

Comparative rates of natural osteological disorders in a collection of Paraguayan birds

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A series of bird skeletons collected in areas of Paraguay without severe human disturbance were examined for osteological abnormalities. The majority of pathological lesions were the result of trauma and a significant portion to the pectoral girdle. Several groups showed a relatively high prevalence rate, e.g. hawks and owls, which is presumably related to the method of food capture. The interpretation of the results is discussed in regards to zooarchaeological analysis for which it is important to separate natural rates of bone disorder from other potential influences before human-induced factors can be implicated.

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Introduction

Virtually no information is available on the 'natural' rates of osteological abnormalities in wild birds. Numerous attempts have been made to quantify such rates, but these relied upon data from museum collections made at least in part in regions with human perturbations. Several types of artefacts are potentially inherent in these studies because of the introduction of man-made factors such as overhead wires, radio towers, motor vehicles, fences, window panes, firearms, etc. In order to determine the natural prevalence of osteological abnormalities in birds, collections must be analysed from areas where human disturbance was minimal.

Although the ornithological literature is filled with reports of teratological monsters and osteological abnormalities, little quantitative information is available on the subject. Tiemeier (1941) examined 6,212 skeletal specimens in the Museum of Natural History, University of Kansas, collection and found 280 (4.5%) with unmistakable bone injuries. In a study of ratite

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osteological abnormalities, Coulon (1966) found 23 of 70 individuals (33%) with degenerative joint disease. Pomeroy (1962) summarized the incidence of bill deformities in birds and found none in a sample of about 5,000 non-passerines and 0.32% in a sample of over 19,427 passerines. Brandwood, Jayes & Alexander (1986) examined the number of healed fractures in a sample of 12,860 bird bones from 12 species and found the rate in Anatidae to be 0.4%, in Laridae between 0.4–0.5%, and in feral pigeons (*Columba livia*) 0.2%. The majority of specimens used in these four studies were from populations that came into contact with human agencies. Further, in the first two studies some captive animals were used. Thus, natural abnormalities could not be completely separated from injuries directly or indirectly induced by man.

Several studies have demonstrated that man plays an important role in the frequency of some abnormalities. Birkhead (1973) found 15 of 186 (8.0%) corvid skulls taken in the United Kingdom with visible deformities, most of which were incurred by shooting. Lidauer (1983) examined the skeletons of 173 *Turdus merula* collected in Vienna, of which 52.9% had healed bone fractures. She attributed this high rate of injury to collisions with window panes and/or accelerating cars. A study of 1,000 wild bird deaths in the United Kingdom revealed that almost 30% of the animals succumbed to injury by trauma (Jennings, 1961). This included overhead wires and impact with motor vehicles. Clearly, a significant bias is included in this data set in that a preponderance of the birds recovered had been salvaged in areas of intense human influence, such as along road sides.

Numerous bird fossils show various types of bone lesions, which, because of their age, are not the result of human agency (e.g. Moodie, 1929; Tasnádi-Kubacska, 1962). Even in cases of clear human association, bone abnormalities are often rare. For example, in his study of bird bone remains associated with North American Indians of the central plains (1400–1675 A.D.), Parmalee (1977) examined 3,100 bird bones of at least 870 individuals and found five cases (0.6%) of osteological disorder. On the other hand, Hargrave (1970) reported that 68 of 145 (47%) macaws (*Ara* spp.) from Pueblo archaeological sites had bone lesions, most of which could be attributed to 'normal accidents' or 'dietary deficiencies' related to the captive rearing of young birds taken from the wild. This second example shows that one serious problem in the interpretation of archaeological material is the lack of information on true 'natural' rates of osteological abnormalities in wild birds. Without such information, inference about human agency in the manifestation of abnormalities found in excavated bird bones is without a comparative basis. In some cases, the role of human involvement is clear. For example, a swan (*Cygnus* sp.) humerus recovered from the Atlantic VI period (6600–4400 B.C.) of Denmark had an arrow-head lodged in it (Noe-Nygaard, 1974).

Some experimental work has been conducted to examine the time needed for wild birds to heal fractured bones. Roggemann (1930) performed laboratory experiments on pigeons and canaries and found that 21 days was generally necessary for the injured animal to regain full flight capabilities. He further noted that bone injuries of active birds took longer to heal than those that remained inactive. Newton & Zeitlin (1977) examined in the laboratory healing rates of different types of fractures in domestic pigeons created by osteotomy. They found that in radial midshaft fractures that were immobilized with external coaptation, motion was still present at one week, the break was slightly movable at three weeks, and complete union took place by five weeks.

The purpose of the present study was to quantify the frequency of osteological abnormalities in birds taken in a region with little human influence. Such baseline information is useful to quantify the adaptive ability of certain animals under heavy stress. It also gives zooarchaeologists a basis to assess potential human agency in the lesion rate of excavated bird bone based on known natural incident rates.

Materials and methods

In the spring and early summer of 1977, 1978 and 1979, expeditions from the University of Michigan Museum of Zoology (UMMZ), led by Dr Philip Myers, visited Paraguay. The group travelled extensively throughout the country for the primary purpose of surveying mammal faunas, and visited the departments of Amambay, Boquerón, Caaguazú, Canendiyu, Central, Chaco, Cordillera, Itapúa, Misiones, Parguari and Presidente Hayes. In 1978 and 1979, Dr Robert W. Storer accompanied the group and jointly collected birds with the other expedition members. Avian specimens were obtained by means of trapping, shooting, netting, and a few were found dead or were brought to the party by local hunters. The majority of the birds collected for skeletons were skinned, eviscerated, and dried in the field, brought back to UMMZ to be cleaned by dermestid beetles and a low-boil water bath. The main purpose of the bird collections was to obtain material for osteological, systematic and comparative studies of species not widely available in the museums of the world. A total of 1,043 bird skeletons was collected on these expeditions, of which 1,025 were used in this study—326 (32%) non-passeriformes and 699 (68%) passeriformes (Table I).

All skeletons were independently checked twice for osteological abnormalities. When found these were classified by the following conditions:

- 1) healed clean fracture with no exostoses.
- 2) healed fracture with exostoses.
- 3) no sign of fracture, but bone with distinct exostoses or myelomic growth.
- 4) developmental disorder with no sign of fracture or exostoses. Radiographs were taken using a low kv machine of bones fitting category 3 to determine if a fracture was hidden by a covering of callus. When an underlying fracture was found the bone was reclassified as category 2.

Since the purpose of the present study was to determine the 'natural' frequency of osteological abnormalities in wild birds, material from localities where possible human agency may have been responsible for disorders was generally excluded. Such potential artefacts included localities near overhead wires, large human population centres, cattle ranches and deforested areas. Nearctic migrants were not included. The systematic arrangement basically follows Meyer de Schauensee (1970) with a few alterations after American Ornithologists' Union (1983). In **Appendix 1** we have listed the material examined for which no osteological disorders were found.

Results

The overall frequency of birds with osteological disorders was 7% (9% in non-passerines and 6% in passerines). Although the sample sizes were not equivalent among the various orders and families of birds examined, striking differences were found in the frequency of osteological disorders among groups (Table I). In two families with substantial sample sizes, no disorders were found: Galliformes ($n=10$) and Apodiformes (all Trochilidae, $n=46$). At the other extreme, several groups with substantial sample sizes had an exceptionally high rate of pathological lesions: 36% in Corvidae ($n=14$), 33% in Ciconiiformes ($n=9$), 25% in Charadriiformes ($n=8$), 13% in Strigiformes ($n=30$), and 13% in Caprimulgiformes ($n=16$). In Table II the specimens for which osteological disorders were discovered, their nature, and bone type are listed.

Of the 79 pathological lesions found in the sample, 68 (86%) cases were traumatic (categories 1–3) and 11 (14%) were non-traumatic in nature. Of the traumatic injuries, 28 (41%) individuals had damage to the clavicle, 13 (19%) to the scapula, and 6 (9%) to the manubrial portion of the sternum. Thus, 47 of the 68 (69%) traumatic injuries were to the pectoral girdle. The preponderance of injuries to the pectoral girdle is rather striking. We assume that these traumas were for the most part the result of impact with solid objects during flight.

TABLE I
Rate of osteological disorders for complete specimens examined

Order or family	#genera examined	#species examined	#specimens examined	#specimens with disorders	% specimens with disorders
Tinamiformes	2	4	12	1	8
Ciconiiformes	7	7	9	3	33
Falconiformes	9	12	19	4	21
Galliformes	3	3	10	0	0
Gruiformes	7	10	32	3	9
Charadriiformes	4	4	8	2	25
Columbiformes	5	7	30	2	7
Psittaciformes	7	7	17	1	6
Cuculiformes	4	4	9	0	0
Strigiformes	7	8	30	4	13
Caprimulgiformes	3	4	16	2	13
Apodiformes	8	9	46	0	0
Trogoniformes	1	3	8	0	0
Coraciiformes	3	4	17	1	6
Piciformes	13	19	63	6	10
Total non-passerines	83	105	326	29	9
Dendrocolaptidae	6	8	54	4	7
Furnariidae	12	19	74	5	7
Formicariidae	11	12	58	2	3
Cotingidae	1	1	1	0	0
Pipridae	3	3	37	1	3
Tyrannidae	32	36	128	7	5
Phytotomidae	1	1	1	0	0
Corvidae	1	2	14	5	36
Troglodytidae	2	2	9	0	0
Mimidae	1	2	4	0	0
Turdidae	1	4	51	6	12
Sylviidae	1	1	3	0	0
Vireonidae	2	2	5	0	0
Icteridae	7	9	37	2	5
Parulidae	3	5	46	2	4
Coerebidae	2	2	8	0	0
Thraupidae	9	11	87	4	5
Fringillidae	20	25	82	3	4
Total passerines	115	145	699	41	6
Total all birds	198	250	1025	70	7

Of the 71 specimens noted with some type of osteological abnormality, 9 (12.7%) had multiple injuries (Table II). None of these was developmental in nature and all are presumed to be the result of traumatic injury. In most cases, these multiple injuries were to adjacent or paired bones, and presumably the result of a single incident. For example, a specimen of *Crypturellus parvirostris* shows considerable exostosis (category 3) on similar portions of the tarsometatarsi; the outer surface of adjacent phalanges of an *Egretta alba* showed osteoporosis (category 3); and both scapuli of a *Tyto alba* were broken, but the left showed some exostosis (category 2), while the right

had cleanly healed (category 1). In a few cases, multiple injuries were not to adjacent bones: a *Rostrhamus sociabilis* had a cleanly healed clavicle (category 1) and an exostotic lower mandible (category 3); a *Certhiaxis cinnamomea* had a fractured sternum (category 1) and tibiotarsus (category 2); and a *Gnorimopsar chopi* had a cleanly healed clavicle and femur (both category 1). Multiple fractures of a single bone were noted for *Tolmomyias sulphurescens* (clavicle) and *Myiospiza humeralis* (scapula).

Discussion

It needs to be stressed that all of the osteological disorders found in the Paraguayan sample represent injuries or growth abnormalities to birds that survived the detrimental effects of the pathological lesion. Those that succumbed are not represented. Thus, this sample approaches the minimum rate of occurrence at large in birds from Paraguay suffering from osteological abnormalities. Some collecting artefacts, such as a preponderance of birds weak from injuries, may bias this figure.

The types of injuries identified from the sample can be divided into two general forms—trauma (categories 1–3) and non-trauma (category 4). Most traumatic lesions are presumably the result of accidental injuries due to collisions or falls. Some traumatic injuries are possibly the result of intraspecific competition, such as male-male aggression, or interspecific conflicts, such as predator/prey interactions. Direct human agency such as shooting or indirect such as collisions with overhead wires, buildings, moving motor vehicles, etc., contribute little to the rate of injury in the present sample. Non-traumatic injuries can be divided into ontogenetic and inherited genetic pathological lesions.

The categories used in the classification of the osteological disorders is simplistic. Several descriptions and classifications have been presented in the literature on bone disorders with particular reference to palaeopathology. The majority of these deal with mammalian lesions (e.g. Chaplin, 1971; Siegel, 1976; Baker, 1978). Those on Aves generally deal with domestic poultry (e.g. Wise, 1975), or in a few cases with wild birds (e.g. Altman, 1969).

The injuries classified under category 3 are probably at least in part the result of ossified haematomata. After a collision or some other form of trauma, sub-periosteal bleeding often occurs and in many cases results in bone swelling and exostosis. Some category 3 injuries might be related to bone marrow osteosarcomas and osteoclastomas, which often manifest themselves as spongy growth of new bone. With the present categorization of osteological disorders it is not possible to identify the manifestation of pathological lesions caused by bacterial tuberculosis, viral osteopetrosis, aspergillosis or other diseases.

A significant portion (69%) of the traumatic injuries were to the pectoral girdle. It is assumed that such lesions were generally incurred by collision with stationary objects. These injuries were confined to the clavicle, scapula and manubrial portion of the sternum. No coracoid lesion was noted in the material examined. This can be interpreted in at least two ways: (1) the coracoid is sufficiently strong to withstand breakage from collisions; or (2) birds that suffer coracoid trauma do not recover and thus are not represented in this sample. If this second point is correct, then it would appear that injuries to the clavicle and scapula are not as serious as to the coracoid, for birds recover from such traumas with some regularity. Clavicle and scapula injuries may not seriously impair flying and foraging abilities, as suggested by the observation that a number of strong flying

TABLE II
Types and distribution of osteological disorders by species¹

Species	scap.	ster.	jugal	clav.	ulna	rad.	hum.	fem.	tibio-tarsus	tarso-meta-tarsus	lower mand.	phalanx
<i>Crypturellus parvirostris</i>										3/3		
<i>Egretta alba</i>												3/3
<i>Syrigma sibilatrix</i>						4						
<i>Theristicus caudatus</i>				4								
<i>Rostrhamus sociabilis</i>				1							3	
<i>Buteo albicaudatus</i>					3							
<i>Geranospiza caerulescens</i>				1								
<i>Micrastur ruficollis</i>		1		1								
<i>Porzana albicollis</i>				4								
<i>P. albicollis</i>				4								
<i>P. albicollis</i>				4								
<i>Vanellus chilensis</i>	4											
<i>Sterna superciliaris</i>				2								
<i>Leptotila verreauxi</i>		1										
<i>L. verreauxi</i>		1										
<i>Pyrrhura frontalis</i>				4								
<i>Tyto alba</i>	2/1											
<i>Otus choliba</i>								2				
<i>O. choliba</i>						4						
<i>O. atricapillus</i>			1									
<i>Nyctidromus albicollis</i>				2								
<i>Caprimulgus longirostris</i>				1								
<i>Ceryle torquata</i>			3									
<i>Colaptes campestris</i>		4										
<i>C. melanolaemus</i>				4								
<i>Piculus chrysochloros</i>				2								
<i>Veniliornis spilogaster</i>				2								
<i>V. spilogaster</i>			3									
<i>Phloeocastes leucopogon</i>		1										
<i>Xiphocolaptes albicollis</i>							3					
<i>Lepidocolaptes angustirostris</i>				3								
<i>L. angustirostris</i>				1								
<i>L. fuscus</i>	1											
<i>Synallaxis albescens</i>				3								
<i>Certhiaxis cinnamomea</i>		1								2		
<i>Phacellodomus ruber</i>				2								
<i>Syndactyla rufosuperciliata</i>									4			
<i>Lochmias nematura</i>										3/3		
<i>Taraba major</i>						1						
<i>Thamnophilus doliatus</i>				2								
<i>Chiroxiphia caudata</i>	1											
<i>Colonia colonus</i>				1								
<i>Machetornis rixosus</i>				2								
<i>Sirystes sibilator</i>				2								
<i>Pitangus sulphuratus</i>				2								
<i>Tolmomyias sulphurescens</i>				2								
<i>Phylloscartes ventralis</i>				2								
<i>Elaenia obscura</i>				2								
<i>Cyanocorax cyanomelas</i>	3											
<i>C. cyanomelas</i>									1			

TABLE II (cont.)
Types and distribution of osteological disorders by species¹

Species	scap.	ster.	jugal	clav.	ulna	rad.	hum.	fem.	tibio-tarsus	tarso-meta-tarsus	lower mand.	phalanx
<i>C. cyanomelas</i>				2								
<i>C. cyanomelas</i>				2								
<i>C. chrysops</i>			3									
<i>Turdus rufiventris</i>				1								
<i>T. leucomelas</i>	1											
<i>T. leucomelas</i>				1								
<i>T. leucomelas</i>	2											
<i>T. amaurochalinus</i>		1										
<i>T. amaurochalinus</i>										1		
<i>Cacicus chrysopterus</i>									1			
<i>Gnorimopsar chopi</i>				1				1				
<i>Basileuterus leucoblepharus</i>				1								
<i>B. leucoblepharus</i>	1											
<i>Thraupis sayaca</i>				2								
<i>T. sayaca</i>	1											
<i>T. sayaca</i>	1											
<i>Tachyphonus coronatus</i>	2											
<i>Trichothraupis melanops</i>	2											
<i>Saltator coerulescens</i>				1								
<i>Sicalis flaveola</i>									1			
<i>Myospiza humeralis</i>	1											
Total category 1	8	6	1	11	0	1	0	1	3	1	0	0
Total category 2	4	0	0	15	0	0	0	1	0	1	0	0
Total category 3	1	0	3	2	1	0	1	0	0	4	1	2
Total category 4	1	1	0	6	0	2	0	0	1	0	0	0
Grand total	14	7	4	34	1	3	1	2	4	6	1	2

¹ Osteological disorder code:

1 = healed clean fracture with no excess bone

2 = healed fracture with excess bone

3 = no sign of fracture, but bone with exostoses or myelomic growth

4 = developmental disorder with no sign of fracture or callus

birds have reduced clavicles and scapuli. It is not clear if birds that feed on the wing, such as swifts and nightjars, are able to fly with fractured clavicles.

For orders with substantial representation in the present sample, there appears to be a correlation between the rate of bone lesion and foraging style. Presumably, the high prevalence rate in the Falconiformes (21%) and Strigiformes (13%) is in part related to their method of food capture. These animals often fly at substantial speeds while hunting and on occasion presumably collide with fixed objects such as tree limbs, vines, etc. Further, injuries could also be incurred by the initial impact of striking prey, and the prey's retaliation if not immediately dispatched. A *Buteo albicaudatus* specimen that was found dead had an injured ulna; it is not known if the death of the animal and the injury were related. The Strigiformes and Caprimulgiformes (13% with injuries) are generally crepuscular or nocturnal birds. Thus, they may be somewhat more likely to collide with objects while flying than diurnally active birds. Within the owl sample there is evidence to support this. A total of 14 *Glaucidium brasilianum*, a diurnally active owl, were examined and no osteological trauma was noted. This is in contrast to the *Otus* owls, which are nocturnal, and of

which two of eight *O. choliba* and one of one *O. atricapilla* had bone disorders. Thus, within owls diurnal species show less injury than nocturnal ones. The Piciformes are generally arboreal and may collide with shrubbery and trees with a higher frequency (10% rate of injury) than non-forest-dwelling groups. This is supported by other arboreal groups, such as the Dendrocolaptidae, which show a similar, but slightly reduced, traumatic injury rate (7%), compared with a more terrestrial family such as the Formicariidae, which has a lower rate (3%). Other groups with substantial sample sizes show few injuries. No cases of trauma were noted in the 46 specimens of hummingbirds (Family Trochilidae) examined. The dietary requirements of this group are very specific and injured animals may not be able to exploit alternative food resources. Further, their extremely small size, combined with high metabolic rate, would not allow fat deposits to suffice during the recuperation period. Thus, it is probable that hummingbirds almost exclusively succumb to traumatic injury. The reason for the exceptionally high injury rate in the Corvidae (36%) is not completely clear. One of the specimens (*Cyanocorax cyanomelas*) was taken near an Indian village. Even if this specimen is excluded, four of 13 (31%) corvids examined had osteological disorders. The lesion rate (12%) in the Turdidae is inflated by two birds with injuries taken in a disturbed area and two near a road. Excluding these four birds, the 'natural' rate of injury in the Turdidae would be two of 47 (4%).

Excluding *Schiffornis*, all of the Cotingidae and Pipridae examined are known to be lekking species. Since lekking males presumably have somewhat regular intraspecific physical conflicts, one might predict that they would show an inflated rate of osteological disorder relative to other Passeriformes. This is not the case. A total of 32 specimens was examined of three lekking species (*Procnias nudicollis*, *Pipra fasciicauda* and *Chiroxiphia caudata*) and one pathological lesion was found.

For the sample as a whole, 34 (3.3%) have disorders of the clavicle, 14 (1.4%) of the scapula, and 7 (0.7%) of the sternum. In his study of the bird skeletal collections in the Museum of Natural History, University of Kansas, Tiemeier (1941) also found these three bones to have the highest lesion rate of any elements, but the frequency was somewhat different: 2.0%, 0.5%, 0.5% (respectively). The Tiemeier material was from a variety of sources including zoological gardens and areas with severe man-made perturbations. On the basis of the increased human factor, one would expect his material to show a higher prevalence of abnormality than the Paraguayan material. However, this is not the case, and no clear explanation can be offered for this observation. It is conceivable that once a bird is injured there is a differential survival rate between those convalescing in areas of human habitation and those in more natural places. Certainly, in towns and cities the presence of domestic cats would affect grounded birds; although this factor could be partially balanced for certain types of birds by the relatively high local availability of seeds and fruits. It might be expected that the greater survival of injured birds in natural areas would lead to a higher rate of detectable bone abnormalities. However, this may be countered by the presence of mammalian carnivores such as foxes, small cats, coatis, marsupials and mustelids.

After experiencing traumatic injury, wild animals often undergo severe physiological and metabolic stress (Cannon, 1929). In some cases, the injury impairs the animal's typical *modus operandi* and they must use alternative means to protect themselves from predators and forage for food or perish. Carnivorous raptors, insectivorous nightjars, and nectarivorous hummingbirds have osteological modifications associated with specialized feeding techniques, and any injury to these bones might affect their foraging abilities. For example, swifts have highly modified bills and feet for aerial foraging, are not adapted to terrestrial life, and any grounding due to injury would seriously limit their feeding. Despite this, some of these animals when under extreme stress and

perhaps grounded convalesce from their injuries. However, it is not known what percentage of animals incur such injuries.

Implications for zooarchaeological analysis

Since little information has been available on the 'natural' prevalence of osteological lesions in wild birds, zooarchaeologists have been hampered in their interpretation of bones with disorders recovered from excavated material. Some baseline data were needed to determine 'natural' rates of such abnormalities before human factors could be implicated. The data presented herein partially fills this void. A hypothetical example would be that an analysis of excavated bird bones from a formerly human occupied site revealed that 40% of the Falconiformes had osteological disorders. Further study showed that many of these lesions were developmental in nature and restricted to leg bones. On the basis of the high rate of disorder relative to the present study and its nature, it would be reasonable to assume that the injuries were not naturally induced and some human factor was responsible. The high rate of developmental leg disorders would be indicative that the birds were maltreated in some way, such as being kept in too small cages. Further, if these bones showed a high incidence of bone disease one might infer that the animals suffered a deficiency or imbalance in important vitamins, nutrients, or minerals during their development which could be construed as further evidence for the caging and rearing of the birds in captivity (Fowler, 1986; Lowenstein, 1986). Thus, such an inference would distinguish between wild birds obtained for food or some other purpose and dispatched during the hunt or soon after capture from birds reared in captivity.

Summary

An analysis of 1025 bird skeletons taken in areas of Paraguay without severe human perturbation showed that 7% of the specimens collected had osteological abnormalities. The majority of the abnormalities were the result of traumatic injury and often to the pectoral girdle. The distribution of injuries across osteological elements and taxonomic groups is discussed. Further, the implications of these findings for zooarchaeological inference is also reviewed.

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REFERENCES

- Altman, I. E. (1969). Disorders of the skeletal system. In *Diseases of cage and aviary birds*: 255–262. Petrak, M. L. (Ed.). Philadelphia: Lea & Febiger.
- American Ornithologists' Union. (1983). *Check-list of North American birds*. 6th edn. Lawrence, Kansas: Allen Press.
- Baker, J. R. (1978). The differential diagnosis of bone disease. In *Research problems in zooarchaeology*: 107–112. Brothwell, D. R., Thomas, K. D. & Clutton-Brock, J. (Eds). London: University of London, Institute of Archaeology Occ. Publ. No. 3.
- Birkhead, T. R. (1973). Frequency of deformed skulls in corvids. *Bird Study* **20**: 144–145.
- Brandwood, A., Jayes, A. S. & Alexander, R. McN. (1986). Incidence of healed fracture in the skeletons of birds, molluscs and primates. *J. Zool., Lond. (A)* **208**: 55–62.

- Cannon, W. B. (1929). *Bodily changes in pain, fear, hunger and rage*. 2nd edn. New York: Appleton.
- Chaplin, R. E. (1971). *The study of animal bones from archaeological sites*. London & New York: Seminar Press.
- Coulon, R. F. (1966). Considerations on degenerative joint disease in ratites and parallelism with arterial lesions. *Acta zool. path. antverp.* No. 39: 85–102.
- Fowler, M. E. (1986). Metabolic bone diseases. In *Zoo and wild animal medicine*: 69–90. Fowler, M. E. (Ed.). Philadelphia: W. B. Saunders & Co.
- Hargrave, L. L. (1970). Mexican macaws. Comparative osteology and survey of remains from the southwest. *Anthrop. Pap. Univ. Arizona* No. 20: 1–67.
- Jennings, A. R. (1961). An analysis of 1,000 deaths in wild birds. *Bird Study* 8: 25–31.
- Lidauer, R. M. (1983). Knochenfrakturen bei Stadtamseln (*Turdus merula*). *Ökologie der Vögel* 5: 111–126.
- Lowenstein, L. J. (1986). Nutritional disorders of birds. In *Zoo and wild animal medicine*: 200–212. Fowler, M. E. (Ed.). Philadelphia: W. B. Saunders & Co.
- Meyer de Schauensee, R. (1970). *A guide to the birds of South America*. Wynnewood, Pennsylvania: Livingston Publishing Co.
- Moodie, R. L. (1929). Excess callus in a Pleistocene bird. *Am. J. Sci.* 17: 81–84.
- Newton, C. D. & Zeitlin, S. (1977). Avian fracture healing. *J. Am. vet. med. Ass.* 170: 620–625.
- Noe-Nygaard, N. (1974). Mesolithic hunting in Denmark illustrated by bone injuries caused by human weapons. *J. Arch. Sci.* 1: 217–248.
- Parmalee, P. W. (1977). Avian pathologies from Arikara sites in South Dakota. *Wilson Bull.* 89: 628–632.
- Pomeroy, D. E. (1962). Birds with abnormal bills. *Br. Birds* 55: 49–72.
- Roggemann, H. (1930). Untersuchungen über die Heilung von Knochenbrüchen bei Vögeln. *Z. wiss. Zool.* 137: 627–686.
- Siegel, J. (1976). Animal palaeopathology: possibilities and problems. *J. Arch. Sci.* 3: 349–384.
- Tasnádi-Kubacska, A. (1962). *Paläopathologie-pathologie der vorzeitlichen tiere*. Jena: Fischer Verlag.
- Tiemeier, O. W. (1941). Repaired bone injuries in birds. *Auk* 58: 350–359.
- Wise, D. R. (1975). Skeletal abnormalities in table poultry—a review. *Avian Pathol.* 4: 1–10.

Appendix 1

Specimens examined without osteological disorders (figure in parentheses is the number examined). Note—specimens listed in Table II are not included below.

TINAMIFORMES—*Tinamus solitarius* (1); *Crypturellus obsoletus* (3); *C. parvirostris* (3); *C. tataupa* (4). CICONIIFORMES—*Syrigma sibilatrix* (1); *Tigrisoma lineatum* (1); *Harpiprion caerulescens* (1); *Theristicus caudatus* (1); *Mesembrinibis cayennensis* (1); *Plegadis chihi* (1). FALCONIFORMES—*Elanus leucurus* (1); *Chondrohierax uncinatus* (1); *Rostrhamus sociabilis* (1); *Buteo magnirostris* (3); *Heterospizias meridionalis* (2); *Buteogallus urubitinga* (1); *Geranospiza caerulescens* (1); *Micrastur ruficollis* (1); *Falco ruficularis* (2); *F. femoralis* (1); *F. sparverius* (3). GALLIFORMES—*Ortalis canicollis* (7); *Penelope obscura* (1); *Pipile jacutinga* (2). GRUIIFORMES—*Aramus guarana* (1); *Rallus sanguinolentus* (1); *Aramides cajanea* (1); *A. ypecaha* (3); *Porzana albicollis* (7); *Laterallus exilis* (1 partial); *L. xenopterus* (2); *L. melanophaius* (2); *L. leucopyrrhus* (9); *Chunga burmeisteri* (2). CHARADRIIFORMES—*Jacana jacana* (1); *Vanellus chilensis* (4); *Gallinago paraguayae* (1); *Himantopus himantopus* (1); *Sterna superciliaris* (1). COLUMBIFORMES—*Columbina talpacoti* (2); *C. picui* (7); *Claravis pretiosa* (2); *Leptotila verreauxi* (8); *L. rufaxilla* (5); *Geotrygon montana* (2); *G. violacea* (2). PSITTACIFORMES—*Ara maracana* (2); *Nandayus nenday* (1); *Pyrrhura frontalis* (8); *Myiopsitta monachus* (1); *Forpus xanthopterygius* (2); *Pionopsitta pileata* (1); *Amazona aestiva* (1). CUCULIFORMES—*Piaya cayana* (3); *Crotophaga ani* (1); *Guira guira* (4); *Tapera naevia* (1). STRIGIFORMES—*Tyto alba* (2); *Otus choliba* (6); *Glaucidium brasilianum* (14); *Athene cunicularia* (1); *Ciccaba virgata* (1); *Strix hytophila* (1); *Aegolius harrisi* (1). CAPRIMULGIFORMES—*Nyctidromus albicollis* (7); *Caprimulgus rufus* (1); *C. longirostris* (1); *Hydropsalis brasiliana* (5). APODIFORMES—*Phaethornis eurynome* (5); *P. pretrei* (4); *Stephanoxis lalandi* (1); *Chlorostilbon aureoventris* (3); *Thalurania glaucopis* (10); *Hylocharis chrysura* (13); *Leucochloris albicollis* (2); *Amazilia versicolor* (7); *Helimaster furcifer* (1). TROGONIFORMES—*Trogon rufus* (2); *T. surrucura* (5); *T. curucui* (1). CORACIIFORMES—*Ceryle torquata* (3); *Chloroceryle americana* (7); *C. amazona* (3); *Baryphthengus ruficapillus* (3). PICIFORMES—*Notharchus macrorhynchus* (1); *Nonnula rubecula* (1); *Pteroglossus castanotis* (2); *Ramphastos dicolorus* (1); *Picumnus temminckii* (5); *P. cirratus* (14); *Colaptes campestris* (2); *C. melanolaimus* (3); *Celeus flavescens* (2); *C. lugubris* (4); *Dryocopus lineatus* (3); *D. galeatus* (1); *Melanerpes flavifrons* (5); *Trichopicus cactorum* (3); *Veniliornis spilogaster* (3); *V. passerinus* (3); *Phloeocastus leucopogon* (1);

P. robustus (4). PASSERIFORMES—DENDROCOLAPTIDAE—*Dendrocincla fuliginosa* (1); *Sittasomus griseicapillus* (22); *Xiphocolaptes albicollis* (1); *X. major* (3); *Dendrocolaptes platyrostris* (9); *Lepidocolaptes angustirostris* (10); *L. fuscus* (2); *Campylorhamphus trochilirostris* (2). FURNARIIDAE—*Furnarius rufus* (9); *F. cristatus* (4); *Schoeniophylax phryganophila* (1); *Synallaxis ruficapilla* (5); *S. frontalis* (2); *S. albescens* (1); *S. cinerascens* (4); *Certhiaxis cinnamomea* (3); *Cranioleuca obsoleta* (2); *Phacellodomus sibilatrix* (1); *P. ruber* (5); *Anumbius annumbi* (1); *Syndactyla rufosuperciliata* (9); *Philydor atricapillus* (3); *P. lichtensteini* (4); *P. rufus* (1); *Automolus leucophthalmus* (4); *Xenops minutus* (2); *Lochmias nematura* (8). FORMICARIIDAE—*Hypoedaleus guttatus* (1); *Taraba major* (4); *Thamnophilus doliatus* (8); *T. caerulescens* (17); *Dysithamnus mentalis* (7); *Myrmorchilus strigilatus* (1); *Herpsilochmus rufimarginatus* (2); *Formicivora rufa* (1); *Drymophila malura* (2); *Pyriglena leucoptera* (7); *Chamaeza campanisona* (1); *Conopophaga lineata* (5). COTINGIDAE—*Procnias nudicollis* (1). PIPRIDAE—*Schiffornis virescens* (6); *Pipra fasciicauda* (15); *Chiroxiphia caudata* (15). TYRANNIDAE—*Xolmis irupero* (1); *Colonia colonus* (2); *Gubernetes yetapa* (4); *Fluwicola pica* (1); *Arundinicola leucocephala* (1); *Satrapa icterophrys* (2); *Machetornis rixosus* (1); *Sirystes sibilator* (4); *Myiozetetes similis* (1); *Pitangus sulphuratus* (8); *Casiornis rufa* (2); *Myiarchus ferox* (4); *M. tyrannulus* (5); *Empidonax euleri* (2); *Myiophobus fasciatus* (2); *Hirundinea ferruginea* (1); *Platyrhynchus leucoryphus* (2); *P. mystaceus* (8); *Tolmomyias sulphurescens* (3); *Todirostrum plumbeiceps* (2); *Idioptilon margaritaceiventer* (15); *Hemitriccus diops* (2); *Pogonotriccus eximus* (1); *Phylloscartes ventralis* (2); *Capsiempis flaveola* (4); *Serpophaga subcristata* (1); *Elaenia flavogaster* (5); *E. parvirostris* (1); *E. obscura* (3); *Suiriri suiriri* (1); *Camptostoma obsoletum* (3); *Leptopogon amaurocephalus* (11); *Corythopsis delalandi* (8); *Pipromorpha rufiventris* (5); *Pachyramphus viridis* (2); *Tityra cayana* (1). PHYTOTOMIDAE—*Phytotoma rutila* (1). CORVIDAE—*Cyanocorax cyanomelas* (3); *C. chrysops* (6). TROGLODYTIDAE—*Donacobius atricapillus* (4); *Troglodytes aedon* (5). MIMIDAE—*Mimus saturninus* (1); *M. triurus* (3). TURDIDAE—*Turdus rufiventris* (14); *T. leucomelas* (19); *T. amaurochalinus* (11); *T. albicollis* (1). SYLVIIDAE—*Poliophtila dumicola* (3). VIREONIDAE—*Cyclarhis gujanensis* (3); *Hylophilus poicilotis* (2). ICTERIDAE—*Molothrus badius* (2); *Cacicus haemarrhous* (5); *C. chrysopterus* (3); *C. solitarius* (4); *Gnorimopsar chopi* (3); *Agelaius cyanopus* (4); *Icterus cayanensis* (8); *Amblyramphus holosericeus* (1); *Pseudoleistes guirahuro* (5). PARULIDAE—*Parula pitiayumi* (4); *Geothlypis aequinoctialis* (4); *Basileuterus culicivorus* (16); *B. leucoblepharus* (13); *B. rivularis* (7). COEREBIDAE—*Conirostrum speciosum* (3); *Dacnis cayana* (5). THRAUPIDAE—*Euphonia pectoralis* (1); *Tangara seledon* (1); *T. cayana* (3); *Thraupis sayaca* (8); *Habia rubica* (5); *Tachyphonus rufus* (10); *T. coronatus* (25); *Trichothraupis melanops* (22); *Pyrrhocomma ruficeps* (5); *Hemithraupis guira* (1); *Cissopis leveriana* (2). FRINGILLIDAE—*Saltator coerulescens* (7); *S. aurantirostris* (3); *Passerina brissonii* (2); *Paroaria coronata* (3); *P. capitata* (2); *Cyanocopsa cyanea* (2); *Cyanoloxia glaucocaeerulea* (2); *Volatinia jacarina* (1); *Sporophila collaris* (2); *S. caerulescens* (3); *S. leucoptera* (1); *Oryzoborus angolensis* (7); *Sicalis flaveola* (3); *Haplospiza unicolor* (5); *Coryphospingus cucullatus* (17); *Arremon flavirostris* (5); *Zonotrichia capensis* (3); *Emberizoides herbicola* (2); *Donacospiza albifrons* (1); *Poospiza torquata* (1); *P. melanoleuca* (4); *Saltatricula multicolor* (1); *Embernagra platensis* (1); *Spinus magellanicus* (2).