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# THE POST-ROOST GATHERINGS OF WINTERING BARNACLE GEESE: INFORMATION CENTRES?

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## 1. INTRODUCTION

Many animals that feed socially and roost communally gather into smaller secondary roosts before they enter or after they leave their main roosts (e.g. Hoffman 1968, Swingland 1976, Siegfried *et al.* 1977, Davis 1979). Barnacle Geese (*Branta leucopsis*) are no exception to this pattern. In their winter quarters, these birds are extremely gregarious, feeding and roosting in large flocks, and form "post-roost gatherings" after leaving their roosts, but before beginning to forage.

One explanation of this phenomenon is that these "pre-" or "post-roost gatherings" are centres to which individuals come because they are able to garner information from other individuals there (Wynne-Edwards 1962, Zahavi 1971, Ward & Zahavi 1973). This information is usually presumed to be about the location of food (see Krebs 1974 for a review) but Wynne-Edwards also envisaged animals trading information about, for example, breeding conditions.

Several investigators have undertaken quantitative tests of the information-centre hypothesis (Krebs 1974, Roell 1978, Loman & Tamm 1980, De Groot 1980). Of these, De Groot has posed the most stringent test. He investigated the ability of individual Weaverbirds, *Quelea quelea*, to

find preferred resources in an indoor aviary. In one experiment, food sources of differing quality were placed in adjacent rooms, to which the birds could fly through small holes in the wall. Each of the birds had experience with only one of the food sources, and yet after roosting with experienced birds, naive birds were able to go directly to the good food source. In another experiment, De Groot showed that naive birds were able to locate water after they had roosted with individuals familiar with the location of the water.

The most detailed field study to date of the behaviour of animals at secondary roosts is that of Stolba (1979) on the baboon *Papio hamadryas*. Stolba described post-roost gatherings where baboons spent approximately 1.5 h before setting out to forage. He marshalled much observational evidence in support of his claim that the post-roost gathering was a centre where the baboons "voted" on where to forage.

Our goal in this article is to quantify aspects of the utilisation of post-roosts by Barnacle Geese, with a view to providing the background to a field test of the information-centre hypothesis. In order to assess the applicability of this hypothesis we decided that it was necessary to determine whether i) the post-roost gathering was in fact a centre for dispersal, ii) whether the pattern of dispersal changed in a manner consistent with changing foraging conditions, and iii) whether use of the post-roost itself varied.

## 2. STUDY AREA

Some 50 000 Barnacle Geese migrate to north-western Europe each autumn from their breeding grounds on Novaya Zemlya. In The Netherlands, concentrations of these birds can be found wintering at several sites (Fig. 1). They remain in The Netherlands until April, when they depart on their spring migration.

The island of Schiermonnikoog serves as winter quarters for 3–4000 of these geese. From their arrival in October until the onset of spring, Barnacle Geese forage in the polder on the island, an extensive tract of dairy pasture. In late

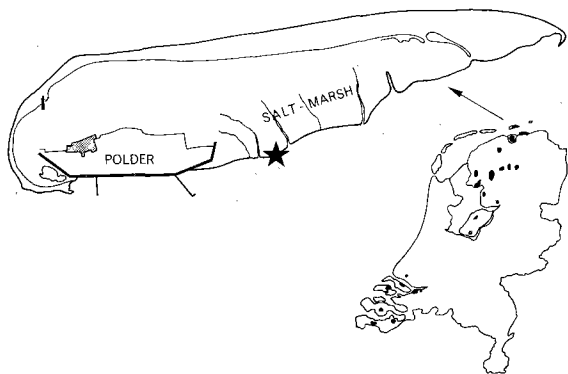


Fig. 1. The island of Schiermonnikoog, showing the main roost (★) and the winter foraging area (the polder). Shaded area = village. Other Barnacle Goose wintering areas in The Netherlands are shown on the map beneath (dark areas).

February, they abruptly shift their foraging activity to the salt-marsh on the island (Prins *et al.* in prep.).

During the winter portion of their residence on Schiermonnikoog, with which we shall be concerned in this article, Barnacle Geese follow a simple routine of roosting and foraging. They leave their roost on the salt marsh each morning at dawn, fly to the polder where they spend 90% of their time foraging (Ebbinge *et al.* 1975), and return to the roost in the late afternoon (Fig. 1). The direct flying time from roost to polder is about five minutes, but the morning roosting flight involves a prolonged stop-over on the mudflats en route to the polder.

### 3. METHODS

We surveyed Barnacle Goose roosting flights on Schiermonnikoog from strategic vantage points. By simultaneously manning two or more such points, a good view could be had of the entire route flown by the geese, and flocks of geese flying between the island and the mainland could easily be spotted. Observers recorded the time, size, direction, origin and landing place of all goose flights seen, employing a standard system of notation so that their records could easily be combined to give a comprehensive account. In all, over 100 roosting flights were monitored, but various factors such as poor visibility, late posting, or the absence of enough observers rendered some accounts unusable. The following analysis utilises the records of 42 morning and 36 evening roosting flights. These were not all from the same or from successive days, and sample sizes are therefore not identical throughout the analysis. Half ( $n = 21$ ) of the morning records are particularly detailed, and we are confident that in these cases we have succeeded in obtaining an exhaustive account of all Barnacle Goose movements on and to and from the island.

To facilitate the analysis of the data, we defined the "moment" at which a roosting flight occurred as the time at which 50% of the geese which eventually did so had arrived on the foraging grounds (in the case of morning flights) or had left them (evening flights). We checked the total number of geese by careful counts of the geese in the polder during the day, when they were easily enumerated. We defined the duration of the morning flight as the length of the inter-

val from the onset of flights in the morning until the "moment" of arrival.

Temperatures were read on most days from a maximum-minimum thermometer. The mean daily temperature was taken to be the average of these readings. On some days we measured the light intensity during roosting flights with a light meter (United Detector Technology, No. UDT-80X), stationed at a standard location and aimed directly skywards.

The bulk of the data reported here were collected from November 1977–February 1978, but are supplemented with observations made in January–February 1980, and December 1980.

## 4. RESULTS

### 4.1. DESCRIPTION OF ROOSTING FLIGHTS

In a typical morning roosting flight, Barnacle Geese began to leave their roost at dawn, and flew in small groups to a site on the mudflats near the foraging grounds. The location of this "post-roost site" varied from day to day, and could be situated almost anywhere along the entire route from roost to foraging site. Occasionally, more than one site was used. We observed post-roost gatherings on 39 of the 42 mornings; on the remaining three mornings, Barnacle Geese flew directly to the polder. Two typical

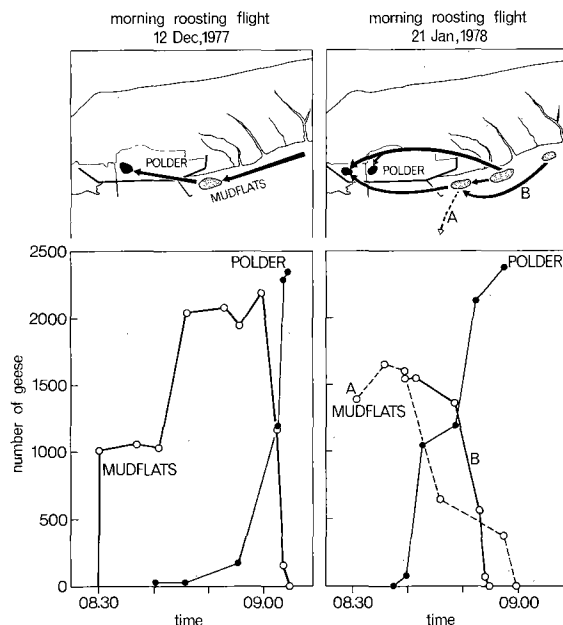


Fig. 2. Two typical morning roosting flights, showing the progression of geese from the main roost to the post-roost sites and finally to the foraging grounds. The graphs below plot the number of geese at the various sites during the observation period.

morning flights are diagrammed in Fig. 2.

The morning roosting flight took up a considerable portion of the day (Fig. 3), lasting almost an hour on average. This meant that over 10% of the daylight period was spent in transit from the roost to the polder, in spite of the fact that the direct flying time was very small.

There were two main reasons for this extended duration. One reason was the uncoordinated manner in which the morning flight proceeded. Geese flew from the roost in groups that were very small compared to those in the evening flight (Fig. 4). Usually, some geese were already foraging in the polder before the last geese had left the main roost.

The main factor contributing to the prolonged duration of the morning roosting flight however,

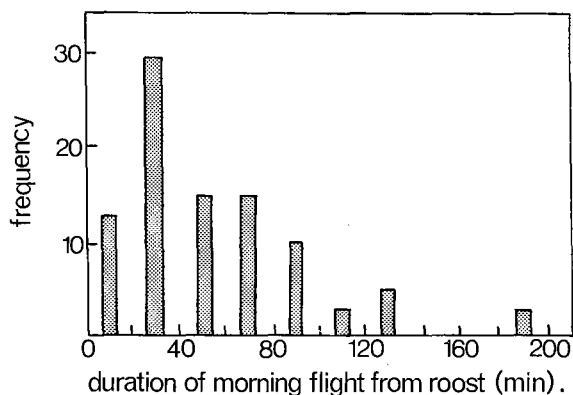


Fig. 3. Frequency distribution of the duration of the morning roosting flights. Average duration is 57 min, although the mode is at 30 min.  $n = 42$ .

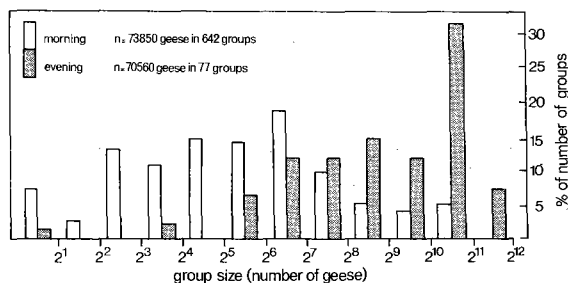


Fig. 4. Frequency distribution of group sizes observed entering or leaving the polder during roosting flights observed on the 21 most complete observation days. Note that the scale on the horizontal axis is exponential. The close agreement of the morning and evening totals (within 5% counting error) makes it unlikely that we missed large scale movements between Schiermonnikoog and the mainland at times other than roosting flights.

was the length of the stay at the post-roost site on the mudflats. Lacking any records, we have estimated the average amount of time spent at the post-roost site by individual geese by the duration of the roosting flight. Although this introduces a slight, albeit consistent, error since flying time is included, it is nonetheless clear from Fig. 3 that a substantial variation exists between mornings.

The evening roosting flights were simpler and more coordinated than the morning flights. Group size of flocks leaving the foraging grounds was very large — the geese generally left the polder in one or two groups (Fig. 4) — and their flight took them directly to their roost.

#### 4.2. DISPERSAL PATTERNS

An important feature of the post-roost traffic was the interchange of individual geese between the mainland and Schiermonnikoog. All geese arriving from the mainland did so in the morning and joined the post-roost gathering, while others left the post-roost site for the mainland. On any particular morning, the traffic flowed predominantly in one direction. Of over 70 000 goose flights recorded in the 21 most complete accounts of morning roosting flights, 25 000 left Schiermonnikoog, and almost 5000 arrived on the island from elsewhere. The close agreement of the counts of Barnacle Geese entering the polder in the morning and leaving in the evening makes it unlikely that we missed large scale movements at other times of the day. In fact, we never observed such movements, except on two occasions when Barnacle Geese returned to Schiermonnikoog around midday after prolonged absences due to freezing weather or snow cover.

Ring sightings confirm that many of the birds foraging on Schiermonnikoog also frequent sites on the adjacent mainland, and that the identity of the individuals foraging on Schiermonnikoog can change radically from day to day (Paul Loth pers. comm.). We lack enough data to understand these movements well, but they are markedly influenced by temperature. Declining temperatures led to shrinkages in the number of Barnacle Geese foraging on Schiermonnikoog, while increasing flock sizes or stability in the numbers of geese were associated with stable

Table 1. Contingency table showing the occurrence of day to day changes in temperature and group size. Expected values in parentheses. The change in temperature is measured as the difference in mean temperature across successive days. Changes of less than 1°C are counted as "no change". Flock sizes on successive days are counted as "no change" if they differ by less than 5% (= approximate counting error)

Changes in temperature	Changes in group size		
	increases	no change	decreases
Increases	13 (8.9)	3 (3.4)	6 (9.8)
No change	14 (11.3)	5 (4.3)	9 (12.4)
Decreases	2 (8.9)	3 (3.4)	17 (9.8)

$\chi^2 = 16.63$ ;  $df = 4$ ;  $P = 0.005$ ;  $n = 72$

and increasing temperatures (Table 1).

#### 4.3. DURATION OF FORAGING

Barnacle Geese spent more time foraging as the mean overday temperature declined (Fig. 5). Foraging time increased at almost twice the rate of estimated metabolic requirements, suggesting that food was more time-consuming to acquire when it was cold. Due to the negative influence of low temperature on the rate of production of new leaves and the leaf extension rate of the pasture grasses on which these birds feed during this period (Peacock 1975, Keatinge *et al.* 1979), we believe that low temperature exercises its influence at least partially through its effect on food availability.

Group size also had an effect on the duration of foraging. Larger groups foraged longer (Fig. 6). This is not confounded with temperature, since groups tend to shrink in size when temper-

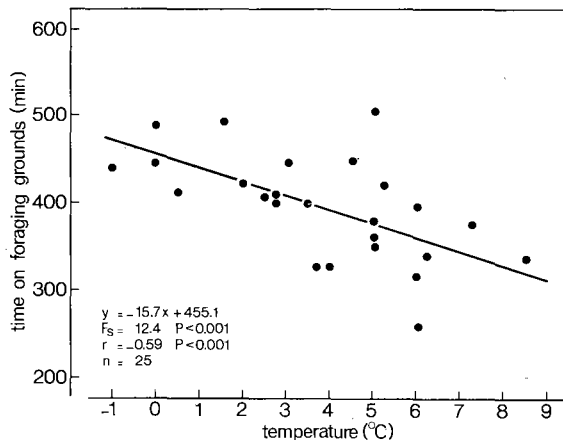


Fig. 5. Duration of foraging as a function of temperature.  $n = 25$ .

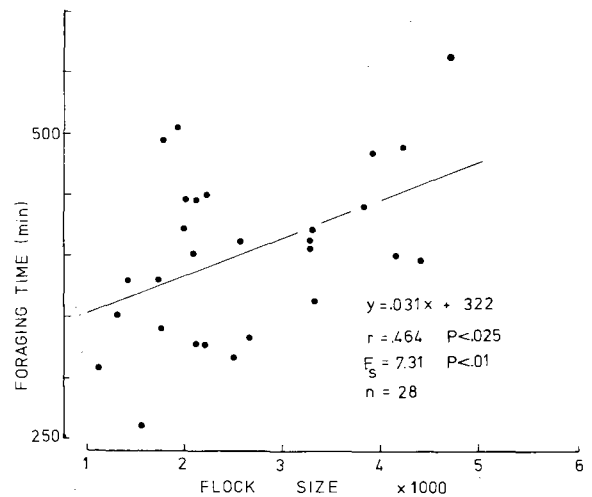


Fig. 6. Duration of foraging as a function of flock size.  $n = 28$ .

atures drop (section 4.2). One explanation for the extended foraging of larger groups is that some form of mutual interference takes place between individuals in flocks. Whatever mechanisms are involved, both large flocks and low temperatures prolong the duration of foraging, and it is possible that both these factors exert their influence by reducing the foraging opportunity for individual Barnacle Geese.

#### 4.4. TIMING OF THE EVENING ROOSTING FLIGHT

The duration of the morning roosting flight displays a strong linear correlation with the lateness of the evening roosting flight on the previous day (Fig. 7). An examination of the factors promoting late departures from the foraging grounds will help clarify the significance of this relationship.

Unlike the roosting flights of many waterfowl (*e.g. Branta canadensis*; Raveling *et al.* 1972) the timing of the evening roosting flight of Barnacle Geese on Schiermonnikoog bears only a loose relationship with light intensity (Fig. 8). Barnacle Geese left the foraging grounds under all light conditions ranging from full sunlight to near dark, though they usually left in the late afternoon.

One important factor leading to late departures is the time of arrival (Fig. 9). Late arrivals on the foraging grounds always led to late departures, but early arrivals had either late or

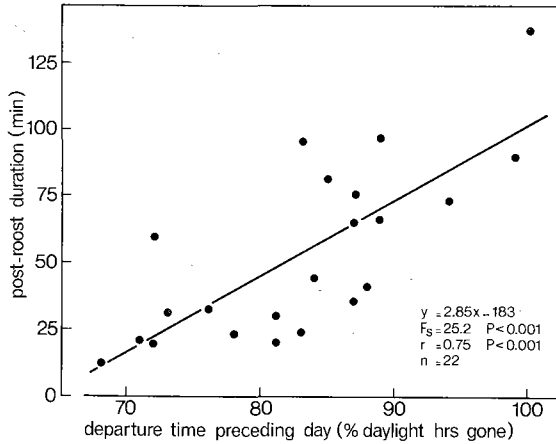


Fig. 7. The duration of the post-roost gathering (for calculation of duration see text) as a function of the lateness of departure on the previous evening, measured as the percentage of daylight hours gone. During the period in which the data were collected, absolute daylength varied by about 10%.  $n = 22$ .

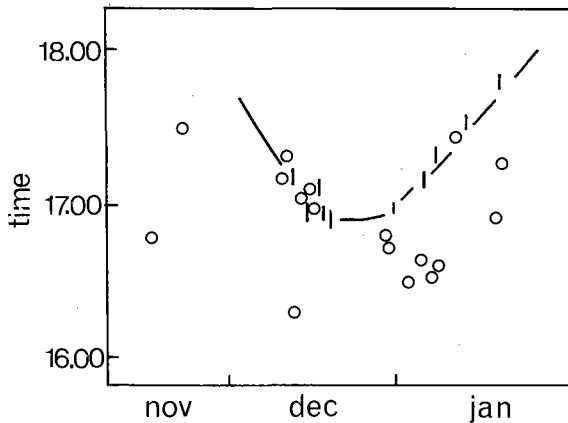


Fig. 8. The timing of the evening roosting flight bears only a loose relationship with light intensity. The vertical bars represent the ten-minute-interval during which the light intensity decreased to  $0.01 \mu$  Watt. The line is fitted by eye.  $n = 17$ .

early departures as their consequence.

Through their influence on the duration of foraging, temperature and group size must also effect the timing of the evening roosting flight. Late departures then, are likely associated with poor foraging conditions, resulting from reduced food availability, interference in some form from flock mates, reduced time for foraging, or any of these factors in concert.

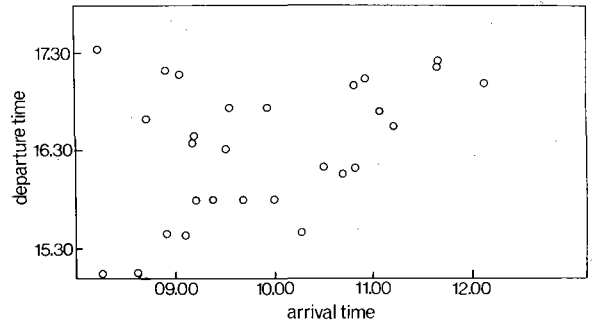


Fig. 9. The time of departure from the foraging grounds as a function of the time of arrival. Late arrivals always lead to late departures, but the departure time after early arrivals is variable. Minimum foraging time was 4.75 h, but the average was 6.75 h.  $n = 28$ .

## 5. DISCUSSION

The results presented here provide empirical support for the following three points. First, the post-roost is a centre for dispersal to and from the island. Second, the pattern of dispersion changes with temperature. Geese are more likely to leave the island when the temperature drops. Finally, increasingly late departures from the foraging grounds cause the geese to spend longer at the post-roost site on the following morning.

Both the Barnacle Goose and its congener the Brent Goose (*Branta bernicla*) are specialist grazers that exploit the new growth of their food plants (Prins *et al.* 1980, Ydenberg & Prins 1981) at least during the spring. In winter, the main food plants of Barnacle Geese on Schiermonnikoog are domestic varieties of the pasture grasses *Lolium perenne* and *Poa pratensis*. *Lolium perenne* at least, is well known to continue its growth throughout the winter, though at a slower rate than in the spring (Peacock 1975, Thomas & Norris 1979, Keatinge *et al.* 1979). In both winter and spring, the rate of appearance of new leaves and the leaf extension rate decline with temperature, and cease altogether at or just above the freezing point (Peacock 1975). In this regard, it is interesting to note that Barnacle Geese abandon Schiermonnikoog entirely during freezing weather. The evidence suggests that they are dependent on the continued growth of their food plants, even in winter, and

that low temperatures do reduce food availability.

This reduction will not, however, affect all flock members equally. Individual birds of several species are well known to differ in their ability to gain access to food under difficult conditions (e.g. Woodpigeons, *Columba palumbus*, Murton *et al.* 1971; Yellow-eyed Juncos, *Junco phaeonotus*, Caraco 1979b; Dark-eyed Juncos, *Junco hyemalis*, Baker *et al.* 1981). In goose flocks, a feeding asymmetry also exists: some positions in foraging flocks are more favourable for feeding than others (Drent & Van Eerden *in press*). Individual Barnacle Geese in possession of good feeding positions in foraging flocks may be forced to seek alternative feeding locations less frequently than those birds in poorer positions. In a radio-tracking study of over 60 Canada Geese, Raveling (1969) found that some birds (usually families) were very fidel to their roost and feeding site, while others (usually single birds) alternated unpredictably between several roosts and feeding areas. One way of explaining this observation is that predictable birds were established in good feeding positions in flocks on their feeding grounds, and that they therefore were never required to search for other feeding sites when conditions deteriorated.

### 5.1. THE POST-ROOST GATHERING

Both Rubenstein (1976) and Caraco (1979a) have modelled the choice individual birds face between remaining in a flock or seeking alternative feeding sites alone. These models both identify several elements that promote the tendency for individuals to abandon groups, including increased competitive inequality among group members, reduced habitat quality or reduced feeding opportunity, and reduced predation. Caraco (1979b, 1980) has provided field evidence in support of his model.

Our hypothesis is that the post-roost gathering facilitates the making of analogous decisions. Assembling at post-roost sites may allow individual geese to gather information relevant to the decision of whether to remain or seek other foraging areas. Information might conceivably derive from several sources including the number of geese already present (*i.e.* the likelihood of obtaining a good foraging position

in the flock), temperature, or the rate of arrival of geese from other areas (a high rate may indicate poor conditions). As foraging conditions worsen, more birds will have to consider making the substantial investment of time, energy, and possibly risk that a switch of foraging site will entail. We suggest that this is the reason that post-roost gatherings increase in duration after late afternoon departures from the foraging grounds: the information on which the decision to leave or stay is based becomes more valuable when the probability of leaving is increased, as it seems to be after late departures from the foraging grounds.

In summary, features of the utilisation of a post-roost gathering by wintering Barnacle Geese are consistent with the interpretation of the post-roost as an information centre. Although the evidence we have presented is largely circumstantial, we believe that it will now be possible to make predictions about the behaviour of individual geese and to test these predictions in a more direct and quantitative manner.

### 6. ACKNOWLEDGEMENTS

We were assisted by many friends while making these observations, but special thanks are due to Theo Boudewijn for his unselfish aid. Bart Ebbing (Rijksinstituut voor Natuurbeheer) ringed the Barnacle Geese and Paul Loth supplied the information on ring sightings. Mike Birkhead and Bruno Ens commented on an earlier draft of this paper. An essential element in our work on Schiermonnikoog was the good-natured co-operation of the Dienst der Domeinen and its overseer on the island, Mr. R. Nieuwenhuis. Dr. R. H. Drent supervised this project, and gave us access to the facilities of the Rijksuniversiteit Groningen on the island. To all these people, we express our thanks.

### 7. SUMMARY

Barnacle Geese wintering on Schiermonnikoog follow a simple routine of roosting and foraging. The morning flight from the roost usually involves a prolonged stop-over at a site en route to the foraging grounds. This "post-roost gathering" is a centre for dispersal to and from the island. The duration of the post-roost gathering is strongly correlated with the lateness of the departure from the foraging grounds on the previous evening. The main factors promoting late departures are low temperatures and large flock sizes, both of which seem to exercise their influence by diminishing foraging opportunity for most individual geese. Flock size also shrinks as temperature declines. Temperature directly affects the rate at which the main food plants of Barnacle Geese produce new material for consumption by these birds, so low temperatures are likely correlated with low food availability. Our hypothesis is that the increase in the

duration of the post-roost gathering following long days of foraging is due to the increased consideration that more geese must give to seeking other foraging sites. The post-roost gathering facilitates the accumulation of information relevant to this decision. Some methods by which information may be acquired are discussed. We emphasize the circumstantial nature of our evidence to date, but we believe that more direct test of this idea in the field can now be undertaken.

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## 9. SAMENVATTING

In noord Nederland overwinterende Brandganzen hebben een eenvoudig patroon van slapen en eten. Op Schiermonnikoog is in de ochtendtrek een lange pauze opgenomen halverwege de slaappleaats en het fourageergebied. Deze ochtendverzamelplaats ("post-roost gathering") is een centrum waarvan de ganzen het eiland verlaten of waar ze naar toekomen als ze het eiland bezoeken. De lengte van deze pauze is sterk gecorreleerd met het tijdstip van vertrek van het fourageergebied op de voorafgaande dag. Een verlaging van de temperatuur veroorzaakt langduriger grazen door de Brandganzen, en ook de groeps-grootte neemt af als het kouder wordt. Aangezien de belangrijkste voedselplanten van de ganzen een geringe bladstrekking (groei) vertonen bij lagere temperaturen, lijkt het aannemelijk dat het latere vertrek en de afnemende groeps-grootte het gevolg zijn van verminderende graas-mogelijkheden. Onze hypothese is dat de duur van de ochtendverzameling toeneemt na een slechte graasdag, omdat meer individuen gedwongen zijn fourageergebieden elders in overweging te nemen. Hierdoor neemt de waarde toe van de informatie waarop de beslissing om te vertrekken (of te blijven) is gebaseerd; deze informatie kan op verschillende manieren, welke in de tekst worden aangestipt, op de ochtendverzamelplaats worden verkregen.