

GUT SIZE, BODY WEIGHT, AND DIGESTION OF WINTER FOODS BY GROUSE AND PTARMIGAN

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ABSTRACT.—A model for grouse and ptarmigan relating the digestibility of their winter foods to their body weights and gut lengths is presented. The observed digestibility of a food depends partly on the “digestive abilities” of the birds eating it, partly on the food’s intrinsic digestibility, and partly on daily intakes. Digestive abilities of the birds vary as much intraspecifically as interspecifically.

Gut lengths and gizzard weights of gallinaceous birds vary with the diet. Birds that eat coarser, more fibrous foods tend to have bigger guts (Leopold 1953, Lewin 1963, Moss 1972, 1974), presumably because coarser foods demand greater intakes and digestive abilities. The digestibility of foods eaten by different populations should be interpretable from measurements of the birds’ guts. This paper provides a simple quantitative model relating the digestibility of a food to its intake and the size of the gut digesting it. Digestibility is an important determinant of nutritive value, food choice, and food intake in vertebrates and, consequently, their foraging behavior.

Several factors that might affect digestibility are not included in the model. Not enough is known about their effects on digestibility to include, for example, ambient temperature, state of molt, and reproductive condition. I minimize the effect of such variables by limiting this paper to fully-grown tetraonid birds in autumn and winter, so that food requirements are approximately those for maintenance at 0°C.

First, one must show how the guts of tetraonids (grouse and ptarmigan) vary in size with the birds’ body weight. The equations describing these average relationships are then used to predict gut sizes from the body weight of a population of interest. One can then use the model to infer what the deviations from these average or predicted values imply about the digestibility of foods eaten by the population.

Moss and Hanssen (1980) gave an account of digestion in tetraonids. Briefly, the gut is generally full of digesta day and night. The crop is filled with food shortly before going to roost and this store is passed into the gut and digested during the night. After being ground in the gizzard, digesta pass through the small intestine. At the junction of the small and large intestines are two long tubular diverticula, the caeca, into which the more liquid fraction of the chyme is diverted and where it ferments. The more fibrous fraction of the chyme passes

by the caecal entrances into the large intestine and is rapidly and regularly egested. The major emptying of the caeca occurs once daily when the bird is about to leave, or has just left, its roost.

METHODS

This paper collates already-published and new information. The data have been collected by different observers at different times and places, using slightly different methods. Body weight in published papers refers sometimes to fresh birds, and sometimes to birds frozen and later thawed. In all samples, except those of Blue Grouse (*Dendragapus obscurus*), weights are without crop contents, but some include the crop membrane and some do not. Fortunately this structure weighs very little. New data presented here are of entire fresh carcasses, with food emptied from the crops, but with gizzards and guts full of digesta.

Gut length was measured after cutting the mesenteries and laying the organ out straight on a flat surface. Lengths can vary by a few centimeters depending on how much the gut is stretched when it is laid out. Usually the weight of the gut itself is allowed to exert tension just sufficient to straighten it. One caecum (the left, according to Arnthor Gardarsson, pers. comm.) is usually slightly shorter than the other. They are usually measured separately, and data from the two are added together here. In one sample (Blue Grouse) the length of only one caecum was measured and I have doubled this.

Gizzards were weighed without gastroliths and digesta, usually including the stomach lining but sometimes not. Based on known weights of gizzards with and without lining (from Blue Grouse and Capercaillie [*Tetrao urogallus*]), I multiplied published data on gizzards without a lining by 1.14. Gut lengths and gizzard weights can vary seasonally within a population: sometimes large (e.g., Pendergast and Boag 1973), sometimes small (e.g., Moss 1972). I have confined this paper to autumn and winter data because they are the most plentiful, in

order to standardize comparisons between populations, and because winter diets are simpler, thereby facilitating inferences about food and gut size.

Sexes and age-classes within a population of grouse often differ in body weight and gut size. In species with big sexual differences in size, data from the two sexes are presented separately, but where such differences are small (under 20%) the data are sometimes combined to increase sample size.

Digestibilities quoted here have been determined from birds both in captivity and in the wild. Captive Red Grouse (*Lagopus lagopus scoticus*) and Capercaillie were hatched and reared as described by Moss (1969). Red Grouse were kept in wire-floored cages and fed pelleted diets (Moss and Hanssen 1980) with a supplement of heather (*Calluna vulgaris*). Capercaillie were fed the same pelleted food as Red Grouse but were given conifer branches as well as heather and kept in a roofed pen with a sand floor. The pen measured 8 ft × 40 ft and was divided into four 8-ft × 10-ft sections interconnected by popholes.

A problem when determining the digestibility of foods eaten by free-living wild birds is to estimate the quantity of caecal droppings produced. Moss (1973) measured this in captives and then assumed that wild birds' droppings consisted of 85% woody and 15% caecal droppings. The documented extremes in captivity are 7% caecal droppings for Spruce Grouse (*Canachites canadensis*) eating pine (*Pinus contorta*) needles (Pendergast 1969) and 25% for Rock Ptarmigan (*Lagopus mutus*) eating bulbils of *Polygonum viviparum* (Moss and Parkinson 1975). Andreev (1979) used quite different assumptions, which gave erratic estimates of digestibility. To make all the data in this paper comparable, I have recalculated digestibilities from Andreev (1979), assuming that in his birds the caecal droppings also comprised 15% of the total.

RESULTS

For ease of presentation, mathematical details and tests of the model are given after the Discussion. Three concepts from the model are necessary for understanding the Results. In general, the digestibility of a food depends on both the food and the animal digesting it. Hence, the term "digestive abilities" is a property of the bird and defined by equation (12) below; for a given set of birds, it is the digestibility, predicted from the birds' mean body weight and gut length, of the average winter food at average intakes. "Relative gut length" is the ratio of the observed gut length to that expected from body weight. "Intrinsic digest-

TABLE 1. Equations relating weight (g) of tetraonids' guts full of digesta to body weight W ; data for Capercaillie, Black Grouse, Willow Ptarmigan, Rock Ptarmigan and Hazel Grouse (*Bonasa bonasia*) from Semenov-Tian-Shanskii (1959), for Spruce Grouse from Pendergast (1969). The column r^2 is the proportion of the variation in the logarithm of organ weight accounted for by variations in $\log W$.

Dependent variable	Equation ^b	r^2
Small intestines	$= 0.035W^{1.05 \pm 0.04}$	0.99
Caeca (both)	$= 0.14W^{0.87 \pm 0.14}$	0.89
Large intestine	$= 0.049W^{0.76 \pm 0.16}$	0.79
Total guts ^c	$= 0.18W^{0.94 \pm 0.07}$	0.97

^a Data for cock and hen Capercaillie were used separately, for other species data for the two sexes were combined, so $n = 7$.

^b Power given \pm SE.

^c Intestines and caeca.

ibility," a property of the food, is not defined explicitly in the model but is related to k_a , the rate of absorption of the food across the gut surface at average rates of food intake.

GUT SIZE AND BODY WEIGHT

The weight of full guts (Table 1) and empty gizzards (Table 2) both increased roughly in proportion to body weight (W). As expected, since guts are roughly tubular, their total length varied approximately as the cube root of W (Table 2). In the model, the empirical relations in these tables are used to predict gut lengths expected from observed body weights.

The small intestines and caeca made up different proportions of the total gut in the different species (Table 3). This complication is ignored in the model, which assumes all sections of the gut to be equivalent, partly for simplicity and partly because not enough data on digestibility are available to do otherwise. The ratio of the combined caeca to small intestine, however, showed no trend with W . Hence variations in this ratio do not bias parameters estimated in the model.

SEX, AGE, AND GUT SIZE

Different sexes and ages within the same populations had different digestive abilities, due

TABLE 2. Organ sizes of tetraonids in relation to body weight (W). Equations were calculated from one sample, marked f in Table 3, from each of the nine species studied. Samples were chosen at random within species, but excluding cock Capercaillie, which might have biased the regressions because they were so big.

Dependent variable	Equation	r^2
Empty gizzard weight (g)	$= 0.0232W^{1.06 \pm 0.16}$	0.86
Small intestine length (cm)	$= 7.32W^{0.41 \pm 0.07}$	0.83
Caeca length (cm)	$= 14.4W^{0.30 \pm 0.09}$	0.59
Large intestine length (cm)	$= 1.57W^{0.33 \pm 0.03}$	0.93
Total gut length (cm)	$= 22.0W^{0.36 \pm 0.06}$	0.86

largely to different relative gut lengths (Table 3). This was clearest in Black Grouse (*Tetrao tetrix*), a species with high sexual dimorphism, but confirmed in Willow Ptarmigan (*Lagopus lagopus*) (Table 3) and Rock Ptarmigan (data in appendix). A difference between the sexes was confirmed in Capercaillie, Blue Grouse and White-tailed Ptarmigan (*Lagopus leucurus*; May 1975) where samples were too small to consider age-classes separately. The pattern seems to be that digestive abilities and relative gut lengths are lowest in old cocks and highest in young hens, with old hens and young cocks intermediate.

DIFFERENCES BETWEEN SPECIES

The ptarmigan (*Lagopus* spp.) had particularly long caeca (Table 3). Ptarmigan eat woodier foods, particularly twigs of deciduous shrubs, than other grouse, and the Willow Ptarmigan eats the highest proportion of, and the thickest, twigs. The caeca are probably sites of lignin and cellulose fermentation (Moss and Hanssen 1980). Certainly the association between woody diets, long caeca and high digestive abilities both within and between species confirms that ptarmigan are particularly well adapted to digesting fibrous foods.

The three species that eat mostly conifer needles as their winter diet—Capercaillie, Blue Grouse and Spruce Grouse—had low digestive abilities. The gizzard of the Spruce Grouse, however, was remarkably large in a population eating pine (*Pinus contorta*) needles and even more so in a population eating spruce (*Picea* spp.) needles. This species is apparently adapted to eating foods that are particularly difficult to grind. If spruce needles are hard to grind this might deter tetraonids from eating them (e.g., Capercaillie eat spruce needles only when pine is scarce; Semenov-Tian-Shanskii 1959).

DIFFERENCES WITHIN SPECIES

Gut lengths and inferred digestive abilities varied as much among populations within species as among species (Table 3). Although Russian and Scottish Capercaillie both ate a winter diet largely of pine (*Pinus sylvestris*) needles, the Russian birds had longer guts. Gut size is known to be influenced by the amount of food eaten (more food, bigger guts) and the daily rhythm of feeding (bigger meals with longer intervals, bigger guts) (Fell 1969). As the Russian birds lived farther north than the Scottish ones, they survived in cooler temperatures and with shorter winter days. This may have increased the amount of food eaten and decreased the amount of time available to eat it, both leading to increased gut size. Also, the pine needles eaten by the different populations

may have differed in intrinsic digestibility (k_a), but I do not have data to test this possibility.

Two samples of birds had unusually short guts, both intestines and caeca: White-tailed Ptarmigan from Colorado and Rock Ptarmigan from Iceland. Both populations are unusual in that they have no Willow Ptarmigan with which to compete. They can therefore eat willow (*Salix*) in winter, almost entirely as in the White-tailed Ptarmigan in Colorado (May 1970), or as long as dwarf willow projects above the snow in the case of Rock Ptarmigan in Iceland (Gardarsson and Moss 1970). The intrinsic digestibility of willow, reflected by its k_a value, was the highest of the observed foods (Table 4); hence, the short guts of the Rock Ptarmigan from Iceland and White-tailed Ptarmigan from Colorado may have resulted from a highly digestible diet.

Scottish Red Grouse, eating almost entirely heather, had the longest guts and the highest digestive abilities of all the populations studied. Scottish Black Grouse, eating mostly heather but also other foods, had longer guts than Russian Black Grouse, which ate mostly birch (*Betula*) catkins and twigs. This finding confirms the hypothesis that a diet of heather is associated with long guts.

DISCUSSION

Present conclusions are tentative because the data in this paper are so heterogeneous in origin. Nonetheless, the data confirm the model based on the purely theoretical premise that A , the calculated external surface area of the gut, limits digestibility. Hitherto, measurements of gut length and digestibility in tetraonid birds have been made with the vague underlying idea that long guts are an adaptation to high intakes of fibrous foods. Now that a quantitative theory is available, we can expect future work to test it with proper rigor. An important question will be whether variables such as ambient temperature, state of molt, and reproductive condition, ignored here, will need to be included in any extrapolation of the model to other seasons and species. This may not be necessary if the main effect of such factors is to alter food intake, because the present model includes intake.

EFFECT OF CAPTIVITY ON GUT SIZE

Birds hatched and reared in captivity had markedly smaller guts and gizzards than wild ones (Table 3), a contrast attributable to their different diets. The pellets eaten by captive grouse contained relatively low levels of crude fiber compared with natural foods (11% vs. 20% or more) and high levels of crude protein (18% vs. 10% or less) (Moss 1972).

TABLE 3. Mean gut lengths (cm), gizzard weights (g) and digestive abilities of tetraonids eating winter foods.

		Age	Sex	Weight (g)	Small int.	Both caeca	Large int.	Gizzard	Relative gut length ^a	Dig. abil. ^b	Ratio caecal sm. int. ^c	Source	Location	Main food items ^d
WILD BIRDS														
Capercaillie														
	♂			3,330	215	184	22	123 ^{se}	1.06	0.34	0.86	STS	68°N, 32°E	<i>Pinus n</i>
	♂			4,200	207	167	19	135	0.91	0.27	0.81		57°N, 4°W	<i>Pinus n</i>
	♀			1,730 ^f	173	136	18	78 ^{ss}	1.04	0.35	0.79	STS	68°N, 32°E	<i>Pinus n</i>
	♀			1,780	153	125	17	76	0.93	0.30	0.82		57°N, 4°W	<i>Pinus n</i>
Black Grouse														
	both			1,110	146	110	12	32 ^{sr}	1.00	0.35	0.75	STS	68°N, 32°E	<i>Betula cbt</i>
	♂	0		1,400 ^f	142	134	16	—	1.00	0.34	0.94	GWJ	57°N, 3°W	<i>Calluna s</i>
	♂	y		1,250	149	129	15	—	1.05	0.36	0.87	GWJ	57°N, 3°W	<i>Calluna s</i>
	♀	0		1,050	136	122	15	—	1.04	0.37	0.90	GWJ	57°N, 3°W	<i>Calluna s</i>
	♀	y		1,050	143	120	15	—	1.06	0.38	0.84	GWJ	57°N, 3°W	<i>Calluna s</i>
Blue Grouse														
	♂			1,060	136	107	15	32	0.98	0.34	0.79	FCZ	49°N, 125°W	<i>Abies, Pinus n</i>
	♀			880 ^f	131	99	15	28	0.99	0.35	0.76	FCZ	49°N, 125°W	<i>Abies, Pinus n</i>
Red Grouse														
	♂	0		685	98	149	15	28	1.16	0.44	1.5	RM1	57°N, 3°W	<i>Calluna s</i>
	♂	0		700	101	158	15	27	1.21	0.46	1.6	RM1	57°N, 3°W	<i>Calluna s</i>
Willow Ptarmigan														
	♂	0		640	97	130	13 ^h	—	1.09	0.41	1.3	EP	68°N, 27°E	<i>Betula cbt</i>
	♂	y		630	98	131	13 ^h	—	1.11	0.42	1.3	EP	68°N, 27°E	<i>Betula cbt</i>
	♀	0		570	93	127	13 ^h	—	1.10	0.42	1.4	EP	68°N, 27°E	<i>Betula cbt</i>
	♀	y		550	94	125	13 ^h	—	1.11	0.42	1.3	EP	68°N, 27°E	<i>Betula cbt</i>
	♂			620	86	129	13	20 ^d	1.05	0.39	1.5	STS	68°N, 32°E	<i>Betula cbt, Salix bt</i>
	♀			590	82	132	13	22 ^a	1.06	0.40	1.6	STS	68°N, 32°E	<i>Betula cbt, Salix bt</i>
	both			500 ^f	81	107	12	16	0.99	0.37	1.3	RM2	63°N, 145°W	<i>Salix bt</i>

TABLE 3. Continued.

	Age	Sex	Weight (g)	Small int.	Both caeca	Large int.	Gizzard	Relative gut length ^a	Dig. abil. ^b	Ratio caeca/sm. int. ^c	Source	Location	Main food items ^d
Spruce Grouse	both		570	—	—	—	38 ^d	—	—	—	LE	60°N, 175°W	<i>Picea n</i>
	both		550 ^f	88	71	13	32	0.83	0.29	0.81	BAP	55°N, 116°W	<i>Pinus n</i>
	both		550 ^f	103	87	13	17	0.97	0.35	0.84	GG	47°N, 92°W	<i>Populus cbt</i>
Ruffed Grouse <i>Bonasa umbellus</i>		♂	520	89	83	12	14	0.90	0.32	0.93	AG	65°N, 21°W	<i>Salix bt, Betula cbt</i>
		♂	520	104	96	12	17 ^d	1.04	0.39	0.92	STS	68°N, 32°E	<i>Betula cbt, Empetrum s</i>
		♂	520 ^f	97	108	12	16	1.06	0.40	1.1	"	57°N, 3°W	<i>Calluna s, Empetrum s, Vaccinium s</i>
Hazel Grouse	both		420	100	93	11	10	1.08	0.42	0.93	RM2	63°N, 145°W	<i>Betula cb</i>
	both		390 ^f	101	86	10	12 ^d	1.07	0.42	0.85	STS	68°N, 32°E	<i>Alnus cbt, Betula cbt</i>
White-tailed Ptarmigan	both		390	78	73	10	—	0.87	0.32	0.94	TM	40°N, 106°W	<i>Salix bt</i>
	both		360 ^f	91	88	11	13	1.06	0.41	0.97	RM2	63°N, 145°W	<i>Betula bt, Alnus c, Salix bt</i>
CAPTIVE BIRDS													
Red Grouse		♂	650	73	106	13	10	0.87	0.30	1.5	RM3	57°N, 3°W	artificial pellets
Capercaillie		♂	4,200	144	119	21	74	0.66	0.18	0.83	RM3	57°N, 3°W	artificial pellets
		♀	1,880	123	87	14	42	0.69	0.20	0.71	RM3	57°N, 3°W	artificial pellets

Where ages are not given, data from young (y) and old (o) birds are combined.

^a L_g/L_{cp} .
^b Digestive abilities, from equation (12).
^c Ratio of lengths of combined caeca and small intestine.
^d Weight of gizzard without lining, given by source, $\times 1.14$.
^e From birds of mean W 3,720 g.
^f Data used for Table 2.
^g From birds of mean W 1,760 g.
^h Not given by EP; data from STS.
ⁱ n = needles, c = cones or catkins, b = buds, t = twigs, s = shoots.
Sources: STS Semenov-Tjan-Shanskii (1959); G.W.J. G.W. Johnstone (pers. comm.); FCZ F.C. Zwickel (pers. comm.); EP Pulliainen (1976); LE L. Ellison (pers. comm.); BAP Pendergast (1969); GG G. Gullion (pers. comm.); AG Arnthor Gardarsson (pers. comm.); TM May (1975); RMI Moss (1967); RM2 Moss (1974); RM3 Moss (1972); otherwise see appendix.

TABLE 4. Digestibilities D of winter diets, and body weights W (g) and relative gut lengths L_o/L_a of tetraonids eating them.

Species	W	L_o/L_a	D (observed)	Digestive abilities	$k_o \times 10^3$	$k_a \times 10^3$	Main food items
Red Grouse ^a	700	1.21	0.46	0.46	52	46	<i>Calluna vulgaris</i> s
Willow Ptarmigan ^a	500	0.99	0.44	0.37	63	77	<i>Salix</i> sp. bt
Spruce Grouse ^a	550	0.83	0.27	0.29	49	34	<i>Pinus contorta</i> n
Rock Ptarmigan ^a	420	1.06	0.37	0.41	48	46	<i>Betula glandulosa</i> cb
White-tailed Ptarmigan ^a	360	1.06	0.45	0.41	57	54	<i>Salix</i> sp. bt, <i>Betula glandulosa</i> cbt, <i>Alnus crispa</i> c
Capercaillie ^{bc}	4,600	1.06	0.33	0.33	53	52	<i>Pinus sylvestris</i> n
Black Grouse ^{bc}	1,000	1.00	0.35	0.35	53	48	<i>Betula</i> sp. c
Willow Ptarmigan ^{bd}	600	1.06	0.35	0.39	47	42	<i>Chosenia arbutifolia</i> bt
Rock Ptarmigan ^{bd}	460	1.04	0.42	0.39	56	50	<i>Betula</i> sp. c, <i>Alnus</i> sp. c
Hazel Grouse ^{bd}	400	1.07	0.38	0.41	48	43	<i>Betula</i> sp. cb, <i>Salix</i> sp. bt, <i>Chosenia</i> sp. bt, <i>Alnus</i> sp. c

^a "Digestive abilities" are as in Table 3; k_o was calculated as for Red Grouse in the text; $k_a = k_o F_o/F_a$.

^b Data directly comparable with Table 3.

^c Data heterogeneous: L_o/L_a from Table 3; W , diet and D (recalculated, see Methods) from Andreev (1979).

^d Diets of two sets of birds (i.e., from Table 3 and Andreev 1979) similar.

^e Diets of two sets of birds different (see Table 3).

More than food is involved, however: successive generations of captive Red Grouse, eating the same food but successively further removed from their wild origins, each had smaller guts than the generation before it (Moss 1972). Furthermore, lengths of the caeca had decreased relatively more than lengths of the small intestine. Hence adaptations to big changes in diet may take generations and differ between parts of the gut.

SEX, AGE, AND GUT SIZE

Different ages and sexes of some species had different gut lengths, suggesting that such birds may eat foods of differing quality. Perhaps the most dominant birds (old cocks) gain access to the best (most digestible) food and the least dominant (young hens) to the poorest.

Pulliainen (1976) suggested that differences in gut length per unit body weight among sexes and age-classes in Willow Ptarmigan may result simply from differences in energy requirements stemming from differences in surface area and body weight. However, the measures of relative gut length, given in Table 3 and calculated from his data, make due allowance for observed average variations in gut length with body weight and still show slight differences among sexes and age-classes. Hence, differences in body size may not be sufficient to explain these differences in gut length in Willow Ptarmigan and they are certainly not an adequate explanation in Black Grouse.

DIET, PREFERENCES, DIGESTIVE ABILITIES, AND CHEMICAL COMPOSITION

Gut length and digestive ability are aspects of the complex of adaptations between a popu-

lation, its preferred foods and its competitors. Within the preferred habitat, a bird's choice of food is restricted by the need to avoid predators, the need to avoid competition from other individuals and species (Moss 1973), and its own morphological, physiological, and biochemical characteristics.

Within these limits, birds clearly prefer certain foods. Willow, Rock and White-tailed ptarmigan all seem to prefer willow in winter if it is available and if a larger species of ptarmigan is not present (Moss 1974).

Preference for willow is often associated with higher content of protein and phosphorus and lower content of fiber (Gardarsson and Moss 1970) but not always (Moss 1973). As well as being more digestible (Table 4), willow may also contain lower concentrations of toxins than birch and alder. Birch may, in addition to possible digestion-inhibiting fat-soluble compounds (Bryant and Kuropat 1980), contain substances promoting loss of sodium (Pehrson 1980). Sodium may be in short supply in snowy continental areas, because it is not an essential plant nutrient and is therefore often in low concentrations in plant material (Moss and Hanssen 1980).

Heather, although well digested by wild Red Grouse, is not usually preferred by tetraonids when other foods are available. This may be because it contains high concentrations of fiber and tannins and low concentrations of protein and phosphorus. Red Grouse detoxify phenolic compounds, such as tannins, and excrete them as ornithuric acid, but this requires nitrogen (Moss and Parkinson 1972). Hence, selection by Red Grouse for nitrogen-rich heather (Moss 1972) not only provides the bird with essential amino acids, but also facilitates detoxication.

ADAPTATION, DIET AND POPULATION DENSITY

The length of a tetraonid's gut is particularly useful for describing nutritional aspects of the bird's ecology because it is so labile, responding quickly to changes in food and environment. This study suggests that "digestibility" is as much a property of the eater as of the food eaten. Some foods are more digestible than others, but this may be apparent only when eaten by animals with comparable digestive abilities. We can now measure the "digestive abilities" of tetraonids in winter as a function of gut length and body weight (equation 12).

The advantages of long and short guts are seen in different contexts. Long guts improve the ability to survive on poor food, but require more energy and nutrients for maintenance. On the contrary, birds with short guts may be able to compete better (as long as enough good food is available; Moss 1975) and can therefore gain access to the best food.

In turn, this can explain why tetraonids feed so selectively and use such a small proportion of the winter food available to them (Semenov-Tian-Shanskii 1959, Gardarsson and Moss 1970, Savory 1978). The better the food they select, the greater their competitive ability. Dominant birds may exclude competitors from the population and so reduce population density. This would increase the amount of food available to them and from which they select their diet.

MODEL PREDICTING DIGESTIBILITY FROM BODY WEIGHT, GUT SIZE AND FOOD INTAKE

MATHEMATICAL OUTLINE

The model does not attempt to mimic the physiological processes of digestion. The main justification for its underlying assumptions is not that they are realistic, but that quantitative predictions of the model are accurate.

The gut is assumed to be a simple cylinder, with both gut and contents having a specific gravity of 1.0. This cylinder has weight and volume G , and is bounded externally by a surface with radius r , length L and surface area A .

Food completely fills the gut and is absorbed at a rate k through each unit area of the bounding surface. The value of k depends partly on the nature of the food and partly on the length of time the food spends in the gut. For a given gut, this time is inversely related to food intake F and so the digestibility D of the food varies inversely as F

$$D = kA/F \quad (1)$$

$$\text{as } A = 2\pi rL$$

$$D = 2k\pi rL/F \quad (2)$$

We are interested in deviations of D and A from their average values for a grouse of a given body weight W . We can therefore write

$$D_o = (k_o A_a / F_o) \cdot (r_o / r_a) \cdot (L_o / L_a) \quad (3)$$

where the subscript a indicates average values for a bird of a given W , and subscript o observed values for a particular set of birds of that W . We can also incorporate deviations in F from the average for a given W by assuming that a bird adjusts its intake so that DF and therefore kA remain constant. This is reasonable because a bird's energy requirements are likely to be similar with different diets. Thus $k_o F_o = k_a F_a$ and

$$D_o = (k_a A_a / F_a) \cdot (r_o / r_a) \cdot (L_o / L_a) \cdot (F_a / F_o) \quad (4)$$

In fact, r and L are correlated, so we can reasonably put $r = L^b$, where b is a constant, and rewrite (4) as

$$D_o = (k_a A_a / F_a) \cdot (L_o / L_a)^{1+b} \cdot (F_a / F_o) \quad (5)$$

Finally, we assume A_a and F_a to be proportional to some power of the body weight W such that $A_a / F_a = CW^c$, where C and c are constants, and so

$$D_o = (k_a CW^c) \cdot (L_o / L_a)^{1+b} \cdot (F_a / F_o) \quad (6)$$

The next step is to incorporate empirical relationships between A_a , L_a , F_a and W .

EMPIRICAL RELATIONSHIPS

Among animals of different weights, food intake increases not in direct proportion to W , but as some lesser power. For tetraonids eating winter foods (Moss and Hanssen 1980) the average relationship is

$$F_a = 0.57 W^{0.73} \quad (7)$$

From Table 1

$$G_a = \pi r_a^2 L_a = 0.18 W^{0.94}$$

and from Table 2

$$L_a = 22.0 W^{0.36}$$

so

$$A_a = 2\pi r_a L_a = 7.05 W^{0.655}$$

Hence the area of gut per unit weight of food (A/F) decreases as

$$A_a / F_a = 12.4 W^{-0.065} \quad (8)$$

and

$$D_a = 12.4 k_a W^{-0.065} \quad (9)$$

So our estimate of C is 12.4 and of c -0.065.

This is an average relationship. For an individual case (equation 6)

$$D_o = 12.4k_a W^{-0.065} \cdot (L_o/L_a)^{1+b} \cdot (F_o/F_a) \quad (10)$$

or

$$D_o = 12.4k_o W^{-0.065} \cdot (L_o/L_a)^{1+b} \quad (11)$$

We can test the theoretical value of c (-0.065) and estimate b by inserting known values of D , W and L_o/L_a (Table 4) in a multiple regression of $\log D$ on $\log W$ and $\log (L_o/L_a)$. This gives the values

$$D = 0.65 W^{-0.09 \pm 0.05} \cdot (L_o/L_a)^{1.31 \pm 0.37} \quad (12)$$

$(R^2 = 0.68).$

This gives an estimate of c (-0.09 ± 0.05) in reasonable agreement with our previous estimate (-0.065) and suggests that b is 0.31 ± 0.37 (SE).

The value of 0.31 for b is likely to be an underestimate if coarser, less digestible foods are associated with longer guts independently of intake. In practice, this is not a disadvantage when predicting D_o , because the same bias would probably recur with a new food whose D_o is being predicted.

Equation (12) can be used to predict the digestibility of the average winter food at average intakes for wild birds; in this paper this is used as a measure of the "digestive abilities" of different populations without the complication due to different diets. The "digestive abilities" of a population are likely to be an adequate predictor of D_o for a new food if k_o for the new food is near the average for other foods. In fact k_o varied much less for the studied foods than did k_a . From data in Table 4

$$k_o = 0.40k_a + 0.033 \quad (r^2 = 0.79).$$

This low variation in k_o was because of a tendency ($r = 0.67$, $P < 0.05$) for high F_o/F_a to be associated with high D_o/D_a . The likely reason is that the high intake (F_o) of an intrinsically highly digestible food (high k_a) tended to reduce the time spent by the food in the gut and hence k_o . It may be that the gut's optimum k_o is about $0.05 \text{ g/cm}^2/\text{day}$ and that intakes of typical winter foods are adjusted to achieve this.

FURTHER TESTS OF THE MODEL

The assumption (equation 1) that D decreases with increasing F when W and G are fixed is confirmed by data from captive Red Grouse which were voluntarily eating different amounts of heather, their natural diet. In these data (Moss and Parkinson 1972)

$$D = 14.9/F + 0.056 \quad (r^2 = 0.76).$$

The known values of D used to derive equation (12) (Table 4) did not involve captive Red Grouse and so we can test the model by using it to predict the digestion of heather by captives. D_o for wild Red Grouse is 0.46 , so

$$0.46 = 12.4k_o W^{-0.09} (L_o/L_a)^{1.31}.$$

Substituting 700 for W , 1.21 for L_o/L_a (Table 3) gives $k_o = 0.052$ for wild Red Grouse eating heather. Applying this to captives ($W = 650$, $L_o/L_a = 0.89$) gives $D_o = 0.31$, a figure reasonably close to the observed value of 0.28 . The assumption that k_o is similar for wild birds and captives is reasonable, as F_o for both is similar (Moss and Parkinson 1972, Savory 1978). Since D_o for wild Red Grouse eating heather was the highest (0.46) observed value and for captives the lowest-but-one (0.28), this prediction was a good test of the model. This example also shows that variation in gut size is at least as important in determining D_o as are intrinsic differences between the studied foods.

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APPENDIX. Sample details for Table 3 (\pm SE). See Table 3 for details of sources.

Species	Season	Age ^a	Sex	n	Weight (g)	Small int. (cm)	Both caeca (cm)	Large int. (cm)	Gizzard (g)
Capercaillie (wild)	Oct.-Nov.	o	♂	2	4,200 \pm 240	207 \pm 11	167 \pm 3	207 \pm 11	135 \pm 16
		o	♀	3	1,780 \pm 27	153 \pm 1	125 \pm 3	153 \pm 1	76 \pm 4
Capercaillie (captive)	Dec.-Jan.	o	♂	2	4,220 \pm 290	144 \pm 15	119 \pm 3	144 \pm 15	74 \pm 1
		o	♀	3	1,880 \pm 72	123 \pm 3	87 \pm 1	123 \pm 3	42 \pm 5
Black Grouse (source GWJ)	Sept.-Dec.	o	♂	15	1,420 \pm 26 ^b	142 \pm 2	134 \pm 4	16 \pm 0.3	—
		y	♂	11	1,240 \pm 17	149 \pm 2	129 \pm 5	15 \pm 0.3	—
		o	♂	29	1,025 \pm 16	136 \pm 1	122 \pm 2	15 \pm 0.2	—
		y	♂	11	1,090 \pm 31	143 \pm 3	120 \pm 4	15 \pm 0.3	—
Blue Grouse (source FCZ)	April	o	♂	2	1,060 \pm 22	136 \pm 3	107 \pm 3	15 \pm 0.2	32 \pm 1
		y	♂	10					
		o	♀	5	880 \pm 31	131 \pm 2	99 \pm 2	15 \pm 0.3	28 \pm 1
		y	♀	12					
Ruffed Grouse (source GG)	Sept.-April	o	♂	5	550 \pm 16	103 \pm 2	87 \pm 3	13 \pm 0.3	17 \pm 2 ^c
		y	♂	3					
		o	♀	1					
		y	♀	4					
Spruce Grouse (source LE)	March-May	y	♂	7	570 \pm 11	—	—	—	38 \pm 1
		o	♀	3					
		o	♀	5					
Rock Ptarmigan	Oct.-Nov.	o	♂	15	530 \pm 7	99 \pm 2	108 \pm 2	12 \pm 0.3	17 \pm 0.5 ^d
		y	♂	8	495 \pm 4	92 \pm 3	109 \pm 4	12 \pm 0.3	16 \pm 0.2
		o	♀	9	500 \pm 10	94 \pm 2	105 \pm 3	12 \pm 0.3	17 \pm 1
		y	♀	8	480 \pm 8	95 \pm 3	110 \pm 3	13 \pm 0.3	15 \pm 0.4

^a y = less than one year old, o = more than one year old.

^b Some weights from A. Watson (pers. comm.); n (for W) 9, 19, 13, 6.

^c n = 2 for gizzards.

^d n for gizzards 10, 4, 3, 3.