American Green-winged Teal are the smallest North American Anas. Because of their small size and early nesting chronology, females may have little ability to use nutrient reserves for egg production or to meet subsequent costs of incubation. Thus, they probably rely heavily on exogenous resources for reproduction. From 21 April to 17 June 1993, we determined diurnal time budgets of breeding Green-winged Teal by observing 12 pairs for 26.4 and 52.0 hours during pre-rapid follicular growth (pre-RFG) and rapid follicular growth (RFG), respectively, and 10 pairs for 20.1 hours during incubation. Females spent more time foraging during RFG (74%) than during pre-RFG (35%). Males spent similar time foraging during pre-RFG and RFG (30% and 35%, respectively). Female Green-winged Teal spent more time foraging during incubation breaks than males and as much or more time foraging than females of other Anas species during RFG and incubation breaks. Time budgets of female Green-winged Teal indicate a strong reliance on breeding area resources for reproduction.

**Keywords:** Behaviour, Body Size, American Green-winged Teal, Rapid Follicular Growth (RFG), Reproduction, Time Budget

The reproductive period has been a major focus in studies of avian time budgets. Female waterfowl have received considerable attention during this period because their nutrient demands for reproduction are high (Alisauskas & Ankney 1992). To meet these nutrient requirements, female waterfowl have evolved various tactics related to the extent of their reliance on endogenous versus exogenous nutrients for reproduction (Owen & Reinecke 1979).

Afton (1980) proposed that structural size is an important factor affecting interspecific variation in nutrient storage and use in breeding waterfowl, i.e., the Body Size Hypothesis. Specifically, smaller temperate nesting ducks should rely more on exogenous nutrients for reproduction than do larger ducks. There are at least three reasons why this should be so: 1) smaller ducks require more food per unit body mass; 2) smaller ducks cannot store (absolutely) as much nutrient as somatic tissue; and 3) it is relatively more costly (expressed as a multiple of basal metabolic rate per day) for smaller ducks to lay eggs (Alisauskas & Ankney 1992). Ankney & Alisauskas (1991) demonstrated a positive relationship between body mass and use of endogenous nutrients for reproduction in temperate nesting ducks.

Dabbling ducks (Anas spp.) show interspecific variation related to body size in regard to whether reserves are obtained either on and/or away from breeding areas. Large-
bodied Mallards *Anas platyrhynchos* (Krapu 1974) and Northern Pintails *Anas acuta* (Krapu 1981) stored fat reserves before arrival on breeding areas and showed no further storage after arrival. Smaller-bodied American Wigeon *Anas americana*, however, stored reserves on breeding areas (Wishart 1983). It is unknown when other dabbling ducks store reserves that they utilize for reproduction.

American Green-winged Teal (*Anas crecca carolinensis*, hereafter Green-winged Teal) are the smallest North American *Anas* (Bellrose 1980). Green-winged Teal may have little ability to use nutrient reserves to mitigate the high costs of egg laying plus subsequent costs of incubation because of their small size, early nesting chronology, and high daily costs of egg production (202% of daily basal metabolic rate) ([see Alisauskas & Ankney 1992; BMR = 73.5 Body Mass$^{0.73}$ (Aschoff & Pohl 1970)]). Consequently, they probably meet most nutrient costs of reproduction through dietary intake on breeding areas.

We describe diurnal time budgets of paired male and female Green-winged Teal breeding in south central British Columbia. We specifically tested the hypotheses that female and male Green-winged Teal spend similar time foraging during pre-RFG, and that females spend more time foraging during rapid follicular growth (RFG) than do male Green-winged Teal. We also examined the prediction that female Green-winged Teal spend more time foraging during RFG and incubation than do female congeners.

**Methods**

**Observations**

We made observations of Green-winged Teal near Riske Creek, British Columbia (Paquette & Ankney 1996). This area is in aspen parkland on the Fraser Plateau of south central British Columbia, about 40 km west of Williams Lake and is described in detail by Boyd & Savard (1987).

We used decoy traps to capture pre-breeding female Green-winged Teal (Sharp & Lokemoen 1987). Females were equipped with a 2.0-3.8 g (<1% body weight) transmitter using methods described by Wheeler (1991). Birds were marked also with uniquely shaped, colour coded, PVC nasal markers (Bartonek & Dane 1964) and U.S.F.W.S. leg bands. We attempted to observe each radio-marked female daily between dawn and 12:00 hours to determine nesting status. When a hen was initially found to be in nesting cover, she was approached on foot, flushed, and the area was searched for a nest. If a nest was found during laying, initiation date was determined by subtracting number of eggs in the nest from the previous Julian day. We assumed a laying interval of one egg per day and that hens flushed off a nest had not laid an egg that day. If the nest was found during incubation, initiation date was determined by candling (Klett et al. 1986) eggs and subtracting number of days incubated and number of eggs in the nest from the Julian day the nest was found (again assuming a laying interval of one egg per day and partial nest depredation had not occurred).

We made observations of time spent in various activities of Green-winged Teal pairs from concealed locations near a wetland or from a vehicle. Activities were observed using a 15-60x spotting scope mounted to a tripod or window mount and were recorded using a Radio Shack Model 100 laptop computer. Sessions were programmed to last 30 minutes during which behaviours were recorded every 10 seconds at an audio signal. We used simultaneous (male-female), focal sampling (Altmann 1974) for measuring activities of individual Green-winged Teal pairs. Activities of focal Green-winged Teal pairs were separated into the following eight categories (Dwyer 1975):

- **Foraging** - searching for or ingesting food.
- **Locomotion** - swimming, walking in shallow water or on the shore of a wetland, or swimming short distances between foraging locations.
- **Resting** - sleeping and loafing.
- **Comfort** - preening, wing flapping, bathing, stretching, body shakes, tail wags and any other activities involved with body maintenance.
- **Alert** - head in an upright posture or head tilted to one side to scan upwards. Alert
birds normally stopped all activities and watched or listened for potential intruders or danger.

Courtship - displays and copulation.
Agonistic - bill threats, chasing, and biting.
Flying.

During observations, unmarked females were seen flying to or from nest sites. These areas were subsequently searched when only the male was observed on the wetland. If a female was flushed, the area was searched and if a nest was found, initiation date was determined as outlined above. A nest trap (Weller 1957) was then placed at the nest site and the female was captured the following day and subsequently marked with a radio backpack and nasal markers.

The study area was divided geographically into 10 wetland groups based on proximity of wetlands. Each wetland group contained 10 wetlands. For the purposes of this study, a wetland was defined as a natural undrained basin or kettle with standing water. Wetlands on the study area are described in detail by Boyd & Savard (1987). Observation periods were: I) morning (dawn - 10:00); 2) mid-day (10:01-16:00); and 3) evening (16:01 - dusk) (Baldassarre et al. 1987). To minimise sampling bias, we randomly selected observation periods and wetland groups. Wetlands in a group were surveyed randomly and when a Green-winged Teal pair was detected we began observations. When a female was incubating, we attempted to observe her daily by waiting near the nest site. To optimise our potential for obtaining observations on incubating females, we randomly selected a female to monitor and monitored the nest site during early morning or late evening hours, when dabbling ducks typically take incubation recesses. When the female left the nest site we began observations.

Analyses

For analyses, Green-winged Teal pairs were classified based on the reproductive status of the female: 1) pre-rapid follicular growth (pre-RFG); 2) RFG; and 3) incubation. Observations classified as during RFG included those that occurred within seven days before laying the first egg (Alisauskas & Ankney 1992) and during laying. Observations categorised as during pre-RFG were those made prior to this period. The respective reproductive status of each pair was then assigned to observation samples by back-dating to each observation date. For analyses, we used only those sessions for which we could assign a known reproductive status to the female.

Occasionally, pairs were obstructed from view by vegetation, disturbed, or the hen flew to the nest and resultant sessions were shorter than 30 minutes. Therefore, we determined the minimum session length that was appropriate for analysis. To do this, we plotted % time spent in each of the four dominant behaviours (foraging, resting, comfort, and locomotion) against observation time in minutes. We used only data from 30 minute sessions and determined, for each minute, the proportion of time that was estimated for each activity. Plots illustrated a relationship that had an asymptote at about 13 minutes (Paquette 1995). Thus, we used sessions that were from 13 to 30 minutes long for analyses.

To avoid pseudoreplication, we calculated mean proportions of male and female behaviours in each reproductive period for each pair. Thus, a sampling unit for analysis was an individual in a pair. Before analyses, proportional data were arcsine square-root transformed to correct for non-normality (Sokal & Rohlf 1981).

We used analysis of variance (ANOVA) (PROC GLM; SAS Inst. Inc. 1990) to determine if individual behaviours differed between stage and sex during pre-RFG and RFG. To elucidate between group differences, the Tukey least significant difference test was performed on the behaviours that had significant ANOVA results. We compared only male-female behaviours during pre-RFG and RFG because during incubation, females spend most of their time on the nest.

Results

We obtained 26.4, 52.0, and 20.1 hours of observations from Green-winged Teal pairs with known reproductive status during pre-RFG, RFG, and incubation, respectively, during
21 April to 17 June 1993. These data were obtained from 12 breeding pairs during pre-RFG and RFG. Two females were killed on the nest during egg laying and thus, data from only 10 of the 12 breeding pairs were collected during incubation.

During pre-RFG, males and females spent similar time \((P > 0.05)\) in all activities (Table 1). However, during RFG, females spent more time foraging than during pre-RFG and also spent more time foraging than did males \((P < 0.05)\). Time that males spent foraging did not differ \((P > 0.05)\) between pre-RFG and RFG.

Females spent less time resting and locomoting during RFG than during pre-RFG \((P > 0.05)\). Time that males spent resting and locomoting, however, did not change \((P > 0.05)\). During RFG, males spent more time resting and locomoting than did females during RFG \((P < 0.05)\).

There was no difference \((P > 0.05)\) in time spent in alert behaviour by females during pre-RFG and RFG. Time spent in alert behaviour by males was higher \((P < 0.05)\) during RFG than during pre-RFG and also was greater \((P < 0.05)\) than time spent alert by females during RFG. There were no differences \((P > 0.05)\) in time spent in comfort, courtship, agonistic, and flying activities between reproductive stage or sex. Courtship, agonistic, and flying activities were observed infrequently. During incubation breaks, females spent most of their time foraging (85.8%).

**Discussion**

Comparison of time budgets of female and male Green-winged Teal pairs, particularly the proportion of time spent foraging during RFG, indicates that females have a strong reliance on exogenous resources for egg production. During pre-RFG, females and males apportioned their time in each activity similarly. During RFG, however, females doubled their time spent foraging, but males showed little increase in foraging activity. Time budgets for other breeding dabbling ducks also show that females spend more time foraging than do males during RFG (Table 2).

The proportion of time spent foraging by paired male and female Green-winged Teal during pre-RFG were similar to average values (males and females combined) reported by Rave & Baldassarre (1989) for Green-winged Teal wintering in Louisiana. They suggested that relatively constant feeding rates from December through March (27.7%-33.3%) reflected a strategy whereby Green-winged Teal relied more on dietary intake than on lipid reserves to survive winter conditions. Thus, foraging effort from December through March by wintering Green-winged Teal probably reflects what is needed to meet daily energy requirements. Similar foraging efforts by Green-winged Teal in Louisiana during winter and in British Columbia during pre-RFG suggest that female Green-winged Teal are foraging during pre-RFG to meet daily energy requirements and were not storing nutrients as somatic tissue. However, this comparison must be made with caution because diets were different between the two areas. Regardless, if female Green-winged Teal were storing nutrients during pre-RFG, the proportion of time females spent foraging would likely have been higher than that of males.

The large amount of alert behaviour by males during RFG may be related to mate guarding from conspecifics. High rates of forced copulation and attempted forced copulation were observed during this study and were also reported by McKinney & Stolen (1982) for captive Green-winged Teal. More importantly, increased alertness by paired males may be related to female energetic requirements and safety. Increased male alertness may protect females from sudden and energetically costly encounters with predators and conspecifics (Derrickson 1977).

Agonistic behaviour towards male conspecifics was low. It appeared that Green-winged Teal avoided (eg often hid in emergent vegetation) confrontation rather than engaged in male-male or male-pair encounters. Encounters with lone males seeking copulation may lead to energetically expensive fleeing tactics by the female, such as diving or flying...
Table 1. Diurnal time budgets of Green-winged Teal pairs breeding near Riske Creek, British Columbia from 21 April to 17 June 1993.

<table>
<thead>
<tr>
<th>Reproductive status</th>
<th>Foraging</th>
<th>Resting</th>
<th>Locomotion</th>
<th>Comfort</th>
<th>Alert</th>
<th>Courtship</th>
<th>Agonistic</th>
<th>Flying</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-FRG* Female</td>
<td>35.3A</td>
<td>40.3A</td>
<td>16.7A</td>
<td>6.3A</td>
<td>0.7A</td>
<td>0.20A</td>
<td>0.00A</td>
<td>0.50A</td>
</tr>
<tr>
<td></td>
<td>SE 6.7</td>
<td>8.9</td>
<td>4.7</td>
<td>1.5</td>
<td>0.3</td>
<td>0.10</td>
<td>0.00</td>
<td>0.11</td>
</tr>
<tr>
<td>(n=12) Male</td>
<td>29.9A</td>
<td>41.8A</td>
<td>13.6A</td>
<td>5.7A</td>
<td>1.2A</td>
<td>3.17A</td>
<td>0.38A</td>
<td>4.25A</td>
</tr>
<tr>
<td></td>
<td>SE 7.6</td>
<td>9.9</td>
<td>3.8</td>
<td>1.5</td>
<td>0.5</td>
<td>3.10</td>
<td>0.30</td>
<td>4.10</td>
</tr>
<tr>
<td>RFG Female</td>
<td>74.0B</td>
<td>9.2B</td>
<td>7.6B</td>
<td>7.3A</td>
<td>1.4A</td>
<td>0.15A</td>
<td>0.01</td>
<td>0.34A</td>
</tr>
<tr>
<td></td>
<td>SE 3.2</td>
<td>2.5</td>
<td>1.3</td>
<td>1.9</td>
<td>0.4</td>
<td>0.10</td>
<td>0.01</td>
<td>0.10</td>
</tr>
<tr>
<td>(n=12) Male</td>
<td>35.3A</td>
<td>29.9A</td>
<td>14.5A</td>
<td>14.1A</td>
<td>4.9B</td>
<td>0.24A</td>
<td>0.03A</td>
<td>1.03A</td>
</tr>
<tr>
<td></td>
<td>SE 6.5</td>
<td>6.7</td>
<td>2.3</td>
<td>3.3</td>
<td>1.3</td>
<td>0.20</td>
<td>0.01</td>
<td>0.40</td>
</tr>
<tr>
<td>Incubation* Female</td>
<td>85.8</td>
<td>2.9</td>
<td>7.7</td>
<td>2.8</td>
<td>0.7</td>
<td>0.02</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>SE 2.9</td>
<td>1.3</td>
<td>2.1</td>
<td>1.0</td>
<td>0.2</td>
<td>0.03</td>
<td>0.03</td>
<td>0.30</td>
</tr>
<tr>
<td>(n=12) Male</td>
<td>38.0</td>
<td>21.3</td>
<td>19.8</td>
<td>12.6</td>
<td>6.5</td>
<td>0.02</td>
<td>0.02</td>
<td>1.76</td>
</tr>
<tr>
<td></td>
<td>SE 7.4</td>
<td>8.4</td>
<td>4.9</td>
<td>4.3</td>
<td>1.9</td>
<td>0.02</td>
<td>0.02</td>
<td>0.80</td>
</tr>
</tbody>
</table>

* Pre-RFG (21 April - 18 May); RFG (12 May-2 June); Incubation (2 May-17 June).

Means within a column sharing same letter are not different (P>0.05), Tukey least significant difference test; Means for incubation not compared to pre-RFG and RFG.

Only includes time spent by pair when female off nest.
Table 2. Diurnal time (%) spent foraging by *Anas* spp. during the breeding season.

<table>
<thead>
<tr>
<th>Species</th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pre-RFG</td>
<td>RFG&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Green-winged Teal</td>
<td>35</td>
<td>74</td>
</tr>
<tr>
<td>Blue-winged Teal</td>
<td>-</td>
<td>59</td>
</tr>
<tr>
<td>Northern Shoveler</td>
<td>69</td>
<td>58</td>
</tr>
<tr>
<td>Gadwall</td>
<td>72</td>
<td>72</td>
</tr>
<tr>
<td>American Wigeon</td>
<td>42</td>
<td>29</td>
</tr>
<tr>
<td>Pintail</td>
<td>25</td>
<td>42</td>
</tr>
<tr>
<td>Mallard</td>
<td>-</td>
<td>37</td>
</tr>
</tbody>
</table>

<sup>a</sup> Excludes time spent at nest.

<sup>b</sup> Estimated from Figure 1 in Dwyer (1975).

(McKinney & Stolen 1982). Female energetic requirements, i.e., high costs of egg production and high foraging rates, have likely influenced this strategy. If egg production is strongly dependent on acquiring exogenous nutrients, then any distraction from foraging during RFG may affect reproductive output and consequently fitness.

Afton (1979) suggested that territoriality in the Northern Shoveler *Anas clypeata* may be related to females' inability to store sufficient body reserves for incubation, and therefore they must rely on breeding ground food resources to meet energy demands. Conversely, Green-winged Teal are not territorial (McKinney et al. 1983) although they, like Shovelers, appear to rely heavily upon food resources obtained on breeding areas. Green-winged Teal nest relatively early and therefore competition for resources may be relatively low at this time. Territoriality is also absent in Northern Pintails, another early nester.

Comparison of the time budgets of female Green-winged Teal to those of other congeners further illustrates female Green-winged Teal's strong reliance on nutrients acquired on breeding areas. Female Green-winged Teal appear to spend as much or more time foraging during RFG and incubation than did females of other *Anas* spp. for which data are available. Thus, it appears that female Green-winged Teal rely as much or more on exogenous nutrient for reproduction than do other congeners. However, such comparisons must be taken with caution because wetland productivity may vary and these species differ in foraging method, diet, and presumably foraging efficiency.

A diurnal activity budget of Green-winged Teal during the reproductive period indicates a strong reliance on breeding area resources for egg production and incubation. This highlights the importance of productive wetlands to female Green-winged Teal on breeding areas (Paquette & Ankney 1996). Further study to quantify the commitment, if any, of nutrient reserves for egg production and incubation by Green-winged Teal is needed.

We thank Thomas Artiss, Sandi Johnson and Floyd Paquette for field assistance. We are especially grateful to Jonathan Thompson for assistance with study design and field work. This study was funded by the Natural Sciences and Engineering Research Council of Canada through a research grant to CDA.
References


