Heart rate as an indicator for daily energy expenditure by Brent and Barnacle geese
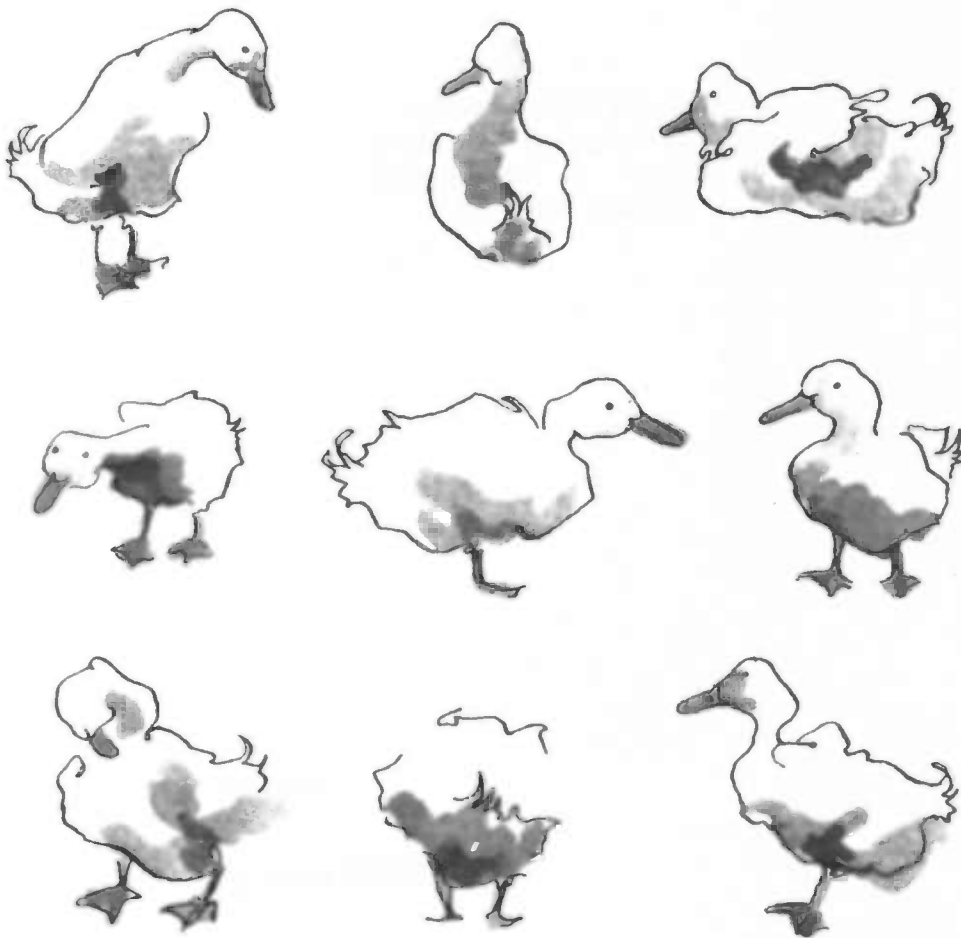
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Heart rate as an indicator for daily energy expenditure
by
Brent and Barnacle geese

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1 Abstract

Brent geese (*Branta b. bernicla*) and Barnacle geese (*Branta leucopsis*) on Schiermonnikoog forage on the grass pastures during the winter and switch during early spring to the saltmarsh. In this study we investigated whether this habitat preference can be explained by daily energy expenditure. To estimate the daily energy expenditure, measurements of time-activity-budgets of the Brent geese in the polder area and on different vegetation types on the saltmarsh were conducted during spring 1999.

Time-activity-budgets can be translated into caloric terms by measuring the average heart rate for specific behaviour. External heart rate loggers were applied on semi-captive Brent and Barnacle geese walking freely in an enclosure. The resting heart rate was calibrated against oxygen consumption in the laboratory to express the heart rate as caloric costs.

Different behavioural parameters could be related to distinct heart rate ranges. Resting had the lowest heart rate, walking had a higher heart rate than foraging. The energetic costs of different behavioural parameters (as assessed by heart rate telemetry) are extrapolated to time-activity budgets of wild Brent geese. When flight is excluded the energy expenditure is lower on the polder than on the saltmarsh. However, flying is very costly, mainly due to disturbance. This results in a higher energy expenditure on the polder than on the saltmarsh., which could play a role in the observed habitat preference for the saltmarsh area as soon as food becomes available there.

2 Contents

3 Introduction

3.1 Heart rate as an indicator for energy expenditure

While obtaining food, birds must spend a certain amount of energy for activities that allow the discovery, capture and handling of food items prior to consumption (Maurer 1996). Thermoregulatory costs, the risk of predation, reproduction or territorial maintenance activities contribute to energy expenditure (Robbins 1993). This also holds for disturbance events (Stock & Hofeditz 1996). Energy expenditure might explain to a large extent the habitat choice. The energetic costs can vary per habitat and season.

The methods that have been used up to present to estimate energy expenditure in free-living birds are:
1. extrapolation from laboratory measurements of oxygen consumption or metabolised energy intake of birds(Nolet *et al* 1992, Woakes & Butler 1983, Bevan *et al* 1995)
2. time-activity studies of free-living birds, quantified in caloric terms by extrapolation of laboratory data, e.g. oxygen consumption or heart rate measurements (King 1974, this study)
3. estimates of energy consumption by a variety of indirect methods in free living birds, e.g. doubly labelled water technique (King 1974)

To estimate energy expenditure the Doubly Labelled Water (DWL) method has been used on free-living animals (Williams *et al* 1993). The method gives an accurate indication of energy expenditure on a 24-hour interval. The birds do not need to carry any registration device and therefore have no extra costs caused by extra weight or stress. The disadvantages of DLW method are that the birds need to be recaptured after a period of time for a blood sample. When one is interested in the energetic cost of specific behaviour, e.g. walking, resting etc., this method cannot be used. The DLW method only gives a single value of metabolic rate over the measuring period, which usually extends to 24 or even 48 hours, recapturing after ten minutes or an hour does not give accurate values.

To determine the energetic costs of specific behaviour as parameters, the oxygen consumption for this trait can be measured under laboratory circumstances (Nolet *et al* 1992, Brunckhorst 1995), e.g. treadmill trials. The disadvantage of this method is that these birds are forced to perform a particular behaviour. Even intense training of captive animals cannot suppress stress reactions in trial situations completely.

An alternative technique for estimating energy expenditure is to use a correlation between heart rate and oxygen consumption (Bevan *et al* 1992, Nolet *et al* 1992, Bevan *et al* 1995, Gessaman 1980). Nolet *et al* (1992) investigated the correlation between oxygen consumption and the heart rate in Barnacle geese. The heart rate and the oxygen consumption were measured while geese were resting, walking or swimming, this all in

laboratory circumstances. The study showed that the heart rate is a good indicator of energy expenditure (Nolet *et al* 1992, Woakes & Butler 1983).

The goal in this study was to estimate the energetic costs of specific behaviour. Heart rate was recorded on free-ranging geese in captivity and the behaviour of the geese was registered. When the heart rate correlates with oxygen consumption, the heart rate can be expressed in caloric terms.

3.2 Daily energy expenditure of Brent geese on Schiermonnikoog

On the Frisian island Schiermonnikoog Brent (*Branta b. bernicla*) and Barnacle (*Branta leucopsis*)geese stage from October until mid-May. During the autumn and winter they forage on the polder[1]. During spring a large proportion of the geese population on the island switch to the saltmarsh. The meadows of the polder are fertilized, which results in a high quality grass during the whole winter, where as the saltmarsh vegetation quality and quantity increases in spring. The habitat switch of Barnacle geese in beginning of March occurs when food quality, as in nutritional proteins, on the polder and saltmarsh are equal (Ydenberg & Prins 1981, Boudewijn 1984).

Geese are selective feeders, showing preference for *Plantago maritima*, *Trichlogin maritima*, *Puccinellia maritima* and *Festuca rubra* (Riddington *et al* 1996, Prop & Deerenberg 1991). Factors such as quality and abundance of food plants affect the habitat preference. The geese select vegetation of low to intermediate standing crop, the food intake tends to be lower at high standing crop. (Van der Wal *et al* 1998).

The major constraint of selective free-ranging herbivores is not the declining rate of intake but an increasing expenditure of energy in foraging. Selective feeding will lead to an increase in the time spent travelling (Murray 1991). Energy expenditure of foraging differs per terrain, per species and per individual. The vegetation structure, as in three-dimensional perspective, could affect the foraging cost and therefore habitat preference. When food is not very abundant or out of reach, due to vegetation structure, the time of discovery and costs of locomotion could reduce the energy intake. The net energy intake over a time period is (Maurer 1996):

equation 1.

$$\frac{E}{T} = \frac{E_T - E_F - E_P - E_I}{T_S + T_H + T_P + T_I}$$

where

E_T = total assimilable energy obtained during foraging
E_F = energy spent searching, pursuing, and handling food
E_P = energy spent in physiological processing of food
E_I = energy spent in interactions with other organisms during foraging
T_S = time spent searching for and pursuing food
T_H = time spend handling food
T_P = time spent during physiological processing of food
T_I = time spent interacting with other organisms during foraging

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[1] pasture land enclosed by dykes

The observed habitat switch is not entirely explained by quality and quantity of food plants. Difference in daily energy expenditure of the geese between the two habitats can possibly cause or affect the habitat switch. During spring the saltmarsh is closed for public and disturbance by human activities is minimised. On the polder the geese forage on agricultural land surrounded by roads. Stock & Hofeditz (1996) investigated the effect of human disturbance on the time-activity budgets of Brent geese in the German Wadden Sea. They observed geese on three different islands, one with no human disturbance, one with only pedestrians, one island with a high level of human disturbance. The study showed that in highly disturbed areas the geese were more in flight, and had to compensate by means of night feeding on the mudflat.

In this study, time-activity budgets of Brent geese were conducted in the two habitats, the polder and the saltmarsh. By calibrating the heart rate with oxygen consumption, the heart rate data of specific behavioural parameters obtained by the captive geese can be expressed in caloric terms. Extrapolating these caloric values to the time-activity budgets of the geese on Schiermonnikoog can give us an estimate of the daily energy expenditure on the two habitats. The hypothesis is that the daily energy expenditure differs between the habitats. The daily energy expenditure of the Brent geese on Schiermonnikoog might explain to an extend the switch form the polder to the saltmarsh.

4 Study site

The study was conducted in spring 1999 on Schiermonnikoog (53° 30' N 6° 15' E), one of the Frisian Waddensea islands in the Netherlands. The polder area excists of fertilised pastures, dominated with *Poa pratensis* and *Lolium perenne* (Bulten 1999). The saltmarsh is mainly dominated by *Puccinellia maritima and Festuca rubra*. During spring (april-july) the saltmarsh is closed for public, to reduce disturbance for breeding birds.

Figure 1 shows a map of Schiermonnikoog, on the east of the island are the saltmarshes. The polder is a pasture area enclosed by dykes.
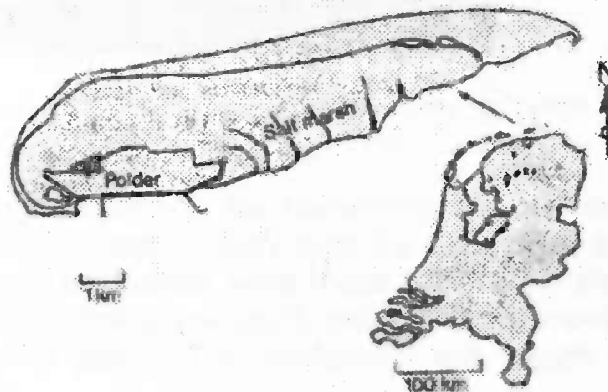
5 Method

5.1 Heart rate telemetry

Heart rates of captive geese were recorded with an adapted heart rate logger for human use, existing of a measuring unit with a transmitter and a registration (logging unit) with receiver (Polar Vantage, Polar Electrop Oy., Kempele, Finland; Bokma 1999).The transmitter was supplied with two 2mm lead-wires, press-stud connected to small gel wetted electrodes (200 medi-trace Mini, Graphic Controls, Buffalo, USA; Bokma 1999). These electrodes were applied on wetted down-freed skin under wings (armpits). The heart rate logger registered an average heart rate over an interval of five or fifteen seconds. For the calibration trails an interval of 15 seconds was used, when measuring the heart rate for specific behavioural parameters an interval of five seconds was used.

Figure 2. Barnacle goose and heart rate logger backpack, the red button with the white patch is one of the two electrodes that were attached to the skin.

The maximum distance between the transmitter and the receiver was one meter, therefore the birds had to carry both the transmitter and the receiver. For this purpose tricot backpacks were made with 18mm elastic bands and pushbuttons. To prevent the geese from opening the pushbuttons, sport tape was used (Hansaplast sport). The backpacks with logger and transmitter weighted ± 80- gram.

Figure 3. Heart rate backpack applied on a barnacle goose (headed to the right).

The backpack was placed under the wings, with the elastics fastened on the breast in front of the legs. The backpack was placed over the electrodes, to prevent the geese from detaching the electrode.

5.2 Calibration

The correlation between heart rate and oxygen consumption was measured for each individual during the night. To limit defeacation during a calibration trial the goose was removed from the group and placed in a box two hours prior to the trial. Before and after the trial the goose was weighed on a digital balance to the nearest gram. The backpack, only containing the transmitter, was attached to the goose. The goose was then placed in a dark, sealed box of 60 or 80 litres. The receiver was placed on top of the box and programmed to measure the average heart rate over an interval of fifteen seconds.

The box with the goose was placed in a climate chamber (Hereus) at a temperature of +15 °C. The box was attached to a respirometer. Dried air (Euro-dry 2001) was blown through the box with an open flow of 300l/h (Brooks model 5850). The outcoming air was blown through Perspex drier tubes containing a molecular filter (type 3Å). Every six minutes a sample of approximately 20 l/h was taken of the outflow during one minute. The oxygen content of the in- and outflowing air (Servomex 1400 gas analyser) and the carbondioxide content of the in- and outflowing air (Servometer Xentra 4100 gas purity analyser) were determined. The temperature in the box was recorded every six minutes. The goose stayed overnight in the respirometer chamber, from 6 pm till 8 am (±14 hours).

The oxygen consumption was calculated according to Hill (1972):

equation 2:

$$VO_2 = Vi \times \frac{(FiO_2 \times (1 - FeCO_2) - FeO_2 \times (1 - FiCO_2))}{(1 - FeCO_2 - FeO_2)}$$

where

VO_2	= Oxygenconsumption	$l \cdot h^{-1}$
Vi	= Air volume that the respirometers enters	$l \cdot h^{-1}$
FiO_2	= Fraction oxygen of the incoming air	
FeO_2	= Fraction oxygen of the outcoming air	
$FiCO_2$	= Fraction carbindioxide of the incoming air	
$FeCO_2$	= Fraction carbindioxide of the outcoming air	

Each individual was measured during two nights. Six night measurements were discarded due to aberrant patterns emerging from over-activity (stress) of the trail bird or bad contact of electrodes with the skin of the trial bird. All other measurements were used to calculate a calibration line. The heart rate and oxygen consumption was averaged over an interval of thirty minutes. A delay in time of 10 to 12 minutes for measuring oxygen consumption occurred because of the volume of the box. The VO_2 that was measured synchronically with the heart rate was corrected for that delay, by calculating the volume of the box and using the flowrate to determine how long it will take for the inflow air to flow out.

5.3 Determining the heart rate for specific behaviour

Brent goose and Barnacle geese were used in this study. The geese were kept in a run (8m by 16m) together with other geese that were not taking part in the study. The geese had unlimited access to water and pelleted food and were able to forage on grass. Every week the pen was moved to a new area to supply the geese with new grass. The geese remained in the group during the measurements.

Heart rate was measured on three Brent geese. Two of the Brent geese showed abnormal behaviour and were excluded from the experiment. Six Barnacle geese were used in the experiment. One female Barnacle goose showed immediately abnormal behaviour and was excluded from the experiment. Another female Barnacle had done many trials, but the logger failed every trial to measure her heart rate. She too was excluded from the data analysis. Eventually one Brent and four barnacle geese were used. Tabel x. shows the details of the geese.

For each trial two geese were captured to apply the heart rate backpacks. This procedure took about fifteen minutes, afterwards the birds were immediately released in the run.

The geese were observed from a distance of 20 meters of the run behind a partition. A timer (Casio) was used with a sound signal every five seconds.

Every five seconds, synchronised with heart rate logging, the behaviour (table 1) of both geese was registered in a database program (Excel 95, Microsoft). 8 Different behaviours were distinguished, see table x. The birds were observed during daytime.

Table 1. The specific behavioural parameters that were observed:

behaviour	description
resting	sitting or standing with eyes closed or head under the wing
sitting	sitting but active
preening	including wing beating
drinking	
foraging	eating grass, meanwhile walking possible
standing	head up or alert
walking	walking when not foraging
interaction	running, flight attempts and interactions with other geese
eating pelleted food	

The average heart rate has been calculated for the behaviour resting, foraging and walking. The behaviour preening was excluded from the analysis. Preening could cause contact problems between the electrodes and the skin, this could lead to measuring an incorrect heart rate. The behaviour drinking and interaction are behaviour with a very short duration. This implies that there were too small sample sizes. It is also possible with behaviour of such short duration that the heart rate that is measured is actually the heart rate of the previous behaviour that had taken place. The behaviour standing is excluded from the analysis. The heart rate could be very low because the goose is at ease or the heart rate is extremely high because the goose looks up in alertness and maybe stress, this will lead to an high variance in heart rate. The behaviour eating pelleted food is an unnatural behaviour and therefore not taken in to the analysis.

5.4 Time-activity budgets of Brent geese

Flocks of Brent geese on the polder and the saltmarsh were observed (see map). A flock was observed for two hours continuously. A flock was scanned (Altmann 1974) with a telescope (Optolyth 60x) and every five seconds randomly a goose was picked and its behaviour (table 1) was recorded. If a flock was disturbed, the source of disturbance and the reaction of the flock was recorded. If geese flew to another location, the time in flight was recorded as well as the flock's destination. On the saltmarsh, approaching the flock often led to disturbance, therefore observations on the saltmarsh were only made from one observation hide.
The time-activity-budget values were averaged per day and arc sin transformed.

5.5 Weather station

A weather station was installed next to the pen to determine the effects of weather parameters on heart rate. A mobile weather station measured windspeed (A100R, rotational anemometer Vector Instruments, Rhyl, UK) and wind direction (potentiometer windvane W200P, VI). Air temperature (H301 thermometer, VI) and net radiation (DRN/301 net radiometer, Didcot instruments Co., Abingdon, UK) were measured 50 centimetres above ground level. The parameters were measured every 2 seconds, and five minutes averages of the measurements were recorded (CR10 datalogger, Campbell, Logan, USA).

Windchill factor was calculated with equation x (ADT 1999), To correct for the effect of the windspeed on the temperature. The equation is based on wind chill factor on humans.

equation 3:

$$T_{wc} = 33 + (T - 33)(.474 + .454 \sqrt{S} - .0545\, S)$$

where:

T_{wc}	= windchill temperature
T	= ambient temperature, $T < 33°C$
S	= windspeed, $S \geq 1.79$ m/s

5.6 Extrapolation of heart rate data to energy expenditure

BMR was calculated by using the correlation between heart rate and oxygen consumption. The tenth recorded time interval with the lowest heart rate was appointed as the basal metabolic heart rate (van der Wal 1992). Using the calibration line (equation 4) the oxygen consumption was estimated. The energetic value of one litre oxygen is equivalent to 5.58 kJ (Eckert et al 1996).

The energetic costs of specific behaviour were determined by using the correlation between heart rate and oxygen consumption. The energetic values of specific behaviour of the Brent geese were used to translate the time-activity budgets into energy expenditure. The fraction of time spent on a specific behaviour was multiplied by the energetic cost of this behaviour.

All analysis in this study have been done with Genearal Linear Models in SPSS 9.0.

6 Results

6.1 Calibration

Each goose was trailed two nights. Correlation between oxygen consumption and heart rate per goose is shown in appendix 1. Appendix 2 shows the heart rate and the oxygen consumption of a goose during a night of calibration.

Variance between individual for the correlation between oxygen consumption and heart rate could not be determined due to the fact that there was a significant difference between nights within a goose (table 2) and because of some individuals only one night was taken in the analysis. One barnacle goose showed no significant difference between nights (table 2).

Table 2: Relation between heart rate and oxygen consumption (VO_2) and the difference between nights. GLM, n.s. = not significant, * p<0.05, ** p<0.01

Goose	Correlation between heart rate and VO_2			effect of night on VO_2	# nights
	F	df	sign	sign	
Barnacle 1	7.016	1,23	*		1
Barnacle 2	35.635	1,23	**		1
Barnacle 3	144.952	1,45	**	**	2
Barnacle 4	399.377	1,23	**		1
Barnacle 5	178.384	1,36	**	n.s.	2
Brent	161.549	1,47	**	*	2

A calibration line is needed to express specific behavioural parameters in energetic costs. Despite the difference between nights and between individuals, the measurements where used to determine a calibration line. The calibration line of the brent goose contained the two nights of measurement, no selection or filtering had been done (table 2). The calibration line of the barnacle geese contained data of three barnacle geese, of one goose only one night. There was a significant difference between the calibration line of the two species (GLM, $F_{1, 162}$ = 453.179, p = .000)(figure 4).

Equation 4: Regression equation of the calibration lines

Barnacle geese: $VO_2 = 0.0182*HR - 0.0955$
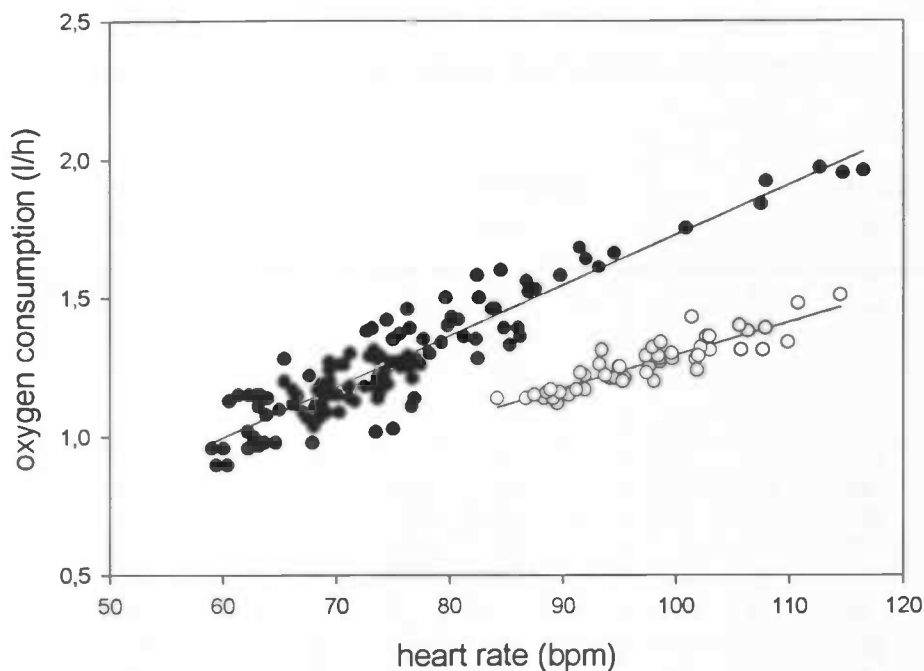
Brent goose: $VO_2 = 0.0120*HR - 0.0963$

Figure 1. Calibration line of the Barnacle geese (●) (r^2 = .8563) and the Brent geese (O) (r^2 = .8015).

6.2 Energetic costs of behaviour

While the geese with heart rate loggers were observed they showed the same behaviour as the other geese in the group. The first hour after the backpack had been applied the geese showed mainly preening behaviour. The heart rate (± 200 bpm) was very high while backpacks were applied, half an hour after release in the run the heart rate of the geese had decreased to daily average heart rate (± 120 bpm)(appendix 1). An hour after application of the backpacks the geese showed the same behaviour as the geese without backpacks, though with a bit more preening behaviour.

The average heart rate was calculated for the behaviour resting, foraging and walking. The behaviour preening, drinking, standing and interaction were placed in the category "remian". The average heart rate of the specific behaviour resting, walking and preening differed significantly within individuals and within species (post hoc test, Tukey). All comparisons between the two species showed significant differences (ANOVA, $F_{1, 18440}$ = 16789.737). Barnacle 4 showed no significant difference in average heart rate between resting and foraging (figure 5). Figure 5 shows the average heart rate for these specific behaviour. Resting showed the lowest heart rate and walking the highest heart rate (table 3 and figure 5).

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Table x. Average heart rate of resting, walking and foraging with standard error and sample size.

| goose	trial	resting				walking				foraging			
		HR		s.e.	n	HR		s.e.	n	HR		s.e.	n
NYJ	124	130	±	1.2	14	103	±	7.9	83	132	±	1.0	148
Brent	132	126	±	0.3	767	131	±	0.9	63	135	±	0.6	201
	135	137	±	0.5	674	166	±	2.2	314	139	±	1.0	127
	153	121	±	0.4	569	196	±	7.6	8				
mean		128	±	3.4	4	149	±	20.3	4	135	±	2.1	3
NUX	104	115	±	8.2	11	141	±	5.7	36	101	±	1.0	174
Barnacle	111	91	±	0.7	203	121	±	4.2	33	96	±	1.3	68
	124	83	±	0.2	1020	118	±	4.5	55	100	±	2.5	64
	135	86	±	0.5	204	112	±	1.7	203	87	±	0.6	32
	138	83	±	0.5	420	112	±	9.0	18				
mean		92	±	6.1	5	121	±	5.3	5	96	±	3.3	4
DIV	141	104	±	0.8	575	122	±	2.1	50	116	±	0.9	156
Barnacle	152	88	±	0.6	816	107	±	3.0	57	99	±	1.0	100
	154	94	±	0.7	754	122	±	2.7	34	101	±	0.4	397
	156					136	±	9.4	10	112	±	1.0	135
	158	78	±	2.1	349	120	±	3.1	7	103	±	.9	337
	162	97	±	5.7	8	65	±	18.3	10	88	±	3.3	3
mean		92	±	5	4.5	112	±	10.1	6	103	±	4.1	6
Y9	159	70	±	0.2	1641	103	±	2.4	99	96.2	±	2	5
Barnacle	160	77	±	0.4	1335	97	±	2.3	101	81	±	0.4	254
mean		73	±	0.2	2976	100	±	1.7	200	81	±	0.4	259
NYD	158	77	±	0.6	511	99	±	1.1	239	74	±	1.4	28
Barnacle													
Barnacle		83	±	4.9	4	108	±	5.2	4	90	±	6.3	4
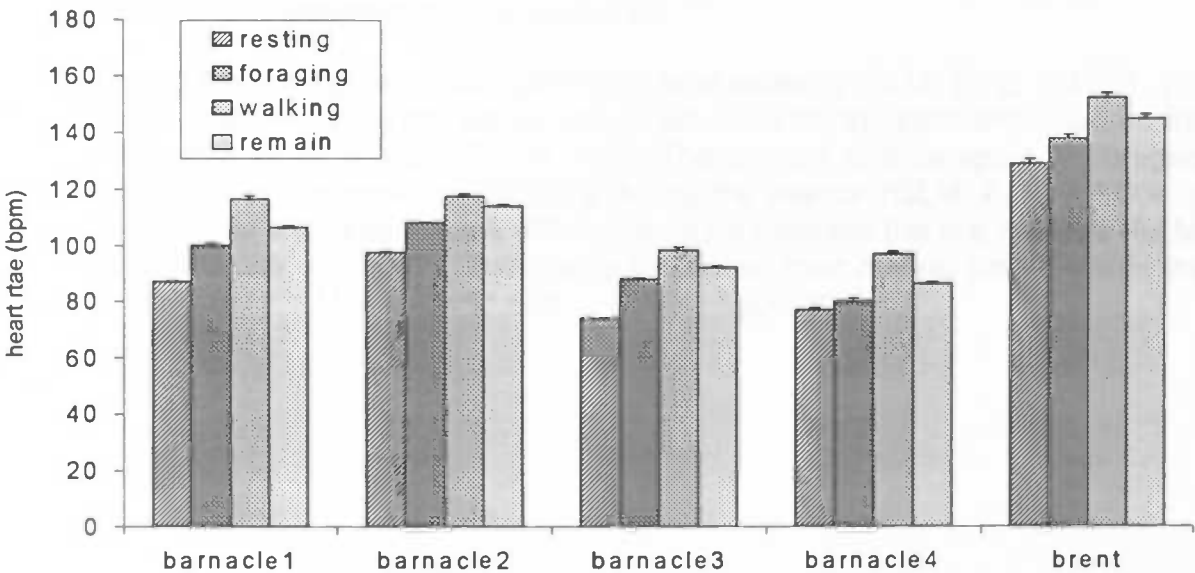
Figure 5: The average heart rate for specific behaviour per individual. mean + s.e., n.s. = non significant, p> 0.05.

6.3 Observation of free-living brent geese

In the beginning of the season, mid March, a large proportion of the Brent geese population of Schiermonnikoog was observed in the polder. Average flock size ranged around 900 birds. Gradually the flock size in the polder decreased towards end of May, as did the total number of geese in the polder (figure 6).
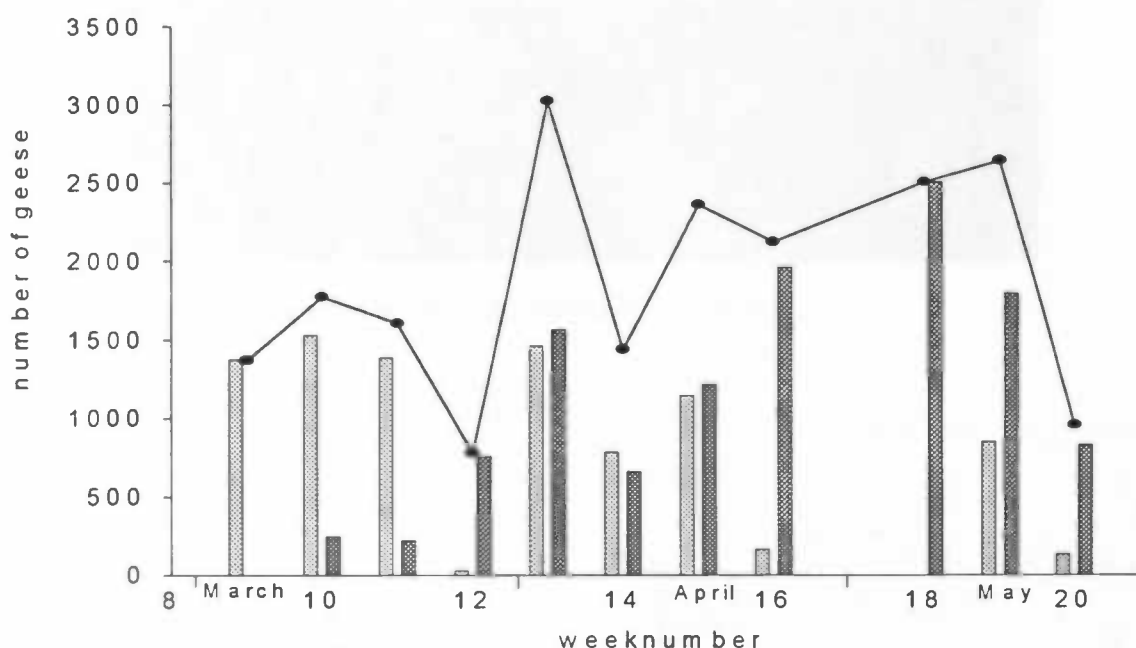

Figure 6. Goose counts of the polder (light grey) and the saltmarsh (dark grey) and total counts (line) on Schiermonnikoog in spring 1999.

During the spring the geese spent less time walking (GLM, $F_{1, 34}$ = 4.201, p = .048). The geese did not significantly walk more on the saltmarsh than on the polder (GLM, $F_{1, 33}$ = 2.450, p = .120). The amount of time spent on foraging did not in- or decrease significantly during the season (GLM, $F_{1, 33}$ = 1.064, p = .310), nor was a significant difference found between the two habitats (GLM, $F_{1, 34}$ = 3.069, p = .089). The geese increased their resting time towards the end of May (GLM, $F_{1, 33}$ = 14.651, p = .001)(figure 8).

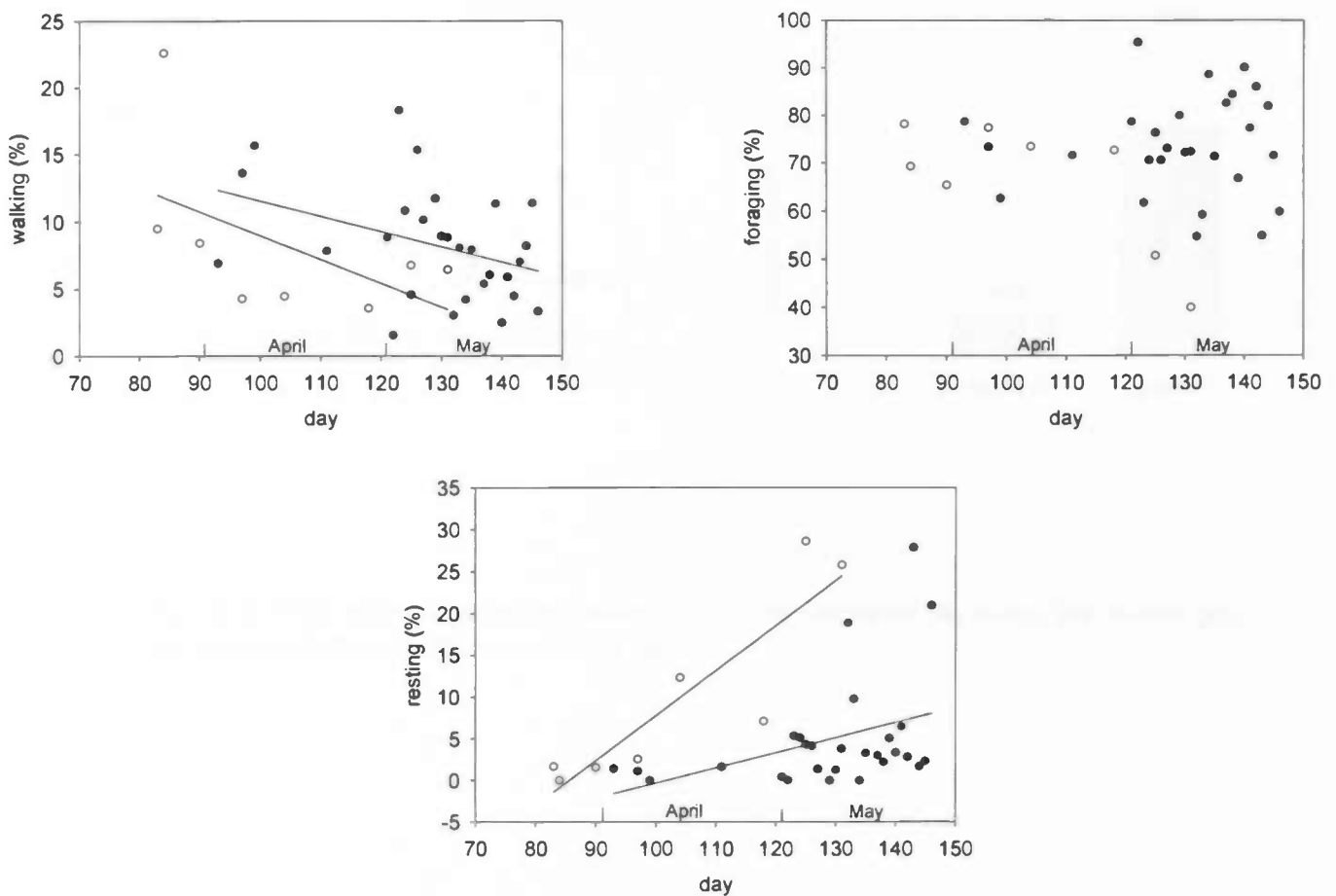Figure 7. Brent geese foraging in the polder on Schiermonnikoog.

Figure 8: Time activity budgets of Brent geese in two habitats on Schiermonnikoog: saltmarsh (↓) and polder (↓). The regression line is shown when a significant relation was found.

Table 4: GLM of factors influencing the time-activity budgets of the brent geese on Schiermonnikoog. n.s. = not significant, * p<.005, ** p<.000

behaviour	difference between polder and saltmarsh		effect of day		interaction between location and day		df
	F	sign.	F	sign.	F	sign.	
resting	1.582	n.s.	23.988	**	3.989	n.s.	1, 32
foraging	2.430	n.s.	3.041	n.s.	3.859	n.s	1, 32
walking	0.030	n.s.	6.643	*	0.211	n.s.	1, 32

The geese tend to fly more in the polder habitat compared to the saltmarsh, but these differences were not significant (GLM, $F_{1, 40}$ = .371, p = .546) (figure 9). In early spring the geese on the polder flew for 44 ± 20 seconds per half an hour. In May the geese flew 19 ± 15 seconds per half an hour in the polder. The geese fly significantly more in the beginning of the season than at the end of the spring (GLM, $F_{1, 41}$ = 10.751, p = .002).
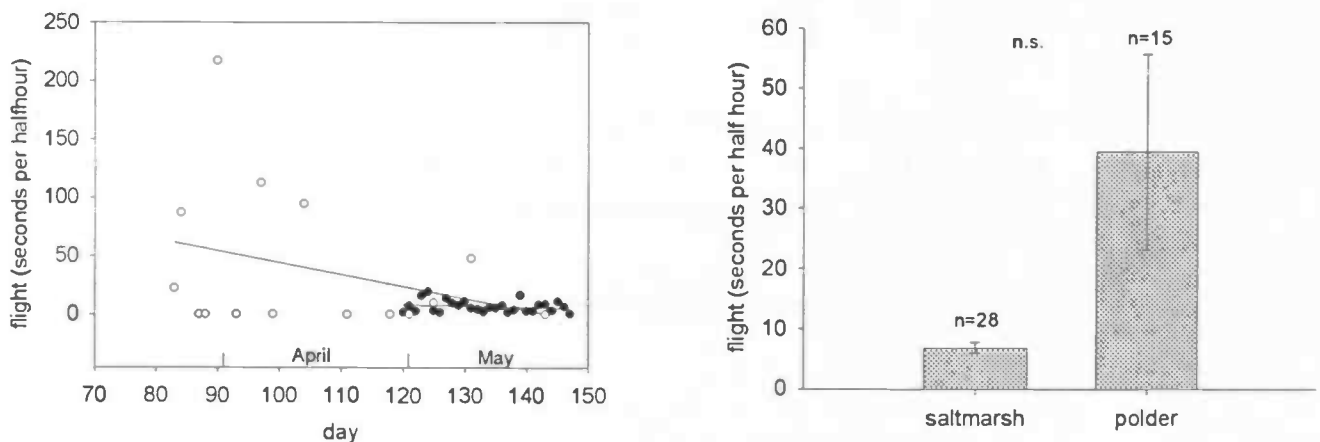

Figure 9. Flight expenditure on the polder (O) and the saltmarsh (●) during the season (a), the average flight expenditure per habitat (b).

7   Weather measurements

A relation was found between the windchill temperature and heart rate (GLM, $F_{1, 555} = 389.087$, $p = .000$)(figure x). The heart rate increased with a decreasing windchill temperature.
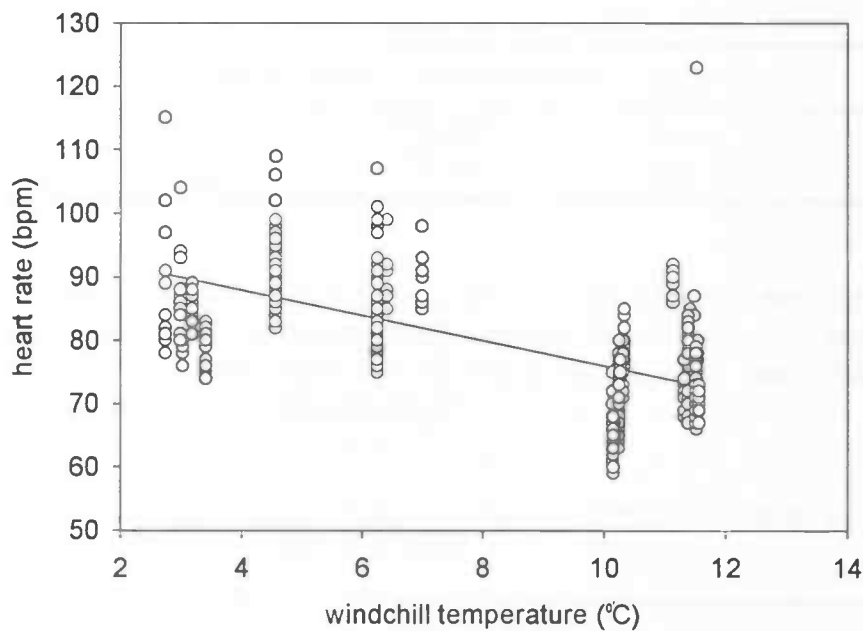

Figure 10. Relation between heart rate and windchill temperature.

7.1 Extrapolation of heart rate data to time-activity budgets

The calibration lines for heart rate and oxygen consumption of the Brent and Barnacle geese were used to express heart rate in energetic terms(equation 4, Eckert *et al* 1996). The basal metabolic rate of the Brent goose and the Brent geese is shown in table 5.

Table 5. BMR estimates from mean rest heart rate for the Brent and Barnacle goose. Oxygen consumption (VO_2) estimated by equation 1.

	Rest HR (bpm)	Calculated VO_2	BMR	BMR *Aschoff & Pohl*
Brent goose	88.3	1.155	6.4	5.13
Barnacle goose	66.9	1.124	6.3	6.57

Table 6. shows the energetic costs of specific behavioural parameters as hasbeen determined by using the average heart rate per behaviour per species. The energetic costs of all behavioural traits were lower for the Barnacle goose than the Brent goose.

Table 6. Metabolic rate of specific behaviour expressed in Watts and as a multiple of the BMR. (* Brunckhorst 1995, ** Nolet *et al* 1992)

	Rest		Walk		Forage	
	MR (W)	BMR	MR (W)	BMR	MR (W)	BMR
Brent goose	9.71	1.3	10.71	1.7	9.75	1.5
Barnacle goose	7.98	1.5	10.69	1.7	9.70	1.6

The MR values in table 6 of the Brent goose were used to convert the time-activity budgets to energy expenditure. Figure x shows that during the spring staging the energy expenditure decreased in both habitats. The energy expenditure decreased with about 0.2 Watts from mid March till end of May (GLM, $F_{1, 33} = 20.348$, p = .000) (figure 11). The energy expenditure on the saltmarsh was significantly higher than on the polder (GLM, $F_{1, 33} = 9.852$, p = .004).
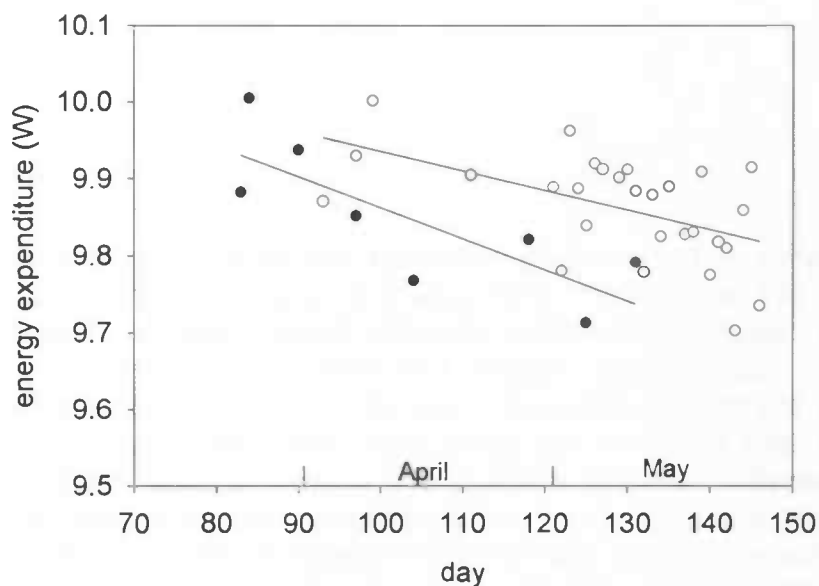
Figure 11. Energy expenditure of Brent geese in the polder (●) and on the saltmarsh (O) during spring staging, when flight is excluded.

To calculate the effect of flight activities on the energy expenditure in the two habitats, the regressions of flight activity against date (figure 9) were used. The costs of flight have a large impact on the energy expenditure. Figure x shows the energy expenditure including flight (10x BMR) during the spring for both habitats. When flight is included in the energy expenditure a significant difference has been found between in energy expenditure between the polder and the saltmarsh (ANOVA, $F_{1, 34}$ = 58.991, p = .000).
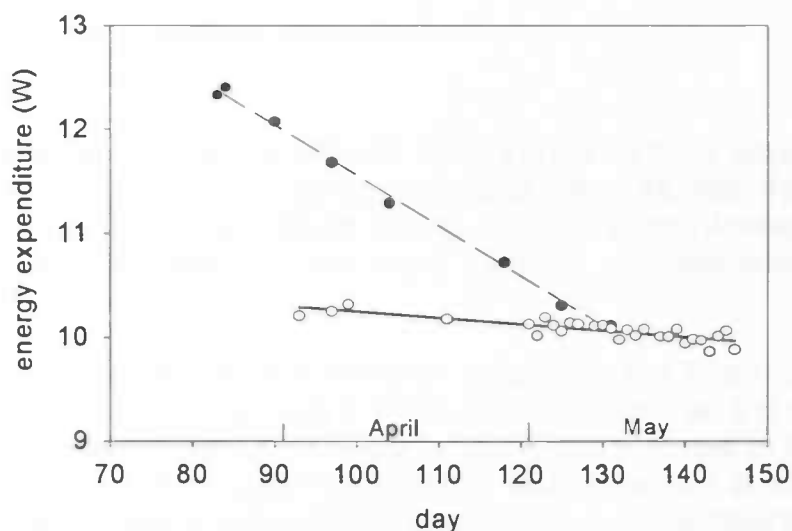

Figure 12. The energy expenditure of Brent geese on the polder (●) and the saltmarsh (O) during day time, including flight costs.

21

8 Discussion

8.1 Calibration

Individual variation in heart rate has been documented in varies studies on species of waterfowl (Wooley & Owen 1978, Nolet *et al* 1992, Gessaman 1980). Nolet *et al* (1992) found individual differences between the geese in the relation between heart rate and oxygen consumption. In this study individual differences could not be study because the sample size was too small. Nolet *et al* (1992) and Ely (1999) did conclude that even though individual differences were found, the average of these individuals could be used for a relation between heart rate and oxygen consumption. Individual differences in correlation between heart rate and oxygen consumption is due to differences in weight and condition of the geese. These individual differences will also be found in the field. Therefore an average of all individuals can be used.

The correlation between heart rate and oxygen consumption of Barnacle geese were compared with the Brent goose, a significant difference was found. The Brent goose uses less oxygen per heartbeat than the Barnacle geese. This is mainly due to the weight difference.

During the calibration trials there appeared to be a significant difference within individuals between nights. The geese sometimes showed an abnormal pattern in their heart rate registration. This pattern was mainly caused by bad contact between the electrodes and the skin. To achieve a more accurate calibration more trials per goose should be measured.

8.2 Energetic costs of behaviour

Ely (1999) found a lack of variation in heart rate for birds engaged in common field behaviours, and supports findings of other studies that reported little variation in energy expenditure among such activities (Wooley & Owen 1978, Weathers *et al* 1984). In this study variation was documented for natural behaviour.

Resting showed for all four barnacle geese and the Brent goose the lowest heart rate. The rest heart rate in the field was higher than the rest heart rate in the respirometer. The geese were probably more at rest in the respirometer than in the field, because in the field rest was measured at daytime and while in the respirometer it is at night in complete silence and darkness.

Foraging has a lower heart rate than the behaviour walking. The usual assumption is that while geese are foraging they're walking too. In this study the assumption can be made that the birds had a higher step rate during

walking than during foraging. Step rate needs to be included because it probably explains the difference.

The Brent goose had a significant higher heart rate than the barnacle geese. This could be due to its behaviour, the goose was very active, implying that resting heart rate is influenced by previous activity. The goose had many interaction with the other geese. Because in this study only one Brent goose observed, it can not be determined whether the higher heart rate is representative for the species. In this study the assumption is made that this Brent goose represents the average Brent goose.

The backpacks with the heart rate telemetry did have influence on the behaviour of the geese. The geese carrying the backpack showed more preening behaviour than the other geese (Wooley & Owen 1978). The longer time expenditure of preening did not affect the measurements of energy expenditure. The heart rate was measured per behaviour and therefore energetic cost of specific behaviour could be determined.

The backpacks do give some extra stress and could increase the heart rate. During and just after application the heart rate was very high (200 bpm), but gradually decreased within in half an hour to an average heart rate. The extra energetic costs of stress and weight caused by carrying a backpack can not be measured. In this study the assumption is made that these factors have little affect on the heart rate. The geese have been trained to get used to carrying the backpacks.

8.3 Observation of free-living Brent geese

The geese in a flock were randomly scanned. Holm (1997) reported in her study that the time budges were not significantly related position of the goose in the flock. The birds on the edge of the flock showed the same behaviour as the birds in the centre of the flock. In this study no distinction was made for the position of the goose in the flock. The flock size in the polder gradually decreased during the season, as did the total number of geese in the polder. This decrease is probably due to the habitat switch to the saltmarsh (Broekman 1998).

The time expenditure on walking decreased during the spring on both habitats. The tiller density increases in the polder during the spring (Bulten 1999). The abundance of the vegetation, e.g. plantago and trichlogin, increases during the spring (Prop & Deerenberg 1991). The increase of abundance could reduce the time of discovery, and therefore, the amount of locomotion.

The geese spent as much time foraging on the polder as on the saltmarsh. Time in the season had no effect on the foraging time of the geese. Stock & Hofeditz (1996) reported in their study that disturbance affects the foraging time. This is supported by the study of Riddington *et al* (1996) on the energy budgets of Brent geese along the north Norfolk coast. The geese are more in

flight on the polder in early spring in this study. It is expected that geese spend less time feeding in high disturbed areas (Riddington *et al* 1996), which means that in this study it is expected that geese spend less time foraging on the polder. In this study the geese spent the as much time on the polder as on the saltmarsh foraging and did not change through the season. The geese would need to compensate for their flight costs and therefore need to spend more time foraging during the day on the polder. It could be that the geese which have been disturbed on the polder feed at night time or partly in the saltmarsh, to balance their daily energy expenditure. In this study no observations have been done at night.

The geese on the polder spend more time resting than the geese on the saltmarsh during day time. This contradicts with the assumption that the geese need to forage more when they are more in flight, as is in the case of the polder versus the saltmarsh. It could be that the geese being observed in the polder mainly rest there and forage on the saltmarsh. Individual tracking needs to be done to determine the exact habitat use of the geese. Another hypothesis is that the geese on the polder feed at, or close to, their maximum possible rate throughout the day (Riddington *et al* 1996). The quality of the pastures is relatively high compared to the saltmarsh. Towards the departure date of the geese, the geese rest significantly more. Due to increase of day length, geese feeding at or near maximum intake can graze less intensively toward the end of May (Riddington 1996).

The geese are significantly more in flight in the beginning of spring than at the end of spring. In the polder the flock size decreases through the season. The effect of flock size on disturbance is also important. Large flocks are likely to be more wary and less tolerant of disturbance than small flocks, simply because there is a greater chance of large flocks containing 'jumpy' members which are liable to startle the rest of the flock (Riddington *et al* 1996). When large flocks are observed in the polder it is more likely that they fly off as a reaction on disturbance than small flocks, large flocks also are more likely to forage near the road (Broekman 1998, this study). Broekman (1998) reported that disturbance is mainly caused by traffic and pedestrians on the road in the polder. Small flocks are able to forage in the middle of the pastures, and therefore, keep enough distance from the road.

8.4   *Estimation of daily energy expenditure*

The basal metabolic rate is estimated using the relation between heart rate and oxygen consumption. Table 5. shows the values estimated by Aschoff & Pohl (1970). The BMR of the Brent goose in this study is much higher than their estimate. This may be explained by the fact that Aschoff & Pohl provide a model for all species, which therefore is not accurate on an individual basis (Kersten & Piersma 1987). The high activity of the Brent goose during the calibration trials could also explain the high BMR. To have a proper BMR estimate more individuals should be calibrated and more trials per individual should be done.

Nevertheless, the difference in BMR between this study and the Aschoff & Pohl will not affect the estimates of energy expenditure of the geese. The correlation between heart rate and oxygen consumption is used to calculate the energetic cost, instead of expressing energetic cost in multiples of BMR.

The energetic cost of resting was the lowest, and walking was the most expensive behaviour. Brunckhorst (1995) and Nolet (1992) found a very high energetic value for walking, 2.8*BMR and 2.4*BMR. The high value found by Nolet could be caused by the fact that the measurements were done in laboratory circumstances. The geese were forced to walk on a treadmill, while in this study the geese walked freely. The effect of stress could be higher in laboratory circumstance, which in turn affects the heart rate.

A relation was found between the windchill factor and the rest heart rate of the geese. We make the assumption the windchill conditions were the same on the two habitats. For more detailed analyses, the costs of thermoregulation have to be taken into account, and intensive measurements of microclimkate have to be conducted for both habitats.

In this study a comparison in energy expenditure between two habitats was made. The energy expenditure of the Brent geese when they are on a location, when flight is excluded, differed significantly between the two habitats. The energy expenditure was higher on the saltmarsh. This is probably due to the higher walking activity and the lower rest activity on the saltmarsh than on the polder. The energy expenditure of the birds is significantly higher on the polder when flight is included.

In this study we were not able to determine the daily energy expenditure, because the geese were not tracked the whole day. No sightings have been done after sun set. It could be that geese forage after dusk to balance their energy budget. On Schiermonnikoog the geese can easily fly from the polder to the saltmarsh or visa versa. The saltmarsh observations that have been reported in this study are done on the east side of the island. The assumption is that the geese who forage there do not fly to the polder. But the geese who forage in the polder do also forage on the saltmarsh. Therefore, the energy expenditure per habitat can be determined, but not the daily energy expenditure of the geese. When individual tracking is done an estimate of daily energy expenditure could be made.

In early spring the flight activity is much higher in the polder than on the saltmarsh. Disturbance is the main factor that causes the birds to fly (Broekman 1998). If flight has such a large effect on the energy expenditure of the geese, it would be expected that the geese would prefer the habitat with the least disturbance. The hypothesis is that the geese forage in the polder in early spring because there is not enough food on the saltmarsh to support all the geese. When the standing crop and quality of the palatable vegetation increases during the spring the geese switch to the saltmarsh.

9   Acknowledgement

10 References

ADT 1999. Calculating Windchill Values. National Center for Atmospheric Research, http://www.atd.ucar.edu/homes/rilling/wc_formula.html

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49: 227-267.

Aschoff, J. & Pohl, H. 1970. Der Ruheumsatz van Vögeln als Funktion der Tageszeit und des Körpergrösse. *J. Orn.* 111:38-47.

Bevan, R.M., Keijer, E. & Butler, P.J. 1992. A method for controlling the feeding behaviour of aquatic birds: heart rate and oxygen consumption during dives of different duration. *J. Exp. Biol.* 162: 91-106.

Bevan, R.M., Speakman, J.R. & Butler, P.J. 1995. Daily energy expenditure of tufted ducks: a comparison between indirect calorimetry, doubly labbelled water and heart rate. *Functional Ecology* 9: 40-47.

Bokma, F. 1999. An appraisal of heart rate as a tool for estimation of thermoregulatory energy expenditure – an experiment with Brent and Barnacle geese. Masters thesis, Zoological laboratory, Groningen University, The Netherlands.

Boudewijn, T. 1984. The role of digestibility in the selection of dpring feeing sites by Brent geese. *Wildfowl* 35: 97-105.

Broekman, M. 1998. Onderzoek naar terreinkeuze van rot- en brandganzen. Stage verslag, Van Hall Instituut, Leeuwarden, The Netherlands.

Brunkhorst, H. 1995. Ökologie und Energetik de Pfeifente (*Anas penelope*) im schleswig-holsteinischen Wattenmeer. Dissertation, Fachbereiches Biologie, Hamburg University, Germany.

Bulten, M.C. 1999. Habitat-preference of foraging Brent geese (*Branta b. bernicla*) in relation to management type. Masters thesis, Zoological Laboratory, University of Groningen, The Netherlands.

Butler, P.J. & Woakes, A.J. 1980. Heart rate, respiratory frequency and wing beat frequency of free flying barnacle geese *Branta leucopsis*. *Journal of Experimental Biology* 85: 213-226.

Eckert, R, Randall, D. & Augustine, G. 1996. Animal physiology, mechanisms and adaptations. Third edition, W.H. Freeman and Company, New York, USA.

Ely, C.R., Ward, D.H. & Bollinger, K.S. 1999. Behavioral correlates of heart rates of free-living greater white-fronted geese. *The Condor* 101:390-385.

Gessamen, J.A. 1980. An evaluation of heart rate as an indirect measure of daily energy metabolism of the American kestrel. *Comp. Biochem. Physiol.* 65A: 273-289.

Hill, R.W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyser. *Journal of Applied Physiology* 33(2): 261-263.

Holm, C. 1997. Time budget and flock structure in spring staging Dark-bellied Brent Geese. *Dansk Orn. Tidsskr.* 91: 109-115.

Kersten, M. & Piersma, T. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* 75: 175-187.

King 1974

Maurer, B.A. 1996. Energetics of avian foraging. In *Avian energetics and nutritional ecology*, ed. C. Carey, pp. 250-279, Chapman & Hall, New York, USA.

Murray, M.G. 1991. Maximizing energy retention in grazing ruminants. *Journal of Animal Ecology* 60:1029-1045.

Nolet, B, A., Butler, P.J., Masman, D. & Woakes, A.J. 1992. Estimation of daily energy expenditure from heart rate and doubly labeled water in exercising geese. *Physiological Zoology* 65: 1188-1216.

Prop, J. & Deerenberg, C. 1991. Spring staging in Brent Geese *Branta bernicla* feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19-28.

Riddington, R., Hassall, M., Lane, S.J., Turner, P.A. & Walters, R. 1996. The impact of disturbance on the behaviour and the energy budgets of Brent Geese *Branta b. bernicla. Bird study* 43: 269-279.

Riddington, R., Hassel, M. & Lane, S.J. 1997. The selection of grass swards by brent geese *Branta b. bernicla*: interactions between food quality and quantity. *Biological Conservation* 81: 153-160.

Robbins, C.T. 1993. Wildlife feeding and nutrition. Second edition. Academic press.

Siple, P.A. & Passel, C.F. 1945. Measurments of dry atmospheric cooling in subfreezing temperatures. *Proc. Amer. Phil.* Soc. 89: 177-199.

Stock, M. & Hofeditz, F. 1996. Time-activity budgets of Brent Geese (*Branta bernicla bernicla*) on saltmarsh in the Wadden Sea – the impact of human disturbance. *Vogelwarte* 38: 121-145.

Wal, R. van der 1992. The energetic costs of moult in the Greylag goose (*Anser anser*). Masters thesis, Zoological Laboratory, University of Groningen, The Netherlands.

Wal, R. van der, Koppel, J. van de & Sagel, M. 1998. On the relation between herbivore foraging efficiency and plant standing crop: an experiment with barnacle geese. *Oikos* 82:123-130

Weathers, W.W., Buttemer, W.A., Hayworth, A.M. & Nagy, K. 1984. An evaluation of time-budgets estimates of daily energy expenditure in birds. *Auk* 101: 459-472.

Williams, J.B., Siegfried, R.W., Milton, S.J., Adams, N.J., Dean, W.R.J., Plessis, M.A. du & Jackson, S. 1993. Field metabolism, wtaer requiremnets, and foraging behaviour of wild ostriches in the Namib. *Ecology* 74(2): 390-404.

Woakes, A.J. & Butler, P.J. 1983. Swimming and diving in Tufted Ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. Exp. Biol.* 107: 311-329.
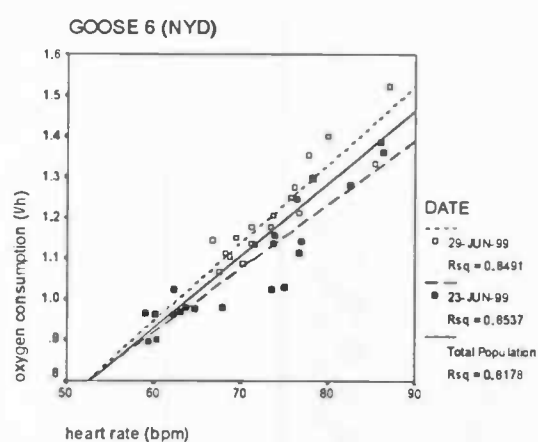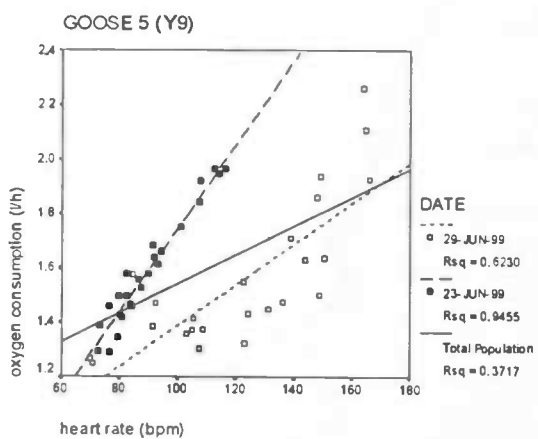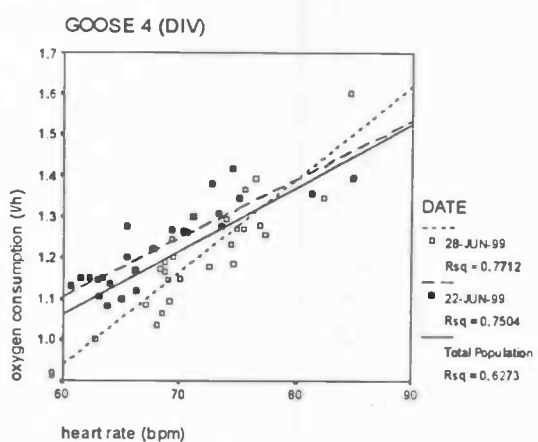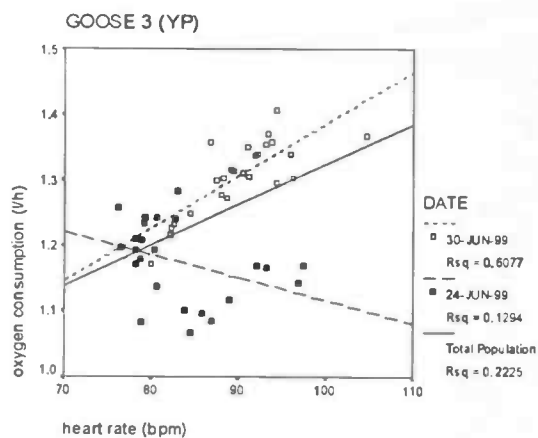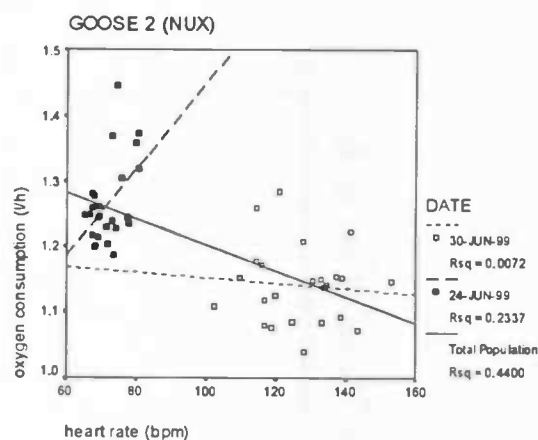
Wooley, J.B. & Owen, R.B. 1978. Energy costs of activity and daily energy expenditure in the Black Duck. *J. Wildl. Manage.* 42: 739-745.
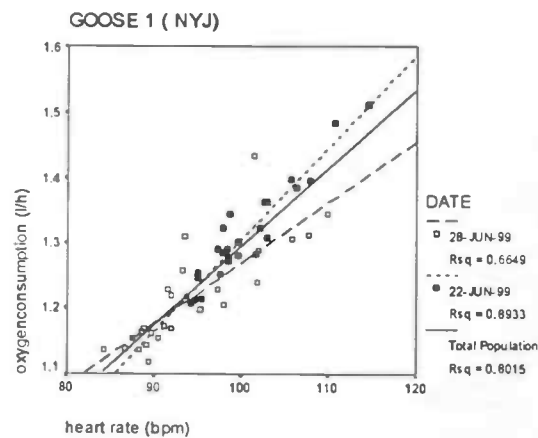
Wooley, J.B. & Owen, R.B. 1980. Energy costs of activity and daily energy expenditure in the Black duck. *J. Wildl. Manage.* 42(4): 739-745.

Ydenberg, R.C. & Prins, H.H.T. 1981. Spring grazing and the manipulation of food quality by Barnacle geese. *Journal of Applied Ecology* 18: 443-453.

11 Appendix

11.1 Appendix 1

GOOSE 1 (NYJ)

DATE
28-JUN-99
Rsq = 0.6649
22-JUN-99
Rsq = 0.8933
Total Population
Rsq = 0.8015

GOOSE 2 (NUX)

DATE
30-JUN-99
Rsq = 0.0072
24-JUN-99
Rsq = 0.2337
Total Population
Rsq = 0.4400

GOOSE 3 (YP)

DATE
30-JUN-99
Rsq = 0.6077
24-JUN-99
Rsq = 0.1294
Total Population
Rsq = 0.2225

GOOSE 4 (DIV)

DATE
28-JUN-99
Rsq = 0.7712
22-JUN-99
Rsq = 0.7504
Total Population
Rsq = 0.6273

GOOSE 5 (Y9)

DATE
29-JUN-99
Rsq = 0.6230
23-JUN-99
Rsq = 0.9455
Total Population
Rsq = 0.3717

GOOSE 6 (NYD)

DATE
29-JUN-99
Rsq = 0.8491
23-JUN-99
Rsq = 0.8537
Total Population
Rsq = 0.8178

nyd 0623