WATERFOWL AND WETLANDS — AN INTEGRATED REVIEW

Edited by
Theodore A. Bookhout

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WATERFOWL AND WETLANDS — AN INTEGRATED REVIEW

Proceedings of a symposium

held at the

39th Midwest Fish and Wildlife Conference

Madison, Wisconsin

5 December 1977

Sponsored by the
North Central Section
The Wildlife Society

Edited by
Theodore A. Bookhout
1979

Printed by La Crosse Printing Co., Inc.
La Crosse, Wisconsin 54601

PREFACE

This volume resulted from a Symposium entitled "Waterfowl and Wetlands — An Integrated Review" held 5 December 1977 at the 39th Midwest Fish and Wildlife Conference, Madison, Wisconsin.

This Symposium was sponsored by the North Central Section of The Wildlife Society. Financial assistance for publication was provided by the U.S. Fish and Wildlife Service, Mississippi Flyway Council, and Mr. Robert Winthrop.

Twelve papers were presented during the Symposium that attempted to summarize our current state of knowledge about dabbling ducks and their habitat needs and preferences throughout the year. The adaptive strategies of dabbling ducks and the implications for management were the common theme of the papers.

The Symposium was organized by Leigh H. Fredrickson and Harold H. Prince. Theodore A. Bookhout accepted the editorial responsibilities and David D. Kennedy directed the fund raising aspects. We express our sincere appreciation to all who have made this volume possible. Special thanks go to the many individuals who served as peer reviewers. They were: C. David Ankney, Dale H. Arner, I. Joseph Ball, Calvin Barstow, James C. Bartonek, David A. Culver, Robert B. Dahlgren, David S. Gilmer, John P. Kelsall, Gregory Lie, Harry G. Lumsden, Sheldon I. Lustick, Frank McKinney, Harvey Miller, Aaron Moen, Nolan G. Perret, Lonnie D. Schroeder, and Joseph Shapiro.

FOREWORD

Management of our waterfowl resource has become both more difficult and more necessary. The driving force behind this reality is the continued development of resources and space on our continent and a "fresh water crisis" looming beyond the "energy crisis" (Wetzel 1978).

Our knowledge of dabbling ducks and their habitat needs has expanded considerably from the classic studies of breeding biology and migration. This is a time when the studies of breeding biology for dabbling ducks can be summarized and future research questions expanded to be more inclusive.

Previous wetland related symposia have not only provided a summary of information, but have served as an important research stimulus for students and biologists. The proceedings from the species-specific symposia on wood ducks in 1964 (Trefethen 1966) and on Canada geese (Hine and Schoenfeld 1968) in 1967, both sponsored by the North Central Section of The Wildlife Society, had a wide distribution, and copies of the original printing are nearly impossible to acquire. Although these efforts are cited extensively, the Saskatoon Wetlands Seminar (1969) provided a more integrated approach to wetland problems and served a wider audience.

Changes in research techniques and new developments in ecological thinking have influenced the direction, interpretation, and application of waterfowl research since the previous symposia were published. Fretwell's (1972) findings that suggest winter is a period of prime importance to survival emphasize the need for a greater understanding of anatid biology between nesting cycles. The efforts of the Northern Prairie Wildlife Research Center indicate new approaches to food habits and feeding studies are essential. The stimulus for energetics work has come from Ricklefs (1974) and King (1972, 1974), and the importance of understanding behavioral responses in relation to habitats has been emphasized by McKinney (1972). The broad generalizations of seasonal use of trophic levels provided by Weller (1975) serve as a base for exciting research.

The collection of papers in this volume is an attempt to provide examples of current thinking and techniques now used by waterfowl experts. The goal of this symposium was to provide a new stimulus for students and others that reflect a new direction for this exciting field — waterfowl and wetlands.

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Published in 1979

SPECIES DISTRIBUTION, HABITATS, AND CHARACTERISTICS OF BREEDING DABBLING DUCKS IN NORTH AMERICA

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Abstract: The abundance and distribution of breeding dabbling duck species vary tremendously in the several landscape forms that extend from north central United States to the Arctic. Within this extensive part of the continent, the northern prairies, including their subclimax parklands, have the largest number of breeding dabblers. Pond abundance within the several prairie associations does not affect all species of dabbling ducks to the same extent. Mallards (*Anas platyrhynchos)* appear to be the least tolerant of the crowding that develops where pond densities are lowest. Mallards predominate as breeders in all landscape forms except the tundra and open taiga of Alaska and Canada, regions where both the pintail (*A. acuta*) and the American wigeon (*A. americana*) are more abundant. The abundance of ponds in the Prairie Pothole Region is the most important single factor regulating the production of mallards and no doubt other dabbling species. Management strategies should consider the effect of pond density upon both the abundance of breeding ducks and the production of young. Temperature, precipitation, and evaporation have both a direct and an indirect effect on the breeding distribution and abundance of the several species of dabbling ducks. These factors determine the ultimate plant associations and they also have a proximate influence on the breeding abundance of waterfowl.

Various species of dabbling ducks breed over the entire North American continent, occupying a diversity of wetland types. They have a broader breeding range and occupy more wetland niches than do diving ducks. Only in the tundra and open taiga are breeding diving ducks more abundant than breeding dabblers. South of the tundra and open taiga, dabbling ducks outnumber divers. Because of their greater adaptability in the exploitation of wetland habitats, dabbling species aggregate about 61% of all breeding ducks. In contrast, diving ducks form only 17% and sea ducks 22% of breeding duck populations.

The disparity between dabblers and divers is even more pronounced in the harvest. Dabbling ducks comprised 86% of hunters' bags in the United States during 1961-70 and diving ducks 14% (Carney et al. 1975). Because of their abundance and importance to the hunter, it is appropriate to conduct a symposium devoted to identification of habitat requirements, population dynamics, and research and management needs of dabbling ducks.

This report examines the principal plant associations occupied by breeding dabblers and explores some of the reasons for the diverse patterns in their distribution. Analyses are focused on the important plant associations extending from the central United States to the Arctic Ocean that are occupied by more than two species of dabblers.

I am indebted to a number of people for contributing to the quality of this paper: R. Pospahala, U.S. Fish and Wildlife Service, for the breeding ground data; V. Wright, Illinois Department of Conservation, for statistical guidance; D. Trauger, U.S. Fish and Wildlife Service, for information on breeding habitats; G. Sanderson, H. Schultz, and H. Henderson, Illinois Natural History Survey, for editorial suggestions.

DERIVATION OF DATA

The bulk of the data used in these analyses was provided by R. Pospahala, U.S. Fish and Wildlife Service. They were derived from the annual aerial surveys of the important waterfowl breeding grounds in North America as described by Hanson and Hawkins (1974). The transects flown on these surveys and their delineation into 50 different strata are shown in Bellrose (1976) and Benning et al. (1978). Strata isolate a particular physiographic unit of the breeding grounds that provides functional means of statistical analysis. Information on the breeding population of ducks in the Intermountain Region was supplied by state and provincial waterfowl biologists. These data were initially supplied to assist me in preparing material for use in *Ducks, Geese, and Swans of North America* (Bellrose 1976). This material has been recast and further analyzed for this report.

AREA OF LANDSCAPE FORM

The principal breeding grounds of dabblers extend in an arc from north central Nebraska and southeastern South Dakota to the Yukon Delta, Alaska. Within this arc the landscape form changes thusly from southeast to northwest: tallgrass prairie, mixed prairie, parkland, closed taiga, subarctic deltas, open taiga, arctic deltas, and tundra. West of the mixed prairie lies the shortgrass prairie, an important adjunct to the prairie breeding grounds. Still farther west are the valleys and basins of the Rocky Mountains, which contain important wetlands for breeding waterfowl. Because this discussion concerns biomes (tundra), plant associations (tallgrass prairie), and physiographic areas (mountain valleys), I use the term landscape form to encompass all three types.

Table 1 shows the approximate number of square miles of each landscape form used by breeding dabbling ducks. Because of similar plant communities, Old Crow Flats is included with the Mackenzie River delta, and the Slave River parklands with the Athabasca delta. The eastern closed taiga embraces Ontario and Quebec.

The tundra east of the Boreal Forest in Canada harbors few breeding dabbling ducks. Because of their limited numbers, it lies outside the area surveyed annually for breeding waterfowl. This vast region covers about 900,000 mi^2, 465,000 of which are on the mainland. Sparsely distributed pintails, perhaps as many as 75,000, breed in the eastern tundra where they are the only important dabbling ducks. But the tundra is highly important to sea ducks and geese, the majority of which breed within its confines.

The renowned Prairie Pothole Region in its traditional definition embraces the climax mixed prairie and the subclimax

Table 1. Population density (ducks/ mi^2) of various species of dabbling ducks among landscape forms of North America, 1955-74.[a]

Landscape form	Square miles	Mallard	Black duck	Wigeon	Gadwall	G. w. teal	Pintail	B. w. and C. teal	Shoveler	Av.	% of total dabblers
Alaskan tundra	48,300	1.18		1.78	0.01	1.14	12.24	0.01	0.21	16.57	2.43
Alaskan open taiga	14,900	3.62		6.84		4.03	6.44		1.21	22.15	1.00
Canadian open taiga	187,500	1.11		1.31	tr[b]	0.56	1.68	tr	0.03	4.69	2.67
Combined open taiga[c]	202,400	1.29		1.72	tr	0.81	2.03	tr	0.12	5.97	3.67
Alaskan closed taiga	18,100	3.01		3.74		2.39	23.08	tr	0.67	32.90	1.81
Northern closed taiga	422,700	4.39	0.02	1.81	0.16	2.06	1.10	1.40	0.81	11.76	15.09
Eastern closed taiga	549,000	0.60	0.80			0.11	0.01			1.52	2.54
Combined closed taiga[c]	989,800	2.26	0.45	0.84	0.07	0.98	0.90	0.60	0.36	6.47	19.44
Canadian Arctic deltas	6,900	5.46		16.62		2.65	23.72	tr	0.84	49.31	1.03
Subarctic deltas	20,170	17.21		7.27	1.05	6.06	6.30	5.21	2.79	45.88	2.81
Parklands	89,458	27.92		7.59	4.41	3.77	11.96	16.72	5.59	77.96	21.17
Mixed prairie	143,124	15.34		3.91	5.22	1.62	15.05	16.85	5.71	63.71	27.68
Shortgrass prairie	145,369	6.76		2.46	1.36	0.82	5.40	3.13	1.40	21.34	9.42
Tallgrass prairie	82,151	3.32			1.10	0.11	1.64	7.30	1.18	14.66	3.66
Combined prairie[c]	460,102	12.93		3.47	3.11	1.52	9.01	10.78	3.52	44.33	61.93
Great Lakes forest	194,000	2.04	0.50	0.15		0.21	0.07	1.84	0.02	4.83	2.84
Intermountain valleys											5.84
Total	1,921,672										100.00

[a] Data from the U.S. Fish and Wildlife Service and from state waterfowl biologists.

[b] Trace.

[c] Subtotals; not included in final total.

parklands that cover 232,582 mi^2, 12% of the waterfowl breeding areas listed in Table 1. In a vegetative sense the Prairie Pothole Region also includes the tallgrass and shortgrass prairie associations, aggregating 460,102 mi^2, or 24% of all the plant communities appraised. I use the broader coverage in this paper. The remnant tallgrass prairie area available to breeding waterfowl lies in western Minnesota, the easternmost counties of the Dakotas, and the Sandhills of Nebraska. Because wetlands become much reduced west of the Missouri River in the Dakotas, this region has been placed in the shortgrass prairie association along with Montana, the southwest corner of Saskatchewan (stratum 33) and the southern tenth of Alberta (stratum 29).

I have been unable to obtain data on the area of valleys and basins amid the ranges of the western mountains. Personnel of the map library at the University of Illinois diligently searched their references but were unable to locate data on the surface area of either the mountain ranges or the valleys and basins. Therefore, I could not appraise the number of breeding ducks per square mile in the intermountain valleys.

Counts of water areas in the Prairie Pothole Region are made in May and July, concurrently with the appraisal of breeding waterfowl populations and their production. The distribution and abundance of May ponds have been summarized by stratum and landscape form in Table 2.

Table 2. The distribution of small wetlands by stratum and landscape form in the northern prairies of North America, 1955-77.

Landscape form	Stratum	Square miles	No. ponds	No. ponds/mi^2
Parklands	26	26,448	440,700	16.7
	30	18,570	240,050	12.9
	31	21,086	441,000	20.9
	34	13,164	482,830	36.7
	38	5,654	42,300	7.5
	40	4,536	162,830	35.9
Total/average		89,458	1,809,710	20.2
Mixed prairie	27	11,274	135,500	11.6
	28	12,890	95,050	7.5
	32	37,912	463,670	12.2
	35	9,044	302,630	33.5
	39	6,552	164,510	25.1
	45	26,625	335,500	12.6
	46	14,238	129,800	9.1
	48	24,589	147,590	6.0
Total/average		143,124	1,774,250	12.4
Shortgrass prairie	29	13,235	85,700	6.5
	33	11,345	95,740	8.4
	41	32,902	113,640	3.5
	42	40,758	107,940	2.7
	43	19,835	92,700	4.7
	44	27,298	100,660	3.7
Total/average		145,369	596,380	4.1
Tallgrass prairie	W. Minnesota	36,500	127,750	3.5
	N. Dakota 47	7,821	24,500	3.1
	S. Dakota 49	15,830	74,410	4.7
	N. Nebraska	22,000	170,940	7.8
Total/average		82,151	397,600	4.8

The abundance and density of water areas vary greatly with stratum and vegetation type (Table 2). As might be expected, the lowest density of ponds occurred in the semi-arid shortgrass prairie association. Compared to it there were 1.2 times as many ponds per square mile in tallgrass prairie, 3 times as many in mixed prairie, and 4.9 times as many in the relatively well-watered parklands.

IMPORTANCE OF LANDSCAPE FORM TO DUCKS

In my appraisal of the breeding distribution of dabbling ducks, 32,396,105 are accounted for (Table 1). The largest proportion of these birds, 27.7%, inhabits the mixed prairie, followed by 21.2% in the adjacent parklands, 9.4% in the shortgrass prairie, and 3.7% in the tallgrass prairie wetlands. Thus, in the traditional definition, the prairie pothole area is occupied by 41% of the population, but, including all grassland associations, it is used by 62% of the breeding dabblers.

Because of its vastness, the Canadian closed taiga, west of central Ontario, supports 15.1% of the breeding dabblers. Intermountain valleys contain 5.8%, the Great Lakes forest region 2.8%, and other landscape forms still fewer.

Another way of evaluating the importance of waterfowl habitats is to assess the density of dabbling ducks using them. This assessment shows that all the grassland associations support a density of 44/mi^2 with slightly higher densities of 49 and 46/mi^2, respectively, in the Arctic delta and subarctic areas. Fertile waters and balanced interspersion between land and water in northern deltas probably account for the unusual density of breeding ducks at such high latitudes. Lowest densities occur in the Great Lakes forest association, the Canadian open taiga, and the northern closed taiga (Table 1).

Compared with similar plant associations in Canada, Alaska has greater concentrations of breeding dabblers. For example, the open taiga in Alaska averages 22.2 dabblers/mi^2; that in Canada averages 4.7/mi^2. The closed taiga in Alaska supports 32.9 dabbling ducks/mi^2, the northern closed taiga in Canada 11.8/mi^2. The coastal tundra of Alaska has 16.6 dabblers/mi^2 compared with probably less than 0.1/mi^2 in Canada.

A comparison of the composition of dabbling ducks in the various landscape forms reveals species differences (Table 3). Pintails predominate through all of

Table 3. The percentage distribution of various dabbling ducks breeding in a variety of landscape forms in North America, 1955-77.

Landscape form	Mallard	Black duck	Wigeon	Gadwall	G.w. teal	Pintail	B. w. & C. teal	Shoveler
Alaskan tundra	7.1		10.7	0.1	6.9	73.8	0.1	1.3
Alaskan open taiga	16.4		30.9		18.2	29.1		5.5
Canadian open taiga	23.7		27.9	tr[a]	11.8	35.9	tr	0.6
Alaskan closed taiga	9.2		11.4		7.3	70.2	tr	2.1
Northern closed taiga	37.4	0.2	15.4	1.4	17.5	9.4	11.9	6.9
Eastern closed taiga	39.4	52.5			7.2	1.0		
Canadian Arctic deltas	11.1		33.7		5.4	48.1	tr	1.7
Subarctic deltas	37.5		15.9	2.3	13.2	13.7	11.4	6.1
Parklands	35.8		9.7	5.7	4.8	15.3	21.4	7.2
Mixed prairie	24.1		6.1	8.2	2.5	23.6	26.4	9.0
Shortgrass prairie	31.7		11.5	6.4	3.9	25.3	14.7	6.6
Tallgrass prairie	22.7			7.5	0.8	11.2	49.8	8.1
Great Lakes forest	42.3	10.5	3.1		4.4	1.4	38.0	0.4
Intermountain valleys	49.4		6.2	9.7	2.9	7.7	20.1	3.9

[a] Trace.

the Arctic habitats as far south as the Canadian closed taiga. That part of the dabbling duck population composed of pintails amounts to 74% on the Alaskan tundra and declines through Alaskan open and closed taiga to 9% in the Canadian closed taiga. It is apparent that pintails prefer the more open tundra and open taiga to wetlands in the closed taiga.

In the Arctic, wigeons rank next to pintails in abundance. Immediately to the south, in the Canadian subarctic deltas and in the northern closed taiga, they occur in slightly greater numbers than the pintail. They also occur in slightly greater numbers in the Alaskan open taiga (Table 1). Wetlands with some wooded vegetation influence mallards more than other dabblers; they rank highest in the closed taiga, subarctic deltas, prairie parkland, Great Lakes forest, and intermountain valleys. In this respect, American green-winged teals (*Anas crecca*) are more like mallards than pintails, but greenwings are like pintails in being more Arctic-oriented.

The latitudinal change in abundance between blue-winged (*A. discors*) and green-winged teals along a line from southeast South Dakota to the Mackenzie River delta is shown in Fig. 1. It is apparent that blue-winged teals have the greatest affinity for prairie pothole habitats, whereas green-winged teals are related to the habitats of the subarctic and Arctic regions.

Cinnamon teals (*A. cyanoptera*) occur almost exclusively in the intermountain valleys, where they have been eminently more successful than have blue-winged teals. In prairie pothole habitats, the blue-winged teal complex is second only to mallards in abundance (Table 1).

Northern shovelers (*A. clypeata*) have exploited most of the areas north of the parklands and subarctic deltas to a greater degree than have blue-winged teals, but they have not been as successful as blue-winged teals in wetlands of the tallgrass prairie or in wetlands of the Great Lakes forest.

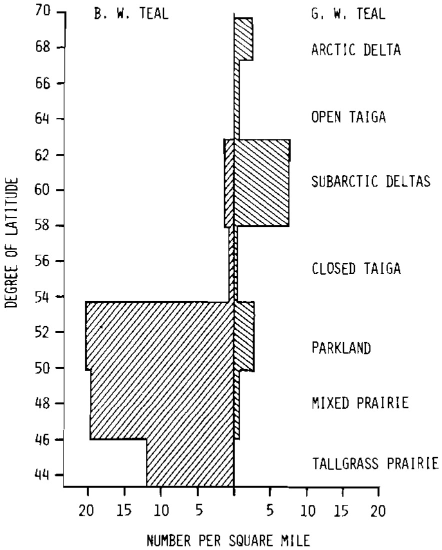

Fig. 1. The latitudinal breeding population distribution of blue-winged and green-winged teals in the various landscape forms, 1955-74.

Gadwalls (*A. strepera*) are limited in viable breeding populations to the prairies and the intermountain valleys. In comparison with other dabblers, their density is the greatest in wetlands of the intermountain valleys and the mixed and tallgrass prairie areas. Only in these landscapes do gadwalls outnumber their close competitors, wigeons.

Three species of dabblers predominate in the all-important Prairie Pothole Region: mallards, blue-winged teals, and pintails. They are of about equal abundance on the potholes of the mixed prairie, but mallards overwhelm the others, particularly pintails, in the parklands.

Although several dabbling duck species breed in the eastern closed taiga east of Manitoba, only mallards and black ducks (*A. rubripes*) have been eminently successful (Table 3). These 2 species together compose 92% of the dabblers utilizing this extensive region. Mallards appear to decline in abundance from west to east, and, conversely, black ducks increase from west to east.

Of the waterfowl breeding in the Precambrian Shield of eastern Ontario, Dennis (1974:55) reported that 23% were black ducks and 7% were mallards (32 and 10%, respectively, of dabbling species). The closed taiga in the clay belt, north of the Precambrian Shield, contained a greater abundance of ducks. There, black ducks composed 17% and mallards 15% of breeding waterfowl (30 and 23%, respectively, of dabbling species). In the open taiga of the Ungava Peninsula, Quebec, Gillespie and Wetmore (1974:147) found that black ducks composed about 80% of the dabbling ducks and 25% of all ducks.

During the last decade, there has been growing evidence that the mallard has increased in the western range of the black duck at the expense of the black duck. Laperle (1974:18) believes that this change is not solely because the mallard is a better competitor but also because it is more adaptable to man's degradation of habitats.

PRAIRIE POTHOLE REGION

The Prairie Pothole Region warrants further analysis because of its importance to breeding dabbling ducks. Table 4 shows that the density of dabbling ducks varies among the several grassland associations as follows: parklands 78/mi^2, mixed prairie 64/mi^2, shortgrass prairie 21/mi^2, and tallgrass prairie 15/mi^2. The parklands have more water areas, 20/mi^2, than the other grassland associations which have: mixed prairie 12/mi^2, shortgrass 4/mi^2, and tallgrass 5/mi^2. On the basis of the number of ducks per pond, there are 5.5 in shortgrass prairie, 5.1 in mixed prairie, 3.9 in parklands, and 3.1 in the tallgrass prairie. The relatively low number of ducks in parkland ponds is partly due to the larger number of ponds.

Among dabbling ducks associated with grasslands, the parklands contain the greatest density of these species: mallards, wigeons, and green-winged teals. The mixed prairie has the greatest densities of gadwalls, blue-winged teals, shovelers, and pintails. Although no species is more abundant in either the shortgrass or tallgrass prairie associations, there are more mallards, wigeons, and pintails per pond in shortgrass prairie strata.

Pond Density and Duck Density

Figure 2 demonstrates the effect of the density of ponds on their occupancy by dabbling ducks. The formula, Duck density = a + b log pond density, gives a better fit (higher R^2) than the simple linear regression when data from all the strata in the Prairie Pothole Region are used. However, when plant associations within the prairie region are separated, the relationship is more complex. Within the tallgrass prairie no relationship exists between the density of ponds and ducks, whereas within the shortgrass prairie the relationship is linear. This fit is best because when pond density is relatively low (as in the shortgrass prairie), numbers of ducks and ponds increase together. But the logarithmic fit demonstrates that where ponds are already numerous, the density of dabbling ducks increases progressively more slowly than the density of ponds. This trend is especially apparent in the Prairie Pothole Region and in its parkland association; where pond density exceeds 12/mi^2, duck density increases slide progressively further behind increases in pond density. At levels up to 12 ponds/mi^2, dabbling ducks are most abundant in mixed prairie strata, least

Table 4. The relationship of dabbling ducks to various breeding ground habitats in the Prairie Region of North America, 1955-74.

Landscape form and stratum	Mallard		Gadwall		Wigeon		G. w. teal		B. w. teal		Shoveler		Pintail		All dabblers	
	SM[a]	PP[b]	SM	PP	SM	PP	SM	PP	SM	PP	SM	PP	SM	PP	SM	PP
Parklands																
26	33.8	2.0	6.8	0.4	8.7	0.5	5.6	0.3	16.2	1.0	6.5	0.4	12.2	0.7	89.8	5.4
30	25.2	2.0	4.2	0.3	8.8	0.7	3.5	0.3	11.4	0.9	5.3	0.4	12.3	1.0	70.6	5.5
31	28.0	1.3	3.3	0.2	8.4	0.4	2.7	0.1	13.4	0.6	6.3	0.3	14.7	0.7	76.8	3.7
34	34.1	0.9	3.4	0.1	6.4	0.2	3.4	0.1	25.6	0.7	4.6	0.1	11.0	0.3	88.5	2.4
38	3.5	0.5	0.3	tr[c]	0.5	0.5	0.6	0.1	5.4	0.7	5.2	0.7	2.9	0.4	18.3	2.8
40	26.9	0.8	4.8	tr	6.8	0.2	4.4	0.1	36.7	1.0	5.7	0.2	9.2	0.3	94.5	2.5
Total/average	27.9	1.4	4.4	0.2	7.6	0.4	3.8	0.2	16.7	0.8	5.6	0.3	12.0	0.6	78.0	3.9
Mixed prairie																
27	22.4	1.9	5.1	0.4	7.8	0.7	2.5	0.2	10.4	0.9	7.7	0.7	20.4	1.8	55.8	6.6
28	14.4	1.9	3.4	0.5	5.3	0.7	1.4	0.2	5.3	0.7	5.7	0.8	25.7	3.4	61.1	8.1
32	20.6	1.7	5.3	0.4	7.1	0.6	2.5	0.2	11.1	0.9	6.2	0.5	20.1	1.6	72.9	6.0
35	20.2	0.6	3.9	0.1	3.9	0.1	3.7	0.1	25.1	0.8	5.2	0.2	14.1	0.4	76.0	2.3
39	11.7	0.5	3.3	0.1	3.1	0.1	3.1	0.1	31.2	1.2	4.4	0.2	7.5	0.3	64.4	2.6
45	10.6	0.8	5.7	0.5	1.4	0.1	0.6	0.1	15.7	1.3	5.0	0.4	10.9	0.9	49.8	4.0
46	8.3	0.9	7.3	0.8	8.6	0.9	0.5	0.1	21.7	2.4	5.0	0.6	9.2	1.0	60.7	6.7
48	7.2	1.2	4.4	0.7	0.4	0.1	0.5	0.1	19.1	3.2	4.1	0.7	7.4	1.2	43.1	7.2
Total/average	15.3	1.2	5.2	0.4	3.9	0.3	1.6	0.1	16.9	1.4	5.7	0.5	15.1	1.2	63.7	5.1
Shortgrass prairie																
29	12.7	2.0	1.8	0.3	3.7	0.6	0.8	0.1	2.5	0.4	3.0	0.5	15.6	2.4	40.0	6.2
33	13.5	1.6	3.0	0.4	5.0	0.6	1.5	0.2	6.2	0.7	4.1	0.5	16.0	1.9	49.3	5.8
41	7.9	2.3	2.5	0.7	3.9	1.1	1.1	0.3	3.0	0.9	1.8	0.5	7.4	2.1	27.5	8.0
42	4.5	1.7	0.6	0.2	1.6	0.6	0.9	0.6	1.3	0.5	0.5	0.2	1.1	0.4	10.4	4.2
43	3.5	0.8	0.4	0.1	1.0	0.2	0.6	0.1	2.3	0.5	0.8	0.2	2.5	0.5	11.1	2.4
44	5.5	1.5	1.0	0.3	1.6	0.4	0.3	0.1	4.9	1.3	0.9	0.2	2.1	0.6	16.3	4.4
Total/average	6.8	1.7	1.4	0.4	2.5	0.6	0.8	0.2	3.0	0.8	1.2	0.3	5.4	1.4	21.3	5.5
Tallgrass prairie																
W. Minnesota	3.0	0.9							3.4	1.0	0.8	tr	0.1	0.3	7.3	2.2
47	2.5	0.9	4.5	1.7	0.2	0.1	0.1	0.1	2.8	1.1	0.9	0.3	1.4	0.5	12.4	4.6
49	4.3	0.9	1.0	0.2	0.3	0.1	tr	0.1	12.0	2.6	2.1	0.4	2.3	0.5	22.0	4.7
Sandhills	3.6	0.5	1.0	0.1			0.1	tr	6.7	0.9	1.6	0.2	1.7	0.2	15.0	1.9
Total/average	3.3	0.7	1.1	0.2	0.1	tr	0.1	tr	7.3	1.5	1.2	0.2	1.6	0.3	14.8	3.1

[a] Ducks/mi .

[b] Ducks/pond.

[c] Trace.

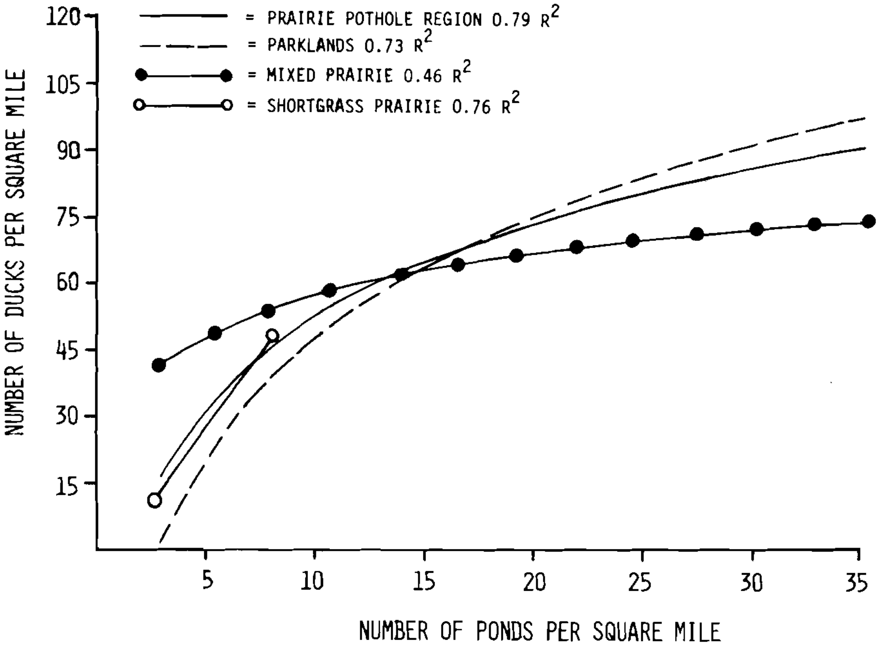

Fig. 2. The number of prairie ponds per square mile among the several strata in parklands, mixed prairie, and shortgrass prairie and the Prairie Pothole Region compared with the number of dabbling ducks per square mile, 1955-74.

abundant in parkland strata, with those of shortgrass strata in between (Fig. 2).

Figure 3 shows the linear regression between pond density and the number of dabbling ducks per pond among strata of the mixed prairie. The coefficient of determination (R^2) suggests that 80% of the reduction in ducks per pond might be explained on the basis of increases in pond density. In the parklands, the reduction in ducks per pond with increases in pond densities among the 6 strata was not as great, and the coefficient of determination indicates that it explained only 32% of the decrease. Still less correlation occurred between pond occupancy and pond density in shortgrass and tallgrass prairie associations, where pond densities are low.

In all four prairie associations, as the number of mallards per pond increases so does the number of other dabbling ducks (Fig. 4). Dabbling ducks other than mallards favor pure grassland communities over the parklands. When there are 1.5 mallards per pond, there are 2.7 other dabbling ducks on ponds of the parkland, 3 on ponds of the tallgrass prairie, and 6 on ponds of the shortgrass and mixed prairie. Among parkland strata, increases in mallards and other ducks per pond are parallel. However, in the other grassland associations numbers of other ducks per pond progressively increase above that of mallards.

I interpret the greater increase of dabbling ducks other than mallards as pond density declines as an indication of differences in space demands among species. It appears that mallards tolerate

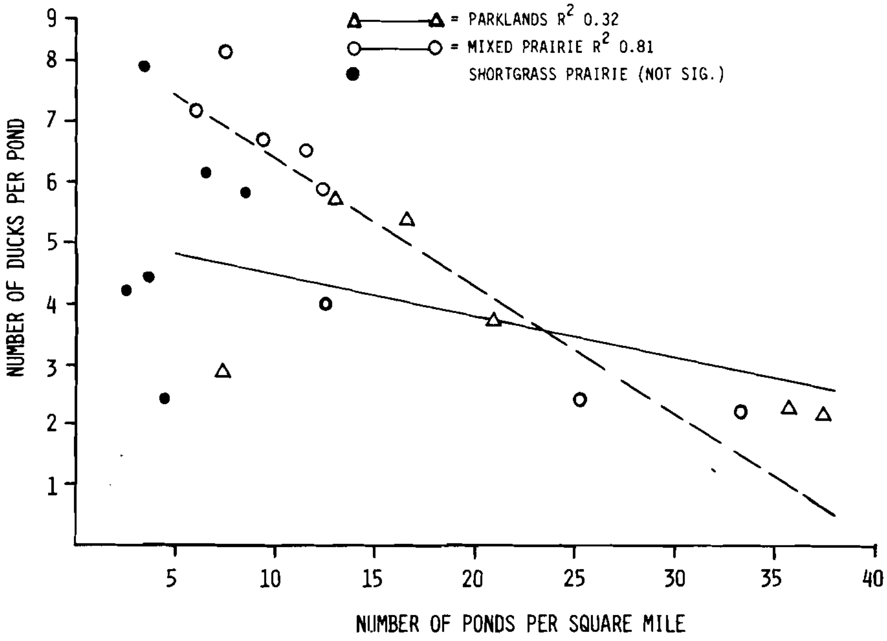

Fig. 3. The number of prairie ponds per square mile compared with the number of dabbling ducks per pond among strata grouped according to parklands or mixed prairie association, 1955-74.

less crowding than do other dabbling ducks. Both mallards (Pospahala et al. 1974) and pintails (Smith 1970) are known to overfly the Prairie Pothole Region in those years that May ponds decline in number. They appear in greater numbers in the areas to the north on lakes of the open and closed taiga and subarctic deltas. My data suggest that other dabbling ducks do not overfly the prairies to the extent that these two species do.

Mallards and pintails are both early-nesting ducks and nest in similar habitats in the Prairie Pothole Region. Because they appear as potential competitors, I examined the effect of reduction in pond density on the comparative abundance of mallards and pintails (Fig. 5). Linear regressions indicate that the density of pintails increases at a higher rate in the shortgrass and mixed prairie associations than in the parklands and tallgrass associations. These findings suggest that breeding pintails prefer the more open grasslands, and that they tolerate greater densities than do mallards. Moreover, other species of dabblers are more tolerant of crowding on prairie ponds. Therefore, they do not overfly the Prairie Pothole Region as often as do mallards and pintails.

Pond Abundance and Mallard Production

The relationship between (1) the size of the continental mallard breeding population and the abundance of ponds in the Prairie Pothole Region and (2) a predicted production of young is shown in Fig. 6. A multiple regression equation,

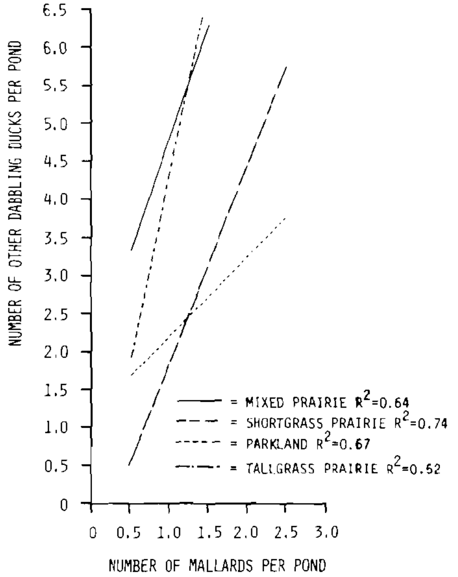

Fig. 4. The relationship between the number of mallards per prairie pond and the number of other dabbling ducks per pond among the several strata in each of four prairie associations, 1955-74.

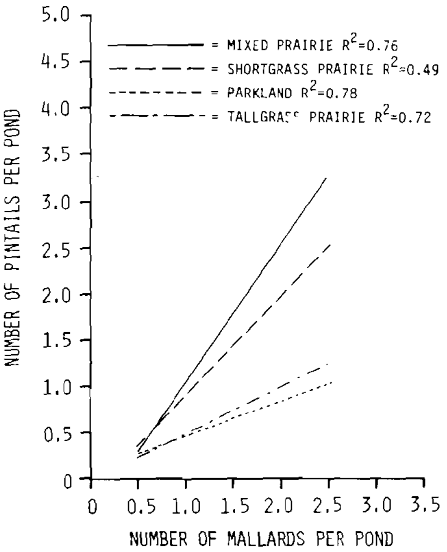

Fig. 5. The relationship between the number of mallards per prairie pond and the number of pintails per pond among the several strata in each of four prairie associations, 1955-74.

Number of young mallards in the fall population = -0.04 log + 0.58 log May breeding numbers + 0.49 log May ponds, was significant with an R^2 of 0.61. It is evident that both the size of the mallard population returning to the breeding grounds and the spring abundance of prairie ponds are important factors governing the size of the fall continental population. Although the number of predicted young rises as the number of May ponds increases, it rises at a decreasing rate.

It is important to realize that from 1955 to 1976 about 42% of the mallards bred outside the Prairie Pothole Region. Yet the production of young from the prairies is such an important component of the fall population that its size greatly influences the entire continental population. The coefficient of determination (Fig. 6) implies that breeding numbers and the number of May ponds in the grassland associations alone account for 60% of the annual variability in the fall numbers of young mallards. Hence, the contribution of young mallards — or the lack of it — from this region produces pronounced variations in the fall population in spite of the production of young from over 40% of the mallards that breed elsewhere. The contribution to the fall population from wetlands of the taiga and subarctic and Arctic deltas should remain quite similar year in and year out because of stable habitat conditions. Actually, potential production might be expected to increase during drought years because the mallard overflight of the prairies adds to the indigenous population. Therefore, it is apparent that, through the period of analysis, the 40% of the mallards breeding outside the prairies contributed fewer than 40% of

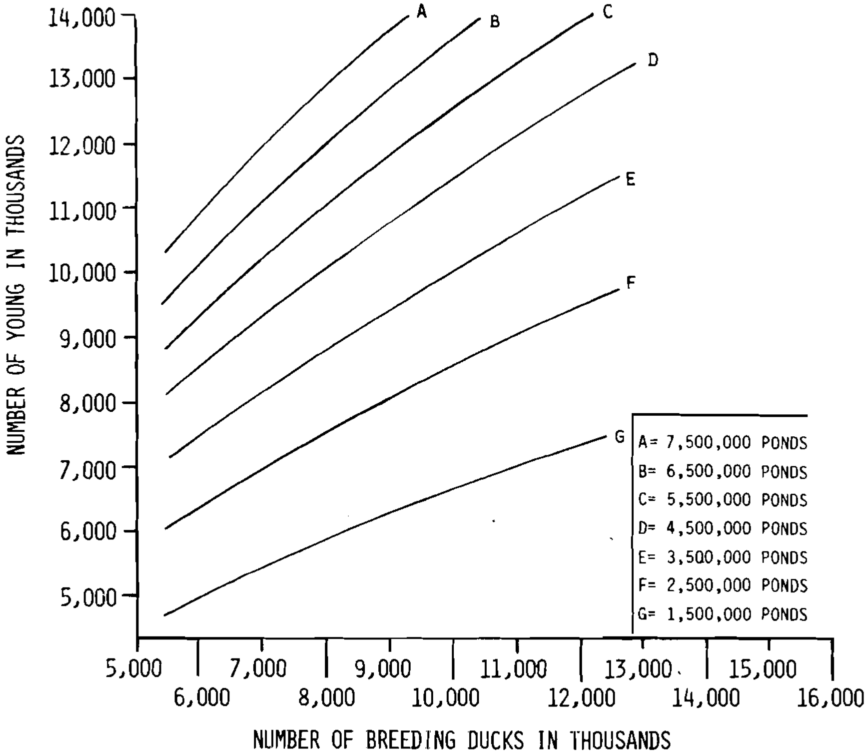

Fig. 6. The predictive influence of mallard breeding numbers and the abundance of May ponds in the Prairie Pothole Region on the number of young in the fall continental population. The analysis is based upon a multiple regression and common logarithmic transformation of the basic data.

the young to the continental population. If it were otherwise, the prairies would not exert such a marked influence on the yearly status of mallards. The adage, "As the prairies go, so go the game ducks," is a supportable truism.

DISCUSSION

Their mode of flight and their feeding habits have enabled dabbling ducks to utilize a greater range and diversity of habitats than do other waterfowl. Among dabbling ducks, the ubiquitous mallard exhibits the greatest adaptability to a variety of breeding habitats and climates. In relation to other species, it achieves its greatest degree of success in the parklands.

Conversely, among the dabbling ducks, black ducks and cinnamon teals have the most restricted breeding ranges over the part of North America considered in this report. The traits that enabled black ducks and cinnamon teals to occupy restricted ranges more advantageously than the closely related mallards and blue-winged teals are not well understood. Although in recent years mallards appear to be invading the western part of the black duck's breeding range, black ducks still sustain the most viable population over their ancestral range. The black duck's breeding range is characterized by a high precipitation-low evaporation ratio. Where this ratio is the highest, the black duck appears to be the most successful at thwarting the encroachment of the mallard.

The cinnamon teal's breeding range is conversely characterized by a low precipitation-high evaporation ratio. This teal reaches its greatest breeding abundance in the Great Salt Lake basin, Utah, followed by the Malheur basin, Oregon, areas that have the lowest precipitation-evaporation ratios (Bellrose 1976). It is in these and other similar areas that the cinnamon teal has been most successful at limiting the encroachment of the bluewing. For example, Wheeler (1965) reported that the blue-winged teal has expanded its range and numbers in northeastern California. Thus, certain climatic conditions appear to be the fundamental reason that black ducks and cinnamon teals have not been overwhelmed by sympatric species that are more numerous and occupy larger ranges.

Gadwalls and blue-winged teals have substantially lower breeding numbers north of the Prairie Pothole Region. They are both late-nesting species, suggesting that warm temperatures are important to their nesting activities. Therefore, temperatures prevailing during the short summer in the Arctic and subarctic appear to be proximate factors responsible for limiting the northward expansion of gadwalls and blue-winged teals.

Both the southern-breeding gadwall and the blue-winged teal have closely related species, the wigeon and the green-winged teal, that manage to maintain substantial breeding populations farther north in the Arctic and subarctic. In similar geographic locations, wigeons nest earlier than gadwalls and green-winged teals earlier than bluewings (Bellrose 1976). The ability of wigeons and greenwings to breed earlier than their relatives may account for their greater abundance in the North.

Perhaps greenwings have minimized competition with bluewings through their greater adaptation to habitats in a harsher climatic region. Otherwise, it might be expected that green-winged teals would be proportionately more abundant in the highly productive Prairie Pothole Region. A similar relationship appears to apply to the wigeon-gadwall distribution. Wigeons predominate north of the Prairie Pothole Region, but both wigeons and gadwalls are about equally numerous in the prairies (Fig. 6).

Mallards do not populate Arctic habitats to the extent that pintails do. Although mallards and pintails vie as the earliest nesters among the dabblers, mallards are probably less able to breed successfully under the more adverse conditions in the Arctic. However, a study of mallard and pintail egg production in the parklands and the Arctic by Calverley and Boag (1977) does not fully substantiate this premise. They found that both mallards and pintails laid fewer eggs per hen in the Arctic than in the parklands. Not only were there fewer eggs per clutch in the Arctic for both species, but there was also a significantly larger proportion of nonlaying females. The reduction in egg productivity was similar for both species. But egg production is only one factor in the number of young produced, and, in the Arctic, pintails may be more successful than mallards in nesting and brood rearing.

The greater concentration of almost all species of dabbling ducks in similar landscape forms in Alaska than in Canada appears to be related to habitat and summer climate. There is a much better interspersion between small water areas and land in the tundra and taiga of

Alaska than in similar landscape forms in Canada. The better interspersion of small water areas in Alaska stems in part from the terrain — the large areas of flat or gently sloping plains along the coast and between the mountain ranges in interior Alaska. Moreover, at similar latitudes, the weather is more moderate in Alaska because of the influence of the Japanese Current on the Bering Sea.

The Arctic Slope of Alaska contains about 12,000,000 mi^2 of tundra wetlands that appear to be excellent for breeding waterfowl. Yet, except for perhaps as many as 20,000 pintails, few other dabbling ducks occur there, apparently because of the short summer and harsh weather. Moreover, most of the pintails that do occur there are nonbreeders, for Eldridge and Derksen (1977, paper presented at 39th Midwest Fish and Wildlife Conference, Madison, WI) found little evidence of pintails breeding on the Arctic Slope.

Temperature, precipitation, and evaporation are weather factors that influence the distribution of breeding dabbling ducks. These factors have an ultimate influence in determining plant associations and, within the vegetation framework, a proximate influence on the breeding birds themselves.

The tapering off in the abundance of breeding dabbling ducks where ponds exceed $12/mi^2$ (Fig. 2) has application to the strategies of acquisition and management of wetlands in the Prairie Pothole Region. This region makes an enormous contribution to the status of the fall continental population of mallards. Both the returning number of mallards to the breeding grounds and the number of May ponds on the prairies have important roles in determining the production of young (Fig. 6). Here, too, management strategy should consider the saturation effect of pond density in the production of young.

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW
Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

NITROGEN AND PHOSPHORUS DYNAMICS IN INLAND FRESHWATER WETLANDS

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Abstract: Few studies have covered even a majority of the important aspects of the biogeochemical cycles of N and P in freshwater wetland ecosystems. Available information is mostly on amounts present at some point in time in various ecosystem components, such as plants, soils, or water. The amounts vary with time and site, and reported values are influenced by methodology. For sediments, in particular, most current methods are inadequate to give meaningful information about nutrient supplies. Standing crops (g/m^2) of N and P are the product of concentration and total plant biomass. Emergents generally have higher standing crop biomass and hence contain more N and P. Processes important in understanding the dynamics of N and P in wetland ecosystems include: water flows into and out of the wetland, rainfall, evapotranspiration, nitrogen fixation, denitrification, animal movements, plant uptake, translocation, decomposition, leaching, animal ingestion and excretion, and a variety of chemical processes. Plants take up nutrients from both sediments and water, and nutrient movements both upward and downward through plants have been demonstrated. Evidence is accumulating that, for submersed and floating-leaved species and even some emergents, the net movement is upward, and substantial quantities of P, and probably N, are moved from the sediments through the plant to the water. Animals are usually considered to be a minor influence on N and P cycles, but occasionally large local concentrations of waterfowl may have detectable effects, particularly on N dynamics. Dense growths of aquatic and marsh plants may require amounts of N and P in excess of the amount present, in available form, at any one time. Therefore the rates at which these nutrients are supplied, cycled internally, and removed from the wetland ecosystem are critical to plant growth. Either or both N and P may be limiting in many marshes. Management practices should be aimed at enhancing supply rates and internal recycling rates while reducing loss rates. Inputs and outputs are mostly via water for P; gaseous exchange is also of major importance for N. Controlling P means careful attention to hydrology, especially during periods when P is mobile. Denitrification is clearly enhanced by rapid and frequent water level fluctuations, which leads to the speculation that N may be conserved by careful water level regulation.

The information on nutrient dynamics in inland freshwater wetlands is largely from fragmented and diverse sources. Relatively few studies have covered a majority of the important aspects of a nutrient cycle in such an ecosystem. Similarly, the number of elements, in their various forms, that have been considered is usually only a part of those that a text in plant physiology would list as nutrients. Perhaps most commonly considered are nitrogen (N) and phosphorus (P), possibly because they are limiting nutrients in many situations. This paper will deal primarily with those two elements.

Because studies and data are scarce, I shall discuss a variety of wetland types, excluding from major consideration only the extensive information on tidal salt marshes. The use of the term "freshwater" in the title will pose little difficulty, for few studies of nutrient cycles have been done in interior saline wetlands.

The dynamics of nutrient relationships are the major emphasis of this discussion, largely because this leads to a better understanding of wetlands and, I believe, the potential for better management. No effort has been made to summarize all available data on the nutrient content of vegetation, or standing crops, but rather only general levels are indicated. Processes by which nutrients are made available to vascular plants will be emphasized with the view that these are of fundamental importance in determining the character of marshes for waterfowl. A rich marsh or poor marsh is characterized basically by the vegetation, which in turn is intimately related to a number of factors, including processes that supply or remove nutrients from the plants.

Wetlands for waterfowl are basically shallow bodies of water and should fall within the general purview of the discipline of limnology. However, limnologists have not done much in wetlands, particularly in the United States. Nevertheless, much of what is known in limnology can be applied, with care, to wetlands. Some wetlands have little or no surface water most of the time, and the relevant literature is then often in agriculture and soils. Particularly rich sources of information for such systems are studies of lowland rice culture and work on peat lands, particularly in Russia.

The conceptual framework used in reviewing N and P cycles in wetlands is the mass balance approach. Simply stated, this says that the change in amount of N or P in the wetland (or any subdivision thereof) at any point or interval of time is a function of the difference between inputs and outputs. We are therefore mostly interested in how much N or P comes in or goes out per unit of time. Quantities present are of interest primarily in determining changes in storages — how much more or less is present at one time compared to another.

ANNUAL BUDGETS

Annual budgets show the balance of imports and exports of N and P as well as the changes in internal storage within the wetland. Examples of such budgets are rare because of the difficulty in obtaining all the required data. In the following sections, I will discuss first the paths of N and P movement into and out of wetlands, then some quantitative data on the rates of N and P movement, and finally look at a few examples of budgets.

Nutrient Import and Export

Nitrogen and phosphorus enter and leave wetlands in or with water and in animal biomass; in addition, N movements include transfers to and from the gas phase in the atmosphere. Water additions occur from groundwater (e.g., springs and seeps), rain, and surface runoff. The volume of water input and the concentration of the various ions must be known to calculate the total amount of, say, N and P being added to the wetland by those routes. Both groundwater and surface runoff may enter by channels (i.e., streams and rivers). Chemistry of groundwater is profoundly influenced by geology, surface water by soils and land use practices, and rainfall by atmospheric dust and pollutants (Likens 1975). Outputs or losses may be via streams, to groundwater, or to evaporation and transpiration. Evaporation losses increase ion concentration and are critical in saline, brackish, and alkali wetlands in interior and western North America, as well as elsewhere around the world.

These various processes in the hydrology of marshes vary greatly in their importance in different wetland types. Virtually the only inputs and outputs of some bogs are rainfall and evapotranspiration, whereas some potholes are fed mostly by groundwater, and yet other marshes are only sheltered parts of rivers. Given all this variation, knowledge of the local hydrology is vital to an understanding of the marsh ecosystem and its management or preservation. Yet there are not many thorough hydrologic studies of wetlands or marshes.

In general, there are two critical hydrologic parameters for wetland ecosystems. The first is water depth and its seasonal variation, about which much is known (e.g., Kadlec 1960, Harris and Marshall 1963, Meeks 1969, Burgess 1969, Weller 1978). The second vital parameter is the flow, flushing, or turnover rate. The importance of water turnover rate has been hinted at in a few wetland studies (Cook and Powers 1958, Kadlec 1960, Andersen 1974), but it is now considered a key parameter in some models of the trophic dynamics of lakes (e.g., Dillon and Rigler 1974). Turnover rate as well as depth, and their seasonal varia-

Table 1. Estimated "average" quantities of N and P (g/m^2/yr) from various sources (from Likens 1975).

Source	N	P
Rainfall	0.80	0.030
Forested area	0.25	0.008
Pastured area	0.85	0.017
Cultivated cropland	0.75	0.440
Citrus farms	2.20	0.018
Muck farms	0.11	0.140
Urban area	0.80	0.350
Feedlot runoff	80	30
Domestic sewage	3,900[a]	800[a]
Septic tanks		
Immediate	2,400[b]	140[b]
Remote	970[b]	14[b]
Domestic ducks	480[c]	90[c]

[a] Grams per capita per year.
[b] Grams per septic tank per year.
[c] Grams per duck per year.

Table 2. Nitrogen and phosphorus inputs (kg/ha/yr) to wetlands by way of precipitation.

Source	NO_3-N+NH_4-N	Total P
Likens (1975), U.S. and Canada	6.6-10	0.04-0.35
Crisp (1966), England	8.2	0.69
Richardson et al. (1978), Great Lakes Region	5.2	0.30
Ulehlova et al. (1973), Czechoslovakia	8	0.60

tions, depend on the dynamic balance between the inputs and outputs of water discussed earlier. Depending on the chemical composition and particulate loads of the incoming and outgoing water, the fertility of the wetland can be markedly affected.

Likens (1975) reviewed the literature on quantities of N and P likely to be brought to a water body from various sources (Table 1). Phosphorus and ammonium-N are relatively easily immobilized in contact with soils, so that contributions from most land uses are not large unless the drainage area is large. Sewage, feedlots, and domestic ducks are high N and P producers, and substantial inputs from any of these sources can lead to enrichment. Some further data on nutrient inputs via rainfall, usually including some "dry fall" or dust, are given in Table 2. Total inputs (loading) of N and P per unit area of marsh are highly variable, depending on the relative proportions of various land uses and sources of N and P in the catchment.

Reliable data on the quantities and nutrient content of a ground water flowing into wetlands are very difficult to obtain. Yet, in some marshes, ground water may be a large part of the annual water supply, and thus presumably also the annual supply of some nutrients. Local geology often has a significant impact on both the quantity and quality of ground water. So little is known of this complex system that it must be considered a major research need.

There is some potential for gain or loss of N and P from marshes by movements of animals or by harvest of marsh vegetation. Waterfowl or marsh bird excreta are potentially the source of large amounts of N and P (Likens 1975 — see Table 1, Davies 1973, McColl and Burger 1976). Waterfowl sometimes consume a significant fraction of the production of macrophytes (Anderson and Low 1976). Crisp (1966) estimated that invertebrate drift and sheep grazing removed 1.7 mg $P/m^2/yr$ and 11.0 mg $N/m^2/yr$ from a Pennine moorland, which is relatively minor — probably less than measurement error on some other inputs and outputs. On the other hand, Vallentyne (1952) estimated 0.15 mg $P/m^2/day$ and 2.26 mg $N/m^2/day$ left a lake surface in the biomass of emerging insects, mostly midges (Tendipedidae), which could be significant if most of those insects left the marsh and were not replaced by immigrants.

Among the major nutrients, C, O, and N can enter and leave wetlands as gases. The role of CO_2 and O_2 in photosynthesis and respiration need not be elaborated here. Molecular N enters or leaves water or sediments by diffusion, but the critical processes adding to or subtracting from the internal N cycle are N fixation and denitrification.

Nitrogen fixation occurs through microbial and algal action, including symbiotic associations of microorganisms and higher plants. Blue-green algae are well known as N fixers (Evans and Barber 1977) and are common in wetlands (Kasischke 1974). Symbiotic N fixation is known in alder (*Alnus* spp.) and sweet gale (*Myrica gale*) (Moore and Bellamy 1974). Nitrogen fixation by microorganisms associated with peat or organic marsh soils has been shown by many studies (Moore and Bellamy 1974). Conversely, N may be limiting for plant growth in saline, brackish, or alkaline interior marshes (Moreau 1976) as it is in the near coastal marine environment (Ryther and Dunstan 1971).

Data from lakes (Likens 1975) suggest a range of N fixation from 0.04 to 4.56 g $N/m^2/yr$, with most values less than 1 g $N/m^2/yr$. Marshes rich in blue-green algae and bacteria, and perhaps generally warmer than lakes, may support somewhat higher rates. Evans and Barber (1977) cite rates ranging from about 0.6 $g/m^2/yr$ for microorganisms associated with *Typha* to 6.0 $g/m^2/yr$ for microorganisms associated with *Glyceria borealis*.

Denitrification, the conversion of NO_3-N to N_2, possibly through intermediate compounds, has been found in many marshes. The process is mostly microbial and requires an anaerobic environment (Patrick et al. 1976). Rates of 2-4 ppm/day for soils and water from southern marshes and swamps have been demonstrated in the laboratory (Patrick et al. 1976). Frequent (order of days) intermittent flooding and drying accelerate the loss (Reddy and Patrick 1976). There is some evidence that this is potentially a major pathway in N cycling in many marshes (Kadlec 1976, Patrick and Reddy 1976). The amount of N loss is related to the close proximity of an aerobic zone in which nitrification can proceed to NO_3 and an anaerobic zone in which the NO_3 is converted to N_2. The process also requires an energy source for the microorganisms, usually in the form of carbon from organic matter. As a result, shallow waters with fluctuations and organic substrates are likely to be sites of high denitrification. Well-oxygenated waters of riverine or lake shore marshes over highly mineral soils probably exhibit much less denitrification activity.

Denitrification loss rates apparently vary widely. Andersen (1974) estimated that 0-54% of the annual N input to 6 shallow Danish lakes was lost through denitrification. Keeney et al. (1971) estimated 63% of the N entering Lake Mendota, Wisconsin, in seepage waters was lost through denitrification. Other estimates for lakes, as summarized by Likens (1975), range from 0.008 mg N/1/day to 300 mg N/1/day. The available information suggests that the middle of that range, a few mg/1/day, is a reasonable first approximation. If the marsh averages about 1 m deep, this loss would be of the same order, but perhaps exceed the input by N fixation. This agrees with Vollenweider's (1968) conclusion that denitrification "normally" exceeds fixation in lakes.

Examples of Annual Budgets

Recently, Carpenter and Adams (1977) summarized the annual imports, exports, and net change of N and P for Lake Wingra in Madison, Wisconsin (Table 3). The net annual gains of both N and P were in excess of the peak standing crops of N and P in *Myriophyllum* biomass. Two relevant studies have been done on ecosystems related to, but somewhat different from, those in interior North America. Andersen (1974) dealt with six shallow Danish lakes (see Table 4) and Crisp (1966) studied an eroding peat bog in England. Andersen found a liberation of P from the sediment in some lakes in summer and deposition in other seasons. Some of his shallower lakes, with shorter water turnover times, showed more P being exported than imported, although Kvind so, Kal so, and Halle so showed reversals; that is, they were net import-

Table 3. Input-output N and P balances (kg/ha) for a hardwater eutrophic lake, Lake Wingra, in Madison, Wisconsin (modified from Carpenter and Adams 1977).

	N	P
Annual imports		
Precipitation	8.14	0.24
Surface runoff	49.64	10.71
Springs	39.86	0.71
Groundwater	10.93	0
Dry fallout	15.29	0.79
Total import	123.86	12.45
Annual exports		
Outlet discharge	17.71	1.03
Groundwater	1.79	0.05
Total export	19.50	1.08
Annual net balance	+104.36	+11.37
Maximum standing crop of N and P in *Myriophyllum spicatum*	19.29	4.14

ers of P one year and net exporters of P in either the preceding or following year. All of Andersen's lakes exported less N than they imported and a substantial amount of the N output was as N_2. Crisp (1966) showed net export of N and P, mostly in the form of erosion loss of peat particulates. A study of nutrient budgets

Table 4. Annual balances of N and P ($g/m^2/yr$) from some shallow water ecosystems in Europe.

Kind of area	Mean depth (m)	Retention time (days)	Year	Input N	Input P	Output[a] N	Output[a] P	Net storage N	Net storage P
Shallow Danish lakes[b]									
Bryrup Lang	5.0	130	1972	84.5	3.92	37.7	1.88	46.8	2.04
			1973	80.5	3.08	36.0	1.77	44.5	1.31
Kvind sø	1.9	14	1972	175.0	16.50	117.9	10.84	57.1	5.66
			1973	149.3	11.40	117.2	16.22	32.1	-4.82
Kulsø	2.2	18	1972	110.6	9.06	90.0	9.88	20.6	-0.82
			1973	107.1	13.18	78.3	12.56	28.8	0.62
Salten lang sø	4.1	59	1972	26.4	3.92	21.6	1.85	4.8	2.07
			1973	23.8	3.18	16.8	1.36	7.0	1.82
Halle sø	ca. 2.8	ca. 38	1972	86.3	2.63	39.4	2.91	46.9	-0.28
			1973	85.3	2.19	40.9	2.05	44.4	-0.14
Stigsholm sø	ca. 1.2	ca. 11	1972	80.4	4.48	62.3	5.19	18.1	-0.71
			1973	81.9	3.26	61.2	4.01	20.7	-0.75
Eroding peat bog[c]									
Total				0.82	0.046-0.069	1.77	0.086	-0.95	-0.017 to -0.040
Total less erosional loss						0.31	0.041	+0.51	+0.005 to +0.028

[a] Nitrogen output includes 0-50% denitrification.

[b] Data from Andersen (1974).

[c] Data from Crisp (1966).

Table 5. Concentrations of N and P (mg/liter) in water flowing into and out of shallow water ecosystems.

Source	Inputs			Outputs		
	TDP	NO_3-N	NH_4-N	TDP	NO_3-N	NH_4-N
Klopatek (1975)	0.17-2.40	0.07-2.03	0.10-2.61	0.10-0.50	0.10-0.68[a]	0.13-1.59[a]
	0.02-0.03	0.17-2.16	0.07-1.69			
	0.04-0.69	0.03-1.51	0.03-5.81			
Kitchens et al. (1975)	0.095-0.393[b]	0.125-0.300	0.015-0.250	0.075-0.100[b]	0.075-0.300	0.020-0.130
Lee et al. (1975)				0.01-0.55[b]	0.10-1.93	0.00-2.1

[a] High values following drainage.
[b] Ortho-PO_4.

for the Okefenokee Swamp (Rykiel 1977), although not dealing with N or P, showed a mixed pattern of net imports for Ca and K, and net losses for Mg, Na, and Cl.

One of the chief difficulties in studying the overall nutrient budgets of marshes is that excellent information on hydrology and nutrient concentration is

Table 6. Nitrogen and phosphorus contents of tissue of vascular aquatic plants from selected studies.

Source	Species	Percent	
		N	P
Boyd (1978)	27 wetland	2.26 ± 0.14[a]	
	35 wetland		0.25 ± 0.02
	submersed (6 sp)	2.56	0.20
	floating-leaved (4 sp)	2.56	0.23
	emergent (8 sp)	1.42	0.19
	Potamogeton diversifolius	2.86	0.27
Kvet (1975)	*Typha latifolia*	1.5-2.0	0.10-0.15
Kvet (1973)	*Phragmites communis*	1.12[b]-5.10[c]	0.084 -0.240[c]
Richardson et al. (1978)	*Chamaedaphne calyculata*	1.71-2.59[c]	0.09-0.22[c]
Brinson and Davis (1976)	*Nuphar luteum*[d]	1.65[e]-5.7[c]	0.48
Bernatowicz (1969)	19 species	1.18-2.82	0.01-0.61

[a] SE.
[b] Stems.
[c] Leaves.
[d] % ash-free dry wt.
[e] Rhizome.

required. Lee et al. (1975:108) put it this way:

> "We hoped it would be possible to make quantitative estimates of the effect of marshes on water quality, in particular, to be able to make mass-balance computations on the amount of chemicals transported through the marsh from various sources, the transformations that take place in the marsh, and the amount that is transported out of it. This was not possible because of the extremely complex hydrology of the marsh system."

In fact, even Crisp's study (1966) suffers from an inability to deal adequately with nutrient inputs from ground water and stream flow over bedrock; and it is considered one of the better studies.

Several investigators have looked at the concentrations of nutrients in inflowing and outflowing, or only outflowing, water (Table 5). However, in the absence of data on the volume of water flowing per unit of time, such data cannot be evaluated in terms of the amounts of nutrients being supplied to or removed from the marsh, either seasonally or annually.

NUTRIENT CYCLES WITHIN WETLANDS

Amounts of N and P in Wetland Components

The storages of N and P in various parts of marsh ecosystems vary substantially, as does information about them. The amount of N and P in plants, animals, soils, and water is a function of both the concentration and the quantity of material containing that concentration. Data on concentration are more common than data on amounts. Perhaps the best data available are those for concentrations of N and P in vascular plant tissue (Table 6). Even here, the underground parts of such plants are not commonly sampled. Two excellent summaries of available data and the variability of nutrient concentration in plant tissues in time, space, plant part, and kinds of plants are available (Boyd 1978, Prentki et al. 1978) and will not be repeated here. Although variations are common, Boyd's (1978) means of 0.25% P and 2.26% N, oven-dry weight basis, are good first approximations. Data on standing crops of N and P (Table 7) are more variable than concentrations because of the additional variability in standing crop biomass of aquatic and marsh plants. Indeed, Boyd and Hess (1970) showed a high correlation between standing crop biomass of cattail (*Typha latifolia*) and g/m^{2}of P ($r=0.69$) and N ($r=0.76$). On the whole, however, stands of emergent vegetation contain 2-4 g P/m^2 and 20-40 g N/m^2, except in peatlands containing *Cladium jamaicense* and *Carex* spp. (Table 7). Submersed and floating-leaved species usually have lower biomass per square meter (e.g., Boyd 1971b), and consequently the standing crop of N and P in areas of submersed vegetation is lower, even though the percentage of N and P may be higher. Reasonable first approximations of standing crops in floating-leaved and submersed species are 10-20 g N/m^2 and 1-2 g P/m^2.

Variation in the ash content of aquatic plants can markedly affect reported nutrient concentrations, depending on whether the basis for calculation is ash-free dry weight or simply dry weight. Kollman and Wali (1976) reported 35.4 to 56% ash content of total dry weight for *Potamogeton pectinatus*, Kvet (1973) 6% for *Phragmites communis*, Boyd and Hess (1970) 1-6% for *Typha latifolia*, and Boyd (1978) 6.1-40.6% for 40 species of wetland plants. Obviously, subtracting as much as 40-50% of the total dry weight to correct for ash content can about

Table 7. Above ground standing crops (g/m^2) of N and P in vascular aquatic plants as reported in selected studies.

Source	Species	N	P
Klopatek (1975)	mixed emergents	16.9	3.7
Kvet (1975)	*Typha latifolia* (maximum)	25.1	1.6
Dykyjova and Hradecka (1973)	*Phragmites communis*	28-46	3-4
Ulehlova et al. (1973)	*Phragmites communis*	23.44	3.67
Kvet (1973)	*Phragmites communis*	18.8-34.7	1.06-2.67
Boyd (1967)	*Chara* spp.	27.6	2.8
	Myriophyllum spp.	9.3	0.9
	Ceratophyllum spp.	16.7	1.3
Steward and Ornes (1975)	*Cladium jamaicense*	5.5-8.9	0.25
Boyd (1971b)	*Justicia americana* (maximum observed)	44.3	2.8
Boyd (1971a)	*Typha latifolia*	5-12	0.7-1.8
Wentz (1976)	*Carex* spp.	4-6	0.2-0.4
Brinson and Davis (1976)	*Nuphar luteum*		0.197

double reported percentages of mineral nutrients. Careful attention is needed, but either approach should give the same standing crop of nutrients. Ash content is usually highest in submersed species, average 21%, next highest in floating-leaved species, average 16%, and lowest in emergent species, average 12% (Brinson and Davis 1976).

Poor analytic technique can also contribute to error in reported nutrient concentrations. For example, neglect of calcium carbonate encrustations that form on underwater plant parts in hard (high bicarbonate) waters can bias dry weight determinations.

The P, N, and other nutrients found in sediments can exist in two phases: dissolved in interstitial waters, or associated with (or in) the solid sediment particles. The solid phase can include: 1) nutrient ions adsorbed on mineral or organic particles, often called exchangeable; 2) oxides, hydroxides, and hydrous oxides, together with coprecipitated ions; 3) nutrients bound in organic matter; 4) nutrients bound with sulfides (mostly metals); and 5) chemicals bound within the crystalline lattice of sediment particles (Brannon et al. 1976). Few studies have carefully distinguished among these forms of nutrients in sediments. More importantly, it is not at all clear in what forms N and P are available

Table 8. Nitrogen and phosphorus content of wetland sediments.

		N			P	
Source	Sediment type	Total (%)	Exchangeable (ppm)		Total (%)	Exchangeable (ppm)
			NO_3-N	NH_4-N		
Klopatek (1975)	ca. 40% organic	1.75				0.005-0.02[a]
Ulehlova et al. (1973)	sand-clay[b]	0.18				
	organic sapropel[b]	0.53				
Schroder (1975)	marl				0.01-0.05	
Fekete (1973)	15% organic, 30% solids				0.55	13.8[b] 35[c]
	24% organic, 15% solids				0.25	65[b] 122.5[c]
Richardson et al. (1978)	peat[b]	2.54			0.09	
	peat[c]					16.9
	interstitial H_2O		0.06	2.10		0.125
Chamie (1976)	litter	1.4-1.8			0.06-0.1	
Boyd and Hess (1970)	various cattail soils[b]					1-116
Brinson and Davis (1976)	biologically available[d]					378
Steward and Ornes (1975)	peat[b]				0.017-0.046	0.5-24
Kadlec (1960)	various[b]		0-37.5			0.25-8.13
	interstitial H_2O		0.04-36.2[e]			0.008-0.151[e]

[a] Bray P-2 procedure.
[b] Dried sediment.
[c] Fresh sediment.
[d] Dried and acid extraction.
[e] Total N and P.

to wetland plants. The assumption is often made that ions dissolved in interstitial water and adsorbed on various particles, which are dynamically related by chemical equilibria, are representative of sediment nutrients available to plants. Other phases are generally insoluble and unavailable, except that under the reducing conditions often prevalent in marsh soils the oxides and hydroxides may dissolve, releasing those nutrients. Aquatic and marsh plant roots are able to function in an anaerobic environment (Sculthorpe 1967) and may be able to utilize nutrients made available under those conditions.

Most analyses of wetland or marsh soils (Table 8) are done by conventional agricultural techniques, which involve drying and grinding the sample prior to analysis. This destroys the anaerobic status of the sediment, and it probably also shifts nutrients among the phases discussed. Consequently, the results of such tests are of dubious value (Brannon et al. 1976). Even measures of "exchangeable" nutrients are biased as much as twofold (Fekete 1973 [see Table 8], Patrick and Mahapatra 1968). Extractant and extraction techniques also affect results. Boyd (1971b) demonstrated continued release of P over 25 repeated extractions of a sediment with P-free water. In agriculture, a large body of empirical data provides the basis for interpreting the results of a standard soil test in terms of crop requirements. In essence, the soil test is an index whose value has been proven by long experience. In wetlands, no such body of empirical data and experience exists. Generally, studies have shown only crude correlations between plant growth and soil and water nutrients (Fekete 1973, Steward and Ornes 1975) and then often with total content, rather than exchangeable. I believe that no satisfactory procedure for assessing the nutrient status of marsh soils is yet available, although several studies such as those of Fekete (1973), Brannon et al. (1976), and Richardson et al. (1978) are contributions toward that goal.

Available data on total P in soils (Table 8) suggest concentrations vary widely but are commonly in the 0.01-0.02% range (dry weight basis). Fekete's (1973) data are much higher, for no obvious reason. Exchangeable amounts (Table 8) also vary widely, but these data are seriously affected by variations in extractant and technique. Table 8 also includes some data on interstitial water, which also are highly variable in the methods used as well as in levels found.

Total N in soils is usually far greater than any other pool of N within the wetland. Much of the soil N is in organic form and unavailable to plants except through decomposition. A reasonable approximation of total N in marsh sediments is 500-1,500 g/m^2 (dry weight basis) of which about 5-15 g/m^2 is considered available.

Converting from concentrations to weights per unit area or volume of N and P in marsh sediments depends on some estimate of the dry weight (the usual basis for concentrations) per unit area of soil in the root zone. Marsh soils vary greatly in water and organic content and therefore in dry weight per unit volume. Hence it is not possible to use standard agricultural conversions. Only a few studies are available that report amounts of N and P per hectare (Table 9), and the results are highly variable. Generally, quantities of total N and P in the soil are substantially larger than the amounts in the plants.

Phosphorus concentrations in surface waters of wetlands (Table 10) are a little higher than in fresh waters in general, which according to Cole (1975) is usually

Table 9. Nitrogen and phosphorus standing crops (kg/ha) in wetland soils.

Source	Soil Type	N Total	N Avail.	P Total	P Avail.
Ulehlova et al. (1973)	organic sapropel sand-clay	5,830 2,700			39.6 37.15
Steward and Ornes (1975)	peat	15,272-15,792	8-13	97-275	0.6-2.8
Schroder (1975)	marl solids			1,600-8,000	
	interstitial H_2O				0.2
Richardson et al. (1978)	peat interstitial H_2O	6,830	7.5 4.32	242	4.5 0.2

about 0.02 mg/l total P. Nitrate concentration seems to be of the same order as other fresh waters, but ammonium is frequently higher. Some of the higher values in Table 10 reflect marsh drainage and reflooding for management purposes, or, in the case of the TDP reported by Komarkova and Komarek (1975), fertilization to increase fish production. Standing crops of N and P in wetlands surface waters are in most cases not reported, although they could easily be calculated if the water depths were known.

Both sediment and surface water N and P concentrations and standing crops vary seasonally, and some of the range in the results reported undoubtedly reflects that variation. I have ignored seasonal variations in the interest of concentrating on general patterns. Klopatek (1975), Kadlec (1976), Kollman and Wali (1976), and Brinson and Davis (1976) discussed seasonal patterns in more detail.

Nitrogen and phosphorus amounts among the consumers (e.g., insects and birds) are usually regarded as small compared to those in plants (Boyd 1971b).

Processes within the Wetland

The processes going on within the wetland can be categorized, roughly, as physical-chemical, microbiological, or macrobiological. Physical-chemical processes include dissolution, precipitation, oxidation-reduction, adsorption, ion exchange, leaching, and formation of complexes. Factors affecting these processes include pH, temperature, oxygen, and kinds and sources of sediments. Most of these are well treated in limnology texts and will not be emphasized in this paper. Delaune et al. (1976) give an excellent summary for salt marshes, much of which is applicable to

Table 10. Nitrogen and phosphorus concentrations (mg/liter) in surface waters of wetlands.

Source	NO_3-N	NH_4-N	Total N	TDP	Total P
Klopatek (1975)	0.10-1.68	0.13-1.59	1.52-4.16	0.10-0.50	0.11-0.69
Ulehlova et al. (1973)	0.44-1.13	0.27-0.79		0.64-1.04	
Boyd (1970b)	0.07	0.09		0.008[b]	
Komarkova and Komarek (1975)	0.001-0.37	0.16-1.36		0.01-8.90	
Steward and Ornes (1975)	0.30-1.01				0.029-0.213
Richardson et al. (1978)	0.039	0.728		0.060	
Kadlec (1960)			0.03-1.79[a]		0.004-0.062
Bernatowicz (1969)	0.00-0.01	0.02-0.26		0.000-0.029[b]	

[a] High values followed drainage of the wetlands.
[b] Ortho-PO_4-P.

other wetlands. Microbiological processes include decomposition and oxidation-reduction, particularly of nitrogen and sulfur compounds. Factors influencing microbial action include pH, carbon energy sources, and oxygen supply. Macrobiological activity may be divided for convenience into plant and animal. Plant uptake of nutrients is essentially a problem in physiological ecology. Stage of growth is important, as are temperature, light, competition, and ratios among the available nutrients. Plants, as well as animals, apparently excrete nutrients, but we really know little of the factors that influence the process. Similarly, there is still some controversy over if, when, and under what circumstances different kinds of marsh and aquatic plants translocate nutrients. Ingestion and excretion by animals are obviously functions of the number and kinds of animals. This in turn is a function of the quality and quantity of habitat provided. In many cases, the animals may be mostly invertebrates. Lamarra (1975) found the rate of recycling of P per gram body weight by animals to be negatively correlated with body size, so smaller animals contribute relatively more to P renewal than do larger animals. Maguire (1974) estimated that only 0.8-1.4% of the N, and presumably P, was cycled by beaver (*Castor canadensis*) populations at the borders of a Michigan peatland.

Rates of nutrient uptake by vascular plants are sometimes calculated from seasonal changes in the total amount in the plants. Such rates may be underestimates, as are rates of biomass production calculated in a similar manner (Prentki et al. 1978, van der Valk and Davis 1978, Whigham et al. 1978). However, Table 11 gives examples of reported rates of P uptake regardless of method of estimation, simply because the data are so few. Daily rates have not been extrapolated to annual rates, because there are few good data on seasonal fluctuations in uptake. Boyd's work (1970b) suggests that in temperate areas most uptake of P by *Typha latifolia* occurs in a short period of active growth, slightly preceding maximum biomass growth. In contrast, Brinson and Davis (1976) found uptake by *Nuphar luteum* in winter, although at less than one-half the summer rate. The data suggest 5-20 mg P/m^2 must be supplied each day during peak daily uptakes, primarily from sediments, inflowing water, rain and dry fall, or decomposition.

Table 11. Rates of P uptake by some wetland vascular plants.

Source	Species	Rate
Prentki (1978)	*Typha latifolia*	3.5 g/m^2/yr
Klopatek (1975)	*Scirpus fluviatilis*	5.3 g/m^2/yr
Steward and Ornes (1973)	*Cladium jamaicense*	0.18 g/m^2/yr
Gaudet (1977)	*Cyperus papyrus* (tropics)	7.8 g/m^2/yr
Boyd (1970b)	*Typha latifolia* (maximum rate)	19.3 mg/m^2/day
	Scirpus americanus (maximum rate)	5.3 mg/m^2/day
Richardson et al. (1978)	Mixed fen	0.17 g/m^2/yr
Brinson and Davis (1976)	*Nuphar luteum* (summer uptake from sediment)	9.3 mg/m^2/day

Table 12. Rates of N uptake by some wetland vascular plants.

Source	Species	Rate
Boyd (1970b)	*Typha latifolia* (maximum rate)	162.7 mg/m^2/day
	Scirpus americanus (maximum rate)	34.4 mg/m^2/day
Klopatek (1975)	*Scirpus fluviatilis*	20.75 g/m^2/yr
Richardson et al. (1978)	Mixed fen	3.0 g/m^2/yr
Boyd (1971a)	*Typha latifolia*	87-279.0 mg/m^2/day
Kvet (1975)	*Typha latifolia*	140.0 mg/m^2/day
Toetz (1973)	*Ceratophyllum*	up to 2 mg NH_4-N/ g dry wt./hr
Gaudet (1977)	*Cyperus papyrus* (tropics)	103.3 g/m^2/yr

Examples of rates of N uptake are presented in Table 12. Many plants can and do take up both N and P in excess of current needs, a phenomenon known as "luxury" uptake (Gerloff and Krombholz 1966). Hutchinson (1975), in an exhaustive review of mineral nutrients in aquatic plants, accepts Gerloff and Krombholz's (1966) estimate of 1.3% N and 0.13% P as the critical or minimum concentration in plant tissue. Higher values, then, presumably reflect some luxury uptake.

Phosphorus is released more rapidly than nitrogen from dead plant material. Boyd (1970a) found that about 50% of the P in cattail was lost in 20 days, whereas in the same period the decrease in biomass was only 20%. Brinson and Davis (1976) estimated the time to lose one-half of the original P content of *Nuphar luteum* aboveground parts as 6 to 9 days, about the same as biomass. For *Justicia americana*, the time for 50% loss was found to be about 13 days in summer, only about one-half the time required for 50% loss of biomass. In contrast, Chamie (1976) found very little change in P concentration in sedge litter over 1 year in a northern peatland. Different species within the same marsh may have very different patterns of decomposition and nutrient release, as shown for *Typha glauca* and *Scirpus fluviatilis* by Davis and van der Valk (1978). Decomposition is very temperature dependent, and in the tropics Gaudet (1977) estimated 84% of the P in *Cyperus papyrus* disappeared in 26 days. He also showed that some of the early loss of P from dead plant material is simply elution; that is, it does not involve microbial action.

Microbial processes important in N cycling within the sediment-water-plant system include decomposition, ammonification, and nitrification. Relatively little of the N content of plant tissue is lost immediately after death (Boyd 1970a, Gaudet 1977, Davis and van der Valk 1978). Depending on the environment, very little change in N concentration of plant litter may take place for months (Boyd 1970a) or years (Chamie 1976). Even in the tropics, Gaudet (1977) found a loss of 26% of the N per m^2 in 26 days, but in the same period there was a one-third loss in biomass. Nitrogen enrichment of litter apparently results from the inclusion of high N content microorganisms that conserve N more than carbohydrate. Nevertheless, there is N mineralization first to NH_4 (ammonification) and then to NO_3(nitrification) which accounts for some contribution of inorganic N to water or soil. The conversion of NH_4 to NO_3 requires oxygen that may not be available for extended periods of time in marsh sediments. Thus it is not uncommon to observe accumulations of NH_4-N in wetlands. This is an acceptable source of N for plants and, within limits, does no harm. Ammonium-N is not a substrate for denitrification and is not converted to N_2 and lost by that route.

Nitrogen is an ingredient in protein and essential to animals. With higher protein content than plants, animals and many microorganisms serve essentially as N concentrators, e.g., the bacteria associated with decomposition as mentioned above. Animals also excrete N as urea, uric acid, or ammonia, generally recycling it in the same area. Some impact of animal excreta on local N concentrations was inferred by Davies (1973) for wintering waterfowl concentrations. He cited an estimate (original reference not given, unfortunately) of 90-250 million tons of N per year excreted by waterfowl. Without data on the area on which this is deposited, or its source, the net impact cannot be evaluated.

Work on eelgrass (*Zostera marina*) (McRoy et al. 1972), salt marshes (Reimold 1972), and freshwater macrophytes (Demarte and Hartman 1974, Schroder 1975, Brinson and Davis 1976, Lamarra personal communication) suggests that living aquatic plants may actually give off P to the surrounding water. The rates vary: 4.4 mg/m^2/day average for total P for *Phragmites communis* (Schroder 1975), 2.5 mg/m^2/day for *Nuphar luteum* in summer (Brinson and Davis 1976), and 2.0-51.5 mg/m^2/day from *Potamogeton alpinus* (Lamarra personal communication).

Senescent but erect structures may lose nutrients by leaching. Klopatek (1975) estimated 2.2 g P/m^2/yr lost by this route from *Scirpus fluviatilis*, and Prentki et al. (1978) estimated 50 mg P/m^2/day from *Typha latifolia*. Some translocation back to roots also occurs at the end of the growing season. Klopatek (1975) estimated that movement as 0.44 g P/m^2/yr in *S. fluviatilis*, Prentki et al. (1978) as 0.59-0.90 g P/m^2/yr in *Typha latifolia*, and Brinson and Davis (1976) as 0.13 mg P/m^2/day in summer in *Nuphar luteum*.

Cycle Syntheses

Brinson and Davis (1976), Klopatek (1975), and Richardson et al. (1978) have attempted to synthesize the N- or P-cycles within a wetland. Even in these cases, the water, vascular plant, and sediment phases received most attention. Two different techniques were used — changes in standing crops and radioisotopes. Brinson and Davis found that their rate of uptake based on isotope techniques was only 11% of uptake based on change in P standing crop. Hence, their data on fluxes (Fig. 1) should be considered in a relative sense only. The important conclusions from Fig. 1 are: 1) uptake of P from both soil and water occurs in all seasons in *Nuphar luteum* in North Carolina; 2) in summer P movement occurs both from sediment through the plant to water and to a lesser degree the reverse; 3) the sediment is the main source of P, and the interstitial and dilute acid extractable fractions are more than 100 times the maximum P in plants; and 4) overall, the plants are a source of P for the water, rather than the reverse.

Klopatek (1975) studied an emergent, *Scirpus fluviatilis*, in Wisconsin, mostly by standing crop determinations. On an annual basis, this species also moves or pumps N and P from sediments to the water (Fig. 2). If it is assumed that water is 50 cm deep and completely enclosed, the annual release of 2.2 g P/m^2would result in a concentration in the water of 4.4 mg P/l, far in excess of the observed

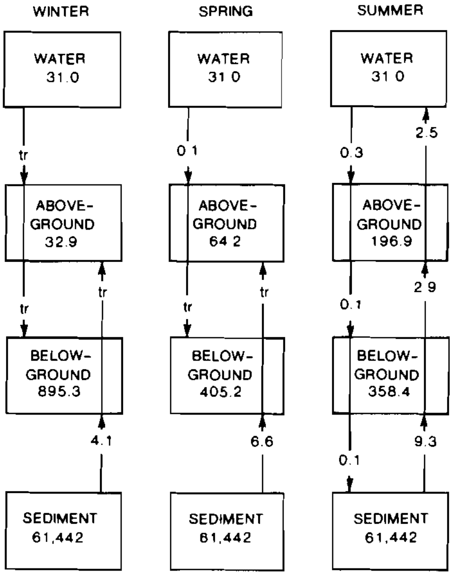

Fig. 1. The daily flux of P (mg) through a square meter of *Nuphar luteum* community during the winter, spring, and summer. Values in the compartments are P mass. Modified from Brinson and Davis (1976).

0.11 to 0.69 mg P/l. Because the excess did not appear in the outflow, some method of immobilization must be postulated. One possibility is that the N and P liberated by macrophytes are taken up by algae and subsequently sedimented. Other workers (e.g., Tilton et al. 1976) have suggested a rapid incorporation in the sediments. Klopatek, whose data are summarized in Fig. 2, suggested that a substantial fraction of "available" P in the sediments was taken up by the plants. Indeed, his data suggested that the concentration of sediment P is reduced during the period of maximum plant uptake. Because of the greater amount of N than P available, relative to uptake, N depletion of the soil seems unlikely. The mechanism preventing N enrichment of the water by the 7.34 g N/m^2 is likely denitrification rather than immobilization as in the case of P, although uptake and sedimentation with algal biomass are also a possibility.

Richardson et al. (1978) used methods similar to Klopatek's in a Michigan fen dominated by *Chamaedaphne calyculuta* and *Betula pumila* (Figs. 3, 4). These are woody plants, so a substantial part of the above ground standing crop persists from year to year. In general, this ecosystem seems to be operating on amounts and fluxes of P about an order of magnitude less than Klopatek's Wisconsin marsh. Nitrogen was also lower, but less so.

Some further impression of N and P in marsh systems can be gained from Ulehlova et al.'s (1973) study of *Phragmites communis* in a fish pond in Czechoslovakia (Table 13). Basing calculations on those data, allowing for a life span of underground parts of 3 years, and subtracting N and P in standing dead indi-

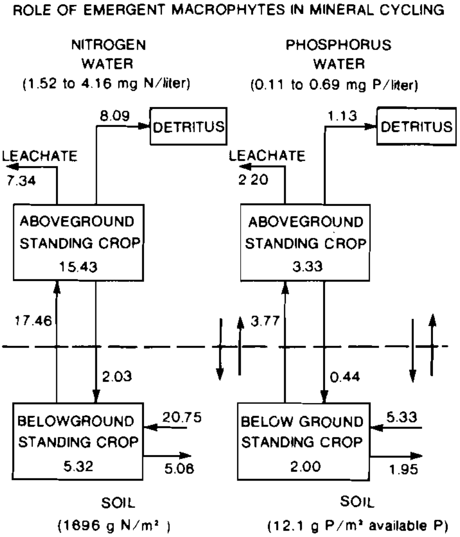

Fig. 2. Flow of N and P through a *Scirpus fluviatilis* stand. Flows are in grams per square meter per year, and compartments are grams per square meter in standing crop. From Klopatek (1975).

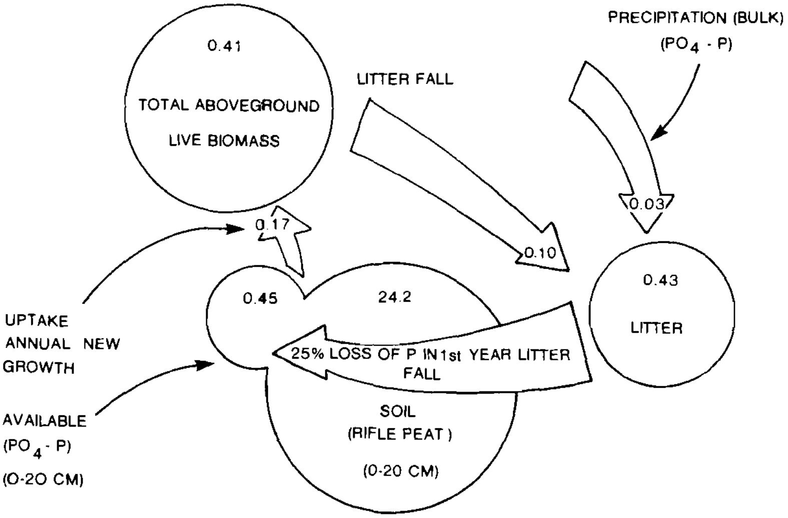

Fig. 3. A preliminary model showing annual P flux and storages for the leatherleaf and bog birch vegetation and soils components of a central Michigan peatland in 1975. All values are in g/m^2. From Richardson et al. (1978).

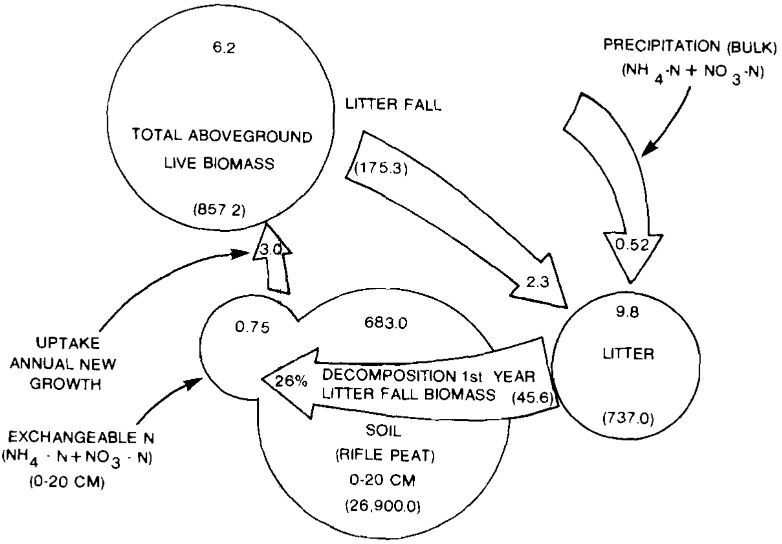

Fig. 4. A preliminary model showing annual N flux and storages for the leatherleaf and bog birch vegetation and soils components of a central Michigan peatland in 1973. Total biomass for each compartment given in brackets. All values are in g/m^2. From Richardson et al. (1978).

Table 13. Nutrient content in a *Phragmites communis* stand (g/m^2) (from Ulehlova et al. 1973).

	N	NH_4	NO_3	P	PO_4
Rainfall	0.80			0.06	
Vegetation					
Living					
Aboveground					
stems	11.14			2.47	
leaves	12.29			1.20	
total	23.44			3.67	
Underground					
rhizomes	19.06			8.45	
roots	2.86			0.92	
total	21.92			9.37	
Total living	45.35			13.04	
Standing dead					
stems	11.33			2.74	
leaves	1.36			0.10	
Total standing dead	12.69			2.84	
Water		0.21	0.55		0.79
Sapropel	583	9.79	4.50		3.96
Bottom soil	270	6.90	2.25		3.75

cate a minimum annual uptake of 6.79 g P/m^2 and 30.75 g N/m^2. The combined standing crops of P and inorganic N in soil and water were inadequate to provide that much P and N, indicating a substantial input during the year. The very high ortho-P content of the water — 1.96-3.19 mg/l as PO_4 — suggests the possibility that the fish pond studied was fertilized.

OVERVIEW AND MANAGEMENT

In preceding sections the data on processes and storages affecting N and P cycling in wetlands were analyzed. The emphasis was on biological processes, with comparative neglect of the physical-chemical. To put the general aspects of these cycles into perspective, let us assume a hypothetical marsh on the eastern edge (about longitude 100° W) of the prairies at mid-latitude. Further assume a marsh of 1 ha, average depth 50 cm, with a 10-ha catchment basin. All water comes from rain, and the excess over evaporation leaves by an outflow channel. The watershed is agricultural land, one-half cropland and one-half pasture. Annual rainfall is 50 cm. Assume 0.5 ha *Typha*, 0.5 ha *Ceratophyllum*, and annual plant uptake of N and P = annual plant loss. Then we can construct hypothetical budgets for water, N, and P, using values selected from existing studies, cited previously, plus some guesses, and allocating residuals to storage in the sediments (Table 14).

The resulting hypothetical balances illustrate several key points. First, such a marsh accumulates nutrients, consistent with generally held opinion. Nitrogen and phosphorus dissolved in the water and available in sediments are grossly inadequate for plant uptake, indicating that the supply must be renewed

Table 14. Hypothetical annual H_2O, N, and P budgets for a wetland.

Process or storage	H_2O (m^3/yr)	P (kg/ha/yr)	N (kg/ha/yr)
Hydrologic			
Precipitation input	5,000	0.25	5
Runoff from cropland (20% precipitation)	5,000	22.0	37.5
Runoff from pasture	5,000	0.85	42.5
Total runoff inputs	10,000	22.85	80.0
Evapotranspiration loss	5,000		
Outflow (0.3 mg P/l, 2 mg N/l)	10,000	3	20
Net change	0	+20.10	+65.0
Internal cycles			
Storage in H_2O (0.1 mg P/l, 1 mg N/l)	5,000	0.5	5.0
Storage in sediment (roughly root zone)			
Total	600-1,600	40-2,000	3,000-17,000
"Available"		3	8
Stored in *Typha* standing crop (3 g P/m^2, 15 g N/m^2)		15	75
Stored in *Ceratophyllum* standing crop (1.3 g P/m^2, 16.7 g N/m^2)		6.5	83.5
Total in above ground plants		21.5	158.5
Plant uptake			
Typha (3.5 g P/m^2, 20 g N/m^2)		17.5	100.0
Ceratophyllum (1.5 g P/m^2, 20 g N/m^2)		7.5	100.0
Total uptake, mostly from sediment		25.0	200.0
Input to H_2O via decomposition and leaching		13.0	80.0
Input to sediment and litter from plant remains		8.0	100.0
Animal consumption (cycled to same year)		2.0	20.0
Release from plants to H_2O (2 mg P/m^2/day, 100 days)		2.0	
Potential net N loss: denitrification-nitrogen fixation	7.0		

rapidly by processes such as runoff and release from sediment storage. Inputs to the water from decomposition and leaching would greatly increase dissolved concentrations unless some mechanisms result in immobilization. Looked at another way, the bulk of the N and P for plant growth apparently comes from and returns to the sediment, with only an ephemeral existence dissolved in surface water. Both the runoff and decomposition inputs to the water could raise P concentrations from about 0.1 mg/l to 2.5-4.0 mg/l and N concentrations from about 1 mg/l to about 16 mg/l. Such concentrations seem to occur rarely, if ever, and hence the inference of some mechanisms re-sedimenting the P and perhaps N. For N, there is the alternative that net gaseous loss (N-fixation minus denitrification) might be a major process, far greater than the 7 kg/ha/yr estimated. Data exist to justify estimates as high as several hundred kg/ha/yr. Chemical precipitation could easily account for the P sedimentation, and there is a clear implication of P enrichment of the sediments. We don't know if this occurs, nor whether that P is available for future plant growth, nor if P concentrations in the interstitial water or surface water increase with time.

From a management point of view, it seems clear that runoff inputs and processes associated with sediment storage are likely to dominate the system. Again, this is consistent with observations that the productivity of marshes is correlated with the fertility of their watersheds. The effects of drawdowns or natural drought on marsh sediments and productivity are reasonably well known (Weller 1978, Kadlec and Wentz 1974). Until recently the possible importance of denitrification in marshes seems to have been less widely appreciated, although it has been considered a serious problem in the culture of rice (Patrick and Mahapatra 1968).

Imports of nutrients, either by runoff or direct addition (fertilization), are to some degree controllable by the manager. Some studies of wetland fertilization are underway or have been completed recently (Kadlec 1976, Boyd 1971a, Odum et al. 1976, Steward and Ornes 1973, Moreau 1976). Plant response has often been less than expected, even under greenhouse conditions (Wentz 1976). In several cases, uptake by sediments and denitrification have removed most of the added N and P, with only a fraction going to the plants (several studies suggest about 25% — e.g., Patrick et al. 1974 reported 17-23% of 56 and 112 kg N/ha) but nevertheless increasing yield substantially.

Sediments vary enormously in the total amount of N and P stored, depending on both physical structure and chemical state. Further, I believe they vary in the ease with which nutrients are flushed out by water movements. Cook and Powers (1958) suggested that marsh drainage at the wrong time could result in a substantial loss of nutrients. To my knowledge, this aspect of the relationship between marsh hydrology and nutrient cycles has not been carefully studied and evaluated. Several workers (Lee et al. 1975, Kadlec 1976, Klopatek 1975) have found higher nutrient levels in water coming from marshes in early spring, which suggests a flushing effect. The importance of this phenomenon to the marsh is not yet clear.

In sum, the overall budgets of N and P seem to be strongly dominated by the rates at which N and P are supplied and removed. Surface runoff seems to be a dominant supply route, perhaps reaching its peak in riverine marshes. Removal seems to be mainly through processes associated with the sediments, but potentially also through water outflow and denitrification. Limnologists have found that the trophic state (fertility) of lakes is dominated by: 1) nutrient import, or loading, and 2) a measure of the time water remains in the lake, or turnover rate.

Aquatic and marsh plants take up and return to water and sediments large amounts of both N and P. Their role in nutrient cycling seems to be one of extracting nutrients from deeper sediments and returning them to surface sediments and to the water to some degree (Prentki et al. 1978). The available evidence does not suggest that vascular plants are very effective in regulating or reducing nutrients in surface waters, although they will certainly respond to increased nutrients with increased growth. This view of the role of aquatic vascular plants in nutrient cycling seems to conflict with the generality that water basins tend to accumulate and store nutrients in the natural process of eutrophication. The conflict is real only to the extent that nutrients are not sedimented in forms unavailable to plants in insoluble minerals or decay resistant organic debris. Certainly the plants tend to keep the soluble and available nutrients in current circulation. It is probably unwise to pursue these generalities further without more information.

What should a manager do? Few marshes suffer from an oversupply of available N and P for growth of plants desirable for waterfowl habitat. Generally, the aim of management will be to conserve and increase supplies of available N, P, and other nutrients. In managing water, the manager should attempt to hold water high in nutrients as long as possible; conversely, water released should be low in nutrients. Mechanisms and processes internal to the marsh may tend to do this naturally, but managing to increase retention time of nutrient rich water should be beneficial. Of course, should excess nutrients, e.g., salt, be a problem, the reverse procedure is called for.

The productivity of marsh sediments is often improved by temporary drainage; hence the frequent practice of periodic drawdown as a marsh management technique. Certainly this practice affects physical and chemical processes, but the microbiological effects may be even more dramatic, e.g., nitrification. Most of our knowledge of drawdown effects is empirical, and some careful research is needed on the processes affected by water level manipulation. For example, water level fluctuations, particularly on a short time scale of, say, a few days, may greatly increase denitrification and lead to N deficiencies. This has not been demonstrated in marshes, to my knowledge, but seems possible and should be considered in future research and management.

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW

Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

SPATIAL AND TEMPORAL HABITAT RELATIONSHIPS OF BREEDING DABBLING DUCKS ON PRAIRIE WETLANDS

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Abstract: The U.S. Fish and Wildlife Service established several waterfowl study areas in Canada during the early 1950's. Annual waterfowl and habitat surveys were conducted near Lousana, Alberta, Redvers, Saskatchewan, and Minnedosa, Manitoba, into the late 1970's. Observations were recorded during an era of wet-dry-wet habitat cycles, liberal-restrictive-liberal hunting regulations, increasing intensity of land use, and accelerating rate of wetland alteration. Data from these areas located in the prairie parklands provide biologists and managers with unique opportunities to assess waterfowl population and production trends over the past three decades. Dramatic shifts in species composition and abundance were documented in response to habitat changes as well as hunting regulations. The species with declining numbers generally tend to be those heavily harvested, whereas the species with stable or increasing populations tend to be those lightly harvested. There are also relationships between breeding chronology and relative abundance: early breeders are not holding up as well as late breeders. Pond occupancy rates indicate that the decline in waterfowl populations is occurring more rapidly than losses of wetland habitat. There is an increasing number of ponds without ducks, suggesting that the available breeding habitat is underutilized. The rapid conversion and intensification of land use is continuing on an ever-increasing scale with impact on both the quality and quantity of wetland and upland waterfowl production habitat. If recent years are any preview of the future, the face and character of prairie Canada may be altered by prevailing socioeconomic conditions. High grain prices have markedly altered agricultural practices in response to world food shortages and populations trends. The upshot of these events has been depressed reproductive potential for several waterfowl species.

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW

Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

SOCIAL INTERACTIONS AND SPACING BEHAVIOR IN BREEDING DABBLING DUCKS

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Abstract: Although dabbling ducks are gregarious during most of the year, pairs of most species seek some degree of isolation during particular phases of the breeding season. The behavioral responses of pairs to conspecifics vary in relation to both breeding status and breeding chronology. In the present paper, discussion centers upon pair-bond characteristics, pair-spacing patterns, pursuit flights, male mate-support roles, and male promiscuity. Strong pair-bonds are generally correlated with low mobility and territoriality, distant threat displays, pronounced male-male hostility, and reduced male promiscuity. Conversely, weak pair-bonds are correlated with increased mobility, reduced territoriality, reduced male-male hostility, and increased male promiscuity. Interspecific differences in evolved breeding strategies are apparent, and appear to reflect differences in habitat characteristics, feeding ecology, and the energetic requirements of breeding females.

WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW
Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

FOODS OF LAYING FEMALE DABBLING DUCKS ON THE BREEDING GROUNDS

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Abstract: Food of laying hens of five species of dabbling ducks collected in the glaciated prairie pothole region of south central North Dakota consisted largely of invertebrates: 99% in blue-winged teals (*Anas discors*) and shovelers (*A. clypeata*); 70% in mallards (*A. platyrhynchos*); 77% in pintails (*A. acuta*); and 72% in gadwalls (*A. strepera*). Snails and aquatic insects dominated the diet of blue-winged teals, snails and crustacea the diet of shovelers, and insects and crustacea the diet of gadwalls. Earthworms were an important food of female mallards and pintails during wet years. Dominant plant components consumed were filamentous algae by gadwalls and plant fruits by mallards and pintails. Factors that influenced the selection of food items were nesting chronology and food availability. Food availability was determined primarily by the life cycle and behavior of invertebrates and current hydrological conditions within the wetland complexes. During years of adequate precipitation, temporary, seasonal, and semipermanent wetlands provided abundant and highly available plant and animal foods successively throughout the breeding season. Prairie wetland complexes provide an important habitat component in the ecology of prairie dabbling ducks. Adequate preservation of waterfowl production habitat requires that the importance of the wetland complex be stressed.

Prairie wetlands traditionally used by breeding waterfowl are being altered or eliminated throughout the glaciated prairie pothole region of North America. The loss of wetlands caused by partial or complete drainage is dramatic and can be readily documented; however, effects of the more subtle ecological changes that alter the structure of plant and animal communities are less obvious and not well documented. Siltation, tillage, and chemical contamination are examples of potentially degrading influences on wetland quality and subsequently on the availability of foods for breeding waterfowl.

The semi-arid climate is a dominant factor affecting the hydrology and consequently the ecology of wetlands in the glaciated prairie pothole region of North

America. An annual moisture deficit, which varies in magnitude and is accompanied by changes in annual and seasonal water levels and dissolved salts, is a dominant feature of the semi-arid climate. Plant and animal communities continually change in response to these fluctuations in water level and salt content (Swanson and Meyer 1977), and periodic droughts produce major changes in plant and animal communities. The dynamic nature of this water regime and the successional changes in the biota that it produces are beneficial for dabbling ducks. Plant and animal foods are often abundant and available at shallow depths to dabbling ducks throughout the breeding season.

Prairie wetlands are shallow, nonintegrated, eutrophic, alkaline, and high in dissolved solids, and contain a low relief, featheredged shoreline. Small changes in water volume produce major changes in the surface area inundated or exposed by drawdown. This interaction of climate and surface geology produces dynamic and productive aquatic ecosystems, which are essential to breeding waterfowl.

Stewart and Kantrud (1971) developed a classification system for prairie wetlands based on species structure of vegetation zones, as determined by water permanence and variations in average salinity. Ephemeral, temporary, and seasonal wetlands typically undergo drawdowns each year and contain plant and animal communities that vary in their tolerance of dry conditions. Invertebrates that thrive on a detritus or algal food chain are abundant during the waterfowl breeding season, and are available to anatids because of the shallow water depths. Temporary and seasonal wetlands also provide loafing sites for pairs and reduce intraspecific strife.

Semipermanent wetlands are flooded throughout the year during wet cycles and undergo drawdowns or dry up during periods of drought. These wetlands contain deep marsh emergent and submerged vascular plants and a number of invertebrate species that are susceptible to dry conditions. As the salt content of the water increases, salt tolerant plant and animal species begin to dominate the biotic communities (Swanson et al. 1974).

Kantrud and Stewart (1977) described use of natural basin wetlands in North Dakota by breeding pairs of ducks. Temporary, seasonal, and semipermanent wetlands were used extensively by pairs of dabbling ducks, whereas permanent lakes were generally used relatively little. Temporary and seasonal wetlands received the highest proportion of annual use by breeding pairs. Tilled wetlands received less use than did undisturbed wetlands.

Adequate assessment of the effects of changes in aquatic ecosystems on waterfowl ecology requires an understanding of the feeding niches occupied by the different species of waterfowl. Knowledge of feeding niches will provide wetland managers with information needed to define critical and threatened habitat, preserve wetlands of highest quality, and efficiently manage existing wetland habitat.

Early investigations of foods consumed by dabbling ducks often combined information derived from different species, sexes, seasons, and geographical areas, and the data were dominated by fall and winter collections. Data were collected during the fall, in part, because of the availability of birds killed by hunters. Few attempts were made to identify foods consumed by dabbling ducks during the breeding period (Perret 1962:4). Some authors pointed out, however, that more animal foods appeared to be consumed during the breeding season than during other times of the year (Martin and Uhler 1939:98, Stewart

1962:44).

Bartonek (1968:92) reviewed 125 published studies of waterfowl food habits and concluded that 95% contained material that biased data in favor of seeds. More recent investigations have pointed out the bias associated with use of the gizzard for food studies when a variety of foods that vary in hardness is consumed (Dillon 1958, Moyle 1961, Perret 1962, Dirschl 1969, Bartonek and Hickey 1969, Swanson and Bartonek 1970).

More recent investigations of foods consumed by dabbling ducks have documented a high incidence of animal foods in the diet of breeding birds (Dirschl 1969, Bartonek 1972), particularly hens (Perret 1962, Swanson and Nelson 1970, Krapu 1974a, Swanson et al. 1974, Serie and Swanson 1976, Landers et al. 1977, Swanson and Meyer 1977). An increase in the consumption of animal foods during egg formation has been demonstrated (Krapu 1974a, Serie and Swanson 1976).

The objectives of this paper are to: (1) describe the foods consumed by the laying hens of five species of dabbling ducks, and (2) assess the role of complexes of wetlands in providing spatial and temporal requirements of ducks during the breeding season.

Appreciation is extended to M. I. Meyer for aid in the laboratory and H. F. Duebbert and A. T. Klett (Northern Prairie Wildlife Research Center) for critical review of the manuscript.

METHODS

Methods used in this study were described by Krapu (1974a), Swanson et al. (1974), and Serie and Swanson (1976). Birds were collected while actively feeding during 1967-76 within the drift plain and Missouri Coteau areas of the Prairie Pothole Region in south central North Dakota. The geology, hydrology, climate, water quality, and biota of this area were described by Eisenlohr (1972), Sloan (1972), Stewart and Kantrud (1972), and Swanson et al. (1974). Actively feeding birds were collected, and only the esophageal contents, measured by volumetric displacement, were tabulated. Food items are expressed as the mean of volumetric percentages (aggregrate percent). Ovaries were examined so that food consumption could be correlated with reproductive condition. Feeding sites were examined to provide a basis for determining food selectivity. Data are presented on two groups of laying gadwalls: (1) those that fed in saline lakes located in glacial outwash, and (2) those that fed in ephemeral, temporary, seasonal, and fresher semipermanent lakes located in end and ground moraines.

RESULTS AND DISCUSSION

Food Selection

Among plant and animal foods consumed by laying female dabbling ducks of 5 species, invertebrates accounted for 99% in blue-winged teals and shovelers, 70% in mallards, 77% in pintails, and 72% in the 2 groups of gadwalls.

Foods selected by laying females varied among species (Table 1). Snails and aquatic insects dominated the diet of blue-winged teals, snails and crustacea the diet of shovelers, and insects and crustacea the diet of gadwalls. Earthworms were an important food of mallards and pintails during early spring. Filamentous algae formed a major part of the plant matter consumed by gadwalls, and fruits were dominant plant parts eaten by mallards and pintails.

Snails are a major food item in the diet of blue-winged teals on the breeding grounds (Dirschl 1969, Swanson et al. 1974). During the laying period, molluscs accounted for 40% of the diet of female

Table 1. Aggregate percent volume of foods consumed by laying female Anatidae collected during 1969-76 in south central North Dakota (number of birds examined shown in parentheses).

Food item	Blue-winged teal[a] (20)	Shoveler[b] (15)	Gadwall (salt)[c] (20)	Gadwall (fresh)[d] (35)	Mallard[e] (15)	Pintail[f] (31)
MOLLUSCA	40	40		4	14	15
Gastropoda	38	40		4	14	15
Lymnaea spp.	28	18		t[g]	14	U[h]
Gyraulus spp.	5	12		t		U
Miscellaneous	5	10		4		U
Pelecypoda	2					
INSECTA	44	5	52	36	14	37
Trichoptera	7	t	1	8		1
Odonata	1	t	2	6	5	
Coleoptera	3	2	16	4	t	3
Hemiptera	1	1	7	t		
Lepidoptera					7	
Diptera	32	2	26	18	2	33
Chironomidae	20	1	26	17	1	20
CRUSTACEA	14	54	20	32	16	14
Anostraca	5	6	t		t	14
Conchostraca	t	7		14	9	t
Copepoda	t	5	5			
Ostracoda	1	3	5	7	t	
Cladocera		33	10	10	6	t
Amphipoda	8			1	1	t
ANNELIDA	1			t	26	11
Oligochaeta	1			t	24	11
Aquatic				t		t
Terrestrial	1				24	11
Hirudinea				t	2	
VEGETATION		t	27	25	3	t
Algae (filamentous)			22	9		
Lemna spp.			t	8		t
Miscellaneous		t	5	8	3	
FRUITS	1	1	1	3	27	23
Echinochloa crusgalli					15	8
Miscellaneous	1	1	1	3	12	15

[a] Swanson and Meyer 1977.

[b] Swanson, unpublished data.

[c] Serie and Swanson 1976. "Salt" gadwalls are those that fed in saline lakes.

[d] Swanson, unpublished data.

[e] Swanson, unpublished data.

[f] Krapu 1974a.

[g] Less than 1 %.

[h] Genera of gastropods unidentified.

blue-winged teals and shovelers, 14% of the diet of mallards, and 15% of the diet of pintails. Shovelers ate a greater proportion of small planorbid snails. Female gadwalls consumed fewer snails (4%) than did the other species. Saline lakes do not support snails, except in adjacent fen areas, but fresher wetlands selected as feeding sites by breeding gadwalls contained high snail populations. The snails selected by gadwalls were a thin shelled, semi-aquatic form (*Succinea* spp.) that was not found in the other ducks.

The dominant snails eaten by all species of ducks examined except the gadwall were *Lymnaea* spp. *Lymnaea stagnalis*, a larger species often abundant in semipermanent lakes, was not found in laying females. Snails are an important food nutritionally because they provide high levels of protein and calcium, both of which are required by laying hens (Krapu and Swanson 1975).

Aquatic insects were major foods in the diet of blue-winged teals (44%), pintails (37%), and the two groups of gadwalls (52 and 36%). Insects accounted for 14% of the diet in mallards and 5% in shovelers. Caddis fly larvae (Trichoptera), dragonflies (Odonata), damselflies (Odonata), predaceous diving beetle larvae (Coleoptera), water boatmen (Corixidae), mosquito larvae (Culicidae), and midge larvae (Chironomidae) were the insects most often eaten. Midge larvae were the insects most often consumed by blue-winged teals, gadwalls, and pintails. This insect contains nutritionally valuable ingredients for breeding females (Krapu and Swanson 1975) and ducklings (Sugden 1973).

Crustaceans were major food items taken by shovelers (54%) and gadwalls (20 and 32%). They accounted for 14% of the diet of blue-winged teals, 16% of the diet of mallards, and 14% of the diet of pintails. Fairy shrimp (Anostraca) that occupied temporary and seasonal wetlands were the primary crustacean in the diet of pintails. The fairy shrimp consumed by blue-winged teals and shovelers, however, were species found only in lakes high in dissolved salts. Clam shrimp (Conchostraca) were an important food of shovelers, mallards, and the gadwalls that fed on lakes in moraines that were low in dissolved salts. Cladocera, copepods, and ostracods were consumed primarily by shovelers and gadwalls. Amphipods were eaten primarily by blue-winged teals, which consumed *Hyalella azteca* by feeding in and around plant stems and terminal buds. Perret (1962:64) also noted that mallards did not use this food. Amphipods, an abundant group found in most semipermanent wetlands and permanent lakes, form a major part of the diet of lesser scaups (*Aythya affinis*) during the breeding season (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Dirschl 1969, Bartonek and Murdy 1970).

Terrestrial earthworms were consumed by dabbling ducks after they were washed into wetlands during early spring storms. Laying mallards and pintails ate earthworms in early spring when this food was abundant in comparison with other invertebrates, which were small or unavailable because of water depth. During springs with little surface runoff, the availability of this food appeared to be limited or reduced. Krapu (1974a) reported that earthworms did not occur in the diet of pintails during 1971 when precipitation was low during April.

Plant matter accounted for 27% of the diet of laying female gadwalls feeding in saline lakes and 25% of those that fed in freshwater wetlands. Although the volumes were similar, the species of plant and animal foods differed. Filamentous algae made up 22% of the plant parts eaten by gadwalls that fed in saline lakes but only 9% of the plant parts eaten by those that fed in freshwater lakes. Duckweed (*Lemna* spp.) accounted for

8%, pondweed (*Potamogeton* spp.) 4%, and bladderwort (*Utricularia vulgaris*) 3% of the diet of female gadwalls that fed on the fresher wetlands.

Mallards and pintails selected similar proportions of plant fruits, which accounted for 27 and 23% of the diets, respectively. In the food of other species, fruits accounted for 1% in laying blue-winged teals and shovelers, 1% in gadwalls that fed in saline lakes, and 3% in gadwalls that fed in freshwater wetlands. Mallards and pintails often fed in tilled ephemeral wetlands located in cropland. The most abundant fruit in their diet was barnyard grass (*Echinochloa crusgalli*), which accounted for 15% of the food of mallards and 8% of that of laying pintails. Barnyard grass formed 71% of the diet of pintail hens that fed on tilled wetlands (Krapu 1974b).

Factors Influencing Food Selection

Food selection by breeding females during egg formation was influenced by bird morphology, nesting chronology, invertebrate behavior, and the species structure of the aquatic biota, which was in turn determined by current and past hydrological conditions.

Morphological characteristics determine the capacity of each species to efficiently extract food items from the wetland environment. Spacing of the lamellae on the bill, for example, determines the minimum size of aquatic organisms that can be filtered efficiently. Shovelers have fine lamellae and feed principally on microcrustacea. Neck length and body size determine maximum feeding depths that can be reached to use food items in the mud-water interface. For example, mallards and pintails can feed at greater depths by tipping than can blue-winged teals.

Certain species of dabbling ducks, particularly the mallard, pintail, and gadwall, have adapted to feeding on domesticated cereal grains. Their bill structure, however, is designed to efficiently extract small food items in a water medium (Goodman and Fisher 1962). Birds observed feeding on tilled wetlands that contained water usually ate small fruits, such as those of barnyard grass. Small fruits and invertebrates often occurred in clusters within the esophagus, suggesting that several are filtered and swallowed as a unit. Small fruits were never abundant in the esophagus of birds that fed in the upland, suggesting that feeding is most efficient in the upland when confined primarily to relatively large fruits that are abundant because of a particular agricultural practice.

Food selection by various species is influenced by the ability to physically process food items of different textures. Gadwalls, for example, have a large muscular gizzard and select fine sand for grit, which is used to process plant tissues such as filamentous algae. This species did not select snails, even when they were abundant at feeding sites, and the few that were eaten were a species with a thin shell. Parts of heavy shelled snails are retained as grit in the gizzards of blue-winged teals and often replace coarse sand used as grit. Perhaps gadwalls avoid coarse shelled snails because they interfere with the grinding action that is required to process plant tissues. Little is known about the relation between morphological characteristics and food selection. Only some of the more obvious differences have been mentioned here, but their influence appears to be significant.

Nesting chronology varies markedly among species of dabbling ducks, and thereby influences food selection during the laying period. A. T. Klett (personal communication) examined 1976 nest initiations of 224 blue-winged teals, 135 mallards, 57 pintails, 56 gadwalls, and 50 shovelers on a study area adjacent to

Interstate 94 in south central North Dakota. Pintails and mallards started nesting in early April, and 50% of the starts were before 3 and 8 May, respectively. Shovelers started their first nests in mid-April and 50% were started by 10 May. The first blue-winged teal nest was found on 26 April and 50% of the nests of this species were initiated by 15 May. Gadwalls started nesting in mid-May and 50% had started before 29 May. Differences in nesting chronology reduce overlap in the use of food resources. Breeding females of each species tend to use a different hydrological phase within the wetland complex, and the hydrology of prairie wetlands changes as the season progresses. Food availability, a major factor influencing food selection, changes in response to phenological and hydrological conditions. Renesting attempts, which are determined by the magnitude of nest destruction on one hand and wetland quality on the other, also influence food selection by extending the laying period. Blue-winged teals held on experimental ponds at the Northern Prairie Wildlife Research Center produced up to five clutches of eggs (Swanson and Meyer 1977) after imposed nest destruction. The renesting effort appears to be strong in years when abundant surface water is present in late spring.

Feeding behavior is a function of interactions among food availability, morphological adaptations, and physiological condition. Consumption occurs when invertebrates are eaten when they move into zones where they are available to feeding waterfowl; nighttime feeding may occur when the availability of invertebrates increases between sunset and sunrise. This occurs, for example, when aquatic insects such as mayflies (Ephemeroptera) or midges emerge, or when beetle or mosquito larvae come to the surface to maintain or replenish their oxygen supply. Crustaceans are consumed when they are unusually abundant or are forced to concentrate on the surface by unfavorable chemical conditions. Certain aquatic invertebrates are made available to ducks when they are concentrated by wind action. The role of invertebrate behavior in the selection of food by waterfowl was discussed by Swanson and Sargeant (1972), Swanson et al. (1974), Serie and Swanson (1976), and Swanson (1977).

When invertebrates become highly available, as during an insect emergence or from a population buildup, morphological differences that influence food selection no longer are a dominant factor influencing feeding efficiency, and several species may consume the same type of food item. For example, when *Daphnia pulex* or *D. magna* populations are unusually dense, all species of prairie nesting dabbling ducks can effectively feed on the large adults. As the population declines and availability of large adults is reduced, only shovelers can continue to feed efficiently on the remaining small individuals.

The Wetland Complex

Invertebrate species structure, population densities, and behavioral characteristics change rapidly within the wetland complex during annual, seasonal, and 24-hour periods (Swanson et al. 1974, Swanson 1977); food availability fluctuates accordingly. A mallard nesting in early April is influenced by a different water regime and invertebrate population than is a gadwall that nests in late May. Water regimes also change with each renesting attempt. Pintail hens, for example, feed principally on fairy shrimp and earthworms in early spring (Krapu 1974a), whereas renesting hens feed primarily on midge larvae (Krapu 1974b).

Wetland classes within the complex are unique in terms of the biotic communities that are produced and the seasonal succession that occurs in the invertebrate community (Swanson et al. 1974). Invertebrate and plant composition may change from one year to the next within a wetland if a major change occurs in hydrology brought about by drought conditions. A seasonal hydrological succession occurs among different classes of wetlands within a complex, providing highly available plant and animal foods that support a variety of waterfowl species throughout the nesting, renesting, and brood rearing period.

Mallards and pintails begin their first nests in early spring, when most of the foods associated with semipermanent lakes are isolated at depths unavailable to dabbling ducks and ice still covers many permanent lakes. Ephemeral and temporary wetlands receive high use at this time. As the season progresses, seasonal wetlands become the major source of food used by renesting mallards and pintails, and shovelers and blue-winged teals are starting their first nest. By late spring, water levels begin to recede on semipermanent wetlands, aquatic insects start to emerge, and submerged aquatic plants extend to the water surface and provide a substrate for invertebrates. Certain semipermanent wetlands provide an abundant and highly available food supply by late spring and early summer. At this time gadwalls are starting their first nests, and renesting dabbling ducks of other species are obtaining food from semipermanent lakes. Semipermanent wetlands also provide food for ducklings.

Wetland hydrology is highly variable from year to year, and normal patterns may reverse in drought years. During the early springs of 1973 and 1977, temporary and seasonal wetlands were dry, and dabbling ducks fed on semipermanent lakes as water levels receded (Swanson and Meyer 1977). When early drawdown occurs, waterfowl production is usually reduced. The hydrological conditions within the wetland complex determine the foods that will be available to breeding ducks during a given period. Different foods were selected by blue-winged teals during a wet period, when many seasonal wetlands contained water, than during a dry year when few were flooded. During wet periods snails were a predominant blue-winged teal food on seasonal wetlands, whereas during years when seasonal wetlands were dry the birds fed principally on chironomid larvae in semipermanent and permanent lakes in drawdown. Food selection by pintail hens during the breeding season also has been shown to be influenced markedly by water conditions (Krapu 1974a).

Feeding Niches

The feeding niche occupied by a given species varies with season and is influenced by the physiological demands and reproductive condition of the bird. Many interacting factors influence food selection and make it difficult to define the feeding niche of each species. The dynamic water regime of the prairies, in association with a high incidence of renesting, tends to mask species differences. Also, the high incidence of invertebrates in the diet of laying females places this segment of the breeding population in a unique category. Large sample sizes would further delineate food selection; however, it is difficult to obtain large numbers of laying females because of the number of females that must be collected to supply a small number that are laying.

Food data have indicated some obvious differences in feeding niches, although some overlap occurs. Shovelers tend to select small crustaceans. Consumption of snails by shovelers was similar in volume to that by blue-winged teals but consisted of a greater proportion of small planorbid species. Gadwalls were similar to shovelers in their use of crustaceans but differed from all other species in their avoidance of snails and greater use of vegetation, particularly filamentous algae. Gadwalls selected similar types of foods even though feeding on wetlands that provided different species of plants and invertebrates. Mallards and pintails differed from the other three species by consuming fruits. Foods of these two species were somewhat similar, and differences reflected in the data may be attributed to sample size. The study of mallard feeding ecology is incomplete and greater differences may be detected in the future. The mallard is more versatile, selecting foods available in several wetland classes, and this characteristic may be found to be a factor in niche separation.

CONCLUSIONS

Female anatids that are producing eggs consume a high proportion (greater than 70%) of small invertebrates (insects, snails, and crustacea). Their ability to obtain these foods during the nesting period depends largely on the types of aquatic habitat that are available. High quality wetland habitats produce an abundant supply of highly available small aquatic animals during the nesting and brood rearing period. Quality aquatic habitat is particularly critical when nest predators destroy a large percentage of the nests, forcing hens to renest after their body reserves already have been expended in previous attempts. A single hen may lay up to five clutches of eggs before a successful hatch is achieved or she terminates her nesting efforts for the year. It is important, therefore, that abundant high quality food be available on the breeding grounds throughout the nesting period. The prairie wetland complex with all of its wetland classes is an important habitat component in the ecology of prairie dabbling ducks, and wetland complexes should be stressed in the preservation of waterfowl production habitat. Land-use practices on the prairies have favored drainage of shallow, non-permanent wetlands into drainage systems or into wetlands located at lower elevations. This practice is altering the natural wetland complex of the prairies, creating larger and more permanent lakes that are less attractive to breeding dabbling ducks (Swanson and Meyer 1977).

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW
Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

NUTRITION OF FEMALE DABBLING DUCKS DURING REPRODUCTION

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Abstract: Females of wild populations of prairie nesting dabbling ducks select diets that contain relatively high levels of animal protein and calcium during the period of egg formation. Experimental studies I conducted at the Northern Prairie Wildlife Research Center in 1975 and 1976 indicate that mallard (*Anas platyrhynchos*) reproduction is adversely affected when hen access to animal matter is curtailed. Hens on a wheat (*Triticum aestivum*) diet laid 46 and 50% fewer eggs than did hens on a control diet during the 1975 and 1976 nesting seasons, respectively. The addition of 10 g of live earthworms (*Lumbricus* sp.) daily to the wheat diet throughout the nesting season markedly improved egg hatchability but egg production remained low, presumably because of a deficiency of total protein or one or more essential amino acids. Hens consuming wheat during the laying of a clutch failed to ovulate an average of 1 day for every 2 eggs laid, whereas hens on the control diet skipped ovulation 1 day for every 4.6 eggs. Mean weights of eggs laid by hens fed the wheat diet during 1975 and 1976 were 12 and 7% less, respectively, than those laid by the control groups. Food deprivation imposed by removal of the control diet for a 3-day period during the laying of each clutch resulted in 45% fewer eggs being laid during the nesting season than among controls fed ad libitum; egg and yolk weights remained similar. Yolks (dry) from eggs produced by hens on control and wheat treatments weighed 11.9 ± 1.3 g and 10.2 ± 1.1 g (mean ± SD), respectively. Mallard ducklings without access to food upon hatching survived longer when hatched from larger eggs. Calcium required for egg formation apparently is derived primarily from the diet during the nesting season. The information presented in this paper underscores the important role of nutrition in determining reproductive potential in dabbling ducks.

The nutrient requirements of free-living populations of dabbling ducks have received limited attention in the scientific literature. This dearth of information has resulted, in part, because advancement in nutrition research on free-living populations of breeding waterfowl requires access to information on food habits, reproductive physiology, and several other aspects of breeding biology.

Knowledge of wetland ecology, and in particular those factors controlling waterfowl food abundance, are also important when nutrient effects on reproductive potential in dabbling ducks are considered. Detailed information on food habits and wetland ecology on the breeding grounds has only recently become available.

Studies of free-living populations of birds during the past decade have shown food selection is influenced by chemical and nutrient composition. Gardarsson and Moss (1970:66) reported that Icelandic ptarmigan (*Lagopus mutus*) selectively fed upon the most nutritious foods available during the breeding period. Moss (1972:424) reported that selection for nitrogen and phosphorus by red grouse (*Lagopus lagopus scoticus*) increased from winter to spring, whereas that for calcium, soluble carbohydrates, and crude fat did not. Food selection has been found to change markedly during the breeding period among certain species of waterfowl. Pintails (*Anas acuta*) feed primarily on plant foods for most of the year but select greater quantities of animal foods during the breeding season, particularly during the period of egg formation (Krapu 1974). Feeding ecology studies of gadwalls (*A. strepera*) (Serie and Swanson 1976), black ducks (*A. rubripes*) (Reinecke 1977), mallards (Swanson et al. 1979), and wood ducks (*Aix sponsa*) (Drobney 1977) have also shown increased consumption of animal matter during the laying period. Among adult breeding hens, nutrient intake must be sufficient to meet energy requirements, replace body constituents lost during normal body processes, and provide the nutrients necessary to produce viable clutches of eggs.

The primary purpose of the present paper is to describe nutrient selection during the breeding period in certain species of prairie-nesting dabbling ducks and to attempt to identify from experimental data those nutrients most likely to be limiting to reproduction. A paucity of published information on dabbling duck nutrition has led me to draw frequently upon relevant literature on other groups of birds. In conclusion, I will discuss dabbling duck nutrition in relation to wetland ecology in the Prairie Pothole Region.

I thank D. G. Jorde, S. Stewart, and J. A. Shoesmith for their assistance in collection of certain data presented in this paper; V. A. Adomaitis for supervising certain chemical analyses; F. B. Lee for supervising rearing of experimental birds; D. H. Johnson for suggestions concerning experimental design; and E. Multer for assistance in literature review. For critical review of this manuscript, I thank D. H. Johnson, M. W. Weller, and W. R. Goforth.

METHODS

Experimental findings that are presented in this paper were obtained with captive mallards reared from eggs of wild origin gathered in south central North Dakota during June 1974. Birds were propagated at the Center and research was conducted during April-June 1975 and 1976.

Treatments were designed to test effects of diet quality and availability on egg production, egg and yolk weight, and egg hatchability. In 1975, treatment effects on egg production, egg weight, and yolk weight were studied, whereas in 1976 the effects of diets on egg production, egg weight, and hatchability were evaluated. Potential genetically induced differences among teatments were minimized by a stratified random selection procedure whereby paired comparisons of treatment effects were made among brood mates. Testing was conducted in outdoor breeding pens situated in an open field on the Center grounds to minimize man-induced disturbance. Control and wheat diets during both years of the study were provided ad libitum. Protein content in the control and wheat diets was 29 and 14%, respectively. Food was removed from pairs on the restricted control diet on the afternoon following the laying of the third egg of a clutch; the food was returned 72 h later. Pairs on the three treatments during each year received oystershells fed ad libitum.

In 1976, earthworms were fed with wheat as one treatment. Each hen on the wheat plus earthworm diet received 10 g live earthworms daily which were weighed on a triple beam balance to the nearest 0.1 g. Earthworms were placed into a water-filled glass pan in selected breeding pens after a partition had been lowered temporarily separating the drake and hen to insure that the hen received the full daily earthworm ration. A plastic floor cover prevented soil invertebrates or other plant and animal matter from becoming available to the pairs.

Pen nest boxes were checked daily to label eggs laid on that date and to document laying patterns. Eggs were removed on the third day after completion of the clutch; each egg was cleaned and weighed to the nearest 0.1 g on a triple beam balance. In 1975, the yolk of each egg laid was separated from other egg constituents in the laboratory and placed in a sealed and labeled plastic vial and stored at -20 C until removed for drying. Yolks were dried in a controlled forced-convection oven until reaching constant weight (48 h). Egg yolks were dried whole for 24 h and separated into quarters for the remaining period. Dry yolks were weighed on a Mettler balance to 0.1 g. In 1976, fertile eggs were incubated to determine hatchability.

RESULTS AND DISCUSSION

Nutrient Selection

During the period of egg formation dabbling duck hens ingest diets that are principally animal matter (Table 1). From the nutritional standpoint, laying pintail, mallard, and gadwall hens are selecting a diet that contains about 28% protein, whereas blue-winged teals (*Anas discors*) and shovelers (*A. clypeata*) consume a somewhat higher protein level. Selection of animal matter during egg formation seems largely independent of the level of availability of plant foods.

Table 1. Percentage of major types of foods consumed by hens of certain species of wild dabbling ducks during the laying period in North Dakota. Data are based upon volumetric measurements of esophageal contents.

	Food type						Percent		
Species	Mollusca	Annelida	Crustacea	Insecta	Seeds	Plant parts	Animal	Plant	Source
Mallard	14	26	16	14	27	3	70	30	Swanson et al. (1979)
Pintail	15	11	14	37	23	tr[a]	77	23	Krapu (1974)
Gadwall (saline)			20	52	1	27	72	28	Serie and Swanson (1976)
Gadwall (fresh)	4	tr	32	36	3	25	72	28	Swanson et al. (1979)
Shoveler	40		54	5	1	tr	99	1	Swanson et al. (1979)
Blue-winged teal	40	1	14	44	1		99	1	Swanson et al. (1974)

[a] Trace.

However, the specific types of animal and plant matter in the diet are strongly influenced by their level of availability. Pintails and mallards, for example, shift to animal foods irrespective of access to cereal grains even though these grains are preferred foods during much of the year.

Most invertebrates consumed by dabbling ducks are primarily protein on a dry-weight basis (Table 2). Amino acid composition of certain of these invertebrates compares favorably with egg protein (Krapu and Swanson 1975). This is an important consideration, because the biological value of protein is high only if all essential amino acids are contained in a proper ratio to the protein being formed (Scott et al. 1969:57).

Among invertebrate foods, calcium is most concentrated in the calcareous exoskeletons of snails. Snails are a major food in the diet of most prairie-nesting dabbling ducks except gadwalls, which feed on crustaceans but consume few snails (Table 1). Snails and certain crustaceans appear to be the principal sources of calcium in the diets of prairie-nesting dabbling duck hens plus being important sources of protein.

Scott (1973:49) indicated that captive breeding ducks and geese should receive 0.5% available phosphorus in diets when fed ad libitum. Most plant and animal foods appear to contain adequate levels of phosphorus (Table 2). Wild breeding ducks may require higher concentrations of key nutrients than is considered adequate in prepared diets, however, because of restricted access to foods.

Most plant foods consumed by dabbling ducks are primarily carbohydrate (NFE), contain relatively low levels of protein (Table 2), and have low concentrations of certain essential amino acids required for egg formation (Krapu and Swanson 1975). Seeds of aquatic and terrestrial plants comprise the bulk of the

Table 2. Nutrient composition of certain plant and animal foods consumed by female dabbling ducks breeding in the Prairie Pothole Region.

Food item		% nutrient composition (dry)					
Scientific name	Common name	Protein	Fat	NFE	Fiber	Ca	P
Plant							
Cladophoraceae[a]	Green algae	16.0	0.2	41.3	22.4	2.9	0.6
Glyceria grandis[a]	Mannagrass (caryopses)	6.0	1.4	76.1	7.9	0.3	0.5
Scolochloa festucacea[b]	Whitetop (caryopses)	8.8	1.9	67.9	16.1	0.4	0.4
Triticum aestivum[b]	Wheat (grains)	18.2	1.7	75.8	2.4	< 0.03	0.6
Echinochloa crusgalli[b]	Barnyard grass (grains)	14.2	0.5	46.6	31.3	< 0.05	0.6
Beckmannia syzigachne[a]	Sloughgrass (caryopses)	7.0	6.5	59.6	20.0	0.5	0.4
Animal							
Oligochaeta[b]	Earthworms	60.2	7.7	12.3	0.4	0.2	1.0
Anostraca[b]	Fairy shrimp	71.9	8.6	1.5	3.9	0.3	1.4
Cladocera[a]	Waterfleas	31.8	1.5	10.9	7.3	11.8	1.2
Amphipoda[a]	Scuds	47.0	5.9	16.5	8.4		
Diptera[b]	Midges (larvae)	66.4	5.8	14.9		0.5	1.3
Gastropoda[b]	Snails (without shell)	58.9	0.1	21.9	0.7	4.2	0.9
Gastropoda[a]	Snails (with shell)	16.9	0.7	5.8	12.4	26.1	0.3

[a] Sugden (1973).

[b] Krapu and Swanson (1975).

plant matter consumed by most species, gadwalls being an exception (Table 1).

Effects of Nutrition on Reproduction

To obtain a better understanding of the underlying basis for selection of animal matter by dabbling duck hens during the period of egg formation, I conducted experiments with mallards to test dietary effects on egg production, egg and yolk weight, and egg hatchability. The results of these studies are examined in this section.

Egg Production. — The number of eggs laid by mallard hens during the nesting season varied directly with the quality of their diet. Hens fed wheat (14% protein) plus supplemental calcium averaged 46 and 50% fewer eggs during the nesting season than did controls on a 29% protein diet (Tables 3, 4). In addition, mallard hens under the stress of a low protein plant diet ovulated at irregular intervals when laying. For example, hens fed the plant diet while laying a clutch averaged 1 day skipped per every 2 eggs laid, whereas hens on the animal diet failed to ovulate 1 day for every 4.6 eggs laid. The latter rate of missed ovulations approaches that which I have observed in field environments. Skipping of days between eggs by mallard hens presumably was caused by inadequate access to total protein or certain essential amino acids. Scott (1973) noted that if a severe deficiency of one or more essential amino acids develops, egg production will cease. From the standpoint of productivity in free-living populations, lengthening of the period required to complete the clutch because of marginal food resources increases the probability of nest destruction.

Lipids stored in the yolk are of critical importance to developing embryos and newly hatched ducklings. However, lipid needs from the diet are small, because hens can either synthesize most lipids from other nutrient sources or can draw upon lipid reserves, particularly early in the nesting season. Lipid reserves, primarily in subcutaneous and visceral fat depots, are substantial in prenesting mallards and pintails and contribute significantly to the lipid requirements needed to form the initial clutch (G. L. Krapu, unpublished data). Whether stored lipids become yolk or are expended as energy for feeding and/or other breeding needs, these reserves lessen nutrient stress during nesting.

Calcium for egg production apparently is obtained principally from food resources available at the time of breeding. Calcium content in femurs from wild mallard hens I sampled increased during the month following hen arrival on the breeding grounds (Fig. 1). This seems reasonable, because the diet of wild mallards is low in calcium during the winter in Louisiana (Junca et al. 1962). Comar and Driggers (1979) used ^{45}calcium to trace the origin of calcium in chicken eggshell and estimated that 60-75% was ingested and the remainder came from body stores. Scott (1973) stated that the calcium in medullary bone is sufficient

Table 3. Egg production, egg weight, and yolk weight (mean ± SD) among mallard pairs on selected treatments at the Northern Prairie Wildlife Research Center, Jamestown, North Dakota, in 1975.

Treatment	No. pairs	No. eggs/pr	Egg wt (g)	Yolk wt (g)
Control	10	31.2±6.1	55.9±4.3	11.9±1.3
Restricted control	7	17.3±9.2	55.6±4.0	11.9±1.2
Wheat	10	16.7±4.4	49.0±3.9	10.2±1.1

Table 4. Egg production and egg weight (mean ± SD) and hatchability rate among mallard pairs on selected treatments at the Northern Prairie Wildlife Research Center, Jamestown, North Dakota, in 1976.

Treatment	No. pairs	No. eggs/pr	Egg wt (g)	Hatchability rate (%)
Control	8	22.6±7.7	55.8±4.0	70.7
Wheat	7	12.4±3.6	51.7±4.8	41.0
Wheat + earthworms	7	11.3±8.3	52.3±4.6	67.9

for 2 or 3 eggs and recommended that prepared diets for breeding ducks and geese contain 2.7% calcium. Egg production in birds is affected when a calcium deficiency exists. Ring-necked pheasant (*Phasianus colchicus*) hens, when fed diets with marginal concentrations of calcium (0.4-1.1% of the diet) during the breeding period, produced eggs at a much lower rate than hens fed diets containing 2.0 to 3.2% (Greeley 1962, Chambers et al. 1966, Hinkson et al. 1970). Grau (1968) noted that most mineral deficiencies result in cessation of egg laying rather than in production of eggs that are deficient in minerals. Snail shells and fragments are abundant on the soil surface of seasonal and semi-permanent wetlands in the Prairie Pothole Region, so calcium is not likely to be a limiting factor in the diets of breeding dabbling ducks that feed upon snails.

A stable source of high quality foods is needed during the nesting season to maintain high levels of egg production. In experimental studies, a 72-h withdrawal of the control diet from mallard hens during each laying cycle resulted in a 45% decline in total number of eggs laid during the nesting season but did not affect egg size or yolk content (Table 3). Breitenbach et al. (1963) reported that

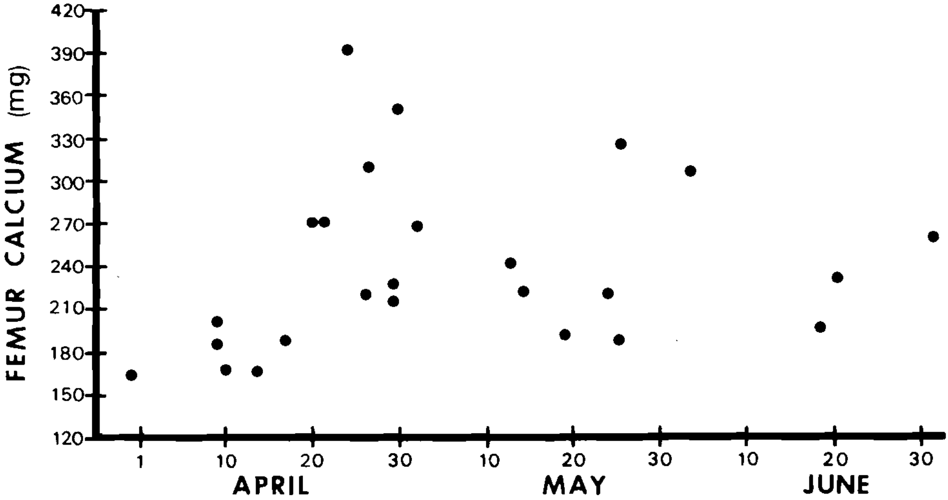

Fig. 1. Calcium content in femurs of 26 mallard hens breeding in North Dakota, by date of collection during 1974-1976 (G. L. Krapu, unpublished data).

ring-necked pheasant hens fed at minimum requirements during the breeding season laid only 9% as many eggs as were laid by controls fed ad libitum. Ivy and Gleaves (1976) reported that level of egg production had an effect ($P < 0.01$) on consumption of food, protein, and energy in chickens.

Selection of invertebrates, particularly larval forms without chitinous exoskeletons, provides an advantage over a plant diet during egg production because of the higher concentration of required nutrients in animal foods and more rapid digestion. Chitin, which forms the structural material of the exoskeleton of many adult insects, is indigestible in non-ruminants (Scott et al. 1969:16). Fisher (1972: 433) noted that birds eat to satisfy two basic needs: the physiological demands of the body and food volume needed to reach satiety. If satiety is fulfilled through bulkiness of the diet the bird will stop eating before the physiological needs are satisfied. In studies of blue-winged teals, invertebrates were digested within minutes, whereas plant foods either required several hours to break down or were passed through the digestive system intact (Swanson and Bartonek 1970).

Egg and Yolk Weights. — My findings indicate diet quality affects egg weight in the mallard. Eggs produced by hens

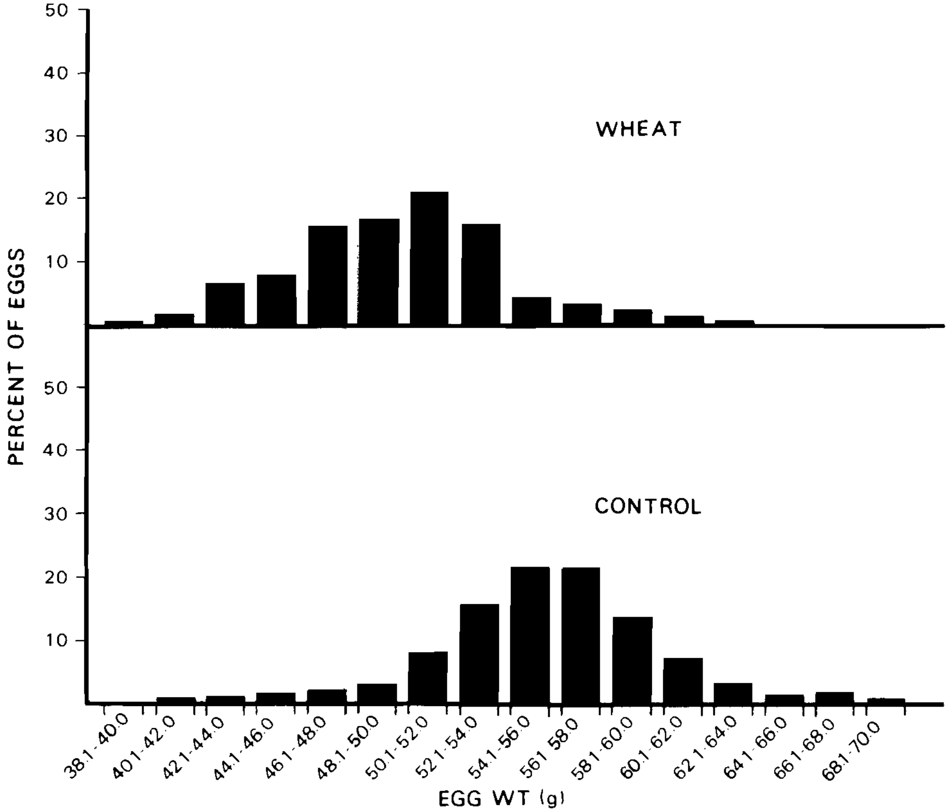

Fig. 2. Mallard egg weight distribution in relation to dietary treatment during 1975 and 1976.

consuming a diet with 29% protein (approximate level of protein in natural diet) were 12% heavier in 1975 and 7% heavier in 1976 than eggs laid by hens fed a 14% protein plant diet (wheat) supplemented with calcium ($P < 0.001$, Tables 3, 4). Egg weight distribution by treatment is shown in Fig. 2. Scott (1973) observed that when the supply of one or more essential amino acids is deficient, the quantity of protein synthesized may be decreased, causing a reduction in egg size. The level of the essential amino acid methionine in the diet of chickens has been shown to affect egg weight (Leong and McGinnis 1952). Concentration of methionine is frequently low in plant foods. Although egg size decreases with a reduction in dietary levels of individual essential amino acids or of total protein, the concentration of amino acids among eggs that are produced is not reduced significantly in chickens (Ingram et al. 1950).

Yolk weights of mallard eggs laid by hens on the plant diet diminished with the decline in egg size. Mean yolk weight (dry) was 14% less (11.9±1.3 to 10.2±1.1g) on the plant diet than on the control diet (Table 3); this is a potential mean loss in energy reserves of about 13.8 kcal to developing embryos and newly hatched young. High fiber content, which is characteristic of many plant foods consumed by dabbling ducks (Table 2), can affect egg and yolk weights. Menge et al. (1974) reported that when powdered cellulose formed 15% of the diet of chickens, adverse effects on egg and yolk weight resulted. Turk and Barnett (1971) reported that the addition of 15% oat (*Avena sativa*) hulls to the diet reduced egg weight in chickens. Limited intake of natural plant foods during egg formation, including those containing relatively high levels of cellulose, probably has evolved, in part, because plant foods contain low concentrations of critical nutrients required for egg production and/or slow digestion rate caused by a high fiber content.

Relationship of Egg Weight to Duckling Survival. — Level of stored nutrient reserves in yolks of dabbling duck eggs affects length of time newly hatched ducklings can survive when food is scarce. In experimental tests, newly hatched mallard ducklings were provided only water in a controlled environment. Ten ducklings from large eggs (>47 g) survived 149.5 h, whereas 6 ducklings from small eggs (<45 g) survived 116.8 h (G. L. Krapu, unpublished data). Research findings presented in this paper suggest the quality of food resources available to breeding hens at nesting can have a significant effect on nutrient reserves available to ducklings at hatching. Newly hatched wild ducklings must often travel long distances to reach water areas with adequate food resources, and access to yolk nutrient reserves reduces nutrient stress during that period.

Egg Hatchability. — Diet quality influenced hatchability rate of eggs laid by mallard hens (Table 4). Selection of some animal matter by laying hens appears necessary solely in view of the deleterious effects on egg viability associated with selection of plant diets. For example, when 10 g of live earthworms were added daily to the wheat diet of each hen, total egg production and egg size remained similar to the wheat treatment, but hatchability rate increased markedly (Table 4). Apparently the addition of the animal matter was adequate to maintain hatchability rates but was inadequate to significantly change the level of egg production. Holm and Scott (1954) reported that hatchability of fertile eggs laid by mallard hens fed an experimental diet with 17% protein was markedly lower than among eggs laid by hens on a 28% protein diet during the third and fourth weeks of laying. In studies of pintails, Krapu and Swanson

(1975) reported an extremely low hatchability rate among hens having access solely to a plant diet (wheat); addition of calcium to the plant diet increased hatchability only slightly.

Dabbling duck hens in captivity continue to lay but at a reduced rate when fed a protein deficient plant diet, but I have concluded that wild hens seldom produce clutches solely from plant diets. I reached this conclusion from data on food selection by wild hens during the laying period (Table 1) and because clutches of wild dabbling ducks characteristically have high hatchability rates. Free-living hens apparently have access to the small levels of animal matter necessary to maintain high levels of hatchability. Vitamin B_{12}, though of critical importance in the diet for egg production and hatchability, is required in only minute quantities. Therefore, when habitat conditions are poor and invertebrates are present in low densities, nesting efforts are more likely to terminate because of a deficiency in total protein or certain amino acids rather than from a reduction in egg viability from a vitamin deficiency.

Animal protein is not necessary to maintain high hatchability rates when diets can be supplemented with vitamins. Cooper and Hughes (1974) have shown that hatchability of eggs produced by chickens fed diets with and without animal matter (fish meal) were similar when the vegetable diet was fortified with a vitamin mixture containing Vitamin B_{12}. A deficiency of several vitamins other than Vitamin B_{12} can also cause lowered hatchability rates (Scott et al. 1969: 108-113), but most vitamins are required in only minute amounts and are present in foods of plant origin; Vitamin B is an exception because it is of animal origin. According to Scott et al. (1969: 59), factors other than Vitamin B_{12} that account for the high superiority of diets with animal protein sources (animal matter) include: (1) calcium and phosphorus levels, (2) other B-complex vitamins, particularly riboflavin, and (3) levels of the essential amino acids lysine and methionine.

Relationship of Female Dabbling Duck Nutrition to Prairie Wetlands

Protein and calcium requirements of dabbling duck females during reproduction are met primarily by feeding on aquatic invertebrates. Dabbling duck access to invertebrates comes through foraging in flooded shallow wetland habitat. During censuses in North Dakota on randomly selected quarter-sections during 1965 and 1967-69, Kantrud and Stewart (1977) found that 60% of the breeding dabbling duck pairs were on seasonal wetlands. Each breeding pair utilizes several shallow wetlands to obtain nutrient requirements. Radio-marked mallard hens used from 7 to 22 natural wetlands during the nesting season (Dwyer et al. 1979).

Annual recruitment in prairie dabbling duck populations varies with the status of water conditions during the nesting season. A strong correlation between number of ponds in July and size of the returning breeding population the following spring has been documented (Crissey 1969). Flooding of shallow basins creates microhabitats conducive to propagation of certain invertebrates that are rich sources of protein and calcium. Breeding by various species of prairie nesting dabbling ducks coincides with periods when these organisms are most accessible. The semi-arid climate has favored those breeding strategies that permit utilization of nutrient sources accessible in a usable form only briefly; pintail and mallard use of earthworms when available after flooding of temporary ponds is a prime example.

My findings indicate that the number and composition of eggs produced by a mallard hen during the nesting season varies with the quality and accessibility of food resources. Dabbling duck hens are physiologically capable of renesting several times after initial nests are destroyed if high quality foods are available at adequate levels. Pintails, mallards, blue-winged teals, gadwalls, and shovelers are all known to renest (Sowls 1955). Radio-marked mallard hens monitored during the nesting season in south central North Dakota made up to four nesting attempts in a single season (G. L. Krapu, unpublished data). Swanson and Meyer (1977) studied experimental ponds and reported that blue-winged teals laid four and five clutches of eggs when each clutch was removed soon after completion. Because dabbling duck hens mobilize a major part of stored nutrients during initial nesting efforts (G. L. Krapu, unpublished data), access to high quality foods is a particularly important factor governing the magnitude of renesting efforts. Water level management in breeding marshes should include consideration of practices that enhance hen access to those protein- and calcium-rich foods sought during the nesting season, thereby adding to recruitment through increased renesting activity.

Nutrient stress caused by deterioration of wetland habitat conditions or other factors during the breeding season reduces nesting activity in dabbling ducks. Securing adequate nutrients, particularly protein, for laying one or more clutches of eggs requires prolonged feeding bouts as shown by the proportion of the daily time budget devoted to feeding during the laying period by hens of various species of dabbling ducks: gadwalls, 75% (Dwyer 1975), shovelers, 57% (Afton 1977), mallards, 55% (Dwyer et al. 1979), and blue-winged teals, 35% (Miller 1976). Feeding time needed to secure adequate nutrients to lay a clutch of eggs is affected by the quality, density, and size of available foods and level of intraspecific interactions with other pairs and other disturbances that curtail feeding activity. Certain species are more tolerant to crowding than are others and tolerance is affected by food abundance. When adequate nutrients are not acquired despite prolonged feeding efforts, yolk deposition is inhibited, follicles collapse, and yolk material is resorbed from the follicles. Drought is a principal natural phenomenon leading to inhibition of laying and follicular atresia. The effects of drought on reproduction in waterfowl can be severe, as reported in several studies (Salyer 1962, Rogers 1964, Smith 1969), but females are long lived, hence populations are capable of withstanding several years of widespread reproductive failures resulting from adverse climatic conditions. Man-induced changes in the environment that either reduce or contaminate food resources, however, pose a serious, long term threat to reproduction in dabbling ducks.

CONCLUSIONS

Reproduction in dabbling ducks is strongly influenced by the quality and abundance of foods accessible to the female from shallow wetlands. Selection of a diet that is principally animal matter during the laying period provides adequate levels of calcium, total protein, and essential amino acids for egg production. Whereas my data suggest hens producing clutches require invertebrates throughout the nesting season, access is particularly important during renesting when stored nutrient reserves have been depleted. The need for ingestion of animal matter during the nesting period to meet nutritional requirements underscores the key importance of maintaining an adequate base of shallow wetland habitat to sustain the desired populations of breeding dabbling ducks.

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW
Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

BIOENERGETICS OF BREEDING DABBLING DUCKS

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Abstract: A thorough understanding of waterfowl reproduction requires an appreciation for the energy requirements of breeding birds. Recent reviews of avian energetics are used as a starting point for this synthesis of information on the bioenergetics of breeding waterfowl. A major obstacle to our understanding is the inability to measure directly the energy needs of free-living birds. The data available for Anatini in particular, and Anseriformes in general, are incomplete and often inconsistent. Such basic information as basal metabolic rates (BMR) and lower critical temperatures (LCT) has not been satisfactorily established. The present analysis is organized around a FORTRAN model that estimates the daily energy requirement during the breeding season as a summation of increments to BMR, and then calculates and partitions the daily energy intake. Manipulation of program parameters and inputs suggested that egg production and behavior, especially flight, are the most energy demanding activities. Analysis of temperature data from Maine indicated that thermoregulation is a minor energy expenditure for the black duck (*Anas rubripes*) during the breeding season. For female dabbling ducks, the daily energy requirement during egg laying is 3.4 times BMR, whereas the requirement for males peaks at 2 times BMR during prenesting. An analysis of the model indicated that the total daily energy requirement and dry matter intake during the breeding season were most sensitive to estimates of BMR, flight time, energy cost for incubation, and percent fiber in the diet. Values for LCT and for the contribution of specific dynamic effect to the energy cost of thermoregulation are more important for wintering than breeding Anatini. Additional research on the above relationships would further our understanding of the energy requirements of waterfowl. The model suggests four strategies used by temperate and arctic nesting waterfowl to meet net energy requirements for reproduction: (1) reliance on exogenous energy supplemented by a small but important endogenous energy reserve accumulated away from the breeding area (e.g., black duck), (2) reliance on exogenous energy supplemented by a small but important endogenous energy reserve accumulated on the breeding area (e.g., wood duck [*Aix sponsa*]), (3) reliance on a large proportion of endogenous energy reserves accumulated away from the breeding area (e.g., blue goose [*Anser caerulescens*]), or (4) reliance on a large proportion of endogenous energy reserves accumulated on the breeding area (e.g., American eider [*Somateria mollissima*]).

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Every organism interacts with a set of environmental factors that may be physical (e.g., temperature, wind), chemical (e.g., quality of the diet), or biological (e.g., courtship and predation). Life history strategies enable birds to maximize their reproductive effort within this sphere of interaction. Part of the strategy is the allocation of available resources during the reproductive period.

Energy is a common denominator for expressing the requirements and activities of a duck during the reproductive season. The consumption of midge larvae (Chironomidae), territorial defense, egg production, and temperature regulation can each be expressed in terms of calories gained and lost. Energy requirements during the breeding season can be met by exogenous sources such as midge larvae or from endogenous stores in the form of fat and protein.

Krapu (1979) has shown that breeding females have specific nutritional requirements (e.g., increased protein and calcium during the egg laying period), and Swanson et al. (1979) have discussed the manner in which birds adjust their feeding habits and choice of foods to meet these nutritional needs. At the same time, however, ducks must also fulfill their energy requirements, and it is the integration of these needs that this symposium is addressing.

The objectives of this paper are to: (1) review studies related to the bioenergetics of breeding dabbling ducks, (2) discuss current methods and their appropriateness for energy studies, (3) provide a detailed energy partition diagram specific for birds, (4) present a model for calculating energy costs during the breeding season, (5) compare the energy requirements of breeding ducks under alternative sets of model parameters and inputs, (6) identify research needs, and (7) examine management decisions as they relate to energy metabolism.

We owe a debt of gratitude to R. E. Ricklefs (1974) for his synthesis of data and ideas on the energetics of avian reproduction, and to A. N. Moen (1973) for his analytical approach to energy relationships. T. J. Shriner, University of Maine, volunteered many hours of programming expertise. This study was supported by funds from U. S. Fish and Wildlife Service Contract No. 14-16-0008-874 and Hatch Act funds administered through the University of Maine Agricultural Experiment Station; computer time was provided by the University of Maine Computing Center.

LITERATURE REVIEW

Gessaman (1973), King (1973), Ricklefs (1974), and Kendeigh et al. (1977) reviewed the concepts and methodology of avian energetics. Ricklefs' data are drawn from a variety of taxa, and his discussions provide only a starting point for anyone working with a particular taxonomic group. Unfortunately, the data necessary to understand the energy relationships of breeding Anseriformes are not available, and limiting the discussion to dabbling ducks compounds the problem. Nevertheless, interest in the bioenergetics of dabbling ducks is increasing and the available data are reviewed below.

Laboratory data on the energy cost of thermoregulation are available for mallards (*Anas platyrhynchos*) (Hartung 1967, Prange and Schmidt-Neilsen 1970, McEwan and Koelink 1973, Smith and Prince 1973), black ducks (Hartung 1967, Berger et al. 1970, Wooley and Owen 1977), and blue-winged teals (*A. discors*) (Owen 1970). Information on changes in body weight and/or composition has been obtained for mallards (Folk et al. 1966), black ducks (Reinecke 1977), blue-winged teals (Harris 1970), pintails (*A. acuta*) (Krapu 1974a, Calverley and Boag 1977), and gadwalls (*A. strepera*) (Oring 1969). Time budgets for various activities during the reproductive period have been calculated for gadwalls (Dwyer 1974, 1975), blue-winged teals (Miller 1976), and black ducks (Wooley and Owen 1978). Incubation behavior has been described for mallards by Caldwell and Cornwell (1975) and blue-winged teals by Miller (1976). Converting time budgets to energy costs is difficult, and data obtained from other taxa are usually applied. For Anseriforms, the cost of swimming has been measured in mallards (Prange and Schmidt-Neilsen 1970), and Wooley and Owen (1978) have attempted to measure the energy cost of a variety of activities in black ducks.

Composition of the diet during the breeding season is available for mallards (Perret 1962), black ducks (Reinecke 1977), blue-winged teals (Swanson et al. 1974), pintails (Krapu 1974a,b) and gadwalls (Serie and Swanson 1976). Proximate nutrient and energy content of waterfowl foods was documented by Bardwell et al. (1962), Driver et al. (1974), Krapu and Swanson (1975), and Reinecke (1977). Digestibility of commercial diets was determined for mallards by Sugden (1971) and for several dabbling species by Miller (1974). Finally, the nutritional requirements for egg production were studied in mallards (Holm and Scott 1954, Foster 1976) and pintails (Krapu and Swanson 1975).

Thus a variety of dabbling ducks has been studied, but the information on particular species is inadequate to describe the energy requirements during the breeding season. Data from several waterfowl species must be combined with information from other avian groups to estimate an energy budget during the reproductive period.

REVIEW OF METHODS

Indirect calorimetry for measuring oxygen (O_2) consumption and/or carbon dioxide (CO_2) production has been used in the laboratory to determine basal (BMR), standard (SMR), or resting metabolic rates (RMR) (King 1974), lower critical temperatures (LCT), and the cost of thermoregulation. Gas exchange, adjusted for the respiratory quotient (RQ), is converted to energy expended in calories (Depocas and Hart 1957).

Digestion trials have been used to measure nutrient retention and to estimate the cost of thermoregulation, tissue growth, and egg production. Generally the energy content of the feces is subtracted from the energy content of the food without a correction for kidney waste. For digestion trials the energy expended is called existence energy (Kendeigh 1949) and is not directly equivalent to BMR, because the birds are free to feed and exhibit limited activity. Both indirect calorimetry and food consumption can be used in the laboratory to assess the energy cost of a treatment such as low temperature. Unfortunately, in the field a duck's thermal environment is modified by temperature, wind, and radiation simultaneously so that it is very difficult to measure the microclimate affecting a bird (Moen 1973, King 1974, Mahoney 1976). The problem is complex, but probably more significant for dabbling ducks in the winter than during the breeding period.

Two methods have been used to obtain estimates of daily energy expenditures (DEE) for birds in the field. Carbon dioxide production, and O_2 consumption if the RQ is known, can be estimated from the turnover rates of D_2O and $H_2{}^{18}O$ within the body (Mullen 1973). Birds are captured and injected with heavy water, blood samples are taken, and the birds are released. After a specified period the birds are recaptured and blood samples again are withdrawn for analysis. This method has been tested on a variety of species with variable success, but to date no waterfowl have been studied. The drawbacks of the technique are (1) the birds must be recaptured, (2) it is expensive, and (3) one does not obtain data on the cost of specific activities during the experimental period.

Daily energy expenditures also can be estimated from time activity budgets for birds at different times of the year if increments to BMR are assumed for specific activities. It is preferable to observe marked individuals for time activity analysis, and in some instances only telemetry is effective, as in determining activity at night. Limited data on the energy expenditure for specific activities by dabbling ducks suggest that the estimates currently in use (Dwyer 1975) are reasonably accurate (Wooley and Owen 1978).

Important information concerning the energy balance of breeding waterfowl can be obtained by monitoring changes in body weight and carcass composition. Reductions in lipid or protein reserves indicate periods of metabolic stress and measure endogenous energy inputs during reproduction. Although few studies of dabbling ducks have measured variations in carcass composition (Reinecke 1977), work on other waterfowl (Ankney 1974, Korschgen 1977, Drobney 1977) has highlighted the value of this technique.

In summary, several methods have been used under both laboratory and field conditions to determine components of the energy budget of dabbling ducks. Much of the work is fragmented and has involved techniques with varying accuracy and precision. Rigorous statistical evaluation has not been possible in most studies.

Laboratory experiments should be more amenable to statistical treatment, but results from studies of related species have been inconsistent. For example, we used data from a variety of studies to estimate LCT and basal metabolic rates. Unfortunately, the data came from experiments that were designed to measure the influence of other parameters such as the effect of oiling (Hartung 1967, McEwan and Koelink 1973), cost of swimming (Prange and Schmidt-Neilsen 1970), cost of flight (Berger et al. 1970), and heart rate-metabolism relationships (Wooley and Owen 1977). Thus differences in objectives and methods have reduced the value of the data for comparative purposes.

AVIAN ENERGY PARTITION

We found it necessary to modify existing energy partitions to obtain a satisfactory model for interpreting the waterfowl data. Our partition (Fig. 1) was derived from Crampton and Harris (1969:58-59) with three modifications. First, the mixture of renal and intestinal waste products in birds is combined within the fecal energy component. Second, we have identified endogenous energy (tissue and fat catabolism) as an alternate source of net energy, and have indicated a potential pathway for the waste heat from catabolism to be used for thermoregulation. The final modification was a separation of the behavioral energy requirement from the maintenance and productive components because of difficulties in assigning specific activities (e.g., preening, feeding, territorial defense) to either a maintenance or productive function.

THE MODELLING PROGRAM

General Features

The energy partition from Fig. 1 provided the conceptual framework for developing a FORTRAN computer model of anatid energy requirements. At present the modelling program deals only with the breeding pair from the time of arrival on the nesting area to the abandonment of the brood by the female or of the female by the male.

The structure of the program is illustrated in the flow diagram of Fig. 2. Complete details of the program are available on request. The components of the energy partition are also the system state variables of the model. The derivation of each component is explained in a

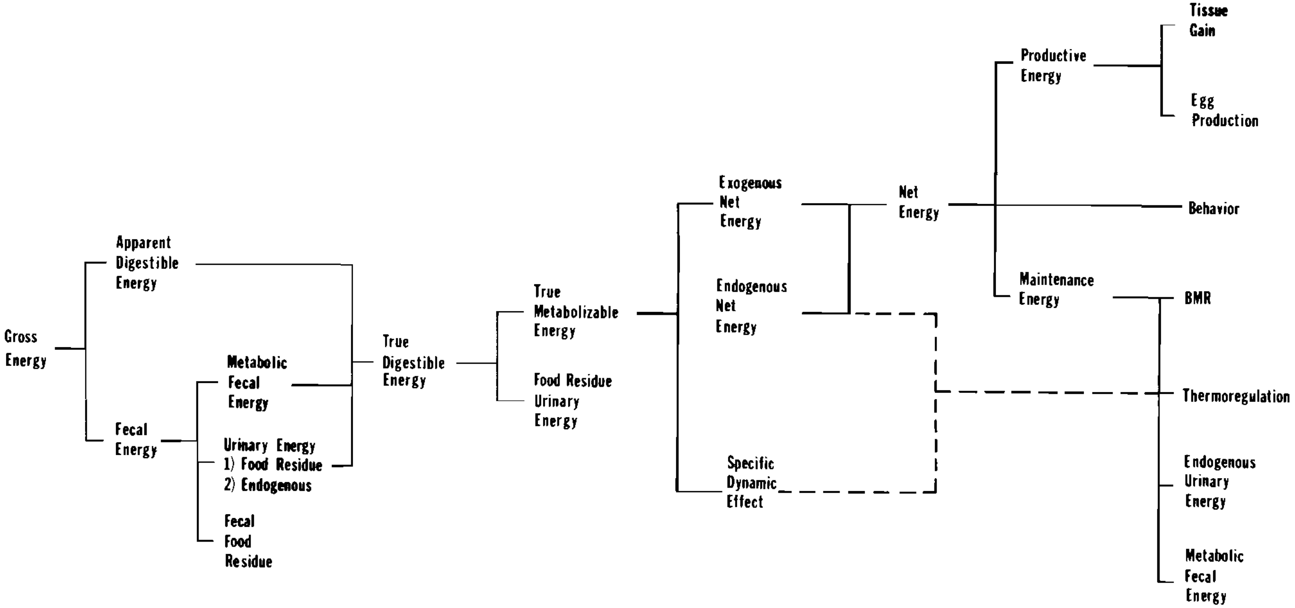

Fig. 1. Avian energy partition modified from Crampton and Harris (1969). The broken lines indicate hypothetical pathways of energy flow.

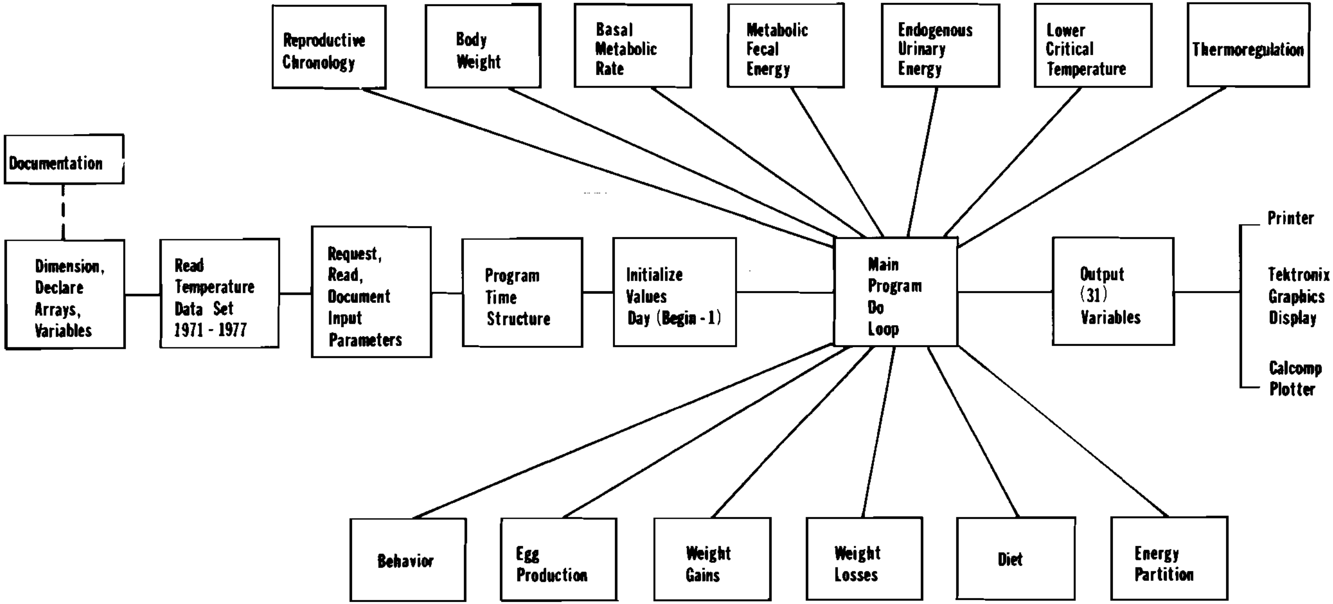

Fig. 2. Flow chart for the computer program modelling the bioenergetics of breeding dabbling ducks.

later section. In its current form the modelling program is strictly deterministic. Program execution requires the input of a temperature data set and 10 variables specifying the size and timing of the reproductive effort; the input variables are summarized in Table 1.

Subroutines TIMING and INTLIZ are called before the main program is entered. TIMING uses the input parameters to develop a time structure for events during the breeding season, including dates for hatching of the clutch, fledging of the juveniles, and molting by the adults. Subroutine INTLIZ provides values for several variables for the day prior to arrival on the nesting area because certain components of the energy partition are functionally dependent upon the daily net energy requirement as well as being terms in the summation used to calculate this value. The program, therefore, must use values from the previous day for these calculations.

The main program is now entered; its primary function is to give access to the 13 subroutines that describe secondary relationships (e.g., body weight) or calculate components of the energy partition. The program terminates with the output of the energy variables to a printer, graphics unit, or electromechanical plotter.

The calculations performed by the modelling program fall in three groups, one dealing with energy requirements, another with energy sources, and a third with the partition of energy intake. The daily net energy requirement is estimated from the maintenance, behavioral, and productive requirements. Once the net energy requirement is known, the contributions from exogenous and endogenous sources can be estimated. Then, the requirement for exogenous energy and estimates of digestive efficiency are combined to derive the gross energy intake that is partitioned as in Fig. 1.

Energy Requirements

The daily net energy requirement, expressed as the sum of the maintenance, behavioral, and productive requirements, was calculated as follows (all units are kcal unless otherwise stated): NRGREQ (DATE) = MAINRG (DATE) + BEHNRG (DATE) + PRONRG (DATE)

Table 1. Input variables required for execution of the modelling program.

Parameter	Interpretation	Value
Specie	Species	1 = Black duck
Agesex	Age and sex	1 = Adult female, 2 = Adult male
Arival	Date of arrival at nesting area	Julian date, i.e., 110
Frsteg	Date first egg laid	Julian date, i.e., 125
Devper	Days required for maturation of a follicle	Approximately 7
Clutch	Clutch size	As desired
Incub	Incubation period in days	23 for black duck
Incost	Energy cost of incubation as increment to BMR	0.0 to desired level
Sdeper	SDE available for thermoregulation	0.0 to 1.0
Unkcst	Energy cost of unknown activity as increment to BMR	0.0 to desired level
Temp 71-77	Daily maximum and minimum temperatures (C) March to July 1971-77	For Orono, ME

The components of maintenance energy are basal metabolic rate, metabolic fecal energy, endogenous urinary energy, and thermoregulation:

MAINRG (DATE) = BMR (DATE) + METFEC (DATE) + ENDUNE (DATE) + HETREG (DATE)

Basal metabolic rate, taken from Wooley and Owen (1977) and others (Hartung 1967, McEwan and Koelink 1973, Smith and Prince 1973), was expressed as:

BMR (DATE) = 75 * Met Body Wt (kg) where Met Body Wt. (kg) = (Body Wt. [kg])$^{0.72}$ Metabolic fecal energy was modelled as a function of body weight, dietary fiber content, and dry matter intake (after Brody 1945:374-397), and was expressed as:

METFEC (DATE) = 0.08 g N * Met Body Wt (kg) * 8.22 kcal/g N Excreted * ([% Dietary Fiber * 100/23.0 + 0.96] + [D.M. Intake (DATE-1) (g)/Maintenance D.M. Intake (DATE-1) (g)])

where N = nitogen, D.M. = dry matter, and maintenance intake = the ratio of maintenance to gross energy intake times dry matter intake. Metabolic fecal energy will increase as dry matter intake increases, and will double with a change in dietary fiber from 0 to 24%.

The endogenous urinary energy estimate was related to the net energy requirement, metabolic body weight, and BMR (Brody 1945:374-397), and was calculated as:

ENDUNE (DATE) = 0.2 g N * 8.22 kcal/g N Excreted * Met Body Wt (kg) * NRGREQ (DATE-1)/BMR (DATE-1)

Thermoregulation was the most difficult component of maintenance energy to model. Ideally the calculation would include (1) seasonal changes in thermal conductance due to molt, (2) variations in body size and thus surface to volume ratio, and (3) differences in plumage conductance among species. Because these data are lacking, we constructed a simplified model that adjusts the lower critical temperature for body size and acclimatization to ambient temperature. The effect of seasonal acclimatization (average temperature previous 14 days) on the lower critical temperature is illustrated in Fig. 3. In our model the adjustment of the lower critical for ambient temperature occurs daily, whereas for the birds this adjustment may be seasonal in relation to feather molts. The effect of body size on lower critical temperature as modelled in the program is shown in Fig. 4. We have assumed that the effects of acclimatization and body size are independent and additive; the lower critical temperature is more sensitive to seasonal acclimatization than to changes in body size. This treatment of lower critical temperatures may not be biologically realistic due to lack of data, but it does adequately represent the available data (McEwan and Koelink 1973, Smith and Prince 1973, Wooley and Owen 1977). Both the illustrations and the modelling program assume that regressions of metabolism on ambient temperature extrapolate to a body temperature of 40 C (see West 1962).

Once the lower critical temperature is established, the number of hours, if any, below the thermoneutral zone is determined by solving for the intersection of the lower critical temperature with a sine curve representing ambient daily temperature (Fig. 5). Daily temperature was modelled with two sine curves having amplitudes equal to the difference between the maximum or minimum and the average temperature, and having a periodicity of one-half the light or dark period. For the time spent below the thermoneutral zone, the effective temperature is defined as the mean of the lower critical and minimum temperatures, and the energy requirement is calculated by solving the equation relating metabolism to temperature (Figs. 3, 4) for metabolic rate at the effective

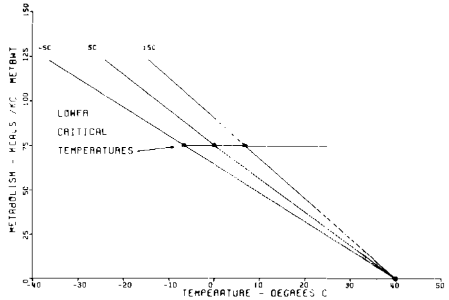

Fig. 3. Effect of temperature of acclimatization (-5, 5, 15 C) on lower critical temperature and metabolic rate of a duck weighing 1 kg.

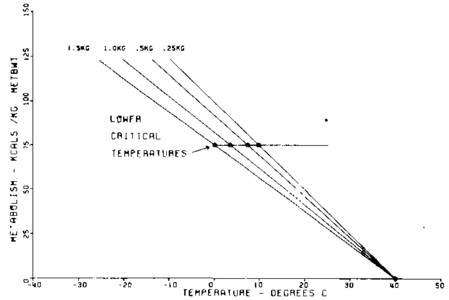

Fig. 4. Effect of body weight (0.25-1.5 kg) on lower critical temperature and metabolic rate for a duck acclimatized to 10 C.

temperature. Finally, the energy increment for thermoregulation is obtained by subtracting BMR from the energy requirement for any time below the lower critical:

HETREG (DATE) = ([75/(Lower Critical Temp [C] - 40)] *Effective Temp - Lower Critical Temp] + 75) * Met Body Wt (kg) * Hours/24.0 - BMR (DATE) * Hours/24.0 - SDEPER * SDENRG (DATE-1) - 0.2 * ENDNRG (DATE-1)

where SDENRG = specific dynamic effect, SDEPER = proportion of SDE available for thermoregulation, and ENDNRG = energy contributed by fat and tissue catabolism.

The productive energy requirement was calculated as the sum of requirements for tissue growth (ovary, oviduct, testis) and egg production:

PRONRG (DATE) = EGCOST (DATE) + TISNRG (DATE)

For estimating the energy increment of egg production, we assumed that the cumulative growth of a follicle is sigmoid and that the energy requirement for each follicle over time is a bell-shaped curve. King (1973:88-92) discussed use of the sine curve as a model for the energy re-

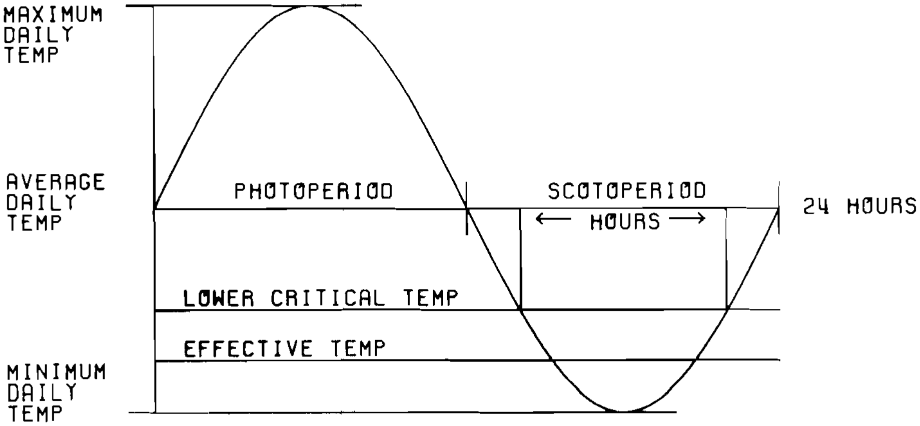

Fig. 5. Use of sine curves as a model for the derivation of the effective temperature and the number of hours spent by a duck below the LCT given the daily maximum and minimum temperatures and photoperiod.

quirement of egg production. As pointed out by Drobney (1977:82), this model does not account for the time difference in yolk and albumen production. The cost of egg production is calculated as the sum of all sine curves representing follicles developing at a given time. In our simulations, the efficiency of egg production (egg energy/metabolizable energy) averaged 73% and was calculated as:

$$\text{EGCOST (DATE)} = \sum_{i=1}^{n} \sin(i)$$

Figures 6 and 7 illustrate the energy requirement for egg production when clutch size is greater and less than the number of days required for follicular maturation. The energy requirement for egg production reaches a plateau when clutch size exceeds developmental period, and the bird can decrease its peak energy requirement for egg production only by reducing its clutch size to less than the developmental period, by producing a smaller egg, or by increasing the laying interval.

Estimates of tissue energy were based on descriptions of testicular, ovarian, and oviductal growth by Johnson (1961), Phillips and van Tienhoven (1962), Drobney (1977), and Calverly and Boag (1977). Nonfat tissue was assumed to have a dry matter content of 25%. Tissue energy was calculated as:

$$\text{TISNRG (DATE)} = 0.25 * \text{Tissue Gain (g)} * 5.65 \text{ kcal/g} + 1.0 * \text{Fat Gain (g)} * 9.45 \text{ kcal/g}$$

where tissue gain is the sum of ovarian, testicular, and oviductal growth.

The energy increment for activity was expressed as a sum of products of the time spent in each activity multiplied by the energetic cost of the activity:

$$\text{BEHNRG} = \text{(DATE)} \sum_{i=1}^{12} \text{Activity (i) (Hours)/24.0} * \text{Cost Activity (i)}$$

where the cost of an activity is expressed as an increment to BMR, and activities 1, . . . , 12) = rest, stand, preen, walk, feed, alert, swim, bathe, chase, unknown, incubate, and fly.

Energy Sources

The daily net energy requirement is satisfied via exogenous and endogenous sources. In the model both fat and structural tissue are considered to be sources of endogenous energy. From 50 to 150 g of fat may be catabolized during the prelaying, laying, and incubation periods (Drobney 1977:59, Reinecke 1977:69). We have assumed a ratio of 1 g per day fat input during prenesting, 2 g during egg laying, and 1 g during incubation; this pattern of weight loss is consistent with

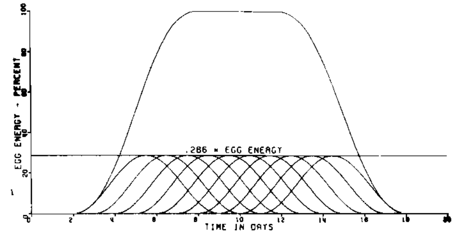

Fig. 6. Percentage of egg energy accumulated in a developing ovary (upper curve) in which the clutch size is greater than the number of days required for the growth of a follicle. Follicular growth was modelled with a sine curve (after King 1973). The maximum daily cost of any individual follicle is 28.6% times the energy content of the egg.

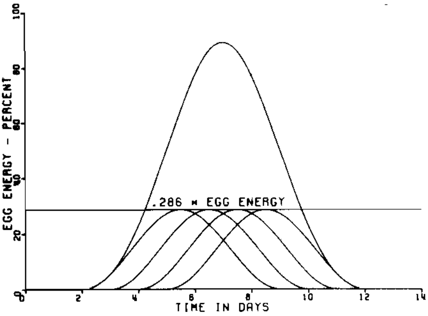

Fig. 7. Percentage of egg energy accumulated in a developing ovary (upper curve) in which the number of days required for the growth of a follicle is greater than the clutch size.

Harris' (1970) data for blue-winged teals. Testicular, ovarian, and oviductal regression were also considered to be sources of endogenous energy. For both fat and tissue catabolism, an efficiency of 80% for conversion to net energy was assumed. Endogenous energy was calculated as:

ENDNRG (DATE) = 0.25 * Tissue Loss (g) * 5.65 kcal/g + 0.8 * Fat Loss (g) * 9.45 kcal/g

Exogenous energy, the portion of the net energy requirement met by dietary intake, was calculated by difference:

EXONRG (DATE) = NRGREQ (DATE) - ENDNRG (DATE)

Energy Partition

The exogenous energy estimate was the basis for calculation of dietary energy intake and its subsequent partition. Metabolizable energy was expressed as the sum of exogenous and specific dynamic effect:

METNRG (DATE) = EXONRG (DATE) + SDENRG (DATE-1)

The sum of metabolizable and food residue urinary energy equalled true digestible energy:

DIGNRG (DATE) = METNRG (DATE) + FRESUE (DATE-1)

Dry matter intake is the digestible energy requirement divided by the digestible energy content per gram of dry matter. In the model digestibility has been adjusted only for the level of dietary crude fiber (see Miller 1974). The equation is:

DINTAK (DATE) = DIGNRG (DATE)/ Digestible energy per g D.M.

where Digestible energy per g D.M. = % Fat * (0.95 - 3.0 * [% Fiber]^2) * 9.45 kcal/g + % Protein * (0.88 - % Fiber) * 5.65 kcal/g + % NFE * (0.96 - 6.0 * [% Fiber]^2)* 4.15 kcal/g

Daily wet matter intake was estimated from dry intake by the equation:

WINTAK (DATE)(g) = DINTAK (DATE) (g)/ % D.M.

The dry matter content of the diet varied with season and with sex of the bird as described in recent literature (Krapu 1974b, Swanson et al. 1974, Serie and Swanson 1976).

Dry matter intake was converted to gross energy with an expression for dietary caloric density, as follows:

GRONRG (DATE) = DINTAK (DATE) (g) * Caloric Density (kcal/g)

where Caloric Density = (% Protein * 5.65 kcal/g) + (% Fat * 9.45 kcal/g) + (% NFE * 4.15 kcal/g) + (% Fiber * 4.15 kcal/g)

Specific dynamic effect was estimated from gross energy intake and dietary composition with data from Ricklefs (1974:168):

SDENRG (DATE) = GRONRG (DATE) * ([% Fat * 0.13] + [% Protein * 0.31] + [% NFE * 0.18])

Food residue urinary energy is related to the difference between dietary protein intake and the current protein requirement. For egg-laying females the model assumes an 18% protein requirement; all other adults require 12% (Scott 1973, Foster 1976). The equation is:

FRESUE (DATE) = (% Dietary Protein - % Protein Required) * DINTAK (DATE) (g) * (8.22 kcal/g N Excreted/6.25 g N/g Protein)

Apparent digestible, urinary, fecal food residue, and fecal energy were all derived from existing variables:

URINRG (DATE) = FRESUE (DATE) + ENDUNE (DATE),
APDNRG (DATE) = DIGNRG (DATE) – METFEC (DATE) – URINRG (DATE),
FECFOD (DATE) = FECNRG (DATE) – METFEC (DATE) – URINRG (DATE),
FECNRG (DATE) = GRONRG (DATE) – APDNRG (DATE)

RESULTS AND DISCUSSION

We completed two types of analyses with the modelling program. In the first we executed the model with what we believe are the best estimates for parameters describing the breeding effort of male and female black ducks. We then manipulated several components of the model to identify those variables to which the daily energy requirement is most sensitive.

Energy Requirements, Sources, and Partition

Several assumptions of the model not discussed above are presented here. For our best estimate of the energy requirements of breeding black ducks, we assumed that (1) the breeding pair arrived on 20 April, (2) the first egg was laid on 5 May, (3) clutch size was 10, (4) incubation required 23 days, (5) the male abandoned the female 10 days into incubation, and (6) the female abandoned the young 5 days before they fledged at 56 days of age. Changes in body weight during nesting can affect the daily energy requirement and the availability of endogenous energy. For our work the annual cycle of body weight for female black ducks was taken from Reinecke (1977:63), and for males from the pattern for mallards described by Dement'ev and Gladkov (1967) (Fig. 8). Endogenous energy inputs were discussed above. Dietary composition varied seasonally, and during egg laying it was approximately 8% fat, 35% protein, 30% NFE, 14% fiber, and 13% ash; dry matter content was 35% (Swanson et al. 1974, Reinecke 1977). Temperature data from 1975 were used, and SDE was not allowed to substitute for any of the energy increment due to thermoregulation. The energetic cost of incubation and unknown activity was subjectively set at 1.5* BMR.

Executing the program with these assumptions generated the output illustrated in Figs. 9-18. The peak energy requirement and dry matter intake (Figs. 9, 10) for females during egg laying were 275 kcal (3.4 * BMR) and 120 g, respectively. Few experimental data are available for comparison. King (1973:94-96) estimated the cost of maintenance plus the production of 1 egg per day at 3.5 times BMR. This did not, however, account for any additional activity asso-

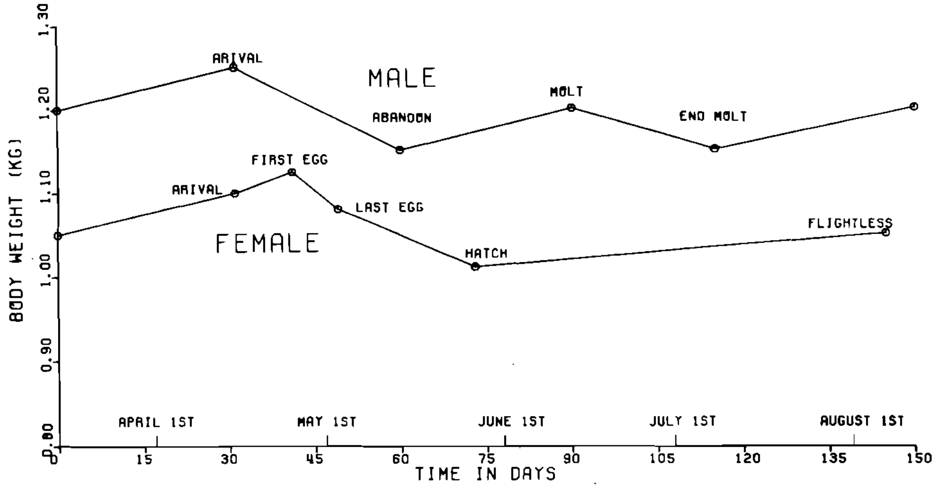

Fig. 8. Annual weight curves for male and female black ducks (after Reinecke 1977, Dement'ev and Gladkov 1967).

ciated with a free existence. In another paper, King (1974:39-40) reviewed estimates of the DEE of free-living birds, most of which were breeding. The majority of the estimates were between 2 and 4 times BMR. Our estimates for dry matter intake are higher than those reported by Foster (1976:40-44) for mallards of comparable size (1,100 g), but his birds were caged and fed a diet containing less than 5% crude fiber.

The energy requirement for males was highest (174 kcal) early in the reproductive season during the period of chasing and increased flight behavior. Maximum dry matter intake (80 g) was only two-thirds that of a female laying eggs, in spite of the larger size of the male.

In Figs. 11-12 the daily net energy requirement is shown as a sum of its components, each of which is further subdivided. The maintenance and behavioral energy requirements fluctuate only slightly, but productive energy increases from zero during prenesting to a value (132 kcal) nearly equal to the sum (143

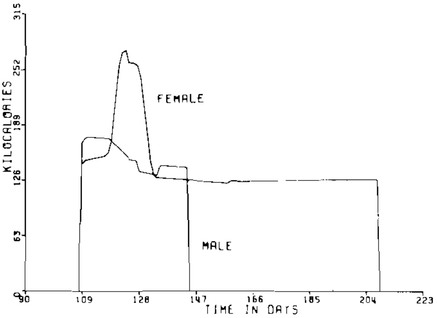

Fig. 9. Total daily energy requirement of a male and female black duck during the breeding season. Time axis is based on Julian calendar (See Table 1).

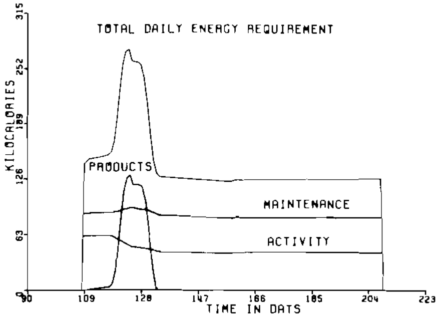

Fig. 11. Partition of the total daily energy requirement of a female black duck during the breeding season. Time axis is based on Julian calendar (See Table 1).

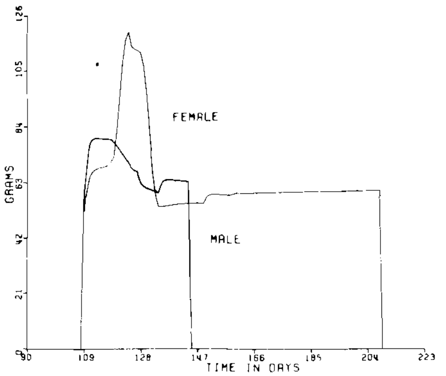

Fig. 10. Dry food intake of a male and female black duck during the breeding season. Time axis is based on Julian calendar (see Table 1).

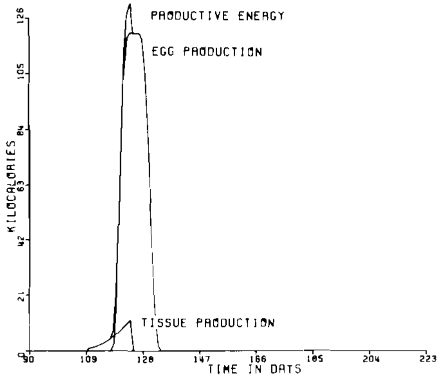

Fig. 12. Partition of the productive energy of a female black duck during the breeding season. Time axis is based on Julian calendar (see Table 1).

kcal) of behavior and maintenance. If the model is realistic, then follicle and oviduct growth causes the peak energy requirement to occur when the first egg is laid (Figs. 11, 12). Behavioral requirements (Fig. 13) are greatest during prenesting when flight activity is high. The energy increment for thermoregulation (Fig. 14) was minimal when we incorporated the 1975 temperature data into the model. We did not consider the effect of wind or solar radiation on the energy cost of thermoregulation, because relevant microclimatic data were unavailable.

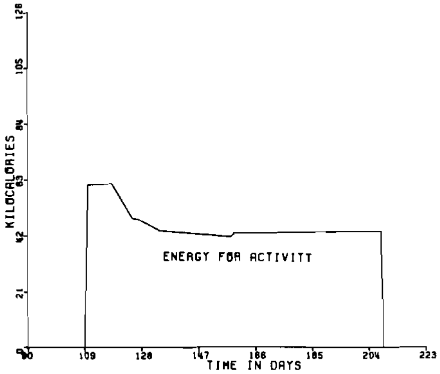

Fig. 13. Energy requirement of a female black duck for activity during the breeding season. Time axis is based on Julian calendar (See Table 1).

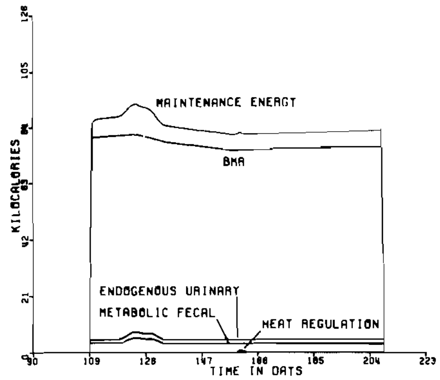

Fig. 14. Partition of the maintenance energy requirement of a female black duck during the breeding season. Time axis is based on Julian calendar (See Table 1).

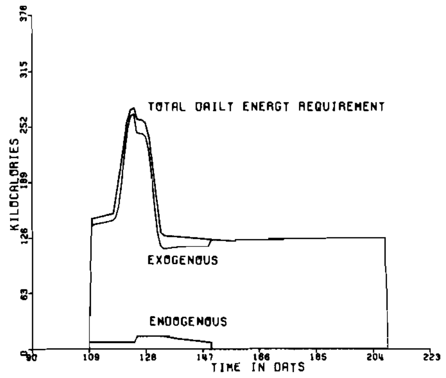

Fig. 15. Relative contributions of exogenous and endogenous energy to the total daily energy requirement of a female black duck during the breeding season. Time axis is based on Julian calendar (See Table 1).

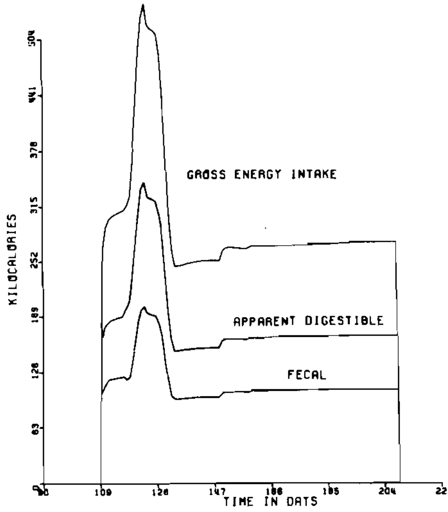

Fig. 16. Partition of the gross energy intake of a female black duck during the breeding season. Time axis is based on Julian calendar (see Table 1).

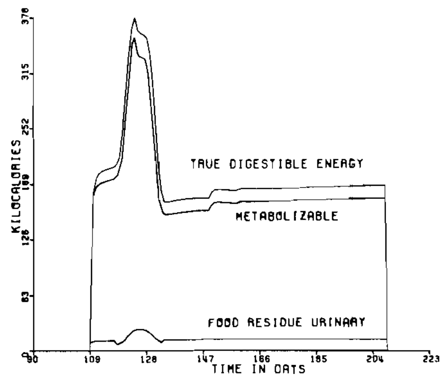

Fig. 17. Partition of the true digestible energy intake of a female black duck during the breeding season. Time axis is based on Julian calendar (See Table 1).

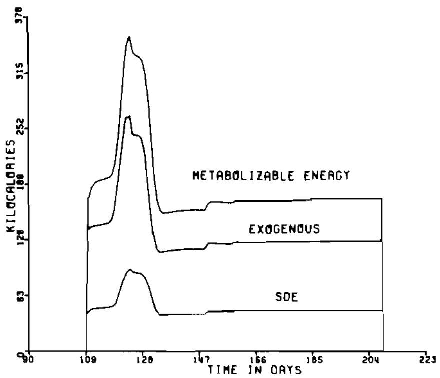

Fig. 18. Partition of the metabolizable energy intake of a female black duck during the breeding season. Time axis is based on Julian calendar (See Table 1).

The relative contributions of endogenous and exogenous energy to the net energy requirement are shown in Fig. 15. With an input of 2 g fat per day during egg laying, endogenous energy was approximately 6% of exogenous. The gross energy intake calculated from the exogenous energy requirement is partitioned in Figs. 16, 17, and 18, which show the magnitude of the inefficiencies associated with digestion and intermediary metabolism. Sugden and Harris (1972), for example, reported that lesser scaups (*Aythya affinis*) metabolized 69% of a commercial ration. In the model metabolizable energy averaged 64% of gross energy for natural diets higher in crude fiber than were commercial preparations

Sensitivity Analyses

In the model, estimates of the daily net energy requirement are dependent on the constant (i.e., 75) used to calculate BMR from metabolic body weight. Although we have chosen 75 as the best estimate for the constant, a wide range of values has been reported (Wooley and Owen 1977, Prince, personal communication). By varying the value of the constant in the model (Table 2), we calculated that an error of 22% in the estimation of BMR (70 versus 90 * Met Body Wt.) would cause an 11 to 12% increase in the energy requirement and dry matter intake. Estimates of energy requirements based on the summation of increments of BMR are therefore sensitive to estimates of

Table 2. Effect of increasing the value of BMR on the daily energy requirement and dry matter intake of female dabbling ducks during laying.

BMR (kcal)	Daily energy requirement		Dry matter intake (g)
	Multiple of BMR	Kcal	
70 * Met Body Wt	3.5	266	116
75 * Met Body Wt	3.4	275	120
80 * Met Body Wt	3.3	283	124
85 * Met Body Wt	3.2	292	128
90 * Met Body Wt	3.1	300	132
100 * Met Body Wt	2.9	317	139

Table 3. Effect of varying the lower critical temperature on thermoregulation and the daily energy requirement of female dabbling ducks during egg laying.

Lower critical temperature (C)	Energy requirement during egg laying (kcal)		Thermoregulation as % of total
	Thermoregulation	Total	
Control	0	2,227	0.0
Control + 2.0	0	2,227	0.0
Control + 4.0	0	2,227	0.0
Control + 6.0	0	2,227	0.0
Control + 10.0	33	2,260	1.5
0.0	0	2,227	0.0
5.0	0	2,227	0.0
10.0	28	2,254	1.2
15.0	88	2,315	3.8
20.0	237	2,465	9.6
25.0	476	2,706	17.6

the metabolic constant.

None of the temperature data sets for spring 1971-77 produced significant energy requirements for thermoregulation. We used the model to simulate a wide range of values for LCT. Relatively large changes in LCT had little effect on the daily energy requirement (Table 3). Incrementing the standard estimate in the model by 10 C caused a 33 - kcal requirement for thermoregulation during the entire laying period. Only at unrealistic LCT values of 20 to 25 C did the requirement for thermoregulation become significant. Despite the insensitivity of the model to changes in LCT during the breeding season, better estimates of LCT are critical for understanding the energetics of wintering waterfowl.

Another aspect of thermoregulation is the potential for heat energy from SDE to offset the cost of exposure to temperatures below LCT (Crampton and Harris 1969). To illustrate this relationship, we varied the availability of SDE from 0 to 80% with LCT at 25 C to generate a significant requirement for heat regulation (Table 4). Even at this elevated LCT the cost of thermoregulation was eliminated with inputs of SDE at 40 to 60%. Kendeigh et al. (1977:146-147) suggested that 100% of SDE may be available for thermoregulation. The availability of SDE may be of little importance to breeding birds but could be highly significant during winter.

The response of the energy requirement to variations in the cost and duration of incubation, unknown, and flight activity was simulated with the model.

Table 4. Effect of increasing the availability of SDE for thermoregulation on daily energy requirements of female dabbling ducks during the entire egg laying period. Lower critical temperature is held at 25 C.

Availability of SDE (%)	Energy requirement			Thermoregulation as % of total
	Thermoregulation (kcal)	Total (kcal)	Multiple of BMR	
0	476	2,706	4.0	17.6
20	291	2,515	3.7	11.6
40	132	2,355	3.5	5.6
60	11	2,235	3.4	0.4
80	0	2,224	3.4	0.0

Table 5. Effect of increasing the energetic cost of flight activity on the daily energy requirement and dry matter intake of female dabbling ducks during prelaying.

Cost of flying (kcal)	Daily energy requirement		Dry matter intake (g)
	Multiple of BMR	Kcal	
8.0 * BMR	1.8	146	66
12.5 * BMR	1.9	150	68
15.0 * BMR	1.9	155	70

Given the amount (15) min) of flight activity per day programmed for the prelaying period, the energy requirement is not very responsive to large changes in the energetic cost of flight (Table 5). However, as flight time was increased from 0.5 to 1.5 h, the energy requirement rose 10 to 20% (Table 6). In the future, modelling may provide a means of relating disturbance, flight activity, energy requirements, feeding time, and rates of energy intake.

Table 6. Effect of increased flight and decreased feeding time on the daily energy requirement of female dabbling ducks during egg laying.

Flight time (h)	Daily energy requirement	
	Multiple of BMR	Kcal
Control	3.4	275
Control + 0.5	3.6	293
Control + 1.0	3.8	311
Control + 1.5	4.0	330

Changing the energetic cost of nightly unknown activity from 1.3 BMR (resting) to 1.7 BMR (feeding) resulted in a 3% increase in dry matter intake (Table 7). The analyses suggest that values for unknown activity currently used for extrapolating from time activity studies to energy budgets are valid.

The existence of an energy requirement for incubation that exceeds normal heat loss is a controversial topic (King 1973, Ricklefs 1974). The data in Table 8 show the effect of varying the cost of incubation from 1.2 to 2.1 BMR. We obtained the latter value by assuming that the clutch of eggs requires as much heat as a bird of similar weight, but with a somewhat lower body temperature. Energy requirements and dry matter intake increased sharply (43%) across this range of values. Field data on the weight losses (Harris 1970) and restricted foraging time available to incubating females (Miller 1976, Caldwell and Cornwell 1975) are more consistent with the lower estimates. Korschgen (personnel communication) believes that incubating female eiders function at a

Table 7. Effect of increasing the energetic cost of unknown activity on the daily energy requirement and dry matter intake of female dabbling ducks during egg laying.

Cost of unknown activity (kcal)	Daily energy requirement		Dry matter intake (g)
	Multiple of BMR	Kcal	
1.3 * BMR	3.3	270	118
1.5 * BMR	3.4	275	120
1.7 * BMR	3.4	280	122

Table 8. Effect of increasing energetic cost of incubation on the daily energy requirement and dry matter intake of female dabbling ducks.

Cost of incubation	Daily energy requirement		Dry matter intake (g)
	Multiple of BMR	Kcal	
1.2 * BMR	1.3	103	44
1.5 * BMR	1.6	125	55
1.8 * BMR	1.9	147	66
2.1 * BMR	2.2	173	77

level just above BMR. A reduction in BMR is known to occur in fasting geese (Benedict and Lee 1937); the relationship of fasting to metabolic rates in incubating waterfowl should be investigated in the field.

The potential contribution of endogenous energy to the daily energy requirement is illustrated in Table 9. Given the assumptions of the model, endogenous energy provides 3% of the requirement during laying. At a level 4 times higher, endogenous sources account for 11% of the daily requirement during egg production. Carcass analysis of female wood ducks (Drobney 1977) has shown that the input of this amount of fat (8 g/day) is realistic. Calverley and Boag (1977) proposed that loss of endogenous energy stores may reduce the clutch size of displaced prairie pintails attempting to breed in the arctic.

Table 9. Effect of increasing endogenous energy on exogenous energy requirement and dry matter intake during egg laying of female dabbling ducks. Control endogenous input was 50 g fat.

Endogenous energy (kcal)	Daily energy requirement (kcal)	Exogenous energy (kcal)	Dry matter intake (g)
Control	275	267	120
Control * 2	275	259	116
Control * 3	274	252	113
Control * 4	274	244	109
Control * 5	274	236	106

The influence of dietary fiber on energy intake is shown in Table 10. The model predicted a 29% increase in dry matter and energy intake in response to a 10% change in crude fiber. Female dabbling ducks that use invertebrate foods during the laying period not only obtain elevated protein levels, but also greatly reduce their dry matter intake.

Energy Metabolism and Reproductive Strategy

On the basis of recent field studies and our simulation analyses, we propose that

Table 10. Effect of varying crude fiber and NFE levels on gross energy and dry matter intake by female dabbling ducks during egg laying.

% Crude fiber	% NFE	Energy requirement as multiple of BMR	Gross energy intake (kcal)	Dry matter intake (g)
9	37	3.4	468	103
11	35	3.4	495	109
12	34	3.4	510	112
13	33	3.4	527	116
14	32	3.4	545	120
19	27	3.4	658	145

temperate and arctic nesting waterfowl have evolved four identifiable strategies for using endogenous and exogenous sources to meet net energy requirements during reproduction. These strategies are (1) reliance on exogenous energy supplemented by a small but important endogenous energy reserve accumulated away from the breeding area, (2) reliance on exogenous energy supplemented by a small but important endogenous energy reserve accumulated on the breeding area, (3) reliance primarily on endogenous energy reserves accumulated away from the breeding area, and (4) reliance primarily on endogenous energy reserves accumulated on the breeding area. We do not intend that all species be placed in one of the categories, but rather suggest that certain points within a continuum can be illustrated.

The simulation analyses indicate that dabbling ducks obtain most of their daily requirement as exogenous energy, whereas endogenous inputs provide a lesser but highly significant energy source that may vary from 6 to 28% of exogenous energy. The data for female pintails (Krapu 1974a) and black ducks (Reinecke 1977) indicate that peak lipid levels occur at the time of arrival in early nesting species. These females probably store nutrient reserves while occupying migrational or wintering habitats.

A second strategy for birds using primarily exogenous energy is the attainment of reserves after arrival at the breeding area. Weight and condition index data (Harris 1970) for blue-winged teals indicate that late nesting may be related to this strategy. Drobney's work (1977) with wood ducks illustrates weight and lipid increases in females that accumulate nutrient reserves after arrival on the breeding ground.

Korschgen's (1977) research on the breeding biology of American eiders nesting on the Maine coast showed that the females are dependent almost entirely upon endogenous fat and protein reserves once laying has begun. Energy stores are obtained by the eiders during a period of hyperphagia in the vicinity of the nesting areas. The arctic nesting blue geese studied by Ankney (1974) illustrate an alternative endogenous energy strategy. Female blue geese feed little before the incubation period and depend like the eider upon nutrient reserves. Unlike the eiders, however, blue geese deposit reserves prior to reaching the nesting area.

Among the selective pressures favoring endogenous energy strategies in the eider and blue goose are the short, harsh breeding season of the goose and the nest predation (Bourget 1973) faced by the eider. For dabbling species, the deposition of lipids prior to egg laying will not affect the net energy requirement during egg production, but may be critical in reducing the exogenous energy requirement to a level within the foraging capabilities of the birds.

Because of data limitations the model has not been used to investigate factors affecting clutch or egg size. In the future, we believe that modelling efforts that incorporate data on body weights, energy content of eggs, and nest predation rates for additional species may offer insight into factors affecting clutch size.

RESEARCH NEEDS

We have shown that the value of several parameters in the model can significantly affect the energy requirements of breeding ducks. Research needs listed below outline studies that could obtain some of the needed data:

1. BMR as a function of metabolic body weight. Current estimates range from 70 to as high as 100. Indirect calorimetry can provide more precise estimates and also measure seasonal variation.

2. Energy requirements for incubation. An opportunity exists with ducks nesting

in cavities or other structures to monitor O_2 consumption by indirect calorimetry. Also, late in the incubation period the heavy water technique could be used. It would be especially interesting to know if BMR drops during the incubation period as Benedict and Lee (1937) have suggested for fasting geese.

3. Time activity analyses. There is a need to measure the activity patterns of females during the reproductive season. Emphasis should be placed on time in flight, because this is the most energy demanding activity. If possible, the impact of increased disturbance to the nesting pair should be evaluated. Also, combining estimates of feeding time and dry matter intake values provided here could allow calculation of estimated rates of resource exploitation.

4. Food digestibility. Detailed studies on food habits should provide an estimate of the proximate analysis of the composite diet to facilitate application in modelling efforts. Artificial diets could then be prepared having the same nutrient and energy content so that the effect of changes in levels of fiber and protein, e.g., could be assessed.

5. Carcass condition. Additional work needs to be done on measuring the levels of carcass fat and protein in reproducing ducks. Nutrient reserves may influence reproductive strategies, including time of laying, clutch size, and ability to renest.

The model is sensitive to parameters that may be especially important during winter:

1. LCT. Although energy costs for thermoregulation are small during the reproductive period, they may be very important in winter. The estimate of the LCT determines the amount of this cost. Few data are available on the relationship of LCT to body size or seasonal acclimatization.

2. SDE. The degree to which SDE can meet the energy requirements of thermoregulation is unknown. Theoretically SDE could reduce these energy costs significantly during critical winter months.

3. Carcass condition. Limited data (Reinecke 1977) suggest that the body weights and energy reserves of young birds are lower than those of adults in severe winter weather. This could influence survivorship rates and physiological condition the following spring.

MANAGEMENT CONSIDERATIONS

The amount of time spent in flight can increase a duck's DEE significantly. In addition, as flight time increases, time available for feeding decreases, reducing the bird's energy intake. Spring trapping, fishing, and the rapid growth of canoeing in the Northeast can cause disturbance to pairs. Isolation is important during this period, and thought should be given to restricting access to major breeding areas until incubation is under way.

Unless our estimates of BMR and LCT are unrealistic, temperature in the spring causes little need for thermoregulation. Instead, temperature affects the phenology of nesting indirectly by regulating ice cover, food availability, and the opportunity for pairs to disperse.

The model has provided good estimates of total daily food requirements and should help us to place other aspects of territory such as the requirements for spacing and isolation in better perspective.

Severe winter conditions can affect the physiological condition of the ducks and may influence endogenous energy stores necessary for early reproduction and large clutch size. In Maine, critical black duck winter feeding areas are kept open by tidal amplitude and current (Hartman 1963). These sites should be identified and protected.

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW
Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

INDIVIDUAL VARIATION AND THE ANALYSIS OF MALLARD POPULATIONS

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Abstract: Scientists interested in social behavior have long recognized the importance of in-depth analysis of individual animals as a technique for exposing underlying population mechanisms. This paper presents evidence that illustrates the importance of applying the same study procedure to gain an understanding of mechanisms that affect population parameters of waterfowl, and that are of interest to waterfowl managers. I studied captive mallards (*Anas platyrhynchos*) and found that laying dates, clutch size, and egg size showed considerable variation among individuals but showed marked consistency within individuals. These results help explain many of the problems inherent in breeding population inventory. The three variables were not significantly different between yearlings and older birds. I hypothesize that, in many species, the measured effects of age on productivity are a consequence of inexperience rather than the breeding strategy. Clutch size, laying date, and renesting potential are not independent variables, although they are often treated as such.

Ecologists have devoted considerable attention to devising methods of trapping and identifying individual animals under study. In most analyses, data on individuals have been used as single measurements in a sample, the characteristics of which lead to inferences on the nature of the population. The goal is to obtain enough measurements to calculate statistical variance terms. This allows a statement about the confidence that the investigator places on his deductions about the population.

More sophistication is achieved when data are obtained on individuals that represent different segments or cohorts of populations. This method has been used in waterfowl research to study the effects of age on reproductive potential (e.g., Trauger 1971, Cooper 1978), renesting potential (e.g., Humburg et al. 1978), population turnover (e.g., Humburg et al. 1978), the effect of restocking with hand-reared waterfowl (e.g., Sellers 1973, Lee and Kruse 1973), migrational homing (e.g. Poston 1974), habitat use and home-range analysis (e.g., Gilmer et al, 1975), and continental and regional characteristics of migration and mortality (e.g., Anderson and Burnham 1976).

Recently, with the expansion of research dealing with adaptive strategies, intensive, long-term observations of individuals have provided clues to why animals respond as they do in various social and environmental contexts. Modern evolutionary theory considers that natural selection occurs at the level of individuals with subsequent effects on the population gene pool (Williams 1966). Significant advances are being made with waterfowl in the area of ecoethology which attempts to integrate ecology, evolution, behavior, morphology, and physiology (McKinney 1973). Future management should benefit greatly from the products of this approach to waterfowl research.

Individual variation is often seen as a nuisance, particularly when it is great. Knowledge of the distribution of variation in certain reproductive characteristics of mallard populations may contribute to more realistic design and interpretation of surveys. This study, conducted under the controlled conditions of captivity, also allows interpretation of the effects of age on waterfowl reproduction. Some of these results have been presented in two other papers (Batt and Prince 1978, 1979). The purpose here is to expand the discussion on certain points and to identify some possibly important considerations for management.

The research was funded by the Ducks Unlimited Foundation and the North American Wildlife Foundation through the Delta Waterfowl Research Station, and by the Michigan State Agricultural Experiment Station. H. Prince, D. Beaver, and W. Conley aided with earlier interpretations of the data. C. Savage and D. Jelinski provided valuable technical assistance.

METHODS

The methods used in this study were described in detail in Batt (1976) and in Batt and Prince (1978, 1979). Basically, I collected initiation date, clutch size, and egg weight data for approximately 80 individual pairs of penned mallards. These were held under standard procedures (Ward and Batt 1972) at the Delta Waterfowl Research Station during 1973, 1974, and 1975. The same pairs were held together for the 3 years of the study. This allowed an examination of the consistency of breeding dates and clutch sizes of individual pairs.

In 1973, 22 pairs of yearlings were compared to 20 pairs of adult breeders (older than 1 year). Six reproductive parameters were compared between the adult and the first year breeders. These were: day first egg laid, day last egg laid, size of first clutch, number of eggs per hen, total number of nesting attempts per hen, and mean egg weight. Unless otherwise stated, comparisons between groups are by one-way analyses of variance (Sokal and Rohlf 1969).

RESULTS

Detailed results were presented in Batt and Prince (1978, 1979). No statistically significant differences were detected among the six parameters compared between the two age groups in 1973. The non-significant age effects allowed pooling of all data for further analyses.

First nest initiation dates varied markedly between individual pairs during the 3 years of the study. There were 58, 50, and 43 days between nest initiation by the earliest and latest pairs in 1973, 1974, and 1975, respectively. There was a significant ($P<0.05$) difference among individual female laying dates for the 3 years but each hen tended to lay near the same date each year. The repeatability (Becker 1975:23) of laying date was calculated to be 0.57 - 0.07 (SE; N of hens = 60). Thus there was marked variation within the sample but considerable consistency by individual females.

Clutch size declined significantly ($P<0.01$) between successive nesting at-

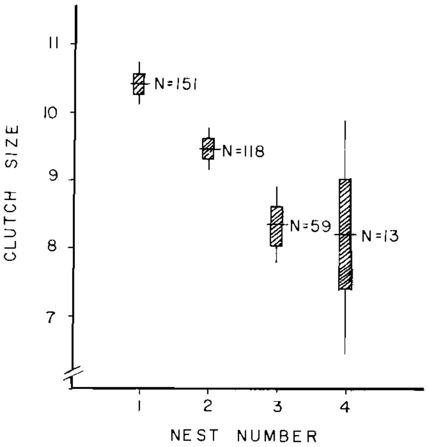

Fig. 1. Clutch size decline between first nests and renests by a captive flock of breeding mallards. Plotted are means, standard errors, and ranges.

tempts. Clutch size was 10.4 ± 0.2 ($\bar{X}$ ± SE; N = 151), 9.5 ± 0.2 (116), 8.4 ± 0.3 (59), and 8.2 ± 0.8 (13) from the first through the fourth nest, respectively (Fig. 1). Analysis of first clutch size and of mean egg weight showed significant ($P<0.01$) differences among individual females but not among years. Repeatability of first clutch size was calculated to be 0.54 ± 0.07 (N of hens = 30).

The clutch size and laying date data were submitted to regression analysis for each of the first three nests for each year of the study. Significant regressions were calculated for the first nest for each year, for the 1974 second nests, and for the 1973 third nests (Table 1). Second nests in 1973 and 1975 and third nests in 1974 and 1975 did not yield significant regression equations. The trend in these data illustrates a decline in number of eggs within and between each successive nest in relation to the time of year that initiation occurred.

All nests for all 3 years' data were combined and submitted to a further regression analysis. The best fit of the data was a curvilinear relationship between initiation date and clutch size (Fig. 3, Batt and Prince 1979).

DISCUSSION

I assumed that all the necessary resources for breeding were provided for the birds in this study, i.e., a mate, space, food, water, and a nest site. The birds were not required to compete for any resources, and inexperience was assumed not to be a factor in the simplified environment of the study. Therefore, the

Table 1. Regression equations for clutch size (Y) and time (X)[a] for the first three nests by individual female mallards in 1973, 1974, and 1975.

Nest sequence	Year	Equation	n	r^2	Significance of r
First	1973	$Y = 22.76 - 0.10X$[b]	45	0.39	0.001
	1974	$Y = 21.76 - 0.09X$	52	0.21	0.001
	1975	$Y = 20.89 - 0.08X$	49	0.12	0.001
Second	1973	$Y = 15.93 - 0.04X$	32	0.08	ns[c]
	1974	$Y = 24.94 - 0.10X$	54	0.20	0.01
	1975	$Y = 9.29 + 0.00X$	37	0.00	ns
Third	1973	$Y = 20.79 - 0.07X$	13	0.36	0.001
	1974	$Y = 17.76 - 0.06X$	31	0.04	ns
	1975	$Y = 4.89 + 0.02X$	20	0.05	ns

[a] Time is in days.

[b] The large-Y-intercept values result from using Julian calendar days.

[c] Not significant.

results probably closely reflected the birds' maximum reproductive capabilities in the captive environment.

Several inferences about the characteristics of wild populations can be made from the data. The lack of significant age-related effects is inconsistent with field data recorded for most species of ducks. Young birds nest later than adults in the ringed-necked duck (*Aythya collaris*) (Mendall 1958), gadwall (*Anas strepera*) (Gates 1962), wood duck (*Aix sponsa*) (Bellrose et al. 1964, Grice and Rogers 1965), blue-winged teal (*Anas discors*) (Dane 1966), black duck (*A. rubripes*) (Coulter and Miller 1968), mallard (Coulter and Miller 1968), and hooded merganser (*Mergus cucullatus*) (Morse et al. 1969). Smaller clutches by yearling breeders have been recorded in the black duck (Stotts and Davis 1960), blue-winged teal (Dane 1966), ring-necked duck (Coulter and Miller 1968), and hooded merganser (Morse et al. 1969). Further, a lower degree of renesting has been recorded for the yearling gadwall (Gates 1962), wood duck (Grice and Rogers 1965), and black duck and mallard (Coulter and Miller 1968). Age-related effects in the field have been little studied in the mallard. However, Dzubin (1969a:152) speculated that young birds may, in general, be less successful than older birds. Bellrose (1976:236) accepted this idea and stated that mallards breed late or not at all in their first year. He believed that during drought years a large proportion of non-breeders are yearlings. These assumptions are not yet substantiated for mallards with data from the field.

Delayed breeding and smaller clutches by yearling waterfowl are often assumed to reflect a reproductive strategy in which some ultimate benefit is gained by those genotypes that follow the typical pattern. I suggest that, in most cases, the lower reproductive potential shown by first-time breeders is a consequence of inexperience rather than a strategy per se. This inexperience seems inevitable since: 1) most yearlings are less than 10 months old and have never been in a breeding marsh in spring, and 2) they must compete with older, more experienced birds.

Young produced in late mallard nests may have several other disadvantages: they may be produced past the peak quality of their brood-rearing habitat and, as a result, have lower fledging success; they have been fledged for a short period of time in early fall and might be less well-equipped to sustain fall migration; and survivors to the subsequent breeding season will be the youngest birds in the population and thereby all age-related effects will be compounded in them.

Under ideal conditions, such as those approached in the captive environment of this study, yearlings were as productive as were older birds. Data from other species suggest that this does not happen in the wild. The most exciting challenge for research is not only to demonstrate age-related effects in the wild, but to identify how birds of different ages react under various habitat conditions and various population densities. Location on the breeding range should also be considered (Calverly and Boag 1977, Batt and Prince 1978).

Many studies have shown that renest clutches have fewer eggs than first nests, and Johnsgard (1973) provided a number of explanations for this phenomenon. However, the relationship that I found of declining clutch size with time, regardless of clutch number, suggests that in the mallard, time alone may be the main factor that correlates with clutch size. This relationship must be tested in the wild where other factors also operate. Population modelers should be interested in this result, because the simple functional relationship with time is easily incorporated into simulation models. Mean clutch size has a direct effect on recruitment rates, which are determinants of population management strategies.

The clutch size-time relationship also has implications for the analysis of age-related reproductive potential. If young birds are forced to nest later because of inexperience with the breeding environment, then we would predict a lower clutch size. Nesting later also allows less time for renesting. Thus, we would expect renesting to occur less in yearling birds. There is a tendency to consider clutch size, initiation date, and renesting potential as three independent parameters for comparison between yearlings and older birds. But my results illustrate that they are probably not. Again, reproductive output appears to be most related to seasonal chronology.

Dzubin (1969b) showed the difficulty of ascribing a given pair of ducks to a particular reproductive status. Problems arise because in the same breeding marsh there may be: 1) breeding resident pairs, 2) prebreeding residents, 3) prebreeding transients, 4) renesting residents, 5) pairs displaced by spacing, or 6) nonbreeders. Smith and Hawkins (1948) speculated that complete turnover of the breeding population of a pond would occur 3 times in a given 6-week season if each pair used a territory for only 2 weeks.

My data suggest that variation in nesting dates by individual pairs accounts for much of the variation observed in the field. Humburg et al. (1978) observed several marked pairs of mallards that were resident and delayed breeding for several weeks past initiation by most pairs. Such studies need to be done in other parts of the continental breeding range to refine current survey techniques.

The wide span of nesting dates and clutch size, along with the consistency demonstrated by individual pairs, indicate the existence of considerable genetic variation in wild mallard populations. This is characteristic of every natural animal population that has been thoroughly studied (Mayr 1963:129). The main cause is that natural environments are variable in time and space and the fitness values of gene complexes are therefore themselves variable. Ankney and Bisset (1976) provided a similar hypothesis on how a wide range of egg weight genotypes survives in the lesser snow goose (*Chen caerulescens*) due to annual variations in the optimum date for young goslings to hatch.

Weather (e.g., Lynch 1964), amongst many other environmental characteristics, varies widely throughout the mallard nesting range and presumably maintains much variation in the gene pool for timing of nest initiation. Historically, optimum nest initiation date probably fluctuated each year relative to earliness or lateness of the transition from winter to spring. At the present time, on the prairies of Western Canada, biologists generally accept the idea that virtually all early mallard nests are lost to agriculture. A large portion of the annual production thus comes from late first nests or from renests, both of which have a lower recruitment potential. Modern cereal crop farming practices limit suitable nesting cover, mechanically destroy early nests, and increase predation on nests and on the nesting hens themselves (Johnson and Sargeant 1977).

In the present mallard nesting environment there may now be selection against early nesters as early nesting hens contribute less to the gene pool. The wide range of individual variation evident in mallards provides a gene pool potentially responsive to directional selection. Although not common, massive shifts in gene frequencies have been recorded in wild populations of several other animals (Mayr 1963:145). The best known case is that of industrial melanism in the Lepidoptera (Kettlewell 1961). A similar shift in significant characteristics in the gene pool is implied in the pink salmon (*Oncorhynchus gorbuscha*) and the Canada goose (*Branta canadensis*), although these cases are somewhat confounded by other factors such as learning and tradition. Early salmon runs were markedly reduced as a result of greater harvest pressure, but later runs thrived under season closures actually intended to preserve the whole stock (Vaughan 1947). Raveling (1978) concluded that extermination of certain Canada goose flocks was the result of over-harvest while other flocks thrived under protection. That the apparent selection against early nesters could change the genetic composition of the continental mallard population is speculation. However, management and research should be aware of this possibility, because a changing recruitment potential would have important implications for management.

CONCLUSION

Waterfowl biologists are primarily concerned with population responses that result from management activities. An understanding of the cause-and-effect relationships of these responses cannot necessarily be gained by analysis at the population level. Population parameters are the measured responses of a sample of individuals, each of which has a unique complement of characteristics from the gene pool. An understanding of the needs and strategies of individuals should be a central focus for research on managed wildlife populations.

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WATERFOWL AND WETLANDS — AN INTEGRATED REVIEW
Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

BIOENERGETICS OF POSTBREEDING DABBLING DUCKS[1]

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Abstract: The postbreeding activities of dabbling ducks are evaluated in terms of energy and time allocation. Although limited data are available for the postbreeding period, the allometric relationship between body weight and basal metabolic rate (BMR) can serve as a basis for understanding energy metabolism. Laboratory estimates of the BMR of mallards (*Anas platyrhynchos*) and increments for maintenance, activity, thermoregulation, and free-living conditions are presented. It is proposed that seasonal variation in energy consumption is relatively stable and amounts to 3x to 4x BMR. Stability is achieved during periods of increased energetic demands by behavioral modifications that result in the conservation of energy. Use-days based on estimated energy expenditures and amounts of available food can be calculated to estimate the carrying capacity of specific areas for dabbling ducks.

Postbreeding activities for North American waterfowl species belonging to the Tribes Cairinini and Anatini are similar. Hochbaum (1944) outlined the major events during this period at the Delta Marsh in Manitoba. Although the activities of all species are not as well understood as those during the breeding period, we know that all species undergo the prebasic molt prior to fall migration and wintering. Males of most species perform a molt migration while females that successfully nest usually stay on the breeding areas with the ducklings (Salomonsen 1968, Gilmer et al. 1977). Unsuccessful females may accompany the drakes to molting areas (Gilmer et al. 1977). The molt migration has been described as a movement from the breeding place to a special molting area that is common to a large number of birds. Hochbaum (1944) described the molting areas of dabbling ducks in Manitoba as large, permanent marshes.

Salomonsen (1968) pointed out that the selective advantage of the molt migration could be the reduction in competition for food between adult males and/or nonbreeders, and the female and ducklings. In North America postbreed-

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[1] Michigan Agricultural Experiment Station Journal Article Number 9102.

ing activities have been described by Wetmore (1921), Munro (1943), Hochbaum (1944, 1955), Sowls (1955), Oring (1964), Grice and Rogers (1965), Coulter and Miller (1968), Bellrose (1976), and Gilmer et al. (1977).

The change in waterfowl behavior from the widely spaced breeding birds to the gregarious molting, migrating, and wintering groups marks a change in the factors that affect survival and fitness. This has been recognized by hunters and waterfowl managers, and techniques to provide food as an attractant are commonly practiced throughout North America. Although techniques to attract postbreeding migrant and wintering birds are successful, the specific needs of each species are not well understood. An analysis of both time and energy allocation is needed to understand the requirements of the postbreeding stages of the life cycle. This is necessary to evaluate the true impact of management recommendations and practices on dabbling ducks. This paper will review the energy conserving and energy demanding processes of energy expenditure for postbreeding dabbling ducks.

ENERGY BUDGETS

Methods

The goal in the analysis of energy expenditures is to estimate the cost of various metabolic activities in free-living birds. King (1974) reviewed the methods that have been used to estimate energy expenditures including laboratory measurements of oxygen consumption, metabolizable energy intake (ME), and time-energy analyses of free-living birds. Energy expenditures of free-living birds can be calculated directly by quantifying their activities in caloric terms or by using indirect measures such as body weights or analysis of crop contents. All of these methods require untested assumptions concerning their relationship to the energetic costs of a free-living bird. Although all these methods can provide useful data, thermal and behavioral models such as the one presented by Owen and Reinecke (1979) in this symposium must be developed before a more rigorous understanding can be achieved.

Basal Metabolic Rate

The metabolic rate of an animal in a thermoneutral zone, at rest, and in a postabsorptive state has been defined as the basal metabolic rate (BMR) (King 1974). King (1974) pointed out that standard metabolic rate (SMR) was originally synonymous with BMR, but has since been confused with fasting metabolic rate (FMR) and resting metabolic rate (RMR). He concludes that BMR is the only measure that has retained a clear definition. BMR is strongly weight-dependent, and can be expressed by the equation:

$$M = aW^b$$

where M is a metabolic parameter, a is a constant, W is body weight, and b is an exponent. This relationship has been further refined by Aschoff and Pohl (1970), who reported that the metabolism of fasted birds in a darkened respiratory chamber has a measurable diurnal rhythm. The metabolic rate during the activity phase of the cycle was about 25% higher than during the resting phase. They proposed that the equation expressing the relationship between body weight and metabolic rate should be computed separately for the rest and activity phases of the diurnal cycle. King (1974) calculated an equation for nonpasserines at rest based on Aschoff and Pohl's equation to be $\text{kcal/h} = 3.60\ W^{0.734}$ where W is body weight in kg. He considered this to be the best estimate of BMR. BMR can be used to formulate energy budgets if rates of energy expenditure for various activities are considered as multiples of BMR (King 1974).

Other indirect estimates of BMR are needed to evaluate the applicability of Aschoff and Pohl's equation estimating BMR to dabbling ducks. Although there are no data for postbreeding birds, I have collected data on the diurnal cycle of mallards fasted for 18 h at rest in a darkened metabolic chamber at a thermoneutral temperature (Prince unpublished). Techniques for measurement of oxygen consumption are presented in Hill (1972). Three female and 3 male mallards in the prebreeding chronological stage (late April) and 6 females that had been incubating eggs from 18 to 22 days were monitored for 28 and 40 h, respectively.

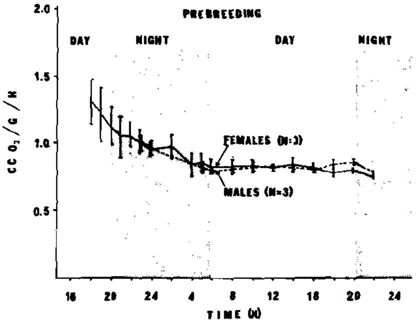

Fig. 1. Metabolic rates of prebreeding male and female mallards at 25 C for a 28-h period expressed in cc O_2/g/h.

The pattern of oxygen consumption for prebreeding birds was similar among individuals (Fig. 1). Their initial consumption was above 1.0 cc O_2/h when they were placed in the chamber in the early evening. Oxygen consumption declined throughout the night to about 0.8 cc O_2/h and remained at a constant level throughout the following day until the run was terminated. Variability was greatest in the early part of the run and decreased with time.

Incubating females were restricted to their nest boxes at least 18 h prior to the run and then O_2measurements were made for 36 h. The straw and down from the nest box and the original number of eggs containing dead embryos were placed in the respiratory chamber with the female. One of the six females actively incubated her clutch of eggs while in the respiratory chamber. Oxygen consumption remained constant at about 1.0 cc O_2/h for the first 20 h (Fig. 2). Oxygen consumption increased significantly on the morning of the second day, decreased to a low point at 1600 h, and increased prior to sunset.

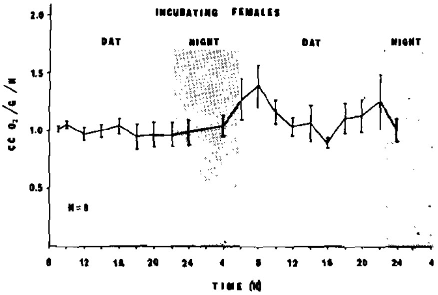

Fig. 2. Metabolic rates of incubating female mallards at 30 C for a 40-h period expressed in cc O_2/g/h.

Although O_2 consumption did fluctuate among individuals, Prince (unpublished) did not observe the diurnal cycle in prebreeding mallards that Aschoff and Pohl (1970) reported for bramblings (*Fringilla, montigringilla*). This is a period of the year when a great deal of nocturnal activity occurs. The diurnal cycle was apparent for the incubating females when the O_2 consumption increased on the morning of the second day of the experimental run. More data are needed for mallards as well as other species to determine the nature of the metabolic cycle.

Because body weight and metabolic

rate were measured in my study, the constant *a* can be calculated. A comparison of the *a* value of the predictive equation and the computed *a* value from my data should give some indication of the applicability of Aschoff and Pohl's equation to mallards as well as its value as a base for an energy model. I examined the data for prebreeding and incubating birds and selected the lowest rate of O_2 consumption for a 30-min period. These values were then converted to kcal per day with a respiratory value of 0.8, and solved the equation $M=aW$ for *a*. There were no significant differences among the calculated *a* values for prebreeding females, males, and incubating females (Table 1). The pooled value of 87.0 ± 2.3 (SE) for *a* is not different from the value of 86.4 for nonpasserines at rest. The Aschoff and Pohl equation appears to be a good estimator of BMR for mallards and possibly other species of dabbling ducks.

Table 1. The *a* values calculated from the equation $M=aW^b$ where m=kcal per day, *a* =constant, and W^b weight to the 0.734 power. The *a* values ($\bar{x}$ + SE) are from the 3 lowest metabolic readings for male and female mallards prior to breeding and incubating females. The chamber temperatures were 25 and 30 C for prebreeding and incubating birds, respectively.

Chronological stage	Female		Male	
	n	Value	n	Value
Prebreeding	3	85.3 ± 3.4	3	88.4 + 1.0
Incubation	6	88.9 ± 4.5	-	-
		Pooled value	87.9 ± 2.3	

Energy Expenditure

Many models have been developed to depict the energy partitioning process. Brody (1945) developed the basic model for the energetics of production in domestic animals. Various foods yield different quantities of metabolizable energy (ME). The net or available energy is the quantity that remains after the calorigenic effect of food (specific dynamic action — SDA) occurs during the process of digestion and molecular transformation of foodstuffs into chemical states.

The concept of productive energy (PE) developed by Kendeigh (1949) and recently summarized by Kendeigh et al. (1977) is basic to understanding the bioenergetics of birds. This concept has been reviewed by Ricklefs (1974), who summarized the relationship between productive energy (available energy minus existence energy) and ambient temperature (Fig. 3). Existence energy (EE) is the energy needed by the animal to stay alive; it includes basal metabolism, SDA, foraging activity, and temperature regulation. PE is the portion available for productive processes. For postbreeding waterfowl this would include molt and migration. Most wintering activity could be included under the EE category. Available energy (AE) has been defined as the maximum rate at which energy can be metabolized by the bird, which is a function of the quantity and quality of food (Ricklefs 1974). Kendeigh (1949) suggested this could be estimated from the metabolic rate of an individual maintaining weight but subjected to maximum cold stress. Estimates of AE for house sparrows (*Passer domesticus*) have been made by observing the lowest temperature that 50% (LD_{50}) of newly caught, locally-acclima-

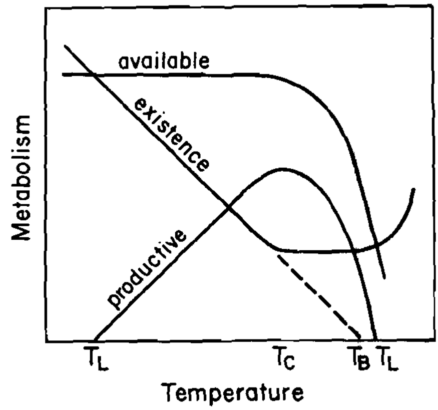

Fig. 3. The relationship between ambient temperature and productive energy (available energy minus existence energy) when T_B= body temperature, T_C=lower critical temperature, and T_L=upper and lower temperature limits of long-term existence (From Ricklefs 1974:173).

tized birds could survive and then solving the EE equation for energy. This procedure is difficult to do and it is unlikely that many estimates of AE for dabbling ducks will be made based on cold tolerance. For instance, Giaja and Males (1928, *in* Brody 1945:284) found that a mallard in a postabsorptive state was able to maintain body temperature for 1h at -100C. Although this extreme example of cold tolerance does not negate the value of the AE concept, it does mean that equipment is a problem and some other standardized procedure is needed.

The highest rate of food consumption by a bird under laboratory condition provides an estimate of the limit of AE. For mallards, laying females consistently consume the greatest quantities of food. Energy requirements for female mallards laying at varied rates are presented in Table 2. The energy needs adjusted to a rate of lay of 1 egg per day ranged from 339 to 389 kcal/bird/day. Purol (1975) reported that female mallards held outdoors and fed a commercial breeder chow metabolized approximately 405 kcal/bird/day during peak egg production in May when ambient temperatures were about 13 C. Although this value would include some of the free-living energy costs, the birds could not fly; the estimate is, therefore, conservative because the birds did not lose weight. Based on these data a value of 450 kcal/day should be used as the best estimate of AE for mallards.

If the BMR as well as the cost of thermoregulation can be estimated for a species, then the cost of some of the productive processes can be compared to the AE. Although estimates of the energetic costs of certain activities can be ex-

Table 2. Estimated energy requirements of mallard females laying 1 egg/day based on metabolized energy consumption by caged females at varied rates of lay. Total needs were estimated on a metabolic cost of 157 kcal per egg produced (Purol 1975).

Study	Location of bird	Metabolized energy (kcal/bird/day)	Rate of lay (no./day)	Energy needs adjusted to 1 egg/day (kcal/bird/day)
Purol (1975)	Michigan (indoors)	289	0.68	339
Foster (1976)	Manitoba (indoors)	265	0.33	370
Foster (1976)	Manitoba (outdoors)	330	0.62	389
Holm and Scott (1954)	New York (outdoors)	325	0.69	373

pressed as an increment of BMR (King 1972, 1974), this can lead to confusion when applied to behavioral data that can be observed and measured for free-living individuals. This happens because there is an overlap and at times an interaction between the existence and productive categories (e.g., foraging and courtship activities). The existence activity takes precedence over the productive category. Thus, the cost of thermoregulation becomes a base for an energy model. These costs are usually met when BMR increments are considered. Increments of BMR can be useful for establishing a dimension among food resources, climatic factors, and waterfowl numbers and activities that occur on specific areas.

ENERGETIC INCREMENTS

Maintenance

Maintenance has been defined by King (1974) as the increase in metabolic rate resulting from neuromuscular tonus and the physical activity associated with wakefulness. I have measured the fasting metabolic rate of mallards in a darkened metabolic chamber at a thermoneutral temperature of 30 C. Three birds per sex were measured over five different chronological periods. The values can be standardized by solving for a in the equation $M=aW$ (Table 3). Although the values of a range from 100.1 to 134.5, there are no significant differences between sex or chronological periods. The pooled value of a is 114.3 ± 3.3 (SE), which is 1.3x above a value computed as the coefficient for the BMR of mallards. This is similar to a difference of 1.24x between the resting and activity phases of the daily cycle for passerines and nonpasserines reported by Aschoff and Pohl (1970). This is the best estimate of minimum energy expenditure of birds that are awake, and it probably more nearly represents the minimum metabolic rate of free-living mallards.

Although there are no significant differences in the calculated a values, some different trends in the a values between sexes were apparent. The largest difference in the values occurred for females and the largest variation about the means was recorded for males. The a value of birds in the prebasic molt was the largest for both sexes, which suggests that the metabolic rate of birds undergoing molt may be slightly elevated.

Locomotion

Tucker (1973) reviewed the theoretical

Table 3. The a values calculated from the equation $M=aW^b$ where M= kcal per day, a= constant and W^b weight to the 0.734 power. The a values ($\bar{x}$ ± SE) are from 6 metabolic readings between 3 to 4 h after the start of the run for male and female mallards at 5 chronological stages at a thermoneutral temperature of 30 C (n=3).

Chronological stage	Female	Male
Winter	100.1 ± 3.7	111.5 ± 12.1
Prebreeding	116.2 ± 9.3	108.4 ± 3.7
Laying[a]	121.9 ± 2.0	111.0 ± 8.0
Incubation[a]	107.6 ± 4.4	110.1 ± 14.2
Molt	134.5 ± 17.3	121.1 ± 18.1
	Pooled value 114.3 ± 3.3	

[a] Male paired with laying or incubating female.

aspects of the energetics of flight. Hart and Berger (1972) empirically analyzed the cost of flight and computed the equation $\text{kcal/h} = 45.5W^{0.73}$ where $W = \text{kg}$. Tucker (1970, 1973) calculated an equation estimating energetic costs that according to King (1974) is not statistically different from the Berger-Hart equations. Tucker's estimate is $\text{kcal/h} = 44.7W^{0.78}$ where $W = \text{kg}$.

The estimated costs of flight for a 1.1-kg mallard calculated with the Berger-Hart and Tucker equations are 49 and 60 kcal/h, respectively. This is a rate of 12.4x and 15.3x BMR, or between 2 and 3 times more than the AE estimate of 450 kcal/day. Raveling and LeFebvre (1967) recommended 12x BMR be used when energetic demands of long range flight are considered. For long distance flights stored energy obviously must be used. A flying time of 2 to 3 h/day would also make an energetic demand comparable to egg production. King (1974) estimated that the flight range of a 1-kg bird would be from 1,800 to 3,800 km with a 25 to 50% body mass loss when fat is used as fuel.

Swimming is another form of locomotion for which there are some estimated energetic costs. Prange and Schmidt-Nielsen (1970) measured the metabolic cost of swimming for mallards. They estimated 0_2 consumption to be 2.2x the resting metabolic level for birds swimming at moderate speeds and 4.1x the resting metabolic level at maximum sustainable speed. When these estimates are contrasted to predicted BMR they are 3.2x and 5.7x BMR (King 1974). Observations of swimming ducks suggest that they swim at rates that optimize the cost of transport (Prange and Schmidt-Nielsen 1970).

Molt

The Anatini have at least two body plumages per year. Weller (1976) outlined the general pattern for adult males as a complete prebasic molt just after breeding, followed by the basic or eclipse plumage, and then another partial or prealternate molt that results in the alternate or breeding plumage. The pattern of molt for adult females is more confused because both plumages are similar. Although there is some variation in terminology, females undergo a complete molt in the summer, after breeding, and another partial molt the following spring prior to the breeding season.

The energetics of molt for postbreeding waterfowl are not well understood. The process places a number of nutritional and energetic demands upon the individual. According to King (1974), a 1-kg bird will have to synthesize about 64 g dry weight of feathers. In addition, there are cardiovascular demands caused by growing feathers as well as a potential for extra thermoregulatory costs. Although King (1974) cited four studies that reported higher 0_2 consumption by molting birds when contrasted with nonmolting individuals, Prince (unpublished data) could find no significant increases in the amount of 0_2 consumed by male or female mallards that were growing new remiges. Prince's (unpublished data) results on mallards were similar to those of Davis (1955) and West (1968) on caged birds that suggested no net increases in caloric cost. If this is true, a modification of behavior would be required to offset the energetic cost of molting.

General descriptions of waterfowl activities during molt suggest there are specific ecological requirements. Weller (1976) pointed out that the birds seek food-rich water areas during the molt periods. During the flightless period mallards and other dabbling ducks frequent areas with dense cover (Munro 1943, Hochbaum 1944, Raitasuo 1964). For mallards there is a large individual variation for the date of molt within sexes (Raitasuo 1964). In addition, males molt 2 to 3 weeks before females (Hochbaum 1944, Boyd 1961, Lebret 1961, Raitasuo 1964). Gilmer et al. (1977) found that drake mallards and some unsuccessful hens left the breeding areas in northwestern Minnesota by early summer and that about one-half of the successful hens remained on the breeding areas and molted. The pattern appears to be to maximize variation among individuals during molt which does reduce intraspecific competition. It is not clear if breeding and brood marshes meet the specific needs of postbreeding mallards (Gilmer et al. 1977).

The ecological needs of dabbling ducks during the molt period require more study. Presently, our waterfowl management strategies do not encompass this period when birds may have requirements as complex as those during the breeding period.

Climatic Factors

Although a general inverse relationship between temperature and metabolic rate is well documented for birds (Kendeigh 1969, King and Farner 1961, King 1974, Ricklefs 1974), the response of individual species will vary with size, thermal conductance of plumage, and thickness of subcutaneous fat. For example, Owen (1970) estimated that outdoor existence energy of blue-winged teals (*Anas discors*) during the fall, winter, and spring increased by 1.7 kcal/bird/day/degree C of decrease. Prince (unpublished data) estimated that mallards will need to produce an additional 2.6 kcal/bird/day/degree C of decrease. The metabolic body weight ($W^{0.734}$) of blue winged teals is 50% that of mallards, which is similar to the 65% difference in the rate of heat loss.

Temperature and/or wind velocity begins to have an observable effect beyond the thermoneutral zone. Sensible heat exchange will be affected by physiological and behavioral adjustments that are made by the bird. The mallard and black duck (*Anas rubripes*) are the only species of *Anas* for which there are enough data to begin to understand the effects of low temperature on energetics. For fasted mallards metabolism begins to increase below the lower critical temperature range of 18 to 25 C at a rate of 2.6 kcal/$W^{0.734}$/day for each degree of decrease (Prince, unpublished data). Although Wooley and Owen (1977) reported a similar pattern for black ducks, the lower critical temperature ranged from 8 to 14 C, which is about 10 C below that for mallards, and the rate of heat production below the lower critical temperature ranged from 2.7 to 3.8 kcal/bird/day, which is higher than that for mallards.

When temperature is considered as a multiple of BMR, then the effect on the mallard can be expressed as $(2.06 - 0.03T)$ x BMR where $T = \text{C}$. Thus, at 0 C a mallard will increase metabolic rate above basal by 2.1x and by 2.7x at -20 C. Although these estimates include heat loss through the feet, a study by Kilgore and Schmidt-Nielsen (1975) on mallards showed that heat loss through the feet becomes more important at low temperatures. They found that loss of heat from feet was 3 to 7% of the simultaneous metabolic heat production between 0 and 20 C and the rate doubled below 0 C.

Freeman (1971) stated that sensible heat exchange between the body and the environment occurs primarily by radiation and convection. The impact of solar radiation on metabolic rates needs to be evaluated, because the zone of thermoneutrality could be depressed on cold, sunny days. Conduction is also important because heat loss through the feet can be significant at low temperatures. This explains why the typical response of a mallard to low temperatures is to reduce activity and rest on ice or land with its feet tucked up against the abdomen (Raitasuo 1964, Reed 1971).

Free-living Conditions

The energetic demands on postbreeding dabbling ducks are diverse and, at times, demanding. The energy needed for maintenance during migration and periods of climatic stress during the winter might approach energetic demands of breeding.

King (1974) suggested that the daily energy expenditure (DEE) in birds and mammals is an allometric function of body weight. This means that energetic costs for DEE of dabbling ducks can be estimated on the basis of their body weight. Values of DEE range from 1.5x to 4.0x BMR for nontorpid, free-living homeotherms; the average for birds is 3.5x BMR (King 1974). These values are very general and include energy output for maintenance, maintenance of social structure, and reproduction.

Although King (1974) indicated that energy expenditures by free-living birds outside the breeding season are unknown, he cited Dolnik (1971), who suggested that an energy utilized by a hypothetical migratory bird might balance out to be fairly stable through the year. This may be the case for dabbling ducks if the cost of egg production for nesting females is excluded. Owen (1970) showed that metabolized energy of captive blue-winged teals was fairly stable throughout the year. Purol (1975) reported that the energy intake by a group of 35 male mallards held in an outdoor pen was fairly stable through the year at about 240 kcal/bird/day, or about 2.5x BMR. If the additional demand of 1 h of flight per day were included for the captive birds, another 50 to 60 kcal should be added to the estimate, yielding 280 to 290 kcal/bird/day (1.1 kg body weight) or at 3.0x BMR. This seems to be a realistic estimate for the DEE of free-living mallards at intermediate (0-20 C) temperatures during the postbreeding period. This does not consider the cost of migration. The estimate is lower than the estimate of 3.6x BMR that Purol (1975) made for a female laying an egg per day (Table 2) or his estimate of 431 kcal/bird/day (4.6x BMR) as the cost of egg laying and free existence.

Biological Factors

Several physiological and behavioral processes affect survival during periods of climatic stress. Prince (unpublished data) did not find a difference in metabolic rates of mallards as a function of season. This implies that insulative covering and/or BMR of mallards throughout the year is the same. This does not seem to be the case for black ducks as evidenced by individual birds acclimated to 19 C producing more heat than those acclimated to 5 C (Wooley and Owen 1977).

Body weights of mallards fluctuate seasonally (Fig. 4). In England, Owen and Cook (1977) recorded the highest weights for males between October and December and for females between November and January. Although Folk et al. (1966) reported a similar seasonal weight pattern in Czechoslovakia, these data are more variable and show a 10 to 12% reduction in weight of both sexes between December and January. Owen (1970) reported a similar weight cycle in captive blue-winged teals.

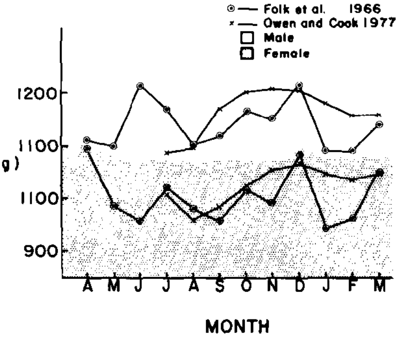

Fig. 4. Body weights of male and female mallards by month.

Owen and Cook (1977) reported that

the condition index (defined as weight/wing ratio expressed as g/cm) of mallards was highest during the winter months. The pattern is similar for blue-winged teals (Owen 1970). This implies that there is a physiological adaptation for mallards and blue-winged teals to build up body reserves prior to periods of cold stress. It would not be surprising for similar patterns to exist for other dabbling duck species.

The condition of mallards can also vary between years on a wintering area. Owen and Cook (1977) observed differences in body conditions of mallards wintering in England that were correlated with the amount of cereal grain available on stubble fields. They suggested that these differences affect winter survival as well as the ability to breed the following summer.

Behavioral changes in mallards occur during periods of climatic stress. Reed (1971) observed activities of 6,000 to 8,000 mallards wintering in southeastern Michigan and described a number of changes in daily activities that were associated with both wind and temperature. These included a reduction of daily feeding flights to 1 per day contrasted with 2 per day during the fall period as reported by Bossenmaier and Marshall (1958) and Winner (1959). Reed (1971) also noted that the birds reduced the duration of feeding flights as the mean 3-day temperature decreased; most of the additional time was spent sitting near water. Rather than increasing foraging activities during periods of extreme climatic stress, mallards reduce their activities and depend on body reserves. Owen and Cook (1977) reported that wintering mallards in England emigrated during long periods of unfavorable weather.

Investigators studying mallards on the northern edge of the wintering range describe their major needs as available food, open water, and protection from hunting (Pulliainen 1963, Moilanen 1971, Reed 1971, Sugden et al. 1974, Cooper and Johnson 1977). A characteristic of all northern wintering flocks is a preponderance of males, suggesting that females are not capable of doing as well in these environs. Smith and Prince (1973) observed such a pattern between sexes for fasting metabolism of mallards. A similar pattern has been reported in the stress response of green-winged teals (*Anas crecca*) wintering on the high plains region of Texas (Bennett and Bolen 1978). More research of the metabolic and physiological response of dabbling ducks to climatic stress might give additional insight to the problem of unbalanced sex ratios.

Body weights of dabbling ducks indicate energetic capabilities and needs (Fig. 5). All species are dimorphic; males are heavier than females and adults are heavier than immatures, based on fall weights reported by Bellrose (1976). The heavier males would require more energy than females and they would also be better able to withstand climatic stress by

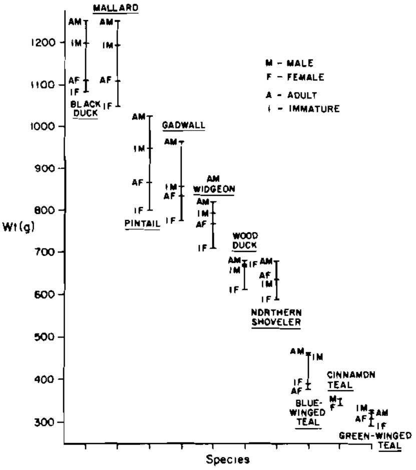

Fig. 5. Fall body weights of dabbling ducks by age and sex (data from Bellrose 1976).

virtue of their larger body size conferring an advantage of endurance (Calder 1974). This differential could be a factor that contributes to disparate sex ratios favoring males, which has been observed in dabbling ducks (Bellrose 1976). The winter distribution of dabbling ducks reported by Bellrose (1976) from north to south is similar to the weight distribution. Mallards and black ducks are species with the more northern distribution, whereas the teal species occur the farthest south. Although many other factors affect winter distribution of dabbling ducks, body size does give an indication for closely related species of the physiological capability to withstand climatic stress.

ENERGY RESOURCES

Use-Days

Food consumption is influenced by many factors. Although nutrition is very important, especially during breeding, this discussion will be limited to energy, which appears to be the most dominant ecological factor during the postbreeding period. Values of ME of plant and animal foods for mallards are presented in Table 4. Although these values would be the best to use for dabbling ducks, estimates of the ME can also be obtained from work done on domestic birds (Scott et al. 1969). Estimates of physiological requirements can be based on the activity increments of BMR that have been previously discussed (Table 5). These values then can be combined with the estimate of BMR based on body weight in order to estimate the amount of energy needed by the bird. Use-days then can be calculated according to the equation:

Table 4. Metabolizable energy (ME) of food items for mallards.

Food item	ME (kcal/g dry matter)	Reference
Wheat (*Triticum* spp.)	3.53	Sugden (1971)
Barley (*Hordeum vulgare*)	3.17	Sugden (1971)
Fall rye (*Secale cereale*)	3.34	Sugden (1971)
Proso millet (*Panicum miliaceum*)	3.57	Purol (1975)
Soldierfly larvae (*Stratiomys* spp.)	2.39	Purol (1975)
Duckweed (*Lemna minor*)	1.43	Purol (1975)
Cellulose	0.20	Purol (1975)

$$\text{Use-days (birds/days/ha)} = \frac{\text{ME of Food (kcal/g)} \times \text{Yield (g/ha)}}{\text{Energy Needs (kcal/bird/day)}}$$

Crop yield data must be converted to a dry weight value for inclusion in the equation. Use-days then can be used to better understand the relationship between the maximum number of birds using a particular habitat and the capacity of that area to support the population.

Environmental-Energy Resource Interactions

Although egg production and time

Table 5. Summary of activity levels and energetic capabilities applicable to postbreeding dabbling ducks as multiples of BMR.

Activity		xBMR	Reference
Maintenance		1.3x	Prince (Unpublished)
Swimming	resting	3.2x	Prange and Schmidt-Nielsen (1970)
	maximum	5.2x	Prange and Schmidt-Nielsen (1970)
Flying		12.4x - 15.3x	Hart and Berger (1972), Tucker (1973)
Temperature (C)	10	1.8x	Prince (Unpublished)
	0	2.1x	Prince (Unpublished)
	-10	2.4x	Prince (Unpublished)
	-20	2.7x	Prince (Unpublished)
Molt		1.3x	Prince (Unpublished)
Free-living	range	1.5x - 4.0x	King (1974)
	birds	3.5x	King (1974)
	fall mallards	3.0x	Prince (Unpublished)
Available energy	(daily)	5.0x	Prince (Unpublished)

spent in flight have been identified by Owen and Reinecke (1979:84) in this symposium as the most energetically demanding activities during the breeding season, the emphasis shifts to molting, flight, swimming, and thermoregulation during the other parts of the year. Much of the selection pressure to maximize fitness with respect to energy during the breeding season is focused on the female, whereas the selection pressures for the remaining part of the year appear to be similar for both sexes. With the intense selection pressures being focused on the female during the breeding season, a differential response by sex might occur during the rest of the year, and females might not be as well adapted to the postbreeding energetic demands as are the males.

Dabbling ducks are best adapted for a climate above 0 C. Although they do winter in areas where temperatures are lower, the energetic demands increase rapidly, and behavioral and physiological adjustments are made that result in the conservation of energy. The range of the DEE appears to be between 3x and 4x BMR. As the DEE approaches 4x BMR the likelihood of mortality would appear to increase as well as the potential to reduce the condition of the bird and the ability to breed the following spring. Research on the impact of winter activities on the reproduction is needed to obtain additional insight into the management of postbreeding dabbling ducks.

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW
Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

HABITAT UTILIZATION BY POSTBREEDING WATERFOWL[1]

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Abstract: Studies of postbreeding waterfowl are needed to elucidate the biology and habitat requirements between breeding seasons. Movements of waterfowl immediately after breeding and habitat characteristics that attract molting waterfowl are poorly understood. Although extensive information is available on factors that stimulate and control migration, information on the nutritional and energy requirements of molting, migrating, and wintering waterfowl is minimal. Nutrition is an important factor in survival, but behavioral and habitat aspects must be understood before the constraints on survival are known. As the loss and deterioration of natural wetland habitats continue, the need to understand the factors that control survival and especially non-hunting mortality becomes increasingly important, because they provide criteria for assigning management priorities.

In North America the major thrust of waterfowl research by conservation agencies and by universities has been to elucidate breeding biology. However, the management of waterfowl probably is more intense and extensive on stopover and wintering areas than on the breeding grounds. The assumption that studies of nonbreeding waterfowl have been neglected is supported by the papers included in a recent bibliography on waterfowl prepared by Reinecke (personal communication) that includes articles from 120 periodicals. Of 174 articles, 116

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[1] Contribution from Gaylord Memorial Laboratory (School of Forestry, Fisheries, and Wildlife, University of Missouri-Columbia and Missouri Department of Conservation cooperating), Edward K. Love Fellowship, and Missouri Agricultural Experiment Station, Project 170, Journal Series Number 8041.

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were related to breeding and 58 to nonbreeding. Only 3 of the 58 articles dealt specifically with postbreeding activities. Other articles on nonbreeding included 35 on migration, 8 on molt, 10 on winter ecology, and 2 on depredations.

Research on postbreeding has been more extensive in Europe than in North America. Undoubtedly, the inaccessibility of many breeding areas and the close proximity to molt and wintering sites used by European species make postbreeding studies more attractive for Europeans than for North Americans.

The paucity of information on postbreeding emphasizes the need for more research to better understand waterfowl biology during the 8 or 9 months when birds are not on breeding areas. Investigation of postbreeding problems are particularly difficult because waterfowl are mobile; waterfowl that congregate on one site may move hundreds of kilometers within 1 day, and some movements may take waterfowl to inaccessible areas. In addition, habitats used and secretive behavior during molt often make study difficult. Biological studies can be further complicated by hunting seasons that restrict research activities on public hunting areas and that may disrupt normal patterns of waterfowl behavior.

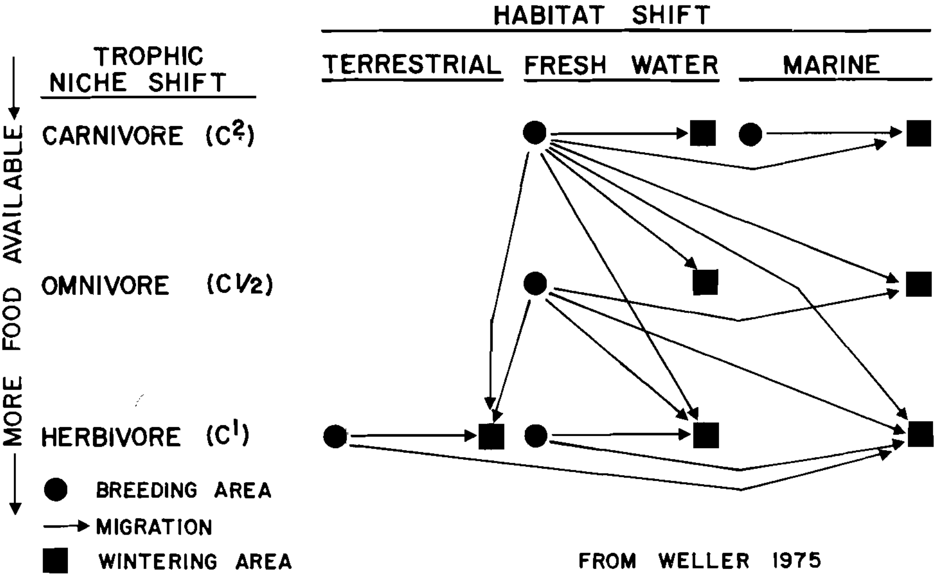
A shift in strategies between breeding and nonbreeding waterfowl has been described by Weller (1975). In North America the strategies of many species change during the annual cycle because of the instability of wetland ecosystems at high latitudes. Freezing and the concurrent lack of food necessitate seasonal migrations to warmer latitudes. An obvious question of great interest is how does the smaller wintering area support the waterfowl from the vastly larger breeding area? Possible explanations suggested by Weller (1975) include: behavioral changes (spacing), a shift in habitats from freshwater to marine, and a shift to a lower trophic level that increases carrying capacities for ducks.

Divers and dabblers that have the greatest flexibility in food habits are the most abundant species. Females of both groups switch to a higher trophic level and consume animal foods that are important during pre-laying and laying. Young rely heavily on invertebrate foods for a few weeks after the hatch as well (Bartonek and Hickey 1969, Krapu 1974a, b).

As young mature and as females complete breeding, they switch to a lower trophic level and feed predominantly on plant matter. Because males do not switch to high protein diets during breeding, they do not show the dramatic shift from one trophic level to another (Krapu 1974b).

Although waterfowl are predominantly a freshwater group, a few species have made the transition to marine habitats. The best examples of anatids adapted to marine environments include kelp geese (*Choephaga hybrida*), herbivores that live almost exclusively on marine algae but both adults and young seek fresh water for drinking (Pettingill 1965); North American brant (*Branta bernicla*) that switch to terrestrial foods and concentrate near the mouths of northern rivers during breeding; and common eiders (*Somateria mollissima*), carnivores that use strictly marine foods during brood rearing. Because cold seas are known for their richness (Ashmole 1971), the abundance of coastal benthos may explain why eiders are abundant species within their habitat range.

There is a definite tendency for waterfowl to shift from unstable freshwater habitats during breeding to more stable and permanent wetlands or marine situations in winter (Fig. 1). A large proportion of the dabblers and divers that nest in the prairie pothole region of North America winter near the coast in Texas and Louisiana. During winter, seed availability is greatest in these



FROM WELLER 1975

Fig. 1. Food and habitat shifts in migratory waterfowl of North America.

southern wetlands (Arner et al. 1974, Knauer 1977), and agricultural production makes field feeding possible (Bossenmaier and Marshall 1958). Waterfowl are opportunists and use these abundant foods when habitat conditions permit.

We believe that techniques developed in recent years for breeding studies can be useful in elucidating postbreeding problems. Our intent is to review some of the postbreeding studies and to attempt to stimulate researchers to investigate the challenging problems associated with postbreeding ecology.

We have divided postbreeding activities into four categories on the basis of probable differences in nutritional and habitat requirements: 1) migration, including both fall and spring movements and staging; 2) postbreeding dispersal; 3) molt, including the complete prebasic molt when birds are flightless and the pre-alternate molt; and 4) wintering, including intermediate stops. Because of a lack of information on postbreeding ecology both within and between species, the categories are tentative. Well defined categories may never be possible because several of these activities may occur concurrently. Despite the possibility for overlap, an understanding of habitat and nutritional requirements during these periods is essential for developing a proper perspective for management. We will discuss migration first and attempt to point out the types of constraints that energy demands may pose for postbreeding waterfowl.

MIGRATION

Migration has probably been studied in more detail and is better understood than any other nonbreeding activity. Lincoln's (1935) suggestion that waterfowl used four major flyways stimulated additional research. Hochbaum (1955) reviewed early concepts of orientation and migratory movements with special reference to waterfowl. His extensive experience with waterfowl suggested that general migratory movements are instinctive, but learned traditions determine use of specific geographical sites. By using data from banding, aerial inventories, radar surveillance, and visual sightings, Bellrose (1976) described the geographical pathways or migration corridors and the numbers of waterfowl that move along each corridor from nesting to wintering areas.

Many key findings on orientation, navigation, and movements have resulted from waterfowl studies. A description of premigratory behavior indicates that on the day of migration blue-winged teals (*Anas discors*) shifted feeding times to midday (Owen 1968). Other behavioral changes included increased wing flapping, turning into the wind, swimming south, less calling, more comfort movements, and especially alert postures prior to departure. Migration movements are not normally initiated under cloud cover, beacause either the sun or stars are necessary for orientation (Hamilton 1962, Bellrose 1966, 1971). Landmarks and wind provide additional cues for navigation once movements are underway (Bellrose 1966, 1971). Emlen (1975) provided a comprehensive review of migration by waterfowl and other birds.

Despite the extensive work on migration, an important problem facing managers is how to estimate the food requirements of migratory waterfowl. This problem is complicated by a number of variables: 1) the number of waterfowl using an area changes from year to year; 2) waterfowl use days can be affected by local temperature, water conditions, and food availability; 3) energy requirements at stopover areas may vary with the condition of birds leaving breeding or molting areas, and if breeding is delayed, hens and young may not have had enough time to store migratory fat before moving south; 4) reduced food availability on preceding stopover areas may increase the number of days spent on an area; 5) low temperatures may increase existence energy requirements and reduce the amount of productive energy for fat synthesis; 6) heavy hunting pressure or other harassment could also increase existence energy requirements and reduce feeding time. Even if the effects of the preceding variables could be established, efforts to estimate food requirements would be hampered by our lack of knowledge of the nutritional requirements of migratory waterfowl.

In the previous paper, Prince described the general relationships between temperature and energy (See Fig. 3, p. 107). Although this figure is not completely accurate with respect to waterfowl under free-living conditions, the relationships between temperature and energy do provide a generalized framework for discussing energy requirements. At the outset, it is important to point out that the existence energy values are normally derived from birds confined to small cages so that activity is restricted. Therefore, there is a curve of unknown form that represents the energy requirement of "free existence." For most temperatures, this curve probably lies above the existence energy curve. This added energy requirement for free existence would reduce the amount of energy available for productive processes. An estimate of the energy requirements for free existence could be made by applying the costs of various activities to time budget data. Unfortunately, this kind of information is not available for waterfowl during migration.

Although ingested (potential) energy is represented as a constant, the actual amount of energy available is probably also variable under free-living conditions. The amount of energy that a bird assimilates can be affected by the physical and chemical properties of the foods

Table 1. Estimated energy costs and time to replenish endogenous fat reserves for migratory waterfowl weighing 1100 g.

Flight time (h)	Distance [a] (km)	Kcal [b] used	Days to replenish fat [c] 480 Kcal intake	Days to replenish fat [c] 390 Kcal intake
2	128	120	0.8(0.6)	1.7(1.0)
4	256	240	1.5(1.1)	3.5(2.0)
6	384	360	2.3(1.7)	5.2(3.0)
8	512	480	3.0(2.3)	6.9(3.9)
10	640	600	3.8(2.8)	8.6(4.9)
12	768	720	4.5(3.4)	10.3(5.9)
14	895	840	5.3(4.0)	12.1(6.9)

[a] Flight time X a flight speed of 64 km/h (Tucker 1971).

[b] Caloric cost of flight/h $=55.7\ W^{0.78}$ (Tucker 1970, 1973, from King 1974).

[c] Based on an estimated existence energy requirement of 3.4 X BMR and potential energy values of 480 and 390 kcal/day. Open figures derived using BMR estimates for mallards; BMR $=87.9\ W^{0.734}$ (Prince, personal communication). Figures in parentheses derived using estimates for nonpasserines at rest; BMR $= 73.5\ W^{0.734}$ (Aschoff and Pohl 1970).

eaten, food availability, and feeding behavior.

Hard seeded food items may be retained in the gizzard for several days and/or they may pass through the digestive tract intact (Swanson and Bartonek 1970). The passage rate of some foods therefore may limit the rate at which energy can be assimilated. Foods that pass through the digestive tract intact are of no nutritive value to the bird and reduce foraging efficiency (energy derived per unit of energy expended in foraging).

Potential energy differs according to the chemical composition of each food because the metabolizable energy (ME) content is variable. The effect of ME on potential energy would probably be most pronounced when food supplies become depleted and the foods being consumed are low in ME.

In addition to its effect on existence energy, temperature may change potential energy through its influence on foraging behavior. After a sudden decrease in temperature, food intake by captive blue-winged teals often decreased or remained the same, suggesting that they were relying partially on fat reserves (Owen 1970). These results indicate that free-living birds may attempt to "wait out" cold snaps, seeking additional food only when body reserves reach a certain low level.

There is some evidence that waterfowl replenish metabolic reserves utilized during migration at stopover areas prior to proceeding on the next leg of their journey (Harris, personal communication). If adequate data were available, it would be possible to estimate the time and energy needed to replenish reserves at various points along the migratory route.

The kind of information needed to make these calculations is not available, but to serve as an illustrative case, we have made some very broad assumptions concerning energy requirements and calculated the number of days needed to replenish fat reserves for migratory flights 2 to 14 h in duration (Table 1). These estimates were computed for a mallard (*Anas platyrhynchos*) weighing 1.1 kg with BMR of $87.9\ W^{0.734}$ (Prince, personal communication), an energy requirement for flight of approximately 55.7 $W^{0.78}$ (Tucker 1970, 1973, from King 1974), a flight speed of 64 km/h (Tucker 1971), and an existence energy requirement of 3.4 X BMR. Maximum potential energy (480 kcal/day) was based on food consumption by penned mallard hens during egg laying (Prince, personal communication). Reduced caloric intake can have a dramatic effect on the time needed to replenish fat reserves. To demonstrate this point, we have reduced the daily caloric intake by 19% (390 kcal/day). This reduction more than doubles the estimated time required for fat replenishment. It should be pointed out that these estimates represent a simplified case and that actual requirements may be greater or less that the figures listed. Our intent in presenting these data is not to define precisely the requirements for migration, but to emphasize that a new approach is needed to allow a more realistic assessment of the food requirements of migratory waterfowl and that this approach requires more information than is currently available.

Past estimates based on waterfowl-use days and food consumption of penned waterfowl probably are lower than actual food requirements. Free-living waterfowl almost certainly incur a greater energy cost as a result of foraging and daily feeding flights than do penned birds under ad libitum food conditions. Energy required for the replenishment of metabolic reserves by migrants must also be established.

To illustrate the point, we have taken our admittedly tenuous estimates and compared them with estimates based on the average intake of corn (71.68 g/bird/day) by mallards during December in Illinois (Jordan 1953). If the ME value of corn (3.43 kcal/g) reported for poultry (Scott et al. 1969:452) is used, the daily intake of metabolizable energy would be 245.86 kcal per bird. This quantity is sufficient to account for only 77 percent of our estimated cost of free existence (320.62 kcal). Even if the 245.86 kcal of energy were sufficient to meet free existence requirements, this amount would not be adequate to meet the needs for productive processes such as replenishment of fat reserves.

Twenty years ago, when wetland habitats were more abundant, generalized estimates of food requirements might have been adequate. However, the currently increasing impact of a man-altered environment predicates a need to better understand and provide for the nutritional requirements of migratory waterfowl. Some possible factors that may influence the energy budgets of present day migrants are outlined in Fig. 2.

The decline in natural wetlands along

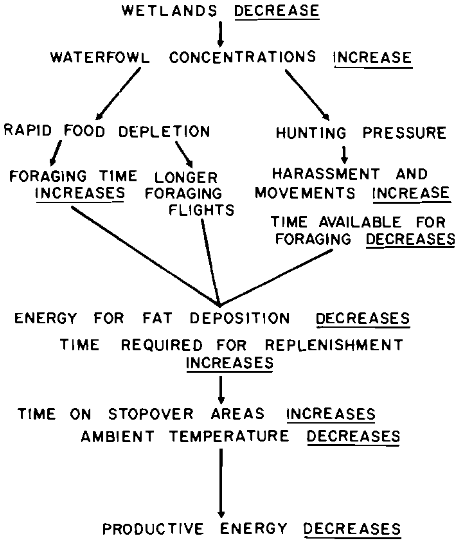


Fig. 2. Potential effects of decreasing wetlands and increased waterfowl concentrations on the energy budgets of migrant waterfowl.

migration corridors has resulted in a greater concentration of waterfowl on many stopover areas. Concentrating waterfowl creates two problems that could adversely affect their energy budgets. First, food supplies become depleted more rapidly. Decreased food availability necessitates increased foraging time and/or longer foraging flights for those species that field feed. Secondly, hunting pressure tends to increase in areas where waterfowl are concentrated. Harassment by hunters could cause increased movements and reduce time available for foraging. Both problems ultimately result in a reduction in the amount of productive energy available for fat deposition and thereby increase the time needed for replenishment. As the duration of stay increases, the effect of declining ambient temperature could compound energy problems by increasing existence energy requirements. It would seem theoretically possible that a combination of these factors could create a situation whereby migrants with depleted fat reserves would be unable to replenish their reserves and, therefore, could not continue migration.

POSTBREEDING DISPERSAL

Many waterfowl have developed molt migrations that are described as mass movements to traditional areas where the pre-basic molt occurs. The molting areas provide food, cover, and isolation when the birds are flightless and vulnerable to predation. This movement of males and nonbreeders may be an adaptation to reduce competition for food on breeding areas (Salomonsen 1968). Postbreeding dispersal is distinct from the fall migration because the direction of flight is often opposite from that of fall movements, breeding females generally do not participate in the movements, and the birds usually congregate on specific geographical areas in large concentrations (Salomonsen 1968). Salomonsen (1968) distinguished several situations in which the molting occurs: 1) on or immediately adjacent to the breeding areas; 2) during the fall or spring migration; 3) on the wintering grounds; and 4) on a special area distinct from the breeding grounds. Typically adults and particularly males and broodless females move to molting areas after breeding, but immatures move directly to these areas from the wintering sites or from the stopover points used during spring movements. He further classified the molting areas on the basis of flock characteristics: 1) individuals or small groups; 2) small flocks of usually no more than a few hundred birds, but occasionally up to a thousand birds; and 3) huge congregations that may number hundreds of thousands of birds.

The initiation of postbreeding activities is variable and depends on the sex, species, and chronology of nesting. The chronology of dispersal from breeding areas is an important constraint on postbreeding strategies. Those species that leave the breeding grounds late in the annual cycle must molt, regain flight, and accumulate sufficient energy reserves for migration prior to freeze-up.

In species that pair annually, most males leave the breeding areas before females with or without broods. Some mallard and wood duck (*Aix sponsa*) drakes may depart during laying, but most leave during early incubation and a few remain with their hens until hatching (Gilmer et al. 1977). In the Chippewa Forest of Minnesota, all male mallards left the breeding area to molt, but 48% of the male wood ducks molted on the breeding area (Gilmer et al. 1977). Most drake pintails (*Anas acuta*), redheads (*Aythya americana*), canvasbacks (*A. valisineria*), and lesser scaups (*A. affinis*) leave in early incubation, whereas most wigeons (*Anas americana*), shovelers (*A. clypeata*), and gadwalls (*A. strepera*) leave in mid-incubation. Blue-winged and cinnamon teals (*A. cyanoptera*) and ruddy ducks (*Oxyura jamaicensis*) generally leave the breeding areas in late incubation (Oring 1964, Bellrose 1976). Ruddy ducks may go through the flightless period on the wintering grounds (Palmer 1976:505). Delayed molt might be in part an adaptation related to late nesting by some birds and late departure from the breeding grounds (Bellrose 1976).

Some broodless wood duck and mallard females leave the breeding area as early as some of the drakes, but most of these nonbreeding females remain several weeks longer than males (Gilmer et al. 1977). Brood females delay their departure from breeding areas until broods are reared, but the time of departure varies with each species.

Female redheads and white-winged scoters (*Melanitta fusca*) consistently leave their broods before the young reach flight stage (Weller 1959, Brown 1977).

MOLT AND POSTBREEDING CONGREGATIONS

Waterfowl concentrations on molting areas may include aggregations of several species in varying numbers. On Swan Lake (310 km^2) in southwestern Manitoba, male pochards were predominant and accounted for 85 to 95% of the molting population (Bergman 1973). In July and August 11,000 dabblers, including 5,000 wigeons, used the area. As many as 3,000 canvasbacks and 20,000 redheads used the lake in early September, but the 2 species segregated themselves. During staging an estimated 50,000 American coots (*Fulica americana*) also used the area in September and lesser scaups occurred in large concentrations in October.

In Alaska, Takslesluk Lake, a 67,340-km^2 molting area on the Yukon Delta, may hold nearly a million ducks of several species (King 1973). Pintails, greater scaups (*Aythya marila*), and oldsquaws (*Clangula hyemalis*) are most common, with nearly 300,000 of each species present. Goldeneyes (*Bucephala* sp.), buffleheads (*Bucephala albeola*), and canvasbacks occur in lesser numbers and generally total less than 25,000. On the Camas National Wildlife Refuge in Idaho, 52,000 molting dabbling ducks that included 25,000 mallards, 20,000 pintails, 5,000 wigeons, and 2,000 teals of 3 species used 4,265 ha of wetlands (Oring 1964).

In Europe molting mute swans (*Cygnus olor*) congregate on traditional molting areas that have been used for at least 350 years (Mathiasson 1973a, b). Some swans appear on the molting areas as early as mid-May and most have departed by mid-November. Flightless swans can be found from mid-June to mid-October, but individual birds are flightless for about 1 month.

Despite a lack of supporting evidence to elucidate evolutionary development of molt migrations, these movements appear to maximize individual fitness. Theoretically food is one important factor in the development of molt migrations (Salomonsen 1968). When immatures, males, and broodless females move from the breeding areas, the competition for foods required for brood rearing is reduced. There is a tendency for waterfowl to shift to molting sites where breeding is limited (Salomonsen 1968). Some high latitude molting areas that are exploited by nonbreeding or postbreeding waterfowl are unsuitable for breeding waterfowl because they are ice-free only for short periods. Ducks that breed in more southern ecosystems may also use tundra wetlands for molting. For example, cavity nesting species such as goldeneyes and buffleheads have moved from boreal forest breeding areas to the tundra for molt (King 1973).

Although large concentrations of birds may use a given molting area, competition for food could be reduced by interspecific differences in foods eaten, feeding habitat, and feeding behavior. On Swan Lake in Manitoba, canvasbacks concentrated near beds of *Potamogeton pectinatus* and *P. richardsonii*, but redheads used a different part of the lake where *Scirpus acutus* occurred as scattered clumps and *P. pectinatus*, *Ruppia occidentalis*, and *Chara* sp. predominated (Bergman 1973).

Molting swans in the Baltic area appear to be attracted to sites with extensive submergent vegetation. Mute swans preferred sites where *Zostera marina* and *Ulva lactuca* were abundant (Mathiasson 1973a). Estimates of food resources required for the equivalent of 94,561 swans for the 5-month period from 22 May to 25 October was 401,523 kg of *Zostera* and 22,832 kg of *Ulva* or a total of 424,355 kg of fresh plant material. There is some evidence that when the carrying capacity of a traditional molting site is reached, molting concentrations develop elsewhere. For example, a molting population in one Baltic area has remained rather constant, but the breeding population has tripled (Mathiasson 1973b).

Our ability to estimate energy and nutrient requirements for molt is severely limited by the lack of data on the timing and duration of molt for free-living waterfowl. Time budget information is essential to assign the costs of daily energy demands, but such data are difficult to obtain because of the secretive habits of molting ducks.

There is some evidence that molt may influence premigratory physiology and behavior. Owen's (1970) work with blue-winged teals suggests that there may be an inhibitory effect of molt on prevernal fat deposition and nocturnal activity.

Waterfowl require isolation on molting areas (Salomonsen 1968). The use of isolated high latitude lakes suggests that birds seek seclusion during the flightless period. In southwestern Manitoba few molting waterfowl were found on lakes where considerable human activity occurred in summer (Bergman 1973). Not only do waterfowl seek out secluded areas for molting, but their behavior is also secretive (Oring 1964, Owen 1970).

WINTERING

Stopover and staging areas may serve as extensions of the wintering areas. This is particularly true when abundant food supplies hold large populations at northern latitudes during mild weather. The use of food resources at higher latitudes reduces the demand for food on wintering habitats and may enable birds to arrive on the wintering areas in better condition.

Recent work on wintering and stopover areas indicates that waterfowl have specific habitat requirements for feeding that allow a variety of ducks to exploit food resources. In March and April in southeastern Missouri, shovelers consistently used water between 17 and 23 cm deep (Taylor 1977) on areas with production of natural foods like millet (*Echinochloa crusgalli*) or smartweeds (*Polygonum* sp.). Pintails used slightly shallower water (14 to 21 cm) and mallards consistently used the shallowest water (11 to 16 cm). These findings suggest that when fields with natural vegetation are flooded too deeply, conditions are unsuitable for feeding by most dabbling ducks. The goal of management on many publicly owned areas is to provide hunting opportunities. When habitat conditions such as water depth are unsatisfactory to attract ducks, not only are food resources unavailable, but hunting opportunities are reduced.

A more sophisticated approach (principal component analyses) to determine wintering requirements of 13 species of waterfowl in Texas from 3 October to 15 December indicated that waterfowl exploited several habitat niches on wintering areas (White and James 1978). Interestingly, the mottled duck (*Anas fulvigula*) restricted its use to the shallowest water and was segregated from all other species. Of the species studied, only mottled ducks bred in the area. The mottled demonstrated habitat preferences different from all other species even though the investigation was conducted during the time of nonbreeding. The other ducks were classified into three groups that exploited water of increasing depths as follows: 1) blue-winged and green-winged teals (*A. crecca carolinensis*) and shovelers; 2) fulvous whistling ducks (*Dendrocygna bicolor*), pintails, gadwalls, wigeons, and ring-necked ducks (*Aythya collaris*); and 3) ruddy ducks, redheads, canvasbacks, and lesser scaups.

In the Louisiana coastal marshes green-winged teals and pintails form large diurnal concentrations on resting areas that have large open expanses and slightly sloping beaches so that whatever the water level, a broad strip of shallow water is available (Tamisier 1976). The three primary daily diurnal activities were: sleeping (8 to 9 h), preening (2 to 3 h and related to molt), and swimming. Feeding was an insignificant diurnal activity. Ducks consistently fed at night, and both the timing and direction of flights were constant. Hunting did not influence daily activity patterns.

SUGGESTED APPROACH TO POSTBREEDING STUDIES

The study of postbreeding ecology should provide an understanding of habitat use and resource allocation in relation to the requirements of the organism. The habitat must therefore be evaluated both in terms of its physical characteristics and how its use relates to the behavioral, physiological, and psychological needs of the organism. Our proposed approach is a comprehensive one requiring the integration of a number of elements (Table 2). Even though waterfowl exploit different habitats and have requirements after breeding that are different from those during breeding, the same basic questions must be answered.

Ultimately research efforts should provide answers to three basic questions: 1) How do postbreeding waterfowl apportion their time and energy; 2) What are the characteristics of the habitat used; and 3) Why is time apportioned among activities and habitats as it is? Because the essential continuity between the organism and the environment is revealed most obviously in energy exchanges and transformations (King 1974: 4), time and energy budget data provide a central framework for evaluating and

Table 2. Suggested areas of research emphasis for the study of postbreeding waterfowl.

Habitat	Foods	Behavior	Physiology
Wetlands used	Foods consumed	Time budget	Condition
Vegetation associations	Feeding habitat	Feeding	Hormones
Chemical and physical characteristics	Chemical composition	Inter- and intraspecific interactions	Nutrition
Meteorological data	Nutritional values	Man's developmental and recreational activities	
	Metabolizable energy		

integrating data on, e.g., habitat selection, food habits, and changes in condition.

On the basis of energetics work during the breeding season, we suggest that productive work include the following components: food and nutrition, habitat, physiology and condition, weather, competition, behavior, and time and energy budgets (Fig. 3). Although a comprehensive discussion of the potential interactions among these components is inappropriate here, we will suggest several approaches that have been successful in our studies. Preliminary time budget studies are useful in identifying habitats used and suggest sites where data on habitat characteristics and food habits should be collected. Once foods are identified, their nutritional values (e.g., chemical composition and ME) should be determined. Carcasses of birds collected can be used to establish baseline data on body and organ weights and measurements and on carcass composition. These data are important in determining changes in condition and how the use of metabolic reserves relates to strategies employed at various stages in the annual cycle.

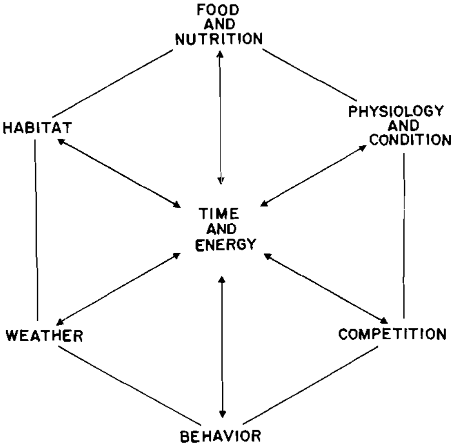


Fig. 3. Use of time and energy budget data for the integration of major elements in the study of postbreeding waterfowl.

Obviously, these are complex problems that are best solved by teams of researchers or in programs with several students working simultaneously. The opportunity to better understand postbreeding ecology is an exciting challenge with a broad range of research opportunities and management applications.

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW
Proc. 1977 Symp., Madison, WI, NC Sect.,
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Published in 1979

WINTER HABITAT OF DABBLING DUCKS — PHYSICAL, CHEMICAL, AND BIOLOGICAL ASPECTS

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Abstract: Each fall some 50 million dabbling ducks representing 10 species depart the northern breeding grounds and make their way southward for the wintering season. Birds begin arriving on the wintering grounds in August and remain through April the following year. Migrant dabbling ducks make use of winter habitat 8 months of the year, and, as a result, are greatly influenced by habitat quality and abundance during that time. Diversity of habitat is an important aspect of meeting the requirements of the many species involved. Important features of winter habitat are presented for the various species and include physical, chemical, and biological aspects. Physical features affecting winter habitat include distribution of aquatic area, water depth, and weather patterns. Important chemical aspects are soil and water salinity and habitat pollution. Major biological considerations are food availability, diseases, and parasites.

The availability of suitable breeding habitat is the major factor affecting continental populations of dabbling ducks in North America; however, the importance of winter habitat should not be overlooked. Certain species, such as blue-winged teals *(Anas discors)*, begin fall migration in August and remain on wintering grounds into the following May, a period exceeding 8 months of the year. Most others use winter habitat in excess of 7 months. Conditions on the wintering grounds can influence the welfare of birds using them and also the breeding condition of birds departing from them in the spring.

The selection of winter habitat by dabbling ducks is, like fall migration, primarily a matter of tradition. Areas visited during a wintering season are usually those visited previously. However, continued use during a wintering season varies with habitat quality and preferences of the individual species, as well as individual birds or groups within a species. The quality of winter habitat encompasses numerous physical, chemical, and biological factors that can change within a period of only a few hours to make an area less attractive or more attractive to ducks. Large-scaled changes in habitat quality can even modify migratory patterns. The purpose of this paper is to review some of the factors affecting winter habitat quality for dabbling ducks.

PHYSICAL ASPECTS OF WINTER HABITAT

Species Preferences

Although dabbling ducks are adapted for use of shallow water areas, feeding and resting habitats selected by the individual species vary. In fact, certain species have different habitat preferences in different parts of their range. For example, the mallard (*A. platyrhynchos*) seems equally at home in the corn fields of the Midwest as it does in the flooded pin oak (*Quercus palustris*) flats of Arkansas or the coastal marshes of Louisiana.

Pintails (*A. acuta*) also display considerable variability in habitat selection; in certain regions they depend heavily on grain and soybean fields for feeding, but elsewhere they may use shallow water marshes and impoundments, even when agricultural crops are nearby. Mallards and pintails feed largely on seeds, and select habitats with an abundance of this food easily available. However, at times pintails will raft on large, shallow water lagoons and feed almost entirely on submerged aquatics. Mallards, on the other hand, are more secretive and in marshes or other aquatic habitats are commonly found in small ponds and potholes.

Blue-winged and green-winged teals (*A. carolinensis*) are the smallest of the dabbling ducks and appropriately select habitats with shallowest waters, often feeding or resting on mud flats. They frequently shift about on local winter habitat in response to changes in water levels.

Gadwalls (*A. strepera*), American wigeons (*A. americana*), and shovelers (*A. clypeata*) are commonly found on shallow, open lakes containing dense growth of aquatic plants. On their arrival to the Louisiana coast in October, gadwalls and wigeons will congregate in large bodies on isolated, brackish lakes, often with as many as 5,000 birds on an area of less than 10 ha. The birds are attracted there by dense wigeongrass (*Ruppia maritima*), remain until stands are depleted, then disperse to other nearby areas. However, they remain mostly in open water habitat, selecting whatever may be available. Gadwalls also occupy lakes in forested bottomlands that contain abundant aquatic growth. Wigeons, however, will disperse to upland areas for feeding and frequently cause damage to green agricultural crops (Horn 1949). During early spring, large flocks of wigeons may be seen feeding out of water on newly sprouted vegetation on the Mississippi River Delta. The shoveler, though more of an opportunistic feeder, remains in aquatic habitat.

The wood duck (*Aix sponsa*), as its name implies, is typically a bird of forested areas, occupying sloughs, streams, lakes, and flooded timber. Exceptions to this have been noted in several areas; in Louisiana wood ducks are occasionally seen in coastal marshes considerable distances from timbered areas, and Bellrose (1976) reported feeding in corn fields.

Cowardin (1969) studied use of flooded timber and marsh by mallards, black ducks (*Anas rubripes*), and wigeons and noted that the birds spent more time resting than feeding in timbered areas and more time feeding than resting in marsh areas. Mallards and black ducks used flooded timber during the fall as a rest area at night and flew out to nearby agricultural fields for feeding during the day. The preference of flooded timber over the adjacent marsh was attributed to the abundance of logs, which provided almost unlimited loafing sites.

Distribution of Aquatic Habitat

The construction of permanent water areas over the past several decades has resulted in broad changes in the distributional pattern of dabbling ducks. Reservoirs constructed for irrigation, flood control, and hydroelectric power have provided permanent water to regions where the absence of available water previously limited winter use by dabbling ducks (Williams 1964). In the short history of reservoir construction in the United States, 1,300 reservoirs were constructed by 1954 with a water storage of 4.5 million surface hectares. By 1964, another 1 million surface hectares were added and the predictions were for a total of 16 million surface hectares by the year 2000 (White and Malaher 1964). Also, farm ponds for livestock watering and fish production literally dot the landscape and constitute a key segment of the winter habitat in many areas. Edminster (1964) estimated that by 1980, 2.5 million farm ponds covering 1.2 million hectares would be available to waterfowl.

The creation of new aquatic habitats occurred at the same time that millions of hectares were being lost because of habitat alterations. Newly constructed water areas receiving greatest use were those in close proximity to agricultural areas. Dabbling ducks, particularly mallards, used the reservoirs and ponds as rest areas and spread out to adjacent grain fields to feed (White and Malaher 1964). The abandonment of traditional wintering areas for the new man-made habitat resulted in a more even distribution of dabbling ducks on the wintering grounds. New areas most readily used were those within or near natural flyways (Edminster 1964).

Although available water is an essential component of dabbling duck winter habitat, the relationship of open water to marsh or terrestrial areas often determines the attractiveness of a particular habitat. Even small wetland areas can provide important wintering habitat if open water areas are properly dispersed. Where adequate water areas are not available, they can be easily developed (MacNamara 1957), and thus provide better distribution of birds and improve opportunity for harvest. Hopper (1972) observed that marshes without adequate open water or a proper interspersion between water and cover are normally avoided by dabbling ducks. Efforts to create more open water in a dense Colorado marsh resulted in increased duck use.

Fresh marshes in southeastern Louisiana that are overgrown with vast, unbroken stands of maidencane (*Panicum hemitomon*) receive little duck use. Opening such stands by prolonged flooding or temporary exposure to brackish water makes the area more attractive to dabbling ducks. In brackish marshes, wiregrass (*Spartina patens*) presents a similar problem, and its gradual encroachment into marsh ponds results in reduced use by ducks.

An excessive amount of open water can also present problems. Large ponds are more exposed to wind and wave action and less attractive to dabbling ducks. Duck use is often limited to coves in such areas, which offer some protection.

Water Depth

Water is an essential element of winter habitat for most species of dabbling ducks and must be present in proper amounts for an area to be attractive. Inadequate amounts and excessive amounts both regulate food availability. Burgess (1969) described methods of regulating dabbling duck use of management units on Squaw Creek National

Wildlife Refuge in Missouri by manipulating water levels. Units were flooded to a shallow depth in the fall to attract ducks, drawn down in December to discourage winter use and move ducks from the refuge, and flooded in spring to attract ducks during northward migration.

In an evaluation of duck use of marsh impoundments in Louisiana, Chabreck et al. (1974) noted several instances where water depth affected duck population levels and distributional patterns. Blue-winged teal use of impoundments was related to water depth, independent of foods present. The area studied normally received high use by blue-winged teals from late August into October; however, brackish water impoundments were mostly dry in August 1970 and contained very few teals as a result. Heavy rains associated with Hurricane "Felice" in mid-September raised water levels, and teal populations were much larger by the following week. The following year a contrasting situation was observed in the brackish water impoundments. Water levels and blue-winged teal populations in late August 1971 were similar to those present in September 1970. Then, Hurricane "Edith" struck the area in mid-September 1971, and over 12 inches of rain fell in the study area. As a result, water depths increased greatly and teal use declined drastically.

Other species were also responsive to changes in water depth and increased or decreased use of an area as water depths changed. Green-winged teals preferred areas with water depths less than 10 cm and moved from areas whenever the water depth increased. Numbers of diving ducks such as lesser scaups (*Aythya affinis*), ring-necked ducks (*A. collaris*), and ruddy ducks (*Oxyura jamaicensis*) generally increased as water depths increased. Gadwalls, wigeons, and shovelers, which feed heavily on aquatic vegetation or animal material, were normally found under a wider range of water levels than most other species of dabbling ducks.

Wills (1965) related water depths to dabbling duck populations on Catahoula Lake in central Louisiana and reported tremendous concentrations of most species during the fall and early winter when depths were less than 0.5 m and favorable for feeding. Deeper flooding in late winter caused most dabblers to abandon the area. The purpose of deeper flooding was to restrict feeding in the lake and prevent the birds from consuming lead shot deposited during the hunting season. Mallards and pintails continued to use the lake as a rest area but moved out into nearby soybean fields to feed.

Weather

Weather patterns are a key factor regulating fall migration of dabbling ducks (Hochbaum 1955), and the behavior of birds on wintering grounds is also greatly affected by weather conditions. Nelson (1954) reported that ducks remain on winter habitat in Utah until lakes and ponds freeze over, thus forcing most birds from the area. Bellrose (1976) noted that over 1 million mallards winter in the Midwest and feed in corn fields when lakes and marshes become frozen. Many birds remain until snow cover becomes too deep for field feeding. Ducks forced southward by adverse weather may return when conditions improve.

Rainfall plays a key role in renovating winter habit (Lynch 1964). Annual plants provide valuable food sources in wetlands, particularly in the Deep South, and summer drying is necessary for germination and growth (Chabreck 1959) Dry summers usually result in abundant growths of annuals in marshes and swamps; however, fall and winter rains are necessary to restore water and make the seeds produced available to wintering birds.

Hurricanes in coastal areas may have adverse effects by sweeping away important aquatic plants in tidal surges (Griffith 1939). Impoundments and other habitat development projects may also be damaged by rushing waters (Ensminger and Nichols 1957). Hurricanes often improve winter habitat by reversing plant succession and improving conditions for growth of annual plants.

CHEMICAL ASPECTS OF WINTER HABITAT

Soil and Water Salinity

In coastal areas, soil and water salinity is usually the major factor regulating plant species composition of lakes and marshes (Penfound and Hathaway 1938). It is also one of the principal factors limiting plant growth in certain western areas (Nelson 1954). The Louisiana coastal marsh has been delineated into 4 vegetational types on a basis of salinity (Chabreck 1972). The types occurred in bands generally paralleling the coastline, contained characteristic floral patterns, and were designated as saline, brackish, intermediate, and fresh. Plant species diversity and the number of duck food plants increased with decreasing water salinity (Chabreck 1970, Martin and Uhler 1939). Palmisano (1972) studied dabbling duck use of these marshes and found greatest duck concentrations in the fresh and intermediate types, which had lowest salinities. The saline type, which was adjacent to the coastline, had highest salinity and lowest dabbling duck use.

Retreat and advancement of vegetational types over a 25-year period were determined by comparing a type map of the Louisiana coast in 1943 (O'Neil 1949) with a type map of the area in 1968 (Chabreck et al. 1968). Comparisons disclosed that the saline type remained unchanged in southwestern Louisiana but widened 3.4 km in the southeast. The brackish type in southwestern marshes was 8.2 km wide on the earlier map but only 4.2 km wide by 1968, a reduction of about 47 percent. In southeastern marshes, the brackish type was 10.6 km wide in 1943 but increased to 13.4 km in width by 1968.

The widening of saline and brackish vegetational types in southeastern Louisiana resulted from saltwater intrusion from the Gulf of Mexico into intermediate and fresh types and was caused by increased canal dredging and stream channelization. The reduction in width of the brackish type in southwestern Louisiana reflects a reduction in water salinities in that area that resulted from saltwater barriers on irrigation projects and special management practices on wildlife refuges. Because dabbling duck use is greater in fresh and intermediate vegetational types, the change represents an improvement of winter habitat in southwestern Louisiana and a deterioration in southeastern Louisiana (Chabreck 1970).

Habitat Pollution

The wide-scale release of chemical pollutants into aquatic and wetland environments is a matter of great concern to waterfowl managers. This concern stems not only from the fact that many pollutants cause mortality, but also because they affect bird behavior and reproductive success and may cause a deterioration of winter habitat.

The discharge of lead shot into the environment by hunters is a form of pollution and occurs nationwide, but the majority of deaths from lead poisoning are within the Mississippi Flyway (Stout and Cornwell 1976). The gradual transfer from lead to steel shot offers a logical alternative for curtailing the problem.

Various other forms of pollution are reported in the literature, and most mortality occurs on the wintering grounds. Oil spills are an important mortality factor in waterfowl, but diving ducks are the group most affected. The nature of winter habitat used by dabbling ducks largely removes them from contact with oil. An oil spill in winter habitat used by dabbling ducks was investigated, but no bird mortality was noted (Chabreck 1973). The oil did, however, act as a repellent to ducks, and habitat use did not return to normal until 6 months after the spills.

Numerous industrial pollutants and insecticides have been investigated to determine their distribution in the environment and effects upon dabbling ducks (Hunt and Ewing 1953, Dustman et al. 1971, Brunch and Low 1973, Longcore and Samson 1973, Heinz 1976, Pearce et al. 1976). Very often the water that enters drainage systems and wetlands used by waterfowl has been used and reused many times and contains a variety of contaminants when it reaches the birds. More effort is needed to properly identify these problems and solve them (Friend 1975).

BIOLOGICAL ASPECTS OF WINTER HABITAT

Food Availability

All major dabbling duck concentration areas have one common component: food is abundant and readily available. By removal of this essential element, an area quickly loses its attractiveness to dabbling ducks. Hawkins et al. (1946) noted a mass exodus of mallards from the Grand Prairie Region of Arkansas into Louisiana and Mississippi caused mainly by the shortage of food. The movement took place in spite of favorable weather conditions and with spring close at hand.

The importance of providing preferred foods in adequate amounts for attracting and holding dabbling ducks on an area is well known. The value of food for attracting birds was the basis for outlawing baiting in areas used for hunting. Also, the use of baits to lure ducks into traps is the most common capture technique used by agencies banding birds. Management programs for ducks usually involve improvement of food supplies by artificial plantings or habitat manipulation to increase growth of natural foods (Davison and Neely 1959, Givens and Atkeson 1959).

Impoundments were constructed on the 50,000-ha Rockefeller Wildlife Refuge in Louisiana during the mid-1950's as habitat management for dabbling ducks. Although less than 20% of the area was impounded, wintering duck populations on the refuge increased from 75,000 to 400,000 birds as a result of the program, and 80% of the ducks were in the impoundments. Vegetational sampling disclosed that species important as duck foods made up 50% of the plants in the impoundments but only 20% of those outside (Chabreck 1959).

Since the 1930's, grain and soybean fields have become an increasingly more important component of the winter habitat of dabbling ducks, particularly mallards, pintails, black ducks and,wood ducks. Many birds have adapted to dry field feeding and have become dependent upon grain and soybeans as a primary source of winter food (Madson 1964, Horn and Glasgow 1964). Mallards have altered their traditional migrational and wintering patterns in response to this immense food supply. Only with a deep snow covering of habitats are some birds discouraged enough to depart for milder climates (Madson 1964).

Diseases and Parasites

Problems of diseases and parasites have no doubt plagued dabbling ducks in winter habitats throughout history. Botulism had been responsible for waterfowl losses for many years before 1910, but that year the first real concern was expressed about its effect on waterfowl populations (Jensen and Williams 1964). Since that time, considerable effort has been placed on tracking outbreaks of diseases and parasites and determining environmental conditions associated with outbreaks. Bird losses may have been overlooked in the past when habitat was plentiful, but as habitat declines and ducks become more crowded, losses become more obvious. Problems have been reported from all winter habitats.

The birds on restricted habitat have also contributed to the problem. Crowding of people or wildlife enhances the spread of contagious and infectious diseases and parasites and causes stress within individuals that makes them more vulnerable to various maladies. Inadequate food supplies and pollutants can disrupt body defense mechanisms, alter host-parasite relationships, and bring on still more disease problems (Friend 1975).

The magnitude of disease and parasite problems in dabbling ducks was investigated by Stout and Cornwell (1976) by analyzing reports and band data. They found that disease mortality in all waterfowl accounted for 87.8% of the total reported non-hunting mortality. Botulism was the major source of non-hunting mortality, and dabbling ducks made up 92% of the band recoveries attributed to botulism. Predation loss was not listed as an important factor affecting waterfowl and represented only 0.1% of all non-hunting mortality reported.

SUMMARY AND CONCLUSIONS

Most literature dealing with continental population of dabbling ducks stresses the importance of breeding habitat for maintaining the resource. Although adequate breeding habitat is essential for maintaining high productivity, the role of winter habitat should not be overlooked. Dabbling ducks occupy winter habitat for 7 or 8 months per year, and the quality of the habitat may determine the condition of birds returning to breeding grounds the following spring.

Conditions within the Atlantic Flyway should serve as a reminder to managers who fail to recognize the importance of wintering grounds. Because of tremendous urban and industrial growth, many former winter habitats in that flyway have been destroyed or have deteriorated to the point where they are no longer attractive to ducks (Addy 1964). In fact, the destruction rate of wintering areas may exceed the loss of breeding grounds, and birds migrating southward in the fall may be adversely affected by overcrowding on the few remaining attractive habitats.

The impact of habitat alteration will vary among species of dabbling ducks. The more adaptable species change with the times and seek out new habitats as former habitats are modified or destroyed. For example, clearing of bottomland hardwoods for soybean farming may have varying effects on different species. Mallards and wood ducks, which previously used the habitat, will be forced to change habitats or seek similar habitat elsewhere. The mallard, being more adaptable, may return to the same area and be equally at home in the soybean field. The wood duck, however, requires a forest environment and must move elsewhere to find similar habitat. Similar habitat in other areas is usually occupied, and its use by displaced birds often results in a problem of overcrowding.

Each fall some 50 million dabbling ducks representing 10 species depart the northern breeding grounds and make their way southward for the wintering season. Habitat requirements vary considerably among species, and diversity of winter habitat must be maintained in order to meet the needs of all species. Diversity should include not only an adequate representation of all habitat types, but also an adequate distribution of all types throughout the winter range.

The winter habitat needs of all species of dabbling ducks cannot be evaluated without full understanding of the habitat requirements of individual species. This understanding should begin by characterizing the physical, chemical, and biological components of the habitats used by each species. This paper has presented a general overview of these components; however, to be useful to managers or decision makers, all components must be quantified to a level that permits reasonable predictions of habitat quality.

Future research should be designed to identify the precise winter habitat requirements of dabbling ducks and the factors affecting habitat quality and to establish mathematical values of each habitat component for the purpose of quality assessments. With this information, winter habitat availability and needs can be determined more accurately.

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WATERFOWL AND WETLANDS —
AN INTEGRATED REVIEW

Proc. 1977 Symp., Madison, WI, NC Sect.,
The Wildlife Society, T. A. Bookhout, ed.
Published in 1979

SYMPOSIUM SUMMARY AND COMMENTS ON THE FUTURE OF WATERFOWL AND WETLANDS

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This symposium on waterfowl and wetlands has been specifically aimed at reviewing recent and ongoing studies relating to habitat dynamics and habitat requirements of North American dabbling ducks. It has the purpose of contributing to a better understanding of the state of our knowledge of these subjects and, perhaps, a better perspective about current and future research and management needs.

The papers presented here today provide us with a wealth of information and experience gained from many years of dedicated field and laboratory work. They contain much more than can be fully digested and absorbed in the short time available to us now. In these closing comments, therefore, I will not attempt an in-depth analysis of them. Instead, I will briefly review what seem to me to be some of the main points, discuss the research trends that seem evident and how they relate to management needs, and, finally, make a few personal observations on the future of waterfowl and wetlands.

An obvious starting point for an overall review of the biology of dabbling ducks is a description of how the various species distribute themselves during the breeding season in the vast and complex array of wetland habitats in North America, and how they relate to these habitats in terms of space, time, and other impinging factors. The first part of this descriptive effort was ably handled by Frank Bellrose, whose unmatched knowledge and experience with North American waterfowl is one of our most valuable assets. His paper shed additional light on how important the so-called prairie pothole country is to breeding dabblers, and why and how other segments of the breeding range differ from it in quantity and quality of habitat, as well as in duck populations.

For the second part of this effort Trauger and Stoudt drew on the important information gleaned from more than 25 years of continuous observations of the fortunes of ducks on 3 specific study areas in the prairies and parklands of western Canada. They described how a combination of weather cycles, intensified land use, differences between species in breeding chronology and possibly other factors, such as hunting pressure, have adversely affected local abundance, species composition, and reproductive success. This paper is important as a case history of what has happened in certain parts of the breeding grounds and could happen in others.

John Kadlec reviewed the state of knowledge about the dynamics of nitrogen and phosphorus abundance and cycles in wetland ecosystems, pointing out their importance in the maintenance of wetland plant and animal communities, and the interrelationships that appear to exist. This is an aspect of natural wetland processes that has, so far, received too little attention and consideration by waterfowl managers. His suggestions about managing wetlands to enhance the supplies and internal cycling of these all-important nutrients warrant the attention of waterfowl managers in relation to maintaining and improving wetlands for waterfowl.

Five of the 11 papers presented today dealt with factors influencing breeding strategies. Indeed, they formed the most important part of the symposium in terms of the attention devoted to one general topic. Thus, Scott Derrickson told us about differences in the behavior of pairs on breeding areas in relation to the status of the pair bond and breeding chronology, and how this may affect the breeding strategies of different species. Swanson, Krapu, and Serie described food selectivity on the breeding grounds by five species of dabblers and how the birds were influenced both by nesting chronology and availability of food resources. They stressed the importance of the entire wetland complex, rather than a selected part of it, to the quality of waterfowl breeding habitat. In a separate but related paper Krapu expanded on the importance of animal food to the reproductive potential of free living prairie ducks, and how lack of this important source of protein can affect production and the quality of eggs.

Owen and Reinecke continued the general topic by presenting a synthesis of information about the energy requirements of breeding ducks with estimates of the needs for daily energy intake and how it is expended. They emphasized the extremely high energy demand on female dabbling ducks during the egg-laying period — a situation where metabolic rates may approach maximum sustainable levels — and pointed out the many gaps in our knowledge about energy needs of ducks in the wild. It is difficult to over-estimate the potential value of such information in helping managers understand the carrying capacity of breeding habitat.

Finally, Bruce Batt described individual variation among captive mallards in laying dates, clutch size, and egg size but found these factors to be consistent from year to year in particular individuals. He suggested that this indicates the existence of previously unrecognized variation within species in basic breeding strategy that may have a genetic basis. If so, this is a mechanism that could provide a means for mallards to adjust their breeding strategy to long term changes in habitat conditions. It also merits consideration in such practical matters as the interpretation of breeding population surveys.

Shifting attention to a different part of the life cycle, Harold Prince led us into the labyrinths of metabolic rates as part of his effort to shed light on the post-breeding behavior of dabbling ducks in terms of energy and time budgets. He pointed out the importance of this for better understanding life history phenomena and adaptive strategies. The usefulness of such information for practical management in the United States is obvious when it is considered that much of our wetland management effort is aimed primarily at the maintenance and welfare of waterfowl during fall and winter rather than the breeding season. Yet, the distribution and movements of waterfowl at these times are often influenced more by events associated with agricultural or other land use trends than by purposeful waterfowl management.

Fredrickson and Drobney continued the discussion of post-breeding waterfowl biology, pointing out the general lack of attention accorded to this part of the life cycle. They identified some obvious and some not so obvious species differences that appear characteristic of the post-breeding period, and noted the inherent difficulty of studying and acquiring information about waterfowl during this period. We must agree with their view that such information is essential and long overdue for better understanding of habitat requirements, food resources, feeding ecology, and nonhunting mortality.

In the final paper, Bob Chabreck discussed factors influencing the quality of wintering dabbling duck habitat based on studies and observations in Louisiana, which contains probably the greatest and most important expanse of wintering habitat in North America. He pointed out that dabbling ducks spend a major portion of their annual life cycle on the wintering grounds and that the quality of winter habitat must be an important factor in determining how well the birds are prepared for breeding. We have not yet begun to understand in detail the influence of winter habitat conditions in the life cycles of the different species of waterfowl. The experience and knowledge already acquired by biologists in Louisiana and elsewhere should provide a point of departure for the necessary studies of the future.

One of the important things about this symposium is not just the variety of thrusts toward better understanding of different aspects of waterfowl biology, but the effort to relate the results to other research and management findings and problems.

A great deal of attention was focused today on such matters as the factors influencing continental breeding ground distribution, specific local habitat and population relationships, social interactions and breeding biology, feeding behavior and nutrient factors in relation to reproductive biology, bioenergetics in relation to distribution and ecology, the management implications of individual variation in nesting behavior within a species, and habitat factors in relation to the ecology of post-breeding and wintering waterfowl. These may appear at first glance to be quite separate and diverse elements, but they are all part of the fabric of waterfowl biology; it is our continuing task to strive to see the whole as well as the parts.

Another important aspect is what appears to be a growing interest in the biology of waterfowl during the post-breeding and wintering periods. An effort to understand the factors affecting waterfowl in this portion of their life cycle, and to apply this knowledge, is essential to a balanced research and management program. We must not overlook the fact that one of the most important roles for the United States in the continental management picture is to provide essential post-breeding and wintering habitat.

These aspects seem to me to indicate a more definite move toward viewing waterfowl in terms of their total environment and their total biology than has been evident in the past. I believe this is not only desirable but essential if we are to continue to improve our understanding of dabbling ducks and other waterfowl populations, and our ability to manage them. Some of the most basic and far-reaching management problems are unlikely to be resolved with any other approach.

For example, let me briefly mention just two problem areas that are of particular interest and concern to management at the present time, and that I believe will require this kind of approach. The first concerns annual mortality and its role in regulating population size. This has long been a major area of research effort, and much progress has been made. But from a practical management standpoint, we need to know much more about the nature and magnitude of hunting and non-hunting mortality, how they are interrelated, and their relative impact on the population status of different species and populations of waterfowl. The importance of this is brought home to us each year when we seek to establish reasonable hunting regulations.

The second concerns the relationship between populations and food resources. What are the roles played by food supplies and availability in regulating waterfowl population size, distribution, and health? The need for information in this area is great, not only in relation to breeding habitat but also in relation to the management of wintering habitat. We have barely scratched the surface of this aspect of waterfowl management.

Answers to these questions are extremely important for determining the degree to which we can improve and refine the management of waterfowl generally, and by species and population units within species. They can only come from broadly based and well integrated studies. No one need expect that an understanding of how waterfowl fit into, and relate to, their total environment will evolve easily or quickly, but the understanding is essential to management and the effort to obtain it should be encouraged.

In regard to the future of waterfowl and wetlands, it seems to be customary to take a very pessimistic attitude. The literature is full of dire warnings about the imminent decline and fall of North American duck populations — perhaps justifiably so. However, it may be worthwhile to remind ourselves that there are other perspectives on the future. I believe that with possibly a few specific exceptions waterfowl are remarkably resilient creatures that are likely to be here in abundance long after you and I are gone.

It is often difficult for people like us, who are so completely immersed in the day-to-day problems and difficulties of waterfowl management and research, to keep in mind that we still have waterfowl in sufficient abundance to provide reasonably good opportunities for hunting and viewing. In some places, and with some species, abundance today is far greater than in historical times. This in itself is the cause of management problems of major concern as, for example, with some present day Canada goose populations.

In some ways this is really quite remarkable. I wonder how many would have anticipated, 30 years ago, that waterfowl would be as abundant today as they are? This is not to say that we don't have serious problems in maintaining waterfowl in abundance. We have plenty, and there is no reason for anyone to be complacent about them. But the problems of assuring that waterfowl will remain at least as abundant in the immediate future as they are today are not insoluble. One of the most important factors in this regard is the great reservoir of public interest in the welfare of waterfowl, and public support for programs to maintain them in relative abundance.

The fact that this is a matter of national policy at the highest level, as spelled out in formal international treaties and commitments with such countries as Canada, Mexico, Japan, and, most recently, the Soviet Union is a reflection of the depth of this public interest and support.

I think the future of waterfowl in this country will be greatly dependent on how well we waterfowl managers and researchers do our job and maintain our credibility with the public as responsible and objective scientists and administrators. I'm sure it is no secret to many in this audience that waterfowl management today is being criticized and occasionally ridiculed by some as archaic, unnecessary, and even inhumane. In part, this attitude seems to be motivated by a strong and growing anti-hunting sentiment. But, there also seems to be a view that if managers would just leave things alone and let nature take care of fish and wildlife, everything would be just fine.

Lynn Greenwalt, Director of the U.S. Fish and Wildlife Service, recently pointed out that the option of letting nature take its course was set aside more than 200 years ago in North America. If we want waterfowl in abundance in the future, we're going to have to manage for it. Most of us know this, and one of our most important responsibilities is to make our knowledge believable and understood by the public. This task is at least as important as the continuing effort to improve our understanding and our management of these most valuable and attractive birds.

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