FEEDING AND DIGESTIVE ORGAN SIZE IN BREEDING LESSER SNOW GEESE

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ABSTRACT.—The Lesser Snow Geese that nest at the McConnell River, Northwest Territories, feed heavily before arriving on the breeding grounds. During laying and early incubation, feeding declines to low levels but increases slightly during late incubation. After their eggs hatch the geese greatly increase their food intake. These changes in feeding activity are correlated with changes in the average sizes of four digestive organs (pancreas, liver, gizzard, and intestine). The large digestive organs characteristic of arriving and post-hatch geese are due to hyperphagia. Previously reported situations that produced decreased size of avian digestive organs did not account for that condition in incubating geese. The decrease in size of digestive organs during incubation is claimed to be innate; its evolution is discussed.—*Department of Zoology, University of Western Ontario, London, Ontario*. Accepted 21 October 1975.

THE concensus among biologists studying tundra-nesting geese has been that breeding adults feed very little between arrival on the breeding ground and hatching of young (Cooch 1958, Barry 1962, Ryder 1970, Harvey 1971). Harvey (1971) showed why it is unadaptive for Lesser Snow Geese (*Chen caerulescens caerulescens*; here includes both blue and white color phases) to leave their territories to feed because predators destroyed the nest.

Quantitative data on the extent of feeding by tundra-nesting geese have been lacking. The present paper shows that breeding Lesser Snow Geese feed little during egg-laying and incubation. This supports Ryder's (1970) theory that in Arctic nesting geese clutch size has evolved in relation to the size of energy reserves that females carry to the breeding grounds. It also provides a new situation for testing the theory that diet and size of digestive organs are related (e.g. Moss 1972, 1974; Anderson 1972).

METHODS

The study was done at the Lesser Snow Goose breeding colony at the mouth of the McConnell River (60° 50′ N, 94° 25′ W), near Eskimo Point, Northwest Territories, Canada. Geese were collected from the time of their arrival to the colony (late May) until the start of the wing molt (late July) in 1971 and 1972.

Birds were placed in the following categories for analysis:

Arriving.— Geese shot from flocks flying northward into the colony. Males had enlarged testes and females had several large ovarian follicles.

Laying.—Birds collected near their nests; both members of a pair were obtained when possible. Females were determined to be laying, or just finished laying, by ovarian examination.

Early incubation.—Incubating geese were collected from nests that had a known history. Females had incubated at least 6 but not more than 11 days, and the males mated to them.

Late incubation.—Females that had incubated at least 17 of the 23-day incubation period and males mated to them.

Failed-nesters.—Geese collected, near the end of incubation, away from the main part of the colony. Only birds that had been seen feeding at least 30 min were taken. All females had defeathered incubation patches and were mated. These pairs probably had lost their nests because Harvey (1971) showed that, at the McConnell River, pairs that leave their territories are very apt to lose their nest contents to jaegers (*Stercoararius* spp.) and gulls (mainly *Larus argentatus*).

Dead.—Geese (all females) found dead or dying during the hatch; all had defeathered incubation patches. The dead birds had starved and the others were starving (Harvey 1971, Ankney 1974).

Post-hatch.—Geese collected during the middle week of the 3-week period from hatch until the onset of the wing molt.

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The intestinal tract was removed from immediately posterior to the gizzard to immediately anterior to the cloaca, the mesenteries were cut, and the intestine was straightened and measured (1972 only). In both years the intestine was indexed as full (> ⅔ full), one-half full (> ⅓ full, < ⅔ full), or empty (< ⅓ full).

Only data on intestinal contents were used as direct evidence that a bird had been feeding. During incubation, data on the contents of the esophagus and proventriculus were apt to overestimate the extent of normal feeding because these contents may have resulted from disturbances caused by collecting activities. Frequently, especially during late incubation, geese were recorded feeding after they had been scared from their nests. When these birds were collected all (10) had full or half-full esophagi and/or proventriculi, but only three had contents in the intestine. The contents of the intestine represented food eaten a considerable time before the bird was shot and thus more likely eaten before its behavior was influenced by human disturbance. Furthermore the upper digestive tract was not used because this would have underestimated the amount of feeding done by arriving and laying geese. Arriving birds were flying when collected and, even if they had fed immediately before taking-off, they would not have had to fly far before the esophagus and proventriculus became empty. To feed, laying geese had to travel to low wet spots where the ground was thawed enough for them to dig for roots; some geese were seen flying or walking to such places. Thus, that birds collected on their territories, where there was little available vegetation, would have contents in the upper digestive tract was unlikely. Rather, if they had been feeding at all, they were more likely to have contents in the intestine. All intestinal contents were removed and the numbers and kinds of parasites were recorded. Gizzards were weighed including the grinding plates but empty of contents. The gall bladder was excised before the liver was weighed. The pancreas was removed and weighed in 1972 only. Tissues were frozen in a sealed plastic bag before drying. The entire pancreas was sliced and dried; sliced subsamples of approximately 25 g from the gizzard and liver were dried. The tissues were freeze-dried in 1971 and oven-dried in 1972. These processes did not remove significantly different amounts of water from comparable samples (Ankney 1974) and the data from each were pooled. The total dry weight of each organ was calculated as:

$$\text{Dry weight} = \frac{\text{Sample Dry Weight} \times \text{Total Wet Weight}}{\text{Sample Wet Weight}} .$$

Statistical tests follow Sokal and Rohlf (1969).

RESULTS

Intestinal contents and parasites.—The gut contents of birds, especially those of geese, are ephemeral. Harwood (1975) found that in Lesser Snow Geese eating green vegetation, the time from ingestion to elimination was about 1.5 hours. Stress may hasten this process and thus data on intestinal contents from those post-hatch geese collected during mass drives (Cooch 1956) were not included because these birds were under stress for at least 1 hour before being collected.

My main interest was in determining the amount of feeding done during egg-laying and incubation. Data from arriving birds are included because they provide a baseline for comparison of subsequent samples. Geese are known to feed extensively after their eggs hatch (Barry 1967), and data from such birds are useful for checking the validity of intestinal content as an index of feeding activity.

The proportion of geese with intestinal contents declined from a high at arrival to almost zero during early incubation (Table 1). During early incubation the territories on my transect contained little green vegetation and, because the geese nested in the drier spots that first became exposed in the spring, no sedge roots (*Carex* spp.) were available. The territories of the geese at the McConnell River are small (100 to 300 m^2; Harvey 1971, C. Von Barloewen pers. comm.). During late incubation some vegetation grew in the goose territories, and the increased proportion of birds with intestinal contents (Table 1) showed the geese ate it.

Predictably all failed-nesters had full or half-full intestines as feeding was a major criterion on whether or not to collect them. Likewise all post-hatch geese had some intestinal content. This indicates that intestinal content was a valid index of the amount of feeding by Lesser Snow Geese.

TABLE 1

SEASONAL VARIATION IN FEEDING BY LESSER SNOW GEESE BREEDING AT THE MCCONNELL RIVER, N.W.T., IN 1971 AND 1972

	Males		Females	
Category[1]	N	% Feeding[2]	N	% Feeding[2]
A	45	76%	78	68%
L	18	44%	44	40%
EI	18	11%	33	9%
LI	22	45%	42	29%
PH	10	100%	16	100%
FN	5	100%	8	100%
D[3]	—	—	26	8%

Chi-square Values[4]

		A	L	EI	LI	LI	
Males	$\chi^2 =$	5.60*	4.99*	5.56*	8.73***	4.90*	
		L	EI	LI	PH	FN	
		A	L	EI	LI	LI	LI
Females	$\chi^2 =$	8.45***	9.63***	4.38*	23.67***	14.29***	4.28*
		L	EI	LI	PH	FN	D

[1] A = arriving; L = laying; EI = early incubation; LI = late incubation; PH = post hatch; FN = failed-nesters; D = dead; categories are defined in the text.

[2] The percentage of birds with full or half-full intestines.

[3] Does not include birds found alive that later died.

[4] From 2 × 2 test for difference in the proportion of birds feeding, e.g. the first value (5.60) shows that there was a significant difference in the proportion of arriving and laying males that were feeding.

* $0.05 > p > 0.01$.

*** $p < 0.005$.

About one-half of the geese arriving on the breeding grounds carried tapeworms (family Anoplocephalidae; Table 2). This proportion declined significantly for both sexes during laying and incubation, but increased significantly after hatch (Table 2). The reduction of tapeworm infestation to very low levels during incubation can be explained in two ways: (1) the tapeworms starved to death, or (2) the life cycle of the tapeworms was so short that these low levels resulted from normal mortality without replacement. Either explanation suggests reduced feeding as the ultimate cause.

TABLE 2

SEASONAL CHANGES IN ABUNDANCE OF INTESTINAL TAPEWORMS IN LESSER SNOW GEESE BREEDING AT THE MCCONNELL RIVER, N.W.T. IN 1971 AND 1972

	Males		Females	
Category[1]	N	% Parasitized[2]	N	% Parasitized[2]
A	45	40%	78	59%
L	18	11%	44	50%
EI	18	0	33	6%
LI	22	0	41	0
PH	22	36%	35	23%
FN	5	40%	8	38%
D	—	—	35	3%

Chi-square Values[3]

		A	L	EI	LI	LI	
Males	$\chi^2 =$	4.95*	2.12NS	0.0NS	9.78***	9.50***	
		L	EI	LI	PH	FN	
		A	L	EI	LI	LI	LI
Females	$\chi^2 =$	1.15NS	16.19***	2.62NS	10.71***	16.76***	1.22NS
		L	EI	LI	PH	FN	D

[1] See Table 1 for definition of symbols.

[2] The percentage of birds with one or more intestinal tapeworms.

[3] See Table 1 for explanation.

* $0.05 > p > 0.01$.

*** $p < 0.005$.

TABLE 3

Seasonal Changes in Dry Pancreas and Liver Weights (g)[1] of Lesser Snow Geese Breeding at the McConnell River, N.W.T., in 1971 and 1972

	Males		Females	
Category[2]	Pancreas	Liver	Pancreas	Liver
A	2.0 ± 0.1 (27)	11.0 ± 0.1 (45)	2.3 ± 0.1 (54)	14.9 ± 0.3 (77)
L	1.4 ± 0.1 (15)	8.0 ± 0.4 (18)	1.5 ± 0.1 (33)	11.0 ± 0.3 (44)
EI	1.4 ± 0.1 (12)	7.4 ± 0.3 (18)	1.2 ± 0.1 (18)	7.4 ± 0.2 (33)
LI	1.6 ± 0.1 (17)	9.0 ± 0.7 (22)	1.1 ± 0.1 (30)	6.3 ± 0.2 (41)
PH	2.6 ± 0.1 (14)	12.6 ± 0.5 (21)	2.3 ± 0.2 (21)	12.6 ± 0.3 (35)
FN	2.2 ± 0.2 (5)	15.2 ± 0.6 (5)	1.3 ± 0.1 (8)	8.4 ± 0.5 (8)
D	—	—	0.7 ± 0.1 (31)	6.6 ± 0.2 (35)

F-values[3]

			A	L	EI	LI	LI	
Males	Pancreas	F =	15.58***	1.01NS	1.48NS	27.90***	6.71*	
	Liver	F =	39.38***	0.34NS	10.84***	30.63***	104.50***	
			L	EI	LI	PH	FN	
			A	L	EI	LI	LI	LI
Females	Pancreas	F =	45.88***	3.83NS	1.26NS	41.89**	1.0NS	8.46***
	Liver	F =	82.47***	85.58***	21.48***	21.70***	15.64***	1.28NS
			L	EI	LI	PH	FN	D

[1] Data expressed as mean ± SE; sample sizes in parentheses.

[2] See Table 1 for definition of symbols.

[3] F-values are from 1-way analysis of variance to establish the significance of the difference between two means; e.g. the first F-value (15.58) shows that there was a significant difference between the mean dry pancreas weights of arriving and laying males.

* $0.05 > p > 0.01$.

** $0.01 > p > 0.001$.

*** $p < 0.001$.

Changes in digestive organs.—Lesser Snow Geese arrived on the breeding grounds with large digestive organs; the dry weights of these organs decreased significantly during egg-laying and incubation and increased significantly after hatch (Tables 3 and 4).

Reduction in dry pancreas weight (Table 3) probably reflected decreased size and number of gland cells with reduced need for digestive enzymes. The significantly heavier pancreases of post-hatch geese compared to late incubation geese and the significantly heavier pancreases of failed-nester males compared to late incubation males are corroborative. The pancreases of failed-nester females showed no significant increase over those of late incubation females but perhaps those particular females had not been feeding for a sufficient time to cause an increase (the mean wet weight of pancreases from failed-nester females was significantly ($p < 0.01$) heavier than that of late incubation females).

Because of the liver's central role in intermediary metabolism it is particularly responsive to dietary changes (Hanson 1962, Pendergast and Boag 1973). A principal liver function is to collect nutrients as they are absorbed from the gut and release them (after the appropriate biochemical conversions) as needed. Thus reduced feeding would lower the amount of nutrients stored in the liver because a fasting goose would rapidly use these nutrients, mainly glycogen and fat (Benedict and Lee 1937). A more detailed histochemical analysis is necessary to determine exactly the factors responsible for changes in mean liver weight. Regardless, reductions of the observed magnitudes, e.g. 60% reduction in female liver weight from arrival until the end of incubation, certainly reflected changes in metabolism (Table 3). The highly significant increases in liver weight of failed-nesters and post-hatch birds (over late incubation birds) suggested that the above reductions in liver weight were correlated with reduced feeding during laying and incubation.

TABLE 4

SEASONAL CHANGES IN DRY GIZZARD WEIGHTS (g)[1] AND INTESTINE LENGTHS (cm)[1] OF LESSER SNOW GEESE BREEDING AT THE MCCONNELL RIVER, N.W.T., IN 1971 AND 1972

	Males		Females	
Category[2]	Gizzard	Intestine	Gizzard	Intestine
A	34.1 ± 0.7 (45)	203 ± 3 (27)	34.7 ± 0.6 (78)	213 ± 2 (53)
L	29.2 ± 1.0 (18)	181 ± 4 (15)	28.8 ± 0.7 (44)	200 ± 2 (33)
EI	27.0 ± 1.0 (18)	171 ± 4 (12)	23.7 ± 0.6 (33)	163 ± 4 (18)
LI	25.7 ± 0.8 (22)	189 ± 4 (17)	21.0 ± 0.4 (41)	165 ± 2 (31)
PH	29.6 ± 0.8 (22)	203 ± 5 (14)	29.5 ± 0.5 (35)	207 ± 3 (21)
FN	32.8 ± 1.5 (5)	209 ± 9 (5)	23.3 ± 0.7 (8)	187 ± 5 (8)
Dead	—	—	18.9 ± 0.3 (35)	186 ± 2 (31)

F-values[3]

			A	L	EI	LI	LI	
Males	Gizzard	F =	14.68***	2.32NS	0.78NS	13.09***	18.68***	
	Intestine	F =	21.82***	3.27NS	7.41*	3.96NS	3.99NS	
			L	EI	LI	PH	FN	
			A	L	EI	LI	LI	LI
Females	Gizzard	F =	38.48***	27.42***	17.24***	154.97***	7.42**	18.34***
	Intestine	F =	16.14***	67.80***	0.22NS	113.98***	15.10***	43.74***
			L	EI	LI	PH	FN	D

[1] Data presented as mean ± SE; sample sizes in parentheses.
[2] See Table 1 for definition of symbols.
[3] See Table 3 for explanation.
* 0.05 > p > 0.01.
** 0.01 > p > 0.001.
*** p < 0.001.

Besides its primary function in digestion, the gizzard could also serve as a protein source to a fasting bird. Thus the significant reductions in gizzard weight could have resulted from either atrophy through disuse or from active catabolism of muscle protein (Table 4). In either case the ultimate cause would have been reduced feeding. The significant increase in gizzard weight of failed-nesters and post-hatch geese showed that feeding and gizzard size were correlated.

It is generally assumed that diet and gut length are related both proximately and ultimately (Leopold 1953, Rieck et al. 1971, Moss 1972, 1974, Pendergast and Boag 1973). Specifically the amount of food eaten is a factor known to affect gut size (Fell 1969). Moss (1972) thought that decreased intestine length of captive Red Grouse (*Lagopus l. scoticus*) was due to reduced food consumption and increased food quality. Therefore it seems likely that the rapid, significant reductions in intestine length from arrivial through early incubation in females and from arrival through laying in males (Table 4), were related to decreased feeding by the geese. This was supported by: (1) significantly greater intestine lengths of failed-nester and post-hatch females over those of late incubation females; and (2) significantly longer intestines of late incubation males compared to early incubation males (Table 4). The trend of increased intestinal length in failed-nester and post-hatch males over late incubation males was corroborative. An explanation of the longer intestines of dead and dying females compared to late incubation females was not apparent as no other evidence suggested that these geese had been feeding. Perhaps this change was preparatory to feeding and occurred in all geese at, or immediately before hatch (see beyond).

DISCUSSION

Quantitative data from this study indicate that previous conclusions concerning reduced feeding by tundra-nesting geese were essentially correct. Most breeding

Lesser Snow Geese, especially females, at the McConnell River rely on their nutrient reserves during laying and incubation. Thus as theorized by Ryder (1970) and Harvey (1971), the number of eggs a female goose lays and her ability to give maximum attentiveness to the eggs during incubation are determined by the size of the reserves she brings to the breeding grounds.

Examination of intestinal contents gave the most direct estimate of the amount of feeding a particular goose had done, but data on intestinal contents were only a measure of feeding activity that occurred a few hours preceding collection. Also the quantity of food in the intestine gave no information on the quality of food consumed. Changes in the incidence of intestinal parasites and in the size of digestive organs were more likely to reflect long-term changes in feeding activity. Several studies (Avery 1969, Denny 1969, Podesta and Holmes 1970) showed that under laboratory conditions waterfowl tapeworms live at least 30 days. The longevity of goose tapeworms in free-ranging birds is unknown. T. G. Neraasen (in litt.) thought that evidence presented here "indicate that the geese feed little during the nesting period and that their tapeworms are lost (through starvation?) and new infections are not acquired during that time."

Reportedly two situations cause increased size of the main digestive organs of birds: (1) reduced quantity or quality of food where the bird attempts to maintain activities energetically similar to those before the reduction (Breitenbach et al. 1963, Moss 1974); (2) hyperphagia concomitant with maintaining or increasing alimentary efficiency (Kirkpatrick 1944, Anderson 1972). Because Lesser Snow Geese feed extensively before and during spring migration (Harvey 1971), the large digestive organs in arriving geese are correlated with the latter situation. Likewise the increased size of digestive organs from post-hatch geese is attributable to increased feeding.

The only situation that reportedly decreases the size of digestive organs is increased quantity or quality of food where the bird maintains activities energetically similar to those previous to the increase. Moss (1972) found that captive Red Grouse exhibited reduced intestine and caecum lengths (data on other digestive organs were not reported) which he attributed to a higher quality diet and reduced food intake. The grouse performed most normal activities of wild birds, e.g. molt and breeding. I have no evidence that nesting Lesser Snow Geese were able to eat higher quality food than that eaten before arrival. Also, data from intestinal contents show a great decrease in food consumption during nesting. Thus I propose that another condition led to the decreased size of digestive organs in nesting geese: a large decrease in food consumption, which was predictable and for which the geese were energenically prepared by large nutrient reserves. This hypothesis suggests no direct causal relationship existed between reduced feeding and digestive organ size. Selection favors geese that do not feed during incubation (Harvey 1971) and there must also be selection for geese whose digestive organs atrophy quickly after egg-laying because "small organs make smaller demands on a bird's metabolism" (Moss 1974). Moss (1972) suggested that annual variation in gut length and caecal length of captive Red Grouse might be innate variation in anticipation of the usual seasonal change in the plane of nutrition that wild birds face. Between arrival and the end of egg-laying Lesser Snow Geese feeding decreased significantly. This period (5–6 days) was considerably shorter than the 2-week period that Lewin (1963) suggested was necessary for diet changes to be reflected in changed caecal length of California Quail (*Lophortyx californicus*). Thus I suggest that the decreases in digestive organ size of the nesting geese were not due to disuse but rather were anticipatory to a behavioral change (not feeding). The significantly longer intestines of dead females (as compared to late incubation females) also indicate an innate change because no evidence showed they had been feeding, and no other digestive organs from dead females showed an increase. Although the decrease in digestive organ size of nesting geese may be innate, the duration of the change is not fixed because failed-nesters had significantly larger digestive organs than did late incubation birds.

Further research under controlled conditions is needed to determine the exact relationship between changes in food intake and changes in digestive organs of breeding Lesser Snow Geese. I have no data on appetite in incubating geese, but predict that it is reduced below normal levels.

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