Travels in a changing world flexibility and constraints in migration and breeding of the barnacle goose

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Box

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Deposition of body stores in pastureland and salt marsh

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Barnacle geese, like many other waterfowl, have increasingly utilised improved grassland during the past 20 years, where forage quality is enhanced due to intensive agricultural fertilization (Van Eerden et al. 2005). It has been argued recently that geese feeding on agricultural pastures benefit from a higher rate of fat deposition, however, at the costs of protein accretion (Prop and Black 1998; Prop and Spaans 2004). However, evidence is inconsistent concerning the questions whether pastureland may represent a second choice habitat (Ebbinge 1992) for arctic geese and whether its usage as foraging site may impair the deposition of body stores and subsequent reproductive success (Prop and Black 1998; Spaans and Postma 2001). Here I investigate changes of body mass and body composition of barnacle geese on the Dutch Wadden Sea island Schiermonnikoog during spring staging period. I compare birds staging in an unmanaged natural salt marsh in the eastern part of the island with birds using heavily fertilised agricultural pastures six kilometres west of it (for a description of the study site see Van der Jeugd et al. 2001; Bos and Stahl 2003).

Methods

The total data set in the present analysis consists of BM measurements on 234 birds of both sexes and two age classes including immature birds (in their second calendar year, determined by presence of juvenile feathers: 11 females, 8 males) and adult birds (i.e., older than 1 year: 109 females, 106 males). By means of isotope dilution (ch. 2, 7) I estimated fat-free mass (FFM) and fat mass (FM) in a subsample of 54 adult females. Birds were sampled (caught, measured and released) at five occasions during the period 18 march to 20 April 2004 from agricultural pastures (three occasions) and salt marshes (two occasions). Further measurements included length of tarsus, head and wing. I use first principal component scores (PC1) generated from a principal component analysis (PCA) of these three structural measurements in order to account for variation in body size.

Results

Table Box D.1 (A) shows results of an analysis on BM comprising all birds in the data set, which are further illustrated in Fig. Box D.1. If corrected for structural size (i.e., including PC1 in the model) females and males did not differ in body mass. A quadratic date effect indicates a levelling off in BM gain towards the end of the study period. Immature birds were 83 g lighter than adults if both sexes are combined and 106 g lighter if only females are concerned (Table Box D.1B). Both sexes combined, pasture birds were on average 73 g lighter than salt-marsh birds. This can be mainly attributed to the condition of males. When females were tested separately no difference in BM between habitats was detected and BM increased linearly with date at a rate 10.3 g d^{-1} throughout the study period (Table Box D.1B), whereas habitat and quadratic date effects remained significant when males alone were tested (model not shown). The rate of BM gain did not differ between habitats regardless if sexes combined or separately are concerned.

FFM of adult females (corrected for differences in structural size) was the same in both habitats and increased with 3.6 g d^{-1} (Table Box D.1C), which should reflect the gain of wet protein mass. For the same sample BM increased at 10.9 g d^{-1} and the difference of 7.3 g d^{-1} is considered to reflect the gain of FM (Fig. Box D.2). Thus FM and wet protein mass contributed with 67% and 33%, respectively, to the BM gain observed during the study period. This translates into a ratio of fat to dry protein of 8.1, assuming a 75% water content in the gained fat-free component (assumed to be mainly muscle tissue; Box B). An analysis of fat-free mass changes over time following the approach suggested by (Lindström and Piersma 1993) assumes a closed population wherein body mass deposition is synchronised among

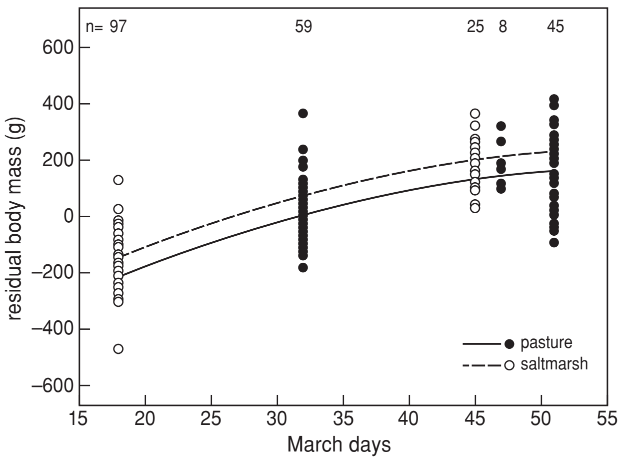

Figure Box D.1. Body mass development of barnacle geese staging in agricultural pastures or salt marsh habitat on the Dutch island Schiermonnikoog. Plotted is the residual body mass (corrected for body size) of both sexes and adult and second calendar year birds combined. See Table Box D.1 for details on the statistical model. Sample sizes are given in the top of the figure.

Table Box D.1. ANCOVA results of body mass for all birds (A), body mass of females only (B) and fat-free body mass of adult females (C) of barnacle geese caught during spring staging on the Dutch island of Schiermonnikoog. PC1 refers to the first principal component from a PCA of tarsus, head and wing. When both sexes were included in the model (as in A) we used PC1 scores from a single PCA over all birds. When only females were concerned (B and C) we used PC1 scores generated for females only. Main effects and all possible two-way interactions were tested and non-significant terms were removed by backward deletion from the models. Some non-significant terms (n.s.) are shown in brackets; given is the F-value when included in the final model. Estimated coefficients (b) with associated standard errors (s.e.) are given only for statistical significant parameters. Note that the "Date" variable refers to March days with the intercept set at March day=0. Coefficients for "Habitat" and "Age" are set relative to reference category "salt marsh" and "adult", respectively.

A) Body mass

Parameter	B	s.e.(B)	df	F	*P*
Intercept	1236	68.8	1	237.93	<0.0005
PC1	109.2	6.7	1	267.14	<0.0005
Date	27.8	4.8	1	34.01	<0.0005
Date^2	-0.2	0.1	1	12.62	<0.0005
Age	-82.5	24.2	1	11.64	0.001
Habitat	-72.6	19.9	1	13.34	<0.0005
(Sex)			1	0.57	n.s.
(Date x Habitat)			1	0.98	n.s.
Final model (R^2= 0.77)			5	152.75	<0.0005
Total			233		

B) Body mass females

Parameter	B	s.e.(B)	df	F	*P*
Intercept	1403	25.05	1	2280.16	<0.0005
PC1	70.4	9.8	1	51.77	<0.0005
Date	10.3	0.7	1	197.50	<0.0005
(Date^2)			1	0.20	n.s.
Age	-106.3	33.7	1	9.98	0.002
(Habitat)			1	1.70	n.s.
(Date x Habitat)			1	1.37	n.s.
Final model (R^2= 0.72)			3	97.01	<0.0005
Total			119		

C) Fat-free mass adult females

Parameter	B	s.e.(B)	df	F	*P*
Intercept	1342	30.1	1	1983.71	<0.0005
PC1	62.1	10.9	1	32.15	<0.0005
Date	3.6	0.8	1	21.13	<0.0005
(Date^2)			1	1.87	n.s.
(Habitat)			1	0.02	n.s.
(Date x Habitat)			1	1.54	n.s.
Final model (R^2= 0.56)			2	31.93	<0.0005
Total			53		

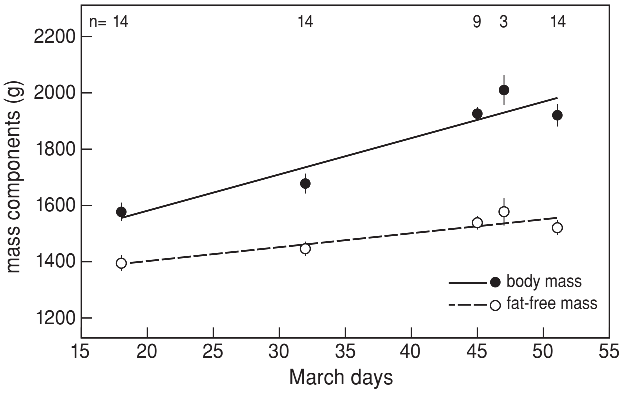

Figure Box D.2. Development of body mass components in adult female barnacle geese during spring staging on the Dutch island Schiermonnikoog. Changes in total body mass (BM) or fat-free mass (FFM) did not differ between geese from agricultural pastures or salt-marsh habitat. Rates of mass increase are 3.6 g d^{-1} for FFM and 10.9 g d^{-1} for BM (10.3 g d^{-1} if BM for all females in the data set is modelled, see Table Box D.1 B and C for statistical models and tests). Sample sizes are given in the top of the figure.

individuals. We know that barnacle geese on Schiermonnikoog belong to populations breeding in Arctic Russia and in the Baltic. The proportion of Baltic birds in the sample likely decreased towards the end of the study period (20 April). Also, it cannot be excluded that birds from these populations differ in their stage of deposition at a given time point or aim for a different composition of stores in general. Van der Meer and Piersma (1994) suggested alternative approaches for an estimate of the composition of body stores, which may account better for individual variation in stage of body store deposition at a given sampling event. I applied their model 2b and regressed FFM corrected for structural size on FM (FM was not related to PC1). This yields a slope of 0.235 indicating a contribution of wet protein to total BM gain of 23.5% (see Fig. Box D.3) and a fat/dry protein ratio of 13.0.

Discussion

I conclude that wet protein comprised a quarter to a third of body stores deposited by adult females during spring staging in the Wadden Sea. Total gain rates and composition of stores appeared to be similar for birds staging in agricultural pastures and salt marshes. Immature birds showed lighter BM than adults, but a difference in BM gain rates between age groups could not be detected. McLandress and Raveling (1981) found similar age effects in giant Canada geese *Branta canadensis maxima* before initiating spring migration in April. Their argument that immature birds may be not in preparation for reproduction as Canada geese almost never nest at this young age seems applicable also for the barnacle goose (Black et al. 2007). It would be of course interesting to know what precisely are the proximate factors preventing them from doing so (e.g., experience, dominance, physiological development).

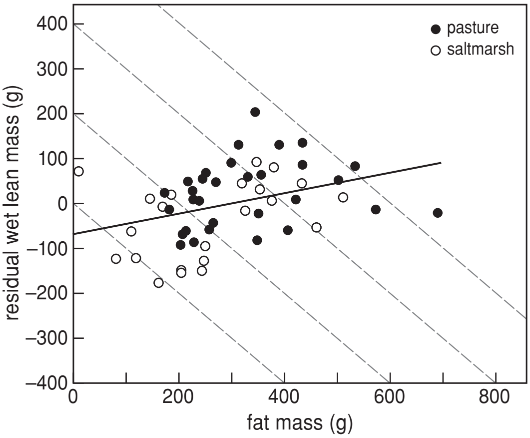

Figure Box D.3. Residual fat-free mass (accounting for PC1) against fat mass of adult female barnacle geese from the Dutch island Schiermonnikoog in spring (same data as in Table Box D.1C and Fig. Box D.2). The slope ($y = 0.235x$; $F_{1,53} = 7.35$, $P = 0.009$) did not differ between geese from different habitats ($F_{1,53} = 2.80$, n.s.) depicted by closed circles (pasture) and open circles (saltmarsh). Diagonal dashed lines are lines of equal body mass.

Adult female giant Canada geese from the same study sampled on 4-7 March and on 4-6 April revealed a ratio of fat to dry protein in the gained body stores of 9.5, which is within the range of estimates for barnacle geese in the Wadden Sea. The composition of stores can be highly variable among goose species and can vary considerably even within species (see Table 8 in Prop and Black 1998). For barnacle geese from the Spitsbergen population staging in northern Norway Prop and Black (1998) recorded fat/protein ratios of stores of 1.2 to 1.4 while using traditional salt-marsh sites but measured a fat/protein ratio of stores of 22.6 for geese using nearby agricultural pastures. Similarly, composition of gained stores may vary during periods of deposition. For instance, comparing body composition of the female giant Canada geese from 4-7 March to an earlier sample taken 12-16 February yields an increase of total BM and FFM but a decrease of fat mass (McLandress and Raveling 1981). Such temporal variation in composition of stores with fat/protein ratios often increasing during pre-migratory deposition has been observed also in several other studies (Alisauskas and Ankney 1992a; Gauthier et al. 1992; but see Sedinger et al. 1992; Battley and Piersma 1997; Prop and Spaans 2004) and may be well controlled by endogenous circannual programs (Dietz et al. 1999).

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