ACTIVITY PATTERNS OF NEARCTIC DABBLING DUCKS WINTERING IN YUCATAN, MEXICO

JOHN D. THOMPSON[1] AND GUY A. BALDASSARRE

Environmental and Forest Biology, State University of New York, College of Environmental Science and Forestry, Syracuse, New York 13210 USA

ABSTRACT.—We spent 1,173 h determining the activity patterns of Blue-winged Teal (*Anas discors*), Northern Shovelers (*A. clypeata*), Northern Pintails (*A. acuta*), and American Wigeon (*A. americana*) in Yucatan, Mexico, from October to March, 1986 to 1988. Feeding (30–50%), locomotion (20–37%), and resting (13–28%) were the dominant behaviors of all species. Preening occurred 4–11%, and ducks spent <4% combined in courtship, comfort, alert, and aggression. Activity patterns generally did not differ within or among species over four phenological time periods during winter, and were similar in the sexes and throughout the day. Activities were similar in all open-water habitats but changed when birds used red mangroves (*Rhizophora mangle*), where resting and preening became dominant. Mild temperatures throughout winter nearly eliminated thermal stress as species spent only 0.0–4.2% of time below their lower critical temperature. We argue that lack of thermal stress increases flexibility in activity patterns and potentially caused the lack of daily, seasonal, and interspecific changes in activity budgets. Such increases in behavioral flexibility and overall energy conservation are probably two major benefits accrued by dabbling ducks wintering in the Neotropics.
Received 2 October 1990, accepted 15 May 1991.

RECENT studies of Nearctic waterfowl have focused on the activities associated with different geographical wintering areas (Paulus 1988). These studies elucidated possible energetic costs and benefits of wintering in given areas, but occurred in temperate climates. This restriction is significant because the winter range of several species of North American waterfowl includes the Neotropics, where environmental conditions are very different from those experienced by conspecifics wintering farther north.

Although migration is an energetically costly event, by choosing to winter in the Neotropics an individual may reap a net benefit by avoiding cold temperatures or food shortages precipitated by snow and ice (Kendeigh et al. 1977). These benefits may influence the activity patterns of wintering ducks by allowing birds to adjust activity patterns to variables other than temperature and food supply (Paulus 1988). We estimated the activity budgets of dabbling ducks wintering in Yucatan, Mexico, to compare and assess potential benefits of wintering in the Neotropics.

STUDY AREA AND METHODS

This study was conducted in the Laguna de Celestun (Celestun Estuary), located on the west coast of the Yucatan Peninsula and adjacent to the village of Celestun (Fig. 1). The Celestun Estuary, part of the Yucatan Lagoons (Saunders and Saunders 1981), is a narrow coastal estuary approximately 25 km long and 0.5–2.5 km wide. It is <1 km inland and is separated from the Gulf of Mexico by a barrier of deciduous scrub thicket, commercial coconut (*Cocos nucifera*) plantations, and smaller seasonal tidal lagoons. The margins of open-water areas support a forest of mangroves (*Rhizophora mangle, Avicennia germinans, Laguncularis racemosa*). The estuary was designated a national park and sanctuary in 1979, but waterfowl hunting is legal immediately adjacent to the park.

The Celestun Estuary and associated wetlands provide the primary wintering area for waterfowl on the Yucatan Peninsula and are the wintering area for approximately 20,000 greater Flamingos (*Phoenicopterus r. ruber*) and 50,000–100,000 American Coots (*Fulica americana*; Baldassarre et al. 1989). From 1970–1988 the number of waterfowl wintering in association with the Yucatan Lagoons averaged >148,000, with Blue-winged Teal (*Anas discors*), Lesser Scaup (*Aythya affinis*), and Ring-necked Ducks (*Aythya collaris*) most abundant (Baldassarre et al. 1989).

A bridge linking Celestun with the mainland bisects the estuary. Our study site (1,200 ha) was the open-water area north of this bridge, and a 0.5-km section south of the bridge. The study area was shallow (<2 m) and ranged in salinity 8–24 PPT. Most of the open water harbored submerged vegetation, including widgeongrass (*Ruppia maritima*), muskgrass (*Chara* spp.), and nitella (*Nitella* spp.).

We quantified activities of Blue-winged Teal, Northern Shovelers (*Anas clypeata*), Northern Pintails

[1] Present address: Max McGraw Wildlife Foundation, P.O. Box 9, Dundee, Illinois 60118 USA.

(*A. acuta*), and American Wigeon (*A. americana*) during four phenological seasons from 7 October to 13 March, 1986–1988. Annual cycle events may influence the behavior of wintering ducks (Heitmeyer 1988). Therefore, birds were sampled within phenological seasons differentiated by migration chronology and weather as follows: (1) *Arrival*—birds begin arriving (October and November), (2) *Early Winter*—bird numbers were stable but winter storm activity (i.e. strong winds and lower temperatures) was minimal (December), (3) *Late Winter*—bird numbers were stable and storm activity increased (1 January to 15 February), and (4) *Departure*—birds migrate from the area (16 February to 15 March). Start and end dates for each phenological season were estimated from migration chronology and long-term weather data, and they were assigned to specific calendar dates for ease of analysis. Migration chronology (J. D. Thompson unpubl. data) was determined by biweekly censuses of the entire study area during both years of the study.

During these seasons, we recorded the behavior of waterfowl in 4 tidal habitats. Habitat 1 (*Lower*) was dominated by widgeongrass and nitella, had sparsely scattered muskgrass, and salinity was 12–24 PPT ($\bar{x}$ = 20.5). Habitat 2 (*Central*) was dominated by nitella and muskgrass, had sparsely scattered widgeongrass, and salinity was 8–20 PPT ($\bar{x}$ = 15.3). Habitat 3 (*Upper*) had a nearly continuous bed of muskgrass, sparsely scattered nitella, and salinity was 10–16 PPT ($\bar{x}$ = 13.5) Habitat 4 (*Mangrove*) had a closed canopy with no submerged vegetation. This habitat was a narrow (<10 m) zone of water and mudflat with overhanging red mangrove branches and prop roots.

We observed from sunrise to sunset during 2 of every 3 days. Each day was divided into 4 equal time blocks (Blocks 1–4) when 2 observers recorded activities of 4 males and 4 females of each species using a focal-animal technique (Baldassarre et al. 1988). Sampling of 4 individuals of each sex and species was the maximum allowable for observers to sample all species within each time block. We attempted to sample both paired and unpaired ducks, however, we observed paired birds rarely on the study area (Thompson 1989). We observed individual birds for 5 min from blinds located throughout the estuary or from a parked vehicle. Activities were recorded at 15-s intervals. Activities were categorized as feeding, resting, locomotion, preening, courtship, comfort, alert, and aggression (Paulus 1980).

Individuals were selected by pointing a 15–60× spotting scope toward a flock and selecting the bird closest to the center of vision. Flocks were selected by partitioning the area around the observation site into 4 equal zones and randomly selecting, without replacement, 1 zone per time block. Species selection was randomized within blocks, and sampling days were assigned randomly, without replacement, to open-water habitat types and blinds. Because of dense vegetation, individual birds were observed in the mangrove type whenever possible. Data were omitted for birds that moved out-of-sight and for observations of <5 min.

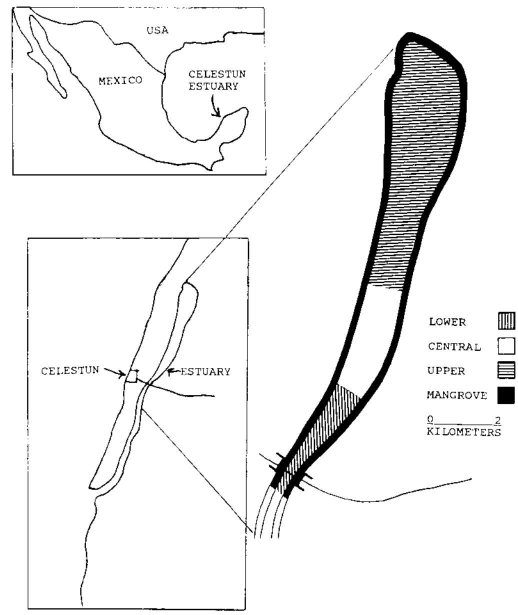

Fig. 1. Location of study area and habitats within the Celestun Estuary in Yucatan, Mexico.

We collected environmental data during each daily time block. Air temperature (°C, recorded every 10 min) and wind velocity (km/h, recorded continuously) were recorded at a portable weather station located at the southern end of the study area (<10 km from observation sites). Cloud cover (%), rainfall intensity, and tide (% of average maximum) were estimated at the beginning of each time block. For analyses, wind velocity was 0–8, 9–16, 17–24, 25–32, and >32 km/h; rainfall intensity was none, light, moderate, and heavy. We obtained long-term weather data recorded in Celestun from the Secretaria de Recursos Hidraulicos, Oficina de Climatologia, Merida, Yucatan.

We used independent sample *t*-tests to compare percent occurrences of each activity between sexes and years. For each species, time spent in each activity between years or sexes differed ($P < 0.05$) in <5% of all seasonal and daily time block comparisons, but most differences were small (<2%). There were few (<4%) differences in activity among daily time blocks. Therefore, we combined data for sexes and years, and all data from blocks were pooled and an average daily percent of time spent in each activity was determined for each species. Sample sizes (Tables 1–4) are the number of days each species was observed per season.

We compared activity among seasons, habitats, and species by analysis of variance (ANOVA) after determining homogeneity of variance and performing arc-

TABLE 1. Mean (±SE) percent of diurnal time spent in each activity within season by Blue-winged Teal in Yucatan, Mexico, 1986–1988. Number of days sampled are in parentheses; different letters within rows indicate statistical significance ($P < 0.05$).

Activity	Arrival[a] (44)	Early Winter (23)	Late Winter (41)	Departure (14)
Feeding	38.0 ± 2.1A	50.4 ± 3.3B	43.4 ± 2.5AB	41.4 ± 6.3AB
Resting	24.7 ± 1.8A	15.6 ± 3.9A	19.7 ± 1.8A	23.3 ± 6.2A
Locomotion	29.9 ± 1.2A	25.6 ± 1.9A	29.7 ± 2.0A	29.6 ± 3.4A
Preening	5.8 ± 0.5A	6.5 ± 1.0A	5.8 ± 0.7A	4.4 ± 0.9A
Courtship	0.0 ± 0.0A	0.0 ± 0.0A	0.1 ± 0.1A	0.1 ± 0.0A
Comfort	1.1 ± 0.1A	1.2 ± 0.2A	1.1 ± 0.1A	0.8 ± 0.1A
Alert	0.4 ± 0.7AB	0.5 ± 0.2A	0.1 ± 0.0B	0.1 ± 0.0B
Aggression	0.1 ± 0.0A	0.2 ± 0.1A	0.1 ± 0.0A	0.3 ± 0.1A

[a] Arrival = 1 October to 30 November, Early = 1–31 December, Late = 1 January to 15 February, Departure = 16 February to 30 March.

sine transformation of nonnormal percentage data (Zar 1974). We used Tukey's studentized range test to compare means following significant ANOVA. Simple correlation analysis (r) was used to determine relationships between activities and environmental variables.

RESULTS

We observed Blue-winged Teal for 368 h (Table 1), Northern Shovelers for 383 h (Table 2), Northern Pintails for 275 h (Table 3), and American Wigeon for 147 h (Table 4). Feeding (30–50%), locomotion (20–37%), and resting (13–28%) were the dominant activities of all species within seasons. Preening occurred 4–11% of the time, and other activities (courtship, comfort, alert, aggression) occurred <4%. Except for feeding by Blue-winged Teal and American Wigeon during Arrival, alert by Blue-winged Teal during Early Winter, and alert by Northern Shovelers during Arrival, activity patterns for each species did not differ ($P > 0.05$) among seasons (Tables 1–4).

Within seasons, activities generally did not vary ($P > 0.05$) among species, and differences that occurred showed few obvious trends (Table 5). Locomotion and alert were most variable among seasons, and behaviors were most different during Arrival. Feeding differed only in American Wigeon during Arrival, after which all species spent similar ($P > 0.05$) amounts of time in feeding, resting, preening, and comfort.

Behavior generally was similar ($P > 0.05$) among open-water habitats but changed within mangrove habitats (Table 6). Blue-winged Teal, Northern Shovelers, and Northern Pintails reduced ($P < 0.05$) locomotion and increased ($P < 0.05$) preening in the mangroves. Northern Pintails rested more ($P < 0.05$) in mangroves, and Northern Shovelers exhibited similar trends. Comfort by Northern Shovelers also was greater ($P < 0.05$) in mangroves than elsewhere. American Wigeon exhibited no habitat-related changes in activity, possibly because they were observed only once in mangroves. Similarly, Northern Pintails were observed once using the Upper habitat.

Tidal amplitude was correlated ($P < 0.001$) with feeding ($r = -0.18$–0.34), resting ($r = 0.15$–

TABLE 2. Mean (±SE) percent of diurnal time spent in each activity within season by Northern Shovelers in Yucatan, Mexico, 1986–1988. Number of days sampled are in parentheses; different letters within rows indicate statistical significance ($P < 0.05$).

Activity	Arrival[a] (44)	Early Winter (24)	Late Winter (40)	Departure (15)
Feeding	38.1 ± 2.2A	45.3 ± 4.9A	40.4 ± 3.8A	50.5 ± 7.2A
Resting	27.5 ± 2.0A	22.1 ± 4.6A	27.6 ± 2.9A	23.4 ± 6.8A
Locomotion	25.0 ± 1.2A	21.7 ± 2.3A	21.6 ± 1.4A	19.7 ± 2.8A
Preening	7.8 ± 0.5A	9.3 ± 1.8A	9.1 ± 1.4A	5.0 ± 0.8A
Courtship	0.0 ± 0.0A	0.0 ± 0.0A	0.0 ± 0.0A	0.0 ± 0.0A
Comfort	1.2 ± 0.1A	1.2 ± 0.2A	1.1 ± 0.1A	1.2 ± 0.2A
Alert	0.3 ± 0.1A	0.3 ± 0.1AB	0.1 ± 0.0B	0.1 ± 0.0AB
Aggression	0.1 ± 0.0A	0.1 ± 0.1A	0.1 ± 0.0A	0.1 ± 0.1A

[a] Arrival = 1 October to 30 November, Early = 1–31 December, Late = 1 January to 15 February, Departure = 16 February to 30 March.

TABLE 3. Mean (±SE) percent of diurnal time spent in each activity within season by Northern Pintails in Yucatan, Mexico, 1986–1988. Number of days sampled are in parentheses; different letters within rows indicate statistical significance ($P < 0.05$).

Activity	Arrival[a] (32)	Early Winter (24)	Late Winter (39)
Feeding	44.9 ± 3.0A	48.3 ± 3.8A	42.1 ± 3.3A
Resting	21.0 ± 1.9A	19.0 ± 4.0A	22.8 ± 2.4A
Locomotion	23.5 ± 1.7A	20.7 ± 2.3A	23.6 ± 2.0A
Preening	7.5 ± 1.0A	9.6 ± 1.3A	9.1 ± 1.4A
Courtship	0.0 ± 0.0A	0.1 ± 0.0A	0.2 ± 0.1A
Comfort	1.6 ± 0.2A	1.3 ± 0.2A	1.3 ± 0.1A
Alert	1.3 ± 0.4A	0.9 ± 0.2A	0.7 ± 0.1A
Aggression	0.2 ± 0.0A	0.1 ± 0.0A	0.2 ± 0.1A

[a] Arrival = 1 October to 30 November, Early = 1–31 December, Late = 1 January to 15 February.

0.18), and locomotion ($r = 0.12$–0.31) for all dabblers except American Wigeon. Feeding decreased, and resting and locomotion increased, when water levels were highest. For American Wigeon, wind velocity was correlated ($P < 0.001$) most strongly with feeding ($r = -0.13$), resting ($r = 0.31$), and locomotion ($r = -0.11$). Correlations between activities and cloud cover, rainfall intensity, and temperature were not significant ($P > 0.05$).

DISCUSSION

Daily and seasonal activity patterns.—Until our study, available evidence indicated that Anatidae exhibited distinct daily and seasonal changes in activity patterns (Paulus 1988). Thus, the relative lack of daily and seasonal changes in activity patterns throughout winter in Yucatan seems significant. We believe that the mild temperatures characteristic of the Neotropics were the most important factor influencing the similarity of these patterns.

Ducks wintering in more northerly areas often exhibit higher feeding rates during nocturnal and early diurnal hours (Paulus 1988). Feeding before and during the colder portions of the day, and resting and preening during the warmer periods, probably achieves a thermodynamic advantage because individuals obtain and use energy when thermal conditions are most demanding (Tamisier 1976, Turnbull and Baldassarre 1987). Jorde (1981) and Hepp (1985) also reported adjustments in activity patterns of wintering waterfowl in response to low temperatures.

Similarly, changes in energetic requirements of wintering ducks are associated with accumulation of lipid reserves, molt, and migration, and are commonly believed to influence seasonal behavior differences. For example, birds typically exhibit high feeding rates in fall (August to November), while acquiring endogenous reserves and undergoing prealternate molt (Paulus 1988). Feeding then decreases and resting increases as birds conserve energy during winter (December to January). Feeding increases during early spring (February to April) due

TABLE 4. Mean (±SE) percent of diurnal time spent in each activity within season by American Wigeon in Yucatan, Mexico, 1986–1988. Number of days sampled are in parentheses; different letters within rows indicate statistical significance ($P < 0.05$).

Activity	Arrival[a] (24)	Early Winter (11)	Late Winter (14)	Departure (12)
Feeding	29.7 ± 3.0A	43.5 ± 5.9AB	41.9 ± 6.4AB	48.7 ± 2.3B
Resting	20.7 ± 2.9A	14.6 ± 2.7A	22.2 ± 5.1A	12.6 ± 1.8A
Locomotion	37.1 ± 2.9A	33.1 ± 5.3A	30.0 ± 5.8A	30.7 ± 2.9A
Preening	11.3 ± 3.1A	6.4 ± 0.9A	5.0 ± 1.2A	6.3 ± 0.9A
Courtship	0.0 ± 0.0A	0.0 ± 0.0A	0.0 ± 0.0A	0.2 ± 0.1A
Comfort	1.0 ± 0.2A	1.3 ± 0.2A	0.7 ± 0.2A	1.2 ± 0.2A
Alert	0.2 ± 0.1A	0.9 ± 0.4A	0.2 ± 0.1A	0.2 ± 0.1A
Aggression	0.0 ± 0.0A	0.2 ± 0.0A	0.0 ± 0.0A	0.1 ± 0.1A

[a] Arrival = 1 October to 30 November, Early = 1–31 December, Late = 1 January to 15 February, Departure = 16 February to 30 March.

TABLE 5. Patterns among species of percent time spent within each activity and season in Yucatan, Mexico, 1986–1988. Only seasons with differences are presented; different letters within rows indicate statistical significance ($P < 0.05$; see Tables 1–4 for means).

Activity/season[a]	Blue-winged Teal	Northern Shoveler	Northern Pintail	American Wigeon
Feeding				
Arrival	AB	AB	A	B
Resting				
Arrival	AB	A	B	AB
Locomotion				
Arrival	AB	AC	C	B
Early	AB	A	A	B
Late	A	B	AB	AB
Departure	AB	A	—	B
Preening				
Arrival	A	AB	A	B
Courtship				
Departure	A	A	—	B
Comfort				
Arrival	A	AB	B	A
Alert				
Arrival	A	A	B	A
Early	AB	A	B	AB
Late	A	A	B	A
Aggression				
Arrival	A	A	B	A
Late	AC	B	A	BC

[a] Arrival = 1 October to 30 November, Early = 1–31 December, Late = 1 January to 15 February, Departure = 15 February to 30 March.

to diminishing food reserves and premigratory hyperphagia (Paulus 1988).

In contrast to temperate wintering areas, temperatures in Yucatan are very mild, and ducks rarely experience *thermal stress* as defined by time spent below lower critical temperature (LCT; Table 7). Blue-winged Teal, Northern Shovelers, Northern Pintails, and American Wigeon experienced temperatures below their LCT only 0.0–4.2% of the time. This contrasts sharply with Mallards and American Wigeon in Alabama, which spent 41–89% and 49–99%, respectively, of time below LCT from November to February (Turnbull 1985). Green-winged Teal in Texas spent 14–96% of the time below LCT from September to March (Baldassarre et al. 1986).

A lack of thermal stress in the Yucatan may explain the absence of both daily and seasonal

TABLE 6. Percent time spent in each activity by habitat for waterfowl wintering in Yucatan Mexico, 1986–1988. Abbreviations: L = Lower, C = Central, U = Upper, and M = Mangrove. The number of observation days is in parentheses. Within species, means for each activity followed by the same letter are not different ($P > 0.05$) among habitat types.

Activity	Blue-winged Teal L (118)	C (30)	U (8)	M (14)	Northern Shoveler L (115)	C (32)	U (10)	M (11)	Northern Pintail L (94)	C (20)	U (1)	M (11)	American Wigeon L (41)	C (22)	U (11)	M (1)
Feeding	43.4A	44.0A	30.8A	39.9A	43.7A	37.9A	38.2A	0.5B	46.6A	41.2A	59.1A	7.7B	37.3A	38.8A	40.9A	12.5A
Resting	20.6A	15.7A	26.0A	24.0A	24.5A	28.3A	22.8A	40.9A	19.2A	19.6A	10.3A	40.4B	17.8A	17.3A	15.0A	22.5A
Locomotion	28.6A	32.7A	37.2A	20.7B	22.7A	23.2A	27.4A	12.6B	23.9A	26.1A	20.9A	10.9B	34.4A	35.0A	34.2A	37.5A
Preening	5.8A	6.2A	3.8A	20.2B	7.6A	9.6A	10.1A	42.9B	7.6A	11.0A	7.8A	40.2B	9.0A	7.2A	8.0A	27.5B
Courtship	0.0A	0.0A	1.3B	0.0A	0.0A	0.0A	0.0A	0.0A	0.1A	0.4B	0.0A	0.0A	0.1A	0.1A	0.2A	0.0A
Comfort	1.1A	1.1A	0.7A	0.8A	1.2A	0.9A	1.4A	3.1B	1.6A	1.1A	1.6A	0.8A	1.0A	1.0B	1.1A	0.0A
Alert	0.3A	0.1A	0.0A	0.4A	0.2A	0.0B	0.0B	0.0B	0.8A	0.5A	0.0B	0.0B	0.3A	0.2A	0.4A	0.0A
Aggression	0.2A	0.2A	0.2A	0.0A	0.2A	0.1A	0.1A	0.0A	0.2A	0.1B	0.3A	0.0B	0.1A	0.4A	0.2A	0.0A

[a] Means < 0.05 shown as 0.00.

TABLE 7. Percentage of time spent below the lower critical temperature (LCT)[ab] of waterfowl in Yucatan, Mexico, 1986–1988.

	1986–1987			1987–1988		
Season[c]	Time below LCT (%)	Temp. when below LCT ($\bar{x}$)	Season temp. ($\bar{x}$)	Time below LCT (%)	Temp. when below LCT ($\bar{x}$)	Season temp. ($\bar{x}$)
			Blue-winged Teal			
Arrival	0.00	—	26.0	0.00	—	24.5
Early Winter	0.00	—	23.7	0.27	16.0	26.5
Late Winter	3.40	14.2	21.7	4.17	14.8	19.0
Departure	0.00	—	23.3	3.59	15.4	23.1
			Northern Shoveler			
Arrival	0.00	—	26.0	0.00	—	24.5
Early Winter	0.00	—	23.7	0.00	13.6	26.5
Late Winter	2.70	13.8	21.7	1.63	13.6	19.0
Departure	0.00	—	23.3	0.98	14.7	23.1
			Northern Pintail			
Arrival	0.00	—	26.0	0.00	—	24.5
Early Winter	0.00	—	23.7	0.00	—	26.5
Late Winter	1.27	12.7	21.7	1.09	13.1	19.0
Departure	0.00	—	23.3	0.00	—	23.1
			American Wigeon			
Arrival	0.00	—	26.0	0.00	—	24.5
Early Winter	0.00	—	23.7	0.00	—	26.5
Late Winter	1.27	12.7	21.7	1.09	13.1	19.0
Departure	0.00	—	23.3	0.00	—	23.1

[a] LCT (°C) = $47.17\ W^{-0.1809}$, where W = body wt. (Kendeigh et al 1977: 135); BWT = 16.3°C, NS = 15.1°C, NP = 14.0°C, AW = 14.2°C.

[b] Body wt. for Blue-winged Teal (360 g), Northern Shovelers (545 g), and Northern Pintails (810 g) from samples collected in Yucatan; for American Wigeon (775 g) from Bellrose (1980).

[c] Arrival = (1 October to 30 November), Early Winter = (1–31 December), Late Winter = (1 January to 15 February), Departure = (15 February to 30 March).

changes in activity patterns because the mild temperatures would reduce energetic demands. The need to accumulate lipid reserves and to conserve energy by resting was reduced (Thompson 1989), and seasonally distinct activity patterns were lost. Similarly, the lack of thermal stress allowed waterfowl in Yucatan to adjust the timing of daily activities to other environmental variables besides temperature (e.g. tide, wind).

Alternatively, the lack of differences in activity patterns may reflect the sanctuary environment. We did not collect data from areas open to hunting, and we made very few nocturnal observations. However, studies of activity budgets from more temperate latitudes also were conducted in sanctuaries (Turnbull and Baldassarre 1987, Bergan et al. 1989, Rave and Baldassarre 1989), or in areas with little hunting pressure (Quinlan and Baldassarre 1984), and birds exhibited distinct changes in both daily and seasonal activity patterns.

Species differences in behavior.—Although some activity patterns differed among species, consistent trends were not evident. In contrast, variation in activity patterns among species of wintering waterfowl in more northerly areas usually is pronounced and has been attributed to differences in the chronology of annual-cycle events (Weller 1965, Hepp and Hair 1983, Miller 1985, Turnbull and Baldassarre 1987) and to differences in diet and energetic requirements (Jorde et al. 1984; Miller 1985; Paulus 1984, 1988; Turnbull and Baldassarre 1987; Rave and Baldassarre 1989). The energetic demands of nonbreeding ducks also vary among species. Generally, larger-bodied species require more energy than smaller birds (Kendeigh et al. 1977, Prince 1979).

Waterfowl species wintering in Yucatan had similar diets (J. D. Thompson unpubl. data). The birds fed only on natural foods as no agricultural land was available. Birds ate primarily small snails (Gastropoda) from October to 15 December and mostly tubercles of muskgrass after mid-December. Although we did not study diets of American Wigeon, they fed in areas dominated by beds of muskgrass, and we suspect that their diets were similar to other species. Muskgrass tubercles were found in the esophagi of American Wigeon collected in Yucatan (Saunders and Saunders 1981).

Diet similarity suggested that, to meet daily energetic requirements, the larger-bodied species (i.e. Northern Pintails) should spend more time feeding than smaller Blue-winged Teals. However, feeding times were similar for all species after Arrival. Reasons for this are unclear, but Pöysä (1983) suggested that larger species of dabbling ducks are better adapted to upending and feed at greater depths. Additionally, it is energetically more profitable for larger species to feed in water depths reached by tipping-up (Pöysä 1983). Ducks in Yucatan fed almost exclusively by tipping-up, which probably was necessary to reach submerged food resources. Presumably, the larger species obtained more food per unit time and spent relatively less energy foraging.

The few interspecific differences in activity budgets observed probably were due to differences in the chronology of annual cycle events.

For example, time spent courting by American Wigeon was higher ($P < 0.05$) than for other species during Departure. Northern Pintails showed similar trends in Early Winter. These differences were probably due to differences in pairing chronology among the four species. Although we observe few paired birds, both Northern Pintails and American Wigeon form pair bonds earlier in the annual cycle than Blue-winged Teal and Northern Shovelers (Weller 1965, Bellrose 1980, Hepp and Hair 1983). Only Northern Pintails and American Wigeon were observed in courting groups.

Influence of habitat and environmental variables.—Habitat-related activity patterns were similar in all species. Resting and preening dominated in red mangroves, while feeding dominated in all open-water habitats. Red mangrove branches and prop roots provided preening and loafing sites, which may be important because very few locations were available for birds to leave the water and preen. Birds in mangroves would climb onto a branch or prop root, preen for a few minutes, and then sleep. Turnbull and Baldassarre (1987) and Rave and Baldassarre (1989) reported similar habitat-based changes in activity, where different habitats were used for various activities.

Although correlations were weak, environmental variables affected waterfowl in Yucatan, especially when high water levels prevented birds from feeding. Feeding decreased when water levels were high. Presumably ducks had difficulty reaching submerged vegetation. Tidal cycles influenced activity patterns (Paulus 1988), and ducks rest during high tides and feed at low tides (Burton and Hudson 1978). Wind also affected activity, largely in the Upper habitat where the estuary was widest, was least influenced by tides, and had the highest wind velocity at the water surface. American Wigeon spent more time feeding in the Upper habitat, while species in other habitats seemingly could not easily reach submerged vegetation. Therefore, waterfowl habitat use and foraging activity may be influenced more by wind velocity and associated wave amplitude of the Upper habitat than by water depth. When tides were high in the Upper habitat, American Wigeon fed on submerged vegetation brought to the surface by diving American Coots. This behavior is similar to Eurasian Wigeon (*Anas penelope*) behavior during floods in Great Britain (Owen and Thomas 1979).

ACKNOWLEDGMENTS

Financial support was provided by the North American Wildlife Foundation through the Delta Waterfowl and Wetlands Research Station. Housing and logistical support were provided at the Ducks Unlimited of Mexico Center for the Investigation of Aquatic Birds in Celestun, Yucatan, Mexico. We especially thank B. J. Sheffer for assistance with all aspects of this study. J. R. Singleton, R. Espino-Barros G., and J. F. Losano M. assisted in various ways.

LITERATURE CITED

BALDASSARRE, G. A., A. BRAZDA, & E. RANGEL-WOODYARD. 1989. The east coast of Mexico. Pp. 407–425 *in* Habitat management for migrating and wintering waterfowl in North America (L. M. Smith, R. Pederson, and R. M. Kaminski, Eds.). Lubbock, Texas Tech. Press.

———, S. L. PAULUS, A. TAMISIER, & R. D. TITMAN. 1988. Workshop summary: techniques for timing activity of wintering waterfowl. Pp. 181–188 *in* Waterfowl in winter (M. W. Weller, Ed.). Minneapolis, Univ. Minnesota Press.

———, R. J. WHYTE, & E. G. BOLEN. 1986. Body weight and carcass composition of nonbreeding Green-winged Teal on the Southern High Plains of Texas. J. Wildl. Manage. 50: 420–426.

BELLROSE, F. C. 1980. Ducks, geese, and swans of North America. Harrisburg, Pennsylvania, Stackpole Books.

BERGAN, J. F., L. M. SMITH, & J. J. MAYER. 1989. Time-activity budgets of diving ducks wintering in South Carolina. J. Wildl. Manage. 53: 769–776.

BURTON, B. A., & R. J. HUDSON. 1978. Activity budgets of Lesser Snow Geese wintering on the Fraser River Estuary, British Columbia. Wildfowl 29: 111–117.

HEITMEYER, M. E. 1988. Body composition of female Mallards in winter in relation to annual cycle events. Condor 90: 669–680.

HEPP, G. R. 1985. Effects of environmental parameters on the foraging behavior of three species of wintering dabbling ducks (Anatini). Can. J. Zool. 63: 289–294.

———, & J. D. HAIR. 1983. Reproductive behavior and pairing chronology in wintering dabbling ducks. Wilson Bull. 95: 675–682.

JORDE, D. G. 1981. Winter and spring staging ecology of Mallards in south central Nebraska. M.S. thesis, Grand Forks, Univ. North Dakota.

———, G. L. KRAPU, R. D. CRAWFORD, & M. A. HAY. 1984. Effects of weather on habitat selection and behavior of Mallards wintering in Nebraska. Condor 86: 259–265.

KENDEIGH, S. C., V. R. DOL'NIK, & V. M. GAVRILOV. 1977. Avian energetics. Pp. 127–204 *in* Granivorous birds in ecosystems (J. Pinowski, and S. C. Kendeigh, Eds.). London, Cambridge Univ. Press.

MILLER, M. R. 1985. Time budgets of Northern Pintails wintering in the Sacramento Valley, California. Wildfowl 36: 53–64.

OWEN, M., & G. J. THOMAS. 1979. The feeding ecology and conservation of Wigeon wintering at the Ouse Washes, England. J. Appl. Ecol. 16: 795–809.

PAULUS, S. L. 1980. The winter ecology of the Gadwall in Louisiana. M.S. thesis, Grand Forks, Univ. North Dakota.

———. 1984. Activity budgets of nonbreeding Gadwalls in Louisiana. J. Wildl. Manage. 48: 371–380.

———. 1988. Time activity budgets of non-breeding Anatidae: a review. Pp. 135–152 *in* Waterfowl in winter (M. W. Weller, Ed.). Minneapolis, Univ. Minnesota Press.

PÖYSÄ, H. 1983. Morphology-mediated niche organization in a guild of dabbling ducks. Ornis Scandinavica 14: 317–326.

PRINCE, H. H. 1979. Bioenergetics of postbreeding dabbling ducks. Pp. 103–117 *in* Waterfowl and wetlands—an integrated review (T. A. Bookhout, Ed.). La Crosse, Wisconsin, LaCrosse Printing Co., Inc.

QUINLAN, E. E., & G. A. BALDASSARRE. 1984. Activity budgets of nonbreeding Green-winged Teal on playa lakes in Texas. J. Wildl. Manage. 48: 838–845.

RAVE, D. P., & G. A. BALDASSARRE. 1989. Activity budget of Green-winged Teal wintering in coastal wetlands of Louisiana. J. Wildl. Manage. 53: 753–759.

SAUNDERS, G. B., & D. C. SAUNDERS. 1981. Waterfowl and their wintering grounds in Mexico, 1937–64. U.S. Fish Wildl. Serv. Resour. Publ. 138.

TAMISIER, A. 1976. Diurnal activities of Green-winged Teal and Pintail wintering in Louisiana. Wildfowl 27: 19–32.

THOMPSON, J. D. 1989. Behavioral ecology and carcass composition of waterfowl wintering in Yucatan, Mexico. Ph.D. dissertation, Syracuse, State Univ. of New York.

TURNBULL, R. E. 1985. Activity budgets of Mallards and American Wigeon wintering at Eufaula National Wildlife Refuge, Alabama-Georgia. M.S. thesis, Auburn, Alabama, Auburn Univ.

———, & G. A. BALDASSARRE. 1987. Activity budgets of Mallards and American Wigeon wintering in east-central Alabama. Wilson Bull. 99: 457–464.

WELLER, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). Auk 82: 227–235.

ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice-Hall.