

FEEDING BEHAVIOUR OF TRUMPETER SWANS *CYGNUS BUCCINATOR*

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We used activity time-budgets to study the feeding behaviour of Trumpeter Swans breeding during 1988–89 on the Copper River Delta, Alaska. Local foods were proximally important for pre-nesting and incubation activities. Females spent more time feeding and had longer feeding bouts than males during pre-nesting, but the pattern was reversed during incubation. During short incubation recesses, females fed with more intensity than males. Although physiologically capable of extended periods of fasting, females appear to rely, in part, on exogenous foods to supplement energy demands of egg laying and incubation. Pairs with young fed less and had shorter feeding bouts than failed breeders, foregoing some feeding opportunities to care for their young. Males fed less and were more vigilant than females during brood rearing, allowing females and young more time to feed undisturbed. Feeding was the principal pre fledging activity of cygnets. Cygnet feeding and non-feeding periods alternated regularly and were relatively uniform in length over time and among broods. The rate at which cygnets can physiologically process green vegetation probably limits the rate of food intake.

Keywords: Trumpeter Swan, Feeding Behaviour, Energetics

Few data are published on the breeding ecology and energetics of wild Trumpeter Swans *Cygnus buccinator* or other swans species. In contrast, the breeding biology and energetics of northern and temperate breeding geese are well documented and may provide models for interpreting Trumpeter Swan behaviour. The Copper River Delta is productive habitat for Trumpeter Swans relative to that occupied outside Alaska (Henson & Cooper 1993). The study of Trumpeter Swan feeding behaviour, particularly on productive habitat, may provide a baseline for evaluating swan feeding strategies outside Alaska.

In *Anserini*, egg laying, incubation, nest building, territorial defense, and moult are costly in terms of energy and nutrients. Waterfowl foraging strategies favour individuals that

maximise nutrient intake per unit of energy expended (Sedinger 1992). Energetics data for breeding waterfowl usually are derived by analysing carcass composition and activity time-budgets (Alisauskas & Ankney 1992, Krapu & Reinecke 1992). Because managers have been unwilling to sacrifice Trumpeter Swans for energetic analysis because of demographic concerns (Weaver 1990), analysis of feeding activity budgets may be the only viable method for gaining reliable knowledge about Trumpeter Swan feeding strategies and energetics.

The period of growth and development is one of the most important yet least understood aspects of waterfowl biology (Sedinger 1992). Young *Anserini* breeding at northern latitudes must acquire enough nutrients within a limited pre fledging period to complete growth and

prepare for migration, yet rely almost exclusively on low-quality plant protein for growth and development (Owen 1980). Poor cygnet growth and survival have been linked to deficiencies in the quality and availability of pre fledging foods, and may limit Trumpeter Swan population growth (Banko 1960, Hansen *et al.* 1971, Page 1976, Holton 1982, Gale *et al.* 1987).

Our objectives were to: (1) document feeding behaviours of Trumpeter Swans breeding on the Copper River Delta; (2) examine the energetic implications of data derived from activity time-budget analysis, and relate these findings to reproductive requirements of female, male, and young birds; (3) relate Trumpeter Swan feeding behaviours to data available for other *Anserini*.

Methods

Study areas

Trumpeter Swans on the Copper River Delta, Alaska (60° and 60°30'N, 144°W), were studied during 1988-89. The delta supported an average of 410 swan pairs from 1980-90 (U.S. Fish & Wildl. Serv., Juneau, Alaska, *unpubl. data*). It is a broad flat expanse of glacial and alluvial deposits formed by the Copper River and adjacent glacial streams that discharge into the Gulf of Alaska (Hansen *et al.* 1971). Trumpeter Swans nested on wetlands formed by glacial action or beaver *Castor canadensis* activity (Hansen *et al.* 1971). Aquatic macrophytes common on the study area included the genera *Menyanthes*, *Carex*, *Equisetum*, *Hippuris*, *Sparganium*, *Nuphar*, *Myriophyllum*, *Chara* and *Potamogeton*.

Field methods

Six nesting territories were studied, with a history of Trumpeter Swan nesting (U.S. Fish & Wildlife Service, Juneau, Alaska, *unpubl. data*). Swan pairs on each nesting territory were observed for about seven hours (range: 4-16 hours) every 2-4 days. The diurnal period increased from 16 hours in April to approximately 21 hours in June and July. All hours of the diurnal period were sampled, but

due to logistical and study site access constraints, we sampled early morning and late evening hours less than late morning, afternoon, and early evening hours. We did not record nocturnal behaviours.

Trumpeter Swans were observed using 85 power Questar telescopes (Questar Corporation, Newhope, Pa.). All observation blinds were located 100-293 m from nest sites. Scan observations (Altmann 1974) of swan feeding behaviours were recorded at six minute intervals with NEC-8300 (NEC Corporation, Tokyo, Japan) portable lap computers. We observed only one family per observation period. We recorded behaviours of females, males and cypnests separately. Individual adults of each pair were sexed by observing unique head and neck feather staining (Cooper 1979, Hawkins 1986), body size, moult patterns and courtship behaviours. Additionally, four adults (one adult each from four pairs) were radio neckbanded in 1988. Cygnet behaviours were recorded for the brood at each scan. When behaviours differed between siblings, the behaviour of the majority was recorded.

Behaviour categories included swimming, walking, flying, stationary (head-up relaxed), alert, preening/bathing, nestbuilding, courtship, agonistic interaction, sleeping or resting, incubation, brooding (sheltering young under the wing), treading (vigorous paddling of feet associated with subsurface feeding) and feeding. Duration of feeding bouts was calculated using six minute activity scans. To accurately calculate the length of swan feeding bouts, we subtracted interruptions in feeding activity of less than 12 minutes from the overall length of the feeding bout. We believed that small breaks in feeding did not result in substantial emptying of the gut, and were usually in response to external stimuli, eg predators, human disturbance or conspecific interactions (Sedinger & Raveling 1988). Furthermore, swans most often began and ended feeding bouts from the nest or shore after engaging in bouts of preening/bathing, providing clear breaks between feeding and nonfeeding periods. During incubation, we calculated adult feeding intensity as the number of bites/minute while grazing on emergent vegetation.

Statistical methods

The breeding season was divided into three periods for data analysis: (1) pre-nesting (included prelaying and laying because we were unable to identify the boundary between the two periods), (2) incubation and, (3) post-hatch/brood rearing. Incubation was subdivided into early, middle and late stages, of approximately 11 days each. The post-hatch period was further partitioned into early brood rearing (hatch to day 30) and late brood rearing (day 31 to fledging) for successful breeders and cygnets.

A single estimate of activity for each daily observation period was calculated as the percent of six minute scans spent in each behaviour during that period. We assumed that the instantaneous activity samples obtained at six minute intervals adequately represented the actual time spent in any given activity. We tested this assumption by comparing feeding data collected at six minute intervals to a subset of feeding data collected at two minute intervals in 1988. We found no difference in the proportion of time recorded in a given activity between the two intervals (Grant 1991). Because swan territories were not equally sampled, mean values were calculated for individual birds by averaging the daily means for each period of the breeding season (ie pre-nesting, incubation, etc.). To assure independent samples, we combined values over two years when it was known or suspected that the same individuals occupied the same territory in 1989 as 1988. Thus every bird in a family group (ie male, female and the brood) contributed one mean value for each statistical test, and the sample size (n) is the number of females, males or broods contributing their mean value to the test. We used paired t -tests to examine sex- and age-related differences in swan behaviour for each period of the breeding season. We used unpaired t -tests to examine differences between the feeding behaviours of pairs with young and failed breeders. We used ANOVA to investigate changes in female feeding during early, middle and late incubation.

Results

Study birds were scanned 12,944 times during 1,295 hours of observation, and data from 7,574 feeding observations were reported for five pairs and five broods (eight nesting attempts; five pairs and four broods in 1988 and three pairs and one brood in 1989).

Pre-nesting

Feeding was the primary diurnal activity of pre-nesting Trumpeter Swans. Females spent more time feeding and had longer feeding bouts than males (**Table 1**). We could not consistently distinguish between the male and female of a fourth swan pair, and therefore combined feeding estimates for both adults. During a three week period, this pair spent about 35-75% of the day feeding ($\bar{x}=56.0\%$, $SE=3.4$, $n=7$ days).

Incubation

Females were restricted to short feeding bouts during recesses away from the nest. Females fed less and had shorter feeding bouts than males (**Table 1**). While grazing on horsetails and sedge, females fed with more intensity than males (female: $\bar{x}=44.2$ bites/minute; male: $\bar{x}=24.7$ bites/minute; $t=3.27$, $P=0.048$, $df=3$). The time that females allocated to feeding varied little with the stage of incubation ($F=1.12$, $P=0.360$, $df=12,2$). Although males did not spend significantly more time feeding during incubation compared to pre-nesting (**Table 1**), a sharp 5-15 day increase in feeding activity was observed at the onset of incubation.

Adults post-hatch

Adults spent about one-third of the day feeding. Females and males did not differ in time spent feeding nor in feeding bout length (**Table 1**). Males were more alert (male: $\bar{x}=7.25\%$; female: $\bar{x}=2.15\%$; $t=2.57$, $P=0.047$, $df=4$) and had more territorial interactions (male: $\bar{x}=0.39\%$; female: $\bar{x}=0.14\%$; $t=2.38$, $P=0.066$, $df=4$) than females. Females alone were responsible for brooding young. Often, males continued to feed during

Table 1. Mean time spent feeding (%) and mean feeding bout length (min) for Trumpeter Swans on the Copper River Delta, Alaska 1988-89.

	Percent time spent feeding			Mean feeding bout length		
	Females	Males	Cygnets	Females	Males	Cygnets
Prenesting	42.1* ^c	31.2	NA	40.4**	30.8	NA
(3) ^a	7.4 ^b	6.8		4.5	4.7	
Incubation	7.8**	36.5	NA	14.6**	30.0	NA
(5)	1.5	4.0		2.2	4.2	
Post-hatch	31.8	32.2	52.7***	32.4	29.1	54.7***
(5)	7.2	2.7	3.0	1.7	3.7	1.6

^a No of pairs/broods^b SE of the Mean^c Two-tailed paired *t*-test comparing (1) male-female feeding budgets **P* = 0.059, ***P* ≤ 0.008 and (2) adult-cygnets feeding budgets ****P* ≤ 0.014**Table 2. Activity time-budgets (%) for adult behaviours during cygnet feeding bouts on the Copper River Delta, Alaska 1988-89.**

Activity	Females	Males	P-value ^b
Feeding	6.76	62.3	0.059
	4.8 ^a	7.2	
Stationary	25.1	25.0	0.971
	5.3	4.6	
Preening	4.7	5.8	0.582
	1.3	2.3	
Alert	2.3	6.8	0.074
	1.5	3.1	

^a SE of the Mean ^b Two-tailed paired *t*-test, *df* = 4

brooding, thereby affecting the overall comparison of post-hatch male and female feeding budgets. To more accurately compare adult activities when young were most vulnerable to predation and disturbance (ie when feeding loosely scattered on the wetland), adult activity budgets during cygnet feeding bouts were compared. When cygnets were feeding, males were more alert and fed less than females (**Table 2**). Adults with young fed less than failed breeders; feeding bouts were also shorter, although the difference was not

significant (**Table 3**). Adults with young spent more time feeding during early brood rearing than late brood rearing (female: *x*=36.6% early & *x*=24.5% late, *t*=6.93, *P*=0.020; male: *x*=33.4% early & *x*=26.5% late, *t*=7.79, *P*=0.016, *df*=2).

Cygnets

Feeding was the principal pre fledging activity of cygnets. Cygnets fed more and had longer feeding bouts than adults (**Table 1**). Although cygnets fed less during late brood rearing than

Table 3. Mean time spent feeding (%) and mean feeding bout length (min) for Trumpeter Swan successful (with young) and failed breeding pairs on the Copper River Delta, Alaska 1988-89.

	Mean feeding %		Mean feeding bouts	
	Successful	Failed	Successful	Failed
Female	25.6	43.7 ^{a,b}	30.0	39.2
	4.3 ^a	5.1	1.7	3.4
Male	29.9	44.4 ^{a,b}	37.2	40.0 [*]
	2.7	1.2	7.6	4.8

^aSE of the Mean^bTwo-tailed unpaired t-test, df = 4 comparing pairs with young to failed breeders *P = 0.100, **P = ≤ 0.030**Table 4. Feeding bouts (min), non-feeding bouts and complete feeding cycles of Trumpeter Swan cygnets on the Copper River Delta, Alaska 1988-89**

Brood Number	Feeding bout	Non-feeding bout	Feeding Cycle ^b
1	58.4	50.4	110.3
	4.5 ^a	3.1	6.1
2	56.4	52.3	108.4
	4.9	2.8	5.3
3	49.3	57.9	108.8
	2.3	6.0	5.5
4	53.0	44.3	104.9
	2.3	4.3	5.7
5	56.6	53.9	113.0
	13.2	7.1	10.0
Mean	54.7	51.9	109.1
	1.6	2.2	1.3

^aSE of the Mean^bFeeding cycle = Feeding bout + Non-feeding bout

early brood rearing ($x=58.0\%$ early and $x=43.6\%$ late, $t=11.00$, $P=0.008$, $df=2$), the length of cygnet feeding bouts did not change between these periods ($t=0.72$, $P=0.518$, $df=2$). Cygnet preening/bathing activity increased over this period ($x=8.9\%$ early & $x=19.9\%$ late, $t=5.38$, $P=0.065$, $df=2$).

Cygnet feeding and non-feeding periods alternated regularly and were remarkably

uniform in length, both over time and among broods (Table 4). Typically, adults initiated a feeding bout from shore or the nest mound. Cygnets then grazed primarily on horsetails (Grant *et al.* 1994) until the neck was clearly distended from impaction of food in the esophagus. When feeding ceased, adults led their brood to shore where cygnets subsequently were brooded by the female.

Discussion

Pre-nesting

Bortner (1985) proposed that Tundra Swans *Cygnus columbianus*, like many northern and temperate breeding geese (Wypkema & Ankney 1979, McLandress & Raveling 1981, Gauthier *et al.* 1984), acquire nutrient and energy reserves for reproduction prior to arrival on the breeding grounds. Local foods are important for nesting efforts of some goose species (Aldrich & Raveling 1983, Ankney 1984, Budeau *et al.* 1991, Gauthier 1993, Bromley & Jarvis 1993). Although the importance of foods from late winter and spring staging grounds has not been examined for Trumpeters, birds on the Copper River Delta exploited local foods extensively during pre-nesting and incubation (Grant *et al.* 1994). These local foods may be required, in addition to endogenous reserves, to meet the energy demands of courtship, territorial defence, nestbuilding, egg laying and incubation.

During pre-nesting, females spent more time feeding and had longer feeding bouts than males. Similar differences have been observed for captive Trumpeter Swans (De Vos 1964), for wild Tundra Swans (Hawkins 1986) and for northern and temperate breeding geese (Fox & Madsen 1981, McLandress & Raveling 1981, Gauthier & Tardif 1991). In this study, males rather than females were primarily responsible for building large nests secure from flooding and egg predators (Henson & Cooper 1992). This strategy may allow females additional time to feed and gain the nutrient and energy resources to supplement the demands of laying and incubation.

Incubation

Female *Anserini* maintain high incubation constancy to minimise the length of the incubation period and to protect the clutch from predation and adverse weather (Owen & Black 1990, Afton & Paulus 1992). Feeding is normally restricted to short bouts during recesses away from the nest. During incubation, female geese rely heavily on endogenous reserves to support metabolism, and can lose

more than 30% of their body mass (Afton & Paulus 1992: **Tables 3-13**). Depletion of female endogenous reserves in geese also is inferred from decreased nest attentiveness during late incubation (Aldrich 1983, Murphy & Boag 1989).

Swans may differ from this general pattern. During incubation, Tundra Swans and Whooper Swans *Cygnus cygnus* feed more (*ie* 234 and 194 minute/day, respectively) than do other *Anserini* (Afton & Paulus 1992: **Tables 3-14**). Female Trumpeter Swans on the Copper River Delta spent more time feeding during incubation ($x=90$ 17 minute/day) than other waterfowl, but less than reported for Tundra and Whooper Swans. Swan feeding studies generally report a strong reliance on submerged aquatic vegetation (Banko 1960, Frith *et al.* 1967, Owen & Kear 1972). In contrast, Trumpeter Swans on the Copper River Delta relied extensively on emergent vegetation which is easier and less time-consuming to harvest (*ie* graze) than submergents (Henson & Cooper 1993, Grant *et al.* 1994). Although constancy declined during late incubation for females on the Copper River Delta (Henson & Cooper 1993), the amount of time spent feeding was unrelated to the stage of incubation. Swans in our study fed primarily on submerged aquatics during pre-nesting and early incubation, but shifted to easily accessible, high protein emergent vegetation from middle incubation to hatch (Grant *et al.* 1994). Because of their large body size and reported fasting endurance (Cooper 1979), Trumpeter Swans probably have the physiological capability of relying primarily on endogenous reserves during incubation (Afton & Paulus 1992). The proximity of abundant food during incubation may have allowed females on the Copper River Delta to offset the loss of endogenous reserves by relying, to an extent, on exogenous foods. A female in our study maintained incubation (in excess of 80% of diurnal and nocturnal activity) of an infertile clutch for two weeks beyond the normal 33 day incubation period, further indicating a reliance on exogenous foods.

Male *Anserini* also catabolize endogenous reserves during nesting, but supplement these reserves with local foods (Ryder 1975, Ankney 1977, Budeau *et al.* 1991). Whereas male Trumpeter Swans were attentive to females

during prelaying, attention shifted to the nest site (ie building, maintenance, guarding and sitting) during laying and incubation (Henson & Cooper 1992). During pre-nesting, male Trumpeter Swans appear to forgo some feeding to defend the territory and build nests secure from flooding and predation. When females begin incubation, males may have more time to feed and replenish the nutrient reserves depleted during pre-nesting. Protection of the female and brood may also depend on the condition of the male at hatching (Ryder 1975, Ankeny 1977).

Activity budgets of adults during post-hatch

Adult Trumpeter Swans with young fed less than failed breeders and appeared to forego some feeding opportunities to care for their young. Similar behaviour is reported in Lesser Snow Geese *Anser caerulescens caerulescens* (Lessells 1987), Bewick's Swans *Cygnus bewickii* (Scott 1980) and Greater Snow Geese *Anser caerulescens atlantica* (Giroux *et al.* 1986). Time spent in brood care reduces adult feeding opportunities and may extend the period required to regain optimal physical condition (Scott 1980). Brood care at the expense of body condition may decrease adult survival and reduce future reproductive output, thereby reducing fitness (Afton & Paulus 1992).

Male Trumpeter Swans may forgo more feeding opportunities than females to protect their young. Similar behaviour has been reported for geese (Harwood 1977, Lazarus & Inglis 1978, Lessells 1987, Sedinger & Raveling 1990). Alert behaviour by the male may reduce predation threats and allow cygnets more time to gain weight undisturbed, thereby protecting immediate male reproductive interests. Females enter the post-hatch period in poorer condition than males and must regain a higher proportion of the energy reserves lost during laying and incubation. Because swans and geese are long-term monogamous, male fitness is enhanced when females gain weight undisturbed and subsequently enter the non-breeding period in relatively good body condition (Sedinger & Raveling 1990).

Cygnet activity budgets

Feeding was the principal cygnet pre fledging activity. Cygnets fed on average 265 minutes/day more, and had feeding bouts that were nearly 24 minutes longer, than either parent (**Table 1**). Des Vos (1964) reported similar data for captive birds. Young geese also feed more than adults before fledging (Giroux *et al.* 1986, Eberhardt *et al.* 1989). Because cygnets must grow rapidly to reach flight stage (within two to three months), they appear to have higher metabolic demands than either adult. Preening and bathing activity increased with cygnet flight feather development during late brood rearing.

Optimization of nutrient uptake

Food availability and the physiological capabilities for processing food likely regulate nutrient intake in waterfowl (Sedinger 1992). Processing rate rather than availability appear to limit the rate of food intake in birds feeding on green vegetation (Kenward & Sibley 1977, Sedinger & Raveling 1988), with food being processed quickly but at the expense of efficient digestion (Sibly 1981). Cygnets in our study grazed over-water on abundant, easily accessible horsetails (Grant *et al.* 1994). Cygnet feeding and non-feeding periods alternated regularly and were relatively uniform in length over time and among broods implying that a period of processing was required, following a feeding bout, to pass sufficient plant material through the gut before cygnets could resume feeding. This pattern suggests nutrient uptake for young swans is optimized by a balance between food intake and digestion. Sedinger & Raveling (1988) report similar data for Cackling Canada Goose *Branta canadensis minima* goslings feeding on green vegetation.

Any function that limits food intake has important implications when evaluating the quality of available brood rearing habitat, both temporally on the same breeding area, or spatially across geographical regions within the Trumpeter Swan range. When food intake is limited by the rate at which it can be processed, adequate nutrient concentrations in available

swan foods become particularly important. The Copper River Delta is productive relative to Trumpeter Swan habitat available outside Alaska (Henson & Cooper 1993). Cygnets already spend >50% of their time feeding on horsetails that are abundant, easily accessible, and relatively high in protein (Grant *et al.* 1994). In less productive habitats, or in years when primary production is decreased, young Trumpeter Swans may be unable to adequately compensate for low levels of nutrients in available foods by simply increasing the quantity of food consumed.

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References

- Afton, A. D., & Paulus, S. L. 1992. Incubation and brood care. In: Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. & Krapu, G. L. (Eds.). *Ecology and management of breeding waterfowl*. Univ. Minnesota Press, Minneapolis. Pp 62-108.
- Aldrich, T. W. 1983. Behavior and energetics of nesting Canada Geese. M.S. thesis, Davis, Univ. California.
- Aldrich, T. W. & Raveling, D. G. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. *Auk* 100:670-679.
- Alisauskas, R. T. & Ankney, C. D. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. In: Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. & Krapu, G. L. (Eds.). *Ecology and management of breeding waterfowl*. Univ. Minnesota Press, Minneapolis. Pp 30-61.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227-267.
- Ankney, C. D. 1977. The use of nutrient reserves by breeding male Lesser Snow Geese. *Can. J. Zool.* 55:1984-1987.
- Ankney, C. D. 1984. Nutrient reserve dynamics of breeding and moulting Brant. *Auk* 101:361-370.
- Banko, W. E. 1960. The Trumpeter Swan: its history, habits, and populations in the United States. *North Am. Fauna* 63. 214pp.
- Bortner, J. B. 1985. Bioenergetics of wintering Tundra Swans in the Mattamuskeet region of North Carolina. M.S. thesis, Univ. Maryland, College Park. 67pp.
- Bromley, R. G. & Jarvis, R. L. 1993. The energetics of migration and reproduction of Dusky Canada Geese. *Condor* 95:193-210.
- Budeau, D. A., Ratti, J. T. & Ely, C. R. 1991. Energy dynamics, foraging ecology, and behaviour of prenesting Greater White-fronted Geese. *J. Wildl. Manage.* 55:556-563.
- Cooper, J. A. 1979. Trumpeter Swan nesting behaviour. *Wildfowl* 30:55-71.
- De Vos, A. 1964. Observations on the behaviour of captive Trumpeter Swans during the breeding season. *Ardea* 52:166-189.
- Eberhardt, L. E., Books, G. C., Anthony, R. G. & Rickard, W. H. 1989. Activity budgets of Canada Geese during brood rearing. *Auk* 106:218-224.
- Fox, A. D. & Madsen, J. 1981. The pre-nesting behaviour of the Greenland White-fronted Goose. *Wildfowl* 32:48-54.
- Frith, H. J., Braithwaite, L. W. & McKean, J. L. 1969. Waterfowl in an inland swamp in New South Wales. II Food. *CSIRO Wildl. Res.* 14:17-64.
- Gale, R. S., Garton, E. O. & Ball, I. J. 1987. *The history, ecology, and management of the Rocky Mountain population of Trumpeter Swans*. U.S. Fish and Wildl. Serv., Missoula, Mont. 314pp.

- Gauthier, G. 1993. Feeding ecology of nesting Greater Snow Geese. *J. Wildl. Manage.* 57:216-223.
- Gauthier, G., & Tardif, J. 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. *Condor* 93:701-711.
- Gauthier, G., Bédard, J., Huot, J. & Bédard, Y. 1984. Spring accumulation of fat by Greater Snow Geese in two staging habitats. *Condor* 86:192-199.
- Giroux, J., Bédard, J. & Bédard, Y. 1986. Time budgets of Greater Snow Geese during the brood rearing period. *Wildfowl* 37:46-50
- Grant, T.A. 1991. Foraging ecology of Trumpeter Swans breeding on the Copper River Delta, Alaska. M.S. thesis, Univ. Minnesota, St. Paul. 82pp.
- Grant, T. A., Henson, P. & Cooper, J. A. 1994. Feeding ecology of Trumpeter Swans breeding in south central Alaska. *J. Wildl. Manage.* 58:774-780.
- Hansen, H.A., Shepard, P.E., King, J. G. & Troyer, W. A. 1971. The Trumpeter Swan in Alaska. *Wildl. Monogr.* 26. 83pp.
- Harwood, J. 1977. Summer feeding ecology of Lesser Snow Geese. *J. Wildl. Manage.* 41:48-55.
- Hawkins, L. 1986. Tundra Swan breeding behaviour. M.S. thesis, Univ. Minnesota, St. Paul. 145pp.
- Henson, P. & Cooper, J. A. 1992. Division of labour in breeding Trumpeter Swans *Cygnus buccinator*. *Wildfowl* 43:40-48.
- Henson, P. & Cooper, J.A. 1993. Trumpeter Swan incubation in areas of differing food quality. *J. Wildl. Manage.* 57:709-716.
- Holton, G. R. 1982. Habitat use by Trumpeter Swans in the Grande Prairie region of Alberta. M.S. thesis, Univ. Calgary, Alberta. 164pp.
- Kenward, R. E. & Sibly, R. M. 1977. A Woodpigeon *Columba palumbus* feeding preference explained by a digestive bottleneck. *J. Appl. Ecol.* 14:815-826.
- Krapu, G. L. & Reinecke, K. J. 1992. Foraging ecology and nutrition. In: Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. & Krapu, G. L. (Eds.). *Ecology and management of breeding waterfowl*. Univ. Minnesota Press, Minneapolis. Pp 1-29.
- Lazarus, J. & Inglis, I. R. 1978. The breeding behaviour of the Pink-footed Goose: parental care and vigilant behaviour during the fledging period. *Behaviour* 65:62-88.
- Lessells, C. M. 1987. Parental investment, brood size, and time budgets: behaviour of Lesser Snow Goose families. *Ardea* 75:189-203.
- McLandress, M. R. & Raveling, D. G. 1981. Changes in diet and body composition of Canada Geese before spring migration. *Auk* 98:65-79.
- Murphy, A. J. & Boag, D. A. 1989. Body reserve and food use by incubating Canada Geese. *Auk* 106:439-446.
- Owen, M. 1980. *Wild geese of the world*. London, Batsford, Ltd.
- Owen, M. & Black, J. M. 1990. *Waterfowl Ecology*. Chapman and Hall, New York.
- Owen, M. & Kear, J. 1972. Food and feeding habits. In: Scott, P. (Ed.). *The Swans* Houghton Mifflin, Boston. Pp. 58-77
- Page, R. D. 1976. The ecology of the Trumpeter Swan on Red Rock Lakes National Wildlife Refuge, Montana. Ph.D. thesis, Univ. Montana, Missoula. 165pp.
- Ryder, J. P. 1975. The significance of territory size in colonial nesting geese: an hypothesis. *Wildfowl* 26:114-116.
- Scott, D. K. 1980. Functional aspects of prolonged parental care in Bewick's Swans. *Anim. Behav.* 28:938-952.
- Sedinger, J. S. 1992. Ecology of pre fledging. Pp109-127
- Sedinger, J. S. & Raveling, D. G. 1988. Foraging behaviour of Cackling Canada goose goslings: implication for the role of food availability and processing time. *Oecologia* 75:119-124.
- Sedinger, J. S. & Raveling, D. G. 1990. Parental behaviour of Cackling Canada Geese during brood rearing: division of labour within pairs. *Condor* 92:174-181.
- Sibly, R. M. 1981. Strategies of digestion and defecation. In: Townsend, C. R. & Calow, P. (Eds.). *Physiological ecology: an evolutionary*

- approach*. Sinauer Associates, Sunderland, Massachusetts. Pp 109- 139
- Weaver, D. K. 1990. Update on the petition to list the RMP Trumpeter Swans as threatened. *Trumpeter Swan Soc. Newsl.* 19(1):5-6.
- Wykema, R. C. P. & Ankney, C. D. 1979. Nutrient reserve dynamics of Lesser Snow Geese staging at James Bay, Ontario. *Can J. Zool.* 57:213-219.