

Underuse of stopover site by migratory swans

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1 Abstract

2 Many migratory birds use a chain of stopover sites to fuel their migration. Under
3 time-minimizing migration, fuelling time and giving-up density at stopovers are
4 predicted to depend on fuelling conditions. Fluctuations in food accessibility likely
5 lead to changes in fuelling conditions, which should in turn be reflected in fuelling
6 time and giving-up density. During their migration, Bewick's Swans *Cygnus*
7 *columbianus bewickii* refuel on belowground tubers of Fennel Pondweed
8 *Potamogeton pectinatus* in shallow lakes. We studied giving-up densities and
9 stopover use of Bewick's Swans (expressed in bird-days) at an autumn stopover site
10 (Lauwersmeer, The Netherlands) during 1995-2008, as dependent on local
11 environmental conditions. High water levels were hypothesized to restrict access to
12 tuber stocks. High water levels at the stopover site were predicted to lead to higher
13 giving-up densities and less bird-days spent at the stopover. Annual variation in
14 giving-up densities and number of bird-days was strongly associated with year-to-
15 year differences in initial tuber biomass density and number of days with high water
16 levels. As predicted, giving-up density increased, and bird-days decreased with the
17 number of days with high water level. We conclude that, in line with time-
18 minimizing migration, changes in fuelling conditions may lead to underuse of a
19 stopover site. Underuse of stopovers by migratory birds has been reported before
20 but only in the sense that more food was left at stopover sites than at wintering
21 sites. In contrast, in our case, dealing with a given stopover site, more food is left
22 behind in some years than in other years.

23

24

25 **Keywords** Bewick's swan · food availability · migratory fuelling · time-minimizing
26 migration · staging site · water level

27

1 **Introduction**

2 Many migratory birds use stopover sites where they fuel for migration (Alerstam
3 and Hedenström 1998). During migration, more time is commonly spent on
4 stopovers than travelling, particularly in birds using flapping flight (Hedenström
5 and Alerstam 1997). Hence, stopover duration largely determines migration speed.

6 Theory predicts that time-minimizing migrants should stay at a stopover as long as
7 the rate of increase in body fuel enables a faster migration than the overall
8 migration speed on their journey (Alerstam 1991; Alerstam and Lindström 1990). In
9 flying animals, fuel load comes with a flight cost (Pennycuick 1975; Kvist et al.
10 2001), and therefore potential flight range, and hence migration speed, is expected
11 to increase at a decelerating rate with fuel load (Alerstam 1991; Alerstam and
12 Lindström 1990). Because fuel load is supposed to increase with fuelling time,
13 diminishing returns of potential flight range are expected with increasing fuelling
14 time (Alerstam and Hedenström 1998). Already at the stopover, carrying and
15 maintaining a given fuel load comes at a cost, and this will further slow down the
16 increase in flight range with fuelling time (Klaassen and Lindström 1996). Moreover,
17 food depletion might cause diminishing returns of potential flight range with
18 fuelling time, because depletion often leads to lower fuelling rates (Nolet and Drent
19 1998; but see Lourenço et al. 2010). Together, fuel load and food depletion
20 determine the optimal fuelling time at a stopover (Alerstam and Lindström 1990;
21 Alerstam 1991). If conditions are unfavourable at a particular stopover site,
22 migrants have been shown to move on (Newton 2006, and references therein) and
23 to depart with low fuel loads, as expected when migrants aim to migrate as fast as
24 possible (Lindström and Alerstam 1992).

25 The main factors determining the fuelling conditions (and hence fuelling time or
26 stopover duration) of a stopover site are its food abundance (Newton 2006), the

1 costs of harvesting that food (Van Eerden et al. 1997b) and food accessibility
2 (Zwarts et al. 1992). Predation risk also affects site use, in particular for small to
3 medium-sized animals, and is often traded-off against food availability (Clark and
4 Butler 1999; Guillemain et al. 2007; Pomeroy et al. 2006; Duijns et al. 2009;
5 Cresswell 1994). These are also the factors known to affect giving-up densities
6 (GUDs), i.e. the food densities remaining after animals have left a food patch (Brown
7 1988; Nolet et al. 2006a). Hence, GUDs at a stopover site have been proposed to
8 reflect the long-term fuelling rates along the migration route (Van Gils and Tijssen
9 2007).

10 Bewick's Swans *Cygnus columbianus bewickii* (Yarrell) fuel their migration by
11 feeding on aquatic macrophytes, especially tubers of Fennel Pondweed *Potamogeton*
12 *pectinatus* (Beekman et al. 1991; Nolet et al. 2001b; Nolet et al. 2001a). During
13 aquatic foraging of these large birds (c. 6.0 kg) predation risk can be neglected,
14 which partly explains why they prefer to forage on water over field feeding (Nolet et
15 al. 2002). For instance, the largest avian predator in their aquatic habitat, the white-
16 tailed eagle *Haliaeetus albicilla*, only exceptionally takes birds of more than 2.5 kg
17 (Cramp and Simmons 1979). Therefore, aquatically foraging Bewick's Swans are
18 well suited to study the effects of fuelling conditions on stopover use without the
19 confounding effects of predation risk.

20 In waterbirds, fuelling conditions may be affected by water depth (De Leeuw et al.
21 1998; Lovvorn 1994; Guillemain et al. 2000; Gawlik 2002). In Lauwersmeer, an
22 important autumn staging site of Bewick's Swans in the Netherlands, within-year
23 (i.e., spatial) variation in GUD was related to water depth (Nolet et al. 2001b), largely
24 due to differences in food accessibility and to a much lesser extent by differences in
25 foraging costs (Nolet et al. 2006a). Because accessibility is directly influenced by
26 water levels, we hypothesize that inter-annual (i.e., temporal) variation in GUD at

1 the stopover site is related to yearly differences in initial food density *and* water
2 level. As the difference between initial and final biomass represents the biomass
3 consumed by swans (Nolet et al. 2006b), both the initial food density and water
4 levels should also influence stopover duration (at the individual or population level).
5 Hence, we predict that lower food accessibility leads to shorter stopover duration
6 and higher GUDs (Fig. 1). Effectively this would result in the underuse of the
7 stopover site in some years, in the sense that food is left unexploited, because it was
8 (temporarily) inaccessible.

9

10

11 **Methods**

12 Study area

13 Lauwersmeer is a shallow freshwater lake (2400 ha, water volume 0.05 km³)
14 formed by damming of a bay of the Wadden Sea in 1969, and recharged by two small
15 rivers. Water levels are strictly regulated, although rapid changes in water level can
16 occur, depending on rainfall, wind direction and state of the tide in the Wadden Sea
17 (determining whether water can be sluiced). Our study site was an inlet (Babbelaar)
18 closed to the public.

19

20 Tuber sampling

21 Tubers were sampled along the north-east shore (53° 20' 27"N, 6° 13' 43"E) of the
22 inlet between 1995 and 2008. Initially (1995-1998), we sampled in three 20 × 20 m
23 plots 100 m apart (plots 11-13 in Fig. 1 of Nolet et al. 2001b). In 1995 we took 18

1 sediment cores per plot (54 cores in total), but in 1996-1998 we doubled this
2 number (i.e. 36 cores per plot, 108 in total). In later years (2001-2008), we sampled
3 the same area in a grid of 200×40 m with 1 m^2 sampling points 20 m apart, taking
4 12 cores per point (396 cores in total). The 20 m distance between sampling points
5 was sufficient to prevent spatial autocorrelation (Nolet and Mooij 2002). Cores were
6 10 cm in diameter and >30 cm deep. These were washed over a 3 mm sieve to
7 collect the tubers, which were taken to the lab, dried for 48 h at 70°C , and weighed
8 (all weights refer to dry weight).

9 Samples were taken in late September or early October, just before the swans
10 arrived, to assess initial tuber biomass density D_i . After the swans had left, usually
11 by mid-November, samples were taken to assess the giving-up tuber biomass
12 density D_f . In March, shortly before sprouting of the tubers, samples were taken to
13 determine the tuber biomass density left after the winter D_s . Sampling plots and
14 points were marked with small bamboo sticks 10 cm above the sediment, well
15 below the water surface, to enable re-sampling at the same locations. From 2001
16 onwards we sampled the same exact 1 m^2 , so for these years we corrected the initial
17 tuber density by subtracting the sampled area ($12 \pi 0.05^2 \text{ m}^2$; i.e. close to 10% of plot
18 area) times D_i (i.e. $D_{ic} = 0.91 D_i$). In the earlier years, sampled area was <1% of plot
19 area, and such a correction was ignored.

20

21 Swan observations

22 With the aid of 20-60× telescopes, Bewick's Swans in the inlet were counted daily
23 from the day the first swans arrived until they had all switched to surrounding
24 arable fields or continued southward migration. Daily numbers were summed to

1 obtain the number of swan-days S per year, linearly interpolating numbers on
2 missing days (comprising 8.6% of the total S).

3

4 Water levels

5 Water levels in Lauwersmeer, obtained from Waterschap Noorderzijlvest, were
6 expressed relative to the Dutch standard (NAP). Daily mean water levels measured
7 at two stations (Zoutkamp, 53° 20' 14"N, 6° 17' 49"E; Nieuwe Robbengat, 53° 23'
8 28"N, 6° 14' 12"E) either side of the Babbelaar were averaged. The distribution of
9 average daily water levels in October – November was right skewed (Fig. 2; Skew =
10 1.81 ± 0.08 SE, Shapiro-Wilk $W = 0.805$, $P < 0.001$), reflecting rapid peaks in water
11 level rise. Rather than using average daily water level, we calculated the number of
12 days with "high" water levels h (i.e. higher than the critical water level) as our
13 independent variable. As the critical water level we took the mean of the observed
14 water levels (-0.81 m NAP), but any critical level between -0.83 and -0.68 m NAP
15 yielded similar results (not shown).

16

17 Statistics

18 Variables were tested for normality with Shapiro-Wilk W test. We compared 7
19 models of final tuber density D_f and swan-days S , respectively, as functions of initial
20 tuber density D_i (or corrected initial tuber density D_{ic} in the case of D_f), days with
21 high water h , and their two-way interactions, in all possible combinations. Akaike's
22 information criterion corrected for small sample size was used to select the most
23 parsimonious model in this model set (Burnham and Anderson 2002). Because the
24 order of models is to some extent dependent on the measurement scale of the

1 variables when including an interaction term, we first normalized all variables x to
 2 x_{norm} ($0 \leq x_{norm} \leq 1$) by taking $x_{norm} = (x - x_{min}) / (x_{max} - x_{min})$, where x_{min} and x_{max} are the
 3 minimum and maximum values of a variable, respectively. We regarded D_f to be a
 4 function of local D_i , hence our choice for D_{ic} when modelling D_f . S , however, was
 5 regarded to be a function of a more global D_i .

6 Swan usage and realized final tuber density were predicted from initial tuber
 7 density and days with high (i.e., above-average) water levels as follows. As the
 8 functional response is nearly linear (Nolet et al. 2002), the foraging time at $h = 0$,
 9 indicated by $t(0)$, to deplete a unit area to $D_f(0)$ can be approximated as:

$$10 \quad t(0) = (1 / (a \cdot \varphi)) \cdot \ln (D_i / D_f(0)),$$

11 where a is the attack rate, and φ is the proportion of foraging time spent feeding
 12 (feeding by head-dipping or up-ending is part of foraging which also includes
 13 digging and breathing pauses). As values we took the average for sandy and clayey
 14 sediments, as both occur in the inlet, giving $\varphi = 0.74$ and $a = 0.00082 \text{ m}^2/\text{s}$ (Nolet
 15 and Klaassen 2009). We assumed that the effective foraging time linearly decreases
 16 with the number of days with above average water levels ($0 \leq h \leq 61$):

$$17 \quad t(h) = t(0) - h / 61 \times t(0)$$

18 The number of swan-days at h days with above average water levels $S(h)$ is then:

$$19 \quad S(h) = (t(h) \cdot A) / (24 \times 60 \times 60),$$

20 where A is the area of pondweed in the inlet ($17.7 \times 10^4 \text{ m}^2$) (Nolet et al. 2006b).

21 Realized final tuber density $D_f(h)$ is obtained after re-arranging:

$$22 \quad t(h) = (1 / (a \cdot \varphi)) \cdot \ln (D_i / D_f(h)),$$

23 which yields:

$$24 \quad D_f(h) = \exp(\ln D_i - a \cdot \varphi \cdot t(h)).$$

25

26

1 **Results**

2 In Lauwersmeer, final tuber density D_f increased with the (corrected) initial tuber
3 density D_{ic} (Table 1, model 3) and number of days with above average water levels h
4 (Table 1, model 2), both variables explaining the final tuber density equally well. The
5 most parsimonious model included both these variables, such that D_f increased with
6 D_{ic} depending on the number of days with above average water levels h (Fig. 3a).
7 This could explain the exceptionally high D_f in 2006 (highest data point in Fig. 3a),
8 when there were many days of above average water levels in Lauwersmeer ($h = 36$).

9 There was little difference in empirical support between the two top models
10 predicting swan-days S , both including the initial tuber density D_i and the number of
11 days with above average water levels h (Table 2, models 1-2). In general, S increased
12 with D_i and decreased with h , and these models only differed in the way the number
13 of days with above average water levels h changed the relationship between S and D_i
14 (i.e., running parallel or divergent; the latter is shown).

15 Using the experimentally derived functional responses yielded very similar patterns
16 of final tuber density (Fig. 3b) and swan usage (Fig. 4b) as the depicted statistical
17 relationships (Fig. 3a and Fig. 4a).

18 The reduction in tuber biomass from November to March ($17.8\% \pm 6.1$ SE, $n = 11$),
19 after the swans had left Lauwersmeer, was not significantly different ($t_{10} = -1.85$, $P >$
20 0.09) from winter mortality without swan grazing (6.5%, assessed using winter
21 exclosures) (Hidding et al. 2012) (Fig. 5). Only in 1996, a relatively large reduction
22 (63%) was measured (Fig. 5; light grey point well below the line).

23

24

1 Discussion

2 Swans left more tuber biomass at the stopover site when more days with high water
 3 levels occurred. In a previous analysis the positive relationship between initial (D_i)
 4 and final (D_f) tuber densities was ascribed to part of the initial tuber biomass being
 5 buried deep, inaccessible to the swans, and the slope of the regression of D_f on D_i
 6 was interpreted as the fraction out of reach of the swans (Nolet et al. 2006b). The
 7 current analysis suggests that this positive relationship results from periods with
 8 high water, which implies that the final tuber density in Lauwersmeer would be
 9 similar in all years, independent of initial tuber density, if water levels would remain
 10 low throughout the stopover period.

11 When considering swan-days S , two models were equally well supported by the
 12 data. According to both these models, S increased with initial tuber density D_i , but
 13 for a given D_i , swan use was lower when more days with high water levels occurred
 14 (i.e, large h). We chose to depict the second most parsimonious model (Fig. 4a),
 15 because it was biologically the most plausible (the most parsimonious model
 16 predicted $S > 0$ at $D_i < 0$), and because it was in line with the most parsimonious
 17 model for D_f . This can be seen by writing model 1 in Table 1 as $D_f = b_0 + b_2 \cdot D_{ic} \cdot h$,
 18 and express it as consumption $C = D_{ic} - D_f = D_{ic} - (b_0 + b_2 \cdot D_{ic} \cdot h) = -b_0 + D_{ic} - b_2 \cdot D_{ic} \cdot$
 19 h . This is very similar in structure as model 2 in Table 2: $S = b_0 + b_1 \cdot D_{ic} + b_2 \cdot D_{ic} \cdot h$.

20 The results of the analyses of final tuber density and swan-days were therefore in
 21 line with each other, and suggest that swans left Lauwersmeer earlier when they
 22 encountered high water, leading to an underuse of the stopover site.

23 The high water levels reduce food accessibility and hence fuelling rate, and induce
 24 the birds to continue migration, in accordance with the hypothesis of time-
 25 minimizing migration. The reduction in tuber biomass from November to March was

1 as expected from winter mortality from other causes than swan predation, as
2 measured in winter exclosures, confirming that there was no measurable swan
3 foraging after our final sampling in November. Only in 1996, the relatively large
4 reduction in tuber biomass between November and March of the following calendar
5 year suggests that the swans returned to forage on the lake when water level had
6 returned to normal. This may be because in that year the water levels dropped to
7 normal again relatively early in autumn (on 9 Nov 1996, only two days after our
8 final sampling, 5000 Bewick's Swans were counted in Lauwersmeer,
9 <http://www.waarneming.nl>). In a way, this exception proves our concept of
10 underuse, because apparently there was food left to be used by swans.

11 Tuber loss due to other causes than swan predation is small over the short
12 exploitation period (3% per month in winter exclosures, Hidding et al. 2009). Hence,
13 the difference between the initial and final tuber density should roughly equal the
14 consumption C by the swans, and the observed patterns of depletion and stopover
15 duration should be reproducible from the functional response of swans feeding on
16 tubers (Nolet et al. 2006b). This functional response model indeed yields very
17 similar patterns as the statistical models, both for D_f (cf. Fig. 3a and 3b) and for S (cf.
18 Fig. 4a and 4b). Apparently, local environmental conditions (initial tuber density D_i
19 and days with above average water levels h) largely explain the annual variation in
20 final tuber density D_f and swan-days S .

21 A rise in bird-days can be due to more birds stopping over at the site or to an
22 increase in stopover duration of individual birds. Whereas there are some
23 indications that staging numbers vary annually with food density at a stopover site
24 (Van Gils et al. 2005), evidence for longer stopover durations at the individual level
25 when resources are plentiful is scarce. In fact, in hummingbirds, the opposite
26 pattern was found, with stopover duration decreasing with resource (i.e., flower)

1 density (Russell et al. 1994). On the other hand, when resource conditions are very
2 poor, birds are found to move on quickly (Newton 2006). Hence, stopover duration
3 may have a humped-shape relationship with resource density: at low resource
4 density, birds leave quickly or skip the site altogether, at intermediate resource
5 density birds make use of the site but need time to refuel, whereas at high resource
6 density birds stay relatively short periods because they are able to rapidly replenish
7 their resources (Schaub et al. 2008). However, birds are predicted to leave a rich site
8 with relatively high fuel loads, which may extend the fuelling period at rich resource
9 densities despite the more rapid fuelling (Lindström and Alerstam 1992; Klaassen
10 and Lindström 1996). So, the increase in swan-days with resource availability is
11 possibly a combination of more swans stopping over and a net increase in stopover
12 duration per swan. Unfortunately, too few marked swans were available to estimate
13 turnover, especially in the later years, to distinguish between these two possibilities.

14 A carry-over effect may cause individuals to stage longer at a site when conditions at
15 the previous site were poor (Bauer et al. 2006). Lower fuelling rates are predicted to
16 lead to lower departure fuel loads (Lindström and Alerstam 1992). Therefore, birds
17 are predicted to arrive relatively lean to a next stopover site, which may cause the
18 birds to stay longer there and, in case of depletable resources, deplete these further.
19 Some studies indeed showed that lean arriving migrants generally stayed longer
20 than fat ones (Cherry 1982; Bairlein 1985; Biebach et al. 1986; Moore and Kerlinger
21 1987; Goymann et al. 2010), or that stopover duration was longer when in a given
22 year body condition at arrival at the stopover site was low (Russell et al. 1994).
23 However, some other studies found no consistent relationship between arrival
24 condition and stopover duration (Safriel and Lavee 1988; Butler et al. 1997; Skagen
25 and Knopf 1994; Lyons and Haig 1995; Holmgren et al. 1993), possibly because
26 departure was triggered more by time schedules or flight conditions (e.g. favourable
27 weather) than by fuelling conditions. The large variation in giving-up tuber densities

1 and swan-days explained by local effects of food density and accessibility, as well as
2 the close fit with the functional response model, suggests that such carry-over
3 effects were small in comparison to local effects.

4 Our study provides clear evidence for underuse of a stopover site, in line with time-
5 minimizing migration. Underuse of stopovers has been reported before but in those
6 cases it was used in the sense that migratory birds leave more food at stopover sites
7 than at wintering sites because on the latter they should reflect energy balance
8 rather than a positive energy budget (Van Eerden et al. 1997a; but see Lourenço et
9 al. 2010; Alonso et al. 1994). Here we show that migratory birds may also underuse
10 a stopover site in the sense that they leave more food behind in some years than in
11 others, because of yearly differences in fuelling conditions.

12

13 **Acknowledgements** Thanks to all who assisted during 15 years of field
14 work, especially: Thijs de Boer, Ten Dekkers, Marcel Klaassen, Raymond Klaassen,
15 Oscar Langevoord, Koos Swart, Peter de Vries, and Erik Wessel. We were introduced
16 to the study system by Jan Beekman, Mennobart van Eerden and the late Rudi Drent.
17 Thanks to Jan Willems (Staatsbosbeheer) for permission to work in the nature
18 reserve, and Waterschap Noorderzijlvest for water level data. Phil Battley, Silke
19 Bauer, Matthieu Guillemain, Anders Hedenström, Raymond Klaassen, Ruedi Nager
20 and Jan van Gils commented on drafts of the manuscript. AGy was supported by the
21 Netherlands Organisation for Scientific Research (NWO grant 814.01.008 to BAN).
22 This is publication 5400 of the Netherlands Institute of Ecology.

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1 **TABLES**

2

3 **Table 1** Top 3 explanatory models to explain final tuber density D_f in Lauwersmeer
 4 in 1995-2008 according to Akaike's information criterion corrected for small sample
 5 size (AICc; $n = 11$). Each model is defined by the listed independent variables:
 6 corrected initial tuber density D_{ic} , number of days with above-average water levels
 7 h , and possible interaction terms (\times). All models with substantial empirical support
 8 (i.e., $\Delta AICc < 2$) are indicated in bold; K is the number of parameters, $\mathcal{L}(m_i|x)$ is
 9 likelihood of model i given the data, and w_i is its Akaike's weight (Burnham and
 10 Anderson 2002). RMSD is the root mean squared deviation of observed on predicted
 11 values of (in this case) D_f , and r^2 the coefficient of determination (i.e. proportion of
 12 the variation in observed values explained by the predicted values of, in this case,
 13 D_f).

14

15

Model	K	Deviance Ratio	$\Delta AICc$	$\mathcal{L}(m_i x)$	w_i	Evidence Ratio	RMSD (g/m ²)	r^2
(1) $D_{ic} \times h$	3	14.0	0.00	1.00	0.53	1.0	3.38	0.61
(2) h	3	18.6	2.41	0.30	0.16	3.3	3.90	0.48
(3) D_{ic}	3	19.7	3.05	0.22	0.11	4.6	4.02	0.45

16

- 1 **Table 2** Top 3 explanatory models for swan-days S in Lauwersmeer in 1995-2008
 2 according to Akaike's information criterion corrected for small sample size (AICc; n
 3 = 11). See also Table 1.

4

Model	K	Deviance Ratio	ΔAICc	$\mathcal{L}(m_i x)$	w_i	Evidence Ratio	RMSD ($\times 10^3$)	r^2
(1) $D_i + h$	4	0.59	0.00	1.00	0.53	1.0	0.65	0.85
(2) $D_i + D_i \times h$	4	0.60	0.61	0.74	0.39	1.4	0.66	0.84
(3) D_i	3	1.25	4.33	0.11	0.06	8.7	1.01	0.63

5

1 **FIGURE LEGENDS**

2

3 **Fig. 1** Optimal fuelling time at a stopover and corresponding giving-up density
4 according to optimal bird migration theory. **a** In migratory birds, potential flight
5 range to the next stopover is expected to increase with fuelling time (T_{fuel}) at the
6 current stopover, but with diminishing returns (see text). Birds are expected to
7 leave a stopover site when the marginal value (tangents) of flight range on fuelling
8 time falls to their expectation for the whole migration (indicated by dots). A
9 reduction in fuelling conditions leads to a slower increase in flight range (grey
10 curve), and hence an earlier departure. Optimal stopover duration (T_{fuel}^*) is
11 predicted to be longer under standard (1, horizontal black bar) than under reduced
12 (2, grey) fuelling conditions. **b** Due to depletion, food density (D) at the stopover is
13 expected to decrease with fuelling time (T_{fuel}), at an increasing rate when more
14 birds settle at the stopover site. A reduction in fuelling conditions leads to a lower
15 depletion rate (grey curve) and a higher giving-up density (D_g ; 2, grey vertical bar)
16 than under standard conditions (1, black bar).

17

18 **Fig. 2** Frequency distribution of daily water level in Lauwersmeer (average of two
19 stations) in Oct-Nov 1995-2008 ($n = 854$); water level aimed for by the water board
20 is -0.93 m NAP (NAP = Amsterdam Ordnance Datum, data Waterschap
21 Noorderzijlvest). Vertical line indicates mean value of -0.81 m NAP.

22

23 **Fig. 3** Final tuber biomass density D_f as a function of corrected initial tuber biomass
24 density D_{ic} and the number of days with high water in Lauwersmeer (h , days). Each
25 data point represents one year in the period 1995-2008, with grey shading
26 according to h values (from white if $h \leq 6$ to black if $h > 30$). The difference from a
27 data point to the $y = x$ line along the vertical equals the consumption (g/m^2) by

1 swans. Error bars indicate 95%-CI. Lines depict **a** most parsimonious model with D_{ic}
2 and h as explanatory variables (model 1 in Table 1); **b** predictions based on linear
3 functional response (see Methods for calculation). When there is no restriction by
4 high water levels ($h = 0$), the best statistical model (Table 1, model 1) predicts a final
5 tuber density $D_f(0) = 9.0 \text{ g/m}^2$.

6

7 **Fig. 4** Swan-days S as a function of initial tuber biomass density D_i and the number
8 of days with high water in Lauwersmeer (h , days). Each data point represents one
9 year in the period 1995-2008, with grey shading according to h values (see Fig. 3).
10 Error bars indicate 95%-CI. Lines depict **a** second most parsimonious model with D_{ic}
11 and h as explanatory variables (model 2 in Table 2); **b** predictions based on linear
12 functional response (see Fig. 3 and Methods for calculation).

13

14 **Fig. 5** Final tuber biomass densities in November (after the swans had left the lake)
15 and March of the following calendar year (at the end of the winter). Each point
16 represents one year in the period 1995-2008, with grey shading according to h
17 values (see Fig. 3). Error bars indicate 95%-CI. Observed tuber biomass densities in
18 March are generally as expected from the winter mortality (m) measured in winter
19 exclosures (line, see text).

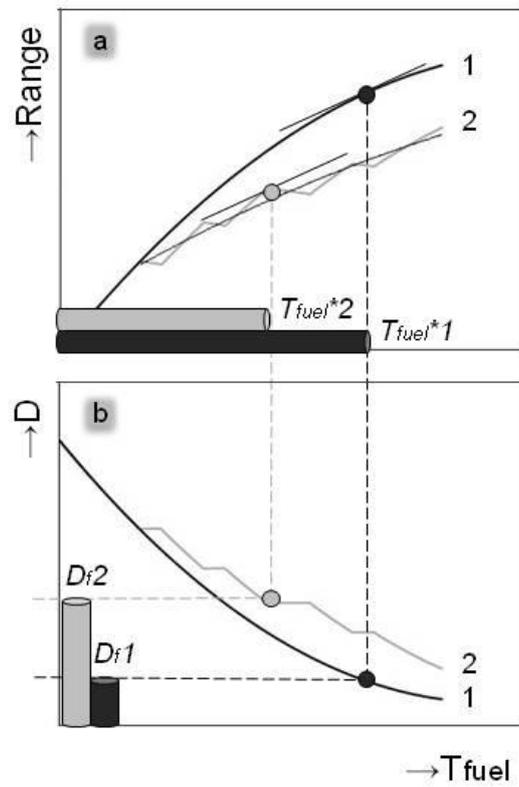


Fig. 1

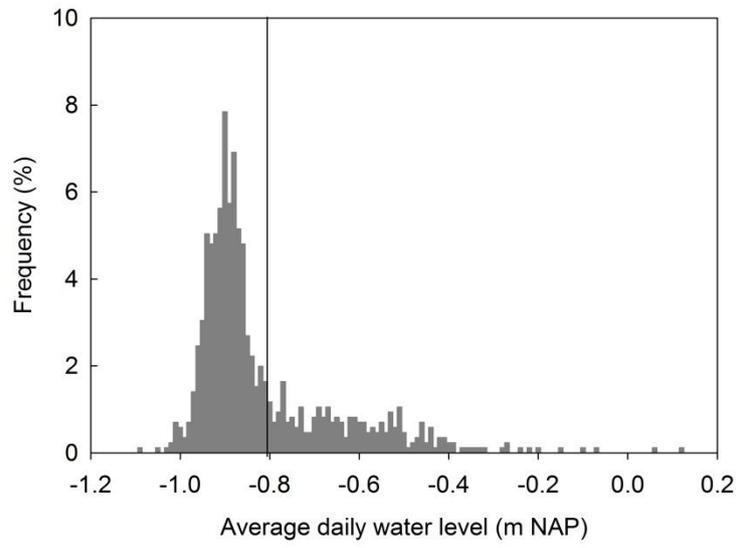


Fig. 2

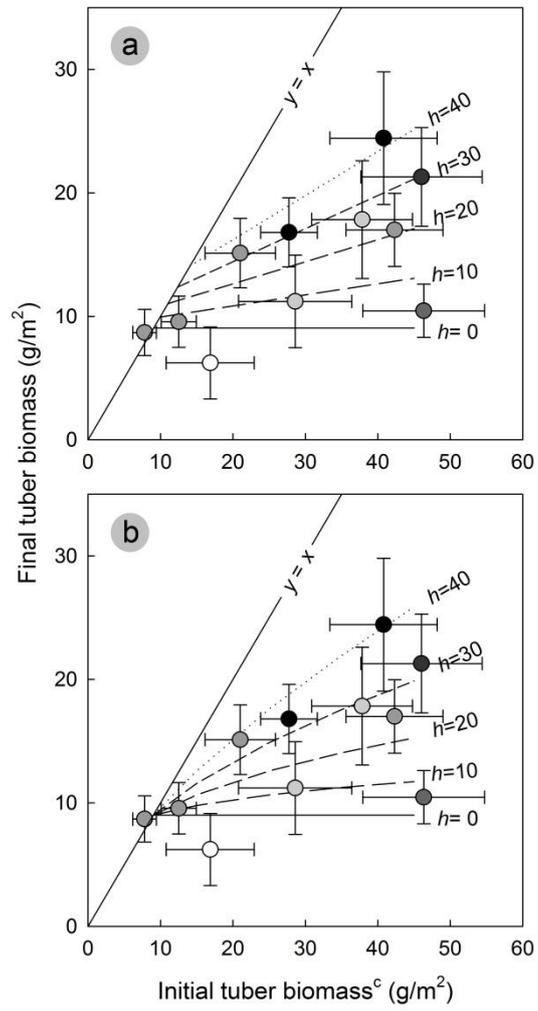


Fig. 3

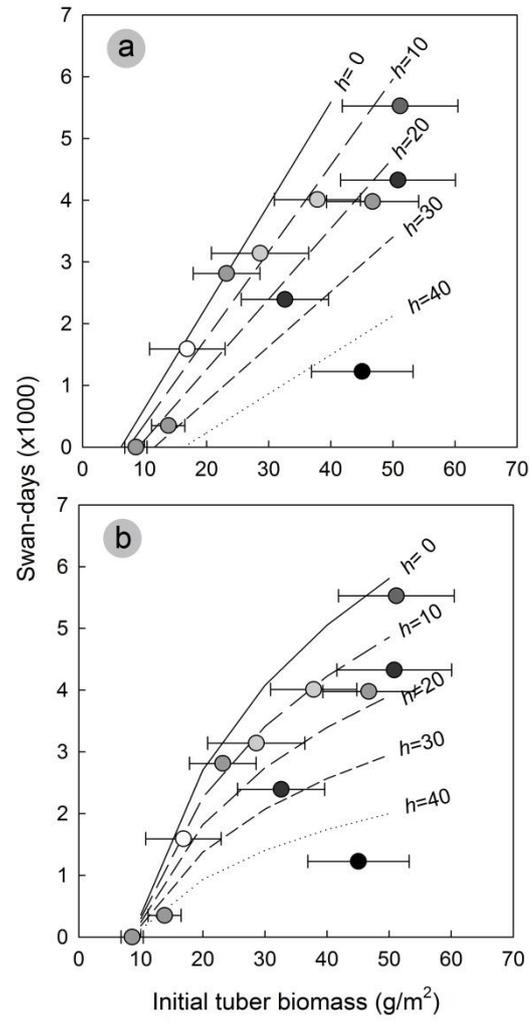


Fig. 4

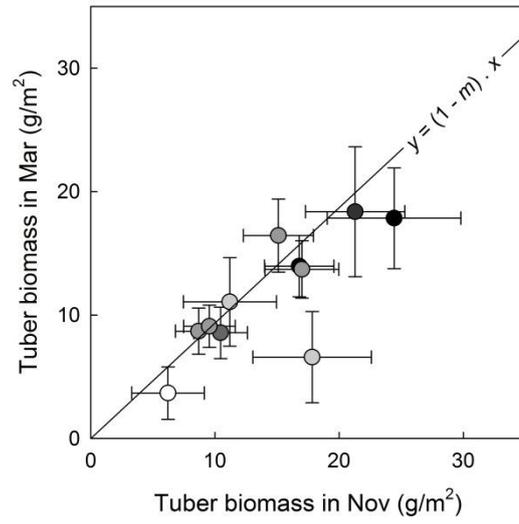


Fig. 5