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FACTORS INFLUENCING THE SIZE OF SOME INTERNAL ORGANS IN RAPTORS

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ABSTRACT.—The size of the small intestine, stomach, kidney, liver and heart were compared among raptor species and considered in relation to hunting strategy and body size. Species relying on rapid acceleration and maneuverability to capture prey in flight, such as sparrowhawk (*Accipiter nisus*), goshawk (*A. gentilis*), and peregrine (*Falco peregrinus*), had the smallest digestive tracts for their size. Species depending more on soaring flight which do not need fast acceleration to capture prey, such as common buzzard (*Buteo buteo*), red kite (*Milvus milvus*), and European kestrel (*Falco tinnunculus*), had heavy digestive organs. In the Strigiformes, the same relationship was found, and species which hunt by active flight, such as barn owl (*Tyto alba*), and long-eared owl (*Asio otus*), had significantly lighter digestive tracts than the tawny owl (*Strix aluco*), a species which mainly hunts from a perch dropping onto its prey from above. Body condition was positively correlated with organ weights, including the heart, but to a lesser extent with linear measures of size such as intestine length.

KEY WORDS: *internal organs; predatory birds; condition.*

Factores que influencian el tamaño de algunos órganos internos en rapaces

RESUMEN.—El tamaño del intestino delgado, estómago, riñones, hígado y corazón, fue comparado entre especies de rapaces que difieren en estrategia de caza y tamaño corporal. Especies basadas en rápida aceleración y maniobrabilidad para capturar presas en vuelo, tales como *Accipiter nisus, A. gentilis* y *Falco peregrinus* tenían el tracto digestivo más pequeño para su tamaño corporal. Especies que dependen más bien de un vuelo de planeo y que no necesitan de una rápida aceleración, tales como *Buteo buteo, Milvus milvus* y *Falco tinnunculus,* tenían órganos digestivos más pesados. En Strigiformes se encontró la misma relación, especies que cazan por vuelo activo, tales como *Tyto alba, Asio otus,* tenían un tracto digestivo significativamente más liviano que *Atrix aluco,* una especie que caza esperando a la presa desde una percha. La condición corporal estuvo correlacionada positivamente con el peso de los órganos, incluyendo el corazón.

[Traducción de Ivan Lazo]

We previously reported that birds of prey show considerable variation in the length of their small intestines (Barton and Houston 1994) and suggested that these differences could be due to adaptations for different styles of predation. We hypothesized that raptors which capture prey by pouncing on it from above would have the longest gut lengths for efficient digestion while species which need to accelerate rapidly to capture active prey, such as predators taking small prey in flight, would have very light organ systems to enable them to accelerate more rapidly. Reduction in the length of the small intestine probably results in less efficient absorption of food but this could still be selected for if this disadvantage were more than compensated for by a higher rate of prey capture. We were able to demonstrate that there was an association between the length of the small intestine and the predatory strategy shown by a species, and that after correcting for differences in body size, those species that specialized in the capture of small birds in flight had small intestinal lengths up to 50% shorter than species with a less active predatory style. The small intestine is responsible for nutrient absorption and is therefore the organ most likely to effect absorption efficiency. We have shown that species with short small intestines digest their food less efficiently, and as a consequence select only prey items of high energy content (Barton and Houston 1993a, 1993b).

This paper considers whether there may be associations between predatory strategy and the weight of other organ systems. We compared the mass of the gizzard, proventriculus, small intestine,

Table 1. Mean wet weights (±SD) of internal organs of various raptors expressed as a percentage of total body weight. Means are based on a combination of the sizes of internal organs of both sexes and sample sizes are given in parentheses.

SPECIES	LIVER	HEART	KIDNEY	STOMACH	SMALL INTESTINE	BODY MASS
Kestrel	3.24 ± 0.46 (14)	1.13 ± 0.14 (12)	1.14 ± 0.22 (10)	2.62 ± 0.34 (12)	0.75 ± 0.42 (18)	180
Merlin	3.24 ± 0.84 (3)	2.20 ± 0.31 (3)	1.10 (1)	1.56 ± 0.32 (3)	0.56 (1)	190
Sparrowhawk	2.63 ± 0.53 (86)	1.12 ± 0.14 (75)	0.81 ± 0.12 (59)	0.95 ± 0.13 (38)	0.63 ± 0.28 (22)	220
Peregrine	2.76 ± 0.43 (3)	1.81 ± 0.05 (3)	0.86 ± 0.2 (3)	1.24 (1)	0.53 ± 0.05 (3)	760
Buzzard	2.15 ± 0.47 (5)	0.86 ± 0.15 (31)	0.92 ± 0.05 (3)	1.48 ± 0.41 (4)	0.99 ± 2.62 (7)	850
Red Kite	—	1.13 ± 0.26 (7)	—	—	—	1040
Goshawk	1.65 ± 0.36 (50)	0.86 ± 0.09 (44)	—	—	0.46 (1)	1110
Long-eared owl	2.10 (2)	0.98 ± 0.28 (6)	0.84 (2)	1.93 (1)	0.75 (2)	270
Barn owl	2.83 (40)	0.87 (38)	0.78 (36)	1.94 (12)	0.42 (2)	310
Short-eared owl	3.17 (2)	1.22 (2)	0.98 (1)	2.48 (1)	1.64 (1)	350
Tawny owl	2.55 ± 0.19 (3)	0.71 ± 0.10 (3)	—	1.91 (2)	1.26 ± 0.38 (3)	460

liver, and kidney between eight species of Falconiformes and four Strigiformes. We also examined heart weight in these species to see if this is heavier in species with an energetic form of prey capture. Finally, we considered the correlation between body condition and the size of these organs.

METHODS

Most of the birds used in this study had been found dead and sent to the Institute of Terrestrial Ecology as a part of their program to monitor pesticide residues. In addition, a sample of goshawks was examined which had been shot under license for game preservation and imported under license (CITES 038371A). Birds were stored frozen at −20°C for up to 6 wk. It is known that freezing has little effect on gut morphology, but prolonged periods between death and freezing can lead to significant loss in tissue weight (Barton and Houston 1992); we therefore discarded any birds which had obviously lain for some time before being frozen.

In order to test our hypothesis, we first needed to categorize the predatory style of each raptor species. For the Falconiformes we did this based on literature review of the proportion of avian prey in each species diet. Species taking more than 75% avian prey were categorized as attackers and included peregrine falcons (*Falco peregrinus*), sparrowhawks (*Accipiter nisus*), and goshawks (*A. gentilis*), while species taking predominantly small mammals and carrion were categorized as searchers and included buzzard (*Buteo buteo*), red kite (*Milvus milvus*), and kestrel (*Falco tinnunculus*) (Brown 1978). Attackers were species which capture prey by high-speed aerial chase, requiring great acceleration and agility with an average hunting success of 13% (Temeles 1985). Searchers, however, were species capturing mammalian prey mainly

Table 2. Correlation between organ size (g) and index of body condition of various species of raptors. Sample sizes given in parentheses.

SPECIES	SEX	GIZZARD	HEART
Sparrowhawk	M	$r = 0.71, P = 0.0018$ (16)	$r = 0.89, P = 0.02$ (6)
	F	$r = 0.53, P = 0.0018$ (32)	$r = 0.63, P = 0.02$ (13)
Peregrine	M	$r = 0.96, P = 0.03$ (4)	$r = 0.96, P = 0.01$ (5)
Kestrel	M	$r = 0.55, P = 0.09$ (10)	—
	F	—	$r = 0.80, P = 0.03$ (7)
Buzzard	M	$r = 0.93, P = 0.0001$ (10)	$r = 0.87, P = 0.0001$ (16)
	F	—	$r = 0.77, P = 0.0003$ (17)
Red Kite	M	$r = 0.69, P = 0.31$ (4)	$r = 0.95, P = 0.004$ (6)
Goshawk	M	$r = 0.33, P = 0.12$ (23)	$r = 0.58, P = 0.002$ (25)
	F	$r = 0.44, P = 0.07$ (18)	$r = 0.79, P = 0.0001$ (19)
Barn Owl		$r = 0.34, P = 0.19$ (16)	$r = 0.78, P = 0.02$ (8)
Tawny Owl		—	$r = 0.72, P = 0.28$ (4)

by dropping on it from above and not depending so heavily on high-speed powered flight, with higher rates of prey capture (Temeles 1985). For the owl species examined, the main difference in hunting strategy between species was that barn owls (*Tyto alba*) and long-eared owls (*Asio otus*) have an active flight mode with prey mainly located while in flight, while tawny owls (*Strix aluco*) are more passive predators, locating prey from perch sites (Cramp and Simmons 1980).

There was some variation in the condition of the birds available for this study. We used dry weights to record organ mass because we did not know the extent to which carcasses had become dehydrated after death. Wet weights were used only from birds known to have died accidentally and whose carcasses were collected shortly after death.

The proventriculus, gizzard, small intestine, liver, kidney, and heart were dissected from 583 carcasses. Stomachs were separated into the proventriculus, whose function is the production and release of gastric secretions, and the gizzard, which provides mechanical digestion and preliminary proteolysis (Duke 1986). The length and width of the proventriculus were measured when laid flat to estimate internal surface area. All other organs were cleaned of mesentery and fat bodies; the heart had the chambers opened and any blood clots removed. All tissues were then oven dried at 70°C to constant weight. The combined weight of proventriculus and gizzard is here referred to as stomach, and the combined mass of proventriculus, gizzard, and small intestine as gut. Falconiformes were analyzed separately by sex, because of their sexual dimorphism, and sufficient data were available to analyze male and female sparrowhawks, peregrine falcons, kestrels, common buzzards, red kites, and goshawks separately. We used a skeletal body size variable to correct for differences in body size between species (Barton and Houston 1994).

We used Principal Components Analysis to identify which of the six body measures were best predictors of body size, and identified the length of the sternum keel (from base of the sternum to anterior edge of the keel)

Table 2. Extended.

Small Intestine Length	Small Intestine Dry Weight
$r = 0.51$, $P = 0.009$ (25)	$r = 0.45$, $P = 0.06$ (18)
$r = 0.06$, $P = 0.72$ (39)	$r = 0.30$, $P = 0.07$ (36)
$r = 0.14$, $P = 0.79$ (6)	$r = 0.95$, $P = 0.01$ (5)
$r = 0.60$, $P = 0.12$ (8)	$r = 0.89$, $P = 0.001$ (9)
$r = 0.15$, $P = 0.63$ (13)	$r = 0.79$, $P = 0.0005$ (15)
$r = 0.60$, $P = 0.01$ (17)	$r = 0.69$, $P = 0.0017$ (18)
$r = 0.09$, $P = 0.70$ (22)	$r = 0.34$, $P = 0.12$ (22)
$r = 0.63$, $P = 0.18$ (6)	$r = 0.99$, $P = 0.0001$(6)
$r = 0.09$, $P = 0.65$ (25)	$r = 0.04$, $P = 0.83$ (25)
$r = 0.35$, $P = 0.13$ (20)	$r = 0.69$, $P = 0.001$ (19)
$r = 0.28$, $P = 0.17$ (24)	$r = 0.37$, $P = 0.14$ (17)
$r = 0.99$, $P = 0.004$ (4)	$r = 0.95$, $P = 0.05$ (4)

and sternum diagonal length (from base of sternum to distal point of coracoid) as the best predictors. We used the product of these two measures as our body size factor and used this factor as the covariate in ANCOVA analysis to correct for body size differences. We log-transformed data on both axes. The Bonferroni method was used for pairwise comparison of adjusted treatment means (Day and Quinn 1989).

Since our study dealt with evolutionary adaptation of digestive organ size with relation to hunting strategy, we considered including a phylogenetic component in our analysis. However, since the species sample was small and we had species with contrasting hunting strategies in the same genus, we decided there would be no advantage to adding a phylogenetic component.

To consider the contribution that each organ makes to total body mass, we used a smaller sample of fresh carcasses to obtain wet weights of liver, kidney, proventriculus, gizzard, small intestine, and heart. The weight of each organ was calculated as a percentage of total body mass.

We dissected the pectoralis muscle from each carcass After weighing, it was dried at 70°C to constant weight. Larger species had 10 g samples of muscle tissue dried, from which total muscle dry weight was estimated from the wet weight of the sample and total muscle. Subsamples were shown to be representative of the whole muscle. A condition index which accounted for body size differences was then calculated by regressing the dry weight of the two pectoral muscles against the skeletal body size measure and saving the residuals. The variables being examined were standardized in the same way, again saving the residuals. Correlations between the two sets of residuals were then examined.

RESULTS

Male and female sparrowhawks and goshawks had the lightest gizzards and stomachs for birds of their size, while red kites and common buzzards had the heaviest. Sparrowhawks had the lightest small intestines and common buzzards and red kites the heaviest. When total mass of the gut was considered, the guts of the goshawk, sparrowhawk, and peregrine were the lightest for their body size and those of the kestrel and common buzzard the heaviest. All comparisons were significant ($P < 0.05$) with no significant heterogeneity in regression slopes. In considering heart weight, there were significant differences among the species examined, but these were not consistent. Among males, kestrels had the largest heart relative to body mass but, in females, goshawks and sparrowhawks were heavier.

Among owls, the tawny owl had a significantly heavier proventriculus, small intestine, and total digestive tract than expected for a bird of this size. There were no significant differences in heart weight between owls.

We were not able to obtain dry weights for liver and kidney tissue but determined their wet weights as a percentage of total body weight (Table 1). This was a less satisfactory method of indicating relative organ size because birds differed in their fat content, gut content, and overall muscle condition making body weight a poor predictor of actual body size (Barton and Houston 1994). To minimize this problem, we only included data from birds which were freshly killed from accidental causes and which seemed to be in good condition. Sample sizes were small but there is no indication that liver, kidney, or heart mass was associated with predatory strategy. Liver and kidney made up approximately the same proportion of body mass across all species. The largest relative heart size was found in the peregrine and merlin (*Falco columbarius*) both of which have high power output requirements. However, the goshawk and buzzard, two species with directly contrasting hunting strategies, had the same relative heart size.

Stomach size was variable. The kestrel had a very large stomach for a bird of its size. Compared to the sparrowhawk, the kestrel had a stomach three times larger. The relative size of the kestrel gut more closely resembled that of the Strigiformes suggesting it might be a dietary adaptation for species feeding largely on small mammals.

We used weight of the pectoral muscle as an index of body condition because this varies considerably and is the largest muscle in the body of a bird. Individuals which we categorized subjectively as having died of starvation had on average only 54% of lean dry pectoral muscle weight compared to that found in individuals which had been killed by collisions. For all species there was a significant positive correlation between condition and the weight of the small intestine (Table 2). The length of the small intestine was also positively correlated with condition in male sparrowhawks, male buzzards and tawny owls. Gizzard weight was also found to be significantly correlated with body condition for sparrowhawks, male peregrines, and male common buzzards. Heart weight was highly correlated with condition in every species except the tawny owl.

DISCUSSION

In an earlier analysis we showed that the length of the small intestine in raptors varied between species and seemed to be strongly associated with the predatory strategy. However, length might not always be the best measure of gut tissue because the alimentary tract can stretch, so that differences in length may not necessarily reflect a corresponding difference in tissue mass. Here we have shown that small intestine tissue weight also varies between species, and that those species with an attacking mode of predation have significantly less intestine tissue than those that do not depend so heavily on rapid acceleration for prey capture. Apart from the small intestine, the stomach size is also important, for this not only involves the mass of the organ itself, but also determines the weight of food that a species can consume. We found that a species such as the sparrowhawk which faces selection pressures to minimize body weight does show small stomach mass. This may accentuate the importance of diet quality between raptors. We showed earlier (Barton and Houston 1993) that species with short intestine lengths are less efficient at digestion and can only maintain body weight when fed on prey species of high calorific value. If they also have significantly smaller stomachs, and so can consume a smaller amount of prey, the difference in organ size emphasizes the need to take prey of high energy content to compensate for the lower overall intake. In Strigiformes, proventriculus and small intestine weight (and also length, see Barton and Houston 1994) was greatest in the tawny owl which is the species with the most passive hunting mode compared to the barn owl or long-eared owl (Barton and Houston 1994).

While there appears to be clear associations between predatory strategy and the total weight of the digestive tract, this is not the case for the liver, kidney, and heart. The size of these organs seems to be strictly determined by metabolic body size, and presumably cannot be reduced in mass without seriously impairing tissue function and the fitness of the bird.

The variations that are found with body condition were perhaps to be expected. When animals enter periods of food deprivation, they depend on endogenous reserves of fat and protein to maintain their metabolic requirements. The extent to which tissue from the alimentary tract is depleted, however, is little known. Our finding that species we examined showed very significant losses of tissue when in poor condition demonstrates that gut tissue is widely used as a reserve. Presumably any reduction in gut tissue has a detrimental effect on digestive efficiency, and so birds do not experience this tissue loss unless they have no alternative. The finding that heart muscle is also significantly lost in birds in poor condition also demonstrates that when birds reach poor body condition even the most vital organs are affected.

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