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A COMPARISON OF DIURNAL TIME BUDGETS FROM PAIRED INTERIOR CANADA GEESE WITH AND WITHOUT OFFSPRING

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Abstract.—Diurnal activities of paired (male and female together without offspring) Interior Canada Geese (*Branta canadensis interior*) were compared to those of parents (pairs with offspring) of the Mississippi Valley Population (MVP) during fall through spring 1984–1985 and 1985–1986. Activities of parents with different numbers of offspring also were compared. The dominant activities of geese were alert, resting and feeding behaviors, which together averaged ≥70% of the diurnal period regardless of social class, habitat, year, season or location. For both males and females, parents spent more time alert than pairs during fall, winter and spring. Parental vigilance probably benefitted young by allowing them greater access to food. Generally, the costs of maintaining this parental vigilance were apparently spread across several activities so that time spent resting or feeding did not differ between parents and pairs. The only exception was for females at Union County Conservation Area (CA) in fall, when the behavioral cost of parental vigilance was less time feeding. Parent males with ≥3 offspring rested less than those with only one offspring. In lake habitats, females with two offspring fed more than females with three offspring. It is suggested that for Interior Canada Geese, diurnal time constraints on parents during fall-spring have only minor influences on the evolution of optimal brood size when compared to constraints during the nesting season.

COMPARACIÓN DE PRESUPUESTOS DE TIEMPO DIURNOS DE INDIVIDUOS DE *BRANTA CANADENSIS INTERIOR* CON Y SIN POLLUELOS

Sinopsis.—Desde el otoño a la primavera de los años 1984–1985 y 1985–1986, se compararon las actividades diurna de parejas de gansos del Canadá (*Branta canadensis interior*) con polluelos y parejas sin progenie. Se compararon además parejas con diferente número de polluelos. El estudio se llevó a cabo en la población de aves del valle de Mississippi. La actividad dominante de los gansos fue estar alerta, descansar y alimentarse, lo que sumó >70% de las actividades sin distinción de clase social, hábitat, localización, temporada o año de estudio. Tanto hembras y machos con polluelos invirtieron más tiempo en estar alerta que parejas sin polluelos durante el otoño, invierno y primavera. La vigilancia parental probablemente benefició a los polluelos al permitirles mayor acceso a fuentes de alimento. Generalmente, el costo de mantener la vigilancia parental se distribuyó entre otras actividades de tal manera, que el tiempo utilizado para descansar y alimentarse no fue diferente entre parejas con y sin polluelos. La excepción fue de hembras durante el otoño en el área de Conservación de Unión County cuando la conducta de vigilar de parejas redujo el tiempo de alimentación de estas. Los machos con mas de tres polluelos descansaron menos que aquellos que tan solo tenían uno.

Interior Canada Geese (*Branta canadensis interior*), like other geese and swans, are perennially monogamous and provide extended biparental care to their precocial young (Owen 1980). Benefits of extended bipa-

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rental care have been suggested as important factors in the evolution of perennial monogamy (Mock 1985). The behavioral costs of this care during fall to spring have received little attention, despite their potential importance to life history tactics of geese (Austin 1990). Barnacle Goose (*Branta leucopsis*) parents that retained young in their family groups during fall and winter spent more time alert and fed less than pairs without offspring (henceforth called pairs) (Black and Owen 1989b). Tundra Swan (*Cygnus columbianus columbianus*) parents spent more time foraging in wetlands than pairs during fall and winter (Earnst and Bart 1991). Foraging produced behavioral and energetic costs to the parents but benefited young by revealing foods (Earnst and Bart 1991). Parent Bewick's Swans (*C. columbianus bewickii*) spent more time alert and less time feeding than pairs during fall, and this allocation may have led to a slower rate of mass gain in parent males (Scott 1980).

Although behavioral costs are associated with extended biparental care in geese, there also may be energetic benefits to parents. A social hierarchy, which allows dominant birds to feed or rest in preferred locations, exists within flocks: large families dominate small families, small families dominate pairs and pairs dominate singles (Black and Owen 1989a, Gregoire and Ankney 1990, Hanson 1953, Raveling 1970). Some forms of parental care may aid current offspring but reduce the parents' potential for raising offspring in the future (Trivers 1972).

Parental care by geese increases with larger broods during the prefledgling period (Forslund 1993, Paine 1992, Schindler and Lamprecht 1987, Sedinger and Raveling 1990, but see Lazarus and Inglis 1978). Posthatch selection pressures, including greater risk of brood predation and costs to the parents, may influence the evolution of optimal clutch size (Forslund 1993, Schindler and Lamprecht 1987). We know of no study, however, that has demonstrated increased parental effort by geese with larger brood sizes during fall to spring (Turcotte and Bedard 1989).

We documented diurnal behavior by parent Interior Canada Geese during fall to spring and examined the effects of changing brood size on this behavior. Our analyses focused on alert, feeding and resting behaviors, because these are the most common activities of Interior Canada Geese during fall to spring and these likely have a greater effect on energy budgets than other behaviors (Caithamer 1989). We compared diurnal time allocated to each of the three activities by parent and paired geese and by parents with different brood sizes.

STUDY AREA AND METHODS

Interior Canada Geese were observed in southeastern Wisconsin near Horicon National Wildlife Refuge (NWR) (43°30′N, 88°38′W) and in southern Illinois near Union County Conservation Area (CA) (37°24′N, 89°23′W). Both areas have a refuge and agricultural and wetland habitats that seasonally attract concentrations of Mississippi-Valley-Population (MVP) Canada Geese (Reeves et al. 1968). Horicon Marsh is a major

staging area during fall and spring whereas southern Illinois is the primary wintering area for the MVP (Tacha et al. 1991).

Data collection.—Geese were observed during the fall, winter and spring of 1984–1985 and 1985–1986. Five seasons were defined on the basis of major migratory movements (Tacha et al. 1991) and other events. Early Fall began with arrival of geese in early October and continued until goose hunting opened (November) in southern Illinois. Early Fall also corresponded closely with goose hunting in southeastern Wisconsin. Late Fall lasted until December when hunting ended in southern Illinois and most geese left Wisconsin and arrived in southern Illinois. Early Winter extended through mid-January when temperatures moderated. Late Winter lasted until large numbers of geese left wintering areas and began their northward migration in February. Lastly, Spring was the period from mid-March to mid-April when large numbers of geese were in southeastern Wisconsin. Observations were collected in southeastern Wisconsin during Early Fall, Late Fall and Spring and in southern Illinois during Early Fall, Late Fall, Early Winter and Late Winter.

We observed geese with a 15–60× spotting scope from a stationary vehicle and recorded the behavior of focal individuals at 10-s intervals with the aid of an electronic metronome and tape recorder. Individual geese were observed for a maximum of 20 min or until they were lost from view. Observations lasting <10 min were discarded.

Behavior was classified into one of eight categories. Sleeping and loafing were categorized as resting. Geese with their head high and neck outstretched were considered alert (Raveling 1970). Swimming and walking were classified as locomotion. Food searching, handling and ingestion were classified as feeding. Simultaneous locomotion and feeding also was classified as feeding. Comfort behavior included any preening, stretching or bathing (McKinney 1965). Head pumping, other threats and biting were classified as agonism (Klopman 1968, Raveling 1970). Greeting ceremony and sexual behavior were categorized as courtship (Klopman 1968, Raveling 1970). Other behavior included drinking, pre-flight head tossing (Raveling 1969a) and all other activities not previously described.

The social status of geese (parent male, parent female, paired male, paired female) was determined from visual cues. Family members and pairs were recognized by their cohesiveness and greeting ceremony (Raveling 1969b, 1970). Age and sex was assessed from plumage, body size and behavioral characters (Caithamer et al. 1993).

Behavioral observations were stratified by habitat type and time of day. Habitat types were grain fields (corn, soybean and milo), forage fields (pastures, winter wheat, alfalfa and clover), wetlands (palustrine systems [Cowardin et al. 1979]) and lakes (lacustrine systems [Cowardin et al. 1979]). Daytime was divided into three 3 periods: the 3 h after sunrise, the 3 h preceding sunset and the remaining midday period. Approximately equal numbers of observations were collected of each social class within each daylight period and habitat type during each season and at

both locations. No geese were observed on lakes in southeastern Wisconsin, however.

Analyses.—The sampling unit was each 10–20 min time budget. Type III sum of squares from General Linear Model (GLM) procedures (SAS Institute 1990) were used to assess the independent effects of social class on proportion of time spent alert, resting and feeding. Proportion of time involved in each activity was arcsine transformed (Sokal and Rohlf 1981) prior to analyses. Habitat, year, season and location were included to account for other potentially important sources of variation and thus allow assessment of the unique effects of social class. A $P \leq 0.05$ was considered significant. Differences among means were identified with Tukey's studentized range test (SAS Institute 1990). Simple means and their standard errors are presented in tables.

Initial analysis determined if subsequent analyses should be conducted by year or location. Location was perfectly confounded with season except during Early and Late Fall. Thus, the first set of tests used data collected from both study sites during Early and Late Fall to determine the effects of year and location on the three activities; social class, season and habitat were included as additional explanatory variables. The second set of tests used data collected during Early Winter, Late Winter and Spring to determine if activities varied by year; social class, season and habitat were again included as additional explanatory variables.

The effects of number of offspring (1, 2, ≥3) on parental behavior were assessed with GLM procedures and Tukey's tests. Models were tested separately for parent males and females with the variables habitat and season included.

RESULTS

A total of 1338 time budgets was collected. Sample sizes from each of the four social classes were nearly equal (range = 323–349). The dominant activities of geese were alert, resting and feeding behaviors, which together averaged ≥70% of the diurnal period regardless of social class, habitat, year, season or location.

Resting, feeding and alert behavior during Early and Late Fall at Horicon NWR and Union County CA varied ($F_{1,642}$ = 9.5–12.3, $P \leq 0.002$) by location but not by year ($F_{1,642}$ = 0.6–3.6, $P \geq 0.058$). Therefore, subsequent analyses of data collected during Early and Late Fall were conducted separately for each location but with years combined and no year-effect included in the models.

Amount of alert behavior during Early Winter, Late Winter and Spring varied ($F_{1,676} = 15.2$, $P \leq 0.001$) by year. Further analyses of activities from Winter and Spring were conducted separately for each year.

Fall.—Time spent alert ($F_{3,233} = 26.8$, $P < 0.001$) and feeding ($F_{3,233} = 2.9$, $P = 0.037$) varied among social classes (main effects) at Horicon NWR. Parents spent about twice as much time alert compared with pairs (Table 1). Parent males fed less than paired females (Table 1), but this effect varied seasonally ($F_{3,233} = 4.0$, $P = 0.009$). Examination of simple

TABLE 1. Percentage of diurnal period spent feeding, resting and alert by social classes of Interior Canada Geese at Union County Conservation Area and Horicon National Wildlife Refuge during Early and Late Fall, 1984 and 1985.

			Feed			Rest			Alert		
Location	Social class	*N*	Mean	SE	Tukey[a]	Mean	SE	Tukey	Mean	SE	Tukey
Union County	Parent male	105	25	2	A	21	2	A	35	2	A
	Paired male	90	33	3	A	27	3	AB	20	3	B
	Parent female	105	34	3	A	30	3	B	14	2	C
	Paired female	95	44	3	B	32	3	B	5	1	D
Horicon	Parent male	65	22	2	A	25	3	A	30	3	A
	Paired male	66	32	4	AB	35	4	A	12	2	B
	Parent female	64	32	3	AB	33	3	A	14	2	B
	Paired female	62	40	5	B	36	4	A	6	1	C

[a] Results of Tukey's studentized range test conducted by area. Different letters within columns indicate differences ($P < 0.05$) among social classes.

effects revealed that parent males fed more often than paired females during Early Fall ($P < 0.05$, Tukey's test), but no differences in time spent feeding were detected among the social classes during Late Fall ($P > 0.05$, Tukey's test). Although there was a main effect of social class on time spent resting ($F_{3,233} = 2.8$, $P = 0.042$), no differences ($P > 0.05$, Tukey's test) were detected among the social classes.

Social classes spent different amounts of time (main effects) feeding ($F_{3,363} = 3.1$, $P = 0.025$), resting ($F_{3,363} = 5.2$, $P = 0.002$) and alert ($F_{3,363} = 30.4$, $P < 0.001$) at Union County CA during Fall. Parent males spent more time alert than paired males (Table 1). Parent females were alert more but fed less than paired females (Table 1).

TABLE 2. Percentage of diurnal period spent feeding, resting and alert by social classes of Interior Canada Geese at Union County Conservation Area and Horicon National Wildlife Refuge during Winter and Spring, 1984–1985 and 1985–1986.

			Feed			Rest[a]		Alert		
Year	Social class	*N*	Mean	SE	Tukey[b]	Mean	SE	Mean	SE	Tukey
1984–85	Parent male	100	29	3	A	28	3	25	2	A
	Paired male	94	36	3	AB	27	3	15	2	B
	Parent female	94	38	3	AB	34	4	9	1	C
	Paired female	89	42	4	B	32	3	5	1	D
1985–86	Parent male	79	29	3	A	26	3	17	2	A
	Paired male	78	33	3	AB	31	3	12	2	B
	Parent female	75	35	4	AB	31	3	8	2	C
	Paired female	77	42	4	B	33	3	2	<1	D

[a] Tukey's studentized range tests not conducted because behavior did not vary ($P > 0.18$) by social class in either year.

[b] Results of Tukey's studentized range test conducted by area. Different letters within columns indicate differences ($P < 0.05$) among social classes.

TABLE 3. Percentage of diurnal period spent feeding, resting and alert by parent Interior Canada Geese with different numbers of offspring. Geese were observed at Union County Conservation Area and Horicon National Wildlife Refuge, Fall through Spring, 1984–1986.

Sex	Number of offspring	N	Feed[a]		Rest			Alert[a]	
			Mean	SE	Mean	SE	Tukey[b]	Mean	SE
Male	1	137	27	2	29	2	A	21	2
	2	111	27	2	24	3	AB	27	2
	≥3	84	26	2	19	3	B	36	3
Female	1	127	33	3	35	3	A	9	1
	2	116	37	3	31	3	A	12	2
	≥3	80	35	3	31	3	A	14	2

[a] Tukey's studentized range tests not conducted because behavior did not vary ($P > 0.05$) by number of offspring.

[b] Results of Tukey's studentized range test conducted by sex. Different letters within columns indicate differences ($P < 0.05$) among parents with different numbers of offspring.

Winter and Spring.—Amount of alert behavior varied among social classes (main effects) during Early Winter, Late Winter and Spring in 1984–1985 ($F_{3,337} = 27.2$, $P < 0.001$) and 1985–1986 ($F_{3,269} = 25.8$, $P < 0.001$). For both sexes, parents were alert more than pairs (Table 2). The interaction of habitat by social class explained a significant amount of variation ($F_{9,337} = 2.2$, $P = 0.025$) in alert behavior during 1984–1985. Amount of alert behavior varied among social classes in grain ($F_{3,105} = 16.6$, $P < 0.001$), forage ($F_{3,107} = 17.0$, $P < 0.001$) and wetland habitats ($F_{3,88} = 4.1$, $P = 0.009$), but not in lake habitats ($F_{3,37} = 1.5$, $P = 0.229$). Parents were alert more than pairs in grain and forage fields ($P < 0.05$, Tukey's test). In wetland habitats there were no differences ($P > 0.05$, Tukey's test) between parent and paired males, or between parent and paired females.

Time spent feeding varied among social classes in both 1984–1985 ($F_{3,337} = 2.8$, $P = 0.043$) and 1985–1986 ($F_{3,269} = 2.7$, $P = 0.046$). In both years, paired females fed more often than parent males, but no other differences in time spent feeding were detected (Table 2). Amount of resting did not vary among social classes (main effects) in 1984–1985 ($F_{3,337} = 1.6$, $P = 0.188$) or 1985–1986 ($F_{3,269} = 0.9$, $P = 0.439$).

Number of offspring.—The number of offspring had a main effect on the amount of time that parent males ($F_{2,277} = 5.9$, $P = 0.003$) rested. Males with only one offspring rested less than males with three or more offspring (Table 3). No differences ($P > 0.05$, Tukey's test) were detected in time spent resting among females with different numbers of offspring (Table 3), although the main effect was significant ($F_{2,270} = 3.1$, $P = 0.047$). The interaction of number of offspring and habitat accounted for a significant ($F_{6,270} = 2.3$, $P = 0.034$) amount of variation in time feeding by parent females. An examination of simple effects revealed an effect ($F_{9,16} = 9.2$, $P = 0.002$) of number of offspring in lake habitat, where

females with two offspring fed more than females with three offspring ($P < 0.05$, Tukey's test).

DISCUSSION

Our study was focused on diurnal activities of geese. We believe that during nocturnal periods over the course of our study, geese largely restricted their activities to resting. We acknowledge that feeding and other activities may have occurred during the night (Raveling et al. 1972), but believe they were limited. In a concurrent study, Caithamer (1989) observed geese in lake and wetland habitats during nocturnal periods and found that they rested 74 and 60% of the time at Union County CA and Horicon NWR, respectively. In another concurrent study (Tacha et al. 1991, unpubl. data), all radio-marked geese located during nocturnal periods near Horicon NWR were found on lakes or wetlands and not in uplands where geese might be expected to feed nocturnally.

Canada Goose parents consistently spent more time alert than pairs during diurnal periods in fall, winter and spring. Parental vigilance may function to protect offspring from feeding competition (Scott 1980) or aid family groups in their search for food (Lazarus and Inglis 1978). Parental vigilance also may have served to protect offspring from predators (Lazarus and Inglis 1978), but this function would have been more important during summer months when goslings are smaller and flightless.

Generally, the costs of maintaining parental vigilance in both sexes were apparently spread across several activities so that time spent resting or feeding did not differ between parents and pairs. The only exception was for females at Union County CA in fall, when the behavioral cost of parental vigilance was less time feeding. The relative difference in time spent alert between parents and pairs and thus parental effort costs, diminished during winter and spring. This pattern of reduced parental costs with maturation of offspring was also noted in Barnacle Geese (Black and Owen 1989b) and swans (Earnst and Bart 1991, Scott 1980).

At some point, the benefits to parents from providing further resource investment in current offspring falls below the expected benefit from investing in future offspring (also see Lazarus and Inglis 1986; Trivers 1972, 1974). Black and Owen (1989b) suggested that in Barnacle Geese this point occurred after the coldest winter months but before spring migration. Interior Canada Geese begin preparing for the next breeding season by increasing their nutrient reserves during spring migration (Gates 1989).

Lesser amounts of diurnal feeding by parent females than paired females at Union County CA in Fall may have represented a true behavioral cost, rather than just behavioral input. In a concurrent study, parent females had smaller lipid reserves than paired females in winter at Union County CA (Gates 1989). Other factors, such as quality of food eaten, also may have influenced body condition. By spring migration both parent and paired females had similar lipid reserves and thus it is unclear if the

reduced feeding time during fall and lower lipid reserves during winter reduced the fitness of parent females.

We suggest that for Interior Canada Geese, diurnal time constraints on parents during fall, winter and spring have only a small functional influence on brood size. The only costs of larger broods that we were able to demonstrate were reduced time spent resting for parent males and decreased time spent feeding for parent females in lake habitats. Constraints on time expenditures during fall to spring are probably not as severe as the physiological constraints on females during egg laying and incubation when they catabolize 30% of their protein mass and exhaust their lipid reserves (Gates 1989). The future reproductive output and survival of parent Canada Geese and the growth and survival of goslings appeared mostly unrelated to brood size in an experiment in which brood sizes were artificially manipulated (Lessells 1986). The sharing of all parental costs by both sexes of Canada Geese during the entire annual cycle may ultimately allow greater offspring survivorship or quality because the needs of offspring may exceed the ability of a single parent to provide the resource (Mock 1985). Further, this sharing may benefit each parent by helping to maintain the reproductive fitness of its life-time mate (Mock 1985).

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