

Quantifying interspecific variation in foraging behavior of syntopic *Anas* (Anatidae)

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Foraging behavior of six *Anas* species was studied during autumn at Long Point Bay, southwestern Ontario. Data were collected using Cody's technique, but statistical analyses identified significant differences among species that could not be discerned from qualitative examination of foraging-behavior curves alone. A relationship between similarity in body size and dissimilarity of foraging behavior was observed.

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Le comportement de recherche de nourriture a été étudié chez six espèces d'*Anas* à l'automne, à la baie de Long Point dans le sud-ouest de l'Ontario. Les données ont été recueillies selon la technique de Cody, mais les analyses statistiques révèlent entre les espèces des différences qui n'ont pas été mises en évidence au seul examen qualitatif des courbes de comportement de recherche de nourriture. Les espèces de tailles semblables ont des comportements de recherche de nourriture qui sont différents.

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Introduction

Waterfowl (Anatidae) are increasingly used as subjects to study community structure and resource partitioning among species (e.g., Stott and Olson 1973; White and James 1978; Lack 1974). Cooccurrence of waterfowl species can be attributed to differential macrohabitat utilization in some cases (e.g., Olney 1964), but usually intensive investigation of microhabitat use and (or) foraging behavior (e.g., Siegfried 1976) is needed to demonstrate differential use of resources. As a part of a project on the organization of waterfowl communities, we initiated this pilot study to examine the applicability of feeding-behavior curves (Cody 1968, 1974) for assessing differences in foraging behavior of puddle ducks (*Anas* spp.). We thought that the technique might be particularly useful for examining diet separation of waterfowl because Siegfried (1976) correlated diet differences with differences in foraging behavior of coexisting diving ducks (*Aythya* spp. and *Oxyura jamaicensis*).

Methods

From 2 October to 13 November, 1977, foraging male puddle ducks of six species (gadwall, *Anas strepera*; wigeon, *A. americana*; green-winged teal, *A. crecca*; pintail, *A. acuta*; mallard, *A. platyrhynchos*; and black duck, *A. rubripes*) were observed with a 40× spotting scope on ponds closed to hunting in Long Point Bay, southwestern Ontario. Data on drakes only were recorded in this study to avoid possible problems of sexually dimorphic behavior.

The duration of a foraging bout (a sequence of feeding activity which was considered finished when the bird began another activity, e.g., preening) and the cumulative time a drake spent tipped up were measured on two stopwatches and the number of 'tip-ups' were counted. Each immersion of a bird's head was considered a 'tip-up.' The distance moved by a foraging individual was estimated using stakes and natural landmarks (e.g., stumps, cattail stands, etc.) at known intervals in the ponds. We calculated the average time for each 'tip-up,' the average time spent moving between 'tip-ups,' the velocity of the bird over the foraging bout, the velocity between 'tip-ups,' and the average distance travelled between 'tip-ups.' (Average refers to the components within individual bouts; means of these averages for each species are reported in Table 1.) Movement during 'tip-ups' was negligible.

Results and Discussion

The mean time spent moving between 'tip-ups,' the mean distance moved between 'tip-ups,' and the mean time spent per 'tip-up' (Table 1) were used to plot feeding-behavior curves for each *Anas* species (Fig. 1). Two general foraging patterns were noted. Gadwall and wigeon, relative to the other species, spent more time moving than tipping up and moved more slowly over longer distances between 'tip-ups' (suggesting fine-grained habitat utilization (Cody 1968)). Pintail and green-winged teal spent relatively more time tipping up than moving and moved quickly over short distances between 'tip-ups' (suggesting coarse-grained habitat utilization). Black duck and mallard were intermediate to these generalist (gadwall-wigeon) - specialist (pintail-green-winged teal) foraging patterns. Although Cody (1968, 1974) reported differ-

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TABLE 1. Means (± 1 SD) of feeding behavior components for six *Anas* species. Lines join species that did not differ at $p < 0.05$.^a Numbers in parentheses are sample sizes. The data were log transformed for analysis

Duration of foraging bout ($F = 4.121, p < 0.002$), ^b s					
Gadwall (22)	Teal (19)	Black (11)	Mallard (24)	Wigeon (25)	Pintail (20)
244.9 \pm 40.7	295.9 \pm 49.7	310.2 \pm 81.3	328.5 \pm 48.6	401.3 \pm 66.0	627.5 \pm 83.1
Total time spent tipped up ($F = 8.804, p < 0.002$), s					
Gadwall	Wigeon	Teal	Black	Mallard	Pintail
89.5 \pm 19.5	127.9 \pm 20.7	202.4 \pm 36.4	206.8 \pm 48.7	211.0 \pm 38.8	477.7 \pm 64.1
Total number of 'tip-ups' ($F = 8.985, p < 0.001$)					
Gadwall	Black	Mallard	Wigeon	Teal	Pintail
26 \pm 5	49 \pm 11	57 \pm 10	58 \pm 9	92 \pm 17	139 \pm 20
Total distance moved ($F = 9.647, p < 0.001$), m					
Gadwall	Mallard	Black	Teal	Wigeon	Pintail
5.0 \pm 0.8	6.9 \pm 1.0	7.6 \pm 2.0	7.9 \pm 1.8	10.2 \pm 1.2	19.3 \pm 2.4
Total time spent moving ($F = 5.058, p < 0.001$), s					
Teal	Black	Mallard	Pintail	Gadwall	Wigeon
93.4 \pm 15.3	103.4 \pm 35.7	117.5 \pm 15.6	149.8 \pm 23.0	155.5 \pm 26.3	273.4 \pm 48.6
Average time per 'tip-up' ($F = 16.210, p < 0.001$), s					
Teal	Wigeon	Pintail	Mallard	Gadwall	Black
2.2 \pm 0.2	2.3 \pm 0.2	3.5 \pm 0.1	3.6 \pm 0.2	3.7 \pm 0.3	4.1 \pm 0.2
Average time spent moving between 'tip-ups' ($F = 31.595, p < 0.001$), s					
Pintail	Teal	Black	Mallard	Wigeon	Gadwall
1.2 \pm 0.2	1.2 \pm 0.2	2.3 \pm 0.4	3.3 \pm 0.6	5.7 \pm 0.6	8.0 \pm 1.1
Velocity over entire foraging bout ($F = 1.165, p < 0.331$), m/s					
Gadwall	Mallard	Black	Teal	Pintail	Wigeon
0.02 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01	0.04 \pm 0.01
Velocity per movement between 'tip-ups' ($F = 9.744, p = 0.001$), m/s					
Gadwall	Wigeon	Mallard	Teal	Black	Pintail
0.04 \pm 0.01	0.06 \pm 0.01	0.08 \pm 0.01	0.10 \pm 0.02	0.10 \pm 0.02	0.16 \pm 0.02
Average distance travelled between 'tip-ups' ($F = 3.679, p < 0.004$), m					
Teal	Pintail	Black	Mallard	Gadwall	Wigeon
0.16 \pm 0.02	0.16 \pm 0.02	0.17 \pm 0.03	0.19 \pm 0.03	0.26 \pm 0.04	0.29 \pm 0.06

^aDuncan's multiple range test.

^bAnalysis of variance.

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differences among *specific* foraging behaviors using feeding behavior curves, we found it difficult to see such differences in Fig. 1. However, most species that he examined had very different foraging velocities whereas the *Anas* species did not (Table 1). To further examine foraging differences, and to obtain more precise measures of these differences, we statistically analyzed the components of foraging behavior (Table 1). For each species pair we tallied the number of feeding behavior components, out of a possible 10, that differed ($p < 0.05$) to index overall differences in foraging behavior (Table 2). In this way, we detected differences between species that were not obvious from the feeding curves. Thus, there are two advantages to analyzing the components of anatid foraging behavior

rather than qualitatively assessing differences from feeding behavior curves: (1) differences in foraging behavior can be detected between species that have similar foraging velocities, and (2) an assessment of the probability that the differences are due to chance can be made.

Some evidence suggests that the differences we observed in foraging behavior are ecologically meaningful. First, body size has been implicated as an important variable in which species may differ and reduce niche overlap (e.g., Brown 1973; Schoener 1970), and Olney (1964) and Siegfried (1976) suggested that it is important in resource partitioning by waterfowl. Green-winged teal and black duck – mallard foraging behavior differed in very few components, but similar-sized species

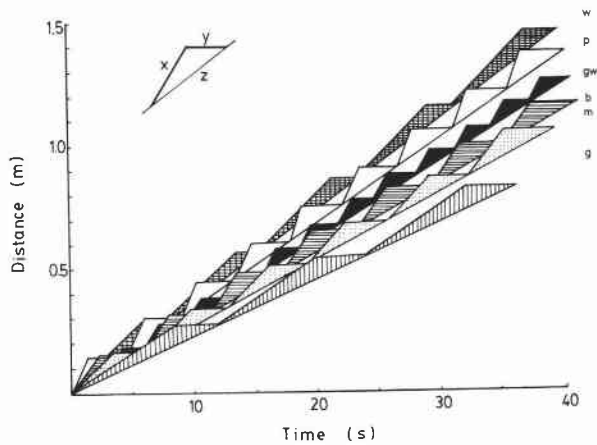


FIG. 1. Feeding behavior curves for six *Anas* species. Each 'sawtooth' is comprised of a diagonal component representing the time and distance travelled between 'tip-ups' (x) and horizontal component representing the duration of a 'tip-up' (y). The diagonal common to all 'sawteeth' (z) for each species represents the velocity over the foraging bout. w , wigeon; p , pintail; gw , green-winged teal; b , black duck; m , mallard; g , gadwall.

TABLE 2. Pairwise comparisons of the number of statistically different ($p < 0.05$) foraging behavior components

	<i>b</i>	<i>g</i>	<i>gw</i>	<i>m</i>	<i>p</i>
<i>g</i>	4				
<i>gw</i>	2	7			
<i>m</i>	0	3	2		
<i>p</i>	6	6	7	6	
<i>w</i>	3	5	3	3	9

NOTE: b , black duck; g , gadwall; gw , green-winged teal; m , mallard; p , pintail; w , wigeon.

differed more (Table 2). To explore this further, we calculated pairwise body-weight ratios (smaller: larger body weights; data from Bellrose (1976)) and plotted these values against the respective pairwise indices of difference in foraging behavior from Table 2 (Fig. 2). Excluding the black duck - mallard pair (see below) there was a significant association ($p < 0.05$, Tukey and Olmstead's corner test; Sokal and Rohlf 1969, p. 538) of increased foraging-behavior differences with increased body-size similarity. This observation is consistent with theoretical (e.g., MacArthur and Levins 1967) and empirical (e.g., Schoener 1970) investigations of the limiting similarity of coexisting species. Second, black duck and mallard were the only species pair that did not differ in at least one component of feeding behavior. Historically, their breeding ranges were largely allopatric and they are considered ecological equivalents (Bellrose 1976); as would be expected, they behaved as one "ecological species" (Cody 1974).

Evaluating foraging behavior using the method

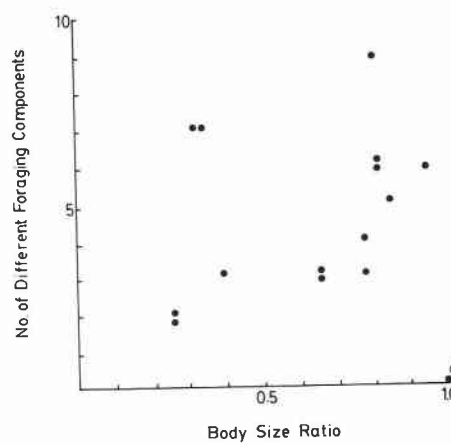


FIG. 2. The relationship between similarity of body size and dissimilarity of foraging behavior for six *Anas* species. a , black duck - mallard.

outlined here showed promise for determining differences in foraging behavior among *Anas* spp. Collecting birds may provide a direct measure of diet differences, but it is not desirable, for example, when studying a community through time. Also, Sugden (1973, p. 12) has pointed out that esophageal and (or) gut contents tend to be variable to the extent that sample sizes must often be governed by logistic, rather than statistical, considerations. Finally, differences in foraging behavior have been linked to differences in diet in several groups of birds (Gibb 1954; MacArthur 1958; Terborgh and Diamond 1970; Siegfried 1976; Baker 1977). The method is being used by one of us (T.D.N.) in an investigation of a waterfowl community in the prairie pothole region of Manitoba.

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