The Condor 99:314–326

ADAPTATIONS TO AND CONSEQUENCES OF AN HERBIVOROUS DIET IN GROUSE AND WATERFOWL[1]

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Abstract. I review diet selection in grouse and waterfowl in the context of their herbivorous diets and discuss adaptations to herbivory in these groups. Both grouse and waterfowl prefer plant foods containing higher concentrations of protein than nonpreferred foods; grouse and small waterfowl include invertebrates in the diet to meet protein demands during periods of high tissue production. Grouse tend to avoid plant foods containing high concentrations of anti-herbivore compounds and the relative roles of these compounds versus nutrients in diet selection by grouse is presently unclear. Grouse and waterfowl have similar digestive morphology, except for the ceca, which are 5 times longer in grouse than in geese. Enlarged ceca are associated with improved nitrogen economy in grouse; evolution of these structures in geese may have been precluded by energetic costs of carrying enlarged ceca during migration.

Key words: grouse, waterfowl, herbivory, nutrition, digestion.

INTRODUCTION

Green leaves typically contain lower concentrations of nutrients and are less digestible than animal tissue or fruits (Robbins 1993). This likely explains why herbivory is practiced by relatively few avian taxa. Herbivory is best known in three groups of birds: (1) grouse, family Tetraonidae in the order Galliformes, (2) geese, swans and some ducks, subfamilies Anserinae and Anatinae in the order Anseriformes, and (3) ratites. Herbivory also occurs in members of the orders Columbiformes (Kenward and Sibley 1977), Gruiformes (Mills et al. 1991) and in the unique Hoatzin *Opisthoeomus hoazin* (Grajal et al. 1989). Because adaptations to herbivory and foraging ecology have been studied most extensively in grouse and waterfowl, I will focus on these two groups in the remainder of this review.

Generally, low nutrient concentrations in plant foods should increase the importance of food quality to herbivorous birds by increasing the nutritional advantage of foraging on those foods with the highest nutrient concentrations. Importance of food quality is further increased by digestive limits on food intake in avian herbivores (Kenward and Sibly 1977, Sedinger and Raveling 1988), which limits the ability to compensate for low nutrient concentration by eating more food. Diet quality has been directly linked to reproductive success in female grouse (Moss et al. 1975, Brittas 1988) and indirectly linked to rate of growth and future fitness in populations of geese (Cooch et al. 1991, Larsson and Forslund 1991, Sedinger and Flint 1991). Herbivorous birds are near the lower end of the size range for endothermic herbivores. Small body size makes it difficult to meet nutritional requirements when feeding on plants because gut capacity scales linearly with body mass, whereas mass-specific nutritional requirements increase with decreasing body mass (Demment and Van Soest 1985). Finally, the necessity for flight has precluded evolution of large complex digestive structures (Dudley and Vermeij 1992) found in numerous mammalian taxa (Robbins 1993). Therefore, behaviors and morphological adaptations that increase rates of nutrient intake and retention can be directly linked to fitness in these two groups of birds. My goals in this review are to describe morphological attributes of waterfowl and grouse with respect to their herbivorous diets, discuss dietary differences between the two groups and bases for diet selection, and examine likely constraints on adaptations to herbivory.

DIETS IN GROUSE AND WATERFOWL

GENERAL DIETARY PATTERNS

Geese feed predominantly on leaves, seeds and underground parts of monocots (Owen 1980). There is, however, seasonal and taxonomic variation in specific attributes of the diet. Geese in the genus *Branta,* including Canada Geese, are

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[1] Received 26 May 1995. Accepted 17 January 1997.

largely restricted from feeding on below-ground structures by their bill musculature, whereas geese in the genus *Anser* are adapted to grub underground parts of plants (Goodman and Fisher 1962). Geese feed predominantly on green leaves during spring and summer, when leaves are actively growing and contain the highest protein content (Harwood 1977, Sedinger and Raveling 1984, Gauthier 1993). Consequently, production of lean tissue is largely restricted to these two periods (Wypkema and Ankney 1979, McLandress and Raveling 1981, Hobaugh 1985). From fall to spring many populations of geese feed predominantly on seeds, including agricultural grains, and underground plant parts (Frederick and Klaas 1982, Alisauskas et al. 1988, Ely 1992). Exceptions to this general pattern include populations of small-bodied geese (Einarsen 1965, Raveling and Zezelak 1991) and some populations in Europe that feed on pasture or other graminoids (Owen 1971, Lorenzen and Madsen 1986).

Consumption of seeds and underground plant parts before spring and fall migration reflects the greater metabolizable energy content of these foods relative to green plants (Joyner et al. 1987, Sedinger et al. 1989, Robbins 1993) when geese must deposit substantial lipid reserves to fuel migration (Ankney 1982, Sedinger and Bollinger 1987). Eating seeds and underground plant parts by geese through winter likely reflects reduced availability of growing graminoids because geese are at endogenously maintained low mass at this time (Hanson 1962, Joyner et al. 1984). However, shifts to agricultural grains have allowed geese to meet their daily energy requirements with less foraging time, and geese using these foods have reduced time spent foraging as a result (Baldassarre and Bolen 1994).

Swans, the largest waterfowl, are believed to feed nearly exclusively on aquatic and terrestrial vegetation and agricultural grains throughout the year (Mathiasson 1973, Owen and Cadbury 1975, Rees 1990). Some species of ducks are exclusively herbivorous outside the breeding season (Paulus 1982, Thomas 1982) but all of these species shift to animal foods to meet protein requirements for breeding and growth (Krapu and Reinecke 1992).

Grouse typically do not feed on monocots (but see Emison and White 1988), except the prairie grouse for which graminoid seeds, including agricultural grains, can be seasonally important in the diet (Aldous 1943, Jones 1966). Most grouse include invertebrates in their diets when producing lean tissue at a high rate, especially during growth (Moss and Hanssen 1980), and some populations also increase consumption of forbs during such periods (Pulliainen 1979, Pulliainen and Eskonen 1982, Norman and Kirkpatrick 1984). Some grouse may eat invertebrates during egg laying (K. Martin, pers. comm.). Beyond these patterns, few generalities exist. Different populations of the same species of grouse may specialize on different foods, depending on local conditions (Table 1), although most grouse species appear to specialize on a few food species throughout their range (Gullion 1966, Bryant and Kuropat 1980). Outside the breeding season grouse generally feed on the leaves or reproductive organs of woody species (Table 1).

DIET SELECTION IN HERBIVOROUS BIRDS

Several studies have demonstrated that geese select foods high in nitrogen (crude protein) and low in cell wall (fiber) content during growth (Sedinger and Raveling 1984, Laing and Raveling 1993, Manseau and Gauthier 1994) and reproduction (Gauthier 1993). Cackling Canada Geese (*Branta canadensis minima*) eat the leaves of arrowgrass (*Triglochin palustris*) at > 4 times the rate expected by chance (Sedinger and Raveling 1984). Arrowgrass leaves contain substantially greater protein levels and lower cell wall levels than other available monocots (Sedinger and Raveling 1984). Lesser Snow Geese (*Anser caerulescens caerulescens*) maintain grazing lawns of *Carex subspathacea* and *Puccinellia phryganodes* (Cargill and Jefferies 1984, Bazely and Jefferies 1986), which contain higher concentrations of protein than less intensively grazed areas during the breeding season, and Lesser Snow Geese concentrate their foraging on these lawns.

During autumn and winter many geese typically switch to foods higher in carbohydrate and lipid, and lower in protein than summer green plants; agricultural cereals have become important foods for wintering geese in North America and Europe (Bossenmaier and Marshall 1958, Lorenzen and Madsen 1986, Alisauskas et al. 1988). This pattern likely reflects the lower protein requirement of geese in fall and winter, relative to the breeding season (Raveling 1979, Se-

TABLE 1. Seasonal diets of waterfowl and grouse including indication of dietary preference based on nutrient content or secondary chemicals.

Time period/bird species	Primary food^{a}	Secondary food^{b}	Evidence for nutrient-based selection^{c}	Evidence for chemical-based selection^{d}	Reference^{e}
Breeding-growth					
Waterfowl					
Anser c. caerulescens	*Carex subspathacea*	*Puccinellia* phryganodes			1
A. caerulescens atlantica			Yes		2
A. c. atlantica	*C. aquatilus*	*Eriophorum scheuchzeri*			3
A. canagicus	*P. phryganodes*	*C. subspathacea*	Yes		4
Branta canadensis minima	*T. palustris*	*C. mackenzei*	Yes		5
Branta canadensis	*Zostera marina*	*Spartina alterniflora*	No	Yes	6
Grouse					
D. canadensis	*Picea* sp.	*Pinus cantorta*	No		7
Lagopus lagopus	Invertebrates	Moss			8
L. lagopus	*Vaccinium myrtillus* leaves	*Eriophorum vaginatum* flowers			46
L. lagopus	*Salix* leaves	Berries			47
L. lagopus	Invertebrates	*Vaccinium* leaves	No		48
L. l. scoticus	*Calluna vulgaris*		Yes		9
L. l. scoticus	*Calluna vulgaris*	Moss			49
L. l. scoticus	*Polygonum bulbils*	Invertebrates			50
L. mutus	*Calluna vulgaris*	*Empetrum nigrum*			10
Bonasa umbellus	Green plants	Sedges			11
B. umbellus	Forbs	Berries			12
Winter					
Waterfowl					
Cygnus c. columbianis	*Potomogetan pectinatus*				13
C. c. bewickii	*Lolium perenne*	*Alopecurus geniculatus*	Yes		14
A. anser	*Scirpus maritima* tubers	*S. litoralis* tubers	Yes		17
A. anser	*Paspalum distichum* stems	*P. distichum* leaves			18
A. c. caerulescens	*Scirpus* sp.	*Spartina* sp.			15
A. c. caerulescens	Forbs	Grasses			15
A. c. caerulescens	Corn	Milo			15
A. a. frontalis	*Lolium perenne*	*Agrostis stolonifera*	Yes		16
A. indicus	*P. distichum* stems	*Pisum sativum* seeds			18
Branta leucopsis	Grass				19
B. canadensis	Millet	Smartweed seeds			20
B. canadensis interior	Oats	Corn			25
B. b. bernicla	*Zostera noltii*	*Enteromorpha* sp.			21

TABLE 1. Continued.

Time period/bird species	Primary food[a]	Secondary food[b]	Evidence for nutrient-based selection[c]	Evidence for chemical-based selection[d]	Reference[e]
B. b. bernicla	*Spergularia media*	*Puccinellia maritima*			22
B. b. bernicla	*Cynosurus* sp. *Lolium* sp.	*Holcus lanatus/Hordeum* sp.			23
B. bernicla nigricans	*Zostera marina*				24
Anas penelope					26
A. penelope	*Cynosurus* sp. *Lolium* sp.	*Holcus lanatus/Hordeum* sp.			23
A. strepera	*Hordeum vulgare* seeds	*Lemna minor*			27
Grouse					
Centrocercus urophasianus	*Artemesia tridentata*			Yes	28
Dendragopus obscurus	*Abies concolor*		Yes		29
D. obscurus	*Pinus contorta*		No		30
D. canadensis	Conifer needles				31
D. canadensis	*Picea* needles				31
Lagopus l. scoticus	*Calluna vulgaris*	*Erica tetralix*	Yes		9
Lagopus l. scoticus	*Salix* twigs	*Empetrum* shoots			50
L. l. lagopus	*Salix* buds, twigs	*Betula glandulosa*			32
L. l. lagopus	*Salix* buds, twigs	*B. glandulosa* twigs			33
L. l. lagopus	*Betula* buds, twigs, catkins				34
L. l. lagopus	*Betula* buds, twigs, catkins	*Salix* buds, twigs			31
L. l. lagopus	*Salix* stems	*B. glandulosa* buds, catkins			35
L. l. lagopus	*Betula* shoots, catkins	*Salix* shoots	Yes		36
L. l. lagopus	*Betula* shoots, catkins	*Salix*		Yes	37
L. mutus	*Salix* buds, twigs	*Betula* cones, buds, twigs			31
L. mutus	*Betula* cones, buds, twigs	*Empetrum nigrum* shoots			31
L. mutus	*Calluna* shoots	*Empetrum nigrum* shoots			31
L. mutus	*B. glandulosa* buds, catkins	*Salix* buds			35
L. mutus	*Empetrum nigrum* leaves	*Equisetum arvense*			38
L. mutus	*Salix* buds, twigs	*Betula* buds, catkins, twigs			32
L. mutus	*Salix* buds, twigs	*Betula* catkins, buds, twigs			31
Lagopus leucurus	*Betula* buds and catkins	*Alnus crispa cones*			32
L. leucurus	*Salix* buds, twigs				31
L. leucurus	*Salix*				39
Tetrao urogallus	*Pinus* needles				31
T. urogallus	*Pinus* needles	Yes	Yes		40
T. urogallus	*Pinus* needles		Yes		41
T. tetrix	*Calluna* shoots				31
Bonas umbellus	*Ostrya virginiana*	*Rosa multiflora*			11
B. umbellus	*Smilax* leaves, fruit	*Kalmia latifolia*			42

TABLE 1. Continued.

Time period/bird species	Primary food[a]	Secondary food[b]	Evidence for nutrient-based selection[c]	Evidence for chemical-based selection[d]	Reference[e]
B. umbellus	*Populus tremuloides* flower buds			Yes	43
B. umbellus	*Rosa woodsei*	*Populus tremuloides* leaves			44
B. umbellus	*Populus tremuloides* flower buds	*Salix* buds	Yes		45

[a] Most abundant food in diet.

[b] Second most abundant food in diet.

[c] Evidence that foods containing higher concentrations of nutrients were eaten more often than expected by chance. Blanks indicate preference was not assessed.

[d] Evident that foods containing higher concentrations of antiherbivore compounds were avoided. Blanks indicate preference based on plant chemistry was not assessed.

[e] (1) Jefferies 1988, (2) Manseau and Gauthier 1993, (3) Gauthier 1993, (4) Laing and Raveling 1993, (5) Sedinger and Raveling 1984, (6) Buchsbaum et al. 1984, (7) Pendergast and Boag 1971, (8) Pulliainen and Eskonen 1982, (9) Moss 1972, (10) Moss and Watson 1984, (11) Korschgen 1966, (12) Norman and Kirkpatrick 1984, (13) Sherwood 1960, (14) Rees 1990, (15) Alisauskas et al. 1988, (16) Owen 1976, (17) Amat et al. 1991, (18) Middleton and van der Valk 1987, (19) Prop and Vulink, (20) Korschgen 1955, (21) Charman 1979, (22) Charman and Macey 1978, (23) Williams and Forbes 1980, (24) Einarsen 1965, (25) Craven and Hunt 1984, (26) Owen and Thomas 1979, (27) Thomas 1982, (28) Welch et al. 1988, (29) Hoffman 1961, (30) Boag and Kiceniuk 1968, (31) Moss 1983, (32) Moss 1973, (33) Andreev 1991, (34) Pulliainen 1976, (35) Thomas 1984, (36) Pulliainen and Iivanainen 1981, (37) Myrberget and Aabakken 1987, (38) Emison and White 1988, (39) Weeden 1967, (40 Linden 1984, (41) Pulliainen 1978, (42) Seehorn et al. 1983, (43) Jakubus and Gullion 1991, (44) Phillips 1967, (45) Doerr et al. 1974, (46) Brittas 1988, (47) Martin and Hik 1992, (48) Spidsø 1980, (49) Savory 1977, (50) Gardarsson and Moss 1970.

dinger et al. 1992), but it also is related to the lower levels of protein in monocots during fall and winter (Alisauskas et al. 1988, Bolen et al. 1989). Foraging on energy-rich seeds and underground plant parts is, of course, important for lipid deposition necessary to fuel fall and spring migration (Raveling 1979, Ankney 1982, Sedinger and Bolinger 1987). Foraging by the smallest geese on green plants during winter (Einarsen 1965, Raveling and Zezelak 1991) is related to the generally greater mass-specific nitrogen requirement in small, compared to large, geese (Brody 1945), but also is associated with the reduced ability of small geese to physically consume foods eaten by larger geese.

In grouse, bases for diet selection are less well understood, but in Red Grouse (*Lagopus lagopus scoticus*), females select new growth of heather (*Calluna vulgaris*) which contains higher nitrogen content than older heather (Moss 1972a). A number of grouse species eat forbs, which can have high crude protein content (Moss and Hanssen 1980), and invertebrates to meet the elevated protein requirements during growth. Most studies have detected positive correlations between crude protein content of foods and preference for these foods by grouse (Hoffman 1961, Gurchinoff and Robinson 1972, Doerr et al. 1974), whereas other studies have failed to detect such associations (Boag and Kiceniuk 1968, Pendergast and Boag 1971).

Several plant species eaten by grouse produce anti-herbivory compounds, but so far only food selection by Ruffed Grouse (*Bonasa umbellus*) (Jakubus et al. 1989), Sage Grouse (*Centrocercus urophasianus*) (Remington and Braun 1985, Welch et al. 1988), and Capercaillie (*Tetrao urogallus*) (Linden 1984) has been shown to be affected by the presence of such compounds. In these species, foraging is concentrated on individual trees or shrubs containing lower levels of anti-herbivory compounds (Bryant and Kuropat 1980). Frequently, grouse prefer older individual trees because such individuals contain lower concentrations of anti-herbivore substances (Bryant and Kuropat 1980). Guglielmo et al. (1996) demonstrated reduced apparent metabolizability of both energy and nitrogen with increased intake of coniferyl benzoate, the principal anti-herbivore compound in male catkins of aspen, eaten by Ruffed Grouse and concluded that reduced efficiency of retaining dietary energy and nitrogen was sufficient to explain avoidance of coniferyl benzoate without invoking toxicity.

Nearly all studies of both grouse and waterfowl that have examined diet selection have detected dietary preferences based on nutrient concentration (Table 1), usually protein. Although the total number of studies is small, these findings suggest that nutrient concentration in foods influences nutrient balance and, ultimately, fitness in wild populations of grouse and waterfowl. Total biomass of potential foods is typically superabundant for grouse and waterfowl (Bryant and Kuropat 1980; pers. observ.). Therefore, preference for foods with higher nutrient concentrations is consistent with the observation that food intake is limited by digestive constraints in herbivorous birds; individuals cannot fully compensate for low nutrient concentration by increasing food intake. In grouse, the situation is more complex because younger portions of trees and shrubs, which contain higher nutrient concentrations, typically also are defended by anti-herbivore compounds (Bryant and Kuropat 1980). For Ruffed Grouse, preferred aspen flower buds tend to contain higher protein and lower anti-herbivore compound concentrations than nonpreferred buds (Jakubas et al. 1989, Jakubas and Guillon 1991, Guglielmo and Karasov 1995), confounding the relative roles of nutrient concentration and anti-herbivore compounds in diet selection. However, selection among a variety of foods, including birch and hazel catkins, by Ruffed Grouse was consistent with an important role of anti-herbivore compounds in diet selection (Guglielmo and Karasov 1995). Resolution of the relative roles of nutrients and anti-herbivore compounds may require use of artificial diets in which nutrients and anti-herbivore compounds can be manipulated independently.

METABOLISM IN HERBIVOROUS BIRDS

Members of the orders Galliformes and Anseriformes have virtually identical mass-specific metabolic rates (Fig. 1). White-tailed Ptarmigan (Thomas et al. 1994) and Blue Grouse (Pekins et al. 1992) had field metabolic rates > 20% lower than other nonpasserines (Nagy 1987). However, Nagy's (1987) equation for nonpasserines contained no waterfowl and only one galliform.

Nevertheless, waterfowl may have higher seasonal nutritional requirements than grouse because they grow faster (Ricklefs 1968, Siregar and Farrell 1980, Sedinger 1992) and produce larger eggs relative to body mass (Lack 1968). Proportional egg weight declines with increasing female weight in both grouse and waterfowl (Lack 1968). In grouse weighing more than 2,000 g, single eggs represented < 3% of female weight. In contrast, for geese weighing > 2,000 g, eggs ranged from 4% to 7% of female weight. Egg weight was 4.3% of female hatching weight in Willow Ptarmigan (Martin et al. 1993) in contrast to 6.1–6.8% of female weight in the somewhat larger American Wigeon and Gadwall (Lack 1968).

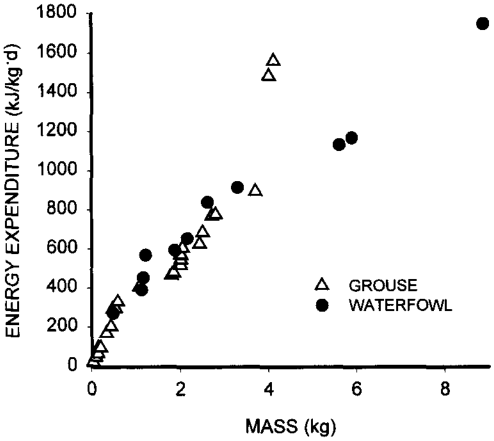

FIGURE 1. Mass-specific daily energy expenditure (standard metabolic rate) of herbivorous grouse and waterfowl. Data from: Lasiewski and Dawson 1967, Zar 1969, West 1972, Rintamäki et al. 1983, Goldstein and Nagy 1985, Bennett and Harvey 1987, Vehrencamp et al. 1989.

Nitrogen intake required for nitrogen balance is higher in waterfowl than in grouse when adjusted for body mass (Analysis of Covariance, $F_{1,4} = 6.99$; $P = 0.057$) (Fig. 2). This result must be considered preliminary because no data are available for larger grouse. It is therefore necessary to assume a similar relationship between mass-specific nitrogen requirement in grouse as in waterfowl. Mass-specific declines in nitrogen turnover (Brody 1945), however, lead me to expect such a relationship between nitrogen requirement and body mass in grouse. It is important to note that both grouse and waterfowl require substantially higher nitrogen intake for balance when feeding than the endogenous losses estimated by Robbins (1993). The higher requirement (up to an order of magnitude) re-

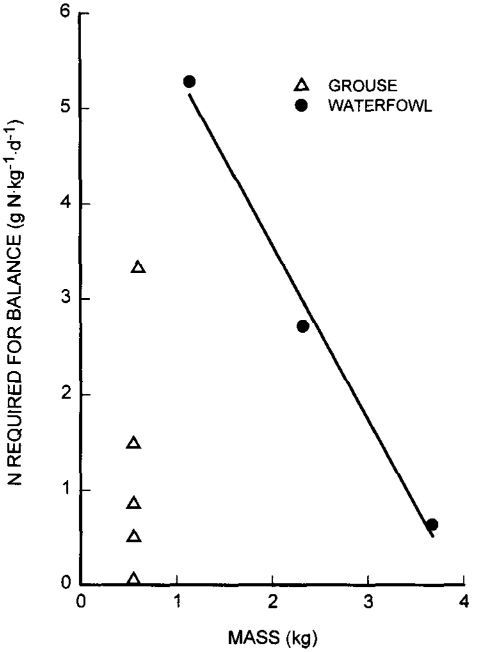

FIGURE 2. Mass-specific daily dietary nitrogen requirement for nitrogen balance in herbivorous grouse and waterfowl. Nitrogen required for balance was estimated by regressing nitrogen excretion against nitrogen intake for studies where both intake and excretion were measured for a sufficient range of intakes. Nitrogen intake required for balance was then calculated from the regression equation as the intake that equaled excretion. Data from: Marriott and Forbes 1970, Moss 1977, Beckerton and Middleton 1983, Guglielmo et al. 1996, Sedinger et al., unpubl. data.

sults primarily from inefficiency of incorporating dietary protein from plant foods. In grouse, nitrogen requirement may be further increased by excretion of nitrogen-containing compounds used to detoxify anti-herbivore compounds in food (Guglielmo 1996; Fig. 2).

Several mechanisms could bring about higher daily mass-specific nitrogen requirements in waterfowl relative to grouse. These include greater losses of nitrogen resulting from a higher rate of metabolic processes necessary to support higher rates of protein production in waterfowl. Greater nitrogen losses could occur even if metabolic reactions involving protein in waterfowl are as efficient as in grouse, because waterfowl have a higher rate of tissue production, and consequently, higher metabolic reactions. It also is possible that metabolic reactions involving nitrogen are less efficient in waterfowl than in grouse. A third hypothesis to explain greater nitrogen requirement in waterfowl is that food intake is higher in waterfowl and greater endogenous nitrogen losses are associated with greater movement of digesta through the gut in waterfowl (Parsons et al. 1982, Sauer et al. 1991). Too few data exist on daily food intake in waterfowl and grouse to assess this hypothesis. Finally, it is possible that grouse retain a greater proportion of dietary nitrogen than do waterfowl because grouse are capable of recycling nitrogen using microbes in their enlarged ceca (see below).

DIGESTIVE ADAPTATIONS

Waterfowl and grouse generally do not differ in the size of digestive organs, when adjusted for body size (Figs. 3, 4). The exception is ceca lengths, which are 4–5 times as long in grouse as in waterfowl of similar size (Fig. 5). I ignored seasonal (Pulliainen and Tunkkari 1983, Thomas 1984) and diet-related (Moss 1972b, Fenna and Boag 1974) variation (up to two-fold) in gut morphology for three reasons. First, some studies (Leopold 1953) did not report collection dates. Second, existing data are insufficient to correct all points in Figures 3, 4, and 5 for seasonal or dietary effects. Most importantly, however, such variation could not have produced the lack of difference between grouse and waterfowl in Figures 3 and 4 or the substantial difference in ceca length between grouse and waterfowl

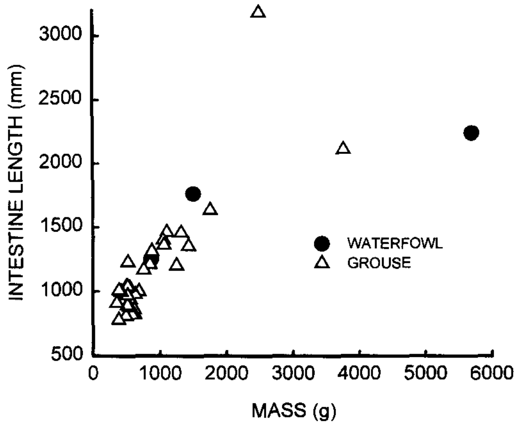

FIGURE 3. Small intestine length (mm) in relation to body mass (g) in herbivorous grouse and waterfowl. Data from: Leopold 1953, Ankney 1977, Moss 1983, Thomas 1984, Moss and Trenholm 1987, Miller et al. 1988, Dawson et al. 1989, MacWilliams and Raveling, unpubl. data.

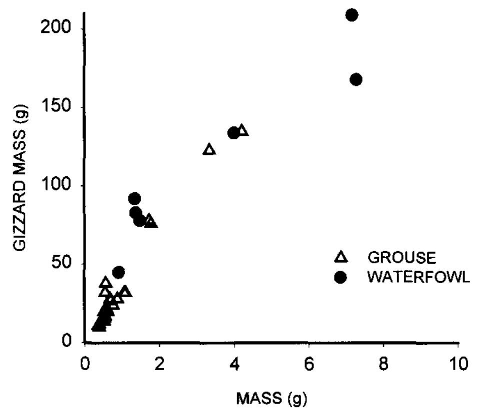

FIGURE 4. Gizzard mass (g) in relation to body mass (g) in herbivorous grouse and waterfowl. Data from: Moss 1983, Thomas 1984, Sedinger 1986, Barnes and Thomas 1987, Miller et al. 1988.

(Fig. 5). I expected a greater difference in digestive tracts because of mass constraints associated with long-distance migrations (Dudley and Vermeij 1992) in waterfowl (Bellrose 1980), which grouse generally do not undertake (Johnsgard 1983). The fact that ceca appear to be released from this constraint in grouse suggests an important role of these structures in grouse, possibly associated with processing a greater mass of digesta in the ceca.

Gasaway et al. (1975) showed that > 20% of digesta reaching the hindgut in Willow Ptarmigan flowed into the ceca. Infrequent production of cecal droppings (once or twice daily) indicates long retention and fermentation times for digesta entering the ceca. Gasaway et al.'s (1975) calculations indicate that cecal fermentation likely contributes less than 5% of the daily energy requirement of free-ranging ptarmigan. Remington (1989) observed a negative correlation between fiber content in the diet of Blue Grouse and ceca size, providing additional evidence that ceca do not function primarily to ferment dietary fiber. Remington (1989) hypothesized that ceca served primarily for digestion of cell solubles, other relatively digestible material, and nitrogenous excretory products.

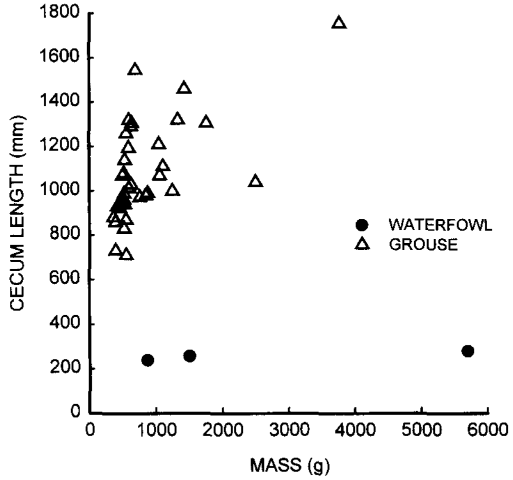

FIGURE 5. Paired ceca lengths (mm) in relation to body mass (g) in herbivorous grouse and waterfowl. References as for Figure 3.

Microbes in the ceca of chickens convert uric acid and urea to ammonia as well as producing ammonia from several amino acids, and labeled nitrogen from these compounds disappeared from the ceca within minutes, suggesting high uptake capacity for nitrogenous compounds (Karasawa 1989). Obst and Diamond (1989) estimated that total uptake capacity for some amino acids was the same for the ceca as for the entire small intestine in grouse. Combinations of peristaltic and antiperistaltic motion are thought to move material from the colon and the junction of the small intestine and colon into the ceca (Björnhag 1989), thus allowing for movement of both nitrogenous waste products and undigested endogenous material (e.g., sloughed intestinal mucosa) into the ceca. The role of ceca in digestion of amino acids is demonstrated by a greater excretion of amino acids in the feces in cecectomized chickens than in controls (Kessler et al. 1981). The potential for grouse ceca to recycle inorganic nitrogen could substantially improve the overall nitrogen balance in grouse and may enable grouse to maintain themselves on the relatively nitrogen poor foods they eat during much of the year.

Recycling excretory nitrogen may be especially important in herbivorous birds because amino acid profiles in plant protein differ from those in tissues produced by the birds (Sedinger 1984). Low concentrations of particular dietary-essential amino acids reduce the maximum potential efficiency of incorporating dietary amino acids into tissue. For example, sulfur-containing amino acids are at low concentrations in most green plants (Sedinger 1984), which limits the total tissue that can be produced. As a result of amino acid imbalances, growing geese retain only 40% of dietary nitrogen when feeding on green plants (Sedinger, unpubl. data), whereas dietary nitrogen retention rates exceed 50% when dietary amino acids are balanced with requirements for tissue production (Sedinger 1992). Therefore, ability to recycle excretory nitrogen could substantially increase nitrogen balance in herbivorous birds.

Grouse ceca, when full, represent about 5% of body mass (Moss 1983), most of which is in the organ itself (Gasaway 1976). Energetic cost of flight increases proportional to $(\text{Mass})^{1.56}$ (Dudley and Vermeij 1992). Therefore, full grouse ceca increase the cost of flight by 8% $(1.05^{1.56})$. Waterfowl typically undergo long migratory flights in which they lose up to 30% of body mass (Sedinger and Bollinger 1987), and substantial mortality, especially of young, occurs during this period (Owen and Black 1989, Schmutz 1993). Selection to minimize mass, particularly during migration, likely has favored smaller ceca in waterfowl compared to grouse.

The relatively small ceca and overall rapid rate of passage of food through the guts of geese may preclude a substantial contribution by their ceca to either energy or protein requirements. I do not view relatively small ceca in geese as evidence that nutrient limitation is less important in geese than in grouse, merely that the balance between costs of cecal mass to flying geese and advantages of the ceca for nutrient balance favors smaller ceca in geese than in grouse. Evolution of relatively small ceca in geese, however, restricts geese to habitats with plant foods containing high concentrations of protein because geese are inefficient at retaining dietary protein.

CONCLUSIONS

Grouse eat plant foods containing lower concentrations of protein than foods of waterfowl, especially during the breeding season. Several species of grouse and small waterfowl (ducks) eat invertebrates during periods of high protein requirement, such as growth or egg production (Table 1). Unfortunately, quantitative data do not exist on the extent to which animal foods contribute to the total nitrogen balance of grouse during growth.

Grouse and waterfowl differ little from each other in the morphology of digestive structures. The principal exception is the ceca, which are 5 times as long in grouse as in comparably sized waterfowl. There is little indication that enlarged ceca contribute substantially to energy balance in grouse. Recent studies, however, indicate a substantial uptake capacity for amino acids in the ceca. Metabolism of urinary excretory products in the ceca and uptake of the metabolic products also has been demonstrated using compounds labeled with ^{15}N. These studies suggest a potentially important role for the ceca in recycling urinary nitrogen and recovering endogenous nitrogen that would otherwise have been lost. Consequently, the ceca could play an important role in nitrogen balance in grouse, as indicated by the lower dietary nitrogen requirement for nitrogen balance in grouse compared to waterfowl. This digestive adaptation may explain how grouse are able to occupy habitats with such poor food quality.

These suggestions must be considered hypotheses requiring further testing because sample sizes are presently small and important physiological mechanisms require further examination. Furthermore, it is not possible to exclude alternative explanations for the larger ceca in grouse, such as water balance (Gasaway et al. 1976), because insufficient data are available for grouse and geese. It is important to estimate dietary nitrogen required for nitrogen balance in a larger range of both grouse and waterfowl species throughout the annual cycle. It also is important to improve our understanding of the role of the ceca in digestion of nutrients. Such studies will require estimates of the portion and composition of the digesta entering the ceca and the turnover time of digesta in the ceca. Monitoring the fates of labeled dietary constituents will play an important role in assessing the role of the ceca in total nutrient balance, as will studies of cecectomized animals. A series of such studies, using relatively natural diets, with both waterfowl and grouse is necessary for understanding the role of ceca in the current ecology and distribution of these two groups of birds.

ACKNOWLEDGMENTS

Time required to prepare this review was provided by a sabbatical leave from the Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks. I wish to thank S. MacWilliams and D. Raveling for providing unpublished data. D. Roby and K. Martin commented on an earlier draft of the manuscript.

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