NUTRITIONAL AND THERMODYNAMIC ASPECTS OF THE ECOLOGY OF BLACK DUCKS WINTERING IN MAINE

DENNIS G. JORDE

1986
MIGRATION JOURNEY

A migration journey of a thousand miles
 begins with the first wing flap,
guided by sun, moon, stars, and gravity
 to lakes, rivers and delta marshes flat.

Over mountains, oceans, and prairies,
 through perilous storms the experienced guide
 the new to destinies
 of hope, accomplishments, and pride.

Thus you have been to me,
 guiding light, migration leader,
 helping to achieve a goal and opening doors
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By
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A DISSERTATION
Submitted in Partial Fulfillment of the
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NUTRITIONAL AND THERMODYNAMIC ASPECTS OF THE ECOLOGY OF BLACK DUCKS WINTERING IN MAINE

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Causes of the 20-year decline of the continental population of black ducks (Anas rubripes) have focused primarily on the breeding grounds; however, there is an urgent need to investigate probable causes affecting their survival at wintering areas. Winter ecology of black ducks along the central coast of Maine was examined between 1982 and 1985 by focusing on the relationships between habitat use and the thermodynamics of microclimates, true metabolizable energy and nutrient content of winter foods, and heat of digestion and thermoregulation.

During winter the selection of microhabitats by black ducks was important in reducing heat loss from wind and maximizing the heat input from solar radiation during the day. Black ducks used shoreline rest sites when solar radiation was available during the day but preferred to swim in open water during the night when water temperatures were often warmer than ambient air temperatures. Measurements of microclimates at rest sites indicated that
small differences in microclimate had a major influence on the energy transfer, especially thermoregulation, of black ducks during winter and caused subtle but crucial changes in behavior, foraging strategy, and distribution.

Animal foods accounted for 96 percent of the diet of black ducks and consisted primarily of periwinkles (*Littorina sp*), blue mussels (*Mytilus edulis*), *Gammarus* (*Gammarus oceanicus*), and soft-shelled clams (*Mya arenaria*). Proximate analyses and force feeding trials indicated that the metabolizable energy obtained from these foods by captive black ducks was influenced by the type and level of food intake. True metabolizable energy per gram of food decreased as fed level increased seemingly because of differences in the rate and efficiency of digestion. *Gammarus* contained the most favorable nutrient content based on gross energy, protein, fat, and true metabolizable energy. The variable amount of energy metabolized from the foods may influence lipid and protein dynamics, foraging strategies, and habitat preference.

Differences in metabolism of black ducks before and after feeding indicated that the heat of digestion or specific dynamic effect (SDE) was compensatory for thermoregulation. Earthworms reduced the energy required for thermoregulation by approximately 50% after feeding. Black ducks had a metabolic rhythm of thermogenesis that cycled at 15 to 20 minute intervals, increased in frequency
when food was digested, and then returned to pre-feeding rhythm patterns. The SDE and nutrient content of foods studied suggest that animal and plant diets of waterfowl have important implications on foraging strategies and survival during winter and on reproductive success during the breeding season.
ACKNOWLEDGEMENTS

First and foremost, I would like to express deep gratitude to my wife, Michele, and children, Benjamin, Johnathon, and Virginia, for their love, understanding, and many sacrifices during my long absences from home.

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I acknowledge other University of Maine faculty, staff, and employees for advice and assistance, especially Dr. William Halteman for statistical and math modeling advice, Dr. Herb Hidu for helping to collect marine organisms, Dr. Stewart Goltz for advice concerning microclimates, Mr. William Cook for conducting chemical analyses, and Ms. Maxine Horn for words of encouragement and friendship.

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assistance during the study.

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in birds has been shown by a number of studies (e.g., Lustick 1969, Krantz and Gauthreaux 1975, Lustick et al. 1978, DeJong 1979). Radiation decreases metabolism and extends the thermoneutral zone to lower ambient temperatures (Heppner 1970, Hayes and Gessaman 1980).

Calculating the cost of thermoregulation requires an understanding of habitat selection, activity patterns, and thermoregulatory physiology of a species (Chappell 1980). The basal metabolic rate (BMR) of birds or standard metabolism of free-ranging birds is related to climate and microhabitats and tends to be higher in cold climates (Weathers 1979). BMR and existence metabolism (EM), which includes activity and heat increment of feeding, increase during periods of decreasing temperature (Kendeigh 1969, Cain 1973).

The influence of microclimate on habitat use, changes in energy budget, and survival of American black ducks (Anas rubripes) is unknown. The objectives of this study were 1) to determine if habitat selection and energetics of black ducks were influenced by the microclimates of different coastal habitats in winter and 2) to study habitat use and foraging behavior of black ducks.

STUDY AREA AND METHODS

The study area was located at Frenchman Bay and Mt.
Desert Narrows between Trenton and Hancock along the north central coast of Maine (Fig. 1). Studies were conducted at the Jordan River estuary, Mt. Desert Narrows, Raccoon Cove, and Skillings River estuary each winter from January through March, 1982-1985. Data for time budget and food habits studies were also collected during December 1982 and 1983. Albright (1981) described geographic, climatic, and physical characteristics of the study area in more detail.

Microclimate data were collected at locations that black ducks were observed and not observed to use as resting areas at Raccoon cove. Each location was monitored for at least 14 days and the observation period at one site overlapped the collecting schedule of a second site by at least 7 days. Temperatures at 20 cm above the soil surface from three measurement probes spaced 10 meters apart, relative humidity, and solar radiation were recorded. Ambient temperature was recorded at 3.6 meters above the ground at each microclimate study site. A hot wire anemometer measured wind velocity at micro- and macroclimate locations 4-5 times each week during 1983 and 1985, and 2-3 times each week during 1984 except when the anemometer was being repaired. Wind velocity was recorded at 10-second intervals for 2 minutes from which an average wind velocity (m/s) was calculated. Wind direction was not determined at microclimate locations because turbulent and eddy air currents were constantly shifting direction.
Figure 1. Study area located along the central coast of Maine. Microclimate study sites are identified along the shore of Raccoon Cove. Telemetry locations of radioed black ducks at high tide are indicated by squares and at low tide by dots.
However, macroclimate wind speed and direction were recorded at a nearby boat access area 10 to 60 minutes before or after wind was recorded at microclimate sites depending on travel time between sites.

Microclimate measurements (except wind) were recorded by an electronic datalogger at one minute intervals, averaged each hour, and automatically stored on cassette tape. Cassettes were taken to the laboratory and data transferred to microcomputer files. Water temperatures were recorded and ice conditions sketched on maps. General weather data at the Southwest Harbor Coast Guard Station, 18 km away, were obtained from the U.S. Environmental Data Service.

A lumped parameter model (Gates 1980) was used to estimate heat exchange and metabolic rates of black ducks using different microclimates in Raccoon Cove. The equation for the lumped parameter model was:

\[ M - cE + Qa = eK1 \ast [Tb + 273 - I(M - cE)] + [K2 \ast 0.5 \ast 0.5 \ast (V/D)] [Tb - Ta - I(M - cE)] \]

where:

- \( M \) = metabolic rate (W/m^2)
- \( c \) = latent heat of vaporization = 2.47E6 to 2.55E6 J/Kg for this study. (See Fritschen and Gay 1979: 132)
- \( E \) = Evaporative water loss estimated by equation
from Gates (1980: 404). $E = 0.351 \text{ W}$

where: $W =$ grams body weight
e = emissivity of plumage = 0.99 (Hammel 1956)
$K_1 =$ Stephan-Boltzmann constant = $5.7 \times 10^{-8}$
$T_b =$ body temperature = 39 C
$I =$ insulative value of feathers = $0.0779 \text{ m C/W}$

for smoothed feather profile and $1.548 \text{ m C/W}$ for ptiloereected feather profile,
estimated using the following equations:

$I = I_1 + I_2 + I_3$

where: $I_1 = d_1/k_1$, $I_2 = d_2/k_2$, $I_3 = d_3/k_3$

(Gates 1980)

where:

d_1 = thickness (in meters) of smooth (0.01 m) and ptiloereected (0.02 m) feathers
estimated from captive black ducks

d_2 = thickness (in meters) of the subcutaneous fat layer (0.0018 m)
estimated from collected black ducks

d_3 = thickness (in meters) of the skin (0.0005 m) estimated from collected black ducks

$k_1 =$ conductivity of feathers (eider down) = $0.013 \text{ w/mC}$

$k_2 =$ conductivity of fat = $0.205 \text{ w/mC}$ (Gates 1980)
\[ k_3 = \text{conductivity of skin} = 0.502 \text{ \( \text{w} \text{m}^{-1} \text{C} \)} \]

\( K_2 = \text{convection constant for forced air} = 3.49 \)

\( V = \text{wind velocity (m/s)} \)

\( D = \text{diameter of black duck body without feathers} = 0.105 \text{ m (estimated from captive black ducks)} \)

\( T_a = \text{Microclimate air temperature (C)} \)

\( Q_a = \text{Shortwave (solar) and longwave (infrared) radiation absorbed by the bird's plumage} \)

\( Q_a \) included shortwave radiation and atmospheric longwave radiation, but not longwave radiation emitted by the ground and surrounding objects (Fig. 2). The equation used to estimate \( Q_a \) was:

\[ Q_a = K_T(1 - a A + a_s - (a A^a a_s)) + L(1 - r A + r_s - r A^2 r_s) \]

where:

\( K_T = \text{total direct solar radiation (W/m}^2) \)

\( a A = \text{albedo (shortwave reflectance) of plumage surface} = 0.164 \text{ for muscovy duck (Cairina moschata) at a low sun angle (Gates 1980: 260)} \)

\( a_s = \text{albedo of substrate surfaces: 1) old snow = 0.85 2) rock = 0.10, and 3) grass = 0.21 (Oke 1978: 15)} \)

\( L = \text{atmospheric longwave radiation estimated by} \)
Figure 2. Thermodynamic diagram of shortwave (solar) and longwave (infrared) radiation used to estimate metabolic heat production by black ducks using different microclimates.
using the equation from Gates (1980: 152):

\[ L = \frac{6}{2} (\text{W/m}) \]

where: \( T \) = microclimate air temperature expressed in degrees Kelvin

\[ rA = \text{longwave reflectance of plumage surface} = 1 - \text{emissivity} = 0.01 \]

where emissivity = 0.99 (Hammel 1956)

\[ rs = \text{longwave reflectance of substrate surface.} \]

For this study 0.08 was used as the estimated value for old snow, rock, and grass surface (Oke 1978: 15)

For this study, respiratory water loss during winter was assumed to be minimal, hence, only one estimate of respiratory heat loss was used in equations to estimate metabolic rates. Compared to other heat losses, conductive heat loss to the environment is usually minimal (Gates 1980). Therefore, conductive heat transfer from the bill, head, and feet of black ducks was not included in the model. Representative body weights selected for use in equations were 1200 g for males and 1000 g for females based on black ducks captured for banding.

Eighteen black ducks were captured in bait traps and fitted with radio transmitters. Marked birds were allowed 7 days to adjust to transmitters before data were recorded for analyses. The location of radio-marked birds, time, and date were recorded on maps at low and high tides.
Visual locations of marked birds were obtained when possible.

Diurnal observations of behavior were made using a 10X spotting scope and 1300mm scope. Nocturnal observations were made with a night-viewing device equipped with either a 300, 400, 800, or 1300 mm lens. Activities of birds were recorded at 15-second intervals. Individual birds were chosen randomly by locating a group of birds in the scope's field of view and, then after looking away and slightly moving the scope either horizontally or vertically or both, observing the individual nearest to the center of the field of view. A minimum of 1 minute and a maximum of 1 hour of continuous data were collected for each individual observed.

Correlation between microclimate variables was examined by generating a matrix of Kendall tau-b coefficients. Differences between paired microclimate variables were tested with paired t-tests using multivariate general linear hypothesis (MGLH) procedures which calculated an F statistic (SYSTAT, Inc. 1985). Behavior data were analyzed using Chi-square analysis. Significance was accepted at P<0.05 unless otherwise stated.
RESULTS AND DISCUSSION

HABITAT USE

Habitat use by black ducks was similar to that of previous studies (e.g. Hartman 1960, Albright 1981, Longcore and Gibbs 1986) and was influenced by the location of principal wintering sites, tidal cycles, microclimates, and ice conditions. Rockweed ledges were the most preferred habitat (36.8 %) whereas unconsolidated beaches were used the least (4.2 %) among diurnal tide periods during this study (Fig. 3). Generally, the use of mud flats, mussel ledges, and open water by black ducks was similar but varied by tide. During the night, black ducks grouped into one or several large flocks and swam or drifted in open water during high tide rather than use roost sites on shore, perhaps to remain in sea water warmer than ambient temperatures (Albright 1981) or to avoid mammalian predators. Also, during the highest tides, most shoreline habitats were flooded and tidelines often extended to the edge of the forest thereby limiting the location and number of suitable resting and loafing habitats. During diurnal high tides, black ducks used rockweed ledges extending from or near shore and open water as resting areas (Table 1)(Fig 1). Also, unconsolidated beaches were occasionally used as rest sites. Black ducks most often flocked along the south facing shorelines near freshwater seeps where microclimates
Figure 3. Influence of the tidal cycle on diurnal habitat use by black ducks along the central coast of Maine during the winters of 1982, 1983, and 1984.
Table 1. Percentages of diurnal habitat use in relation to low, rising, high, and ebbing tides by radioed black ducks at two principal wintering sites along the central coast of Maine.

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<tr>
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<th>Raccoon Cove</th>
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<th>Jordan River/ Mt. Dessert Narrows</th>
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<tr>
<td></td>
<td>Low</td>
<td>Rise</td>
<td>High</td>
<td>Ebb</td>
</tr>
<tr>
<td>Mud Flat</td>
<td>12.6</td>
<td>10.3</td>
<td>0.0</td>
<td>9.9</td>
</tr>
<tr>
<td>Mussel Ledge/Bar</td>
<td>8.3</td>
<td>3.4</td>
<td>0.0</td>
<td>5.7</td>
</tr>
<tr>
<td>Rockweed Ledge</td>
<td>8.3</td>
<td>3.4</td>
<td>3.8</td>
<td>6.9</td>
</tr>
<tr>
<td>Unconsolidated Beach</td>
<td>0.0</td>
<td>2.3</td>
<td>0.8</td>
<td>1.5</td>
</tr>
<tr>
<td>Open Water</td>
<td>0.8</td>
<td>0.8</td>
<td>20.2</td>
<td>0.8</td>
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were more favorable, although east-facing rockweed ledges and sand beaches near freshwater seeps were also used. Occasional extensive ice formations forces birds to rest on the ice or use nearby ice-free habitats until ice conditions have abated (Albright 1981, Longcore and Gibbs 1986). Patterns of habitat use changed during mid tide as rockweed ledges and the shallowest areas of mudflats and mussel bars were exposed (Table 1). Black ducks flew and swam to forage in tidal channels, mud flats, rockweed ledges, and mussel bars presumably because invertebrates were more abundant and accessible there. Different habitat types were used during rising and ebb tides at principal wintering sites. For example, mud flats (30.8 %) were used most often at Raccoon Cove whereas rockweed ledges (41.8 %) and mussel bars (30.0 %) were frequently used at the Jordan River (Table 1). During low tide black ducks preferred mud flats, mussel ledges, and rockweed ledges (Table 1). During the night, black ducks used the same habitats at low tide as used during the day except they seemed to avoid exposed surfaces and preferred to use areas still covered by shallow water. These habitat types were abundantly scattered throughout the study area which resulted in a wide distribution of bird locations (Fig. 1).

Ice interacted with high tides to restrict or limit the amount and distribution of habitats that black ducks could use, similar to results reported by Albright (1981) and
Longcore and Gibbs (1986). For example, Evan's cove became icebound during periods of extreme cold which, forced the ducks to move to Raccoon cove until temperatures warmed and the tides moved ice from the cove. However, in general, black ducks rarely shifted between wintering sites (Fig. 1), although these two sites were only 5 - 6 km apart.

BEHAVIOR

General Patterns

The behavior of black ducks was strongly influenced by tidal cycles similar to observations by Albright (1981). During this study, sleeping was the dominant behavior during rising and high tides as habitats used for foraging became flooded (Fig. 4). Swimming was an important activity during each tide period but was greatest (26.6%) during rising tide and lowest (14.0%) during high tide. Walking, which was mostly associated with foraging activity, was observed more often during low tide. Resting and comfort movements were also common behaviors and were similar within tide periods except during ebbing tides when resting (7.7%) was observed more often than comfort activity (4.8%).

Black ducks were more alert during ebbing and low tides while they foraged in exposed tidal areas (Fig. 4). Although time spent in aggressive encounters was low compared to other behaviors, aggression was greatest during
the ebbing tide when black ducks vied for foraging and resting sites. Grandy (1972) and Albright (1981) observed little aggression among black ducks, especially on feeding areas. Also, similar to Albright (1981), courtship (including copulation) and pairs of black ducks were observed throughout winter, although courtship was a rare or infrequent daily activity. Courtship was observed more often during high tide, which may represent the brief period when energy from food digestion was most available for courtship and when foraging areas were inassessable. Stotts (1958) reported that in Maryland black ducks form pairs during early fall and continue pairing throughout winter until about 90% are paired by the time they reach the breeding grounds.

Generally weather conditions during this study were mild and black ducks were not observed huddling at diurnal resting sites. However, severe weather forces black ducks to group tightly (Grandy 1972) and Albright (1981) observed black ducks huddling together at roost sites and vying for thermally optimal sites. Black ducks were observed to congregate while swimming in open water during the night, possibly to 1) reduce heat loss by convection, 2) increase longwave heat exchange with adjacent birds, and 3) enhance foraging success while feeding on invertebrates. Also, in response to increased energy requirements for thermoregulation during low ambient temperatures, black
ducks are sedentary to conserve energy (Hickey 1980, Albright 1981).

Foraging Behavior

Black ducks most often swam and occasionally flew from resting areas to foraging habitats. During the day, they often foraged for gammarus (Gammarus oceanicus) and periwinkles (Littorina spp.), individually or in small groups, among rock ledges covered with rockweeds that were the first habitats exposed as the tide receded. They then foraged for soft-shelled clams (Mya arenaria), blue mussels (Mytilus edulis), and other invertebrates on mud flats and mussel bars at low tide.

During the night, black ducks most often swam but occasionally flew to feeding sites. Also, they foraged during the same tidal periods and used the same habitats at night as during the day, but foraging patterns differed. Flocks were larger, concentrated into smaller areas, and occasionally included common goldeneyes (Bucephala clangula). Foraging behavior at night seemed more intense than during the day. Also, birds avoided walking on exposed mudflats and other surfaces during the coldest nights, presumably to prevent mud and other material from freezing on their bills and feet.

Foraging activity of black ducks was largely dictated by the tidal cycle (Fig. 5). Of all foraging behavior,
Figure 5. Percent of time black ducks spent foraging during each of four, 3-hour segments of diurnal tide periods along the coast of Maine during winter.
including drinking, 79% occurred during ebbing and low tides. Feeding activity during ebbing tide was 2.6 times greater than during rising tide. Only 6% of foraging activity occurred during high tide because most of the food was inaccessible.

Dabbling with head submerged was most often observed, but tipping was also a common behavior (Table 2). Tipping (69%) and head submerged (45 and 49%) were observed more during ebbing and rising tides whereas pecking on water (63%) and on mud surface (69%) were more common during low tide, especially on mussel bars. Ducks foraging on blue mussels often shook their heads vigorously from side to side to tear mussels loose from byssus threads anchoring the mussels to rocky substrate and other mussels. Feeding pause and bill shake were more common during rising tide, presumably because exposed substrate had cooled or frozen and the ducks were attempting to prevent mud from sticking or freezing to their bills. Feeding pauses with bill tucked into back feathers (sleeping posture) was greatest during ebbing tide when the birds seemingly were acclimating their bills to foraging in cold water and substrates. This behavior was also common (30%) before rising tide, possibly because exposed substrate surfaces had reached the coldest temperature. Ducks drank water more often during high tide and least often during the ebbing tide. Drinking was most often observed at
Table 2. Partitioning of foraging behavior by black ducks during four 3-hour tide periods along the central coast of Maine during the winters of 1982 to 1985.

<table>
<thead>
<tr>
<th></th>
<th>Low</th>
<th>Rising</th>
<th>High</th>
<th>Ebbing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tipping</td>
<td>12/ 1 a</td>
<td>13/ 2</td>
<td>6/ 2</td>
<td>69/ 4</td>
</tr>
<tr>
<td>Head Submerged/</td>
<td>34/55</td>
<td>15/62</td>
<td>6/69</td>
<td>45/74</td>
</tr>
<tr>
<td>Not Swimming</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head Submerged/</td>
<td>33/ 4</td>
<td>16/ 5</td>
<td>2/ 2</td>
<td>49/ 6</td>
</tr>
<tr>
<td>Swimming</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pecking Water</td>
<td>63/ 9</td>
<td>6/ 2</td>
<td>3/ 3</td>
<td>28/ 4</td>
</tr>
<tr>
<td>Surface</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pecking Mud or</td>
<td>69/26</td>
<td>11/11</td>
<td>1/ 2</td>
<td>19/ 7</td>
</tr>
<tr>
<td>Soil Surface</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feeding Pause/</td>
<td>29/ 4</td>
<td>35/13</td>
<td>12/12</td>
<td>25/ 4</td>
</tr>
<tr>
<td>Bill Shake</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feeding Pause/</td>
<td>17/ 0</td>
<td>30/ 2</td>
<td>6/ 1</td>
<td>46/ 1</td>
</tr>
<tr>
<td>Bill In Feathers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drinking</td>
<td>29/ 1</td>
<td>23/ 2</td>
<td>36/ 9</td>
<td>12/ 0</td>
</tr>
</tbody>
</table>

a Row Percent/Column Percent
freshwater seeps along shore and at channels where fresh water drained across the mud flats.

Black ducks were relatively sedentary during winter and left resting areas primarily to forage in nearby habitats. Black ducks at the Jordan River regularly flew 1-4 km to forage among mussel beds and mudflats at Mt. Desert Narrows. Ducks at Raccoon Cove swam or flew 5 m - 2 km to foraging sites within the cove. However, black ducks at the Skillings River usually swam to nearby rockweed ledges and sheltered coves along the estuary, although some ducks often flew 3-5 km to forage at Raccoon Cove. On some coastal areas black ducks may fly 18 km or more to feeding sites (Hickey 1980) compared with flights of 40 km to agricultural habitats at inland wintering areas (Reed 1971). Feeding flights and the use of foraging habitats is reduced or curtailed by periods of cold temperatures and extensive ice cover (Hartman 1960, Hickey 1980, Albright 1981). Black ducks remain near feeding sites during cold weather (Grandy 1972). Temperature influences foraging of black ducks but no data are available to indicate if temperature directly affects the ducks or if it affects the availability of foods (Grandy and Hagar 1971). Also, decreasing temperatures reduce foraging activity of black ducks on a diet of marine organisms (Grandy and Hagar 1971, Albright 1981), but has an opposite effect on food consumption of mallards on a diet of small grains (Sugden
1979). Generally, food dictates the selection of habitat during winter (Hilden 1965).

MICROCLIMATE

Wind

Wind velocity between north and south microclimate sites were variable (Fig. 6). Generally, wind velocity was less along the north shore, which was sheltered by high banks and adjacent forest. Ambient wind velocities at 1.8 m above the ground were -0.2 to +2.2 m/sec higher than wind at 20 cm above the ground among microclimates. During periods of cold temperatures dark colored birds select microclimates with little or no wind (Midtgard 1978), and may reduce convective heat loss by moving or orientating in relation to the wind profiles of microclimates (Calder and King 1974:301). Resting sites along north shorelines lessened the effect of prevailing NW winds and provided more favorable microclimates for black ducks, similar to observations reported by Longcore and Gibbs (1968).

At each microclimate site, the velocity of air current 20 cm above ground among three probes was similar (p<0.05) except for sites N1 and SW2 (Table 3). However, wind velocities between several probes (20 cm above ground and ambient wind (1.8 m above ground) were different (p<0.05). The wind at probe height was in constant flux and continuously changed velocity and direction, whereas
Figure 6. Ambient wind velocity between paired microclimate sites along the shore of Raccoon Cove during the winters of 1983, 1984, and 1985. Measurements at 20 cm above the ground are indicated by solid symbols and at 180 cm by open symbols. Julian date is in paranthesis.
Table 3. Comparison of wind velocity (m/s) at probes 10 m apart and 20 cm above the ground between paired microclimate study sites located along the shore of Raccoon Cove during winters 1983 and 1984. Julian date is in parenthesis.

<table>
<thead>
<tr>
<th></th>
<th>N1 vs NW1 (39-44)</th>
<th>N1 vs NW1 (47-55)</th>
<th>N1 vs SW1 (51-63)</th>
<th>NW1 vs S1 (57-66)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probe 1</td>
<td>1.1 ±0.3</td>
<td>1.7 ±0.5</td>
<td>0.7 ±0.3</td>
<td>1.4 ±0.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.0 ±0.2</td>
<td>1.2 ±0.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.3 ±0.5</td>
</tr>
<tr>
<td>Probe 2</td>
<td>0.8 ±0.2</td>
<td>1.6 ±0.4</td>
<td></td>
<td>1.0 ±0.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.6 ±0.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Probe 3</td>
<td>0.5 ±0.1</td>
<td>1.7 ±0.4</td>
<td>0.7 ±0.1</td>
<td>0.9 ±0.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.9 ±0.3</td>
<td>1.1 ±0.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.2 ±0.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.1 ±0.4</td>
</tr>
</tbody>
</table>
velocity and direction of ambient wind tended to fluctuate less. Usually, the degree of mixing of air between different heights increases as ambient wind increases (Oke 1978), which likely influenced the thermodynamics of microclimates and subsequent heat exchange and habitat use by black ducks.

For example, at low wind speed, dark plumage has a much greater radiative heat load than light plumage even though radiation penetrates deeper into light plumage. However, at high wind speeds (8 m/s) disturbance of the boundary layer of black plumage lowers the radiative heat load below that of light plumage (Walsberg et al. 1978). Hence, dark plumage is an advantage only when wind speed is low. Therefore, black ducks probably selected microclimates that enhanced the radiation heat load of their dark plumage.

Temperature

Microclimate temperatures at probe height (20 cm) were different between habitats \( p<0.05 \) except for SE-1 vs NW-1 \( p<0.08 \) (Table 4). However ambient temperatures between sites were different only for sites N-1 vs NW-1 and SE-1 vs NW-2 \( p<0.001 \). Temperatures between north sites were more highly correlated \( \tau > .927 \) than between south vs NW-1 sites \( \tau > .826 \) and south vs NW-2 sites \( \tau > .694 \) because of the influence of solar radiation and shelter from prevailing NW winds.
Table 4. Paired comparisons of temperature (°C), solar radiation (W/m²), and relative humidity (%) between paired microclimate sites during winter 1984. Julian date in parenthesis.

<table>
<thead>
<tr>
<th></th>
<th>NI vs NW1 (38-44)</th>
<th>SW1 vs NW1 (45-53)</th>
<th>SE1 vs NW1 (54-58)</th>
<th>SE1 vs NW2 (60-65)</th>
<th>SE1 vs NW2 (68-74)</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>146</td>
<td>214</td>
<td>108</td>
<td>135</td>
<td>107</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Probe (20 cm)</td>
<td>-4.0 *** -4.8</td>
<td>2.1 * 1.9</td>
<td>2.1 ns 2.4</td>
<td>-5.7 *** -4.8</td>
<td>-9.6 * -9.1</td>
</tr>
<tr>
<td></td>
<td>+0.6</td>
<td>+0.6</td>
<td>+0.2 +0.2</td>
<td>+0.4 +0.5</td>
<td>+0.4 +0.5</td>
</tr>
<tr>
<td>Ambient (360 cm)</td>
<td>-3.8 *** -4.5</td>
<td>2.4 ns 2.4</td>
<td>2.6 ns 2.6</td>
<td>-5.6 *** -4.8</td>
<td>-9.5 ns -9.1</td>
</tr>
<tr>
<td></td>
<td>+0.6</td>
<td>+0.6</td>
<td>+0.2 +0.2</td>
<td>+0.4 +0.5</td>
<td>+0.4 +0.5</td>
</tr>
<tr>
<td>Solar Radiation</td>
<td>72.7 * 77.2</td>
<td>42.6 *** 65.3</td>
<td>47.4 *** 96.5</td>
<td>57.7 *** 160.0</td>
<td>32.2 *** 85.3</td>
</tr>
<tr>
<td></td>
<td>+11.6 +12.5 +6.2 +9.0 +8.0 +17.1</td>
<td>+8.1 +19.0 +6.5 +16.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Relative Humidity</td>
<td>- 76.1</td>
<td>- 80.4</td>
<td>- 80.4</td>
<td>- 56.1</td>
<td>- 55.9</td>
</tr>
<tr>
<td></td>
<td>+1.6</td>
<td>+1.2</td>
<td>+1.8</td>
<td>+1.8</td>
<td>+2.3</td>
</tr>
</tbody>
</table>

a Sample size

b

*** = p<0.001, ** = p<0.01, * = p<0.05, ns = not significant
Although most differences in temperature among probes at each microclimate site were less than 1°C, they were different (p<0.05). Average ambient temperatures at 360 cm above the ground were warmer than probe temperatures at 20 cm above the ground except at NW-2, which may have been influenced by additional accumulation of ice at the site when data were collected. In general, probe temperatures tended to be 0 to 0.9°C and ambient temperatures 0 to 0.8°C warmer along the north shore of Raccoon Cove than at sites along the south side of the cove (Fig. 7), which were exposed to the NW wind.

Differences in microclimate temperatures between closely spaced temperature probes indicated that energy transfer was variable within habitats and could influence the distribution and spacing of black ducks at coastal resting sites. Small differences (<1.0°C) between microclimate temperatures have biological significance. For example, if the energy expenditure for thermoregulation by black ducks is 10.88 KJ/bird/day per degree°C below the lower critical temperature (LCT) for black ducks (Wooley and Owen 1977). The energy content of Gammarus (Gammarus oceanicus) which is a major food of black ducks (Chapter 2) is 14.73 KJ/g dry weight. Therefore, a 0.2 to 1.0°C difference between microclimate temperatures would increase daily energy expenditure by 2.18 to 15.06 KJ/bird/day; approximately 0.3 to 1.3 g dry weight or 85 to 429
Figure 7. Microclimate temperature within and between paired microclimate sites located along the shore of Raccoon Cove during the winters of 1983, 1984, and 1985. Numbers above or below the symbols are the number of 1-hour observations recorded. ns = not significant (p<0.05).
individual gammarus per day. The importance of these differences in temperature was difficult to determine because the energy required to obtain this amount of gammarus and the thermodynamic interactions with other weather variables were not known. However, small differences in temperatures within microclimates may have important implications concerning the energy balance, which in turn may affect behavior and habitat use by black ducks.

Solar Radiation

Direct solar radiation was $22.7$ to $102.3 \text{ W/m}^2$ greater at sites along north shores ($p < .001$) (Table 4) (Fig. 8). Between north shore microclimates, site N-1 received more solar radiation ($4.5 \text{ W/m}^2$) than NW-1 ($p < 0.05$), although average daily radiation patterns were similar (Fig. 8a). In general, south shore sites received less solar radiation because they were shaded by the adjacent forest. Correlations between solar radiation and microclimate and ambient temperatures were not as high as expected ($0.332 > \tau > 0.050$), and indicated that other environmental variables (e.g. cold fronts and wind) influenced temperatures of these coastal resting sites.

South-facing resting sites used during the day by black ducks along the coast of Maine received more sunlight than north-facing sites (Fig. 8), possibly giving the duck's dark plumage an important thermal advantage not available
Figure 8. Examples of paired measurements of solar radiation amicroclimate temperatures at sites along the shore Raccoon Cove. Plotted values are hourly averages of data recorded at one-minute intervals. Julian date in parenthesis.
during the night. Solar radiation causes an effective increase in plumage temperature thereby reducing the surface and body core temperature differential and limiting heat loss (Lustick 1969). Solar radiation may also lower LCT by as much as 10 °C for dark birds compared to light birds which would decrease metabolism and food requirements (Lustick 1969). Wind lessened the thermal advantage of solar radiation by decreasing the thickness and insulative value of the boundary layer of air surrounding the ducks.

Relative Humidity

Average relative humidity (RH) was 78 percent at NW-1 during warm temperatures and ranged from 31 to 100 percent, whereas RH at NW-2 was 56 percent during cold weather and ranged from 21 to 98 percent during the recording period. Relative humidity influences evaporative water loss and heat exchange between an animal and its environment, and is especially important at high temperatures. Because cold air contains less water vapor (Schmidt-Nielsen 1975), relative humidity probably has little influence on habitat use by black ducks during winter.

ENERGETICS

Thermodynamics and Metabolic Rate

Maximum diurnal radiation (shortwave and longwave)
absorbed by black ducks using different habitats was 730 to 944 W/m² whereas estimated nocturnal radiation (longwave) absorbed by the ducks from the surrounding environment was 150 to 217 W/m² (Table 5). Total radiation was 102 to 217 W/m² greater and convective heat exchange was 315 to 520 W/m² greater during the day than at night. Therefore, average radiation received by black ducks during most days increased surface temperatures of plumage above ambient temperature. Also, metabolic heat production (thermoregulation) was 40 to 61 W/m² greater at night because the thermodynamic influence of ambient temperature, net radiation, and convection increased heat exchange from the bird to the environment. Heat loss at the highest microclimate temperature recorded during the day (14.4 C) could be balanced with heat generated by basal metabolism without thermoregulation. For example, solving the equation using microclimate temperatures of 14.4 and 11.4 C estimated energy for thermoregulation to be 0 to 9 W/m², respectively. This indicated that the LCT for black ducks was between these temperatures, which is in close agreement with the LCT of 12 C estimated by Wooley and Owen (1977).

Metabolic rates estimated for paired microclimate sites were greater for locations along the more exposed south shore during the day (Table 5). Similarly, DeWoskin (1980) reported that differences in wind speed, air temperature, and solar radiation between open and sheltered
Table 5. Estimated diurnal and nocturnal (in parenthesis) energy partitioning by female black ducks for paired comparisons of microclimates. Calculations are based on body weight of 1000 g and a smooth feather profile.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Wind (m/s)</th>
<th>Metabolic Heat</th>
<th>Absorbed Radiation</th>
<th>Emitted Radiation</th>
<th>Convection</th>
</tr>
</thead>
<tbody>
<tr>
<td>N1</td>
<td>11.3</td>
<td>14</td>
<td>777</td>
<td>462</td>
<td>329</td>
</tr>
<tr>
<td>vs</td>
<td>(-17.9)</td>
<td>(0.01)</td>
<td>(75)</td>
<td>(157)</td>
<td>(234)</td>
</tr>
<tr>
<td>NW1</td>
<td>10.5</td>
<td>18</td>
<td>871</td>
<td>444</td>
<td>446</td>
</tr>
<tr>
<td>vs</td>
<td>(-19.8)</td>
<td>(0.02)</td>
<td>(77)</td>
<td>(150)</td>
<td>(228)</td>
</tr>
<tr>
<td>SW1</td>
<td>8.7</td>
<td>17</td>
<td>825</td>
<td>449</td>
<td>393</td>
</tr>
<tr>
<td>vs</td>
<td>(-3.8)</td>
<td>(0.40)</td>
<td>(57)</td>
<td>(217)</td>
<td>(228)</td>
</tr>
<tr>
<td>NW1</td>
<td>8.0</td>
<td>7</td>
<td>917</td>
<td>501</td>
<td>423</td>
</tr>
<tr>
<td>vs</td>
<td>(-4.7)</td>
<td>(0.40)</td>
<td>(59)</td>
<td>(212)</td>
<td>(284)</td>
</tr>
<tr>
<td>SE1</td>
<td>11.4</td>
<td>18</td>
<td>748</td>
<td>446</td>
<td>319</td>
</tr>
<tr>
<td>vs</td>
<td>(-6.7)</td>
<td>(0.40)</td>
<td>(61)</td>
<td>(203)</td>
<td>(276)</td>
</tr>
<tr>
<td>NW1</td>
<td>14.4</td>
<td>0</td>
<td>944</td>
<td>537</td>
<td>407</td>
</tr>
<tr>
<td>vs</td>
<td>(-6.4)</td>
<td>(0.40)</td>
<td>(61)</td>
<td>(205)</td>
<td>(278)</td>
</tr>
<tr>
<td>SE1</td>
<td>4.9</td>
<td>25</td>
<td>732</td>
<td>414</td>
<td>342</td>
</tr>
<tr>
<td>vs</td>
<td>(-13.5)</td>
<td>(0.40)</td>
<td>(69)</td>
<td>(174)</td>
<td>(251)</td>
</tr>
<tr>
<td>NW2</td>
<td>5.1</td>
<td>8</td>
<td>941</td>
<td>494</td>
<td>455</td>
</tr>
<tr>
<td>vs</td>
<td>(-14.4)</td>
<td>(0.40)</td>
<td>(70)</td>
<td>(170)</td>
<td>(248)</td>
</tr>
<tr>
<td>SE1</td>
<td>-0.1</td>
<td>30</td>
<td>730</td>
<td>393</td>
<td>367</td>
</tr>
<tr>
<td>vs</td>
<td>(-19.2)</td>
<td>(0.40)</td>
<td>(76)</td>
<td>(152)</td>
<td>(231)</td>
</tr>
<tr>
<td>NW2</td>
<td>-1.3</td>
<td>13</td>
<td>944</td>
<td>467</td>
<td>490</td>
</tr>
<tr>
<td>vs</td>
<td>(-19.8)</td>
<td>(0.40)</td>
<td>(76)</td>
<td>(150)</td>
<td>(230)</td>
</tr>
</tbody>
</table>
areas increases metabolic rate by 20% in open areas, which affects timing of foraging behavior. Estimated metabolic rates were not different between locations during the night when wind velocities were similar because shortwave radiation was not available and differences in longwave radiation did not produce changes in heat transfer.

Greatest radiation received between paired microclimates did not increase the difference between temperatures by more than 3°C (20 cm above ground), probably because free and forced convection mixed ambient and boundary layer air that prevented stratification of temperatures. Therefore, the effect of solar radiation on warming ambient air seems less important than warming the plumage surface by absorbed radiation. Weathers and Nagy (1980) emphasized out the importance of including the influence of solar radiation on the metabolism of free-living birds when estimating daily energy expenditures, otherwise the estimates will be low.

The energy budget of an organism is determined by 1) operative environmental temperature (environmental temperature plus conduction, convection, and radiation), 2) thermal conductance of insulation, and 3) effective metabolic heat production (metabolic heat plus evaporative cooling). Solving the lumped parameter model equation for changes in environmental conditions provided insight into the biological implications of these changes (Table 6).
Table 6. Equivalent number of additional food items required by a 1000 g female black duck to balance increased metabolic rate associated with changes in weather variables during winter. Baseline weather conditions for initial calculations using the lumped parameter model were: temperature = -15 C, wind = 0.01 m/s, solar radiation = 300 W/m**2, photoperiod = 10 hours of daylight. Number of food items (wet weight) needed were based on the diet of collected black ducks and true metabolizable energy of these foods (Chapter 2).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Change</th>
<th>Energy Cost (KJ)</th>
<th>Number of Food Items</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Gammarus</td>
<td>Periwinkle</td>
</tr>
<tr>
<td>Temperature (C)</td>
<td>-1</td>
<td>0.76</td>
<td>17</td>
</tr>
<tr>
<td>Wind (m/s)</td>
<td>+1</td>
<td>14.44</td>
<td>328</td>
</tr>
<tr>
<td>Solar Radiation (W/m2)</td>
<td>-100</td>
<td>20.02</td>
<td>455</td>
</tr>
</tbody>
</table>
For example, differences of shade between north and south microhabitats or a change in overcast skies influenced solar radiation and substantially increased additional food intake. Similarly, a change in wind velocity also resulted in a substantial increase in food intake to balance increased metabolic rate. Predicted wind velocity would influence metabolic heat production less at south microclimate sites because solar radiation and resulting changes in microclimate temperatures were less (Fig. 9). Differences in estimated metabolic rates between NW1 and SE1 were $17 \text{ W/m}^2$ when wind velocity was $0.1 \text{ m/s}$ compared to less than $4 \text{ W/m}^2$ when wind velocities were greater than $1.0 \text{ m/s}$ for black ducks with a smooth plumage profile. Also, the influence of wind on metabolic rate was less when feathers were erected to increase insulation. Ptiloerection reduced estimated metabolic rate by almost 50 percent (Fig. 9). At temperatures below LCT, heat loss is proportional to the insulative value of the birds integument and the temperature difference between the body and external environment (Birbebak 1966). Both the convective and radiative rates of heat exchange between a bird and its environment are functions of plumage surface temperature (Hill et al. 1980).

SUMMARY

The foraging activity of black ducks was strongly
Figure 9. Influence of wind on estimated metabolic rate of black ducks with erected (a) and smooth (b) feather profiles and using north and south microclimates during midday (maximum incoming radiation and microclimate temperatures).
influenced by the timing and height of tides similar to previous studies (Hickey 1980, Albright 1981). Tide dictates food availability by exposing foraging habitats at different times of the day and by moving ice on and off of feeding sites (Grandy and Hagar 1971). Foraging activity of black ducks may also be timed to tide cycles and photoperiod when many invertebrates are most active on the substrate surface or in the water column. Foster and Moreton (1981) reported that intertidal invertebrates emerge at the mud surface shortly after the retreat of tide. However, the availability of intertidal organisms may be lower during very cold periods because some organisms may avoid extreme environmental conditions by tidal migration or periods of dormancy (Purschke 1981). Supercooled water has less severe effects on intertidal organisms than ice formation (Purschke 1981). Marine invertebrates evade thermal stress and are resistant to desiccation (Newell 1979). This may explain why black ducks first foraged for gammarus and other invertebrates among rockweed covered ledges during the day and night where the rockweed presumably protected these invertebrates from freezing and desiccation when the ledges were exposed up to 8 hours during tidal cycles.

During winter the selection of microhabitats by black ducks reduced the effects of wind and maximized the warming effect of solar radiation during the day. Therefore,
microclimate measurements were more representative of the black ducks' environment than gross or macroclimate measurements similar to previous studies (Francis 1968, Schulte and Porter 1974, Jorde et al. 1984). Small changes in microclimate variables could have a major influence on the energy transfer, especially thermoregulation, and survival of black ducks during winter and cause subtle but crucial changes in behavior, foraging strategy, and distribution. The thermodynamics of coastal microclimates coupled with long-term variation in foraging habitats and aquatic food base could determine true habitat availability rather than apparent habitat availability of coastal wintering areas. Variation in true habitat availability probably causes short and long-term changes in the maximum population size of black ducks that a given wintering area can support. The animal diet of black ducks (Chapter 2) was closely adapted to their energy transfer with the environment during winter and to tidal cycles. Subtle changes in weather patterns or the aquatic food base could explain the redistribution and population decrease of wintering black duck populations along the coast of Maine and at other wintering areas throughout the species' range.
LITERATURE CITED


Francis, W.J. 1968. Temperature and humidity conditions in potential pheasant nesting habitat. J. Wildl. Manage. 32:36-46.


CHAPTER 2

NUTRITION OF FOODS USED BY BLACK DUCKS DURING WINTER

Much attention has been focused on behavior and foraging strategies of waterfowl based on time and energy budgets (e.g., Paulus 1986). However, little is known about the nutritional requirements of waterfowl, especially during winter and migration (Fredrickson and Drobney 1979, Prince 1979) or about the nutritional value and ease at which natural foods are metabolized. Sugden (1973) used metabolizable energy to determine the value of foods eaten by waterfowl, however, Sibbald (1976) emphasized the importance of using true metabolizable energy (TME) to determine the value of foods and he developed a bioassay to measure TME of poultry foods. Until now the TME method has been applied to mainly plant material during waterfowl nutrition studies (K. Reinecke, unpublished data). Yet many waterfowl consume animal foods during part of the year.

The metabolic role of invertebrate foods in the bioenergetics of black ducks (Anas rubripes) wintering along the coast of Maine is not known. The objectives of this study were 1) to determine the foods used by wintering black ducks and 2) to determine the nutrient content and true metabolizable energy of these foods.
METHODS

Foods were obtained from 18 black ducks collected in the mid-coastal region of Maine at Mt. Desert Narrows, Raccoon Cove, and the Skillings River during December to March 1982-84. Ducks were collected during daylight hours at three principal habitats used for foraging: mud flats, blue mussel beds, and rockweed ledges. Birds were observed feeding for at least 15 minutes before they were collected. Food in esophagi was preserved in 5% formalin or frozen and later sorted, identified, counted, and weighed wet and dry. Samples were dried at 55°C for at least 24 hours to constant weight.

The TME study was conducted from October through December 1983, and July through December 1984. Black ducks used during the study had finished molting and were sexually quiescent. The principal foods of black ducks identified during this study were collected from coastal habitats used by wild black ducks and fed to captive birds during feeding trials. Periwinkles (Littorina spp.), soft-shelled clams (Mya arenaria), and blue mussels (Mytilus edulis) were placed in a refrigerator for about 24 h before trials, while gammarus (Gammarus oceanicus) was collected and immediately frozen until used during the feeding trials. Clams and blue mussels were kept in aerated seawater until fed to ducks. Subsamples of food were removed before feeding trials, dried at 55°C in a forced-air drying
oven, and analyzed for fat, crude protein, ash, caloric content, calcium carbonate (CaCO3), and percent moisture. Gammarus were spun at slow speed in a centrifuge to standardize the moisture content of samples forced-fed to ducks. Periwinkles, clams, and blue mussels were placed on a paper towel to remove excess moisture before samples were weighed and fed to ducks. The size of foods fed were similar to those removed from the esophagi of collected black ducks and ranged in length from 4 to 25 mm for gammarus, 2 to 7 mm for periwinkles, 3 to 10 mm for soft-shelled clams, and 2 to 12 mm for blue mussels.

The experimental flock consisted of 5 female and 4 male black ducks that were either F1 or F2 offspring from wild parents. Two alternate females and 1 male were maintained under the same environmental conditions as the experimental group. The alternate male was used during trial 2. Throughout the nutrition studies, black ducks were held in 30 x 50 cm wire-mesh cages in an environmental chamber and acclimated to local winter photoperiod (10 h light/14 h dark). Ambient temperature was maintained at 20 C until the last 4 weeks of trials when temperature was lowered to 5 C. Water and a maintenance diet of pelleted food containing about 17 percent crude protein, 3 percent crude fat, 4 percent crude fiber, and supplemental vitamins and minerals were provided ad libitum. No grit was supplied during the study to reduce variability of feces
weight and chemical composition. Earthworms (Lumbricidae),
gammarus, periwinkles, and blue mussels were fed to ducks 2
to 5 days before feeding trials to acclimate birds to test
diets of animal matter. Sugden (1973) found no difference
in percent of food metabolized between birds acclimated 5-6
days and 9-10 days, and Sibbald and Slinger (1963)
recommended 3-4 days acclimation for diets high in fiber.

Three weeks were required to conduct one feeding trial
for each food item studied. Gammarus was fed during three
trials (9 weeks) at an ambient temperature of 20 °C and
during one trial at 5 °C. Periwinkles, clams, and mussels
were fed during one trial each at an ambient temperature of
20 °C. During each week of a trial, the ducks were starved
21 hours before feeding to allow alimentary tracts to
empty. Birds were weighed immediately before feeding and
24 hours later after excreta were collected. Food was
force-fed at 3 amounts (5, 15, and 25 grams, wet weight)
using modified 10 cc plastic syringes. The amount of food
fed to a duck was rotated every week of the three-week
trial so that each duck received the same amount (5, 15,
and 25 g) of food during a trial. Water dispensed from a
squeeze bottle was given to the bird immediately before and
after force-feeding, and food was gently palpated down the
esophagus, which helped prevent food from being
regurgitated.

After force-feeding, each duck was returned to its
percent dry weight) of the diets of 18 black ducks collected during 1983-84 (Fig. 1). Periwinkles, gammarus, and blue mussels composed 68 percent of the total diet while soft-shelled clams, crabs (Pinnixa savana), clam worms (Nereis spp.), and isopods each accounted for approximately 6 percent. Plant matter consisting of sea lettuce (Ulva lactuca) and other plant material comprised about 4 percent of the diet.

Although the diets were somewhat different between foraging areas, gammarus, periwinkles, soft-shelled clams and blue mussels were the foods most often consumed at each feeding site (Table 1). Crabs occurred more often in the diet at Mt. Desert Narrows (MN) whereas isopods (Jaera baltica) were a common food eaten at Raccoon Cove (RC). Thirteen foods were consumed at MN compared to 9 at RC, which probably reflected different habitat characteristics (eg. tidal flow), diversity of the food base, or sample size. Flocks of wintering black ducks were predictable and tended to forage in localized areas; therefore, differences among localized habitats could have influenced food availability, diet, and foraging behavior.

Previous studies indicated that animal foods comprise most of the diet of black ducks wintering along coastal areas of the eastern United States and Canada. Invertebrates such as clams, snails, and blue mussels are most important (Grandy 1972b), although other animal foods
Figure 1. Diet of black ducks wintering at Raccoon Cove and the Jordan River along the coast of Maine during 1983 and 1984. Data are expressed as aggregate percent dry weight.
Table 1. Esophageal contents of black ducks collected in Maine during winter, 1983 and 1984.

<table>
<thead>
<tr>
<th>ANIMAL</th>
<th>Percent occurrence</th>
<th>Aggregate percent dry weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MN/JR (n=10)</td>
<td>RC/SR (n=8)</td>
</tr>
<tr>
<td>Crangon septemspinosa</td>
<td>20</td>
<td>13</td>
</tr>
<tr>
<td>Cumacea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Edotea triloba</td>
<td>10</td>
<td>Tr</td>
</tr>
<tr>
<td>Gammarus oceanicus</td>
<td>90</td>
<td>75</td>
</tr>
<tr>
<td>Pelebus balthica</td>
<td>40</td>
<td>10</td>
</tr>
<tr>
<td>Jaera marina</td>
<td>10</td>
<td>50</td>
</tr>
<tr>
<td>Littorina spp.</td>
<td>60</td>
<td>88</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>70</td>
<td>63</td>
</tr>
<tr>
<td>Mytilus edulis</td>
<td>70</td>
<td>38</td>
</tr>
<tr>
<td>Nassarius spp.</td>
<td>10</td>
<td>13</td>
</tr>
<tr>
<td>Nereis spp.</td>
<td>20</td>
<td>13</td>
</tr>
<tr>
<td>Pinnixa sayana</td>
<td>50</td>
<td>13</td>
</tr>
<tr>
<td>Skenea planorbis</td>
<td>30</td>
<td>25</td>
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<tr>
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<td>40</td>
<td>25</td>
</tr>
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<td>Tr</td>
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<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PLANT</td>
<td>Ulva lactuca</td>
<td>63</td>
</tr>
<tr>
<td></td>
<td>Zostera marina</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Unknown</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tr</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tr</td>
</tr>
</tbody>
</table>

1 MN=Mt. Desert narrows, JR=Jordan River, RC=Raccoon Cove, SR=Skillings River
2 Tr=trace (<0.5 perce
(Grandy 1972b), cordgrass (*Spartina* spp.) (Hartman 1960, Grandy 1972b), eelgrass (Mendall 1949), plant seeds (Hartman 1960), and algae (Lynch 1939, Grandy 1972b)) are also eaten in small amounts. Grandy (1972a) reported that vegetative matter was not important to black ducks during winter. However, Hartman (1960) noted that the winter diet of Black ducks in Maine contains 25 percent plant material, though only gizzards were examined which probably biased the importance of plant foods (Swanson and Bartonek 1970). The amount of plant food in the diets of wintering black ducks is most likely related to availability (Hartman 1960). For example, black ducks in Raccoon Cove foraged among windrows of sea lettuce and ate this algae during the short period in early winter when tides deposited green leaves of sea lettuce at the tide line. During cold winters or extended periods of cold and ice, foods present in wintering areas may be limited by the amount of ice in different tide zones (Hartman 1960, Albright 1981), thereby influencing the intensity of foraging and availability of different foods (Grandy 1972b).

The ability of Black ducks and other waterfowl to change behavior and adapt to a wide range of diets within and among seasons and geographic areas has recently become evident (Jorde and Owen, in press). Diets of black ducks wintering in coastal habitats was almost exclusively animal matter. The diet of black ducks at inland wintering sites
includes snails, fish, invertebrates, sugarbeets, small grains, and other plant material, and is occasionally limited by ice and snow (Winner 1959, Reed 1971). Similarly, mallards wintering among black ducks and using the same habitats along the coast of Maine most likely had similar diets high (>90%) in animal matter, whereas mallards at inland wintering areas may have diets containing 97 percent plant material (Jorde et al. 1983). This ability of waterfowl to adapt to different diets and foraging habitats clearly focuses the importance of understanding the nutritional role of diets within and among seasons and geographic areas.

METABOLIZABLE ENERGY

Body Weight Change During Digestibility Trials

Body weights of black ducks used during feeding trials ranged from 930 to 1211 g for males and 845 to 1132 g for females. Individual ducks generally maintained body weight throughout the nutrition studies. The difference between beginning and ending weights averaged +74 g for males and -18 g for females. Weight losses during the 24-hour period following forced-feeding did not differ by sex (t-test, p>0.05), therefore data were pooled for additional analyses.

Average body weight of males and females decreased 4 to 31 g during the 24-hour trial period following force-
feeding (Fig. 2). Males and females regained 28 and 21 grams, respectfully, during the following 6-day recovery period. Weight loss was not different (t-test, p>0.5) between amounts of food fed (5, 15, 25 g) for each food fed except for gammarus and soft-shelled clams at 5 g amounts (t-test, p<0.05). Black ducks lost the most weight when fed periwinkles and lost the least weight when fed blue mussels. Loss of body weight during the endogenous trial (about 26 g) was greater than during any feeding trials (t-test, p<0.05) except for periwinkles. Although the difference in body weight change between the periwinkle and endogenous trials was not significant, black ducks lost more weight when fed 5 and 25 g of periwinkles than during the endogenous loss trials. This weight loss indicated that periwinkles may have had little energy value and supported Grandy and Hagar's (1971) hypothesis that snails were eaten primarily for their value as grit. Although endogenous weight loss indicated that starved black ducks weighing 1000 g would loose 25 percent of total body weight in about 10 days, free-ranging birds could loose twice as much weight per day because periods of cold weather would also exert greater energy demands on fat reserves for thermogenesis (Chapter 3). There were no differences in weight change of black ducks fed gammarus when ambient temperatures during the trials were 20 C and 5 C.
Figure 2. Change in body weight of captive black ducks during the 24-hour period following force-feeding different foods during nutrition studies. G=gammarus, P=periwinkle, S=soft-shelled clam, B=blue mussel, and E=endogenous loss.
Nutrient and Energy Content of Food

Gammarus contained the most favorable nutrient content based on gross energy, protein, and fat (Table 2). Protein was 3 - 8 times higher and fat was 4 - 12 times higher in gammarus than in blue mussels, periwinkles, or soft-shelled clams. Ash was 59 - 64 percent and CaCO$_3$ 72 - 76 percent lower in gammarus than in these other foods. The ratio of organic matter (OM) to ash was much greater in gammarus.

Periwinkles averaged 88 percent shell material and 12 percent organic matter. Shell material was 97 percent ash of which 96 percent was CaCO$_3$. Ninety-nine percent of shell material after ashing in a muffle furnace was CaCO$_3$, thereby confirming that no significant loss of CaCO$_3$ had occurred during the ashing process (Paine 1966).

The gross energy content of gammarus changed throughout the year (one-sample t-test, P<0.05) (Fig. 3). Gross energy content was highest from April through June with a peak of 16.69 KJ/g occurring during May. Energy content decreased in July and remained low until February. The lowest energy content in gammarus (14.73 KJ/g) occurred during December when most black ducks arrived on the wintering areas in Maine.

Composition of Excreta

Excreta from ducks fed gammarus contained more nitrogen
Table 2. Nutrient composition and energy content of fresh marine foods (dry weight) fed to captive black ducks. Gammarus were collected during July to December, periwinkles and soft-shelled clams during September, and blue mussels during October.

<table>
<thead>
<tr>
<th></th>
<th>Gammarus</th>
<th>Periwinkle</th>
<th>Soft-shelled clam</th>
<th>Blue mussel</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moisture (%)</td>
<td>76.2</td>
<td>34.7</td>
<td>57.9</td>
<td>63.7</td>
</tr>
<tr>
<td>Nitrogen (%)</td>
<td>7.6(11.3)</td>
<td>1.5(12.3)</td>
<td>1.0(10.6)</td>
<td>2.5(12.5)</td>
</tr>
<tr>
<td>Crude Protein (%)</td>
<td>47.5(70.5)</td>
<td>9.4(77.0)</td>
<td>6.3(67.0)</td>
<td>15.6(78.0)</td>
</tr>
<tr>
<td>Fat (%)</td>
<td>4.6(6.8)</td>
<td>0.6(4.9)</td>
<td>0.4(4.3)</td>
<td>1.1(5.5)</td>
</tr>
<tr>
<td>Ash (%)</td>
<td>32.6</td>
<td>87.8</td>
<td>90.6</td>
<td>80.0</td>
</tr>
<tr>
<td>Carbohydrate (%)</td>
<td>15.3</td>
<td>2.2</td>
<td>2.7</td>
<td>3.3</td>
</tr>
<tr>
<td>Calcium Carbonate (%)</td>
<td>19.7</td>
<td>81.7</td>
<td>81.2</td>
<td>70.9</td>
</tr>
<tr>
<td>Organic Matter:Ash</td>
<td>2.1:1</td>
<td>0.1:1</td>
<td>0.1:1</td>
<td>0.3:1</td>
</tr>
<tr>
<td>Gross Energy (KJ/g)</td>
<td>14.73</td>
<td>1.13</td>
<td>0.92</td>
<td>2.18</td>
</tr>
<tr>
<td>Gross Energy (ash free) (KJ/g)</td>
<td>21.88</td>
<td>17.41</td>
<td>18.03</td>
<td>16.74</td>
</tr>
</tbody>
</table>

a Percent ash-free dry weight

b Total nitrogen * 6.25

c Estimated carbohydrate = 100 - crude protein + fat + ash

d Gross energy content of organic matter
Figure 3. Monthly change in gross energy content of gammarus collected at Mt. Desert Narrows during 1983 and 1984.
and less CaCO₃ and ash than periwinkles, soft-shelled clams
3 and blue mussels (Table 3). Fecal nitrogen excreted by
males and females was similar (p>0.05). The percent
of nitrogen in excreta decreased as the intake of food
increased, except for periwinkles at 15 and 25 g levels,
which were similar. The higher levels of fecal nitrogen
recorded when gammarus were fed probably resulted from the
greater protein content in gammarus and subsequent
metabolic turnover and excretion of nitrogen. Maynard et
al. (1979) reported that apparent digestibility of protein
was a function of the level of dietary protein. The amount
of CaCO₃ and ash in fecal matter increased when higher
levels of food were fed indicating that calcium and other
mineral intake exceeded metabolic needs and the excess was
excreted.

Nitrogen, CaCO₃ in excreta from birds fed fresh
periwinkles without shells (soft tissues only) were less
than when gammarus, soft-shelled clams, and blue mussels
were fed because periwinkle soft tissues contained very
little or no skeletal material (Table 3).

During endogenous loss trials, male black ducks
excreted 2.8 times more CaCO₃, 1.9 times more ash, and
1.51 KJ less energy than females (Table 4). Females may
have deposited more calcium or excreted excess CaCO₃ over
a longer period, perhaps in response to physiological
processes associated with retention of calcium for egg
Table 3. The amount of nitrogen, calcium carbonate and ash in excreta collected 24 hours after force feeding black ducks four foods at 5, 15, and 25 grams intake (wet weight).

<table>
<thead>
<tr>
<th></th>
<th>Gammarus (g)</th>
<th>Periwinkle (g)</th>
<th>Soft-shelled Clam (g)</th>
<th>Blue Mussel (g)</th>
<th>Periwinkle w/o shell (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nitrogen</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0.255</td>
<td>0.245</td>
<td>0.244</td>
<td>0.111</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>0.344</td>
<td>0.306</td>
<td>0.284</td>
<td>0.169</td>
<td>0.257</td>
</tr>
<tr>
<td>25</td>
<td>0.441</td>
<td>0.448</td>
<td>0.219</td>
<td>0.210</td>
<td>0.383</td>
</tr>
<tr>
<td><strong>CaCO3</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>-</td>
<td>4.150</td>
<td>-</td>
<td>2.660</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>0.444</td>
<td>7.237</td>
<td>7.104</td>
<td>5.334</td>
<td>0.160</td>
</tr>
<tr>
<td>25</td>
<td>1.319</td>
<td></td>
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<td></td>
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<tr>
<td><strong>Ash</strong></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>1.452</td>
<td>1.767</td>
<td>-</td>
<td>3.287</td>
<td>0.739</td>
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<tr>
<td>15</td>
<td>2.172</td>
<td>5.194</td>
<td>6.314</td>
<td>6.394</td>
<td>1.234</td>
</tr>
<tr>
<td>25</td>
<td></td>
<td>7.723</td>
<td>8.410</td>
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Table 4. Proximate analysis of excreta from black ducks during endogenous loss experiments.

<table>
<thead>
<tr>
<th></th>
<th>Nitrogen (%)</th>
<th>CaCo3 (%)</th>
<th>Ash (%)</th>
<th>Gross Energy (KJ/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MALE</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.275 +0.07(6)</td>
<td>0.371 +0.04(2)</td>
<td>0.396 +0.06(5)</td>
<td>13.81 +0.59</td>
</tr>
<tr>
<td></td>
<td>ns</td>
<td>ns</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>FEMALE</td>
<td>0.236 +0.03(6)</td>
<td>0.134 +0.11(2)</td>
<td>0.212 +0.07(6)</td>
<td>15.32 +0.84</td>
</tr>
</tbody>
</table>

^a Mean ± standard error (sample size)
^b ns = not significant (p>0.05), ** = p<0.01
Table 3. The amount of nitrogen, calcium carbonate and ash in excreta collected 24 hours after force feeding black ducks four foods at 5, 15, and 25 grams intake (wet weight).

<table>
<thead>
<tr>
<th></th>
<th>Gammarus (g)</th>
<th>Periwinkle (g)</th>
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<th>Blue Mussel (g)</th>
<th>Periwinkle w/o shell (g)</th>
</tr>
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<tbody>
<tr>
<td><strong>Nitrogen</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>5</td>
<td>0.255</td>
<td>0.245</td>
<td>0.244</td>
<td>0.111</td>
<td>-</td>
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<tr>
<td>15</td>
<td>0.344</td>
<td>0.306</td>
<td>0.284</td>
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</tr>
<tr>
<td>25</td>
<td>0.441</td>
<td>0.448</td>
<td>0.219</td>
<td>0.210</td>
<td>0.383</td>
</tr>
<tr>
<td><strong>CaCO3</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>-</td>
<td>4.150</td>
<td>-</td>
<td>2.660</td>
<td>-</td>
</tr>
<tr>
<td>15</td>
<td>0.444</td>
<td>7.237</td>
<td>7.104</td>
<td>5.334</td>
<td>0.160</td>
</tr>
<tr>
<td>25</td>
<td>1.319</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Ash</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>-</td>
<td>1.767</td>
<td>-</td>
<td>3.287</td>
<td>-</td>
</tr>
<tr>
<td>15</td>
<td>1.452</td>
<td>5.194</td>
<td>6.314</td>
<td>3.287</td>
<td>0.739</td>
</tr>
<tr>
<td>25</td>
<td>2.172</td>
<td>7.723</td>
<td>8.410</td>
<td>6.394</td>
<td>1.234</td>
</tr>
</tbody>
</table>
Table 4. Proximate analysis of excreta from black ducks during endogenous loss experiments.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Nitrogen (%)</th>
<th>CaCo3 (%)</th>
<th>Ash (%)</th>
<th>Gross Energy (KJ/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MALE</td>
<td>0.275</td>
<td>0.371</td>
<td>0.396</td>
<td>13.81</td>
</tr>
<tr>
<td></td>
<td>±0.07(6)</td>
<td>±0.04(2)</td>
<td>±0.06(5)</td>
<td>±0.59</td>
</tr>
<tr>
<td>b</td>
<td>ns</td>
<td>ns</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>FEMALE</td>
<td>0.236</td>
<td>0.134</td>
<td>0.212</td>
<td>15.32</td>
</tr>
<tr>
<td></td>
<td>±0.03(6)</td>
<td>±0.11(2)</td>
<td>±0.07(6)</td>
<td>±0.84</td>
</tr>
</tbody>
</table>

\( ^{a} \) Mean ± standard error (sample size)
\( ^{b} \) ns = not significant \((p>0.05)\), ** = \( p<0.01 \)
production (Fisher 1972). Higher percent ash for males indicated a shorter retention time of excess calcium.

True Metabolizable Energy

The metabolizable energy obtained by captive black ducks was influenced by the type and level of food fed ($F=14.5$, $df=6,139$, $P<0.001$). Different patterns of metabolizable energy among input levels were observed for TMEN/g and TMENA/g values (Table 5). For example, TMEN/g decreased as food intake increased, which indicated differences in the rate and efficiency of digestion. The ducks obtained more true metabolizable energy (TMEN) from gammarus at 15 g (33.83 KJ) and 25 g (53.18 KJ) food input levels (wet wt.) than from the other foods (ANOVA, $p<0.01$, $r=0.85$), whereas TMEN among foods at 5 g amounts were similar ($p>0.05$) (Table 5). Further, TME and TMEN at different feeding levels increased sharply for gammarus as compared to the other foods tested (Table 5).

Based on grams dry weight (TMEN/g), gammarus provided more energy at all feeding levels ($p<0.01$) than other foods (Fig. 4). Also, for each food item, the 5 g amount produced the highest ME ($p<0.05$), indicating that digestion, absorption, and passage rate in the alimentary tract of small amounts of food were more efficient than for larger amounts of food intake. For gammarus, the TMEN/g values were not different ($p>0.05$) indicating that the
Table 5. True metabolizable energy (TME) of four foods (grams dry weight) fed to captive black ducks.

<table>
<thead>
<tr>
<th>Grams Fed</th>
<th>TME</th>
<th>TMEN</th>
<th>TME/g</th>
<th>TMENa/g</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet Dry</td>
<td>(n)</td>
<td>a</td>
<td>b</td>
<td>b</td>
</tr>
<tr>
<td>Gammarus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 1.19 (29)</td>
<td>15.36</td>
<td>12.27</td>
<td>9.70</td>
<td>9.02</td>
</tr>
<tr>
<td>15 3.57 (34)</td>
<td>41.76</td>
<td>33.83</td>
<td>9.14</td>
<td>11.36</td>
</tr>
<tr>
<td>25 5.95 (30)</td>
<td>62.84</td>
<td>53.18</td>
<td>8.86</td>
<td>11.56</td>
</tr>
<tr>
<td>Periwinkle</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 3.27 (5)</td>
<td>10.29</td>
<td>8.16</td>
<td>2.52</td>
<td>7.30</td>
</tr>
<tr>
<td>15 9.80 (4)</td>
<td>14.64</td>
<td>12.41</td>
<td>1.27</td>
<td>6.90</td>
</tr>
<tr>
<td>25 16.33 (7)</td>
<td>18.95</td>
<td>16.39</td>
<td>1.12</td>
<td>8.09</td>
</tr>
<tr>
<td>Soft-shelled Clam</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 2.11 (5)</td>
<td>10.88</td>
<td>8.18</td>
<td>3.89</td>
<td>4.79</td>
</tr>
<tr>
<td>15 6.32 (8)</td>
<td>14.39</td>
<td>9.72</td>
<td>1.54</td>
<td>6.33</td>
</tr>
<tr>
<td>25 10.53 (6)</td>
<td>16.65</td>
<td>11.43</td>
<td>1.09</td>
<td>3.22</td>
</tr>
<tr>
<td>Blue Mussel</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 1.82 (6)</td>
<td>16.23</td>
<td>9.33</td>
<td>5.15</td>
<td>11.32</td>
</tr>
<tr>
<td>15 5.45 (8)</td>
<td>21.13</td>
<td>14.24</td>
<td>2.61</td>
<td>6.56</td>
</tr>
<tr>
<td>25 9.08 (6)</td>
<td>26.78</td>
<td>17.08</td>
<td>1.85</td>
<td>4.99</td>
</tr>
</tbody>
</table>
Table 5. continued.

- **a** TME = True metabolizable energy corrected for calcium carbonate (CaCO₃) (Paine 1966)
- **b** TMEN = TME corrected for CaCO₃ and nitrogen (Sibbald 1983)
- **c** TMEa = TME corrected for CaCO₃, ash, and nitrogen
- **d** Mean (+ standard error)
Figure 4. True metabolizable energy per gram of 4 foods fed at 3 levels of input. G=gammarus, M=blue mussel, C=soft-shelled clam, and P=periwinkle.
energy obtained per gram of dry weight of gammarus did not vary among feeding levels tested (Fig. 4). TMEN/g of the other foods declined (p<0.01) as feeding levels increased from 5 to 15 g and from 15 to 25, except for periwinkles from 15 to 25 g (P>0.05). The TMEN/g for gammarus (8.86 to 9.70 KJ/g) fed to black ducks was less than apparent ME values obtained by Sugden (1973) when fresh gammarus were fed to lesser scaup (Aythya affinis) (12.76 KJ/g) and similar to greater than ME for blue-winged teal (Anas discors) (9.71 KJ/g). However, TMENa/g of 25 g of periwinkles (1.12 KJ/g) was considerably below the apparent ME of snails (Lymnaeidae) (9.67 KJ/g) reported by Sugden (1973).

Compared to gammarus, ash content (primarily CaCO₃) was higher in periwinkles, clams and mussels and seemingly contributed to the low TMEN/g values obtained. In almost all instances the TMEN/g values were less than gammarus suggesting that factors other than ash content reduced the TME values. For example, the ratio of TMEN/g values for gammarus and periwinkles was 3.8:1 to 7.9:1 while on a TMENa/g basis it was 1.2:1 to 1.6:1. Possibly the presence of high levels of ash in the shell component of invertebrates reduced the digestibility of soft tissues, or the high levels of CaCO₃ inhibited digestion. Soft-bodied invertebrates (eg. gammarus) evidently are more digestible and provide more TME/g. Hence, waterfowl feeding on soft-
bodied animal foods are able to obtain more energy per gram of food, can process these foods more rapidly, and can consume larger amounts of food during feeding bouts than if they consume bivalves or other molluscs.

The variable amount of energy metabolized from gammarus, periwinkles, soft-shelled clams, and blue mussels by captive black ducks indicated that natural foods in the diet of wild black ducks probably influenced foraging strategies and habitat preference. Jorde and Owen (unpublished data) found that black ducks foraged intensively for gammarus among rockweed ledges until this habitat was exposed by the ebbing tide.

Black ducks probably selected specific foods based on palatability, digestibility, and ability to maintain optimal nutritional balance. Changes in seasonal abundance, availability, and quality of individual foods in localized foraging areas (e.g., different caloric content of gammarus) (Fig. 4) may alter a bird's nutritional balance. Small amounts of different foods in the diet of black ducks may have been consumed to supplement the diet with essential vitamins and minerals or possibly could have been incidental foods.

The high TME, fat, and protein of gammarus emphasized the importance of this food to wintering black ducks to meet daily energy needs, provide stored energy reserves, and may influence foraging activity. Daily storage rates
of energy are dependent on frequency of feeding, meal size, and rates of energy expenditures between meals (Hainsworth et al. 1981). Foraging activity may also decrease when energy reserves are replenished. For black ducks, the greater intake of periwinkles, soft-shelled clams, and blue mussels, and differences in quantities consumed are not eaten solely for energy or nutrient content. The importance of these foods may be related to abundance and relative ease of obtaining them (Grandy and Hagar 1971). However, periwinkles and mussels do not seem to be consumed in proportion to abundance in marine habitats used by wintering black ducks. Perhaps lower ME or excess calcium in diets of periwinkles and blue mussels triggers protective metabolic feedback that reduces consumption of these foods. Excess calcium in the diet of animals, although not toxic, may adversely affect the balance of other essential minerals that may cause stress and disease (Maynard et al. 1979).

During periods when food is limited by cold weather and ice, black ducks rely on stored fat reserves and protein for maintenance energy (Reinecke et al. 1983). Therefore, gammarus and similar foods that have high lipids and ME available for fat deposition and protein replacement would be particularly important in the diet of wintering black ducks following prolonged periods of cold weather and weight loss (Chapter 3). Stored fat supplements limited
or deficient food resources when food is limited. Protein (eg. muscle tissue) probably is not replaced or is catabolized for thermogenesis when fats are nearly depleted. For some birds a large proportion of their caloric needs are obtained from muscle protein during periods of starvation (Grammeltvedt 1978) leading to a loss of body mass followed by a gradual decrease of body temperature and metabolism (Prinzinger et al. 1981). During cold weather, body weights of black ducks decrease when foraging habitats are limited by ice cover (Albright 1981). Gammarus and soft-shelled clams are the first invertebrate foods covered by ice that forces black ducks to feed on lower quality blue mussels and periwinkles. Body weight, fat reserves, and muscle protein of starved black ducks most likely rebounds at a rate dependent on abundance and nutritional quality of available foods when severe weather conditions abate.
LITERATURE CITED


CHAPTER 3
THE COMPENSATORY ROLE OF HEAT OF DIGESTION (SDE) ON THERMOREGULATION IN BLACK DUCKS

Energy flow from an organism to its environment must be balanced by an equal amount of energy intake (termed existence metabolism, EM) to meet maintenance requirements. Kendeigh (1974) stated, "the concept and measurement of existence metabolism is of considerable ecological importance both theoretically and for birds under natural conditions". For birds, EM is partitioned into basal metabolism (BM), foraging activity, heat of digestion or specific dynamic effect (SDE), and thermoregulation (Kendeigh et al. 1977, Prince 1979). SDE is an increment of metabolism that produces heat independently of other thermoregulatory processes. SDE represents the work of catabolizing food and is dependent on the nutritional content and quantity of foods consumed (Ricklefs 1974). The metabolic rate of animals assimilating food is higher than those in a post-absorptive state because of chemical and muscular processes (Kleiber 1961). Energy from SDE could be used to compensate for metabolic heat production for thermoregulation (Kleiber 1961). Theoretically, as ambient temperature decreases, and the rate of food intake increases, a greater proportion of heat generated by SDE...
could supplement the heat needed for thermoregulation and may be 100 % compensatory at some point below lower critical temperature (LCT)(Kendeigh et al. 1977). Therefore, SDE may be an important increment of heat production for birds during winter or periods of cold weather (Owen and Reinecke 1979).

Many authors assume that heat generated by SDE is fully compensatory for thermoregulation in birds (Owen and Reinecke 1979). Yet, this concept has neither been tested for birds (Kendeigh et al. 1977) nor have the effects on SDE of different natural foods been studied. The objectives of this study were to 1) determine if and to what degree specific dynamic effect compensates for thermoregulation in Black ducks (Anas rubripes) and 2) determine the SDE of several natural foods important to waterfowl and other birds.

METHODS

Metabolic rates of heat produced were defined as:

**BASAL METABOLISM (BM)** -- energy requirements of fasting, resting birds exposed to temperatures in the thermoneutral zone (TNZ)(Kendeigh et al. 1977, p. 129) (Fig. 1),

**STANDARD METABOLISM (SM)** -- energy requirements of fasting, resting birds exposed to temperatures below LCT (Kendeigh et al. 1977 p. 134),

**EXISTENCE METABOLISM (EM)** -- energy requirements of resting birds digesting food and exposed to
Figure 1. The influence of specific dynamic effect (SDE) on lower critical temperature (LCT) and metabolic heat production. a = basal metabolic heat (BM), b = existence metabolism (EM) in the thermoneutral zone composed of basal heat + heat from digestion (SDE), c = standard metabolic heat (SM) composed of basal heat + heat from thermogenesis, d = existence metabolism below lower critical temperature and composed of basal heat + heat from thermogenesis + SDE. Heat increment of feeding (animal activity) was assumed to = 0.
temperatures in TNZ (EM\textsubscript{tnz}) and below LCT (EM\textsubscript{lct}).

Each trial of the experiment was conducted in four steps: 1) determine basal metabolism (no food or thermoregulation). Ambient temperature was maintained in the thermal neutral zone (TNZ) and O\textsubscript{2}\textsubscript{CO} measured while the bird was in a post-absorptive state. 2) determine EM\textsubscript{tnz} for a force-fed diet (BM + SDE, no thermoregulation). Ambient temperature was maintained in TNZ, food force-fed, and O\textsubscript{2}\textsubscript{CO} measured during the digestive and absorptive state. 3) determine standard metabolism (SM) by measuring O\textsubscript{2}\textsubscript{CO} for thermoregulation (post-absorptive state). Ambient temperature was maintained below lower critical temperature (LCT) and O\textsubscript{2}\textsubscript{CO} measured while the bird was in a post-absorptive state. 4) determine EM\textsubscript{lct} including thermoregulation and SDE. Ambient temperature was maintained below LCT, the same diet used in step 2 was force-fed, and O\textsubscript{2}\textsubscript{CO} measured during the digestion and absorption state.

The compensatory effect of SDE for thermoregulation was determined by comparing energy used (KJ/bird/hour) among the 4 steps of the experiment. First, SDE was determined as the difference between steps 1 and 2 (EM\textsubscript{tnz} - BM), and thermoregulation was estimated as the difference in energy used between steps 1 and 3 (SM - BM). These results (BM + SDE + thermoregulation) were compared to energy used during step 4 (EM\textsubscript{lct}). The BM content of
steps 2 and 4 was assumed to be the same value estimated in step 1. The null hypothesis (no compensatory SDE) would be accepted if results of step 4 were similar to the sum of the energy for BM + SDE + thermoregulation. Less energy expenditure during step 4 would indicate that heat energy from SDE compensated to some extent for thermogenesis.

An open circuit respiration system with an oxygen (O) analyzer and an infrared carbon dioxide (CO) analyzer was used to measure O used and CO produced by the experimental bird (Fig 2). The system was calibrated to standard gas mixtures and zeroed to ambient air. Throughout each trial the system was checked for zero and the analyzers adjusted if necessary. Electrical signals from the analyzers were recorded every 1 to 4 seconds by dataloggers programmed to calculate maximum, minimum, mean, and standard deviation of these signals at one-minute intervals during the trial. These values were automatically stored on cassettes by the datalogger and data transferred to a microcomputer via an interface for analyses.

The rate of O2 consumption was corrected for standard temperature and pressure (STP), and liters of O2 consumed per hour calculated as the percent of O2 used times STP flow rate. Energy used (KJ/bird/hour) was calculated as the absorptive or post-absorptive caloric equivalent of RQ times the liters of O2 consumed.
Figure 2. Open circuit respiration system. Arrows indicate direction of air flow. F=dririte filter, FM=flow meter, M=metabolism chamber, MS=mechanical switch, P=vacuum pump, S=electrical switch, a=exhaust, b=environmental chamber air, ac=outside air, d=spiro analyze air, e=direct analyze air, and v=environment chamber air input to metabolism chamber.
One trial using one male or one female black duck was conducted each day. Each bird was used on alternate days to allow the other bird to recover from the previous trial. Before a trial, food was removed and bird was starved 18 hours (21 hours before force-feeding) to permit its alimentary canal to empty and to reach post-absorptive state. Three hours before force-feeding, the bird was weighed, placed in a 21w x 36l x 26h cm plexiglass metabolism chamber, and basal/standard metabolism measured. After 3 hours the duck was removed from the chamber, weighed, and force-fed 20 grams of food using modified 10 cc plastic syringes. Water dispensed from a squeeze bottle was given to each bird immediately before and after force-feeding, and food was gently palpated down the esophagus. After force-feeding, the duck was returned to the metabolism chamber for 4-5 hours to measure metabolism during digestion. Food and water were withheld while the bird was in the metabolism chamber. At the end of the trial, the duck was immediately weighed and returned to its holding cage within the environmental chamber.

The activity component of EM was minimized by 1) using a small metabolism chamber that discouraged locomotor activity and encouraged a resting posture (Fig. 3), 2) acclimating birds to the metabolism chamber thereby eliminating escape or fright behavior and associated elevated metabolism, 3) force-feeding birds to eliminate
Figure 3. Metabolism chamber. a=input environment chamber air, b=input temperature and relative humidity probe, c and d=metabolism chamber temperature probes, e=output temperature and relative humidity probe, f=output metabolism chamber air, g=wire mesh screen, and h=stainless steel pan.
locomotor activity associated with feeding, and 4) selecting the most docile ducks in the captive flock. The metabolism chamber was covered except on the side where gas was being drawn into the analysis line. The bird remained orientated in that direction with its head 3-5 cm from the gas outlet port (Fig. 3).

The experimental ducks were F2 generation from wild parents and were raised in the plexiglass metabolism chambers until 3 weeks old when they were transferred to a large pen and kept isolated from adult birds until about 4 months old. Thereafter, they were allowed to mix with other captive adult black ducks. The test birds were 20 months old when used in the SDE experiment. To avoid seasonal biases, trials were conducted when the birds were not undergoing reproduction, molt, migratory unrest, or growth.

Variability of SDE, which is related to the level and amount of food in the diet, was reduced by force-feeding 20 g (wet weight) of food during each trial. Gammarus (Gammarus oceanicus) were spun at low speed in a centrifuge and earthworms (Lumbricidae) placed on a paper towel to standardize the moisture content of the samples that were force-fed. Earthworms and gammarus were fed 2 to 7 days before SDE experiments to acclimate birds to animal food. Earthworms were selected as an invertebrate test food because they contain a high level of protein, the
major metabolic component of SDE, and they are an important natural food of waterfowl (Krapu and Swanson, 1975) and other birds (Sperry 1940, Krohn 1969). Corn (Zea mays) was selected because it induces considerable gizzard activity, has an amino acid imbalance, which provides excess amino acids for energy, and is a major plant food in the diet of waterfowl wintering in colder climates (Jorde et al. 1983).

Throughout the SDE study, experimental birds were held in 30 x 50 cm wire-mesh cages in an environmental chamber and acclimated to local winter photoperiod (10 h light/14 h dark). Ambient temperature was maintained at 20 C for the experiments within the TNZ (LCT=8 to 12 C, Wooley and Owen 1977). Experiments below TNZ were conducted at +2 and -3 C. Water and a maintenance diet of pelleted food were provided ad libitum between trials. No grit was supplied during the study.

Time series analysis and analysis of variance using multivariate general linear hypothesis (MGLH) procedures (SYSTAT, Inc. 1985) were used to analyze respiration data. significance was accepted at p<0.05. KJ equals KJ/bird/hour unless otherwise stated in the text.

RESULTS AND DISCUSSION

Twenty-two SDE trials were conducted during the experiment. Earthworms were fed during 18 trials (9 trials
in TNZ and 9 below LCT) and corn fed during 4 trials (2 in TNZ and 2 below LCT). Of 9 trials below LCT during which earthworms were force-fed, 7 trials were at 2 C and 2 at -3 C. The percent O2 used, CO2 produced, and estimated energy expenditures did not differ by sex (F=0.288, P<0.64), therefore data were combined for analysis.

Body weights of birds changed less than 1.3 percent during each trial and were within the constant weight limit (1-2 %) suggested for studies of EM (Kendeigh et al. 1977). Female weight (Y=1071 g) increased 5.4 percent and male weight (Y=1238 g) decreased 3.2 percent during the 48-day experiment.

SDE In The Thermoneutral Zone

EM (16.99 KJ) of black ducks force-fed earthworms was 3.56 KJ higher than BM (13.43 KJ) (F=34.56, P<0.01), and represented the heat increment of feeding or SDE (EM-BM) (Fig. 4). Assuming BM was not affected by food type, the SDE for 20 g of corn (wet wt.) was 4.77 KJ and 1.21 KJ greater than for an equal amount of earthworms. Protein and CHO metabolism, muscular activity by the gizzard to digest corn, and greater dry weight of corn most likely increased the SDE of corn. The amount of heat that the muscular digestive process contributed to SDE was not determined, however, all muscular and chemical heat generated by digestion were assumed to be compensatory SDE.
Figure 4. Compensatory relationship of SDE on the metabolism of black ducks force-fed 20 g of earthworms (e) and corn (c) at different temperatures. Numbers above bars are sample sizes. Black dots indicate expected values if SDE were not compensatory and triangles indicate expected values if SDE were 100 percent compensatory.
SDE associated with corn formed a greater percentage of EM than that from earthworms (Table 1). The ratio of SDE to BM was higher for corn than earthworms, and was within the range compiled by Ricklefs (1974).

SDE Below The Lower Critical Temperature

SM (21.67 KJ) was 8.224 KJ higher than BM at 2 C (F=103.9, p<0.001) which represented the energy cost for thermoregulation (SM-BM) (Fig.3). EM (21.17 KJ) after feeding earthworms was not different (F=01.647, p>0.256) than SM (21.67 KJ), but 4.06 KJ less than expected if SDE was not compensatory for thermogenesis. Therefore, SDE from earthworms was not fully compensatory but reduced the energy required for thermoregulation by 49 percent.

The compensatory trend of SDE associated with corn was similar to earthworms. EM (20.96 KJ) was 0.71 KJ less than SM and 5.48 KJ less than expected if SDE was not compensatory. Energy for thermoregulation was reduced 52 percent by SDE from corn. Also, the SDE derived from corn formed a higher component percentage of EM than the SDE derived from earthworms although both component percentages decreased between TNZ and LCT (Table 1).

Although only four trials were conducted at -3 C, SM (25.19 KJ) was 11.76 KJ greater than BM and represented a 42.6 percent increase in energy expended for thermoregulation than at 2 C. After force-feeding
Table 1. Component percentages of existence metabolism (EM) and standard metabolism (SM) at temperatures within the thermoneutral zone (TNZ) (20°C) and below lower critical temperature (LCT) (2°C) of black ducks force-fed earthworms and corn.

<table>
<thead>
<tr>
<th></th>
<th>SM LCT (2°C)</th>
<th>EM earthworm TNZ LCT (2°C)</th>
<th>EM corn LCT (2°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BM (%)</td>
<td>62.0</td>
<td>79.1</td>
<td>63.4</td>
</tr>
<tr>
<td>SDE (%)</td>
<td>0</td>
<td>20.9</td>
<td>16.8</td>
</tr>
<tr>
<td>Thermogenesis (%)</td>
<td>38.0</td>
<td>0</td>
<td>19.8</td>
</tr>
</tbody>
</table>


earthworms to the ducks, EM (29.79 KJ) was 4.60 KJ greater than SM; 1.05 KJ higher than expected (28.74 KJ) if SDE was not compensatory. EM higher than expected at -3 C does not preclude SDE from being compensatory. Other possibilities for higher than expected EM include: 1) the energy needed for thermogenesis was much greater than the energy content of the earthworms, 2) less efficient digestion at lower ambient temperatures resulting in less SDE, and 3) the colder temperature may have stimulated a change in metabolism to convert food into energy (eg. timing or chemical) whereby the compensatory role of SDE was greatly reduced or eliminated. Also, SM at -3 C may have been influenced by catabolism of body tissues and shivering. Most likely SDE was not great enough to compensate for thermoregulatory needs and fat catabolism and shivering were stimulated to balance heat loss. The ambient temperature at which captive ducks begin to shiver or catabolize tissues was not determined for this study.

Respiratory Quotient

Respiratory quotients (RQ) of black ducks in the post absorptive state (no food) were slightly higher than RQ's expected for birds during starvation (RQ < 0.70) (Table 2). RQ's associated with post digestion decreased as temperature decreased suggesting that more body fat was catabolized to carbohydrates for thermoregulation.
Table 2. Respiratory Quotients (RQ) associated with metabolic rates of black ducks in a post-digestive state and after force-feeding 20 g (wet weight) of food within the thermoneutral zone (TNZ) and below lower critical temperature (LCT).

<table>
<thead>
<tr>
<th>Temperature</th>
<th>No Food</th>
<th>Earthworms</th>
<th>Corn</th>
</tr>
</thead>
<tbody>
<tr>
<td>TNZ 20°C</td>
<td>0.765</td>
<td>0.723</td>
<td>0.885</td>
</tr>
<tr>
<td>&lt;LCT 2°C</td>
<td>0.755</td>
<td>0.743</td>
<td>0.880</td>
</tr>
<tr>
<td>&lt;LCT -3°C</td>
<td>0.722</td>
<td>0.647</td>
<td>-</td>
</tr>
</tbody>
</table>
In the TNZ, RQ's were highest for corn (0.885) and indicated mixed combustion of protein and CHO. Below LCT at 2 C, RQ's associated with earthworms were not different from RQ's at 20 C (F=1.053, p>0.352). The RQ's of corn were similar between TNZ and LCT. RQ was 13 % less between 2 C and -3 C when earthworms were fed, which indicated that the birds may have catabolized endogenous lipids (Table 2). However, RQ values less than 0.70 are also characteristic of animals that rapidly consume food within 1-2 hours once each day (Romijn and Lokhorst 1966).

Patterns of RQ between different temperatures indicated that corn provided more energy and compensatory SDE from CHO and protein than earthworms. Energy required by many species of birds is provided mostly by CHO (about 87 %) and protein with a corresponding RQ between 0.85 and 0.95 for mature fowl (Freeman 1971). Because the RQ above 20 C was greater than 0.70, catabolism of lipids did not seem to bias the results of the SDE experiment.

Metabolic Rhythm

Black Ducks had a definite non-diurnal metabolic rhythm of oxygen consumption that cycled at an average of 15 to 20 minute intervals and was influenced by food digestion (Fig. 5a). Within the TNZ at 20 C, rhythm amplitude increased (F=12.18, p<0.001) when 20 g of
Figure 5. Percent oxygen used before force-feeding (Graph A) and after force-feeding 20 g of earthworms (Graph B) to black duck #9 during SDE trial #4. The arrow (Graph B) indicates a change in rhythm. Temperature was below LCT at 2 C. Data smoothed by time series statistical methods.
earthworms were fed. Frequency was lower but not different (F=3.522, p>0.069) from that for BM (Table 3). Below LCT at 2 C the amplitude decreased (F=5.325, p<0.05) and frequency increased (F=5.386, p<0.05) when food was force-fed compared to SM. Frequency was not different between TNZ BM and LCT SM (F=0.154, p>0.698) and TNZ EM and LCT EM (F=0.031, p>0.861).

The data suggest that the metabolic rhythms observed during this study seem to be related to metabolic processes of digestion (SDE) and thermoregulation that are superimposed on a 12 h diurnal or crepuscular rhythm reported for poultry (Barott et al. 1938). The diurnal rhythms in poultry are believed to be caused by muscular activity and a corresponding deep body temperature which is influenced by age (Barott et al. 1938, Freeman 1971). However, the metabolic rhythms of SDE and thermoregulation recorded during this study are believed to be associated with protein and CHO breakdown products of food that enter the intestine, are absorbed into the blood, and assimilated by cells within minutes after eating (Hill 1971). These breakdown products are available for heat production and influence temperature regulation. Thermogenesis seems to operate like a thermostat and furnace whereby metabolic heat production is stimulated to cycle on and off (see Fig. 5) as a function of cooling rate determined by conditions of the environment and organism. Food digestion and
Table 3. Amplitude and frequency of metabolic rhythm associated with digestion of 20 g of earthworms by black ducks at two environmental temperatures.

<table>
<thead>
<tr>
<th></th>
<th>Within TNZ (20 C)</th>
<th>Below LCT (2 C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BM</td>
<td>EM</td>
</tr>
<tr>
<td>Amplitude (% O2 used)</td>
<td>0.338 ± 0.009</td>
<td>0.369 ± 0.007</td>
</tr>
<tr>
<td></td>
<td>(59)</td>
<td>(66)</td>
</tr>
<tr>
<td>Frequency (minutes)</td>
<td>18.8 ± 1.2</td>
<td>15.5 ± 1.1</td>
</tr>
<tr>
<td></td>
<td>(35)</td>
<td>(42)</td>
</tr>
</tbody>
</table>

a Mean ± standard error (sample size)
b * = p<0.05, ** = p<0.01
c Time between peaks of oxygen used
associated SDE heat production may shift the proportion of heat generated at different sites (eg. inner body core vs outer body core) and affect cooling rates. Figure 5 indicates that the amplitude and frequency of "thermostatic" metabolic rhythm changes when food is digested, absorbed, and assimilated. Following these processes, catabolism of excess amino acids stored during assimilation decreases the frequency of metabolic rhythm for a short period of time followed by a return to the pre-feeding rhythm pattern (see arrow on graph b, Fig.5).

Relationship Between Nutrient Content and SDE of Foods

Nutritional studies have shown that SDE is considerably greater with protein diets than with carbohydrates (CHO) or fat diets (Kriss et al. 1934, Kleiber 1961) and that individual amino acids have different SDE (Brody 1945). Amino acids not needed for protein synthesis or in excess of any limiting amino acids are stored in body tissues for a few hours before conversion to nitrogen, carbon dioxide and water, carbon molecules for fat, and heat energy (Sturkie 1965, Maynard et al. 1979, Scott et al. 1982). Ingested CHO and fat are stored as glycogen or triglycerides if not immediately required for catabolic processes (Freeman 1971). The metabolic pathways to convert protein into fat reserves are more complicated and energetically expensive than processes to retain CHO.
and fat components of food as lipid reserves (Hazelwood 1972). Therefore, protein may provide compensatory SDE for thermogenesis first while CHO and fat are stored as lipid reserves to provide energy for thermogenesis when protein and SDE are no longer available.

Corn contained more dry matter, ash, fat, CHO, and gross energy than gammarus and earthworms, but similar amounts of protein (Table 4). The protein in corn contains limited amounts of several essential amino acids (Fisher 1972). Therefore, the excess amino acids could provide compensatory SDE for thermogenesis enabling more dietary CHO and fat to be stored as lipid rather than be used for thermoregulation, according to Rubner's compensating theory (Kleiber and Dougherty 1934). Also, under conditions of fasting or starvation that reduce glycogen stores, the high CHO content of foods like corn produces a substantial rise in SDE when glucose is converted to glycogen (Wilhelmi 1935). The CHO content of corn is 6 to 8 times greater than its protein content, and 19 and 35 times greater than the CHO in gammarus and earthworms, respectively. In contrast, the CHO content of gammarus and earthworms was less than their protein contents (Table 4).

The composition and amounts of essential, limiting, and excess amino acids in the diet of birds may have important implications on the seasonal biological quality of foods, especially for waterfowl that winter in cold climates and
Table 4. Nutrient content (g) and gross energy (KJ) in 20 g of foods fed to or used by black ducks.

<table>
<thead>
<tr>
<th></th>
<th>Gammarus</th>
<th>Earthworms</th>
<th>Corn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water</td>
<td>15.24</td>
<td>16.30</td>
<td>1.20</td>
</tr>
<tr>
<td>Dry Matter</td>
<td>4.76</td>
<td>3.70</td>
<td>18.80</td>
</tr>
<tr>
<td>protein</td>
<td>2.26</td>
<td>2.22</td>
<td>1.65 - 2.44</td>
</tr>
<tr>
<td>fat</td>
<td>0.22</td>
<td>0.16</td>
<td>0.86</td>
</tr>
<tr>
<td>CHO</td>
<td>0.73</td>
<td>0.39</td>
<td>13.72</td>
</tr>
<tr>
<td>ash</td>
<td>1.55</td>
<td>0.93</td>
<td>1.77 - 2.93</td>
</tr>
<tr>
<td>Gross Energy</td>
<td>47.28</td>
<td>57.26</td>
<td>299.39</td>
</tr>
</tbody>
</table>

a National Research Council  
b Sibbald (1979)  
c Sugden (1973)  
d Estimated CHO = dry matter - protein - fat - ash  
e Food and Agricultural Organization  
f Estimated ash = dry matter - protein - fat - CHO  
g Gross energy = 14.73 KJ/g * (dry matter - ash)  
h Gross energy = 20.67 KJ/g * (dry matter - ash)  
i Gross energy = 17.58 KJ/g * (dry matter - ash)
require considerable energy for thermogenesis to survive.

Biological Implications of SDE and Nutrient Content

Different SDE, RQ and nutritional content of earthworms and corn suggested that the biological quality of these and other animal and plant foods in the diets of waterfowl may influence their foraging strategies, survival, and reproductive success. For example, the diet of black ducks wintering in coastal areas contains mostly animal matter (eg. Hartman 1960, and Chapter 2), which has high water content and is digested rapidly. Because of the high water content and low CHO and fat components, large quantities of animal foods must be consumed to balance dietary and energy needs. Therefore, foraging strategies are lengthy feeding bouts twice each day in response to favorable tide periods (Table 5). Because food resources are often scattered and patchy, black ducks digest food continuously while foraging. If black ducks consumed and digested a maximum of 25 g of animal foods (eg. gammarus or blue mussels) per 30-40 minutes (Grandy 1972) and foraged 12 hours/day, they could consume 450 g/day of animal matter to obtain about 1063 KJ of energy (Table 5). The larger protein content in this amount of food compared to fat and CHO could provide compensatory SDE during the long foraging periods thereby conserving fat for thermogenesis during the non-foraging periods of each day. In contrast, the diets of mallards
Table 5. Differences in foraging time, amount of food eaten, and nutrient composition between an animal and plant diet consumed by waterfowl during winter. Numbers in parenthesis represent the animal diet needed to obtain the same amount of energy contained in the plant diet.

<table>
<thead>
<tr>
<th></th>
<th>Anamal Diet</th>
<th>Plant Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>Gammarus</td>
<td>Corn</td>
</tr>
<tr>
<td>Feeding bouts</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Foraging time</td>
<td>12 hour/day</td>
<td>0.7-3.6 hour/day</td>
</tr>
<tr>
<td>Food eaten (g dry weight)</td>
<td>450 (734)</td>
<td>120</td>
</tr>
<tr>
<td>Number of food items</td>
<td>24,190 (39,471)</td>
<td>470</td>
</tr>
<tr>
<td>Food composition</td>
<td></td>
<td></td>
</tr>
<tr>
<td>water (g)</td>
<td>342.9 (559.3)</td>
<td>7.2</td>
</tr>
<tr>
<td>dry matter (g)</td>
<td>107.1 (174.7)</td>
<td>112.8</td>
</tr>
<tr>
<td>protein (g)</td>
<td>50.9 (83.0)</td>
<td>9.9 - 14.7</td>
</tr>
<tr>
<td>fat (g)</td>
<td>4.7 (4.7)</td>
<td>5.2</td>
</tr>
<tr>
<td>CHO (g)</td>
<td>16.4 (26.7)</td>
<td>82.3</td>
</tr>
<tr>
<td>ash (g)</td>
<td>34.9 (57.0)</td>
<td>10.6 - 17.6</td>
</tr>
<tr>
<td>gross energy (KJ)</td>
<td>1063.4 (1735.2)</td>
<td>1735.2</td>
</tr>
</tbody>
</table>
wintering at midcontinent areas contain mostly plant foods, especially corn which is high in dry matter and digested more slowly than animal matter. Therefore, the foraging strategy of these mallards is to forage intensively for shorter periods of time, rapidly consume large quantities of food once (perhaps twice) each day, and then fly back to roosts or resting areas to digest the food (Jorde et al. 1983). Generally, agricultural foods such as corn are relatively concentrated and easy to locate, hence mallards can consume an estimated maximum of 120 g of corn in less than 45 minutes to obtain 1700 KJ of energy (Table 5). At a digestion rate of 10 g/hour, 120 g of corn would take 12 hours to digest during which the protein and amino acid imbalance could provide compensatory SDE thereby enabling most of the CHO to be converted to lipids for future needs (Jorde and Krapu, in review).

Compensatory SDE and composition of CHO, fat, protein and energy in the diets of wintering waterfowl may influence the length of time required to regain lipid reserves and protein following periods of cold weather (Fig. 6). For example, diets of corn and gammarus may have similar protein content but the high CHO content of corn probably enables individuals to regain body weight and lipid reserves sooner than individuals using animal diets, especially if protein provides compensatory SDE. Also, some diets of animal matter may require waterfowl to
Figure 6. The influence of severe cold temperatures on the loss and recovery rates of lipid and protein components of the body weight of waterfowl having plant and animal diets during winter.
consume larger, if not impossible, numbers of food items to obtain similar amounts of energy contained in plant diets (Table 5). The energy cost of foraging for an equivalent amount of energy from animal foods may be greater than the amount of energy obtained from the food. The influence of plant and animal diets on an individual's physical condition and ability to recover from periods of cold weather may be more important during late winter or early spring when waterfowl are preparing for migration and reproduction. For example, successive periods of cold during late February and March may cause ducks to deplete lipids and catabolize protein. When periods of intense cold weather are stressfull enough to deplete fat and protein and cause winter mortality, diets of animal matter may not provide adequate nutrients to replace lipida and protein in time to meet nutrient and energy requirements for migration and reproduction (Fig. 6). Hence, migration may be delayed or reproductive condition and breeding success may be lower in individuals that cannot attain optimal reproductive condition on the breeding grounds. As a result, nesting attempts may be delayed, fewer eggs may be laid, or hatchlings may be in poorer physical condition and have higher mortality (Krapu 1981, Pehrsson 1982).

During winter, productive energy (PE) needs (eg. growth, molt, reproduction) of waterfowl are lower than at other seasons of the year (Prince 1979). Therefore, less
proteins or fewer amino acids are needed for these processes, therefore the excess amino acids are converted to heat energy and provide more compensatory SDE for thermogenesis. During periods of cold, energy obtained from fat and CHO could be supplemented or compensated by SDE from excess amino acids for thermoregulation. Thus, a larger percent of the fat and CHO components in the diet could be partitioned into body fat reserves rather than be catabolized for thermoregulation, as suggested for mallards wintering in northern climates (Jorde and Krapu, in review). On the basis of actual and potential compensatory SDE and nutrient content as a waterfowl food, corn is particularly suited for providing energy to survive long periods of cold and to enhance migratory fattening. However, low protein content and limited essential amino acids of corn does not meet the dietary needs of breeding waterfowl. The protein in earthworms and other animal foods provides a better dietary amino acid balance needed for reproduction by waterfowl (Krapu and Swanson 1975). During winter, animal foods seem to provide sufficient energy and nutrients most of the time but not during prolonged or closely repeated periods of extreme cold weather.
LITERATURE CITED


BIOGRAPHY OF THE AUTHOR

Dennis G. Jorde was born in Rugby, North Dakota, on August 22, 1947. He graduated from Towner High School, Towner, North Dakota, in May, 1965. He served in the United States Navy from August 1965 to December 1971.

Dennis graduated from the University of North Dakota, Grand Forks, in May 1977 as a 4-year honors student and received a bachelor of science degree in fishery and wildlife management. He enrolled in the graduate program at the University of North Dakota where he graduated with a master of science degree in biology in August 1981.

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