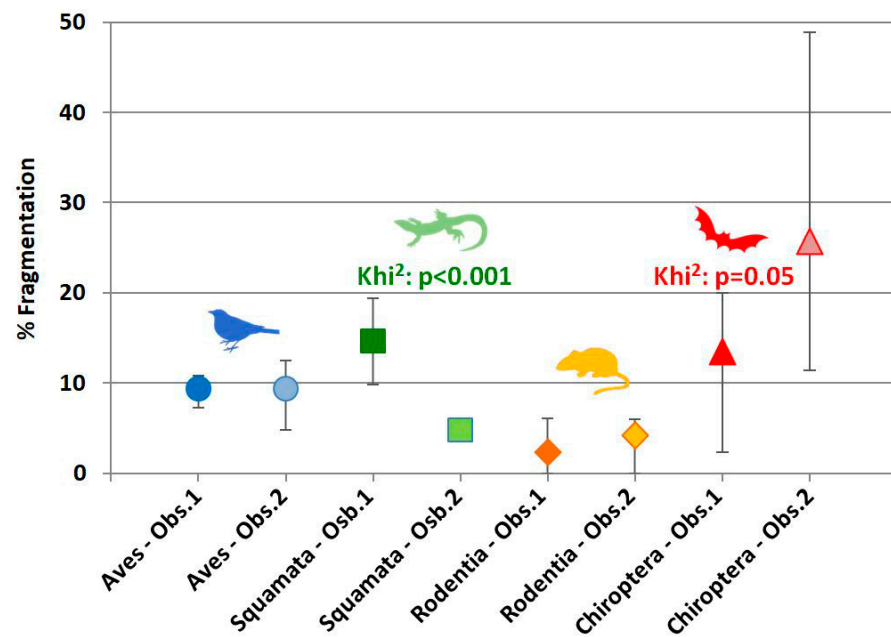
### 3.3. Fragmentation

From a global point of view (Table S5, mean values from the two observers), the fragmentation rate is very low, and intact bones represent between 80% and 97% of the material, all taxa combined. Bats show the higher variability in the percentage of fragmentation between the elements. The most fragmented elements are generally the longest and the finest, such as bat radius or bird tarsometatarsus. Conversely, the less fragmented elements are often more robust, such as rodent femora or bird carpometacarpus. Proximal parts (fragmentation categories 1 and 2) are generally better preserved than distal parts (fragmentation categories 4 and 5) (cf. detailed data in Table S5).

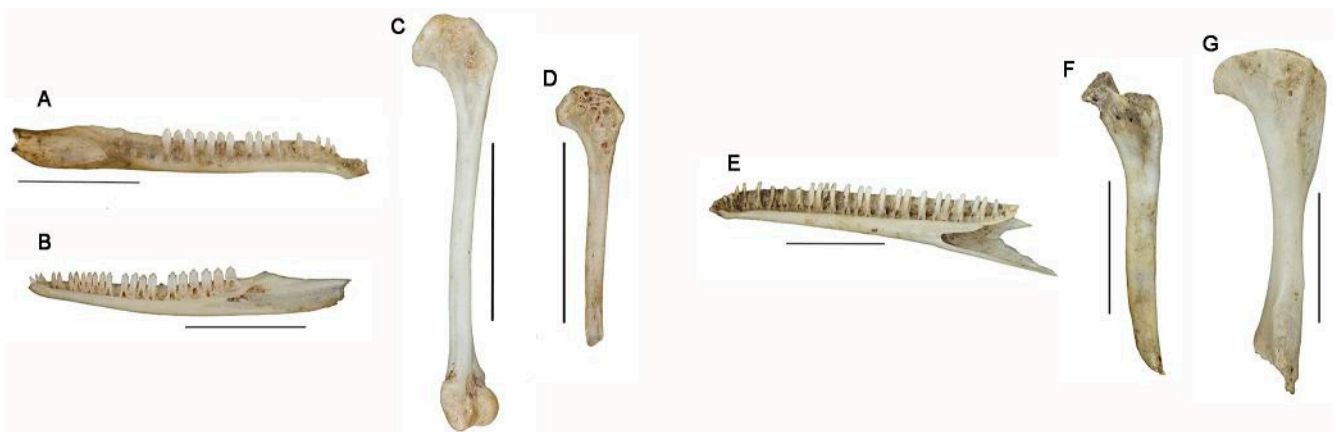
Figure 4 shows the percentages of fragmentation obtained by each observer for each faunal group. For birds and rodents, there is little variability between observers, but for squamates and bats the differences are significant (Figure 4). For squamates, this is probably due to the previously mentioned difference in anatomical identification, as observer 1 has identified more numerous elements corresponding to smaller and fragmented bones. For bats, two factors may be responsible for this result: (1) one of the observers considered the quasi-complete elements as complete, and the other as fragmented; (2) the absence of some extremities was attributed either to fragmentation or extreme digestion according to the observers.

### 3.4. Modifications of Bone Surface

Examples of digestion traces observed on the material are given in Figures 5 and 6. The two squamate species (*Thecadactylus rapicauda* and *Anolis* sp.) were separated because they displayed different patterns of digestion. In geckos *s.l.*, including *Thecadactylus* spp., the skeleton may be less mineralized and less robust, and thus generally less preserved and less represented in the deposits. Moreover, as *Anolis* sp. and *Thecadactylus rapicauda* are generally found in different sites, this variation might also be related to differences between several individual barn owls, which would contribute to the formation of the considered samples.



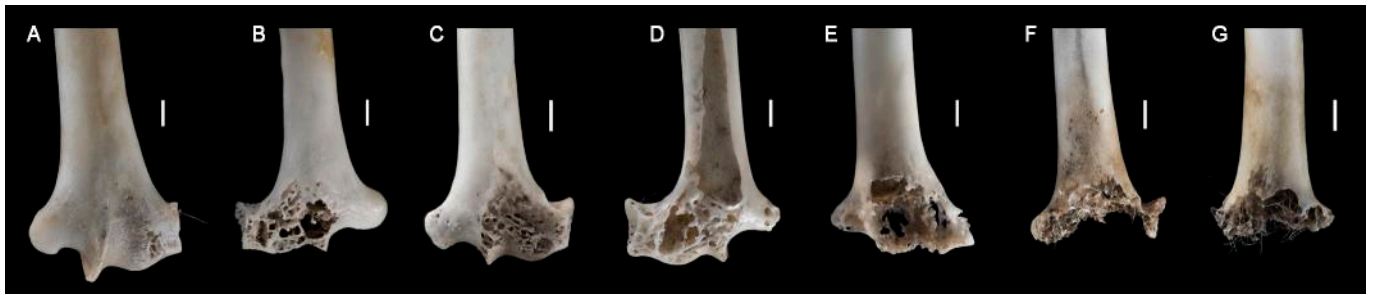
**Figure 4.** Percentage of fragmentation for each observer and for each faunal group, all sites combined (detailed data in Table S5). The error bars represent the values for the most and the least fragmented elements, which may vary from one group to another.



**Figure 5.** Example of digestion traces observed on squamate remains. (A–D) *Anolis* sp. (Salisbury, n°2): (A) left dentary with moderate digestion on the extremity and loss of anterior and posterior teeth, (B) right dentary not digested, (C) complete humerus not digested, (D) humerus with moderate digestion on the proximal part and loss of distal extremity. (E–G) *Thecadactylus rapicauda* (Canefield, n°30): (E) right dentary with light digestion on the anterior extremity, (F) femur with moderate digestion on the proximal and distal parts, (G) humerus with dissolved distal part. Scale = 5 mm. Pictures: S. Bailon.

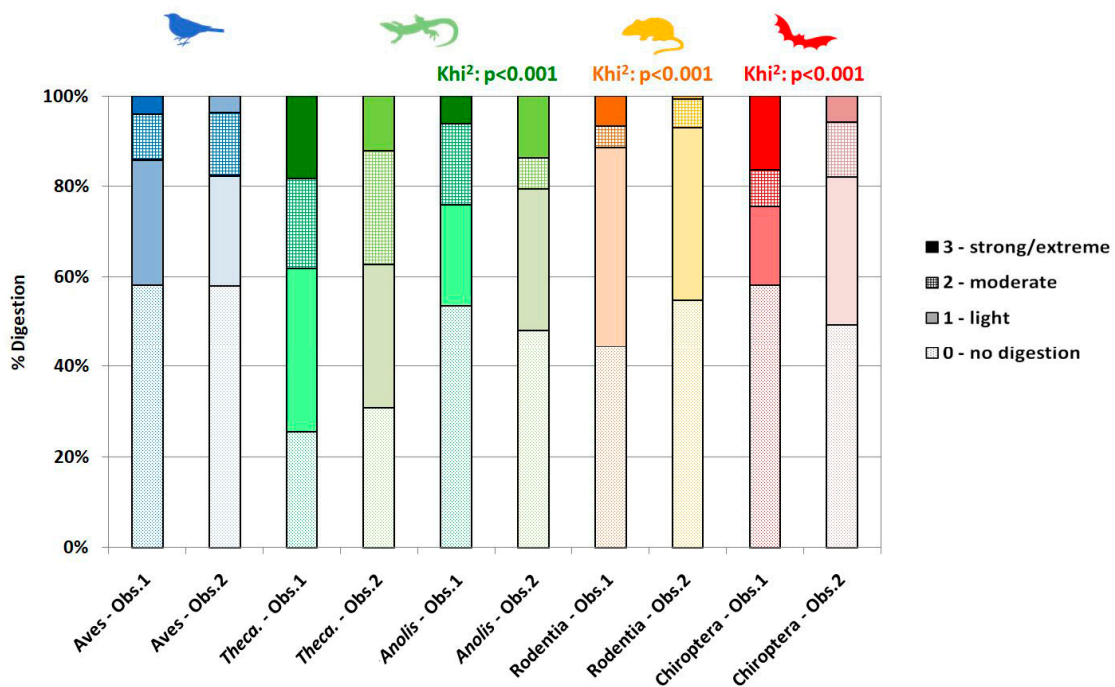
For all considered taxa, approximately half of the material is digested, except for *Thecadactylus rapicauda*, which presents higher percentages of digestion (~70%) with a dominance of light digestion, but also with more moderate to strong grades (Table S6). For birds and rodents, most of the digested bones show light to moderate grades. For bats and *Anolis* sp., we observed a higher representation of strong digestion.

We also chose some relevant examples so that we could look at the variability that may exist between elements of the same species and between different parts of the same element, independent of the observer effect.



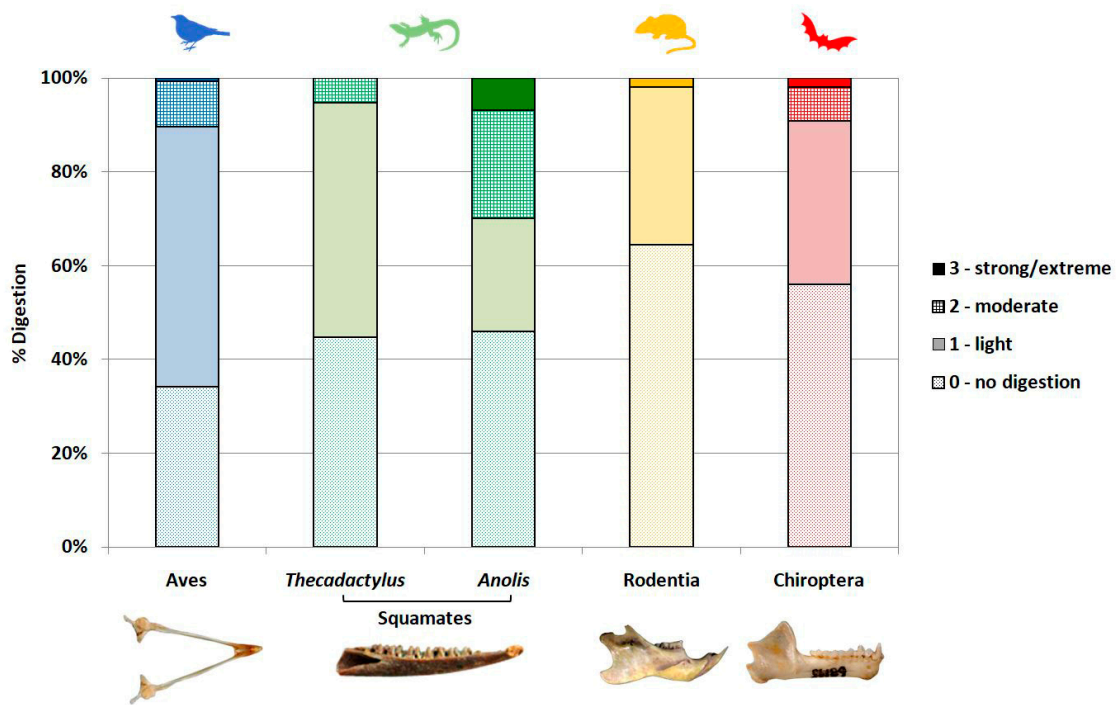
**Figure 6.** Example of digestion traces observed on bat remains. Posterior view of distal humerus: (A) *Brachyphylla cavernarum*, right humerus (Salisbury 2015, n°29) slightly digested; (B) *Artibeus jamaicensis*, left humerus (Salisbury 2015, n°12) moderately digested; (C) *Ardops nicholsii*, right humerus (Salisbury 2015, n°15) moderately digested; (D) *Artibeus jamaicensis*, left humerus (Salisbury 2015, n°32) strongly digested; (E) *Brachyphylla cavernarum*, right humerus (Salisbury 2015, n°31) extremely digested; (F) *Ardops nicholsii*, right humerus (Salisbury 2015, n°9) extremely digested; (G) *Ardops nicholsii*, left humerus (Salisbury 2015, n°15) extremely digested. Scale = 1 mm. Pictures: D. Cochard.

Regarding the differences between observers, we see that for birds and *Thecadactylus rapicauda* results are similar, while for *Anolis* sp., rodents and bats, differences are statistically significant (Figure 7). The main differences in the percentage of digestion are observed in ulna for squamates, mandible, proximal femur and distal tibia for rodents, and proximal humerus for bats (Table S6).



**Figure 7.** Percentages of digestion grades quoted for each observer and for each faunal group, all sites combined (detailed data in Table S6).

For example, with the same anatomical element, the pattern of digestion may differ according to the species. Such inter-taxa variability was notably observed for mandibles and dentaries (Figure 8). Globally, digestion more strongly affects bird mandibles and lizard dentaries than small mammal mandibles. In contrast, there is no significant difference in the digestion pattern between bird and bat femora for example, because these elements are relatively short and robust with a similar shape and size.



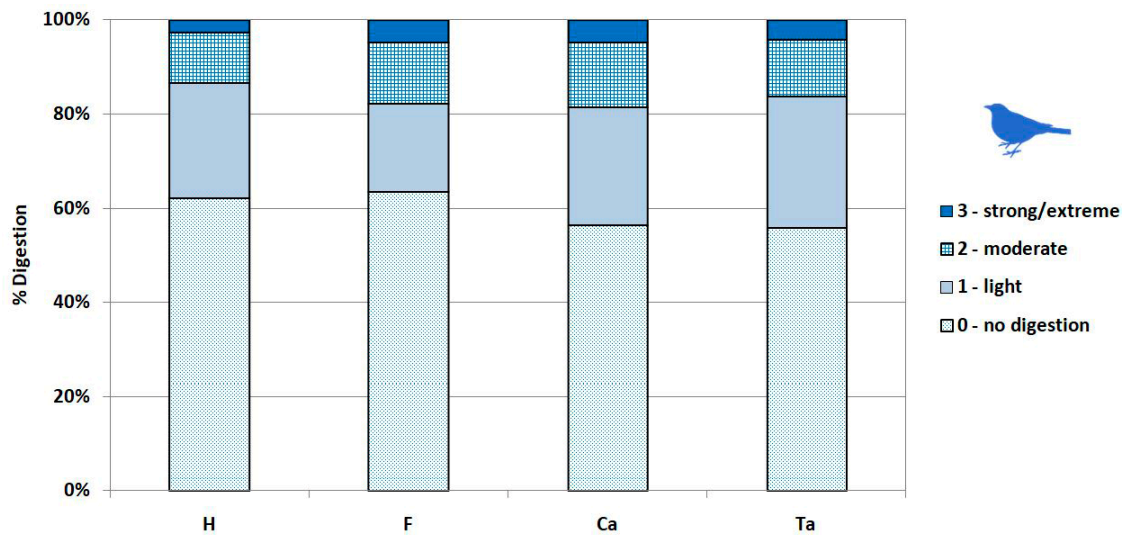
**Figure 8.** Digestion pattern on mandibles/dentaries (mean values of the data from the two observers for each taxon; detailed data in Table S6).

Regarding differences between elements within the same faunal group (intra-taxa variability), we see, for example, that the bat radius is much more digested than the femur (Figure 9, Table S6). This is probably due to the size and shape of bones: the radius is very long and narrow, and often exceeds the pellet size, making it more exposed to digestion. In contrast, among birds there is no significant difference in the pattern of digestion between the four long bones examined (humerus, femur, carpometacarpus and tarsometatarsus), because these elements all display a relatively short size in the considered species (Figure 10).



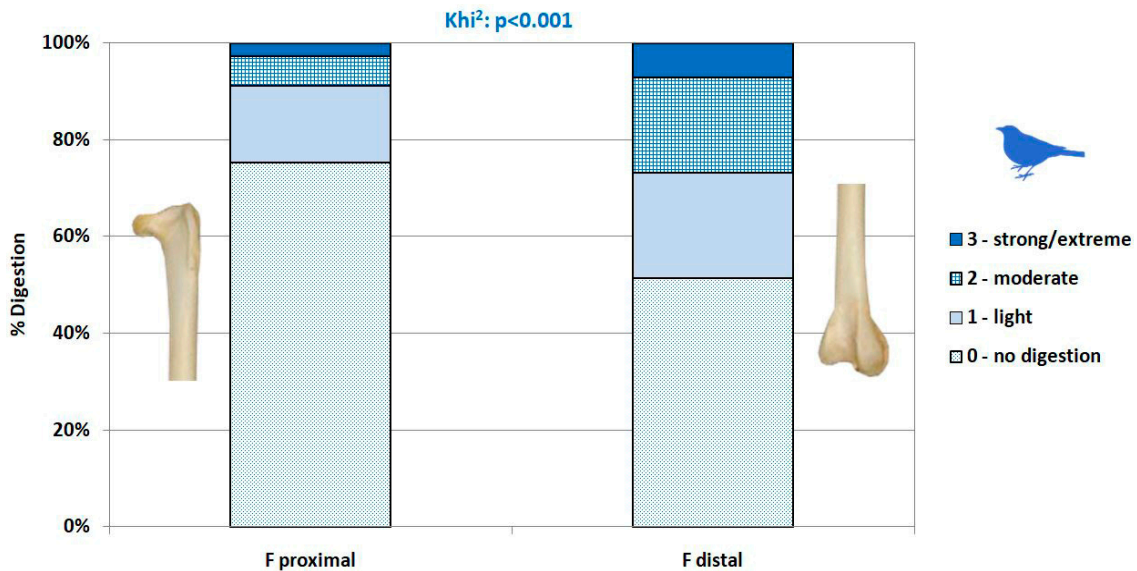
**Figure 9.** Digestion pattern on bat radius and femur (mean values of proximal and distal parts from the two observers; detailed data in Table S6).





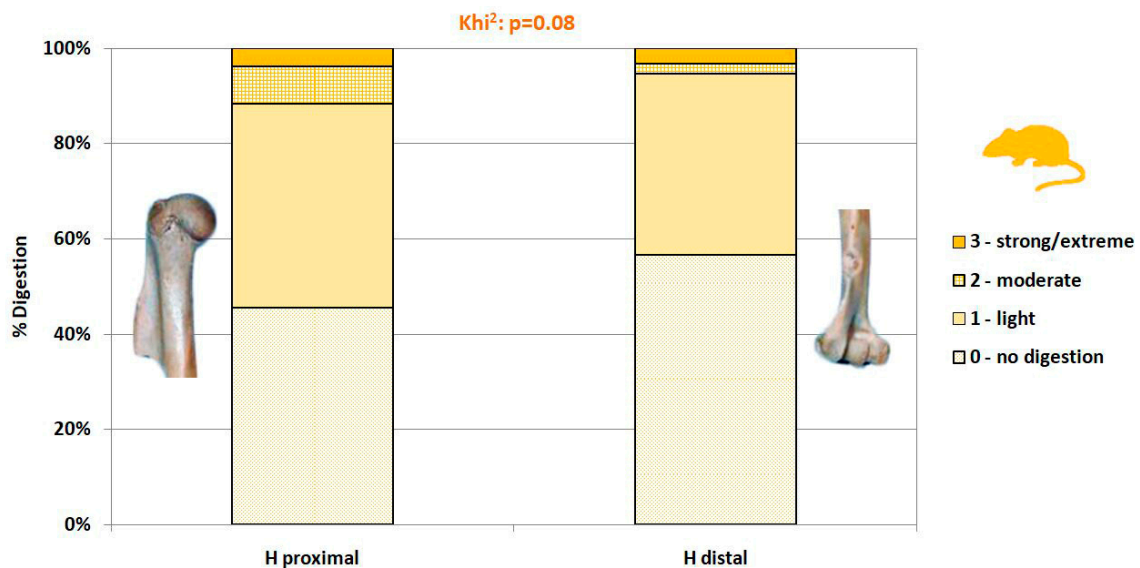
**Figure 10.** Digestion pattern on bird long bones (mean values of proximal and distal parts from the two observers; detailed data in Table S6).

However, differences can be observed between different parts when comparing the same element. This is the case for bird femora, for which the distal part is more digested than the proximal part (Figure 11). Consequently, within the same bone, the pattern of digestion can differ considerably. The same observation can be made for rodent and bat femora, while the reverse is observed for bird tarsometatarsus and small mammal tibia (proximal part more digested than distal part). In contrast, the digestion pattern is quite similar between proximal and distal parts for rodent humeri, for example (Figure 12).



**Figure 11.** Digestion pattern on proximal and distal bird femur (mean values of the data from the two observers; detailed data in Table S6).





**Figure 12.** Digestion pattern on proximal and distal rodent humerus (mean values of the data from the two observers; detailed data in Table S6).

#### 4. Discussion

We present here a synthesis and a discussion of our results on the studied *Tyto insularis* assemblages and a comparison with data of the diet from assemblages produced by representatives of the Barn Owl family in the West Indies. As no other taphonomic analysis has been performed on Barn Owl accumulations in the study region, we considered data from diverse geographic areas.

##### 4.1. Diet of *Tyto Insularis* in Dominica

According to our study, the feeding habits of *Tyto insularis* from the island of Dominica include several bird species (belonging to three size classes), two lizard species, two rodent species and six bat species, with most of the preys weighing less than 100 g. Our observations show that birds are the main prey of *Tyto insularis* in the three studied sites and that a significant difference exists for the other prey taxa. The representation of lizards and bats is higher in “natural” environments (Grand Bay, Salisbury), while a greater representation of rodents is observed in the more anthropized site (Canefield). Moreover, as the samples analyzed in the present study were collected at two different periods (June 2014 and January 2015), a seasonal effect may exist between Grand Bay and Canefield on the one hand, and Salisbury on the other. The expected effect could be a decrease in black rat populations in the dry season, which is very clear in dry forest environments [33]. This seasonality effect may be the same for bats and forest birds and lizards, but it deserves further analyses.

Our results partly differ from the previous studies of the diet of *Tyto alba* and *Tyto glaucops* in the West Indies. Indeed, these studies predominantly show a general pattern indicating that the preferred prey in the Caribbean islands are, from most to least abundant, commensal rodents > birds > squamates/amphibians/bats, with few records of invertebrates such as insects and crustaceans [2,6–8,34,35]. For *Tyto glaucops* in Hispaniola, [2] identified in several pellet samples around 40 vertebrate taxa (including five bat species), and the large pellet sample studied by [35] led to the identification of 125 vertebrates (including 13 bat species). According to [12], a sample composed of 57 pellets produced by *Tyto insularis* in Dominica yielded at least 28 species of vertebrates, including seven bat species, and the most abundant species in terms of MNI (*Anolis* cf. *oculatus*) was not the most important in terms of biomass (*Rattus* cf. *rattus*). Hispaniola is a larger island than Dominica, and the studied material for *Tyto glaucops* is more abundant than for *Tyto insularis*, which may explain the higher species richness in the diet of *Tyto glaucops* com-

pared to *Tyto insularis*, but both of them appear as opportunist predators. Thus, barn owls appear to have a broad spectrum of prey species with a few species dominating, probably depending on environmental conditions (specific diversity and abundance of prey in the environment) and seasonality, and *Tyto insularis* may exhibit a more varied diet than *Tyto alba* in the Caribbean [12].

#### 4.2. Taphonomic Impact of *Tyto Insularis* on Small Vertebrate Bone Assemblage

##### 4.2.1. Remarks on the Size/Weight Classes of Preys

For the present study we chose to consider only three size/weight classes according to the taxa we identified in the *Tyto insularis* assemblages. To apply the developed methodology to other predators, additional classes may be added according to their diet range and the size of hunted preys. For example, for the study of eagle-owl pellet assemblages, we can add at least one or two more classes (size category 3: 300 to 500 g including, for example, birds of pigeon size and adult *Rattus norvegicus*; size category 4: more than 500 g including larger birds, squamates, rodents and lagomorphs).

##### 4.2.2. Anatomical Representation

For squamates, the fact that one of the observers considered and identified smaller and more fragmented elements than the other has meant that, compared to the other taxa, the radius and tibia are underrepresented, and this has impacted all the subsequent taphonomic analyses.

We also observed that in “terrestrial taxa” (lizards, rodents), posterior elements are slightly more represented than anterior elements, while the opposite is true in “flying taxa” (bats, birds). This may be explained by several hypotheses: an anatomical specificity, the mode of consumption by the predator, a differential preservation or a sample effect. The first hypothesis is the most likely, since it is the limbs that ensure propulsion and are therefore the largest and most “robust” and the least subjected to differential conservation. Moreover, a reliable interpretation of these profiles remains difficult considering the sample size.

Our results are difficult to compare directly with other taphonomic analyses of Barn Owl pellet assemblages (*Tyto alba*) in varied geographical areas, which generally consider more element categories for the anatomical representation, and only for small mammals (e.g., [14,15,36,37]). However, it is interesting to note that most of them show a good preservation of “robust” bones, like mandibles, humeri, femora and tibiae, which are the elements we chose to consider and for which we observed a similar representation in small mammals.

##### 4.2.3. Fragmentation

Despite some differences between observers (for squamates and bats), we generally observed that the fragmentation rate was very low, with a great majority of bones being complete, all taxa combined. The maximum percentage of fragmentation was obtained for bat radius (34%), the most elongated bone, which is more sensitive to breakage. These observations are in keeping with data on *Tyto alba*, which are known to present a low fragmentation of skulls and post-cranial elements and a high preservation rate of intact bones (e.g., [14,15,36,37]).

##### 4.2.4. Digestion

Previous analyses of digestion traces on small vertebrate bones accumulated by barn owls have focused mainly on rodent incisors, molars and proximal femora, and are thus again difficult to compare directly with our results. Generally, *Tyto alba* produces low percentages and grades of digestion, with some moderate grades (e.g., [14,15,36,37]). In our study, we have shown that more or less half of the articular extremities are digested, all taxa combined (except *Thecadactylus rapicauda*), with a majority of light to moderate grades. In focusing on proximal femora of rodents, we see that on average 44% are digested,

and 70% of them with a light intensity (Table S6), which is in keeping with the available data for *Tyto alba* (for example [15], 37.8% digested, among them 55% with light intensity). Moreover, [15] also noticed that 30.5% of bird remains were digested, of these 79.5% with light intensity, while in our study we obtained respectively 42% and 62%.

However, there can be important differences in the digestion pattern between taxa coming from the same pellets produced by the same predator. There may also exist a high variability between elements of the same species and between different parts of the same element. This variability in the evaluation of the digestion can be due either to an observer effect or to specific osteological characteristics of bones. For example, digestion more strongly affects bird mandibles and lizard dentaries than small mammal mandibles. This may be due to the very thin skin on lizard dentaries. For bird mandibles, this may result from the bone structure and/or the presence of rhamphotheca of keratin on their beak bone. In rodents, mandibles are protected by strong masticatory muscles, which may explain why digestion traces are weaker on these bones. As another example of inter-taxa variability, we observed that *Thecadactylus rapicauda* displays both a higher percentage of digestion and a higher proportion of moderate and strong grades for humerus and femur than all the other taxa. Currently, the role of peculiar bone structure specificities in this pattern remains unknown.

For lizards, the differences between observers may be due to the first step of the study—namely, the anatomical identification. For rodents, the main reason is that digestion is very difficult to evaluate on rodent mandibles and distal tibia. For bats, the main cause is probably the same as for the fragmentation—the absence of extremities is attributed to either fragmentation or extreme digestion, according to the observers. Moreover, as for rodent ulna, observation of digestion on bat tibia is difficult. More generally, the major reason may be that the two observers have evaluated differently the limit between digestion grades, notably between light and moderate grades. These differences do not follow a particular trend or pattern—that is, a specific observer will not necessarily over- or under-evaluate digestion compared to another researcher. Differences are randomly distributed; each researcher seems to evaluate digestion grades differently. Consequently, an error range may exist, and this must be taken into account when comparing reference models established by different people.

#### 4.3. Degree of Inter-Observer Differences and Potential Outcomes

The differences identified between the two observers are not strong enough to bias the taphonomic description of the assemblage. The discrepancies observed in the quantification of the lizard ulna, which subsequently biased the quantification of the digestion traces on the same assemblage, encourage the consideration of criteria that are not too difficult to assess. Indeed, lizard ulnae are small and lack easily recognizable morphological criteria, which makes them difficult to identify, even by paleontologists who are very familiar with this group. In contrast, only minor and insignificant differences were observed in the quantification of the other lizard bones. For bats (and small mammals in general), the absence of certain extremities may be due either to fragmentation or extreme digestion. In the case of extreme digestion there may be loss of a proximal or distal end, and the bone may then be considered “incomplete” from the point of view of the fragmentation pattern, instead of “complete” with extreme digestion. To avoid this type of “error” in the future, a clear characterization and definition of the indices allowing the observers to distinguish one or the other phenomenon will have to be clearly established.

However, when deciding whether an observation discrepancy is significant or not, we must consider the level of precision adhered to in the description of the taphonomic impact of a predator on a bone assemblage. In that respect, our results warn against the use of very minor taphonomic differences. Indeed, in addition to a fall in the variation between different observers, such variation might also indicate individual differences between specimens of the same species related to age/size/sex or environmental conditions.

It is clear that defining the category of predator (cf. [14,16]) responsible for the constitution of a bone accumulation is possible in spite of these different biases, however, distinguishing different predators of the same category might be more complex. To address this issue, the replication of our study protocol to compare different predators of similar size and lifestyle would be needed to assess whether the observer bias would make such a distinction meaningless or not using minor taphonomic differences.

4.4. Towards an “Inter-Taxa Calibration”

To help conduct multi-taxa analyses, we tried to establish an “inter-taxa calibration” on the basis of the digestion pattern.

Table 5 shows a proposition of classification based on the percentage of digestion. The same anatomical element is classified differently according to the considered species. For example, rodent mandibles are less digested (and more difficult to observe) than squamate dentaries or bird mandibles. For the same taxon, there are differences from one element to another, with a greater or lesser extension of values.

Table 5. Classification of the considered anatomical elements according to taxa and percentages of digestion.

	<30% Digested	30–50% Digested	50–80% Digested	>80% Digested
Aves		Hum, CMC, Fem, TMT	Md	
Squamata ( <i>Thecadactylusrapicauda</i> )			Md, Hum, Ulna, Tib	Fem
Squamata ( <i>Anolis</i> sp.)	Ulna	Tibia	Md, Hum, Fem	
Rodentia	Md	Hum	Ulna, Fem, Tib	
Chiroptera		Md, Fem, Tib	Hum, Radius	

Another proposition of classification based on the grades of digestion (Table 6) gives a result that is a little bit different from the previous one. Thus, the calibration will be different according to the considered parameter: percentage of digestion, grades of digestion, or other taphonomic impacts.

Table 6. Classification of the considered anatomical elements according to taxa and grade of digestion.

	Majority Not Digested	Majority Light Digestion	Majority Moderate Digestion	Majority Strong Digestion
Aves	Hum, CMC, Fem, TMT	Md		
Squamata ( <i>Thecadactylusrapicauda</i> )		Md, ulna, Tib	Hum	Fem
Squamata ( <i>Anolis</i> sp.)	Md, Hum, Ulna, Fem, Tib			
Rodentia	Md, Hum, Tib	Ulna, Fem		
Chiroptera	Md, Hum, Ulna, Fem, Tib			Radius

5. Conclusions

The present study focused on the analysis of pellet samples produced by *Tyto insularis* in Dominica. The prey spectrum reflects the diet of an opportunistic predator that exploits a variety of small vertebrates available in the environment. From a global point of view and for all the studied taxa, the taphonomic impact of *Tyto insularis* on prey bones seems very similar to that of *Tyto alba*: good preservation of mandibles and long bones and a high rate of complete bones, with more or less half of the material being digested with a majority of light to moderate grades.

From a methodological point of view, our work is an attempt to lay the foundations for a clear and simplified study protocol for the collaborative taphonomic analysis of multi-taxa assemblages. To do so, we defined a protocol that aims to limit the potential biases between observers and to allow for inter-taxa comparisons.

As a result, we observed high similarities in the taphonomic results obtained for the considered faunal groups, but some differences emerged at several levels: between observers, between taxa, between elements and even between different parts of the same element. There may be several reasons for these differences, including the way each person observes and evaluates digestion traces, and the way each part of the skeletal elements is affected by digestion.

However, the identification of these factors will remain out of reach until more comparison points using the same approach are available. Similar attempts considering other observers and taxa with the same protocol will open the way to understanding the taphonomic variability according to additional factors (predator age, season, environment and prey availability) and then to the application of our approach to multi-taxa microvertebrate fossil and sub-fossil assemblages.

From a regional point of view, this study constitutes the first neo-taphonomic comparison point available in the whole insular Caribbean for taphonomic studies of microvertebrate assemblages. Therefore, we hope that similar approaches will be further developed in the area to help the understanding of the accumulation process of the numerous fossil and sub-fossil assemblages investigated up until now and in the future. These studies will be of fundamental importance to better understand the biases that affect the vision of the paleobiodiversity provided by fossil and sub-fossil assemblages.

**Supplementary Materials:** The following are available online at <https://www.mdpi.com/article/10.3390/quat4040038/s1>. Figure S1: Examples of digestion grades considered in the present study on bird ulnae; Table S1: Detailed data on the proportions of the prey species found in the three studied pellet samples from the island of Dominica, by site and by observer; Table S2: Detailed data on the size categories of the prey taxa found in the three studied pellet samples from the island of Dominica, by site and by observer; Table S3: Detailed data on the percentage of anatomical representation (PR) for each faunal group, by site and by observer; Table S4: Ratios calculated with the considered anatomical elements for each faunal group and each site, all observers combined; Table S5: Detailed data on the number of identified specimens (NISP) fragmented and percentage of fragmentation (PF) for each faunal group, by site and by observer; Table S6: Detailed data on the percentage of digestion (PD) for each faunal group, by anatomical element and by observer.

**Author Contributions:** E.S., S.B., C.B., D.C., M.G. and V.L. contributed to the choice and implementation of the taphonomic methodology, to the material analysis and to the result interpretations. E.S. collected, combined and compared the databases of all specialists. E.S. designed and wrote the original draft. All authors have read and agreed to the published version of the manuscript.

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