

Preliminary observations of diurnal feeding patterns of Swan Geese *Anser cygnoides* using two different habitats at Shengjin Lake, Anhui Province, China

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Abstract

Swan Geese *Anser cygnoides* wintering at two different areas of Shengjin Lake fed either by grubbing below ground rhizomes of *Vallisneria asiatica* or by grazing the above ground primary production of sedges *Carex* sp. and Canary Grass *Phalaris arundinacea* leaves. Activity budgets were compiled from geese using the two different foods and feeding behaviours showed little appreciable difference in time spent feeding (c. 50% of daylight hours) or resting (c. 30%), which were similar to previous observations from Poyang Lake of the species feeding on *Vallisneria*. In the absence of evidence of night feeding, the extended periods spent resting during the day suggests that the species is well able to meet its energetic needs at present foraging rates. However, to understand fully the profitability of the two habitats, detailed studies are required on the energetics of goose exploitation of *Carex* and *Phalaris* leaves and of *Vallisneria* rhizomes, including the effects of food depletion on the profitability of both habitats, and in relation to changes in body stores accumulated by the geese throughout the winter season. This is especially important if availability of these foods is likely to change at Shengjin Lake and at the many other lakes in the Yangtze River basin as a result of the hydrological effects of the Three Gorges Dam project, as these sites are the main winter strongholds for the global Swan Goose population.

Key words: *Anser cygnoides*, feeding ecology, grazing, grubbing, Swan Goose, *Phalaris arundinacea*, Shengjin Lake, *Vallisneria asiatica*.

The Swan Goose *Anser cygnoides* is confined to the Eastern Palearctic, where it breeds in west and central Mongolia, northeast China and adjacent parts of Russia, as well as on Sakhalin Island and adjacent parts of the Russian mainland (Kear 2005). It winters almost exclusively in China, at a few sites on the Yellow and East China Seas and at several recessional wetlands and large lakes along the middle and lower Yangtze River, as well as in small numbers elsewhere (Perennou *et al.* 1994; Lu 1996; Miyabayashi & Mundkur 1999). The species is categorised as vulnerable (BirdLife International 2008) and population estimates vary between 60,000 and 100,000 (Wetlands International 2006; BirdLife International 2008; Cao *et al.* 2008), with accounts referring to fragmentation and contraction of the breeding range contributing to “substantial reductions” from previous times (Lu 1996; Miyabayashi & Mundkur 1999; Goroshko 2001; Poyarkov 2001; Kear 2005). Although new evidence (Cao *et al.* 2008) suggests that declines have not been as severe as previously thought, the species remains in decline and at threat from extensive habitat loss, hunting, damming of major rivers, over exploitation and general habitat loss (BirdLife International 2008; Kear 2005); range contraction on the wintering grounds of the Yangtze floodplain has occurred during the last 50 years (Cao unpubl. data). The principal food item on the freshwater wintering grounds is considered to be the over-wintering rhizomes of *Vallisneria asiatica*, which the species extracts from soft muddy substrates in recessional wetlands (Lu 1996). The accessibility and extraction of these plant organs is highly dependent upon

hydrological conditions; high water levels put rhizomes beyond the reach of the geese, but severe water level recession dries the substrate, rendering the food supply inaccessible. The reliance on particular water levels at critical periods of the winter may explain the very large between-year fluctuations at specific sites which are a feature of the species (e.g. Fox *et al.* 2008) and which creates particular challenges to constructing population trend assessments. The construction of the Three Gorges Dam gives additional cause for concern in this respect, given that the control of flows in the Yangtze River is likely to affect water levels down stream, lowering the levels at periods of maximum inundation in the summer, but prolonging high levels later into the winter. Such changes in the water regime may have adverse effects on wintering Swan Geese, given their reliance on specific water levels for their food supply. For this reason, it is important to understand the feeding ecology of the species under different hydrological conditions in order to assess its potential to shift between different feeding habitats, and to appraise its vulnerability to changes in water regimes at key sites.

We undertook a brief study of the feeding behaviour of Swan Geese at Shengjin Lake in the Yangtze River system in February 2008, comparing two sites where the geese were seen to be consistently feeding throughout the winter, but where they exploited different habitats using different foraging techniques. At one site, the geese fed on the below-ground *Vallisneria asiatica* rhizomes which the species extracted from soft mud. Meanwhile, at the same time approximately 8 km away elsewhere on the

same lake, a separate flock of Swan Geese fed on the above ground fresh green biomass of Canary Grass *Phalaris arundinacea* and a sedge *Carex* sp. (probably *C. thunbergii*), both of which were very abundant over extensive areas of mudflats that were becoming colonised by flowering plants following water level recession. Swan Geese are reported to feed principally on roots in winter, especially those of *Vallisneria asiatica* (Kear 2005), which may suggest that the graminoid habitats represent an alternative or secondary habitat, widely available at Shengjin Lake. These differences in foraging behaviour provided an opportunity to compare time budgets of geese feeding on below ground storage organs and those grazing on above ground green plant material. This may have some management relevance in the future should the relative availability and abundance of these two habitats alter as a result of hydrological changes in the Yangtze River. In particular, we make the prediction that, because *Vallisneria* rhizomes are highly nutritious (although not necessarily more so than grass, Lu & Zhang 1996), the grazing birds would feed for longer periods because they may require longer periods of feeding during the daylight hours to attain the same energetic intake from grass.

Study Area and methods

Shengjin Lake

Shengjin Lake (30°16'–30°26'N, 116°58'–117°11'E) is a large shallow freshwater lake with a shoreline extending to 156 km at 11 m above sea level lying south of the Yangtze River (Fig. 1). The area experiences a subtropical monsoon climate with dry

winters and a rainy season from April to June. Spring flooding raises water levels to a maximum of 17 m ASL in summer, depositing extensive silt, after which water table recession through autumn and early winter to 10 m ASL exposes extensive mud flats, grasslands, sedge meadows and seasonal wetlands (Research Institute for Yangtze Water Resources Protection 1999). Dominant submerged macrophytes include *Ceratophyllum demersum*, *Potamogeton malainus* and *Vallisneria spiralis*, floating species include *Euryale ferox*, *Trapa maximowiczii* and *Nymphoides peltatum* and the dominants of exposed drying mudflats include *Phalaris arundinacea*, *Carex unisexualis*, *C. cinerascens* and *Polygonum lapathifolium* (Ramsar Site Information Service 2008). The site is state owned and its 13,300 ha are protected within the Shengjin Lake National Nature Reserve, which was established in 1987 and is managed by the Government of Anhui Province. Management includes establishment of a research station at the site and designation of 33,340 ha around the lake as a Waterbird Conservation Area. Proposals for management include restrictions on grazing and cutting of aquatic vegetation, on fishing techniques, a complete ban on hunting, and prevention of pollution from industrial effluents. A publicity campaign and programme of conservation education is being developed to convince the local people of the need to conserve the lake and its wildlife, since 13 towns and 46 villages (total population of about 80,000) are situated in the area (Jiang *et al.* 2007). Most of the villagers are dependent on cultivation of cotton and rice on the plains around the lake, whilst others

graze livestock on the lake shore and fish the waters of the lake which are an essential source of food for many local residents.

Study sites

Data on Swan Goose activity budgets was recorded at two discrete sites on 23 and 24 February 2008 (Fig. 1). The first was an area of recently exposed mudflats at 30°25'N 117°08'E, some 10 km southeast of the bridge over the Yangtze River at Anqing. Here the flats were dry and relatively firm,

covered in a dense carpet of a small *Rorippa* sp. punctuated with dense patches of *Carex* sp. and *Phalaris arundinacea*. The second was part of a relatively enclosed bay approximately 80 m wide at 30°23'N 117°04'E, with a shoreline of open soft mud with no covering surface vegetation, approximately 10–20 m wide where the geese fed exclusively on subterranean parts of *Vallisneria*. A series of fish traps covered part of the shoreline, including areas used by the geese.

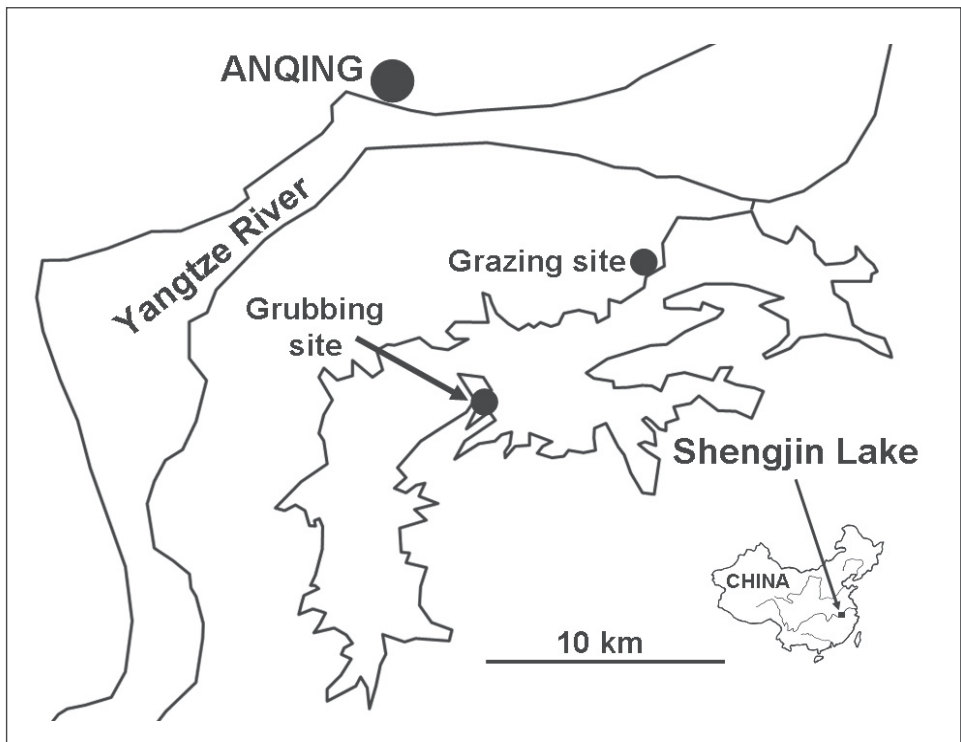


Figure 1. Location of Shengjin Lake Nature Reserve, China (inset bottom right) and places at the lake used by Swan Geese for grubbing (feeding on *Vallisneria*) and for grazing (feeding on *Carex*/*Phalaris*), as described in the text.

Compilation of activity budgets

Data on Swan Goose activity were compiled by using 20–60x telescopes to undertake scan samples of visible flocks at 15 min intervals during the day. The behaviour of each successive individual was recorded as it was encountered in the field of view on scanning from one end of the flock to the other. The geese were viewed from cover at a range of 200–800 m without causing disturbance to the birds (Altmann 1974). The following behaviour classes were allocated to each bird: walk, feed (whether standing or swimming), stand, preen (including wing flap and other plumage care), alert (standing with the body and bill held slightly above the horizontal), drink, loaf (on water), swim, fly, sit, sleep (both sitting and standing with head on back) and agonistic interactions (both given and received). Sitting and sleeping were grouped into a “resting” category for analysis. Scan samples were compiled from dawn until dusk, although single scans were occasionally missed when birds were disturbed. As far as possible, the entire flock was sampled at both observation sites comprising between 131–470 individuals at the first site and 69–146 geese at the second. Numbers fell during periods when the geese were disturbed and displaced from a site, but it was considered highly unlikely that individuals moved between the two sites.

Results

Based on the average proportions of Swan Geese scanned every 15 min, the geese grazing on *Carex/Phalaris* flats fed for 53.1% (s.e. ± 3.27) and rested for 29.4% (s.e.

± 2.76) of the daylight hours. This compared with 49.4% ± 4.23 and 33.8% ± 4.75 for geese grubbing for *Vallisneria* rhizomes. There was a distinct diurnal rhythm to feeding, with most intensive feeding activity towards sunset and slightly elevated feeding activity at first light. Least foraging in both habitats occurred during the middle part of the day when geese exhibited most resting behaviour (Fig. 2).

Discussion

The results showed that there was little appreciable difference between the time invested by Swan Geese feeding on the *Carex/Phalaris* flats compared to those grubbing for *Vallisneria* rhizomes; both spent approximately 50% of the 12 daylight hours foraging. For the geese grubbing for *Vallisneria* rhizomes, this conforms to earlier observations made by Lu & Zhang (1996), who found feeding constituted 57% (s.e. $\pm 7\%$) of daylight hours and resting 22% (s.e. $\pm 9\%$) amongst Swan Geese at Poyang Lake. These authors also found that 90% of the diet at this site consisted of *Vallisneria* rhizomes, on which this species clearly specialises at certain sites. The lack of difference in time invested in feeding activity between rhizome-grubbing and grazing birds at Shengjin was contrary to expectations, because it is well recognised that most grazing geese spend a greater period of their time foraging than do rooters and seed-gleaners (e.g. Madsen 1985). This is because grass tends to be less digestible than plant storage organs that are often rich in soluble carbohydrates (Owen 1980). *Vallisneria* rhizomes are energy-rich (3.4 \pm

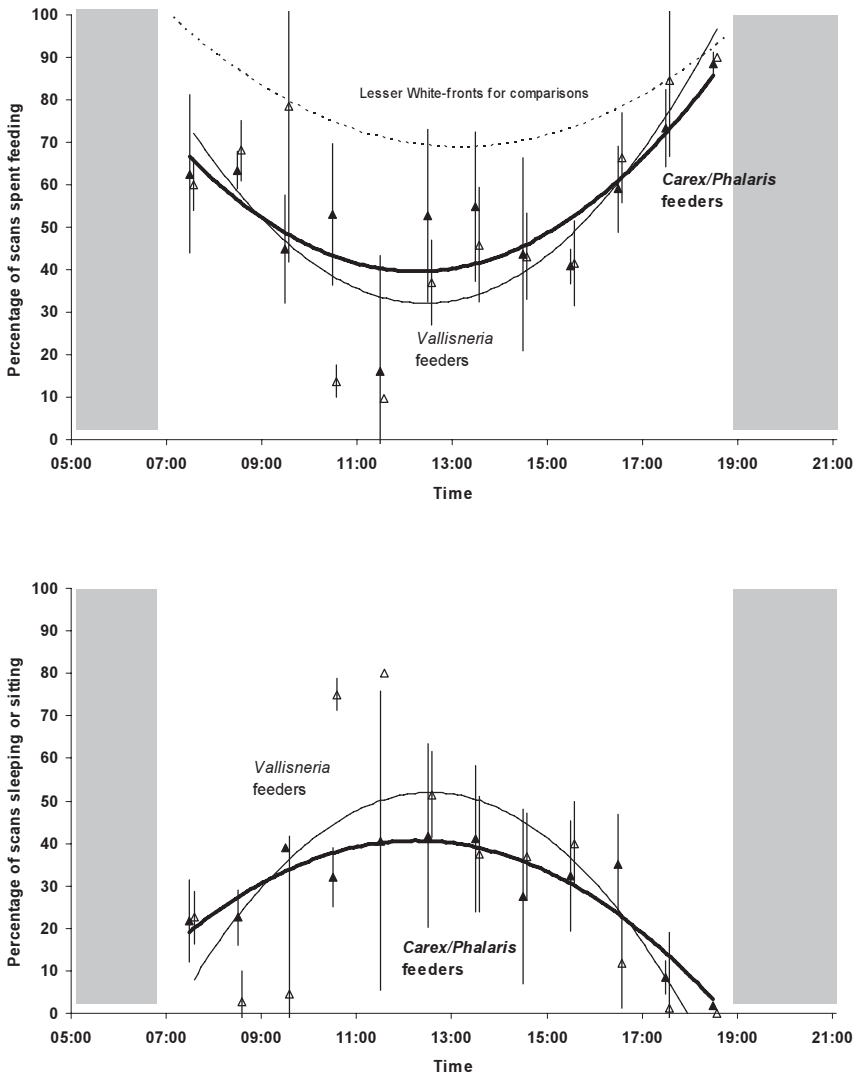


Figure 2. Daily activity patterns of Swan Geese at Shengjin Lake, showing the mean (\pm 95% confidence intervals) hourly percentage of scan samples with birds feeding (upper) and resting (sleeping and sitting combined, lower). Open triangles represent the geese feeding on *Vallisneria* rhizomes; solid triangles represent the geese grazing on *Carex* sp. and *Phalaris arundinacea*. Shaded areas indicate the period of darkness at the time of the study. Fitted least square polynomial regression models are shown simply as a visual guide and for general comparisons with similar data from Lesser White-fronted Geese at East Dongting Lake (from Fox *et al.* 2008).

0.11 kcal g⁻¹ dry weight) but also relatively low in fibre and ash (Lu & Zhang 1996), making the handling time involved in excavation and consumption profitable where rhizome densities are sufficiently high. The same authors found that the leaves of *Carex* sp. had higher potential energy content (3.6 ± 0.09 kcal g⁻¹ dry weight), but high ash content (and very likely fibre content). In contrast, the leaves of *Phalaris arundinacea* are large compared to many similar grass species, and may also be potentially relatively energy-rich (4.58–4.71 kcal g⁻¹ dry weight), as well as being high in protein content (27.4–32.2% dry weight content) and not excessively high in fibre (27.4–32.2%) or lignin (2.7–4.2%, Ingalls *et al.* 1965). This would also suggest that a large goose would be able to harvest large quantities of available forage from the above ground parts of this plant, especially where the grass is common, as is the case on the flats where the observations took place at Shengjin Lake.

Observations made at the time indicated that Swan Geese invest considerable search time in probing and grubbing substrate before each *Vallisneria* rhizome was found, and that each required prolonged handling time before being finally eaten. Such investment in successfully locating and consuming rhizomes may offset the energetic benefits of consuming such a high quality food item, but without more detailed studies of the relative energy intake rates versus foraging costs, it is not possible here to compare *Vallisneria* profitability with the sustained intake of more locally abundant, more accessible and more energy-rich monocotyledonous leaves at the second site. It may be, as in the case of Lesser Snow

Geese *Anser caerulescens caerulescens* feeding by grubbing on saltmarshes in Louisiana compared to those grazing on the green shoots of rice (Jónsson & Afton 2006), that the relatively higher work load required for grubbing probably leads to higher handling times (before ingestion) per unit of food (see Keating *et al.* 1992). In that case, grubbing Lesser Snow Geese actually spent longer foraging in the marshes compared to those grazing in the rice fields, contrary to expectations. Hence, although below ground storage organs present an apparently rich food source, the costs of extraction and hence ultimate intake rates may offset profitability against other foods (such as above-ground monocotyledon leaves) where search and handling times are lower and intake rates potentially higher.

Overall, Swan Geese showed remarkably low levels of feeding activity at both study sites. Herbivorous geese in temperate wintering areas typically spend up to 90% of daylight hours grazing to achieve their energetic requirements (e.g. Owen 1972), so the finding that Swan Geese used so little grazing time when exploiting *Carex*/*Phalaris* flats is unusual. However, observations of the same species grazing at nearby Poyang Lake reported similar low levels of feeding at that site in the early 1990s (Lu & Zhang 1996). Nevertheless, the difference in comparison to Lesser White-fronted Geese *Anser erythropus* which fed for a mean of 78% of the same daylight period at nearby East Dongting Lake (Fox *et al.* 2008) is highly pronounced. This marked difference suggests that Swan Geese can attain their energy requirements in less time than other studied species, but is this really the case?

It is generally assumed that, amongst grazing geese, foraging takes precedence over all other activities (Owen 1980). Owen (1972) showed that preening, drinking and resting were amongst the main non-feeding activities of geese under pressure to feed during limited hours of daylight. Plumage care and taking water took up a constant and minimal amount of time throughout the winter, but as the daylight hours increased later in the season, the absolute time spent resting increased. Owen (1980) took this to indicate that resting is an indication of the ability of the geese to attain their necessary nutritional and energetic income, rather than an essential element of the diurnal rhythm. If this were to be the case, the extended periods of resting witnessed amongst the Swan Geese under observation at Shengjin Lake would seem to indicate that these birds had very little difficulty meeting their daily energetic needs under observed conditions exploiting two different types of food item, derived from different habitats.

Both flocks of geese were observed to be disturbed by people during the observations, and in both cases this caused geese to put to flight to remote refuge areas where they loafed, preened and drank before ultimately returning to feed. At both sites, the disturbance took place fortuitously at a similar time of day (late morning) and turned out to be of similar duration. On the basis of Owen's view of the function of rest, this suggests that despite a single disturbance, the geese were still able to find substantial periods in which to rest, implying the geese could also tolerate higher rates of disturbance.

However, we should perhaps be more prudent in our conclusions. The larger body size and bill enables the Swan Goose to take in larger bite sizes and therefore very much greater amounts of food per unit time than other species of the genus *Anser*. It may be that the Swan Goose simply fills the gut faster, without necessarily being able to digest and process the volume of food any more efficiently than other smaller species. This digestive bottleneck may enforce Swan Geese to cease feeding and rest in order to digest the gathered food more efficiently, but this seems unlikely, since resting was least when the geese fed most. Geese exhibit rapid throughput of food in the alimentary canal, so unless resting was evenly distributed through the feeding period, the digestive bottleneck does not seem a likely explanation for patterns of resting in this case, especially amongst the grazing birds which likely ingested a greater bulk of food than the rhizome grubbers (although the relative intake rates need to be quantitatively determined). However, the fact that the geese are resting for prolonged periods of the day compared to other congeners need not imply that the geese are able to tolerate higher disturbance levels, because disturbance induced stress is clearly different from other forms of resting. Relationships between volumetric food ingestion and retention times have rarely been studied in geese (see Prop *et al.* 2005), and never to our knowledge in Swan Geese, so there are opportunities for innovative captive feeding studies to look at these issues.

Furthermore, although Swan Geese at both sites were observed flying to open

water to roost at dusk and come from open water onto the feeding sites at sunrise, it remains possible that they were feeding at night (although Lu & Zhang 1996 rejected this possibility amongst Swan Geese feeding at Poyang Lake), which may be an alternative potential explanation to the low rate of investment in feeding during the daylight hours. The moon was full at the time of the observations, so it is important that any future study investigates the possibility of night-time feeding being associated with the phases of the moon. This investigation was restricted to a very short period in the annual non-breeding cycle, so perhaps we were witnessing the birds feeding in times of food abundance compared to that seen at times of greater unpredictability in their stochastic feeding resource. Perhaps as hydrological conditions change (within and between years) Swan Geese need to be as efficient as possible in their feeding ecology and retain possibilities for investing far greater time in foraging under less favourable feeding conditions.

Swan Geese showed dichotomous feeding strategies at different parts of the same wintering site. Observations and constancy of numbers in each site suggested no interchange between birds using the two feeding areas, indicating that different flocks grazed the above ground parts of high biomass graminoids or extracted below ground storage organs of a water plant in muddy substrates exposed by water level regression.

More research is urgently needed relating to this species if its precise ecological needs are to be identified and

refuge management focussed on providing the best possible conditions and habitat for the species. One priority would be to establish whether there are changes in habitat use through the course of a winter at this important site in response to depletion and changes in food profitability. In other species, grubbing is often highly seasonally dependent, for example, on arrival in arctic areas prior to the onset of above ground primary production (Fox *et al.* 2006), but it is not known to what extent this may be the case at Shengjin Lake. For instance, Lu & Zhang (1996) mention that Swan Geese at Poyang Lake fed on the below ground parts of *Carex* sp. which we did not witness at Shengjin Lake, suggesting that these birds may modify their exploitation of the same habitat in response to changes in seasonal food quality and availability. Furthermore, it is essential that detailed studies be carried out on the energetics of exploitation of *Carex* and *Phalaris arundinacea* and of *Vallisneria* rhizomes, including the effects of food depletion on the profitability of both habitats, in relation to changes in body stores accumulated by the geese throughout the winter season, to understand fully the profitability of the two habitats. This is especially important if the balance between the two habitat types is likely to change in the future as a result of the Three Gorges Dam project, which is likely to have an effect on the hydrology of Shengjin and many other lakes in the Yangtze River basin where the global population of the Swan Goose has its main winter strongholds.

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References

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.
- BirdLife International 2008. Species factsheet: *Anser cygnoides*. Available at <http://www.birdlife.org/datazone/species/index.html> (accessed on 19/9/2008).
- Cao, L., Barter, M. & Lei, G. 2008. New Anatidae population estimates for eastern China: implications for current flyway estimates. *Biological Conservation* 141: 2301–2309.
- Fox, A.D., Francis, I.S. & Bergersen, E. 2006. Diet and habitat use of Svalbard Pink-footed Geese *Anser brachyrhynchus* during arrival and pre-breeding periods in Adventdalen. *Ardea* 94(3): 691–699.
- Fox, A.D., Cao, L., Barter, M., Rees, E.C., Hearn, R.D., Cong, P.H., Wang, X., Zhang, Y., Dou, S.T. & Shao, X.F. 2008. The functional use of East Dongting Lake by wintering geese. *Wildfowl* 58: 3–19.
- Goroshko, O.A. 2001. Swan Goose in the Eastern Transbaikalia and Mongolia. *Casarca* 7: 68–98.
- Ingalls, J.R., Thomas, J.W., Benne, E.J. & Tesar, M. 1965. Comparative response of wether lambs to several cuttings of alfalfa, birds foot trefoil and reed canary grass. *Journal of Animal Science* 24: 1159–1164.
- Jiang, H.X., Xu, W.B., Qian, F.W. & Chu, G.Z. 2007. Impact of habitat evolvement and human disturbance on wintering water birds in Shengjin Lake of Anhui Province, China. *Chinese Journal of Applied Ecology* 18: 1832–1836.
- Jónsson, J.E. & Afton, A.D. 2006. Different time and energy budgets of Lesser Snow Geese in rice-prairies and coastal marshes in southwest Louisiana. *Waterbirds* 29: 451–458.
- Kear, J. 2005. *Bird Families of the World: Ducks, Geese and Swans*. Oxford University Press, Oxford, UK.
- Keating, J. F., Robel, R. J., Adams, A.W., Behnke, K.C. & Kemp, K.E. 1992. Role of handling time in selection of extruded food morsels by two granivorous bird species. *Auk* 109: 863–868.
- Lu, J. 1996. Distribution and bioenergetics of wintering swan geese (*Anser cygnoides*) in the Yangtze River valley, China. *Gibier Faune Sauvage* 13: 327–335.
- Lu, J. & Zhang, J. 1996. Feeding ecology of three wintering goose species at Lower Yangtze River, China. *Chinese Ornithological Research*, pp.143–152. China Forestry Publishing House, Beijing, China.
- Madsen, J. 1985. Relations between change in spring habitat selection and daily energetics of Pink-footed Geese, *Anser brachyrhynchus*. *Ornis Scandinavica* 16: 222–228.
- Miyabayashi, Y. & Mundkur, T. 1999. *Atlas of Key Sites for Anatidae in the East Asian Flyway*. Wetlands International – Japan, Tokyo, and Wetlands International – Asia Pacific, Kuala Lumpur. Available at: <http://www.jawgp.org/anet/aaa1999/aaaen dx.htm> (accessed on 17/11/2008).

- Owen, M. 1972. Some factors affecting food intake and selection in White-fronted Geese. *Journal of Animal Ecology* 41: 79–92.
- Owen, M. 1980. *Wild Geese of the World*. Batsford, London, UK.
- Perennou, C., Mundkur, T., Scott, D.A., Follestad, A. & Kvenild, L. 1994. *The Asian Waterfowl Census 1987–91: Distribution and Status of Asian Waterfowl*. Asian Wetland Bureau Publication No.86 and International Waterfowl Research Bureau Publication No.24. AWB, Kuala Lumpur, Malaysia and IWRB, Slimbridge, UK.
- Poyarkov, N.D. 2001. The Swan Goose: its origin, numbers, dynamics, biology and conservation. *Casarca* 7: 51–67.
- Prop, J., van Marken Lichtenbelt, W.D., Beekman, J.H. & Faber, J.F. 2005. Using food quality and retention time to predict digestion efficiency in geese. *Wildlife Biology* 11: 21–29.
- Ramsar Site Information Service 2008. An updated web resource accessible at: <http://ramsar.wetlands.org/Portals/15/China.pdf> (accessed on 17/11/2008).
- Research Institute for Yangtze Water Resources Protection 1999. *Yangtze Basin Flood Control Project, China: Environmental Impact Assessment*. Report E-291 to World Bank, Research Institute for Yangtze Water Resources Protection, Wuhan. Available at: http://www-wds.worldbank.org/servlet/WDSContentServer/WDSP/IB/2000/06/24/000094946_0001290532161/Rendered/INDEX/multi_page.txt (accessed on 17/11/2008).
- Wetlands International 2006. *Waterbird Population Estimates – Fourth Edition*. Wetlands International, Wageningen, The Netherlands.