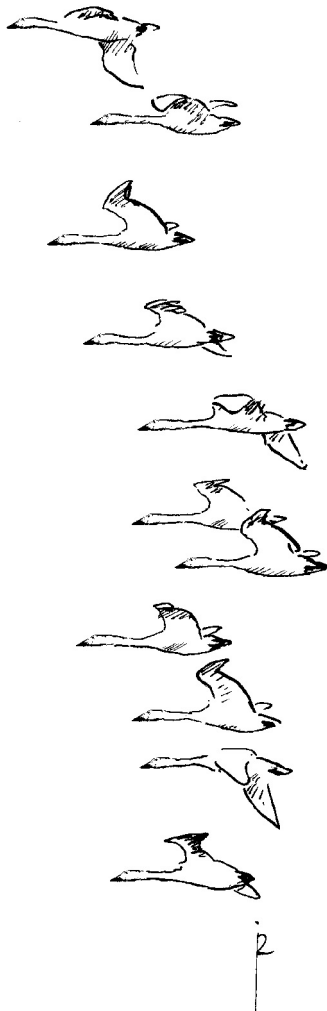


Speed of spring migration of Tundra Swans *Cygnus columbianus* in accordance with income or capital breeding strategy?

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Large migratory birds may bring along stores in order to survive adverse conditions and produce a clutch upon arrival ('capital breeders') or they may acquire all the necessary resources on the breeding grounds ('income breeders'). Whether birds are capital- or income-breeders may depend on the distance between the last stopover site and the breeding grounds and the length of the summer season. The degree of capital-breeding may therefore differ among flyway populations of the same species. I used migration speed as a proxy for the degree of capital-breeding, and compared the observed migration speeds of satellite-tracked Tundra Swans *Cygnus columbianus* from all four main flyway populations with those predicted by an allometric model for 6-kg waterfowl. Average overall spring migration speed of Tundra Swans was 52.2 km d⁻¹, close to that predicted under a capital-breeding strategy (i.e. carrying the stores for the whole clutch and allowing for 8 days of starvation). This migration speed was in accordance with the speed at which the ice retreats in spring. However, the energy stores for clutch formation and survival on the breeding grounds may be primarily put on at the last stopover. Tundra Swans ('Whistling Swans') in the Nearctic, and especially in the Western Nearctic, make use of the rapid advancement of spring on their last leg and accelerate their migration speed accordingly, and so probably rely on income-breeding. In the Western Palearctic, Tundra Swans ('Bewick's Swans') are faced with a slow advancement of spring on their last track, and they may fare better by building up stores on the last stopover and bring these to the breeding grounds. This may not be an option for swans in the Eastern Palearctic, as they are confronted with a very long last leg. The variation in migration speeds on the last leg suggests a large variation in the degree of capital-breeding among flyway populations of Tundra Swans.

Key words: allometry, bird migration, capital-income breeding, Bewick's Swan, migration speed, satellite tracking, stopover ecology, Whistling Swan

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INTRODUCTION

Migratory birds may bring body stores to the breeding grounds in order to survive adverse conditions and produce a clutch upon arrival. Birds that bring along stores are termed capital breeders, whereas birds that do not are termed income breeders (Drent & Daan 1980). Migratory birds alternate energetically expensive flights with feeding bouts at stopover sites, and the speed of migration is more determined by fuelling rate than flight speed (Hedenström & Ålerstam 1998). In income breeders the stopover time is wholly spent on fuelling stores for the next flight, whereas in capital breeders part of it is spent on fuelling reserves for survival at the breeding grounds and stores for egg formation. Because capital breeders do not use their whole energy load to fuel flight, they pay a cost in terms of a reduction in flight distance of the next leg. Migration speed, defined as the flight distance divided by the stopover time plus flight time, can therefore be used as a proxy for the degree of capital breeding.

Body size is probably the main factor affecting the use of capital vs. income breeding. Allometric scaling relationships between potential flight distance and body size indicate that capital breeding is an option for large long-distance migrants but less so for small ones (Klaassen 2003). In accordance with this, isotope analyses indicated income breeding in arctic waders (<250 g) (Klaassen *et al.* 2001). Focussing on larger birds (>250 g), other factors than body size may affect whether a capital or income breeding strategy is actually being used. If the distance between the last stopover site and the breeding grounds is large, capital breeding may not be possible because all stores are needed to cover the flight distance (Choinière & Gauthier 1995, Klaassen 2003). Also, if the summer season is relatively long, income breeding may be favoured because birds are expected to arrive on the breeding grounds as soon as possible to gain access to limited resources (Kokko 1999).

Swans *Cygnus* spp. are the largest long-distance migrants that use flapping flight. Theoretically, their speed of migration should be low

because their flight speed and fuelling rate rise less steeply with body mass than their flight costs (Hedenström & Ålerstam 1998). In addition, because of their large size, the time needed for successful breeding is long (Rahn & Ar 1974). Migratory swans are therefore expected to be among the most time-stressed of all birds (Rees *et al.* 1996), and capital breeding may be the only way to complete the breeding cycle in time. Their relatively large size also means that swans were among the first birds to be equipped with satellite transmitters (Beekman *et al.* 1996). With the aid of these transmitters it is possible to measure the chronology of the migration of individual birds.

Tundra Swans *Cygnus columbianus* breed in tundra regions around the north pole, and winter in temperate regions of the coastal areas of the Pacific and Atlantic Ocean, spending as much as half of the year on migration between these regions. Individuals of all four main flyway-populations have been tracked on their migration by satellite: the western and eastern population of Whistling Swan *Cygnus c. columbianus* in North-America (Nearctic), and the western and eastern population of Bewick's Swan *Cygnus c. bewickii* in Eurasia (Palearctic). I compared these four in order to identify possible differences in migration trajectories and schedules among the flyway populations that may be related to the degree of capital breeding. Specifically, their migration speed was compared with that of Tundra Swan-sized waterfowl using an income- or capital-breeding strategy, as predicted by a modified version of an allometric model developed by Klaassen (2003).

METHODS

Tundra Swans belonging to one of the four main flyway populations were equipped with platform transmitting terminals (PTTs) from NTT/Toyocom (Tokyo, Japan) or Microwave Telemetry (Columbia, Maryland). The transmitters weighed 30–185 g comprising, together with the attachment tools, 1.3–4.0% of the body weight (Table 1). The signals of the PTTs were picked up by a TIROS-NOAA

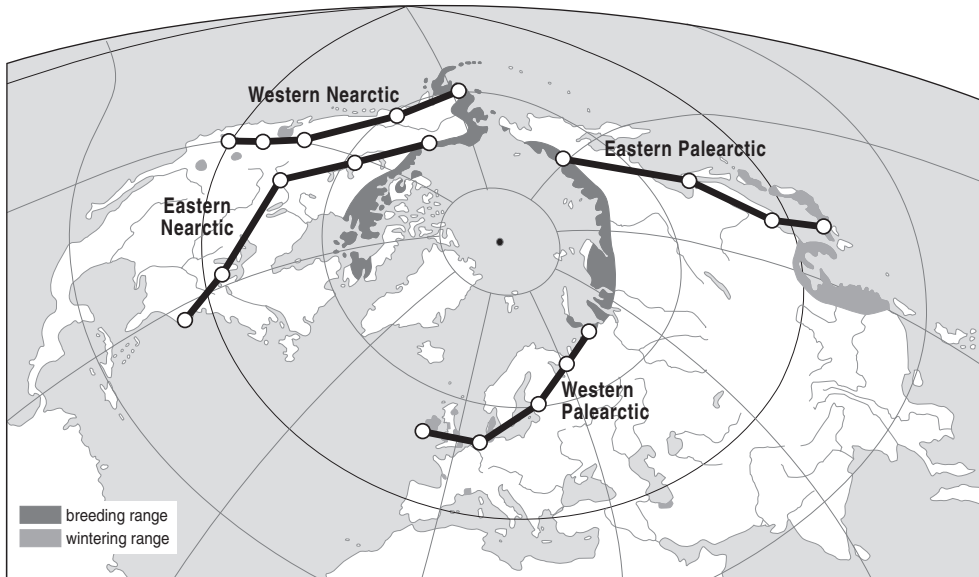


Figure 1. Schematic representation of the migratory trajectories of Tundra Swans from the four flyway populations. Circles denote main wintering, stopover and breeding sites. Breeding and wintering range from Cramp & Simmons (1977).

satellite, that relayed its data to a ground-based ARGOS processing centre. The location of the transmitter is determined from the Doppler shift as successive signals are received. The processed data include time, latitude, longitude and an index of the accuracy of the location. During the migration typically one valid location was obtained per day per bird (Beekman *et al.* 1996).

Locations were grouped into stopovers by pooling fixes of different individuals that were closer to each other than to other fixes; when available the stopovers as defined by the original studies were used (Beekman *et al.* 2002, Petrie & Wilcox 2003) (Fig. 1). If the exact arrival or departure dates were not known, the median date between the last fix at one stopover and the first fix at the next was

Table 1. Published accounts of Tundra Swans tracked by satellite.

Flyway ^a	Range of transmitter weight ^b (g)	Number tracked	Number successful ^c		Year		Reference
			spring	autumn	spring	autumn	
WN	30–50	9	2 (1)	4 (2)	1995	1994	Ely <i>et al.</i> 1997
EN	30–95	12	11 (1)	8 (1)	1998–2000	1998–2000	Petrie & Wilcox 2003
WP	185	3	3	0	1990		Nowak <i>et al.</i> 1990
WP	45–95	18	2 (1)	5 (5)	1993,1996	1998	Beekman <i>et al.</i> 2002
EP	83	4	2 (1)	0	1990		Higuchi <i>et al.</i> 1991
EP	89–105	8	2	0	1994,1997		Kamiya & Ozaki 2002

^aWN = Western Nearctic, EN = Eastern Nearctic, WP = Western Palearctic, EP = Eastern Palearctic.

^bExcluding attachment tool (harness and/or neck-collar).

^cData for at least one leg of the migration; number for complete migration given in brackets.

used. The duration at a given stopover site i T_i was calculated as the departure date minus the arrival date. Body mass increases in the first few weeks after arrival on the wintering site, but remains relatively constant in December–January (Evans & Kear 1978). Preparation for migration will take place after this date and I assumed it to be of similar duration as the average stopover duration (see Results). As the distance between the successive stopovers D_{ij} the great circle distance was calculated from the latitudes and longitudes of the centres of stopovers i and j (Imboden & Imboden 1972). The migration speed on this stretch $V_{migr_{ij}}$ was calculated as:

$$V_{migr_{ij}} = \frac{D_{ij}}{\frac{D_{ij}}{V_{flight}} + T_i} \quad (1)$$

where V_{flight} was assumed to be a ground speed of 20 m s⁻¹ (Beekman *et al.* 2002). $V_{migr_{ij}}$ was averaged over the individuals tracked on this stretch. As individuals were generally tracked in more than one year (Table 1), these migration speeds do not refer to a specific year. Overall migration speed was calculated as:

$$V_{migr} = \frac{\sum D_{ij}}{\frac{\sum D_{ij}}{V_{flight}} + \sum T_i} \quad (2)$$

For each stopover a representative weather station was chosen out of the c. 1000 weather stations in the world climate information database of the Netherlands' meteorological office KNMI (see <http://www.knmi.nl/product/>), and its mean monthly air temperatures averaged over 1961–1990 were taken. Assigning the mean value to the median date of each month, per stopover site the day number d_0 at which the daily temperature was 0°C was calculated by linear interpolation. The speed of the onset of spring on a given stretch from site i to j $V_{spring_{ij}}$ was subsequently calculated as:

$$V_{spring_{ij}} = \frac{D_{ij}}{d_{0j} - d_{0i}} \quad (3)$$

Overall speed of the onset of spring was calculated as:

$$V_{spring_{ij}} = \frac{\sum D_{ij}}{d_{0k} - d_{0i}} \quad (4)$$

where the subscript k denotes the breeding site.

The expected speed of migration for a Tundra Swan was calculated by setting V_{migr} equal to (Hedenström & Ålerstam 1998):

$$V_{migr} = \frac{V_{flight} \times P_{fuel}}{P_{fuel} + P_{flight}} \quad (5)$$

where V_{flight} is flight speed, P_{flight} is the power requirement of flight and P_{fuel} is the rate of energy deposition during (re)fuelling. These variables were derived from allometric relationships for birds (where available for waterfowl Anseriformes) (Table 2). This V_{migr} is the migration speed of an income breeder. Its stopover duration T_{fuel} is:

$$T_{fuel} = \frac{E_{load}}{P_{fuel}} \quad (6)$$

where E_{load} is the maximum load L (g; Table 2) multiplied by the energy density of the stores (30 kJ g⁻¹; Jenni & Jenni-Eiermann 1998). The resulting maximum flight distance D_{max} is:

$$D_{max} = E_{load} \times \frac{V_{flight}}{P_{flight}} \quad (7)$$

A capital breeder has to allocate part of the stores to its clutch and part to reserves for survival. I calculated the energy needed for the clutch by multiplying the energy per egg and the clutch size (Table 2), assuming a synthesis efficiency of 77% (Rahn *et al.* 1985). This efficiency does not account for the production of ovary and oviduct (Carey 1996), so I added the energy content of these, assuming a synthesis efficiency of 100% (Table 2). I also calculated the energy needed to survive 0–8 days at the field metabolic rate for waterfowl (Stahl *et al.* 2001), using an energy density of the reserves of 30 kJ g⁻¹ (Jenni & Jenni-Eiermann 1998). These energy needs were converted in flight distance by dividing them by the locomotion cost of flying and also converted in fuelling time by dividing them by the rate of

Table 2. Allometric relationships used to derive migration speeds of waterfowl. M is body mass (g).

Variable	Symbol	Unit	Equation	Group	Reference
Observed flight speed	V_{flight}	$m\ s^{-1}$	$10.4\ M^{0.075}$	waterfowl	Clausen <i>et al.</i> 2002
Flight power	P_{flight}	W	$0.150\ M^{0.868}$	flapping birds	McWilliams <i>et al.</i> 2004
Maximum deposition rate ^a	P_{fuel}	W	$0.0789\ M^{-0.34}\ (M^{-1/2}\ L)$	birds	Lindström 2003
Maximum load	L	g	$1.98\ M^{0.948} - M$	flapping birds	Hedenström & Alerstam 1992
Field metabolic rate		W	$0.0897\ M^{0.656}$	waterfowl	Stahl <i>et al.</i> 2001
Energy per egg		J	$4.7\ 10^3\ M^{0.68}$	waterfowl	based on Rahn <i>et al.</i> 1975, Sotherland & Rahn 1987
Energy in ovary/oviduct		J	$655.5\ M^{0.938}$	birds	Walsberg 1983
Observed clutch size		–	$40.4\ M^{-0.26}$	waterfowl	data Cramp & Simmons 1977

^aCalculating lean body mass as $M - 1/2 L$ and assuming an energy density of stores of $30\ kJ\ g^{-1}$ (Jenni & Jenni-Eiermann 1998).

energy deposition during refuelling P_{fuel} . As the migrants were assumed to fuel to their maximum load, the duration at a stopover site should not change with the degree of capital breeding (only the proportion used for refuelling for the next flight), but the distance of the subsequent flight should be less for a capital breeder than for an income breeder. Hence, migration speed of an income-breeder can (also) be written as:

$$V_{migr} = \frac{D_{max}}{\frac{D_{max}}{V_{flight}} + T_{fuel}} \quad (8)$$

whereas for a capital-breeder the distance $D = D_{max} - E_{store} \times V_{flight} / P_{flight}$ instead of D_{max} was used in equation 8, where E_{store} stands for the required energy stores for clutch production and survival reserves.

RESULTS

As shown previously by Klaassen's (2003) allometric model, the maximum flight distance does not change greatly with body mass, but allocating part of the energy stores to a clutch would reduce the flight distance much more in small than in large waterfowl (Fig. 2A). Similarly, saving part of the energy stores as reserves for its own survival after

reaching the breeding grounds would result in a disproportionately greater reduction in flight distance in small than in large waterfowl. Consequently, the allometric model predicts that there is more scope for capital breeding in large waterfowl species than in small ones. In fact, full capital breeding as defined here (i.e. carrying the stores for the whole clutch and allowing for 8 days of starvation), would not be possible for waterfowl smaller than c. 1 kg (Fig. 2A and Fig. 3A). In terms of stopover duration, the same trends hold, except that the stopover duration is not reduced when stores are carried, but part of the stopover period is being used for storage rather than refuelling for flight (Fig. 2B). With mean female body masses of 5.7 kg for the Palearctic populations (Cramp & Simmons 1977) and 6.3 kg for the Nearctic populations (Limpert & Earnst 1994), Tundra Swans are in the range where capital breeding is an option (Fig. 2).

Average overall spring migration speed of Tundra Swans is $52.2\ km\ d^{-1}$ (Table 3). This is much slower than the migration speed predicted by the allometric model under an income-breeding strategy, and in fact close to that predicted under a full capital-breeding strategy. When this is compared with the spring migration speeds of other waterfowl species from which satellite tracking data are available, Tundra Swans fall on the trend

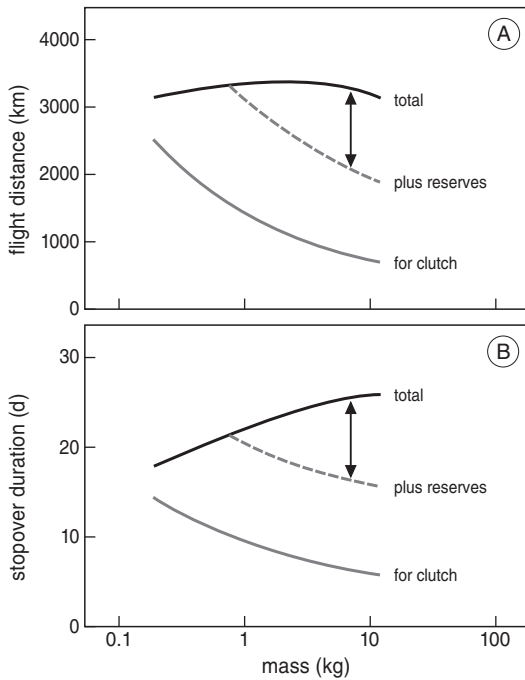


Figure 2. Migratory performance of waterfowl according to allometric relationships (Table 2). The black lines indicate the (A) maximum flight distance and (B) corresponding stopover duration of waterfowl that uses all its stores for migratory flight (i.e. income breeder). The flight distance traded-in and the stopover duration needed, respectively, to accumulate the stores to supply the energy for the whole clutch are indicated by the grey lines. Those for an additional starvation of 8 days are indicated by the dashed grey lines. The arrows indicate the remaining flight distance and the remaining ‘fuel-for-flight’ stopover duration, respectively, of a Tundra Swan-sized full capital breeder.

of an increase in capital breeding with body mass, from bringing 40% of the stores to the breeding grounds in the Northern Pintail to 90% in Tundra Swans and close to 100% in Whooper Swans (Fig. 3B).

When the migration speeds are calculated from one site to the next (Table 4), a different picture emerges. Up to the last stopover a migration speed of c. 50 km d⁻¹ is reached in all flyway populations, but the migration speed over the last leg

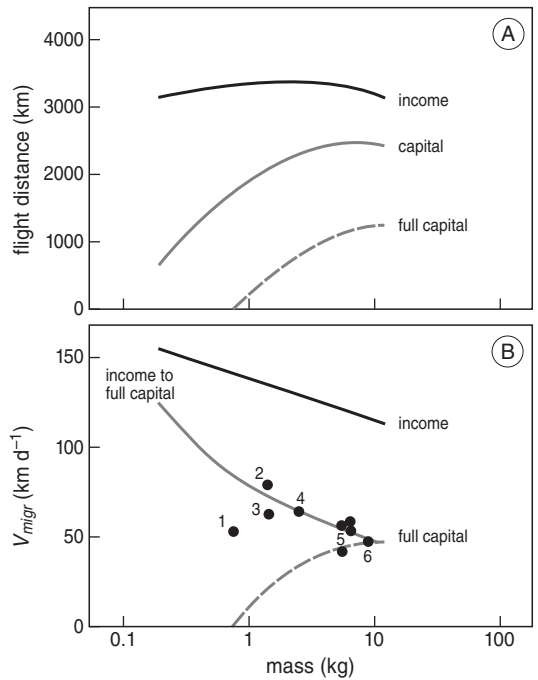


Figure 3. (A) Resulting maximum flight distances of different-sized waterfowl using an income-breeding strategy, a capital-breeding strategy (clutch but no survival reserves) or a full capital-breeding strategy (i.e. enabling the immediate production of a clutch as well as allowing for 8 days of starvation). (B) Corresponding migration speeds V_{migr} . Grey line indicates (log-linear) gradient from 100% income-breeding in a hypothetical 100 g waterfowl species to full capital-breeding in a 10 kg swan. Dots indicate observed overall spring migration speeds against mean female body mass (Cramp & Simmons 1977) in satellite-tracked waterfowl species: (1) Northern Pintail *Anas acuta* (using direct Alaska migration, Miller et al. 2005), (2) Light-bellied Brent Goose *Branta bernicla hrota* (Clausen et al. 2003), (3) Dark-bellied Brent Goose *Branta bernicla bernicla* (Green et al. 2002), (4) Greenland White-fronted Goose *Anser albifrons flavirostris* (Fox et al. 2003), (5) Tundra Swan (four dots, this study), and (6) Whooper Swan *Cygnus cygnus* (Kanai et al. 1997).

(i.e. last stopover plus last flight) is considerably higher in three of the four populations (Fig. 4A). The migration speed may be constrained by climatic conditions. Outside the breeding season, the mean daily temperature that Tundra Swans

Table 3. Mean overall spring migration speed V_{migr} (km d^{-1}) of Tundra Swans of the four main flyway-populations in comparison with the speed of the onset of spring (ie. retreat of 0°C isotherm). n indicates the number of individuals on which the estimate is based.

Flyway ^a	One-way distance(km)	V_{migr} (km d^{-1})	V_{spring} (km d^{-1})
WN	5300	53.6 ($n = 2$)	51 ^b (68°)
EN	5500	57.8 ($n = 11$)	56 (65)
WP	3950	41.1 ($n = 5$)	55 (36)
EP	4350	56.3 ($n = 4$)	48 (62)
Mean \pm SE		52.2 \pm 3.8	52.5 ^b \pm 1.8

^aSee Table 1 for abbreviations. ^bExcluding last leg.

^cIncluding last leg.

encounter is $4.1^\circ\text{C} \pm 3.9$ SD ($n = 42$). During this period they are generally just one site further south than where sub-freezing temperatures are normal (Table 5). I therefore looked at how fast the 0°C isotherm moves northward as a measure of the speed of the onset of spring. This speed V_{spring} is again c. 50 km d^{-1} up to the last stopover on all flyways. On the last leg, however, it varies greatly among the flyways, with a high V_{spring} in Western Nearctic and a low one in the Western Palearctic (Fig. 4B). Whereas the high V_{spring} in the Nearctic seems to enable a high V_{migr} on the last leg to the breeding grounds, Tundra Swans in the Palearctic migrate finally nearly twice as fast as V_{spring} (cf. Fig. 4A and B).

Table 4. Migration speed $V_{migr_{ij}}$ (from given site to the next) of Tundra Swans tracked by satellite calculated from mean stopover durations and flight distances.

Flyway ^a	Site ^b	Timing ^c	Region	Distance to next site (km)	Stopover duration (d)	$V_{migr_{ij}}$ (km d^{-1})
WN	W		California	900	^d 24	37.1
	S1	I Feb– I Mar	Great Basin	1100	23	46.5
	S2	II Mar– I Apr	Northern Prairie	1800	39	45.0
	S3	II Apr	Yukon-Alaska	1500	10	138.0
	B	May	Alaska (Y-K Delta)			
EN	W	II Feb	Atlantic Coast	1000	16	60.3
	S1	Mar	Great Lakes	1500	25	58.0
	S2	Apr	Northern Prairie	1500	37	39.6
	S3	May	Northern Boreal Forest	1500	14	100.9
	B		Arctic Coast			
WP	W		North Sea countries	1100	^d 24	45.1
	S1	Mar	Germany/Denmark	1000	23	42.4
	S2	Apr	Baltic/Finnish Gulf	1100	30	35.9
	S3	May	White Sea	750	17	43.0
	B		Barentsz Sea Coast			
EP	W		Honshu (Japan)	800	^d 24	33.0
	S1	Apr	Tumangan River/Hokkaido	1350	37	35.7
	S2	May	Lower Amur River/N-Sakhalin	2200	14	144.0
	B		Northern Siberia			

^aSee Table 1 for abbreviations. ^bW = wintering site, S = stopover site, B = breeding site. ^cI = first half, II = second half of month.

^dAverage stopover duration (see text).

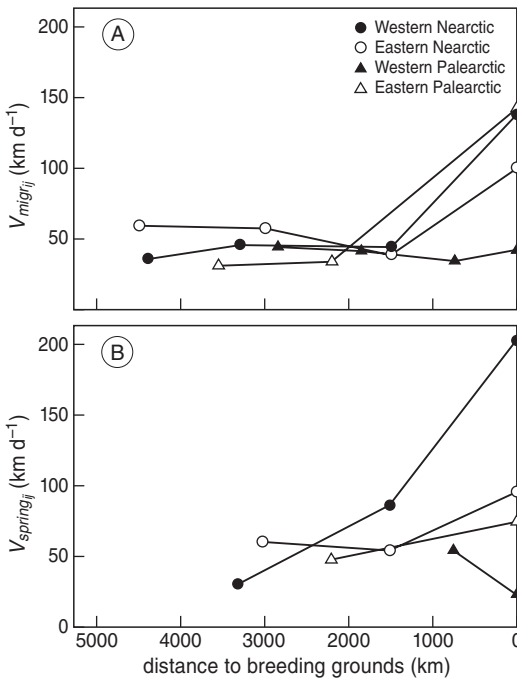


Figure 4. (A) Migration speeds $V_{migr_{ij}}$ per stopover site of satellite-tracked Tundra Swans belonging to four flyway populations: Western Nearctic (WN), Eastern Nearctic (EN), Western Palearctic (WP), and Eastern Palearctic (EP). Migration speeds are plotted relative to the distance to the breeding grounds after the flight. (B) Speed of the onset of spring $V_{spring_{ij}}$ from one site to the next along the migration routes of the Tundra Swans. For some sites at lower latitudes $V_{spring_{ij}}$ cannot be calculated because mean monthly temperatures are above zero during the whole year.

When the migration speeds over the last leg are plotted, only the Western Palearctic Tundra Swans still fall on the line predicted by the allometric model under a full capital-breeding strategy (i.e. enabling the immediate production of a clutch and allowing for 8 days of starvation). The Eastern Palearctic and Western Nearctic Tundra Swans are now even above the line for income-breeding. The Eastern Nearctic Tundra Swans are somewhere in between; they could carry energy reserves for a few days of starvation or trade this for part of the energy stores for a clutch (Fig. 5).

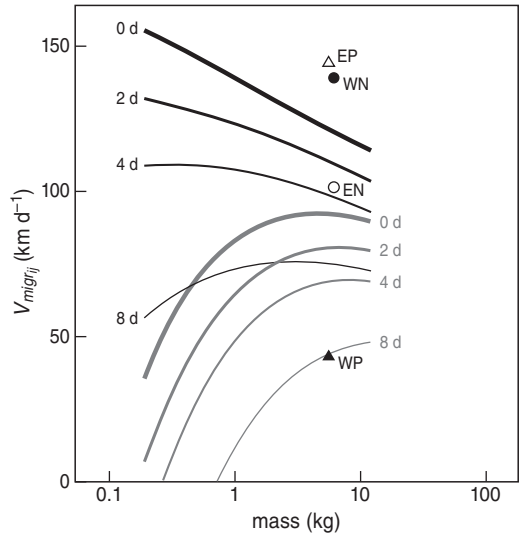


Figure 5. Lines give the migration speeds V_{migr} of different-sized waterfowl using an income-breeding (in black) or a capital-breeding strategy (i.e. enabling the immediate production of a clutch, in grey), depending on the reserves carried into the breeding grounds to allow for a given number of days of starvation. Dots represent the observed migration speeds $V_{migr_{ij}}$ during the last leg of satellite-tracked Tundra Swans belonging to four flyway populations (see Fig. 4 for abbreviations).

DISCUSSION

Interestingly, and in contrast to migratory passerines (Fransson 1995, Bauchinger & Klaassen 2005), spring migration in swans is thought to be slower rather than faster than autumn migration (Rees *et al.* 1997, Petrie & Wilcox 2003). Two main and not mutually exclusive hypotheses have been put forward to explain this phenomenon (Petrie & Wilcox 2003): (1) ice-cover delays spring and speeds up autumn migration, and (2) swans need to carry stores to the breeding grounds. The

Table 5. Mean air temperatures (°C) per month at representative weather stations within the breeding, stopover and wintering sites of Tundra Swans of four flyway populations. Gray shading indicates mean temperatures below 0°C. Whereabouts of swans indicated in bold.

Flyway ^a	Site	Station	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
WN	breeding	Bethel	-14.1	-14.4	-10.4	-4.7	4.4	10.3	12.8	11.6	7.3	-1.4	-8.4	-13.1
	stopover 3	Burwash	-22.3	-17.9	-11.2	-2.0	5.2	10.3	12.5	10.6	5.0	-3.0	-14.5	-20.2
	stopover 2	Edmonton	-14.2	-10.8	-5.4	3.7	10.3	14.2	16.0	15.0	9.9	4.6	-5.7	-12.2
	stopover 1	Pocatello	-4.8	-1.6	2.4	7.2	12.0	17.1	21.4	20.4	15.0	8.9	2.0	-4.0
	winter	Stockton	7.2	10.3	12.3	15.2	19.3	22.9	25.4	24.9	22.6	18.1	11.7	7.2
EN	breeding	Inuvik	-28.9	-28.5	-24.1	-14.1	-0.7	10.6	13.8	10.5	3.3	-8.2	-21.5	-26.1
	stopover 3	Yellow Knife	-27.9	-24.5	-18.5	-6.2	5.0	13.1	16.5	14.1	6.7	-1.4	-14.8	-24.1
	stopover 2	Saskatoon	-17.5	-13.9	-7.0	3.9	11.5	16.2	18.6	17.4	11.2	4.8	-6.0	-14.7
	stopover 1	Buffalo	-4.6	-4.1	1.0	7.3	13.7	18.8	21.7	20.6	16.6	10.6	4.7	-1.5
	winter	Kaap Hatteras	7.0	7.5	10.9	14.9	19.4	23.4	25.7	25.8	23.4	18.6	13.9	9.4
WP	breeding	Naryan Mar	-18.9	-17.3	-11.9	-7.6	-0.5	7.3	13.3	10.3	5.6	-2.1	-9.7	-14.3
	stopover 3	Archangelsk	-14.6	-12.2	-6.0	-0.4	6.5	12.5	15.7	13.2	7.8	1.5	-4.6	-10.5
	stopover 2	Tallinn	-5.5	-5.7	-2.2	3.4	9.7	14.5	16.3	15.3	10.8	6.3	1.2	-2.9
	stopover 1	Hamburg	0.5	1.1	3.7	7.3	12.2	15.5	16.8	16.6	13.5	9.7	5.1	1.9
	winter	Rosslare	6.3	5.9	6.8	8.2	10.5	13.1	14.9	14.9	13.6	11.5	8.4	7.2
EP	breeding	Iirnej	-33.4	-33.2	-28.9	-18.2	-2.7	9.4	12.1	8.5	0.6	-14.6	-28.4	-33.2
	stopover 2	Nikolajevsk	-23.2	-19.7	-11.9	-2.0	5.1	12.9	16.6	15.7	10.4	1.5	-10.3	-20.3
	stopover 1	Vladivostok	-13.1	-10.3	-2.5	4.4	9.6	12.9	17.3	19.5	15.3	8.2	-1.3	-9.5
	winter	Yonago	3.8	4.0	6.9	12.4	17.1	20.9	25.5	26.5	22.0	16.2	11.2	6.6

^aSee Table 1 for abbreviations.

observed migration speeds of satellite-tracked swans are in support of both hypotheses, but in some flyway populations swans seem to be more likely to carry stores to the breeding grounds than in others.

Contrary to most current models of migratory and stopover behaviour (e.g. Gudmundsson *et al.* 1991, Weber *et al.* 1998; but following Klaassen 2003), the allometric model does not take the transport cost of stores into account. Aerodynamic theory predicts that the costs of carrying stores should increase sharply with the amount of stores (Pennycuik 1989). This would mean that the last flight distance should be short if stores were to be carried into the breeding grounds. The only empirical test of this assumption to date found a much

more gradual increase in transport costs with storage load (Kvist *et al.* 2001). Incorporating such small increases in transport cost would only suggest an accuracy that is simply not attained with the kind of modelling used here.

To get an idea of how accurate the allometric model is, I made two calculations for a 6-kg waterfowl species that could be held against observations. The model predicts a maximum flight distance of 3278 km. This is only slightly further than the observed record for Tundra Swans, which stands at 2895 km covered by an Eastern Nearctic bird flying from the Northern Prairie to the Atlantic Coast (i.e. skipping the Great Lakes) in four days in autumn (Petrie & Wilcox 2003). Similarly, the stopover duration predicted by the

model (25.3 d) compares favourably with the observed $23.8 \text{ d} \pm 2.9 \text{ SE}$ ($n = 12$ stopovers) during spring migration of Tundra Swans (Table 4). These agreements give confidence that the predictions of the allometric model, however crude the model is, give a good approximation of the real migration speeds depending on the breeding strategy.

In Tundra Swans overall spring migration speed appears to be in accordance with capital breeding. At the same time, the speed of migration seems to be constrained by the onset of spring as ice-cover would prevent feeding on aquatic resources. These are the main resources for Tundra Swans on their final stopover site, at least in the Eastern Nearctic (Northern Boreal Forest, Petrie & Wilcox 2003), Western Palearctic (White Sea, Nolet *et al.* 2001), and Eastern Palearctic (Lower Amur River, Kanai *et al.* 1997). From this one might conclude that Tundra Swans make the best out of a bad job by putting on stores during stopover while waiting for the next stopover (or the breeding grounds) to become available.

However, if one is to use migration speed as a proxy for the degree of capital breeding, it may be better not to consider the whole migratory trajectory, because the energy stores for the clutch formation and survival on the breeding grounds may be primarily put on at the last stopover. When considering the last leg of the migration, a great variation in the predicted degree of capital breeding among flyways appears. Eastern Nearctic and especially Western Nearctic birds make use of the rapid advancement of spring on their last leg and accelerate their migration speed accordingly. The presumed strong competition for territories would induce an early arrival on the breeding grounds (Kokko 1999). This may be much more important than bringing stores to the breeding grounds, in particular in the Western Nearctic birds because their length of the breeding season in Alaska is relatively long (Table 5), giving them plenty of time to gather resources on the breeding grounds. The Western Palearctic birds are faced with a slow advancement of spring on their last track, but have the advantage that this last leg is relatively short (Table 4). They may fare better by building up

stores on the last stopover and bring these to the breeding grounds. In contrast, the Eastern Palearctic birds are confronted with a very long last leg (Table 4), which precludes capital breeding. On the breeding grounds, Tundra Swans feed primarily on terrestrial resources (Limpert & Earnst 1994, Rees *et al.* 1997), so they may be less prone to sub-freezing temperatures upon arrival there, but it would be interesting to know how the Eastern Palearctic Tundra Swans survive after arriving so early in Northern Siberia after such a long flight.

Weather patterns at subsequent stopover sites are generally correlated (Cooke *et al.* 1995, van der Graaf 2006), so swans should be able to predict, at least to some extent, the ice conditions at their next stopover site. However, the annual variation in the onset of spring tends to increase with latitude (van der Graaf 2006). In order to test whether swans are really constrained by the advancement of spring, one should therefore ideally compare the timing of swan migration in several years with the weather conditions of those specific years. This would require considerably more satellite trackings than are currently available.

The observed spring migration speeds predict that the degree of capital breeding differs among flyway populations, with a high degree in the Western Palearctic to a low degree in Western Nearctic and Eastern Palearctic. This is in agreement with the time lag between arrival date on the breeding grounds and laying date, which is presumably short in the Western Palearctic (indicative for capital breeding) and long in Alaska (indicative for income breeding) (Klaassen *et al.* 2006). Whether these flyway populations can really be characterized as capital or income breeders remains to be tested. This can possibly be done by comparing stable isotope ratios in eggs and those in the females' food sources on the breeding grounds (Klaassen *et al.* 2001, Gauthier *et al.* 2003, Morrison & Hobson 2004). The stable isotope ratios from aquatic food plants of swans differ considerably from those of terrestrial ones (Nolet *et al.* 2000). As the food source probably changes from primarily aquatic on the last

stopover to primarily terrestrial on the breeding grounds in at least three of the four flyway populations (see above), this method should in principle be able to discriminate between income or capital breeding in Tundra Swans.

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SAMENVATTING

Grote trekvogels kunnen er in theorie voor kiezen om lichaamsreserves mee te torsen naar de broedgebieden om bij aankomst gelijk een legsel te produceren en eventuele ongunstige weersomstandigheden te overleven ('kapitaal-broeders') of om alle benodigde nutriënten op de broedgebieden zelf te verzamelen ('inkomsten-broeders'). Of trekvogels kapitaal- dan wel inkomsten-broeders zijn, zou kunnen afhangen van de afstand tussen de laatste pleisterplaats en het broedgebied, maar ook van de lengte van het broedseizoen. Daarom zou de mate van kapitaal-broeden tussen verschillende trekpopulaties van dezelfde soort kunnen verschillen. Van de Kleine Zwaan *Cygnus columbianus* komen vier trekpopulaties voor die

op de toendra's broeden van respectievelijk Europa, Azië (*C. c. bewickii*, 'onze' Kleine Zwaan), Alaska en Canada (*C. c. columbianus*, die 'Fluitzwanen' worden genoemd). Als maat voor de mate van kapitaal-broeden heb ik de treksnelheid gebruikt. De treksnelheid van met satellietzenders uitgeruste zwanen van deze vier trekpopulaties heb ik vergeleken met de voorspelde treksnelheid van een 6 kg zware watervogel, die in verschillende mate reserves meestorst naar het broedgebied. Gemeten over de hele trekroute van het overwinteringsgebied naar het broedgebied was de gemiddelde treksnelheid 52,2 km/dag, hetgeen in overeenstemming is met de voorspelde treksnelheid van een kapitaal-broeder. Deze treksnelheid is ook in overeenstemming met de snelheid waarop het ijs zich in het voorjaar terugtrekt. Het is echter waarschijnlijk dat het grootste deel van de reserves pas op de laatste pleisterplaats voor het broedgebied wordt aangelegd.

Fluitzwanen in Noord-Amerika, en dan vooral in Alaska, maken gebruik van de snelle inval van het voorjaar en versnellen hun trek op het laatste traject zodanig dat ze vermoedelijk geen reserves meenemen. In Europa hebben Kleine Zwanen daarentegen te maken met een langzame ontwikkeling van de lente op het laatste deel van hun trekroute. Zij zouden er dus beter aan doen om reserves aan te leggen op hun laatste pleisterplaats en deze mee te nemen naar de broedgebieden. Dit is wellicht geen optie voor zwanen in Azië, die te maken hebben met een extreem lang laatste traject van hun trekroute. De variatie in waargenomen treksnelheden tijdens het laatste deel van de trek naar de broedgebieden suggereert dat tussen de verschillende trekpopulaties van Kleine Zwanen en Fluitzwanen ook een grote variatie bestaat in de mate van kapitaal-broeden.

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