MORPHOLOGICAL ADAPTATION AND DIGESTION IN RELATION TO RAPTOR FEEDING ECOLOGY

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CANDIDATE'S DECLARATION

I declare that the work recorded in this thesis is entirely my own unless otherwise stated and that it is of my own composition. No part of this work has been submitted for any other degree.

Nigel W.H. Barton

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CONTENTS

SUMMARY

1. An integral part of the study was to relate intestinal morphology to digestive efficiency in raptors. The source of morphology data was carcasses handed in by the public. The environmental conditions and time for which carcasses were exposed were unknown, as were the storage procedures following collection. The validity of using gut morphology data from carcass analysis was tested by assessing the extent to which small intestine length and weight in two-week old cockerels (*Gallus gallus*) changed under different experimental conditions of time and temperature post-mortem. Intestine weight decreased significantly with increases in time and temperature. Intestine length changed to a lesser extent and was chosen as the preferred measure when restricted to using carcass data.

2. Having determined which measure of gross gut morphology to use, data from Falconiformes and Strigiformes were used to quantify interspecific differences in small intestine length, the region of the gut responsible for food absorption. The study assessed the influence of predatory behaviour and prey type on morphological adaptations of the flight musculature and gut. Falconiform species were categorised as either 'attackers' or 'searchers' depending on the degree to which active, powered pursuit is required for prey capture. Attacking species feed predominantly on avian prey, requiring extreme agility, speed and acceleration for prey capture. Searchers feed largely on relatively slow-moving mammals and carrion. Weight minimisation is very important in terms of flight energetics and it was hypothesised that attackers would minimise the weight of internal organs which are not important for flight, such as intestinal mass. Searchers which do not require such agility and acceleration for prey capture would be expected to have longer, heavier intestines. It is further considered whether the absolute length or weight of the gut is important or whether it is the weight associated with gut contents that influences the size of the digestive tract. A skeletal body-size

measure was determined to enable calculation of intestine length independent of body-size and shape differences. Attacking species were found to have a small intestine which was up to 50% shorter than found in searchers of equivalent body-size. Strigiformes which locate prey by active flight also had intestinal tracts shorter than expected. It is hypothesised that these interspecific differences in gross gut morphology result in corresponding differences in digestive efficiency.

3. The size of the small intestine, stomach, liver, kidney and heart were compared between species and considered in relation to hunting strategy and body size for several raptor species. The extent to which these organs are affected by differences in body condition and parasite burden was examined. No relationship was found between parasite burden and intestine length. There was a strong correlation between body condition and organ size. Condition, fat content and parasite burden were shown to be related. Attacking species were found to have a small stomach and intestine for their size; searchers had large, heavy digestive organs. The more active owl species also had a lighter digestive tract. The scaling of intestine length, area and volume with body-mass was discussed.

4. It was hypothesised that the relatively long small intestine found in searchers such as the Red Kite (*Milvus milvus*) and Common Buzzard (*Buteo buteo*) is adaptive and results in increased digestive efficiency, whereas a short digestive tract as found in the Sparrowhawk (*Accipiter nisus*), Peregrine Falcon (*Falco peregrinus*) and Goshawk (*Accipiter gentilis*) is selected for higher flight performance but results in reduced digestive efficiency. In order to test this hypothesis, it was necessary to find an appropriate method to measure digestion. The study aimed to test the suitability of titanium dioxide as a nutritional marker for measuring digestive efficiency in raptors. Such a method would enable a larger sample of birds to be used since it would allow the use of birds which could not be tethered under experimental conditions and those which are permanently kept in

large aviaries. Birds which had been trained by falconry techniques were used to compare the use of a marker with results based on total faecal collection. Titanium dioxide is supposedly inert. However, complete recovery of the marker was not achieved and titanium dioxide was determined not to be a suitable marker for digestion studies in raptors. Total faecal collection was therefore used throughout the remainder of the study for measuring food passage and digestive efficiency.

5. The more quickly a bird can process food, the sooner it can revert to its most efficient flying weight. Unless there is a compensatory increase in hydrolysis or absorption rate, raptor species shown to have short digestive tracts would be predicted to have reduced digestive efficiency. Species with long digestive tracts would be predicted to have high digestive efficiency. Attackers could either slow the rate of food passage to compensate for a shorter digestive tract or pass food through the gut at the same rate as species with a long digestive tract, suffering the predicted consequence of reduced digestive efficency. Attackers were found to have a short intestine and short food retention time. Searchers had a long intestine and corresponding long retention time. There was no evidence for a compensatory mechanism by which food passage could be slowed in species with a relatively short digestive tract. The effect of different diets on the rate of digestion was also considered.

6. The effects of intestine length and food retention times on digestive efficiency were determined. Both were shown to be positively correlated with digestive efficiency. Searchers feeding on relatively easily caught prey and carrion had long intestines and a high digestive efficiency. Raptors specialising on fast-moving, avian prey had short intestines and reduced digestive efficiency. Efficiency varied between 75% in attackers and 82% in searchers. It was hypothesised that raptors

with reduced efficiency might compensate by eating food of a higher quality. Food quality was quantified for 6 diets and the ability of Peregrines and Buzzards to utilise 2 contrasting diets (rabbit, *Oryctolagus cuniculus* and pigeon, *Columba livia*) was examined by measuring their efficiency on both diets and also their direct influence on body-mass. The Buzzard had a high digestive efficiency on several diets, the Peregrine appears to compensate for its short digestive tract by eating food of high nutritional quality. The relative quality of fresh prey compared to carrion was also examined and the value of carrion as a food source was discussed.

CHAPTER 1

General Introduction

Background

Digestive efficiency is of ecological significance because it influences both the feeding rate and the foraging time of an animal, as well as its impact on the environment through its rate of depletion of resources. The less efficient an animal's digestion the more food it is likely to require, and conversely, the more efficiently an animal digests its food, the less it requires. Nevertheless, very little has been published on the efficiency of digestion in wild animals and until recently, few people had investigated raptor digestion or energetics, primarily because of difficulties encountered with such species in the laboratory and in the field. Of those papers published, most are concerned with metabolic rates and body size, flight energetics and responses to climatological factors (Graber 1962, Gatehouse and Markham 1970, Gessaman 1972,1987, Duke *et al.* 1973, Kirkwood 1979,1980, Koplin *et al.* 1980, Stalmaster and Gessaman 1982). Only in recent years have digestive studies changed from the purely descriptive to analytical in an attempt to understand the cause-effect basis of foraging and to examine the possible constraints imposed on food processing and energy utilisation which affect daily behaviour patterns and ultimately individual fitness.

Digestion studies.

The understanding of factors determining dry-matter digestibility are basic to predicting energy digestibility and for most herbivore, granivore and carnivore diets, dry-matter and energy-digestibility are virtually synonymous (Robbins 1983). In Falconiformes, passage is readily relatable to food intake (Duke *et al.* 1976, Fuller *et al.* 1979, Fuller and Duke 1979, Duke *et al.* 1980) and it has been assumed in previous studies that because virtually all raptor species eat meat, they will have approximately equal digestive efficiencies (Kirkwood 1979, 1981, Stalmaster and Gessaman 1982, Hamilton 1985, Tollan 1988, Castro *et al.* 1989, Karasov 1990). Assimilation efficiencies and food passage rates are however interactive, competing processes. The amount of food absorbed is directly related to the mean residence time of digesta in the gut, and the rate of hydrolysis and absorption (Penry and Jumars 1987, Karasov 1990, Karasov and Levey 1990). If insufficient time is available for complete hydrolysis, then increasing passage rates may reduce assimilation efficiency. The more quickly a bird can process food, the sooner it can revert to its most efficient flying weight (Sibly 1981). I predict that raptor species which require high flight performance will have rapid throughput of digesta with a reduction in digestive efficiency, whereas raptors which can afford to carry an increased food load for longer would be expected to have a correspondingly higher digestive efficiency. I hypothesise therefore that foraging strategy in raptors is directly related to digestive efficiency and prey requirements.

Raptor foraging strategies.

Different foraging strategies are associated with differences in flight morphology (Andersson & Norberg 1981, Norberg 1986). Raptors have developed their own modifications of beak, feet, gut and aerodynamic design in response to selection pressures associated with pursuing, capturing, killing, eating and digesting their prey. Aerial predation is energetically costly and most raptor species employ several hunting methods to provide energy for fuelling their daily activity costs (Jaksic & Carothers 1985). Generally there are differing strike and success rates associated with each (Tarboton 1978, Village 1983). Prey suitability is determined by availability, nutritional value and the predator's ability to catch a particular prey type.

The Falconiformes exhibit a wide range of hunting strategies from the soaring, carrion-feeding vultures to the bird-eating specialists such as the small falcons and sparrowhawks. From one extreme to the other, there is an increasing requirement for acceleration, agility and rapid, powered pursuit. Buzzards, some eagles and vultures do not require a high degree of aerial agility and acceleration for prey capture and feed for much of the year on carrion, exclusively in the case of vultures. Many of the sparrowhawks, goshawks and falcons feed almost entirely on highly manoeuvrable avian prey. Attack success on avian prey is characteristically low (Temeles 1989) and very active raptor species should show specialised morphological adaptations for success. Within the Strigiformes, the Barn Owl, *Tyto alba* and the Long-eared Owl, *Asio otus* are more active in flight than the Tawny Owl *Strix aluco*, (Cramp 1985) although the differences are not as pronounced as within the Falconiformes.

Food processing constraints.

Contrary to the assumption that raptors have equal digestive efficiencies, previous studies have shown that several raptor species suffer food processing constraints (Kaufman *et al.* 1980, Temeles 1989, Kirkwood 1983). The physical capacity of the gastro-intestinal tract to hold and process food can limit intake when foods of low nutrient density (Hainsworth and Wolf 1972), low digestibility or infrequent availabilty are ingested and another meal cannot be ingested until gastro-intestinal bulk is reduced by either digestion, absorption or passage. Such constraints have also been found in other species. Intake of brassica by Woodpigeons (Kenward & Sibly 1977) is limited by the rate at which this food can be processed. For raptor species relying heavily on flight, decisions must be made on whether to eat as much of a prey item as their gut capacity will allow, in which case they gain energy but also probably incur subsequent energetic flight costs because of increased load, or whether to deliberately eat less than they are anatomically capable (or cache the food), if by doing this they subsequently have greater flight performance and so can maintain high capture rates (Rijnsdorp *et al.* 1981, Masman *et al.* 1986).

As already mentioned, one way to reduce the high costs associated with flight hunting for any aerial predator is to keep body weight at the lowest possible level (Sibly 1981, Rijnsdorp *et al.* 1981). This could be achieved by reducing the weight of parts of the body other than skeletal musculature, such as the intestine and, therefore its capacity for carrying gut contents. Therefore one might expect to find long digestive tracts, long retention times and efficient digestion in those species which do not require speed and agility for prey capture, such as soaring species feeding on less manoeuvrable prey. Small falcons and hawks (active pursuers of aerial prey) depend on acceleration and agility for prey capture and so might be expected to have reduced intestine length, rapid throughput times and consequently a reduced digestive efficiency. Such a relationship was found by Houston (1988) during a study of large, mammalian carnivores with contrasting hunting techniques.

Gut morphology.

Studies of the ecomorphology of birds have shown that interspecific differences in the gross morphology of the digestive tract reflect differences in the feeding ecology of closely related and/or sympatric species of birds (Thomas 1984, Kehoe and Ankney 1985). Omnivorous animals show a high degree of plasticity in gut anatomy depending on food type. When eating less digestible or more fibrous food, intestine length has been shown to increase; when eating more digestible food intestine length decreases (Savory & Gentle 1976, Al-Joborae 1980, Kehoe & Ankney 1985, Barnes & Thomas 1987, Kehoe *et al.* 1988). Changes in gut morphology may allow a bird to increase its digestive efficiency on a particular diet and may allow species to be more opportunistic in selecting diets, however there are few studies which show a direct relationship between gut morphology and digestive efficiency (Partridge & Green 1984). Bird guts do not necessarily operate in a manner that maximises digestive efficiency; maximising the rate of energy gain per gram of food with minimisation of digesta volume may sometimes occur at the expense of digestive efficiency (Sibly 1981, Penry & Jumars 1987). This would appear to be an adaptive strategy which many raptor species might adopt. The aim of this study was to examine the behavioural, morphological and physiological determinants of digestion and to relate them to some aspects of feeding ecology in wild raptors.

Each chapter of the thesis has been written with its own introduction in which specific hypotheses are proposed. There is a discussion at the end of each chapter with a general discussion to conclude. The study was structured as follows:

Thesis structure and predictions.

The first hypothesis was that there might be size-independent differences in gut morphology related to foraging strategy. The only source of such data was from carcasses handed in for pesticide analysis. These varied greatly in their age and storage conditions and it was therefore necessary to assess the reliability of carcass data to determine an appropriate measure of gross gut morphology (length or weight) to use in an interspecific comparison of digestive organ morphology in raptors. I restricted the analysis to the small intestine, since this is the organ responsible for food absorption. Chapter 2 describes a controlled experiment to test the effects of time, temperature and storage procedure post-mortem on length and weight of the small intestine in 2-week old cockerels (*Gallus gallus*) and determines which measure is most appropriate.

Chapter 3 applies the gut morphology measure to the raptor data. Carnivorous birds such as raptors feed almost exclusively on meat and so diet-related differences in gut morphology would not be expected. The chapter examines whether there are interspecific differences in length of the digestive tract and assesses the possible influence of diet and predatory behaviour on morphological adaptations of the gut. It was hypothesised that in those species which require a high degree of agility and acceleration for prey capture, a short digestive tract, carrying a small digesta load and with rapid throughput, would be adaptive since weight minimisation is very important for flight manoeuvrability and performance. In species feeding mainly on carrion and adopting a soaring, searching hunting mode where prey is usually caught by a relatively simple search and pounce technique, without the need for an active chase, it was predicted that these species would have developed longer, heavier intestines with slow throughput which should be comparatively efficient at digestion.

Chapter 4 examines species differences in some other body organs and considers these in relation to hunting strategy and body size. It also looks at the extent to which they are affected by body condition and parasite load.

The results of Chapter 3 are used to predict the effect of small intestine length on digestive efficiency in raptor species with different foraging strategies. In order to test the hypothesis, an accurate method was required for determining digestive efficiency in raptors. Chapter 5 describes these methods. I was only interested in the amount of food absorbed from the gut on a dry-matter basis and the method used required only the collection of faeces and pellets, not uric acid. Two methods were compared, one of which used an inert, nutritional marker which could potentially be used with untethered birds in aviaries. The other relies on total excreta collection and necessitates the use of falconry trained birds or birds in close confinement. The main benefit of the first method is that it would allow the use of a larger sample of birds. The use of a marker proved to be inaccurate and total collections were used in subsequent feeding trials.

One way in which a raptor species with a relatively short digestive tract might compensate for a predicted digestive constraint would be to slow the passage of food in the gut. Chapter 6 examines whether compensatory mechanisms are found in species with short guts and considers the effect of different diets on the rate of digestion.

The initial chapters established the validity of using carcass data, showed interspecific differences in gut morphology and established an accurate method for measuring digestive efficiency. Chapter 7 uses these predictions in a comparative study of digestive efficiency in raptors. It is also considered whether intestinal morphology might be related to prey type or meat quality, such that species feeding largely on spatially or temporally unpredictable food sources such as carrion, might have larger intestinal tracts than predicted in order to digest each meal as efficiently as possible. It is generally assumed that raptor prey types are of equivalent nutritional value. Six potential prey types are analysed to consider what factors might contribute to the quality of prey animals and whether active, rapid-pursuit species compensate for a reduced digestive efficiency by feeding on prey of higher quality. It is also considered how the quality of fresh prey compares with that of carrion. Comparatively few species will eat carrion and I speculate on why this food source is not utilised more widely by predatory birds.

REFERENCES

Al-Joborae, F.F. (1980) The influence of diet on the gut morphology of the Starling (*Sturnus vulgaris L.* 1758.) Unpublished Ph.D. thesis, University of Oxford, Oxford.

Andersson, M. & Norberg, R.A. (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15:** 105-130.

Barnes, G.G. & Thomas, V.G. (1987) Digestive organ morphology, diet and guild structure of North American Anatidae. *Can. J. Zool.* **65:** 1812-1817.

Castro, G., Stoyan, N. & Myers, J.P. (1989) Assimilation efficiency in birds: a function of taxon or food type? *Comp. Biochem. Physiol.* **92A:** 271-278.

Drobney, R.D. (1984) Effect of diet on visceral morphology of breeding wood ducks. *Auk* **101:** 93-98.

Duke, G.E., Ciganek, J.C. and Evanson, O.A. (1973) Food consumption and energy, water and nitrogen budgets in captive great horned owls (*Bubo virginianus*). *Comp. Biochem. Physiol.* **44A:** 238-292.

Duke, G.E., Evanson, O.A. & Jegers, A. (1976) Meal to pellet intervals in 14 species of captive raptors. *Comp. Biochem. Physiol.* **53A:** 1-6.

Duke, G.E., Fuller, M.R. & Huberty, B.J. (1980) The influence of hunger on meal to pellet intervals in barred owls. *Comp. Biochem. Physiol.* **66A:** 203-207.

Fuller, M.R. & Duke, G.E. (1979) Regulation of pellet egestion: the effects of multiple feedings on meal to pellet intervals in great horned owls. *Comp. Biochem. Physiol.* **62A:** 439-444.

Fuller, M.R. Duke, G.E. & Eskedahl, D.L. (1979) Regulation of pellet egestion: the influence of feeding time and soundproof conditions on meal to pellet intervals of red-tailed hawks. *Comp. Biochem Physiol.* **62A:** 433-438.

Gatehouse, S.N. & Markham, B.J. (1970) Respiratory metabolism of three species of raptors. *The Auk* **87:** 738-741.

Gessaman, J.A. (1972) Bioenergetics of the Snowy Owl (*Nyctea scandiaca*). *Arctic and Alp. Res.* **4(3):** 223-238.

Gessaman, J.A. (1987) Energetics. *In* Giron Pendleton, B.A., Millshap, B.A., Cline, K.W. & Bird, D.M. (eds) *Raptor Management Techniques Manual.* Washington, D.C.: Natl. Wildl. Fed.

Graber, R.R. (1962) Food and oxygen consumption in three species of owls (Strigidae). *Condor* **64:** 473-487.

Hainsworth, F.R. & Wolf, L.L. (1972) Crop volume, nectar concentration, and hummingbird energetics. *Comp. Biochem. Physiol.* **42:** 359-366.

Hamilton, K.L. (1985) Food and energy requirements of captive barn owls (*Tyto alba*). *Comp. Biochem. Physiol.* **80A:** 355-358.

Houston, D.C. (1988) Digestive efficiency and hunting behaviour in cats, dogs and vultures. *J. Zool.* **216:** 603-605.

Jaksic, F.M. & Carothers, J.H. (1985) Ecological, morphological and bioenegetic correlates of hunting mode in hawks and owls. *Ornis Scandinavica* **16:** 165-172.

Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Stud. Avian Biol.* **13:** 391-415.

Karasov, W.H. & Levey, D.J. (1990) Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiol. Zool.* **63:** 1248-1270.

Kaufman, L.W., Collier, G. Hill, W.L. & Collins, K. (1980) Meal cost and meal patterns in an uncaged domestic cat. *Physiology and Behav.* **25:** 135-137.

Kehoe, F.P. & Ankney, C.D. (1985) Variation in digestive organ size among 5 species of diving ducks. *Can. J. Zool.* **63:** 2339-2342.

Kehoe, F.P., Ankney, C.D. & Alisauskas, R.T. (1988) Effects of dietary fibre and diet diversity on digestive organs of captive Mallards (*Anas platyrhynchos*). *Can. J. Zool.* **66:** 1597-1602.

Kenward, R.E. & Sibly, R.M. (1977) A woodpigeon (*Columba palumbas*) feeding preference explained by a digestive bottleneck. *J. Appl. Ecol.* **14:** 815-826.

Kirkwood, J.K. (1979) Partition of food energy for existence in the Kestrel (*Falco tinnunculus*) and the Barn Owl (*Tyto alba*). *Comp. Biochem. Physiol.* **63:** 495-498.

Kirkwood, J.K. (1980) Energy and prey requirements of the young free-flying kestrel. *Ann. Rep. Hawk Trust* **10:** 12-14.

Kirkwood, J.K. (1981) Energy and nitrogen exchanges during growth in the kestrel (*Falco tinnunculus*). *Proc. Nutr. Soc.* **40:** 6.

Kirkwood, J.K. (1983) A limit to metabolizable energy intake in mammals and birds. *Comp. Biochem. Physiol.* **75A:** 1-3.

Koplin, J.R., Collopy, M.W., Bammann, A.R. & Levenson, H. (1980) Energetics of two wintering raptors. *The Auk* **97:** 795-806.

Masman, D., Gordijn, M., Daan, S. & Dijkstra, C. (1986) Ecological energetics of the kestrel: field estimates of energy intake throughout the year. *Ardea* **74:** 24-39.

Norberg, U. (1986) Evolutionary convergence in foraging niche and flight morphology in insectivorous, aerial hawking birds and bats. *Ornis Scandinavica* **17:** 253-260.

Partridge, L. & Green, P. (1984) Intraspecific feeding specialisations and population dynamics. *In* Sibly, R.M. & Smith R.H. (eds), *Behavioural Ecology-Ecological Consequences of Adaptive Behaviour.* Oxford: Blackwell Sci. Publ.

Penry, D.L. & Jumars, P. A. (1987) Modelling animal guts as chemical reactors. *Am. Naturalist.* **129:** 69-96.

Rijnsdorp, A., Daan, S. & Dijkstra, C. (1981) Hunting in the kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. *Oecologia* **50:** 391-406.

Robbins, C.T. (1983) *Wildlife Feeding and Nutrition.* New York: Academic Press.

Savory, C.J. & Gentle, M.J. (1976) Effects of dietary dilution with fibre on the food intake and gut dimensions of Japanese Quail. *Br. Poult. Sci.* **17:** 561-570.

Sibly, R.M. (1981) Stategies of digestion and defecation. *In* Townsend, C.R. & Calow, P. (eds), *Physiological ecology: an evolutionary approach to resource use.* Sunderland, MA: Sinauer Associates, Inc.

Stalmaster, M.V. & Gessaman, J.A. (1982) Food consumption and energy requirements of captive bald eagles. *J. Wild. Manage.* **46:** 646-654.

Tarboton, W.R. (1978) Hunting and the energy budget of the black-shouldered kite. *Condor* **80:** 88-91.

Temeles, E.J. (1989) Effect of prey consumption on foraging activity of Northern harriers. *The Auk* **106:** 353-357.

Thomas, V.G. (1984) Winter diet and intestinal proportions of rock and willow ptarmigan and sharp-tailed grouse in Ontario. *Can. J. Zool.* **62:** 2258-2263.

Tollan, A.M. (1988) Maintenance energy requirements and energy assimilation efficiency of the Australasian harrier. *Ardea* **7:** 181-186.

Village, A. (1983) Seasonal changes in the hunting behaviour of kestrels. *Ardea* **71:** 117-124.

CHAPTER 2

Post-mortem changes in avian gross intestinal morphology.

N.W.H. Barton & D.C. Houston

The data presented in this chapter form the basis of a paper in press in the Canadian Journal of Zoology (1992).

ABSTRACT

The effects of time and temperature *post-mortem* on small intestine length and small intestine weight are examined in two-week old cockerels (*Gallus gallus*) to assess the reliability of data from carcasses which had been exposed to unknown environmental conditions after death. It was established whether freezing and refrigeration before analysis affected weight and length of the small intestine. Intestine weight decreased significantly with increases in temperature and time *post-mortem*. Intestine length increased but to a lesser extent. Freezing and/or refrigeration of carcasses soon after death did not significantly affect intestine weight or length upon thawing. It was concluded that intestine length should be used in preference to intestine weight when the source of carcasses and the conditions to which they were subjected are unknown.

INTRODUCTION

The alimentary tract of birds and mammals is capable of rapid size changes in response to factors such as diet quality and food quantity (Moss 1974; Savory and Gentle 1976; Ankney 1977; Drobney 1984; Thomas 1984; Kehoe and Ankney 1985; Kehoe *et al.* 1988; Sibly *et al.* 1990). For example, Starlings (*Sturnus vulgaris*) increase small intestine length by 20% when changing from an insect to a seed diet (Al-Joborae 1980). To quantify these changes, reliable measurement techniques are required. A problem encountered in some studies, is that carcasses are used which have been frozen, refrigerated or left in the field for some time before *post-mortem* analysis. Storage conditions might influence measurements taken from the digestive tract due to changes in muscle tone, or tissue breakdown. Authors have reported carcasses to be either frozen whole as soon as possible after death (Miller 1975; Pulliainen and Tunkkari 1983; Thomas 1984; Whyte and Bolen 1985); refrigerated before freezing (Paulus 1982; Kehoe and Ankney 1985) or intestines removed and frozen separately (Pulliainen 1976).

Apart from the study of Robel et al. (1990) who examined time-related changes in digestive organ morphology in Dark-eyed Juncos (*Junco hyemalis*) up to 90 minutes *post-mortem*, (during which no significant changes in intestinal morphology occurred), there is no published information on the effect of *post-mortem* changes in intestinal morphology. This study used two-week old cockerels (*Gallus gallus*) to investigate the effects of time, temperature and freezing on *post-mortem* changes in gross intestinal morphology of the small intestine.

METHODS

Chicks were fed and watered *ad lib.*, maintained at 20°C with continuous lighting and killed simultaneously using CO_2 when 14 days old. They were randomly divided into 12 groups of 10 and weighed. Each group corresponded to one of 12 treatments shown in table 1.

Table 1. Treatments used to examine *post-mortem* changes in dry small intestine weight and small intestine length in 12 randomly selected groups of 10 two-week old cockerels. The adjusted means from ANCOVA are shown.

GROUP	TREATMENT	ADJUSTED MASS (g)	ADJUSTED LENGTH(mm)
1.	dissected immediately after death	0.80	953
2.	dissected after 24 hours at 5°C	0.65	954
3.	dissected after 48 hours at 5°C	0.70	1006
4.	dissected after 72 hours at 5°C	0.64	1052
5.	dissected after 1 week at 5°C	0.48	1089
6.	dissected after 24 hours at 20°C	0.67	1079
7.	dissected after 48 hours at 20°C	0.48	1046
8.	dissected after 72 hours at 20°C	0.45	1069
9.	dissected after 1 week at 20°C	0.33	1059
10.	deep frozen immediately after death	0.60	955
11.	deep frozen, thawed, frozen, thawed	0.47	1069
12.	deep frozen after 48 hours at 5°C	0.58	1076

Groups 10 and 12 were thawed for dissection 1 week after freezing. Group 11 was frozen for 1 week, thawed overnight and re-frozen for 2 days before thawing and dissecting.

All chicks were dissected by one author (N.W.H.B.). Keel length was measured (from base of sternum to furthermost point of keel). The intestinal tract was stripped of fat and mesentery and the small intestine separated at the ileo-cecocolic junction and at the gizzard before being measured using Leopold's straight ruler technique (Leopold 1953). A full wet weight was taken, intestines were opened along the complete length, washed, towel-dried and re-weighed for calculation of small intestine contents. Body mass was corrected for contents. Small intestines (herein referred to as intestines) were oven dried at 75°C to constant weight.

Statistical Analysis

Variables were examined for skewness and kurtosis, residuals were plotted against predicted values from regression analysis to check the underlying assumptions of regression statistics. Linear regression was used to help determine the most appropriate body-size variable.

Body mass and keel length measure two different quantities. Keel length is a measure of skeletal body size, body mass is more a measure of body condition, chicks which are large skeletally not necessarily being of large mass and *vice versa.* It is known from previous studies that gross intestinal morphology changes with body condition (Thaysen and Thaysen 1949; Steiner *et al.* 1968). It was therefore necessary to check that the different treatment groups did not differ in body condition. This was done by analysis of covariance (ANCOVA) with body mass as the dependent variable and keel length as covariate.

Assuming equal condition between treatment groups, ANCOVA was used to detect treatment differences in small intestine length and weight, keel length being used as the covariate. The Bonferroni method (Day and Quinn 1989) was used for pairwise comparisons between adjusted treatment means.

RESULTS

There was no evidence to suggest that intestine length or intestine weight did not increase linearly with body-size (as measured by keel length), plots of residuals against predicted values showing random scatter. All the assumptions of ANCOVA were met.

Analysis of Covariance

With body mass as the dependent variable and keel length as covariate, no significant treatment differences were found ($F_{11,107}=1.58$, $P=0.114$) and regression slopes could be assumed homogeneous ($F_{11,96}=0.84$, $P=0.600$). Any differences between treatments cannot therefore be attributed to condition differences between treatment groups.

With small intestine dry weight as the dependent variable and keel length as covariate, there was a significant treatment effect ($F_{11,106}=11.65$, $P<0.0001$) with homogeneity of slopes ($F_{11,95}=0.79$, $P=0.647$). With small intestine length as the dependent variable and keel length as the covariate, there was again a treatment effect ($F_{11,107}=3.05$, $P<0.001$) and homogeneity of slopes ($F_{11,96}=1.72$, $P=0.08$). Table 1 shows adjusted means from the ANCOVA for dry small intestine and intestine length. Pairwise comparisons of adjusted means for small intestine length and small intestine weight were compared by the Bonferroni method. All significant pairwise comparisons ($P<0.05$) between adjusted means for small intestine weight are shown in table 2. Only 3 significant pairwise differences were found for small intestine length between treatments (treatment 5 with treatments 1, 2 and 10, $P<0.05$).

Table 2. Significant treatment differences for small intestine dry weight using ANCOVA followed by the Bonferroni method ($P<0.05$).

		1	2	3	4	5	6	7	8	9	10	11	12	
	1					*		*	*	*		*	*	dissected immediately after death
T	2					*		*	*	*		*		24 hours at 5°C
R	3					*		*	*	*		*		48 hours at 5°C
E	4								*	*		*		72 hours at 5°C
A	5						*							1 week at 5°C
T	6							*	*	*		*		24 hours at 20°C
M	7													48 hours at 20°C
E	8													72 hours at 20°C
N	9										*		*	1 week at 20°C
T	10													frozen immediately after death
	11													frozen, thawed, frozen, thawed
	12													frozen after 48 hours at 5°C

DISCUSSION

A carcass stored at 5°C for up to 72 hours has the same dry small intestine weight as one which was fresh. Similarly, intestines from fresh carcasses did not differ significantly from those of carcasses left at 20°C for up to 24 hours. Carcasses left for longer than 24 hours at 20°C, or for 1 week at 5°C, had significantly lighter intestines than did those of freshly killed animals.

An animal which is killed, frozen immediately and later thawed has an intestine with the same weight as when it was killed. However, if a carcass is frozen and thawed several times before the intestine is removed for examination (for example if carcasses are examined by several researchers at different times, being frozen inbetween examinations for storage or for transport purposes) then the intestine will have become significantly lighter.

The results in Table 1, and the 3 significant differences detected by the Bonferroni method, show that there were also changes in intestine length with time and temperature, length increasing with both variables. However, changes were less than changes in the dry weight of the small intestine. The most likely explanation for weight changes is that the gut tissue begins to decompose with increasing time and temperature and this material is lost when the intestine is washed and dried.

Apparently, intestine length is less susceptible to change than is intestine weight. Carcasses used to examine intestinal morphology can be frozen after death or refrigerated for 3 days before analysis without significantly affecting intestine weight or length. If the source of carcasses is unknown, then an analysis of small intestine weight either as a measure of intestine size or to examine effects of dietary, seasonal, sex or age differences should be treated with caution. If the same information can be gained by examining intestine length, then this is the preferred measure. Nevertheless, the results of studies from carcasses of unknown origin should always be interpreted with care, regardless of whether intestine length or intestine weight are reported. Also, length and weight changes of the intestine in live birds are not always correlated and so it should not be assumed that they are comparable measures of gross intestinal morphology (Kehoe *et al.* 1988).

REFERENCES

AL-Joborae, F. (1980) The influence of diet on the gut morphology of the starling (*Sturnus vulgaris*). D.Phil. thesis, University of Oxford, England.

Ankney, C.D. (1977) Feeding and digestive organ size in breeding lesser snow geese. *Auk*, **94:** 275-282.

Day, R.W. and Quinn, G.P. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs*, **59(4):** 433-463.

Drobney, R.D. (1984) Effect of diet on visceral morphology of breeding wood ducks. *Auk*, **101:** 93-98.

Kehoe, F.P. and Ankney, C.D. (1985) Variation in digestive organ size among five species of diving ducks (*Aythya* spp.). *Can. J. Zool.* **63:** 2339-2342.

Kehoe, F.P., Ankney, C.D. and Alisauskas, R.T. (1988) Effects of dietary fiber and diet diversity on digestive organs of captive Mallards (*Anas platyrhynchos*). *Can. J. Zool.* **66:** 1597-1602.

Leopold, A.S. (1953) Intestinal morphology of gallinaceous birds in relation to food habits. *J. Wildl. Manage.* **17:** 197-203.

Miller, M.R. (1975) Gut morphology of mallards in relation to diet quality. *J. Wildl. Manage.* **39:** 168-173.

Moss, R. (1974) Winter diets, gut lengths and interspecific competition in Alaskan ptarmigan. *Auk*, **91:** 737-746.

Paulus, S.L. (1982) Gut morphology of gadwalls in Louisiana in winter. *J. Wildl. Manage.* **46:** 483-489.

Pulliainen, E. (1976) Small intestine and caeca lengths in the willow grouse (*Lagopus lagopus*) in Finnish Lapland. *Ann. Zool. Fennici*, **13:** 195-199.

Pulliainen, E. and Tunkkari, P. (1983) Seasonal changes in the gut length of the willow grouse (*Lagopus lagopus*) in Finnish Lapland. *Ann. Zool. Fennici*, **20:** 53-56.

Robel, R.J., Barnes, M.E., Kemp, K.E. and Zimmerman, J.L. (1990) Influences of time postmortem, feeding activity and diet on digestive organ morphology of two emberizids. *Auk* **107:** 669-677.

Savory, C.J. and Gentle, M.J. (1976) Effects of dietary dilution with fibre on the food intake and gut dimensions of Japanese Quail. *Br. Poult. Sci.* **17:** 561-570.

Savory, C.J. and Gentle, M.J. (1976) Changes in food intake and gut size in Japanese Quail in response to manipulation of dietary fibre content. *Br. Poult. Sci.* **17:** 571-580.

Sibly, R.M., Monk, K.A., Johnson, I.K. and Trout, R.C. (1990) Seasonal variation in gut morphology in wild rabbits (*Oryctolagus cuniculus*). *J. Zool.(London)*, **221:** 605-619.

Steiner, M., Bourges, M.R., Freedman, L.S. and Gray, S.J. (1968) Effect of starvation on the tissue composition of the small intestine in the rat. *Am. J. Physiol.* **215:** 75-77.

Thaysen, E.H. and Thaysen, J.H. (1949) Morphological changes in the gastrointestinal tract of the white rat following inanition. *Acta Pathol. Microbiol. Scand.* **26:** 370-379.

Thomas, V.G. (1984) Winter diet and intestinal proportions of rock and willow ptarmigan and sharp-tailed grouse in Ontario. *Can. J. Zool.* **62:** 2258-2263.

Whyte, R.J. and Bolen, E.G. (1985) Variation in mallard digestive organs in winter. *J. Wildl. Manage.* **49:** 1037-1040.

CHAPTER 3

Morphological adaptation of the digestive tract in relation to feeding ecology of raptors.

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The data presented in this chapter form the basis of a paper submitted to Functional Ecology 1992.

ABSTRACT

The study examined some aspects of gross morphology in Falconiformes and Strigiformes. It is hypothesised that in predatory birds, hunting strategy might influence the relative size of skeletal musculature and length of the digestive tract. Falconiform species were categorised as either 'attackers' or 'searchers' depending on the degree to which active, powered pursuit is required for prey capture. Attacking species feed predominantly on avian prey, requiring extreme agility, speed and acceleration for prey capture. Searchers feed largely on relatively slow moving mammals and carrion. Comparisons between species of attackers and searchers showed that the former had heavier pectoral muscle mass, larger areas for flight muscle attachment and higher linearised wing loadings. Strigiformes had a pectoral muscle mass only half the size of attacking Falconiformes and had a correspondingly smaller sternum area. A skeletal body-size measure was determined to enable calculation of intestine length independent of body-size and shape differences. Attacking species have a small intestine which is 20-30% shorter than would be predicted on the basis of body-size and 50% shorter than found in searchers of equivalent body-size. Strigiformes which locate prey by active flight also have intestinal tracts shorter than expected. The likely effects of intestine length on digestive efficiency and food utilisation are discussed and it is suggested that in predatory birds, some species have evolved alimentary tracts that are shorter than necessary for maximum digestive efficiency in order to enhance prey capture.

INTRODUCTION

Efficient utilisation of energy is an essential component of the daily cycle. The extent to which an animal can utilise food energy depends largely on the anatomical and physiological properties of the digestive tract, which in turn influence optimal feeding strategies (Maynard Smith 1978, Sibly 1981). Omnivorous animals with a varied diet show a high degree of plasticity in their gut anatomy depending on food type. When eating less digestible or more fibrous food their intestine length increases (Savory & Gentle 1976, Al-Joborae 1980, Kehoe & Ankney 1985, Barnes & Thomas 1987, Kehoe *et al.* 1988) . Carnivorous birds and mammals feed almost exclusively on meat, which varies little in composition and so diet-related anatomical differences would not be expected. Nevertheless, variation in gut length has been found among meat-eating species.

Among predatory mammals, cats have shorter digestive tracts and 10% lower digestive efficiency than dogs of equivalent body-size. Houston (1988) suggested that these differences may have arisen because of different selective pressures acting on those predators which rely on rapid acceleration to catch prey and those which use a sustained chase technique. Thus, cat species, which usually rely on a rapid sprint to capture their prey, would tend to reduce the weight of all parts of the body other than skeletal musculature. Lower inertia enables them to reach maximum speed faster. Such species might develop short, light digestive tracts, which would be selected if they resulted in higher hunting success, even if they showed a reduced digestive efficiency. Other species such as dogs and Hyaenas (*Crocuta crocuta*), however, usually hunt by a long, sustained chase which eventually exhausts the prey. This technique does not require rapid acceleration, and in such predators one would expect selection for efficiency of digestion, even if this were at the expense of a longer and heavier tract.

The study tests this hypothesis for two Orders of predatory birds, the Falconiformes and Strigiformes and assesses the influence of diet and predatory behaviour on morphological adaptations of the musculature and gut. Raptors attack a considerable range of prey species, requiring differing degrees of agility for prey capture. This results in species-specific hunting strategies (Jaksic & Carothers 1985). Weight minimisation is very important in terms of flight energetics (Sibly 1981). The initial hypothesis is that predatory birds which catch prey by brief periods of sustained chase might be expected to allocate a greater proportion of their body mass to flight musculature and to minimise the weight of internal organs which are not important for flight, such as the intestinal mass. This category includes species such as sparrowhawks, goshawks and large and small falcons which chase agile prey (mainly other bird species), and where the aerial hunt is highly complex, energy demanding and frequently unsuccessful. This contrasts with species such as vultures, large eagles, buzzards, kites and owls which attack relatively slow-moving prey, usually mammals, and where the attack is simple, direct and with a high success rate. Hunting strategies in these species usually consist of long periods of watching from perches, or soaring flight to survey the ground. The prey is most often caught by a surprise pounce from above, without an active chase. These latter species might be expected to have developed longer, heavier intestines which are comparatively efficient at digestion. It is further considered whether it is the absolute size of the intestine that is important (length or weight) or whether it is the weight associated with gut contents to be carried that influences the size of the digestive tract. Secondarily it is considered whether intestinal morphology might be related to prey type or meat quality, such that species feeding largely on spatially and temporally unpredictable food sources, such as carrion, might have larger intestinal tracts than predicted in order to digest each meal as efficiently as possible.

METHODS

Raptor carcasses were obtained from the Institute of Terrestrial Ecology, Cambridge, the Scottish Office Agriculture and Fisheries Department, Edinburgh the Ministry of Agriculture, Fisheries and Food, Tolworth, Surrey and some additional carcasses were received from various individuals. Most of these birds had been found dead in the field and sent to laboratories for pesticide analysis. The state of preservation was therefore very variable. Goshawk (*Accipiter gentilis*) carcasses were obtained from the Ministry of the Environment Environmental Protection and Nature Conservation Department, Finland after licenced collection for game protection.

583 individuals were obtained from 23 species of Falconiformes and Strigiformes: 135 Sparrowhawks (*Accipiter nisus*), 23 Peregrines (*Falco peregrinus*), 76 Kestrels (*Falco tinnunculus*), 77 Buzzards (*Buteo buteo*), 9 Red Kites (*Milvus milvus*), 59 Goshawks (*Accipiter gentilis*), 14 Merlins (*Falco columbarius*), 4 Hobbies (*Falco subbuteo*), 1 Rough-legged Buzzard (*Buteo lagopus*), 1 Eleonoras Falcon (*Falco eleonorae*), 7 Hen Harriers (*Circus cyaneus*), 2 Marsh Harriers (*Circus aeruginosus*), 10 Golden Eagles (*Aquila chrysaetos*), 1 Tawny Eagle (*Aquila rapax*), 2 Lanner Falcons (*Falco biarmicus*), 1 Saker Falcon (*Falco cherrug*), 36 Tawny Owls (*Strix aluco*), 91 Barn Owls (*Tyto alba*), 11 Long-eared Owls (*Asio otus*), 6 Little Owls (*Athena noctua*), 4 Short-eared Owls (*Asio flammeus*), 12 Snowy Owls (*Nyctea scandiaca*) and 1 Ural Owl (*Strix uralensis*). Only species for which large samples were available were used in most of the analysis.

Whole, part carcasses and intestinal tracts were stored frozen at -20^{o}C. Data were collected on age, sex (by dissection), month of year killed, cause of death and location.

The following measurements were taken:

Wing length (nearest mm)

Measured from the wrist (carpometacarpal joint) to the tip of the longest primary with the wing folded straight and flattened against a ruler. Birds in moult were excluded from the analysis.

Tail length (nearest mm)

Measured from the skin between the central pair of rectrices to the tip of the same feathers with the tail folded and flattened.

Tarsus length (nearest 0.1mm)

Measured with calipers from the joint between the tibia and the metatarsus to the joint at the base of the middle toe.

Keel length (nearest 0.1mm)

The maximum length measured after dissection with caliper tips placed at the base of the sternum and the anterior edge of the keel.

Diagonal length (nearest 0.1mm)

Measured after dissection with caliper points placed at base of sternum and distal point of coracoid.

Body-mass (nearest g)

Mass was adjusted for crop, stomach and gut contents.

Wing span (nearest mm)

Birds were placed on their backs with wings spread to their full extent. The distance between wing tips was measured.

Wing area (nearest cm^2)

(See Pennycuick 1989). The body was held beside the edge of a table with the distal end of the coracoid bone against the table edge. The wing was spread to its fullest extent, the leading edge forming a straight line. The wing was traced following the outline of individual feathers, the area measured using a digitiser.

Wing loading

Body mass divided by total wing surface area (without body area). For cases where no body mass was available, wing loading was estimated using the mean mass of live, healthy birds.

Linearised wing loading - LWL (see Jaksic and Carothers 1985, Mendelsohn *et al.* 1989).

$$\text{LWL} = (\text{Body Mass})^{1/3}(\text{Wing Area})^{-1/2}$$

As species increase in size, body mass increases at a faster rate than wing area. Wing loading (g/cm^2) is therefore inherently heavier in larger birds. In a comparative study such as this, linearised wing loading is more appropriate than wing loading, because it enables differences (independent of body-size) to be examined.

Intestinal measurements:

For descriptions of the avian gastrointestinal tract, see Ziswiler and Farner (1972) and Duke (1986).

Small intestine length (nearest mm)

The intestinal tract was separated post gizzard adjacent to the pyloric sphincter and at the cloaca. The tract was stripped of fat and mesentery, placed unstretched in a straight line and the length measured from the cut-off point at the gizzard to the ileo-cecocolic junction (Leopold 1953).

Anterior, middle and posterior widths of intestine (nearest mm)

Small intestine was opened along the whole length and flattened. Gut contents were washed out and the width measured at both ends and the mid-point. Small intestine volume was calculated using the mean width (circumference) and intestine length to compute the volume of a cylinder.

Skeletal measurements and intestinal morphology data for all carcasses examined are shown in appendices 2-7.

Analysis

The analysis consists of 5 sections: 1) determination of a body-size variable to allow an interspecific comparison of small intestine length independent of body-size. 2) Examination of how sternum design and the measures used to compute the body-size variable differ between species and how they relate to requirements for active, powered pursuit of prey. 3) Use of the body-size measure in covariance analysis to compare small intestine length, between species with contrasting hunting strategies. 4) An estimation of the extent to which small intestine length for each species deviates from expected values. 5) Assessing the functional significance of the results obtained. Unless otherwise stated, significance levels are two-tailed and tested at the 5% level with means and standard errors shown where applicable.

Much of the interpretation of the results is dependent on the initial categorisation as to whether a particular raptor species is a searcher or an attacker and whether a certain prey species is difficult or easy to catch. Temeles (1985) quotes median hunting success for falconiform species to be lowest for avian prey (12.95%) and increases from mammals (22.60%) through fish (58.00%) to invertebrate prey (82.00%). This relationship holds for different raptor species and for individual raptor species feeding on different prey types. The Falconiformes were divided into 2 groups depending on their requirement for active chase. Those species with more than 75% avian prey in the diet (Brown

1978) were categorised as attackers: (Sparrowhawk, Peregrine, Merlin, Hobby, Goshawk, Lanner, Saker, Eleonoras Falcon). Species feeding predominantly on mammals and carrion were categorised as searchers (Buzzard, Red Kite, Golden Eagle, Kestrel, Hen Harrier, Marsh Harrier, Rough-legged Buzzard, Tawny Eagle). The Strigiformes (Tawny Owl, Barn Owl, Short-eared Owl, Long-eared Owl, Little Owl, Snowy Owl, Ural Owl) and Falconiformes were compared separately in the analysis for phylogenetic reasons: these two families are unrelated (Sibley & Ahlquist 1990). Within the Strigiformes, and for which sufficient data were available, those species with a more active search mode (Barn Owl and Long-eared Owl) were compared with a less active species, the Tawny Owl (Cramp 1985).

Throughout the analysis, small intestine length is used as the measure of gross-intestinal morphology. The small intestine is the longest section of the gut and the region responsible for nutrient absorption and is, therefore, the region of the tract likely to have most influence on digestive efficiency. The study only examines interspecific differences in the small intestine but recognises the importance of the gizzard, proventriculus, colon and cecae (Strigiformes only) in digestion.

A body-size variable was computed and used in analysis of covariance to examine the relationship between small intestine length and hunting strategy/foraging mode for attackers, searchers and Strigiformes. Small intestine length was also compared within the Orders Falconiformes and Strigiformes. The Bonferonni method was used for pairwise comparison of adjusted treatment means (Day and Quinn 1989).

RESULTS

Computation of a body-size variable.

In interspecies comparisons, it is implicit that the body-size measure used to remove the confounding body-size variable should be comparable across all species being examined. Weight is not a suitable measure of body-size because it varies with the condition of the bird, and so only skeletal variables should be used to determine size (Piersma & Davidson 1991). Raptor species differ in both size and shape, some having longer wings than others for example, and so a univariate measure of body-size should not be used as a body-size variable across species (Freeman and Jackson 1990). For the same reason, a generalised body-size variable (principal component factor) computed by Principal Components Analysis (PCA, see Jolicoeur 1963) is not directly applicable to derive a generalised body-size variable in an interspecies comparison. However, the factor loadings derived from the PCA can be used. Factor loadings indicate how much of the variation within each univariate body measure is explained by the principal component factor and were used here to identify those body measures most important in measuring body-size.

PCA analysis was carried out using measures of wing, tail, tarsus, keel and diagonal for males and females of 6 falconiform species (Sparrowhawk, Peregrine, Kestrel, Buzzard, Red Kite and Goshawk). Only one factor was extracted and Table 1 shows that the factor loadings for each of the variables did differ between species and sex, demonstrating the importance of recognising body shape as well as size differences in interspecific comparisons. Data were not available for male Kestrels and female Red Kites. In most species, factor loadings for wing, keel and diagonal were high and therefore contributed most to the computation of the first principal component. Factor loadings for tarsus and tail length were low and therefore those variables contributed very little. A second factor was computed using only wing, keel and diagonal to see if wing length contributed sufficiently to merit use in a computed body-size variable. Table 2 shows that this measure was least important. It is also the variable which might be expected to differ most between species, whereas keel length and diagonal, which are both skeletal measures of the trunk skeleton would be expected to be a more accurate reflection of body-size. Only one factor was computed for the Strigiformes because of lack of data for tail and tarsus lengths (Table 3). The variable used to correct for body-size in this study was therefore taken to be a combination of keel length and diagonal length: (keel x diagonal)$^{1/2}$, and this is referred to as BODY. The square root was taken to compare body-size with the linear measure of small intestine length.

Table 1. Factor loadings for each of the variables (wing, tail, tarsus, keel and diagonal) in the PCA for males and females of each species. Only one factor was extracted and the solution not rotated.

	SPARROWHAWK	PEREGRINE	KESTREL	BUZZARD	RED KITE	GOSHAWK
			MALES			
WING	0.91	0.81	-	0.29	0.97	0.79
TAIL	0.39	0.18	-	0.34	0.21	0.01
TARSUS	0.60	0.54	-	0.79	0.59	0.55
KEEL	0.83	0.82	-	0.44	0.72	0.82
DIAGONAL	0.88	0.88	-	0.80	0.91	0.80
			FEMALES			
WING	0.71	0.88	0.20	0.69	-	0.71
TAIL	0.30	0.15	0.50	0.67	-	0.56
TARSUS	0.14	0.96	0.37	0.49	-	0.45
KEEL	0.76	0.13	0.93	0.51	-	0.84
DIAGONAL	0.65	0.82	0.67	0.85	-	0.94

Table 2. Factor loadings for each of the variables (wing, keel and diagonal) in the PCA for males and females of each species. Only one factor was extracted and the solution not rotated.

	SPARROWHAWK	PEREGRINE	KESTREL	BUZZARD	RED KITE	GOSHAWK
			MALES			
WING	0.61	0.14	0.44	0.12	0.50	0.25
KEEL	0.82	0.82	0.86	0.77	0.94	0.87
DIAGONAL	0.86	0.91	0.83	0.95	0.90	0.81
			FEMALES			
WING	0.52	0.01	0.25	0.52	0.88	0.77
KEEL	0.77	0.89	0.85	0.68	0.94	0.89
DIAGONAL	0.83	0.83	0.82	0.86	0.96	0.93

Table 3. Factor loadings for each of the variables (wing, keel and diagonal) in the PCA for four owl species (sexes combined). Only one factor was extracted and the solution not rotated.

SPECIES	TAWNY OWL	BARN OWL	LONG-EARED OWL	SNOWY OWL
WING	0.29	0.27	0.59	0.91
KEEL	0.53	0.76	0.74	0.98
DIAGONAL	0.75	0.46	0.92	0.91

Relationship between skeletal size and hunting strategy.

Figure 1 demonstrates that neither keel nor diagonal would have been suitable by themselves as univariate measures of body-size. Attacking species have a long keel relative to diagonal length and searching species with a soaring flight have a short keel relative to diagonal length. Least squares regressions for keel length on diagonal length were significant for attackers ($R^2=0.997$, $F_{1,3}=904.9$, $P<0.0001$), searchers ($R^2=0.999$, $F_{1,4}=4366$, $P<0.0001$) and Strigiformes ($R^2=0.960$, $F_{1,4}=98.2$, $P<0.001$).

ANCOVA was run across the three groups (attackers, searchers and Strigiformes) using diagonal as covariate and keel length as the dependent variable. Adjusted means differed significantly ($F_{2,13}=216.01$, $P<0.001$) with homogeneity of slopes ($F_{2,11}=0.6.92$, $P=0.266$). Adjusted mean keel lengths were 61.6mm, 53.5mm and 49.1mm for attacking Falconiformes, searching Falconiformes and Strigiformes respectively. Keel length for attacking Falconiform species was significantly longer than for searchers or Strigiformes (Bonferonni, $P<0.05$). Searching Falconiformes had significantly longer keels than Strigiformes ($F_{1,9}=56.65$, $P<0.01$) with homogeneity of regression slopes ($F_{1,8}=0.76$, $P=0.41$).

From the above analysis it can be implied that attackers have a larger sternum surface area for flight-muscle attachment with consequent benefits for powered, attacking flight. Wet pectoral mass as a percentage of total body mass from birds known to have died from accidents, not malnutrition, were as follows: for attacking Falconiformes; Sparrowhawk = 19.3% (n=29), Peregrine = 18.7% (n=2), Goshawk = 18.2% (n=46). For searching Falconiformes; Buzzard = 11.6% (n=18), Red Kite = 15.2% (n=7). Kestrel = 11.9% (n=7). For Strigiformes; Barn Owl = 9.5% (n=5), Tawny Owl = 11.3% (n=2). As a proportion of body-mass, attacking raptors therefore tend to have a greater pectoral muscle mass than searchers or Strigiformes. For the supracoracoideus muscle as a proportion of total body mass, results were: Sparrowhawk = 1.03% (n=6), Peregrine = 1.03% (n=2), Goshawk = 0.91% (n=43), Kestrel = 0.81% (n=2), Buzzard = 0.60% (n=16), Red Kite = 1.04% (n=7), Barn Owl = 0.57% (n=2), Tawny Owl = 0.58% (n=2).

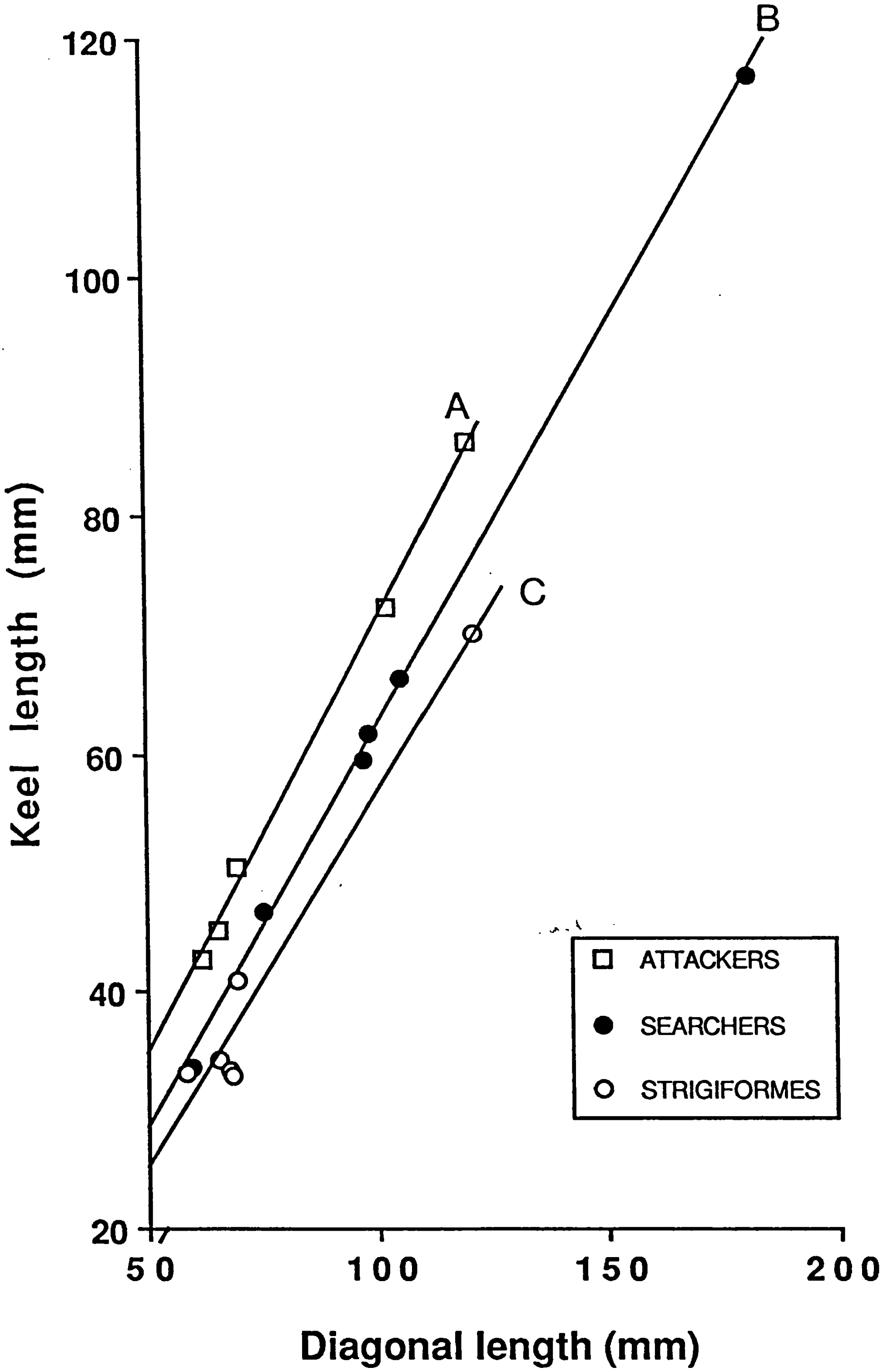
Figure 1.

Regressions of keel length (mm) against diagonal length (mm) for 17 species of Falconiformes and Strigiformes. Points are means for each species (sexes combined).

A: attacking Falconiformes: $y = 0.73x - 1.67$.

B: searching Falconiformes: $y = 0.67x - 5.16$.

C: Strigiformes: $y = 0.63x - 6.16$.


120
100
80
60
40
20
Keel length (mm)
50
100
150
200
Diagonal length (mm)
A
B
C
□ ATTACKERS
● SEARCHERS
○ STRIGIFORMES

Interspecific differences in intestine length.

Small intestine lengths of attackers (Sparrowhawk, Peregrine, Merlin, Goshawk, Lanner, Saker and Eleonoras Falcon), searchers (Buzzard, Red Kite, Hen Harrier, Golden Eagle, Rough-legged Buzzard, Tawny Eagle) and Strigiformes (Barn Owl, Tawny Owl, Little Owl, Long-eared Owl, Short-eared Owl, Ural Owl and Snowy Owl) were compared. For each species (sexes combined), a small intestine length and a BODY measure was calculated by taking the average of the means for each sex. Separate regression lines were drawn through the species means for each group (Fig. 2). Within group regressions were significant for attackers ($R^2=0.71$, $F_{1,5}=12.3$, $P<0.02$), searchers ($R^2=0.64$, $F_{1,4}=6.98$, $P<0.05$) and Strigiformes ($R^2=0.53$, $F_{1,6}=6.68$, $P<0.05$). Small intestine length for a given body-size differed significantly between groups ($F_{2,18}=5.60$, $P=0.013$) with homogeneity of regression slopes ($F_{2,16}=0.25$, $P=0.783$). Adjusted means were 698mm, 945mm and 677mm for attackers, searchers and Strigiformes respectively. Small intestine length does not differ significantly between the attacking Falconiformes and the Strigiformes but both groups have shorter small intestines than the searching Falconiformes.

In order to determine precisely which species and to what extent species differed from one another, interspecific differences within the Falconiformes and Strigiformes were examined by analysis of covariance for those species for which I had relatively large sample sizes. Many of the species examined are reversed size dimorphic to differing degrees (Andersson & Norberg 1981). If sexes are combined for each species and regression lines drawn within species, significant intraspecific regressions between intestine length and body-size result, but significant heterogeneity arises between species because of differences in the regression slopes as a consequence of some species being more size dimorphic than others. For this reason sexes have been analysed separately.

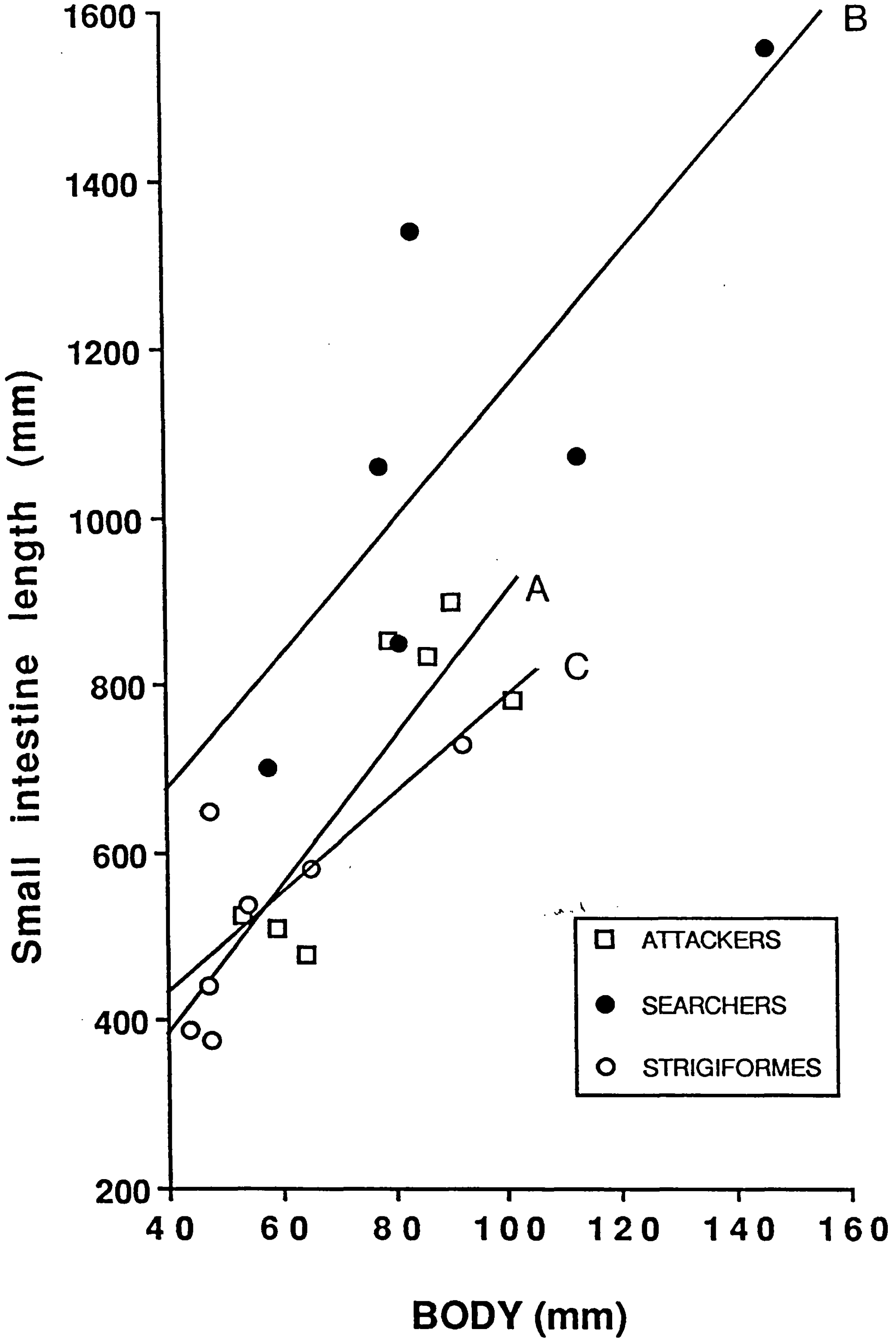
Figure 2.

Regressions of small intestine length (mm) against BODY (mm) for 20 species of Falconiformes and Strigiformes. Points are means for each species (sexes combined).

A: attacking Falconiformes: $y = 8.74x + 32.41$.

B: searching Falconiformes: $y = 6.96x + 416.8$.

C: Strigiformes: $y = 5.45x + 229.5$.


Small intestine length (mm)
1600
1400
1200
1000
800
600
400
200
40
60
80
100
120
140
160
BODY (mm)
B
A
C
□ ATTACKERS
● SEARCHERS
○ STRIGIFORMES

Falconiformes

The species analysed were Sparrowhawk, Goshawk, Peregrine, Kestrel, Buzzard and Red Kite. Small intestine length for a given body-size differed significantly for both males ($F_{5,89}=75.56$, $P<0.001$) and females ($F_{5,101}=87.10$, $P<0.001$) with no significant heterogeneity in regression slopes for either males ($F_{5,84}=0.77$, $P=0.574$) or females ($F_{5,96}=1.40$, $P=0.232$). Adjusted means are shown in Table 4 and significant species differences in Table 5. The Buzzard and the Red Kite have the longest small intestine relative to body size, the Kestrel is intermediate and the Sparrowhawk, Peregrine and Goshawk all have a relatively short small intestine. Species differences for males and females are very similar. From searchers to attackers there is a large reduction in size of the small intestine, independent of body-size. The differences are significant for species with different foraging strategies across a size range, and for species within a similar size range (eg. Goshawk, Buzzard and Red Kite). Some factor other than allometry causes interspecific differences in the gross gut morphology of raptors.

Table 4. Adjusted mean small intestine length for 6 Falconiformes. Those species which capture prey by attacking, active pursuit (Sparrowhawk, Peregrine, Goshawk) have relatively short intestines. The Kestrel Buzzard and Red Kite which do not require the same degree of rapid acceleration and agility have relatively long intestinal tracts.

	ADJUSTED SMALL INTESTINE LENGTH	
SPECIES	MALES	FEMALES
1. GOSHAWK	445	426
2. PEREGRINE	619	775
3. SPARROWHAWK	669	774
4. KESTREL	862	1013
5. BUZZARD	951	1111
6. RED KITE	1304	1200

Table 5. Pairwise comparison of adjusted small intestine length from ANCOVA for males and females of each species. * denotes significant pairwise differences, Bonferonni, $P<0.05$)

		MALES						FEMALES					
		1	2	3	4	5	6	1	2	3	4	5	6
SPARROWHAWK	1	–			*	*	*	–		*	*	*	*
PEREGRINE	2		–	*	*	*			–	*	*	*	*
KESTREL	3			–		*	*			–		*	*
BUZZARD	4				–	*	*				–		*
RED KITE	5					–	*					–	*
GOSHAWK	6						–						–

It is possible that differences in small intestine length are compensated for by corresponding differences in gut volume. That is, species with short intestines relative to body size have wide guts resulting in the same gut capacity as a species with a long but narrow gut. Least squares regression of small intestine length against volume, using species' means, shows this not to be the case, intestine volume increasing with intestine length ($r_{13}=0.97$, $P<0.0001$). Species with short intestines have a smaller gut capacity than species with long intestines and a longer intestine also corresponds to a larger surface area.

Strigiformes

The species analysed were Tawny Owl, Barn Owl and Long-eared Owl. The Tawny Owl differs in hunting strategy from the other two species. It does not search in active flight, instead detecting prey by perch hunting. Sample sizes for other species were too small to be included in the analysis. The degree of size dimorphism is generally less in Strigiformes than Falconiformes and so the sexes were combined by taking the average of the sex means. Small intestine length for a given body-size differed significantly between species ($F_{2,32}=23.10$, $P<0.001$) with homogeneity of regression slopes ($F_{2,30}=0.50$, $P=0.614$). Adjusted means were 578mm, 385mm and 439mm for Tawny Owl, Barn Owl and Long-eared Owl respectively. Tawny Owls have a small intestine significantly longer than that found in Long-eared Owls which is significantly longer than found in Barn Owls.

Calculation of intestine length independent of body-size.

It is not apparent whether the relationship between small intestine length and the body-size variable can be assumed linear or isometric (Packard and Boardman 1988), or to what extent the position of the line may be biased by the range of species available. However, covariance analysis as described in the previous section is the most suitable method for scaling to body-size if allometric functions are not precisely known (Herrera 1986). In Fig. 3, mean small intestine length was plotted against mean BODY (standard errors shown) for 8 species of Falconiform, separated by sex, and 4 Strigiformes (sexes combined) using data in appendix 1. As a standard against which to measure each species, an isometric line was drawn through the combined means of the 8 points (Buzzard, Red Kite, Peregrine and Goshawk, by sex). The line was drawn through the origin and ($y=1005$; $x=87.2$). Those species above the line apparently have small intestines longer than predicted from the isometric body-size relationship, species below the line have intestines shorter than predicted. All the attacking falconiform species have short small intestines independent of body-size, the searchers have relatively long intestines. For example, independent of body-size, the small intestine length of the Red Kite is approximately twice that found in the Goshawk.

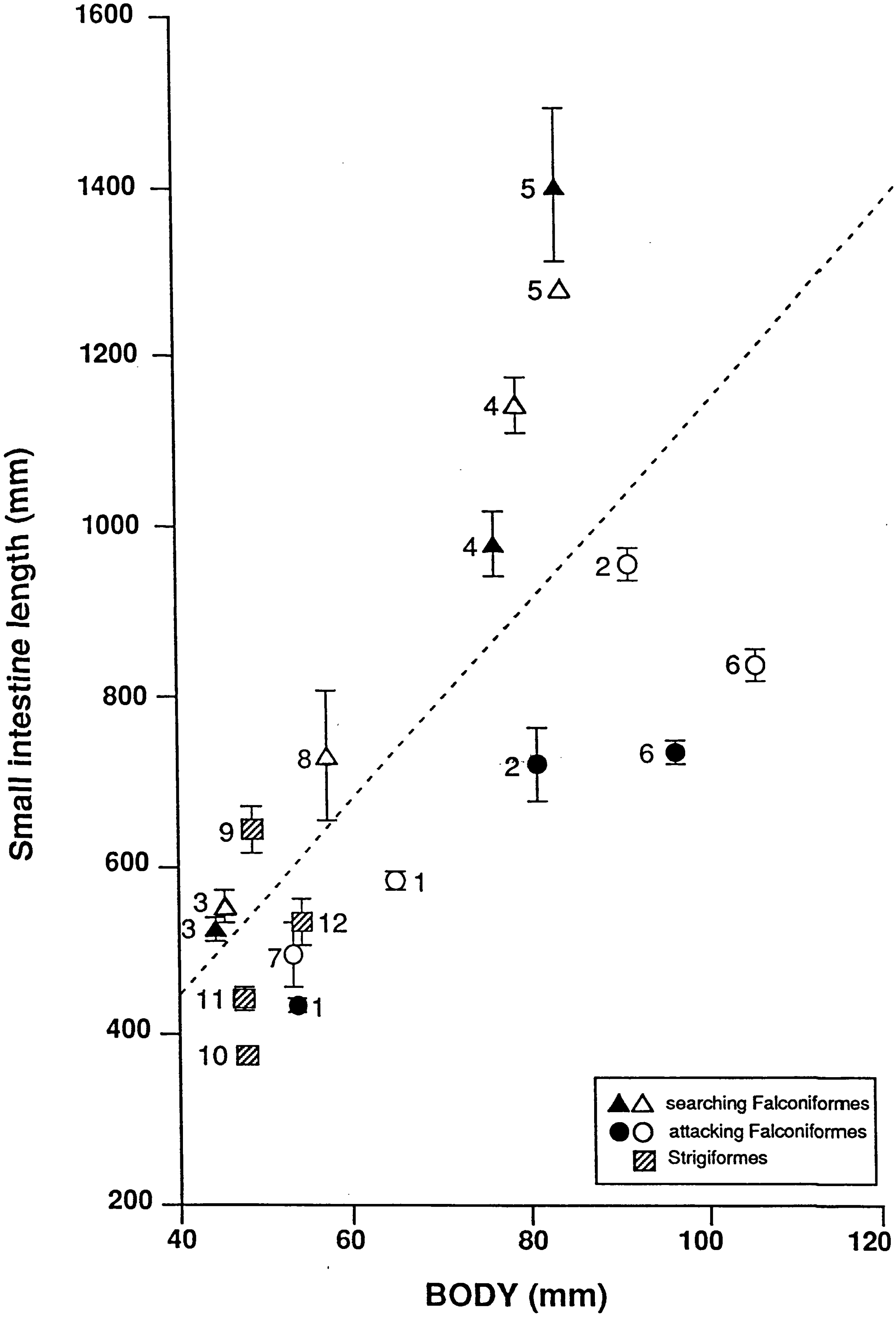
Figure 3.

Diagrammatic relationship of small intestine length against body-size (BODY) for 8 falconiform species (separated by sex) and 4 strigiform species (sexes combined). Standard errors are shown. The dashed line was fitted as described in the text to give a standardised value against which the measured intestine lengths could be compared for species and sexes differing in size.

Species codes (sample sizes in parentheses):

1: male Sparrowhawk (37), female Sparrowhawk (52); 2: male Peregrine (10), female Peregrine (6); 3: male Kestrel (9), female Kestrel (15); 4: male Buzzard (22), female Buzzard (31); 5: male Red Kite (7), female Red Kite (2); 6: male Goshawk (31), female Goshawk (18); 7: female Merlin (3); 8: female Hen Harrier (4); 9: Tawny Owl (10); 10: Barn Owl (50); 11: Long-eared Owl (8); 12: Short-eared Owl (3).

Solid symbols represent males, open symbols represent females.



Small intestine length (mm)
1600
1400
1200
1000
800
600
400
200
40
60
80
100
120
BODY (mm)
1
2
3
4
5
6
7
8
9
10
11
12
▲△ searching Falconiformes
●○ attacking Falconiformes
▨ Strigiformes

It is difficult to correct for body-size between species, and there is probably no method that is perfect. One source of bias in the body-size variable that has been used in this study could occur if species with the same basic body volume and mass had different sternum structures, as has been shown in Fig. 1. For example, attacking species might be slightly more streamlined than searching species, and so two species of the same fundamental body-size may have different sternum measures and so be given different BODY indices. The relationship between intestine length and the computed variable BODY might therefore be due to body shape differences rather than real body-size. By using two linear body measurements to derive the size variable instead of one, this potential source of bias is reduced. However, to check the validity of the body-size variable BODY, the analysis for interspecific differences in intestine length was re-run using mass as the covariate. It resulted in no essential differences from the analysis using BODY as the measure of body-size.

Relationships with wing loading.

It was hypothesised that those species which require rapid, powered acceleration to catch difficult prey types (particularly highly manoeuvrable, avian prey species) should have a body-size which is a compromise between increased muscle mass for powered attacks (as already shown) and weight reduction in those body components which are not essential in order to increase agility and acceleration. Linearised wing loading is a meaningful measure of flight capability independent of body-size. Species with high LWL (falcons and accipiters) are capable of rapid, active pursuit; species with a low LWL (kites, buzzards, harriers and eagles) are suited to soaring, searching flight. Table 6 summarises data collected from this study and from the literature for mass, wing areas and linearised wing loading. Typical values for LWL are: attackers (0.22-0.28); searchers (0.18-0.21); Strigiformes (0.16-0.28).

Table 6. Mass, wing areas and linearised wing loading for Falconiformes and Strigiformes used in the analysis.

SPECIES	SEX	MASS (g)	ref[a]	WING AREA (cm^2)	s.e.	n	ref[b]	LWL	n	ref[c]
SPARROWHAWK	M	149	3	560	15.2	3	2	0.225	3	2
	F	290	3	785	18.7	5	2	0.233	5	2
PEREGRINE	M	540	(3)	954	17.1	5	2	0.264	4	2
	F	985	(4)	1344	16.1	5	2	0.272	4	2
KESTREL	M	160	1	703	-	1	2	0.210	1	1
	F	200	1							
BUZZARD	M	756	1	2007	27.4	7	2	0.203	6	2
	F	940	1	2217	27.4	4	2	0.208	6	2
RED KITE	M	930	1	2902	-	1	1	0.181	1	1
	F	1137	1							
GOSHAWK	M	893	(34)	1521	8.1	34	2	0.249	32	2
	F	1335	(18)	1926	15.7	19	2	0.250	18	2
MERLIN	M	162	1	-	-	-	-	0.263	-	3
	F	212	1							
HEN HARRIER	M	346	1	1382	-	1	1	0.200	1	1
	F	527	1							
TAWNY OWL	M	410	4	1086*	15.5	17	2	0.234	17	2
	F	515	4							
BARN OWL	M	288	2	1046*	20.9	10	2	0.207	10	2
	F	330	2							
S.E. OWL	M	320	5	1437*	-	1	1	0.166	1	1
	F	374	5							
L.E. OWL	M	250	6	1166*	-	2	2	0.190	2	2
	F	295	6							

Sources:

a. (1) Cramp & Simmons 1980, (2) Cramp 1985, (3) Newton 1986, (4) Hirons et al. 1984, (5) as cited in Lundberg 1986, (6) Wijnandts 1984.

b. (1) as cited in Jaksic and Carothers 1985, (2) this study.

c. (1) as cited in Jaksic and Carothers 1985, (2) this study, (3) calculated from data in Cade 1982. See methods for calculation of LWL.

Reference numbers in parentheses indicate data from this study and the corresponding sample size.

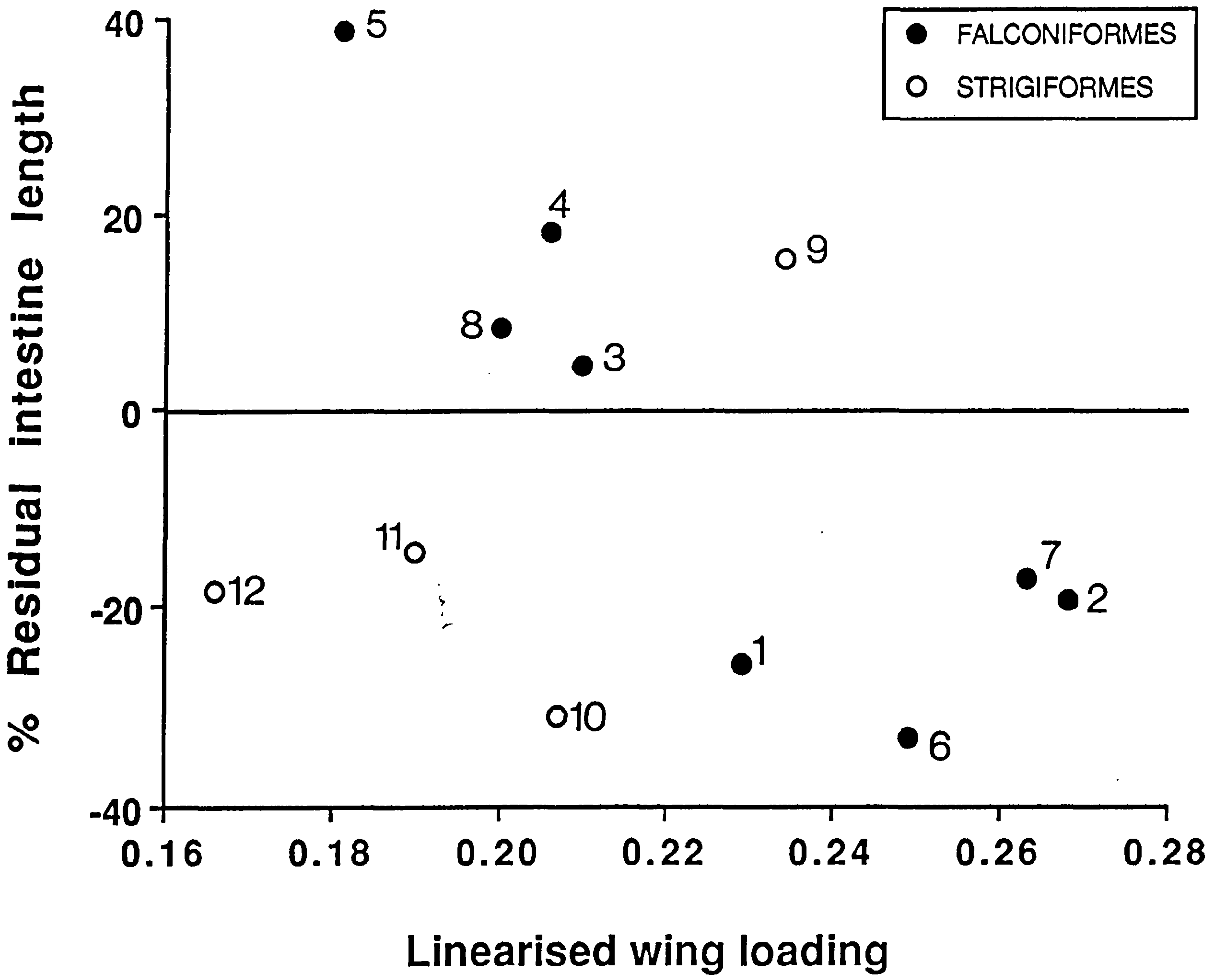
* sexes combined.

To consider the relationship between small intestine length and LWL, the residual values from Fig. 3 were calculated as a percentage of the predicted values (Appendix 1) in order to standardise for body-size differences. If small intestine size (length) is related to aerial manoeuvrability, it would be expected that the standardised residual intestine length would be negatively correlated with LWL (Fig. 4). Standardised residual intestine length and LWL were calculated for each species. Small intestine residuals were significantly correlated with LWL for falconiform species (r_S=-0.79, n=8, P<0.05).

Figure 4.

Correlation between residual small intestine length as calculated from data in Appendix 1 and linearised wing loading using data from Table 6. For Falconiformes the correlation is significant (r_s=-0.79; n=8; P<0.02).

Species codes are as in Fig. 3. The residuals were calculated as a percentage of the predicted values to correct for body-size differences.


● FALCONIFORMES
○ STRIGIFORMES
% Residual intestine length
40
20
0
-20
-40
0.16
0.18
0.20
0.22
0.24
0.26
0.28
Linearised wing loading
1
2
3
4
5
6
7
8
9
10
11
12

DISCUSSION

This chapter is based on the hypothesis that in raptors (Strigiformes and Falconiformes) hunting strategy adopted by a species may influence the morphology of the digestive tract. In particular, species adapted for rapid acceleration during the attack, and where the prey is difficult to catch, would be expected to gain an advantage by reducing, wherever possible, the weight of parts of the body other than the skeletal musculature. The shortening of the digestive tract results in a lighter gut, as well as a reduced weight of gut contents and this might be selected if costs of reduced digestive efficiency were outweighed by the benefits of greater hunting success. Those raptors specialising in the capture of small birds in flight have the most active form of pursuit; speed, acceleration, extreme agility and manoeuvrability are required. The searching raptors which eat predominantly ground mammals, or carrion, do not need to develop such rapid acceleration and agility in the attack and show a far higher success rate in prey capture (Temeles 1985). Searching species also rely heavily on soaring flight rather than powered flapping flight. These two factors mean that in searching raptors extreme strategies to reduce body-mass may not be so necessary. In such species one might expect selective pressure for the most efficient digestion and comparatively longer digestive tracts.

Species of both Falconiformes and Strigiformes were compared and I will consider first the Falconiform species. The proportion of avian prey in the diet was used as the criterion for categorising species as attacking raptors or searching raptors. It is well established that the success rate of attacks on avian prey is substantially lower than that on mammals, invertebrates or carrion (Table 7).

Comparisons between species of attackers and searchers showed that the former had heavier pectoral muscle mass, larger areas for muscle attachment on the keel and higher linearised wing loadings. These all result in the ability to achieve higher power output in flight and faster flight speeds. The size of the

Table 7. Capture success rates (attack on specific prey item) for raptor species feeding on different prey types.

SPECIES	ATTEMPTS	DIET	% SUCCESS	REFERENCE
Goshawk	79	Birds	6.3	Kenward (1982)
Sparrowhawk	190	Birds	12.1	Rudebeck (1951)
Merlin	139	Birds	5.0	Rudebeck (1951)
	343	Shorebirds	12.8	Page and Whitacre (1975)
Peregrine	252	Birds	7.5	Rudebeck (1951)
	674	Birds	7.7	Dekker (1980)
Kestrel	87	Birds	31.0	Shrubb (1982)
	-	Mammals	50.0	Shrubb (1982)
	54	Mammals	25.9	Village (1983)
	67	Invertebrates	52.2	Village (1983)
Golden Eagle	72	Mammals	29.2	Collopy (1983)
Hen Harrier	291	Mammals	8.3	Schipper *et al.* (1975)
	20	Birds	5.0	Temeles (1985)
	130	Mammals	7.7	Temeles (1985)

supracoracoideus muscle is larger in attackers such as Peregrine, Goshawk and Sparrowhawk than in searchers such as Buzzards. This is presumably because in active hunters it is important to develop a fast upward stroke because it leads to more rapid recovery of the wing and a shorter time interval between wing beats. Rapid wing recovery is not so important for species that are chiefly reliant on soaring flight. The Red Kite is an apparent exception having a supracoracoideus as large as those of attacking raptors. Red Kites do not have the strength or the aggression shown by many raptors, but they do have a very characteristic flight pattern with a strong, deep, wing beat and a comparatively long wing, also occasionally hovering (Cramp & Simmons 1980). A large supracoracoideus muscle would give the Red Kite the required powered upstroke for such a buoyant flight.

It has been shown here that attackers have considerably shorter intestinal tracts than do searchers, which in some species resulted in intestinal tracts being

20-30% shorter than predicted from their body-size and only half the length of similar-sized species of searchers. These interspecific differences in gross gut morphology presumably have some effect on digestive efficiency. The small intestine is the region of the gut where nutrient absorption takes place, and one might expect a reduced length to result in a lower efficiency of digestion. This is known to occur in some mammalian carnivores, where cats have 10% lower digestive efficiency than dogs and shorter digestive tracts (Kendall *et al* 1982, Houston 1988) and this study on digestive efficiency in a variety of raptor species shows that on average the attacking raptor species have digestive efficiencies about 7% lower than those of searching raptors. A number of studies on species with an omnivorous diet, such as Starlings (*Sturnus vulgaris*) and voles (*Microtus ochrogaster*), have shown that as the quality of the diet declines, the small intestine length is increased (Al-Joborae 1980, Hammond & Wunder 1991) presumably because increased length maintains energy requirements on food of low nutrient content.

The Strigiformes are an unrelated group of birds to the Falconiformes and their predation techniques are not directly comparable with either attacking or searching Falconiformes. The flight behaviour of owls is very variable and none of the owl species considered here are active pursuit predators after small birds. Most species feed on small mammals or invertebrates by dropping on them from above, and so the predation technique is in some ways similar to the searching predators among the Falconiformes. Owls do, however, differ considerably from searchers in their flying techniques. None of them use soaring flight to any extent, whereas this method of flight is important for most searching Falconiformes. Strigiformes have a low wing loading and use a slow quartering flight which is achieved by having a low body weight and relatively large wing surface area. The owl species available for this study show two different hunting methods. The Tawny Owl spends long periods perch hunting, pouncing on detected prey from a perch rather than during flight. The Short-eared, Long-eared and Barn Owls all fly for long periods using active flapping flight, and locate suitable prey items during these flights (Cramp 1985).

Strigiform species had relative pectoral muscle masses which were only about half that of attacking Falconiformes and they had smaller sternum areas for muscle attachment. This included those species that undertake long periods of powered flight. It suggests that the large muscles of the attacking Falconiformes are mainly to achieve the rapid speed necessary for the hunt, rather than being needed for routine flying. Owls have much lighter muscle masses because they do not need rapid acceleration to catch prey. Owls also have comparatively small supracoracoideus muscles, again suggesting that they are not adapted to rapid wing beat and fast flight speed. Although the predatory strategy of owls is similar to that of the searching Falconiformes, they rely on flapping rather than soaring flight and so are far more influenced by the need to reduce body weight. Their intestine length is therefore somewhat shorter than in a soaring, searching raptor. It is however noteworthy that the Tawny Owl, which does not use powered flight to anything like the extent of the other three owl species studied was found to have a 45% longer gut length. It also had a longer than expected gut length in relation to its linearised wing loading, while those owl species which locate prey while on the wing all had intestinal lengths shorter than expected.

I suggest that in raptors, some species have evolved alimentary tracts that are shorter than necessary for maximum digestive efficiency because this results in enhanced prey capture. This explanation may account for one aspect of diet specificity that is so far unaccounted for in raptors. In many habitats, meat-eating birds have two alternative sources of food. They can either kill their own prey, or scavenge off animals that they find dead. Despite the fact that carrion is often freely available to predatory birds, it is striking how comparatively few species take advantage of it. Those species which do scavenge will, at some seasons of the year, often obtain a high proportion of their total diet from this source, and among the species available for this study this would include the Common Buzzard, Red Kite and Golden Eagle (Cramp & Simmons 1980). Other species such as Peregrine Falcons, Goshawks and Sparrowhawks also have carrion available in the habitat but this is not eaten on a regular basis (Cramp & Simmons 1980). Why should some meat eating birds avoid feeding on carrion while others take it readily? Predation is an energetically demanding and at times dangerous activity, with a real risk of injury during the attack. Why should some species choose to face these risks in killing their own prey rather than taking carrion that is available at none of these costs ? One reason could be that carrion is a food of lower quality than fresh meat for a variety of reasons: it may have lost some energy content or nutritional quality through microbial activity, the meat is not at body temperature and it may contain products from bacterial metabolism which render it unpalatable, impede digestion or have a toxic effect (Janzen 1977). If as I suggest, some raptors have evolved digestive tracts that are less than optimum for digestive efficiency, it might be expected that these species would be least able to deal with carrion as a food. All of the species studied here which were found to have notably shorter than expected gut lengths were species which do not regularly include carrion in their normal diet (Cramp & Simmons 1980), while those species with considerably longer than expected gut lengths were the Red Kite and the Buzzard, which scavenge extensively. A consequence of the development of reduced digestive tracts to facilitate active predation may be that it limits active hunters to the extent with which they can exploit carrion as a food resource.

REFERENCES

Al-Joborae, F.F. (1980) *The influence of diet on the gut morphology of the Starling (Sturnus vulgaris L. 1758)*. Unpublished Ph.D. thesis, University of Oxford.

Andersson, M. & Norberg, R.A. (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15:** 105-130.

Barnes, G.G. & Thomas, V.G. (1987) Digestive organ morphology, diet and guild structure of North American Anatidae. *Can. J. Zool.* **65:** 1812-1817.

Barton N.W.H. Ph.D. thesis (in preparation), Univ. of Glasgow.

Brown, L.H. (1978) *British Birds of Prey*. London: Collins.

Cade, T.J. (1982) *The Falcons of the World.* London: Collins.

Collopy, M.W. (1983) Foraging behaviour and success of Golden Eagles. *Auk* **100:** 747-749.

Cramp, S. (1985) *Handbook of the birds of Europe, the Middle East and North Africa. Vol. 4.* Oxford: Oxford University Press.

Cramp, S. & Simmons, K.E.L. (1980) *Handbook of the birds of Europe, the Middle East and North Africa. Vol. 2.* Oxford: Oxford University Press

Day, R.W. & Quinn, G.P. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59(4):** 433-463.

Dekker, D. (1980) Hunting success rates, foraging habits and prey selection of Peregrine Falcons migrating through central Alberta. *Can. Field-Nat.* **94:** 371-382.

Duke, G.E. (1986) Alimentary canal: secretion and digestion, special digestive functions and absorption. *In* P.D. Sturkie (ed), *Avian Physiology 4th ed.* New York: Springer-Verlag.

Freeman, S. & Jackson, W.M. (1990) Univariate metrics are not adequate to measure avian body size. *Auk* **107:** 69-74.

Hammond, K.A. & Wunder, B.A. (1991) The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster. Physiological Zoology* **64:** 541-567.

Herrera, C.M. (1986) On the scaling of intestine length to body size in interspecific comparisons. *Ornis Fenn.* **63:** 50-51.

Hirons, G.J.M., Hardy, A.R. & Stanley, P.I. (1984) Body weight, gonad development and moult in the Tawny Owl (*Strix aluco). J. Zool.*, Lond. **202:** 145-164.

Houston, D.C. (1988) Digestive efficiency and hunting behaviour in cats, dogs and vultures. *J. Zool.* **216:** 603-605.

Jaksic, F.M. & Carothers, J.H. (1985) Ecological, morphological and bioenergetic correlates of hunting mode in hawks and owls. *Ornis Scandinavica* **16:** 165-172.

Janzen, D.H. (1977) Why fruits rot, seeds mould and meat spoils. *Am. Nat.* **111:** 691-713.

Jolicoeur, P. (1963) The multivariate generalisation of the allometry equation. *Biometrics* **19:** 497-499.

Kehoe, F.P. & Ankney, C.D. (1985) Variation in digestive organ size among 5 species of diving ducks. *Can. J. Zool.* **63:** 2339-2342.

Kehoe, F.P., Ankney, C.D. & Alisauskas, R.T. (1988) Effects of dietary fibre and diet diversity on digestive organs of captive Mallards (*Anas platyrhynchos*). *Can. J. Zool.* **66:** 1597-1602.

Kendall, P.T., Holme, D.W. & Smith, P.M. (1982) Comparative evaluation of net digestive and absorptive efficiency in dogs and cats fed a variety of contrasting diet types. *J. Small Anim. Pract.* **23:** 577-587.

Kenward, R.E. (1982) Goshawk hunting behaviour and range size as a function of food and habitat availability. *J. Anim. Ecol.* **51:** 69-80.

Leopold, A.S. (1953) Intestinal morphology of gallinaceous birds in relation to food habits. *J. Wildl. Mgmt.* **17:** 197-203.

Lundberg, A. (1986) Adaptive advantages of reversed sexual size dimorphism in European owls. *Ornis Scandinavica* **17:** 133-140.

Maynard Smith, J. (1978) Optimization theory in evolution. *Ann. Rev. Ecol. Syst.* **9:** 31-56.

Mendelsohn, J.M., Kemp, A.C., Biggs, H.C., Biggs, R. & Brown, C.J. (1989) Wing areas, wing loadings and wing spans of 66 species of African raptors. *Ostrich* **60:** 35-42.

Newton, I. (1986) *The Sparrowhawk.* Calton: Poyser.

Packard, G.C. & Boardman, T.J. (1988) The misuse of ratios, indices and percentages in ecophysiological research. *Physiol. Zool.* **61:** 1-9.

Page, G. & Whitacre, D.F. (1975) Raptor predation on wintering shorebirds. *Condor* **77:** 73-78.

Pennycuick, C.J. (1989) *Bird flight performance: a practical calculation manual.* Oxford: Oxford University Press.

Piersma, T. & Davidson, N.C. (1991) Confusions of mass and size. *Auk* **108:** 441-444.

Rudebeck, G. (1951) The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. *Oikos* **2:** 65-88; **3:** 200-231.

Savory , C.J. & Gentle, M.J. (1976) Effects of dietary dilution with fibre on the food intake and gut dimensions of Japanese Quail. *Br. Poult. Sci.* **17:** 561-570.

Schipper, W.J.A., Buurma, L.S. & Bossenbroek, P. (1975) Comparative study of hunting behaviour of wintering Hen Harriers *Circus cyaneus* and Marsh Harriers *Circus aeruginosus. Ardea* **63:** 1-29.

Shrubb, M. (1982) The hunting behaviour of some farmland Kestrels. *Bird Study* **29:** 121-128.

Sibley, C.G. & Ahlquist, J.E. (1990) *Phylogeny and Classification of Birds.* New Haven & London: Yale University Press.

Sibly, R.M. (1981) Strategies of Digestion and Defaecation. *In* C.R. Townsend & P. Calow (eds), *Physiological Ecology: An Evolutionary Approach to Resource Use.* Massachussetts: Sinauer Associates.

Temeles, E.J. (1985) Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *Am. Naturalist* **125:** 485-499.

Temeles, E.J. (1989) Effect of prey consumption on foraging activity of Northern Harriers. *Auk* **106:** 353-357.

Village, A. (1983) Seasonal changes in the hunting behaviour of Kestrels. *Ardea* **71:** 117-124.

Wijnandts, H. (1984) Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* **72:** 1-92.

Ziswiler, V. & Farner, D.S. (1972) Digestion and the digestive system. *In* D.S.Farner & J.R. King (eds), *Avian Biology. Vol. 2* London: Academic Press.

Appendix 1. Summary statistics for the computed body-size variable (BODY) and actual small intestine length. The predicted small intestine length was calculated as shown in the text. Residual deviation is the absolute difference between predicted and actual. Residuals standardised for body-size differences are calculated as a percentage of the predicted values.

SPECIES	SEX	n	BODY (mm)	ACTUAL SMLENGTH (mm)	s.e.	n	PREDICTED SMLENGTH (mm)	RESIDUAL DEVIATION (mm)
SPARROWHAWK	M	31	53.3	436	8.0	37	614	-178
	F	55	65.0	581	12.0	52	750	-169
PEREGRINE	M	13	80.9	718	42.0	10	933	-275
	F	7	91.4	954	20.2	6	1054	-100
KESTREL	M	19	44.0	525	13.4	9	507	+ 18
	F	27	45.3	551	17.5	15	522	+ 29
BUZZARD	M	23	76.6	979	37.0	22	883	+ 96
	F	25	79.2	1143	31.2	31	913	+230
RED KITE	M	6	83.4	1401	88.0	7	962	+439
	F	2	84.2	1280	-	2	971	+309
GOSHAWK	M	34	96.4	730	13.5	31	1111	-381
	F	22	105.8	832	19.0	18	1220	-388
MERLIN	F	5	52.8	494	38.0	3	597	-103
HEN HARRIER	F	1	57.1	729	74.2	4	671	+ 58
TAWNY OWL	*	6	48.1	641	28.1	10	555	+ 86
BARN OWL	*	29	47.4	378	9.5	50	546	-168
L.E.OWL	*	9	47.3	444	14.0	8	545	-101
S.E.OWL	*	2	53.8	531	26.9	3	620	- 89

SMLENGTH = small intestine length
* represents data for sexes combined

Appendix 2 - Body measurements for British falconiform species used in the analysis.

SPECIES	SEX (M/F)	MASS (g)	WING (mm)	TAIL (mm)	KEEL (mm)	DIAGONAL (mm)	TARSUS (mm)
SPARROWHAWK							
(*Accipiter nisus*)	M	132±17.4	197±4.5	146±4.8	45.4±2.0	62.5±1.6	54.0±1.5
		(49)	(56)	(55)	(32)	(53)	(12)
	F	233±37.0	233±5.9	173±4.5	55.4±1.5	75.9±1.8	61.8±1.4
		(64)	(73)	(70)	(57)	(72)	(24)
GOSHAWK							
(*Accipiter gentilis*)	M	893±80.2	322±5.0	236±34.0	82.3±2.6	113.5±3.2	78.6±1.7
		(34)	(35)	(34)	(33)	(33)	(34)
	F	1333±101.3	362±7.6	269±5.2	90.3±3.2	127.2±3.0	86.8±2.5
		(18)	(18)	(18)	(19)	(19)	(19)
PEREGRINE							
(*Falco peregrinus*)	M	505±98.5	309±14.0	146±8.0	68.0±3.0	96.0±3.6	48.3±3.0
		(12)	(14)	(14)	(13)	(14)	(9)
	F	917±113.6	354±9.6	171±6.8	76.7±1.9	109.7±2.9	53.3±1.7
		(6)	(8)	(8)	(7)	(8)	(7)
KESTREL							
(*Falco tinnunculus*)	M	165±40.7	240±12.3	156±11.2	33.2±1.9	58.4±1.8	39.0±0.7
		(30)	(32)	(31)	(20)	(30)	(2)
	F	160±31.7	251±10.0	162±10.5	33.9±1.7	60.3±2.2	39.4±1.1
		(35)	(40)	(36)	(28)	(38)	(8)
MERLIN							
(*Falco columbarius*)	M	142±24.1	203±7.1	116±2.6	41.5±2.1	59.7±4.4	36.9
		(4)	(5)	(4)	(3)	(5)	(2)
	F	170±30.5	220±9.6	127±3.6	44.0±1.6	63.5±5.0	39.4±0.6
		(5)	(7)	(7)	(5)	(5)	(3)
HOBBY							
(*Falco subbuteo*)	M	165	257	129	-	64.0	-
		(1)	(1)	(1)		(1)	
	F	304±67.7	289	147	45.0±1.5	66.8±1.0	34.5
		(3)	(1)	(1)	(3)	(3)	(2)
COMMON BUZZARD							
(*Buteo buteo*)	M	643±155.1	382±12.0	208±9.7	60.8±3.2	96.6±3.3	77.7±3.2
		(15)	(30)	(28)	(26)	(27)	(16)
	F	795±177.2	398±10.4	215±7.9	62.3±3.1	100.8±3.3	77.0±2.7
		(24)	(29)	(30)	(25)	(28)	(12)

SPECIES	SEX (M/F)	MASS (g)	WING (mm)	TAIL (mm)	KEEL (mm)	DIAGONAL (mm)	TARSUS (mm)
HONEY BUZZARD (*Pernis apivorus*)	M	470 (1)	365 (1)	220 (1)	62.5 (1)	95.5 (1)	52.0 (1)
ROUGH-LEGGED BUZZARD (*Buteo lagopus*)	M*	535 (1)	425 (1)	205 (1)	63.0 (1)	105.0 (1)	-
RED KITE (*Milvus milvus*)	M	788±131.2 (5)	473±31.7 (6)	336±17.8 (5)	66.4±1.1 (6)	104.4±1.9 (7)	55.5±3.0 (5)
	F	943 (2)	498 (2)	326 (2)	66.5 (2)	106.8	56.5 (2)
HEN HARRIER (*Circus cyaneus*)	M	381±130.1 (3)	332 (2)	204 (2)	47.4 (2)	73.0 (1)	62.0 (2)
	F	371 (2)	339 (2)	219 (2)	46.0 (1)	77.7 (2)	72.4 (2)
MARSH HARRIER (*Circus aeruginosus*)	F	573 (2)	390 (1)	217 (2)	59.5 (2)	97.0 (2)	89.5 (2)
GOLDEN EAGLE (*Aquila chrysaetos*)	M	3525±171 (4)	599±8.5 (4)	320 (1)	114±2.9 (5)	172.2±4.1 (5)	99.0 (1)
	F	-	660 (1)	330 (1)	120±5.3 (3)	191.9±12.3 (3)	-

* denotes birds which died in captivity.

Appendix 3 - Body measurements for British Strigiform species used in the analysis.

SPECIES	SEX (M/F)	MASS (g)	WING (mm)	TAIL (mm)	KEEL (mm)	DIAGONAL (mm)	TARSUS (mm)
TAWNY OWL (_Strix aluco_)	M	417±42.9 (4)	256±3.0 (5)	151±6.5 (5)	32.2 (2)	68.5 (2)	48.4 (2)
	F	481 (1)	267 (2)	159 (2)	33.5 (1)	67.5 (1)	45.5 (2)
BARN OWL (_Tyto alba_)	M	268±47.6 (31)	292±9.9 (32)	114±4.9 (31)	33.1±3.4 (12)	66.9±1.5 (34)	56.5 (1)
	F	272±45.0 (38)	290±10.4 (37)	115±4.4 (38)	33.6±3.6 (16)	67.2±2.7 (35)	-
LONG-EARED OWL (_Asio otus_)	M	205±33 (3)	290±4.5 (5)	140±1.6 (4)	32.9±1.5 (4)	62.1±1.6 (4)	38.3 (2)
	F	261±71 (4)	299±2.9 (4)	141±1.6 (5)	35.5±3.2 (6)	67.8±4.1 (5)	41.9 (2)
SHORT-EARED OWL (_Asio flammeus_)	M	294 (2)	307 (2)	135 (2)	41.5 (1)	69.5 (2)	-
	F	-	305 (1)	141 (1)	40.0 (1)	69.0 (2)	-
LITTLE OWL (_Athena noctua_)	M	167±16.6 (3)	164±7.9 (4)	77±3.8 (3)	33.0 (1)	58.0 (1)	-
	F	153 (1)	160 (2)	79 (1)	-	-	-
SNOWY OWL (_Nyctea scandiaca_)	M*	958±220.9 (3)	423 (2)	212±2.9 (3)	70.0±4.0 (3)	119.0±4.6 (3)	57.0 (1)
	F*	1118±185 (3)	408±23.6 (3)	217±11.3 (3)	70.3±3.5 (3)	123.3±5.0 (3)	52.0 (1)

Appendix 4 - Body measurements for miscellaneous species which had been kept and died in captivity.

SPECIES	SEX (M/F)	MASS (g)	WING (mm)	TAIL (mm)	KEEL (mm)	DIAGONAL (mm)	TARSUS (mm)
ELEONORAS FALCON (*Falco eleonorae*)	F	320 (1)	300 (1)	-	52.5 (1)	78.5 (1)	35.0 (1)
LANNER FALCON (*Falco biarmicus*)	M	545 (1)	345 (1)	193 (1)	57.0 (1)	92.0 (1)	52.0 (1)
	F	740 (1)	345 (1)	184 (1)	64.0 (1)	98.0 (1)	55.0 (1)
SAKER FALCON (*Falco cherrug*)	F	945 (1)	400 (1)	232 (1)	73.0 (1)	112.0 (1)	-
HARRIS HAWK (*Parabuteo unicinctus*)	F	735 (1)	355 (1)	245 (1)	72.0 (1)	108.0 (1)	89.0 (1)
TAWNY EAGLE (*Aquila rapax*)	F	1620 (1)	545 (1)	235 (1)	90.0 (1)	142.0 (1)	85.0 (1)
BONELLIS EAGLE (*Hieraaetus fasciatus*)	F	2065 (1)	470 (1)	260 (1)	99.0 (1)	143.0 (1)	- (1)
CHANGEABLE HAWK EAGLE (*Spizaetus cirrhatus*)	F	1400 (1)	397 (1)	248 (1)	82.0 (1)	120.0 (1)	95.0 (1)
URAL OWL (*Strix uralensis*)	-	-	300 (1)	215 (1)	46.0 (1)	92.0 (1)	52.0 (1)

Appendix 5 - Intestinal measurements for British falconiform species used in the analysis.

SPECIES	SEX (M/F)	SMALL INTESTINE LENGTH (mm)	COLON LENGTH (mm)	TOTAL LENGTH (mm)	SMALL INTESTINE DRY WEIGHT (g)	ANTERIOR WIDTH (mm)	MIDDLE WIDTH (mm)	POSTERIOR WIDTH (mm)
SPARROWHAWK (*Accipiter nisus*)	M	436±49.2 (37)	42±8.3 (18)	469±49.1 (22)	0.194±0.088 (32)	12±1.3 (13)	7.5±0.8 (13)	6±1.1 (13)
	F	581±86.3 (52)	56±13.2 (29)	646±82.7 (32)	0.305±0.159 (51)	14±1.5 (18)	9±1.1 (18)	7±2.0 (18)
GOSHAWK (*Accipiter gentilis*)	M	730±75 (31)	82±11.5 (33)	811±80.8 (31)	0.831±0.263 (31)	21±2.3 (30)	12±1.6 (30)	11±1.8 (30)
	F	832±80 (18)	103±13.6 (17)	942±81.6 (17)	0.984±0.326 (18)	24±5.9 (18)	14±2.7 (18)	12±2.7 (18)
PEREGRINE (*Falco peregrinus*)	M	718±134.7 (10)	50±7.1 (6)	752±144.4 (7)	0.438±0.203 (5)	20±4.4 (8)	11±2.1 (7)	10±3.6 (7)
	F	954±49.6 (6)	49±5.2 (5)	1002±54.9 (5)	0.684±0.111 (3)	20±1.5 (3)	12.5±0.7 (3)	12.5±0.7 (3)
KESTREL (*Falco tinnunculus*)	M	525±40.2 (9)	48±13.5 (5)	587±69.5 (16)	0.183±0.105 (12)	16±5.5 (5)	10±1.6 (5)	9.6±1.8 (5)
	F	551±68.0 (15)	50±6.0 (7)	613±78.2 (20)	0.170±0.130 (18)	16±2.8 (8)	11±1.6 (7)	10.4±1.8 (8)
MERLIN (*Falco columbarius*)	M	435 (1)	40 (1)	563±78.9 (3)	0.069 (1)	-	-	-
	F	524 (2)	42 (2)	570±50.7 (3)	-	14 (2)	9 (2)	11 (2)
HOBBY (*Falco subbuteo*)	M	-	-	495 (1)	-	-	-	-
	F	640 (1)	36 (1)	676 (1)	0.208 (1)	-	-	-

SPECIES	SEX (M/F)	SMALL INTESTINE LENGTH (mm)	COLON LENGTH (mm)	TOTAL LENGTH (mm)	SMALL INTESTINE DRY WEIGHT (g)	ANTERIOR WIDTH (mm)	MIDDLE WIDTH (mm)	POSTERIOR WIDTH (mm)
COMMON BUZZARD (*Buteo buteo*)	M	979±172.5 (22)	88±18.6 (14)	1111±213.7 (13)	1.291±1.131 (23)	20±3.8 (19)	13±2.4 (19)	13±2.4 (19)
	F	1143±173.7 (31)	101±27.7 (23)	1261±192.6 (23)	1.400±0.603 (30)	20±4.1 (22)	13.5±2.8 (22)	13.3±3.3 (22)
HONEY BUZZARD (*Pernis apivorus*)	M	430.0 (1)	50.0 (1)	480.0 (1)	0.281 (1)	16.0 (1)	11.0 (1)	10.0 (1)
ROUGH-LEGGED BUZZARD (*Buteo lagopus*)	M*	850.0 (1)	90.0 (1)	940.0 (1)	0.519 (1)	20.0 (1)	14.0 (1)	11.0 (1)
RED KITE (*Milvus milvus*)	M	1401±235 (7)	56±6.5 (5)	1357±167.4 (5)	1.020±0.339 (7)	17±1.9 (5)	12±2.2 (5)	11±3.4 (5)
	F	1280.0 (2)	67.0 (2)	1347.0 (2)	0.979 (2)	21.0 (2)	16.0 (2)	14.0 (2)
HEN HARRIER (*Circus cyaneus*)	M	756±170 (3)	78±23.7 (3)	834±191 (3)	0.318±0.121 (3)	-	-	-
	F	650.0 (1)	55.0 (1)	813.0 (2)	0.809 (1)	-	-	-
MARSH HARRIER (*Circus aeruginosus*)	F	1247.0 (2)	78.0 (2)	1325.0 (2)	0.548 (2)	15.0 (1)	10.0 (1)	7.0 (1)
GOLDEN EAGLE (*Aquila chrysaetos*)	M	1258±176 (4)	73±5.8 (3)	1257±120 (3)	-	28±1.5 (3)	19±5.0 (3)	14±4.0 (3)
	F	1855.0 (2)	160.0 (1)	2350.0 (1)	-	-	-	-

Appendix 6 - Intestinal measurements for British Strigiform species used in the analysis.

SPECIES	SEX (M/F)	SMALL INTESTINE LENGTH (mm)	COLON LENGTH (mm)	TOTAL LENGTH (mm)	SMALL INTESTINE DRY WEIGHT (g)	ANTERIOR WIDTH (mm)	MIDDLE WIDTH (mm)	POSTERIOR WIDTH (mm)
TAWNY OWL (*Strix aluco*)	M	638±87.6	78±25.2	716±109	0.994±0.463	20.0	16.0	14.0
		(5)	(5)	(5)	(5)	(1)	(1)	(1)
	F	660.0	98.0	758.0	1.300	22.0	12.0	10.0
		(2)	(2)	(2)	(2)	(1)	(1)	(1)
BARN OWL (*Tyto alba*)	M	367±66.7	47±12.5	396±47.6	0.196±0.085	20±2.2	16±2.7	12±2.2
		(24)	(8)	(8)	(17)	(12)	(12)	(9)
	F	389±66.9	47±11.9	438±76.9	0.264±0.232	20±2.6	17±2.7	9±2.9
		(26)	(11)	(12)	(21)	(13)	(13)	(10)
LONG-EARED OWL (*Asio otus*)	M	427±22.5	50.0	465.0	0.265±0.105	16±2.6	10±2.0	9±3.8
		(3)	(2)	(2)	(3)	(3)	(3)	(3)
	F	454±46.3	75±17.3	540±47.7	0.441±0.139	16.0	10.0	9.0
		(5)	(3)	(3)	(5)	(2)	(2)	(2)
SHORT-EARED OWL (*Asio flammeus*)	M	519.0	74.0	592.0	0.788	-	-	-
		(2)	(2)	(2)	(2)			
	F	555.0	-	-	0.698	-	-	-
		(1)			(1)			
LITTLE OWL (*Athena noctua*)	M	394.0	-	-	0.306	20.0	13.0	13.0
		(2)			(1)	(1)	(1)	(1)
	F	385.0	-	-	-	-	-	-
		(1)						
SNOWY OWL (*Nyctea scandiaca*)	M*	705±100	60.0	650.0	1.005±0.269	19±0.6	14±1.5	13±2.6
		(3)	(1)	(1)	(3)	(3)	(3)	(3)
	F*	755.0	80.0	840.0	1.441	22.0	13.0	12.0
		(2)	(1)	(1)	(2)	(2)	(2)	(2)

Appendix 7 - Intestinal measurements for miscellaneous species which had been kept and died in captivity.

SPECIES	SEX (M/F)	SMALL INTESTINE LENGTH (mm)	COLON LENGTH (mm)	TOTAL LENGTH (mm)	SMALL INTESTINE DRY WEIGHT (g)	ANTERIOR WIDTH (mm)	MIDDLE WIDTH (mm)	POSTERIOR WIDTH (mm)
ELEONORAS FALCON								
(*Falco eleonorae*)	F	480	-	-	-	-	-	-
		(1)						
LANNER FALCON								
(*Falco biarmicus*)	M	685	-	-	0.402	-	-	
		(1)			(1)			
	F	855	55	910	0.720	19	14	14
		(1)	(1)	(1)	(1)	(1)	(1)	(1)
SAKER FALCON								
(*Falco cherrug*)	F	900	-	-	-	-	-	-
		(1)						
HARRIS HAWK								
(*Parabuteo unicinctus*)	F	915	-	-	0.982	-	-	-
		(1)			(1)			
TAWNY EAGLE								
(*Aquila rapax*)	F	1075	60	2135	1.723	25	11	10
		(1)	(1)	(1)	(1)	(1)	(1)	(1)
BONELLIS EAGLE								
(*Hieraaetus fasciatus*)	F	1060	-	-	1.958	-	-	-
		(1)			(1)			
CHANGEABLE HAWK EAGLE								
(*Spizaetus cirrhatus*)	F	720	-	-	0.907	21	11	10
		(1)			(1)	(1)	(1)	(1)
URAL OWL								
(*Strix uralensis*)	-	580	72	652	0.489	-	-	-
		(1)	(1)	(1)	(1)			

CHAPTER 4

The effects of body condition and parasite burden on digestive organ size with a comparison of internal body organs.

ABSTRACT

The size of the small intestine, stomach, kidney, liver and heart were compared between species and considered in relation to hunting strategy and body size for several raptor species. The extent to which these organs are affected by differences in body condition and parasite burden was examined. The Sparrowhawk, Goshawk and Peregrine had the smallest stomach and intestine for their size. The Common Buzzard, Red Kite and Kestrel had heavy digestive organs. The Tawny Owl had a significantly larger digestive tract than the Barn Owl and the Long-eared Owl. The scaling of intestine length, area and volume with body-mass was discussed. Body condition was positively correlated with organ weights but to a lesser degree with intestine length. A significant correlation was found between body condition, fat content and parasite burden.

INTRODUCTION

In Chapter 3, differences in small intestine length were found between raptor species. Such differences might largely be the result of long-term evolutionary adaptation and it was hypothesised that maintaining optimum flight performance is one of the main selection pressures determining gut morphology. The intestine is, however, also affected in the short-term by dynamic adaptations. Diet, temperature and season (Barnes & Thomas 1987, Kehoe *et al.* 1988, Karasov 1990, Sibly *et al.* 1990, Brugger 1991) are all known to have an effect on intestinal morphology. These intraspecific adjustments presumably enable animals to maintain their metabolic requirements through adjusted food intake, throughput and assimilation. Body condition, parasite burden and the effects of illness and malnutrition (Thaysen & Thaysen 1949, Ankney 1977) also affect gut morphology and must have some effect on its functioning as a digestive organ.

This chapter examines the relationship between intestine length, intestine weight and differences in body condition and parasite burden and predicts the effect these changes are likely to have on digestion. The small intestine is responsible for food absorption and therefore the organ most likely to affect digestive efficiency. However, I have also analysed the gizzard, proventriculus, liver, kidney and heart to consider both their overall size in relation to hunting strategy and body-size and the extent to which they are influenced by body condition and parasite load.

METHODS

Interspecific comparison of digestive organ size and heart size independent of body-size

Data were collected from carcasses for proventriculus area and dry weight of the proventriculus, gizzard, small intestine and heart. The proventriculus and gizzard serve different functions and so were considered separately. The primary function of the proventriculus is the production and release of gastric secretions, whereas the function of the gizzard is mechanical digestion and preliminary proteolysis (Duke 1986). Stomachs were dissected into proventriculus and gizzard. The proventriculus was placed flat and the length and width measured to the nearest millimetre to give an estimate of internal surface area. Organs were oven dried at 70^{O}C to constant weight.

The combined weight of proventriculus and gizzard was calculated and is referred to as 'stomach'. The combined mass of proventriculus, gizzard and small intestine was also calculated and is referred to as 'gut'. This enabled an interspecific comparison of specific organs, as well as a combination of organs to examine interspecific differences in the total weight of the digestive system. All organ sizes were compared by ANCOVA. Falconiformes were analysed separately by sex. Sufficient data were available for a comparison of organ size in male Sparrowhawk (*Accipiter nisus*), Peregrine (*Falco peregrinus*), Kestrel (*Falco tinnunculus*), Common Buzzard (*Buteo buteo*), Red Kite (*Milvus milvus*) and Goshawk (*Accipiter gentilis*). For females, sufficient data were available for only Sparrowhawk, Kestrel, Common Buzzard and Goshawk. The comparison for Strigiformes was restricted to the Tawny Owl (*Strix aluco*), Barn Owl (*Tyto alba*) and Long-eared Owl (*Asio otus*).

The data were collected from dissections in Chapter 3. Sample sizes were small for some species and not truly random and so the extent to which the data could be analysed was limited. Size-independent differences in organ size were examined using ANCOVA with log-transformed data on both axes. The skeletal body size variable derived in the previous chapter and referred to as BODY was used as the covariate in ANCOVA to correct for body size differences. The Bonferonni method was used for pairwise comparison of adjusted treatment means (Day & Quinn 1989).

The relative proportion of each of the body organs in relation to body-mass.

The previous section examined organ size differences for each species independent of body-size. This section considered the contribution each organ makes to body-mass. For a smaller sample of carcasses, wet weights were available for liver, kidney, proventriculus, gizzard, small intestine and heart. Each organ was calculated as a percentage of total body-mass to examine the proportion contributed by each organ.

For 25 raptor species, small intestine length, area and volume were calculated and the scaling of each measure with body-mass (kg) was compared. Intestines were opened along the entire length and flattened. The width was measured at both ends and the mid-point. Area was calculated as (intestine length x mean width). Volume was calculated using the mean width (circumference) and length to compute the volume of a cylinder. Data were log-transformed on both axes.

The relationship between organ size, body condition and the effects of starvation and parasite burden.

During the course of routine dissections, helminths (worms) found in the digestive tract were removed and counted. No distinction was made between size of parasites. Cause of death was assessed during the dissection and based on criteria routinely used by the Institute of Terrestrial Ecology (Newton *et al.* 1982). Birds were categorised as having died either from starvation or collision and represented individuals in poor and good condition respectively to examine the degree to which body condition deteriorates during starvation.

To calculate a condition index, the pectoralis muscle was dissected from each carcass. Any external fat was removed, the muscle weighed to 1mg and placed on a pre-weighed petri dish. In some cases the whole pectoralis muscle was dried, in others a 10g sub-sample was cut from the middle of the muscle block. Sub-samples were shown to be representative of the whole muscle. Samples were dried to constant weight in a fan-assisted oven at 70°C. Using the total muscle wet weight and the sub-sample wet weight, an estimate of total muscle dry weight was calculated. Samples were packaged in filter paper and run through the Soxhlet apparatus for 8 hours using AR chloroform as the solvent. Following fat extraction, the samples were re-dried to constant weight in the oven and the lean dry weight and percentage fat content in the muscle calculated.

A condition index accounting for body-size differences was calculated by regressing the dry weight of the pectoral muscle (excised pectoral x 2) against BODY (the skeletal body-size measure derived in Chapter 3) and saving the residuals. The variables being examined were standardised in the same way, again saving the residuals. Correlations between the two sets of residuals were then examined. Dry weight was used in preference to lean dry weight as it explained a greater proportion of the variance in each of the organs measured. Correlations were examined between organ-size, body condition, fat content and parasite burden.

RESULTS

Interspecific comparison of digestive organ-size and heart size independent of body-size.

Summary statistics for the organs measured are given in appendices 1 & 2. The results of ANCOVA are shown in Tables 1,2 & 3 for male Falconiformes, female Falconiformes and Strigiformes (sexes combined) respectively. Male and female Sparrowhawks and Goshawks had the lightest gizzard and stomach (proventriculus + gizzard) for their size. The Red Kite and the Common Buzzard had a heavy gizzard and heavy stomach. When the total mass of the gut was considered, the Goshawk, Sparrowhawk and Peregrine had the lightest for their body-size, the Kestrel and the Common Buzzard the heaviest. The Sparrowhawk had the lightest small intestine, the Common Buzzard and the Red Kite the heaviest. Although the Goshawk has a light stomach, it has a large proventriculus area in both sexes. Kestrels had the largest heart relative to body-mass. In the Strigiformes, the Tawny Owl had a heavier proventriculus, small intestine and total digestive tract. No significant differences were found between the Barn Owl and the Long-eared Owl. All differences are 2-tailed and significant at the 5% level.

The relative proportion that each of the organs small intestine, liver, kidney and heart contribute to body-mass.

Organ sizes relative to body-mass are summarised in Table 4. Of those organs measured, the liver constitutes the largest percentage of body-mass (1.65% in the Goshawk to 3.24% in the Merlin and the Kestrel), followed by the stomach, heart, kidneys and intestine (0.46% in the Goshawk to 1.64% in the Short-eared Owl) respectively. The only organ to show any significant change in proportion with increasing size was the liver ($F_{1,8}$=8.25, R^2=0.50, P=0.02). The tendency was for smaller livers in larger species. The stomach ($F_{1,8}$ =1.08, P=0.33), heart

($F_{1,9}=0.42$, $P=0.53$), kidney ($F_{1,6}=0.48$, $P=0.51$) and intestine ($F_{1,9}=0.12$, $P=0.74$) comprised the same proportion of body-mass across all species analysed.

For Falconiformes and Strigiformes combined and using the data shown in Appendix 3 intestine length scaled with $(\text{body-mass})^{0.38}$, intestine area scaled with $(\text{body-mass})^{0.50}$ and intestine volume with $(\text{body-mass})^{0.63}$. All the regressions were significant ($r_{24}=0.83$, $P<0.0001$; $r_{19}=0.88$, $P<0.0001$; $r_{19}=0.88$, $P<0.0001$) for length, area and volume respectively. For Falconiformes only, length, area and volume scaled to body-mass with exponents 0.32, 0.45 and 0.62 respectively, each of the regressions being significant ($r_{16}=0.84$, $P<0.001$; $r_{13}=0.87$, $P<0.001$; $r_{13}=0.88$, $P<0.001$). For Strigiformes length, area and volume scaled to the exponents 0.37, 0.47 and 0.52 ($r_6=0.89$, $P<0.02$; $r_5=0.93$, $P<0.05$; $r_5=0.86$, $P=0.06$) respectively.

The effects of condition on organ size

Correlations for small intestine length and weight, gizzard weight and heart weight against the condition index are shown in Tables 5-8 respectively. For small intestine length, only male Sparrowhawks, male Buzzards and Tawny Owls showed significant positive correlations with condition. Individuals in good condition had longer intestines than those in poor condition. In all the other species, small intestine length was not correlated with condition. Small intestine weight was significantly and positively correlated with condition in almost all species (Table 6). Gizzard weight was also found to be significantly correlated with body condition for Sparrowhawks, male Peregrine and male Common Buzzard. Heart weight was highly correlated with condition in every species except the Tawny Owl. Individuals show a considerable reduction in pectoral muscle weight during starvation. Using lean dry pectoral muscle, individuals which died of starvation had lost 54% of their pectoral muscle weight compared with individuals which had been killed by collision.

The relationship between parasite burden, body condition and fat content.

Out of 380 individuals of 6 raptor species, 20% had one or more intestinal helminths. No significant differences were found between species. The number of parasites was very variable with up to 70 nematodes being found in the small intestine of some individuals. Length and dry weight of the small intestine were not correlated with parasite number in any species after controlling for condition differences. Only Goshawks showed a significant negative correlation between the amount of pectoral fat and parasite number ($r_{13} = -0.50$, $P<0.05$). Goshawks with more parasites had less intramuscular fat. I also examined whether individuals with no parasites had more pectoral fat than individuals with one or more parasites: in Sparrowhawks no correlation was found ($n=50$, $U=240$, $P=0.27$, Mann-Whitney U-test) but in Common Buzzards the individuals with less pectoral fat were those with more parasites ($n=39$, $U=76.0$, $P<0.005$; Mann-Whitney U-test). Pectoral muscle lean dry weight was also significantly and negatively correlated with parasite burden in Common Buzzards ($n=39$, $U=71.0$, $P=0.003$; Mann-Whitney U-test) and tended towards significance for Sparrowhawks ($n=50$, $U=200.5$, $P=0.06$; Mann-Whitney U-test). Dry pectoral muscle weight was not significantly correlated with parasite burden for any species.

Table 1. A comparison of digestive organ size and heart size for males of 6 Falconiform species. Species are in order of increasing organ size after the inequality.

	LINES[a]	SLOPES[b]	SIGNIFICANT DIFFERENCES (P<0.05; 2-tailed)
PROVENTRICULUS WEIGHT	$F_{5,64}=25.25$; $P<0.001$	$F_{5,59}=0.87$; $P=0.509$	1 < 2,3,4,5,6; 2 < 3,4,5,6.
GIZZARD WEIGHT	$F_{5,65}=131.9$; $P<0.001$	$F_{5,60}=1.14$; $P=0.350$	1 < 2,5,4; 6 < 2,5,4.
INTESTINE WEIGHT	$F_{5,79}=13.13$; $P<0.001$	$F_{5,74}=0.39$; $P=0.855$	4 > 1,2,3; 5 > 1.
PROVENTRICULUS + GIZZARD WEIGHT	$F_{5,61}=83.2$; $P<0.001$	$F_{5,56}=0.89$; $P=0.492$	1 < 2,5,4,3; 6 < 5,4,3; 2 < 4,3.
GUT WEIGHT	$F_{5,53}=34.92$; $P<0.001$	$F_{5,48}=0.80$; $P=0.553$	1 < 5,4,3; 6 < 5,4,3; 2 < 4,3.
PROVENTRICULUS AREA	$F_{5,47}=7.15$; $P<0.001$	$F_{4,43}=0.99$; $P=0.425$	2 < 3,4,5,6; 1 < 4,5,6.
HEART WEIGHT	$F_{5,59}=3.39$; $P<0.01$	$F_{5,54}=0.86$; $P=0.512$	3 > 1,6.

GUT WEIGHT = PROVENTRICULUS + GIZZARD + SMALL INTESTINE DRY WEIGHT (g).
1 = Sparrowhawk
2 = Peregrine
3 = Kestrel
4 = Common Buzzard
5 = Red Kite
6 = Goshawk

Lines[a]: F-statistic to test differences in elevation of lines.
Slopes[b]: F-statistic to test homogeneity of regression slopes.

Table 2. A *comparison of digestive organ size and heart size for* females of 4 falconiform species. Species are in order of increasing organ size after the inequality.

	LINES[a]	SLOPES[b]	SIGNIFICANT DIFFERENCES (P<0.05; 2-tailed)
PROVENTRICULUS WEIGHT	$F_{3,70}=33.81$; $P<0.001$	$F_{3,67}=1.09$; $P=0.359$	1 < 4,6; 6 > 1,3.
GIZZARD WEIGHT	$F_{3,78}=162.9$; $P<0.001$	$F_{3,75}=1.06$; $P=0.372$	1 < 6,3,4; 6 < 3,4.
INTESTINE WEIGHT	$F_{3,90}=24.18$; $P<0.001$	$F_{3,87}=0.92$; $P=0.436$	1 < 4; 3 < 4.
PROVENTRICULUS + GIZZARD WEIGHT	$F_{3,69}=106.7$; $P<0.001$	$F_{3,66}=0.93$; $P=0.444$	1 < 6,3,4; 6 < 4.
GUT WEIGHT	$F_{3,60}=46.45$; $P<0.001$	$F_{3,57}=1.30$; $P=0.283$	1 < 6,4,3; 6 < 4.
PROVENTRICULUS AREA	$F_{3,44}=26.45$; $P<0.001$	$F_{3,41}=4.47$; $P<0.01$	6 > 1,3,4; 4 > 1,3.
HEART WEIGHT	$F_{3,55}=20.73$; $P<0.001$	$F_{3,52}=1.02$; $P=0.391$	6 < 1,4,3; 1 < 4,3; 4 < 3.

GUT WEIGHT = PROVENTRICULUS + GIZZARD + SMALL INTESTINE DRY WEIGHT (g).

1 = Sparrowhawk
3 = Kestrel
4 = Common Buzzard
6 = Goshawk

Lines[a]: F-statistic to test differences in elevation of lines.
Slopes[b]: F-statistic to test homogeneity of regression slopes.

Table 3. A comparison of digestive organ size and heart size for Strigiformes (sexes combined). Species are in order of increasing organ size after the inequality.

	LINES[a]	SLOPES[b]	SIGNIFICANT DIFFERENCES ($P<0.05$; 2-tailed)
PROVENTRICULUS WEIGHT	$F_{2,19}=19.8$; $P<0.001$	$F_{2,17}=0.59$; $P=0.566$	9 > 10,11.
GIZZARD WEIGHT	$F_{2,19}=2.25$; $P=0.132$	$F_{2,17}=0.05$; $P=0.948$	no significant differences.
INTESTINE WEIGHT	$F_{2,24}=11.37$; $P<0.001$	$F_{2,22}=1.00$; $P=0.384$	9 > 10.
PROVENTRICULUS + GIZZARD WEIGHT	$F_{2,19}=4.13$; $P<0.05$	$F_{2,17}=0.12$; $P=0.892$	9 > 11.
GUT WEIGHT	$F_{2,16}=7.69$; $P<0.005$	$F_{2,14}=0.72$; $P=0.504$	9 > 10,11.
PROVENTRICULUS AREA	$F_{2,5}=1.84$; $P=0.252$	$F_{2,3}=0.29$; $P=0.770$	no significant differences.
HEART WEIGHT	$F_{2,14}=0.14$; $P=0.870$	$F_{2,12}=0.42$; $P=0.669$	no significant differences.

GUT WEIGHT = PROVENTRICULUS + GIZZARD + SMALL INTESTINE DRY WEIGHT (g).

9 = Tawny Owl
10 = Barn Owl
11 = Long-eared Owl

Lines[a]: F-statistic to test differences in elevation of lines.
Slopes[b]: F-statistic to test homogeneity of regression slopes.

Table 4. Internal organ size as a percentage of total body weight. Sexes combined, sample size in parentheses.

SPECIES	LIVER	HEART	KIDNEY	STOMACH	SMALL INTESTINE	BODY MASS (g)
KESTREL	3.24 (14)	1.13 (12)	1.14 (10)	2.62 (12)	0.75 (18)	180
	0.46	0.14	0.22	0.34	0.42	
MERLIN	3.24 (3)	2.20 (3)	1.10 (1)	1.56 (3)	0.56 (1)	190
	0.84	0.31	-	0.32	-	
SPARROWHAWK	2.63 (86)	1.12 (75)	0.81 (59)	0.95 (38)	0.63 (22)	220
	0.53	0.14	0.12	0.13	0.28	
PEREGRINE	2.76 (3)	1.81 (3)	0.86 (3)	1.24 (1)	0.53 (3)	760
	0.43	0.05	0.20	-	0.05	
BUZZARD	2.15 (5)	0.86 (31)	0.92 (3)	1.48 (4)	0.99 (7)	850
	0.47	0.15	0.05	0.41	2.62	
RED KITE	-	1.13 (7)	-	-	-	1040
		0.26				
GOSHAWK	1.65 (50)	0.86 (44)	-	-	0.46	1110
	0.36	0.09				
HEN HARRIER	-	-	-	1.10 (1)	0.66 (1)	440
LONG-EARED OWL	2.10 (2)	0.98 (6)	0.84 (2)	1.93 (1)	0.75 (2)	270
		0.28				
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 (3)	0.71 (3)	-	1.91 (2)	1.26 (3)	460
	0.19	0.10			0.38	

Table 5. Correlation between small intestine length and condition index.

SPECIES	SEX	n	r	P
SPARROWHAWK	M	25	0.51	0.009
	F	39	0.06	0.72
PEREGRINE	M	6	0.14	0.79
	F	0	-	-
KESTREL	M	8	0.60	0.12
	F	13	0.15	0.63
BUZZARD	M	17	0.60	0.01
	F	22	0.09	0.70
RED KITE	M	6	0.63	0.18
	F	-	-	-
GOSHAWK	M	25	-0.09	0.65
	F	20	0.35	0.13
BARN OWL	*	24	0.28	0.17
TAWNY OWL	*	4	0.99	0.004

Table 6. Correlations between small intestine dry weight and condition index.

SPECIES	SEX	n	r	P
SPARROWHAWK	M	18	0.45	0.06
	F	36	0.30	0.07
PEREGRINE	M	5	0.95	0.01
	F	0	-	-
KESTREL	M	9	0.89	0.001
	F	15	0.79	0.0005
BUZZARD	M	18	0.69	0.0017
	F	22	0.34	0.12
RED KITE	M	6	0.99	0.0001
	F	-	-	-
GOSHAWK	M	25	0.04	0.83
	F	19	0.69	0.001
BARN OWL	*	17	-0.37	0.14
TAWNY OWL	*	4	-0.95	0.05

Table 7. Correlations between gizzard dry weight and condition index.

SPECIES	SEX	n	r	P
SPARROWHAWK	M	16	0.71	0.0018
	F	32	0.53	0.0018
PEREGRINE	M	4	0.96	0.03
	F	0	-	-
KESTREL	M	10	0.55	0.09
	F	0	-	-
BUZZARD	M	10	0.93	0.0001
	F	0	-	-
RED KITE	M	4	0.69	0.31
	F	0	-	-
GOSHAWK	M	23	-0.33	0.12
	F	18	0.44	0.07
BARN OWL		16	0.34	0.19

Table 8. Correlations between heart dry weight and condition index.

SPECIES	SEX	n	r	P
SPARROWHAWK	M	6	0.89	0.02
	F	13	0.63	0.02
PEREGRINE	M	5	0.96	0.01
	F	0	-	-
KESTREL	M	1	-	-
	F	7	0.80	0.03
BUZZARD	M	16	0.87	0.0001
	F	17	0.77	0.0003
RED KITE	M	6	0.95	0.004
	F	-	-	-
GOSHAWK	M	25	0.58	0.002
	F	19	0.79	0.0001
BARN OWL	*	8	0.78	0.02
TAWNY OWL	*	4	0.72	0.28

DISCUSSION

Body condition measured by pectoral muscle weight has a significant effect on digestive organ size and heart size. Organ weight is low in poor condition birds and high in birds in good condition. Muscle protein appears to be mobilised because of inanition, however, the extent to which internal organs are affected and the consequences are largely unpublished. Ankney (1977) showed that Lesser Snow Geese (*Chen caerulescens*) arriving on their breeding grounds had large digestive organs. During egg-laying and incubation the dry weight of digestive organs decreased, increasing again after hatch. Gizzard weight decreased either from atrophy through disuse or from active catabolism of muscle protein. Ankney suggests that the decrease in digestive organ size may not be through disuse but anticipatory to a behavioural change. The results of this chapter provide evidence that changes in organ size are directly influenced by body condition. However, this does not necessarily preclude the possibility of innate changes as suggested by Ankney.

Although body condition did affect intestine length in some species, intestine weight was affected to a far greater extent and so length changes in some studies could be an innate response, rather than a change arising from changes in body condition. It is more likely that intestine length changes will influence digestive efficiency more than intestine weight changes (assuming area changes proportionately with length). Mayhew (1985) also showed a significant, positive correlation between condition index and intestine length in female Wigeon (*Anas penelope*) but not in males. It is possible that birds with long guts (either genotypically or phenotypically derived) attain better condition than birds with short guts since they are able to process more food per unit time or are able to extract more nutrients from a limited amount of food. Few significant correlations were found between condition and small intestine length which strengthens the interpretation of interspecific differences in intestinal morphology found in Chapter 3 and supports the use of length rather than weight as a measure of gross gut morphology in analyses bound to using carcass data (Chapter 2). However, this does not exclude the use of dry weight for indicating trends, especially since significant correlations are less likely to have occurred by chance than non-significant correlations.

Condition, fat content and parasite burden were all found to be correlated. However, it is difficult using carcass data to establish cause and effect. Birds in poor condition might have been more susceptible to parasitism. Alternatively, parasites could have been the cause of poor condition found in some birds. Very few parasites were found in birds in good condition with high fat contents, whereas virtually all birds which were parasitised had low condition and minimal fat reserves. A bird in deteriorating body-condition with parasites requires more food and because of the additional parasitic burden would be expected to use up its fat resources.

Intestine, gizzard and heart weight are all positively correlated with condition, catabolism occuring in starving birds. Jackson (1915) showed a decrease in intestinal weight of 57% during starvation in rats, this compared to only a 35% reduction in body-mass. The animals were still active whilst starving and so had to provide energy from somewhere to maintain their BMR. It was concluded that atrophy of the intestine was caused by the deficiency of calories and primarily by the lack of protein. Birds facing starvation draw on all possible protein reserves which presumably makes these organs less efficient. The heart becomes less effective as a pump, the digestive tract less efficient at food turnover which is why animals on a starvation diet are less efficient at digestion when returned to a normal diet (Thaysen & Thaysen 1949).

It has been suggested that metabolic rate and gut-size might be related. Metabolic rates are known to vary between tissues, high rates being found in kidney, brain and heart, low rates in skeleton, skin and muscle (Daan *et al.* 1990). There is a positive relationship between the size of digestive organs and the energetic demands they impose on the bird's metabolism (Moss 1972, Ankney 1977). It would be more costly for Buzzards and Kites to maintain their long digestive tracts than Peregrines, Sparrowhawks and Goshawks with short digestive tracts, however the benefits gained from having a long gut and hence an increased surface area for absorption, together with a less costly flight mode may result in an overall energy gain.

For the sample of species available, liver was the only organ found to be smaller in larger species, presumably because the metabolic demands are less in larger species. For kidney and heart there was no significant difference in organ size between large species and small species. Nevertheless, the Merlin and Peregrine do appear to have relatively large hearts for their body size weighing approximately 2% of body-mass. The Common Buzzard, Red Kite and Goshawk all have hearts weighing about 1% of body-mass. Kidney size remained constant at about 0.9% of body-mass for all species included in the analysis.

Daan *et al.* (1990) found that mass-independent variations in the lean dry weight of the kidney and heart, and energy requirements during parental care are associated with size-independent interspecific variations in basal metabolic rate. However, species-specific variations in BMR after correcting for body-mass, were not found to be associated with mass-independent variations in the size (dry weight) of the gut in avian species. They postulated that in order to support a high energy expenditure during parental care (DEE_{par}), parent birds must develop a large metabolic apparatus to sustain energy requirements during the period of offspring care. Species with relatively low DEE_{par} should sustain requirements with smaller heart and kidneys and vice versa. High values of DEE would be expected in males during the nestling period, consistent with the fact that the male has the largest share in food provisioning (King 1974, Masman *et al.* 1988a, 1988b).

Jackson (1990) found that for seabird species (flying species and penguins), total intestine volume scaled with (body mass)$^{1.09}$, and when only flying species were included in the analysis, gut volume scaled with (body-mass)$^{0.81}$, suggesting that an increasing proportion of body-mass was allocated to skeletal and muscular flight components with increases in body-size. Karasov (1990) assumed scaling exponents with body-mass for avian intestine length, area and volume of $(\text{mass})^{0.33}$, $(\text{mass})^{0.66}$ and $(\text{mass})^{1.0}$ respectively. The exponents found in this study when intestine length was scaled with body-mass are as predicted by Karasov (1990) and Jackson (1990). However, the exponents for intestine area and intestine volume are less than expected. As, shown, intestine length, area and volume are determined by variables other than body-size to the extent that species such as the Goshawk have an intestinal capacity far less than predicted on the basis of body-size alone. Consequently the scaling exponent with body-size is less than predicted. Although the exponents for area and volume are less than the predicted 0.66 and 1.0 respectively, this is likely a result of significant interspecific differences in intestine size for species of approximately equal body-size. When interpreting scaling relationships of intestine size with body size, interspecific differences should therefore be taken into consideration. Gut size cannot be assumed equal for species of equal body-size and scaling relationships will depend greatly on the species used in the analysis.

It is difficult to separate the effects of diet, flight requirements, metabolism and allometry in explaining organ size. In Chapter 3, the Goshawk, Sparrowhawk and Peregrine were all shown to have a short small intestine for their body-size. They have been shown in this chapter to also have relatively small stomachs and a light total digestive tract (gut). The Common Buzzard, Red Kite and Kestrel all have large, heavy digestive tracts for their body-size. Intestine weight is relatively constant across all species despite the fact that very large differences were found in intestine length (Chapter 3). The Strigiformes had very large stomachs for their body-size. This is presumably because they swallow their prey whole and do not have a crop for food storage. The Goshawk and Sparrowhawk also had a small stomach weight which might improve flight agility and acceleration when chasing prey.

It was hypothesised in Chapter 3 that some species have reduced intestine length to reduce the weight of internal organs to increase the powers of acceleration and agility in species with high flight requirements. These results show that the intestine makes up a very small proportion of body-mass and so although the above hypothesis could be adaptive, it seems more likely that the capacity of the digestive tract would have a greater adaptive influence on flight energetics. Species with short guts have faster throughput and carry less weight of digesta so returning to an optimal flying weight more quickly.

REFERENCES

Ankney, C.D. (1977) Feeding and digestive organ size in breeding Lesser Snow Geese. *Auk* **94:** 275-282.

Barnes, G.G. & Thomas, V.G. (1987) Digestive organ morphology, diet and guild structure of North American Anatidae. *Can. J. Zool.* **65:** 1812-1817.

Brugger, K.E. (1991) Anatomical adaptation of the gut to diet in Red-winged Blackbirds (*Agelaius phoeniceus*). *Auk* **108:** 562-567.

Daan, S., Masman, D. & Groenewold, A. (1990) Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *Am. J. Physiol.* **259:** R333-R340.

Day, R.W. & Quinn, G.P (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59:** 433-463.

Duke, G.E. (1986) Alimentary canal: secretion and digestion, special digestive functions and absorption. *In* P.D. Sturkie (ed), *Avian Physiology 4th ed.* Springer-Verlag: New York.

Jackson, C.M. (1915) Changes in the relative weights of the various parts, systems and organs of young albino rats held at constant body weight by underfeeding for various periods. *J. Exp. Zool.* **19:** 99-156.

Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Studies in Avian Biology* **13:** 391-415.

Kehoe, F.P. & Ankney, C.D. (1985) Variation in digestive organ size among five species of diving ducks (*Aythya* spp.) *Can. J. Zool.* **63:** 2339-2342.

Kehoe, F.P., Ankney, C.D. & Alisauskas, R.T. (1988) Effects of dietary fibre and diet diversity on digestive organs of captive Mallards (*Anas platyrhynchos*). *Can. J. Zool.* **66:** 1597-1602.

King, J.R. (1974) Seasonal allocation of time and energy resources in birds. *In* R.A. Paynter (ed), *Avian Energetics.* Cambridge, MA: Nuttal Ornithol. Club.

Masman, D., Daan, S. & Beldhuis, H.J.A. (1988a) Ecological energetics of the Kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. *Ardea* **76:** 64-81.

Masman, D., Daan, S. & Dijkstra, C. (1988b) Time allocation in the kestrel, *Falco tinnunculus*, and the principal of energy minimization. *J. Anim. Ecol.* **57:** 411-432.

Mayhew, P.W. (1985) The feeding ecology and behaviour of wigeon (*Anas penelope*) Ph.D. thesis, University of Glasgow.

Moss, R. (1972) Effects of captivity on gut lengths in Red Grouse. *J. Wildl. Mgt.* **36:** 99-104.

Newton, I., Bell, A.A. & Wyllie, I. (1982) Mortality of Sparrowhawks and Kestrels. *British Birds* **75:** 195-204.

Sibly, R.M., Monk, K.A. Johnson, I.K. & Trout, R.C. (1990) Seasonal variation in gut morphology in wild rabbits (*Oryctolagus cuniculus*). *J. Zool., Lond.* **221:** 605-619.

Thaysen, N.H. & Thaysen, J.H. (1949) Morphological changes in the gastro-intestinal tract of the white rat following inanition. *Acta path. microbiol. scand.* **26:** 370-379.

Appendix 1. Summary statistics for organ size in male Falconiformes and Strigiformes.

MALES		SPARROWHAWK	PEREGRINE	KESTREL	BUZZARD	KITE	GOSHAWK	TAWNY OWL	BARN OWL	L.E.OWL
BODY (mm)		53.3	80.9	44.0	76.6	83.4	96.4	48.1	47.4	47.3
	MEAN	478	954	429	1362	1645	2251	716	764	620
PROVENTRICULUS	s.d.	92	142	-	436	178	264	37	248	103
AREA (mm^2)	n	14	3	1	11	3	27	2	4	5
	MEAN	0.175	0.430	0.388	0.615	0.890	0.965	0.393	0.171	0.142
PROVENTRICULUS	s.d.	0.041	0.168	0.688	0.148	0.329	0.117	0.081	0.045	0.052
DRY WEIGHT (g)	n	37	5	20	11	6	27	6	27	5
	MEAN	0.178	1.110	0.876	1.235	1.366	0.709	0.749	1.030	0.946
GIZZARD	s.d.	0.041	0.387	0.189	0.377	0.561	0.109	0.350	0.276	0.377
DRY WEIGHT (g)	n	35	5	21	11	5	29	7	28	5
	MEAN	0.194	0.438	0.183	1.291	1.020	0.831	0.938	0.234	0.375
INTESTINE	s.d.	0.088	0.203	0.105	1.131	0.339	0.263	0.556	0.183	0.150
DRY WEIGHT (g)	n	32	5	12	23	7	31	9	38	8
	MEAN	0.351	1.540	1.264	1.843	2.246	1.663	2.317	1.201	1.088
PROV. + GIZZARD	s.d.	0.076	0.545	0.741	0.513	0.927	0.219	0.232	0.307	0.429
DRY WEIGHT (g)	n	35	5	20	10	5	27	4	27	5
	MEAN	0.588	2.014	1.235	2.802	3.261	2.508	3.352	1.444	1.482
TOTAL DRY WEIGHT (g)	s.d.	0.135	0.811	0.275	0.893	1.267	0.413	0.813	0.363	0.488
(PROV.+ GIZ.+ INT.)	n	25	4	10	10	5	26	5	24	5
	MEAN	0.360	1.940	0.325	1.439	2.516	2.165	0.660	0.567	0.575
HEART	s.d.	0.124	1.134	0.007	0.566	1.108	0.282	0.184	0.148	0.167
DRY WEIGHT (g)	n	11	5	2	20	7	29	8	11	6

Appendix 2. Summary statistics for organ size in female Falconiformes.

FEMALES		SPARROWHAWK	PEREGRINE	KESTREL	BUZZARD	KITE	GOSHAWK
BODY (mm)		65.0	91.4	45.3	79.2	84.2	105.8
	MEAN	599	721	483	1493	2215	2929
PROVENTRICULUS	s.d.	108	-	134	237	-	446
AREA (mm^2)	n	18	1	9	8	2	15
	MEAN	0.260	0.490	0.773	0.768	0.905	1.411
PROVENTRICULUS	s.d.	0.062	-	0.225	0.124	0.134	0.247
DRY WEIGHT (g)	n	49	2	31	13	2	16
	MEAN	0.277	2.250	0.773	1.672	1.550	1.046
GIZZARD	s.d.	0.075	-	0.225	0.419	-	0.223
DRY WEIGHT (g)	n	48	1	31	17	2	17
	MEAN	0.305	0.684	0.170	1.400	0.979	0.984
INTESTINE	s.d.	0.159	0.111	0.130	0.603	-	0.326
DRY WEIGHT (g)	n	51	3	18	30	2	18
	MEAN	0.536	2.740	0.976	2.490	2.455	2.391
PROV. + GIZZARD	s.d.	0.125	-	0.296	0.495	-	0.544
DRY WEIGHT (g)	n	48	1	27	12	2	16
	MEAN	0.835	3.279	0.974	4.057	3.434	3.279
TOTAL DRY WEIGHT (g)	s.d.	0.245	0.810	0.302	1.154	-	0.810
(PROV.+ GIZ.+ INT.)	n	44	16	13	12	2	16
	MEAN	0.542	2.390	0.352	1.900	2.535	2.835
HEART	s.d.	0.211	1.225	0.145	0.724	-	0.544
DRY WEIGHT (g)	n	21	3	8	21	2	19

Appendix 3. Small intestine length, area and volume for raptor species of different body-mass and skeletal size.

SPECIES	INTEST. LENGTH (mm)	INTEST. AREA (mm^2)	INTEST. VOLUME (mm^3)	BODY MASS (g)	BODY (mm)
SPARROWHAWK	509	4977	3829	183	59.1
PEREGRINE	836	12000	13903	711	86.1
KESTREL	538	6636	6860	163	44.6
BUZZARD	1061	16252	20884	719	77.9
RED KITE	1340	20918	25909	866	83.8
GOSHAWK	781	12181	15491	1113	101.1
MERLIN	524	5623	4862	170	52.9
ROUGH-LEGGED BUZZARD	850	12750	15219	535	81.3
HONEY BUZZARD	430	5918	5807	470	77.2
ELEONORAS FALCON	480	-	-	320	64.2
HEN HARRIER	703	-	-	376	57.9
GOLDEN EAGLE	1556	26587	43175	3525	146.6
CHANGEABLE HAWK EAGLE	720	10080	11230	1400	99.2
BONELLIS EAGLE	1060	17667	23431	2065	119.0
TAWNY EAGLE	1075	16483	20113	1620	113.0
LANNER FALCON	855	13395	16700	740	79.2
HARRIS HAWK	915	-	-	735	88.2
SAKER FALCON	900	-	-	945	90.4
TAWNY OWL	649	9527	11888	449	47.3
BARN OWL	378	5707	7284	270	47.4
LONG-EARED OWL	441	5082	4866	233	47.1
LITTLE OWL	390	5443	6642	160	43.7
SHORT-EARED OWL	537	-	-	294	53.8
URAL OWL	580	-	-	-	65.1
SNOWY OWL	730	11268	14001	1038	92.2

N.B. To ensure independence of data points in the regression, means for each variable were calculated for each species by taking the average of the means for the sexes.

CHAPTER 5

The use of titanium dioxide as an inert marker for digestion studies in raptors.

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The data presented in this chapter form the basis of a paper published in Comparative Biochemistry and Physiology (1991): 100A: 1025-1029.

ABSTRACT

The study aimed to test the suitability of titanium dioxide as a nutritional marker for measuring digestive efficiency in raptors. Markers are of most benefit in situations where total collection of faeces cannot be made. This would enable a larger sample of birds to be used since it would allow the use of birds which could not be tethered under experimental conditions and those which are permanently kept in large aviaries. The total collection and marker-ratio methods were used simultaneously allowing a direct comparison. Complete recovery of the inert marker was not achieved and titanium dioxide was determined not to be a suitable marker for digestibility studies involving raptors. Total collection of faeces is a more accurate method to determine food absorption. Samples containing the marker were analysed using a colorimetric procedure. Freezing sample solutions prior to colorimetric analysis can produce misleading results. The percentage food absorbed from the intestine in Falconiformes was found to be about 85% by dry weight.

INTRODUCTION

During a comparative study of digestive efficiency in raptors it was necessary to find an appropriate method to measure digestion. Previous work on assimilation efficiencies, food metabolizability and energy requirements in raptors has relied on measuring total food input and total excreta output (Kirkwood 1979, Hamilton 1985, Campbell and Koplin 1986, Tollan 1988). Such a method is unsuitable , however, in situations where total collection of excreta cannot be made. This is likely to occur in larger raptor species and wild caught individuals which are not suited to confinement under experimental conditions. In such situations, markers have frequently been used in nutritional studies of digestion (Kotb and Luckey 1972). These methods assume that the marker is not absorbed during its passage through the gastro-intestinal tract, and so the amount of food absorbed by the bird can be determined from the ratio of marker in samples of the food and faeces. It is not necessary to know total food intake or faecal production, and so this method is particularly suited to wild birds housed in large aviaries. This study compares the use of titanium dioxide (TiO_2) as an inert marker to determine the digestive efficiency of raptors, with results obtained by total faecal collection. It also considers whether the presence of the marker influenced digestive efficiency. No previous study has considered the use of a nutritional marker for raptor studies. In the past, chromic oxide (Cr_2O_3) has been successfully used as a marker for other bird species (Lloyd *et al.* 1955, Dansky and Hill 1952, Savory and Gentle 1976, Savory 1980). However, because of the potential carcinogenicity of Cr_2O_3 it has largely been replaced by TiO_2, a white, tasteless, metal oxide, that has been used to measure apparent digestibility, food intake and rates of food passage in domestic fowls (*Gallus gallus)* and Japanese quail (*Coturnix coturnix japonica*) (Peddie *et al.* 1982, Savory 1986, Savory and Hodgkiss 1984). Peddie *et al.*(1982) achieved 97.5% recovery of the marker in poultry; Njaa (1961) recovered 98% in rats.

METHODS

Captive individuals from eleven species of British raptor were used: 8 Common Buzzards (*Buteo buteo*), 5 European Kestrels (*Falco tinnunculus*), 3 Northern Goshawks (*Accipiter gentilis*), 2 European Sparrowhawks (*Accipiter nisus*), 2 Golden Eagles (*Aquila chrysaetos*), 2 Red Kites (*Milvus milvus*), 1 Peregrine Falcon (*Falco peregrinus*), 1 Hobby (*Falco subbuteo*), 4 Long-eared Owls (*Asio otus*), 3 Tawny Owls (*Strix aluco*) and 3 Barn Owls (*Tyto alba*). All, with the exception of juveniles, were partially in moult. Trials were conducted at the Falconry Centre Herbert Schmidt in Bad Wörishofen, West Germany during June and July 1990. Birds were kept indoors at prevailing ambient temperature, photoperiod and humidity. Temperature fluctuated between 10 and 20^{o}C , humidity between 45 and 55%.

Birds which had been previously trained using falconry techniques, or were accustomed to being tethered to perches, remained so for the course of the trial. Those species which had never been tethered were housed free-flying in individual pens (3m x 4m x 2.5m) during the trial. Each Strigiform was untethered in a holding box (1m x 1m x 1m) with one horizontal perch. Birds were weighed prior to the trials, during and at the end of the trial to ensure their weight remained within ± 2% of their initial body weight (Stalmaster and Gessaman 1982).

To measure total faecal production a clear plastic sheet was secured beneath each bird: this also allowed for the collection of pellets. It was possible to separate the faeces from the uric acid in Falconiformes and Strigiformes. In the case of Strigiformes the boxes were lined with plastic, and a sliding tray on the base of the box enabled faecal collections without undue disturbance to the birds. Birds in individual pens were left undisturbed and all faeces and pellets collected at the end of each trial. All other birds were cleaned daily and sheets washed following each collection. The birds had been fed a diet of day-old chicks (*Gallus*

gallus) for several weeks prior to the trial and were fed the same diet during the trial. Stomach, yolk sac and intestine were removed from each chick since these parts were often rejected by the falcons and the puncture of the yolk sacs caused spillages that were difficult to quantify. All food was weighed before presentation to the birds. Birds were fed at the same time once daily, Falconiformes being fed at 10 a.m., Strigiformes at 8p.m. to correspond approximately to their normal hours of feeding. Prior to feeding, pellets and total faeces from the previous day were collected. Each trial lasted 16 days during which time no water was available for drinking or bathing. Apart from feeding time, birds were left undisturbed. Faecal samples and pellets were stored at -20°C. Fifty 'day-old' cockerels were taken at random, prepared in the same way as those being fed and dried at 70°C for 7 days to constant weight in a convection oven. This sample was used to calculate dry food intake from wet food intake (0.225 x wet food weight).

For the marker trials, birds were fed without marker for the first 8 days of the trial followed by 8 days feed with the marker. Titanium dioxide was added to a concentration of 0.2% (2g per dry kg). Using the total dry weight of food, the amount of titanium dioxide required for each individual was determined. This amount of marker was scattered on the inside of each chick in approximately equal amounts (if 4 chicks were to be fed, about one quarter of the marker was added to each). Birds were encouraged to eat all food provided during their feed. Accurate 'total collections' were only made from the tethered birds, these results serving as a comparison for the accuracy of the 'marker-ratio' method. Quantitative analysis of faeces from these tethered birds also allowed us to determine whether all of the marker was recovered.

Calculating efficiency by 'total collection'

Faecal and pellet samples were dried in a fan-assisted oven at 70°C for 7 days to constant weight. They were then cooled in a dessicator and weighed to 1mg. Apparent digestive efficiency was calculated as:

$$1 - \left(\frac{\text{DM faecal output(g)}}{\text{DM food intake(g) - DM pellet output(g)}} \right) \times 100$$

Calculating efficiency by 'marker-ratio' method

The initial 3 days of collections were not used for this analysis since a period of 2-3 days is required for the marker to equilibrate in the gastro-intestinal tract (Peddie *et al.* 1982) . All faecal samples were ground and analysed but only those from day 3 onwards were used to calculate digestive efficiency . One gram dry faecal sub-samples were used for titanium analysis. Whole pellets were also analysed for titanium content.

The analytical method followed Peddie *et al.*(1982), with the following adjustments to suit the semi-automated system, a Technicon autoanalyser II. The method is a colorimetric determination. To make the Hydrogen Peroxide solution, 960ml of distilled water was degassed by bubbling argon through the solution and 40ml of 30% w/v Hydrogen Peroxide added with 1ml BRIJ-35 (15% solution). To keep the chemical 'environment' constant, 15g Na_2SO_4 was dissolved in 1 litre of 10% H_2SO_4 for the wash solution. Sample aliquots were thawed overnight and run at 40 per hour, standards and blanks being inserted every 15 samples. Blanks were made as for sample preparation. Standards were made by dilution giving two ranges, 0 - 10mg/100ml for pellets and 0 - 20mg/100ml for faecal samples. For the lower range a linear calibration curve was fitted; for the higher range a quadratic was a slightly better fit. Having determined the concentration of titanium dioxide in food, pellet and faecal samples, the apparent digestive efficiency was calculated as :

$$1 - \left(\frac{TiO_2 \text{ g/kg in food entering the intestine}}{TiO_2 \text{ g/kg in faeces}} \right) \times 100$$

The ratio of TiO_2 in food entering the intestine accounts for losses of the marker through pellet regurgitation. All mean values are given ± 1 standard deviation.

RESULTS

Analytical method

The accuracy of the titanium analysis was tested by taking replicates from the same aliquot. They did not differ significantly in the concentration of TiO_2 detected (Wilcoxon, $T = 6$, $n=12$, n.s.).

It was important to thoroughly mix the samples after thawing, and failure to do this led to inaccuracies. Two aliquots of equal volume were taken from each of twenty sample solutions. 20 of the aliquots were thoroughly shaken 2 hours before the analysis, 20 were not shaken at all (Table 1). The difference in quantity of TiO_2 detected between the two aliquots for each of the 20 samples was calculated and expressed as a percentage of the mean. Aliquots which had been shaken prior to analysis showed significantly less deviation than those which were not shaken (Mann-Whitney U-test, $P<0.001$). This suggests freezing influences the dispersion of titanium in the solution.

Table 1. Shaking samples before analysis improves accuracy during the colorimetric procedure.

SAMPLE NUMBER	WITHOUT SHAKING		SAMPLE NUMBER	WITH SHAKING	
	Aliquot 1	Aliquot 2		Aliquot 3	Aliquot 4
1	10.03	9.94	11	10.11	10.10
2	7.64	7.62	12	8.93	8.91
3	5.61	5.26	13	6.78	6.77
4	3.61	3.65	14	4.31	4.30
5	1.82	1.87	15	2.23	2.23
6	9.50	9.33	16	11.03	11.01
7	7.29	7.53	17	8.55	8.56
8	5.30	5.60	18	6.70	6.70
9	3.99	4.07	19	4.88	4.88
10	2.33	2.32	20	2.79	2.80

Analysis of samples from feeding trials

To see if addition of the marker affected digestion, dry matter efficiencies calculated from 'total collections' were compared for 8 days 'before' and 8 days 'during' addition of the marker. For species where only one individual was available, the two treatments were compared using a t-test on arcsine-square root transformed data. In cases where more than one individual for a species was available, two-way ANOVA was used to account for any individual differences. The Red Kites had a significantly reduced apparent digestive efficiency ($F_{1,27}=7.1$, $P<0.02$) following addition of the marker, the Hobby had a significantly increased apparent digestive efficiency ($t_{13}=2.29$, $P<0.05$). None of the other four species (Sparrowhawk, Kestrel, Peregrine, Buzzard) showed significant differences.

To see if the efficiencies using the 'marker-ratio' method are comparable with those for the 'total collection' method, efficiencies calculated by the two methods were compared for 4 consecutive days during which both treatments were used

(Table 2). Species were analysed separately using either a t-test or two-way ANOVA as in the previous analysis. The percentage digestive efficiency calculated from the two methods differed significantly, the 'marker-ratio' method being less for each species. There were also individual differences within a species for the Red Kite ($F_{1,12}$=10.04, P<0.01) and the Kestrel ($F_{3,26}$=10.23, P<0.001).

Table 2. To compare the apparent digestive efficiencies for the 'marker-ratio' method and the 'total collection ' method. Means are for species, not individuals, to give some indication of the differences in magnitude between the two methods. Significance values account for individual differences within a species.

SPECIES	Number of Individuals	MEAN WITHOUT TiO_2	MEAN WITH TiO_2	SIGNIFICANCE
RED KITE	2	85.1	76.2	$F_{1,12}$ = 118.96, P < 0.001
HOBBY	1	83.8	80.1	t_6 = 3.46, P < 0.02
BUZZARD	4	87.7	82.1	$F_{1,28}$ = 48.95, P < 0.001
PEREGRINE	1	87.4	82.5	t_6 = 4.69, P < 0.005
SPARROWHAWK	1	88.1	83.5	t_6 = 4.65, P < 0.005
KESTREL	4	86.7	79.0	$F_{1,26}$ = 119.52, P < 0.001

The marker technique assumes that there is no absorption or retention of the marker compound, recovery from the faeces approaching 100%. The amount of TiO_2 recovered from the raptor trials, however, was extremely low and variable between individuals and species, the mean percentage recovery being 67.5 ± 11.44 (Table 3).

Digestive efficiencies based on the 'marker-ratio' method will only be identical to the efficiencies from 'total collection' if there is complete recovery of the TiO_2. If, however, there is incomplete recovery of the marker, the efficiencies from the two methods will differ. Table 4 and Fig.1 show that for the falconiform species studied here, there is a clear relationship between the recovery of the marker and the accuracy of the digestibility figure derived from the marker method ($r_{11}=0.687$, $P<0.02$, 2-tailed).

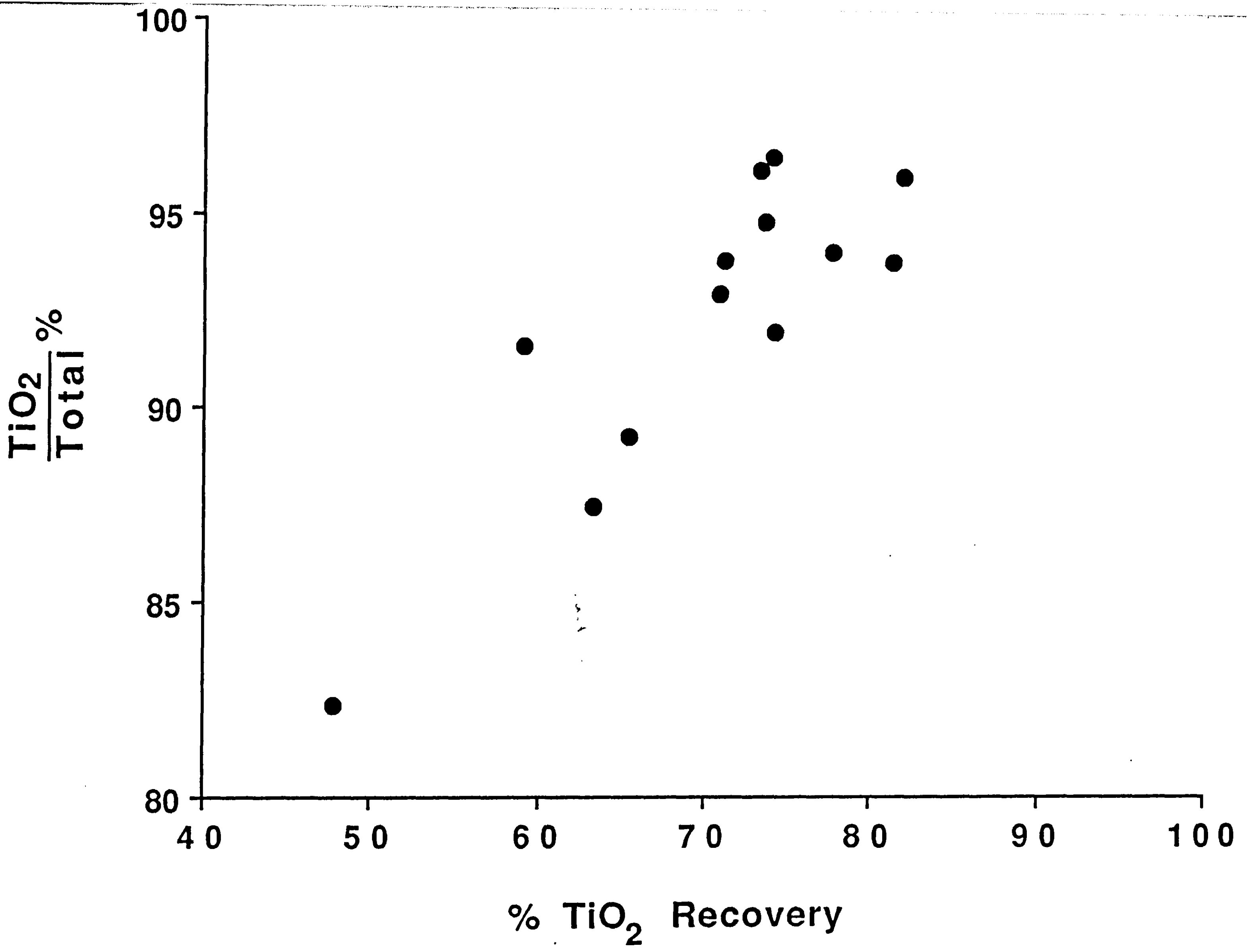
The mean dry-matter percentage efficiency for the Falconiformes is 86.35 ± 1.6 (n=13) and for the Strigiformes 90.69 ± 4.61 (n=10). The difference is significant (Mann-Whitney U-test, $P<0.05$). In falconiform species, pellets contained 2.3% ash whereas Strigiform pellets contained 15.6% ash, the difference being significant ($t_{29}=18.24$, $P<0.001$). Faeces from Falconiformes and Strigiformes contained 27.4% and 18.0% ash respectively, this difference is also significant ($t_{31}=3.07$, $P<0.005$). The differences found are because the Falconiformes have a much higher acidity in the stomach and thus more of the ash is digested (Duke *et al.* 1975).

Table 3. Amounts of TiO_2 recovered in pellets and faeces over a 6-day period during which time TiO_2 was fed daily.

SPECIES	TiO_2 added to food (g)	% TiO_2 recov. in pellet	% TiO_2 recov. in faeces	% RECOVERY
RED KITE	0.3522	2.21	63.26	65.47
RED KITE	0.3906	0.97	62.42	63.39
HOBBY	0.1679	0.59	73.55	74.20
BUZZARD	0.3251	3.04	78.32	81.36
BUZZARD	0.3594	8.76	64.50	73.26
BUZZARD	0.3555	2.05	71.62	73.67
BUZZARD	0.3455	2.75	56.41	59.16
PEREGRINE	0.2647	1.47	72.65	74.12
SPARROWHAWK	0.2031	4.87	66.32	71.19
KESTREL	0.1890	7.88	69.79	77.67
KESTREL	0.1790	2.51	68.38	70.89
KESTREL	0.1711	0.76	47.11	47.87
KESTREL	0.1478	2.57	79.30	81.87
TAWNY OWL	0.2282	2.80	49.20	52.00
TAWNY OWL	0.1802	1.00	43.00	44.00
TAWNY OWL	0.2480	2.38	67.90	70.00

Figure 1.

Relationship between the amount of TiO_2 recovered for each individual and how closely the 'marker-ratio' method approximates to the 'total collection' method for Falconiformes only ($r_{11} = 0.687$, $P < 0.02$, 2-tailed).



$\frac{TiO_2}{Total}$ %
100
95
90
85
80
40
50
60
70
80
90
100
% TiO_2 Recovery

Table 4. Mean percentage apparent digestive efficiencies from the ‘total collection’ and ‘marker-ratio’ methods for all species used, with ‘marker-ratio’ efficiency calculated as a percentage of ‘total collection’ efficiency.

SPECIES	MEAN % TOTAL EFFICIENCY	6 DAYS MEAN % TiO_2 EFFICIENCY	% RECOVERY 6 DAYS	$\frac{\%TiO_2}{\%TOTAL}$ X 100
RED KITE	86.41	77.06	65.47	89.18
RED KITE	85.56	74.79	63.39	87.41
HOBBY	83.22	76.50	74.20	91.93
BUZZARD	87.79	82.27	81.36	93.71
BUZZARD	87.43	83.98	73.26	96.05
BUZZARD	86.36	81.81	73.67	94.73
BUZZARD	86.78	79.45	59.16	91.55
PEREGRINE	85.62	82.54	74.12	96.40
SPARROWHAWK	88.98	83.42	71.19	93.75
KESTREL	86.64	81.38	77.67	93.93
KESTREL	83.61	77.65	70.89	92.87
KESTREL	87.67	72.22	47.87	82.38
KESTREL	86.45	82.87	81.87	95.86
BUZZARD	-	79.16	-	-
BUZZARD	-	83.92	-	-
BUZZARD	-	83.95	-	-
GOSHAWK	-	82.57	-	-
GOSHAWK	-	83.90	-	-
GOSHAWK	-	84.40	-	-
GOLDEN EAGLE	-	85.73	-	-
GOLDEN EAGLE	-	88.17	-	-
TAWNY OWL	88.10	78.35	52.00	88.93
TAWNY OWL	88.08	77.64	44.00	88.15
TAWNY OWL	84.25	80.53	70.00	95.58
BARN OWL	97.02	79.18	-	-
BARN OWL	96.90	-	-	-
BARN OWL	96.28	87.89	-	-
LONG-EARED OWL	91.06	-	-	-
LONG-EARED OWL	86.10	81.92	-	-
LONG-EARED OWL	88.40	72.97	-	-
LONG-EARED OWL	90.72	80.83	-	-

DISCUSSION

The results show that digestive efficiencies based on the 'marker-ratio' method are not accurate because of incomplete recovery of the marker. Several factors could account for this. Birds were closely watched to ensure that they ate the food without loss of marker. Even if some TiO_2 had been lost at ingestion this would have resulted in higher 'marker-ratio' efficiencies than expected, not lower ones as found here. If some mixing of uric acid and faeces occurred in the colon, TiO_2 might be lost in this way. To check for this the titanium content of uric acid samples was measured, but found to be negligible (mean = 0.03 ± 0.045 mg/g; n=12).

The low recovery of titanium could have been caused by incomplete recovery of faeces. However, the mean daily variation in percentage efficiency based on dry-matter collections for 12 individuals was 3% which would imply no substantial irregular losses of faecal material. Unless the marker passes through the gastro-intestinal tract in concentrated pulses, recoveries of 60-70% would imply a loss of 30-40% of the faeces, which is improbable. It is possible that TiO_2 takes much longer than expected to reach equilibrium in these species. However, from day 2 onwards, there was little variation in percentage efficiency and since percentage recoveries were based on day 2 onwards this factor would also seem unlikely. The two most likely causes for the low recovery rates are:

a) the TiO_2 is retained in the bird, though not necessarily absorbed.

b) TiO_2 is lost during sample preparation - grinding, ashing, dissolution.

Fig. 1 implies that the birds are indeed retaining the marker. All samples were selected for analysis entirely at random and so if the analytical procedure was at fault, one would expect errors of TiO_2 concentrations to be randomly distributed between all individuals. This does not appear to be the case since some individuals retain more TiO_2 than others and the higher the percentage recovery the significantly closer the digestive efficiency based on the 'marker-ratio' method is to the expected. Disproportionately low and high efficiencies calculated on the 'total collection' method could also account for the relationship, however efficiencies derived from this technique for individuals were relatively constant.

Titanium dioxide in raptors does not satisfy the criteria in Kotb and Luckey (1972) for nutritional markers. There is incomplete recovery of the marker and in some species the marker appears to affect apparent digestibility. 'Total collection' is a better method to determine apparent digestibility. The degree to which food is absorbed from the intestine in raptors is similar to that found in other Carnivores (Robbins 1983). Greater digestion of bones by Falconiformes was reported by Duke *et al.* (1975) and Clark (1972). The amount of pellet ash in this study for both Falconiformes and Strigiformes is less than that found by Clark (1972) and Duke *et al.* (1975), and this difference is most likely a reflection of the incomplete bone ossification in day-old chicks used in this study.

REFERENCES

Campbell, E.G. and Koplin, J.R. (1986) Food consumption, energy, nutrient and mineral balances in a Eurasian Kestrel and a Screech Owl. *Comp. Biochem. Physiol.* **83A:** 249-254.

Clark, R.J. (1972) Pellets of the short-eared owl and marsh hawk compared. *J. Wildl. Mgt.* **36:** 962-964.

Dansky, L.M. and Hill, F.W. (1952) Application of the chromic oxide indicator method to balance studies with growing chickens. *J. of Nutr.* **47:** 449-459.

Duke, G.E., Jegers, A.A., Loff, G. and Evanson, O.A. (1975) Gastric digestion in some raptors. *Comp. Biochem. Physiol.* **50A:** 649-656.

Hamilton, K.L. (1985) Food and energy requirements of captive Barn Owls *Tyto alba*. *Comp. Biochem. Physiol.* **80A:** 355-358.

Kirkwood, J.K. (1979) The partition of food energy for existence in the Kestrel (*Falco tinnunculus*) and the Barn Owl (*Tyto alba*). *Comp. Biochem. Physiol.* **63A:** 495-498.

Kotb, A.R. and Luckey, T.D. (1972) Markers in Nutrition. The Commonwealth Bureau of Nutrition. *Nutrition Abstracts and Reviews* **42:** 813-845.

Lloyd, L.E., Rutherford, B.E. and Crampton, E.W. (1955) A comparison of titanic oxide and chromic oxide as index materials for determining apparent digestibility. *J. of Nutrition*. **56:** 535-537.

Njaa, L.R. (1961) Determination of protein digestibility with titanium dioxide as indicator substance. *Acta Agriculturae Scandinavica* **11:** 227-241.

Peddie, J., Dewar, W.A., Gilbert, A.B. and Waddington, D. (1982) The use of titanium dioxide for determining apparent digestibility in mature domestic fowls (*Gallus domesticus*). *J. agric. Sci.* **99:** 233-236.

Robbins, C.T. (1983) *Wildlife Feeding and Nutrition.* London: Academic Press.

Savory, C.J. (1980) Meal occurrence in japanese quail in relation to particle size and nutrient density. *Anim. Behav.* **28:** 160-171.

Savory, C.J. (1986) Influence of ambient temperature on feeding activity parameters and digestive function in domestic fowls. *Physiology and Behav.* **38:** 353-357.

Savory, C.J. and Gentle, M.J. (1976) Changes in food intake and gut size in Japanese quail in response to manipulation of dietary fibre content. *Br. Poult. Sci.* **17:** 571-580.

Savory, C.J. and Hodgkiss, J.P. (1984) Influence of vagotomy in domestic fowls on feeding activity, food passage, digestibility and satiety effects of two peptides. *Physiology and Behav.* **33:** 937-944.

Stalmaster, M.V. and Gessaman, J.A. (1982) Food consumption and energy requirements of captive Bald Eagles. *J. Wildl. Mgt.* **46:** 646-654.

Tollan, A.M. (1988) Maintenance energy requirements and energy assimilation efficiency of the Australasian Harrier. *Ardea* **76:** 181-186.

CHAPTER 6

The influence of gut morphology on digestion time in raptors

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The data presented in this chapter form the basis of a paper submitted to Comparative Biochemistry and Physiology 1992.

ABSTRACT

It is assumed that the primary determinant of digestive efficiency in animals is the length of time for which food is retained in the digestive tract. Unless there is a compensatory increase in hydrolysis or absorption rate, raptor species with short digestive tracts independent of body-size would be predicted to have reduced digestive efficiency. This study examined interspecific differences in mean food retention times in relation to digestive efficiency and feeding ecology of raptors. Captive individuals from raptor species with contrasting foraging strategies and gut morphology data from wild raptor carcasses were used. European Sparrowhawk, Peregrine and Hobby have a short small intestine relative to body-size resulting in rapid digesta throughput and a short mean retention time. The Common Buzzard, European Kestrel and Red Kite have a long, high-capacity digestive tract, independent of body-size, with a corresponding long mean retention time. Diet also affected mean retention time. In Peregrine Falcons and Common Buzzards, rabbit passed through the gut more quickly than pigeon and Peregrines digested both diets more quickly than Buzzards. There was no evidence for a compensatory mechanism by which food passage could be slowed in species with a relatively short digestive tract. The costs and benefits of interspecific differences in mean retention times are discussed with respect to feeding adaptations in raptor species occupying specialist and generalist foraging niches.

INTRODUCTION

Two factors contribute to the overall weight of the digestive tract: the length of the gut itself and the quantity of digesta it contains. It has already been shown that there is considerable variation in the gut length of different species of birds of prey. I here consider the role of food passage time in raptors and whether this is influenced by predatory strategy.

Unlike many animal species, raptors do not take small quantities of food continuously, but eat one or more large meals at discrete intervals each day. The more quickly a bird can process this food, the sooner it can revert to its most efficient flying weight (Sibly 1981). However, assimilation efficiency and food passage rates are interactive, competing processes (Robbins 1983). The amount of food absorbed is directly related to the mean retention time of digesta in the gut, and the rate of hydrolysis and absorption (Penry & Jumars 1987, Karasov 1990, Karasov & Levey 1990). If insufficient time is available for complete hydrolysis, then increasing passage rates will reduce assimilation efficiency. Birds therefore face decisions as to whether to retain food in the gut for the optimum time for maximum digestive efficiency, or to increase food passage rate, with a consequent fall in energy absorption, in order to regain maximum flight performance and so increase the likelihood of making further kills that day.

Scavenging species such as the Common Buzzard (*Buteo buteo*) and the Red Kite (*Milvus milvus*) are opportunist predators, as demonstrated by the wide range of live prey and carrion in the diet (Cramp & Simmons 1980, Davies & Davis 1973, Tubbs 1974). They feed on a spatially and temporally unpredictable food supply and so one might expect them to utilise each meal as efficiently as possible and show comparatively slow throughput times. Presumably such species maintain a sufficient retention time for food in the gut to optimise energy absorption. However, species with an active, chasing form of predation which have a comparatively short digestive tract could adopt two different strategies. Firstly they could adopt a slower rate of throughput of the food, so that although their digestive tract were short, they retained it within the absorptive region of the gut for longer and so compensated to some extent for the reduced area for nutrient absorption. Alternatively, they could pass food through the gut at the same rate, or faster than species with long digestive tracts, suffering a reduced efficiency of digestion and face the consequent need to kill prey more frequently. This chapter reports on feeding trials to study digesta passage in a range of raptor species for which gut morphology data had previously been collected (Chapter 3). Two different feeding trials were conducted. In the first a range of different species were fed on the same diet, and the rate of faecal production determined in order to compare their throughput times in relation to gut anatomy. Secondly, two species, the Common Buzzard and the Peregrine Falcon were fed on diets of different quality to see if the rate of digestion was influenced by prey type.

METHODS

Captive individuals from 7 raptor species were used: 2 Red Kites (*Milvus milvus*), 4 Common Buzzards (*Buteo buteo*), 5 European Kestrels (*Falco tinnunculus*), 3 Peregrine Falcons (*Falco peregrinus*), 2 Hobbies (*Falco subbuteo*), 2 European Sparrowhawks (*Accipiter nisus*) and 1 Honey Buzzard (*Pernis apivorus*). All were accustomed to being tethered and remained so for the duration of the trials. Two experiments were conducted, the first to examine interspecific differences in food throughput and the effects of meal size on throughput rate and assimilation efficiency. The second looked at differences in throughput related to prey type. Birds were maintained and samples collected as in Barton & Houston (1991). They were fed a known amount at 10 a.m. and faeces were collected every 2 hours for up to 16 hours with a final collection after 24 hours. Only the faecal portion was collected and appearance of black/green faeces signified the end of digestion for each meal. Lights were left on for 16 hours after feeding. Transit time is taken as the time to first appearance of the faeces. It is assumed that faecal production is a direct indication of flow of digesta through the gut and that one of the main determinants of food passage is small intestine length.

Interspecific and meal-size differences in digesta throughput.

Birds were fed a diet of day-old cockerels (*Gallus gallus*) with yolk sac, stomach and intestine removed to avoid spillage. Each individual was fed an equal amount of food. For the Kestrel, Sparrowhawk and Hobby, 2 cockerels (60g wet weight) were sufficient for a good-sized crop. For the Peregrine, Red Kite and Buzzard it was only a small meal. These larger species were also fed 5 cockerels (150g wet weight) which was a good-sized meal for them but exceeded the crop capacity for the small Falconiformes. Small and large meals were fed to the same individuals to examine whether different-sized meals were digested to differing extents and to compare the time taken for large and small volumes of digesta to pass through the gut. Faecal output was calculated at 2-hourly intervals as a percentage of the total 24-hour faecal output. Throughout the study, a 2 chick meal is referred to as a 'small meal' (whether fed to a large or a small bird), a 5 chick meal as a 'large meal'. Trials were in triplicate for the Peregrines and duplicate for the other species.

The influence of prey type on digesta throughput.

Two raptor species were used: 4 Common Buzzards and 3 Peregrine Falcons. On 2 consecutive days, each individual was given a known amount of rabbit meat (*Oryctolagus cuniculus*) without fur or bone. On 2 subsequent days they were fed the same quantity of pigeon meat (*Columba livia*) without feather or bone. Individuals were fed slightly different amounts depending on their body-mass, but were fed equal amounts of rabbit and pigeon. The quantity of food given was calculated for both diets as that sufficient to provide the metabolisable energy requirements for maintenance (ME_m) for individuals and species of differing body-size, using Kirkwood's (1981) equation:

$ME_m = (110 \times M^{0.679} \times 4)/4.5$ where M is body-mass in kg and assuming raptor diets have a calorific value of 4.5 kcal/g and 25% water content (calculated from preliminary studies). The aim was to examine throughput differences caused by prey type, rather than interspecific differences in digestive efficiency. In this experiment, faeces were only collected at 2-hourly intervals up to 12 hours after feeding, with a final collection after 24 hours.

Gut morphology measurements.

Intestine length and volume were measured for 8 raptor species. To measure intestine length, the intestinal tract was placed unstretched in a straight line and the length measured from the cut-off point at the gizzard to the ileo-cecocolic junction (Leopold 1953). Intestine volume was calculated by opening the small intestine along the whole length, measuring the width at both ends and at the mid-point and using the mean width (circumference) to compute the volume of a cylinder.

Data analysis - calculation of mean retention time.

The length of time for which digesta were retained in the gut (mean retention time) was calculated for each species using the formula given by Warner (1981).

$$t = \sum_{i=1}^{n} m_i t_i \; / \; \sum_{i=1}^{n} m_i$$

where t is the mean retention time of digesta in the gut and m_i is the absolute amount of faeces excreted at time interval t_i after feeding. Mean retention times were calculated up to 14 hours after feeding and used to compare digesta throughput for different species feeding on the same diet of cockerels and for 2 species (Peregrine Falcon and Common Buzzard) feeding on 2 different diets (rabbit and pigeon). Kruskal-Wallis one-way analysis of variance was used to establish significant interspecific differences. Pairwise differences were tested by determining confidence intervals at the 5% level (Siegel & Castellan 1988). All tests were 2-tailed.

Calculation of apparent digestive efficiency.

Using the methods described in Barton and Houston (1991), apparent digestive efficiency was calculated as:

$$1 - \left(\frac{\text{dry faeces(g)} + \text{dry pellets(g)}}{\text{dry food intake(g)}} \right) \times 100$$

Correlations were examined between mean retention time, small intestine length and apparent digestive efficiency.

RESULTS

Interspecific differences in digesta throughput.

The data clearly show a pattern of digestion similar to that found in other carnivores (Sibly 1981). Raptors had a short retention time associated with a relatively short and simple gastro-intestinal tract and there was a peak of faecal output marking the time of maximum digesta throughput. There were, however, interspecific differences in throughput. I will first consider those differences and then examine differences in throughput within species fed different-sized meals and different food types.

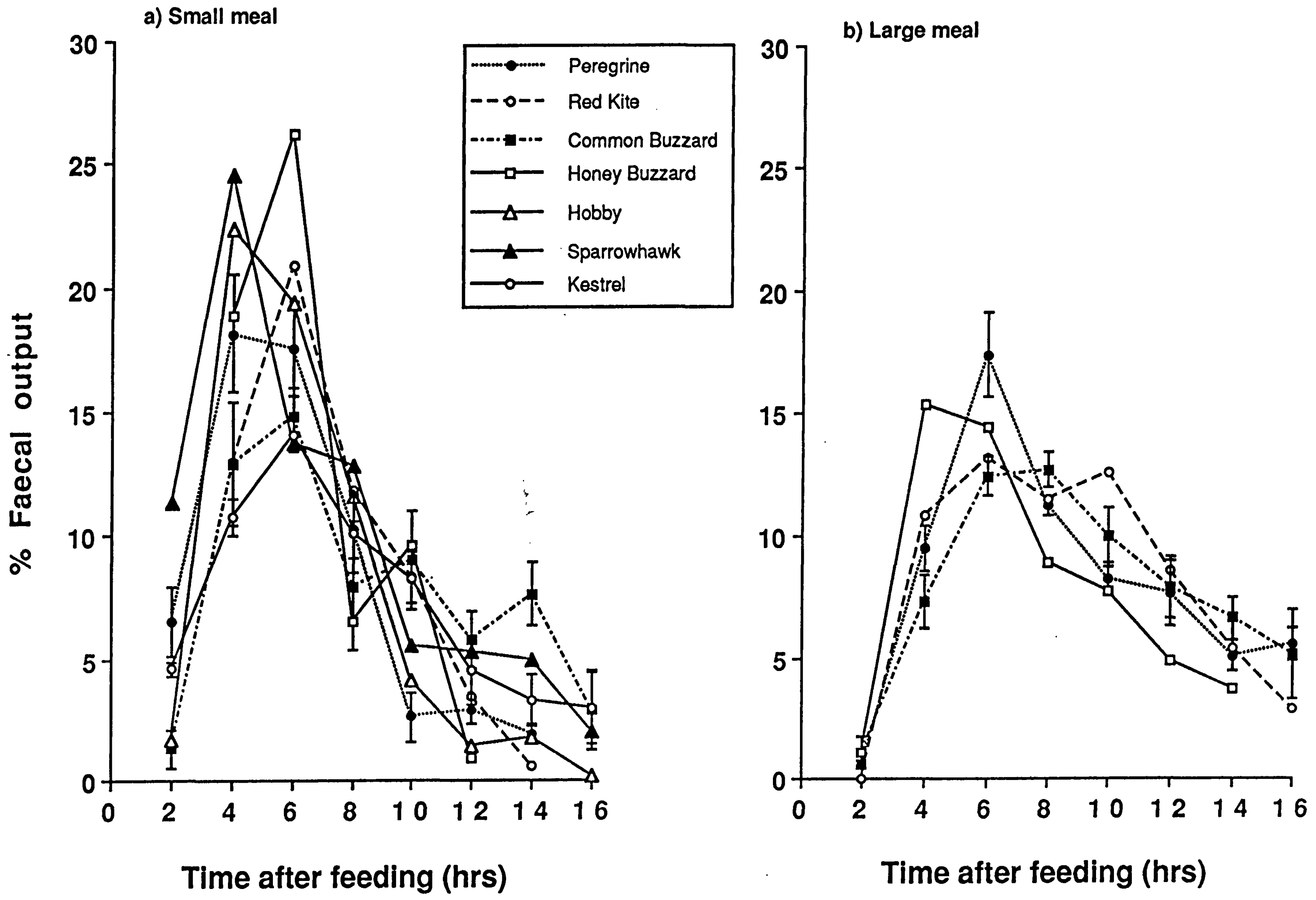
In Fig. 1a, the percentage of the total 24-hour faecal output is shown at each 2-hourly interval for 7 raptor species digesting a small meal (60g wet weight of cockerel). All of the species had a peak faecal output at 4-6 hours, followed by further output until 16 hours after feeding when defaecation stopped. Initially, throughput was faster in the Sparrowhawk, Peregrine, Hobby and Honey Buzzard. Peak faecal output was about 25% of the total for these species after 4 hours compared to 10-15% in the Common Buzzard and the Red Kite. Transit time (time for first appearance of digesta) was shorter in the Sparrowhawk, Peregrine and Kestrel, a higher percentage of faeces being excreted after 2 hours in these species. Transit time for the Common Buzzard and the Red Kite was longer, there being no faecal excretion from the Red Kite until 4 hours after feeding and very little in the Common Buzzard after 2 hours. The significance of these results can be clearly seen in Fig. 2a where the same data were plotted cumulatively. The Sparrowhawk digested more of its meal (80%) and more quickly than all the other species, followed by the Hobby, Honey Buzzard, Peregrine, Red Kite, Kestrel and Common Buzzard respectively. Most species excreted 55-60% of the total faecal output after 16 hours, only the Hobby and the Sparrowhawk produced more.

A similar pattern was found for the 4 species which were also fed a large meal (Fig. 1b). All 4 species had a transit time of 2 hours. Peak faecal output was reached most quickly in the Honey Buzzard after 4 hours, followed by the Peregrine, Red Kite and Common Buzzard at 6-8 hours. The Common Buzzard and the Red Kite retain digesta for longer and again, all 4 species had excreted 60% of total faecal output after 16 hours (Fig. 2b).

Figures 1a and 1b.

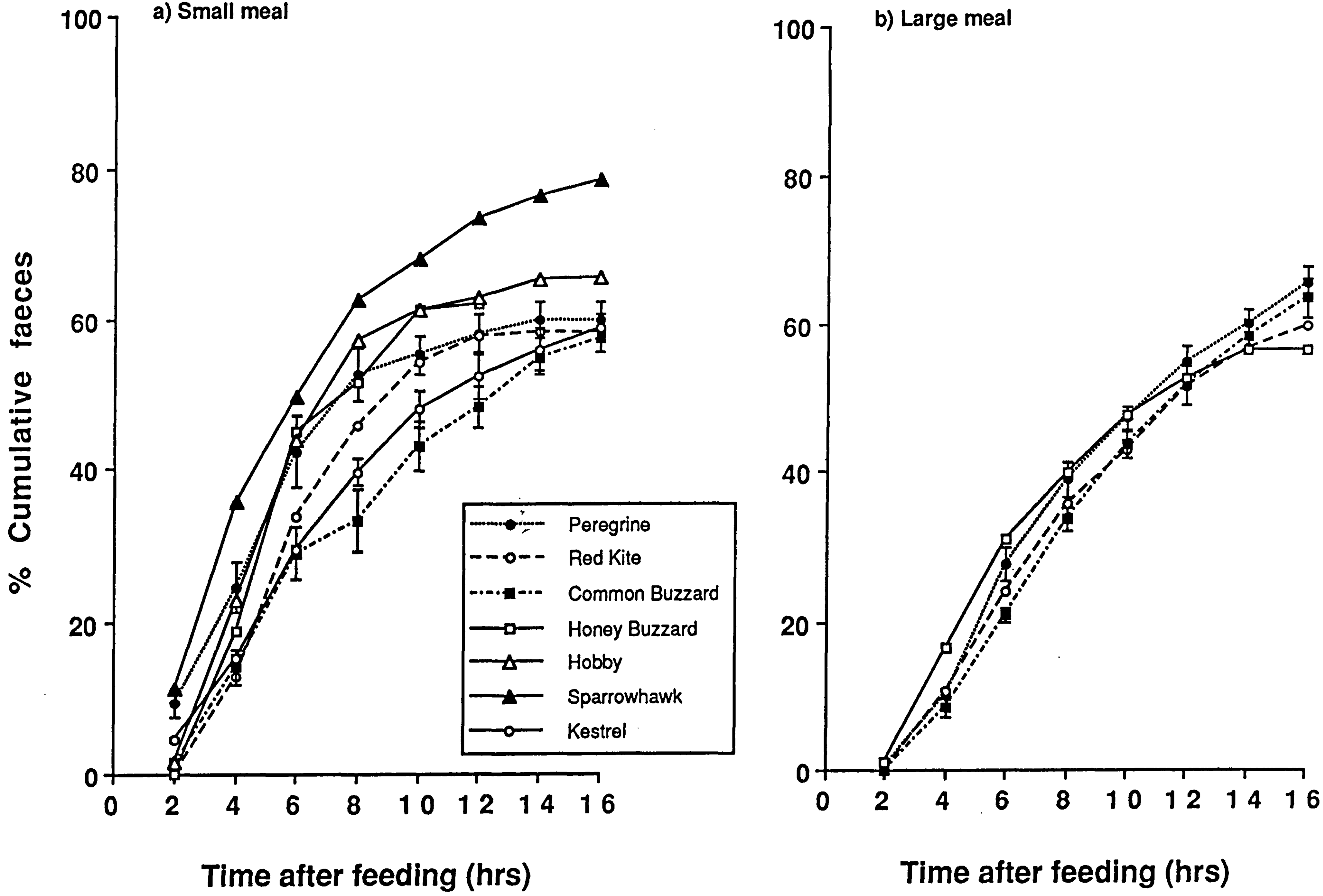
Percentage of total 24-hour faecal output at 2-hourly intervals post-feeding for 7 raptor species fed a small meal (60g wet weight of day-old cockerel) and a large meal (150g wet weight). Means and standard errors are shown. Trials were in triplicate for the Peregrines and in duplicate for the remaining species. Sample sizes for species were:

2 Peregrine Falcons (*Falco peregrinus*); 4 Common Buzzards (*Buteo buteo*);
4 European Kestrels (*Falco tinnunculus*); 2 Red Kites (*Milvus milvus*);
2 Hobbies (*Falco subbuteo*); 2 European Sparrowhawks (*Accipiter nisus*);
1 Honey Buzzard (*Pernis apivorus*).


a) Small meal
b) Large meal
% Faecal output
Time after feeding (hrs)
Time after feeding (hrs)
0
5
10
15
20
25
30
0
2
4
6
8
10
12
14
16
Peregrine
Red Kite
Common Buzzard
Honey Buzzard
Hobby
Sparrowhawk
Kestrel

Figures 2a & 2b.

Cumulative faecal output at 2-hourly intervals post-feeding for 7 raptor species fed a small and a large meal. Numbers of individuals are the same as in Fig. 1. Means and standard errors are shown.


a) Small meal
b) Large meal
% Cumulative faeces
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
Time after feeding (hrs)
Peregrine
Red Kite
Common Buzzard
Honey Buzzard
Hobby
Sparrowhawk
Kestrel

Time for excretion of 10%, 30% and 50% of total 24-hour faecal output is shown for each species feeding on 2 and 5 chicks (Table 1). For a small meal, the Sparrowhawk, Hobby, Peregrine and Honey Buzzard excrete a larger percentage of their faecal output more quickly than the Kestrel, Common Buzzard and Red Kite. For the large meal, the Peregrine and Honey Buzzard again excrete a larger proportion of their faeces more quickly.

Table 1. Mean time (hours) for passage of 10%, 30% and 50% of the total 24-hour faecal output in 7 raptor species fed a small meal (2 chicks) and a large meal (5 chicks). Sample sizes are in parentheses after the species' name.

FAECAL OUTPUT	10%		30%		50%	
NO. OF CHICKS	2	5	2	5	2	5
	Time (hrs)		Time (hrs)		Time (hrs)	
Sparrowhawk (2)	2	-	3.5	-	6	-
Hobby (2)	2.5	-	4.5	-	6.75	-
Peregrine (3)	2	4	4.5	6.5	7.5	10.5
Honey Buzzard (1)	3	3	5	5.75	7.5	11
Red Kite (2)	3.5	3.75	5.75	7	9	11.75
Kestrel (5)	2.75	-	6	-	10.5	-
Common Buzzard (4)	3.25	4.25	6.5	7.5	12.5	11.75

Individuals fed meals of different sizes.

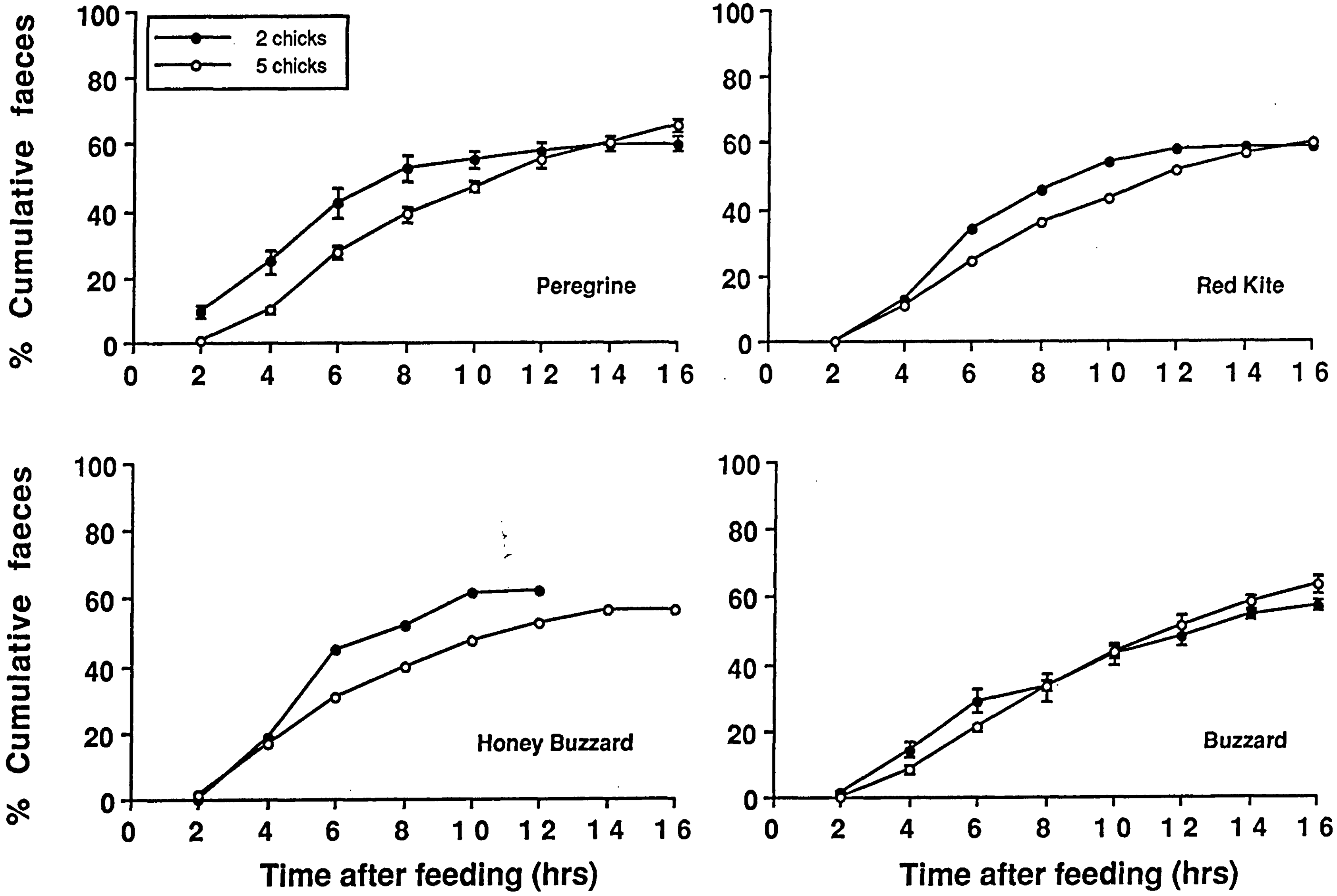
The cumulative faecal output for the 4 species (Peregrine, Red Kite, Common Buzzard and Honey Buzzard) fed a small and a large meal are shown in Fig. 3. Throughput is not in direct proportion to meal size. For both meal sizes, about 60% of the total faecal output is excreted after 16 hours. In absolute terms, more bulk of digesta passed through the gut when fed a large meal (150g) than a small meal (60g).

The percentage digestive efficiency (total dry excreta output as a percentage of dry food intake) for birds fed both a small and a large meal were respectively for Peregrine (74.2% and 78.3%), Common Buzzard (78.8% and

Figure 3.

Cumulative faecal output for 4 raptor species to compare faecal output when fed a small meal (60g wet weight) and a large meal (150g wet weight). Trials were in triplicate for the Peregrines and duplicate for the Common Buzzard, Red Kite and Honey Buzzard. Sample sizes were:

3 Peregrine Falcons; 4 Common Buzzards; 2 Red Kites; 1 Honey Buzzard.


2 chicks
5 chicks
% Cumulative faeces
Peregrine
Red Kite
Honey Buzzard
Buzzard
0
20
40
60
80
100
0
2
4
6
8
10
12
14
16
Time after feeding (hrs)

79.2%), Red Kite (74.5% and 79.0%) and Honey Buzzard (71.1% and 78.1%). When individuals were considered separately, a large meal was always digested more efficiently than a small meal (Wilcoxon's test for matched pairs, $T=6$, $P<0.05$).

Mean retention times.

Results for mean retention times are summarised in Table 2. The sample sizes for each species were relatively small and so rather than attempt to test the significance of every pairwise comparison, only the mean retention times for Peregrine, Kestrel and Common Buzzard were statistically analysed. The 3 species were chosen *a priori*. I initially hypothesised that the ultimate determinant of passage rate is foraging strategy. These 3 species have contrasting foraging strategies (Cramp & Simmons 1980) and acceptable sample sizes. The results for the remaining 4 species should be interpreted with caution but in the light of the results, do appear to be real. For a small meal, Peregrines, Kestrels and Common Buzzards differed in their mean retention times ($KW=7.09$, $P<0.05$, Kruskal-Wallis 2-tailed). The time for which digesta was retained in the gut of the Kestrel did not differ significantly from either the Buzzard or the Peregrine, however the Peregrine had a significantly shorter mean retention time than the Buzzard ($P<0.05$, multiple comparison test - Siegel & Castellan 1988). For the 4 species eating a large meal, no significant differences in retention time could be detected ($KW=5.58$, $P>0.05$, Kruskal-Wallis).

Table 2. Mean retention time in hours (with standard errors), small intestine length and apparent digestive efficiency for the 7 raptor species used in the analysis (sample sizes in parentheses).

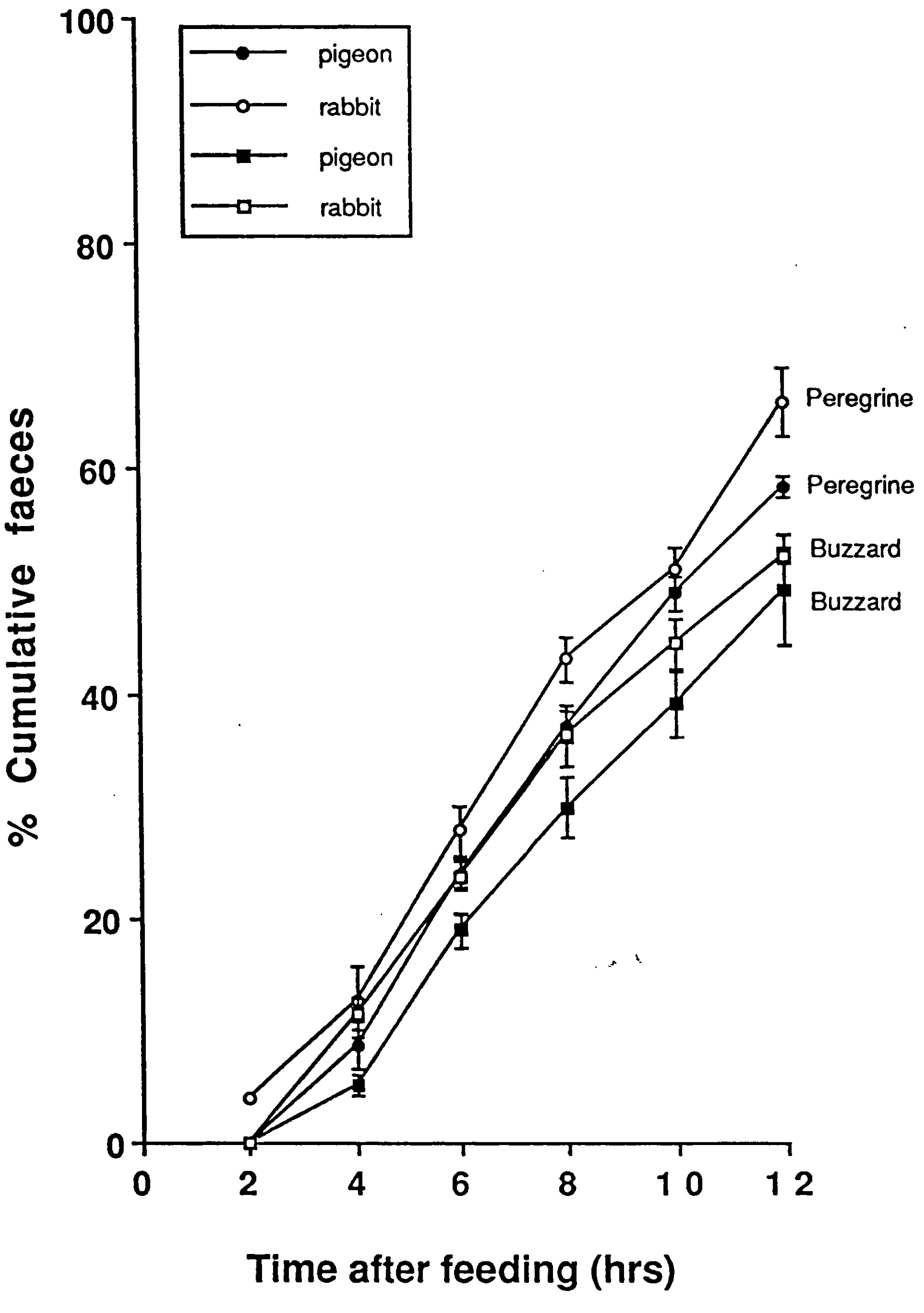
SPECIES	MEAN RETENTION TIME (HOURS) Small Meal	Large Meal	Intestine Length (mm)	Digestive Efficiency %
Sparrowhawk (2)	6.30	-	509	79.28
Hobby (2)	6.35	-	640	80.36
Peregrine (3)	6.02±0.33	8.03±0.10	718	78.85
Honey Buzzard (1)	6.31	7.30	430	75.92
Red Kite (2)	7.49	8.40	1340	81.97
Kestrel (5)	7.19±0.12	-	538	80.18
Common Buzzard (4)	8.00±0.54	8.55±0.25	1061	81.74

The influence of prey type on digesta throughput.

Prey type influenced time taken for food to pass through the gut (Fig.4). In Peregrines and Common Buzzards, rabbit passed through the gut more quickly than pigeon. Mean retention times for Common Buzzards and Peregrines were significantly longer for the pigeon diet than for the rabbit (T=1, $P<0.05$, Wilcoxon's matched pairs).

Figure 4.

Cumulative faecal output for 3 Peregrines and 4 Common Buzzards during the initial 12 hrs of digestion. Trials were duplicated for each individual. Individuals were fed the same wet mass of pigeon and rabbit. Means and standard errors are shown.



% Cumulative faeces
100
80
60
40
20
0
0
2
4
6
8
1 0
1 2
Time after feeding (hrs)
pigeon
rabbit
pigeon
rabbit
Peregrine
Peregrine
Buzzard
Buzzard

Gut morphology

Data summarising the size and capacity of the digestive tract for 8 raptor species are shown in Table 3. Relative to body-mass, the Peregrine, Sparrowhawk, Hobby and Honey Buzzard have a small intestine volume less than expected (Fig. 5). They are also the species with more rapid throughput (Tables 1 & 2). The Red Kite and the Common Buzzard have the capacity to carry a greater mass of gut contents than species of approximately equivalent body-mass such as the Goshawk (*Accipiter gentilis*). Similarly, the Kestrel has a greater gut capacity than the Sparrowhawk. Small intestine length and small intestine volume were shown to be significantly and positively correlated ($r_{11}=0.95$, $P<0.0001$).

Table 3. Gut morphology data for 8 raptor species.

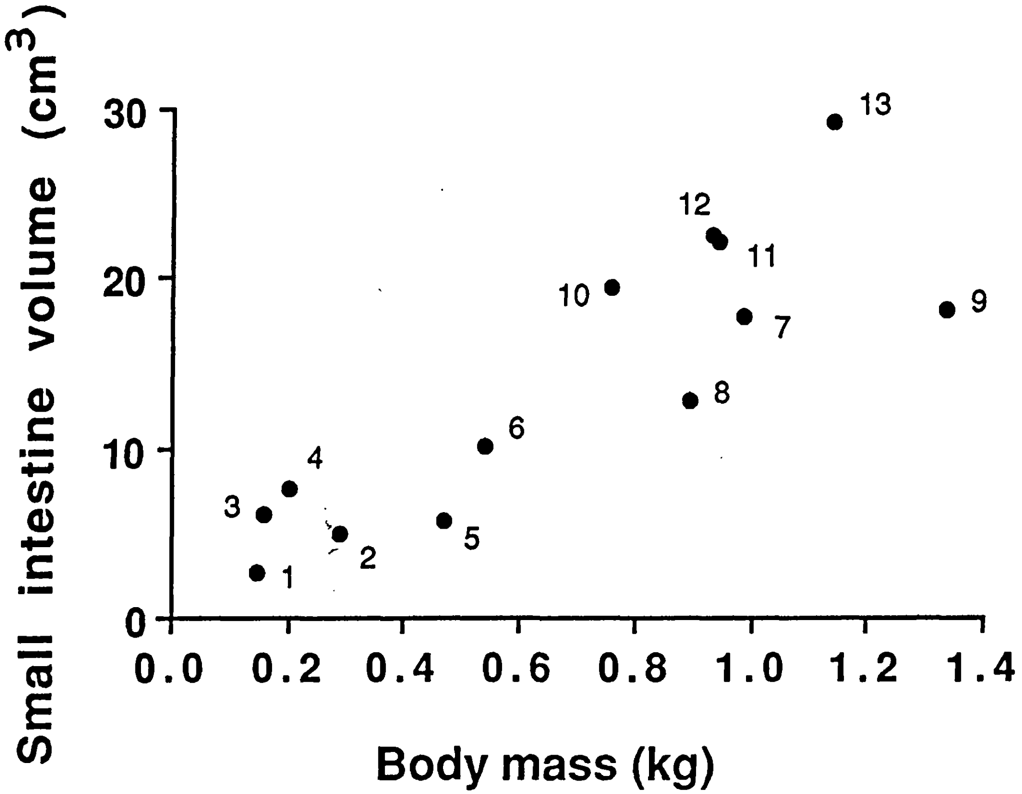
SPECIES	SEX	BODY MASS(g)	SMALL INTESTINE LENGTH (mm)	(n)	SMALL INTESTINE VOLUME (cm^3)	(n)
SPARROWHAWK	M	149	436	37	2.61	13
	F	290	581	52	5.05	18
KESTREL	M	160	525	9	6.08	5
	F	200	551	15	7.64	6
PEREGRINE	M	540	718	10	10.12	7
	F	985	954	6	17.69	2
COMMON BUZZARD	M	756	979	22	19.51	18
	F	940	1143	31	22.26	22
RED KITE	M	930	1401	7	22.49	5
	F	1137	1280	2	29.33	2
GOSHAWK	M	893	730	31	12.78	31
	F	1335	832	18	18.21	20
HOBBY	F	304	640	1	-	-
HONEY BUZZARD	M	470	430	1	5.81	1

Figure 5.

Small intestine volume plotted against body-mass to show interspecific differences in gut capacity independent of body-size.

Species codes are:

1) male Sparrowhawk; 2) female Sparrowhawk; 3) male Kestrel; 4) female Kestrel; 5) male Honey Buzzard; 6) male Peregrine; 7) female Peregrine; 8) male Goshawk; 9) female Goshawk; 10) male Common Buzzard; 11) female Common Buzzard; 12) male Red Kite; 13) female Red Kite.


Small intestine volume (cm3)
30
20
10
0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Body mass (kg)
1
2
3
4
5
6
7
8
9
10
11
12
13

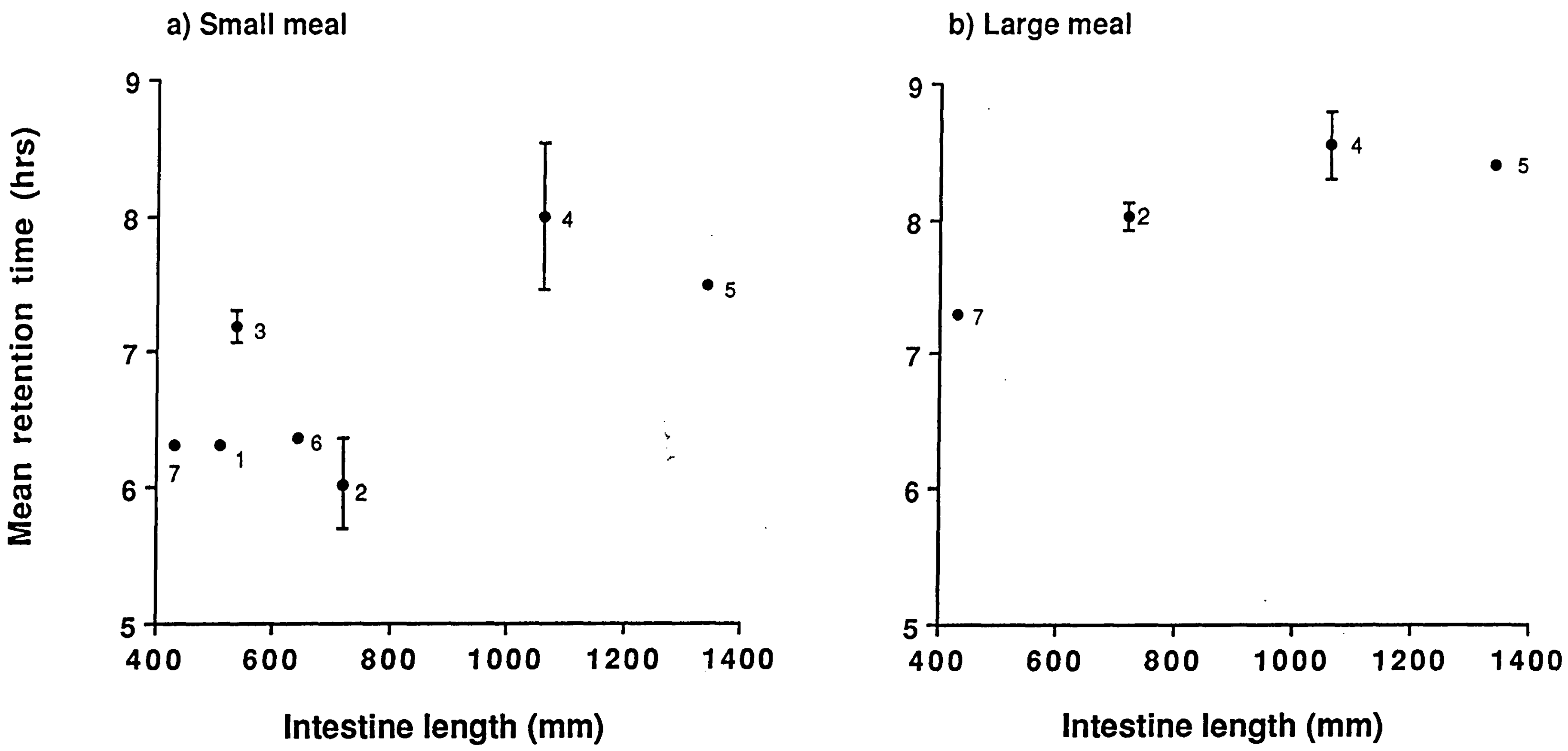
The correlation between small intestine length and mean retention time was not significant for a small meal ($r_S=0.536$, $n=7$, $P>0.05$ 2-tailed). The data did, however, show some evidence that those species with longer intestines retained food for longer even though the relationship was not significant (Figs. 6a & b). There was no direct evidence that species with short intestines increase their food retention time to increase digestive efficiency. Mean retention time and digestive efficiency were significantly and positively correlated ($r_S=0.82$, $n=7$, $P<0.05$ 2-tailed). A higher digestive efficiency was found in the Red Kite and the Common Buzzard which had longer intestines and longer retention times than in the Peregrine and the Sparrowhawk which had shorter intestines and shorter mean retention times.

Figures 6a & b.

The relationship between mean retention time and small intestine length for birds fed a small meal (Fig. 6a) and those fed a large meal (Fig 6b).

Species codes are:

1=Sparrowhawk; 2=Peregrine; 3=Kestrel; 4=Common Buzzard; 5=Red Kite; 6=Hobby; 7=Honey Buzzard.


a) Small meal
b) Large meal
Mean retention time (hrs)
9
8
7
6
5
400
600
800
1000
1200
1400
Intestine length (mm)
1
2
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DISCUSSION

It was hypothesised that the main determinant of digestive efficiency in raptors is the length of the small intestine and the time for which digesta is retained in the digestive tract. This chapter assesses whether small intestine length directly influences digesta retention time and digestive efficiency and suggests ways in which species might overcome these apparent digestive constraints. The most likely explanation for the relationship between digestive efficiency and small intestine length is that retention time of digesta is directly proportional to gut length and volume. Alternatively, throughput of digesta might in some way be slowed down in short guts, allowing longer for absorptive processes (Sibly 1981).

Various methods have been used to measure food passage most commonly using markers (Gasaway *et al.* 1975, Warner 1981, Duffy *et al.* 1985). However, attempts to use a marker during digestion studies on raptors were unsatisfactory (Barton & Houston 1991) and the most accurate method proved to be total faecal collection as used here. Parameters known to affect rate of food passage include temperature (Savory 1986), season (Prop & Vulink 1992), fasting (Harlow 1981), moulting (Jackson 1990) and prey type (Karasov & Diamond 1983, Jackson 1990, Barton this study). This chapter considers only the influence of gross gut morphology and prey type on digesta retention times.

The results provide evidence that digesta retention times are related to small intestine length. The Sparrowhawk, Hobby, Honey Buzzard and Peregrine, species with short intestines relative to body-size, had shorter transit times, reached their peak faecal output more quickly and digested more food during the initial 14 hours of digestion. The Kestrel, Red Kite and Common Buzzard, species with relatively long digestive tracts had longer transit times, a peak faecal output lagging behind other species by about 2 hours and excreted food more slowly over the initial stages of digestion. The above pattern of digestion was also found when species were fed a large meal. The Peregrine and Honey Buzzard had shorter mean retention times than the Common Buzzard and Red Kite. Many of the seabird and penguin species used by Jackson (1990) retained food for up to 70 hours after feeding, allowing time for a large number of faecal collections. Japanese Quail (Savory & Gentle 1976) and Starling (Al-Joborae 1980) eat continuously and produce droppings at much shorter intervals allowing more frequent and therefore more precise timings. As a consequence of the high digestibility of a protein diet, raptors excrete relatively few faeces and so a 2-hourly collection interval was most suitable.

A decision made by many animals is whether to eat one large meal or several small ones. Whether individuals were fed a small meal (60g) or a large meal (150g) only 60% of the faeces from that meal were excreted during the initial 16 hours of digestion. Thus, a larger volume of digesta passed along the digestive tract after the large meal than the small meal. There was no evidence that this caused reduced digestibility in the large meal, large meals were actually digested more thoroughly than small meals suggesting that it is more beneficial to eat one large meal than several small ones. The disadvantage is a higher flight cost caused by the greater load (Andersson and Norberg 1981). For species with a high basal metabolic rate which need to catch prey frequently, such as the small falcons and accipiters, rapid throughput of small meals would be beneficial in maintaining their flight energy requirements and at the same time an optimum body-mass for flight agility and hunting success.

In a study of seabird foraging ecology, Jackson (1990) found no such differences in assimilation efficiency when birds were fed meals of different sizes. In King Penguins (*Aptenodytes patagonicus*), mean retention time did not differ for meals of different size after 18 hours although small meals were excreted more quickly during the initial stages of digestion, the same as found for raptors during this study. This initial period of increased faecal output might be an adaptive strategy of rapid digestion to reduce flight costs in species with expensive foraging modes. An alternative explanation is that the more easily digestible portions of a meal move through the digestive tract more quickly. However, this would seem unlikely due to the fact that a very uniform food type such as rabbit, also produced this initial period of rapid digestion. In studies by Prop and Vulink (1992) and Harlow (1981), length of time for which digesta remained in the gut did influence assimilation efficiency. Thus, the results of this study suggest that species with long retention times relative to body-size would have high assimilation efficiencies and conversely, those species with a short digestive tract relative to body-size would have short retention times and reduced digestive efficiency.

Faecal excretion ceased after 16 hours in all species. One reason for this is lights were switched off at this time. It is possible that the digestive processes slow down at nighttime, the birds sleep and defaecation recommences at dawn when birds awaken, by which time most of the digesta had passed through the gut and was probably in the colon ready for excretion. It would be expected that over the initial 16 hour digestion period a larger proportion of a small meal would be digested and excreted compared to the proportion of a large meal digested in the same time. However, a greater absolute mass was digested from the large meal. I suggest that this result is a combination of a circadian rhythm and lack of bulk stimulus required for defaecation. When fed a small meal, most food appears to have been digested and excreted 8-10 hours after feeding, at which time the cumulative curve had reached a plateau (Fig. 3). This could be because insufficient bulk was in the colon and so faecal pressure was not high enough for defaecation. When fed a large meal, the cumulative curve is increasing at a greater rate but seems to stop during the nocturnal part of the digestive cycle. This does not mean that digestion ceased, although there is evidence to suggest that digestion slows down during the night. Pellets were also cast at dawn, supposedly a mechanism by which diurnal raptors ensure being able to start feeding again shortly afterwards (Duke 1987). Virtually all of the faeces had also been excreted by the time of pellet egestion and so diurnal raptors would be at their optimum flying weight at this time of day.

Prey profitibility is an important consideration for raptors. It is clear that even subtle differences in diet must be considered when interpreting throughput data and digestive efficiency. Both rabbit and pigeon are high in protein content, but the lower water content and high fat content of pigeon result in longer mean retention times. Such differences in prey retention times might result in differences in digestive efficiency and so prey choice could be an important determinant in overcoming the apparent digestive constraints which one would predict from these results.

For raptors it seems as if there are 2 alternative digestion strategies depending on the foraging niche they occupy. The Peregrine, Sparrowhawk and Hobby which chase active prey have a short digestive tract resulting in rapid throughput and short mean retention times relative to their body-size. The benefit of such a strategy is that the load incurred by catching and ingesting prey is rapidly reduced enabling a return to a more efficient flying weight. The Common Buzzard, Kestrel and Red Kite have a long, high capacity digestive tract relative to body-size with a long mean retention time. The Honey Buzzard is an apparent anomaly. It is not a very active predator but nevertheless has a short digestive tract. Honey Buzzards feed predominantly on the larvae of social Hymenoptera, perhaps a food with high digestibility for which only a short digestive tract would probably be required.

It seems that in raptors, there is no compensatory mechanism by which food passage can be slowed in species with a relatively short digestive tract. It is suggested that a direct consequence of these results is a high digestive efficiency in raptors such as the Common Buzzard and the Red Kite enabling them to occupy a generalist feeding niche. The Sparrowhawk, Peregrine and Hobby are specialists on agile prey, the benefits of which presumably outweigh the apparent digestive constraint of short food retention time and predicted reduction in digestive efficiency.

REFERENCES

Al-Joborae, F.F. (1980) The influence of diet on the gut morphology of the Starling (*Sturnus vulgaris L.* 1758). Unpublished Ph.D. thesis, University of Oxford.

Andersson, M. & Norberg, R.A. (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol J. Linn. Soc.* **15:** 105-130.

Barton, N.W.H. & Houston, D.C. (1991) The use of titanium dioxide as an inert marker for digestion studies in raptors. *Comp. Biochem. Physiol.* **100A:** 1025-1029.

Cramp, S. & Simmons, K.E.L. (1980) *Handbook of the Birds of Europe, the Middle East and North Africa. Vol. 2.* Oxford: Oxford University Press.

Davies, P.W. & Davis, P.E. (1973) The ecology and conservation of the Red Kite in Wales. *British Birds* **66:** 183-224; 241-270.

Duffy, D.C. (1985) Two methods of measuring food transit rates of seabirds. *Comp. Biochem. Physiol.* **82A:** 781-785.

Duke, G.E. (1987) Gastrointestinal Physiology and Nutrition. *In* Giron Pendleton, B.A., Millshap, B.A., Cline, K.W. & Bird, D.M. (eds), *Raptor Management Techniques Manual.* Washington, D.C.: Natl. Wildl. Fed.

Gasaway, W.C., Holleman, D.F. & White, R.G. (1975). Flow of digesta in the intestine and cecum of the Rock Ptarmigan. *The Condor* **77:** 467-474.

Harlow, H.J. (1981) Effect of fasting on rate of food passage and assimilation efficiency in badgers. *J. of Mammalogy* **62:** 173-177.

Jackson, S. (1990) Seabird digestive physiology in relation to foraging ecology. University of Cape Town.

Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Studies in Avian Biology* **13:** 391-415.

Karasov, W.H. & Diamond, J.M. (1983) Adaptive regulation of sugar and amino acid transport by vertebrate intestine. *Am. J. Physiol.* **245:** G443-462.

Karasov, W.H. & Levey, D.J. (1990) Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiol. Zool.* **63:** 1248-1270.

Leopold, A.S. (1953) Intestinal morphology of gallinaceous birds in relation to food habits. *J. Wildl. Mgt.* **17:** 197-203.

Penry, D.C. & Jumars, D.L. (1987) Modeling animal guts as chemical reactors. *Am. Nat.* **129:** 69-96.

Prop, J. & Vulink, T. (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Functional Ecology* **6:** 180-189.

Robbins, C.T. (1983) *Wildlife Feeding and Nutrition*. New York: Academic Press.

Savory, C.J. (1986) Influence of ambient temperature on feeding activity parameters and digestive function in domestic fowls. *Physiology and Behav.* **38:** 353-357.

Savory, C.J. & Gentle, M.J. (1976) Effects of dietary dilution with fibre on the food intake and gut dimensions of japanese quail. *Br. Poult. Sci.* **17:** 561-570.

Sibly, R.M. (1981) Stategies of digestion and defecation. *In* C.R. Townsend & P. Calow (eds). *Physiological Ecology: an Evolutionary Approach to Resource Use.* Massachussetts: Sinauer Associates.

Siegel & Castellan (1988) *Non-parametric Statistics for the Behavioural Sciences.* New York: McGraw-Hill.

Tubbs, C.R. (1974) *The Buzzard.* London: David & Charles.

Warner, A.C.I. (1981) Rate of passage of digesta through the gut of mammals and birds. *Nutr. Abs. Rev.* **B51:** 780-820.

CHAPTER 7

A comparison of digestive efficiency in birds of prey.

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The data presented in this chapter form the basis of a paper submitted to Ibis 1992.

ABSTRACT

Raptors exhibit a wide range of foraging strategies associated with their prey. Differences in how they hunt and what they catch has resulted in size-independent differences in length of the small intestine, the region of the digestive tract responsible for food absorption. The study used 10 raptor species to examine the functional significance of these differences. Dry matter apparent digestive efficiency was calculated for each species fed a diet of day-old cockerels. For Falconiformes and Strigiformes efficiencies varied between 75% and 82%, digestive efficiency being positively correlated with intestine length.

Generalist species with a wide prey spectrum and feeding on relatively easily caught prey and carrion had long intestines and high digestive efficiencies. Raptors specialising on fast-moving, avian prey had short intestines and reduced digestive efficiency. The Peregrine Falcon and the Common Buzzard were used as examples of specialist and generalist feeders respectively. Rabbit and pigeon were fed to both. Buzzards digested both diets more efficiently than Peregrines. Body-mass changes were used to examine the nutritional value of the two diets to each species. Buzzards gained body-mass when eating rabbit, Peregrines lost mass. Both species gained mass when feeding on pigeon. It seems that diet quality, not just quantity, is essential in understanding raptor food requirements. Generalist raptors have high efficiencies on several diets, specialists compensate for their reduced efficiency by eating food of high nutritional quality. Various aspects of prey quality are examined.

INTRODUCTION

The amount an animal eats depends on how efficiently it can use its food. The less efficient an animal's digestion the more food it is likely to require, and conversely the more efficiently an animal digests its food, the less it requires. Energy requirements for daily and seasonal activities must be balanced by sufficient energy intake. The efficiency with which an animal digests its food therefore influences foraging activity and subsequent energy availability (Kendeigh 1949, Karasov 1990). It has been suggested that some species suffer food processing constraints (Karasov *et al.* 1986b, Temeles 1989) in that there is an upper limit to metabolizable energy intake (Kirkwood 1983) and consequently a ceiling to energy expenditure (Drent & Daan 1980, Bryant & Tatner 1991). Species might therefore be expected to maximise digestive efficiency.

This chapter examines digestive efficiency in the Falconiformes and Strigiformes. It has previously been assumed that because virtually all raptor species eat meat, they will have approximately equal efficiencies (Kirkwood 1979, Castro *et al.* 1989, Karasov 1990). There are, however, reasons to suppose that this may not be the case. The principal organ involved in food absorption is the small intestine (Robbins 1983). Chapter 3 found size-independent differences in intestine length up to 50% between raptor species. The Falconiformes were divided into 2 groups depending on their requirements for active chase. Those species with more than 75% avian prey in the diet (Brown 1978) were categorised as attackers such as Sparrowhawk (*Accipiter nisus*), Peregrine (*Falco peregrinus*), Hobby (*Falco subbuteo*) and Goshawk (*Accipiter gentilis*). Species feeding predominantly on mammals and carrion were categorised as searchers such as Common Buzzard (*Buteo buteo*), Red Kite (*Milvus milvus*), Golden Eagle (*Aquila chrysaetos*) and Kestrel (*Falco tinnunculus*). Within the Strigiformes, those species with a more active search mode, Barn Owl (*Tyto alba*) and Long-eared Owl (*Asio otus*) were compared with a less active species, the Tawny Owl (*Strix aluco*).

Attackers, specialists on fast-moving, agile prey were found to have relatively short digestive tracts. Generalist searchers feeding on relatively slow-moving prey or carrion were found to have long digestive tracts.

I suggest that these differences may have arisen because different styles of predatory behaviour may give rise to different selection pressures. Thus, predators which need to accelerate rapidly when chasing after active prey might be expected to show extreme strategies for weight reduction in the body, such as a reduced size of the digestive tract. Other predatory species which rely more on soaring flight, and whose predation method is a pounce onto prey from above, might not be so constrained. There is, presumably, an optimum gut length for maximum digestive efficiency. Any reduction in the length of the gut might be expected to result in less efficient food absorption in the absence of a compensatory increase in absorption rate (Karasov 1990). Birds would be expected to develop the optimal gut anatomy unless a shorter tract resulted in a higher rate of prey capture to compensate for the lower digestive efficiency. In this chapter I consider whether the differences that have been recorded in small intestine length between species do actually result in differences in digestive efficiency. To do this I report on a series of feeding trials in which the same quality diet was fed to ten different raptor species to consider whether there was any correlation between apparent digestive efficiency and gut length.

I also speculate on the implications of such variation for prey selection in raptors. For generalist feeders and those species feeding on a spatially and temporally unpredictable food supply, efficient digestion of a wide range of food types would be adaptive. For specialist hunters such as those feeding predominantly on avian prey, adaptation to one food type may entail a drop in digestive efficiency on other food types. Falconers have been aware for centuries that prey species differ considerably in quality. Woodford (1977) comments "When dieting hawks, the quality as well as the volume of meat must be taken into account. Woodpigeon is twice the feeding value of an equal amount of rabbit.

Rabbit is good for Goshawks and as a change for Peregrines, but it is too light and poor in food value for smaller hawks. Young house pigeons are nourishing food for all hawks, grouse are very rich and should be fed sparingly. Hare is much more nourishing than rabbit. Blackbirds, thrushes and other small birds are all excellent food for small hawks." This suggests that if some predatory birds are less efficient at digesting prey than others, those species with reduced digestive ability may not be able to utilise 'low quality' prey and so have reduced prey availability compared to species with high digestive efficiency.

I considered whether this may occur by a series of feeding trials in which digestive efficiency was compared for a specialist, attacking hunter, the Peregrine Falcon and a generalist, searching hunter, the Common Buzzard, on two diets of different quality, these being pigeon and rabbit meat. Finally I analysed meat samples from six prey species to consider what factors might contribute to the quality of prey animals. I considered the relative quality of fresh prey compared to carrion which had been left for varying periods of time. Comparatively few raptor species will eat carrion and I speculate on why this food source is not taken more widely by predatory birds.

METHODS

Digestive efficiency of ten raptor species fed the same diet.

A diet of day-old cockerels (*Gallus gallus*) was fed to captive individuals from 10 raptor species: 2 Red Kites, 2 Golden Eagles, 5 Common Buzzards, 4 European Kestrels, 11 Peregrine Falcons, 2 European Hobbies, 2 European Sparrowhawks, 3 Tawny Owls, 3 Barn Owls and 4 Long-eared Owls. The falconiform species were accustomed to being handled daily and had been trained by falconry techniques (Glasier 1978). They had previously been tethered and remained so for the duration of the trial. Each Strigiform was untethered in a holding box (1x1x1m) with one horizontal perch. Birds were weighed at the beginning, during and end of the feeding period in an attempt to maintain their body mass within ±2% of their initial mass (Stalmaster & Gessaman 1982). Birds were kept indoors at prevailing ambient temperature, photoperiod and humidity.

To achieve adequate sample sizes it was necessary to use birds from three different locations. Two feeding trials were conducted in June/July at average midday temperatures between 20 and 30°C and relative humidity 40-50%. One trial had to be conducted in November/December at ambient temperatures of -5°C to 0°C and relative humidity 40-55%.

Early attempts to measure digestibility using a marker technique were unsuccessful (Barton & Houston 1991) and total weight of food and faeces were used to determine apparent digestive efficiency. To measure total faecal and pellet production a clear plastic sheet was secured beneath each bird. For the Strigiformes a sliding tray on the base of the box was lined with plastic. It was possible to separate the faeces from the uric acid in Falconiformes and Strigiformes. Samples were collected and sheets washed daily. The birds had been fed a diet of day-old chicks prior to the trial and were fed the same diet during the trial. Stomach, yolk sac and intestine were removed from each chick to minimise spillage and leftovers. Food was weighed before presentation to the birds.

Falconiformes were fed daily at 10 a.m. and Strigiformes at 8 p.m.

Feeding trials lasted an average of 10 days. A random sample of chicks was taken during each trial, prepared in the same way as those being fed and then dried at $70^{o}C$ to constant mass. The calculated water content was then used to convert wet food intake to dry mass. Faecal samples and pellets were stored at $-20^{o}C$ and were dried to constant mass at $70^{o}C$, cooled in a dessicator and weighed to 1mg. Apparent digestive efficiency was calculated as:

$$1 - \left(\frac{\text{dry faeces(g)} + \text{dry pellets(g)}}{\text{dry food intake(g)}}\right) \times 100 .$$

Intestine length independent of body-size was calculated by plotting intestine length against a calculated value for skeletal body-size, drawing a line through the points and measuring the extent to which each species deviated from the predicted value of small intestine length. Species were therefore classified as having intestine lengths longer or shorter than predicted on the basis of the magnitude of residuals from the line. If a large and a small bird have the same residual, the small bird effectively has a longer intestine relative to body-size. Therefore, percentage residual intestine length was calculated by taking the residual deviation from the predicted length, as a percentage of the predicted small intestine length.

Comparison of digestive efficiency for Peregrine Falcon and Common Buzzard.

Two diets were used, wild-caught rabbit (*Oryctolagus cuniculus*) and domestic pigeon (*Columba livia*). Two approaches were used to examine food utilisation, the first was to determine apparent digestive efficiency, the second to look at the direct effect that feeding each diet had on changes in body-mass.

The feeding trials were conducted at temperatures between 0 and $10^{o}C$ and involved 4 Common Buzzards and 4 Peregrine Falcons. At the start of each trial, birds were judged to be at their falconry 'flying weight' (Glasier 1978) with little or no fat reserves.

Food was freshly killed and stored frozen. Each bird was fed a known and equal amount of rabbit meat for 8 consecutive days and pigeon meat for 8 consecutive days. The food was fed without fur, bone or feather so that pellets would not be produced. All external fat was stripped from the meat. It is recommended to feed captive raptors roughage at least once a week for normal digestive functioning (Glasier 1978) and so after feeding the rabbit diet for 8 days, whole day-old cockerels were fed for 2 days during which time no data were collected. The birds were then fed on the pigeon diet. The experimental procedure, sample collection and storage were as previously described. Birds were weighed at the same time each day prior to feeding in order to measure body-mass changes on the two diets.

The quantity of food given was calculated for both diets as that sufficient to provide the metabolisable energy requirements for maintenance (ME_m) for individuals and species of differing body-size, using Kirkwood's (1981) equation

$$ME_m = (110 \times M^{0.679} \times 4)/4.5$$

where M is body-mass in kg and assuming raptor diets have a calorific value of 4.5 kcal/g and 25% water content (calculated from preliminary studies).

Nutritive values of natural diets.

Some aspects of the nutritive value of six diets were considered: domestic pigeon (*Columba livia*), rabbit (*Oryctolagus cuniculus*), hare (*Lepus capensis*), pheasant (*Phasianus colchicus*), crow (*Corvus corone*) and sheep. A fresh meat sample was taken from carcasses of each meat type. Water, fat and nitrogen contents were determined by freeze-drying, Soxhlet extraction (chloroform solvent) and Kjeldahl techniques respectively and amino acid analysis was undertaken. Energy content was determined by macro-bomb calorimetry.

To consider the changes that might occur when carcasses were left as a source of carrion I left whole carcasses at sites where they were ventilated but not exposed to precipitation on a soil substrate at ambient temperatures in December/January (mean minimum temperature 2^{o}C, mean maximum temperature 8^{o}C). Meat samples were then taken at weekly intervals for 7 weeks. These carrion samples were analysed for fat-free calorific content to see if exposure time affects the energetic value of the meat and therefore its value as a food source.

RESULTS

How comparable are captive birds with wild birds ?

An underlying assumption in using captive animals is that the basic physiological processes of digestion are comparable between wild and captive states. There is some evidence that birds kept in captivity can develop very different gut morphology than those in the wild (e.g. Red Grouse; *Lagopus lagopus*, Moss 1972, Barnacle Geese; *Branta leucopsis*, Owen 1975), however these differences are associated with a difference in diet in captivity. In the case of raptors, the captive diet does not differ substantially from that taken in the wild. In addition, this study is concerned with interspecific comparisons and so any changes which are a consequence of the captive state, provided they affected all species equally, would not be expected to affect the overall comparative result.

It is difficult to test the above assumption because of the problems in conducting digestion trials on unrestrained animals (Barton & Houston 1991). However, a small sample of carcasses was available from birds which had died in captivity and this enabled a basic comparison of the gross gut morphology between wild and captive birds. Wild bird intestines are from carcasses which had been found dead in the field and sent to laboratories for pesticide analysis. Intestine length has been shown to be the most appropriate measure of gross gut morphology (Chapter 2). Table 1 shows the 95% confidence interval from captive and wild carcass data for each species studied. The mean values for captive species were within the 95% C.I. in each case.

Table 1. Mean small intestine lengths from a small sample of several raptor species which had died in captivity compared with the 95% confidence intervals for small intestine lengths using data from carcasses found in the wild (data from Chapter 3).

		WILD INTESTINE LENGTH (mm)			CAPTIVE INTESTINE LENGTH (mm)		95% CONFIDENCE INTERVAL
SPECIES	SEX	mean	n	s.d.	mean	n	
SPARROWHAWK	F	582	51	86	570	1	582 ± 24
PEREGRINE	F	952	3	77	957	3	952 ± 191
	M	745	4	92	708	5	745 ± 146
KESTREL	F	557	10	79	513	3	557 ± 56
RED KITE	F	1175	1	-	1385	1	-
	M	1497	2	2	1362	5	-
LONG-EARED OWL	F	458	3	64	460	1	458 ± 159

Digestive efficiency for ten species on the same diet.

The feeding trials reported here had to be performed at two different times of year and temperature conditions and so differences between the birds used in December ($0^{o}C$) and those used in July ($>20^{o}C$) might have been caused by seasonal differences in digestive efficiency rather than individual or species differences. Digestion data for each individual are summarised in Table 2 ($0^{o}C$) and Table 3 ($>20^{o}C$). To see whether seasonal differences were not significant, and therefore whether the data could be combined, apparent digestive efficiency was measured for the same 9 individuals at $20^{o}C$ and at $0^{o}C$ (Table 4).

Table 2. Digestive efficiency and food intake data for 7 raptor species fed a diet of day-old cockerel at $0^{o}C$.

SPECIES	SEX(M/F)	BODY (g) MASS	DAILY WET FOOD INTAKE (g)	% DIGESTIVE EFFICIENCY	NO. OF DAYS	S.D.
RED KITE[a]	M	1000	184	78.66	11	3.13
RED KITE[b]	F	1270	184	79.47	10	2.91
HOBBY[c]	M	195	48	78.45	9	1.52
HOBBY	F	190	56	77.85	4	1.90
COMMON BUZZARD[d]	F	1000	139	77.16	8	2.76
COMMON BUZZARD[e]	M	820	118	76.66	8	4.22
COMMON BUZZARD[f]	F	795	167	80.22	8	2.38
COMMON BUZZARD[g]	M	775	130	76.90	10	1.62
HONEY BUZZARD	F	940	122	75.92	8	3.51
GOLDEN EAGLE	M	3750	451	80.31	6	2.49
PEREGRINE	M	575	143	75.02	13	1.14
PEREGRINE	M	510	143	75.08	11	1.54
PEREGRINE[h]	M	565	141	75.83	14	1.57
KESTREL	F	210	80	77.10	15	2.05
KESTREL[j]	M	195	62	77.17	7	1.68

Table 3. Digestive efficiency and food intake data for 10 raptor species fed a diet of day-old cockerel at 20°C.

SPECIES	SEX(M/F)	BODY (g) MASS	DAILY WET FOOD INTAKE (g)	% DIGESTIVE EFFICIENCY	NO. OF DAYS	S.D.
RED KITE[a]	M	950	160	82.44	13	3.28
RED KITE[b]	F	1210	185	81.50	11	2.35
HOBBY[c]	M	165	46	80.36	15	1.46
COMMON BUZZARD[d]	F	900	132	80.79	14	1.79
COMMON BUZZARD	F	750	111	81.09	14	5.88
COMMON BUZZARD[e]	M	730	112	82.14	14	2.18
COMMON BUZZARD[f]	F	800	131	82.92	13	2.92
COMMON BUZZARD[g]	M	730	116	80.80	10	1.82
GOLDEN EAGLE	F	-	246	79.04	7	1.85
PEREGRINE[h]	M	535	101	78.85	13	2.44
PEREGRINE	F	740	101	73.49	8	1.76
PEREGRINE	M	600	78	73.81	7	0.77
PEREGRINE	F	770	91	71.81	7	3.20
PEREGRINE	F	896	134	75.42	7	1.30
PEREGRINE	M	566	94	77.05	7	2.71
PEREGRINE	F	750	129	75.27	7	2.52
PEREGRINE	M	570	117	75.52	6	1.71
PEREGRINE	M	580	82	76.19	6	1.84
SPARROWHAWK	F	260	64	79.28	6	2.45
KESTREL	F	195	66	77.21	8	2.28
KESTREL[j]	F	210	59	79.83	8	1.19
KESTREL	F	180	46	83.99	8	1.46
KESTREL	M	180	55	79.69	15	1.72
TAWNY OWL	*	495	79	82.80	13	3.60
TAWNY OWL	*	550	77	82.60	10	4.80
TAWNY OWL	*	415	79	81.90	12	4.60
BARN OWL	*	280	67	77.50	11	3.40
BARN OWL	*	255	71	79.40	9	8.30
BARN OWL	*	295	68	78.30	11	2.50
LONG-EARED OWL	*	275	64	79.90	6	6.60
LONG-EARED OWL	*	255	77	79.40	11	1.20
LONG-EARED OWL	*	265	62	74.40	9	5.20
LONG-EARED OWL	*	315	57	76.60	8	2.60

* sex undetermined

Table 4. Digestive efficiency for the same 9 individuals in summer (>20^{o}C) and winter (0^{o}C) fed on a diet of day-old cockerel.

SPECIES	SUMMER % EFFICIENCY	WINTER % EFFICIENCY	DIFFERENCE
RED KITE[a]	82.44	78.66	3.78
RED KITE[b]	81.50	79.47	2.03
HOBBY[c]	80.36	78.45	1.91
COMMON BUZZARD[d]	80.79	77.16	3.63
COMMON BUZZARD[e]	82.14	76.66	5.48
COMMON BUZZARD[f]	82.92	80.22	2.70
COMMON BUZZARD[g]	80.80	76.90	3.90
PEREGRINE[h]	78.85	75.83	3.02
KESTREL[j]	79.83	77.17	2.66

mean percentage difference=3.23%, n=9, s.d.=1.11.

There was, however, a significant 3% difference between the median digestive efficiency at 20^{o}C (summer) and at 0^{o}C (winter) ($T=0$, $P<0.001$, Wilcoxon's test for matched pairs). Data from winter and summer feeding trials were therefore not combined in subsequent analyses. The day-old chick diet was equivalent in water content for each feeding trial (ANOVA, $F_{2,36}=0.412$, $P=0.665$, data were arcsine transformed). Inaccurate estimation of dry food intake from wet food intake could not therefore account for any differences found.

Across the falconiform species in summer, dry matter digestive efficiency varied between 71.8% and 82.9% with a mean value of 78.6% (n=23, s.d.= 3.31%). Using those species for which both intestinal morphology data and digestive efficiency data were available, the relationship between intestine length (% residual intestine length) and digestive efficiency was examined. For this analysis, only those individuals were used which had their apparent digestive efficiency measured simultaneously. This reduces sample size but minimises any bias caused by different experimental conditions. From Fig. 1 small intestine length and digestive efficiency were positively correlated for birds measured at

$20^{o}C$ ($r_s=0.82$, $n=9$, $P<0.01$ 2-tailed) but not at $0^{o}C$ ($r_s=0.7$, $n=5$, $P>0.05$).

The mean apparent digestive efficiencies for Peregrines, Buzzards and Red Kites were 75.3%, 81.5% and 82.0% respectively (all measured in summer conditions). The median digestive efficiency for the 9 Peregrines was significantly less than for the 2 Red Kites ($P<0.01$, Mann-Whitney U-test) and the 5 Common Buzzards ($P<0.01$, Mann-Whitney U-test). Mean digestive efficiency for the Tawny Owl, Barn Owl and Long-eared Owl were 82.4%, 78.4% and 77.6% respectively (Table 3), the Tawny Owl having a significantly higher digestive efficiency than the Barn Owl and the Long-eared Owl ($P<0.05$, Man-Whitney U-test).

Figure 1.

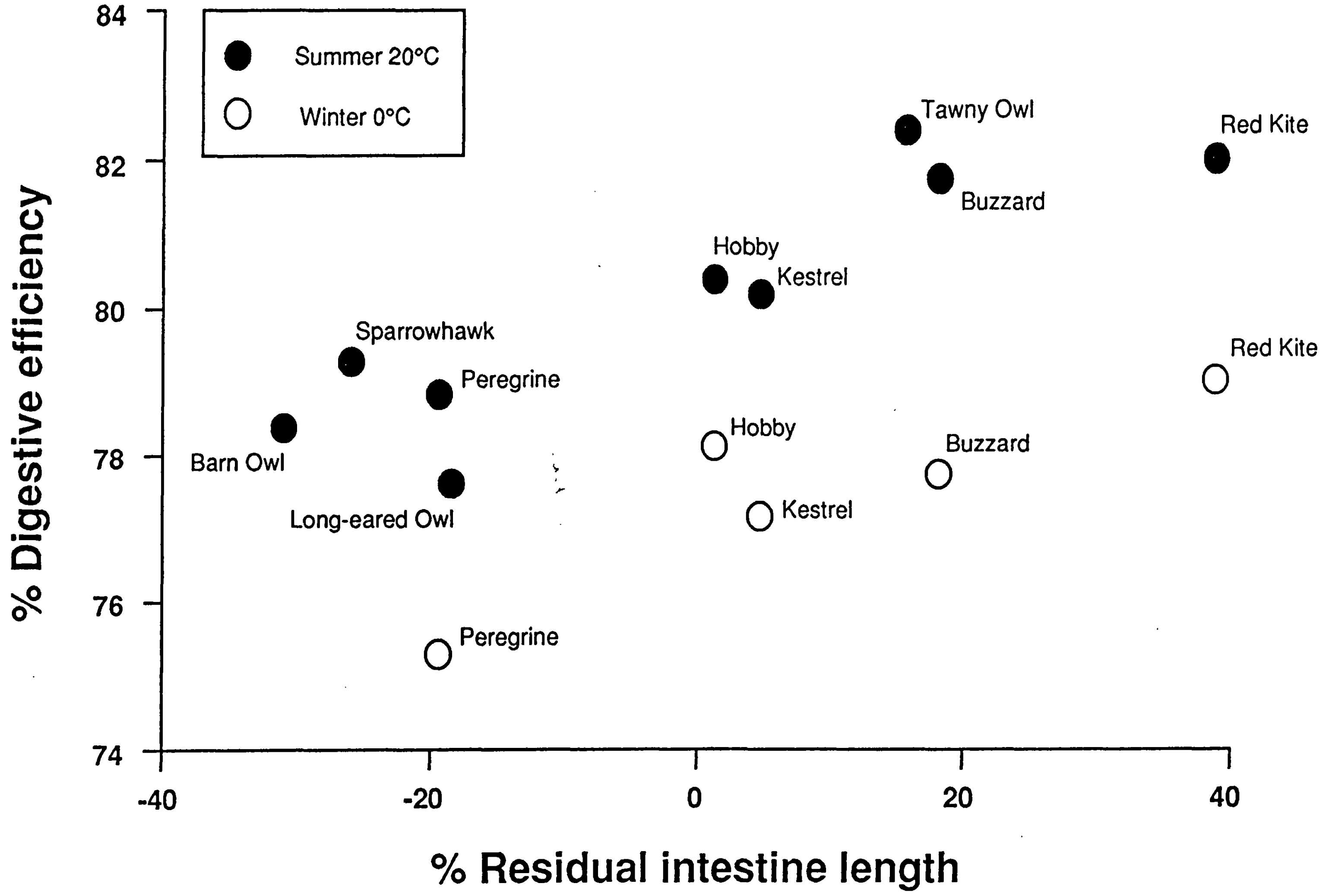
The relationship between digestive efficiency and small intestine length. The % residual intestine length is the residual of the small intestine, calculated as a percentage of the predicted small intestine length for each species (see methods). A full description for the calculation of residual and predicted intestine lengths is given in Chapter 3.

Percentage digestive efficiency values are means for each species. Sexes were combined for carcass data and efficiency data.

Sample sizes for summer were: 2 Red Kites (9); 5 Common Buzzards (53); 4 Kestrels (24); 1 Hobby (1); 1 Peregrine (16); 1 Sparrowhawk (89); 3 Tawny Owls (10); 3 Barn Owls (50); 4 Long-eared Owls (8).

Sample sizes for winter were: 2 Red Kites; 4 Common Buzzards; 2 Kestrels; 2 Hobbies; 3 Peregrines.

Sample sizes for intestinal morphology are in parentheses.


Summer 20°C
Winter 0°C
% Digestive efficiency
84
82
80
78
76
74
% Residual intestine length
-40
-20
0
20
40
Tawny Owl
Red Kite
Buzzard
Hobby
Kestrel
Sparrowhawk
Peregrine
Red Kite
Barn Owl
Hobby
Buzzard
Long-eared Owl
Kestrel
Peregrine

Apparent digestive efficiency for Peregrines and Buzzards feeding on rabbit and pigeon.

The apparent digestive efficiency for Peregrines and Buzzards feeding on the two diets are summarised in Table 5. Very high apparent digestive efficiencies were found in both Peregrines and Buzzards (93-97% of the food intake being absorbed). There was no significant difference in the efficiency with which Buzzards ($P>0.05$, Mann-Whitney U-test) or Peregrines ($P>0.05$, Mann-Whitney U-test) digested rabbit and pigeon. Buzzards digested rabbit 2.14% more efficiently than Peregrines ($P<0.05$, Mann-Whitney U-test) and pigeon 1.69% more efficiently ($P<0.05$, Wilcoxon rank-sum test).

Table 5. Digestive efficiency data for 4 Peregrines and 4 Buzzards fed for 8 days on each of 2 diets, rabbit and pigeon. Mean and standard deviation are given for each species on each diet.

SPECIES	WET FOOD INTAKE (g)	RABBIT MEAN % EFFICIENCY	DAYS FED	S.D.	PIGEON MEAN % EFFICIENCY	DAYS FED	S.D.
PEREGRINE 1	92.0	93.83	8	1.07	-	-	-
PEREGRINE 2	67.1	95.29	8	0.81	94.43	8	0.70
PEREGRINE 3	65.1	94.41	8	0.96	93.89	8	0.63
PEREGRINE 4	64.3	93.17	8	1.85	93.96	8	1.16
MEAN		94.17 %			94.09 %		
n		4			3		
s.d.		0.90			0.29		
BUZZARD 1	92.0	96.72	8	0.88	95.79	8	0.84
BUZZARD 2	84.0	96.93	8	0.36	96.28	8	0.50
BUZZARD 3	77.1	95.45	8	1.39	95.33	8	0.66
BUZZARD 4	76.0	96.14	8	0.67	95.73	8	1.09
MEAN		96.31 %			95.78 %		
n		4			4		
s.d.		0.66			0.39		

Changes in body-mass.

When feeding on rabbit for 8 days, the Peregrines lost an average of 5.01% of their initial body-mass, the Buzzards gained 2.78%. When fed the same mass of pigeon, the Peregrines gained an average of 1.81% of initial body-mass and the Buzzards gained 7.17% (Fig. 2). Buzzards gained significantly more mass than Peregrines when fed on either rabbit or pigeon ($P<0.05$, Mann-Whitney U-test). Buzzards gained significantly more mass when feeding on pigeon than on rabbit ($P<0.05$, Mann-Whitney U-test). Peregrines also gain more mass when feeding on pigeons than on rabbits ($P<0.05$, Wilcoxon rank-sum test).

Food composition.

Results for the composition of the 6 diets examined are summarised in Tables 6 and 7. The largest differences were found in fat content which varied between 0% in the pheasant and 40% in sheep. Nitrogen values, which can be used to approximate protein content, were high, those species with high fat content generally having lower nitrogen values or protein content. Gross energy values varied between 23.2kJ/g in pheasant with low fat and 29.5kJ/g in pigeon with high fat content. Only a small amount of variation was found in the amino acid composition of the 6 diets (Table 7).

Fat content ($F_{5,39}=96.4$, $P<0.0001$), gross energy ($F_{5,39}=30.39$, $P<0.0001$) and lean energy content ($F_{5,39}=13.2$, $P<0.0001$) differed significantly across the 6 prey species. Pigeon had a higher fat content than rabbit, crow, pheasant and hare (Scheffé, $P<0.05$). No fat was extracted from pheasant using chloroform as the solvent. Sheep had a significantly higher gross energy value than all other species. Pigeon had a significantly higher gross energy value than pheasant and had the highest lean energy content. Crow had the lowest lean energy content.

Figure 2.

Body-mass change over an 8-day period to compare the effect of feeding an equal wet weight of rabbit and pigeon to Buzzards and Peregrines. Each individual was fed the same amount of the 2 diets. Birds were weighed every 2 days and individuals showed either a gradual gain or loss in mass. Lines are drawn from starting mass to final mass to emphasise the direction of change for each individual.

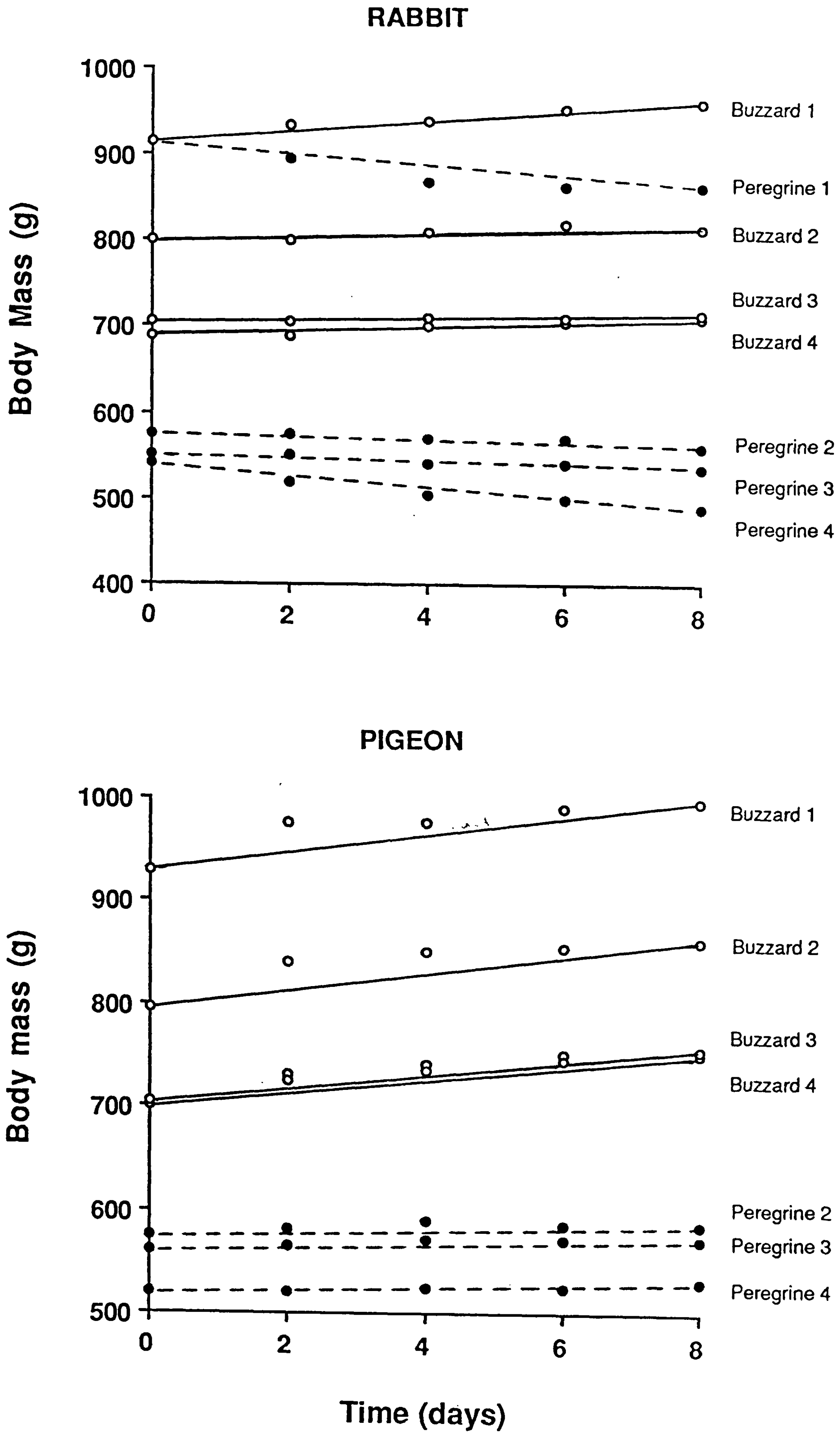

RABBIT
Body Mass (g)
1000
900
800
700
600
500
400
0
2
4
6
8
Buzzard 1
Peregrine 1
Buzzard 2
Buzzard 3
Buzzard 4
Peregrine 2
Peregrine 3
Peregrine 4
PIGEON
Body mass (g)
1000
900
800
700
600
500
0
2
4
6
8
Buzzard 1
Buzzard 2
Buzzard 3
Buzzard 4
Peregrine 2
Peregrine 3
Peregrine 4
Time (days)

Table 6. Water, fat, nitrogen and energy composition of fresh food and 7-week old carrion for 6 possible raptor prey items.

PREY TYPE	WATER CONTENT %	FAT CONTENT %	NITROGEN CONTENT g/kg	GROSS ENERGY kJ/g	LEAN ENERGY kJ/g	LEAN CARRION kJ/g
RABBIT	74.25±1.04	5.0±1.6	144	24.72±0.58	23.22±0.49	22.90
n	10	10		10	10	
PIGEON	72.21±1.41	20.7±2.6	130	25.67±0.45	23.86±0.54	23.79
n	10	10		10	10	
PHEASANT	72.43	0.0±0.0	148	23.18±0.19	22.19±0.16	22.28
n	1	5		5	5	
HARE	74.79	11.7±2.3	138	25.16±0.85	23.54±0.81	22.67
n	1	5		5	5	
SHEEP	73.09	40.3±1.8	120	29.51±2.18	23.66±0.85	22.60
n	1	5		5	5	
CROW	69.61	8.6±1.2	113	24.26±0.13	21.82±0.23	21.79
n	5	5		5	5	

Rabbit and pigeon were also compared separately to allow a more thorough interpretation of the feeding trial in which these two diets were fed to Peregrines and Buzzards. Rabbit and pigeon differed in fat content (5% and 21% respectively; $t_{18}=17.6$, $P<0.0001$), dry matter (74.25% and 72.21%; $t_{18}=3.49$, $P<0.005$) and gross energy value (24.72kJ and 25.67kJ; $t_{18}=3.86$, $P<0.001$), all tests being 2-tailed.

Carrion samples were fat-extracted to compare their lean energy content with the lean energy value of the fresh samples (Table 6). For each prey type, samples from individual carcasses were pooled to give one carrion sample for each prey type. Although weekly samples were taken it was found that there was no significant difference between lean energy content in the 7-week old carrion samples and that of fresh meat ($T=6$, $P>0.05$, Wilcoxon matched pairs), and so analysis was not carried out for the fresher carrion samples.

Table 7. Amino acid composition for 6 potential raptor prey items. All values are given in g/kg of sample.

PREY TYPE	AMINO ACID																
	ASP	THR	SER	GLU	PRO	GLY	ALA	VAL	ILE	LEU	TYR	PHE	HIS	LYS	ARG	CYS	MET
RABBIT	59	41	36	105	23	29	62	47	29	66	29	30	24	82	39	8	19
PIGEON	58	37	34	96	23	28	59	39	25	61	26	28	20	75	68	8	17
PHEASANT	58	37	35	105	22	28	62	40	26	62	27	27	37	88	124	8	19
HARE	56	37	34	100	23	29	60	48	32	67	31	31	26	75	122	9	24
SHEEP	48	33	29	93	20	25	52	39	28	56	24	25	23	73	69	6	15
CROW	46	29	27	76	20	24	52	43	25	54	22	25	17	59	108	13	10

DISCUSSION

It is hypothesised that size-independent differences in gross-intestinal morphology influence the efficiency with which raptor species with contrasting foraging strategies and prey types digest their food. Differences in intestine length up to 50% have been found between raptor species (Chapter 3). Generalist feeders which capture their prey by soaring, searching flight and feed largely on carrion and easily caught prey have considerably longer guts than active, attacking raptors feeding on difficult prey species. Although some animal species also show differences in gut morphology at the microscopic level (Karasov *et al.* 1985), such differences are most likely to be found between species feeding on radically different diets and so are not thought to be an important feature of digestive morphology and physiology in raptors. Gross differences in gut morphology are likely the result of selection pressures due to a predator's hunting strategy and prey species. This study aimed to show a direct relationship between the morphological, physiological and behavioural adaptations exhibited by raptors.

These data support the hypothesis that small intestine length, independent of body-size, influences digestive efficiency, those species with long intestines absorbing more food than species with short intestines. Of the Falconiformes studied, the Red Kite and Common Buzzard had the highest digestive efficiencies of about 82% of total food intake. The Peregrines had a mean digestive efficiency of 75%, other species being intermediate when feeding on a diet of day-old cockerel. High digestive efficiencies are indicative of the high digestibility of the protein diet and for most herbivore, granivore and carnivore diets, dry matter and energy digestibilities are virtually synonymous (Robbins 1983). On a dry-matter basis, the Common Buzzard and the Red Kite absorbed 7% more food from the digestive tract than the Peregrine. It has previously been suggested that birds with long guts are adapted to process more food per unit time (Savory & Gentle 1976) but that the digestive efficiency remains the same. This does not appear to be the case for raptors.

The Common Buzzard and the Red Kite are similar in many aspects of their prey preferences and foraging. They have a wide prey spectrum (Cramp & Simmons 1980), scavenging extensively and feeding predominantly on relatively easily caught prey items, particularly during the winter months (Davies and Davis 1973, Tubbs 1974). Although prey is not difficult to catch, it is sometimes difficult to find and they must often spend periods of time without food (Brown 1978). It would be expected that such species should have adaptations which enable them to digest a wide range of food items as efficiently as possible. In contrast, species such as the Peregrine, Merlin and Sparrowhawk have specialised prey requirements feeding almost entirely on avian prey (Cramp & Simmons 1980). Such prey is abundant, but it is difficult to catch. I suggest that the generalist species show adaptations for maximum digestive efficiency, whereas the specialists are constrained in their ability to digest food by the overriding aerodynamic requirements for capture of a difficult prey.

A 7% difference in digestive efficiency is extremely important in terms of food requirements, especially for predatory birds with energy expensive foraging modes. For species of approximately equal size, this would mean a 7% difference in the amount of food they must catch, assuming species utilise prey in a similar way (Fox 1977). Food requirements vary with body-size. Buzzards, kites and eagles require approximately less than 10% wet weight of their body-mass per day, large falcons and accipiters 10-15%, small falcons and accipiters 20-25% (Craighead and Craighead 1969, Brown 1978, Kirkwood 1981). These differences in prey requirements may be the result not just of metabolic differences but also of differences in digestive efficiency resulting from the selective pressures of different foraging strategies on gut morphology. It is not known why efficiency should be greater at higher temperatures but temperature-related or seasonal metabolic differences and bulk of food intake could be responsible.

There is a limit to how much food an animal can process (Sibly 1981, Kirkwood 1983). The more quickly it processes its food, the sooner it can feed again but, the less efficient it is at assimilating the food. Small falcons and accipiters must often feed several times per day. Therefore, although efficiency on a per meal basis is lower than that found in Buzzards and Kites, the advantages of a smaller digestive tract, faster throughput of digesta and more efficient capture rates probably outweigh the advantages to be gained by trying to achieve maximum digestion of each meal. In the specialist hunters, the benefits to be gained from feeding on a narrow and difficult to catch prey spectrum (Newton 1979) must exceed the morphological, behavioural and physiological constaints which result from adaptations required for filling this specialised niche.

Calculations of prey requirements based on digestive efficiency data for a single diet, assume that raptor species feed on diets of equivalent nutritional quality. If the diet of wild Peregrine Falcons was of a higher quality than that of Common Buzzards, then this might compensate for their lower digestive efficiency. Alternatively, specialist feeders might have a higher digestive efficiency when feeding on their chosen prey type. To consider this possibility, pigeon and rabbit were fed to Peregrines and Buzzards and the composition of these and other diets were analysed. Buzzards were found to have significantly higher digestive efficiencies than Peregrines when fed on both rabbit and pigeon. Rabbit and pigeon differed in fat content (5% and 20% respectively), dry matter content (74.25% and 72.21%) and gross energy value (24.72kJ and 25.67kJ). Therefore, by wet weight, a Peregrine is gaining more when eating pigeon than it would by eating the same amount of rabbit. When fed an equal wet weight of rabbit and pigeon, the actual dry mass of pigeon is 7.9% more. Not only are Peregrines eating more on a dry matter basis, but that food is also of higher calorific value. Further, birds cannot digest protein completely (Fisher 1972). The theoretical calorific value for protein is 22.59kJ/g but only 17.99kJ/g is available. Therefore, meat with a high proportion of fat is energetically more valuable than a diet such as rabbit which is virtually all protein (Table 6). The reduction in digestive efficiency caused by a shorter gut might therefore be compensated for by the different composition of the diets, not by digesting preferred prey more thoroughly. Animals with limited digestive capabilities and which retain food for short periods might therefore have to select high quality food. Peregrines would indeed appear to eat only high quality prey but this does not appear to be the case for Buzzards. It is worth noting that rabbit meat is not typical of mammalian prey, being white meat and containing little fat.

The resultant changes in body-mass over 8 days reveal the importance of diet quality as well as quantity. Buzzards maintained their body-mass on both diets, Peregrines could only maintain their mass when feeding on pigeon. In both species, pigeon is also digested more slowly than rabbit (Chapter 6). Previous studies have shown that increasing fat levels slow the passage of digesta, increasing the digestibility of other nutrients in the diet (Mateos *et al.* 1982). The slower throughput together with the higher calorific value of pigeon (Table 6) might account in part for the increase in body-mass when fed on pigeon than when eating rabbit. However, neither species showed a significantly higher digestive efficiency feeding on pigeon. The leaner rabbit meat might be easier to digest than pigeon so that different passage rates do not affect overall differences in digestive efficiency. It seems, therefore, that the high fat content associated with some prey species, makes them more suitable than others. Taylor *et al.* (1991) found that American Kestrels (*Falco sparverius*) fed on a moderate lipid diet increased their food consumption by 40%. Birds on a low lipid diet increased their food consumption by more than 120%. They concluded that a predator's total food consumption and the subsequent kill rates vary greatly depending on the lipid content of the prey it catches. Even if a predator feeding on starving prey could catch enough individuals to satisfy its energetic demands, it might not be able to eat enough to meet its caloric needs before reaching satiation.

I also considered whether specialists such as Peregrines might have particular requirements for amino acids specific to certain prey types but no real differences in the quantity of individual amino acids could be found in any of the diets analysed (Table 7) and I conclude that protein composition is unlikely to be an important factor.

The results found for Hobby, Kestrel and Sparrowhawk can similarly be interpreted in terms of their feeding ecology, however sample sizes were smaller for these species and so a more tentative interpretation would be necessary. Of the Strigiformes studied, the Tawny Owl had the highest digestive efficiency and the Barn Owl and the Long-eared Owl both had comparatively low digestive efficiencies associated with a shorter gut. The Tawny Owl like the Common Buzzard feeds on a diverse range of prey species including mammals, birds, reptiles and insects. The Barn Owl and Long-eared Owl feed almost exclusively on small mammals (Mikkola 1983) but occasionally on birds. As in the Common Buzzard and the Red Kite, a long gut may allow the Tawny Owl to feed on less profitable prey items whereas the Barn Owl and Long-eared Owl with reduced gut size may be limited to feeding on small mammals in order to maintain their nutritional requirements.

The Red Kite and the Common Buzzard feed extensively on carrion whereas the Peregrine, Sparrowhawk and Goshawk take this diet only rarely. In Scotland, especially in winter, carrion is a widely abundant food source, both from sheep and deer carcasses and road kills of smaller prey. It is notable among meat eating species that comparatively few species utilise carcasses even though scavenging would appear to be an easy way to obtain a meal. This raises the question of why so few species take advantage of this food source. It is likely that carrion represents a poorer quality diet than freshly killed prey. If this were the case then, for reasons outlined above, one might expect active hunters to be inefficient at digesting such a diet. Several factors might cause carrion to be of lower quality than the same prey species freshly killed. Firstly, carrion is usually low in fat and energy content because many of the animals found as carrion have died from starvation (Taylor *et al.* 1991). Secondly, meat from a kill is already at body temperature, whilst carrion needs to be heated from ambient temperature before digestion can start. Thirdly, carrion will contain many micro-organisms which are starting to break down the food. These bacteria might have two effects. One is that many of the toxins and products of microbial metabolism seem to be designed to specifically deter vertebrates from feeding on the food, either by rendering the meat unpalatable, impeding vertebrate digestive enzymes or by a direct toxic action (Janzen 1977). I investigated whether these effects could be experimentally tested, but had to abandon this aspect because of the large number of bacteria that might be involved, and the extremely diverse range of bacterial metabolites. The other effect could be that by their routine metabolic activity the micro-organisms break down the food sufficiently to significantly reduce its overall energy content. This aspect was investigated by measuring the calorific value of carrion up to 7-weeks old. However, this showed that there was no significant decline in calorific value compared to fresh meat. I therefore conclude that other factors must be responsible for the lower 'quality' of carrion, and for the limited range of species which use this food.

REFERENCES

Barton, N.W.H. & Houston, D.C. (1991) The use of titanium dioxide as an inert marker for digestion studies in raptors. *Comp. Biochem. Physiol.* **100A:** 1025-1029.

Barton, N.W.H. & Houston, D.C. (1992) In Press. Post-mortem changes in gross intestinal morphology. *Can. J. Zoology.*

Brown, L.H. (1978) *British Birds of Prey.* London: Collins.

Bryant, D.M. & Tatner, P. (1991) Intraspecies variation in avian energy expenditure: correlates and constraints. *Ibis* **133:** 236-245.

Castro, G., Stoyan, N. & Myers, J.P. (1989) Assimilation efficiency in birds: a function of taxon or food type ? *Comp. Biochem. Physiol.* **92A:** 271-278.

Craighead, J.J. & Craighead, F.C. (1969) *Hawks, Owls and Wildlife.* New York: Dover.

Cramp, S. & Simmons, K.E.L. (1980) *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. 2.* Oxford: Oxford University Press.

Davies, P.W. & Davis, P.E. (1973) The ecology and conservation of the Red Kite in Wales. *British Birds* **66:** 183-224; 241-270.

Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* **68:** 225-252.

Fisher, H. (1972) The nutrition of birds. *In* Farner, D.S. & King, J.R. (eds), *Avian Biology, Vol. 2.* London: Academic Press.

Fox, N.C. (1977) Diet values and the food consumption of New Zealend Falcons. *Raptor Res.* **11:** 59-62.

Glasier, P. (1978). *Falconry and Hawking.* London: B.T. Batsford Ltd.

Hammond, K.A. & Wunder, B.A. (1991). The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Michrotus ochrogaster. Physiological Zoology* **64:** 541-567.

Janzen, D.H. (1977) Why fruits rot, seeds mould and meat spoils. *Am. Nat.* **111:** 691-713.

Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinents and ecological implications. *Studies in Avian Biology* **13:** 391-415.

Karasov, W.H., Solberg, D.H. & Diamond, J.M. (1985) What transport adaptations enable mammals to absorb sugars and amino acids faster than reptiles? *Am. J. Physiol.* **249:** G271-G283.

Karasov, W.h., Petrossian, E., Rosenberg, L. & Diamond, J.M. (1986) How do food passage rate and assimilation differ between herbivorous lizards and non-ruminant mammals ? *J. Comp. Physiol.(B)* **156:** 599-609.

Kendeigh, S.C. (1949) Effect of temperature and season on energy resources of the English Sparrow. *Auk* **66:** 113-127.

Kirkwood, J.K. (1979) The partition of food energy for existence in the Kestrel (*Falco tinnunculus*) and the Barn Owl (*Tyto alba*). *Comp. Biochem. Physiol.* **63A:** 495-498.

Kirkwood, J.K. (1981) Maintenance energy requirements and rate of weight loss during starvation in birds of prey. *In* Cooper, J.E. & Greenwood, A.G. (eds), *Recent Advances in the Study of Raptor Diseases.* Keighley, U.K. Chiron Publ.

Kirkwood, J.K. (1983) A limit to metabolisable energy intake in mammals and birds. *Comp. Biochem. Physiol.* **75A:** 1-3.

Kirkwood, J.K. (1985) Food requirements for deposition of energy reserves in raptors. *In* Newton, I. and Chancellor, R.D. (eds), *Conservation Studies on Raptors*: Proceedings of the ICBP World Conference on Birds of Prey, 1982.

Mateos, G.G., Sell, J.L. & Eastwood, J.A. (1982) Rate of food passage (transit time) as influenced by level of supplemental fat. *Poult. Sci.* **61:** 94.

Mikkola, H. (1983) *Owls of Europe.* London: Poyser.

Moss, R. (1972) Effects of captivity on gut lengths in Red Grouse. *J. Wildl. Mgmt.* **36:** 99-104.

Newton, I. (1979) *Population Ecology of Raptors.* Berkhamsted: Poyser.

Owen, M. (1975) Cutting and fertilizing grassland for winter goose management. *J. Wildl. Mgmt.* **39:** 163-167.

Prop, J. & Vulink, T. (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Functional Ecology* **6:** 180-189.

Robbins, C.T. (1983) *Wildlife Feeding and Nutrition.* New York: Academic Press.

Savory, C.J. & Gentle, M.J. (1976) Changes in food intake and gut-size in Japanese Quail in response to manipulation of dietary fibre content. *Br. Poult. Sci.* **17:** 571-580.

Sibly, R.M. (1981) Strategies of digestion and defaecation. *In* C.R. Townsend & P. Calow (eds), *Physiological Ecology: An Evolutionary Approach to Resource Use.* Massachussetts: Sinauer Associates.

Stalmaster, M.V. & Gessaman, J.A. (1982) Food consumption and energy requirements of captive Bald Eagles. *J. Wildl. Mgt.* **46:** 646-654.

Taylor, R.L., Temple, S.A. and Bird, D.M. (1991) Nutritional and energetic implications for raptors consuming starving prey. *Auk* **108:** 716-719.

Temeles, E.J. (1989) Effect of prey consumption on foraging activity of Northern Harriers. *Auk* **106:** 353-357.

Woodford, M. (1977) *A Manual of Falconry, 3rd ed.* London: A. & C. Black.

CHAPTER 8

GENERAL DISCUSSION

Discussion

The study used a comparative approach to examine the causes and consequences of morphological adaptation in raptors, enabling a test of hypotheses relating to the functional significance of the interspecific differences found (Clutton-Brock & Harvey 1991). The relationship between body size and prey size would appear to be most critical in predatory birds since aspects of body size determine an animal's ability to chase and capture prey. Apart from Houston (1988) this is the only study to have shown a relationship between gut morphology and foraging strategy. Inevitably, it is difficult to establish what the main selection pressure is since foraging strategy and diet are directly related.

I suggest that prey availability and abundance are additional factors contributing to the digestive adaptations found in this study. One of the advantages of feeding on a diet which is difficult to catch is that there is less competition (Lack 1946) and a greater prey abundance (Schoener 1969, Gittleman 1985). For species such as the Sparrowhawk, Peregrine and Goshawk, birds are their staple diet and because they are specialist predators, it enables them to utilise a food source that is abundant. Without extreme morphological adaptation of external and internal body components, such prey would be unavailable. The Red Kite, Common Buzzard and Golden Eagle feed on a wide range of prey species, most of which are less abundant and patchily distributed. It would be difficult for those raptors to find sufficient food if they specialised on only a few prey species. Hence they show generalist adaptations to exploit a larger number of less abundant prey species.

The nutritional characteristics of prey are important determinants of ecological adaptations shown by predatory species. An extreme example is the difference between freshly killed avian prey and a carcass such as sheep or rabbit which has been dead for several days. I have already discussed possible reasons as to why carrion is utilised by some species and not others. The digestive constraints found in attacking raptors limits them to the food they can utilise regularly whereas the greater digestive efficiency found in scavenging species enables them to utilise a wide range of prey. There are also other factors which determine food availability. For example, attacking species, which in general are smaller than scavenging species to match the agilty of their highly manoeuvrable prey (Andersson & Norberg 1981) might be outcompeted at carcasses or simply unable to break open larger animals if they are the first to arrive at a carcass. They maybe occupy habitats where carrion is scarce or they could be so specialised that their search image restricts them to the number of prey species they encounter. Nevertheless, there is clearly some difference in digestive physiology or food composition which limits prey suitability and therefore prey availability.

It is important to recognise that a prey type which enables an animal to maintain its energy requirements on a short-term basis might not be adequate for them to breed. Captive breeding studies have assessed the merits of various diets for improved production (Dierenfeld *et al.* 1989). Species such as the Common Buzzard produce chicks which fledge on seemingly poor diets. Peregrines fed on the same diet often lay eggs with low hatchability, chicks with poor fledging success or they do not lay at all (pers obs.). Although this study established the requirement of a high quality diet such as pigeon for Peregrines, more work is required on the specific dietary requirements of raptor species.

Not only do generalist species have a comparatively high digestive efficiency but they presumably are more tolerant of food which has been exposed to micro-organisms and bacterial breakdown. Most carrion results from animals which have died through illness and starvation. Scavenging species would appear to be very resistant to disease transmitted via carcasses. The reasons why scavengers are so resilient are unknown and warrant further study.

Food preferences are necessarily generalisations, since diet changes throughout the year, more avian prey being taken by some species during the breeding season and males and females sometimes differing in their prey selection

(Cramp & Simmons 1980). Prey species also differ depending on the extent to which the population of a raptor species is migratory and the habitat it lives in. For example, diet composition for continental Red Kites differs from British Red Kites, with more reptiles and invertebrates being taken in populations living in warmer climates (Cramp & Simmons 1980). However, the morphological adaptations shown by raptors with contrasting foraging strategies and prey preferences undoubtedly reflect the ability of species to occupy different predatory niches.

Most other studies which have determined digestive efficiency in raptors have been referred to throughout this thesis. Such data could not be used for a comparative assessment of digestion and foraging strategy. In most cases, only a small number of species were used and feeding trials were reportedly under a wide range of temperature, diet and experimental conditions. The data in this study were collected from raptors for which several individuals of each species were available and species were tested simultaneously, thereby assuring comparable experimental conditions and validating the use of a comparative approach. It is because of the differences in design of previous studies that the initial assumption of approximately equal digestive efficiencies across raptor species arose. It is hoped that this study and the interpretation of the results will provide answers to some otherwise unexplained observations from wild bird studies which could only be tested through captive studies such as this.

REFERENCES

Andersson, M. & Norberg, R.A. (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15:** 105-130.

Cramp, S. & Simmons, K.E.L. (1980) *Handbook of the birds of Europe, the Middle East and North Africa Vol. 2.* Oxford: Oxford University Press.

Clutton-Brock, T.H. & Harvey, P.H. (1991) Comparative approaches to investigating adaptation. *In* Krebs, J.R. & Davies, N.B. (eds), *Behavioural Ecology.* London: Blackwell Scientific Publications.

Dierenfeld, E.S. Sandfort, C.E. & Satterfield, W.C. (1989) Influence of diet on plasma vitamin E in captive Peregrine Falcons. *J. Wildl. Manage.* **53(1):** 160-164.

Gittleman, J.L. (1985) Carnivore body size: Ecological and taxonomic correlates. *Oecologia* **67:** 540-554.

Houston, D.C. (1988) Digestive efficiency and hunting behaviour in cats, dogs and vultures. *J. Zool.* **216:** 603-605.

Lack, D. (1946) Competition for food by birds of prey. *J. Anim. Ecol.* **15:** 123-129.

Schoener, T.W. (1969) Models of optimal size for solitary predators. *Am. Nat.* **103:** 277-313.