A comparison of behaviour and habitat use by Bewick's Swans *Cygnus columbianus bewickii* at wintering sites in China and Europe: preliminary observations

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Abstract

The dynamics and behaviour of the Northwest European population of Bewick's Swans *Cygnus columbianus bewickii* has been studied over several decades, yet relatively little is known about the more numerous Eastern population of the species. Comparisons of the two populations could help explain why the Northwest European population is in decline. Here we describe for the first time the swans' use of a wintering site (Shengjin Lake) in China, comparing these findings with studies made of Bewick's Swans wintering at Slimbridge, UK. First birds arrived in late October at both sites, and swans remained at Shengjin Lake until late March, which approximates to the time that Bewick's Swans spend at wintering sites across Europe. Monthly swan counts did not correlate significantly with water level variations at Shengjin Lake (and by implication food accessibility). However, more extensive monitoring, both of water depth and food abundance, is required to understand whether fluctuating water levels affect site use by the birds. There was no significant difference between the two sites in the proportion of birds recorded feeding throughout the day, though this may reflect a high level of variance in the swans' feeding activity. A bimodal pattern in feeding activity recorded for the swans in China is similar to feeding patterns recorded for Bewick's Swans at Slimbridge. Breeding success recorded for Bewick's Swans in the Eastern population was significantly higher than for those in the Northwest European population every year from 2007 to 2010 inclusive. Further studies should investigate whether this is attributable to the carry-over effects of swans in the Eastern population feeding on aquatic vegetation in traditional wetland habitats during winter, as opposed to the farmland used by swans wintering in Europe.

Key words: aquatic vegetation, Bewick's Swan, breeding success, feeding behaviour, population differences.

Bewick's Swans *Cygnus columbianus bewickii* breed across the tundras of high-arctic Russia, from Cheshskaya Bay in Arkhangelsk to Chaun Bay in Chukotka (Rees 2006), but different populations appear to encounter very different conditions in their wintering ranges. The Northwest European population feeds almost exclusively on agricultural habitats at its wintering sites in western Europe (Dirksen *et al.* 1991; Limpert & Earnst 1994; Rees *et al.* 1997a). In contrast, Bewick's Swans from the Eastern population wintering in China exploit natural freshwater wetland systems (Cong *et al.* 2011), which are considered to be the traditional feeding habitats for the species following observations that swans in the Netherlands spent the whole winter in aquatic habitats during the 1930s and 1940s (Brouwer & Tinbergen 1939). Studies of Bewick's Swan feeding ecology in Europe have shown that, despite their general tendency to feed on farmland during the winter months, the swans still select aquatic vegetation, particularly the tubers of pondweeds *Potamogeton* sp., on arrival in the wintering range, then move to feed on arable land and improved pasture as the winter progresses (Dirksen *et al.* 1991; Laubek 1995; Nolet *et al.* 2002). This suggests that aquatic vegetation remains an important food source for the birds, despite a substantial reduction in wetland habitats across Europe due to the drainage and eutrophication of wetlands during the 20th century, and an increase in the swans' use of arable habitats from the 1970s onwards (reviews in Dirksen *et al.* 1991; Robinson *et al.* 2004; Rees 2006).

Whereas the Northwest European Bewick's Swan population is currently in decline (Rees & Beekman 2010) there is currently no evidence for a decrease in the more numerous Eastern population which winters in China, Japan and Korea. A total of 81,000 Bewick's Swans were counted in eastern China in the early 21st century (Cao *et al.* 2008a), of which >90% were found in the Yangtze River valley, on Poyang Lake and the lakes of Anhui Province (Cao *et al.* 2010). There is some evidence, however, for the swans' distribution in the Yangtze River valley becoming more restricted since 1996 (though it is not known whether there has also been a decline in numbers wintering in the region; Cao *et al.* 2008b). Moreover, Shengjin Lake, a site of international importance for the species where > 4,000 Bewick's Swans (*c.* 5% of the Eastern population) were recorded in winters 2003/2004 and 2004/2005 (Barter *et al.* 2004, 2006) received fewer swans in subsequent winters, which coincided with a decline in numbers of other tuber-feeding species wintering at the site such as Swan

Goose *Anser cygnoides* and Hooded Crane *Grus monacha* (Cheng *et al.* 2009; Zhang *et al.* 2010; Fox *et al.* 2011; Cong *et al.* 2011).

The differences in winter habitat use by swans from the two populations may affect not only the birds' nutrient intake, but also influence their feeding activity. Earlier studies of swans wintering in Gloucestershire, southwest England, have shown diurnal and seasonal variation in food intake, with a higher proportion of birds in the flock feeding at the start and end of the day than in the middle (Bowler 1996; Rees 2006) and a greater proportion of the day spent feeding at the end of the winter (February) when the biomass of grass in the fields was lowest (Bowler 1996). There is substantial variation in feeding activity recorded for Bewick's Swans grazing on pasture, however, with 33% of adults feeding during observations made during the 1990s (Bowler 1996), compared with 54% for swans in fields at the same site during the mid 1980s (Rees & Bowler 1991) and 60% for Bewick's Swans on the fens at the Ouse Washes, southeast England, in the 1970s (Cadbury 1975; Scott 1980).These estimates of the Bewick's Swans' daily feeding activity are within the range reported for Whooper Swans wintering in Britain and Ireland (40% and *c.* 60%; O'Donoghue & O'Halloran 1994; Rees *et al.* 2005), and are also similar to the activities of the more sedentary (non-migratory) Mute Swans (36% of the day feeding, Keane & O'Halloran 1992), but feeding activity is markedly higher for other wildfowl wintering in Europe: 90% feeding for European White-fronted Geese *Anser albifrons* (Owen 1972), 70% for Pink-footed Geese *Anser brachyrhynchus* (Giroux & Patterson 1995), 75–85% for Barnacle Geese *Branta leucopsis* (Ebbinge *et al.* 1975), 74% for Eurasian Wigeon *Anas penelope* (Mayhew 1988) and 60% for Gadwall *Anas strepera* (Paulus 1984). Whether the relatively low proportion of time spent feeding is attributable to the Bewick's Swans' feeding habitat, and the extent to which this is influenced by the time of year and other factors, remains unclear. For instance, Bewick's Swans feeding on stoneworts *Chara* sp. when staging at Matsalu Bay, Estonia, during spring migration spent 59% of their time feeding (and 24.5% sleeping) over a 10-day period in 1988, but only 25.5% of their time was spent feeding (compared with 38.2% sleeping and 12.3% preening) on the day when large numbers of birds landed in the area. This was thought to be due to the birds needing to rest following a long flight to the migratory site (Rees & Bowler 1991). Nolet & Klaassen (2005) and Nolet *et al.* (2007) similarly found that swans in aquatic habitats devoted 60–75% of their time to feeding at spring staging sites, attributing this to habitat quality and to the birds restoring the body reserves used during their long-distance migration.

Given the marked difference in the winter diet of Bewick's Swans wintering in Europe, compared with those in China, and also the vulnerability of wetlands in the Yangtze River valley to habitat change (especially the collapse of submerged macrophyte communities, Fox *et al.* 2011), information on habitat use and activity budgets for Bewick's Swans wintering in China is required to provide advice on the protection and management of wintering sites throughout the range. We therefore describe here, for the first time, within-winter changes in Bewick's Swan numbers at an internationally important site (Shengjin Lake in Anhui Province), in relation to variation in water levels at the site. Additionally, diurnal feeding patterns and food intake rates were studied for comparison with published data on the feeding behaviour of Bewick's Swans wintering in Europe. In particular, given that Bewick's Swans in China exploit natural foods in wetland habitats throughout the winter, which may provide a more nutritious diet than the arable crops used by swans wintering in Europe, we aimed to determine whether Bewick's Swans in China spent less time foraging in the day than those wintering on agricultural land. Finally, productivity data recorded for Bewick's Swans in the Northwest European and Eastern populations are compared, to determine whether there is any evidence for differences in breeding success for the two populations in recent years.

Methods

Study Site

The Shengjin Lake National Nature Reserve (30°15'–30°30'N, 116°55'–117°15'E) lies south of the Yangtze River and is the only wetland National Nature Reserve in Anhui Province (Fig. 1). The protected area, which covers 333 km^2, includes Shengjin Lake – a large and shallow, permanent, fresh water lake with a 165 km shore-line – as well as small lakes, fishponds, rice paddies and forests. Lake water comes from three rivers flowing directly into the lake (catchment area 1,548 km^2) and from the Yangtze River via a sluice built in 1965. During the summer flood season the maximum lake area is 140 km^2 (water level = 17.0 m a.s.l.; Wusong, unpubl. data); the water level falls to less than 10 m a.s.l. during September to February (dry season) causing the lake area to decrease to approximately 34 km^2 (Cheng & Xu 2005). Coordinated counts of Bewick's Swans and other waterbirds have been made at Shengjin Lake since winter 2004/05, with 4,333 swans recorded in January 2004, 5,429 in February 2005, 1,007 in February 2008 and 1,778 in February 2009 (Cong *et al.* 2011). In winter 2008/09, count frequency was increased, with systematic complete counts of Shengjin Lake being undertaken nine times from mid-October 2008 to mid-April 2009, to determine whether Bewick's Swan abundance and distribution across the lake was consistent throughout the winter. The following winter, thirteen counts were made between mid-October 2009 and mid-April 2010. Counts were made by two teams of observers visiting observation points (Sites 1–4 in Fig. 1) around the lake in a single day, using the methods described by Cao *et al.* (2011). Habitat assessment in summer 2008 found that Straight Vallisneria *Vallisneria spiralis* is the dominant submerged macrophyte at Site 1; Site 2 has three fish ponds where Rigid Hornwort *Ceratophyllum demersum* is the main vegetation; and Site 3 is a sedge *Carex* sp. meadow (University of Science and Technology of China, unpubl. data). Vegetation at Site 4 was not accessible, so the type of food available there for the swans is not known.

In order to determine whether swan numbers and distribution varied with water levels, a broad-brush measure of seasonal

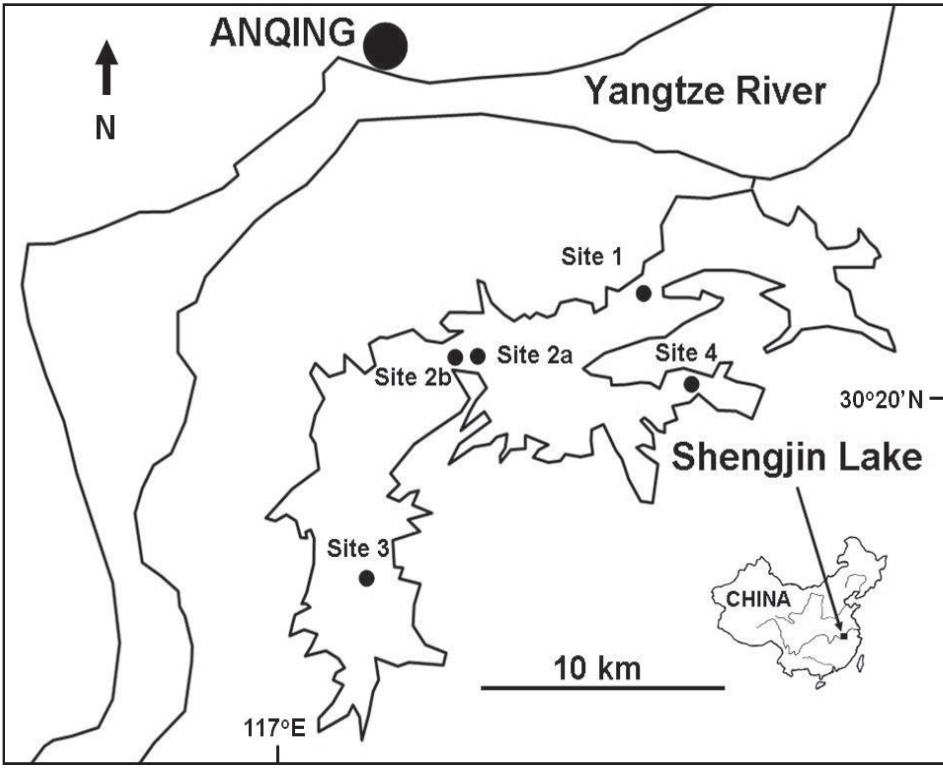

Figure 1. Map of Shengjin Lake, illustrating the four main count sites around the lake: Site 1; Site 2a and 2b, Site 3 and Site 4.

variation in the depth of water in the lake was determined from water depth data recorded at the Huangpen sluice, which controls the influx of water from the Yangtze River into Shengjin Lake. This describes only the amount of water coming into the lake, however; dams within the lake system also regulate flow and influence water depth in different parts of the lake, depending on whether the sluices are open or closed.

Behavioural observations: flock scans

The behaviour of the swans was recorded by making flock scans at approximately 15 min intervals throughout the day from dawn to dusk, over three days in winter 2007/08 (from 23–25 February 2008 inclusive), seven days in winter 2008/09 (on 4 November, 29 December, 1 and 16 January, 8 and 21 February and 19 March) and two days in winter 2009/10 (on 12 and 25 March 2010). All birds in view from the observation point (usually one or two groups of >100 individuals, seen on either side of the causeway at Site 2 in Fig. 1, treated as a single flock because the birds moved from one side to the other) were scanned using a telescope, working systematically from one end of the group to the other and recording each swan's activity as the bird first comes into view. The swans' behaviours were grouped into seven main categories: feeding (with sub-categories of head-dipping, up-ending, digging, grazing, surface-feeding, trampling and food handling), resting (which included sleeping, sitting, standing and loafing), aggression, comfort activity (including preening, flapping and bathing), movement (swimming, walking and flight), drinking and alert. Thus the proportion of birds present recorded feeding or engaged in other activities was determined for each scan.

Behaviour data recorded within each hour were averaged to give the mean proportion of birds in the flock seen feeding, resting and engaging in other activities for each hour of the day. Hourly samples of flock activity make it possible to describe diurnal patterns in the birds' activities (Owen 1972; Bowler 1996; Rees *et al.* 2005). The hourly figures were again averaged to assess any within-winter and between-winter variation in the swans' activities (especially the proportion of time spent feeding) at Shengjin Lake.

Flock scan data recorded in winters 1990/91, 1991/92 and 1992/93 for Bewick's Swans wintering at Slimbridge, Gloucestershire, UK (51°44.6'N, 2°24.2'W), a site of international importance for swans in the NW European population, were compared with the observations made in winter 2008/09 in this study to determine whether there was a major difference in the behavioural patterns of swans from different populations feeding on different food sources: primarily aquatic habitat at Shengjin Lake and grassland at Slimbridge. Methods were the same in both studies (*i.e.* scans were made at *c.* 15-min intervals and summarised by hour) except that adults and cygnets were considered separately at Slimbridge (Bowler 1996). Only 2008/09 data were considered for China, because the temporal spread (all day and across winter) was similar to the spread of the Slimbridge observations. Two scans made in February 2008 of >1,000 Bewick's Swans in a flock of 15,000 Bewick's Swans at Fengsha Lake, Anhui Province, China (30°93'–30°94'N, 117°61'–117°62'E), 75 km northwest of Shengjin Lake, are also presented for comparison. However, too few observations were made at Fengsha Lake to permit analyses of site differences in the activities of Bewick's Swans wintering in China.

Behavioural observations: feeding intensity

The feeding intensity of swans near the bridge at Shengjin Lake was monitored in February 2008 and December 2009, using similar but slightly different methods. In both years, feeding intensity was recorded as the time (in seconds) that the swan's head was under water, when the bird was feeding either by head-dipping or up-ending. In 2008 a single focal individual was followed continuously for up to 10 head-up and head-down motions during a feeding bout, with the duration of each successive head-up and head-down being timed using a stop-watch. When the scan was completed, or if a swan stopped feeding during an observation bout, then observations switched to the next bird to the right to ensure that data were being recorded for different individuals. To increase the number of individuals sampled, in winter 2008/09 the time that a feeding swan spent with its head under water was again recorded, but on this occasion just one head-dip was timed before moving to the next bird in the flock. Feeding intensity was taken as the duration of time that the swan had its head under water for each head dip, rather than the proportion of time that the head was under, to permit use of data from both winters in the same analysis. The age, location on the lake and, where possible, the breeding status (*i.e.* parent, paired or single) of each swan were also recorded. Bays used on either side of the road to the north of the bridge in February 2008 were classed as Ponds 1 and 2, and one additionally used to the south of the bridge in December 2009 (in addition to Pond 2) was classed as Pond 3. Observations made outside these areas were grouped as Pond 4.

Statistical analysis

Generalised linear models (GLMs) with identity link functions were used to determine whether the proportion of time that the swans spent feeding (arcsine transformed) at Shengjin Lake varied with the time of day (hour), season (month) or between years (for the winters 2007/08, 2008/09 and 2009/10). Year (included as a factor), month and time of day (included as variates), and quadratic functions of month and hour (testing for any curvilinearity in the relationship between month or hour and the proportion of swans seen feeding in each hour) were included as explanatory variables in the initial maximal model. Although month may be confounded by year due to only one month's data being available for two of the three years, both month and year were included at the outset, but were also tested separately. The first month of the winter with behavioural observations (November) was coded as 1, and subsequent months were coded consecutively. Non-significant variables were omitted sequentially from the model, the least significant variable being omitted first, so that the final model was parsimonious. Two-way interaction terms for significant variables were also tested in the model. Parameter estimates were taken from the final minimum adequate model.

Generalised linear mixed models (GLMMs) tested whether the swans' feeding intensity (time with head under water) varied significantly with year, month, time of day and the age (*i.e.* adult or cygnet) and location of the bird. Bird identity was included as a random effect, to control for known repeat observations made of the same individuals in 2008; year and month were treated as factors and time of day (hour) as a continuous variable in the model; year and month were both treated as factors because feeding intensity data were recorded in only two months (December and February) in 2008/09, as well as in February 2008.

The hourly mean percentage of Bewick's Swans recorded as feeding at Shengjin Lake was averaged, and variance in the data (calculated from the s.d. of the mean of the hourly values) was determined, for comparison with the results of the study of Bewick's Swan behaviour at a European wintering site (Slimbridge, U.K.; Bowler 1996). Student t-tests assessed whether there was a significant difference in the overall percentage of birds feeding at the two sites.

Variation in the breeding success of the two populations was investigated by collating age ratios published for a sample of birds from both western Europe (at sites in the U.K., Netherlands and Germany; Hustings *et al.* 2009; Hornman *et al.* 2011; WWT Waterbird Monitoring Reports 2008–2011 (WWT 2011); and W. Tijsen pers. comm.) and from China and Japan (Cong *et al.* 2011; K. Kazuo pers. comm.; this study) for winters 2007/08 to 2010/11 inclusive. The percentage of cygnets in a wintering flock was not recorded in China prior to 2007/08, so earlier years are not considered here. Chi-squared tests were used to determine whether there was a significant difference between the populations in the proportion of juveniles recorded each winter. Means are given ± s.d. throughout.

Results

Within-winter variation in numbers and distribution

The repeated counts of Bewick's Swans at Shengjin Lake in winter 2008/09 found that the first birds had arrived by 24 October and remained at the site at least until 31 March 2009; a span of 159 days. No birds were present on the first count day (15 October) or during the last coordinated count on 15 April. Numbers varied between 260 and 460 birds in the early part of the winter, but increased markedly to a peak of 1,788 in late-February, before decreasing again in March. Only 39 swans were recorded on 31 March (Fig. 2a), and just three birds were seen (albeit on a non-count day) on 3 April.

There was no significant correlation between water levels at the entrance to Shengjin Lake and the maximum number of Bewick's Swans counted on the lake on that day (Spearman's rank correlations: $r_s = 0.32$, $n = 6$, n.s., in 2008/09; $r_s = 0.28$, $n = 9$, n.s., in 2009/10; Figs. 2a,b; surveys before the swans arrived in autumn and after they departed in spring were omitted). Similarly, in most cases the proportion of the swans recorded on different parts of the lake did not correlate significantly with the water levels recorded (Spearman's rank correlations: $r_s = 0.58, –0.33, 0.68$ and $–0.32$, $n = 6$, for sites 1–4 respectively, n.s. in each case, in 2008/09; $r_s = –0.14, –0.82, –0.30$ and 0.03, $n = 9$, $P = 0.007$ for site 2, n.s. for sites 1, 3 and 4 in 2009/10; Figs. 2a,b).

Variation in feeding behaviour

A total of 75 scans were recorded over 26 h for flock sizes varying between 37–190 Bewick's Swans (mean flock size = 124 ± 35.3) in February 2008, 458 scans over 82 h for flocks of 9–653 swans (mean = 191 ± 131.9) in winter 2008/09 and 69 scans over 19 h for flocks of 119–458 swans (mean = 317 ± 89.6) in March 2010. Overall, 50.9 ± 19.6% of swans were recorded feeding throughout the study period. The percentage of swans recorded as feeding varied between winters, from 47.8 ± 15.4% in winter 2007/08 to 46.5 ± 17.7% in 2008/09 and 73.8 ± 16.9% in 2009/10. The swans also spent a high proportion of their time resting: 44.0 ± 14.2% in 2007, 32.9 ± 17.4% in 2008 and 15.9 ± 11.1% in 2009; 32.5 ± 17.9% throughout the study. Movement, comfort and other activities accounted for < 20% of the day.

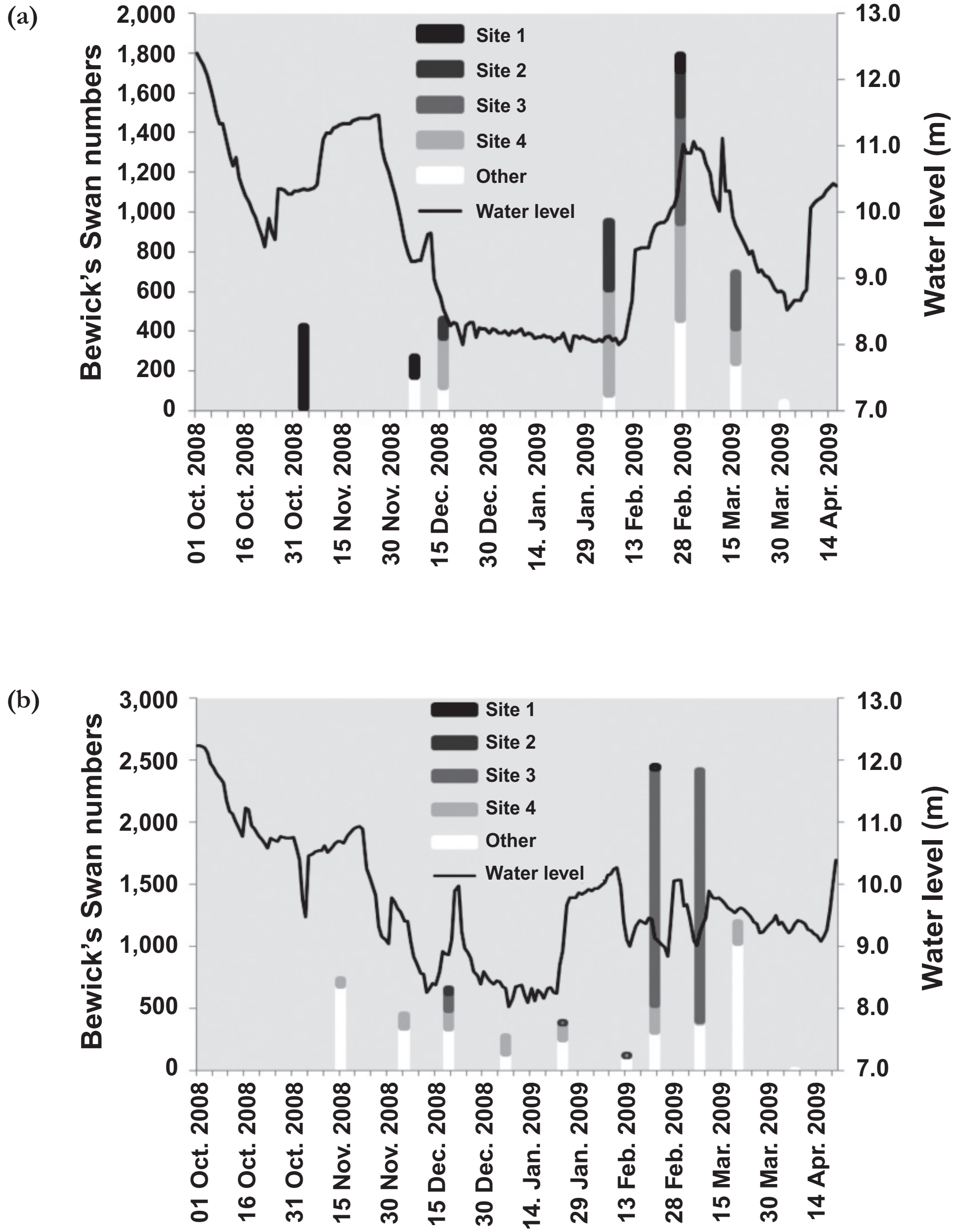

Figure 2. Water levels (line) and Bewick's Swan numbers (bars) at the Shengjin Lake National Nature Reserve in (a) winter 2008/09, and (b) winter 2009/10.

By including both year and month in the initial maximal model, the amount of time that the birds were feeding was found to differ significantly between years and with the quadratic time effect (hour^2) (GLM: $F_{3,122}$ = 20.12, P < 0.01). Feeding activity recorded in winter 2009/10 was significantly higher than in both 2007/08 ($t_{1,122}$ = 6.10, P < 0.001) and 2008/09 ($t_{1,122}$ = 7.17, P < 0.001), but winters 2007/08 and 2008/09 did not differ from each other ($t_{1,122}$ = –0.05, n.s.). When winter was omitted from the analysis, however, because of its potential to confound month effects, feeding activity was found to vary significantly across months ($t_{1,122}$ = –3.23, P = 0.002 for month; $t_{1,122}$ = 4.17, P < 0.001 for month^2; Fig. 3) and again within the day ($t_{1,122}$ = 2.02, P < 0.05 for hour^2; Fig. 4) (GLM: $F_{3,122}$ = 14.19, P < 0.01 for the final minimum adequate model). The significance of hour^2 reflected the non-linear trend in the swans' feeding patterns during the day, with the proportion of birds feeding increasing up to 10:00 h, decreasing a little in the middle of the day, then increasing again to a peak in numbers feeding at 17:00 h (Fig. 4). A similar pattern was found when analyses were confined to data recorded in the 2008/09 winter only; *i.e.* when observations were made in most months during the winter. A linear increase in feeding activity during the day proved significant, but month was not statistically significant (GLM: $F_{1,80}$ = 6.69, P = 0.01 for hour; $F_{1,79}$ = 2.71, P = 0.10, n.s. for month).

There was a significant negative correlation between the swans' feeding and resting activity during the study (Spearman's rank: r_s = –0.86, P < 0.001; Fig. 4). Feeding intensity, recorded as the proportion of time that the swans had their heads down under water during feeding bouts did not vary significantly with the time of day, but did vary with the location and age of the bird (*i.e.* whether adult or cygnet) (GLMM: $F_{3,598}$ = 9.12, P < 0.001 for location; $F_{1,703}$ = 6.22, P = 0.013, for age). Mean

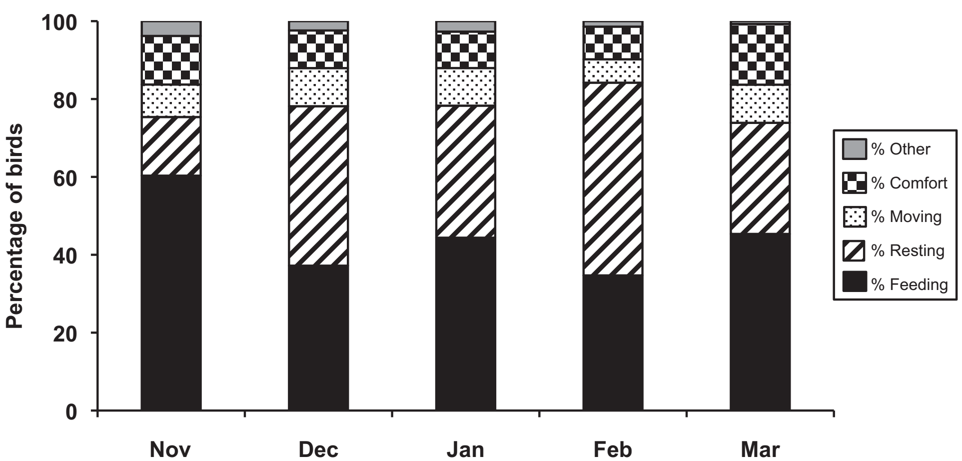

Figure 3. Variation in Bewick's Swan activities across months at Shengjin Lake in winter 2008/09.

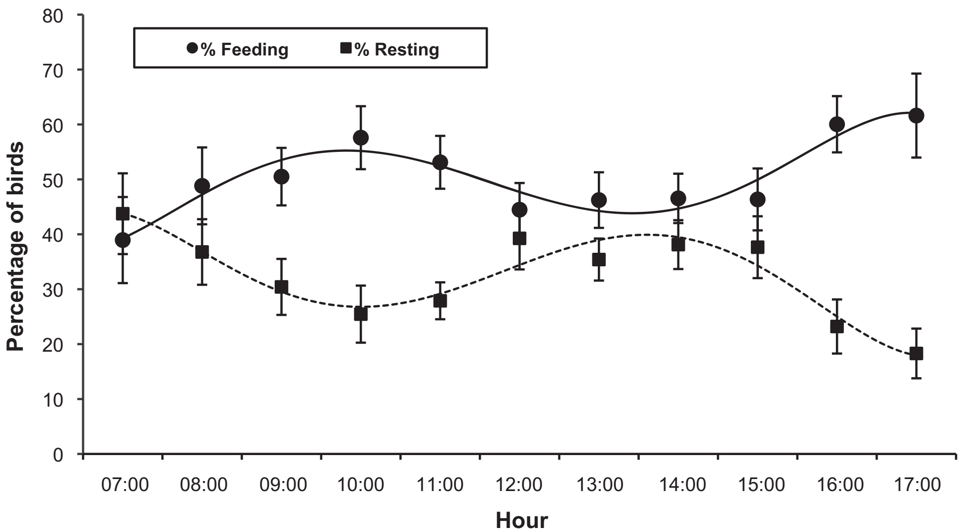

Figure 4. Diurnal variation in Bewick's Swan feeding and resting activity (mean of the percentage hourly activity recorded each day ± s.e. bars), recorded during flock scans at Shengjin Lake in winters 2007/08, 2008/09 and 2009/10, with polynomial trend lines.

duration with head-down feeding was 14.8 ± 8.1 s in Pond 1, 12.5 ± 7.7 s in Pond 2, 12.0 ± 6.5 s in Pond 3 and 13.9 ± 6.5 s outside these areas. Cygnets spent less time with their heads down during feeding bouts than adult swans (observed mean duration = 11.3 ± 5.6 s and 13.3 ± 7.7 s respectively). Differences in feeding intensity between the two main observation periods (13.9 ± 8.0 s head-down feeding in February 2008; 12.7 ± 7.3 in December 2009) was not quite significant (GLMM: $F_{1,\ 697}$ = 3.80, P = 0.052, n.s.) but more extensive observations are required to confirm any meaningful variation in feeding intensity within winters and between years. Preliminary analysis found that the feeding intensity recorded for adult swans in Pond 2 did not differ between years (mean duration with head-down feeding = 11.4 ± 7.4 s, n = 52, in February 2008; 12.8 ± 7.9 s, n = 302, in December 2009; unpaired t-test: t_{72} = –1.25, n.s.).

Comparison of the feeding activities of Bewick's Swans wintering in China with those from the Northwest European population

The percentage of Bewick's Swans recorded as feeding during the day was higher both at Shengjin Lake and at Fengsha Lake, China, than at Slimbridge in the U.K., but there was also a large amount of variance in the data (Table 1). Thus although 50.9% (± 19.6%) of the birds were found to be feeding at Shengjin Lake, compared with 32.8% (± 26.1%) of adults and 39.3% (± 32.3%) of cygnets seen at Slimbridge, the differences in the mean percentage of birds recorded as feeding did not differ significantly between

Table 1. Activities recorded for Bewick's Swans in winter, at one site in Europe (Slimbridge, Gloucestershire, U.K.; n = 1,208 and n = 815 hourly scans for adults and cygnets respectively in winters 1991/92–1993/94; Bowler 1996) and at two sites in China (Shengjin Lake and Fengsha Lake; n = 126 and n = 2 hourly scans respectively in winters 2007/08–2009/10; this study).

Activity	Site	Adult % activity (s.d.)	Cygnet % activity (s.d.)
Feed (graze)	Slimbridge	32.77 (± 26.09)	39.29 (± 32.34)
Rest	Slimbridge	32.56 (± 24.15)	28.28 (± 27.96)
Comfort	Slimbridge	16.56 (± 14.36)	17.55 (± 20.79)
Alert	Slimbridge	8.81 (± 9.26)	5.73 (± 10.73)
Movement	Slimbridge	7.19 (± 7.46)	7.63 (12.51)
Interaction	Slimbridge	1.45 (± 3.27)	0.85 (3.37)
Drink	Slimbridge	0.66 (± 1.85)	0.67 (2.87)
Feed (head-dip/up-end)	Shengjin Lake	50.88 (± 19.62)	
Rest	Shengjin Lake	32.53 (± 17.94)	
Comfort	Shengjin Lake	6.66 (± 4.55)	
Alert	Shengjin Lake	0.20 (± 0.67)	
Movement	Shengjin Lake	8.19 (± 6.11)	
Interaction	Shengjin Lake	0.96 (± 1.22)	
Drink	Shengjin Lake	0.02 (± 0.09)	
Feed (head-dip/up-end)	Fengsha Lake	47.27 (± 24.37)	
Rest	Fengsha Lake	11.28 (± 7.12)	
Comfort	Fengsha Lake	7.54 (± 6.87)	
Alert	Fengsha Lake	0.07 (± 0.09)	
Movement	Fengsha Lake	33.15 (± 10.39)	
Interaction	Fengsha Lake	0.71 (± 0.09)	
Drink	Fengsha Lake	0	

these two sites (Student's t-tests: t = –0.32, d.f. = 48, n.s. on comparing adults at Slimbridge with all birds at Shengjin Lake; t = –0.18, d.f. = 264, n.s. on comparing cygnets at Slimbridge with all birds at Shengjin Lake). The percentage of birds recorded as feeding during the two scans made on one day at Fengsha Lake (47.27 ± 24.37%) fell between the Slimbridge and Shengjin Lake values (Table 1).

Productivity of Bewick's Swans in the NW European and Eastern populations

The proportion of cygnets recorded among Bewick's Swans aged in the Eastern population was markedly higher than for swans aged in Northwest Europe each winter from 2007/08 onwards (Table 2). Overall, there were 15.34% cygnets (n = 2,654 swans aged) in the Eastern population compared with 3.86% cygnets (n = 9,609 swans aged) in Europe in 2007/08; 11.60% compared with 6.09% (n = 8,502 and n = 5,302 respectively) in 2008/09; 28.60% compared with 7.00% (n = 2,832 and n = 7,472) in 2009/10; and 18.65% compared with 10.53% (n = 8,154 and n = 7,275) in 2010/11. The higher proportion of cygnets among birds sampled in the Eastern population was statistically significant for each of the winters (χ^2_1 = 460.8 for 2007/08, χ^2_1 = 115.3 for 2008/09, χ^2_1 = 850.9 for 2009/10, and χ^2_1 = 201.0 for 2010/11; $P < 0.001$ in each case).

Discussion

Whilst the dynamics and behaviour of the Northwest European population of Bewick's Swans have been studied over several decades (Rees 2006), relatively little is known about the more numerous Eastern population of the species, which winters mainly in China and Japan. Information on population differences in winter feeding ecology is important as it may help to indicate potential reasons for the decrease in the Northwest European population during the 21st century (Worden *et al.* 2006; Rees & Beekman 2010) at a time when the Eastern population is clearly more numerous (Cong *et al.* 2011) and, despite the lack of coordinated population-level monitoring or extensive conservation management, seems to be stable or increasing (Wetlands International 2006; K. Kazuo, pers. comm.). Moreover, information on the swans' use of wintering sites in China is of value for advising on the management and protection of these areas. The wintering period, which extended from late October to late March in 2008/09, is longer than is usually recorded for Bewick's Swans wintering in the British Isles, where the first individuals likewise arrive in mid to late October but, even allowing for annual variation in weather conditions, most start their spring migration in February to early March and all have departed by mid-March (Rees 2006). It does however approximate to the time that the swans spend at wintering sites across Europe, with most birds leaving the Netherlands by the end of March (Rees *et al.* 1997b) and migration through staging sites in the Baltic countries (notably Estonia) generally occurring in April (Luigujõe *et al.* 1996). Satellite telemetry results suggest swans normally leave Japan in the last days of March and early April (Kamiya & Ozaki 2002).

The increase in numbers at Shengjin Lake during February 2009, to a peak of 1,788 in late-February, indicates either that the swans are congregating at the lake due to disturbance or reduced access to food resources at other wintering sites (*e.g.*

Table 2. Bewick's Swan breeding success recorded for the NW European population and the Eastern population. (Source: [1] = WWT Waterbird Monitoring Reports 2008–2011; [2] = Hustings *et al.* 2009 and Hornman *et al.* 2011; [3] = W. Tijsen pers. comm.; [4] = this study; [5] = K. Kazuo pers. comm).

Population	Country	Site	Winter	Month	No. aged	No. juvs	% juvs
NW Europe	UK	Various[1]	2007/08	Nov–Jan	2,278	107	4.7
	Netherlands	Various[2]	2007/08	November	7,331	264	3.6
	UK	Various[1]	2008/09	Nov–Jan	1,025	66	6.4
	Netherlands	Various[2]	2008/09	December	4,277	257	6.0
	UK	Various[1]	2009/10	Nov–Jan	5,561	506	9.1
	UK, Nths, Germany and Denmark	Various[3]	2009/10	December	7,472	523	7.0
	UK	Various[1]	2010/11	Nov–Jan	4,308	465	10.8
	UK and Nths	Various[3]	2010/11	December	7,275	766	10.5
Eastern	China	Shengjin Lake[4]	2007/08	February	214	29	13.6
	China	Fengsha Lake[4]	2007/08	February	2,440	378	15.5
	China	Shengjin Lake[4]	2008/09	Nov–Jan	1,452	222	15.3
	Japan	Various[5]	2008/09	Dec–Jan	7,050	764	9.8
	China	Shengjin Lake[4]	2009/10	Dec–Mar	1,508	224	14.9
	Japan	Various[5]	2009/10	Dec–Jan	1,324	214	16.2
	China	Wuchang Lake[4]	2010/11	November	1,417	596	42.1
	China	Shengjin Lake[4]	2010/11	December	69	18	26.1
	Japan	Various[5]	2010/11	Dec–Jan	6,668	907	13.6

through varying water levels or depletion of the food supply), or potentially that the site is used as an initial staging area by swans that winter further south. Future observations should help to clarify whether the late winter peak in numbers is a consistent pattern. Counts made in winter 2009/10 found a similar pattern, with about 2,400 Bewick's Swans at the site from mid February to early March compared with *c*. 800 swans seen in late October and early November, but this was not evident in winter 2010/11 when the peak count of 450 swans was made in January (Cong *et al.* 2011; University of Science and Technology of China, unpubl. data). *Vallisneria* tubers, an important food source for Bewick's Swans wintering in the Yangtze River floodplain (Barzen *et al.* 2009; Zhang *et al.* 2010), appear to be declining at some key Bewick's Swan sites (Fox *et al.* 2011), and vegetation surveys found no *Vallisneria* in Shengjin Lake in summer 2010 compared to 7.7 km^2 of continuous *Vallisneria* in four discrete beds in the southern end of the Upper Lake in 2000 (Liu *et al.* 2001; Fox *et al.* 2011). Thus any pattern of a late February influx of birds during or immediately prior to their migration is likely modified by local food availability for the birds.

There was no evidence from the present study for water levels at Shengjin Lake affecting numbers and distribution of Bewick's Swans at the site, but the water depth measure (taken as the depth at the entrance to the lake) was rather crude. More systematic measures of water depth across the lake, along with sampling to record variation in the abundance and distribution of *Vallisneria* tubers and other potential food for Bewick's Swans in the lake, should help to clarify this issue. Additionally, more frequent counts would perhaps be able to describe a short-term response by the birds to short-term changes in water levels, which would help to separate site-use determined by water levels from the general seasonal changes in numbers (*i.e.* increasing numbers in autumn and decreases in spring) at the site. Studies of Bewick's Swans feeding on pondweed tubers in Europe have demonstrated that the swans prefer to take tubers in shallow water than in deep areas in the first instance (Nolet *et al.* 2001), so further investigation of the influence of water levels on the swans' use of Shengjin Lake is important for advising on how best to manage the site for the birds.

Preliminary analysis of the behaviour of Bewick's Swans wintering at Shengjin Lake in winters 2007/08 to 2009/10 inclusive found that on average the birds spent > 50% of the day feeding, but that there was significant variation in the proportion of birds recorded as feeding both within the day and between years. The bimodal feeding pattern recorded, with higher feeding activity noted in the morning and late afternoon and a more quiescent period in the middle of the day, is similar to patterns recorded for Passeriformes (Gibb 1956; Morton 1967; Verbeek 1964) and wildfowl (Owen 1972; Ebbinge *et al.* 1975; Amat 1986; Mooij 1992), including geese feeding on *Vallisneria* tubers in China (Fox *et al.* 2008a,b) and earlier studies of swan species (Bowler 1996; Rees *et al.* 2005; Tatu *et al.* 2007). In the case of wildfowl, this may be attributable to birds with relatively poor ability to digest their food needing to maximise their energy intake immediately before and after the overnight roost (when feeding activity generally is much lower), particularly at wintering sites where night-time temperatures may fall well below zero. Whether food intake by swans wintering at Shengjin Lake is indeed constrained by day length warrants further investigation, however, as Bewick's Swans feeding on pondweed tubers in the Netherlands feed at night (Nolet *et al.* 2007). Unlike Barnacle Geese *Branta leucopsis* grazing on grass swards, where the peck rates of grazing birds were more rapid at the start and the end of the day (Ebbinge *et al.* 1975) there was no similar bimodal pattern in the swans' feeding intensity, but the difference in feeding intensity recorded for swans in different parts of the lake (*i.e.* the significant location effect) may reflect variation in food density and accessibility (patch profitability), as indicated for Bewick's Swans feeding on pondweed tubers in the Netherlands (Nolet *et al.* 2001; Nolet & Mooij 2002; Nolet *et al.* 2007). That cygnets in China spent a lower proportion of time with their head under water during feeding bouts than adult swans appears to differ from observations made in April–May 1988 of Bewick's Swans at Matsalu Bay, Estonia, an important staging area for the Northwest European population, where cygnets fed more intensively (*i.e.* had their heads down continuously for longer periods) than the adult birds (Rees & Bowler 1991). Cygnets in Estonia also looked up for longer periods than paired birds whilst feeding, however, so it seems that looking around is an important component of cygnet behaviour at both sites, perhaps to maintain contact with the parent birds.

Overall, there was no significant difference between Bewick's Swans wintering at Shengjin Lake with those wintering at Slimbridge in the proportion of birds recorded feeding throughout the day, though this may due to the high level of variance in the swans' feeding activity. The amount of time that the swans at Shengjin Lake spent feeding was significantly higher in winter 2009/10 than in the previous two years, but similar variability has been recorded at Slimbridge, where 32.8% of adults and 39.1% of cygnets were recorded feeding in winters 1990/91–1992/93 (Bowler 1996; Table 1) but 54.3% of Bewick's Swans (both adults and cygnets) were recorded as feeding (68.5% at the start of the winter; 48.5% at the end of the winter) in 1986/87 (Rees & Bowler 1991). The variability in feeding activity reflects that reported in studies of other swan species (Keane & O'Halloran 1992; O'Donoghue & O'Halloran 1994; Rees *et al.* 2005; Nolet *et al.* 2007) and may be attributable to a range of factors affecting the birds' behaviour such as season, weather, field location, crop type and the number of days that the flock has been using a field. But feeding activity in both the eastern and western populations was still markedly lower than for other wildfowl wintering in Europe (Owen 1972; Giroux & Patterson 1995; Ebbinge *et al.* 1975; Mayhew 1988; Paulus 1984). Thus, although there is currently no evidence to suggest that the amount of time spent feeding during the day differs significantly between swans at the Slimbridge and Shengjin Lake wintering sites, further and more extensive behavioural observations are required to confirm whether this is the case and to explain any differences found between the two populations. This does not necessarily reflect a similarity in the calorific and nutrient value of the food ingested by swans at the two sites. Although some supplementary grain is provided for the swans at Slimbridge (Rees 2006), their main food is Common Ryegrass *Lolium perenne* (Rees 1991). Ryegrass has slighter greater crude energy content (*e.g. c.* 18 kJ g^{-1} Palladino *et al.* 2009) than *Vallisneria* tubers (*c.* 15 kJ g^{-1}; Fox *et al.* 2011) but energy assimilation rates are far higher for tubers (87%; Fox *et al.* 2011) than grass, which has a far higher fibre content than plant storage organs (Prop *et al.* 2004). Tubers also contain more protein than some other foods utilised by Bewick's Swans in Europe, such as sugar beet (14·8 *versus* 6·6% of organic matter; Van Eerden *et al.* 1997). Thus, even if the amount of time spent feeding by swans from the different populations is the same, differences in food utilised by the Northwest European population and the Eastern population in winter (*i.e.* farmland and aquatic vegetation respectively; Rees 2006; Cong *et al.* 2011) may result in substantial differences in the average daily intake of energy and other nutrients during the winter.

The percentage of cygnets recorded for Bewick's Swans in the Eastern population was significantly higher than for those in the Northwest European population every year from 2007 to 2010 inclusive. Whether this is attributable to the swans in the Eastern population being in better body condition through their feeding on traditional wetland habitats, as opposed to farmland, remains to be seen, but the correlation between winter body condition and productivity the following summer (*i.e.* the carry-over effect of the winter food supply) has been demonstrated for some goose populations (Inger *et al.* 2010; Morrissette *et al.* 2010), and for individuals birds (Bowler 1996; Studds & Marra 2005). Poorter (1991) hypothesised that reproduction was higher when more aquatic resources are eaten by the swans, and he used this to explain a reduction in the reproductive output of the Northwest European Bewick's Swan population from 1955 onwards. However, this decrease in reproduction can be better explained by density-dependence (the population showed a large increase during Poorter's study period) and a lower breeding density for the Eastern population may likewise explain their greater breeding success.

Several other factors may also contribute to or explain the current differences in the dynamics of the two populations, including the frequency and location of staging sites which are poorly known for the Eastern population. Based on the satellite telemetry studies of Higuchi *et al.* (1991) and Kamiya & Ozaki (2002) to establish distances between stopover sites, Nolet (2006) calculated that because west Palearctic Bewick's Swans are faced with slow advancement on their final migratory leg to the breeding grounds, the degree of capital breeding (*i.e.* where the body reserves required for egg laying are developed at the staging areas rather than the breeding grounds) would be far greater amongst this flyway population than in the east Palearctic swans. Swans in the Eastern population are faced with a long (2,200 km;

Nolet 2006 p. 585) last leg, which energetically would preclude capital breeding. This may mean that the reproductive output in this flyway population is more subject to conditions on the breeding areas, and therefore more susceptible to variation in weather conditions across the swans' breeding grounds in the Russian arctic. Variation in breeding habitat quality therefore may accommodate further increases in numbers in the eastern part of the range. More detailed studies to determine whether variation in winter food supply has a significant effect on the productivity of individual Bewick's Swans, and the extent to which traditional foods are important for survival and productivity, would help to inform habitat management and protection for the swans throughout their different wintering ranges. Other potential reasons for differences in the breeding success between the two populations, such as variation in climate and predator levels across the breeding range, should also be assessed.

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Photograph: Mark Barter (right) and Richard Hearn (left) counting Bewick's Swans in the distance at Fengsha Lake, China, by Eileen Rees.