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Behavioral Energetics of Wintering Black Ducks

University — Université

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Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M.Sc.

Year this degree conferred — Année d'obtention de ce grade

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BEHAVIORAL ENERGETICS
of
OVERWINTERING BLACK DUCKS (Anas rubripes)

by

© LYNN BRODSKY, B. Sc.

A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfilment of the requirements for the degree of
MASTER OF SCIENCE

Department of Biology
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1982

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ABSTRACT

Wintering activities of Black ducks (Anas rubripes) were examined near Ottawa, Ontario at three discrete sites differing considerably on the basis of available energy, to determine how environmental conditions influenced their behavior.

Ducks responded to colder temperatures by reducing energetically costly activities and increasing resting or foraging activity. This trend was consistent at each site but was most pronounced at the low energy site.

Initiation of courtship occurred earliest at the high energy site. In addition, these ducks had progressed furthest through the sequence of courtship by the time of spring dispersal.

Diving black ducks had lower foraging success than ducks tipping up and these differences were attributed to the lack of morphological adaptations required for diving and/or inexperience in utilizing diving as a foraging method.

Black ducks roosted in a sheltered habitat, spent more time here on cold days and adopted specific postures and orientations which reduced heat loss while roosting.

ACKNOWLEDGEMENTS

To Patrick J. Weatherhead, whose endless support and valuable guidance have aided me immeasurably.

To H.G. Merriam and C.A. Barlow for their continued encouragement and constructive advice throughout my years of study at Carleton.

To my dear friends, Connie Gaudet, Judy Geggie and Marty Leonard for moral support and helpful suggestions.

To Jan Sharkey-Thomas for her warm hospitality and her generosity in providing food for one hungry population of wintering ducks.

To Carleton University and NSERC for their financial assistance.

And finally, to Michael and Jessie for their most appreciated field assistance on weekends and for tolerating my long working hours.

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GENERAL INTRODUCTION

The black duck (Anas rubripes) is one of the common dabbling duck species in North America. Its range is restricted to the central and eastern regions of the continent (Johnsgard 1975). Because of its economic importance and its recreational value, much work had been done to elucidate the breeding biology of this species (e.g. Stotts and Davis 1960, Coulter and Miller 1968, Reinecke 1980). However, as with most avian research, little work has been done on the post-breeding ecology which encompasses sixty percent of the annual cycle. One period during the post breeding stage, particularly interesting because of its influence on the subsequent breeding season, is the winter. Most black ducks utilize the marine habitats of the eastern United States as wintering grounds (Johnsgard 1975), but several populations are known to winter in more northerly regions such as Ontario, Quebec and the maritime provinces (Godfrey 1979).

The winter period poses special problems for black ducks, especially those that winter at their northern extreme because of cold temperatures and lowered food supply. Calder and King (1974) argued that thermoregulation aids birds in surviving periods of environmental stress, and the literature abounds with studies concerning the physiological (increased fat

deposits) and morphological (plumage insulation) adaptations which enable birds to tolerate these extreme conditions (see Kendeigh et al. 1977 for a comprehensive review). However, few studies to date have concentrated on the behavioral adjustments birds adopt in response to winter conditions, although several authors have stressed its importance (Dawson and Hudson 1970, Calder and King 1974). The ultimate aim of this study was to examine the activities of black ducks wintering in Eastern Ontario and to determine how they modify their behavior in order to tolerate the stresses imposed by a winter environment.

The first chapter deals with time-energy budgeting in this species. Pianka (1974) suggested that varying the time-energy budget is a potent means of coping with environmental stress and the manner in which an organism budgets its available resources is of fundamental importance in determining how well adapted it is to its environment. The aim of this chapter was to determine if black ducks modify their time-energy budgets in response to environmental conditions and if the degree of these modifications reflect the level of environmental stress.

Chapter 2 specifically examines courtship behavior which usually peaks during the winter months. Prince (1979) stated that most of the available time and energy resources are required for individual maintenance

activities in the winter since thermoregulatory costs are high and food supplies are low. However, ducks must allocate resources to courtship activity to realize future reproductive success. The aim of this chapter was to determine how the availability of resources influences the courtship activity of black ducks.

The third chapter involves the foraging activities of wintering black ducks. Black ducks normally feed by tipping up in shallow water areas, however cold temperatures restrict the foraging activities of black ducks to deep, fast flowing areas, forcing diving activity. The purpose of this chapter was to examine the foraging success of diving black ducks when compared with ducks tipping up and to determine what factors influence their foraging success.

Chapter 4 considers the modes of behavioral thermoregulation adopted by wintering black ducks. The aim of this chapter was to determine if black ducks adjust their roosting behavior in response to climatic conditions and if so, do these adjustments serve to lower thermoregulation costs.

**CHAPTER 1. TIME-ENERGY BUDGETING IN
WINTERING BLACKS DUCKS**

INTRODUCTION

King (1974) argued that both an organism's abiotic and biotic environments significantly influence the ways in which it allocates its available resources. Abiotic factors such as microclimatological agents will determine how much energy an animal must ingest in order to be in an energy balance with its environment (Schoener 1971), and thus dictate how much time and energy must be devoted to foraging. Biotic factors, such as the intensity of competition and predation will influence how much time and energy an animal must devote to resource defence and in defence against predators (Pianka 1974). To understand the complex interactions between an organism and its environment, and to ascertain what physiological and behavioral modifications they adopt to survive the pressures imposed by their environment, recent studies in avian ecology have focussed on how birds allocate their available time and energy resources. One method frequently used to study these interactions is the estimation of time-energy budgets. This requires the initial construction of a time-activity budget which describes the allocation of time resources to various activities such as foraging, locomotion and resting. To obtain a time-energy budget from this information, the energetic costs of these activities must be estimated

and multiplied by the amount of time spent per activity. The critical element in this procedure is the estimation of the energy costs of the various activities, and in the past decade, several techniques such as heart rate telemetry (Owen 1969) and doubly labelled water (Utter and Lefebvre 1973) have been developed to estimate these costs (for a general overview see Gessamen 1973).

Although interrelated, time and energy are basically separate resources. Wolf and Hainsworth (1971) postulated that energy intake (requiring the use of time) for essential activities, and the allocation of time for these same activities cannot simultaneously be maximized. It follows therefore, as a reasonable hypothesis, that natural selection favors those animals that are able to optimize the allocation of time and energy resources required for self-maintenance and reproduction (Verner 1965).

Pianka (1974) argued that varying the time-energy budget is a potent means of coping with environmental stress and thus the manner in which an organism allocates or budgets their available resources is of fundamental importance in determining how well adapted it is to its environment. Hainsworth (1981) stated that animals must have a carefully regulated time-energy budget such that energy inputs equal energy outputs. Therefore, the time-energy budget adopted by an organism should exhibit a degree of flexibility in order to meet

the constraints imposed by the environment. One way to test this hypothesis is by examining the time-energy budgets of organisms during environmentally stressful periods.

Many studies have tested this hypothesis on waterfowl species because of their ease of observation. Several studies (Siegfried 1974, Dwyer 1975, Bruggers and Jackson 1977, Asplund 1981, Titman 1981) have examined time-activity budgets in waterfowl during the breeding period when females are under energetic stress since they require a large amount of energy to maintain themselves, as well as produce eggs. King (1973) estimated that egg production in ducks required an increase of 50 to 70 percent above the daily energy intake necessary for general maintenance. Because the female assumes sole responsibility for the nest and invests more energy than the male in reproduction, the general hypothesis that was tested in these studies was that the time-activity budgets of females would differ from males as a result of differences experienced in terms of energetic stress. All of these studies report that the time budgets differed between males and females mainly as a result of the differences in time spent foraging. Since females required more resources for reproduction, they increased the amount of time spent foraging, thereby increasing energy stores.

Although the stress imposed on female ducks during the breeding season is high (Owen and Reinecke 1979), the energetic stress imposed upon both male and female ducks during the winter months is among the most critical in the animals' life (Smith and Prince 1973). Kricher (1973) reported that winter presents a very distinct series of stresses to avian populations, differing considerably from those during the nesting season. Prince (1979) argues that the energetic demands on post-breeding ducks are diverse and at times so demanding that the periods of climatic stress experienced by birds in winter may approach the energetic demands of breeding.

The ability of birds to survive cold temperatures and reduced food supply during winter depends on insulative, metabolic and other physiological responses, as well as behavioral responses, which favor homeostasis (Chaffee and Roberts 1971). Calder and King (1974) discuss in detail the many physiological attributes adopted by birds such as increased feather insulation, increased fat deposits, which enable them to reduce energetic stress. Studies dealing with these physiological adaptations abound in the literature (see Kendeigh et al. 1977 for a comprehensive review). However, to date few studies have examined the behavioral adaptations adopted by birds in order to reduce winter stress, apart from studies concerning

migration and torpidity (King 1974).

In light of the modifications in the time-activity budgets adopted by female ducks during the breeding season, one could hypothesize that wintering ducks, in response to both climatic and energetic stress, modify their behavior to cope with the environmental pressures experienced in winter. The energetic cost of thermoregulation increases as the difference between body temperature and ambient temperature increase thereby making energetic costs of thermoregulation greater on colder days. Furthermore, Kontogiannis (1968) stated that the energy cost of activity was greater at higher levels of climatic stress and West (1968) argued that vigorous activities serve to reduce the insulative capacity of the feathers and thus increase heat loss. Therefore, as climatic stress is heightened, modifications to time-energy budgets would increase as the organism attempts to tolerate the stress imposed by the environment. For instance, Bennett and Bolen (1978) determined that the onset of severe weather, particularly decreasing ambient temperatures served to increase stress levels in wintering Green-winged Teal (Anas crecca).

The modifications adopted by wintering birds should not only account for the climatic stress imposed upon the bird, but should also reflect the energetic stress experienced. It is hypothesized that a greater resource

base (in terms of energy) would enable an organism to tolerate climatic stress better than one with fewer resources and the degree of modification adopted would be less since they would have more energy remaining after thermoregulatory costs to devote to other activities. If the food supply is poor, the degree of modification adopted should be greater in order to economize scarce resources as organisms attempt to meet the energetic demands they are experiencing.

The purpose of this study was to examine time-activity budgeting in three populations of black ducks (Anas rubripes) wintering in a cold temperate region, and differing considerably on the basis of available energy and to determine i) what climatic variables best define climatic stress; ii) do the modifications ducks adopt in response to climatic stress serve to balance their daily energy budget, and if they do, iii) does the degree of behavioral modification adopted reflect the level of energetic stress experienced. I hypothesize that the time-activity budget of the populations will vary in response to differing levels of climatic stress, and the degree of modification adopted will be greatest in the population with the least amount of energy available.

STUDY AREAS

All study areas were located within 20 km of Ottawa, Ontario. Site A, located near Manotick Ontario on the Rideau River supported 250 black ducks as well as approximately 450 mallards. Weekly counts of this population indicated that the size remained constant throughout the study period. Fast flowing water from a dam situated 200 m upstream prevented the Rideau River from freezing in the vicinity of the roost site. The feeding station, where 50 kg of cracked corn was provided daily by a local resident, was located 3 km north of the roost. Ducks made daily flights to and from this feeding station. There were approximately 185 ducks which overwintered at site B (located at Shirley's Bay on the Ottawa River) throughout the study period. A creek flowed into this bay carrying in warmed tertiary wastes from a nearby sewage treatment plant. This effluent prevented ice formation in the shallow waters in the bay area which contained a high density of aquatic plants. The ducks obtained these aquatic plants by tipping upside down in the water. The smallest population overwintered at site C on the Rideau River near Carleton University. In December, approximately 250 black ducks were observed to dabble and tip-up in the shallow waters at this site. However, the cold temperatures froze the shallow waters and only deep,

fast flowing areas remained open. Because of this reduction in foraging area, the majority of these ducks flew to other wintering grounds, leaving only ten ducks. Although these remaining ten ducks did not follow the flock, they were observed to fly short distances on several occasions (due to disturbance), as well as fly from this wintering site in early spring demonstrating that they were not injured and that they could in fact fly.

METHODS

Assessing Available Energy Resources

To determine the extent of the difference in energy available to ducks in each of the three sites, the quantity of food at each site was estimated.

Site A: The quantity of food available daily per duck was estimated by dividing the weight of corn provided by the number of ducks feeding. The energetic value of corn obtained from Kendeigh and West (1965) was expressed as a dry weight measure, but the weight of corn estimated in this study included moisture content. The weight was thus reduced by 15 per cent (Wiens and Dyer 1975) to allow for water content and then multiplied by the energetic value in order to obtain an estimate of daily energy intake.

Sites B and C: The sizes of the foraging areas used by ducks throughout the study period were measured. To estimate the density of vegetation in these areas, two sets of fifteen random samples were obtained. Sampling was done by placing a frame of known size into a randomly chosen area and collecting all of the vegetation within the frame. At site B, a 0.5 square metre frame was used for collecting samples, while at site C, a 0.01 square metre frame was used. Samples were not collected until late March to avoid disturbing

the foraging ducks. One set of samples was collected from open water areas where the ducks had been foraging all winter, and a second set was obtained from frozen areas immediately adjacent to the open areas by digging through the ice layer. Open area samples allowed identification of the plant species taken by the ducks.

Samples were taken from frozen areas to estimate the plant density of the open water areas before the black ducks began feeding there, assuming that the density of plants in the frozen areas immediately adjacent to the open areas was the same before the black duck arrived. Physical characteristics such as turbidity, water depth, water velocity and substrate were measured at both frozen and open water areas and were found to be very similar.

The vegetation samples were identified to genus. With these aquatic plants, little interspecific variation exists with regard to energetic values in winter (Cummins and Wuycheck 1971) and thus classification to the generic level was sufficient. The samples were weighed with an electronic balance and after drying in a 60 degree C oven for three days, were reweighed. This dry weight was converted to a density measure by dividing by the size of the sampling frame used for collection.

Assessing the Influence of Environmental Stress
on the Allocation of Resources

To determine the behavioral modifications adopted by ducks in response to differing levels of climatic and energetic stress, the activities of ducks at the three sites were examined under a wide range of temperatures, windspeeds and cloud cover. The activities of ducks at sites A, B and C were recorded using the scan sampling technique (Altmann 1974). The activity of the duck furthest to the left of the population was initially examined and recorded for a five second period and then the activity of the duck to the immediate right of that just observed was similarly monitored.. This procedure was repeated until all the population had been examined and then it was reinitiated, beginning again with the duck furthest to the left. The activities which were monitored include foraging, resting, swimming, flight, comfort (preening, bathing etc. as described by McKinney (1960) and courtship. The entire population was examined in this manner for a sixty minute period yielding approximately 720 observations. A spotting scope was used permitting accurate observations up to 50 m away. Observations were made during the period of 14 January to 21 March at site A; 12 January to 28 February at site B and 1 January to 21 March at site C.

For each hour of observation, temperature and

windspeed were recorded with a hot wire anemometer and cloud cover (percentage of sky covered in clouds) was estimated in order to obtain a measure of the environmental conditions experienced and thus assess the ducks' behavior with regard to these conditions. All daylight hours were sampled (from 0700 to 1700 EST) with equal frequency to prevent any temporal biases. The total number of hours of observation was 175 at site A; 135 at site B and 190 at site C.

The proportion of observations in which a given activity was recorded was determined by dividing the number of times a particular activity was observed during a time period by the total number of observations obtained during that same time period. These proportions were then used to construct an overall time budget.

RESULTS

Assessing Available Energy Resources

While ducks at site A fed exclusively on cracked corn, the vegetation samples showed the principle foods at sites B and C to be water milfoil (Myriophyllum) and filamentous algae (Cladophora) respectively. Although invertebrates were observed on the underside of rocks at site C, it is unlikely the foraging ducks could dislodge these rocks to obtain the invertebrates (see Chapter 3).

To determine the biomass of food available per duck at each site, the total estimated biomass at a site was divided by the number of ducks feeding. Multiplying this value by the energy value of the food at that site and dividing by the number of days the ducks were resident at the site provided an estimate of the energy available per duck per day (Table 1). From these calculations, it is apparent that ducks at site A had the most energy available, ducks at site B an intermediate amount and ducks at site C the least.

Although the ducks at site A had the greatest amount of energy available and ducks at site C the least, the estimated g/duck/day did not differ considerably in magnitude. Therefore, the differences in available energy are due primarily to the differences in the energy content of the food source.

Table 1-1. Estimated energy available to ducks at sites A, B and C.

Food Source	A			B	C
	<u>Zea mays</u>	<u>Myriophyllum</u>	<u>Cladophora</u>		
Energetic Value in dry g/m ²	18.0	13.4	8.8		
Estimated density in dry g/m ²	--	13.1 ± 4.9	11.6 ± 4.2		
Estimated size of foraging area in m ²	--	62,500	2,750		
Total biomass in g	2.76 × 10 ⁶	8.19 × 10 ⁵	3.14 × 10 ⁴		
Number of foraging ducks	550	185	8		
Number of days ducks at the site	65	67	65		
Estimated g/duck/day	77.2	66.1	61.3		
Estimated available energy in kJoules/duck/day	1390.9	885.7	539.8		

These estimates of the amount of energy (ME) available per duck are presumably too high since these values are based strictly on energetic values of the food and not on the metabolizable energy these foods provide for ducks. For instance, although the energetic value of cracked corn is 18.0 kJoules/g dry wt., Hill (1969) estimated the ME as 14.2 kJoules/g in domestic ducks (Anas spp.). Although this overestimation is consistent for each site, the relative magnitude of this overestimation likely differs as a result of differences in assimilation efficiencies (AE) of the foods consumed. Ricklefs (1976) stated that the AE derived from plant material varies with the proportion of cellulose, lignin, and other indigestible materials found within plants. He reported that the AE for seed diets, such as cracked corn at site A, can be as high as 80 per cent, while the AE for mature foliage such as Myriophyllum and Cladophora found at sites B and C respectively, is only 30 to 40 percent. Sugden (1973) determined the ME of 18 species of plant foods found commonly in the diet of wild ducks. He found the ME derived from both Myriophyllum and Cladophora to be less than 40 percent of the gross energetic value. Although the ME values measured with captive ducks may not reflect values for the same food in the wild, they indicated the relative ME of the different food items and demonstrated that the ME of corn is higher than that of the two aquatic

plants. These differences in AE would serve to further increase the differences in the amount of energy available between site A and sites B and C. Thus the assumption of substantial differences in energy available per duck at sites A, B and C (ratio of 2.5:1.5:1 respectively) is valid and conservative.

Assessing the Influence of Climatic Variables on Behavior

In order to determine what climatic factors influenced the percent time devoted to a particular activity, a multiple linear regression (MLR) analysis was performed. Since one of the stipulations of this model is that residuals are normally distributed, Kolmogorov-Smirnov tests were performed to ensure that this in fact was the case.

Using the SPSS MLR program (Nie et al. 1975), a number of statistical parameters were computed. The overall F test was calculated to determine if the independent variables (climatic factors) significantly contributed to the prediction of the dependent variable (percent time spent/activity). The cumulative R value, which represents the proportion of variation in the dependent variable explained by the independent variable, was calculated to determine how well the latter predicted the former. Since a stepwise regression program was employed for the calculations,

the order of inclusion of the independent variables was determined by the respective contribution of each variable to the explained variance. Regression coefficients (B) were calculated to measure the linear association between the amount of time spent in an activity versus the particular environmental parameter. The partial F test was also calculated in order to assess whether or not the addition of any specific independent variable in the regression model significantly improved the prediction of the dependent variable given that the other variables are in the model.

i) Foraging

The MLR analysis (Table 2) revealed that the length of time spent foraging at site A was independent of the environmental parameters measured. However, the significant negative regression coefficient calculated for site B between temperature and time spent foraging implies that as temperature decreased, the amount of time spent foraging increased. Conversely, at site C, a significant positive B value suggests, as climatic stress increased, the time spent foraging decreased. These results indicate that ducks at site A did not modify their foraging activity in response to differing

Table 1-2. Multiple linear regression analysis to determine the effect of climatic variables on percent of time spent foraging.

Site A (N = 175 hours)				
Weather Variables	Cumulative R^2	B	B Std.E.	Partial F
Cloud Cover	.032	-1.12	.465	5.86
Windspeed	.054	-0.61	.266	5.17
Temperature	.064	-0.42	.293	2.04
Overall F = 3.65				
Site B (N = 135 hours)				
Weather Variables	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.268	-1.38	.274	25.43**
Windspeed	.273	0.34	.094	0.75
Cloud Cover	.277	-0.12	.073	0.48
Overall F = 19.36**				
Site C (N = 190 hours)				
Weather Variables	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.452	1.42	.101	198.41**
Windspeed	.550	-0.53	.083	41.15
Cloud Cover	.551	0.11	.017	0.36
Overall F = 76.24**				
p < 0.01 *				
p < 0.001 **				

levels of climatic stress, but the other two populations did in fact respond by either increasing or decreasing the amount of time allocated to foraging activity.

ii) Resting

Time spent resting was also correlated with temperature at all three sites (Table 3). At sites A and C, temperature and time spent resting were negatively correlated. Also, resting activity increased as windspeed increased. Ducks at sites A and C were thus observed to respond to periods of high climatic stress by increasing the amount of time resting. This increase in resting activity at site C is concomitant with the observed decrease in foraging activity.

Ducks at site B rested less at lower temperatures, as indicated by the positive regression coefficient calculated. They responded somewhat differently to periods of climatic stress from the other two populations. Rather than increase the amount of time devoted to resting, they increased the time devoted to foraging.

iii) Locomotion: Swimming and Flight

A significant amount of the variation observed in the time spent swimming at all three sites was explained by temperature (Table 4); as temperature decreased, the amount of time spent swimming also decreased. Therefore

Table 1-3. Multiple linear regression analysis to determine the effect of climatic variables on the percent time spent resting.

Weather Variables	Site A (N = 175 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.17	-1.21	.221	30.00**
Windspeed	.205	0.55	.201	7.44
Cloud Cover	.221	0.67	.351	3.59
Overall F = 16.22**				

Weather Variables	Site B (N = 135 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.205	-1.54	.254	36.60**
Windspeed	.255	0.47	.161	8.54
Cloud Cover	.264	0.48	.366	1.71
Overall F = 15.70**				

Weather Variables	Site C (N = 190 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.465	-2.35	.160	214.42**
Windspeed	.564	0.85	.131	31.82
Cloud Cover	.564	0.04	.021	0.02
Overall F = 80.44**				

p < 0.01 *

p < 0.001 **

Table 1-4. Multiple linear regression analysis to determine the effect of climatic variables on percent of time spent swimming.

Weather Variables	Site A (N = 175 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.225	0.41	.065	40.20**
Windspeed	.251	-0.15	.059	6.09
Cloud Cover	.252	-0.04	.010	0.16
Overall F = 19.19**				

Weather Variables	Site B (N = 135 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.142	0.33	.087	13.72**
Windspeed	.202	-0.18	.056	10.37*
Cloud Cover	.218	0.21	.126	2.78
Overall F = 12.21**				

Weather Variables	Site C (N = 190 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.267	0.42	.049	74.47**
Windspeed	.338	-0.19	.040	22.86*
Cloud Cover	.363	-0.24	.086	7.38
Overall F = 35.33**				

p < 0.01 *

p < 0.001**

ducks at all 3 sites modified the time allocated to swimming in response to differing levels of climatic stress.

Only ducks at site A flew regularly. Ducks at sites B and C roosted and foraged in the same area and thus the need for flight was negligible. Ducks at site A fed approximately 3 km from their roost and thus they had to fly each day to and from their roost to feed. The duration of a one way flight was approximately 11 minutes from the time they left the roost until they landed (see Chapter 4). Short flights were also observed while at the feeding station where these birds flew from the water to feed. As well, these birds were quite timid, and thus easily disturbed which increased the time spent flying. The ducks left their roost in the morning to feed and returned in mid-afternoon. Therefore, the length of time spent in flight during an observation period was dependent upon the time of day and the amount of disturbance observed. However, as indicated in Table 5, the amount of time spent flying was independent of the environmental parameters measured.

iv) Comfort Activity

Although comfort activities include such behaviors as bathing and wingflapping, the most prevalent comfort activity adopted by ducks was preening (accounting for

Table 1-5. Multiple linear regression analysis
to determine the effect of climatic variables
on percent of time spent flying.

Weather Variables	Site A (N = 175 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.004	0.03	.190	.66
Windspeed	.005	0.09	.173	0.27
Cloud Cover	.006	0.24	.302	0.16
Overall F = 1.05				
p < 0.01 *				
p < 0.001 **				

over 90 percent of the comfort activity observed). For the purposes of this study therefore, the terms comfort activity and preening will be considered synonymous. Only a small amount of the variation observed in the time spent preening at each site was explained by the environmental variables (Table 6) and therefore fluctuations in these parameters did not influence preening activity. Therefore, ducks from each population did not modify the time allocated to preening in response to differing levels of climatic stress.

v) Courtship

The effect of environmental parameters on the time spent in courtship activities was analyzed only for site A because ducks at sites B and C initiated this activity considerably later (see Chapter 2). and thus too few data were available for analysis.

A significant amount of variation observed in the time spent courting was explained by temperature (Table 7). As the temperature increased, ducks at site A spent significantly more time courting.

Table 1-6. Multiple linear regression analysis to determine the effect of climatic variables on percent of time spent in comfort activity.

Weather Variables	Site A (N = 175 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Cloud Cover	.012	0.28	.214	1.72
Temperature	.020	0.18	.435	1.70
Windspeed	.022	0.08	.123	0.42
Overall F = 1.73				

Weather Variables	Site B (N = 135 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.058	-0.29	.133	4.55
Windspeed	.074	-0.13	.085	2.27
Cloud Cover	.080	-0.18	.019	0.92
Overall F = 3.84				

Weather Variables	Site C (N = 190 hours)			
	Cumulative R^2	B	B Std.E.	Partial F
Temperature	.065	0.44	.114	4.99
Windspeed	.078	-0.08	.059	3.27
Cloud Cover	.083	-0.42	.201	0.88
Overall F = 4.59				

$p < 0.01$ *
 $p < 0.001$ **

Table 1-7. Multiple linear regression analysis to determine the effect of climatic variables on percent of time spent courting.

Weather Variables	Site A (N = 175 hours)			
	Cumulative R ²	B	B Std.E.	Partial F
Temperature	.375	0.99	.101	98.05**
Windspeed	.376	0.05	.041	0.21
Cloud Cover	.376	-0.21	.159	0.02
Overall F = 34.36**				
p < 0.01 *				
p < 0.001 **				

Influence of Climatic Stress on Allocation of Time and Energy Resources

To test the hypothesis that the observed modification of behavior in response to environmental stress actually resulted in a reduction of energy expenditure, the time-budgets and daily energy expenditure at two climatic extremes were compared.

i) Time

The information obtained from scan-sampling was used to estimate the time-activity budgets at 0 and -20 degrees C (Figures 1-1 to 1-3). The time-activity budget of ducks at -20 degrees C was estimated from data collected at -17 to -23 degrees C and for 0 degrees C from data collected at -3 to 3 degrees C by dividing the time spent in a particular activity per hour by the number of hours of observations (based on at least 30 hours of observations from each site). In order to obtain a measure of the amount of time spent daily per activity these estimated mean percentages were converted to mean hours spent per activity by multiplying each by ten (based on there being ten hours of daylight per day at this time of year). Since data were available for all daylight hours at this temperature range at each site, the estimated mean number of hours spent per

Figure 1-1. Time-activity budgets
of ducks at site A at
0 and -20 degrees C

Figure 1-2. Time-activity budgets
of ducks at site B at
0 and -20 degrees C.

Figure 1-3. Time-activity budgets
of ducks at site C at
0 and -20 degrees C.

activity on a daily basis provided a reasonable measure of the time-activity budgets at both -20 and 0 degrees C.

To determine if the amount of time spent in a particular activity at 0 degrees C differed significantly from time spent at -20 degrees C, student t-tests were computed (Ostle and Mensing 1975). There were at least 59 degrees of freedom for each t-test calculated. At site A, the amount of time allocated daily to foraging, flying and preening did not differ significantly at the two temperature regimes ($t = .13$, $p > 0.05$; $t = .08$, $p > 0.05$; $t = .34$, $p > 0.05$, respectively). However, the time spent resting increased significantly ($t = 3.99$, $p < 0.01$) while a significant decrease in the time spent swimming ($t = 3.16$, $p < 0.01$) and courting ($t = 6.80$, $p < 0.01$) was observed at -20 when compared to 0 degrees C. At site B only the time spent preening did not differ significantly ($t = 0.6$, $p > 0.05$). Since significantly more time was devoted to foraging at the higher level of climatic stress ($t = 6.6$, $p < 0.005$), less time was available for other activities such as resting which was notably reduced ($t = 2.41$, $p < 0.01$). A significant decrease in the amount of time allocated to swimming ($t = 4.60$, $p > 0.01$) and courtship ($t = 5.86$, $p > 0.01$) was observed.

Ducks at site C significantly reduced the time

U allocated to swimming ($t = 4.03$, $p < 0.01$) and courtship ($t = 1.75$, $p < 0.05$) at -20 degrees C. This population also reduced the amount of time foraging at -20 degrees C ($t = 6.36$, $p < 0.01$), while the time allocated to preening remained constant ($t = 0.64$, $p > 0.05$). Resting activity significantly increased at -20 degrees C ($t = 8.66$, $p < 0.01$).

ii) Energy

To ascertain the extent to which the behavioral modifications adopted by ducks in response to heightened periods of climatic stress served to conserve energy, I computed what the 0 degree C time budget would cost a duck if it employed it at -20 degrees C and then compared it to the cost of the time budget actually observed at -20 degrees C. The difference between the costs of a 0 degrees C time budget and those actually realized by the ducks using their modified time budget would indicate the magnitude of the energy savings. For the purposes of this study, the daily energy expenditure was determined by calculating the energy expended for each activity, using estimates derived by Wooley and Owen (1978). Since these estimates are expressed only as multiples of resting metabolic rate (RMR), it was necessary to initially estimate this value.

Most energetic studies employ the basal metabolic rate (BMR) rather than RMR to estimate daily energy

V

budgets. BMR is the minimum rate of heat production in a resting bird in a thermally neutral environment while not digesting or absorbing food (King and Farner 1974). RMR includes BMR, thermoregulatory metabolism and the heat liberated in the digestion of food. RMR is a more appropriate measure of metabolic rate for this study since BMR is only associated with temperatures within the zone of thermoneutrality whereas RMR accounts for temperatures below this zone, i.e. below the lower critical temperature. The lower critical temperature is defined as the point where insulation reaches its maximum capacity below which the body cannot maintain its internal temperature without an increase in heat production. For black ducks acclimated to 5 degrees C, the lower critical temperature was determined to be 8 degrees C (Wooley and Owen 1977). Since all temperatures in this study were well below this value, the RMR is the most appropriate measure of metabolism.

A general inverse relationship between temperature and metabolic rate is well documented for birds (Hartung 1967, Kendeigh 1969, Smith and Prince 1973). Wooley and Owen (1977) discovered a linear relationship between metabolism and temperature below the lower critical temperature (LCT) of 8 degrees C. They estimated that the rate of heat production increased below LCT 11.3 to 15.9 kJoules/day for every degree below LCT. Therefore it was necessary to account for ambient temperature when

determining daily energy expenditure (DEE). The regression equation, developed by Wooley and Owen (1977) relating ambient temperature (T) to resting metabolic rate (RMR) in black ducks: $RMR = 4.742 - 1.407T$, was used in this study to estimate the RMR at -20 degrees C. It is important to note that this equation was obtained from radiq-equipped ducks acclimated for 4-6 weeks at 5 degrees C. Wooley and Owen (1977) reported that the RMR in radio-equipped birds was 19% greater than the RMR in birds without the transmitters since the radio stimulated either increased activity or emotional stress which in turn stimulated metabolism. Therefore, the value calculated for RMR was reduced by 19% yielding a value of 25.61 kjoules/hr.

The cost of each activity at -20 degrees C was estimated by multiplying the RMR at -20 (in kjoules/hour) by its corresponding cost expressed as a multiple of RMR. These multiples were taken directly from Wooley and Owen (1978) with the following modifications. Ducks at A did not dabble or tip up for their food but rather walked along the ice pecking at the corn. This closely resembled walking activity estimated at 1.7 RMR. Ducks at site B fed naturally so the feeding value of 1.8 RMR was employed. At C, ducks foraged by diving. The activity monitored by Wooley and Owen which closely resembled this diving activity was bathing, which was measured at 2.9 RMR.

Flight costs were estimated from equations developed by Kendeigh et al. (1977) for non-passerines (Metabolic rate while flying = $0.333 \times W^{\frac{1}{2}}$). Since this equation is weight dependent, a measure of the weight of black ducks was necessary. To be consistent with the other estimates of activity costs, the weight value utilized was the mean weight of black ducks used in Wooley and Owen's study for the estimation of RMR: 1180 g. Energy expenditure of birds in sustained flight is independent of the ambient temperature since the excess heat generated by flight muscle eliminates the need for additional temperature regulation while flying (Kendeigh et al. 1977). Therefore, flight costs were assumed to be the same regardless of temperature. Using the conversion values described above, the costs of the 0 and -20 degrees C time budgets were calculated for each site (Tables 8-10). Recall that the time-activity budgets estimated were based on diurnal observations only. Therefore, in order to obtain a measure of total DEE, the activity for the 14 remaining nocturnal hours were also considered. The nocturnal activities of ducks were monitored for at least ten hours at each site. Since all of the ducks were observed to sleep at these times, it was assumed that the nocturnal activity consisted entirely of resting.

The decrease in swimming and courtship activity coupled with the increase in the time spent resting at

-20 degrees C served to decrease the total daily energy expenditure of ducks at A (Table 8). If a duck adopted the 0 degrees C time budget at -20 degrees C, it would increase its daily energy costs by 13 percent since the DEE for this time budget was 972.3 kJoules while it was 858.1 kJoules for the time budget actually observed at -20 degrees C. At B, the cost of the 0 degrees C time budget and the -20 degrees C time budget did not differ significantly since the modifications only served to reduce the DEE by less than 1 percent (from 842.8 to 837.0 kJoules: Table 9). Although the energy devoted to courtship and swimming was notably reduced, the increased amount of energy devoted to foraging at -20 degrees C (almost a 40% increase) nullified this reduction. By reducing the energetically costly activities such as foraging, swimming and courtship, and by increasing the time spent resting, a cheap behavior metabolically, ducks at site C reduced their DEE. If ducks at site C adopted the time budget at 0 degrees C rather than the time budget at -20 degrees C during extremely cold temperatures, their daily energy costs would increase 27 percent (Table 10).

Table 1-8. Allocation of energy resources
at site A at 0 and -20 degrees C (kjoules).

	0	-20
Foraging	108.9	108.9
Resting	56.3	118.3
Flight	96.7	96.7
Swimming	39.4	16.9
Preening	87.2	92.2
Courtship	192.1	30.7
Sleeping	394.4	394.4
Total DEE	972.3	858.1

Table 1-9. Allocation of energy resources
at site B at 0 and -20 degrees C (kjoules).

	0	-20
Foraging	212.1	318.1
Resting	64.8	45.1
Flight	--	--
Swimming	39.4	5.6
Preening	78.4	73.8
Courtship	53.7	--
Sleeping	394.4	394.4
Total DEE	842.8	837.0

Table 1-10. Allocation of energy resources
at site C at 0 and -20 degrees C (kjoules).

	0	-20
Foraging	215.4	0
Resting	95.9	225.4
Flight	--	--
Swimming	56.3	--
Preening	96.8	92.2
Courtship	46.3	--
Sleeping	394.4	394.4
Total DEE	905.1	317.6

DISCUSSION

The results from this study support the contention that wintering ducks modify their time-activity budgets in response to climatic and energetic stress. Of the three climatic parameters measured: ambient temperature, wind speed and cloud cover; the former was determined to be the most important in defining climatic stress since behavioral adjustments in the ducks' daily activity patterns at all sites could primarily be attributed to variations in temperature.

The differences observed between the -20 and the 0 degrees C time-activity budget of ducks at all three sites resulted from modifications in the time allocated to foraging activity (except at A), resting, swimming and courtship. The fact that these time-activity budgets were found to differ significantly at two climatic extremes experienced in winter clearly demonstrates that black ducks responded to differing levels of climatic stress by modifying their allocation of time resources. Whether these modifications to the time devoted to different activities aided the animal in tolerating periods of climatic stress and whether the modifications adopted were influenced by the level of energetic stress experienced by the individual will now be discussed.

The fact that ducks at all sites reduced the amount

of time spent swimming and courting in response to low ambient temperatures and spent a similar amount of time preening daily suggests that some of the behavioral adjustments (or lack of, in the case of preening) to the time-activity budgets were consistent regardless of the level of energetic stress experienced by the population.

Swimming and courting are two of the more energetically costly activities. West (1968) reported that vigorous activities, such as locomotion and courtship, during cold weather reduce the insulative capacity of the feathers, and thus increase heat loss. Therefore, by significantly decreasing the amount of time devoted to these activities, ducks at all sites reduced energy costs.

Preening stimulates the oil gland to secrete a substance containing fats, fatty acids and wax. In ducks, the secretion of the oil gland maintains the water repellant quality of the feathers and it is generally thought that without this secretion, the feathers lose most of their normal function as a flight mechanism and more importantly, in this case, as a heat insulating medium (Elder 1954).

Elder (1954) compared heat loss in normal ducks with those whose preening gland had been removed, and found that the glandless birds suffered a severe increase in heat loss. Without preening, severe matting and deranging of the feathers result which reduce the

insulative quality of the plumage. Hartung (1967) reported that ducks with plumage in poor condition suffered greater heat loss and were subsequently found to have higher metabolic rates as a result of the increased thermoregulatory costs. In this study, the fact that differing levels of climatic stress had little influence on the amount of preening implies that ducks must allocate a certain amount of time daily to maintain their body plumage. Although preening is almost twice as costly as resting activity, ducks at all sites would stand to gain little by reducing the amount of time devoted to preening since preening serves to decrease the thermal conductivity of the plumage (Calder and King 1974), and is thus important in controlling heat loss. In view of this, one may expect that ducks should actually increase the amount of time devoted to preening at low temperatures in order to further reduce heat loss from the body when it would be most significant. However, the fact that the amount of time spent preening did not increase at low temperatures implies that there is an upper limit on plumage insulation, i.e. ducks would realize little energetic benefit by increasing the amount of time preening because the insulating properties of the feathers would not increase indefinitely.

Some of the modifications in the time-activity budget adopted by black ducks differed considerably

between populations and the differences observed in adjustments to foraging, flight and resting activity are thought to reflect the specific ecological circumstances experienced by the three populations.

Kendeigh (1945) stated that the maintenance of food reserves becomes more critical at low air temperatures because metabolism is higher and more energy is required to compensate for higher thermoregulatory costs. An increase in food intake permits the buildup of fat stores during the day which are subsequently utilized for thermoregulation during the cold nights. When the environmental temperature is low, the increased energy required for thermoregulation leads to the necessity of more intensive feeding (Shilov 1968).

Schoener (1971) discussed optimal length of feeding periods and argued that animals should expand their feeding periods during times when they have greater energy requirements, such as under periods of climatic stress. Chaffee and Roberts (1971) referred to several studies on passerine birds which demonstrated a linear increase in food intake as ambient temperatures decrease. Cain (1973) also reported that gross energy intake in the Black-bellied tree duck (Dendrocygna autumnalis) increased with lowering temperatures. Moreover, Jordan (1953) found food intake of mallards to be inversely related to air temperature. Therefore, by increasing the amount of time spent foraging, ducks can

increase the amount of food ingested and thus compensate for the higher thermoregulatory costs experienced at cold temperatures.

The results of the present study, however, show that ducks do not always increase foraging in response to lower temperatures, but rather, dependent upon the nature of food and foraging methods, can increase, maintain or decrease time spent foraging.

Kontogiannis (1968) argued that the amount of feeding during the daytime is determined largely by the amount of energy lost during the preceding night that needs to be replaced. Since cold temperatures during the day are typically associated with cold nights, the significant increase in foraging activity observed at site B at low ambient temperatures is understandable. However, only ducks at this site were observed to modify their foraging activity in this manner in response to low temperatures.

The amount of time spent foraging by ducks at site A was not influenced by environmental conditions, but rather was dictated by the amount of time necessary for the population to consume the food provided daily. Since the same number of ducks fed each day and the quantity of food did not vary, the amount of time spent feeding was the same regardless of temperature. Once all of the corn had been eaten, there was no other food source available to the ducks. Thus increasing the

amount of time spent foraging at A. would serve little purpose in terms of increasing food stores. In comparison, ducks at site B had an unlimited daily food source and they could effectively obtain more energy through feeding when demanded by cold temperatures.

The fact that ducks at site C decreased their foraging time during periods of high climatic stress contradicts the feeding strategy theory discussed above. However this result may be explained by the foraging method adopted by ducks at site C. These ducks did not forage by tipping up, but by diving since the water was too deep to permit successful tipping up.

Since the amount of energy required for diving is approximately twice that needed for tipping-up, it is more costly energetically for a dabbling duck to obtain food by diving and hence the energetic gain from foraging is less. Furthermore, the food the ducks are diving for at site C (Cladophora) is lower energetically than the food at site B due to its high ash content (Cummins and Wuycheck 1971), so the amount of energy gained when feeding is less. The estimated success of diving was found to be considerably less (see chapter 2). Therefore, diving was not only more costly energetically but also was not as efficient as the foraging method used by ducks at site B. Ducks at site C did not increase the time spent foraging in response to low ambient temperatures because unlike ducks at site

B, the costs incurred through foraging likely exceeded the benefits realized, and thus it was not profitable. This explains why ducks at site C reduced foraging time in an attempt to balance their energy budget. This result agrees with the observation that sudden drop in temperature resulted in a reduction of food intake by Blue-winged Teal (Anas discors) (Owen 1970). These birds may attempt to wait out cold snaps and seek additional food only when body reserves reach some low level. Hickey (1980) also found that the decreased availability of food resources coupled with increased cost for heat regulation reduced the amount of foraging activity in black ducks wintering in Prince Edward Island. Ducks at site C, by adopting a similar strategy as ducks in the above two studies at low ambient temperatures, realized a reduction in energy costs which served to counteract the influence of heightened costs of thermoregulation.

Flight is the most metabolically expensive activity of any bird species (King 1973). By remaining at the same site all winter, ducks at site B and C reduced the need for flight thereby conserving energy.

Although the energetic cost of flying per se does not increase as temperatures decrease (Kendeigh et al. 1977), flight costs would increase an already high daily energy expenditure (resulting from increased thermoregulation costs on colder days). One might

expect therefore, that birds might forego flying on cold days in order to conserve energy. For example, LeFebvre and Raveling (1967) found that on cold days (less than -20 degrees C), Canada Geese (Branta canadensis) would remain at their roost site and not fly in search of food, and they attributed this behavior to the high costs of flight and the necessity of conserving energy on cold days. Common goldeneye (Bucephala clangula) wintering on the upper Mississippi River remained near their roosting site on cold days (below -20 degrees C) rather than fly long distances in search of food (Sayler and Afton 1981). However, the fact that daily flight activity was observed in this study, regardless of the ambient temperature, suggests it was more profitable for the black ducks to fly to their feeding station and forage (accounting for flight costs) than it would be for them to remain inactive at the roost site.

Most activities of free-living birds under natural conditions are energy-demanding (Kendeigh et al. 1977). However, there are some activities which are energy-conserving, and by adopting these activities, ducks can reduce energy costs. One such activity is resting which is, metabolically speaking, the cheapest behavior.

By increasing the amount of time resting at low ambient temperatures, ducks at site A and C balanced their energy budgets by reducing their daily energy

expenditure at a time when energy costs were highest. Smith and Prince (1973) also reported that mallards wintering in Michigan increased the time allocated to resting activity in response to cold temperatures since they too could not combat cold temperatures by increasing energy input. At site B however, ducks reduced the amount of time resting at cold temperatures in favor of increasing the amount of time allocated to foraging because they could feasibly balance their energy budgets by increasing foraging activity.

The calculation of the energy costs at sites A and C support the interpretation that the modifications to the time-activity budget adopted in response to climatic stress do indeed serve to reduce energy costs thereby balancing the ducks' daily energy budget.

Ducks at all sites reduced metabolically expensive activities such as swimming and courtship (and foraging at site C) at low ambient temperatures. West (1968) reported that vigorous activities, such as courtship and locomotion during cold weather reduce the insulative capacity of the feathers and thus increase heat loss. These modifications served to significantly reduce the daily energy expenditure of ducks at sites A and C at a time when thermoregulatory costs are highest. In spite of these modifications, the daily energy expenditure was not significantly reduced at site B, because the energetic costs of foraging exceeded that of resting and

thus increasing the time devoted to foraging instead of resting would only serve to increase daily energy costs. However, although this increase in foraging did not reduce DEE, the significant decline in both courtship and swimming did, since if these modifications were not implemented, the DEE would have been even greater than that estimated. Furthermore, the increase in foraging time resulted in an increase in energy ingested by the animal, thereby providing more energy when costs are greatest. The fact that the modifications adopted by ducks at B served to increase the energy inputs rather than decrease the energy output, implies that the ducks at B adopted a somewhat different strategy which nevertheless enabled these birds to better tolerate low ambient temperatures.

The overall time budget differences recorded between sites reflect the differences in available energy. Ducks at the high energy site A devoted the most time to energetically costly activities such as courtship and flight while ducks at site C allocated most of their time to the energy conserving resting activity. Ducks at the intermediate energy site B spent most of their time foraging. Because the nature of the food source and the foraging methods differed considerably between sites B and C, ducks at site B did not need to spend the majority of their day resting like ducks at site C in order to balance their daily energy

~~budget.~~ However, because ducks at site B did not have as much energy as ducks at site A, they were unable to devote as much time to metabolically costly activities.

Differences in available energy were also found to influence the degree of behavioral modification adopted in response to low temperatures. Because ducks at site A had more energy available than ducks at site C, one would expect that daily energy costs would be reduced more at site C relative to site A in response to low temperatures in order to suit their lower energy source. The fact that the modifications adopted by ducks at site C resulted in a 21% reduction in energy costs while ducks at site A reduced costs by only 11% clearly demonstrates that ducks at site C modified their behavior to a greater extent as was dictated by their available resources. However, it is interesting to note that the daily energy costs of ducks at sites A and C did not differ considerably at warmer temperatures. This suggests that at milder temperatures, when thermoregulatory costs are low, ducks at site C need not be as economical. The fact that they foraged at milder temperatures likely increased their available energy explaining why energetically costly activities were observed at this time.

The wintering black ducks in this study were found to respond to differing levels of climatic stress by modifying their allocation of time and energy resources.

These modifications should enhance the survival of these organisms through the balancing of energy inputs with energy outputs, thus allowing them to better tolerate periods of climatic stress. The degree of modification differed considerably between high and low energy stressed populations, demonstrating that the ducks were able to modify their behavior to suit the energetic demands imposed by their environment.

Therefore, one can conclude that a degree of flexibility exists in the time-energy budget of black ducks, and it is this behavioral flexibility, coupled with morphological and physiological adaptations, which enabled black ducks to cope with the climatic and energetic pressures imposed by a winter environment.

CHAPTER 2. INFLUENCE OF THE AVAILABILITY OF
RESOURCES ON THE COURTSHIP ACTIVITY
OF BLACK DUCKS

INTRODUCTION

An individual must allocate its available resources not only to self-maintenance activities to ensure individual survival but also to reproductive activities to realize the future success of its genes. The amount of time and energy an animal can devote to reproductive activities is dictated by the resources allocated to maintenance activities which is in turn determined by the organism's internal and external environment (Schoener 1971). Utter (1971: cited in King 1974) proposed a hypothetical model to explain this hierarchy in maintenance and reproductive activities. Initially, he identified three "priority" levels associated with different activities.

Priority level I is associated with individual maintenance activities such as feeding, preening and resting. Priority level II, in addition to the activities of level I, includes aggressive encounters, courtship displays etc. Priority level III adds the costs of reproduction (egg production, feeding the young) to the aforementioned levels.

Utter proposed that successively higher ranges of energy output are required to reach a higher priority level. He states that the ability to attain the next higher "success" level depends upon environmental attributes such as the availability of time and energy

resources and the individuals ability to optimize the exploitation of these resources, where optimizing in this context refers to obtaining adequate resources with minimal time and/or energy expenditure. Therefore, the availability of resources will determine when an individual will ascend to a higher priority level. The aim of this study was to test this hypothesis by examining the behavior of three populations of black ducks differing considerably on their availability of resources during the winter period when they are known to ascend from Priority Level I to Level II.

McKinney (1975) regarded the time spent in courtship as an expense that individual ducks must balance against other costs involved with individual survival. Prince (1979) stated that most of the available time and energy resources are required for individual maintenance activities (Priority level I) in the winter since thermoregulatory costs are high and food supplies are often low. However, in spite of the winter being a time of high maintenance costs and reduced food availability, ducks must allocate time and energy to courtship activity during this period in order to realize future reproductive success.

The courtship behavior of black ducks can potentially be influenced in a number of ways, three of which are: i) when it is initiated; ii) how much time and energy is spent in this activity; and iii) the type

of displays adopted while courting. The stage of courtship can be assessed by the display adopted by the courting drakes. There are three main courtship displays which differ not only in their visual appearance (see Lebreton 1961 for a description), but also in their intensity. The gruntwhistle is a low intensity display associated with early courting activity. It is incited by a corresponding low intensity display of the female. The head up-tail up display is of intermediate intensity and usually occurs after the onset of courtship. The highest intensity display is the down up display which is associated with the peak of courtship activity, usually leading to copulation (Johnsgard 1960).

The specific hypotheses to be tested are that the population with the most abundant resources will initiate courtship (i.e. ascend to the more advanced priority level) earlier; devote more time and energy to this activity and reach higher stages of courtship sooner than populations with fewer available resources.

STUDY AREAS

This study was conducted at three discrete sites (A, B and C) located within a 20 km radius of Ottawa, Ontario (see Chapter 1 for a description). The combination of differences in food quality (in terms of energetic value), quantity and foraging costs (see chapter 1) produced major differences between the three sites in terms of the availability of time and energy resources. ~~Since ducks at site A~~ had the richest food source, the cheapest foraging method and devoted only a few hours each day to foraging activity, they had the greatest amount of time as well as energy available after maintenance costs. Ducks at site B were intermediate in terms of available energy since the energetic value of their food source and the metabolic cost of their foraging technique was between that of sites A and C. However, due to the extended amount of time spent foraging, these ducks had little time available for other activities. Ducks at site C had the lowest amount of energy available since their food source was the poorest energetically and their foraging method the costliest metabolically. However, because they spent little time foraging they had the time available to devote to other activities.

METHODS

The behavior of ducks was examined at site A from 14 January to 21 March 1982; at site B from 12 January to 28 February 1982, and at site C from 1 January to 21 March 1982. To ensure that any differences in courtship activity between sites was not due to the absence of available mates, sex ratios were determined at each site. Females were distinguished from males by bill color (yellow in males, olive green in females) and by the presence of bill spots (Godfrey 1979).

In order to determine when courtship activity was initiated, each population was observed at least every second day. Ducks at a particular site were said to have initiated courtship by the regular appearance of one of the three courtship displays in their daily behavioral repertoire, i.e. when courtship activity comprised over 5% of the daily time-activity budget. After courtship had been initiated, the percent of time spent courting and the frequency of use of the 3 types of displays at each site was estimated using the scan-sampling technique (see Chapter 1). Observations were made through a spotting scope which permitted accurate measurements up to 50 metres away and thus prevented disturbance of the ducks. Observations were

obtained equally from all daylight hours to avoid temporal biases, thus enabling an estimate of the mean amount of time devoted daily to courtship.

RESULTS

At each of the three sites there was a predominance of male ducks. At site A, there were 137 males and 113 females (1.2:1); at site B there were 108 males and 77 females (1.4:1); and at site C there were 6 males and 4 females, which because of predation was later reduced to 5 males and 3 females (1.6:1). Because approximately 40% of the ducks at all sites were female, differences observed in courtship behavior between sites cannot be attributed to the number of potential mates.

The date at which courtship was initiated and the percent of time allocated to this activity differed considerably between the three sites (Figure 1). In spite of cold January temperatures (mean temperature -20 degrees C) producing high maintenance costs, ducks at site A initiated courtship at this time prior to ducks at sites B and C. Furthermore, they also spent substantially more time at this activity compared with other sites. Ducks at site B initiated courtship in mid-February when the temperatures increased (mean temperature -10 degrees C) thereby reducing maintenance costs and the need for an extended foraging period. These ducks not only initiated courtship three weeks later than ducks at site A but also allocated

Figure 2-1. Initiation of and percent time spent in courtship activity by ducks at each site throughout the winter.

temperature -5 degrees C) when maintenance costs were considerably lower. Nonetheless, they devoted little time to this activity. At all three sites, the percent of time devoted to courtship gradually increased with time.

The percent of time devoted to each of the three displays was found to differ considerably throughout the study period both within and between sites (Figure 2). In spite of the differences in initiation time of courtship behavior between sites, the pattern of display utilization was very similar at all sites. When courtship began, the most prominent display was the low intensity gruntwhistle. Gradually the frequency of the higher intensity head up-tail up display increased. At the conclusion of the study, the down up display was observed to increase in frequency at both sites A and C. Ducks at site B left their wintering site on 28 February 1982, and thus analysis of their courting displays was not possible during the latter part of the study. However, at this time, the ducks at site A used the down up display most frequently while for those at site C, the low to intermediate displays were the most frequent.

Figure 2-2. Percent of time spent by courting drakes in three courtship displays at each site throughout the winter.

DISCUSSION

The patterns of courtship behavior observed at the three sites were consistent with Utter's hypothesis which stated that the availability of resources will influence when an individual will ascend to a higher priority level. Moreover, the fact that ducks at the three sites allocated differing amounts of time to courtship activities demonstrates that the availability of resources will also dictate how much time and energy is apportioned to activities associated with higher priority levels. The population at site A having both more time and energy available for non-maintenance behavior began courtship sooner, spent more time per day engaged in this activity and had progressed further through the sequence of courtship behaviors by the time of spring dispersal. Ducks at site B exhibited courtship patterns intermediate to those at sites A and C. These ducks had fewer energy resources than ducks at site A explaining why they initiated courtship later. The lack of time resources further contributed to the reduction of time allocated to courtship. Therefore, although ducks at site B may have had the energy available to ascend to a higher priority level, they did not have the time available to devote to activities

available energy resources required for higher cost activities. Although these ducks had ample time available, they did not have the energy required to initiate courtship activity and thus were the last to ascend to Priority level II. These results suggest that both time and energy resources are critical in the attainment of a higher priority level, unlike Utter's model which primarily stressed the importance of energy resources.

Since the sequence/ of courtship activity did not vary between sites, the order of displays adopted by courting ducks must be independent of the availability of resources. Johnsgard (1960) stated that it is the stimulus provided by the female that establishes the display adopted by the male. Therefore, from these results, it appears that courting black ducks initially adopt low intensity displays and, as the stimuli increase, higher intensity displays are assumed regardless of available resources.

The availability of resources does, however, influence the courtship stage of the individual since the intensity of courtship display varied between the three sites at any one time.

Since the most prominent courtship display adopted by ducks at site A at the conclusion of the study was

Ducks at site C were thought to be at only the early to intermediate stages of their courtship activity since their most frequent displays were the low intensity gruntwhistle display and the intermediate intensity head up-tail up display. This demonstrates that a greater resource base enables a duck to reach the peak of its courtship phase prior to those with fewer resources.

Since it is at the peak of courtship activity when pair formation is thought to occur (Johnsgard 1960), it is reasonable to conclude that pair formation had occurred at site A but not at the other sites. It was earlier demonstrated that the sequence of courtship displays was the same at all sites. This implies that ducks at the other sites would reach the peak of their courtship later than ducks at site A because they were still in the early stages of courtship when the study was concluded. This suggests that upon arrival on the breeding grounds, the ducks at site A would be able to initiate reproductive activities prior to ducks at sites B and C since they would have already formed pairs.

Earlier breeding is thought to be advantageous for waterfowl for several reasons (Sayler and Afton 1981). It permits priority in nest site selection on the breeding ground, favors renesting attempts and allows earlier molt and subsequent greater accumulation of body

migration and thus more likely to survive (Owen and Cook 1977).

Therefore, the results from this study clearly demonstrate that the availability of both time and energy resources and the individuals ability in optimizing the exploitation of these resources, influences when an individual will ascend to a higher priority level, and how much time and energy is apportioned to activities associated with this priority level, which in turn, may ultimately influence the fitness of the individual.

CHAPTER 3. DIVING ACTIVITY IN BLACK DUCKS

INTRODUCTION

The black duck (Anas rubripes) is a dabbling or surface feeding duck. Although they usually feed by tipping up or dabbling in shallow waters, they have also been reported to forage in deeper waters by diving (Kutz 1940, Kear and Johnsgard 1968).

Diving is associated mainly with winter foraging activity since it is during these cold months when the typical shallow water feeding areas of black ducks freeze. Bourget and Chapdelaine (1975) stressed the importance of diving behavior in dabbling ducks which winter in cold regions. They measured the dive time of three species of surface feeding ducks (including the black duck) at unknown depths and found differences in mean dive times between species and attributed this to physiological differences. They argued that diving is inefficient for the surface feeding ducks examined but they did not quantify the success of this foraging technique. Apart from this, little is known about the diving activity of the black duck, even though it appears to be an important foraging strategy adopted by these ducks during the energetically stressful winter period.

A comparison between foraging methods adopted by wintering black ducks was made in order to characterize diving activity in a dabbling duck. Since these ducks

are not morphologically or physiologically designed for diving, it is hypothesized that this foraging technique is less efficient than one normally adopted by black ducks. The aim of this study was to determine if the success of diving and tipping up differ, and if so, to examine factors, both biotic and abiotic which contribute to these differences.

STUDY AREAS

Black duck foraging activity was examined at two locations: Shirley's Bay on the Ottawa River, and the Rideau River in Ottawa, Ontario. Ducks at both locations were initially observed to forage by tipping up. However, at the Rideau River site, cold temperatures prompted the freezeover of the typical shallow water feeding areas of black ducks, resulting in the onset of diving activity. Water depths at the shoreline where ducks were feeding were measured daily to determine at what water depth ducks began diving. The area where the ducks were observed to dive had a rocky bottom which was covered with the freshwater algae, Cladophora. At Shirley's Bay, a creek carrying warmed tertiary wastes from a nearby sewage treatment plant heated the shallow waters and thus prevented them from freezing. At this site, ducks fed mainly on water milfoil (Myriophyllum spp.). Quadrat sampling indicated that food density did not differ significantly between sites (see Chapter 1).

METHODS

Diving was examined on 16 days during December 1981 to March 1982 on the Rideau River and tipping up during 10 days in January and February 1982 on the Ottawa River. On each sampling day, foraging activity was monitored for at least 2 hours between 0800 and 1600 EST. All observations were made using a spotting scope which permitted accurate measurements from 50 metres and all times were recorded with a stopwatch. On each day of observation, several foraging parameters were measured.

The length of a foraging bout was examined in order to determine how long a duck could continually tip-up or dive before it required a rest. This sequence of feeding activity was measured by recording the length of time an individual duck foraged before it switched to another activity.

The number of forages during a sixty second period was also recorded to obtain some comparative measure of the foraging rate between diving and tipping up. Timing and counting began when the duck first submerged and counting was terminated after a 1 minute period.

The length of an individual dive or tip-up was recorded in order to compare the length of time required to secure food. The length of the forage was measured from the time the duck's head was immersed under water

until it resurfaced. After 10 such forages had been measured for an individual duck, another foraging duck, selected at random, was similarly monitored.

Pause length was examined in order to compare the length of time required to rest between forages. A pause was measured as the time elapsed between two dives or tip-ups. For every tip-up measured, pause length was determined, and to ensure accuracy of time and not lose sight of diving ducks, pause times were recorded for every second dive.

The number of successful dives or tip-ups was measured for individual ducks in order to compare the relative success of these foraging methods. Success rate was measured by recording the number of successful forages in a total of 20 dives or tip-ups. A forage was classified as successful if the duck resurfaced with food hanging from its bill. Due to the nature of the food sources at each of the foraging sites, the presence of food in the bill was readily observed.

The temperature $[T(a)]$ and windspeed (W) were recorded for each sampling period and converted to windchill values $[T(c)]$ using the following formula obtained from the Environment Canada Weather Office:

$$T(c) = 33 - [(0.227\sqrt{W} + 0.45 - 0.0118 W)(33 - T(a))].$$

After each sampling period, the depth of water the ducks were foraging in was also recorded. These environmental factors were measured to determine if they influenced

any of the foraging parameters examined.

RESULTS

Ducks on the Rideau River were observed to tip up when the water depth at the shoreline was less than 50 cm deep. At this depth, and greater, ducks were observed to forage exclusively by diving. The mean value of each of the foraging parameters measured over all sampling periods was calculated (Table 1) and Student t-tests were performed to determine if the measures characterizing diving activity differed significantly from tipping up. The length of the foraging bout was considerably greater for ducks tipping up ($t = 128.5$, $p < 0.001$) than those diving. The foraging rate also differed significantly. The results suggest that the rate of diving is lower than tipping since a significantly greater number of tip-ups were recorded in a 60 second period ($t = 41.2$, $p < 0.001$). This results from the greater forage and pause length recorded for diving black ducks. Overall mean dive lengths were found to be significantly greater than mean tip-up length ($t = 27.9$, $p < 0.001$). This is likely due to the differences in water depths since in deeper waters (such as those at the diving site), ducks would take longer to swim to the bottom to secure their food than in the shallower waters where the ducks tipped up. Pause lengths were also significantly greater ($t = 96.9$, $p < 0.001$) when diving.

Table 3-1. Tipping vs. diving: A comparison of foraging methods used by black ducks in winter.

		Tipping up	Diving
Foraging bout:	mean	180+30 min	13+5.5min
	range	75-360 min	7-20 min
	N	20	26
Forage length:	mean	5.5+0.7 s	7.6+2.7 s
	range	4-7 s	5-15 s
	N	200	1315
Forages/min:	mean	10+1.4	4+2.1
	range	9-13	2-8
	N	200	315
Pause length:	mean	1.0+0.5 s	7.9+3.9 s
	range	1-2 s	4-21 s
	N	400	621

When tipping up, the black duck remained under water for approximately 6 seconds. Upon resurfacing, the duck would often have food in its bill which it would swallow and then immediately tip-up again. Diving black ducks however would resurface, eat any food they had obtained and then rest for several seconds before diving again. This explains why the pause length of diving black ducks was greater.

In addition to the differences recorded in the forage and pause times, the degree of variation between diving and foraging also differed. The F-ratio revealed that the variances observed in the time of individual forages and pauses for diving were significantly greater ($F = 3.86$, $p < 0.01$, $df = 198, 1312$ for forage time; $F = 7.8$, $p < 0.01$, $df = 398, 618$ for pause time) than ducks tipping up. This implies that diving is a more variable foraging activity. Since the foraging variables measured for tipping up were relatively constant, it is assumed that they were not influenced by the measured windchill temperature which varied considerably during the sampling period (-30 to 0 degrees C). One measure which did remain relatively constant at this site was the water depth which varied only from 40 to 45 cm, and this consistency likely accounts for the small variation recorded in the forage times. However, for diving black ducks, the foraging parameters were sufficiently variable to warrant further analysis in an attempt to

explain some of the variation observed.

The ducks were observed to dive in 3 discrete areas which differed considerably in water depth. The mean dive and pause times in seconds for forages measured at each of the three depths were compared (Figure 1). A one-way analysis of variance revealed that the mean dive lengths differed significantly ($F = 192.6$, $p < 0.01$, $df = 2, 1312$) such that the mean dive time at 3.8 m was significantly greater than the mean dive time at 2.7 m ($t = 24.12$, $p < 0.01$, $df = 988$), while the mean dive time at 2.7 m was significantly greater than the mean dive time at 2.0 m ($t = 25.08$, $p < 0.01$, $df = 808$). A one-way analysis of variance revealed that the mean pause times did not differ significantly between different depths ($F = 2.3$, $p < 0.05$, $df = 2, 618$).

Windchill temperatures measured during the diving periods ranged from -25 to -6 degrees C. Linear regression analysis indicated that windchill temperature did not influence dive time (Figure 2), however as the windchill temperature decreased, the mean pause time recorded increased (Figure 3). Pause time, however, was independent of dive time (Figure 4).

Foraging success did not vary considerably between sampling days (mean success rates for all sampling periods: 13.8 ± 1.4 for tipping; 8.2 ± 1.1 for diving) suggesting that a gradual decline in food density did not influence foraging success. For ducks tipping up,

water longer when diving. Although the pause times are somewhat greater for the diving ducks, if one compares the length of time needed to pause between dives relative to the dive time, it becomes apparent that black ducks require a much greater rest between dives. For common goldeneyes, a pause of less than half the length of the dive was required before the bird dives again (Dow 1964), but in the black duck, the pause was at least three-quarters the dive length. This suggests that diving is energetically more costly for black ducks than for diving ducks such as goldeneyes and mergansers. Dow (1964) found that the duration of the pause in diving birds was positively correlated with water depth and thus it follows that the duration of the pause was also correlated with dive length. Morrison et al. (1978) reported similar findings. However, the pause length of diving black ducks did not increase as water depth increased, nor did it increase as dive length increased. This suggests that some factor other than water depth and dive length influenced the pause length. The fact that pause length was found to increase as windchill temperature decreased suggests that at cold windchill temperatures, the black duck requires a longer rest between dives, i.e. a longer recovery period is necessary before it can dive again. Kontogiannis (1968) states that activity costs are greater at low temperatures. Therefore it would be more costly

Figure 3-1. Mean duration of dive
and pause length at
different water depths.
Fine lines represent
standard deviation about
the mean.

Figure 3-2. Changes in dive length at different temperatures. Large dots indicate the mean dive length recorded at a particular temperature. Fine lines represent standard deviation about the mean.

Figure 3-3. Changes in pause length at different windchill temperatures. Large dots indicate the mean pause length recorded at a particular windchill. Fine lines represent standard deviation about the mean.

Figure 3-4. Relationship between pause length and dive length. Large dots represent mean pause length recorded at a particular dive length. Fine lines represent standard deviation about the mean.

138 of the 200 forages (69%) were observed to be successful, but only 135 of the 320 dives (42%) monitored were successful. Therefore tipping up was a more profitable method of foraging.

DISCUSSION

Godfrey (1979) reported that the length of a black duck, exclusive of the tail, is 44 cm thus explaining why the ducks in this study tipped up in waters up to this depth but dived at depths greater than 50 cm.

There are several reasons as to why the foraging success of diving black ducks was considerably less than ducks tipping up. Schoener (1971) for example, argued, that foraging success is related to prey density, predator mobility and experience.

Since the density of food estimated at the areas where ducks were tipping up and diving was not significantly different (see chapter 1), differences in the foraging success between diving and tipping up cannot be attributed to this factor. If density influenced foraging success, one would expect that it would decrease over time as the food resources became depleted. However, since foraging success remained relatively constant over the sampling periods, one can assume that density was not a factor influencing foraging success in this study, leaving predator mobility and experience as possible explanations.

The bodies of black ducks are morphologically designed for shallow water foraging methods such as tipping up and dabbling. Typical diving ducks generally have smaller wings, short heavy bodies, wider feet and

small short tails enabling them to swim and dive with greater efficiency in deep waters (Raikow 1973). Because black ducks lack these morphological features, they likely experience reduced mobility while diving which may consequently lower their foraging success. Furthermore, since tipping up is the more common foraging method adopted by black ducks, the experience they have diving is conceivably less and this fact may also contribute to their reduced foraging success while diving.

Black ducks foraged for significantly longer periods of time when tipping up than when diving because diving is metabolically more costly (see Chapter 1), and thus more rest is needed after a shorter period of time.

The fact that the ducks tipped up more often in a minute than they dived implies that their foraging rate is greater. Assuming that the same quantity of food was obtained per forage (i.e. a "bill-full"), the ducks have the potential to ingest almost twice as much food during the same time period when tipping up than when diving. Furthermore, this finding coupled with the fact that ducks can forage for longer periods of time when tipping demonstrates that on a daily basis, ducks are able to forage more and thus theoretically ingest more food.

When the ducks dived in deeper water, the length of time they remained under water increased because of the

increased time required to swim down to lower depths and secure food and then resurface. Conversely, the length of tip-ups remained constant throughout all sampling periods because the water depth remained constant. Since no relationship was observed between forage length and windchill temperature, forage length is likely a direct function of water depth.

Dow (1964) examined the diving times of seven species of diving birds, including four species of diving duck, and observed that dive times increased as water depth increased. Similarly, Morrison et. al. (1978) found a significant positive correlation between dive times of Cormorants (Phalacrocorax spp.) and water depth.

The actual dive times measured for black ducks were significantly shorter than those measured by Dow (1964) for ducks that normally foraged by diving. For example, the mean dive time of the Common Goldeneye (Bucephala clangula) was 24 seconds and for the Red-breasted Merganser (Mergus serrator) 42 seconds in one to two meters of water. In 2.0 m of water, the mean dive time recorded for black ducks in this study was 5.5 seconds. Szijj (1965 cited in Bourget and Chapdelaine 1975) examined dive times in the mallard (Anas platyrhynchos) and reported that the range of diving times in one to two metres of water was 4 to 6 seconds, which are very similar to those recorded in this study for the Black

duck. These differences in dive times between diving and dabbling ducks are thought to be primarily a result of the morphological differences previously discussed, as well as physiological differences which enable diving ducks to remain under water for extended period of time (Johnsgard 1975). These differences may also reflect differences in diving birds since it would take longer to secure mobile prey such as fish.

Several explanations can be offered as to why the pause length recorded between forages was significantly greater in diving black ducks than in tipping up ducks. The pause between forages has two functions: one is to enable the bird to resurface and eat whatever food items it has obtained from the water, another function is to allow the bird to resume breathing since while under water, it does not exchange gases. Therefore the longer the time spent under water, the longer the pause required. However at a depth of 2.0 m, the mean dive time was not significantly different from the mean tip up time ($t = 0.79$, $p > 0.05$, $df = 723$). This implies that diving causes greater physical strain on a dabbling duck than tipping does and thus necessitates a longer rest period.

When relating the pause length of ducks which normally dive to those recorded for diving black ducks, a major difference is evident. One would expect pause times to be greater in diving ducks since they are under

water longer when diving. Although the pause times are somewhat greater for the diving ducks, if one compares the length of time needed to pause between dives relative to the dive time, it becomes apparent that black ducks require a much greater rest between dives. For common goldeneyes, a pause of less than half the length of the dive was required before the bird dives again (Dow 1964), but in the black duck, the pause was at least three-quarters the dive length. This suggests that diving is energetically more costly for black ducks than for diving ducks such as goldeneyes and mergansers. Dow (1964) found that the duration of the pause in diving birds was positively correlated with water depth and thus it follows that the duration of the pause was also correlated with dive length. Morrison et al. (1978) reported similar findings. However, the pause length of diving black ducks did not increase as water depth increased, nor did it increase as dive length increased. This suggests that some factor other than water depth and dive length influenced the pause length. The fact that pause length was found to increase as windchill temperature decreased suggests that at cold windchill temperatures, the black duck requires a longer rest between dives, i.e. a longer recovery period is necessary before it can dive again. Kontogiannis (1968) states that activity costs are greater at low temperatures. Therefore it would be more costly

energetically to dive at colder temperatures (although the water temperature would remain relatively constant), since upon resurfacing, heat from the body would be lost more rapidly to the environment. Thus it appears diving is more stressful for the dabbling duck at low ambient temperatures, explaining the longer pause lengths recorded between dives. Since the pause duration was longer at cold temperatures, the foraging rate decreased. This implies that diving would be even less efficient at cold temperatures in terms of energy ingested per unit time. However, since the number of tip-ups per minute remained constant over all temperatures, the foraging rate did not vary.

The results from this study clearly demonstrate that the foraging rate and success of diving black ducks was considerably less than black ducks tipping up. Differences in foraging parameters, such as the length of the foraging bout and forage and pause times, served to reduce the foraging rate of diving black ducks. Environmental conditions such as low windchill temperatures and increased water depth further reduced the foraging rates of diving black ducks and thus accentuated the differences between tipping up and diving. Foraging success was also lower because of the reduced mobility of diving black ducks (due to the lack of morphological adaptations required for diving) and/or the black duck's inexperience in utilizing diving as a

foraging method.

In spite of reduced foraging success, black ducks wintering in this area resorted to diving as a means to secure food due to the lack of shallow water feeding areas. The fact that no ducks died due to starvation attests to the usefulness of adopting an alternate feeding strategy and indicates that this behavioral plasticity enhanced their survival during the stressful winter period.

CHAPTER 4. BEHAVIORAL THERMOREGULATORY MECHANISMS
IN WINTERING BLACK DUCKS

INTRODUCTION

Behavioral thermoregulation is an important and sometimes crucial supplement to physiological modes of thermoregulation and takes such forms as: selecting a sheltered roost site; sunbathing; and postural adjustments which serve to minimize heat loss (King 1974). Dawson and Hudson (1970) argued that the physiological capacities of birds in relation to survival and energy expenditure are greatly augmented by behavioral adjustments that tend to reduce the costs of thermoregulation. The purpose of this study was to examine the modes of behavioral thermoregulation adopted by Black ducks (Anas rubripes) wintering in a cold environment.

Nocturnal periods are critical in the resistance of birds to winter temperatures since it is generally the coldest time of the day, and a period when the bird is not feeding (Kendeigh 1960). Birds roosting in the open experience rapid heat loss through radiation and strong winds (Shilov 1968) and therefore roosts should be well sheltered in order to minimize thermoregulation costs. However, another factor which must be considered when selecting a roost site is the distance from the feeding area. Since flight costs are high (Kendeigh et al. 1977), roosts should be located near the feeding area in order to minimize these costs. Yom-tov et al. (1977)

discovered that many birds arriving at their roost flew long distances daily, thereby negating any potential thermal benefit obtained from the roost. Therefore, there appears to be several factors which can potentially influence roost site selection. One of the aims of this study was to determine whether the roost site selected by wintering black ducks was energetically profitable, such that the energetic savings realized at the roost outweighed the necessary flight costs.

A variety of factors, such as light intensity and ambient temperature are known to influence the time birds leave and return to roost. Krantz and Gauthreaux (1975) stated that varying light intensities influenced the roosting responses of brown-headed cowbirds (Molothrus ater) so that on brighter days the birds left the roost earlier and returned to roost later. Eastwood et al. (1962) also related flights from starling roosts to light intensity and concluded that decreased light intensity resulting from clouds caused the birds to remain at their roosts longer. However both starlings (Sturnus vulgaris) and chickadees (Parus carolinensis) were found to leave their sheltered roost later and return earlier on cold days (Jumber 1956, Pitts 1976, respectively). Another aim of this study was to examine roost arrival and departure in wintering black ducks and to determine what environmental factors influence their roosting responses.

While at the roost site, birds spend the majority of their time resting. The posture and orientation adopted by birds while resting are ecologically significant since they can be adjusted to reduce heat loss (Rising 1979) and thus should be dependent upon such factors as light intensity, temperature and wind. For example, Midtgard (1978) reported that the postures adopted by mallards (Anas platyrhynchos) were influenced by the weather. The third aim of this study was to examine the posture and orientation of resting ducks and to determine if these wintering birds adjust their positioning in response to environmental conditions.

METHODS

Black duck roosting and resting behavior was studied on the Rideau River, 20 km south of Ottawa. Observations, using a spotting scope which permitted accurate observation from 50 m away, were made along a 0.5 km stretch of the river near the roost site or from a bridge located south of the roost. The ducks roosted along the shoreline in snow or ice from 14 January to 12 March, 1982. The roost site was surrounded on both sides by sloping banks supporting many large trees. The ducks flew from their roost site, approximately 3 km north, each day to a feeding station which supplied 50 kg of cracked corn every morning at approximately 11:00 EST.

There were only two areas of open water in this vicinity: the roost and the feeding station (i.e. only two possible roost sites since black ducks must roost near water according to Johnsgard 1975). Therefore, microclimatological data were collected concurrently at these sites on nine separate occasions to determine if the roost site was sheltered relative to the feeding site. Both temperature and windspeed were measured with a hot wire anemometer placed 0.5 m above the ground.

In order to calculate flight costs using the method outlined in Kendeigh et al. (1977) (see chapter 1), the approximate length of time required to fly from the

roost to the feeding station was determined. The flight duration was measured by two observers with synchronized watches, one which recorded the time and number of ducks leaving the roost and the other, the time and number arriving at the feeding station. Since the ducks would leave the roost in discrete groups, at least several minutes apart, accurate measurements of flight duration were obtained.

The total number of ducks leaving and returning to roost in five minute intervals was recorded for 16 morning and afternoon flight periods. Counts for a morning flight period began when the first birds left the roost, and were continued until the last duck departed for the feeding area. Afternoon counts began when the first bird returned to roost and ceased when the first major break (greater than 20 minutes) occurred in arrival times or when it became too dark to observe returning birds. This method accounted for at least 90% of the roosting population.

Air temperature and windspeed were measured and cloud cover was estimated (percent of the sky covered in clouds) for each flight period, observed in order to determine what environmental factors influenced roost responses. The times recorded in the morning were converted to minutes after sunrise and for the afternoon to minutes before sunset. Sunrise/sunset times were obtained from the Environment Canada Weather Office

(ECWO).

The time for 50 percent of the birds to leave the roost in the morning and the time for 50 percent to return was calculated. Regression analysis was used to examine the relationship between the time birds left and returned to roost with windchill temperature and cloud cover. Windchill temperature, $T(c)$ was calculated using the ambient temperature, $T(a)$ and windspeed, W (measured with a hot-wire anemometer placed 0.5 m above ground near the roost) and the following formula obtained from ECWO:

$$T(c) = 33 - [(0.227\sqrt{W} + 0.45 - 0.0118 W)(33 - T(a))].$$

The postures and orientation of ducks while resting were recorded on 18 separate occasions from 20 January to 12 March 1982 in order to observe resting behavior under varying temperatures, windspeeds and cloud cover. The postures adopted by ducks resting on the ice were recorded along with the temperature and windspeed to determine if the posture used was influenced by the windchill temperature.

The orientation adopted by resting ducks on clear and overcast days was also recorded along with the wind speed and direction to determine if these factors influenced the direction of the birds while resting.

RESULTS

Although the temperatures recorded concurrently at the roost and the feeding sites were similar, the windspeeds differed considerably (Table 1), suggesting that the roost site provided more shelter than the feeding station. Large trees surrounding the roost provided an effective windbreak from the prevalent northwesterly winds. The windchill temperature was computed for each observation period and the mean difference in the two sites over the 9 observation periods was approximately 5 Celcius degrees. Wooley and Owen (1978) determined that a decrease in temperature of 5 Celcius degrees raised the resting metabolic rate (RMR) of black ducks approximately 4.18 kjoules per hour. Therefore, a duck at the roost site would have a lower RMR and would realize a reduction of energy costs of approximately 80 kjoules/day based on the 20 hours spent daily at the roost.

On average, it took a black duck 11 minutes to fly from the roost and land at the feeding station. Cost of daily flight to and from the roost was thus estimated at 48 kjoules. Therefore, the metabolic saving realized by ducks at the roost site outweighed the necessary flight costs.

Multiple linear regression analysis was employed to examine the relationship between the time 50% of the

Table 4-1. Comparison of temperature and
windspeed conditions at the feeding station (F)
and at the roost (R).

Date	Temperature	Windspeed	Windchill
Jan 24 (F)	-10	18	-19
Jan 24 (R)	-10	12	-14
Jan 25 (F)	-21	20	-33
Jan 25 (R)	-20	10	-26
Jan 30 (F)	- 9	15	-15
Jan 30 (R)	- 9	8	-11
Jan 31 (F)	-15	22	-27
Jan 31 (R)	-15	11	-21
Feb 6 (F)	-10	25	-22
Feb 6 (R)	-10	14	-18
Feb 7 (F)	-16	20	-28
Feb 7 (R)	-16	15	-23
Feb 21 (F)	+ 3	18	- 4
Feb 21 (R)	+ 4	11	0
Feb 25 (F)	-12	28	-26
Feb 25 (R)	-12	15	-18
Mar 7 (F)	- 3	15	- 8
Mar 7 (R)	- 2	9	- 4

birds left and returned to roost and the windchill temperature and cloud cover at this time.

Windchill temperature explained a significant amount of the variation observed in both the time the birds left and returned to roost (Tables 2 and 3). Cloud cover, however, in both morning and afternoon flight periods, had little effect on the roosting responses of ducks in this study. On cold days (less than -25 degrees C), ducks were observed to leave the roost 100 minutes later and return 160 minutes earlier than on warm days (greater than -2 degrees C) (Figure 1). After feeding, the ducks would return to their roost at least 75 minutes earlier on cold days than on warm days (Figure 2).

When sleeping, black ducks noticeably fluffed out their feathers, formed large tight huddles, tucked their bills under their scapular feathers and their feet under their bodies (Posture IV). However during the day, they adopted this and three other postures illustrated in Figure 3. The differences in the appearance of these 4 postures represent differences in the exposed surface area of the duck (taken from Mitgard 1978). Posture I has a maximum exposed surface area and is observed mainly on warm days, especially sunny ones when the bird exposes its feet to the sun's rays. Posture II, represents a 4% decrease in exposed surface area and Posture III a 9% decrease. Posture IV, observed

Table 4-2. Multiple linear regression analysis to determine the effect of windchill and cloud cover on the time birds left their roost.

Weather Variables	Cumulative R^2	B	B Std.E.	Partial F
Windchill	.810	4.61	.491	58.87**
Cloud Cover	.819	1.03	.980	1.10

Overall F = 27.66**

p < 0.01 *
p < 0.001 **

Table 4-3. Multiple linear regression analysis to determine the effect of windchill and cloud cover on the time birds returned to their roost.

Weather Variables	Cumulative R^2	B	B Std.E.	Partial F
Windchill	.828	-4.47	.251	49.46**
Cloud Cover	.835	0.37	.601	3.66

Overall F = 35.45 **

p < 0.01 *
p < 0.001 **

Figure 4-2. The effect of windchill temperature on the time (expressed in minutes after sunrise) at which 50% of the ducks left their roost.

Figure 4-2. The effect of windchill temperature on the time (expressed in minutes before sunset) at which 50% of the ducks returned to their roost.

Figure 4-3. Postures adopted by resting black ducks. Percentages indicate the reduction of exposed surface area (After Mitdgard 1978).

I

II

4%

III

9%

IV

12%

predominantly on cold days represents a 12% decrease in exposed surface area. The total number of ducks observed in any one of the four postures at a particular windchill range was determined (Table 4). A chi-square test on this contingency table was used to determine if the posture adopted by the resting duck was independent of the windchill temperature. The results from this analysis suggest that the postures adopted by resting ducks are not random ($\chi^2 = 1721.6$, $p < 0.001$, $df = 9$), but rather dependent upon windchill temperature.

Only data collected when skies were clear or completely overcast were used in the analysis of the orientation of resting ducks (Figure 4). Moreover, only those periods when the direction of the wind was opposite to the direction of the sun were used when determining if wind speed and direction influenced orientation.

In order to determine if the orientation of resting ducks was dependent upon the direction of the wind or sun, chi-square tests were performed. All tests had one degree of freedom. The results for condition A imply that at low wind speeds, resting ducks do not orient their bodies randomly ($\chi^2 = 28.4$, $p < 0.001$), but rather facing towards the sun. However, under overcast conditions and low wind speed (condition B), a random orientation was observed ($\chi^2 = 0.12$, $p > 0.05$) suggesting that orientation is independent of environmental

Table 4-4. Number of ducks adopting resting postures I-IV at different windchill temperatures

Windchill	Postures			
	I	II	III	IV
< -20	4	6	205	436
-20 to -11	54	139	346	104
-10 to 0	331	171	119	18
> 0	233	24	13	5

Figure 4-4. Orientation of black ducks in winter with respect to sun and wind. The number of ducks facing a particular quadrant is given. Position of sun and wind direction are indicated.

- A. Clear skies
Windspeed ≤ 10 kph

- B. Overcast
Windspeed ≤ 10 kph

- C. Clear skies
Windspeed > 10 kph

- D. Overcast
Windspeed > 10 kph

conditions. However, the orientation of ducks under conditions C ($\chi^2 = 155.8$, $p < 0.001$) and D ($\chi^2 = 25.8$, $p < 0.001$) demonstrates that regardless of sky conditions, ducks orient their bodies dependent upon the direction of strong winds.

DISCUSSION

The roost site selected by black ducks was sheltered from strong northwesterly winds unlike the feeding station, perhaps explaining why ducks roosted in a separate area from where they fed. Although there were perhaps sites which were better sheltered, there were only two open water areas where the birds could roost: the feeding station and an area located 3 km south (the chosen roost). The fact that the energetic savings realized by ducks roosting at the chosen roost site exceeded the metabolic costs of daily flight from the roost to the feeding station implies that the selection of a roost site by ducks in this study was energetically profitable.

Most species roost communally only during the post-breeding season when they face an unevenly distributed and somewhat lowered food supply (Lack 1968). Coupled with this is the problem of shortening day length resulting in less time to forage. Shilov (1968) states that the feeding activity of birds starts earlier in the winter months (with respect to sunrise times) in order to compensate for the shortening daylength and the increased energy demands due to costs related to maintaining body temperature. Thus in order to maintain an energy balance, these birds must forage for as long as possible during the daylight hours, so

that at the first sign of light, these birds leave their roosts to forage and return only when they can no longer search for food. This explains why many studies have reported the relationship between light intensity and roost responses. For example, Hochbaum, (1955) stated that daily feeding flights of waterfowl were governed by metabolic and solar cues. Parr and Scott (1978) found that Wood duck (Aix sponsa) roost flights were controlled primarily by light. Raveling et al. (1972) reported that light intensity at dawn and dusk appear to be important factors regulating the onset of daily flight activities in Canada geese (Branta canadensis). Common goldeneyes (Bucephala clangula) started their morning flights later on those days with fog, and evening arrival times at the roost were earlier on overcast days (Sayler and Afton 1981).

The fact that this study revealed no relationship between cloud cover and time leaving or returning to roost can be explained by considering the nature of the food supply. The ducks did not have to search actively for their food as did the birds in the other roosting studies cited above and thus did not leave the roost at sunrise or earlier to begin foraging. The shortened daylength did not influence the foraging success of ducks at this site and thus they did not need to remain foraging until the light intensity reduced visibility, at sunset or sometime later. The uniqueness of their

food supply therefore explains why roosting responses were not governed by light intensity.

The fact that windchill temperature accounted for at least 80% of the variation observed in the time the birds left or returned to roost suggests that it was a critical factor influencing roost responses in this study. As demonstrated earlier, the roost site in this study provided a more favorable microclimate for ducks and by spending more time at this site on colder days, the ducks can reduce thermoregulation costs.

The large tight huddles that ducks formed while sleeping at their roost served to reduce the amount of surface area exposed and thus reduced heat loss to the environment (Calder and King 1974). Huddling behavior also served to lower metabolic rates which are known to increase as ambient temperatures decrease (Wooley and Owen 1977). Shilov (1968) stated that in a close gathering of birds, the temperature within the group is significantly higher than the external temperature and thus the effective maintenance of body temperature is possible at a relatively lower energy cost.

Fluffing of the feathers increases the thickness of the plumage which is thought to reduce the rate of heat conduction away from the body (Shilov 1968). Also, the sleeping position that ducks adopted at the roost further reduced exposed surface area as well as protecting those areas (legs, feet and bill) which are not covered by

feathers and are thus subject to rapid heat loss (Dawson and Hudson 1970).

The fact that the postures adopted by resting ducks were dependent upon the windchill temperature suggests that ducks adjusted their resting posture in response to environmental stress. By tucking their head under their wing, they reduced heat loss through the head which would otherwise be high because of the short feathers which cover it. In addition, heat loss from the feet was minimized since they were tucked under the body. Overall, this posture reduced the exposed surface area of the duck to the greatest degree and assuming heat loss is reduced by the same magnitude (Midtgard 1978), the advantage of retracting the extremities is obvious, especially on the cold days when this posture was most prevalent.

By orienting their body towards the sun (termed sunbathing by Midtgard 1978), a duck could obtain maximum insolation. Exposure to sunshine appears to have the same functional effect on energy metabolism as a rise in the ambient temperature, and the degree to which this effect is produced is said to depend upon the characteristics of the incoming radiation and the properties of the surface upon which it falls (Gessaman 1973). Heat absorbed from insolation cannot be used as energy for activities such as foraging or locomotion, but it is of value in reducing heat loss from the body,

thereby reducing thermoregulation costs (Kendeigh 1960). For example, the metabolic rate of the cardinal (Cardinalis cardinalis) in the sun and in the shade differed by up to 50% (Porter and Gates 1969). Furthermore, a decrease in caloric intake was observed in the white crowned sparrow (Zonotrichia leucophrys) on days when they were exposed to early morning sunlight (Morton 1967). Therefore, sunbathing appears to be an important behavior in wintering birds, and by adopting this behavior, wintering black ducks have likely reduced thermoregulation costs.

Windspeeds greater than 10 kph ruffled the plumage of ducks that did not orient their bodies facing into the wind. This would increase the rate of heat loss in these birds since ruffling the feathers disrupts and displaces them, exposing the downy layer. This, in turn, causes a reduction in the interface between the body and the environment, thereby increasing thermal conductance to the atmosphere (Calder and King (1974). Since the majority of ducks faced into the wind when resting, they did not experience this problem and thus reduced heat loss on windy days.

Three modes of behavioral thermoregulation were examined in this study. Wintering black ducks were observed to: i) roost in a sheltered habitat; ii) spend more time in this habitat on cold days; and iii) adopt postures and orientations while roosting which minimized

heat loss either through retraction of poorly insulated body parts or by reducing disruption of the insulation layer. It is thought that these behavioral adjustments enhanced the survival of these ducks as they likely served to lower thermoregulation costs.

GENERAL DISCUSSION

Wintering black ducks modified their behavior in a number of ways as a means to tolerate the stresses imposed by a winter environment. For example, they adjusted their daily time-activity budget in response to differing levels of climatic and energetic stress. The strong relationship observed between ambient temperature and the amount of time spent in many of the activities led to the conclusion that climatic stress is best defined by temperature. At low temperatures (high climatic stress) when thermoregulation costs are highest, ducks reduced energetically costly activities in favor of: i) increasing metabolically cheap behaviors, thereby reducing energy outputs; or ii) increasing foraging activity, thereby increasing energy inputs. In addition, the level of energetic stress experienced influenced time-activity budgeting. The ducks with high energy resources spent more time in non-maintenance activities such as courtship while ducks with fewer energy resources restricted their activities to mainly cheap maintenance behaviors such as preening and resting. This demonstrates that ducks are able to modify their behavior in response to the levels of climatic and energetic stress they are experiencing, and this plasticity in time-energy budgeting favored the maintenance of homeostasis.

Behavioral flexibility was also evident in the courtship behavior of black ducks. Ducks require both time and energy after maintenance costs in order to initiate courtship behavior. Ducks at the high energy site were able to initiate courtship earlier than ducks at the other two sites, in spite of high maintenance costs, because they had the available resources. Ducks at the lower energy sites initiated courtship later, when maintenance costs were lower (due to higher ambient temperatures) and thus they had the resources (both time and energy) available to devote to courtship. In this respect, ducks modified both the time they began courting and the time spent in this activity to suit their environmental surroundings.

The foraging behavior of black ducks also incorporated a degree of flexibility which was thought to contribute to the survival success of these wintering birds. Black ducks generally forage by dabbling or tipping up in shallow water. However, due to ice formation, the only open waters for one population were deep fast flowing areas which prompted these ducks to begin diving for their food. Although not physiologically or morphologically designed for diving, adopting this atypical foraging method enabled these ducks to secure an otherwise unobtainable food source.

Selecting an energetically profitable roost site, adopting postures which reduce heat loss from poorly insulated body parts and orienting their bodies facing the wind to reduce the disruption of the insulating plumage layer and facing the sun to receive maximum insolation were several of the behavioral thermoregulatory mechanisms employed by wintering black ducks. These behavioral modifications which reduced thermoregulation costs by reducing heat loss, were both quick and cheap ways of coping with climatic stress: quick in that they can be employed when stress occurs and cheap because they require no additional energy expenditure.

The ability of these birds to adjust their foraging, courtship and resting behavior to suit fluctuating climatic conditions illustrates several facets in the behavioral repertoire of the black duck which can be readily modified and serve to enhance survival during the winter months. The behavioral adjustments adopted clearly augment physiological and morphological adaptations and thus should be considered in future studies involving animals and their ability to cope with the stresses imposed by their environments.

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