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The Behaviour of Whooper Swans (*Cygnus cygnus*) wintering in a tidal Environment.

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INTRODUCTION

Studies of the Whooper Swan (*Cygnus cygnus*) in Europe and the U. S. S. R. have concentrated on birds using freshwater or terrestrial habitats in winter (eg Venables & Venables 1950; Airey 1955; Hewson 1964, 1973; Henty 1977; Brazil 1981a, 1981b) or using freshwater in summer (eg Haapanen et al 1973a, 1973b, 1977; Brazil 1981a, 1981c, 1982a; Krechmar 1982a, 1982b), while studies of the behaviour or ecology of birds wintering on the sea have not been reported. The closely related Trumpeter Swan (*Cygnus buccinator*) has been studied at estuarine sites where they are influenced by the tidal cycle, but their ecology rather than their behaviour has been described (McKelvey 1981).

In Britain and Ireland, the western extremity of the species' winter range, the Whooper Swan is primarily a bird of coastal or inland marshes, inland lakes or rivers and in some areas bays or estuaries. Since the hard winters of the 1940's they have increasingly used agricultural land (Owen & Kear 1972). In Scotland where the species has been studied in detail, birds observed at tidal bays were found to also visit nearby agricultural land and/or freshwater lakes. The increasing use of terrestrial habitats in Britain is considered to have markedly affected the behaviour of this species. Because it proved difficult to find birds using *only* a tidal site, only the behavioural patterns of those birds commuting between a night-time aquatic roost and a day time foraging area on farmland and those roosting *and* foraging at a freshwater site have been compared previously (Brazil 1981a, 1981b). The behaviour of birds at a tidal site was expected to differ from the behaviour of birds at either of the other two main habitats, since it would be influenced by both the diurnal and tidal cycles. Birds were expected to feed over low tides and roost over high tides.

Large numbers of Whooper Swans have been observed on the sea in Iceland (Brazil pers obs 1978—80), but only during migration or the summer moult. At these times the daylight period is much longer than in winter and the energetic requirements of the birds are presumed to be very different from those of birds in winter. Studies in Iceland have mainly concentrated on breeding biology (eg Bulstrode et al 1973; Brazil 1981a, 1981c, 1982a), the behaviour of non-breeders and on moult (Brazil 1981a). The same is also true of Scandinavia (Haapanen et al 1973a, 1973b, 1977; Myberget 1981).

In Japan, the eastern extremity of the species wintering range, the Whooper Swan is a common winter visitor from October until April with on average c13,000 birds occurring in Hokkaido and northernmost Honshu, approximately twice the number wintering in the British

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方　　法

基礎資料は，行動を4つのカテゴリーに分け，タイム・バジェット法によって得た．すなわち，“採餌”には，水中に頭を没している個体と，頭を上げ下げしている最中の個体(Fig. 1−a) すべてを含み，“羽づくろい”には，翼のばたつかせや排糞など，羽づくろいの過程の一部として行われる短時間の行動をはじめ，体の手入れ行動 (Fig. 1−b) のすべてを含む．“就塒”には，眼をあけているか否かにかかわらず，流水中や海岸に立っている．あるいは水面に浮いている個体を含む．典型的な姿勢 (Fig. 1−c) は，頭を背にのせ，背羽に一部をくるみこんでいるものであるが，風の強い時には，風上にむかって首をまげ，首の下部に頭をつける姿勢 (Fig. 1-d) をとる．“頭あげ”には，頭を体の位置よりも上げている個体をすべて含む．群の構成個体を30分おきに走査し，各行動カテゴリーに該当する個体数を数えた．結果は2時間ごとにまとめ，時刻 (Fig. 2) と，高潮時刻からの時間 (Fig. 3) との関係で示した．人工的な給餌が行われていない所が，この研究には好ましいので，ほぼ自然状態で採餌していると思われた青森県大湊のオオハクチョウを対象とし，1980年3月2日から7日にかけて調査を行った．

結　　果

大湊のオオハクチョウは，大湊湾の海岸線と，芦崎の先端部との2か所に分布していた．芦崎では，就塒が優占的行動で，採餌がそれについでいた．海岸線では，頭あげと羽づくろいが普通にみられ，採餌は20%以下であった．日周期と潮汐周期の影響を分離するには，資料が十分とはいえないが，ある程度の傾向はみられた．すなわち，芦崎では，採餌は，時刻でグルーピングすると日中に多く，潮汐でグルーピングすると低潮時に多かった．これと反対に，就塒は，朝と午後に多く，高潮時に増加した．他方，海岸線では，採餌は，潮汐の状況とは関係なく，一日中おおむね同じ程度みられた．また就塒は，日の出以降減少し，高潮以降増加した．

議　　論

今回の結果は，陸上あるいは淡水生息地の採餌状況で得られた結果とは，明らかに異なっていた．芦崎では，採餌が，日中あるいは低潮時に多く，就塒は，高潮時に多かった．これは，水位に変化のある環境では，高潮時に水中植生の採餌が困難になるため，就塒が行われ，低潮時には採餌が行われるという，当初の予想を裏づけるものである．

海岸線での採餌は，潮汐の状況と関係なく，一日中おおむね同じ程度みられた．これは，汀線の構造上，海岸線では，一日中採餌が可能で，排水管から餌が供給された可能性もあるためと考えられた．

Isles and Ireland (OSJ 1974; Brazil 1982b, 1983; Brazil & Kirk unpubl). It is frequently encountered at inland lakes, marshes, rivers, rice stubble fields (especially when close to large lakes as at Izunuma, Miyagi-ken), on the sea and rarely on other types of farmland, (although in early spring 1984 a large flock was observed on snow free meadows in central east Hokkaido, at a great distance from the nearest wintering sites (Brazil & Yamamoto pers. obs.).

Small differences have been shown to exist between birds from opposite extremes of the extensive palearctic range of this species, for example in bill patterns (Brazil 1981d), but no behavioural differences are known to exist other than those related to regional differences in the availability of food types. Feeding occurs on rice in the east for example, and on root crops and other cereal grains in the west. Studies in Japan have concentrated primarily on numbers and distribution (eg Horiuchi 1981; Nakanishi 1981; Brazil 1983) and migration (Matsui et al 1981; Ohmori 1981a) while ecology and behaviour have received less attention (but see Kakizawa 1981).

Japan, with several marine wintering sites seems to present the ideal opportunity for studying the effect of the tide on the behaviour of Whooper Swans, however in the time available for this study (February and March 1980) it proved difficult to find a site where food was not provided by visitors or by a resident 'swan-keeper'. Sites where swans occur (Whooper, Bewick's (*C. columbianus bewickii*) and Mute (*C. olor*) are extremely popular for 'sight-seeing', and feeding the birds plays an important role in this interest (see Hatakeyama 1981). The food given, consisting mainly of cereals, rice, waste tea and bread (Ohmori 1981b) provides bulk and carbohydrates, but is low in nutritional value and considered inappropriate for the birds (Tamada 1981). It should be noted however, that birds studied in Scotland selected cereal grains (rich in carbohydrates) during the autumn and mid-winter even in a region where freshwater lakes with aquatic vegetation were available; they switched to growing grass with its higher protein content only during the latter part of the winter and in the spring prior to the migration and the ensuing breeding season (Brazil 1981a). Thus the kind of food given in Japan, while not the most suitable, may be sufficient and certainly serves to attract birds into concentrations and leads to ice-free areas being maintained for them. Birds may be tempted to remain at sites in the north, where food is given rather than moving further south. By saving them the risks of onward migration, artificial feeding may contribute to their survival, but in areas prone to sudden freezing weather it may have the adverse effect of retaining birds which might otherwise have escaped extremely severe conditions. Large numbers of Whooper Swans have frozen to death at Odaito, east Hokkaido for example, where feeding takes place on a daily basis (Abe 1968). The birds affected however may be mainly non-or failed breeders, there being some evidence of selective migration by families away from the northernmost sites (Brazil 1983).

Except at sites with resident 'swan-keepers', feeding does not follow a regular pattern, the number of visitors and the amount of food given varies greatly from day to day and during the day. Even where 'swan-keepers' provide a fixed amount of food at a given time each day the behaviour of the birds follows no obvious pattern, with birds moving between natural and artificial feeding areas throughout the day.

Feeding methods used by Whooper Swans, including those for fresh and salt water are

described by Brazil (1984), but the feeding *pattern* of birds wintering on the sea seems so far to have been ignored. The aim of this brief study therefore was to compare the diurnal behaviour of Whooper Swans on the sea with that of birds in freshwater and terrestrial environments.

METHODS

Time budgets have been used to provide the basic material for this study as they have for many other species of waterfowl (eg Pintail (Krapu 1974) and Gadwall (Dwyer 1975)). The methods used for studying Whooper Swans feeding terrestrially are described in Brazil (1981b) and the basic behavioural categories are the same for birds at aquatic sites: *feeding, preening, roosting* and *head-up*. The definitions of these categories are slightly altered by circumstances however. On water *feeding* includes all birds with their heads submerged or in the act of raising or lowering their heads into or out of the water (see Fig 1a). *Preening* includes all comfort movements including those of very brief duration which are often performed as part of the preening sequence, such as wing-flapping and defaecation (see Fig 1b). *Roosting* includes birds standing (in shallows or on beaches) or floating with their eyes open or closed. In the typical posture (see Fig 1c) the head rests on the back, partially tucked in amongst the back feathers, however when the wind is strong birds face into it with their necks curved so that the head lies almost horizontally on the lower neck pointing forwards similar to the 'busking' threat display of the Mute Swan (see Fig 1d). *Head-up* includes birds with the head and neck raised above the level of the body (Fig 1e). A continuum of positions are included in this category since it was not practical to separate *head-up* from extreme head-up, as has been done in studies of goose behaviour (eg Lazarus & Inglis 1977).

The behavioural categories used were all mutually exclusive, thus the behaviour of flock members could easily be assingned to a single category during scans. Scans were made every 30 minutes and the results were combined into two hour time blocks from all dates studied and expressed in relation to time of day (see Fig 2) or tide (see Fig 3). Clearly a site where aritificial feeding did not occur, or rarely, occurred was desirable for this study. Data were initially collected at both Odaito, and at Kominato, Aomori-ken, but were finally discarded since artificial feeding was found to disrupt their behavioural rhythm. A site at Ominato, Mutsu Bay, Aomori-ken was found where people rarely visited the swans and where birds were considered to be feeding under essentially natural conditions. At this site swans were studied from March 2−7, 1980 (see Fig 4).

RESULTS

Birds were found to occupy two areas at Ominato, either the shore-line of the bay or the shore-line and point area of a nearby peninsula (c750−1,000m away). The groups using these areas were not isolated, nor were they presumed to be completely separate from other groups in the Ominato area. On the other hand birds were consistent in using both areas and little movement was observed to, or away from, these sites. *Roosting* was found to be the dominant behaviour at the point especially in the mornings and afternoons (Fig 2) or over high tide (Fig 3) with *feeding*, the second most important, at its highest during the middle of the day (Fig 2) or at low ride (Fig 3) whereas along the bay shore *head-up* and *preening* were much commoner, *feeding* took up less than 20% of time and occurred at almost the same rate regardless of time

or tide, while *roosting* took up little time, but occurred more in the morning or from high tide onwards. Birds from the bay-shore moved to the point to roost and while roosting at the bay shore invariably occurred on water,at the point it usually occurred on shore.

Although six days are not adequate to separate the effects of tide from those of time of day, certain trends are apparent. At the point for example, *feeding* tended to peak during the middle of the day if the data are grouped according to time (Fig 2) or towards low tide, if grouped according to tide (Fig 3). Conversely *roosting* occurred more in the mornings and afternoons and possibly increased over high tides. Along the bay-shore *feeding* occurred throughout the day at approximately the same level regardless of tidal state. *Roosting* however decreased from dawn onwards and increased after high tide.

During the observation period the numbers using the point increased (Pearson's correlation coefficient r=0.492, p=

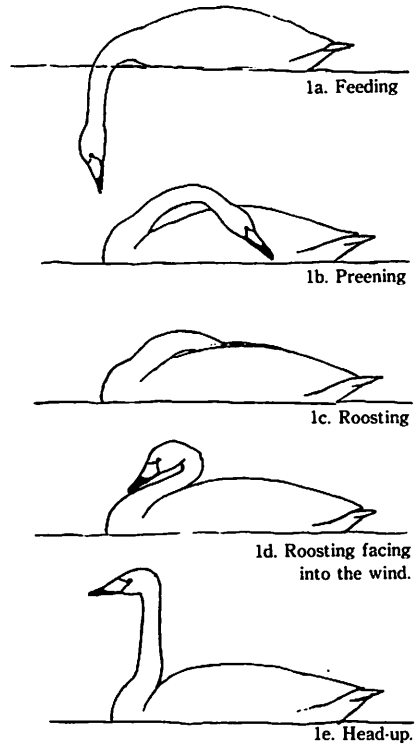

Fig. 1. Behavioural categories of Whooper Swans on the sea.

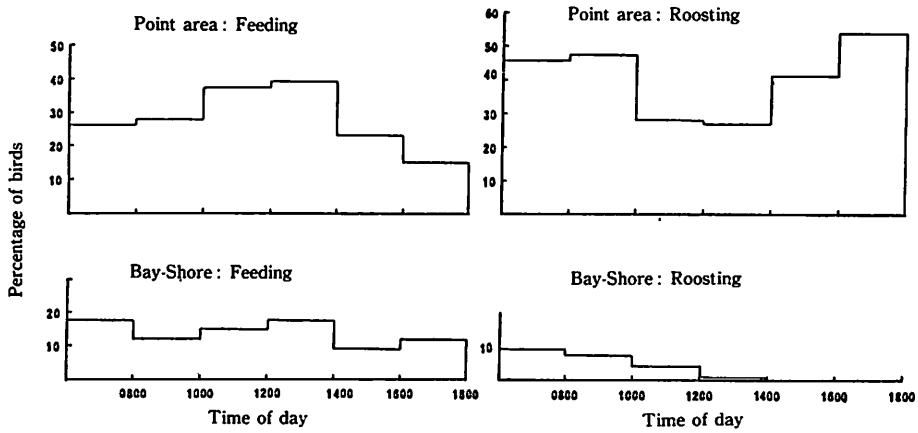

Fig. 2. Time budget of Whooper Swans at Mutsu Bay, Japan, 1980 in relation to the time of day.

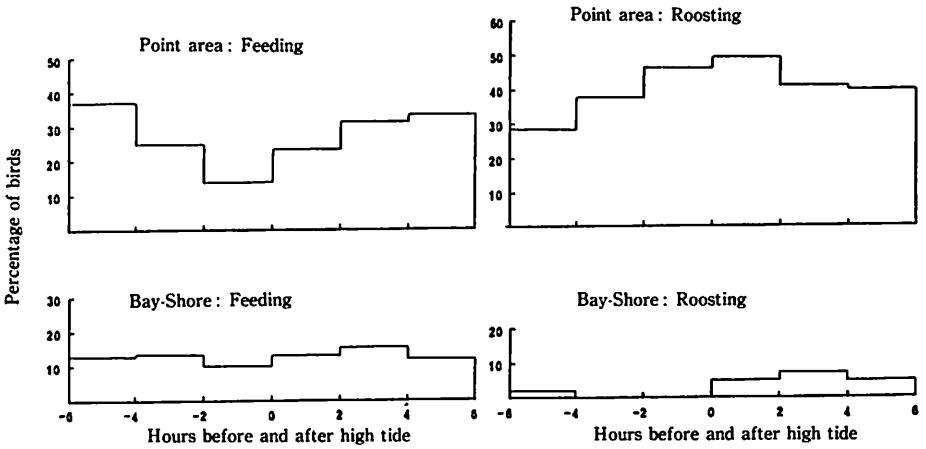

Fig. 3. Time budget of Whooper Swans at Mutsu Bay, Japan, 1980 in relation to the tide.

0.001) and the numbers along the bay shore declined ($r=-0.287$, $p=0{,}002$) there being a significant negative correlation between numbers at these two localities ($r=-0.451$, $p=0.001$). The proportion of the flock which was roosting at the point increased as numbers increased ($r=0.342$, $p=0.002$) and decreased as numbers increased at the bay shore ($r=-0.412$, $p=0.001$). *Feeding*, conversely decreased as numbers increased at the point ($r=-0.379$, $p=0.001$) and increased as numbers increased at the bay shore ($r=0.392$, $p=0.001$). The data thus supported the subjective impression that birds moved to the point to roost. Since *feeding* and *roosting* are mutually exclusive these complementary results were to be expected.

On a rising tide, feeding at the point and preening at the bay-shore decreased with time ($r=-0.494$, $p=0.009$ and $r=-0.551$, $p=0.005$ respectively) while *head-up* at the bay-shore increased with time ($r=0.478$, $p=0.011$). On a falling tide *head-up, roosting* and *preening* at the bay-shore were correlated with time and tide (see table 1). The result of using Kendalls partial rank correlation was to raise the r values of both variables (Table 2) suggesting that time and tide were counter active in their effect on behaviour during the study period.

DISCUSSION

Whooper Swans feeding on farmland have been shown to have a bimodal feeding rhythm (with some seasonal variation) with a high morning peak, a lull during the middle of the day and a high afternoon peak. *Roosting* is particularly prevelant during the mid-day feeding lull, while *preening* occurs throughout the day (Brazil 1981a, 1981b). Similar bimodal patterns have been reported for dabbling ducks (eg Henty 1975) and for geese (eg Owen 1972; Ebbinge et al 1975). In strong contrast, at a fresh water site in Scotland feeding increased steadily from dawn until c14 : 00hrs reaching an afternoon plateau (Brazil 1981b), a pattern similar to that of *C. olor* and *C. c. bewickii* on the Ouse Washes, England (Owen & Cadbury 1975). In Scotland *roosting* was the dominant activity in the morning, *preening* peaked at 18% between 11 : 00 and 12 : 00 hrs, while

. *head-up* occurred throughout the day at between 18 and 47% (Brazil 1981b).

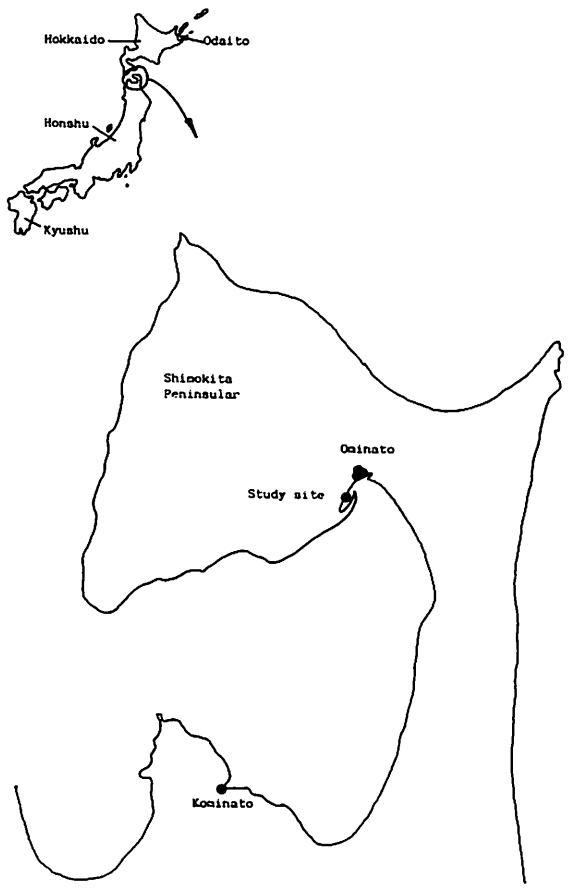

Fig. 4. Japan : showing sites mentioned in the text, and the study area at Ominato, Aomori-ken.

While the data presented here are too few to fully explain the combined relationship between time of day, tidal state and swan behaviour, the results are clearly different from those obtained from either terrestrial or freshwater feeding situations. There was for example, no evidence of an increase in feeding to an afternoon plateau as on fresh water, nor of a bimodal pattern as on land with morning and afternoon peaks separated by a mid-day lull, in fact the reverse was apparent, *feeding* tended to peak during the middle of the day at the point, or over low tide, while *roosting* was highest in the morning and afternoons, lowest at mid-day and occurred more over high tides. Feeding decreased as the tide rose. These results confirmed expectations, since where variation in water height puts submerged vegetation out of reach of the birds, feeding at high tide will be difficult or impossible, thus birds should roost, while at low tide feeding should occur.

It should be noted that the behaviour of birds along the bay-shore was somewhat different from that of birds at the point and that the number using the bay-shore declined as the numbers increased at the point (these being significantly correlated). *Feeding* at the point appears to be related to the state of the tide, while feeding at the bay-shore continued at approximately the same level throughout the day. The structure of the shore line may have been such that birds were able to feed throughout the day at the bay shore, but not at the point and some food may have been available from waste-pipe outlets. The reason for the shift of birds from bay-shore to point during the period is not clear. A much longer study covering the full change of tides at different times of day is clearly desirable to fully demonstrate this behaviour.

Table 1. The correlation of behaviour with time *or* state of tide.

Behaviour	Correlated variable	r	Significance
Head-up	Time	0.532	0.001
	Tide	−0.251	0.029
Roosting	Time	−0.412	0.001
	Tide	0.397	0.001
Preening	Time	−0.588	0.001
	Tide	0.340	0.004

Table 2. Partial correlation of behaviour with time *and* state tide.

Behaviour	Correlated variable	Variable hald constant	r
Head-up	Time	Tide	0.557
	Tide	Time	−0.296
Roosting	Time	Tide	−0.453
	Tide	Time	0.432
Rreening	Time	Tide	−0.622
	Tide	Time	0.414

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潮汐の影響をうける環境で越冬するオオハクチョウ (Cygnus cygnus) の行動について (抄訳)

マーク・ブラジル

はじめに

ヨーロッパやソビエト連邦のオオハクチョウの研究は，冬期には，淡水または陸上生息地，夏期には，淡水生息地のオオハクチョウを研究の対象としており，海水域で越冬している場合の行動の研究は，いまだみられない．潮汐の影響をうける環境に生息するオオハクチョウが，潮汐のない環境に生息する場合と比較して，日周期と潮汐周期の両方に影響をうける可能性があるという点で，異なった行動を示すということは，十分に予想されることである．海岸部にオオハクチョウの越冬地がある日本は，この研究に好適である．