Adaptive radiation of the digestive system, heart and wings of *Turdus pilaris, Bombycilla garrulus, Sturnus vulgaris, Pyrrhula pyrrhula, Pinicola enucleator* and *Loxia pytyopsittacus*

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A study is made of the comparative morphology of *Turdus pilaris, Bombycilla garrulus, Sturnus vulgaris, Pyrrhula pyrrhula, Pinicola enucleator* and *Loxia pytyopsittacus* from specimens found dead in autumn and winter in N Finland, mainly in Oulu and its vicinity. All recordings were made per unit fat-free body weight. The least migratory species, *Pyrrhula pyrrhula* and *Pinicola enucleator,* which feed largely on buds, have the relatively longest intestines, relatively small livers, high plumage weights, low body weight/wing area and blunt wing-tips, while the migratory birds, *Turdus pilaris, Bombycilla garrulus* and *Sturnus vulgaris,* which feed on berries and insects (and seeds), have relatively short intestines, larger livers, lower relative plumage weights, pointed wing-tips and higher proportions of hand wing within the total wing area. The granivorous *Loxia pytyopsittacus,* known for its irruptive flights, has relatively pointed wing-tips, a high proportion of hand wing within the total wing area, a relatively short intestine, small liver and low relative plumage weight. The smallest heart in relative terms is that of *Turdus pilaris* and the largest liver that of *Bombycilla garrulus.* All the species have small caeca.

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Introduction

The ability of an animal to secure ample energy and nutrient supplies from its environment, and to mobilize these physiologically, determines to a large extent its life-history, distribution, abundance, the season and extent of such activities as migration, reproduction and moulting, and its interactions with other individuals of its own and other species. Birds have different adaptations which enable them to exploit different resources. A good example is the beak modifications found in Darwin's finches, connected with different food habits on the Galapagos Islands (see Lack 1947). The adaptive radiation of the European finches was studied by Newton (1967, 1972), and general reviews have been published by Morse (1971, 1975).

When studying the food habits of passerine birds occurring in northern Finland (Pulliainen 1971, 1972, 1973, 1978, 1979a, b, Pulliainen & Hakanen

1972, Pulliainen & Tuomainen 1978, Pulliainen et al. 1978, Pulliainen & Erkinaro 1978), the senior author was struck by the great variation in the morphology of passerines which utilize rowan-berries *(Sorbus aucuparia).* A detailed study seemed justified, and the following species were selected for study: the Fieldfare *Turdus pilaris,* Waxwing *Bombycilla garrulus,* Starling *Sturnus vulgaris,* Bullfinch *Pyrrhula pyrrhula,* Pine Grosbeak *Pinicola enucleator* and Parrot Crossbill *Loxia pytyopsittacus.* The present paper provides information on the wings, plumage, heart, liver and intestine of these birds.

Material and methods

The birds examined (65 Waxwings, 24 Bullfinches, 15 Pine Grosbeaks, 9 Parrot Crossbills, 3 Starlings and 3 Fieldfares) had all died accidentally during the autumn and winter, mainly in the city of Oulu and its vicinity, and until examination were stored in plastic bags at —20°C. Some weight was lost before and after freezing, but how much was not known.

Sexing and ageing were carried out according to Svensson (1976), and the sex checked internally. The following measurements were made from each carcass: wing length (maximum method according to Svensson 1976), intestine length from gizzard to cloaca, caeca length, liver weight, heart weight (without blood), plumage weight after drying for about four hours at +60°C, wing-tip pointedness index according to Holynski (1965) and Busse (1967), wing area and hand wing area in cm^2.

After dissection the whole carcass without the contents of the digestive tract was ground, homogenized and extracted with ethanol in order to record the soluble fat content.

The laboratory work was carried out by the authors Helle and Tunkkari, and Mrs. Riitta Harjula, and this paper was written by Pulliainen.

Results

The fat content (%) of the carcasses is presented in the following tabulation:

	Mean	*SE*	*SD*	Range	*N*
B. garrulus	13.2	1.2	8.1	0.5—35.0	46
P. enucleator	8.9	1.4	5.1	3.1—19.6	14
P. pyrrhula	9.9	0.9	4.4	1.5—19.9	22
L. pytyopsittacus	8.0	0.7	1.8	5.4—10.2	7
S. vulgaris	6.0	4.6	8.0	1.1—15.2	3
T. pilaris	7.3	3.0	5.2	1.5—11.4	3

Passerine birds in the north store fat daily in autumn and winter. Newton (1972:253) emphasizes that many birds, such as the Bullfinch, must replenish their fat every day in winter in order to survive. Birds which die early in the morning are thus lighter than ones dying late in the afternoon. The great variation recorded in the fat contents of the carcasses led us to the conclusion that it was best to use fat-free body weights in the calculations presented here.

Table 1 shows the body weights (with and without fat), the relative lengths of the intestine and caeca and the relative weights of the heart, liver and feathers of the six species studied. The Bullfinch and Pine Grosbeak have relatively long intestines, small livers (as has also the Parrot Crossbill), and relatively high plumage weights. The Waxwing has the largest liver in relative terms and the Fieldfare the smallest heart. All six species have small caeca (combined length 0.2—2.9 cm) as compared with those of, for instance, *Lagopus* spp. (combined length over 100 cm; see Pulliainen 1976).

Table 2 shows that the body weight per unit wing area is smallest in the Bullfinch and greatest in the Parrot Crossbill. The wing-tip pointedness indices are greatest in the Waxwing and Starling and smallest in the Bullfinch and Pine Grosbeak, in which the proportions of hand wing within the total wing area are also smallest.

TABLE 1. Body weight, body weight without fat, relative length of intestine and caeca, and relative weights of heart, liver and plumage in the Waxwing, Bullfinch, Pine Grosbeak, Parrot Crossbill, Starling and Fieldfare (mean ± *SD*).

	Body weight (g)	Body weight without fat (g)	Relative length of intestine (mm/g of body weight)	Relative length of caeca (% of intestine length)	Relative weight of heart (% of body weight without fat)	Relative weight of liver (% of body weight without fat)	Relative weight of plumage (% of body weight without fat)	*N*
B. garrulus	62.1± 9.14	54.0± 5.51	4.7±1.41	2.2±0.51	1.9±0.38	7.4±2.27	7.0±1.38	50
P. pyrrhula	31.5± 3.41	28.9± 2.58	21.8±3.55	0.3±0.12	1.8±0.26	2.4±0.61	9.3±1.23	22
P. enucleator	52.6±10.47	47.6± 7.66	19.2±3.63	0.7±0.65	1.7±0.13	3.0±0.52		13
L. pytyopsittacus	51.3± 4.39	47.6± 4.15	7.0±3.07	0.7*	1.9±0.10	2.0±0.27	6.9±0.85	7
S. vulgaris	70.7±12.74	66.0±10.20	5.3±1.10	2.2±0.21	1.8±0.21	4.4±0.32	6.9±1.24	3
T. pilaris	102.7±22.68	94.4±16.30	4.0±0.70	1.7±0.50	1.4±0.22	4.2±1.10	8.0±0.58	3

*only one measurement

Discussion

Although birds as a group have a particularly homogeneous body plan (Bock 1969), species differ widely in their general shape and morphology, according to their diets, habitats and general life styles. Morse (1975) assumes that the interactions over food sources are most important in leading to adaptive radiation, although anti-predator mechanisms may also have a high selective value.

Relatively few birds feed heavily upon green-plant material, though a number consume quantities of buds (reviewed in Morse 1975). More species feed on dry seeds (granivorous), and may make a particularly heavy impact upon seeds of trees. Several families, mostly tropical, feed primarily upon fruit (frugivorous). Insects are exploited by more families of birds than any other food category (insectivorous), and most primarily herbivorous species feed their young partially or totally upon insects or other animal material, only a few species being able to raise young on an entirely plant diet.

Buds are a particularly important food for the Pine Grosbeak and Bullfinch in winter, the former feeding on buds of spruce *(Picea abies)* and willow *(Salix* spp.) (e.g. Pulliainen 1974) and the latter especially on buds of cultivated fruit trees (Newton 1964) and other wild trees (Erkamo 1948). Both species also feed on berries (e.g. *Sorbus aucuparia, Vaccinium* and *Rubus),* extracting the seeds and discarding the soft parts (Newton 1972, Pulliainen 1978, 1979a). The same technique is used by the Parrot Crossbill when extracting seeds from rowan-berries (v. Haartman et al. 1963—72), but this species feeds mainly on conifer seeds (Newton 1970, Pulliainen 1972), although insects are also accepted (Pulliainen 1972). The

TABLE 2. Body weight per unit wing area, wing-tip pointedness index and relative area of hand wing in the Waxwing, Bullfinch, Pine Grosbeak, Parrot Crossbill, Fieldfare and Starling (mean ± *SD*) (numbers of measurements in brackets).

	Body weight per wing area (g/cm²)	Wing-tip pointedness index	Proportion of hand wing in the total wing area (%)
B. garrulus	0.43±0.06 (51)	97.3±12.89 (64)	60.8±1.46 (5)
P. pyrrhula	0.27±0.03 (18)	43.6± 3.43 (23)	54.7±4.71 (5)
P. enucleator	0.34±0.06 (13)	54.1± 4.72 (13)	56.7±2.95 (5)
L. pytyopsittacus	0.44±0.04 (9)	80.6± 4.95 (9)	60.7±4.56 (5)
T. pilaris	0.36±0.03 (3)	89.0±9.07 (3)	58.5±2.14 (3)
S. vulgaris	0.39±0.09 (3)	93.3±33.87 (3)	62.9±4.80 (3)

three other species feed mainly on invertebrates in summer and various berries when available, swallowing them whole (Siivonen 1940, 1941, 1943, Toivari & Hytönen 1941, v. Haartman et al. 1963—72, Pulliainen 1978), but the starling also feeds on seeds in autumn and winter (Wiens & Dyer 1977). The Waxwing is possibly the most frugivorous of them all (Siivonen 1941), and Morse (1975) regards it as the most frugivorous species in the temperate zone.

In northwestern Europe these six species also differ in their migrations. The Pine Grosbeak breeds in the northern coniferous forests, migrates just a few hundred kilometres to the south and returns by February-March (Pulliainen 1979b), while the Bullfinch may perform short- or long-distance movements (v. Haartman et al. 1963—72). The Parrot Crossbill, like other Crossbill species, is known for its irruption movements (Newton 1970). The autumn and early winter movements of the Fieldfare and Waxwing depend greatly on the availability of rowan and other berries, the birds concentrating wherever crops are plentiful (Toivari & Hytönen 1941, Tyrväinen 1975, Saurola 1977), while the huge overwintering flocks of the Starling migrate to winter in southern agricultural landscapes (see Wiens & Dyer 1977). Starlings born in Finland winter mainly in Western Europe (Saurola 1978). All these six species may also overwinter in Finland in varying numbers (Hildén et al. 1973, Sammalisto 1974, 1978).

According to Herpol (1967), the small intestine tends to be relatively long in herbivorous and granivorous birds, and relatively short in carnivorous, insectivorous and frugivorous ones, although there may be difficulties in separating variations due to diet from variations due to body size and taxonomic position. The present data (Table 1) suggest that adaptation to a bud diet involves an exceptionally long intestine, the relative length of the intestine of the granivorous Parrot Crossbill being only a third of that of the

Pine Grosbeak and Bullfinch, two species which Newton (1972) regards as closely related. The relative lengths of the intestine of the insectivorous-frugivorous Starling, Fieldfare and Waxwing were of the same magnitude, and shorter in relative terms than that of the Parrot Crossbill.

According to the review by Moss (1972), intestine size depends on hormones, intestine microbes, parasite load, rhythm of feeding, composition of diet and amount of food eaten (see also Pulliainen 1976). A long intestine may also serve as a thermogenetic and/or heat-conserving organ, both peristaltic and segmenting movements being involved (Vonk & Postma 1949). Here the least migratory birds, the Pine Grosbeak and Bullfinch, which winter furthest north, had relatively the longest intestines (Table 1). It has also been shown that cold exposure causes an increase in peristalsis in sheep and cattle (Christopherson 1976; see also White 1979).

One major difference between the Crossbill and the other species is that the Crossbill rears its young on seeds alone (Newton 1967, Pulliainen & Tuomainen 1978), while the others require animal matter for this purpose. Although the relative length of the intestine of the Parrot Crossbill is only 1.5 times that of the Waxwing, the former can digest seeds, while the seeds of rowan-berries pass through the digestive tract of the Waxwing unaltered (Pulliainen & Erkinaro 1978). There must be other differences in the digestive systems of these two species as well, which may also explain the occasional consumption of buds by the Crossbills (Turček 1961).

All these six species have a pair of caeca, but these are small (Table 1). Mitchell (1901) and Naik & Dominic (1963) classified the caeca of birds into the following categories: (a) intestinal type, (b) glandular type, (c) lympho-epithelial type and (d) non-functional and vestigial. Most of the passerine birds have the third type, which is much reduced and infiltrated by lymph cells (Ziswiler 1967). It is likely that the present species have the third or fourth category.

The liver in birds produces bile, but it may also serve for storage of lipids and glycogen, intermediary metabolism, synthesis of proteins and glycogen, and formation of uric acid (Ziswiler & Farner 1972). According to Magnan (1910), the liver is smallest in relative terms in carnivores and granivores and largest in piscivores and insectivores. Here the granivorous Parrot Crossbill had relatively the smallest liver, but the bud-feeders, the Pine Grosbeak and Bullfinch, also had small livers, while the Starling and Fieldfare had relatively larger and the Waxwing the largest liver (Table 1).

Vorontsov (1962) suggested that the number of liver lobes in mammals is reduced with adaptation away from a proteinaceous diet (see also Perrin & Curtis 1980). Herpol (1967) found the total proteolytic capacity of newly hatched Domestic Pigeons *Columba livia domestica* to be very high compared with that of the adults, corresponding with a change from a protein-rich to a protein-poor diet. The spruce-bud diet of the Pine Grosbeak is rather poor in protein (Pulliainen 1974), but the conifer and rowan seed diet of the Parrot Crossbill is much richer in this respect (Pulliainen 1971, 1973, 1974, 1978).

The Waxwing has a relatively large liver (Table 1), but no gall bladder, the organ for storing and concentrating bile (Ziswiler & Farner 1972). Birds which have a gall-bladder have the advantage of delivering very concent-

rated bile into the intestine at the beginning of a digestive period, the bile functioning mainly to emulsify fats. Such an organ would seem to be unnecessary to the frugivorous Waxwing, which utilizes only the flesh of the berries, from which the sugars and other constituents are presumably easily absorbed in the intestine. Berries can pass through the digestive tract in as little as 12 minutes in the Blackcap *Sylvia atricapilla*, for instance (Groebbels 1932). This feeding and digestion pattern presupposes an almost continuous passage of berries through the digestive tract during the active period. The frugivorous Waxwings may also need a large liver as a detoxification organ, as toxins are more often present in fruits than in buds or animal matter.

The feeding strategy of the Waxwing also involves risks in that there may be no berries available over vast areas. It is thus important for the birds to have fat reserves. In fact the fat content of the Waxwings appeared to be on average greater than that of the other birds studied, even including those wintering in the north.

According to 'Rensch's Rule' (1938), the most mobile birds especially those migrating to cooler climates to nest, have relatively narrower and more pointed wings than the less mobile birds of warmer regions. The wing-tip pointedness indices (Table 2) were greatest for the long-distance migratory birds, the Waxwing (97.3), Starling (93.3) and Fieldfare 89.0). A slightly lower value was recorded for the irruptive Parrot Crossbill (80.6), and the lowest ones for the least migratory birds, the Pine Grosbeak (54.1) and Bullfinch (43.6). The proportion of the hand wing within the total wing area was smallest in the latter two species, as was also the body weight per unit wing area (Table 2).

According to the 'Heart Rule' (Hesse 1921), the heart/body weight ratio in birds is higher in colder than in warmer climates (for experimental evidence, see May & Deaton 1974). Theoretically, a smaller bird also needs a more efficient circulation system and a relatively larger heart than a larger bird in order to maintain its homeothermic condition at low temperatures (see also Pulliainen 1980). The heart/body weight ratios of the Waxwing, Parrot Crossbill and Starling were 1.8 or 1.9, and the relative weights of the plumage (6.9—7.0 %) and the body weights (without fat, 51—71 g; Table 1) were also of the same magnitude. The Bullfinch and Pine Grosbeak had similar heart/body weight ratios (1.7—1.8), but clearly higher plumage weights (9.3 and 10.5 % respectively), while the largest of these birds, the Fieldfare, had the smallest heart (1.4 % of the body weight) and moderate plumage weight (8.0 %).

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Selostus: **Räkättirastaan, tilhen, kottaraisen, punatulkun, taviokuurnan ja isokäpylinnun ruoansulatuskanavassa, sydämessä ja siivissä ilmenevistä sopeutumista**

Syksyllä ja talvella Oulussa ja sen lähiympäristössä tapaturmaisesti kuolleiden räkättirastaiden, tilhien, kottaraisten, punatulkkujen, taviokuurnien ja isokäpylintujen ruoansulatuskanavassa, sydämessä ja siivissä ilmeneviä sopeutumia tutkittiin suorittamalla kaikki vertailut rasvattoman ruumiinpainon yksikköön. Silmuja syövillä punatulkuilla ja taviokuurnilla, jotka suorittavat useimmiten lyhyitä muuttomatkoja, on suhteellisesti pisin suoli, pieni maksa, tuuhea höyhenpuku, alhainen ruumiinpaino siiven pinta-alaa kohti ja alhainen siiven terävyysindeksi.

Tyypillisillä muuttolinnuilla, räkättirastaalla, tilhellä ja kottaraisella, jotka syövät sekä marjoja että hyönteisiä (kottarainen myös siemeniä), on sitä vastoin suhteellisen lyhyt suoli, edellisiä suurempi maksa ja ohuempi höyhenpuku, korkea siipien terävyysindeksi ja edellisiä suurempi käsiosan osuus siiven kokonaispinta-alasta. Invaasioistaan tunnetulla ja siemeniä syövällä isokäpylinnulla on suhteellisen korkea siiven terävyysindeksi, lyhyt suoli, pieni maksa, ohut höyhenpuku ja suuri käsiosan osuus koko pinta-alasta (taulukot 1 ja 2). Suhteellisesti pienin sydän todettiin tutkituista linnuista suurimmalla, räkättirastaalla, kun taas suhteellisesti suurin maksa on tilhellä (taul. 1). Kaikilla lajeilla on lyhyet umpisuolet.

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