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FEEDING STRATEGIES OF BEWICK'S SWANS
(Cygnus columbianus bewickii)
IN WINTER

by

Jonathan Mark Bowler

A thesis submitted to the University of Bristol in accordance with the requirements for the degree of Doctor of Philosophy in the Faculty of Science, Dept of Zoology

June 1996

ABSTRACT

This study investigates the ecology of Bewick's Swans Cygnus columbianus bewickii wintering at Slimbridge, Gloucestershire and considers their roost-site choice, habitat selection and activity budgets, in order to elucidate factors affecting return rates and reproductive success.

An abdominal profile (AP) scale was developed to assess body condition. AP was significantly correlated with condition indices, demonstrating for the first time that mass can be predicted from AP. AP scores of individual swans increased during the winter, reaching a peak in spring, and were influenced by sex, social class and dominance rank.

Two main roost sites were identified at Slimbridge to which individuals proved faithful within a winter: the "Rushy Pen" and the "Grounds Pens". Swans from the two roost groups used different feeding sites. Those from the Grounds roost visited fields close to the roost-site, whereas swans from the Rushy Pen ranged further afield. Swan distribution on the fields was determined primarily by the extent of flooding, with heavier swan use on more flooded fields. Rushy Pen birds also selected swards with a high protein content, whilst Grounds birds visited fields low in both protein and biomass per unit area. These differences in feeding site selection reflected differences in foraging behaviour. At the Grounds roost, swans fed for longer and on larger amounts of provisioned grain per swan, than in the Rushy Pen. Field selection was therefore more critical for the Rushy Pen swans. Swans responded to changes in food supply during the winter by selecting different feeding sites and by altering their feeding rates, although individual foraging strategies varied with respect to social class and roost group.

Adult swans spent approximately one third of their time feeding on the fields during the day, one third resting and one third in other activities. Parental protection enabled cygnets to spend significantly more time feeding than adults. Feeding was most frequent in early February when food availability was lowest. Increasing protein levels towards the end of the season led to an increase in the number of swans seen feeding, perhaps because they were developing fat reserves to fuel their spring migration. Females spent more time feeding than males, and had faster peck rates and slower step rates. Male parents had slow peck rates, and were more vigilant and aggressive than other males, suggesting that they were protecting their mate and offspring from conspecific feeding competition and/or predation at the cost to themselves of reduced food intake. Time spent feeding by females increased with the dominance rank of the pair, whilst time spent in vigilance and movement decreased. Males were less vigilant and fed more intensively on swards with a high protein content. They invested more effort into protecting their mates and/or offspring when food quality was low. The protection afforded by a dominant male enabled its mate and cygnets to have faster peck rates and slower step rates, hence effecting the extent to which they could build up fat reserves as reflected in their AP scores. Female AP score at the end of the winter had a significant positive effect upon breeding success. The lower AP scores of paired females in the Grounds roost compared to those in the Rushy Pen were a product of less successful foraging strategies and resulted in reduced breeding success.

Mean return rate of swans to Slimbridge was 66%. Single adults had lower return rates than paired birds, whilst cygnets and yearlings had the lowest return rates. Return rates did not relate directly to foraging performance of adult swans. Male dominance rank and its effect on female foraging performance may influence the return rate of pairs. Females from the Grounds roost had higher return rates than those from the Rushy Pen, despite their poorer foraging performance, suggesting that they benefitted in other ways e.g. reduced levels of aggression, by returning to a smaller familiar roost.

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AUTHOR'S DECLARATION

The work presented in this dissertation, unless indicated to the contrary in the text or acknowledgements, represents original research carried out by the author. The major part of the work has not at the time of submission appeared elsewhere. One published paper (Bowler 1994) includes some of the results described in Chapter 2 and is included in Appendix 1. Some management implications of the results are included in Appendix 2.

The views expressed in the dissertation are those of the author and not of the University of Bristol.

Jonathan Mark Bowler

TABLE OF CONTENTS

Page No.

CHAPTER 1. INTRODUCTION

CHAPTER 2. TWO MEASURES OF THE QUALITY OF SWANS: DOMINANCE RANK AND CONDITION AS ASSESSED BY ABDOMINAL PROFILE

A) DOMINANCE RANK

2.3 Results

B) CONDITION AS ASSESSED BY ABDOMINAL PROFILE

CHAPTER 7. RETURN RATES AND BREEDING SUCCESS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1 INTRODUCTION

1.1 BACKGROUND TO THE STUDY

The Bewick's Swan Cygnus columbianus bewickii is a wholly migratory species that breeds in the arctic tundra of Russia, from the Kanin Peninsula west to the Chukota Sea. At least two populations exist: swans breeding east of the Lena Delta winter mainly in Japan, China and Korea, whereas those breeding west of the Urals winter in northwest Europe, primarily in the Netherlands and Britain, with smaller numbers in Germany, Denmark, Ireland, Belgium and France (Ogilvie 1972a, Beekman et al. 1994a). The species was a regular winter visitor to the Caspian and Aral Sea areas of central Asia (Dement'ev et al. 1952), but now only a few hundred birds visit Iran (Perennou et al. 1994), with even smaller numbers in the Ukraine and Turkey. Important migratory sites for the western population have been identified in the Netherlands, Germany and the Baltic countries, particularly Estonia (see Evans 1982, Rees & Bowler 1991), although staging areas further east into Russia itself are less well known (Rees 1991, Beekman et al. 1994b). The western population was stable at around 16,000-17,000 in the 1980s (Dirksen & Beekman 1991, Rose & Scott 1994) but fluctuates due to marked annual variation in breeding success. The eastern population is larger at 25,000-30,000 birds (Mineyev 1991, Rose & Scott 1994), but has not been studied in detail.

The winter range of the western population has undergone considerable changes within the last century. Numbers have declined in Scotland where Bewick's Swans were common in the 19th century particularly on the Hebridean Islands of Tiree and South Uist (Baxter & Rintoul 1953, Ogilvie 1969). It is also less common than formerly in Ireland, where it has undergone a considerable decline in the last century (Ruttledge 1966), but numbers have increased rapidly in England where it began wintering regularly only in the 1920's (Ogilvie 1969, Cramp & Simmons 1977). Reasons for these changes are thought to be linked to both habitat change and climatic conditions. The species formerly occurred mostly on shallow lakes and marshes in northwest Europe where it fed primarily on aquatic vegetation, but it has increasingly made use of flooded pastures and arable land. Depletion of submerged macrophytes in the Netherlands (particularly the pondweeds Potamogeton spp.) through water pollution, drainage and land reclamation encouraged a shift to grass leys and semi-natural grassland after 1968 and subsequently to cereals and root crops (Poorter 1991). On the Ouse Washes in Norfolk/Cambridgeshire the species has, since 1972-73, increasingly switched from a diet of soft grasses on semi-natural wet grassland on the Washes themselves to adjacent waste crops of potatoes and sugar beet and to cereals (Owen & Cadbury 1975). During monthly surveys conducted in Britain and Ireland during the 1990-91 winter, only 23.8% of the Bewick's Swans were found on permanent inland waters, and the majority (60.1%) were recorded on arable land (Rees et al. in press).

Wintering sites are scattered but individuals may return to a particular site for many years (Scott 1966, Evans 1980, Rees 1989). The study site at Slimbridge, Gloucestershire, England (51°44'N, 02°25'W) lies towards the western edge of the winter range. Numbers of swans wintering at Slimbridge have increased from less than 20 birds in the 1950's (Ogilvie 1969) to daily totals in excess of 350 by 1968-69 (Evans 1978) and some 200-300 swans now winter regularly at the site. Bewick's Swans began to winter at Slimbridge on a regular basis in the early 1960's (Scott 1966) and roosted initially on the River Severn and on the adjacent salt-marsh known as the Dumbles (Rees 1982). As the swan flock built up, birds began to roost in the Rushy Pen, to which they were attracted by evening feeds of provisioned grain under floodlights. Within the three hectare enclosure of the Rushy Pen is "Swan Lake", which is a shallow, one hectare pool system, that has gradually been enlarged since its initial development in 1953. Although the majority of the swans continue to roost in the Rushy Pen, since the late 1970's an increasing number have roosted on pools some 400 m away, within the Trust's enclosures (Fig. 1.1), collectively known as the 'Grounds roost'. Bewick's Swans are generally present at Slimbridge from mid-October until early March but the numbers concerned, together with the precise timing of arrivals and departures varies considerably from year to year, and is often related to climatic variables (Evans 1979a, Rees 1982).

Bewick's Swans wintering at Slimbridge have been the subject of a detailed long-term research programme (see Evans 1979b, Rees 1988). All swans recorded at the site since 1964 have been individually identified, both by their unique black and yellow bill markings (Scott 1966, Evans 1977, Scott 1978a, Rees 1981) and by their coded leg rings (Ogilvie 1972b), allowing detailed study of aspects of their life cycle and ecology. These have included biometrics (Evans & Kear 1978), movements (Evans 1982, Rees 1988, Rees 1991), timing of spring migration (Rees 1982, Rees 1989), conflict of choice within pairs regarding migratory movements (Rees 1987), migratory tradition (Evans 1980, Rees & Bacon in press), feeding ecology (Rees 1990, Rees & Bowler 1991), population dynamics (Evans 1978), mate fidelity and longevity (Rees et al. 1996), functional aspects of the pair bond and prolonged parental care (Scott 1980a & b), breeding success (Scott 1988), and the social behaviour of swans wintering at the Welney Wildfowl & Wetlands Trust Refuge, Norfolk (Scott 1978b, 1980c).

Wildfowl exhibit a range of feeding behaviours and select food in relation to its profitability, usually measured as the amount of energy and/or specific nutrients gained per unit time (Owen & Black 1990). Herbivorous grazing geese can sometimes manipulate the growth of plants to maintain its quality (Prins et al. 1980), although sward depletion can result in a net energy deficit particularly during the mid-winter period when grass growth may stop (Owen et al. 1992). The annual cycles of several species of geese have been shown to be adapted to variation in food quality (e.g. Sedinger & Raveling 1984, Prins & Ydenberg 1985, Owen & Black 1989), so that energetically demanding phases of the life cycle such as migration and breeding are tuned to the availability of high quality foods. Rees (1990) analyzed the distribution of Bewick's Swans wintering in Gloucestershire in relation to habitat variables at the feeding sites, including sward length, biomass and protein content of green grass, and depth of flooding. The study concluded that the swans occurred most frequently and in greatest numbers where the highest biomass of green grass was available. The percentage of protein in the vegetation was a relevant secondary factor. Flooded pasture also appeared to be preferred, although the absolute depth of flooding did not have a significant effect upon their site selection. However, the total variation in the count data accounted for in the study was low (32.6%) and this was attributed to grazing pressure from other waterfowl species (over 70% of the variation in the data was accounted for when this variable was added). Although the swans dispersed over a wider area as the food supply diminished, the influence of social factors upon feeding site selection and changes in the swans' feeding activities in relation to food supply were not considered in detail. The current study aims to investigate these factors more fully.

Bewick's Swans have been shown to exhibit a wide range of aggression and threat behaviours (Scott 1978b). These include such activities as head-low threats, aggressive vocalisations, half-opened wings, physical attack, pecks and chases, as well as avoidance behaviour exhibited by submissive birds. The outcome of such encounters leads to the establishment of a dominance rank within the flock, with families tending to dominate pairs, which in turn tend to dominate single individuals (Scott 1978b). Larger families also dominate smaller families (Scott 1980b) and prolonged parental care may bring the benefit of access to the best resources for all members of the family, although the presence of more mouths to feed may involve measurable costs to the parents (Scott 1980b). The costs and benefits of aggressive behaviour have also been investigated, with the benefits of winning an encounter being seen as both a short-term gain of immediate access to a resource, and a long-term gain of resource access throughout the rest of the winter achieved by the consequent increase in social rank. There may also be a reduction in the frequency of further aggressive encounters since subordinate birds tend to avoid birds which have already beaten them in a previous encounter. Costs of fighting have been found to include both direct injury and temporary post-fight exhaustion, with a potential decrease in social rank resulting in reduced access to resources (Scott 1978b). The dominance rank of individual birds can be calculated each season from the proportion of opponents beaten in relation to the total number with which aggressive encounters were observed to take place. Such a rank is a valuable measure of the position of a bird in the hierarchy of the flock which can then be related to a wide range of variables including diurnal activities, roost-site selection, feeding site selection, feeding intensity, likelihood of return to Slimbridge, breeding success and body condition. One measure of body condition that can be measured remotely in the field is Abdominal Profile (AP) in which the shape of the abdomen immediately below the tail is coded according to a scale and which reflects fat deposition in the omental depot (Owen 1981). Initially developed for geese, a similar six-point AP index was adapted for use on Bewick's Swans from photographs taken of birds at Slimbridge during the 1990-91 winter (see Bowler 1994, Appendix 1), which was subsequently used for the duration of the study.

1.2 AIMS OF THE STUDY

The primary aim of the study is to determine how the Bewick's Swans vary their foraging strategies in relation to food supply during the winter, thus presumably optimising their food intake. Herbivorous grazing birds have been shown to compensate for declining food stocks in winter by pecking more rapidly (e.g. Owen et al. 1992), increasing the proportion of time spent feeding (e.g. Amat 1986a), and changing feeding patch or diet (e.g. Madsen 1985, Ydenberg & Prins 1985). Individual responses may vary according to social class, dominance rank, sex, age and previous experience of the site. In flocks of grazing Brent Geese Branta bernicla, the first birds to arrive at a plot of vegetation have higher intake rates and make a different selection from the plants available than birds further back in the flock. Differences in the intake rates and diet of 'early' and 'late' individuals related to their subsequent body condition (Prop & Loonen 1988) and ultimately to their subsequent breeding success (Teunissen et al. 1985).

Since parental care is prolonged in the Bewick's Swan, with cygnets associating with their parents throughout the first winter, the question of whether families adapt their feeding strategies for the benefit of their cygnets, perhaps at some cost to the parents, is also addressed.

In addition, the presence of distinct roost groups amongst the Bewick's Swans at Slimbridge allows an exploration of roost-site choice and function, and to compare the success of different foraging strategies employed by swans from the roost groups in terms of subsequent return rates to the site and breeding performance.

The analyses will show whether birds of high dominance rank are able to gain access to the best resources available in the Slimbridge area, allowing them to achieve better body condition prior to departure for the breeding grounds in spring (as assessed by AP), and hence have a measurable effect upon subsequent return rates to the site and breeding success.

1.3 GENERAL METHODS

All Bewick's Swans arriving at Slimbridge since 1964 have been individually identified as part of a long-term study investigating various aspects of their life history and ecology (for full description of this work and methods, see Rees (1988)). The current author took over the main recording work for this study in 1989. New swans arriving at the site were sexed both by cloacal examination upon catching the birds for ringing and in the field by observing the relative size and behaviour of paired birds; males are generally larger than females (Evans & Kear 1978) and tend to be more aggressive than their mates during dominance disputes (Scott 1978b). Age was determined by the extent of juvenile grey plumage remaining on an individual; birds in their first winter (cygnets) are predominantly grey and in addition normally remain with their parents, second-winter birds (yearlings) retain a variable amount of grey feathers on the head and neck, whilst the feathering of adult birds is completely white (Cramp & Simmons 1977). Yearlings may also sometimes accompany their parents during their second winter. Social class was recorded by daily observation of individual swans in order to discern the presence or absence of a mate, cygnets (if any), and other associates. Birds were placed into one of three main social classes: families, pairs (without cygnets), and singletons, and in some cases these classes or 'swan units' (consisting of all related swans within the pair or family) were used for analysis. A small number of swans, including former offspring associating with their parents and siblings associating with each other, were placed in a separate class ('other'). For more detailed analyses the social status of each swan was further calculated from a combination of its age and social class, giving rise to nine different categories: breeding adult, paired adult (without cygnets), single adult, family cygnet (with one or both parents), single cygnet (parents absent), family yearling (associating with parents), single yearling (not associating with parents), family adult (former offspring aged >2 years associating with parents), trio (group of three siblings associating together but not with their parents).

A daily register of individual swans present at Slimbridge is kept throughout the winter and data concerning each individual is added to an ORACLE database at the end of each winter. Data stored for each swan includes: name, age when first seen, sex, ring codes and biometrics, together with annual data: arrival and departure dates at Slimbridge for the swan each winter, identity of mate, number of cygnets, recapture dates, additional biometrics, and sightings away from the Slimbridge area.

1.4 THE STUDY AREA

The study was based on observations of the Bewick's Swans wintering at Slimbridge, Gloucestershire, England. The first birds typically arrive in mid-October and numbers continue to build up during the course of the winter, reaching a peak in January or February. Swans begin to depart on the start of the spring migration to their breeding grounds in arctic Russia in late February and only the occasional straggler will remain by the end of March (see Bowler *et al*. 1994 for example). During their stay at Slimbridge the swans typically roost on pools within the fox-proof enclosures of the wildfowl collection of the Wildfowl & Wetlands Trust, where they also receive supplementary feeds of grain (see Fig. 1.1). The swans flight out, in the morning, to the mainly pasture fields and scrapes of the Slimbridge refuge, and to the fields of adjoining farms, where they spend the daylight hours. The pasture fields have mostly been improved, are reseeded on rotation and receive regular inputs of nitrogen-based fertilisers. The swards are dominated by *Lolium perenne*, but also contain a mixture of *Phleum pratense*, *Agrostis stolonifera*, and *Poa* spp., with *Alopecurus geniculatus* abundant in damp depressions. Other species present include *Holcus lanatus*, *Hordeum secalinum* and clover *Trifolium* spp. (Rees 1990). Swans may disperse more widely along the valleys of the Rivers Severn and Avon depending on local flood conditions (see Rees 1990) and may roost at alternative roost sites away from Slimbridge. During the current study only three additional local sites, Walmore Common, Ashleworth Ham and the Avon Meadows lying to the north along the valleys of the Rivers Severn and Avon were used by Bewick's Swans in any numbers. Fieldwork therefore was concentrated in the Slimbridge area. Visits to Walmore Common were restricted to once a month for habitat recording purposes except when swans were reported to be present in large numbers by voluntary observers. Ashleworth Ham was only used by Bewick's Swans for a brief period in February 1993, whilst the Avon Meadows were only occasionally used by very small numbers of swans (<10), and neither site features in the study. At Slimbridge, birds were followed on a day to day basis from the roost-sites to the feeding areas.

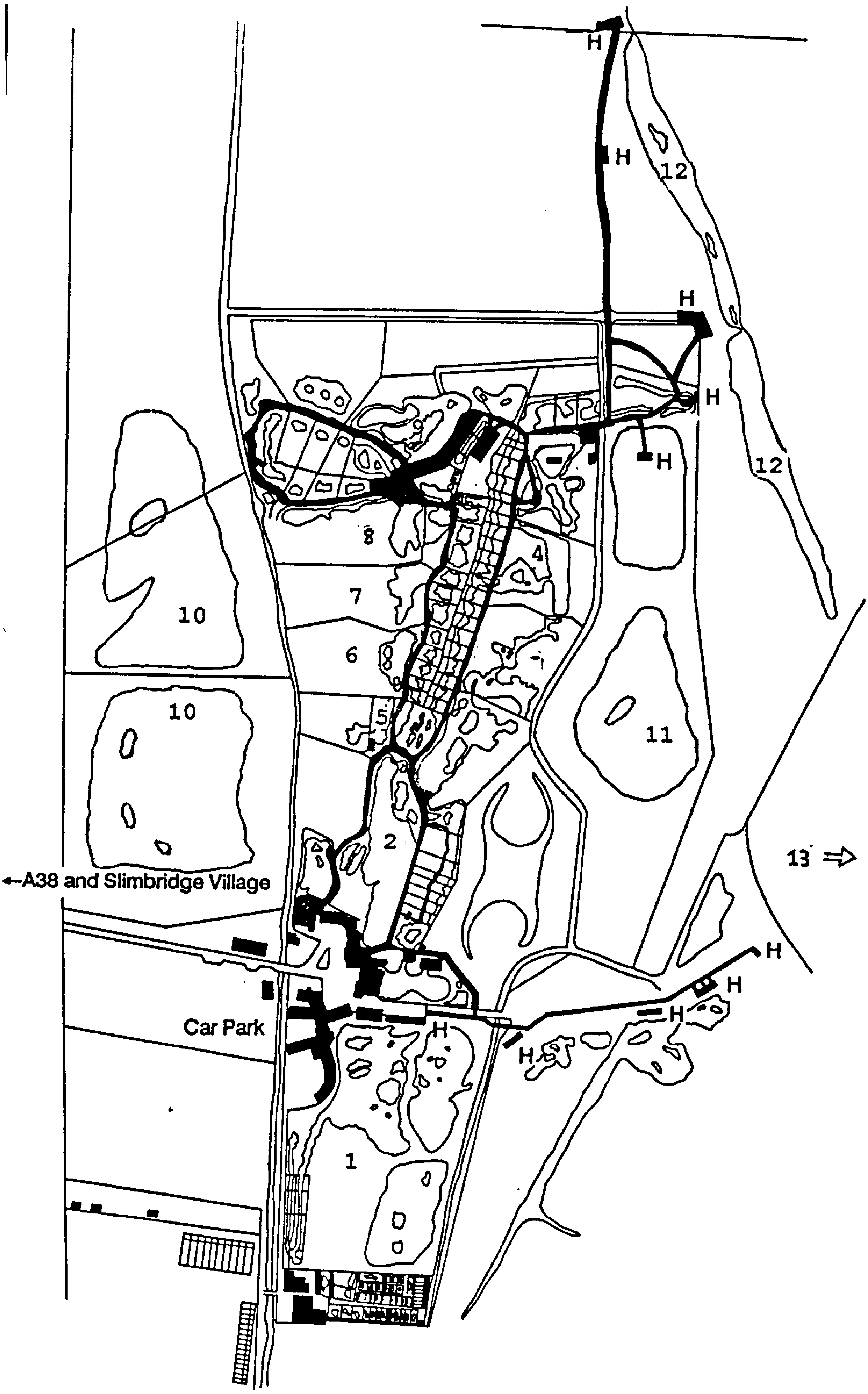
FIG 1.1. MAP OF THE ENCLOSURES AT SLIMBRIDGE SHOWING THE ROOST-SITES USED BY BEWICK'S SWANS 1989-1993

1. Rushy Pen

The "Grounds" roost
2. Big Pen
3. Tundra Pen
4. North American Pen
5. Andean Pen
6. Asian Pen
7. European Pen
8. Hybrid Pen
9. African Pen

Occasional roost-sites
10. New South Lake
11. Long Ground Scrape
12. South Finger Scrape
13. River Severn

H = Hide



CHAPTER 2 TWO MEASURES OF THE QUALITY OF SWANS: DOMINANCE RANK AND CONDITION AS ASSESSED BY ABDOMINAL PROFILE

The daily distribution of Bewick's Swans at the roost sites and feeding sites in the Slimbridge area (considered in the following chapters) may be influenced by a number of variables pertaining to the individual birds themselves e.g. fighting ability, body condition, previous experience of the site, and social class. Social class and experience (measured as the number of winters that a swan had previously been recorded at Slimbridge) were recorded in all cases as part of the Wildfowl & Wetland Trust's long-term study of the Bewick's Swans at Slimbridge. This chapter considers two measures of individual 'quality'; dominance rank, and body condition as assessed by abdominal profile, which will be used in subsequent chapters in order to investigate their influence upon the observed distribution and foraging strategies of individual swans.

A) DOMINANCE RANK

2.1 INTRODUCTION

Dominance hierarchies have been studied amongst a wide range of animal groups, both in captivity and in wild situations, including ungulates (e.g. Clutton-Brock et al. 1979), primates (e.g. Harcourt & Stewart 1987) and birds (e.g. Henderson & Hart 1995, Koivula et al. 1995, D'Eath in litt.). Amongst Willow Tits Parus montanus, dominant individuals (mostly males) were able to gain more mass during a day's foraging than subordinates (mostly females, Koivula et al. 1995), and needed to carry smaller reserves as a buffer against periods of food shortage (Clark & Ekman 1995), whilst amongst Jackdaws Corvus monedula dominance rank was positively correlated with the more efficient provisioning of offspring and the raising of larger annual broods (Henderson & Hart 1995). Amongst gregarious species of Anatidae which form large flocks in winter, an individual's position in the social hierarchy or dominance rank has important associated benefits, both in the short-term such as access to the prime feeding areas (e.g. Black & Owen 1989) and in the long-term such as life-time breeding success (Scott 1988). Dominance rank may therefore be taken as one measure of pair bond quality. Bewick's Swans exhibit a range of displays during aggressive encounters. The series of displays are usually performed in a set order of increasing intensity depending on the quality of the opposition (see Scott 1978b). Displays range from head-low threats to physical combat, where opponents grapple and beat each other with their wings. Male swans tend to be more actively involved in aggressive interactions than their mates and offspring, if any, but such associates may lend support by approaching and joining in the display (Scott 1978b). 'Success' in an encounter can usually be determined from the activities of the swans concerned, following the aggressive encounter. The unit emerging victorious from an encounter will frequently perform a triumph display, whilst the losing unit will usually swim away quietly with heads bowed. Results of a number of aggressive encounters establish the position of a unit in the social hierarchy of the flock.

Factors affecting success in aggressive encounters and the position individuals reach within dominance hierarchies has been considered amongst wildfowl species by a number of authors including Raveling (1970), Scott (1980a & b), Lamprecht (1986), Black & Owen (1989), Mulder et al. (1995). Amongst migratory swans and geese, where the offspring associate with their parents during the first winter and adults are normally monogamous, the rank of an individual in the dominance hierarchy has been shown to be related to its pairing and breeding success during the previous summer, with families dominating over pairs without offspring, which in turn are dominant over singletons (Raveling 1970, Scott 1980a, b, Lamprecht 1986, Black & Owen 1989, Mulder et al. 1995). The effect of the size of the unit upon dominance rank has been investigated by several workers. Scott (1980a), Lamprecht (1986) and Mulder et al. (1995) could not find a significant correlation between family size and dominance rank amongst Bewick's Swans, Bar-headed Geese Anser indicus and Blue Geese Anser caerulescens caerulescens respectively, although the first two studies showed that the dominance of a given male was reduced when its mate was absent. Black and Owen (1989) working on Barnacle Geese Branta leucopsis showed that large families were more likely to be successful in aggressive encounters than small families but again could not find a direct relationship between family size and dominance rank. More recently however, Einarsson (1995) found a positive correlation between dominance rank and brood size amongst Whooper Swans Cygnus cygnus wintering in south west Scotland. Black & Owen (1984) suggested that because parents did not increase their family size by adopting stray juveniles during the winter, optimum brood size (as far as winter performance was concerned), may not be the largest. Lamprecht (1986) suggested that the differing results may have arisen from differences in flock stability in each of the studies, and suggested that dominance rank might be retained over several years, through individual recognition between members of a stable flock. Of equal importance however may be the sample sizes used to calculate dominance rank (Black & Owen 1989), since the accuracy of dominance ranks calculated by monitoring the outcome of aggressive interactions between known individuals will improve with the size of the sample for each unit.

The current study attempted to test the hypothesis that dominance rank is positively correlated with unit size by obtaining data on the outcomes of very large numbers of aggressive encounters between known individuals. The large amount of data gathered also permitted an investigation of the consistency of dominance rank between winters, for birds that a) did not exhibit a change in social class and b) birds that did exhibit a change in social class between years. Since it has been shown that cygnets may assume their parents dominance and that this effect may continue into the second winter (Scott 1980b), the hypothesis that offspring of dominant parents may assume higher rank when they return in subsequent winters than offspring of lower ranking parents was also tested. In addition, the effect of increasing age (number of years of experience at Slimbridge) upon dominance rank was investigated amongst singletons prior to pairing for the first time to test the theory that dominance rank increases with age.

Black and Owen (1989) showed that amongst Barnacle Geese, young pairs increased their rate of aggressiveness in the winter prior to entering the breeding contingent of the population. Such an increase might be reflected by an increase in dominance rank in the winter prior to a successful breeding season, which, being a function of a pairs' ability to work together in aggressive encounters, should be a reasonable indicator of a pairs' ability to hold a territory and to breed. This was tested for in the current study.

Dominance rank is influenced by the size of the male and the proximity of the mate in Bewick's Swans (Scott 1980b), and by age amongst Bar-headed Geese (Lamprecht 1986), although amongst Barnacle Geese both body size and age had only a secondary effect on dominance rank after unit size had been taken into account (Black & Owen 1989). Moreover the intensity of agonistic behaviour varies according to the rank of the opponent, so that minimal effort is used to win (e.g. Black & Owen 1989, Rees 1988). These aspects of agonistic behaviour have been investigated in detail elsewhere and are not considered further here.

2.2 METHODS

Detailed records of aggressive encounters amongst the Bewick's Swans at Slimbridge were kept throughout the period 1989-90 to 1992-93. In all cases, the identities, sex and social class of the participating units, together with the outcome of the encounter were noted. Observations were made throughout the day, except during the distribution of grain at the roost sites, since the outcome of aggressive interactions during feeding melees has been found to be less predictable than that on field sites (Scott 1978b). Observations were made at the feeding sites as well as at the roost sites since Scott (1980c) found that dominance relationships between individual units were consistent at different locations. Encounters involving units from which an adult member was missing were not included in the analysis since both male and female swans are less successful in encounters when their mates are absent (Scott 1980a).

A simple value of dominance was calculated by dividing the number of successful encounters for a given unit by the total number of encounters in which it was seen to be involved. An augmented dominance value was then derived by the addition of a) units that beat other birds dominant to the focal unit and b) units that were beaten by subordinate swans, as used by Scott (1978b) and Rees (1988). The augmented values are considered preferable to the original ratio in that they take into account the "quality" of the opposition. Dominance values recorded for units involving fewer than five encounters or ten augmented encounters were omitted from the analyses. Interactions involving the same opponents were included only once unless the outcome differed, since dominance relationships tend to be stable throughout a season (Scott 1978b) and inclusion of repeated encounters might bias the dominance values obtained.

In order to explore the relative effects of age, experience and sex upon dominance rank, a generalised linear model was fitted to the data using GLIM (NAG 1986). Only data pertaining to single birds were included in this analysis in order to remove the confounding effects of social class and breeding success. Four variables were examined in relation to dominance rank since it was thought that they might explain the variation between individuals: year, age (in years), experience (number of years recorded previously at Slimbridge), and sex. The interactions between all six pairs of the above variables were also added to the model. Sex and year were coded and treated as factors, and a normal error distribution was assumed. The statistical significance of the explanatory variables and their interactions were determined by fitting the full model and inspecting the changes in deviance with respect to the changes in degrees of freedom. The most non-significant (*P* > 0.05) variables were than progressively removed from the model. The final model was thus the most parsimonious (see Crawley 1993).

2.3 RESULTS

a) The effect of unit size upon dominance rank

A total of 3948 aggressive encounters were recorded during the period 1989-90 to 1992-93. From these interactions it was possible to calculate augmented dominance values for 422 swan units including 143 singletons, 179 pairs, 11 single-parent families and 87 two-parent families (see Table 2.1). In addition the dominance ranks of two 'trios' of yearlings were also calculated.

Families had a significantly higher dominance rank than pairs which in turn had a significantly higher dominance rank than singletons (see Table 2.1). One-parent families had a mean dominance rank intermediate between that of two-parent families and pairs. Amongst two-parent families, dominance increased with the size of the family (Fig. 2.1) and there was a strong positive correlation between the two variables (Spearman's rank correlation, $\underline{r}_s = 0.381$, $\underline{n} = 87$, $\underline{P} < 0.01$). For two-parent families dominance rank can be approximated by the equation:

$Y = 0.685 + 0.052 * X$ ($\underline{F} = 15.12$, $\underline{P} < 0.001$, df = 86)

where Y = dominance rank and X = number of cygnets in family.

The dominance rank of successful pairs which returned with more cygnets than in the previous year tended to increase (Table 2.2a), although the difference in rank between consecutive years was not significant. Similarly the dominance rank of successful pairs which returned with fewer cygnets than in the previous year tended to decrease (Table 2.2b), although again the difference in rank between consecutive winters was not significant. The dominance rank of successful pairs returning with the same number of cygnets as in the previous year however, did increase significantly (Table 2.2c). This latter spurious result may be due to the small sample size, since there is no logical reason why birds returning with the same number of cygnets should do better than those with an increased number of cygnets.

Pairs that had former offspring associating with them had a significantly higher dominance rank than those which did not (Table 2.3a). This relationship was also suggested for singletons which were associating with a sibling (Table 2.3a), although sample size was small. The suggestion that families, with former offspring also associating, had higher dominance ranks than those which did not (Table 2.3a), is biased by the fact that former offspring tended to associate with larger families (Table 2.3b). When the dominance ranks of families with the same number of cygnets were investigated separately, those with former offspring also associating tended to have higher dominance ranks than those which did not (in all cases except in families with one cygnet) but small sample sizes precluded any significant results (Table 2.3c).

b) The effect of change in social class upon dominance rank

Although the dominance rank of singletons returning the following winter with a mate increased significantly (Table 2.4b), their rank as pairs was still significantly lower than that of birds paired for at least one previous winter (Table 2.5a). Similarly the dominance rank of singletons returning the following winter with both a mate and cygnets ($n = 4$) was found to increase significantly between consecutive winters (Table 2.4c). Pairs which had been unsuccessful in one year but returned the following winter with cygnets also experienced a significant increase in dominance rank (Table 2.6b).

Reduction in social rank would be expected to result in a decrease in dominance rank although individual recognition between members of a relatively stable flock between years might allow some retention of dominance rank (Lamprecht 1986). Successful breeders returning in the subsequent winter without young generally lost dominance rank ($n = 31$, 21 exhibited a decrease in rank, 10 exhibited an increase in dominance rank) but the difference was not significant (Table 2.7) and these pairs had significantly higher ranks than pairs without young in both winters (Table 2.5b). However, members of successful pairs which returned alone in the subsequent winter experienced a significant decrease in dominance rank between winters (Table 2.8). Members of pairs which had been unsuccessful in one year and returned alone (without their mate) in the following year did not show a significant decrease in dominance rank between winters (Table 2.9), but the sample size was small.

c) Consistency of dominance rank

The dominance rank of singletons which had also been singletons in the previous winter, generally increased between years (15 out of 21 cases, see Table 2.4a), although there was no correlation between the ranks of individuals between years (Spearman's rank correlation r_s = -0.078, P > 0.1, n = 21).

The dominance rank of pairs without cygnets whose social class and mate remained unchanged from the previous year also increased significantly between years (Table 2.6a), and the ranks recorded for individual pairs in each season were closely correlated (Spearman's rank correlation r_s = 0.500, P < 0.01, n = 44). A regression was fitted to the data-set and the following predictive formula was derived:

DR2 = 0.315 + 0.518*DR1 (F = 13.56, P = 0.001, df = 43).

where DR1 = dominance rank in year 1 and DR2 = dominance rank in year 2.

The dominance rank of unsuccessful pairs in winter at Slimbridge which went on to breed successfully in the following summer was found to be significantly higher than that of pairs which did not return with cygnets in the following winter (Table 2.10a). However when the analysis was rerun, omitting all pairs that had ever bred successfully in a previous season (since these pairs may have retained dominance rank), the significance of the result was lost (Table 2.10b). The dominance rank of singletons which subsequently found a mate and bred successfully the following summer, was significantly higher than that of singletons which returned with a mate but without cygnets (Table 2.11). There was no evidence to suggest that the dominance rank of singletons in the winter prior to finding a mate was significantly higher than that of singletons which did not find a mate (Table 2.12).

d) Heritability of dominance

Sample sizes for this analysis were rather small since each record required full information on the dominance rank, age and sex of the bird in question, together with the dominance rank of its' parents when it was a cygnet. Only the sample sizes of males in their second and third winters were large enough to permit analysis. Individuals which continued to associate with their parents were not included in the analysis since their dominance rank would be greatly enhanced by the presence of family members. The dominance rank of the parents would depend to some extent on the size of the family during the individuals' first winter, but since the two factors are likely to be closely correlated, family size was not taken into account for this analysis. Dominant parents were taken to be those with ranks above 0.84 (an arbitrary figure chosen to split the sample into two similar sized groups), less dominant parents were taken to be those with ranks below 0.84.

There was no significant difference between dominant and less dominant parents in the dominance rank of male offspring in their second winter (Table 2.13a). Moreover, there was no correlation between the dominance of the offspring and of the parents during its first winter (Spearman's rank correlation $r_s = 0.074$, $P > 0.1$, $n = 7$). Dominance ranks of males in their third winter again did not depend on whether they were the offspring of dominant and less dominant parents (Table 2.13b), and there was no correlation between the dominance of the offspring and of the parents during its third winter (Spearman's rank correlation $r_s = 0.700$, $P > 0.1$, $n = 5$).

e) The effect of age

The effect of age upon dominance rank can best be investigated amongst singletons since an individuals' dominance rank generally increases upon acquiring a mate. Moreover, yearlings are significantly smaller (in terms of weight) than adults (Evans & Kear 1978), which will also have a direct bearing upon their fighting ability. Dominance rank tended to increase with age in years amongst male singletons (Fig 2.2), irrespective of the number of years that individuals had visited Slimbridge (all individuals of known age were included in the analysis), and the two variables were significantly correlated (Spearman's rank correlation $r_s = 0.354$, $P < 0.05$, $n = 38$). There was no obvious relationship between dominance rank and age amongst female singletons (Fig. 2.2) and there was no significant correlation between the two variables (Spearman's rank correlation $r_s = 0.140$, $P > 0.1$, $n = 23$). Males had higher mean dominance ranks than females in all age categories but small sample sizes precluded significant differences between the two sexes, in any year category.

Variation in the dominance rank of single birds was associated with age, experience (number of years recorded previously at the site) and sex (Table 2.14). There were no significant interactions between these variables. Amongst singletons, males had higher dominance ranks than females (Fig. 2.3). Dominance rank tended to increase with both age and experience (Figs. 2.4 & 2.5), although there was some evidence to suggest that dominance rank was lower amongst older birds (> 12 years old).

2.4 DISCUSSION

In accordance with similar studies on dominance hierarchies in species of wildfowl which form large flocks in winter (e.g. Raveling 1970, Scott 1980b, Lamprecht 1986, Black & Owen 1989) families were dominant over pairs without cygnets, which in turn were dominant over singletons. Moreover there was a significant positive linear relationship between unit size and dominance rank amongst two-parent families. This relationship has not been found in previous studies and may reflect the very large number of aggressive interactions involved in the calculation of dominance in the current study, thereby increasing the accuracy of the resultant dominance ranks. Moreover single-parent families ranked intermediately between two-parent families and pairs without cygnets, whilst pairs which had former offspring associating (and therefore a larger unit size) had significantly higher dominance ranks than those which did not. Trios of yearlings (n = 2) ranked intermediately between singletons and pairs.

The relationship between unit size and dominance differs from that found in Lamprecht's (1986) study of Bar-headed Geese, which indicated that assistance in encounters by other members of a unit had a negligible effect on the outcome of goose conflicts. It does however agree with studies of animals such as gorillas (Harcourt & Stewart 1987), and Bewick's Swans at Welney, Norfolk (Scott 1978b), which show that individuals assess each other's fighting ability through perceiving specific cues in an opponent (theoretical review in Parker 1974), and that the presence of 'helpers' can improve the fighting ability of an individual. Indeed, in the current study closely-matched families of similar size and rank were observed to recruit temporarily former offspring present prior to an aggressive encounter (but which had previously been chased away by members of the families), and such encounters would then often involve a number of fights between different individuals from the two families. The number of swans in a given unit therefore seems likely to have a bearing on both its perceived and actual fighting ability. The tendency for former offspring to associate with larger families, rather than smaller families, suggests that there is more to be gained by family and former offspring alike from an increase in dominance rank towards the top of the hierarchy, since former offspring which were unwanted as associates by a family (usually smaller or subordinate families) were repeatedly chased away by the parents whenever they approached the family unit. Such behaviour demonstrated amongst Barnacle Geese (Black & Owen 1984) was taken to suggest that the optimum size of a family unit may not simply be the largest. Optimum unit size may be that which allows its' members to achieve the best access to the resources available within the social hierarchy operating at the time.

An increase in an individual's social class between winters was associated with an increase in dominance rank, thus confirming the positive relationship between dominance rank and unit-size. However since the dominance rank of newly-formed pairs was significantly lower than that of birds which had been paired for at least one previous winter, it is clear that other factors than unit size are also operating. Rees et al. (1996) using the data sets obtained in the current study showed that amongst the 23 pairs whose ranks were recorded in all four years, dominance rank increased linearly with pair duration. Moreover since there was no association between pair duration and dominance rank for years when the birds accompanied by cygnets were treated separately, the authors argued that the increase in dominance rank associated with pair duration could be attributed to the improved breeding success of the pair rather than to improved fighting ability (Rees et al. 1996). However, the current analysis revealed that the dominance rank of individual pairs without cygnets (omitting those which exhibited a change in mate) tended to increase from one year to the next, suggesting that dominance rank did increase with pair-bond duration alone, perhaps from a combination of increased age, experience and fighting ability of the pair. Rees et al. (1996) only looked at birds which had bred at some point in their life (and did not include unsuccessful pairs), so the difference in results between the two studies is likely to stem from differences in sample size.

There was consistency between years in the dominance rank of pairs both with, and without, cygnets. Singletons did not show consistency in dominance rank between years, although their dominance rank tended to increase from one year to the next. The increasing familiarity with the site of returning singletons may have permitted them to exploit the food resources more efficiently and gain weight, which would improve their fighting ability. Reduction in social class in the current study was found to have less predictable results than an increase in social class, suggesting that there was some retention of dominance rank. Pairs which had bred successfully one year, but returned without cygnets in the next year, did not show a significant decrease in dominance rank; indeed they retained significantly higher dominance ranks than pairs which had not bred successfully in either year. This agrees with the findings of Rees (1988) and again indicates that there may have been some retention of dominance rank perhaps through individual recognition between members of a relatively stable flock. Flock stability between years at Slimbridge is high; some 40-50% of the adults and yearlings recorded at Slimbridge each winter have been recorded before at the site (see Bowler et al. 1993 for example), whilst allegiance to particular roost sites at Slimbridge is even higher (see Chapter 3). However, since members of successful pairs which returned alone in the subsequent winter did experience a significant decrease in dominance rank between winters, it seems likely that dominance rank can not be retained following a severe loss of social status.

There was no evidence for an increase in dominance rank amongst single swans prior to attracting a mate, as suggested for Barnacle geese (Black & Owen 1989). Dominance ranks recorded for pairs which bred successfully the following summer were significantly higher than that for pairs which failed to rear any cygnets. When pairs which had bred successfully in a previous season were removed from the analysis, the significance of the relationship was lost, indicating that there was no significant increase in dominance rank in the winter prior to breeding amongst first-time breeders. These results suggest that it is generally the same group of dominant birds that breed year after year i.e. dominance gives rise to reproductive success (through holding breeding territories and breeding early), and that this is consistent for individuals.

There was no direct evidence to suggest that the dominance ranks of offspring were related to those of their parents during the winter in which they had first appeared as cygnets. Scott (1980b) found evidence to suggest that cygnets assumed their parents dominance and that this effect continued into the second winter. In the current study, offspring from dominant families were generally more dominant than those from less dominant families and it may be that the small sample sizes precluded any significant results. An additional complication is that former offspring were more likely to associate with large families. Since family size and dominance rank were closely linked, and offspring associating with their parents were excluded from the analyses, very few singleton offspring from the most dominant pairs were included in the sample.

Dominance rank increased with age for two to six year old singletons, and age (in years) was found to be a good predictor of dominance rank for single swans. Adult size has been achieved by the second year (Evans & Kear 1978) so this yearly increase in dominance is likely to relate to an improvement in fighting ability gained through experience rather than to an increase in fighting strength, and indeed both age and experience (defined as the number of winters which an individual had been recorded previously at the site) were found to contribute to the dominance rank of singletons. There was some evidence to suggest that the dominance rank began to decline amongst older singletons (> 12 years old). This probably does not represent a genuine decline in dominance rank amongst older birds but instead may highlight the low dominance rank of old singletons (particularly old females) which had failed to attract a mate. Although dominance did generally increase with age amongst female singletons, there was no significant correlation between age and dominance rank, unlike amongst male singletons, and females tended to rank lower than males of the same age. This concurs with Scott (1980a) who showed that dominance was related to body size and, since females are generally smaller than males (Evans & Kear 1978), females would be expected to rank lower than males. In addition female fighting is not normally a determinant of the dominance rank of a pair. Both male and female singletons stand to gain significantly in terms of increased dominance rank by forming a pair. However, since there is evidence to suggest that Bewick's Swans exhibit age assortative pairing (Rees et al. 1996), it is the females which stand to gain the most from finding a mate. This may help to explain in part, the observation that the age of females at first pairing is generally lower than for males (Evans 1979b).

2.5 SUMMARY

1) The outcomes of 3498 aggressive interactions between individually identified swan units were recorded during the study. From the outcomes of these interactions, the augmented dominance ranks of 422 swan units were calculated including 143 singletons, 179 pairs, 11 single-parent families, 87 two-parent families and two 'trios' of yearlings.

2) Families were dominant over pairs without cygnets which in turn were dominant over singletons. Single-parent families had intermediate dominance ranks between those of two-parent families and those of pairs without cygnets. Trios of yearlings ranked between pairs without cygnets and singletons.

3) A significant positive linear relationship was discovered between unit size and dominance rank amongst two-parent families which differed from some other published studies. This may have resulted from the very large sample sizes involved, which in turn permitted a very accurate determination of dominance rank. It is argued that the number of swans in a unit has a bearing on both its perceived and its actual fighting ability. Former offspring tended to associate with larger families suggesting that there is more to be gained by the family and former offspring alike towards the top end of the hierarchy. However since unwanted former offspring were repeatedly chased away by family units, the optimum size for a family unit in winter may not always be the largest.

4) There was evidence to suggest that dominance rank was retained by pairs, accompanied by offspring in one winter, upon returning without young the following season. Such retention may be possible because of the high level of winter site fidelity, which allowed individual recognition between members of the wintering flock. Severe loss of social status (i.e. loss of mate), did however cause a significant decrease in dominance rank.

5) There was consistency between years in the dominance rank of individual pairs, both with and without cygnets. The dominance rank of singletons increased between years but ranks for individuals did not exhibit consistency between years.

6) The dominance rank of individual pairs without cygnets increased from one year to the next, indicating that pair-bond duration had a positive effect upon rank, probably through a combination of improved cooperation between members of the pair, increased age and experience leading to an improvement in fighting ability.

7) There was no evidence to suggest that there was a significant increase in dominance rank amongst singletons in the winter prior to finding a mate. Similarly there was no evidence to suggest that the dominance rank of pairs in the winter prior to their first successful breeding season was significantly higher than for unsuccessful pairs.

8) Although offspring from high-ranking families in general had higher dominance ranks than those from less dominant families, upon returning as singletons in subsequent years, small sample sizes precluded any conclusive evidence for the heritability of dominance.
9) Generalised linear models were used to examine the variation in dominance rank amongst single birds; variables which statistically accounted for some of the variation included sex, age (in years) and experience (number of years previously recorded at site). Dominance rank tended to increase with both age and experience, although the relationship between dominance rank and age was less clear for females than for males. The lack of correlation between age and dominance rank amongst female singletons was expected since female size/fighting ability is not normally a determinant of the dominance rank of a pair. Male singletons tended to rank higher than females of the same age. Assuming that Bewick's Swans exhibit age-assortative mating, it is the female singletons that stand to gain the most, in terms of increased dominance rank, from pair formation.

B) CONDITION AS ASSESSED BY ABDOMINAL PROFILE

2.6 INTRODUCTION

The choice of wintering site is important since the fat reserves developed by the swans prior to the spring migration serve to fuel the c4,500 km return flight to the summer breeding grounds and may also affect condition upon arrival at the nest sites, depending on food availability at migratory sites along the route. Snow cover may severely reduce the availability of food during the pre-nesting period (pers. obs.) so the quantity of stored fat reserves could directly affect egg production in females, territorial defence activity in males, and therefore ultimately breeding success (Harvey 1971), as demonstrated for other arctic nesting species (Ankney & MacInnes 1978, Drent & Daan 1980, Aldrich & Raveling 1983, Ebbinge & Spaans 1995).

The current study investigates the acquisition of fat reserves by individual swans whilst over-wintering at Slimbridge as assessed by their abdominal profile (AP). Fat content is a good indicator of 'condition', defined as the fitness of a bird to cope with its present and future needs (Owen 1981). The abdominal (omental) fat depot is an important one and although it comprises only 10% of the total body fat in Red-billed Duck Anas erythrorhyncha, there was a close correlation between abdominal fat and total fat content in this species (Woodall 1978). The mass of the abdominal fat has also been found to be a good predictor of total body fat in Blue Geese and Canada Geese Branta canadensis (Thomas & Mainguy 1983). The use of AP as a technique for obtaining a field score of physiological reserves is well established amongst Branta geese (Owen 1981, Owen & Black 1989, Johnson & Sibly 1993). It has also been applied to grey geese (Loonen et al. 1991, Van Eerden et al. 1991, Warren 1990, Mayes 1991, Boyd & Fox 1995) and to a shorebird, the Red Knot Calidris canutus (Wiersma & Piersma 1995). Of the three species of swan that occur naturally in Europe the Bewick's Swan is most akin to geese in size. Moreover, the relatively short distance between the tail and the lowest point of the belly causes fat accumulation in this area (as revealed by the dissection of swans that had died by colliding with power-lines) to produce similar profiles to those seen in geese. An AP scale similar to the one described by Owen (1981) was developed for the study. The validity of using this method was assessed by comparing biometric data recorded upon catching swans for ringing, with abdominal profiles made during observations of the same individuals in the field. A number of variables are likely to affect AP including time, year, social class, dominance rank and sex. Correlates of AP were investigated with respect to these variables in order to test whether:

1) AP changed during the course of the winter and whether the swans exhibited pre-migratory fattening. Evans & Kear (1978) showed that Bewick's Swans at Slimbridge increased in weight during the first half of the winter, but weight data immediately prior to departure in spring were sparse.

2) AP varied between winters. Differences in the quantity and quality of food supply between winters, perhaps as a result of climatic conditions, might be expected to affect AP scores, assuming food is limiting.

3) AP varied between the sexes. Females might be expected to have higher AP scores than their mates towards the end of the winter, since they may rely on stored body reserves for breeding, as well as for fueling migration to the breeding grounds in spring.

4) AP varied between birds of differing social class. Swans from the dominant family class might be expected to have higher AP scores than low-ranking singletons, since their dominance may allow them access to the best resources. However, the effect of 'more mouths to feed' may also be relevant.

5) AP varied with the position of a bird in the social hierarchy of the Slimbridge herd (dominance rank).

The results of the current analysis formed the basis of a paper (Bowler 1994, see Appendix 1).

2.7 METHODS

a) Abdominal Profiles

During the winters 1990-91, 1991-92 and 1992-93 the condition of individual swans was assessed by recording their AP on a near-daily basis from arrival in mid-October to departure at the end of March. Because of the effect of food intake on AP (Loonen et al. 1991), records were taken only in the afternoon at feeding sites and at the evening roost, in order to ensure that all swans had had the opportunity to feed, prior to having their AP scored. An AP scale reflecting the shape of the belly between the tail and legs with scores from 1 to 6 was developed from photographs and observations taken in the 1989-90 winter (see Fig. 2.6).

The validity in using an AP score to assess body condition in swans was tested by comparing biometric data recorded for birds caught during the winters to their AP scores obtained within two days of the catch date. Measurements taken included weight, tarsus length, skull length and wing length (maximum chord). Three condition indices were calculated based on the mass divided in turn by a) wing-length, b) skull-length and c) tarsus length, to account for differences in the overall size of the individual (Owen & Cook 1977). The cube of these three measurements was also calculated in order to investigate the relationship between mass and volume as in Fox et al.(1992), but these transformations compounded sampling variance, so the results using linear measurements only are presented here.

b) Statistical analyses

Correlates of Abdominal Profile score

For each individual a weighted median AP score for each half-month period was taken to prevent bias for frequently resighted birds. Weighted medians as devised by Owen & Black (1989) were used for the analyses:

$WM = (m\,(nm) + (n^{+} - n^{-}))\,/\,nm$

where WM = weighted median, m = median value, nm = number at median value, n^{+} = the number above and n^{-} = the number below.

Weighted medians were used instead of means, since a 'mean' profile assumes that the intervals between the index values are equal, which is not necessarily true.

Co-variate analysis of the data was performed initially using the PROC GLM command in the SAS statistical package to fit a generalized linear model and then investigated further using GLIM (NAG 1986). Four variables were examined in relation to abdominal profile since it was thought that they might explain the variation between individuals: date (in half-months), year, social class (i.e. paired with cygnets, paired without cygnets, single adult, single yearling, cygnet from a family, lone cygnet, yearling associating with a family, or adult associating with a family) and dominance rank. Male and female birds were treated separately because of their differences in size (Evans & Kear 1978) and to monitor sex differences in condition during the winter. The interactions between all six pairs of the above variables were also added to the model. Sex, year and social class were coded and treated as factors. In order to assess the statistical significance of the explanatory variables and their interactions, a full model was initially fitted and the Type III sums of squares inspected (SAS/STAT 1990). The most non-significant ($P > 0.05$) variables were then progressively removed from the model. The final model was thus the most parsimonious (see Crawley 1993).

2.8 RESULTS

a) Comparisons with biometric data

There was a significant positive correlation between change in AP and change in mass for individual swans caught in December 1990 and again in January 1991 (Pearson's correlation test $r = 0.645$, $n = 48$, $P < 0.01$). The condition indices (mass/morphometric measurement) using both skull-length and tarsus-length correlated positively with AP (Pearson's correlation tests $r = 0.321$, $n = 68$, $P < 0.01$ for males and $r = 0.461$, $n = 58$, $P < 0.01$ for females; $r = 0.323$, $n = 68$, $P < 0.01$ for males and $r = 0.521$, $n = 58$, $P < 0.01$ for females respectively, Fig. 2.7). Regressions were fitted to these data-sets and the following predictive formulae for estimating the mass of birds for which biometric data and AP is known were derived (95% confidence limits given in Fig. 2.7):

i) males. $M/T = 47.17 + 3.17 * AP$ ($F = 7.69$, $P < 0.007$, df $= 67$)

$M/S = 32.50 + 1.94 * AP$ ($F = 7.58$, $P < 0.007$, df $= 67$)

ii) females. $M/T = 37.50 + 4.90 * AP$ ($F = 20.88$, $P < 0.001$, df $= 57$)

$M/S = 25.60 + 2.73 * AP$ ($F = 15.13$, $P < 0.001$, df $= 57$)

where M = mass (g), T = tarsus length (mm) and S = skull length (mm).

The condition index based on wing-length was not significantly correlated with AP.

b) Correlates of Abdominal Profile

The APs of males and females were analyzed separately, and for both sexes the variation in the observed AP was significantly reduced by the addition of the explanatory variables year and date in half-month intervals, as well as the social class of the individual and, for females only, its dominance rank (Table 2.15). In addition there were significant interactions between year*half-month, and half-month*social class, indicating that APs recorded in each half-month varied according to social class and also from year to year.

i) Seasonal variation

Time of year had a significant positive effect on AP (Table 2.15) with AP scores generally increasing during the winter period, and differing little from the expected values of the linear model except in October (Fig. 2.8). Lowest AP scores were observed upon arrival in the second half of October and higher profiles were recorded prior to departure in the second half of March. For both sexes, profiles tended to reach a peak in the second half of January and then again in March (Fig. 2.8). There was a slight reduction in profiles in February (Fig. 2.9) although this was only marked in the 1990/91 winter (Fig. 2.9). Gain in AP was most marked between the second half of October and the first half of November with birds on average increasing one half-score. AP gain was steady and more gradual over the rest of the winter.

ii) Year

Year had a significant effect on AP (Table 2.15). The pattern of increase in AP varied significantly between the three winters for both males and females (Fig. 2.9) with AP scores in the 1991/92 and 1992/93 winters generally rising more slowly than in the 1990/91 winter. The pattern of increase for each winter, however, was similar between the two sexes. Mean AP upon arrival in October differed significantly between winters for both sexes (Kruskal-Wallis X^2 approximation test, $X^2 = 7.355$, $P = 0.025$, df = 2, n = 24 for males and $X^2 = 8.384$, $P = 0.015$, df = 2, n = 21 for females) but profiles prior to departure in late March did not differ significantly between years ($X^2 = 3.510$, $P = 0.187$, df = 2, n = 73 for males and $X^2 = 1.651$, $P = 0.438$, df = 2, n = 75 for females).

iii) Sex

Female AP scores were consistently higher, on average, than male scores throughout the winter (Fig. 2.8) and this difference was significant when all data were combined (Kruskal-Wallis X^2 approximation, $X^2 = 113.06$, df = 1, $P < 0.001$. Mean = 3.931, SD = 0.744, n = 1545 for males and mean = 4.203, SD = 0.789, n = 1457 for females). Combination of the data for this analysis was considered justified since the half-monthly means for both sexes were very similar to the predicted values and the sample sizes for the two sexes were also very similar within each half-month (Fig. 2.8).

iv) Social class

Mean AP scores varied significantly between the different social classes (Table 2.15 & Fig. 2.10). The mean AP of swans in the adult classes were very similar to the predicted class means; differences between these classes were investigated further using the Kruskal-Wallis $\underline{X}^2$ approximation test (df = 1 for all comparisons). Data for paired birds, and for birds with a mate plus cygnets, were combined in order to investigate the effect of presence of a mate. Amongst males, birds with a mate had a significantly lower AP score than those without a mate ($\underline{X}^2 = 38.166$, $\underline{P} < 0.001$, $\underline{n} = 972$ and 205 respectively), whilst amongst females, birds with a mate had significantly higher AP scores than those without a mate ($\underline{X}^2 = 85.712$, $\underline{P} < 0.001$, $\underline{n} = 967$ and 223 respectively). In addition male birds with a mate had a significantly lower AP score than females with a mate ($\underline{X}^2 = 252.83$, $\underline{P} < 0.001$, $\underline{n} = 972$ and 967 respectively). Amongst adults, single males had a significantly higher AP score than single females ($\underline{X}^2 = 19.465$, $\underline{P} < 0.001$, $\underline{n} = 205$ and 223 respectively, see Fig 2.11). Amongst male yearlings, there was no significant difference in AP between birds associating with their parents and singletons ($\underline{X}^2 = 1.992$, $\underline{P} = 0.158$, $\underline{n} = 16$ and 94 respectively). Amongst female yearlings however, birds associating with their parents had significantly lower AP scores than singletons ($\underline{X}^2 = 10.212$, $\underline{P} < 0.001$, $\underline{n} = 43$ and 49 respectively). The interaction term social class*month also had a significant effect upon AP (Table 2.15) as mentioned earlier, and this was particularly marked for cygnets.

v) Dominance rank

The effect of dominance rank upon AP differed markedly between the two sexes (Fig. 2.11). When data from all social classes were combined, AP for females increased significantly with dominance rank (Table 2.15 & Fig. 2.11), whilst for males AP tended to decrease with dominance rank although this relationship did not reach significance and this factor was therefore removed from the generalised linear model.

There was a significant negative correlation between AP and dominance rank for males with a mate (Pearson's correlation $\underline{r} = -0.092$, $\underline{P} < 0.01$, $\underline{n} = 948$), and a significant positive correlation for females with a mate (Pearson's correlation $\underline{r} = 0.110$, $\underline{P} < 0.001$, $\underline{n} = 940$). Amongst cygnets AP increased significantly with increasing dominance rank (Pearson's correlation $\underline{r} = 0.106$, $\underline{P} < 0.002$, $\underline{n} = 908$).

2.9 DISCUSSION

The strong significant positive correlations observed between the AP index developed in this study with both change in mass of individual swans and condition indices involving mass/tarsus and mass/skull, indicate the suitability of this technique for assessing the body condition of Bewick's Swans in the field. Moreover they indicate for the first time that it is possible to predict mass from the AP of known individuals for which biometric data are available, thereby precluding the need for repeated capture to monitor body condition. The considerable overlap between values of adjacent profiles (see Fig. 2.7), however, suggests that predictions may not be very precise. The lack of correlation between AP and a condition index based on mass/wing is interesting as this was found to be the best indicator of condition in Mallard Anas platyrhynchos (Owen & Cook 1977). Wing measurements are less reliable than bone measurements, however, as there may be considerable variation between observers in the degree of wing flattening during measuring (Owen & Montgomery 1978), and this effect may be compounded on the larger swan wing. In addition, differences between seasons in feather-tip abrasion and in feather growth, following the moult in August, will add to the variability. Wing length had the lowest coefficient of variation of measurements in an earlier study of Bewick's Swans (Evans & Kear 1978), but over 90% of the measurements included in their analyses were taken by just one person, which was not the case in the current study. The advantage of the AP technique is that it precludes the need for the repeated capture of birds in order to monitor differences in body condition within and between years.

The change in AP recorded over the winter (Fig. 2.8) is similar to graphs plotted of change in mass of swans wintering at the site in previous winters (Evans & Kear 1978). Mass was lowest upon arrival and rose quickly to reach a maximum in late December/early January. Similarly AP scores were lowest on their arrival and peaked in January. The drop in AP recorded between late January and early February is supported by a decrease in mass amongst birds caught during the second half of the winter (Evans & Kear 1978), a pattern also shown by other wildfowl species including Canada Geese (Elder 1946), Greylag Geese Anser anser (Matthews & Campbell 1969), Mallard (Owen & Cook 1977), Common Teal Anas crecca (Fox et al. 1992) and diving duck (Ryan 1972).

Two hypotheses have been put forward to explain similar weight patterns in Dunlin Calidris alpina (Pienkowski et al. 1979): i) that abundant early winter food enabled birds to store surpluses which later compensate for inadequate food resources and ensure survival until

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Two hypotheses have been put forward to explain similar weight patterns in Dunlin Calidris alpina (Pienkowski et al. 1979): i) that abundant early winter food enabled birds to store surpluses which later compensate for inadequate food resources and ensure survival until food becomes more abundant, and ii) that reserves form an insurance against the risk of future inclement conditions and that with increasing day-length the benefit of reserves becomes diminished (as the risk of severe weather declines) compared with the costs of carrying unnecessary weight, particularly during migration. In small birds such as passerines, there is likely to be a trade-off between the risks of starvation and predation (McNamara & Houston 1990), and increasing uncertainty of feeding conditions has been shown to promote an increase of internal and external reserves in tits Parus spp. (Ekman & Hake 1990, Hurly 1992). Heavier birds are probably less agile and loss of unnecessary body reserves may be advantageous to reduce the risk of predation (Owen et al. 1992). The first hypothesis predicts that birds would be unable to recover mass lost during cold spells while the second predicts that birds would regain weight rapidly to return to optimal mass levels for the time of year. The Bewick's Swans at Slimbridge graze predominantly on improved pasture and shift feeding site throughout the winter selecting fields with the highest green biomass and on the basis of protein content (Rees 1990), and receive complementary feeds of grain at their roost-sites. The birds increase their frequency of feeding in February when food availability is lowest (Chapter 4), but were still able to achieve similar high AP scores in all three winters prior to departure in late March. It seems unlikely therefore that food supply is a limiting factor except, perhaps, during prolonged periods of severe weather in February. Since all three winters during the current study were generally mild and lacked any prolonged periods of sub-zero temperatures, the AP gains observed were presumably close to their optimum. The decrease in AP during early February is a result of both decreasing food quantity (Chapter 4) and quality (Rees 1990); this therefore supports the view of the second hypothesis. The increase in AP prior to migration in March, found in the present study, agrees with the increase in mass amongst some age classes of Bewick's Swans at Slimbridge (Evans & Kear 1978). However the full weight gain prior to departure was not known since catching immediately prior to departure is discouraged to minimize possible disturbance.

The high AP scores achieved prior to the start of migration to the breeding grounds mirror similar gains recorded amongst Greenland White-fronted Geese Anser albifrons flavirostris in Ireland (Warren 1990 and Mayes 1991) and amongst Pink-footed Geese Anser brachyrhynchus in Scotland (Boyd & Fox 1995). Pre-migratory fattening was not evident amongst Common Teal caught and weighed at Abberton Reservoir in Essex, although they had gained and then lost body condition during the course of the winter, indicating that they may be able to gain weight at sites en route to nesting areas in order to improve body condition in readiness for reproduction (Fox et al. 1992). The fact that Bewick's Swans exhibit marked pre-migratory fattening suggests that they may be unable to gain weight sufficiently at migratory sites to achieve the necessary body condition for nesting upon arrival at the nesting areas, particularly since the conspecific Whistling Swan Cygnus columbianus columbianus of North America loses weight throughout the winter on its eastern wintering grounds (Maryland and North Carolina) and departs on spring migration at lowest weight (Limpert et al. 1987). The difference in weight change patterns during the winter between the two subspecies is difficult to explain since they are ecologically very similar, both travel large distances between arctic breeding grounds and more temperate wintering areas and stop off at a few key migratory sites. Limpert et al. (1987) suggested that the daily supplemental feeds of grain may have allowed the swans at Slimbridge to maintain a higher body weight at a lower energy cost by spending large proportions of their time at the provisioned site. However, results from the current study indicate that swans from the Grounds roost, which were able to feed for longer at the grain feeds and to obtain more grain per bird (Chapter 6) than those from the Rushy Pen roost (which instead relied more heavily on field feeding), in general had lower AP scores (Chapter 3), so it seems unlikely that the provision of grain at Slimbridge can account for the differences in weight change between the two sub-species. Depletion of the available food supplies could account for the loss of weight seen in Whistling Swans during the winter, however the failure to gain weight during March and April prior to departure for migratory sites further north is surprising, and suggests that for Whistling Swans from Maryland and Carolina (but not Bewick's Swans from Slimbridge) the energetic costs of migrating with a heavy fat load outweigh the risks of inclement weather further north and failure to gain weight at sites en route to the nesting areas in order to improve body condition in readiness for reproduction. The migratory staging areas for Whistling Swans seem likely to be important for accumulating reserves for breeding (Limpert & Earnst 1994), as they are for many arctic-nesting geese (see Ebbinge & Spaans 1995, for a review). Amongst Bewick's Swans the level of fat accumulation prior to migration is likely to be important; it has been shown to influence both migration survival in Barnacle Geese (Owen & Black 1989) and breeding success in Blue Geese (Ankney & MacInnes 1978).

The pattern of AP gain over the three winters was very similar (Fig. 2.9). Mayes (1991) showed that AP scores of Greenland White-fronted Geese varied significantly between birds feeding on semi-natural and intensive farmland. The similarity in AP score gain each winter at Slimbridge indicates that the quantity and quality of food available did not vary between years. This again suggests that food supply at Slimbridge may not have been a limiting factor. The significant variation in AP upon arrival to the site in late October may reflect seasonal variation in the quantity and quality of food available at sites along the migratory route from the Russian breeding grounds, or in the timing of that migration.

Male birds had a significantly lower mean AP score than females when all classes were treated together and this difference is most marked prior to migration. Studies on geese have suggested that males protect their mates during the pre-breeding season (e.g. Hanson 1953, Inglis 1976, Fox & Madsen 1981, Johnson & Sibly 1990) thereby allowing them to acquire more food and ultimately to breed more successfully. Since females with a mate had a significantly higher mean AP score than males with a mate, this would also appear to be true for Bewick's Swans during the pre-migratory fattening stage. Moreover males with a mate had a significantly lower mean AP score than single males implying that the protection of their female partners incurs the cost of a reduction in their own intake of food and/or more activity. In a similar study, Boyd & Fox (1995) showed that amongst Pink-footed Geese staging at spring migratory sites in Scotland, paired females had higher median AP scores than paired males, but that unpaired adults had lower AP scores. A small sample of ringed birds however meant that the AP scores of unpaired adult males and females were not treated separately.

The relationship between AP and dominance rank for the two sexes (Fig. 2.11) is a function of the differences already described between social classes since, in general, singletons are subordinate to pairs which in turn are subordinate to families (Scott 1978b). Low-ranking single males have higher mean AP scores than higher ranking males with a mate, whilst low-ranking single females lacking the protection of a mate have lower mean AP scores than higher-ranking females with a mate. Moreover the AP of females with a mate increases with the dominance rank of the pair. This is consistent with the observation that the dominance rank of a pair is related to the size of the male (Scott 1978b), since large dominant males would allow better protection of their mates and enable them to gain access to the best food resources. Conversely the AP of males with a mate decreases with increasing dominance rank of the pair, highlighting the cost to the male of maintaining a high dominance level, to the benefit of its mate. The positive correlation between AP and dominance rank amongst cygnets implies that they also benefit from the increased protection afforded by a dominant male parent. This concurs with Scott (1980b) who demonstrated that parents intervened in aggressive encounters involving the cygnets and that their presence had an inhibitory effect upon other individuals from threatening the cygnets, thus protecting them from feeding competition. There was no evidence, in terms of increased AP, to suggest that yearlings benefit by associating with their parents during the winter.

There was little variation between the mean AP scores of different social classes within each sex category (Fig. 2.10). Only cygnets differed significantly (negatively) from the null model. The social class*half-month effect for cygnets however was strongly positive indicating a greater increase in AP during the winter than predicted by the model. Cygnets are also known to put on weight more rapidly than other age categories (Evans & Kear 1978) suggesting that parental care may permit increased food intake, not only to allow for high weight gain but also for continued growth since cygnets are still smaller than yearlings and adults (Evans & Kear 1978).

2.10 SUMMARY

1) An Abdominal Profile (AP) scale was developed to assess body condition of Bewick's Swans in the field in winter. Change in AP score for individual birds correlated significantly with change in their body mass. In addition AP was significantly correlated with condition indices that were designed to remove the potential confounding effects of variation in size between individuals. This indicated the validity of the technique which can be used to assess body condition without catching and measuring the birds, and demonstrates for the first time that mass can be derived from AP. There was considerable overlap between the values of adjacent profiles, however, indicating that predictions for individual birds may not be very precise.

2) AP scores were lowest upon arrival of the birds at their wintering sites in late October and highest prior to departure on spring migration in late March. Profiles reached a peak in January before declining slightly in February. Reasons for this pattern of change in AP are discussed, together with the implications of pre-migratory fattening.

3) There was little variation in the seasonal pattern of AP scores between winters, suggesting that food supply may not have been a limiting factor.

4) Females had significantly higher AP scores than males throughout the winter and this difference was most marked prior to migration.

5) The effect of social dominance upon AP was opposite for the two sexes; low-ranking single males had higher AP scores than higher-ranking paired males, whilst low-ranking single females had lower AP scores than higher-ranking paired females. This suggests that females benefit from the presence of a mate, perhaps due to the male's ability to defend feeding areas, but that this incurs a cost to the male in terms of its reduced fat levels. Both the benefit to the female and the cost to the male increase with the dominance rank of the pair. AP scores of cygnets also increased with dominance rank of the family unit, indicating that they benefit from the presence of a dominant male parent. There was no evidence, in terms of increased AP, to suggest that yearlings benefit by associating with their parents during the winter.

Table 2.1 Dominance values calculated for Bewick's Swans at Slimbridge during the study period 1989-90 to 1992-93 (the number of encounters involved is given in brackets). NB two social units comprising three associating yearlings or 'trios' omitted (mean = 0.453).

		Dominance values			
Winter		Singletons	Pairs	Two-parent Families	One-parent Families
1989-90	mean	0.156	0.483	0.842	0.560
	S.D.	0.182	0.254	0.132	0.296
(n=379)	n	14	20	17	13
1990-91	mean	0.081	0.390	0.770	0.244
	S.D.	0.086	0.175	0.155	0.345
(n=1040)	n	21	37	34	2
1991-92	mean	0.091	0.452	0.801	0.560
	S.D.	0.147	0.232	0.130	0.299
(n=1300)	n	55	50	29	6
1992-93	mean	0.161	0.576	0.921	-
	S.D.	0.191	0.259	0.081	-
(n=1229)	n	53	72	7	0
Total	mean	0.122	0.493	0.807	0.503
	S.D.	0.164	0.245	0.142	0.301
(n=3948)	n	143	179	87	11

Comparison of dominance rank between the social classes (Kruskal-Wallis Chi-square comparisons, df = 1 in all cases).

	Chisq.	P
Singletons v pairs	150.54	<0.001
Pairs v two-parent families	87.48	<0.001
Single-parent families v pairs	0.06	>0.81
Single-parent families v two-parent families	2.22	>0.13

Table 2.2 Comparison of the dominance rank of successful pairs between consecutive winters which:

a) exhibited an increase in family size (Mann-Whitney U comparison).

Dominance values

	Winter 1			Winter 2				
	mean	S.D	n	mean	S.D.	n	W	P
Pair	0.783	0.137	6	0.880	0.116	6	31.00	>0.23

b) exhibited a decrease in family size (Mann-Whitney U comparison).

Dominance values

	Winter 1			Winter 2				
	mean	S.D	n	mean	S.D.	n	W	P
Pair	0.884	0.078	9	0.855	0.119	9	88.50	>0.82

c) exhibited no change in family size (Mann-Whitney U comparison).

Dominance values

	Winter 1			Winter 2				
	mean	S.D	n	mean	S.D.	n	W	P
Pair	0.870	0.099	10	0.909	0.078	10	56.0	<0.001

Table 2.3a Comparison of the dominance values obtained by units which did and did not associate with former offspring (Kruskal-Wallis Chi-square comparison, df = 1 in all cases).

Dominance values

	Associating with former offspring			Not with former offspring				
	mean	S.D	n	mean	S.D.	n	Chi-sq.	P
Singletons	0.407	0.368	2	0.118	0.159	141	2.89	<0.09
Pairs	0.740	0.170	11	0.477	0.241	168	11.62	<0.001
Families (two-parent)	0.857	0.151	15	0.796	0.139	72	3.52	<0.065

Table 2.3b Comparison of the size of families which did and did not associate with former offspring.

Number of cygnets

	Former offspring associating	No former offspring associating	K.W. Chi-sq	P
mean	2.800	2.250	3.36	<0.07
S.D.	1.082	1.045		
n	15	72		

Table 2.3c Comparison of the dominance values obtained by families of different size which did and did not associate with former offspring (Mann-Whitney U comparison, df = 1 in all cases).

Dominance values

	Associating with former offspring			Not with former offspring				
Family size: Number of cygnets	mean	S.D	n	mean	S.D.	n	U	P
1	0.436	0.435	3	0.701	0.182	24	350.0	>0.29
2	0.867	0.188	2	0.759	0.194	27	395.5	>0.43
3	0.845	0.116	9	0.807	0.145	17	224.0	>0.78
4	0.931	0.046	5	0.859	0.116	11	83.0	>0.25

Table 2.4 Comparison between consecutive winters of the dominance rank of singletons which:

a) returned as a singleton (Mann-Whitney U comparison).

Dominance values							
Winter 1 Singleton			Winter 2 Singleton				
mean	S.D	n	mean	S.D.	n	W	P
0.058	0.080	21	0.165	0.149	21	553.0	<0.015

b) subsequently returned with a mate (Mann-Whitney U comparison).

Dominance values							
Winter 1 Singleton			Winter 2 Pair				
mean	S.D	n	mean	S.D.	n	W	P
0.100	0.175	12	0.520	0.216	12	87.00	<0.001

c) subsequently returned with a mate and cygnets (Mann-Whitney U comparison).

Dominance values							
Winter 1 Singleton			Winter 2 Pair & cygnets				
mean	S.D	n	mean	S.D.	n	W	P
0.237	0.154	4	0.716	0.091	4	10.00	<0.03

Table 2.5 Comparison of the dominance values obtained by paired birds in relation to their social status in the preceding winter (Kruskal-Wallis Chi-square comparison, df = 1 in all cases).

a) Comparison of the dominance rank of pairs which had been singletons in the preceding winter with those which had had a mate (but no cygnets).

	Dominance values							
	Singletons in preceding winter			Pair only in preceding winter				
	mean	S.D	n	mean	S.D.	n	Chi-sq.	P
Pairs	0.366	0.224	25	0.503	0.226	80	5.99	<0.015

b) Comparison of the dominance rank of pairs which had returned with cygnets in the preceding winter with those which had not.

Dominance values

	Pair & cygnets in preceding winter			Pair only in preceding winter				
	mean	S.D	n	mean	S.D.	n	Chi-sq.	P
Pairs	0.688	0.208	38	0.503	0.226	80	15.23	<0.001

Table 2.6 Comparison between consecutive winters of the dominance rank of unsuccessful pairs which:

a) returned without cygnets (Mann-Whitney U comparison).

Dominance values

Winter 1 Pair			Winter 2 Pair				
mean	S.D	n	mean	S.D.	n	W	P
0.445	0.223	44	0.546	0.234	44	2215.5	<0.035

b) subsequently returned with cygnets (Mann-Whitney U comparison).

Dominance values

Winter 1 Pair			Winter 2 Pair & cygnets				
mean	S.D	n	mean	S.D.	n	W	P
0.424	0.147	17	0.735	0.146	17	178.00	<0.001

N.B. There was an increase in rank in all 17 cases.

Table 2.7 Comparison between consecutive winters of the dominance rank of successful pairs which subsequently returned without cygnets (Mann-Whitney U comparison).

Dominance values

Winter 1 Pair & cygnets			Winter 2 Pair only				
mean	S.D	n	mean	S.D.	n	W	P
0.780	0.141	31	0.694	0.220	31	1068.5	>0.19

Table 2.8 Between winter comparison of the dominance rank of successful paired swans which subsequently returned without their mate (Mann-Whitney U comparison).

Dominance values							
Winter 1 Pair & cygnets			Winter 2 Singleton				
mean	S.D	n	mean	S.D.	n	W	P
0.679	0.200	6	0.242	0.249	6	55.00	<0.015

Table 2.9 Comparison between consecutive winters of the dominance rank of unsuccessful paired swans which subsequently returned without their mate (Mann-Whitney U comparison).

Dominance values							
Winter 1 Pair only			Winter 2 Singleton				
mean	S.D	n	mean	S.D.	n	W	P
0.311	0.278	4	0.302	0.218	4	17.00	>0.88

Table 2.10 Comparison of the dominance rank of unsuccessful pairs which subsequently returned the next winter with cygnets with those that returned without cygnets (Kruskal-Wallis Chi-square comparison, df = 1).

a) All pairs included in analysis.

	Dominance values							
	Returned with cygnets			Returned without cygnets				
	mean	S.D	n	mean	S.D.	n	Chi-sq.	P
Pair	0.620	0.214	22	0.484	0.241	76	5.17	<0.03

b) Excluding pairs that had bred in a previous year.

	Dominance values							
	Returned with cygnets			Returned without cygnets				
	mean	S.D	n	mean	S.D.	n	Chi-sq.	P
Pair	0.546	0.187	12	0.462	0.241	49	0.07	>0.79

Table 2.11 Comparison of the dominance rank of singletons which subsequently returned the next winter with a mate and cygnets, with those that returned with a mate only (Mann-Whitney U comparison).

	Dominance values							
	Returned with a mate plus cygnets			Returned with a mate only				
	mean	S.D	n	mean	S.D.	n	W	P
Singleton	0.237	0.154	4	0.100	0.175	12	85.00	<0.05

Table 2.12 Comparison of the dominance rank of singletons which subsequently returned the next winter with a mate, with those that returned without a mate (Kruskal-Wallis Chi-square approximation test, df = 1).

	Dominance values							
	Returned with a mate			Returned without a mate				
	mean	S.D	n	mean	S.D.	n	Chi-sq.	P
Singleton	0.169	0.224	23	0.110	0.144	63	0.671	>0.41

Table 2.13 Comparison of the dominance rank of the offspring of dominant families (rank score >0.84) and less dominant families (rank score <0.84), when they returned as singletons in subsequent winters (Mann-Whitney U comparisons).

a) Amongst two year-old males

	Dominance rank of independent offspring							
	From dominant families			From less dominant families				
	mean	S.D	n	mean	S.D.	n	W	P
Singletons	0.126	0.186	4	0.086	0.150	3	10.0	>0.58

b) Amongst three year-old males

	Dominance rank of independent offspring							
	From dominant families			From less dominant families				
	mean	S.D	n	mean	S.D.	n	W	P
Singletons	0.406	0.049	3	0.130	0.148	2	5.0	>0.14

Table 2.14 Linear model using maximum likelihood estimates fitted to dominance rank of singletons (N.S. variables omitted).

Variable	F ratio	d.f.	P
Age	4.016	1, 59	<0.05
Experience	5.901	1, 59	<0.025
Sex	4.464	1, 59	<0.05

Table 2.15 Linear model using maximum likelihood estimates fitted to abdominal profile. Sexes treated separately.

a) Males

Variable	F ratio	d.f.	P
Half-month	26.64	1,1545	<0.001
Year	44.98	2,1546	<0.001
Status	2.32	8,1562	<0.02
Half-month*year	14.65	2,1546	<0.001
Half-month*status	6.69	8,1562	<0.001

b) Females

Variable	F ratio	d.f.	P
Half-month	74.85	1,1359	<0.001
Year	17.79	2,1360	<0.001
Status	5.81	8,1366	<0.001
Dominance	18.56	1,1359	<0.001
Half-month*year	7.04	2,1360	<0.001
Half-month*status	3.71	8,1366	<0.001

Fig. 2.1. The dominance rank of Bewick's Swan familes (mean and S.E. bar) by family size (all data for the 1989-90 to 1992-93 winters included, n = 87).

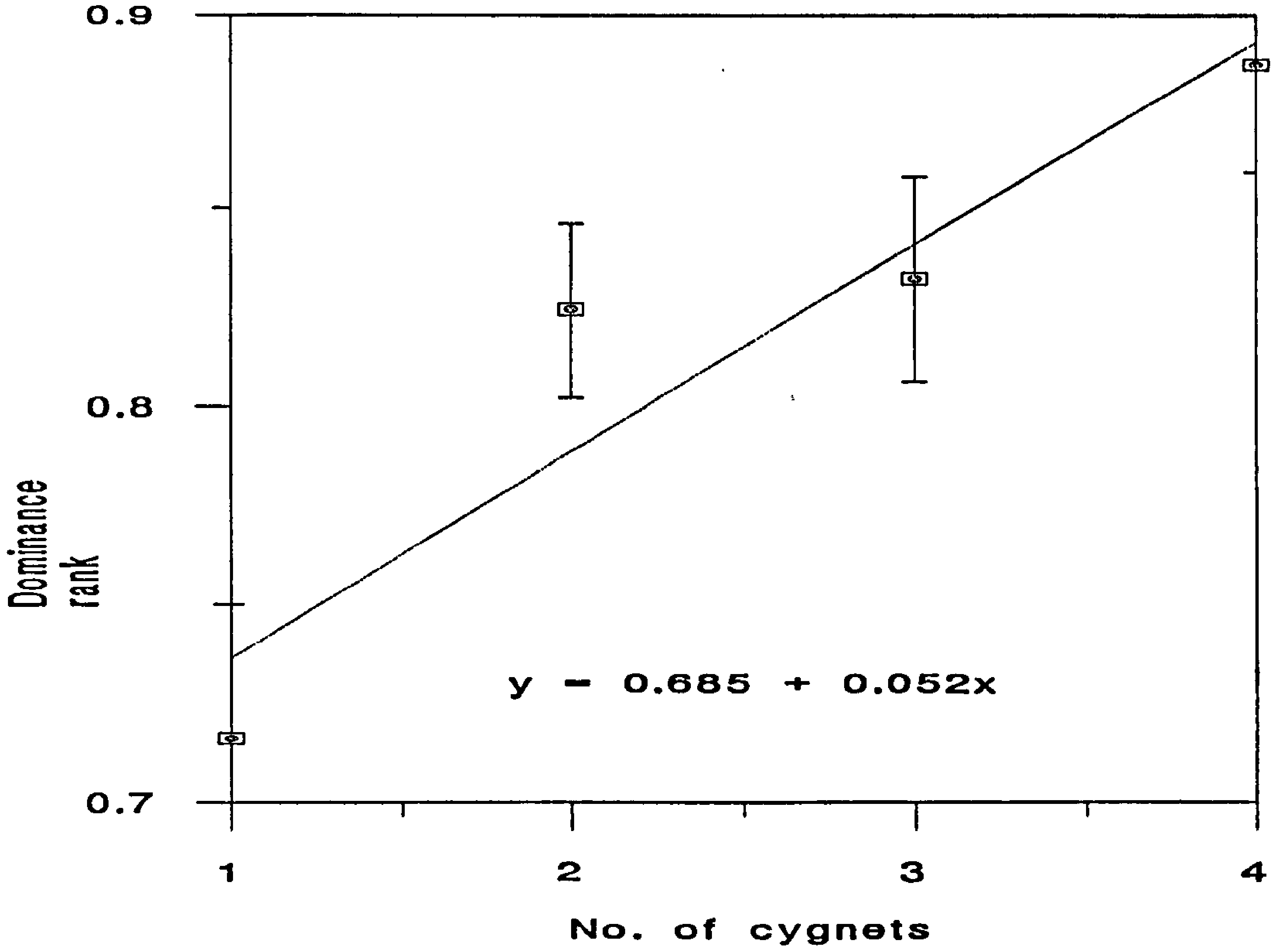


Fig. 2.2. Dominance rank with age for single male and female Bewick's Swans at Slimbridge 1989-90 to 1992-93 winters inclusive (mean and SE bar, n = 38, 23 for males and females respectively).

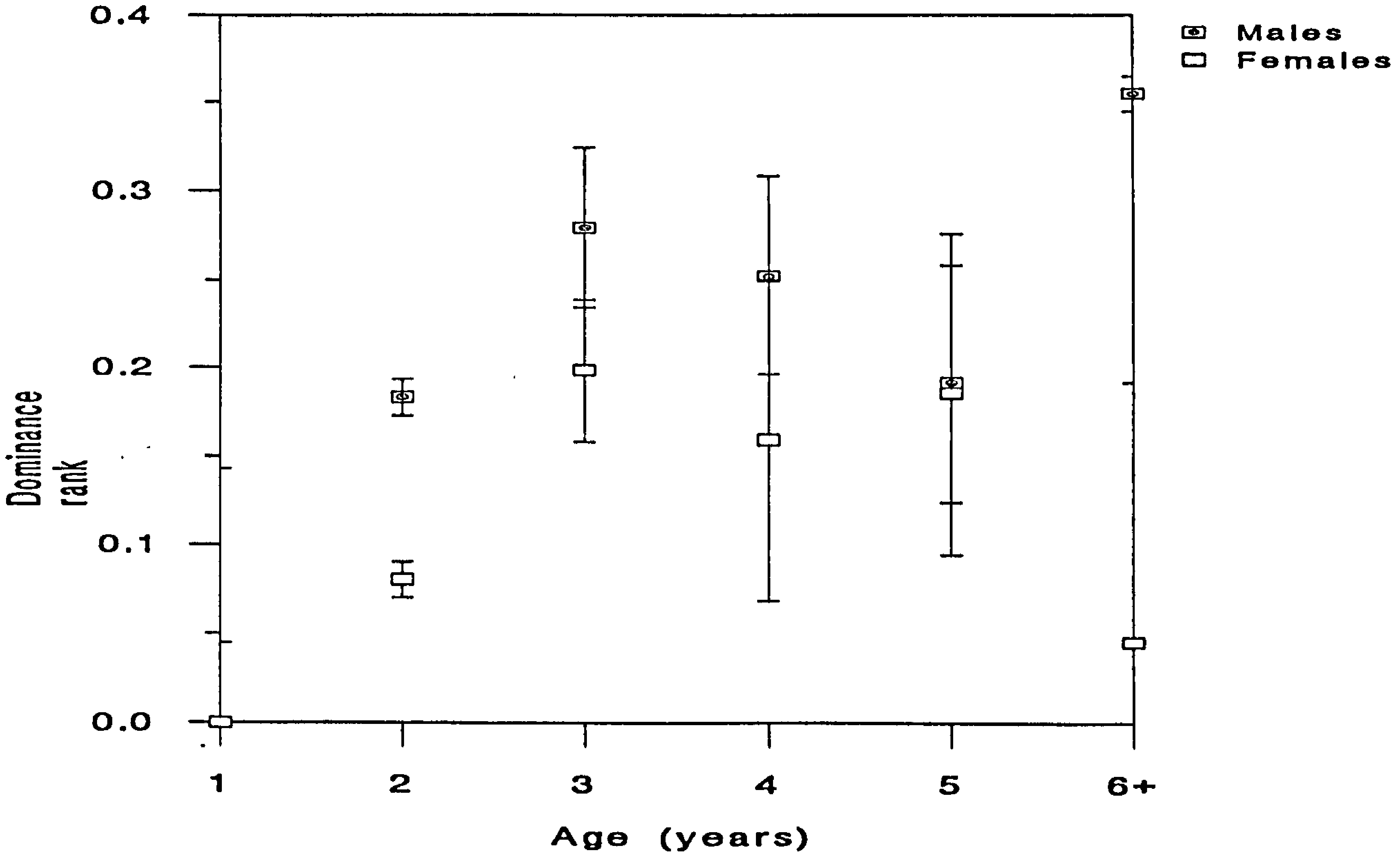


Fig. 2.3. The dominance rank of single Bewick's Swans at Slimbridge by sex for the winters 1989-90 to 1992-93 inclusive (mean and S.E. bar, n = 38 for males, n = 23 for females), plus predicted values from a generalised linear model (white rectangles).

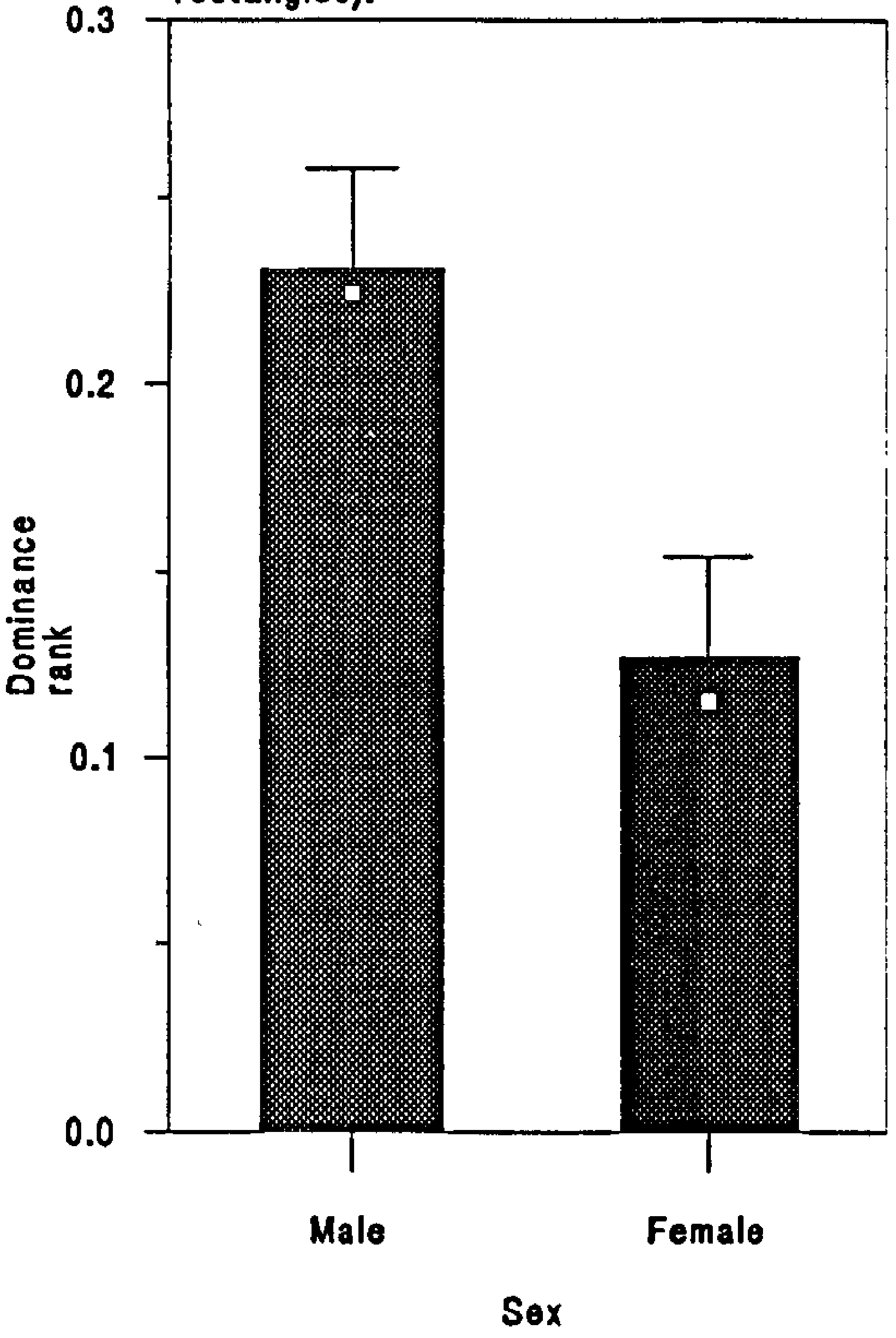


Fig. 2.4. The dominance rank of single Bewick's Swans with age in years for the winters 1898-90 to 1992-93 inclusive (mean and S.E. bar, n = 61), plus predicted values from a generalised linear model (white rectangles).

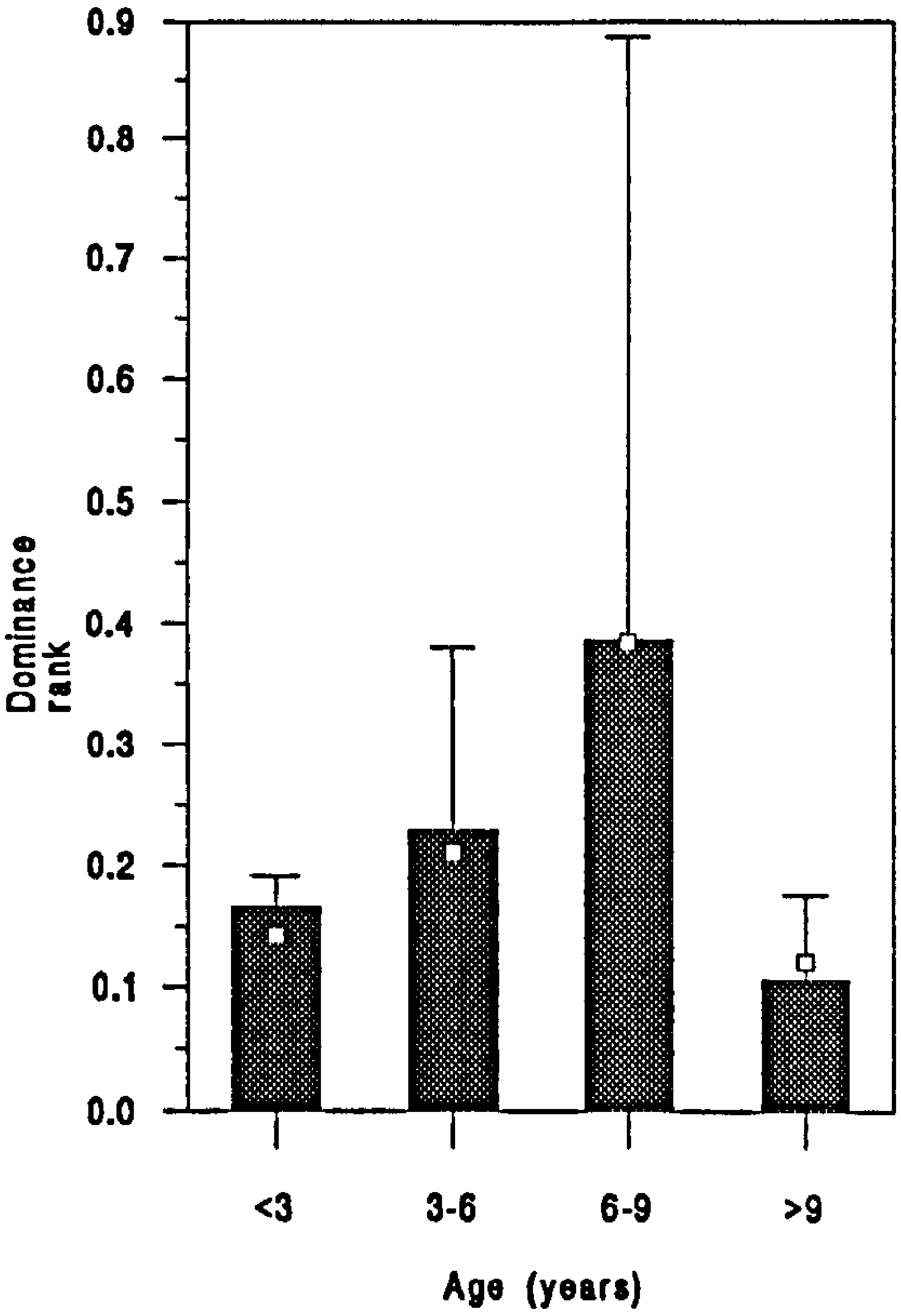


Fig. 2.5. The dominance rank of single Bewick's Swans at Slimbridge with experience (see text) for the winters 1989-90 to 1992-93 (mean and S.E. bar, n = 61), plus predicted values from a generalised linear model (white rectangles).

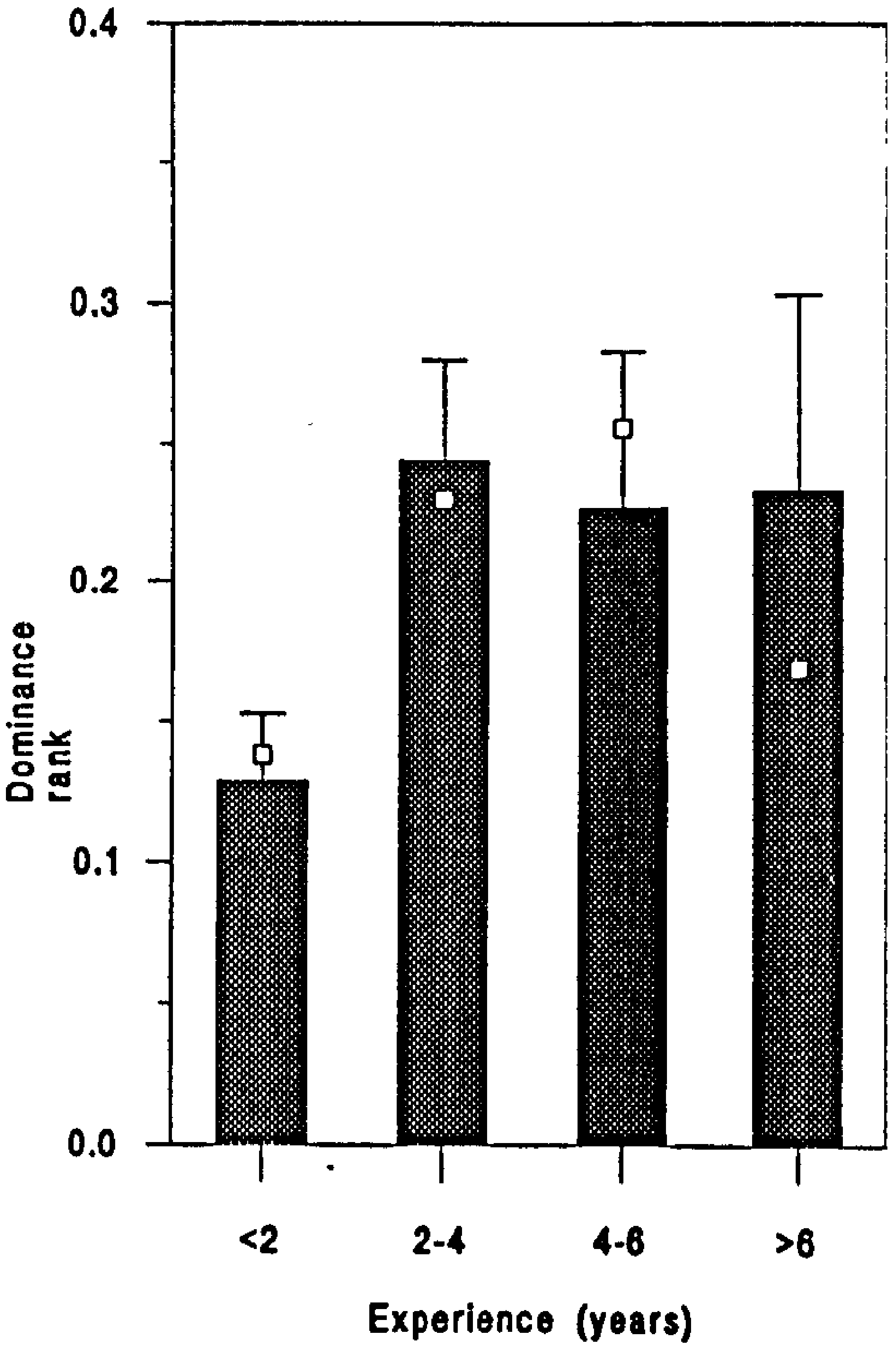
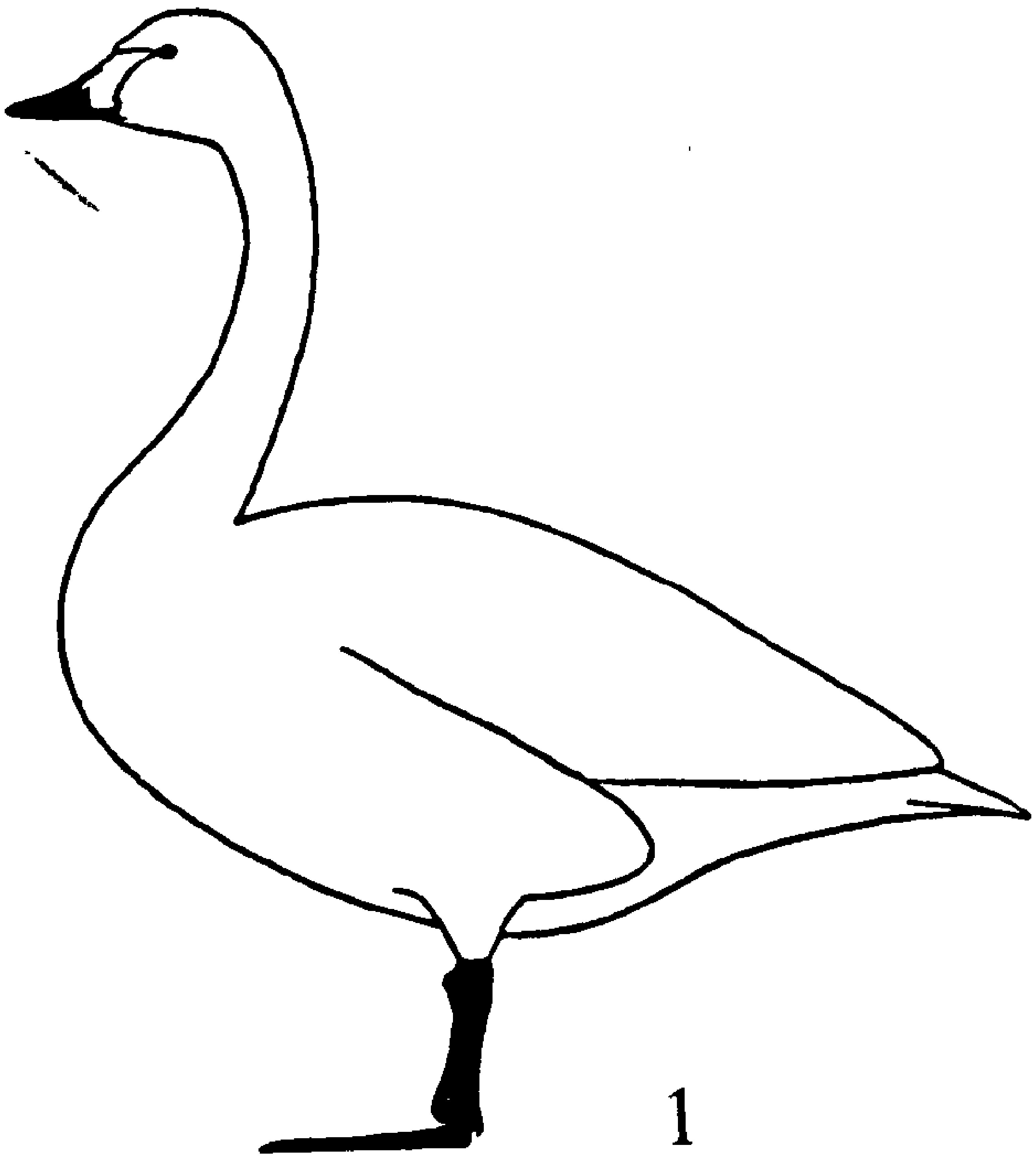


Fig. 2.6



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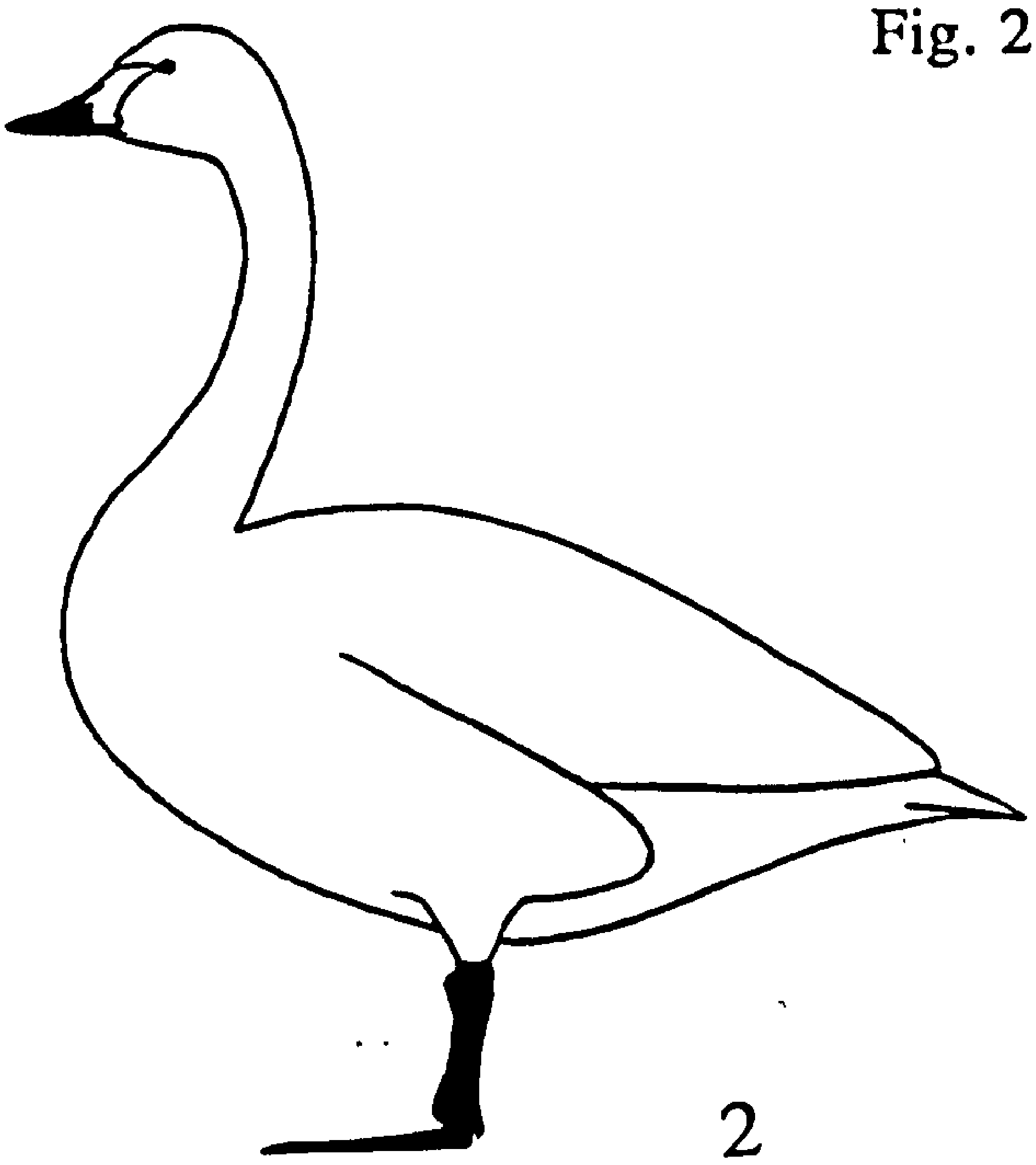

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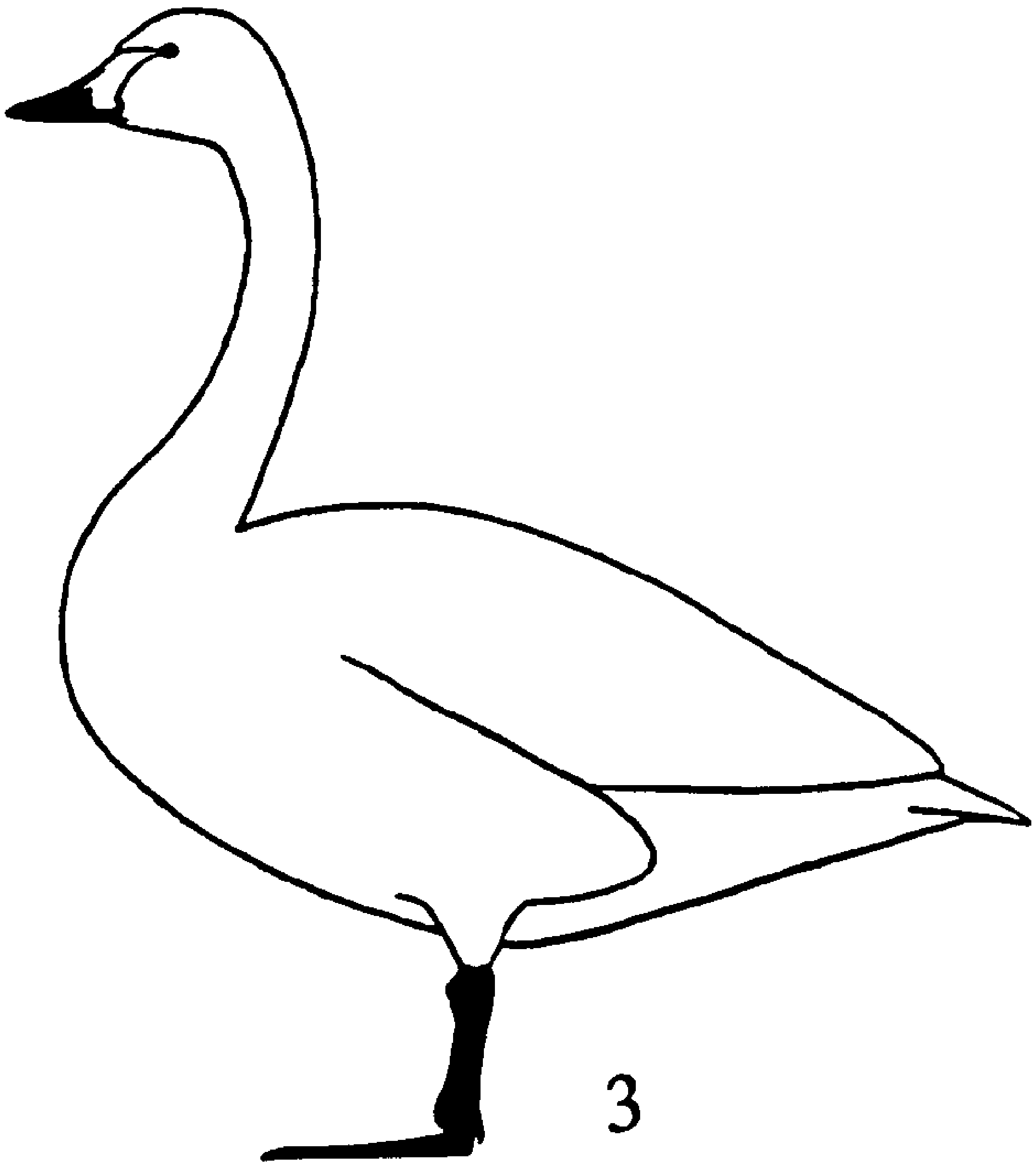

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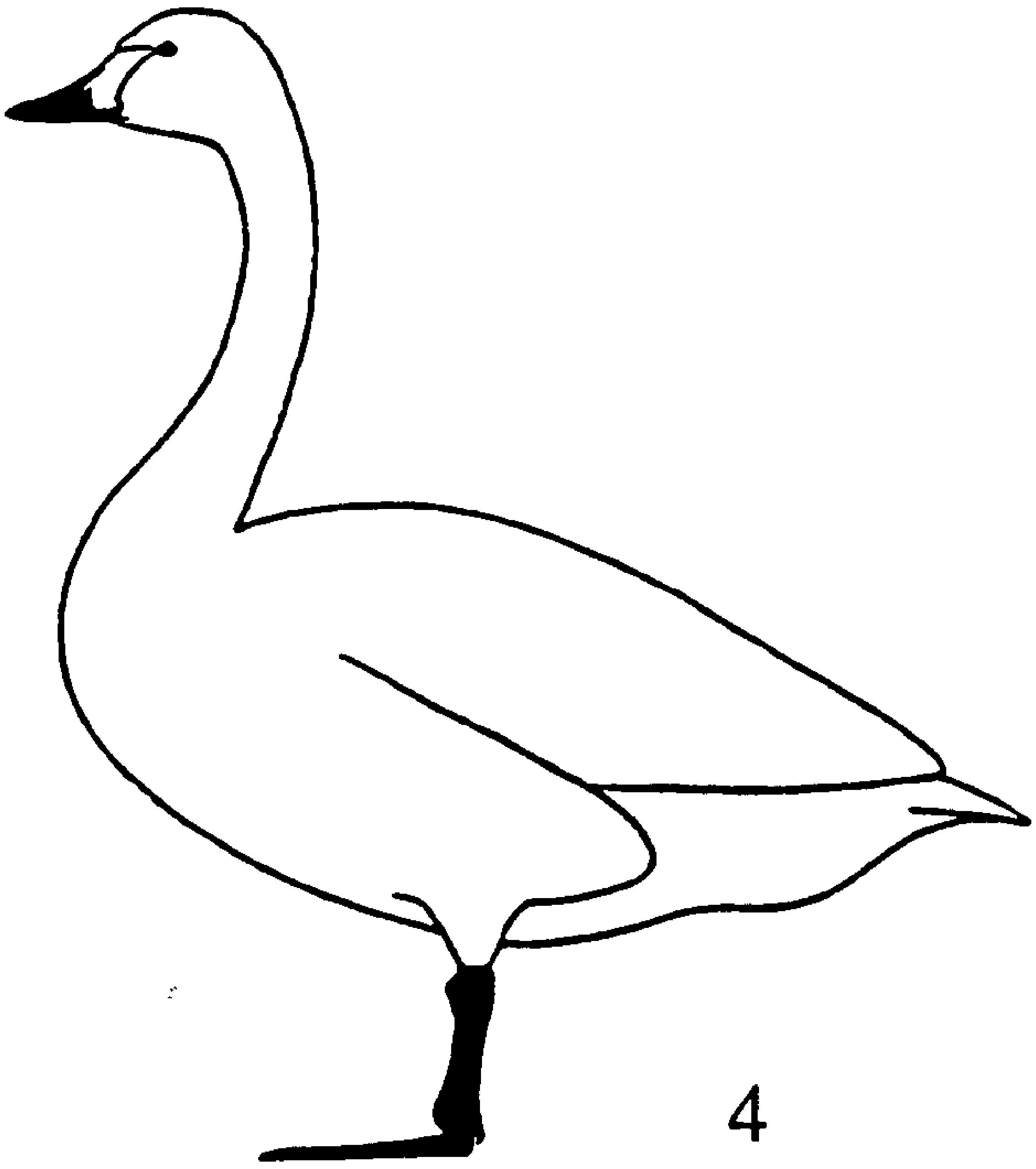

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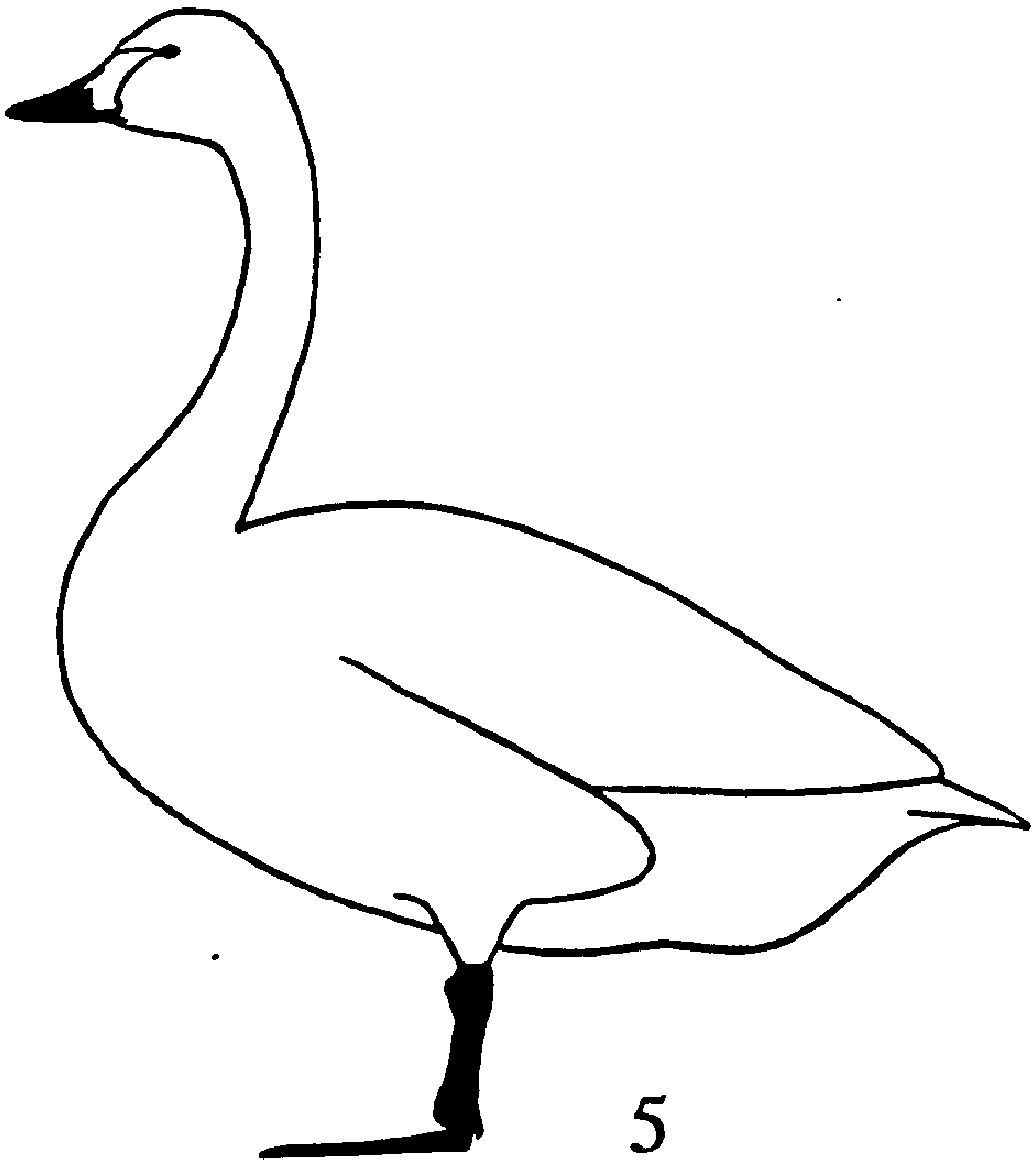

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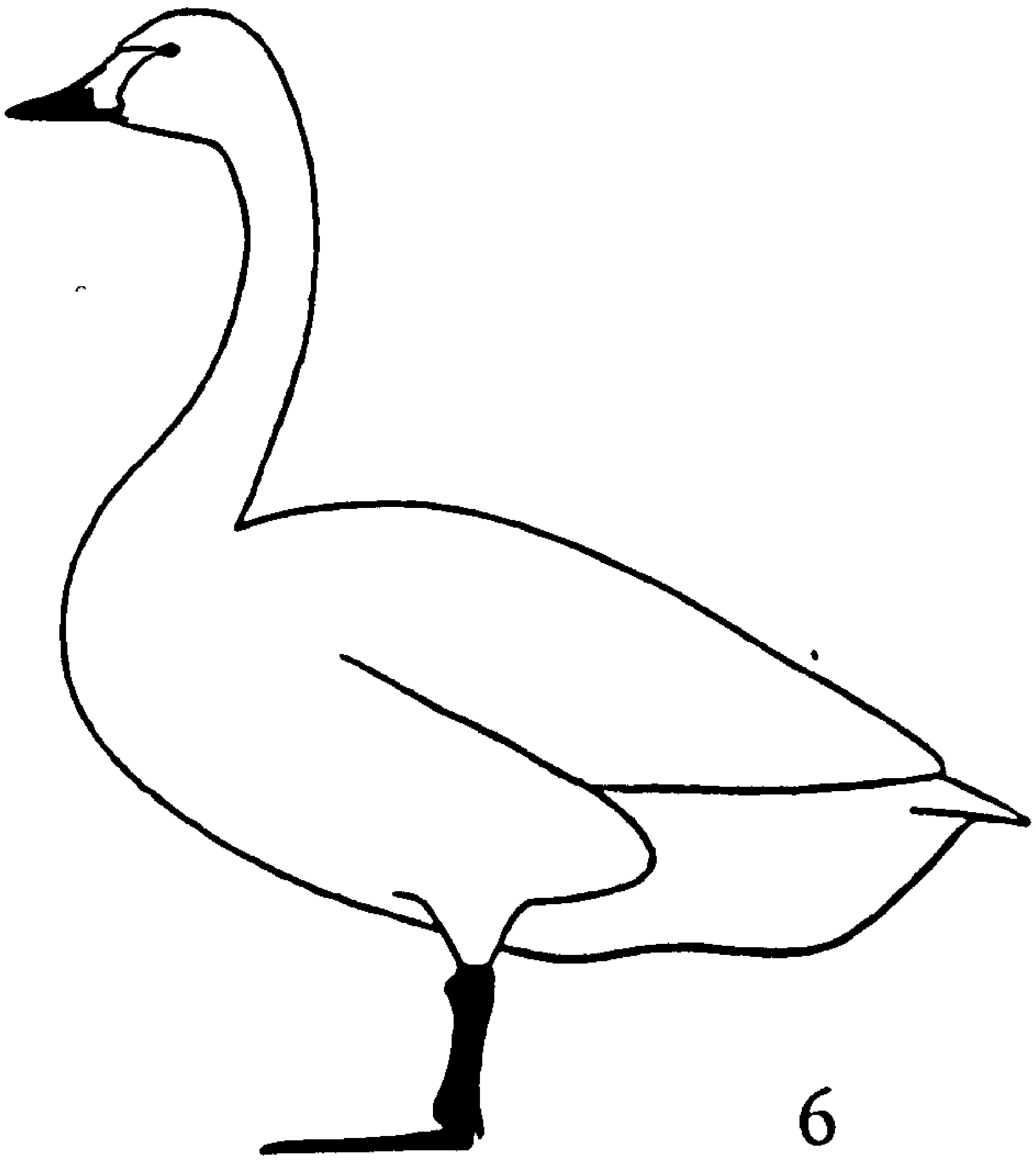


6

Legend for Fig. 2.6

Fig. 2.6 Classification point values (1-6) of abdominal profiles of Bewick's Swans used for assessing body condition in the field.

1 Very concave

2 Concave

3 Straight

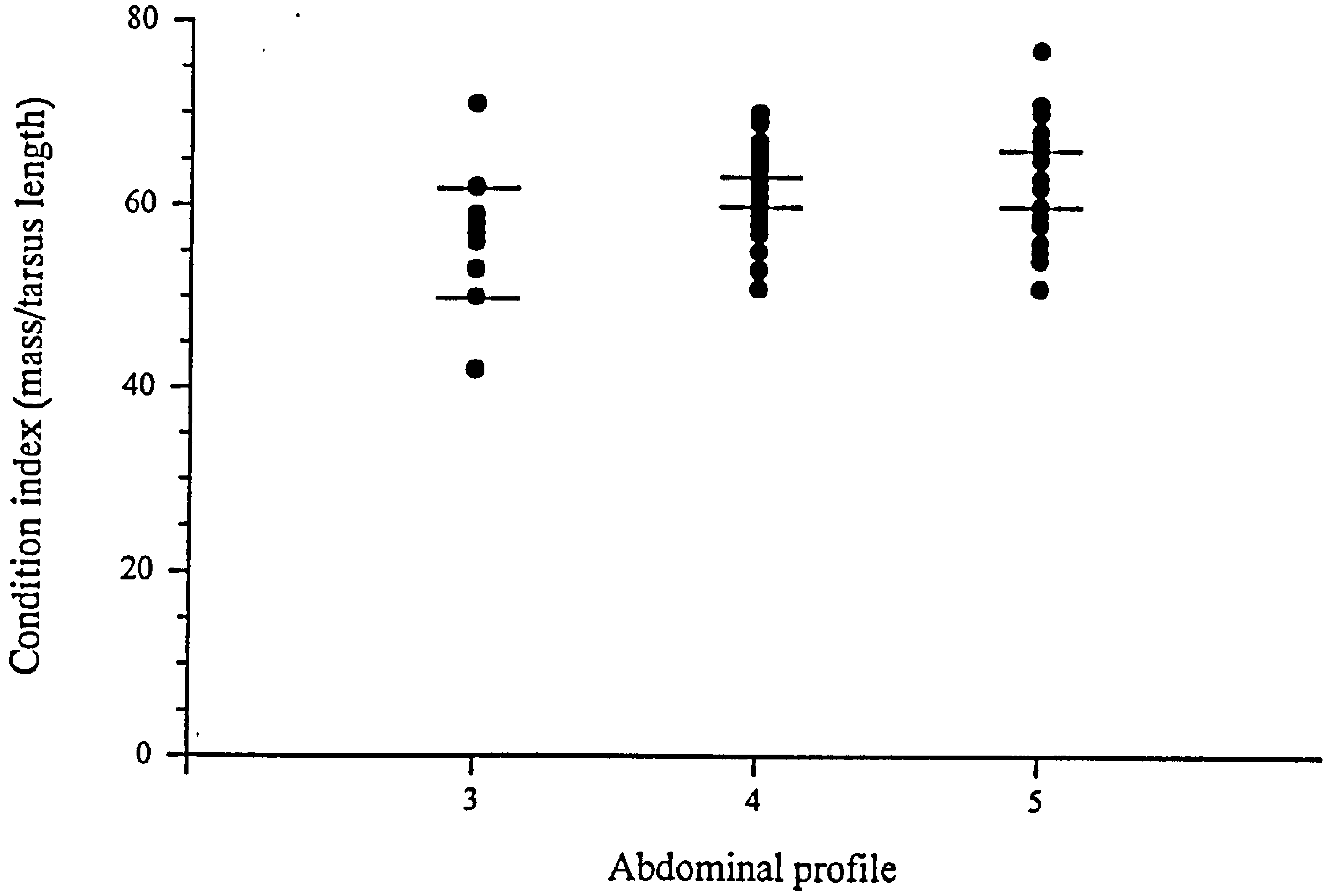
4 Convex

5 Very convex

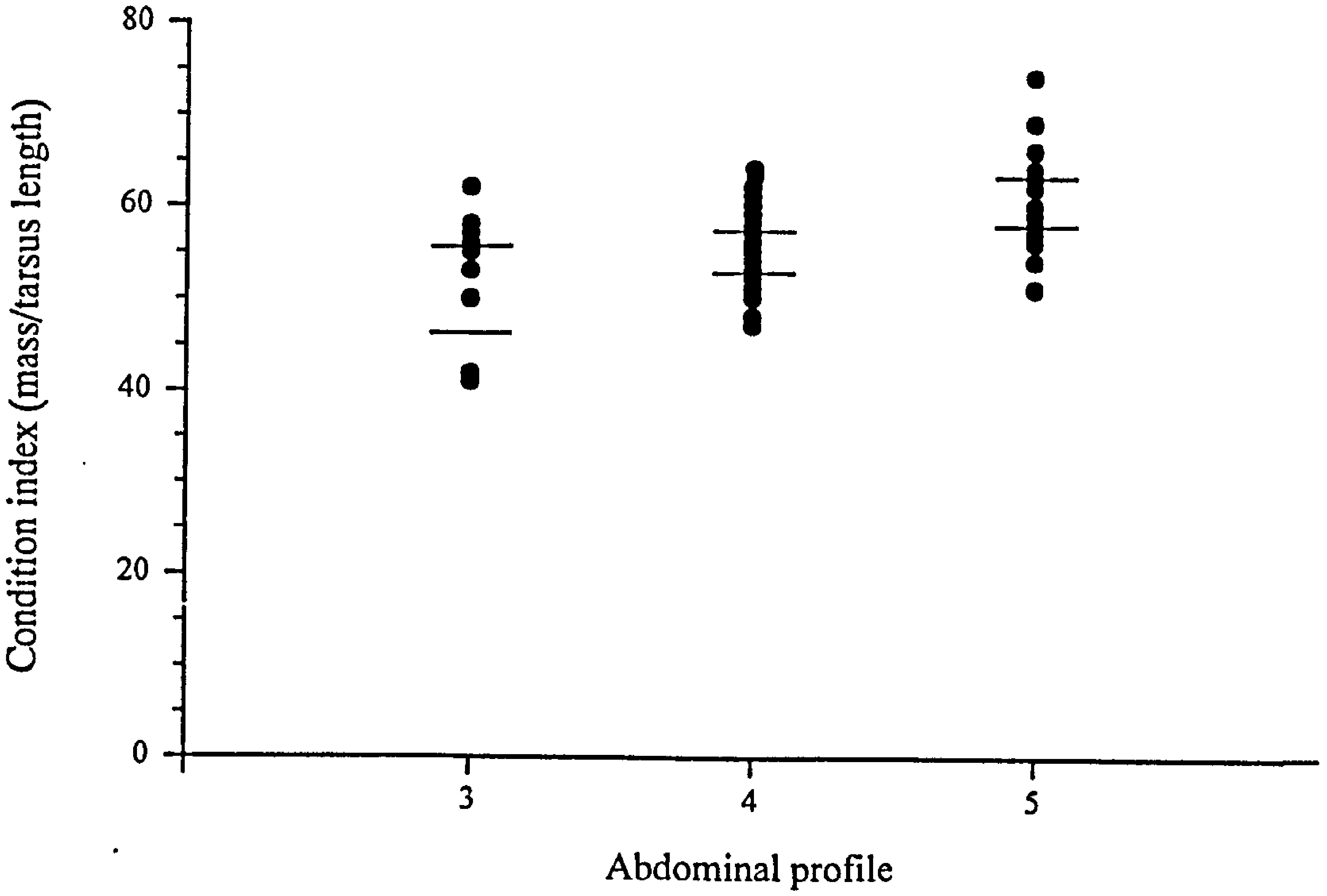
6 Sagging

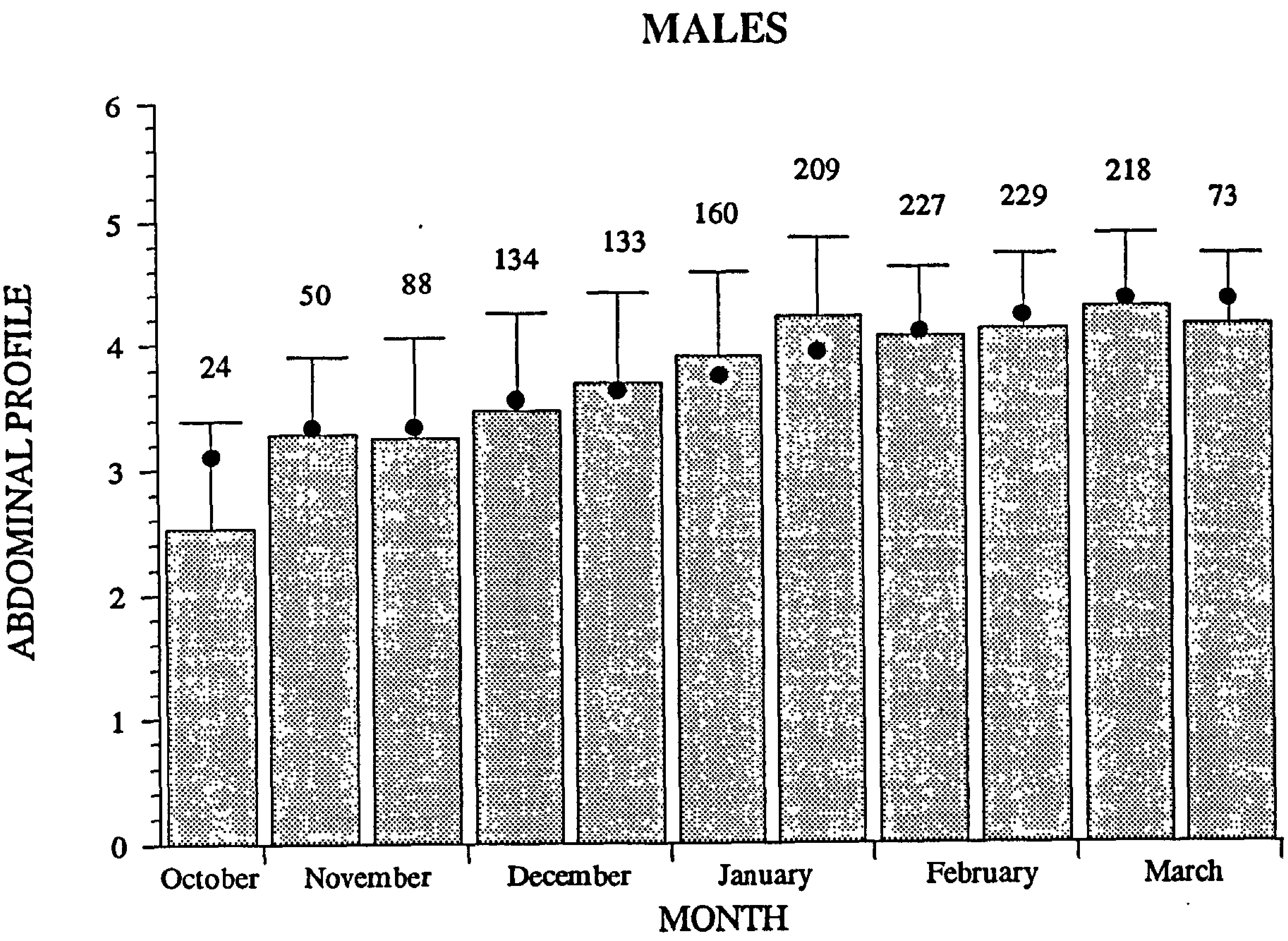
Fig. 2.7. Condition index values, mass/tarsus length, plotted against Abdominal profile. All data points plotted plus 95% confidence limits of the mean value for each profile score.

a) Males. $y = 47.17 + 3.17x$; $F = 7.69$, $P < 0.007$, $df = 67$



b) Females. $y = 35.7 + 4.90x$; $F = 20.88$, $P < 0.001$, $df = 57$





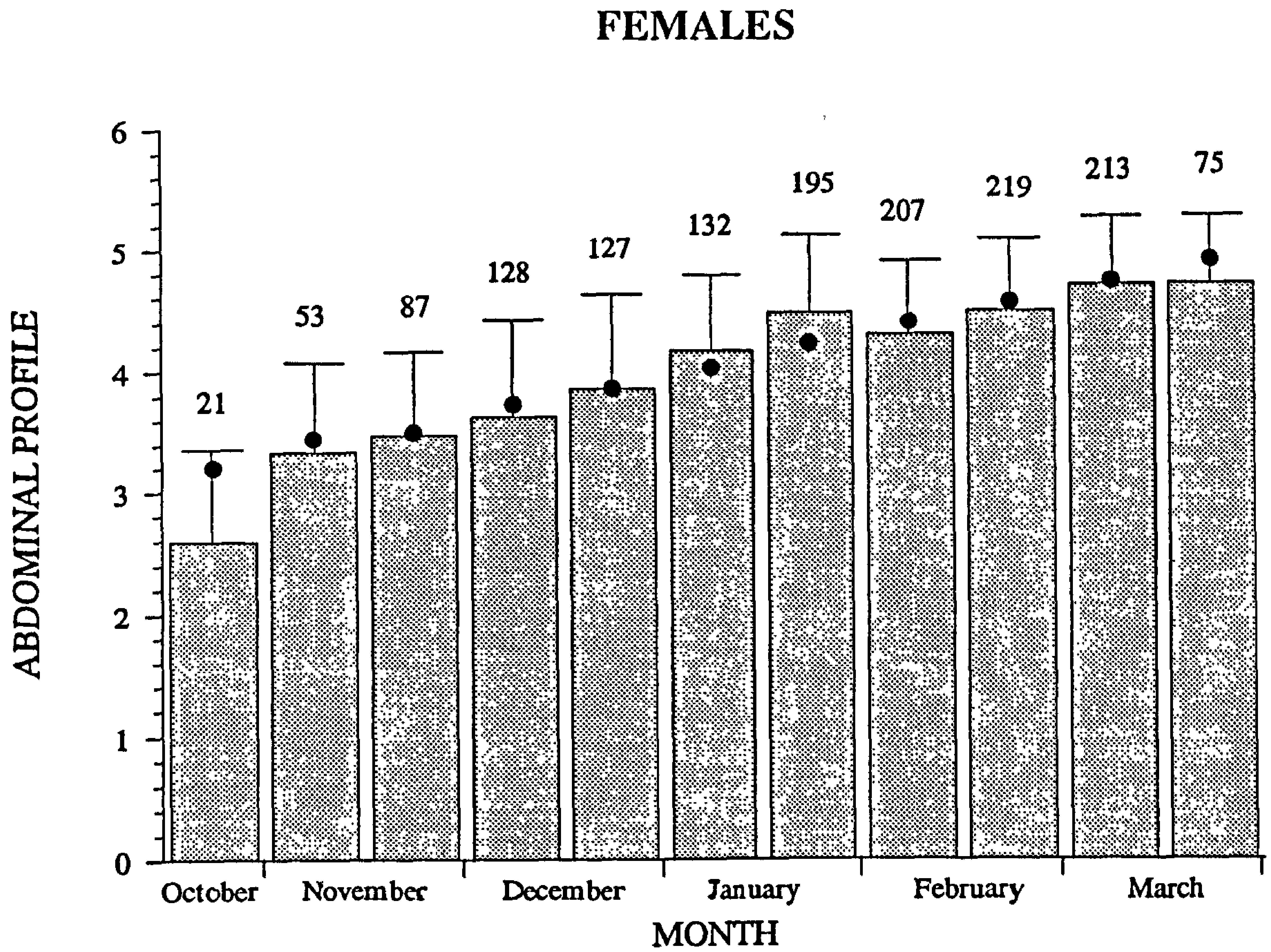
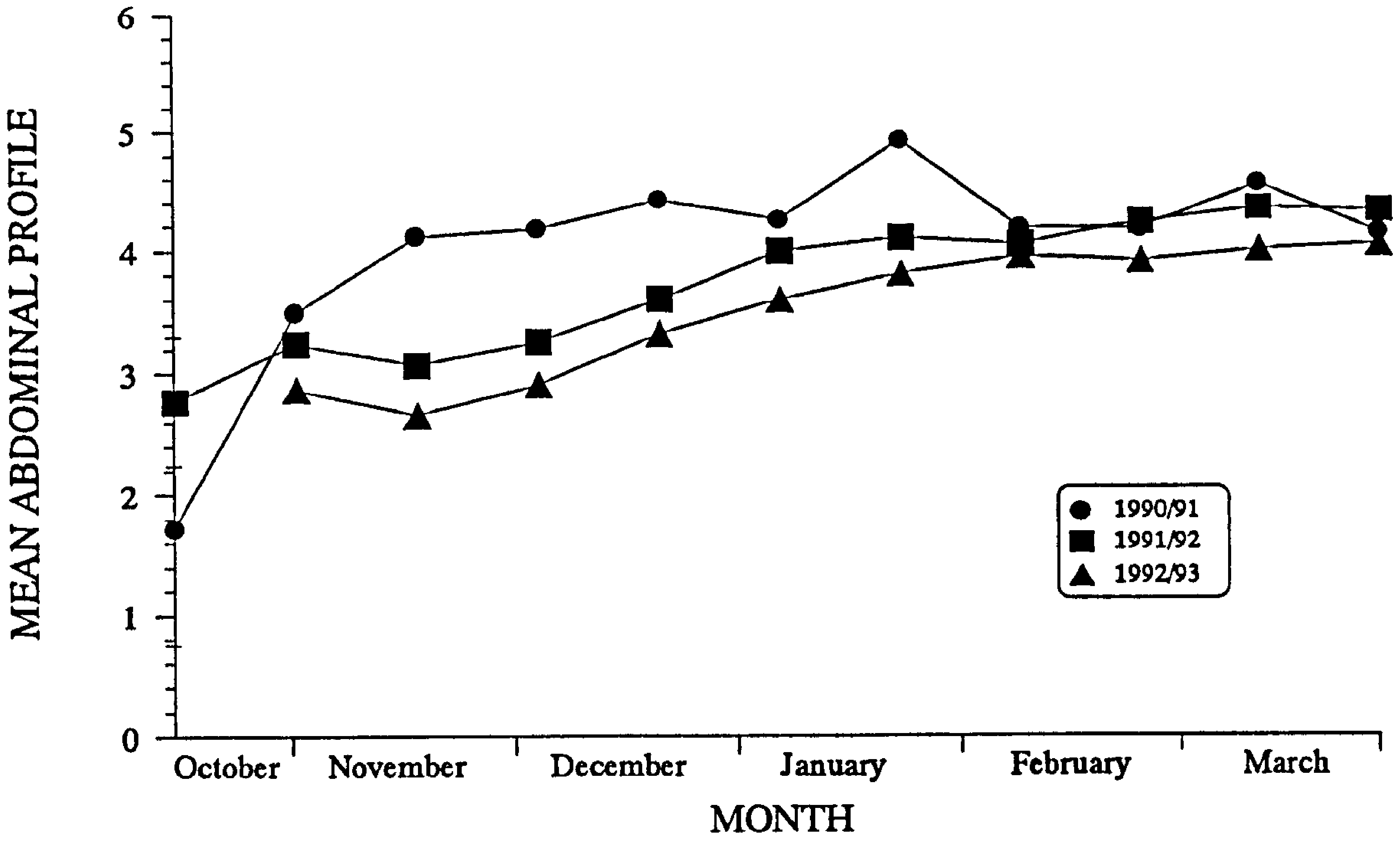


Fig. 2.8. Mean abdominal profile score for all winters combined (1990/91-1992/93) plotted by half-month (histogram plus SD), and the fitted values from a generalised linear model (see text). The number of different individuals involved in each half-month is given above each histogram.

MALES



FEMALES

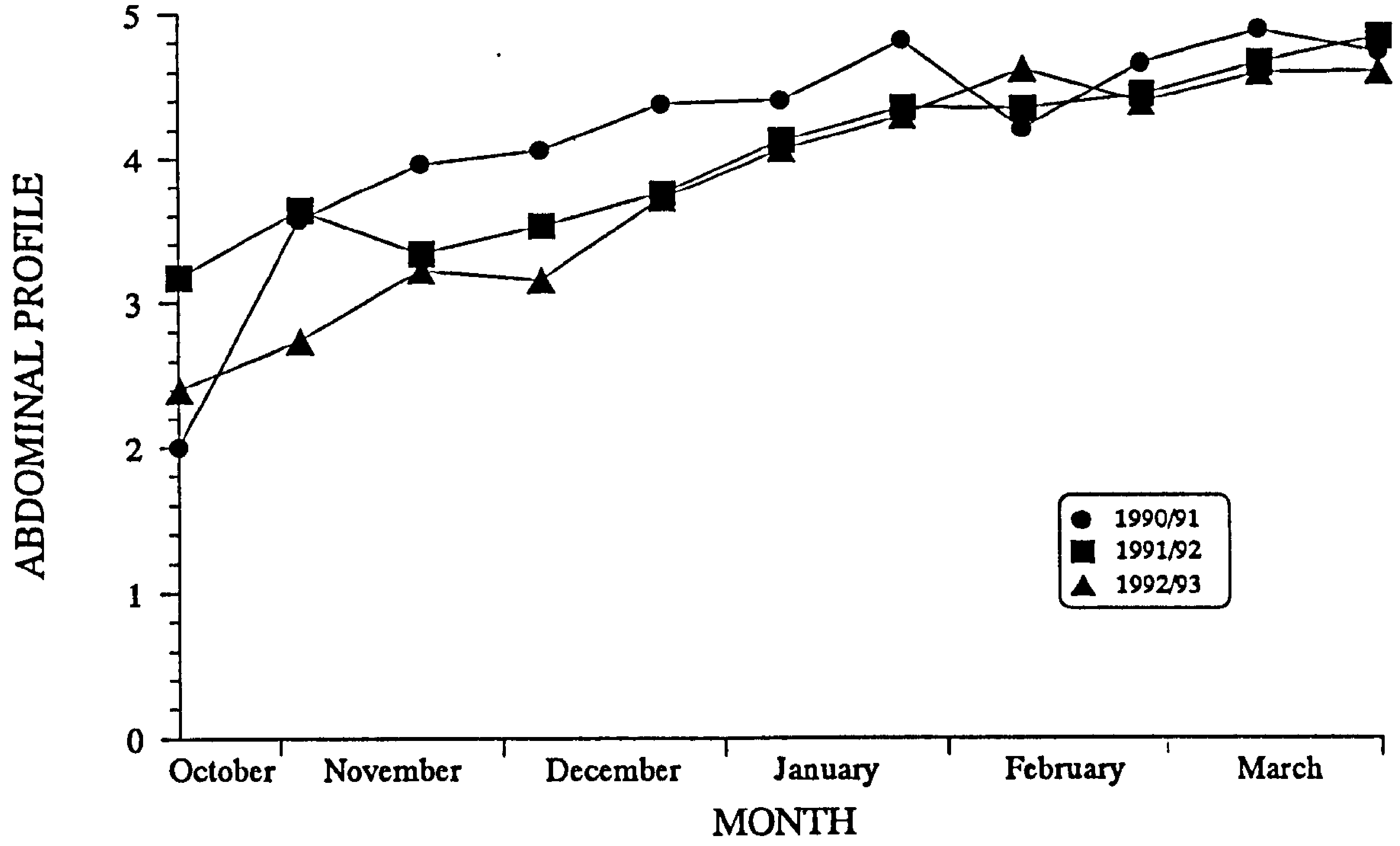


Fig. 2.9. Mean abdominal profile plotted by half-month for each winter (1990/91 - 1992/93) recorded for Bewick's Swans at Slimbridge, all classes combined. Sample sizes as follows: males: n = 396, 713, 434, females: n = 427, 626, 404 for the 1990/91, 1991/92 and 1992/93 winters respectively. Half-monthly means involving less than five birds have been omitted.

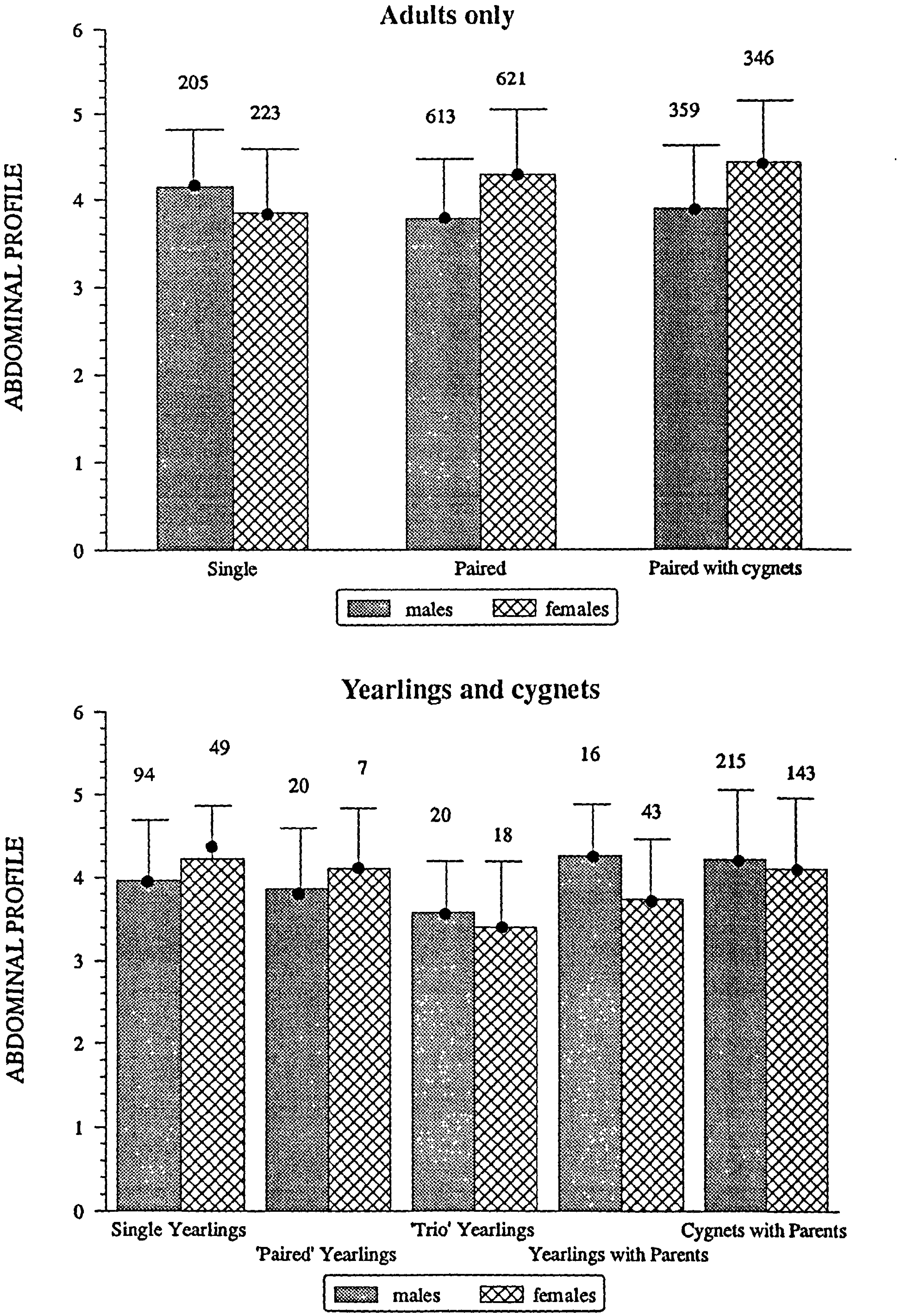


Fig. 2.10. Mean abdominal profile for each social class (histogram plus SD) and the fitted values derived from a linear model (see text). The number of individuals involved in each category is given above each histogram. Categories where APs were recorded for less than five individuals (i.e. single cygnets and adults associating with their parents) have been omitted.

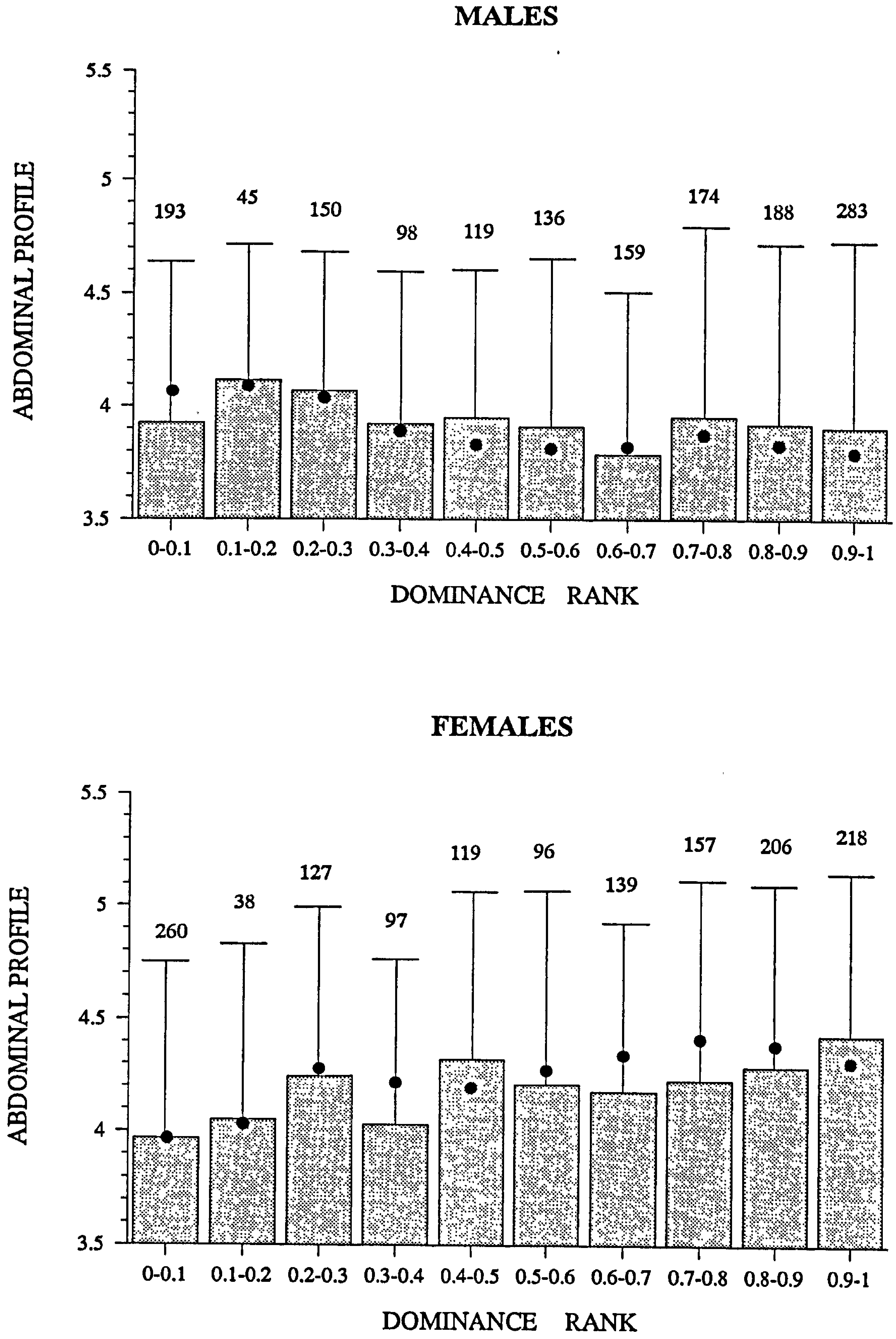


Fig. 2.11 Mean Abdominal Profile score plotted against dominance rank (histogram plus SD) and the fitted values from a linear model (see text). The number of individuals involved in each category is given above each histogram.

CHAPTER 3 ROOST-SITES: DISTRIBUTION AND FUNCTION

3.1 INTRODUCTION

Communal roosting has been documented amongst many species of social-feeding birds and its function has been investigated by several workers. Defence against predation has been suggested as an important role of communal roosts (Lack 1968), the cost of an increased likelihood of detection being overcome, either through an earlier detection of the predator by increased group vigilance ('many eyes' hypothesis, Pulliam 1973), or by a dilution or confusing effect (Hamilton 1971, Kenward 1978). Communal roosting amongst solitary feeders is rare however, and in the treecreepers Certhia sp. and the Northern Wren Troglodytes troglodytes is confined to periods of cold weather when clumping together enables the birds to conserve heat. Since these birds stop using communal roosts when the weather improves, it seems that there is no other advantage, and perhaps some disadvantage, for solitary feeders roosting communally (Zahavi 1971). Both wrens and treecreepers exhibit cryptic camouflage and generally secretive behaviour, in order to reduce predation levels when foraging alone. A number of anti-predator adaptations, including increased vigilance, more rapid transmission of alarm, reduced levels of intra-specific aggression and aerial evolutions, have been demonstrated in communal roosts but these may have evolved in response to increased predation associated with the congregation of large numbers of birds (Zahavi 1971). Species which roost communally also tend to feed socially. There are several possible explanations for this: 1) they use the same anti-predator mechanisms during the day and night, 2) there is only a limited suitable food supply within range of the roost, so all members use the same feeding sites 3) flocking behaviour increases foraging efficiency, as individuals increase their food intake rate through local enhancement around newly discovered food patches (Krebs & Davies 1987) 4) birds which are seeking information on patchy and localised food can more efficiently do so from a communal roost (Zahavi 1971). When the food supply deteriorates and its distribution becomes uneven, birds tend to form fewer and larger roosts (Ward & Zahavi 1973) which suggests the role of communal roosts in improving foraging ability. Birds may continue to use communal roosts when food supplies are plentiful however, and this may be a form of 'insurance' against the risk of losing a hitherto good feeding place. Birds losing a feeding place can immediately go to a new feeding place instead of searching at random over a large area (Ward & Zahavi 1973). Although both the quality and quantity of food at different sites will vary, not all members of a roost-group will feed at the 'best' site. The foraging performance of an individual will depend on the size, density and flock structure at each feeding site, which in turn will influence its decision of where to feed.

Ward (1965) suggested that for the Red-billed Quelea Quelea quelea communal roosts act as information centres, in which birds lacking a good feeding place follow out of the roost, in the morning, birds which know of good feeding sites; but could give no direct evidence to support this attractive hypothesis. The information-centre hypothesis has been investigated by several workers (Krebs 1974, Roell 1978, Loman & Tamm 1980, De Groot 1980, Ydenberg et al. 1983). For a critical review, see Rickner & Heeb (1995). De Groot (1980) working with weaverbirds in an indoor aviary, investigated the ability of individuals to find preferred resources. In one experiment he allowed each bird to visit just one of several food sources of variable quality. Although each bird had had experience with only one of the food sources, naive birds were able to go directly to the good food source after roosting with experienced birds. Barnacle Geese wintering in the Netherlands gather into smaller secondary roosts after they leave their main roosts but before dispersing to the feeding areas (Ydenberg et al. 1983). These post-roost gatherings acted as centres for dispersal to the feeding grounds and lay between the roost-sites and the feeding areas. Ydenberg et al. (1983), argued that because the gatherings increased in duration following late afternoon departures from the foraging grounds on the preceding day, and the probability of birds switching to a different feeding site also then subsequently increased, there was evidence to suggest that the post-roost gathering was acting as an information centre.

Bewick's Swans are social feeders, feeding together in groups both during the day and on moonlit nights. They also roost communally on or around the edges of areas of open water at night during winter. Birds from several feeding areas may converge at night at a given roost and be able to switch to another feeding site by following other birds out to the feeding grounds the following morning. There is thus an opportunity for an exchange of information concerning feeding areas, through clues either broadcast deliberately or given out involuntarily, by birds which have had varying degrees of success in foraging during the day. At Slimbridge there are no post-roost gatherings; swans generally fly directly from the roosts to the feeding sites. Levels of disturbance at the roost-sites are low however, and together with supplementary feeding, allow birds to stay at the roost well into the morning, providing ample time at the roost-site itself for information exchange to occur. Although food may not be limiting in the Slimbridge area in winter, it is certainly patchy in terms of both biomass and protein content on a spatial and temporal basis (Rees 1988 and data from this study) and therefore selection of a feeding site is likely to be important.

The current study aimed to investigate the factors affecting roost-site selection at Slimbridge on both a day-to-day and a seasonal basis by attempting to answer the following questions:

1) Do separate roost groups exist and if so, do the swans using different roosts differ in terms of social class, dominance rank, experience or condition, as assessed by abdominal profile.

2) Do birds differ in their fidelity to a particular roost site within a winter and is fidelity affected by social class, experience or condition. High-ranking swans might be expected to be more faithful to a roost-site than low-ranking singletons (Raveling 1969), since their rank may allow them access to the good and/or predictable resources. The presence of two distinct roosts allowed an investigation of the theory that roosts serve as centres for information exchange, by comparing the condition and feeding site selection of individuals which made use of both roost sites, with those of individuals which were more consistent in their choice of roost site. It should be noted however, that this investigation is difficult since the decision by an individual bird of where to roost could depend on both historical and contemporary factors.

3) Does parental roost site choice influence the roost site selection of their offspring when they return in subsequent years, as found in Canada Geese (Raveling 1979a).

4) Do changes in social status, including the acquisition, loss or change of mate, affect the roost site choice of swans between winters, and if so, does this reflect a drop in dominance rank or the loss of the effect of the partner's roost site preference.

5) Do birds from different roost sites differ in their use of feeding sites during the day.

3.2 METHODS

A total of nine different pens, each containing a pool and located within the enclosures of the WWT collection at Slimbridge were used as roosting sites by the swans during the course of the study. These included the Rushy Pen in front of the Director's House, and eight pens located within the "Grounds" of the collection: the Asian, European, Big, Tundra, African, Andean, North American and Hybrid pens (see Fig. 1.1). Small numbers of swans were also seen roosting occasionally at four other sites on the refuge; the New South Lake, the Long Ground Scrape, the South Finger and the River Severn itself. Swans using these alternative roost-sites could not be identified individually because they usually arrived well after dusk. However, use of these additional roosts was rare, and the small amount of data pertaining to these roost areas therefore was excluded from the analyses.

The number of Bewick's Swans roosting at Slimbridge was monitored each winter (1989/90 -1992/93) by making regular counts of the roost sites. Counts were conducted daily at the main roost on the Rushy Pen and three times a week at the "Grounds" roost-sites located within the main enclosures holding the Trust's collection of captive waterfowl. The counts in the "Grounds" were conducted either at dusk, or in the early morning prior to the birds' departure to the feeding areas. Counts of swans in the Rushy Pen were made both early in the morning and in the evening under floodlit conditions. Where more than one roost count was conducted per pen per night, the highest count was used for analysis. Checks of alternative roost-sites, known to be used occasionally by small groups of roosting swans, were made only once a week unless reported by another member of staff.

The identity of individual swans using each of the roost-sites was also recorded during the evening and early morning observations throughout the study period in order to establish patterns of roost usage by individual birds. Swan units which spent more than 50% of their roost-nights in the Rushy Pen during a winter were defined as Rushy Pen units; swan units which spent more than 50% of their roost-nights in the grounds were classified as Grounds units. This arbitrary cut-off point was used in order to classify all birds, including those which only appeared for a few days at the site, although a 75% cut-off point would have been adequate to classify the vast majority of birds.

In order to monitor the use made of feeding sites by swans from the two roost groups, all fields in the vicinity of Slimbridge were searched on a near-daily basis for swans during the study period (1989-90 to 1992-93 winters inclusive). Swan flocks encountered were counted and the identities of swan units within each flock recorded. The identities of all units could not always be ascertained, depending on conditions in the field, but efforts were made to identify as many swans as possible by a combination of leg-rings and/or bill patterns. On occasions when birds were known to be present at other more distant sites (e.g. Walmore Common, some 10.5 km NNE of The New Grounds and the Avon Meadows, some 40 km NE of the New Grounds), the numbers and identities of swans in these flocks were also checked. Orthogonal comparisons were conducted between fields within the MGLH module of the Systat statistical package. Effectively these are planned contrasts between fields which aimed to highlight differences and similarities in the numbers of swan units identified on different fields from the two roost groups.

3.3 RESULTS

a) Location of roost-sites and roost totals

The number of swans using each roost-site varied greatly both during the course of the winter and between winters (Fig. 3.1a-e) reflecting in part, variation in the total number of birds in the area. The Rushy Pen generally contained the largest number of roosting swans throughout the study period (mean roost total of nights when at least one swan was present at Slimbridge = 88.91), although on a few occasions the combined number roosting in the Grounds Pens was higher than the Rushy total, particularly when overall numbers at the site were low. The Asian Pen contained the largest number of roosting swans of the Grounds Pens (mean roost total of nights when at least one swan was present at Slimbridge = 13.39), followed by the European, Tundra, Big and African Pens (mean roost totals = 9.87, 5.93, 4.77 and 1.27 respectively). The Andean, Hybrid and North American pens all had mean roost totals of less than one swan.

Interchange of swan units between adjacent pens in the grounds was frequent. On windy evenings birds returning to roost in the grounds were observed to overshoot a particular pen on attempting to land and to end up in an adjacent pen. On such occasions members of family units could be located in different pens although the unit would normally regroup prior to roosting for the night. This interchange, together with the close proximity of the Grounds pens to each-other (see Fig. 1.1) promotes the lumping of data concerning all units roosting in the Grounds pens, hereafter referred to as the Grounds pens roost. Swan units which were recorded roosting on more than 50% of the nights that they were present at Slimbridge during the winter in the Grounds pens roost were classified as 'Grounds units', whilst units which were recorded roosting on more than 50% of the nights that were present at Slimbridge in the Rushy Pen were classified as 'Rushy Pen units'.

The proportion of swans roosting in the Grounds pens varied significantly between the four winters (see Fig 3.1, Chi-square test, $\underline{X}^2 = 35.55$, $\underline{P} < 0.001$, df = 3) but there was no obvious trend in the data during the study period.

b) Comparison of roost-groups

i) Unit proportions and family size

Chi-squared tests comparing the Rushy Pen and the Grounds roost-groups revealed that there were no significant differences in the proportion of singletons, pairs and families utilising the two roost areas (Table 3.1). Brood sizes recorded for families seen at the two roost-sites also did not differ significantly (Mann-Whitney U test, $W = 2333$, $P > 0.9$, $n = 102$ and 34, for the Rushy Pen roost and Grounds roost respectively).

ii) Dominance rank

A breakdown of the dominance rank of swans from the two roost-groups is given in Table 3.2. There was no significant difference in terms of dominance rank between the Rushy Pen and the Grounds roost-groups, for singletons, two-parent families or single-parent families. However pairs from the Grounds had significantly higher dominance ranks than those from the Rushy Pen (Table 3.2). There was a sufficient number of observations of aggressive encounters between units from the two roost-groups when they mixed in feeding flocks on the fields, in order to remove the possibility that birds in one roost-group were consistently more subordinate/dominant than those in the other.

iii) Experience

Experience was taken to be the number of winters that a given swan had previously been recorded at Slimbridge. For paired birds, including those with cygnets, the number of winters that the more experienced member of the pair had spent at Slimbridge was used in the analysis.

Swans roosting in the Rushy Pen had significantly more previous experience than those roosting in the Grounds (Table 3.3). There was no significant difference in experience between the two main roost groups for singletons, pairs or families when these classes were investigated separately, although the result for families approached significance (Table 3.3).

There was no difference in the proportion of 'new' swans to the site (i.e. swans which had not previously been identified at Slimbridge) recorded at the Rushy Pen and Grounds roosts

(Chi-square = 0.4, $P > 0.5$, df = 1, see Table 3.4). The proportion of new birds at the alternative roost-sites was significantly higher than in the two main roost-sites (Chi-square = 22.05, $P < 0.001$, df = 1); indeed only two (5.7%) of 35 units seen roosting outside the Rushy Pen/Grounds Pen roosts had been recorded at Slimbridge in previous winters (Table 3.4).

iv) Abdominal profile

Abdominal profiles of individual birds were recorded during the 1990/91 to 1992/93 winters inclusive (see Chapter 2). Swans roosting in the Rushy Pen had significantly higher APs than those roosting in the Grounds Pens, when data for all three winters were combined and the sexes treated separately (Table 3.5). The abdominal profile sample was biased, however, both in terms of number of records per year (Kruskal-Wallis Chisq. = 28.693, $P < 0.001$, df = 1) and social class (Kruskal-Wallis Chisq. = 47.728, $P < 0.001$, df = 1); but not in terms of month or dominance rank. The analyses therefore were repeated for each of the social classes; data for all three years were again combined since variation in AP score between years was not great (see Fig. 2.9). In general, birds from the Rushy Pen roost had higher AP scores than those from the Grounds roost with the exception of yearlings associating with their parents (Table 3.5). The differences were statistically significant for paired and single adult males, breeding and paired adult females, and for cygnets from families.

v) Roost-site fidelity

The swans roosting in the Grounds pens were present for a significantly greater number of roost-nights than those in the Rushy Pen when all data were treated together (Table 3.6). This relationship held true for the winters 1989/90, 1990/91 and 1991/92 but not 1992/93.

Swan units from the three main social classes were investigated separately. Both singletons and paired birds seen in the Grounds were present for a significantly greater number of roost-nights than swans from the same social classes seen in the Rushy Pen (Table 3.6). There was no significant difference between the number of roost-nights that families spent in the Grounds Pens and in the Rushy Pen. However, birds roosting in the Rushy Pen (mean = 94.78% roost nights in Rushy Pen) were significantly more faithful to their roost-site when present at Slimbridge than those in the Grounds (mean = 87.94%

of roost-nights in Grounds Pens, see Table 3.7). This relationship held true for singletons and pairs when these social classes were investigated separately, but not for families, although the result for families approached significance.

Data for the two roost-groups were combined to investigate fidelity to the primary roost-site by units from the three main social classes (Table 3.8). Singletons were significantly less faithful to their primary roost-site than both pairs and families (Kruskal-Wallis Chi-square approximation test (df = 1 for all comparisons), Chi-sq. = 42.40, $P < 0.001$, and Chi-sq. = 36.05, $P < 0.001$, respectively). There was no significant difference in fidelity to the primary roost-site between pairs and families (Chi-sq. = 0.66, $P > 0.4$).

There was no significant correlation between roost-site fidelity, measured as the percentage of roost-nights each swan unit was present at its primary roost, and the experience of the unit (Spearman's rank correlation $r_s = -0.045$, $P > 0.1$, $n = 757$ for the Rushy Pen and $r_s = -0.044$, $P > 0.1$, $n = 253$ for the Grounds Pens). Similarly there was no significant correlation between experience and roost-site fidelity when data for the two main roost-groups were lumped together and the three main social classes treated separately (Spearman's rank correlations, $r_s = -0.042$, $P > 0.1$, $n = 644$ for singletons; $r_s = 0.025$, $P > 0.1$, $n = 230$ for pairs and $r_s = -0.058$, $P > 0.1$, $n = 136$ for families).

c) Roost-site selection

i) Roost-site change within a season

Although roost-site interchange within a season between individual pens in the Grounds roost area was frequent, interchange between the Grounds roost and the geographically distinct Rushy Pen roost was comparatively rare. For example during the 1992/93 winter a Grounds pair named Striker and Melba were recorded on 24 nights in the Asian Pen, 16 nights in the Tundra Pen and 3 nights in the European Pen, but only once on the Rushy Pen during their stay of 119 days at Slimbridge. The identity and number of anomalous units (i.e Grounds units present at the Rushy Pen roost, and Rushy Pen units at the Grounds roost) were recorded on all nights when the roost-sites were monitored and subsequently analyzed with respect to 1) date in season 2) total number of swans roosting at Slimbridge and 3) the percentage of Grounds units present in the roost total at Slimbridge.

1) Grounds units in the Rushy Pen

A total of 156 different Grounds units were observed roosting in the Rushy Pen on one or more occasions during the study period. The number of Grounds units present each night varied widely from 0 to a maximum of 26 on 16.03.93, with a mean value of 2.523 (n = 499, SD = 3.728). The number of units present correlated significantly with half-month (Spearman's rank correlation, r_s = 0.440, P < 0.01, n = 499), with the number of units steadily increasing through the winter to a peak in late-March immediately prior to departure (see Fig 3.2a). The number of Grounds units seen in the Rushy Pen also correlated positively with both the number of birds in the Rushy Pen roost and the total number of birds roosting at Slimbridge. There was also an inverse relationship between the number of Grounds units seen roosting in the Rushy Pen and the percentage of all birds present at Slimbridge seen roosting in the Grounds (Table 3.9).

In order to investigate the reasons for the presence of Grounds units in the Rushy Pen roost, linear regressions were conducted to explore the following hypotheses:
i) The number of Grounds units in the Rushy Pen was related to the total number of swans roosting at Slimbridge.
ii) The number of Grounds units in the Rushy Pen was related to the number of swans in the Rushy Pen roost.
iii) The number of Grounds units in the Rushy Pen was related to the number of swans in the Grounds roost.
iv) The number of Grounds units in the Rushy Pen was related to the percentage of Grounds birds in the total roost.
Linear regressions conducted on the number of Grounds units observed roosting in the Rushy Pen revealed that only 3.7% of the variance in the dependent variable could be explained by the total number of birds roosting at Slimbridge (F = 12.49, P = <0.001, df = 330). In addition only 5.9% of the variance could be explained by the total number of birds in the Rushy Pen (F = 30.06, P < 0.001, df = 482) and 2.2% by the total number of birds in the Grounds Pen (F = 7.70, P = 0.006, df = 337). However 12.5% of the variance in the dependent variable could be explained by the percentage of Grounds birds in the total roost (F = 47.20, P < 0.001, df = 330).

2) Rushy Pen units in the Grounds

A total of 81 different Rushy Pen units were observed on occasion to roost in the Grounds

Pens during the study period. The number of Rushy Pen units present each night ranged from none to a maximum of ten on 25.11.91, with a mean value of 1.537 (n = 369, SD = 2.135). The number of units present was significantly negatively correlated with half-month (Spearman's rank correlation, $r_s = -0.103$, $P < 0.05$, $n = 369$) with the number of units generally decreasing through the winter from a peak in the second half of November (see Fig 3.2b). Numbers during the arrival period in October-early November were lower. The number of Rushy Pen units in the Grounds was also positively correlated with the number of birds in the Grounds roost, the number of birds in the Rushy Pen roost, the total number of birds roosting at Slimbridge and the percentage of all birds present at Slimbridge seen roosting in the Grounds (Table 3.9). In order to investigate the reasons for the presence of Grounds units in the Rushy Pen roost, linear regressions were conducted to explore the hypotheses set out previously.

Linear regressions conducted on the number of Rushy Pen units observed roosting in the Grounds Pens revealed that 23.6% of the variance in the dependent variable could be explained by the total number of birds roosting at Slimbridge ($F = 98.64$, $P < 0.001$, df = 320). In addition 14.2% of the variance could be explained by the total number of birds in the Rushy Pen ($F = 58.94$, $P < 0.001$, df = 356) and 24.9% by the total number of birds in the Grounds Pen ($F = 107.89$, $P < 0.001$, df = 327), although these two measures were closely correlated with the total number of swans roosting at Slimbridge. Less than 0.1% of the variance in the dependent variable could be explained by the percentage of Grounds birds in the total roost ($F = 0.14$, $P = 0.705$, df = 320).

ii) Comparison of mobile versus immobile units

A comparison of the swan units that did, on occasion, roost at a secondary roost with those that did not, might indicate possible reasons for such movements.

Unit proportions. Chi-square tests revealed that amongst Grounds units observed roosting in the Rushy Pen there were significantly more pairs and significantly fewer singletons than expected (Table 3.10a). There was no difference in the proportion of Grounds families that did and did not roost in the Rushy Pen. There were no significant differences in the proportion of Rushy Pen units that occasionally roosted in the Grounds Pens compared with those that did not, for each of the three main social classes (Table 3.10b).

Experience. Grounds units observed roosting in the Rushy Pen had significantly more previous experience of Slimbridge (in winters spent at the site) than those that were not observed on the Rushy Pen (Table 3.11a). When investigated by class this relationship remained significant for singletons and near significant for families. There was no significant difference in the experience of pairs that did or did not roost in the Rushy Pen. However, previous experience of Slimbridge did not affect the number of Rushy Pen units seen roosting occasionally in the Grounds Pens (Table 3.11b). Similarly there were no differences between the two groups when the three social classes were investigated separately.

Abdominal Profiles. Only data for the month of February were used for the analysis of Grounds birds using the Rushy Pen since high numbers of Grounds birds visited the Rushy Pen during February, and most of the birds did not leave on spring migration until March. The average abdominal profile score (mean of the two half-monthly medians calculated earlier - see Chapter 2) for February was calculated for each bird and the birds were then placed into one of three categories:

1) Grounds birds observed roosting in the Rushy Pen during the month
2) Grounds birds not observed roosting in the Rushy Pen during the month
3) Rushy Pen birds

Grounds birds observed roosting in the Rushy Pen had lower abdominal profile scores than Grounds birds that did not roost on the Rushy Pen in all the sex and class categories considered except for adult males with cygnets (Table 3.12a). Sample sizes were small, however, and only amongst cygnets did the low profiles for the Grounds birds that switched roost sites prove significant. Grounds birds roosting in the Rushy Pen also had lower abdominal profiles than the Rushy Pen birds themselves for all categories considered, but again this proved significant only for cygnets.

Only data for the month of November were used for the analysis of Rushy Pen birds using the Grounds since Rushy Pen birds visited the Grounds pens most frequently during this month. The average abdominal profile score (mean of the two half-monthly medians calculated earlier - see Chapter 2) for November was calculated for each bird and the birds were then placed into one of three categories:

1) Rushy Pen birds observed roosting in the Grounds Pens during the month
2) Rushy Pen birds not observed roosting in the Grounds Pens during the month
3) Grounds birds

There were no significant differences between the abdominal profiles of Rushy Pen birds observed roosting in the Grounds and those of Rushy Pen birds that did not roost in the Grounds in any of the categories considered (Table 3.12b). Rushy Pen birds occasionally seen roosting in the Grounds had lower abdominal profiles than the Grounds birds themselves in some categories, but not in others (see Table 3.12b). Amongst paired females (without cygnets) the profile scores of Rushy Pen birds which occasionally roosted in the Grounds were significantly higher than those of the Grounds birds.

iii) Roost-site choice in relation to parental roost use

Cygnets generally stay with their parents throughout the first winter (Evans 1979b). Lone cygnets do occur; six were recorded during the study period (1.9% of all cygnets seen). These had presumably become lost from their parents during autumn migration. Roost-site choice of cygnets arriving at Slimbridge for the first time therefore is dictated mainly by parental roost-site preference. Birds returning in their second year (i.e. as yearlings), can act independently of their parents although associations between parents and their year-old offspring are frequent (42 cases during the study period). Some offspring continue to associate with their parents over several years; 23 swans associated with their parents in their third year during the study period. Some birds returning in their fourth winter (i.e. three years old) arrived with a mate. As change in social status may influence roost-site choice, only the roost use of birds in their second and third winters was investigated. All data concerning birds observed during the study period (1989-90 to 1992-93 winters inclusive) were used for this analysis, including data from earlier years for swans of known parentage, in order to improve sample size.

1) Second winter

Of 63 birds of known parentage, observed during the study period which had returned to Slimbridge in their second winter, 43 associated with their parents and the other 20 were unattached (data concerning birds whose parents did not return to Slimbridge were omitted from this analysis). A further 20 birds, known to still be alive, wintered without their parents at alternative sites (see Table 3.13a). All but one of the yearlings returning to Slimbridge frequented the same primary roost-site that they had used in the previous season. There was no difference between yearlings associating with their parents and those that did not do so, in the likelihood of their returning to the same primary roost-site used in the previous winter (Chisq. = 0.48, $\underline{P} > 0.4$, df = 1). Indeed, the only bird to change its primary roost-site between its first and second years was associating with its parents, which had also switched roost-site.

2) Third winter

Of 50 birds of known parentage, which had returned to Slimbridge in their third winter, 23 associated with their parents and 27 were unattached (data concerning birds whose parents did not return to Slimbridge were again omitted from this analysis). A further 15 birds, wintered at alternative sites without their parents (see Table 3.13b). All but two of the birds returning to Slimbridge used the same primary roost-site in their first and third winters. There was no difference between birds associating and not associating with their parents in the likelihood of their frequenting the primary roost-site used in their first winter (Chisq. = 1.77, $\underline{P} > 0.1$, df = 1).

iv) In relation to change in social status

The effect of a change in social status upon roost-site choice was investigated by summarising the roost data for each unit in each winter of the study period. This was taken as the proportion of nights on which a given swan unit was identified on the Rushy Pen in relation to the total number of nights that the unit was known to be roosting at Slimbridge, to give an index of fidelity to the Rushy Pen roost. All birds, from any social class, that visited Slimbridge for a minimum of five days during a winter, and for at least two winters running, were included in the analysis. Data concerning units that spent two or more consecutive winters away from Slimbridge were excluded as their social status during their absence was not known.

Variation in the roost use index between seasons (calculated by subtracting one index from the other) was calculated for the most experienced member of each unit only, in order to avoid duplicating data for paired birds. Pair formation in Bewick's Swans is thought to occur in the spring at the start of the breeding season (Scott 1978b). Of the 49 cases of pairing or re-pairing included in this study just two (4.1%) involved the pairing of birds that had previously visited Slimbridge independently of each other. Roost-use indices calculated for members of these two pairs, both before pairing and during the first year of the pair bond, were included in the analysis. Change in roost use was analyzed in relation to paired status, classified according to whether:

1) a bird arrived with a new mate

2) a bird did not arrive with a new mate and their was no change in its social status (i.e. remained single / paired to the same mate)

3) a bird arrived alone, having lost its mate since leaving Slimbridge at the end of the previous season.

A provisional analysis of all the data revealed significant differences in roost-site change between the three groups described above, indicating that a change or acquisition of a mate affects roost-site selection. There were significant differences between the two main roost-groups in the change in roost-site indices recorded for all three categories, however (Table 3.14), so the analysis was re-run for the two roost groups separately to clarify the situation. Amongst birds from the Grounds roost, birds arriving with a new mate exhibited a significantly higher change in roost-site use than those arriving with no change in social status (Mann-Whitney U test, $\underline{W} = 4389$, $\underline{P} < 0.001$, $n = 35$ and 260 respectively). There were near- significant differences between birds arriving with a new mate and birds arriving alone without their mate of the previous season ($\underline{W} = 238$, $\underline{P} < 0.07$, $\underline{n} = 35$ and 30 respectively); and between birds with no change in social status and birds arriving alone without their mate of the previous season ($\underline{W} = 4508$, $\underline{P} < 0.06$, $\underline{n} = 260$ and 30 respectively). There was no significant difference between the sexes in the change in roost-site use for swans arriving with a new mate, or between males and females arriving alone without their mate of the previous season (Table 3.15).

Amongst birds from the Rushy Pen roost there were no significant differences between any of the three groups although a trend was suggested that birds arriving with a new mate exhibited a larger change in roost-use than those arriving with no change in social status ($\underline{W} = 37708$, $\underline{P} < 0.1$, $\underline{n} = 15$ and 91 respectively). In addition there was no significant difference in the change in roost-site use between males and females arriving with a new mate, or between males and females arriving alone without their mate of the previous season (Table 3.15).

When only those birds recorded with a mate were considered (i.e. excluding singletons that had never paired) the differences between the groups became more significant (see Table 3.16). Amongst units from the Grounds roost, birds arriving as singletons, having lost their mate of the previous season, exhibited a significantly larger change in roost-use than those arriving with no change in social status.

d) Field-site choice in relation to roost-group

Two of the swans' feeding sites were some distance from Slimbridge: Walmore Common (10.5 km) and the Avon meadows at Bredon's Hardwicke (c40 km, see Fig. 3.3). The remaining 19 fields were all within 2000 m of the roost-sites at Slimbridge (see Fig 3.4). Additional fields in the area, both on and off the reserve, were used on occasion by small numbers of swans. The identity of swans feeding at these alternative sites was not recorded, either because close approach was difficult and liable to cause undue disturbance to the swans and other wildfowl on the reserve, or because the birds used the field very briefly and there was insufficient time to record ring numbers or bill patterns.

Swans identified at Slimbridge were also recorded on 21 different fields in the Slimbridge area during the course of the study (Table 3.17). They also dispersed over 13 different fields at Walmore Common, but these data were lumped together owing to the mobile nature of the swans on the common. Birds frequently moved between adjacent fields on the common during the course of a day, and in addition the availability of grazing on the fields at the site was strongly affected by flood conditions (see Chapter 4). During flood conditions swan could move between fields by swimming, without the need for flight, since the fences separating the fields were frequently under water.

The percentage of swans identified in the feeding flocks ranged from 4 to 100%. The mean percentage of swans identified amongst the 612 feeding flocks investigated was 68.35%, pertaining to 7455 swan units observations (2443 Grounds units, 5012 Rushy Pen units). Lowest identification rates were on large fields where it was difficult to approach the birds such as JB's field (36.68%) and the Canal fields (37.44%). Highest identification rates of swans were in fields adjacent to hides on the Slimbridge reserve such as the Top New Piece (81.93%) and the Tack Piece (76.44%), and on the River Severn (97.50%) since birds using the river could be identified as they returned to the pens at the end of the day (see Table 3.17). There was no evidence of a bias towards the identification of ringed birds (predominantly from the Rushy Pen) in the feeding flocks; indeed there was a bias towards the identification of the largely unringed Grounds birds (Table 3.18). There were no significant correlations between the percentage of birds identified from the two roost groups and month, or between the percentage of birds identified from the two roost-groups and time of day (Table 3.18). The percentage of birds identified from the two roost groups did correlate with the total number of birds in the flock however; the percentage of Grounds units significantly decreased as flock size increased while the percentage of Rushy Pen units significantly increased as flock size increased (Table 3.18). This may be because there were fewer Grounds units than Rushy Pen units, and Grounds units were therefore less likely to form a high proportion of large flocks.

Since the swan units were identified in the fields, the use of the fields by swans from the two roost groups could be investigated in order to see if there were any differences in their use of the feeding sites. Feeding site choice by birds from the two roost groups, with respect to social and habitat variables will be investigated in Chapter 4. Data recorded for three fields on the south side of the Gloucester-Sharpness canal (collectively known as the "Canal fields") were combined for the analysis, since swans were observed to move readily between them during the course of a day and the sample size for each of the fields was small. Moreover there were no significant differences in terms of the proportion of units identified from the two roost groups between the three fields (Mann-Whitney U tests, $\underline{P} > 0.288$, df = 1, in all cases). Otherwise the fields used by the swans (Fig. 3.4) were treated as separate feeding sites.

The number of units from the two roost groups identified in each flock were investigated separately. The count data were transformed for analysis since Bartlett's tests revealed heterogeneity in the group variances for swans from both roost-sites. Heterogeneity in the group variances were reduced by the transformation $x^1 = \log (x + 1)$. Three of the field sites on which feeding flocks were recorded were omitted from analysis (the Avon Meadows, Tin Shed and South-east road field) as the sample sizes were low ($n < 5$ for all three sites) and there was no variance in the number of units identified for at least one of the roost groups.

i) Grounds Pen units.

An analysis of variance, using field identity as a categorical variable, revealed that 27.4% of the variance in the transformed number of Grounds units identified in feeding groups could be accounted for by the fields alone ($\underline{F}$-ratio = 14.82, $\underline{P} < 0.001$, $\underline{n} = 604$).

Orthogonal comparisons highlighted significant differences, in terms of the number of Grounds units identified, between logically selected suites of feeding sites (Fig. 3.5, df = 1 in all cases). Walmore Common was significantly different from the 15 sites lying less than 2000 m from the Grounds roost ($\underline{F} = 23.18$, $\underline{P} < 0.001$) and the isolated Fifty acre field was significantly different from the remaining 14 sites ($F = 29.51$, $P < 0.001$). Of the remaining 14 sites, the ten managed by WWT did not differ significantly from the four fields not managed by WWT although a trend was suggested ($F = 3.25$, $P < 0.08$). Of the four fields not managed by WWT, the two fields situated on the low-lying 'Moors' were significantly different from the two located on higher, well-drained land in terms of the number of Grounds Pen units seen at each site ($F = 17.02$, $P < 0.001$). The two Moors fields also differed from each-other ($F = 4.47$, $P < 0.05$) but the two well-drained fields did not do so ($F = 1.82$, $P > 0.1$). Of the ten remaining sites managed by WWT, the seven lying close to the Grounds roost (< 600 m) were significantly different from the three more distant (>600 m) sites ($F = 3.90$, $P < 0.05$); the River Severn site was not significantly different from the two remaining WWT managed, more distant fields, although a trend was suggested ($F = 3.19$, $P < 0.08$) and the two remaining more distant, WWT managed fields were not significantly different from each-other ($F = 0.96$, $P > 0.3$). Of the remaining seven WWT managed sites lying close to the Grounds roost, the four containing permanent water-filled scrapes were significantly different from the three that did not contain scrapes ($F = 8.21$, $P < 0.005$); of the three fields without scrapes, the two lying south of the entrance road to WWT were not significantly different from the field lying to the north although a trend was suggested ($F = 3.28$, $P < 0.08$) and the two lying south of the road were not significantly different from each-other ($F = 1.68$, $P > 0.19$). Of the four sites containing scrapes lying close to the grounds roost, the one tidally inundated site (the Dumbles) was significantly different from the three non-tidally inundated sites ($F = 67.49$, $P < 0.001$); the site lacking grass pasture (the Long ground) was significantly different from the remaining two pasture fields ($F = 27.51$, $P < 0.001$) which in turn were significantly different from each-other ($F = 10.58$, $P < 0.001$).

ii) Rushy Pen units.

An analysis of variance, using field identity as a categorical variable revealed that 36.8% of the variance in the transformed number of Rushy Pen units identified in feeding groups could be accounted for by the fields alone (F-ratio $= 11.25$, $P < 0.001$, $n = 604$).

Orthogonal comparisons highlighted significant differences, in terms of the number of Rushy Pen units identified, between logically selected suites of feeding sites (Fig. 3.6, df = 1 in all cases). Walmore Common was significantly different from the 15 sites lying less than 2000 m from the Rushy Pen roost ($F = 11.25$, $P < 0.001$). The isolated Fifty acre field was not significantly different from the remaining 14 sites ($F = 2.70$, $P > 0.1$) and was therefore retained for inclusion in further analyses. Of the 15 sites lying within 2000 m of the Rushy Pen, the eleven managed by WWT were significantly different from the four fields not managed by WWT ($F = 4.68$, $P < 0.05$). Of the four fields not managed by WWT, the two low-lying 'Moors' fields were not significantly different from the two located on higher, better-drained land ($F = 1.78$, $P > 0.15$). The two Moors fields did not differ significantly from each-other ($F = 0.09$, $P > 0.7$) but the two better-drained fields were statistically different from each-other ($F = 11.72$, $P < 0.001$). Of the eleven remaining sites managed by WWT, the five lying close to the Rushy Pen roost (< 600 m) did not differ from the six more distant (> 600 m) sites ($F = 0.41$, $P > 0.5$). The River Severn site differed significantly from the five remaining WWT managed, more distant fields, ($F = 5.14$, $P < 0.025$). The two more distant fields containing permanent water-filled scrapes differed significantly from the three that did not contain scrapes ($F = 7.26$, $P < 0.01$). The two more distant fields with scrapes differed significantly from each-other ($F = 7.16$, $P < 0.01$). Of the three more distant fields without scrapes, the two pasture fields differed significantly from the sugar-beet (Seventeen-acre) field ($F = 6.63$, $P < 0.01$) and the two remaining pasture fields differed significantly from each-other ($F = 5.25$, $P < 0.025$). Of the remaining five WWT managed sites lying close to the Rushy Pen roost, the three containing permanent water-filled scrapes did not differ from the two that did not contain scrapes ($F = 0.11$, $P > 0.7$) and the two fields without scrapes did not differ from each-other, although a trend was suggested ($F = 3.28$, $P < 0.08$). Of the three remaining sites containing scrapes lying close to the Rushy Pen roost, the site lacking field grazing (the Long ground) was significantly different from the remaining two fields ($F = 29.11$, $P < 0.001$) which did not differ from each-other ($F = 2.73$, $P > 0.1$).

iii) Relative field use by the two roost-groups.

The proportion of birds identified in the feeding flocks which were Grounds Pen units, varied between 0 and 100%, and the overall field means for the study period between 2.78% (SE road field) and 91.69% (Long Ground, see Table 3.19). The proportion of Rushy Pen units identified in the feeding flocks varied between 0 and 100%, and the overall field means between 8.31% (Long Ground) and 97.22% (SE road field).

Chi-square tests were used to determine whether the occurrence of swan units from the two main roost-groups on each field differed significantly from each other, in comparison with the numbers seen at all other fields in the vicinity (Table 3.19). The Avon Meadows were excluded from this and further analyses because of the small number of observations made at this site ($n = 1$). There was a significant difference in the proportion of swans units identified from the two roost-groups on all but three of the 18 field-sites considered, namely the North Middle road field, the Tin Shed Ground and the River Severn. There were significantly more Grounds Pen units than expected on the Long Ground, New South Lake field, Pylon Field, Moors field B, South Middle Field, South Middle Extension and Top New Piece. There were significantly more Rushy Pen units than expected on the 17-acre field, the canal fields, the Dumbles, the Fifty-acre, JB's field, the North middle road field, the South-east road field, the Tack Piece and Walmore Common.

iv) Distance from roost-site

The distance of each field utilised by the swans during the study from the roosting sites was measured simply on the OS map from the central point of the field to the central point of the Grounds and Rushy Pen roost areas (see Table 3.20). There was no significant correlation between distance from each roost and the proportion of swan units from the two roost-sites when all fields (except the Avon Meadows) were considered.

The analysis was re-run omitting Walmore Common because it was known that the majority of the swans also roosted at Walmore when feeding on the Common. There was a significant negative correlation between distance from the Grounds roost and the percentage of Grounds units identified on the fields when data from Walmore Common were omitted from the analysis (Spearman's rank correlation $\underline{r}_s = -0.507$, $\underline{P} < 0.05$, $\underline{n} = 18$, see Fig. 3.7), although the suggested positive relationship between distance from the Rushy Pen and the percentage of Rushy Pen units identified on the fields was not statistically significant ($\underline{r}_s = 0.255$, $\underline{P} > 0.1$, $\underline{n} = 18$, see Fig. 3.8).

v) Field selection by anomalous roost units

Feeding site selection by swans in relation to roost-group membership, was also investigated by locating units on the feeding grounds which had spent the previous night in the roost group of which they were not normally members.

During the study, a total of 237 Grounds units and 131 Rushy Pen units were located at a feeding site, having spent the previous night at the 'wrong' roost-site. In order to investigate the true composition of the feeding flocks joined by these units, the anomalous units were not included when calculating the number of units identified on the fields from the two roost-groups. The roost-group composition of feeding flocks that were joined by birds which had roosted at the wrong roost-site during the previous night was significantly different to the composition of flocks not joined by these anomalous units when all feeding flocks were considered (Table 3.21). There were significantly more Rushy Pen units and significantly fewer Grounds units than expected present in feeding flocks joined by Grounds birds which had roosted in the Rushy Pen, and significantly fewer Rushy Pen units and significantly more Grounds units than expected present in feeding flocks joined by Rushy Pen birds which had roosted in the Grounds.

Moreover, the number of Grounds units that had roosted in the Rushy Pen during the previous night, and which were recorded in the fields, was positively correlated with the percentage of Rushy Pen units identified and negatively correlated with the percentage of Grounds units identified in the feeding flocks (Table 3.22). Similarly, the number of Rushy Pen units that had roosted in the Grounds during the previous night and which were recorded in the fields, also correlated positively with the percentage of Grounds units identified and negatively with the percentage of Rushy Pen units identified in the feeding flocks (Table 3.22).

3.4 DISCUSSION

The two main Slimbridge roosts, although differing in size, were very similar to each other in terms of composition. There were no significant differences in social structure between the birds using the two roosts and there was no difference in the likelihood of a new swan unit arriving at Slimbridge for the first time joining either roost group. The much smaller peripheral group of swans roosting on the scrapes, where supplementary feeding did not occur, was composed almost entirely of birds with no previous experience of the site. The Rushy Pen units were more experienced than Grounds units in terms of the number of winters that they had previously visited Slimbridge, but this relationship was restricted to families. This may be due to the family class including a higher proportion of the oldest and most experienced birds, many of which were roosting on the Rushy Pen before the Grounds roost became established. It is possible that the initial movement of birds to the Grounds roost in the late 1970's involved less successful and less experienced paired birds.

Dominance rank similarly did not differ between swans from the two roost groups, except amongst pairs without cygnets, which were of significantly lower rank in the Rushy Pen roost. This difference may be important since it suggests that amongst pairs of higher rank, those in the Grounds roost might be less likely to return to Slimbridge with cygnets than those in the Rushy Pen. Since the abdominal profiles of paired females both with and without cygnets, and of paired males without cygnets, was significantly lower in the Grounds roost than in the Rushy Pen roost, there is a clear indication that Grounds pairs are in poorer body condition than Rushy Pen pairs. In addition both single males and cygnets from families achieved lower AP scores in the Grounds roost than in the Rushy Pen roost. Only yearlings still associating with their parents had significantly higher AP scores in the Grounds roost than in the Rushy Pen. The question therefore arises of why any units roost in the Grounds. Clearly there must be some benefits to the swans in doing so, and these will be investigated in the following chapters. One benefit may be reduced levels of aggressive interaction at the roost caused by the presence of related birds, since the roost-site choice of former offspring is dictated by that of their parents. This seems likely, since the frequency of aggressive encounters at the feeding sites was influenced by the relative proportions of birds from the two roost-groups present, with significantly fewer interactions amongst flocks composed largely of birds from the Grounds roost (see Chapter 5). This concurs with D'Eath (1995, in litt.) who showed that domestic hens *Gallus domesticus* more readily approached, and began feeding, near a flockmate, than near an unfamiliar conspecific. Unfortunately, because only a small number of swans returning to Slimbridge were ringed at the site as cygnets, it was not possible to calculate the relative proportions of closely related birds in the two roost-groups.

Roost-site fidelity was very high compared to the results of similar studies on roost use by geese in winter, and this may reflect the lack of disturbance at the roosts. Pink-footed Geese Anser brachyrhynchus, for example, have been found to be very mobile and may switch roost-sites throughout the winter in response to disturbances, in addition to night-feeding and snowfall (Giroux 1991). The higher level of fidelity shown by families and pairs to their primary roost site, compared to singletons, agrees with Raveling (1969) who found that amongst Canada Geese, some birds (usually families) were very fidel to their roost-site, while others (usually single birds) alternated unpredictably between several roosts. There are a number of hypotheses which might explain this observation:

1) More experienced birds have acquired a greater knowledge of the fighting abilities of their neighbours from previous years, giving rise to consistency in the distribution of individuals. Since singletons were generally less experienced than birds from the pair and family classes in the current study (Table 3.3), they might be expected to be less consistent in their choice of roost-site.
2) Unattached birds exhibited exploratory dispersal at the roost-sites, in order to acquire information for use when they return with a mate and/or cygnets.
3) Predictable birds were established in good feeding positions in flocks on the feeding grounds, and that they therefore were never required to search for other feeding sites when conditions deteriorated (Ydenberg et al. 1983).

At Slimbridge the available biomass of grass on the surrounding fields during the study was lowest in January and February (see Chapter 4) and this was the period when swans from the Grounds roost appeared in largest numbers in the Rushy Pen roost. The Grounds birds that roosted on occasion in the Rushy Pen during February were mostly from the singleton and pair only classes, and generally had lower AP scores than those from the same social class that did not roost in the Rushy Pen, also supporting this view. That these more mobile units were also significantly more experienced than those that did not leave the Grounds roost further suggests that they may have been able to use previous knowledge of the site in order to decide if and when to switch roost-site.

Possible benefits to the Rushy Pen birds of occasionally roosting in the Grounds were less clear. There were no significant differences in the social class, experience or abdominal profiles of Rushy Pen units that did and did not roost on occasion in the Grounds early in the winter. Moreover, differences in the abdominal profiles for all birds were least upon arrival (see Chapter 2). However, since the number of Rushy Pen units in the Grounds was highest in November, when food availability in the fields was high and declined later in the winter as the food supply diminished (see Chapter 4), it may be that units were investigating alternative feeding sites by roosting in the Grounds, before returning to the Rushy Pen roost as food availability declined. Exploration of feeding sites may have been helped by the very high proportion of all birds present at Slimbridge, seen roosting in the Grounds, during this period.

Several authors (e.g. Ward 1965, Zahavi 1971, Loman & Tamm 1980, De Groot 1980) have postulated that one function of communal roosts amongst species which feed socially on patchy or localised food may be to allow an exchange of information concerning the food supply between individual members of the roost, although see Rickner & Heeb (1995). The use of the Rushy Pen roost as a centre for information-exchange is inferred by the increased presence of less-successful Grounds units during the period of lowest food availability in February. Moreover, since the APs of the immigrant Grounds units in February were generally lower than those of Rushy Pen units from the same social class, and the immigrants tended to a) join the Rushy Pen group in the evening (often having first visited the Grounds roost) and b) feed in flocks dominated by Rushy Pen birds following a night spent roosting in the Rushy Pen, information-exchange at the roost seems likely. It is possible that some Grounds birds may visit the Rushy Pen in the evening, in order to make use of two evening feeds (the Rushy Pen evening feed is later than the evening feed in the Grounds), and then simply follow the Rushy Pen birds out to their feeding areas. However, such exchange is rare early in the winter, when abdominal profiles are at their lowest, following the migratory flight from Russia, and an additional feeding opportunity would seem to be equally desirable.

The mechanisms of information-transfer at roost-sites may vary between species. Ydenberg et al. (1983) postulated that amongst Barnacle Geese utilising post-roost gatherings, such information might include the number of geese already present, temperature and the rate of arrival of geese from other areas. Ward & Zahavi (1973) speculated that there would be marked behavioural differences between successful individuals which have come to a roost from places where they found sufficient food, and the unsuccessful birds which did not. Hungry birds for example might be more restless and wakeful. They postulated that this distinctive behaviour may also serve to indicate the 'mood' of the roost and amongst Starlings, Grackles and Queleas, the expression of 'mood' may take the form of a loud chattering chorus during roost assembly and into the night. Since Bewick's Swans at Slimbridge do not exhibit post-roost gatherings and communal 'chattering' is rare except on nights preceding mass departure from the site at the start of the Spring migration, another mechanism of information exchange seems likely. I speculate that for Bewick's Swans and for species of Branta and Grey geese, a possible mechanism for exchange is the comparison of the Abdominal Profiles of birds from the same social class and of similar dominance rank. Abdominal profile, is a good indicator of condition (Owen 1981) and is an obvious feature in the field to the well-trained eye of an observer and presumably to other members of the flock. Amongst large unicoloured swans, abdominal profile can be measured with care; amongst Branta and grey geese the lower abdomen is prominently white compared to the rest of the body feathering, and AP is very conspicuous.

Choice of roost-site for birds which first appeared at Slimbridge as cygnets is heavily influenced by their parents. Cygnets associate closely with their parents in the first winter and adopt their feeding and roost-sites. Subsequent roost-site choice appears to be determined by the experience gained in the first winter, for at least the second and third seasons prior to pairing. Former offspring still associating with their parents might be expected to retain the parental roost-site choice, but birds returning to Slimbridge that did not associate with their parents showed a high level of roost-site fidelity when returning as yearlings or three-year old birds. These findings agree with those of Raveling (1979), who found that 78% of yearling Canada Geese used the same primary roost area that they had used the previous year as immatures. He did however find a tendency for yearlings that did not associate with their parents or siblings to be less faithful to the roost area of their previous experience, although the trend did not achieve significance. Return to traditional roost-sites may facilitate reunification of family members, not only on a day-to-day basis during the winter when, for example, a cygnet may become temporarily separated from its parents, but also on a seasonal basis as former offspring often arrive independently prior to reunification with their parents and subsequent association for the course of the winter. The presence of familiar non-associating former offspring at the traditional roost may help to minimize both the frequency and intensity of aggressive encounters, for former offspring and parents alike. Non-associating former offspring do, on rare occasions, rally around their relatives during long-lasting, and therefore important, aggressive encounters with other units, thereby helping to strengthen both their own position and that of their relatives in the dominance hierarchy of the roost group and helping to reduce further aggressive encounters. Raveling (1979) also suggested that the local stratification caused by the assemblage of related Canada Geese helps to maximise acquisition of the most desirable roost locations, and to promote efficient use of food resources.

Roost-site choice in subsequent winters may be influenced by the acquisition of or change of mate. For both roost-groups there was evidence to suggest that birds, of either sex, returning to Slimbridge with a new mate were more likely to change their roost-site. Since all but two (4.1%) of the new mates were new birds to the site, it seems likely that the lack of experience of Slimbridge of the new partner affected the choice of roost-site by the pair. Moreover, there was some evidence to suggest that the loss of a partner also caused birds, returning as singletons, to exhibit a higher than expected change in roost-site use. This may reflect the loss of the effect of the partner's roost-site preference and/or a reduction in dominance rank caused by the change in status. However, there was no significant difference between males and females in terms of the percentage change in roost-site choice following loss of a partner. It seems likely therefore that it is the loss of the effect of the partner's roost-site preference that causes the change, since single females are subordinate to single males in terms of dominance rank (see Chapter 2) and widowed females would thus have been expected to exhibit a greater change in roost-site preference than males.

There was a significant difference in the distribution of swans from the two roost-groups at feeding sites in the Slimbridge area, with certain fields being utilised more heavily by birds from the Grounds roost and others more heavily by birds from the Rushy Pen roost. The proportion of Grounds units in the feeding flocks decreased with distance from the roost, whereas the proportion of Rushy Pen birds in feeding flocks tended to increase with distance from their roost. Such differences might indicate differences in foraging strategies relating to a trade-off between the cost involved in flying to a feeding area and the quantity and quality of food available. It has been suggested amongst Starlings Sturnus vulgaris that birds may "patch-sit" by using the roost-site closest to an especially rich food source (Morrison & Caccamise 1985). Swans in this study would on occasion roost on flood-waters at a number of feeding sites when conditions were suitable, thereby reducing the cost of travelling to and from the feeding site. This may also have the added benefit of reduced competition from other birds from the Slimbridge roost which may otherwise have gained information concerning the location of the feeding site.

3.5 SUMMARY

This chapter investigated the use made of roost-sites by Bewick's Swans at Slimbridge during the winter.

1) The two main roosts appear to be very similar in terms of population structure but a difference was detected in the dominance rank of pairs without cygnets which were of significantly lower rank in the Rushy Pen roost. It was inferred from this that, amongst pairs of higher rank, those in the Grounds roost may be less likely to return to Slimbridge with cygnets, than those in the Rushy Pen. In addition swans from the Grounds roost generally had lower APs than those from the Rushy Pen roost indicating that they were in poorer body condition. One reason for roosting in the less successful Grounds roost may be reduced levels of aggressive interaction caused by the presence of related birds.

2) Families and pairs were more faithful to their roost-site than singletons within a winter.

3) Less successful Grounds units switched roost-site to the Rushy Pen during February when the food supply in the fields was lowest. The APs of these birds were generally lower than for birds from the same social class which remained in the Grounds roost, and lower than those of the same social class in the Rushy Pen roost. Since the immigrants tended to follow the Rushy Pen birds to their feeding grounds, it is suggested that information transfer was occurring at the roost. It is postulated that this information exchange may be by comparison of the APs of birds of similar rank.

4) Choice of roost-site for single birds which first appeared at Slimbridge as cygnets was determined mainly by the experience of their first winter (i.e. by the roost-site choice of their parents), regardless of whether or not they continued to associate with their parents in subsequent years.

5) Birds returning to Slimbridge with a new mate were more likely to exhibit a change in roost-site use, suggesting that both members of a pair influence roost-site choice. Previously-paired birds returning as singletons similarly were more likely to exhibit a change in roost-site use. There was no difference in the observed change in roost-site use between males and females returning as singletons, suggesting that it was the loss of the partner's roost-site choice, rather than the loss of dominance rank which caused this change.

6) Birds from the two roost groups used different feeding sites, with those from the Grounds roost tending to utilise fields close to their roost-site, whereas swans from the Rushy Pen roost tended to range further afield.

Table 3.1 Breakdown of swan units by social class within the two main roost-groups.

a) By social class

	Grounds Pens					Rushy Pen						
Winter	89-90	90-91	91-92	92-93	Tot	89-90	90-91	91-92	92-93	Tot	Chi Sq.	P
Class												
Singles	29	17	33	83	162	102	138	128	114	482	0.00	NS
Pairs	12	7	12	26	57	38	39	50	46	173	0.20	NS
Families	12	11	11	0	34	27	33	34	8	102	0.90	NS
Other	0	1	4	3	8	0	7	6	7	20		
Total					261					777		

b) By family size

	Grounds Pens					Rushy Pen				
Winter	89-90	90-91	91-92	92-93	Tot	89-90	90-91	91-92	92-93	Tot
Family size: (no. of cygs)										
1	5	2	3	0	10	7	10	7	2	26
2	2	2	3	0	7	7	9	12	5	33
3	5	4	4	0	13	9	8	8	1	26
4	0	3	1	0	4	4	6	7	0	17
Mean					2.32					2.33
S.D.					1.04					1.04

Table 3.2 Dominance rank of swan units by social class within the two main roost-groups (1989-1992 winters inclusive). Mann-Whitney U Test comparison between roost-groups (df = 1 for all comparisons).

	Grounds Pens			Rushy Pen				
	Mean	S.D.	n	Mean	S.D.	n	W	P
Singles	0.110	0.175	45	0.127	0.149	94	6851	0.217
Pairs	0.578	0.235	44	0.497	0.242	109	7891	0.043
Two-parent families	0.830	0.114	20	0.800	0.147	68	2989	0.713
One-parent families	0.484	0.276	6	0.525	0.359	5	32	0.784

Table 3.3 Number of previous winters spent at Slimbridge for swans of each social class within the two main roost-groups (1989-1992 winters inclusive). Kruskal-Wallis Chi-square Approximation Test - comparison between roost-groups (df = 1 for all comparisons).

	Grounds Pens			Rushy Pen				
	Mean	S.D.	n	Mean	S.D.	n	Chisq.	P
Singles	0.920	2.201	162	0.853	2.350	482	0.156	0.693
Pairs	3.579	3.190	57	4.353	4.867	173	0.019	0.890
Families	4.971	3.572	34	7.186	5.883	102	2.729	0.099
All	2.063	3.087	253	2.506	4.359	757	4.630	0.031

Table 3.4 Comparison of the number of new swan units joining the Slimbridge roost-groups (1989-1992 winters inclusive).

Previous experience of site (yrs)	n	Grounds Pens	(%)	Rushy Pen	(%)	Other sites	(%)
0	580	133	22.9	414	71.4	33	5.7
1+	465	120	25.8	343	73.8	2	0.4
Total	1045	253	24.2	757	72.4	35	3.3

Table 3.5 Abdominal Profiles of swans by social class within the two main roost-groups (1989-1992 winters inclusive). Kruskal-Wallis Chi-square Approximation Test - comparison between roost-groups (df = 1 for all comparisons).

	Grounds Pens			Rushy Pen				
	Mean	S.D.	n	Mean	S.D.	n	Chisq.	P
Adult males								
Single	3.74	0.77	17	4.18	0.63	223	11.66	0.001
Paired	3.66	0.80	166	3.80	0.69	473	7.68	0.006
Breeding	3.83	0.69	56	3.90	0.77	305	2.40	0.122
Adult females								
Single	3.90	0.70	71	3.89	0.74	201	0.07	0.798
Paired	3.97	0.82	167	4.39	0.74	483	7.52	0.006
Breeding	4.11	0.79	64	4.50	0.69	291	9.27	0.002
Cygnets								
Family	4.09	0.70	249	4.26	0.78	708	51.61	0.000
Yearlings								
Single	3.77	0.81	83	3.89	0.79	244	1.30	0.255
Family	4.45	0.42	4	4.17	0.57	11	5.63	0.018
All males	3.71	0.74	251	3.97	0.74	1371	26.51	0.000
All females	3.95	0.80	370	4.27	0.77	1193	50.87	0.000

Table 3.6 Roost-night totals of swan units within the two main roost-groups (1989-1992 winters inclusive). Kruskal-Wallis Chi-square Approximation Test - comparison between roost-groups (df = 1 for all comparisons).

a) By winter

	Grounds Pens			Rushy Pen				
	Mean	S.D.	n	Mean	S.D.	n	Chisq.	P
1989/90	49.83	33.99	53	25.48	26.14	167	23.36	0.000
1990/91	71.49	45.96	35	51.74	50.69	210	5.05	0.025
1991/92	70.46	36.86	56	55.56	48.29	212	3.93	0.047
1992/93	59.53	41.87	109	51.27	31.86	168	1.28	0.258
All	61.75	40.41	253	46.91	43.23	757	26.46	0.000

b) By social class

	Grounds Pens			Rushy Pen				
	Mean	S.D.	n	Mean	S.D.	n	Chisq.	P
Singles	53.83	39.24	162	38.12	40.60	482	24.94	0.000
Pairs	77.54	37.96	57	61.27	42.82	173	6.25	0.012
Families	71.68	40.95	34	64.13	44.66	102	0.62	0.433

Table 3.7 Roost-site fidelity (measured as the percentage number of roost nights spent at the primary roost-site out of the total number of roost nights seen at Slimbridge) of swan units by social class within the two main roost-groups (1989-1992 winters inclusive). Kruskal-Wallis Chi-square Approximation Test - comparison between roost-groups (df = 1 for all comparisons).

	Grounds Pens			Rushy Pen				
	Mean	S.D.	n	Mean	S.D.	n	Chisq.	P
Singles	88.10	13.91	162	94.21	11.70	482	41.65	0.000
Pairs	87.11	13.46	57	96.72	8.14	173	48.58	0.000
Families	91.85	11.42	34	92.53	13.39	102	3.12	0.078
All	87.94	15.41	253	94.78	11.17	757	10.63	0.001

Table 3.8 Fidelity of swan units to their primary roost-site by social class.

	Units n	Obs. n	Obs. per unit	Observations at roost-site Primary	(%)	Secondary	(%)
Singles	644	27094	42.07	24767	91.4	2327	8.6
Pairs	230	15020	65.30	14069	93.7	951	6.3
Families	136	8977	66.01	8385	93.4	592	6.6

Table 3.9. Comparison of the number of swan units roosting at secondary roost-sites and roost number variables. Spearman's rank correlations.

a) Grounds units in the Rushy Pen (GINR)

	r_s	P	n
GINR v half-month	0.440	<0.01	499
GINR v number of birds in Rushy Pen	0.267	<0.01	330
GINR v number of birds in Grounds	-0.087	>0.1	338
GINR v total roosting at Slimbridge	0.244	<0.01	331
GINR v % Grounds birds in total roost	-0.396	<0.01	331
GINR v number of Rushy units in Grounds	-0.033	>0.1	354

b) Rushy Pen units in the Grounds (RING)

	r_s	P	n
RING v half-month	-0.103	<0.05	369
RING v number of birds in Rushy Pen	0.456	<0.01	357
RING v number of birds in Grounds	0.643	<0.01	328
RING v total roosting at Slimbridge	0.586	<0.01	321
RING v % Grounds birds in total roost	0.180	<0.01	321
RING v GINR	-0.033	>0.1	354

Table 3.10 Use of secondary roost-sites by swan units from the three main social classes. Chi-square comparisons (df = 1 in all cases)

a) Grounds units in the Rushy Pen

Social class	Roosted in Rushy Pen No	Yes	Chi-square	P
Singletons	72	90		
Not singletons	25	65	6.78	<0.001
Pairs	13	44		
Not pairs	84	111	7.65	<0.001
Families	12	22		
Not families	85	133	0.17	>0.60

b) Rushy Pen units in the Grounds

Social class	Roosted in the Grounds No	Yes	Chi-square	P
Singletons	425	57		
Not singletons	251	24	1.76	>0.10
Pairs	159	14		
Not pairs	517	67	1.60	>0.20
Families	92	10		
Not families	585	71	0.10	>0.70

Table 3.11 Experience (measured as the number of previous winters spent at Slimbridge) of swan units utilising secondary roost-sites from the three main social classes. Mann-Whitney U comparisons unless stated otherwise indicated (df = 1 in all cases).

a) Grounds units in the Rushy Pen

Social class	Roosted in the Rushy Pen	n	Experience mean	SD	W	P
Single	No	72	0.45	1.32		
	Yes	90	1.21	2.53	5173	0.030
Pair	No	13	3.43	3.34		
	Yes	44	3.80	3.25	397	0.679
Family	No	12	3.58	4.23		
	Yes	22	5.82	3.00	159	0.067
All	No	97	1.27	2.58		
	Yes	156	2.61	3.30	10323	0.000

b) Rushy Pen units in the Grounds

Social class	Roosted in the Rushy Pen	n	Experience mean	SD	W	P
Single	No	425	0.86	2.40		
	Yes	57	0.91	2.20	101822	0.106
Pair	No	159	4.15	4.76		
	Yes	14	6.36	5.73	13580	0.154
Family	No	92	7.19	6.05		
	Yes	10	7.20	4.32	4712	0.769
					Kruskal-Wallis Chi-square	
All	No	676	2.49	4.38		
	Yes	81	2.63	4.24	0.724	0.395

Table 3.12 Comparison of the Abdominal Profiles of units utilising secondary roost-sites with those not utilising secondary roost-sites. Some categories omitted where data too scant for analysis. Kuskal-Wallis Chi-square comparisons (df = 1) in all cases.

a) Grounds birds in the Rushy Pen - February only

	Grounds birds not roosting in the Rushy Pen			Grounds birds roosting in the Rushy Pen			Rushy Pen birds		
	mean	SD	n	mean	SD	n	mean	SD	n
Breeding males	3.50	0.00	2	3.88	0.13	3	4.15	0.48	24
Chi-square				3.16			1.11		
P				0.08			0.29		
Significance				N.S.			N.S.		
Paired males	4.00	0.60	12	3.84	0.47	4	3.92	0.48	55
Chi-square				0.87			0.44		
P				0.35			0.51		
Significance				N.S.			N.S.		
Breeding females	4.48	0.62	7	4.35	1.41	3	4.96	0.45	25
Chi-square				0.01			0.29		
P				0.91			0.59		
Significance				N.S.			N.S.		
Paired females	4.50	0.43	13	4.38	0.54	8	4.67	0.57	44
Chi-square				0.23			2.52		
P				0.63			0.11		
Significance				N.S.			N.S.		
Family cygnets	4.81	0.30	10	4.37	0.35	13	4.76	0.42	60
Chi-square				7.94			10.04		
P				0.005			0.002		
Significance				**			**		
Single yearlings	4.21	0.43	6	4.33	0.58	3	4.16	0.64	26
Chi-square				0.02			0.02		
P				0.89			0.88		
Significance				N.S.			N.S.		

b) Rushy Pen birds in the Grounds - November only

	Rushy Pen birds not roosting in the Grounds				Rushy Pen birds roosting in the Grounds				Grounds birds		
	mean 2	SD	n		mean 1	SD	n		mean 3	SD	n
Breeding males	3.27	0.80	15		3.42	0.83	3		3.51	0.74	4
Chi-square				0.23				0.00			
P				0.63				0.99			
Significance				N.S.				N.S.			
Paired males	3.30	0.88	14		3.50	-	1		3.00	0.64	12
Chi-square				0.00				0.91			
P				0.95				0.34			
Significance				N.S.				N.S.			
Single males	3.27	0.80	15		4.00	-	1		2.00	-	1
Chi-square				0.00				-			
P				0.95				-			
Significance				N.S.				N.S.			
Breeding females	3.85	0.66	14		3.50	-	1		3.92	0.14	3
Chi-square				0.35				2.00			
P				0.55				0.16			
Significance				N.S.				N.S.			
Paired females	3.63	0.72	19		4.25	0.66	3		3.34	0.37	13
Chi-square				2.10				5.31			
P				0.15				0.02			
Significance				N.S.				*			
Single females	3.09	0.77	7		3.87	0.71	3		3.50	-	1
Chi-square				0.00				-			
P				0.95				-			
Significance				N.S.				N.S.			
Family cygnets	3.37	0.60	45		3.13	0.18	45		3.28	0.82	18
Chi-square				0.50				0.33			
P				0.48				0.57			
Significance				N.S.				N.S.			
Single yearlings	2.95	0.45	9		2.50	1.00	4		2.90	0.74	5
Chi-square				2.17				0.61			
P				0.14				0.43			
Significance				N.S.				N.S.			

Table 3.13 Roost-use by birds returning to Slimbridge in their second and third winters in relation to their roost area experience as cygnets (only birds of known parentage included).

a) Second year

Social group	Sex	n	Primary roost area relative to previous year Same	 Different	 (Absent)
With parents					
	male	12	12 (100%)	0 (0%)	(0)
	female	17	16 (94.1%)	1 (5.9%)	(0)
	unknown	14	14 (100%)	0 (0%)	(0)
	Total	43	42 (97.7%)	1 (2.3%)	(0)
Without parents					
	male	12	12 (100%)	0 (0%)	(13)
	female	7	7 (100%)	0 (0%)	(7)
	unknown	1	1 (100%)	0 (0%)	(-)
	Total	20	20 (100%)	0 (0%)	(20)

b) Third year

Social group	Sex	n	Primary roost area relative to previous year Same	 Different	 (Absent)
With parents					
	male	10	10 (100%)	0 (0%)	(0)
	female	10	10 (100%)	0 (0%)	(0)
	unknown	3	3 (100%)	0 (0%)	(0)
	Total	23	23 (97.7%)	0 (0%)	(0)
Without parents					
	male	12	12 (100%)	0 (0%)	(6)
	female	11	9 (81.8%)	2 (18.2%)	(8)
	unknown	4	4 (100%)	0 (0%)	(1)
	Total	27	20 (100%)	0 (0%)	(15)

Table 3.14 Change in roost-use between seasons with respect to mate change, - all data included (see text). Mann-Whitney U comparisons between roost groups.

	Change in roost-use (%)							
	Grounds units			Rushy Pen units				
Mate change	n	mean	SD	n	mean	SD	U	P
No change (single/same mate +/- cygnets)	260	6.65	12.37	91	16.46	21.13	4181.5	0.000
Arrived with new mate	35	12.47	21.54	15	58.43	32.21	689.0	0.000
Arrived alone having lost a mate	30	6.45	12.16	11	33.35	32.56	518.0	0.001

Table 3.15 Comparisons betwen the sexes of roost-site fidelity (determined by roost-use indices) upon changing a mate (Mann-Whitney U tests).

a) Arrived with a new mate

i) Rushy Pen

		Change in roost use (%)			
Sex	n	mean	SD	W	P
Male	22	13.38	24.92	382.0	0.774
Female	11	8.90	11.93		

ii) Grounds Pen

Male	8	53.74	28.26	55.5	0.605
Female	6	58.70	38.70		

Table 3.15 (con.)

b) Arrived alone having lost a mate

i) Rushy Pen

Sex	n	Change in roost use (%) mean	SD	W	P
Male	20	6.96	12.72	312.5	0.929
Female	10	5.43	11.54		

ii) Grounds Pen

Sex	n	Change in roost use (%) mean	SD	W	P
Male	5	25.70	29.50	28.0	0.784
Female	6	39.70	36.30		

Table 3.16 Change in roost-use between seasons with respect to mate-change - excluding data concerning singletons that had never paired (see text). Mann-Whitney U comparisons.

Mate change	n	Rushy Pen units mean	SD	n	Grounds units mean	SD
No change	187	6.01	11.53	61	15.33	20.90
New mate	35	12.47	21.54	15	58.43	32.21
Lost mate	30	6.45	12.16	11	33.55	32.56

Mann-whitney U comparisons between mate change groups:

	Rushy Pen units W	P	Grounds units W	P
No change v new mate	20241	0.076	2019	0.000
No change v lost mate	20418	0.912	2101	0.050
New mate v lost mate	1252	0.202	238	0.069

Table 3.17 Field usage by swans seen at Slimbridge 1989/90 - 1992/93 (for location of fields see Figs 3.3 & 3.4).

Field	Number of flocks	Percentage of birds identified		Sum of units identified	
		mean	S.D.	a) from Grounds roost	b) from Rushy Pen roost
17 acre	17	51.910	20.124	52	226
Avon meadows	1	69.231	-	1	4
Canal 1	9	35.977	29.245	12	44
Canal 2	5	40.141	13.428	7	28
Canal 3	2	37.264	18.011	4	14
Dumbles	88	71.216	27.990	132	402
Fifty acre	10	63.465	28.816	8	85
JBS	19	36.684	22.852	41	317
Long Ground	47	60.631	29.087	188	28
North middle road	4	54.960	29.832	8	27
New south lake field	5	71.839	15.588	81	29
Pylon	19	66.282	27.350	189	316
Pylon B	5	55.264	9.894	38	23
River Severn	3	97.500	4.330	14	33
South-east road	4	46.994	35.764	1	25
South middle road	86	66.123	29.009	510	351
South middle ext.	11	75.215	25.738	40	34
Tack piece	106	76.444	25.511	334	2266
Tin shed	3	62.176	38.575	3	9
Top new piece	115	81.934	22.658	744	370
Walmore Common	31	50.143	23.764	36	381
	612	68.354	28.301	2443	5012

Table 3.18 Comparison of the percentage of swan units from the two main roost-groups identified in feeding flocks and i) percentage of flock identified, ii) month, iii) time of day (hour) and iv) flock-size. Spearman's rank correlations, n = 612 flock checks in all cases.

	r_s	P
% Grounds units v % of flock identified	0.188	< 0.01
% Rushy units v % of flock identified	-0.196	< 0.01
% Grounds units v month	0.001	> 0.1
% Rushy units v month	0.010	> 0.1
% Grounds units v hour	0.019	> 0.1
% Rushy units v hour	-0.021	> 0.1
% Grounds units v flock-size	-0.359	< 0.01
% Rushy units v flock-size	0.362	< 0.01

Table 3.19 Comparison of the roost source of swan units identified on individual fields (for location of fields see Figs 3.3 & 3.4).

	Sum of units identified			
Field	Grounds	Rushy	Chisq.	P
17 acre	52	226	25.93	<0.001
Canal fields	23	86	6.84	<0.025
Dumbles	132	402	16.93	<0.001
Fifty acre	8	85	24.97	<0.001
JBS	41	317	77.57	<0.001
Long Ground	188	28	341.13	<0.001
North middle road	8	27	1.57	>0.2
New south lake field	81	29	84.62	<0.001
Pylon	189	316	5.33	<0.025
Pylon B	38	23	24.34	<0.001
River Severn	14	33	0.19	>0.6
South-east road	1	25	9.91	<0.005
South middle road	510	351	309.43	<0.001
South middle ext.	40	34	15.37	<0.001
Tack piece	334	2266	719.35	<0.001
Tin shed	3	9	0.33	>0.5
Top new piece	744	370	687.86	<0.001
Walmore Common	36	381	116.79	<0.001
	2443	5012		

Table 3.20 Numbers of swan units identified on fields from the two main roost groups, and distances of the fields from the roost-sites (for location of fields see Figs 3.3 & 3.4).

	Percentage of units identified				Distance of field (metres) to: a) Grounds roost b) Rushy Pen roost	
	Grounds		Rushy			
Field	mean	S.D.	mean	S.D.	a	b
17 acre	23.28	19.69	76.72	19.69	637	919
Canal fields	24.02	32.43	75.98	32.43	969	1319
Dumbles	31.52	35.39	66.13	37.50	561	652
Fifty acre	10.13	19.93	89.87	19.93	1646	1274
JBS	14.03	10.82	85.39	10.90	1606	1678
Long Ground	91.69	16.78	8.31	16.78	163	385
North middle road	16.56	14.50	83.44	14.50	585	422
New south lake	74.33	10.28	25.68	10.28	237	378
Pylon	37.54	22.38	58.76	24.10	1693	1884
Pylon B	59.85	10.40	37.07	12.98	1379	1611
River Severn	29.93	1.88	70.07	1.88	1022	844
South-east road	2.78	5.56	97.22	5.56	696	711
South middle road	65.68	32.15	33.65	32.38	456	489
South middle ext.	61.85	37.72	38.15	37.72	478	681
Tack piece	17.84	26.99	81.61	27.27	613	341
Tin shed	48.61	45.71	51.39	45.71	563	896
Top new piece	73.10	27.45	26.83	27.33	449	756
Walmore Common	11.24	13.60	86.79	14.57	10550	10750

Table 3.21 Comparison of composition of feeding flocks on the fields that were joined by anomalous roost units, with those that were not joined by anomalous roost units. Chi-square comparisons (df = 1 in both cases).

a) Grounds birds roosting in the Rushy Pen (GINR)

	Flock composition			
	Total Grounds units	Total Rushy units	Chi-sq.	P
Joined by GINR	656	1713	19.60	<0.001
Not joined by GINR	1550	3168		

b) Rushy Pen birds roosting in the Grounds Pens (RING)

	Flock composition			
	Total Grounds units	Total Rushy units	Chi-sq.	P
Joined by RING	616	800	126.42	<0.001
Not joined by RING	1590	4081		

Table 3.22 Comparison of the number of anomalous roost units identified in feeding flocks on the fields with flock composition. Spearman's rank correlations, n = 612 in all cases.

a) Grounds units roosting in the Rushy Pen (GINR)

	r_s	P
Tot GINR v % Rushy Pen units in flock	0.112	<0.02
Tot GINR v % Grounds units in flock	-0.156	<0.01

b) Rushy Pen units roosting in the Grounds (RING)

	r_s	P
Tot RING v % Rushy Pen units in flock	0.104	<0.02
Tot RING v % Grounds units in flock	-0.100	<0.05

Fig. 3.1a. The daily mean number of Bewick's Swans roosting in the two main roost groups at Slimbridge during the 1989-90 winter by half-month.

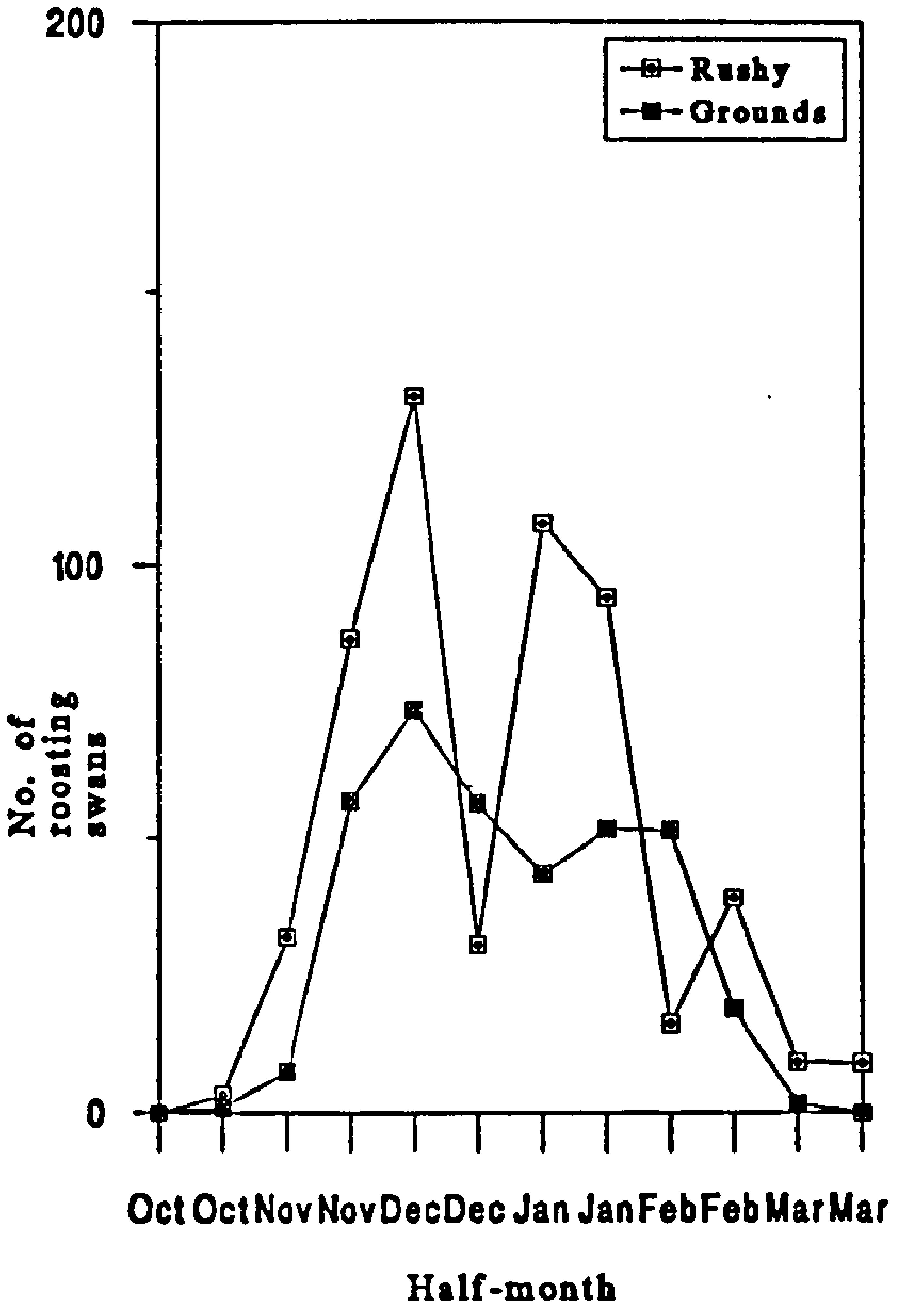


Fig. 3.1b. The daily mean number of Bewick's Swans roosting in the two main roost groups at Slimbridge during the 1990-91 winter by half-month.

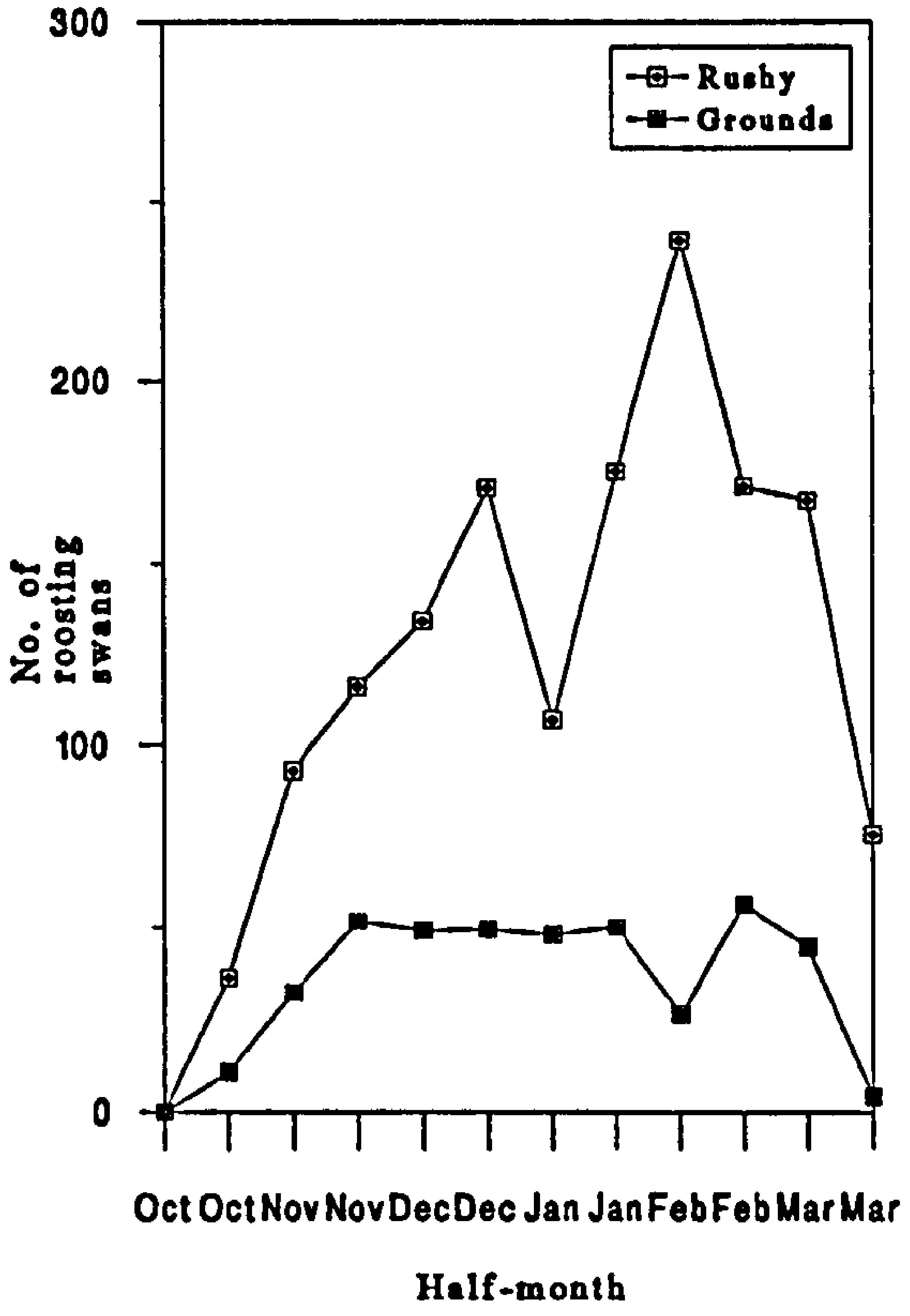


Fig. 3.1c. The daily mean number of Bewick's Swans roosting in the two main roost groups at Slimbridge during the 1991-92 winter by half-month.

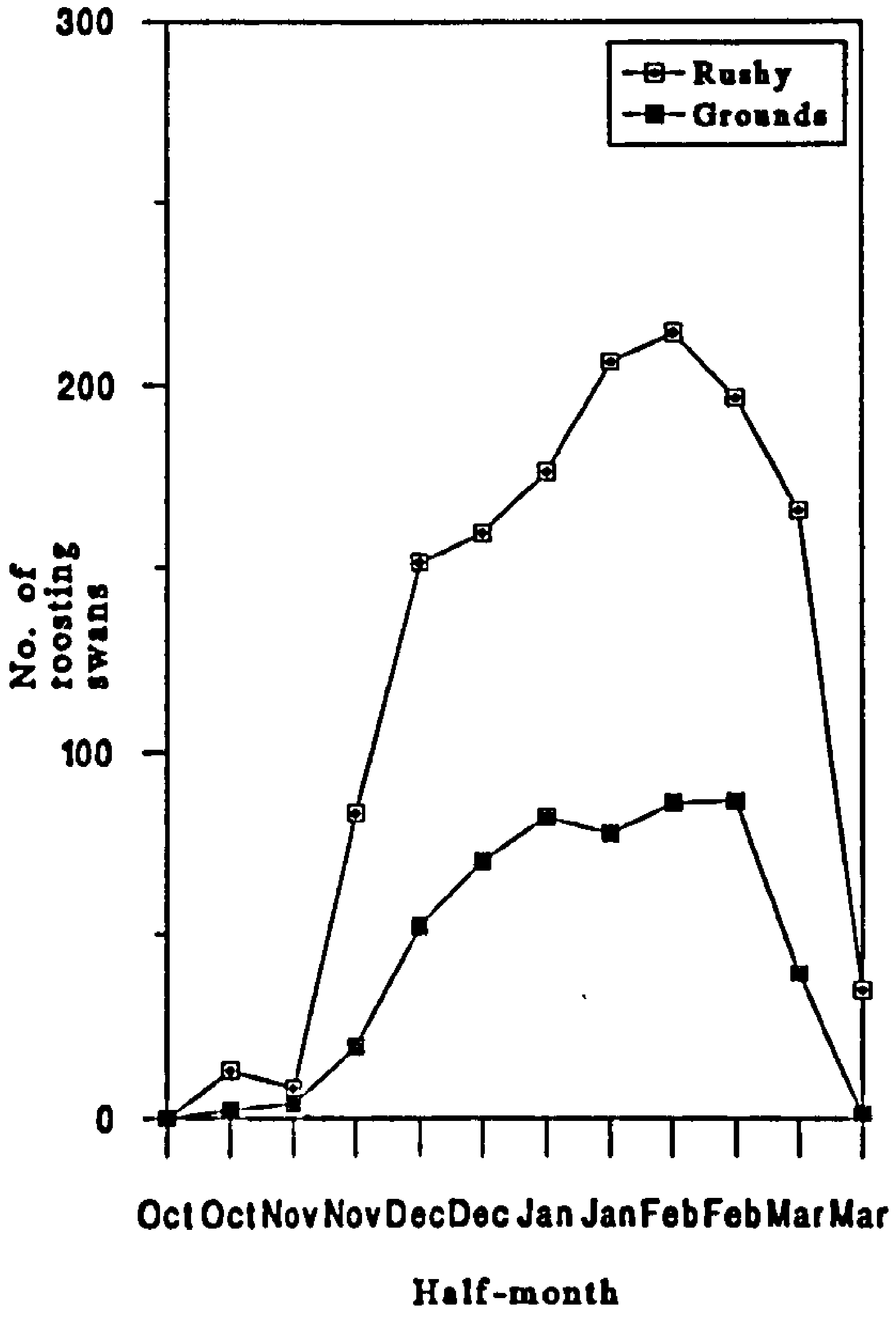


Fig. 3.1d. The daily mean number of Bewick's Swans roosting in the two main roost groups at Slimbridge during the 1992-93 winter by half-month.

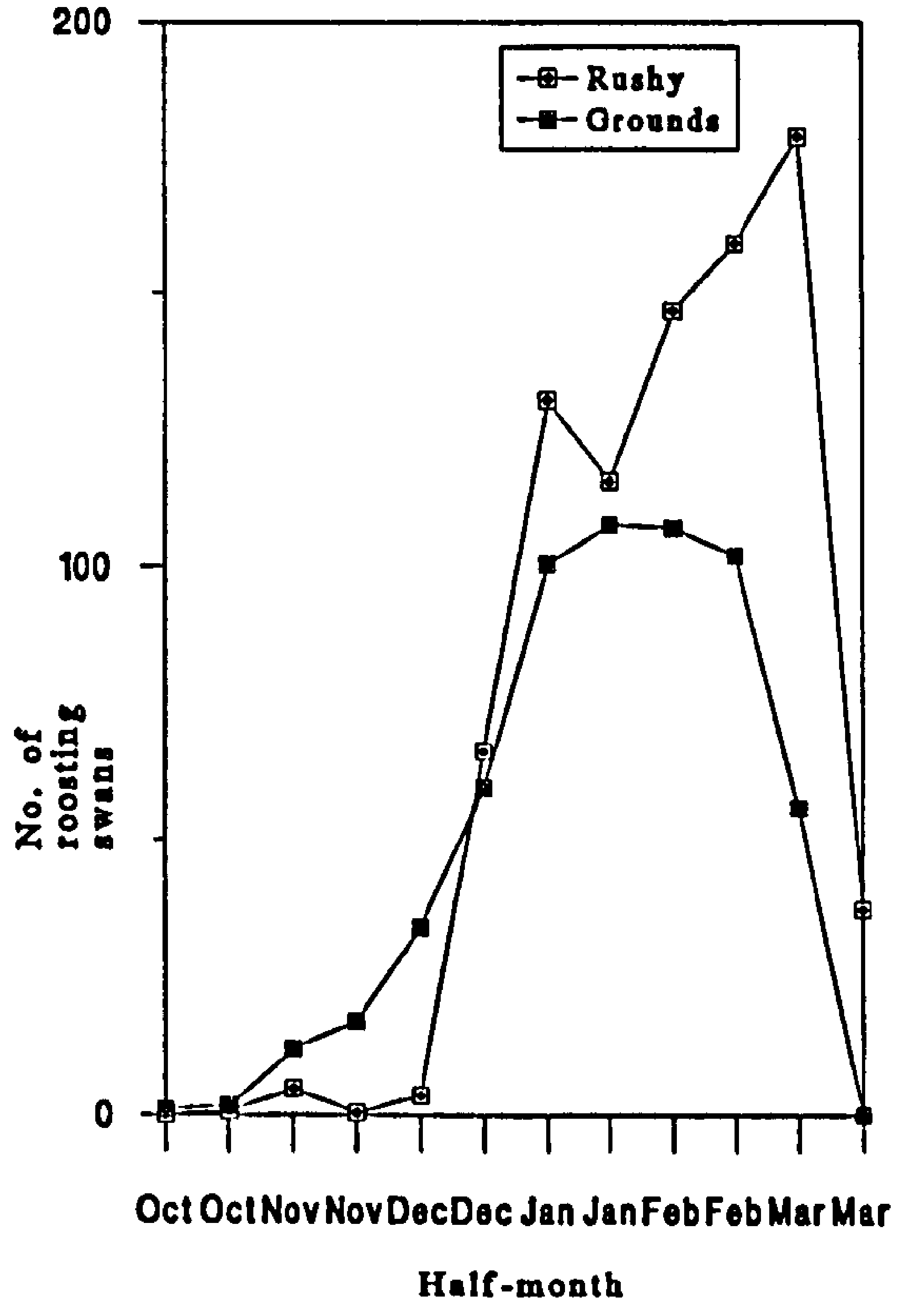


Fig. 3.1e. The daily mean number of Bewick's Swans roosting in the two main roost groups at Slimbridge by half-month, data for the winters 1989-90 to 1992-93 combined (mean and S.E. bar).

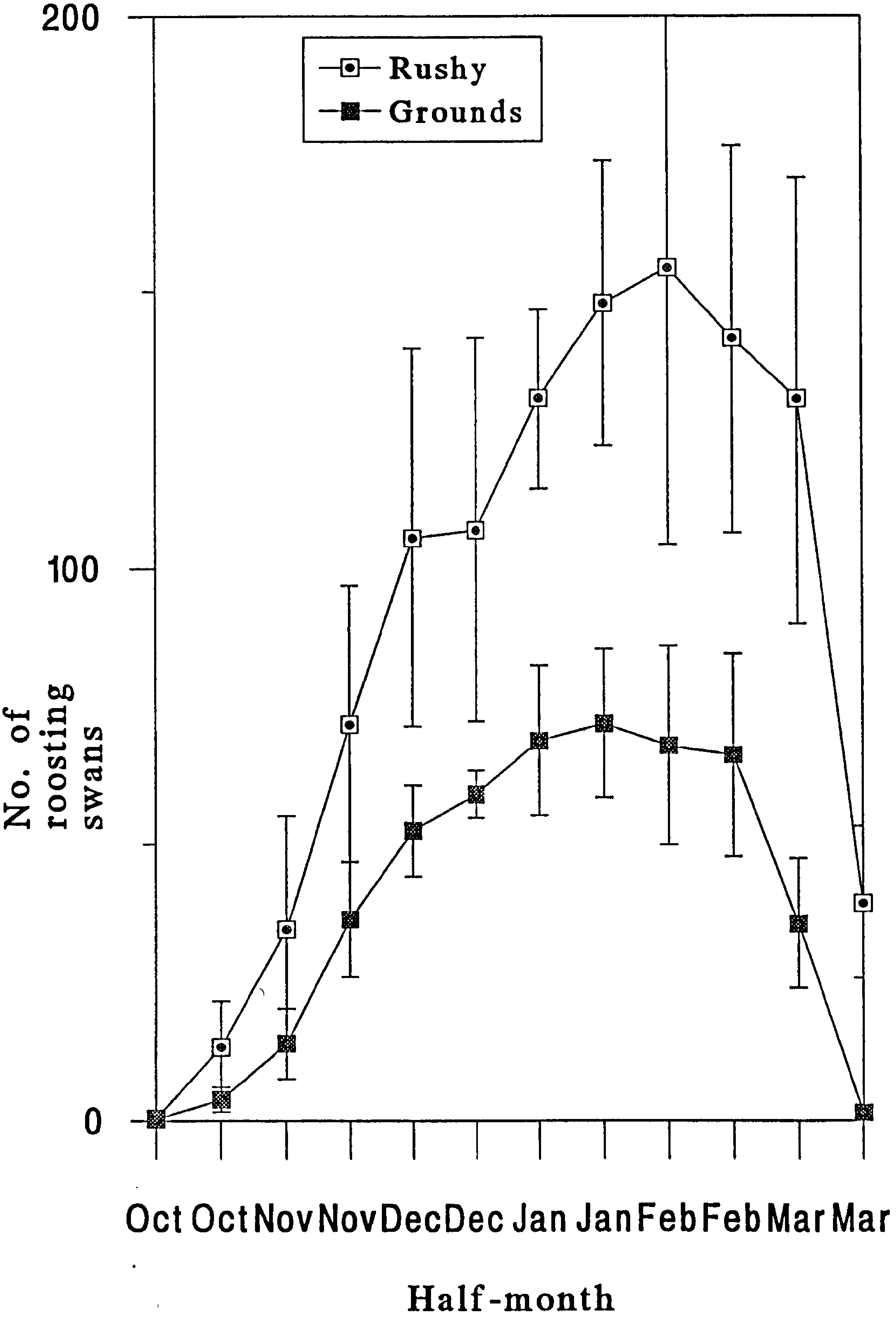


Fig. 3.2a. The daily mean number of Grounds units roosting in the Rushy Pen by half-month, data for the winters 1989-90 to 1992-93 winters combined (mean and S.E. bar, n = 507).

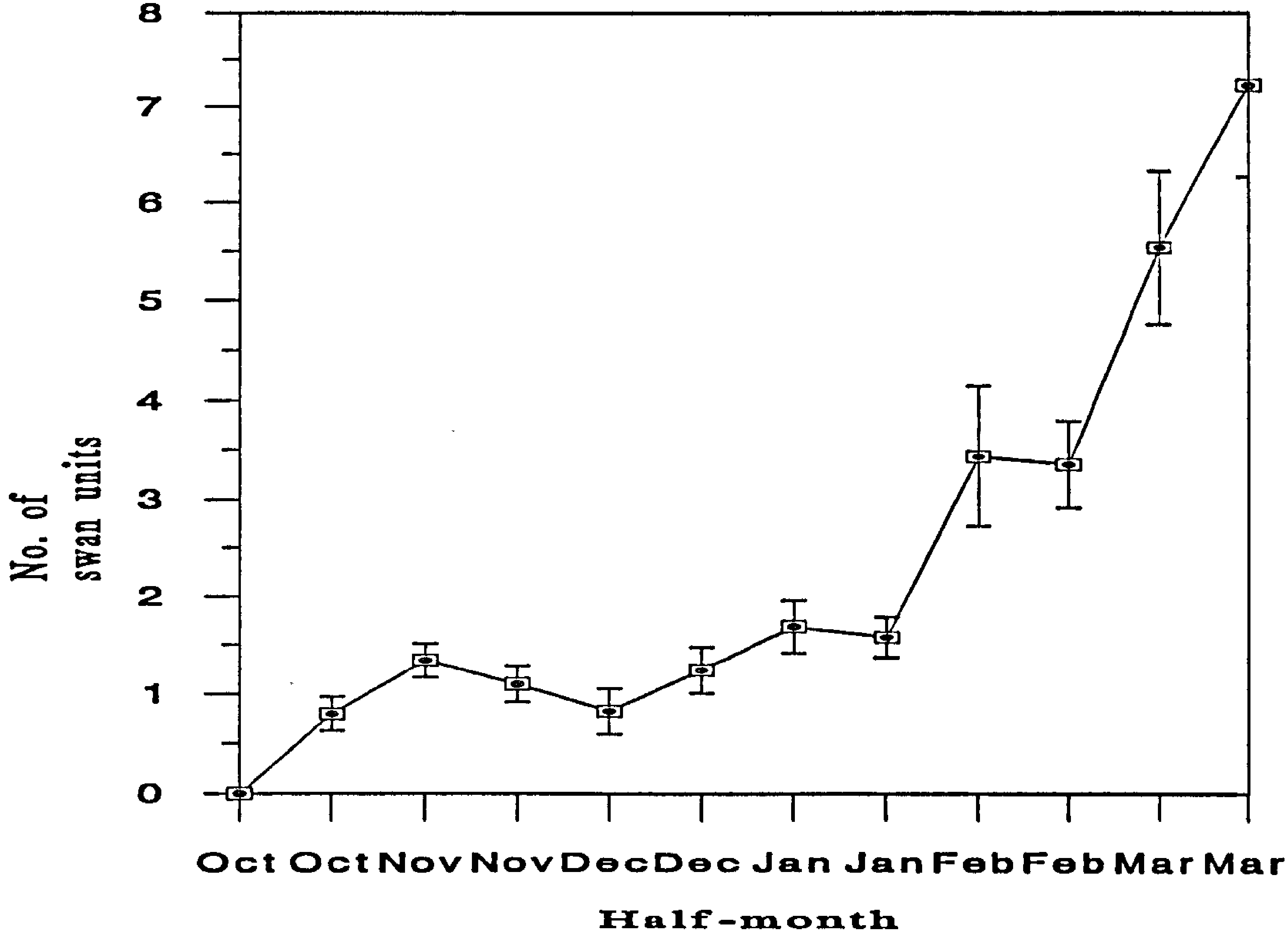


Fig. 3.2b. The daily mean number of Rushy Pen units roosting in the Grounds by half-month, data for the 1989-90 to 1992-93 winters combined (mean and S.E. bar, n = 357).

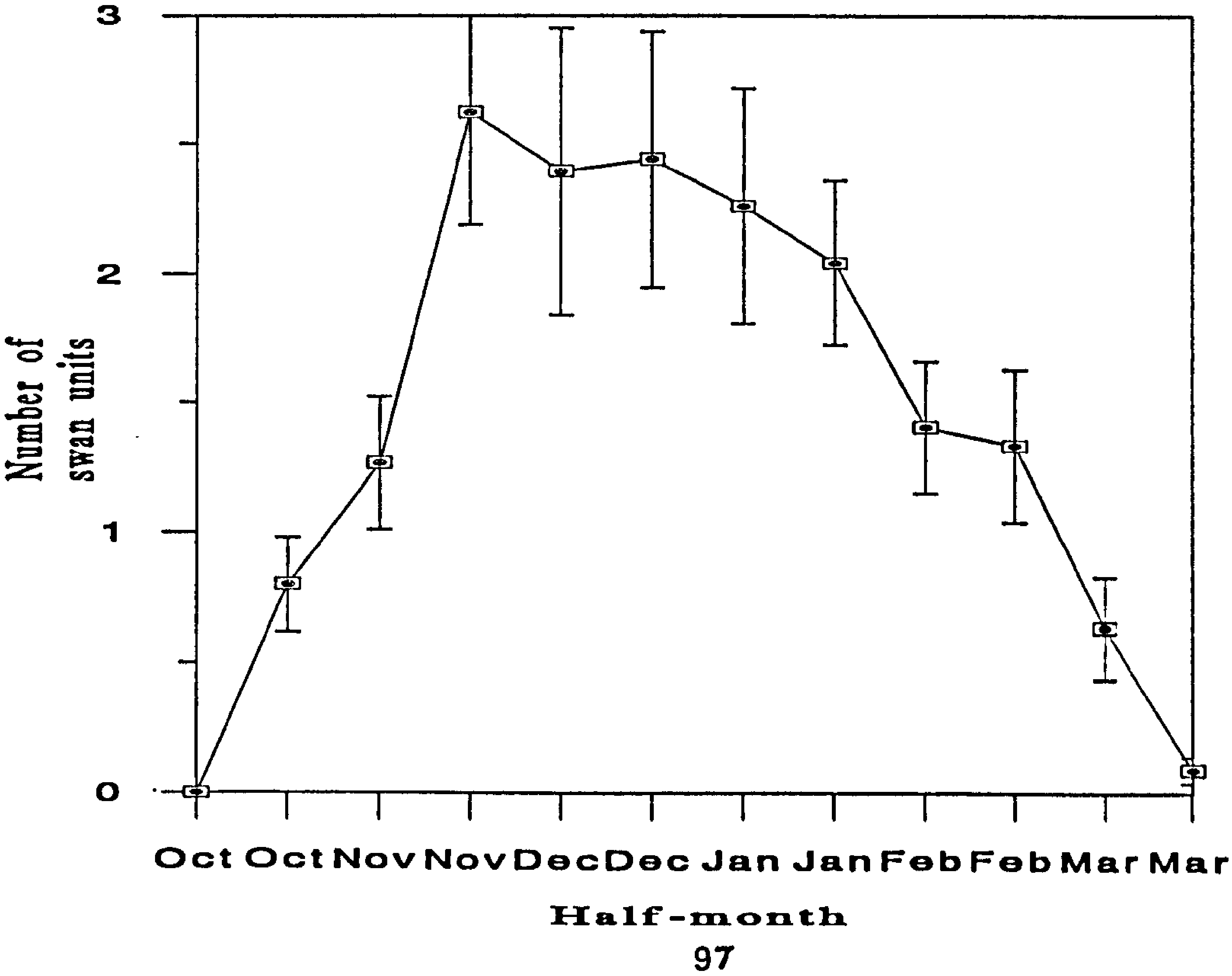
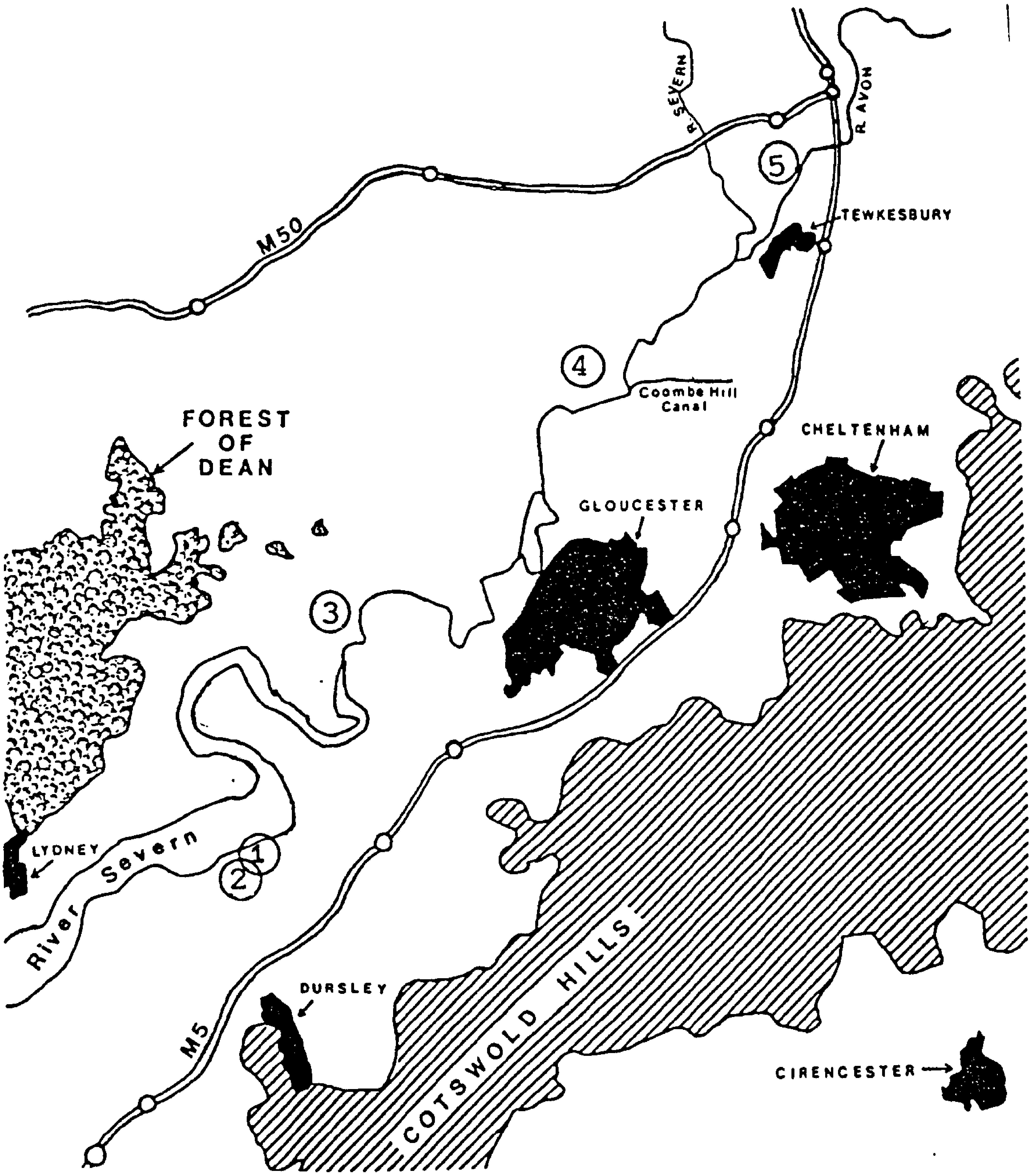
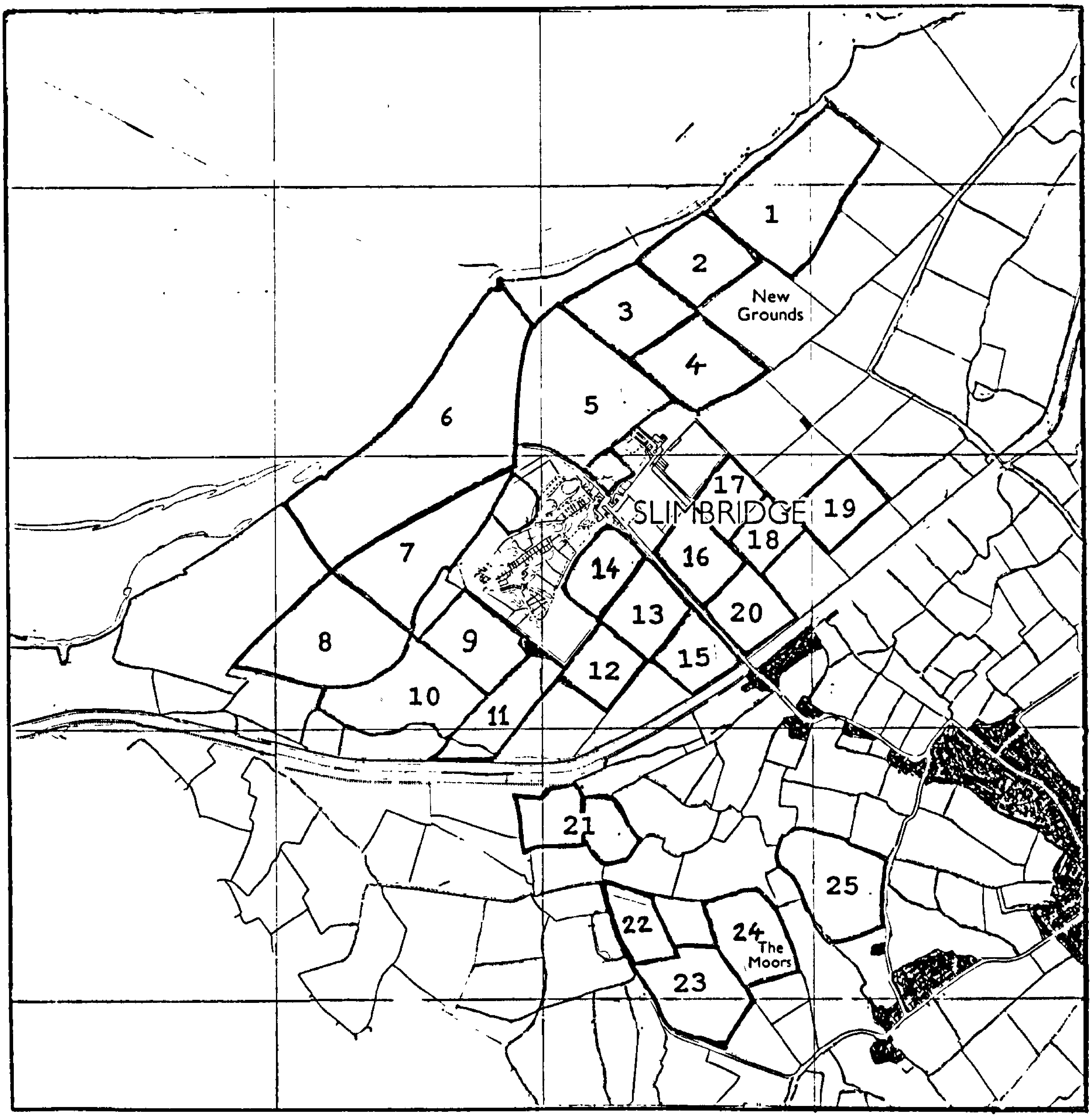


Fig. 3.3. The location of sites in the Severn valley regularly used by Bewick's Swans during the 1989-90 to 1992-93 winters inclusive (adapted from Rees 1988)



Key: 1 New Grounds, Slimbridge
2 The Moors, Slimbridge
3 Walmore Common
4 Ashleworth Ham
5 Avon meadows

Fig.3.4. Fields in the Slimbridge area used by Bewick's Swans during the period 1989-90 to 1992-93



Fields on the Slimbridge WWT reserve

1 Fifty Acre
2 Severn Ground
3 Goose House Ground
4 Ox Piece
5 Tack Piece
6 Dumbles
7 Top New Piece
8 Bottom New Piece
9 Tin Shed
10 Four Score
11 Seventeen Acre
12 South Middle Extension
13 South Middle
14 New South Lake ground
15 South East Road
16 North Middle Road
17 North North Middle Road
18 North North East Road
19 Hurn's
20 North East Road

Beyond reserve

21 Canal Fields
22 Pylon A
23 Pylon
24 Pylon B
25 JB's

Fig 3.5 Dendrogram showing the similarities and differences between logically selected suites of fields, in terms of their use by swans from the Grounds roost, as revealed by Orthogonal comparisons (Key: ** P<0.01, * P<0.05, NS P>0.05, + more, - less).

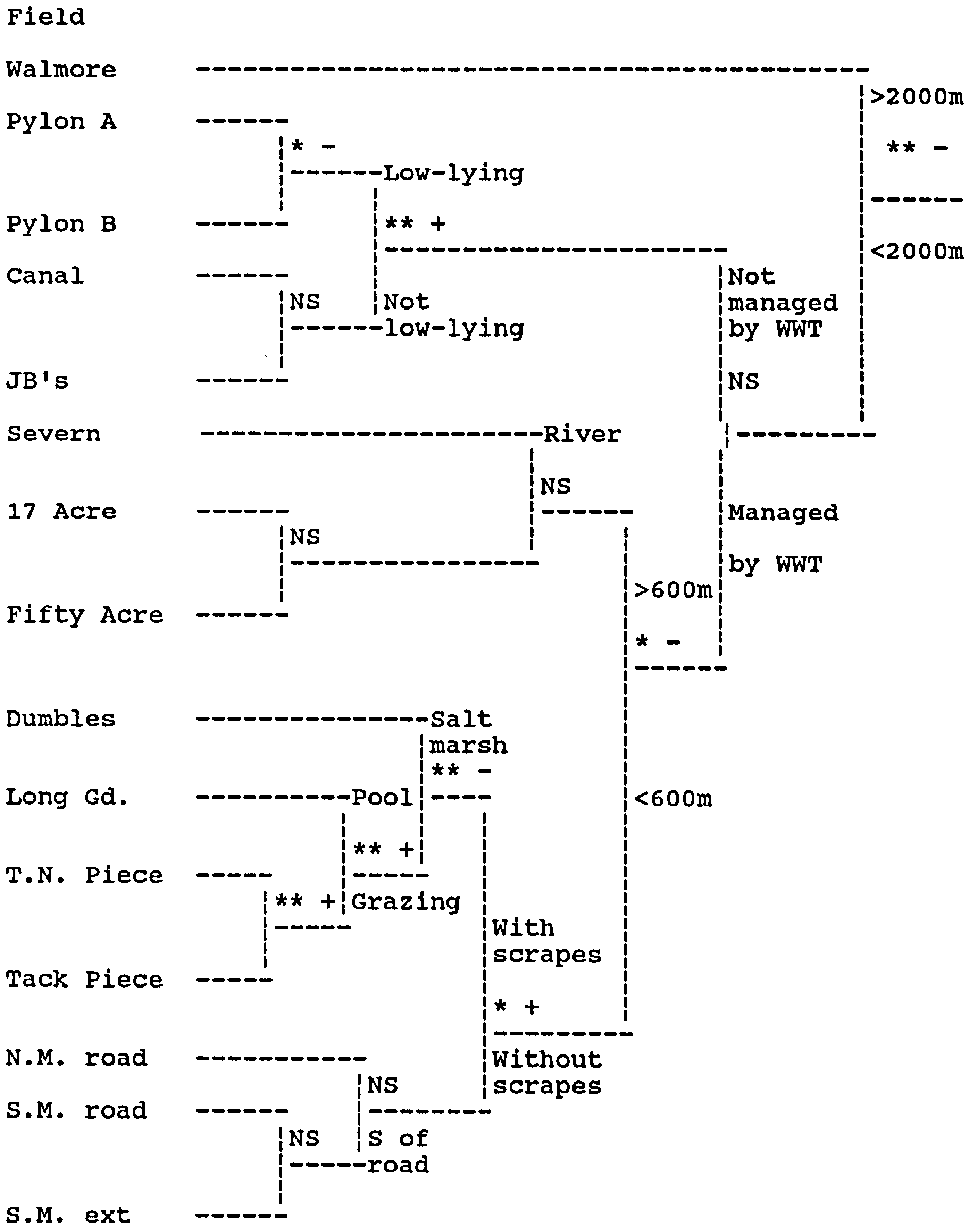


Fig 3.6 Dendrogram showing the similarities and differences between logically selected suites of fields, in terms of their use by swans from the Rushy Pen roost, as revealed by Orthogonal comparisons.

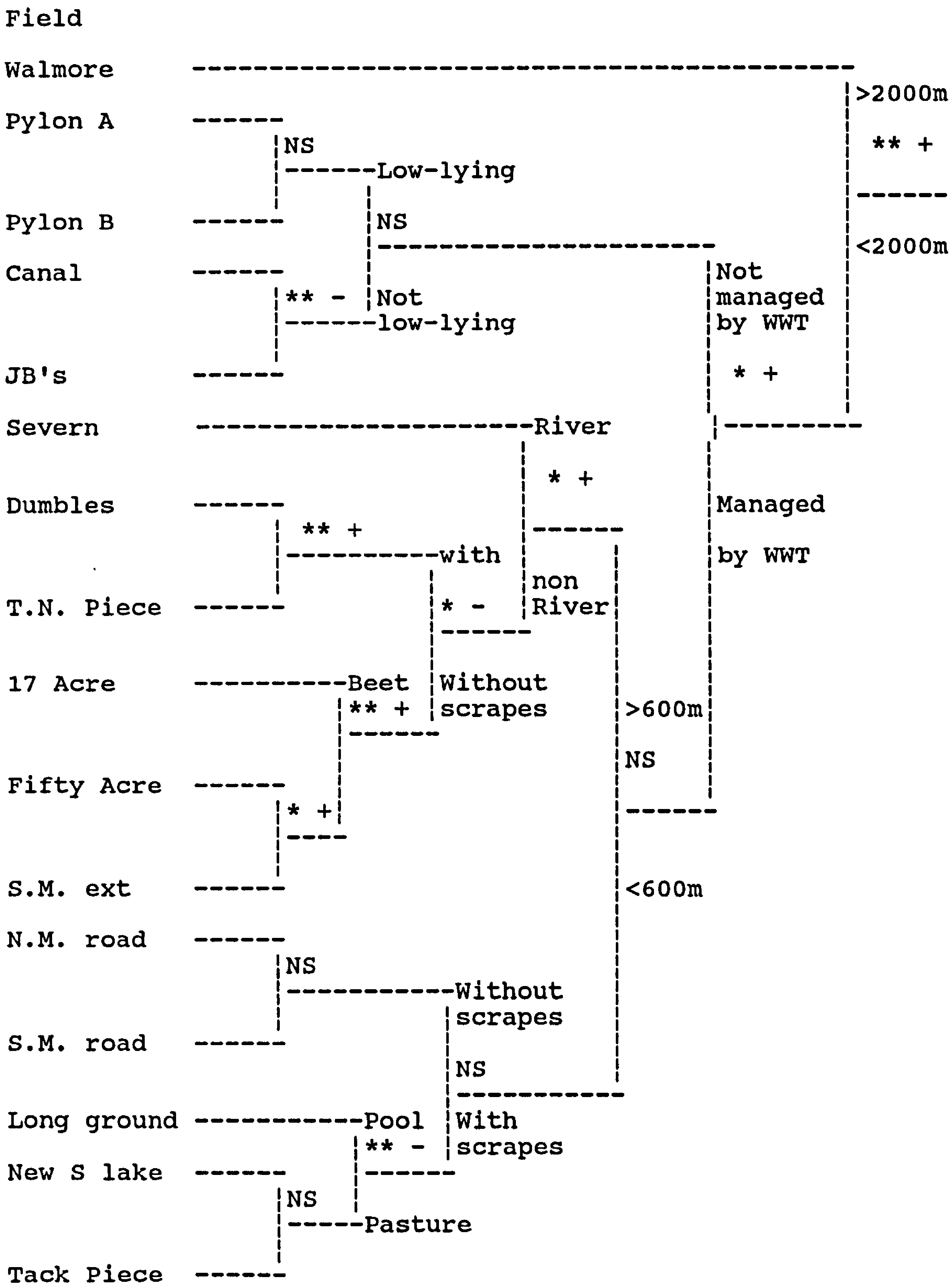


Fig 3.7 The proportion of Grounds units at the feeding sites with distance from the Grounds roost (mean per field for winters 1989-90 to 1992-93 inclusive plus S.E. bar. Walmore Common excluded).

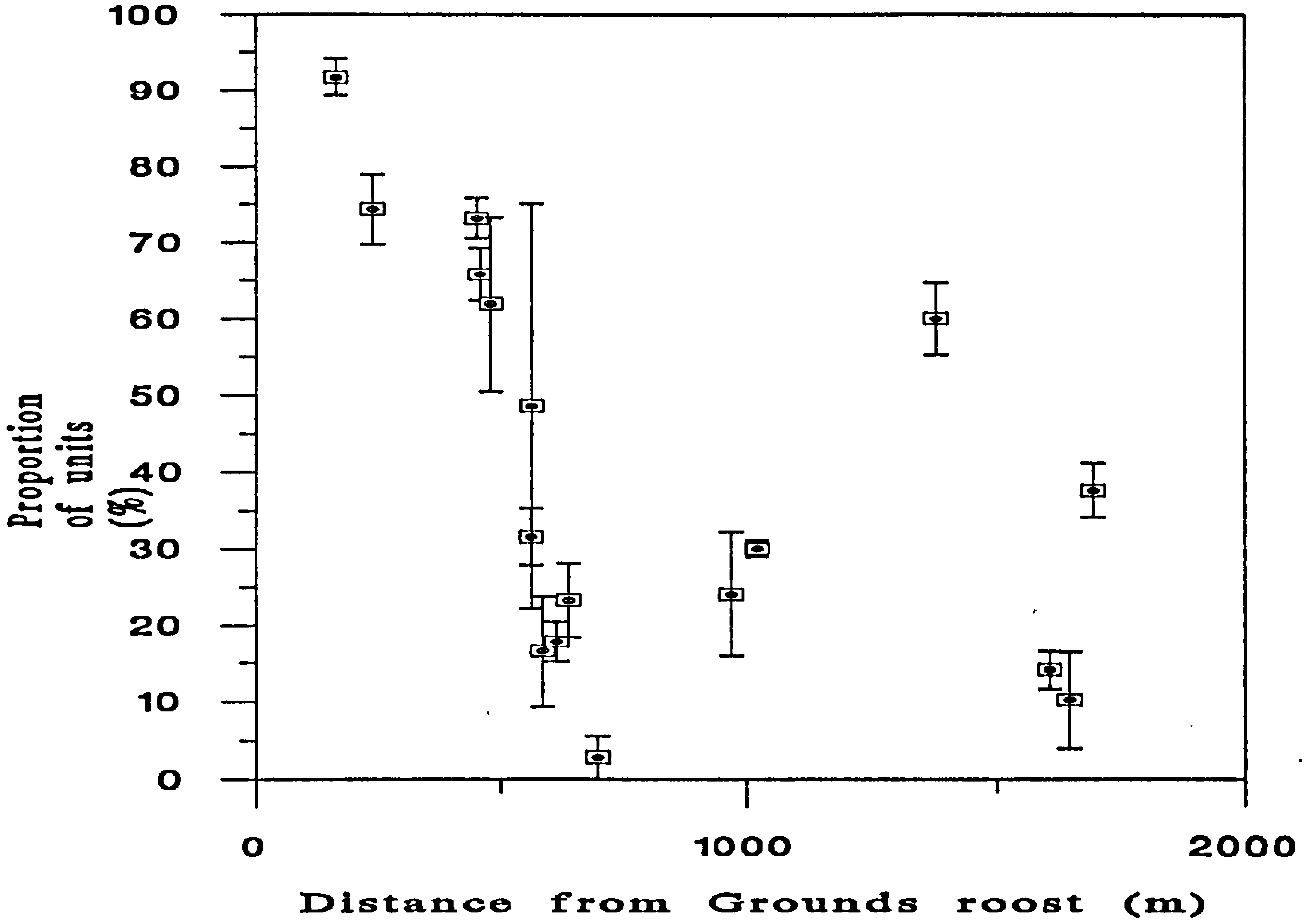
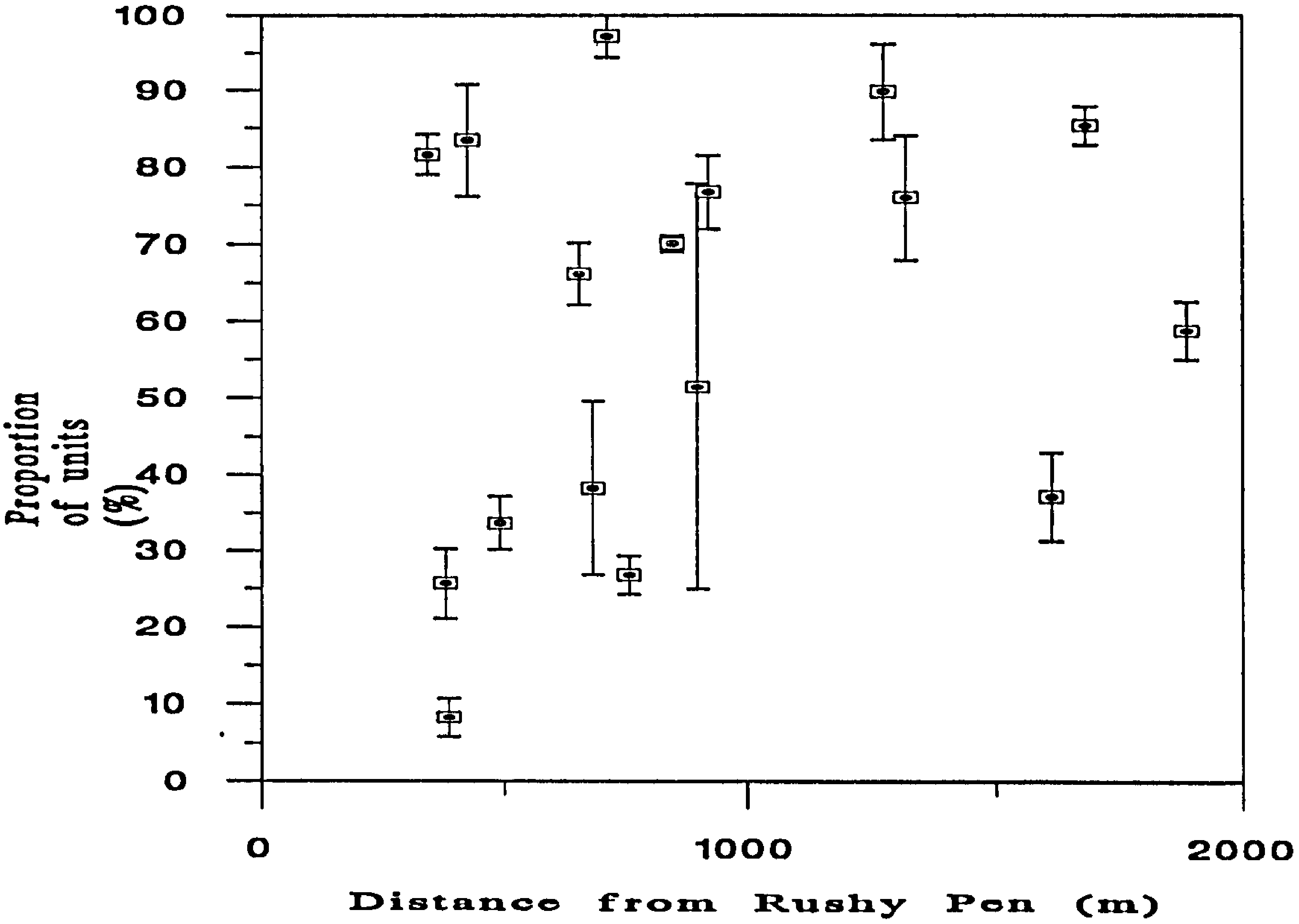


Fig 3.8. The proportion of units from the Rushy Pen at the feeding sites with distance from the Rushy Pen roost (mean per field for 1989-90 to 1992-93 winters inclusive plus S.E. bar. Walmore Common excluded).



CHAPTER 4 CHANGES IN THE DISTRIBUTION OF THE SWANS AT FEEDING SITES DURING THE WINTER

4.1 INTRODUCTION

The general pattern of swan distribution on the Slimbridge fields was established during the first two winters of fieldwork (1989-90 and 1990-91). Changes in this pattern of use were investigated in greater detail during the 1991-92 and 1992-93 winters in relation to habitat variables.

Feeding site selection amongst herbivorous grazing wildfowl in winter has been investigated in detail by a number of authors, including work conducted on Greater White-fronted Geese Anser albifrons (e.g. Owen 1971, 1972a and 1973a), Bean Geese Anser fabalis (Sutherland & Allport 1994), Brent Geese (e.g. Ranwell & Downing 1959, Summers & Critchley 1990, McKay et al. 1994, Rowcliffe et al. 1995), Barnacle Geese (e.g. Drent & Swiestra 1977, Owen et al. 1977, Black et al. 1991, Black et al. 1992), Eurasian Wigeon Anas penelope (Owen 1973b, Mayhew 1985, Mayhew & Houston 1989) and Bewick's Swans (Rees 1990). The nutrient quality and digestibility of grass vary greatly according to the stage of growth (Gill et al. 1989), and this may have a profound influence on herbivore feeding patterns (McNaughton 1979). If the digestibility and intake maxima occur under different grazing pressures, the herbivore will face a trade-off dependent on its specific requirements and digestive strategy (Rowcliffe et al. 1995). Owen (1971) demonstrated that Greater White-fronted Geese grazing on the Dumbles at Slimbridge were highly selective in their choice of vegetation zone, and that the basis of this selection may have been in relation to sward height, the proportion of live material in the sward, vegetational composition and its nutritive value. Ranwell and Downing (1959) found pronounced seasonal differences in the food of the Brent Goose in Norfolk, with birds showing a clear preference in autumn for one food source, Zostera, over another, Enteromorpha. Owen (1971) suggested that this selection had a nutritional basis since the main Zostera species (Z. nana) contained three times more protein and six times as much soluble carbohydrate as Enteromorpha. Similarly Owen (1973b) showed that food selection by Eurasian Wigeon in Somerset could partly be explained by differences in nutritive value, but that other factors such as digestibility and physical characteristics probably also played a part. Buchsbaum et al. (1984) suggested that deterrent secondary metabolites (mostly phenols) had a primary role in determining food palatability in Canada Geese. However, in a multi-factor experiment in which phenol and protein content and height of grass were manipulated simultaneously, Gauthier & Bedard (1990) found no evidence to show that phenol content played a primary role in determining food preference in Snow Geese Anser caerulescens hyperboreus; instead, protein content of plants was found to be a more important factor. Water content of the vegetation may also be relevant however, since it has been found to be correlated both to protein content and to the ease with which vegetation was broken up in the gizzard, thereby controlling the availability of nutrients to the bird (Owen et al. 1977).

The relationship between feeding site selection and the quantity of food available has been demonstrated to differ amongst species of grazing wildfowl. Feeding site selection will be influenced by the effect of diminishing returns when birds are grazing on a depleted food supply, and by the ability of the birds to respond to variable pay-offs over time (e.g. Caracao et. al 1990, Houston & McNamara 1982). Bean Geese in Norfolk, for example, tended to select sites with grass swards of high biomass (Sutherland & Allport 1994), however as the swards were depleted by increased grazing, particularly by stock and Eurasian Wigeon, the consequent reduction in intake rates resulted in an increasing redistribution to other sites. Eurasian Wigeon have been shown to prefer swards that had been grazed short by cattle (Rijnsdorp 1986), although Mayhew & Houston (1989) showed that Eurasian Wigeon were prepared to risk feeding further from the water if grass biomass was greater further away. Brent Geese in Norfolk were found to select fields with a high percentage of live grass, (Summers & Critchley 1990), but of these, the fields with the shortest grass and fewest thistles were then used most intensively. The authors suggested that the selection of fields may initially have been on the basis of their colour, with geese preferring dark green vegetation (high percentage of live grass or biomass) to pale green (with a correspondingly low percentage of live grass or biomass), but the relative importance of food quantity and food quality was not established. Owen (1980) demonstrated that geese tend to select grasses with a high protein content, but suggested that the basic cause for this was the need for energy, since grass has a very high protein content and geese were therefore more likely to be short of energy. Summers & Atkins (1991) similarly showed that although small leaves of Aster tripolium on a Norfolk salt-marsh contained proportionately more protein and water-soluble carbohydrates than large leaves, Brent Geese did not select the most nutritious leaves but instead selected the mid-sized leaves in order to maximise their intake of nutrients. The advantage of food with a high protein content is the availability of highly digestible constituents (protein and soluble carbohydrates) which are an important energy source (Prop et al. in prep). Nutritional requirements may change during the course of the winter. McKay et al. (1994), for example showed that Brent Geese in Sussex, switched from winter cereals to pasture in early winter. The switch in feeding site selction did not appear to be in response to relative changes in nutrient quality and the authors concluded that Brent Geese may maximise dietary protein early in the winter, perhaps to replace that lost during migration, and thereafter attempt to maximise water soluble carbohydrates.

Rees (1990) demonstrated that Bewick's Swans in Gloucestershire occurred most frequently and in greatest numbers at sites where the highest biomass of green grass was available, and that the percentage of protein was a relevant secondary factor. When other grazing species of waterfowl were also present, site usage became more closely correlated with maximum sward-length, which, perhaps surprisingly, did not correlate significantly with biomass, possibly because the grazing activity of geese and Eurasian Wigeon caused some 'thinning' of the sward. The total variation in the count data accounted for by habitat variables in the study was low, however (32.6%), and this was attributed to grazing pressure from other waterfowl species (over 70% of the variation in the count data was accounted for when this variable was added). The influence of social factors was not considered in detail and the current study aims to investigate these factors more fully.

The chapter set out to answer the following questions:
1) Do swans from different social classes differ in terms of feeding site selection, and does the proportion of cygnets at a feeding site decrease with flock size. This would be predicted if families were monopolising the best food resources as shown amongst Brent Geese (Lambeck 1990) and demonstrated experimentally amongst Blue Geese (Mulder et al. 1995).
2) How does swan distribution at the feeding sites vary, both within and between winters.
3) How does food quantity and quality change during the course of the winter, and what affect do these changes have upon swan distribution at the feeding sites. Swans might be expected to concentrate at sites with the highest biomass of green grass available and/or highest protein levels (Rees 1990), although the extent of flooding may also be relevant through its effects on digestive ability (Owen et al. 1977).
4) Does the grazing activity of other Anatidae affect swan distribution at the feeding sites. In a previous study, increased grazing by other wildfowl lead to a reduction in the number of swans using a field (Rees 1990).
5) Do swans from the two roost groups differ in their distribution at the feeding sites and if so, how does their selection of feeding sites differ in relation to the quantity and quality of food available.

4.2 METHODS

a) Swan numbers

The numbers of swans on the fields of the Slimbridge refuge, on adjacent farmland, and at Walmore Common (the only other more distant site known to be used regularly by the Slimbridge swans during the study period), were counted on a near-daily basis (see Chapter 3, for location of fields see Figs. 3.3 & 3.4). Since the numbers varied considerably, both during the course of a winter, and between winters, the count data were transformed in order to permit analysis. Firstly the maximum count (y) for each field on a given day, or "y swan-days", was recorded (see Owen 1972b). Where a field was not counted for a short period (usually one to three days), the mean of the counts made immediately before and after this period was used as an estimate of the number of swans present on the days with missing data. Monthly swan use of a given field was calculated by summing the swan-days for each field by month and dividing this figure by the total number of swan-days for all fields in the month. This figure was then multiplied by one hundred in order to give percentage monthly swan use (see Rees 1990).

Rees (1988) demonstrated that Bewick's Swans were attracted in large numbers to potatoes put out on the Slimbridge refuge and that this masked the effect of other habitat variables upon swan distribution. During the current study, potatoes were distributed on just one field, the Tack Piece, and attracted swans from the two roost groups in both winters in which detailed habitat data were collected (1991-92 winter: December - March inclusive, 1992-93 winter: January only). Data concerning this field therefore were removed prior to the calculation of the total number of swan-days for each month, in order to remove the potentially confounding effects of the availability of potatoes on the distribution of the swans.

b) Habitat variables

Sward-length

Length of grass sward on the fields was monitored monthly. Average sward height was calculated from the mean of twenty measurements taken per field of extended grass blades (ground level to tip). The grass blades selected for measurement were the nearest to the marked corner of a ruler thrown randomly twenty times in the field.

Biomass

Standing green biomass is a good measure of the quantity of food available in a field. Mayhew et al. (1984) calculated green biomass by using a spectrophotometer to measure the ratio of Far Red to Red radiation reflected by the vegetation. However, the FR/R ratio correlates closely with green biomass only under constant light conditions. Since habitat sampling of the fields was conducted mostly at night, in order to prevent the disturbance of feeding swans, the use of a spectrophotometer was not feasible for this study. Instead biomass was estimated by clipping all grass from within a quadrat of 10 x 25 cm thrown randomly into the parts of each field where swans had been recently observed grazing. Swans mostly graze in the centre of fields and swards therefore tend to increase at the edges. Grass was clipped from ground level with scissors and placed into polythene bags. Live (green) grass was separated out from the dead and placed in an oven at 100° C for 24 hours. The removal of dead grass is assumed valid since it has been shown that Greater White-fronted Geese take a diet of up to 80 % green matter from a sward containing up to 50 % dead grass (Owen 1972a). The crop contents of one Bewick's Swan, which flew into power cables during the current study, contained only green grass although it had spent the day feeding on a sward containing up to 20% dead grass. The samples of dried green grass were then weighed and the subsequent weights multiplied by 40 in order to give grammes of live green grass per m^2. A minimum of two samples were taken per field per month. Sampling was conducted monthly on those fields of the Slimbridge refuge that had been used regularly by swans during the previous two winters, the adjacent 'Moors' fields, and at Walmore Common. Additional fields were sampled once they had been visited by swans in appreciable numbers during a given month. Heavy flooding at Walmore Common prevented sampling of the central field (Field C) in February 1991, and February 1992.

Protein content

Grass samples collected for protein analysis were obtained by hand-plucking the swards between thumb and forefinger, thereby simulating the pecking action of the swans (see Rees 1990). The samples were sorted into live and dead material. The dead grass was discarded and the live grass was dried for 24 hours at 100°C in an oven. Samples were again collected monthly, dried and stored in desiccators prior to analysis. The samples were analyzed in the laboratories of Waterfall & O'Brien, Bristol, by the Kjeldahl technique in order to determine percentage Nitrogen content. This figure was then multiplied by 6.25

to approximate crude percentage protein content (as in Ydenberg & Prins 1981, Mayhew 1985).

Percentage water cover

The percentage water cover of a field was estimated by eye, either from the edge of the field or from a higher vantage point where possible. If no surface water could be seen, but water was known to be lying due to the swans drinking and/or splashing water during aggressive interactions, coverage was taken as 1% (ground checks were made during habitat sampling sessions at night to verify this). Depth of standing water on a field was not found to be a significant factor in the selection of fields by Bewick's Swans in the Slimbridge area by Rees (1990); water depth therefore was not considered further in the current study. Similarly field size did not influence the percentage swan-days recorded for each site during the winter (Rees 1990), and this factor was not considered further here.

c) Statistical analyses

Field use by units from the three main social classes (i.e. families, pairs and singletons) were first investigated separately to see if there were any differences in their use of the feeding sites (see Table 4.1a). Analyses of variance, which included field identity as a categorical variable, were conducted, and orthogonal comparisons were then used to highlight similarities and differences between selected suites of fields. Criteria used for grouping fields included: distance from the roost site, field management (WWT or non - WWT), presence/absence of a permanent water-filled scrape, habitat type (pasture, sugar beet or river), low-lying / not low-lying. Yearlings still associating with their parents were omitted from analysis, since their choice of feeding site was thought to be influenced by the movements of their parents. The number of units identified in each flock was transformed for analysis since Bartlett's tests revealed heterogeneity in the group variances for each social class. In this instance heterogeneity in group variance was reduced by the transformation: $x^1 = \log(10x + 1)$. Two of the field sites on which feeding flocks were recorded were omitted from analysis (Avon Meadows, and Tin Shed field) as the sample sizes were low ($n < 5$ for both sites) and there was no variance in the number of units identified for at least one of the roost groups. The distance of a field from the Slimbridge roosts was taken to be the mean of the two measurements from the Rushy Pen roost and the Grounds roost (see Chapter 3).

The effect of the independent variables in influencing feeding site selection by the swans (measured in terms of the mean number of swan-days recorded for each field each month) was determined by co-variate analysis using GLIM (NAG 1986). Co-variate analysis was chosen in order to identify the individual variables from a number of inter-related variables, which had a significant effect upon field selection. Seven variables were examined initially in relation to field use since it was thought that they might explain variation in the monthly swan count data: year, time (coded by month), protein content, sward-length, biomass, percentage water cover and presence/absence of supplementary feeds of potatoes (coded as 1/0). Year and presence/absence of potatoes were treated as factors. A binomial error distribution was used in which monthly swan totals for each field were divided by the total number of swan-days in the relevant month (the binomial denominator). This distribution was used since the number of swans both using and not using a field was known in each month. Moreover since the distribution does not use the percentage field use as the response variable, the sample size information could be retained for each month. Over-dispersion of the data was compensated for, in cases where the residual deviance was considerably larger than the residual degrees of freedom, by the use of the WILLS.MAC programme. This macro assumes that the variance is not npq (where n is the size of the sample, p is the proportion of swan-days in a month on a given field and q is $1-p$) but $npqs$, where s is an unknown scale parameter ($s > 1$). The macro calculates an estimate of s by dividing the Pearson X^2 value by the degrees of freedom, and uses this estimate to set a scale directive in the model (Crawley 1993). The number of combined effects entered into the initial model was reduced by first determining which of the seven variables were significant, then including the interaction of these variables as factors in the model. Only two were found to have a near-significant effect on the distribution of swans: percentage water cover and biomass, and these were included in the main model. The statistical significance of the explanatory variables, and their interactions, was then determined by fitting the full model and inspecting the changes in deviance with respect to the change in the degrees of freedom (Crawley 1993). The most non-significant ($P > 0.05$) variables were then progressively removed from the model. The final model was thus the most parsimonious (see Crawley 1993).

Rees (1990) demonstrated that there was a strong inverse correlation between Bewick's Swan days on fields at Slimbridge and their use by other grazing wildfowl, particularly Greater White-fronted Geese and Eurasian Wigeon. A further model was therefore run as before but including two additional variables, goose-days (including use by feral Canada and Greylag Geese) and wigeon-days, which were calculated monthly in the same way as swan-days, from reserve reports (D.B. Paynter pers comm.). Goose/wigeon-days were looked at in two ways:

1) Goose/wigeon-days for the **same** month in which swans were seen in a field to investigate any inter-specific 'competition'.

2) Goose/wigeon-days for the **previous** month in which swans were seen in a field, because their grazing may have affected sward composition/biomass.

Only the 20 fields used by the swans at the New Grounds were included in this analysis, since daily goose and duck count data for the more distant sites were not available. Mean distance from the two main roost-sites (see Chapter 3) was added as a variable.

A final model aimed to investigate the differences in the extent to which swans from the two roost-groups frequented the different fields. The dependent variable was the number of units from each of the two roost-groups identified per month, expressed as a ratio of the total number of swan units identified on that field in that month. The effects of all independent variables, including distance from the two roost-sites, were considered initially, using a log linear model (with Binomial error structure) in GLIM, and the most parsimonious model was derived as before.

4.3 RESULTS

a) Field use in relation to social class

i) Families

An analysis of variance, including field identity as a categorical variable, revealed that 15.5% of the variance in the number of families identified in feeding groups could be attributed to the fields alone (F-ratio $= 6.78$, $P < 0.001$, $n = 608$).

Orthogonal comparisons highlighted significant differences, in terms of the number of families identified, between logically selected suites of feeding sites (Fig. 4.1, df = 1 in all cases). Walmore Common was not significantly different from the 16 sites lying less than 2000 m from Slimbridge ($F = 0.04$, $P > 0.8$). Of the remaining 16 sites, the twelve managed by WWT did not differ significantly from the four fields not managed by WWT ($F = 0.18$, $P > 0.05$). Of the four fields not managed by WWT, the two low-lying Moors fields were significantly different from the two located on higher, well-drained land ($F = 10.35$, $P < 0.001$). The two Moors fields did not differ from each-other ($F = 3.46$, $P > 0.05$) and the two well-drained fields were significantly different from each-other ($F = 5.29$, $P < 0.025$). Of the twelve remaining sites managed by WWT, the six lying closest to the Slimbridge roost (< 600 m) did not differ significantly from the six more distant (>600 m) sites ($F = 0.00$, $P > 0.9$). The River Severn site did not differ from the five remaining WWT managed, more distant sites ($F = 0.93$, $P > 0.3$). Of the five remaining WWT managed more distant sites, the one root crop field (Seventeen-acre) was differed significantly from the four pasture fields ($F = 5.38$, $P < 0.025$). The two remaining fields containing permanent water-filled scrapes did not differ significantly from the two without scrapes ($F = 1.49$, $P > 0.2$). The two fields with scrapes differed from each-other ($F = 31.21$, $P < 0.001$), but the two remaining more distant, WWT managed fields without scrapes did not differ significantly from each-other ($F = 0.10$, $P > 0.75$). Of the remaining six WWT managed sites lying close to the Slimbridge roost, the one site lacking field grazing did not differ from the five pasture sites ($F = 1.68$, $P > 0.1$); the two pasture sites containing permanent water-filled scrapes did differ significantly from the three that did not contain scrapes ($F = 4.28$, $P < 0.05$) but were not significantly different from each-other ($F = 1.02$, $P > 0.3$). Of the three fields without scrapes, the two lying south of the entrance road to WWT did not differ from the field lying to the north ($F = 1.57$, P

> 0.2) and the two lying south of the road did not differ from each-other ($F = 1.68$, $P > 0.1$).

ii) Pairs

An analysis of variance, including field as a variable, revealed that 12.6% of the variance in the number of pairs identified in feeding groups could be attributed to the fields alone (F-ratio $= 5.33$, $P < 0.001$, $n = 608$).

Orthogonal comparisons highlighted significant differences, in terms of the number of pairs identified, between logically selected suites of feeding sites (Fig. 4.2, df = 1 in all cases). Walmore Common did not differ significantly from the 16 sites lying less than 2000m from the Grounds roost ($F = 2.69$, $P > 0.1$). Of the remaining 16 sites, the twelve managed by WWT did not differ from the four sites not managed by WWT ($F = 0.59$, $P > 0.4$). Of the four fields not managed by WWT, the two low-lying Moors fields differed significantly from the two located on higher, well-drained land ($F = 5.21$, $P < 0.025$). Both the two Moors fields and the two well-drained fields were significantly different from each-other ($F = 4.50$, $P < 0.05$, and $F = 6.20$, $P < 0.025$, respectively). Of the twelve remaining sites managed by WWT, the six lying closest to the Slimbridge roost (< 600 m) did not differ significantly from the six more distant (> 600 m) sites ($F = 0.44$, $P > 0.5$). The River Severn differed significantly from the five remaining WWT managed, more distant fields ($F = 4.73$, $P < 0.05$). Of the five remaining WWT managed more distant fields, the one root crop field (Seventeen-acre) did not differ significantly from the four pasture fields ($F = 3.64$, $P > 0.05$); the two remaining fields containing permanent water-filled scrapes did not differ from the two without scrapes ($F = 0.00$, $P > 0.9$). The two fields with scrapes and the two fields without scrapes did not differ significantly from each-other ($F = 1.45$, $P > 0.2$ and $F = 0.08$, $P > 0.7$, respectively). Of the remaining six WWT managed sites lying close to the Slimbridge roost, the one site lacking field grazing differed significantly from the five pasture sites ($F = 4.20$, $P < 0.05$). The two pasture sites containing permanent water-filled scrapes differed significantly from the three that did not ($F = 7.36$, $P < 0.01$) but not from each-other ($F = 0.65$, $P > 0.4$). Of the three fields without scrapes, the two lying south of the entrance road to WWT did not differ from the field lying to the north ($F = 0.01$, $P > 0.9$) or from each-other ($F = 2.05$, $P > 0.1$).

iii) Singletons

An analysis of variance, including field as a categorical variable revealed that 15.4% of the variance in the number of singletons identified in feeding groups could be attributed to the fields alone (F-ratio = 6.71, $P < 0.001$, $n = 608$).

Orthogonal comparisons highlighted significant differences, in terms of the number of singletons identified, between logically selected suites of feeding sites (Fig. 4.3, df = 1 in all cases). Walmore Common did not differ significantly from the 16 sites lying less than 2000m from the Grounds roost ($F = 1.29$, $P > 0.2$). Of the remaining 16 sites, the twelve managed by WWT did not differ significantly from the four sites not managed by WWT ($F = 1.87$, $P > 0.1$). Of the four fields not managed by WWT, the two low-lying Moors fields did not differ significantly from the two located on higher, well-drained land ($F = 1.63$, $P > 0.2$). The two well-drained fields differed significantly from each-other ($F = 13.94$, $P < 0.001$) but the two Moors fields did not do so ($F = 0.06$, $P > 0.8$). Of the twelve remaining sites managed by WWT, the six lying closest to the Slimbridge roost (< 600 m) did not differ significantly from the six more distant (> 600 m) sites ($F = 0.06$, $P > 0.8$). The River Severn site did not differ significantly from the five remaining WWT managed, more distant fields ($F = 3.00$, $P > 0.08$). Of the five remaining WWT managed more distant fields, the one root crop field (Seventeen-acre) differed significantly from the four pasture fields ($F = 8.31$, $P < 0.005$). The two remaining fields containing permanent water-filled scrapes did not differ significantly from the two without scrapes ($F = 0.06$, $P > 0.8$). In addition, the two fields with scrapes and the two without scrapes did not significantly differ from each-other ($F = 0.83$, $P > 0.3$ and $F = 0.13$, $P > 0.7$, respectively). Of the remaining six WWT managed sites lying close to the Slimbridge roost, the one site lacking field grazing did not differ significantly from the five pasture sites ($F = 3.62$, $P > 0.05$); the two pasture sites containing permanent water-filled scrapes differed significantly from the three without scrapes ($F = 7.40$, $P < 0.01$) but did not significantly differ from each-other ($F = 0.94$, $P > 0.3$). Of the three fields without scrapes, the two lying south of the entrance road to WWT did not differ significantly from the field lying to the north ($F = 1.74$, $P > 0.1$) or from each-other ($F = 1.69$, $P > 0.1$).

iv) Relative field use by birds of different social class

Chi-square tests were used to determine whether the number of units of each social class recorded at the feeding sites differed from field to field (Table 4.1b). There was a significant difference between the proportion of families identified and the number of units from the other two social classes on nine of the 18 field-sites considered. There were significantly more family units than expected on the Seventeen-acre field, Canal fields, JB's field, Long Ground and Top New Piece; and significantly fewer family units than expected on the Dumbles, Pylon Field, Moors field, and the South Middle field. There was a significant difference between the proportion of pairs identified and the number of units from the other two social classes on six of the 18 field-sites considered. There were significantly more pairs than expected on the Moors field B and the South Middle road field; and significantly fewer pairs than expected on the 17-acre field and JB's field. There was a significant difference between the proportion of singletons identified and the number of units from the other two social classes on three of the 18 field-sites considered. There were significantly more singletons than expected on the Dumbles and significantly fewer pairs than expected on the Long Ground and the Top New Piece.

There were no significant correlations between the percentage of units identified in a flock from each of the three social classes and mean distance from the two Slimbridge roost-sites, excluding the anomalous Walmore Common site (Spearman's rank correlations, n = 18, r_s = -0.217 for families, $P > 0.1$, r_s = 0.090 for pairs, r_s = 0.392, $P > 0.1$ for singletons), although the trend was negative for families (Fig. 4.4) and positive for singletons (Fig. 4.5). There was no obvious trend for pairs without cygnets (Fig. 4.6).

v) Field use and percentage of cygnets

The percentage of cygnets identified at the feeding sites varied significantly between years, reflecting the differences in breeding success between seasons (see Table 4.2). There was no significant difference between the 1990-91 and 1991-92 winters in the percentage of cygnets identified at the feeding sites and data from these two winters were selected for the following analysis.

The percentage of cygnets identified at the feeding sites was significantly negatively correlated with flock-size (Spearman's rank correlation r_s = -0.231, $P < 0.01$, n = 335). There was no significant correlation between the percentage of cygnets identified at the feeding sites and distance from the Slimbridge roost when all feeding sites were included in the analysis (r_s = -0.089, $P > 0.1$, n = 17) or when the anomalous Walmore Common site was omitted (r_s = -0.199, $P > 0.1$, n = 16).

b) Swan numbers

Variation in the percentage swan-days recorded for each field each month is given in Table 4.3. The extent to which swans visited fields in the Slimbridge area was not consistent between the two (1991-92 and 1992-93) winters (Table 4.3c).

i) The 1991-92 winter (see Table 4.3a).

A total of 39 different feeding sites were used by swans during the course of the winter, including 11 fields at Walmore Common. The first arrivals in October used several fields on the Slimbridge refuge and at Walmore Common, with the highest numbers being recorded on the Dumbles (Slimbridge refuge) and at Walmore (Table 4.3a, see Fig 3.4). Although November was largely dry, many birds transferred to Walmore Common (58% of swan-days for the month), where they grazed during the day and used a newly created pool on the Common to roost. The percentage of swan-days was also high at the Pylon Field (the Moors) in November, where light flooding proved attractive to swans throughout the month. In December the swans returned to the Slimbridge refuge from Walmore Common, and were attracted in large numbers to potatoes placed around the edges of the scrapes in the Tack Piece. The potatoes were supplied weekly for the rest of the winter and attracted large numbers of swans until their departure in March. Moderate flooding at Walmore Common in February encouraged swans to return to the site to feed and roost on the flooded meadows for the rest of the winter. Swans also frequented the permanent scrapes on both the Top New Piece and the Long Ground (Slimbridge refuge) throughout the winter.

ii) The 1992-93 winter (see Table 4.3b).

A total of 30 different feeding sites were used by swans during the course of the winter, including 13 fields at Walmore Common. The swans concentrated at just two fields on the Slimbridge refuge in October with numbers on the Dumbles accounting for 84% of swan-days. Walmore Common remained dry throughout the month and received no swans until November when heavy rain resulted in deep flooding at the site. Around 50% of swan-days recorded in both November and December were at Walmore. At Slimbridge the Dumbles received the highest proportion of swan-days in November, but birds also started visiting the South Middle, where 10-20% of swan-days were recorded each month for the rest of the winter. The swans returned from Walmore during a cold spell at the end of December, as the flood-waters on the common first froze over and then drained away. Further heavy rain in mid-January, however, caused both the floods and the swans to return to the site later in the month. February and March were largely dry and there were no Bewick's Swans at Walmore in either month. The widespread flooding in January encouraged the swans at Slimbridge to use a wide range of feeding sites both on and off the reserve. Potatoes put out along the edges of the scrapes on the Tack Piece at the end of January attracted large numbers of swans for the rest of the winter, but smaller numbers also made use of several other feeding sites on the reserve, particularly prior to their departure on spring migration in March. The number of swans flighting to the mudflats of the River Severn, increased greatly in March in both winters (Table 4.3c).

iii) During all winters (1989-90 to 1992-93, see Table 4.3d).

The number of fields utilised by swans each month was investigated in order to see if there was evidence for a wider dispersal of swans during the mid-winter period as the food supply diminished. The greatest numbers of fields visited were in December and January with fewer at the start and end of the winter (Table 4.3d). However, this pattern of increasing dispersal during the mid-winter months may simply reflect the number of swans present in the area. The number of fields utilised each month was positively correlated with the total monthly swan-days (Pearson's correlation, $r = 0.639$, $P < 0.01$, $n = 24$). Fig 4.7 shows the linear relationship between the mean number of fields utilised during each month of the winter and mean monthly swan-days.

c) The habitat variables

Sward-length. There was considerable variation in sward-lengths, both between fields and during the winter season, with mean sward-length ranging from 27 mm (the Dumbles in March 1992) to 243 mm (Walmore Common field A in December 1992). Sward-lengths were greatest at the start of the winter, in October, and declined steeply as the winter progressed, reaching a minimum value in January (Fig. 4.8). Sward-length increased from January onwards as grass growth increased over grazing pressure. However, mean sward-length in March was still lower than in October.

Biomass. Biomass of vegetation recorded each month followed the same pattern as the sward-length values. Mean biomass declined from October to a minimum value in January, before increasing through February and March (Fig. 4.9). Biomass is closely linked to sward-length and the two variables correlated significantly with each other (Pearson's rank correlation, $\underline{r} = 0.551$, $\underline{P} < 0.01$, $\underline{n} = 85$). Mean monthly biomass values ranged from 15.78 g/m^2 (Fifty Acre field in March 1992) to 213.53 g/m^2 (Fifty Acre field in October 1992).

Protein content. The percentage of crude protein in the vegetation recorded each month ranged from 17.5% (Dumbles in November 1992) to 33.5% (Pylon Field, the Moors in March 1993). The pattern of mean monthly percentage protein during the winter differed from that of sward-length and biomass; minimum values occurred in November, and protein content increased each month thereafter, reaching a peak in March (Fig. 4.10). This pattern is rather different from those obtained by Rees (1988) and Mayhew (1985) where protein levels decreased mid-winter and then increased again in March. Since there were no differences in sampling, the difference may stem from the extremely mild nature of the 1991-92 and 1992-93 winters which permitted the grass to continue growing throughout. This seems likely since in a similar study conducted during the 1991-92 winter in Sussex, the protein content of grass pasture followed an almost identical pattern to that recorded in the current study (McKay et al. 1994).

Percentage water cover. The percentage of the field covered by water was linked to both rainfall and to the level of the River Severn. Very high water levels in the river, due to a combination of westerly winds, high spring tides, and heavy rainfall in the preceding days, caused direct flooding of one field lying beyond the sea-wall (the Dumbles) and indirect flooding of the fields at Walmore Common, by reducing the capacity of the drainage system at the site to discharge surface water into the Severn. Mean monthly water cover varied from 0% on many fields during drier months to 67.7% on the central field at Walmore Common (Walmore Field C) in December 1992. Mean monthly water cover generally increased during the winter reaching a peak in December and then declined again in the New Year (Fig. 4.11).

d) Initial model - Habitat variables only

Variation in the percentage of swan-days recorded for each field each month was attributed to the percentage water cover and mean biomass at a near-significant level (Table 4.4). There was no significant interaction between these two variables. The remaining variables which had originally been included; year, month, protein content and sward-length, did not have a significant effect and were subsequently dropped from the model.

Water cover. Percentage water cover had a positive effect on the use of fields by swans at a near-significant level (Table 4.4), with swan use generally increasing as the percentage of field covered by water increased, although at higher levels of percentage water cover, however, swan use appeared to decline (Fig. 4.12). An example of the effect of a flood event on the numbers of Bewick's Swans using the Dumbles, caused by high spring tides in February 1992 is given in Fig. 4.13.

Biomass. Mean biomass of grass available had a negative effect on the use of fields by swans, at a near-significant level, when habitat variables alone were considered (Table 4.4), with swan use generally decreasing as biomass increased (Fig. 4.14), although the trend in the observed data was variable.

e) Second model - Competition with other grazing Anatidae

1) Within a month

Variation in the percentage of swan-days recorded for each field each month was associated with monthly variation in the percentage water cover, protein levels and goose-days at these sites (Table 4.5). There were no significant interactions between any of the three variables considered in the final model. The remaining variables which had originally been included; year, month, sward-length, and mean distance from the roost-sites, did not have a significant effect and were subsequently dropped from the model.

Water cover. As in the previous analysis, percentage water cover had a significant positive effect on the use of fields by swans (Table 4.5), with swan use generally increasing up to a certain level as the percentage of field covered by water increased, but then decreasing with more extensive flooding. The addition of other grazing wildfowl to the model did not affect this relationship (Fig. 4.15).

Protein. Percentage protein content of grass available had a significant negative effect on the use of fields by swans when other grazing wildfowl were added to the model (Table 4.5), with swan use generally decreasing as protein content increased (Fig. 4.16).

Goose-days. Monthly percentage goose-days had a significant negative effect on the use of fields by swans in the same month (Table 4.5), with swan use generally decreasing as goose-days increased, although the trend was not uniform (Fig. 4.17).

2) Effect of grazing from the previous month

When percentage goose-days and wigeon-days for a given month were replaced by the relevant figures from the previous month, variation in the percentage of swan-days recorded for each field each month was associated with monthly variation in percentage water cover, and percentage wigeon-days in the previous month (Table 4.6). In addition there was a significant, perhaps coincidental, interaction between water cover and wigeon-days in the previous month. The remaining variables which had originally been included; year, month, sward-length, biomass, percentage protein content, mean distance from the roost-sites and percentage goose-days from the previous month, did not have a significant effect and were dropped from the model.

Water cover. As in the two previous analyses, percentage water cover had a significant positive effect on the use of fields by swans (Table 4.6), with swan use generally increasing as the percentage of field covered by water increased, although the observed results were rather different from the predicted values. The addition of other grazing wildfowl in the previous month to the model did not affect this relationship (Fig. 4.18).

Wigeon-days. Percentage wigeon-days in the previous month had a significant positive effect on the use of fields by swans (Table 4.6). Predicted swan use generally increasing as wigeon-days in the previous month increased, although observed swan use did not show such a trend (Fig. 4.19).

f) Third model - factors affecting the distribution of swans from the two roost-groups

i) Rushy Pen roost

When all variables were considered, variation in the proportion of all units identified in the fields from the Rushy Pen roost-group, was associated with distance from the roost-site only (Table 4.7a). The highly significant positive relationship between distance from the roost-site and swan-use by swans from the Rushy Pen roost (see Fig. 4.20), masked the effect of other variables and therefore the model was rerun, omitting this variable.

When distance from the roost-site was removed from the model, variation in the proportion of all units identified on the fields from the Rushy Pen roost was associated with percentage water cover, percentage of protein in the grass sward, and year (Table 4.7b). There were no significant interactions between any of the three variables considered in the final model.

Water cover. Percentage water cover initially had a significant positive effect on the use of fields by swans from the Rushy Pen roost (Table 4.7b), with the proportion of swans from the Rushy Pen roost generally increasing as the percentage of field covered by water increased (Fig. 4.21); however, the proportion then decreased as flooding became more extensive.

Protein. Percentage protein had a significant positive effect on the use of fields by swans from the Rushy Pen roost (Table 4.7b), with the number of swans from the Rushy Pen roost generally increasing as protein content increased (Fig. 4.22).

Year. Year had a significant effect on the proportion of Rushy Pen units identified on the fields (Table 4.7b) with a significantly lower mean proportion of Rushy Pen units identified per field (compared to Grounds units) in the 1992-93 winter (38.32%) than in 1991-92 (63.43%). This may reflect the higher proportion of swans roosting in the grounds in 1992-3.

ii) Grounds roost

When all variables were considered, variation in the proportion of all units identified in the fields from the Grounds roost-group, was associated with distance from the roost-site only (Table 4.8a). The highly significant negative relationship between distance from the roost-site and swan-use by swans from the Grounds roost (see Fig. 4.23), masked the effect of other variables and therefore the model was rerun, omitting this variable.

When distance from the roost-site was omitted from the model, variation in the number of units from the Grounds roost identified on the fields was associated with mean biomass of grass, percentage protein content of the sward, and year (Table 4.8b). There were no significant interactions between any of the three variables considered in the final model.

Biomass. Mean biomass of grass had a significant negative effect on the use of fields by swans from the Grounds roost (Table 4.8b), with the number of swans from the Grounds roost generally decreasing as mean biomass increased (Fig. 4.24).

Protein. Percentage protein content of the sward had a significant negative effect on the use of fields by swans from the Grounds roost (Table 4.8b), with the number of swans from the Grounds roost generally decreasing as percentage protein content increased (Fig. 4.25).

Year. Year had a significant effect on the number of Grounds units identified on the fields (Table 4.8b) with a significantly higher number of Grounds units identified in the 1992-93 winter (61.68%) than in 1991-92 (36.57%). This may reflect the higher proportion of swans roosting in the Grounds in 1992-93.

4.4 DISCUSSION

There were significant differences in the use made of fields by birds from the three main social classes. The proportion of families identified in the flocks tended to decrease with distance from the Slimbridge roost-sites, whilst the proportion of singletons tended to increase. This suggests that the high-ranking families were able to establish themselves at feeding sites closer to the roost, in order to reduce time and energy spent searching for, and flying to, more distant sites; whereas low-ranking singletons were forced to fly further afield. In a similar situation in northeast Scotland, Giroux & Patterson (1995) monitored the daily movements of individual Pink-footed Geese from their roost sites to feeding areas, and showed that unpaired birds had seasonal activity ranges which were twice as large as those of juveniles. Flying has been demonstrated to be the activity with the highest energy costs per unit of time amongst wintering geese in the Lower Rhine area of Germany (Mooij 1992), thereby placing a premium on feeding sites closest to the roost. The negative correlation between the percentage of cygnets in a flock and flock size agrees with similar findings on the Whooper Swan in winter (e.g. Hewson 1964, Salmon & Black 1986) and on the conspecific Whistling Swan, both at feeding sites in North Dakota during autumn migration (Earnst 1994) and on the wintering grounds in Maryland (Bart et al. 1991). Lambeck (1990) found that amongst Brent Geese small flocks (<100 birds) had extremely varying age ratios and suggested that such a partitioning of birds related to differences in carrying capacity and quality between feeding areas on the one hand, and the dominance hierarchy in the population on the other. It seems likely that higher-ranking families might be able to dominate preferred food resources i.e. those which are close to the roost-site and/or of high quality and quantity. In an experimental study Mulder et al. (1995), demonstrated that during the brood-rearing phase, families of Blue Geese fed for longer in high biomass plots and spent more time in 'defending' such plots from other broods. Families can also exploit the best resources in smaller flocks during the winter where competition from conspecifics is reduced, since the male parent can devote more of its high vigilance budget (see Chapter 6) from scanning for intra-specific competitors, to scanning for potential predators.

The daily distribution of Bewick's Swans wintering at Slimbridge was determined primarily by percentage water cover at the feeding sites. Monthly swan use increased with water cover on the fields in all the models considered, irrespective of grazing pressure from other wildfowl. The more distant feeding site at Walmore Common was used by large numbers of swans only when it was extensively flooded, despite having both a higher mean biomass and a higher mean percentage protein content of the grass sward than at the Slimbridge refuge throughout. Rees (1990) showed that Bewick's Swans mainly fed on flooded pasture but that precise depth of flooding did not have a significant effect upon food site selection. Swans tended to feed on floodwater, which has been suggested may be for safety or to drink (Rees 1990). However since birds feeding on totally dry and undisturbed fields were always observed to fly to an adjacent water source at least once during the day, safety is unlikely to be the main factor. Water sources were used for drinking and bathing and it seems likely that the advantage of feeding at a flooded site is that it removes the need for commuting to another water source. In a similar situation amongst Greater White-fronted Geese grazing at Slimbridge, close proximity to pools was found to reduce time spent in activities other than feeding (Owen 1972b). Water aids the digestive process by increasing the ease with which vegetation is broken up in the gizzard, thereby controlling the availability of nutrients to the bird (Owen et al. 1977). Grass that has been submerged for some days may therefore become more palatable. Certainly, Bewick's Swans at Slimbridge selectively graze the grass Alopecurus geniculatus which is most abundant in the damp depressions of fields (Rees 1990). Swans may be unable to find food in very deep water (Owen & Cadbury 1975), and on heavily flooded fields feeding activity was mostly concentrated along the edges of the floodwater. There was some evidence to suggest that percentage swan-days was lower on very heavily flooded fields.

The presence of other wildfowl on the fields also affected the extent to which the swans used each site, as found by Rees (1990). There was no association between swan numbers and the numbers of Eurasian Wigeon using the fields within the same month. In dry weather wigeon mainly use fields containing scrapes with permanent standing water, to which they flew for drinking and bathing, and especially to escape from predators (Mayhew & Houston 1989). The use of other fields by wigeon on the refuge was therefore limited to periods of heavy flooding. Greater White-fronted and feral geese are less tied to fields containing scrapes which they use primarily as drinking and bathing sites (Owen 1972b, 1973b). Grazing geese, like Bewick's Swans, feed primarily in the centre of fields (Owen 1972b) and the percentage of goose-days recorded for each field had a significant effect upon the distribution of Bewick's Swans within the same month, with swan-days declining as goose-days increased. Since geese and swans were frequently seen grazing in the same field and interspecific aggression was very rare, it seems unlikely that the two compete directly for grazing. Heavy usage by geese significantly depletes the biomass of vegetation, however (Rees 1990) and the addition of percentage goose-days to the model removed the earlier apparent negative association between percentage swan-days and biomass, when habitat variables were investigated alone.

A comparison of the percentage of swan-days recorded in one month with the percentage of goose and wigeon-days recorded during the previous month showed that although goose-grazing did not affect the subsequent use of fields by swans, wigeon grazing had a positive effect upon swan use in the following month. This unexpected relationship may result in part from the fact that Eurasian Wigeon, like swans, prefer fields containing a water source (Mayhew & Houston 1989); the interaction term of percentage wigeon-days in previous month*percentage water cover, perhaps coincidentally, also had a significant effect upon percentage swan-days. The strong preference for wetland areas shown by Eurasian Wigeon, restricts their feeding to a narrow strip near the water (Owen 1973b, Mayhew & Houston 1989), and swans were rarely seen feeding in the same parts of the fields as wigeon. Swans tend to feed in the centre of fields and therefore have access to a greater quantity and choice of feeding areas. Since neither biomass nor sward-length had a significant effect it seems unlikely that wigeon grazing was having a direct effect upon the distribution of swans in the following month. Moreover, wigeon grazing led to a significant decrease in the protein content of the sward in the following month (Spearman's rank correlation r_s = -0.458, $P < 0.01$, $n = 40$).

The negative relationship between percentage swan-days and biomass, revealed when habitat variables were investigated alone, contrasts with the positive relationship between these two variables found by Rees (1990). Similarly the significant negative relationship between swan numbers and protein content revealed when grazing pressure from other wildfowl was included in the model, also differs from Rees (1990). Both relationships appear to contradict conventional rules concerning optimal foraging strategy. However when the distribution of swans was investigated with respect to roost-group origin it was clear that the two groups of birds were selecting fields for different reasons. Swans from the Rushy Pen roost spent a greater proportion of their time feeding (Chapter 6) and selected fields on the basis of high protein content, as well as percentage water cover. Swans from the Grounds roost, conversely, spent less time feeding on the fields and there was a strong negative correlation between field usage and distance from the roost site. When distance from the roost-site was removed from the model, Grounds units appeared to select fields on the basis of low biomass and low protein content. The selection of feeding sites by the Grounds units thus seemed to be at odds with conventional optimal foraging theory, although a tendency for birds to select fields closer to the roost-site than expected given the habitat distribution, has also been demonstrated for Red-breasted Geese Branta ruficollis (Sutherland & Crockford 1993), and amongst Common Cranes Grus grus during the early and late parts of the winter season when numbers of birds in the roost were low (Bautista et al. 1995). This apparently odd selection of feeding sites may stem from reserve management policy at Slimbridge where there is less intensive agriculture on the refuge than on neighbouring farms; the presence of water and a short flight (flight is energetically very expensive, e.g. Mooij 1992), may be the overriding factors influencing field choice by Grounds units i.e. there was enough food, although not necessarily of the highest quality available. The selection of feeding sites by swans from the Rushy Pen roost agreed more closely with the results of other authors investigating feeding site selection. Moreover, since protein levels in the grass increased towards the end of the winter, the results suggest that swans from the Rushy Pen roost were concentrating their feeding on swards of high protein content prior to the spring migration to the breeding grounds. These findings suggest that swans from the Rushy Pen roost were selecting their feeding sites more critically than swans from the Grounds roost. This, in turn, may be due to swans spending less time feeding on the provisioned grain in the Rushy Pen, where there was greater competition for the food from other swans, geese and ducks, than swans in the smaller Grounds pens (Chapter 6), and therefore needing to obtain more food on the fields. This theory is supported by the significant negative correlation between distance from the roost-site and the proportion of families found on a field. Since families generally ranked highly in the dominance hierarchy (Chapter 2) they were likely to benefit most from the grain feeds (Chapter 6), and therefore may also need to rely less heavily on food supply from the fields.

Biomass of the sward might have been expected to have had a positive effect on the percentage of swan-days since it has been shown that geese have to consume a larger amount of grass to meet their energy requirements than to fulfil their protein needs (Prop et al. in prep). However, since in grasses, the metabolizable energy and the protein content are positively related, selection for plants containing a high proportion of protein would be favourable for the energy budget as well (Prop et al. in prep). The basic cause for the selectivity for grasses with a high protein content may therefore be the need for energy (Owen 1980). Moreover, since protein digestion occurs rapidly, optimizing protein intake (by high turnover rates of food) is probably more important than increasing the efficiency of carbohydrate digestion (by retaining food for longer periods of time) (Buchsbaum et al. 1986).

The higher proportion of Grounds units, and lower proportion of Rushy Pen units, identified on the fields during the 1992-93 winter compared to 1991-92, may have resulted from the higher proportion of swans roosting in the Grounds in 1992-93. However since the proportion of Grounds units identified per field per month in 1992-93 was higher than the overall proportion of Grounds units roosting at the site, it suggests that Grounds birds predominated in small flocks at a number of sites, whilst Rushy Pen birds were concentrated in larger flocks at fewer sites.

Although the number of fields used by the swans was highest during the mid-winter months of December and January, the evidence for increased dispersal as the food supply diminished was not conclusive since there was a direct linear relationship between the number of fields and the monthly swan-day total, indicating that dispersal increased as the number of swans increased (numbers were highest during the mid-winter period), perhaps in relation to optimal flock size and density.

It seems likely that the swans were eating invertebrates during their visits to the River Severn in March, since they appeared to be feeding in shallow water at low tide, and there was no evidence of any vegetation on the tidal flats. The most abundant estuarine invertebrates in areas used by the swans were an amphipod Corophium sp. and a polychaete worm Nereis sp. (M. Bell pers. comm.). Bewick's Swans have not previously been recorded feeding on estuarine invertebrates, although the conspecific Whistling Swan feeds heavily on estuarine molluscs (Mya arenaria and Macoma baltica) during the winter in Chesapeake Bay, Maryland (Stewart & Manning 1958, Earnst & Bart 1991). Very young Bewick's Swans may feed on both adult and immature mosquitoes on their Russian breeding grounds (pers. obs.), and in eastern Siberia the tadpole shrimp Notostraca forms an important part of the diet for breeding birds (Kondratiev 1991). Use of invertebrate foods which are rich in protein (Owen 1980) may be important as nutritional requirements change at certain stages of the life cycle. Alisaukas & Ankney (1992) for example, attributed the changing diet of Blue Geese as they migrated northwards on spring migration to their breeding grounds in arctic Canada, to changing nutritional requirements from protein to carbohydrates.

4.5 SUMMARY

This chapter investigated the use of feeding-sites by Bewick's Swans in the Slimbridge area during the winter in order to elucidate the factors that influenced choice of feeding site.

Field choice was first investigated in relation to social class in order to see if there were differences between the classes in their choice of a feeding site. Habitat variables including sward-length, biomass, protein content and percentage of water cover were then investigated in relation to overall swan use of the fields. The effect of grazing pressure from other species of wildfowl, including Eurasian Wigeon, Greater White-fronted Geese and feral geese was also considered, together with the influence of roost-site use.

1) The use made of the feeding sites differed significantly between the three main social classes. Families tended to utilise the fields closest to the roosts and singletons used fields further away, suggesting that high-ranking families could dominate their preferred feeding sites, close to the roost, whilst low-ranking singletons were forced to travel further afield.

2) The proportion of cygnets in the feeding flocks decreased with flock size. It was inferred from this that families may be able to dominate their preferred food resources i.e. those close to the roost and/or of high quality/quantity.

3) Biomass and sward-length were closely correlated and both measures declined during the winter, reaching their respective minimum values in January. Both measures then increased through February and March. Protein levels declined between October and November, but increased from December onwards, reaching the maximum level of the study period in March. Flooding on the fields was most frequent during periods of heavy rainfall in November, December and January, reaching maximum levels in December.

4) The distribution of Bewick's Swans wintering at Slimbridge was determined primarily by the percentage of water cover at the feeding sites. Swan use increased with increasing water cover. Water itself, aids the digestive process, thereby controlling the availability of nutrients to the bird, and swans grazing on dry fields were seen flying to water sources during the day in order to drink, as well as to bathe. Close proximity to water may reduce the time spent in activities other than grazing (see Chapter 5). There was some evidence to suggest that swan use declined on heavily flooded fields, presumably because deep water reduced the amount of grazing available to the swans.

5) The percentage of goose-days recorded for fields on the Slimbridge refuge had a significant effect upon the distribution of swans within the same month, with the use of a field by swans declining as goose use increased. This was thought to be related to a decrease in biomass resulting from heavy goose usage, although biomass itself did not

prove to be significant in the model.

6) There was a significant positive relationship between percentage wigeon-days in one month and swan use in the following month. This unexpected relationship may be linked to the preference shown by both species for fields containing a water source. Since biomass and sward-length did not have a significant effect upon the overall distribution of the swans, it is unlikely that wigeon grazing was having a direct effect upon the distribution of swans in the following month.

7) There was a significant difference in field usage between swans from the two roost-sites (Chapter 3). Distance from the roost-site was the most important variable affecting distribution of swans from the two roost-sites on the fields; the number of Rushy Pen units identified increased with distance from roost-site whilst the number of Grounds Pen units identified decreased with distance from roost-site. Swans from the Rushy Pen roost selected fields on the basis of high protein content, as well as percentage water cover. Field selection by swans from the Rushy Pen roost was therefore in line with conventional optimal foraging strategy. Field choice by swans from the Grounds roost appeared to be less critical with significant negative relationships between the number of Grounds units identified and both protein and biomass. These unexpected relationships may be a spin-off of reserve management; the presence of water and a short flight may be the overriding factors influencing field choice by Grounds units.

8) It was argued that differences in the selection of field sites by birds from the two roost-sites could be explained by differences in foraging behaviour. Swans from the Rushy Pen spent less time feeding on provisioned grain at the roost-site, where there was greater competition for the food from other swans, geese and ducks, than those in the pens of the Grounds roost-site, and more time feeding on the fields. The selection of feeding site was therefore more critical for swans roosting in the Rushy Pen than those roosting in the Grounds.

9) There was a direct linear relationship between the number of fields used by the swans and the monthly swan-day total, suggesting that dispersal increased as the number of swans increased (numbers were highest during the mid-winter period), rather than as a direct response to a decline in food supply.

10) A large increase in the use made by the swans of the River Severn at low tide was noted in March immediately prior to their departure on the first step of their return migration to the Russian breeding grounds. It is likely that the birds were utilising an invertebrate food source, which has not previously been documented for Bewick's Swans during the winter. The use of a protein-rich invertebrate food source in spring may reflect the swans' nutritional requirements at the start of migration.

Table 4.1 Breakdown of swan units identified on individual fields in the Slimbridge area 1989/90 - 1992/93 by social class (for location of fields see Figs 3.3 & 3.4).

a) Total units identified

	Sum of units identified		
Field	Families	Pairs	Singles
Slimbridge refuge:			
17 acre	100	57	116
Dumbles	109	178	246
Fifty acre	29	23	40
Long Ground	94	58	65
North middle road	10	9	16
New south lake field	27	36	46
River Severn	11	15	21
South-east road	9	7	10
South middle road	143	355	364
South middle ext.	22	26	26
Tack piece	664	862	1091
Tin shed	5	1	6
Top new piece	356	337	418
Canal fields	45	26	37
JBS	132	68	158
Pylon	109	178	234
Pylon B	3	36	24
Walmore Common	121	128	175
	1990	2400	3097

b) Chi-square comparisons (Significance levels: *** = P < 0.001, ** = P < 0.01, * = P < 0.05, N.S. = P > 0.05).

	Families v rest		Pairs v rest		Singles v rest	
Field	Chi-sq.	P	Chi-sq.	P	Chi-sq.	P
17 acre	14.67	***	16.25	***	0.14	N.S.
Dumbles	11.05	***	0.47	N.S.	5.42	*
Fifty acre	1.17	N.S.	2.13	N.S.	0.17	N.S.
Long Ground	32.08	***	2.92	N.S.	11.99	***
North middle road	0.07	N.S.	0.65	N.S.	0.27	N.S.
New south lake field	0.18	N.S.	0.05	N.S.	0.03	N.S.
River Severn	0.24	N.S.	0.00	N.S.	0.22	N.S.
South-east road	0.86	N.S.	0.31	N.S.	0.09	N.S.
South middle road	49.81	***	37.27	***	0.29	N.S.
South middle ext.	0.38	N.S.	0.32	N.S.	1.19	N.S.
Tack piece	3.00	N.S.	1.44	N.S.	0.19	N.S.
Tin shed	1.40	N.S.	3.11	N.S.	0.38	N.S.
Top new piece	19.96	***	1.78	N.S.	7.53	**
Canal fields	12.78	***	3.02	N.S.	2.28	N.S.
JBS	20.42	***	29.45	***	1.18	N.S.
Pylon	9.19	***	1.14	N.S.	2.91	N.S.
Pylon B	15.51	***	18.34	***	0.27	N.S.
Walmore Common	0.88	N.S.	0.72	N.S.	0.00	N.S.

Table 4.2 The proportion of cygnets identified in feeding flocks on the fields by season.

	Proportion of cygnets identified in flocks (%)			Overall proportion of cygnets at Slimbridge (%)
Winter	mean	S.D.	n	
1989-90	20.76	16.47	131	21.84
1990-91	28.51	18.74	192	23.11
1991-92	26.39	15.31	143	22.89
1992-93	1.84	3.38	125	3.77
All	20.66	18.30	593	17.90

Mann-Whitney U test comparisons between winters (df = 1 in all cases).

Winters	W	P	
89/90 v 90/91	17912	<0.001	**
90/91 v 91/92	33110	>0.45	N.S.
91/92 v 92/93	27980	<0.001	**
89/90 v 91/92	15923	<0.001	**
89/90 v 92/93	22593	<0.001	**
90/91 v 92/93	41439	<0.001	**

Table 4.3. Monthly usage of fields in the Slimbridge area by Bewick's Swans - data expressed as monthly percentage swan-days (for location of fields see Figs 3.3 & 3.4. N.B. data from the Tack Piece are included).

a) 1991-92 winter

		Percentage Swan-days					
Field	Field no.	Oct	Nov	Month Dec	Jan	Feb	Mar
Slimbridge refuge:							
Fifty Acre	1	0	4.64	2.48	0	0	0
Severn Ground	2	0	0	1.64	0	0	0
Tack Piece	5	0	0.82	45.08	35.81	27.46	13.59
Dumbles	6	23.89	1.21	0	0.41	5.66	0.49
Top New Piece	7	18.58	5.37	17.54	18.98	18.80	29.49
Bottom New Piece	8	1.33	0	0	0	0	0
Seventeen Acre	11	0	0	0	9.14	0	0
South Middle	13	0	0.34	4.80	0.44	0	0
New South Lake	14	10.62	1.69	0.96	3.34	9.20	2.48
South East Road	15	3.98	0	2.54	1.85	0	0
North Middle	16	0	1.79	0	0.30	0	0
N. N. Middle	17	0	0	0	0.98	0	0
N. N. East	18	0	0	1.24	0	0	0
North East	20	0	0	1.08	0	0	0
Long Ground		17.70	0.50	8.69	11.55	9.47	16.81
River Severn		0	0.82	0.46	2.20	0.11	22.72
Slimbridge area (outside refuge):							
Canal fields	21	0	0	11.60	0	0	0
Pylon	23	2.21	25.16	0	8.14	3.52	0
J.B.s	25	2.21	0	0	0	0	0
Frampton Marsh		0	0	0	0	0.82	0
Walmore Common		19.47	57.58	1.27	0	24.97	14.41
Total swans counted		226	2067	3232	7076	7337	4106
No. of days counted		7	30	31	31	29	23

b) 1992-93 winter

Field	Field no.	Percentage Swan-days Month Oct	Nov	Dec	Jan	Feb	Mar
Slimbridge refuge:							
Fifty Acre	1	0	0	0	0	0	0.96
Goose House	3	0	0	0	0	0	0.16
Ox Piece	4	0	0	0	0.21	0	11.49
Tack Piece	5	0	0	9.21	31.69	13.03	36.26
Dumbles	6	84.21	21.53	1.01	10.25	10.55	10.09
Top New Piece	7	15.79	0.58	1.06	7.26	0	0
Tin Shed	9	0	0	0	0.29	0	0
Four Score	10	0	0	0	0	0	1.15
South Middle	13	0	14.01	19.80	18.57	11.16	9.47
South East Road	15	0	0	0	0.80	0	0
North Middle	16	0	0	1.58	1.68	0	0
N. N. East	18	0	0	0	0.34	0	0
Long Ground		0	6.83	9.29	8.82	8.35	11.98
River Severn		0	0	0.26	3.56	7.71	17.08
Slimbridge area (not on refuge):							
Pylon A	22	0	0	10.38	0	0	0
Pylon	23	0	0	0	1.43	49.21	1.37
Walmore Common		0	57.05	47.41	15.10	0	0
Total swans counted		57	864	3854	7015	7055	3221
No. of days counted		13	30	31	31	28	31

c) Overall percentage swan-days for the winters 1991-92 and 1992-93.

Field	Field no.	Percentage Swan-days Winter 1991-92	1992-93
Slimbridge refuge:			
Fifty Acre	1	0.73	0.16
Severn Ground	2	0.22	0.00
Goose House	3	0.00	0.03
Ox Piece	4	0.00	2.03
Tack Piece	5	27.26	12.89
Dumbles	6	2.25	7.08
Top New Piece	7	19.28	2.98
Bottom New Piece	8	0.01	0.00
Tin Shed	9	0.00	0.11
Four score	10	0.00	0.20
Seventeen Acre	11	2.68	0.00
South Middle	13	0.80	17.30
New South Lake	14	4.57	0.00
South East Road	15	0.92	0.30
North Middle	16	0.03	0.94
N. N. Middle	17	0.09	0.00
N. N. East	18	0.17	0.13
North East	20	0.14	0.00
Long Ground		10.50	10.61
River Severn		4.68	7.14
Slimbridge area (outside refuge):			
Canal fields	21	1.55	0.00
Pylon	23	5.71	18.55
Pylon A	22	0.00	2.11
J.B.s	25	0.02	0.00
Frampton Marsh		0.25	0.00
Walmore Common		17.32	17.51
Total swans counted		24044	22066
No. of days counted		151	164

d) Number of fields used by the swans per month and total monthly swan-days for the winters 1989-90 to 1992-93

	Number of fields used per month					
	Oct	Nov	Dec	Jan	Feb	Mar
1989-90	2	6	11	12	6	3
1990-91	5	13	12	10	13	10
1991-92	9	11	14	13	9	7
1992-93	2	5	9	13	6	9
mean	4.50	8.75	11.50	12.00	8.50	7.25
S.D.	3.22	3.86	2.08	1.41	3.32	3.10

Total monthly swan-days

	Oct	Nov	Dec	Jan	Feb	Mar
1989-90	19	3568	3777	4839	1388	27
1990-91	763	3975	6447	8917	8663	6477
1991-92	226	2067	3232	7076	7337	4106
1992-93	57	864	3854	7015	7055	3221
mean	266	2619	4327	6962	6111	3458
S.D.	343	1429	1440	1668	3226	2668

Table 4.4. Linear model using maximum likelihood estimates fitted to monthly percentage swan-days on fields in the Slimbridge area. Habitat variables only. Final model: deviance = 48.85, df = 61.

Variable	F ratio	d.f.	P
% water cover	3.190	1, 62	<0.10
Mean biomass	2.961	1, 62	<0.10

Table 4.5. Linear model using maximum likelihood estimates fitted to monthly percentage swan-days on fields in the Slimbridge area. Habitat variables (sward-length, biomass, % protein content of grass and % water cover of field), plus percentage goose-days and percentage Wigeon-days within the same month (N.S. variables omitted). Final model: deviance = 32.86, df = 33.

Variable	F ratio	d.f.	P
% water cover	5.443	1, 34	<0.05 *
% protein	4.269	1, 34	<0.05 *
% goose-days	5.049	1, 34	<0.05 *

Table 4.6. Linear model using maximum likelihood estimates fitted to monthly percentage swan-days on fields in the Slimbridge area. Habitat variables (sward-length, biomass, % protein content of grass and % water cover of field) plus percentage goose-days and percentage Wigeon-days in the previous month (non-significant results excluded). Final model: deviance = 58.21, df = 63.

Variable	F ratio	d.f.	P
% water cover	13.617	1, 64	<0.001 **
% Wigeon-days (previous month)	16.590	1, 64	<0.001 **
% water-cover* Wigeon-days (previous month)	6.941	1, 64	<0.025 *

Table 4.7a. Linear model using maximum likelihood estimates fitted to monthly percentage swan-days of birds from the Rushy Pen roost, on fields in the Slimbridge area. All variables considered including distance from roost-site. Final model: deviance = 114.57, df = 97.

Variable	F ratio	d.f.	P
Distance from roost-site	38.041	1, 98	<0.001 **

Table 4.7b. Linear model using maximum likelihood estimates fitted to monthly percentage swan-days of birds from the Rushy Pen roost, on fields in the Slimbridge area. All variables considered excluding distance from roost-site. Final model: deviance = 43.19, df = 37.

Variable	F ratio	d.f.	P
% water cover	6.895	1, 38	<0.025 *
% Protein	4.282	1, 38	<0.05 *
Year	6.999	1, 38	<0.025 *

Table 4.8a. Linear model using maximum likelihood estimates fitted to monthly percentage swan-days of birds from the Grounds roost, on fields in the Slimbridge area. All variables considered including distance from roost-site. Final model: deviance = 115.33, df = 97.

Variable	F ratio	d.f.	P
Distance from roost-site	41.669	1, 98	<0.001 **

Table 4.8b. Linear model using maximum likelihood estimates fitted to monthly percentage swan-days of birds from the Grounds roost, on fields in the Slimbridge area. All variables considered excluding distance from roost-site. Final model: deviance = 39.22, df = 33.

Variable	F ratio	d.f.	P
Mean biomass	12.577	1, 34	<0.005 **
% Protein	4.259	1, 34	<0.05 *
Year	6.489	1, 34	<0.025 *

Fig 4.1 Dendrogram showing the similarities and differences between logically selected suites of fields, in terms of their use by families, as revealed by Orthogonal comparisons (Key: ** P<0.01, * P<0.05, NS P>0.05, + more, - less).

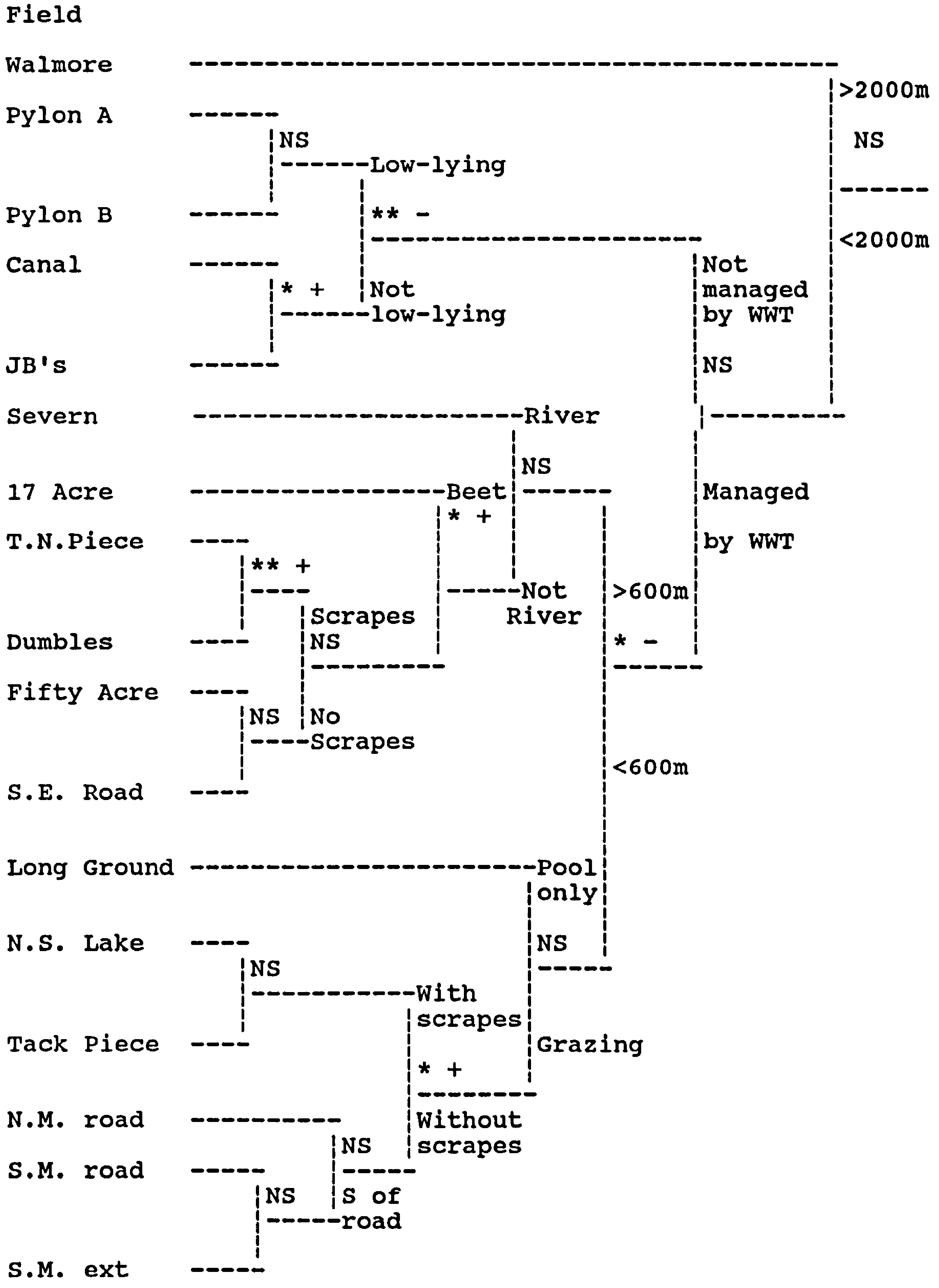


Fig 4.2 Dendrogram showing the similarities and differences between logically selected suites of fields, in terms of their use by pairs without cygnets, as revealed by Orthogonal comparisons (Key: ** P<0.01, * P<0.05, NS P>0.05, + more, - less).

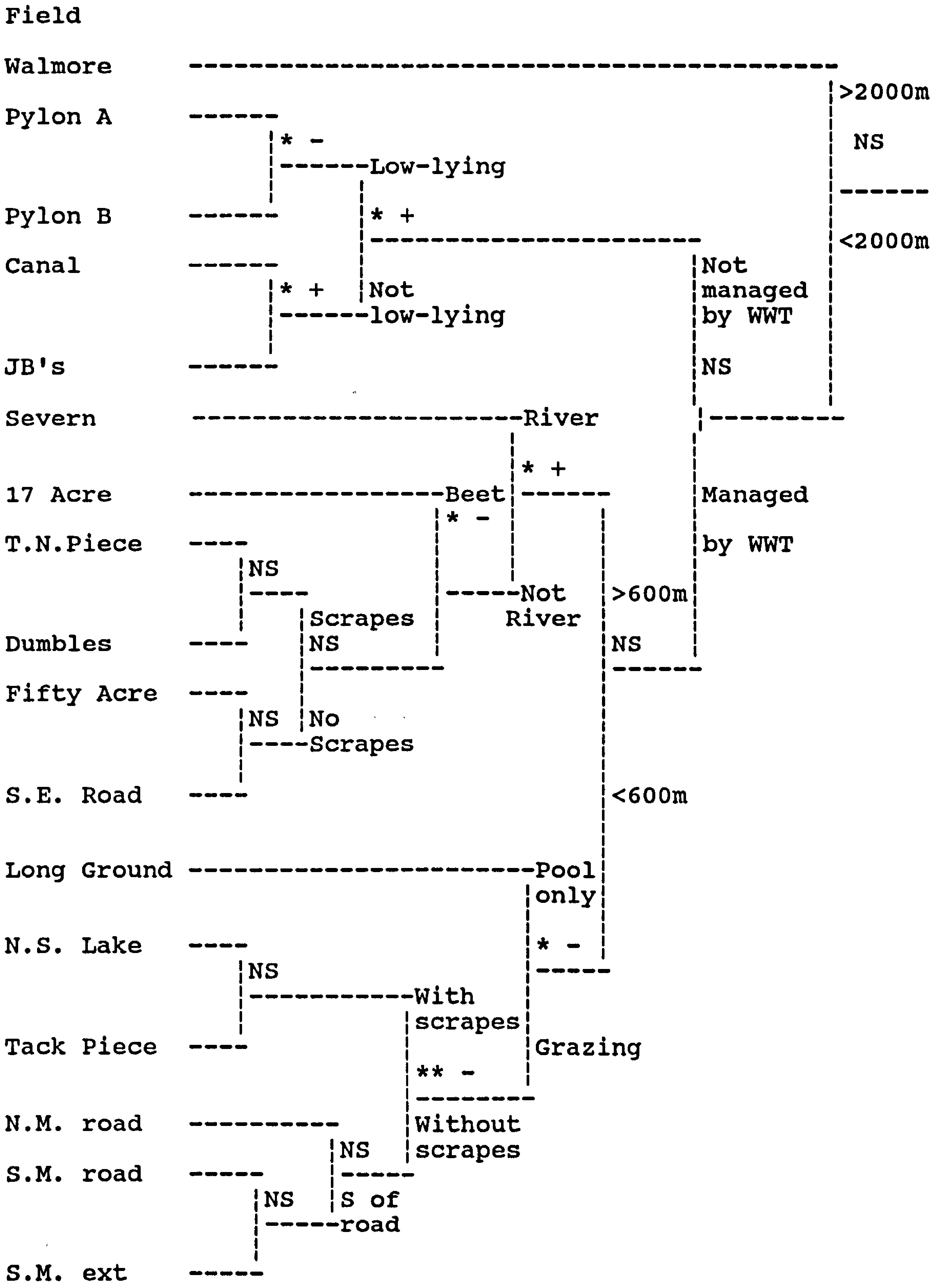


Fig 4.3 Dendrogram showing the similarities and differences between logically selected suites of fields, in terms of their use by singletons, as revealed by Orthogonal comparisons (Key: ** P<0.01, * P<0.05, NS P>0.05, + more, - less).

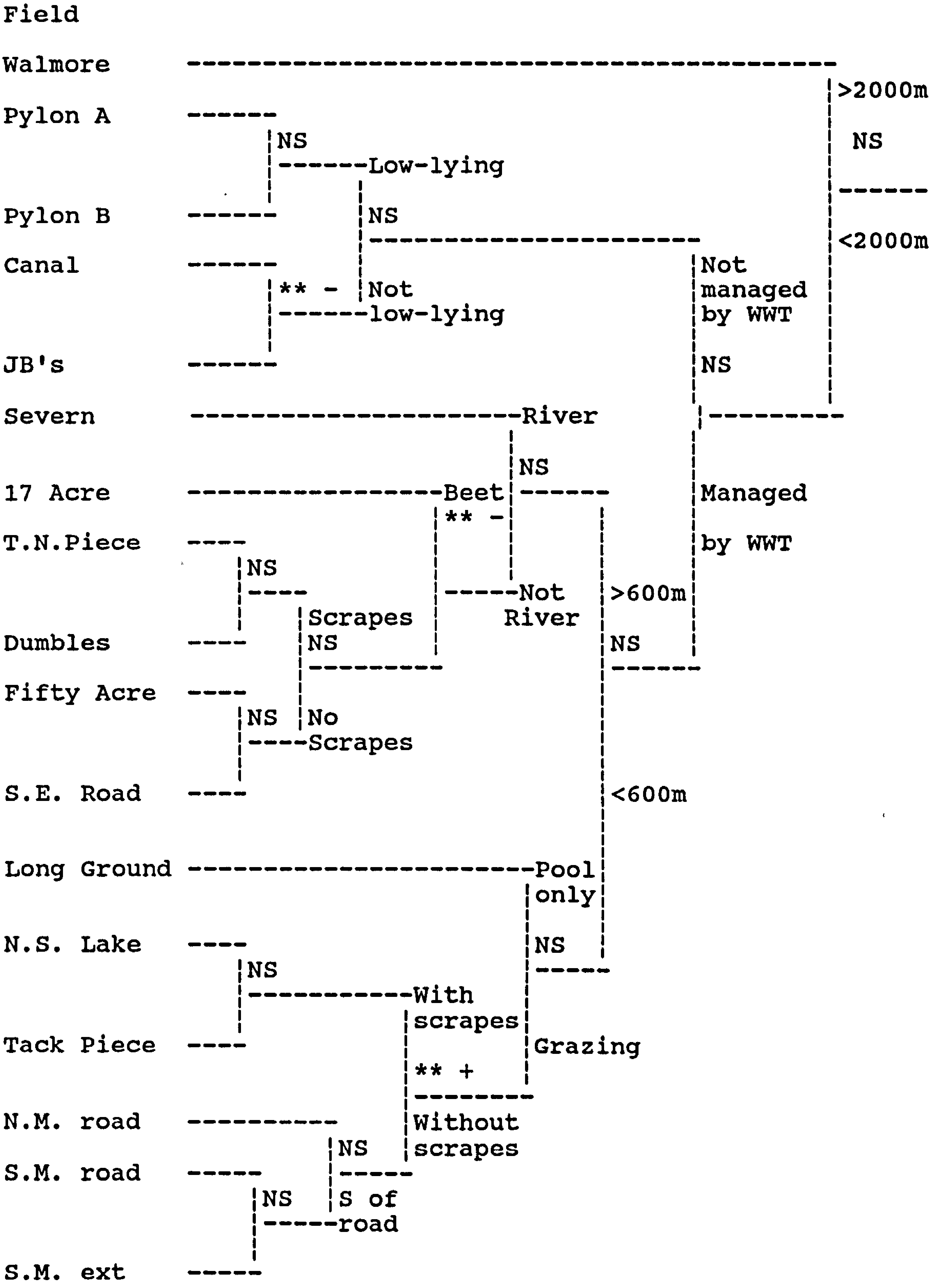


Fig. 4.4. The proportion of swan familes at the feeding sites with mean distance from the Slimbridge roosts (mean per field for 1989-90 to 1992-93 winters inclusive plus S.E. bar. Walmore Common excluded).

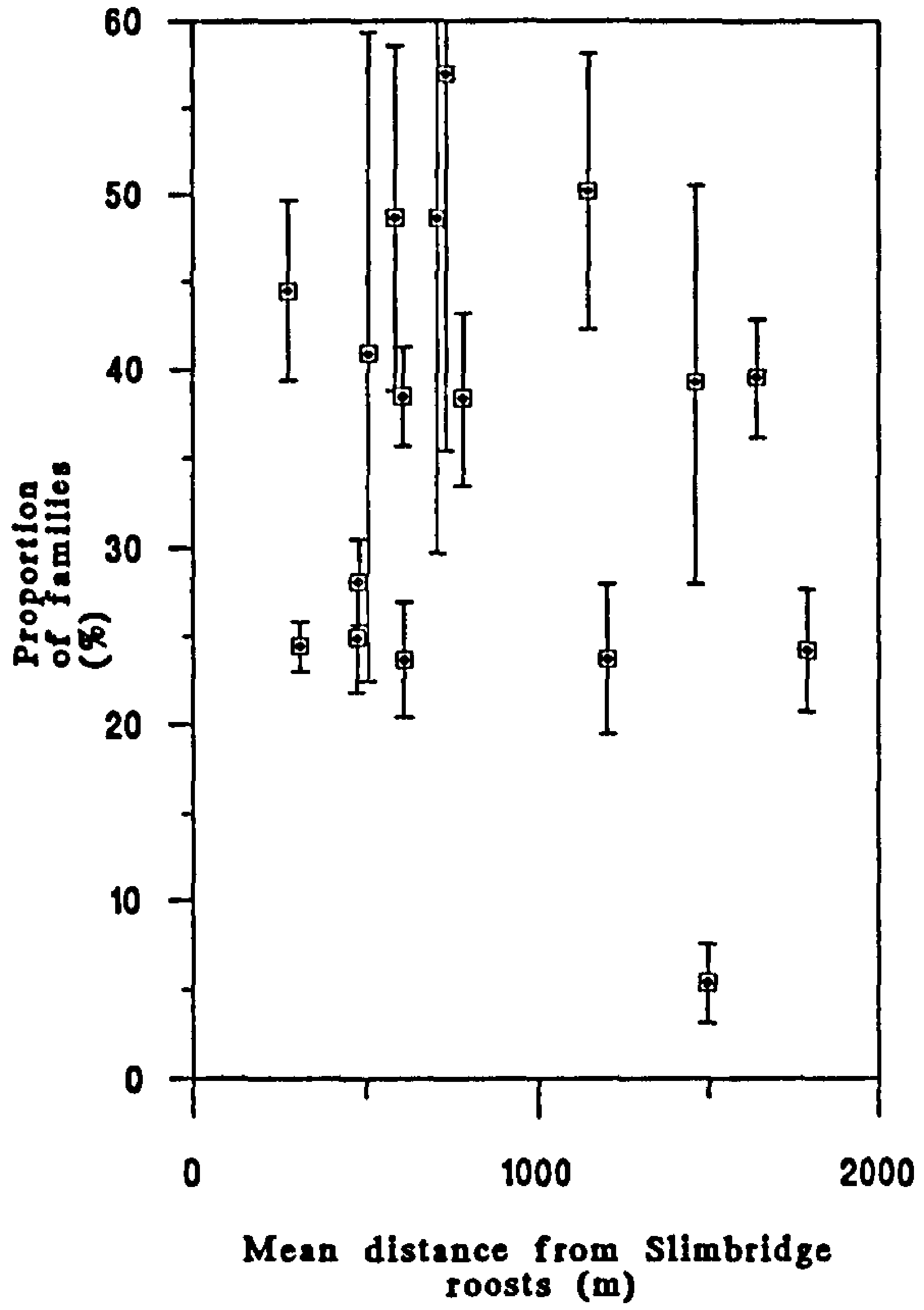


Fig. 4.5. The proportion of single swans at the feeding sites with mean distance from the Slimbridge roosts (mean per field for 1989-90 to 1992-93 winters inclusive plus S.E. bar. Walmore Common excluded).

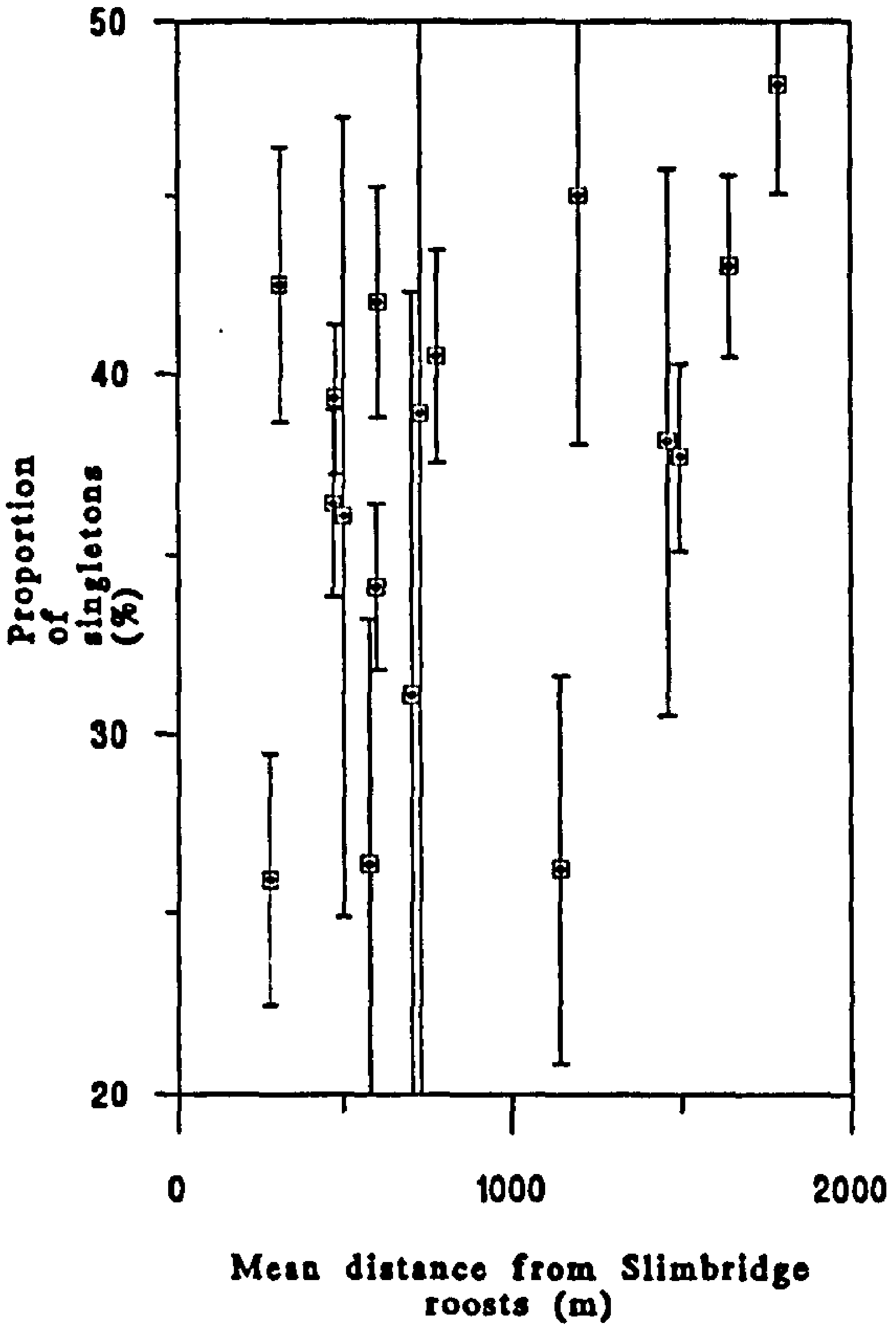


Fig. 4.6. The proportion of swan pairs (without cygnets) at the feeding sites with mean distance from the Slimbridge roosts (mean per field for 1989-90 to 1992-93 winters inclusive plus S.E. bar. Walmore Common excluded).

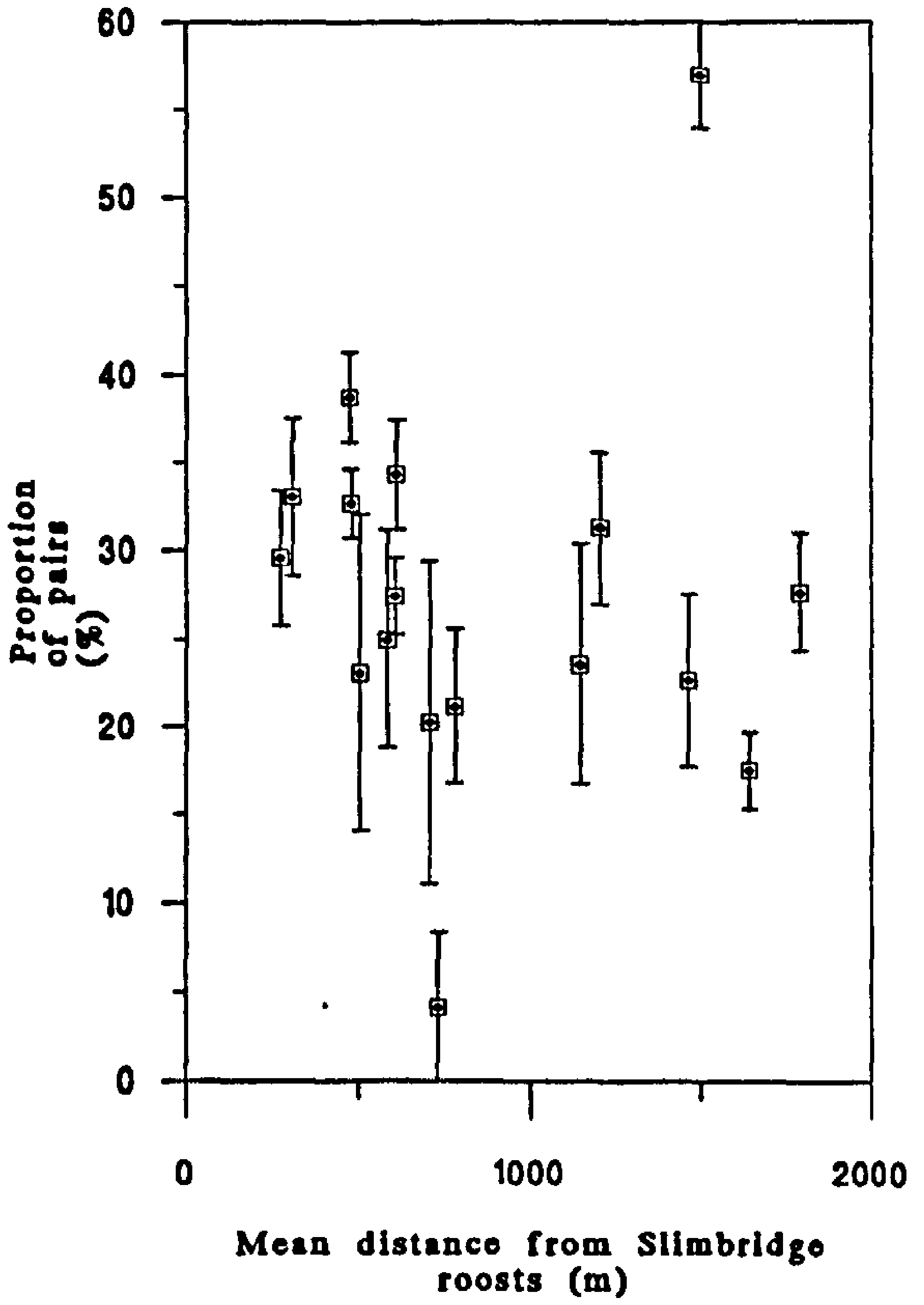


Fig. 4.7 The mean number of fields used by Bewick's Swans per month during the winter with mean monthly swan-days (mean per month of four winters, 1989-90 to 1992-93).

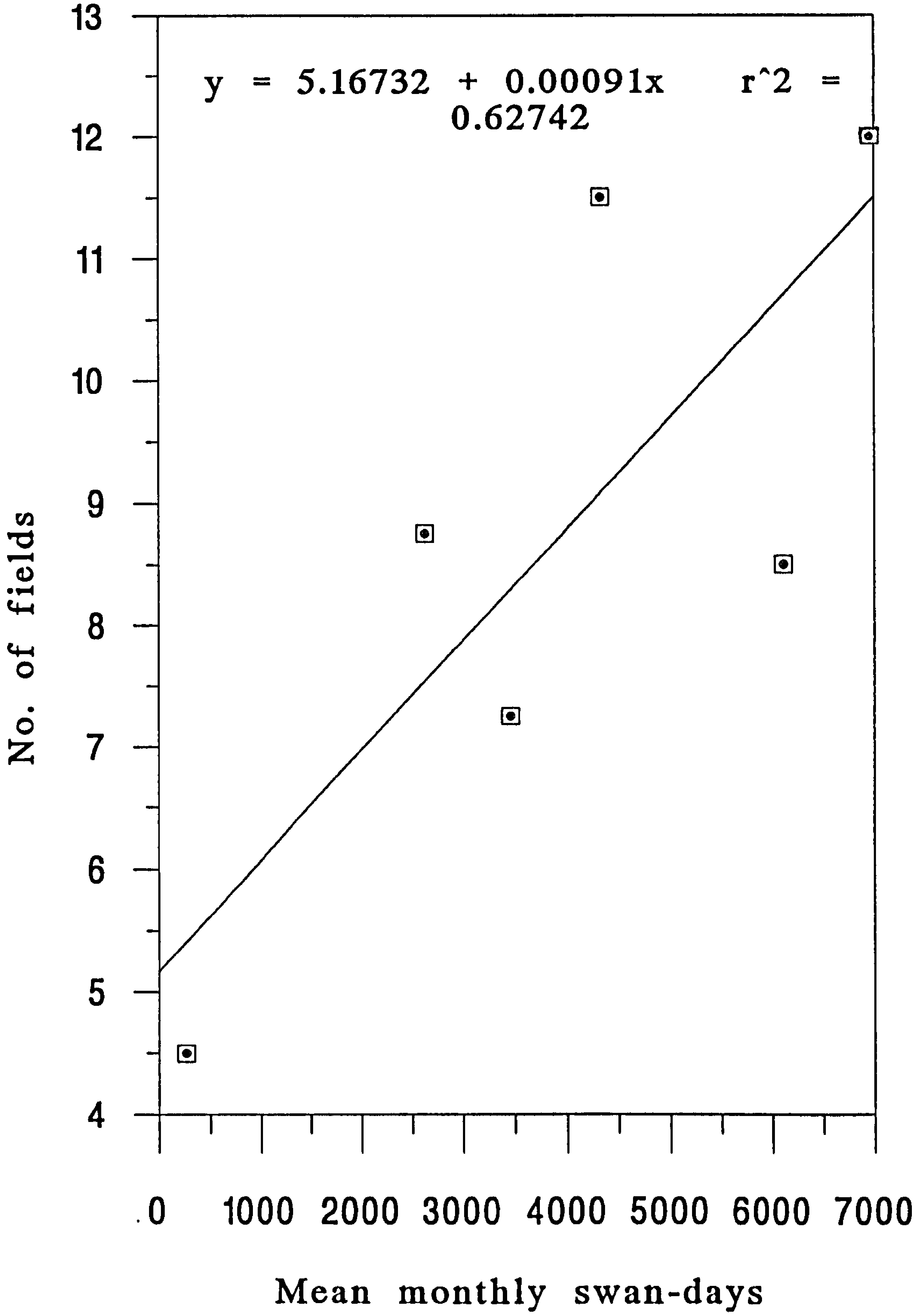


Fig. 4.8. Mean monthly length of grass swards at the feeding sites. Data from the 1991-92 and 1992-93 winters combined (mean and S.E. bar, n = 98).

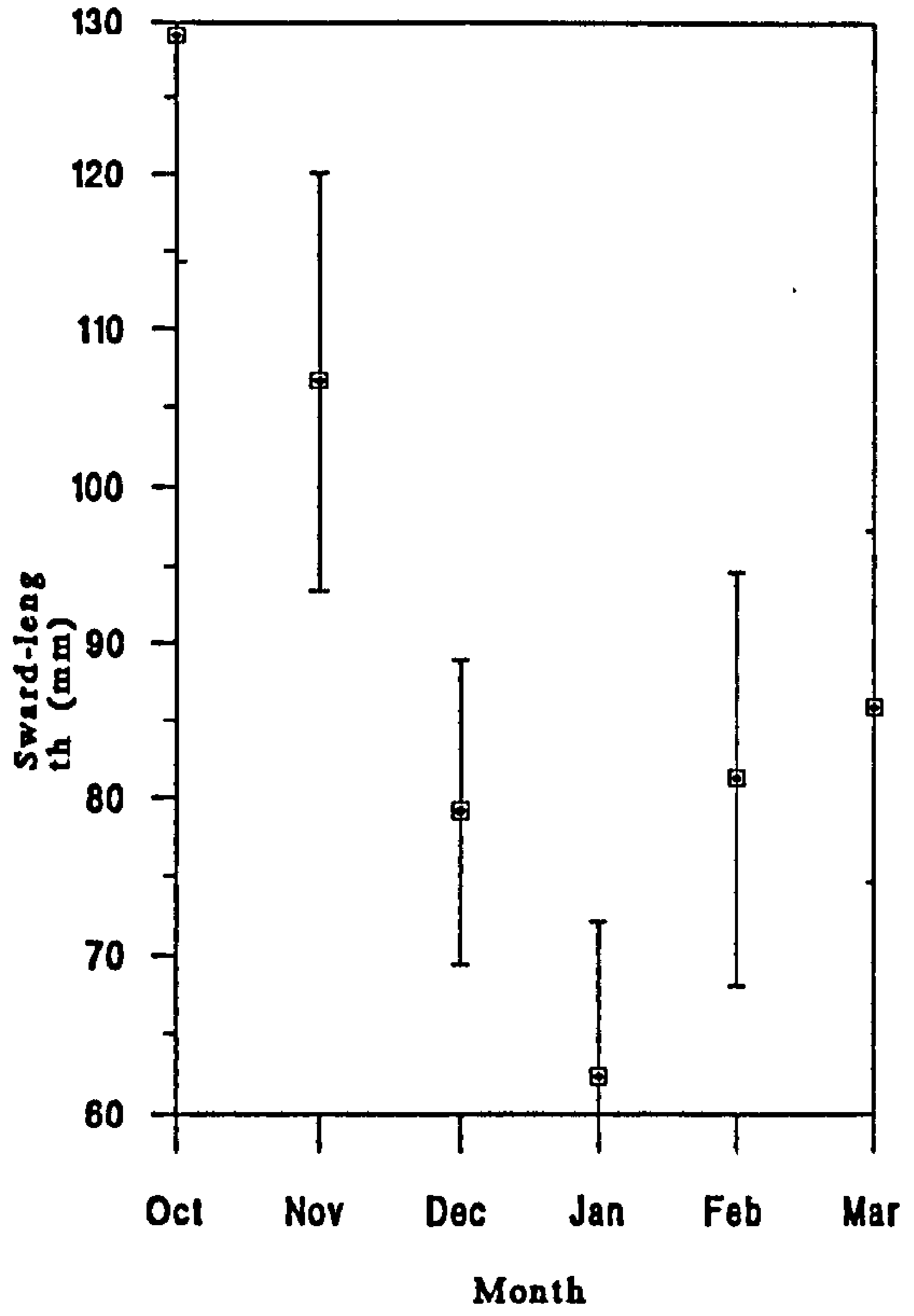


Fig. 4.9. Mean monthly biomass of grass swards at the feeding sites. Data from the 1991-92 and 1992-93 winters combined (mean and S.E. bar, n = 97).

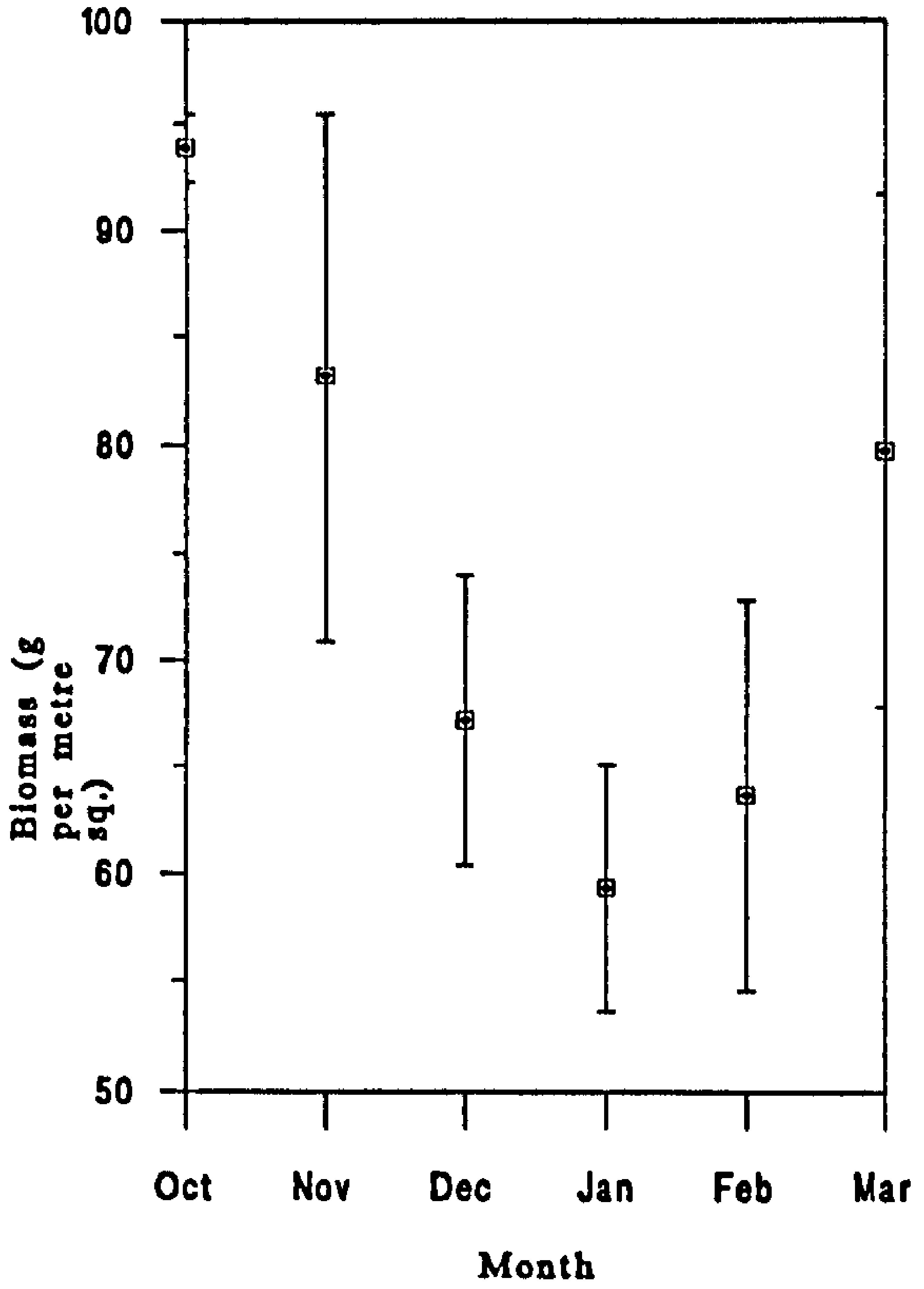


Fig. 4.10. Mean monthly percentage protein content of grass swards at the feeding sites. Data from the 1991-92 and 1992-93 winters combined (mean and S.E. bar, n = 78).

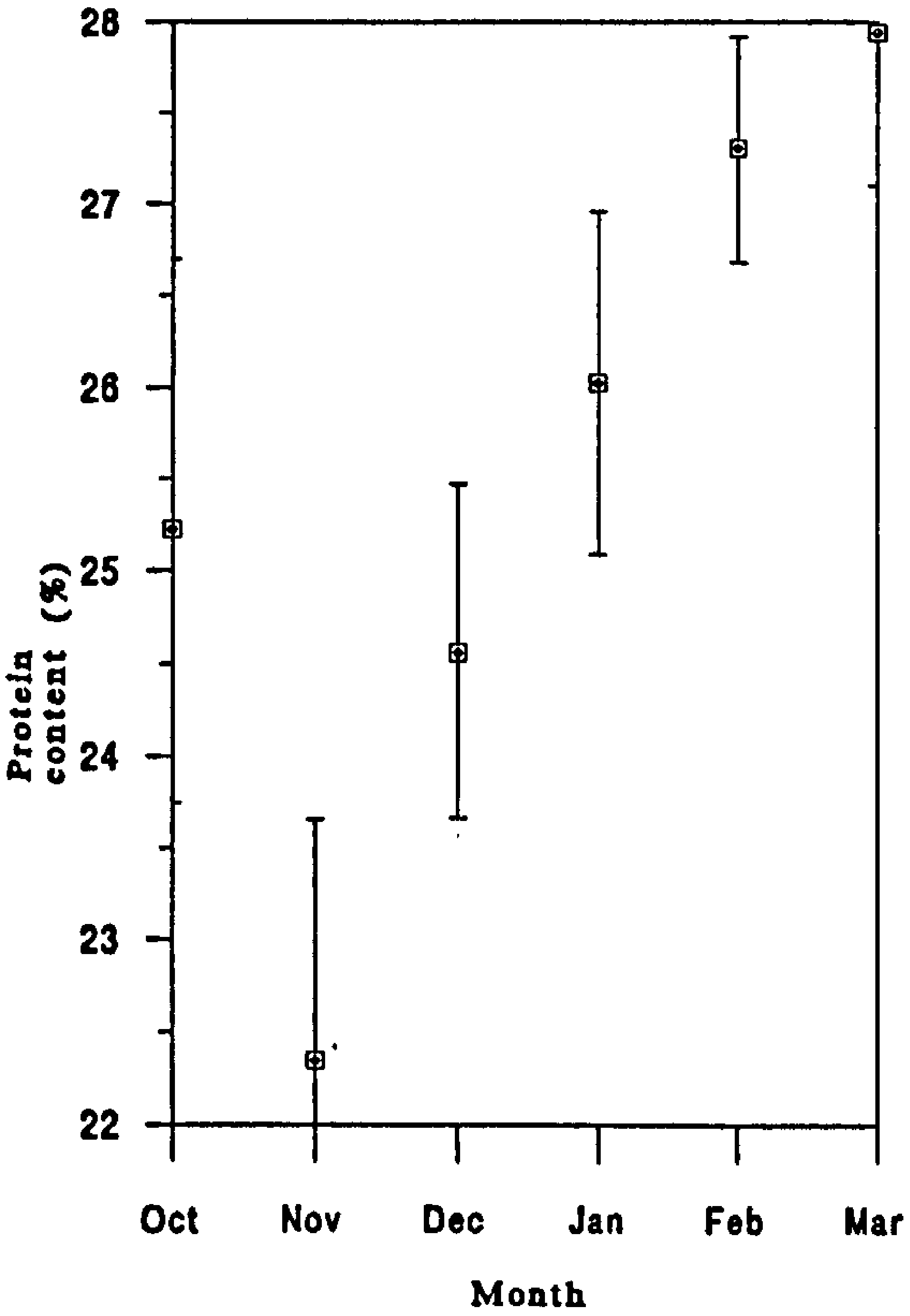


Fig. 4.11. Monthly percentage water cover at the feeding sites. Data from the 1991-92 and 1992-93 winters combined (mean and S.E. bar, n = 159).

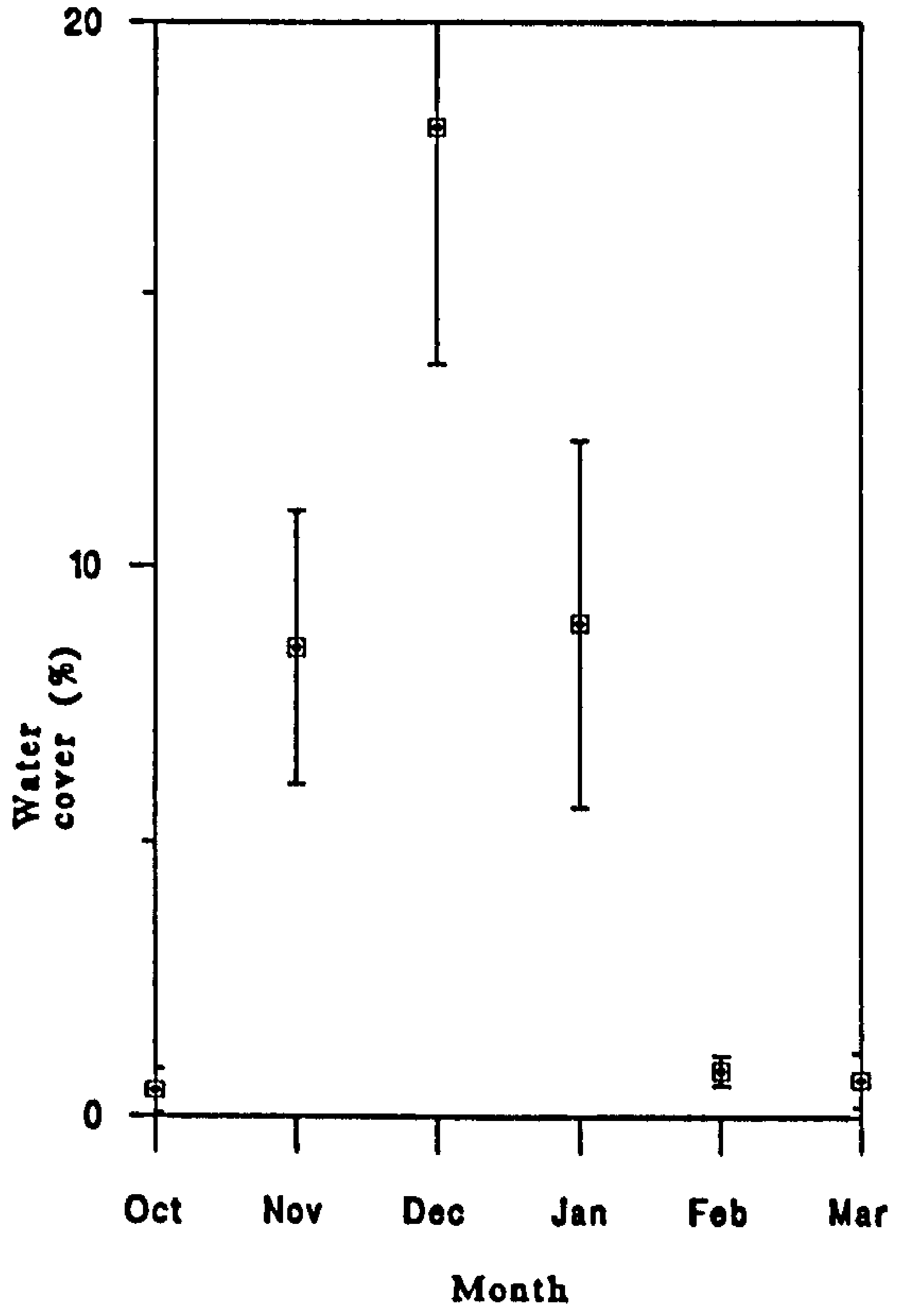


Fig. 4.12. Monthly swan-days in relation to percentage water cover at the feeding sites (histogram and S.E. bar), plus predicted values from a generalised linear model (white rectangles). Data from the 1991-92 and 1992-93 winters combined (n = 149).

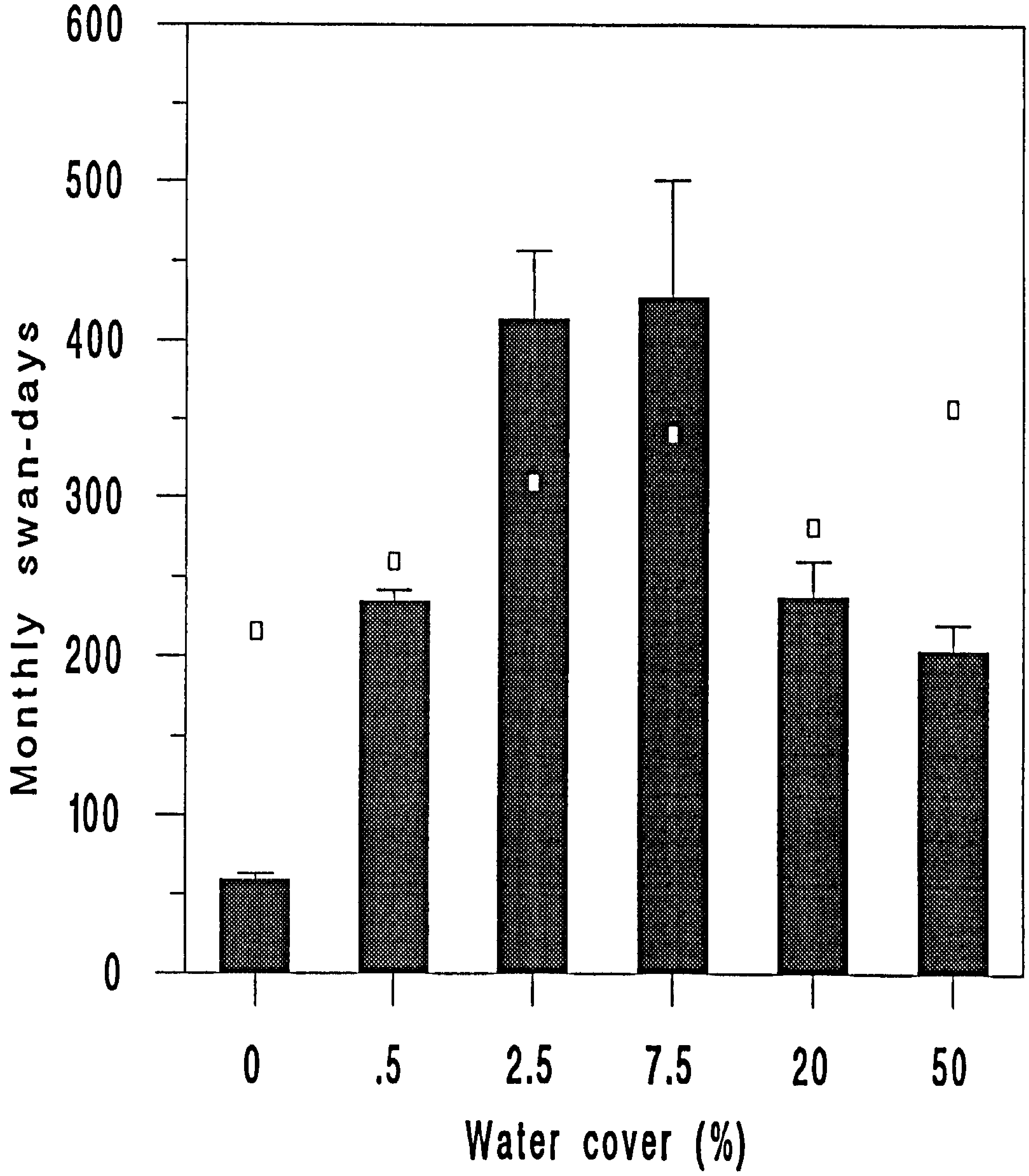


Fig. 4.13. Maximum daily swan counts on the Dumbles during February 1992 in relation to flooding from high spring tides.

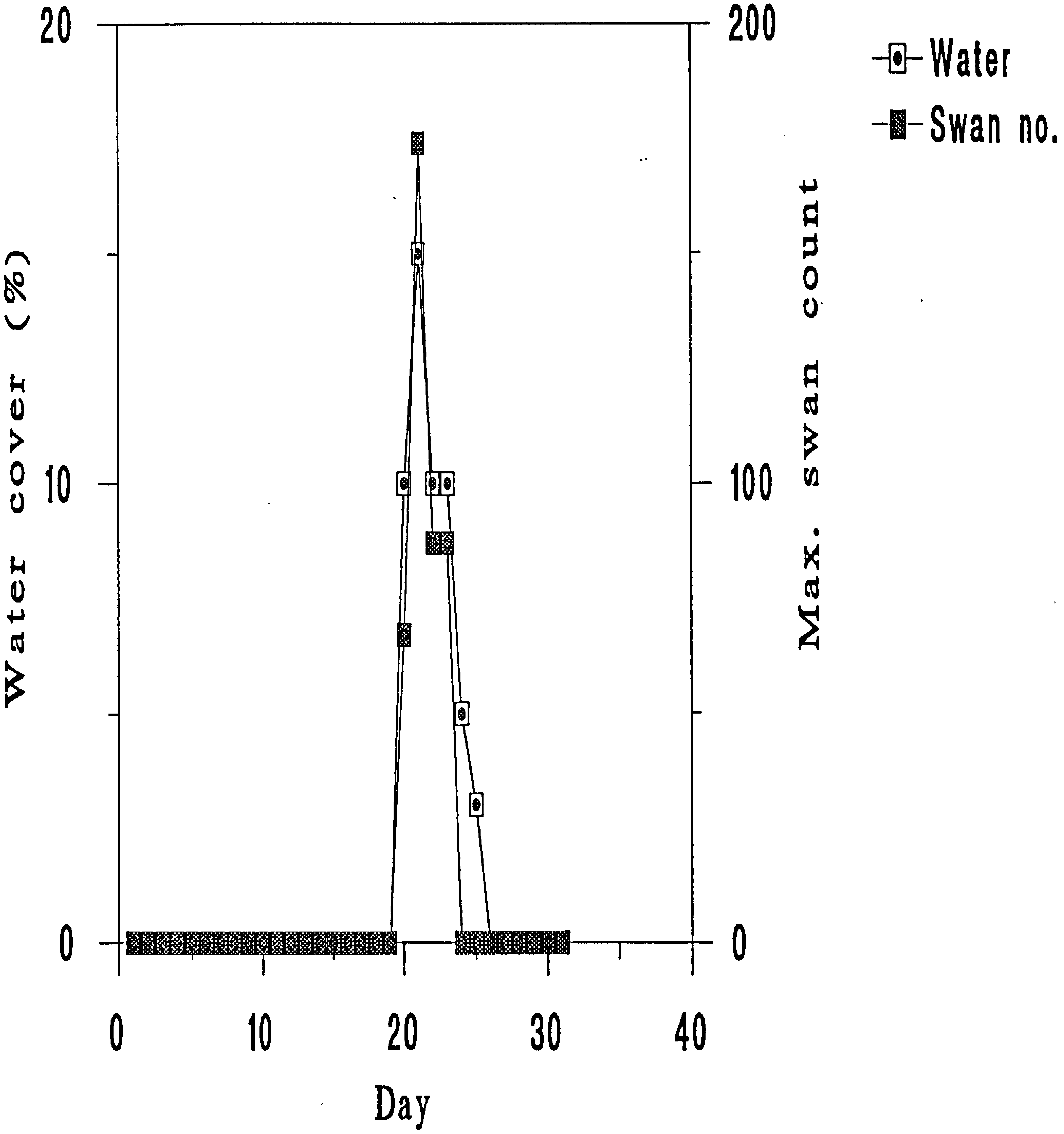


Fig. 4.14. Monthly swan-days in relation to biomass of sward at the feeding sites (histogram and S.E. bar) plus predicted values from a generalised linear model (white rectangles). Data from the 1991-92 and 1992-93 winters combined (n = 81).

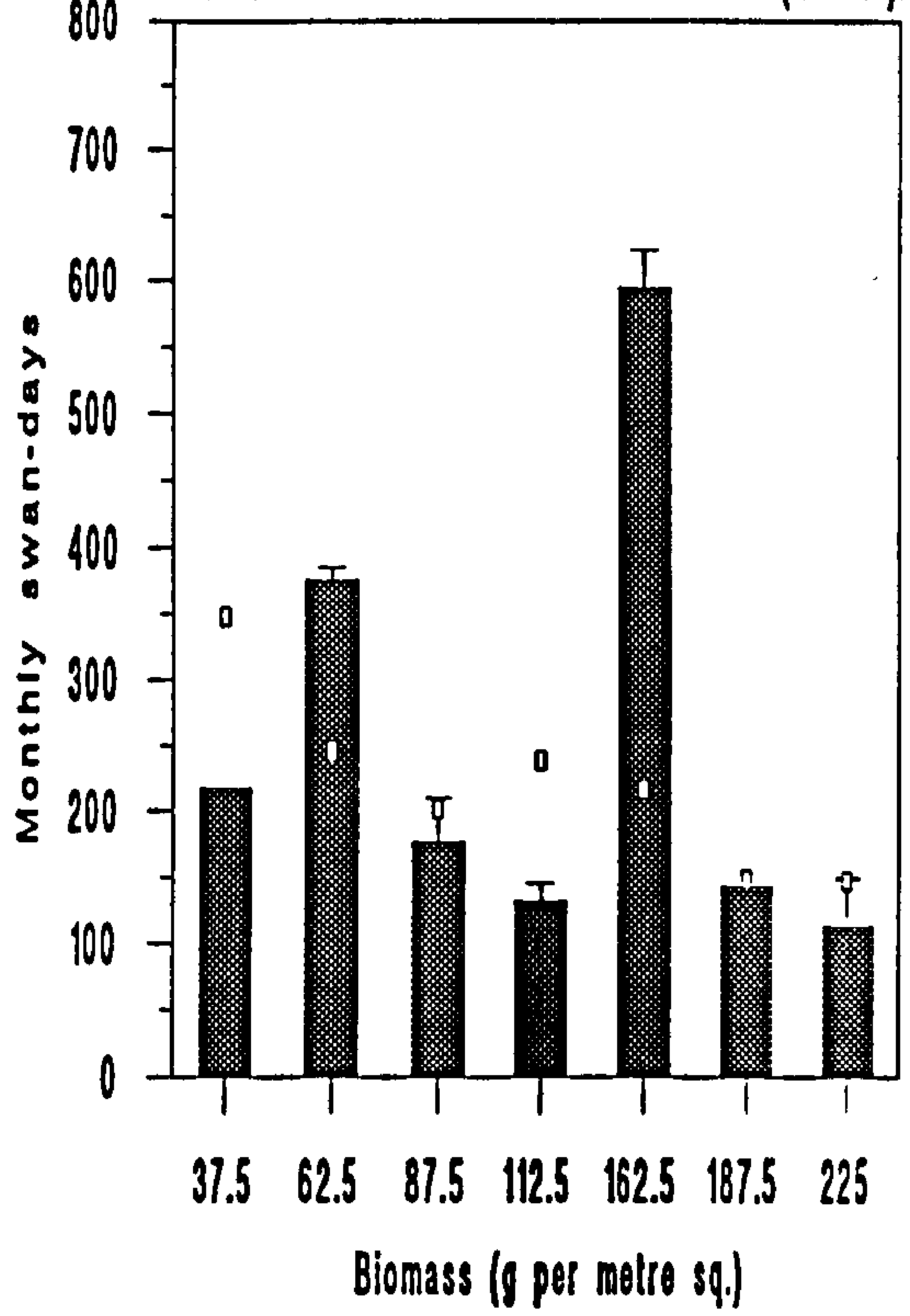


Fig. 4.15. Monthly swan-days in relation to percentage water cover at the feeding sites (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 149).

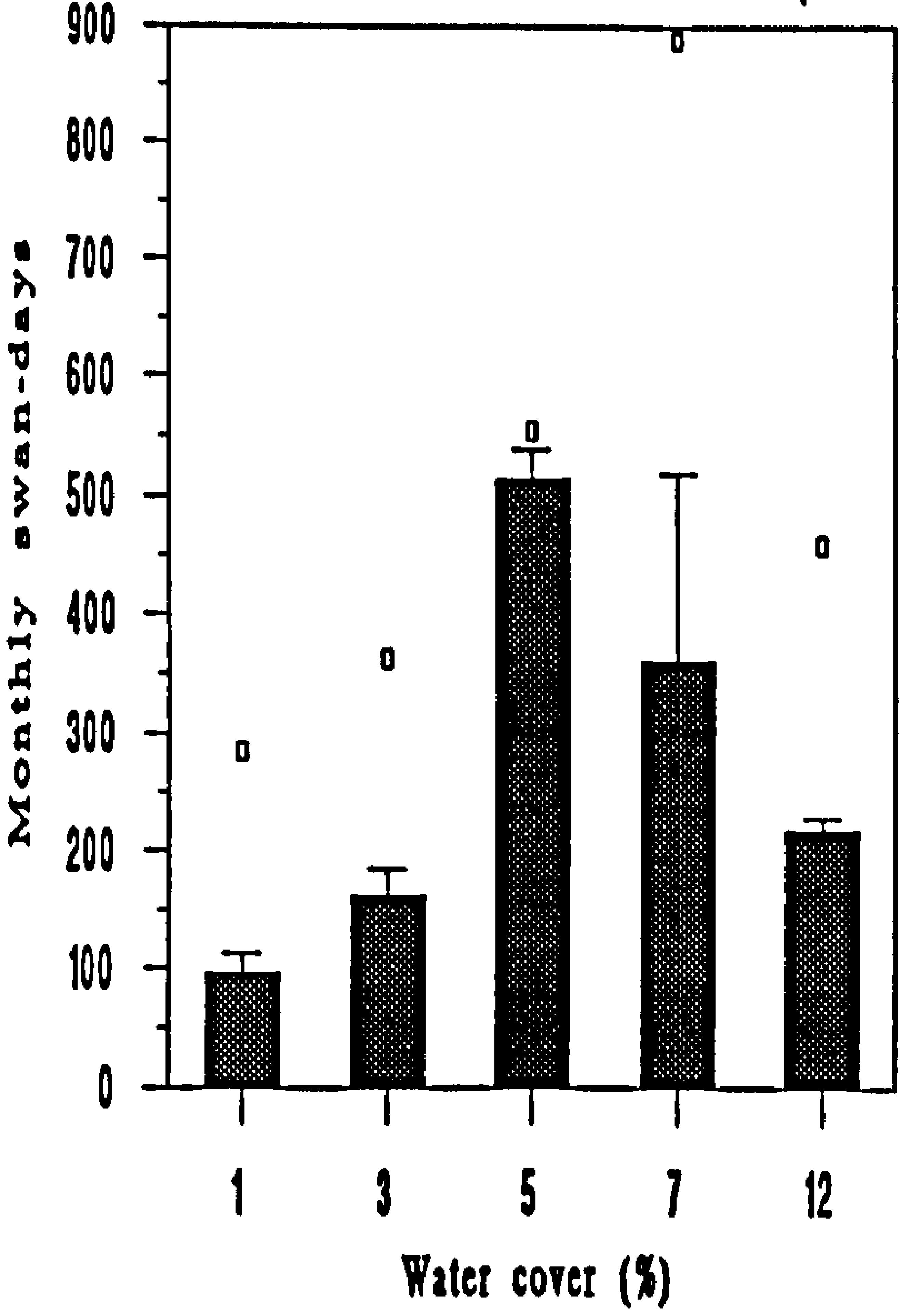


Fig. 4.16. Monthly swan-days in relation to the percentage protein content of the grass sward at the feeding sites (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 70).

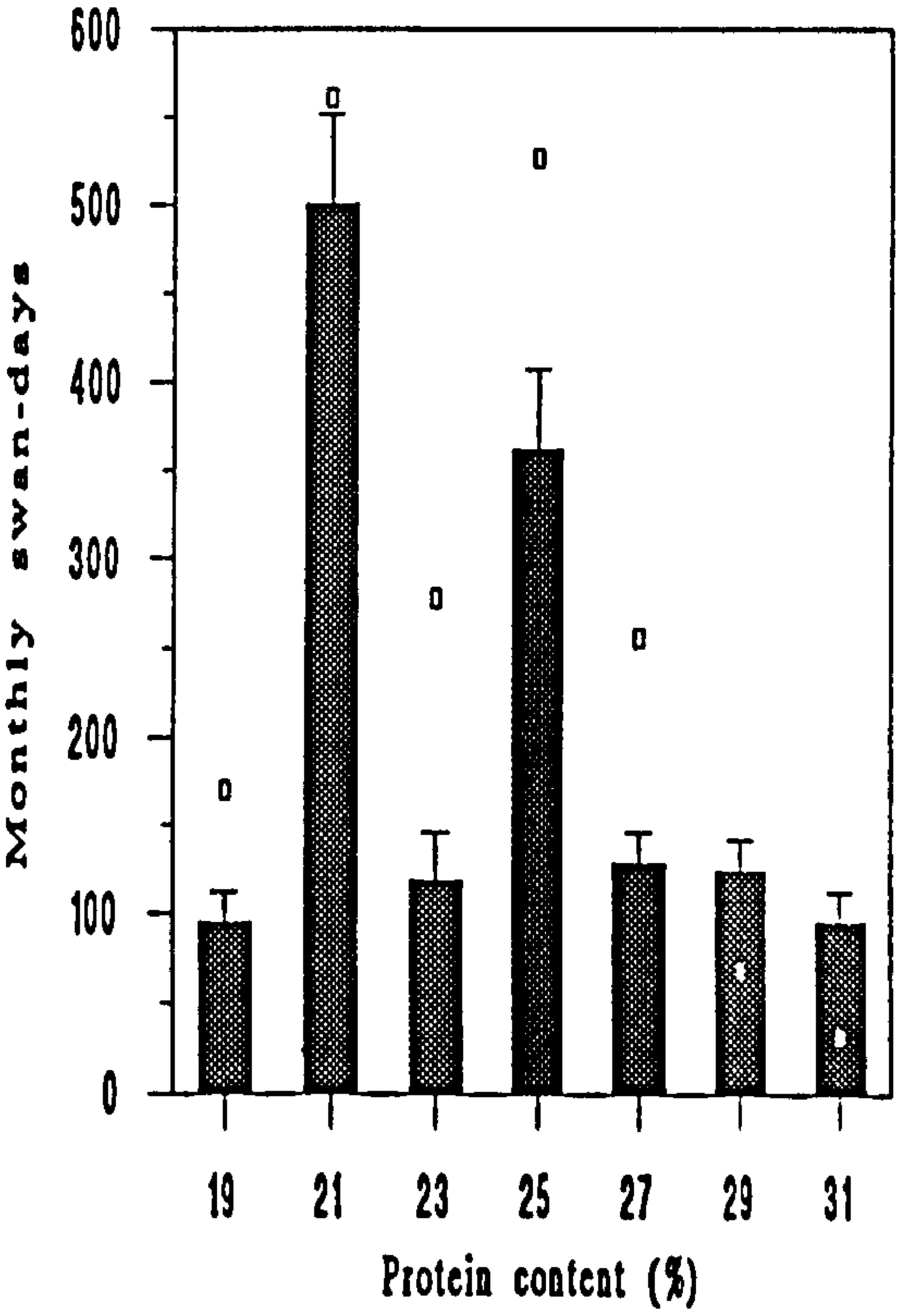


Fig. 4.17. Monthly swan-days in relation to monthly goose-days at the feeding sites (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 75).

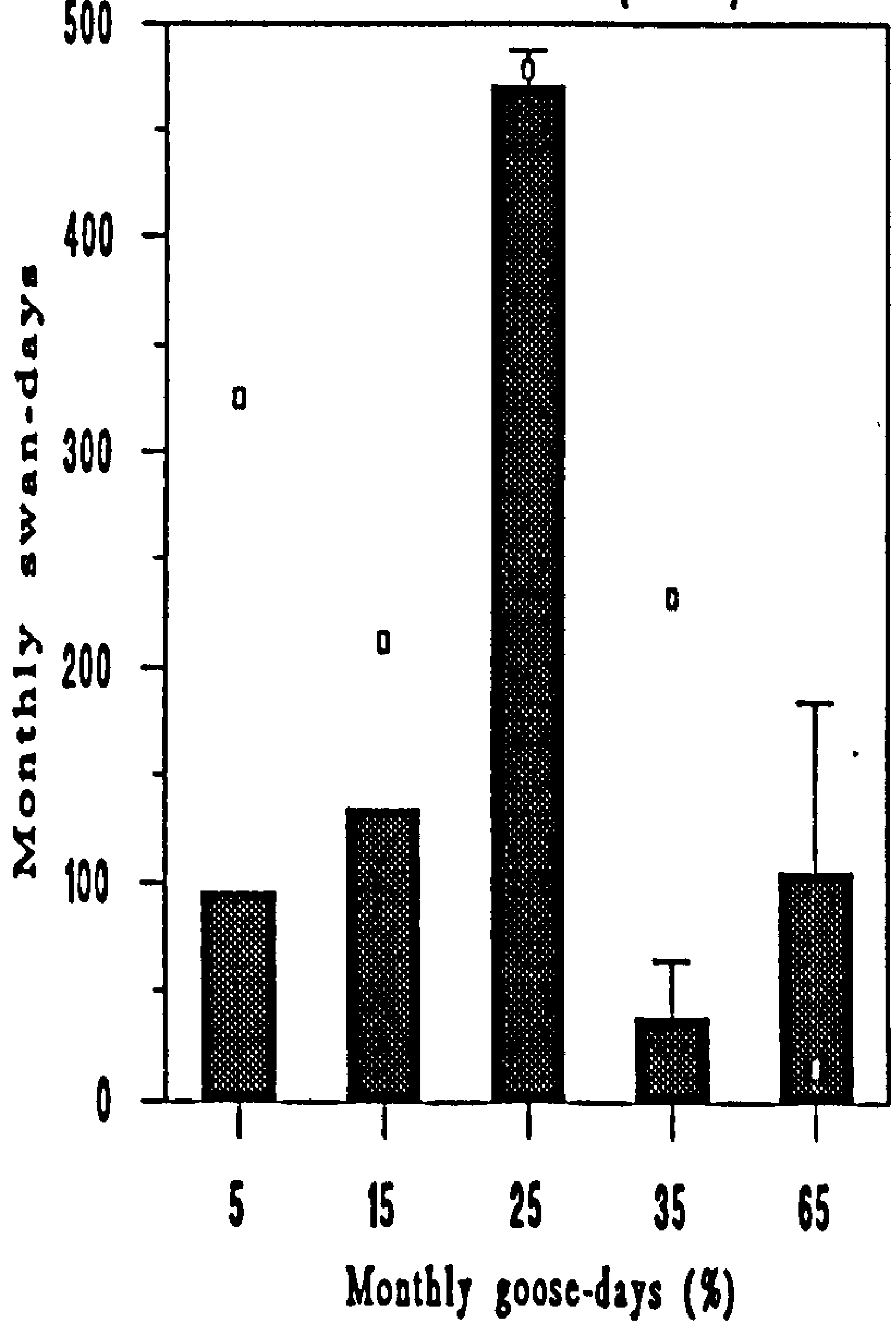


Fig. 4.18. Monthly swan-days in relation to percentage water cover at the feeding sites (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 149).

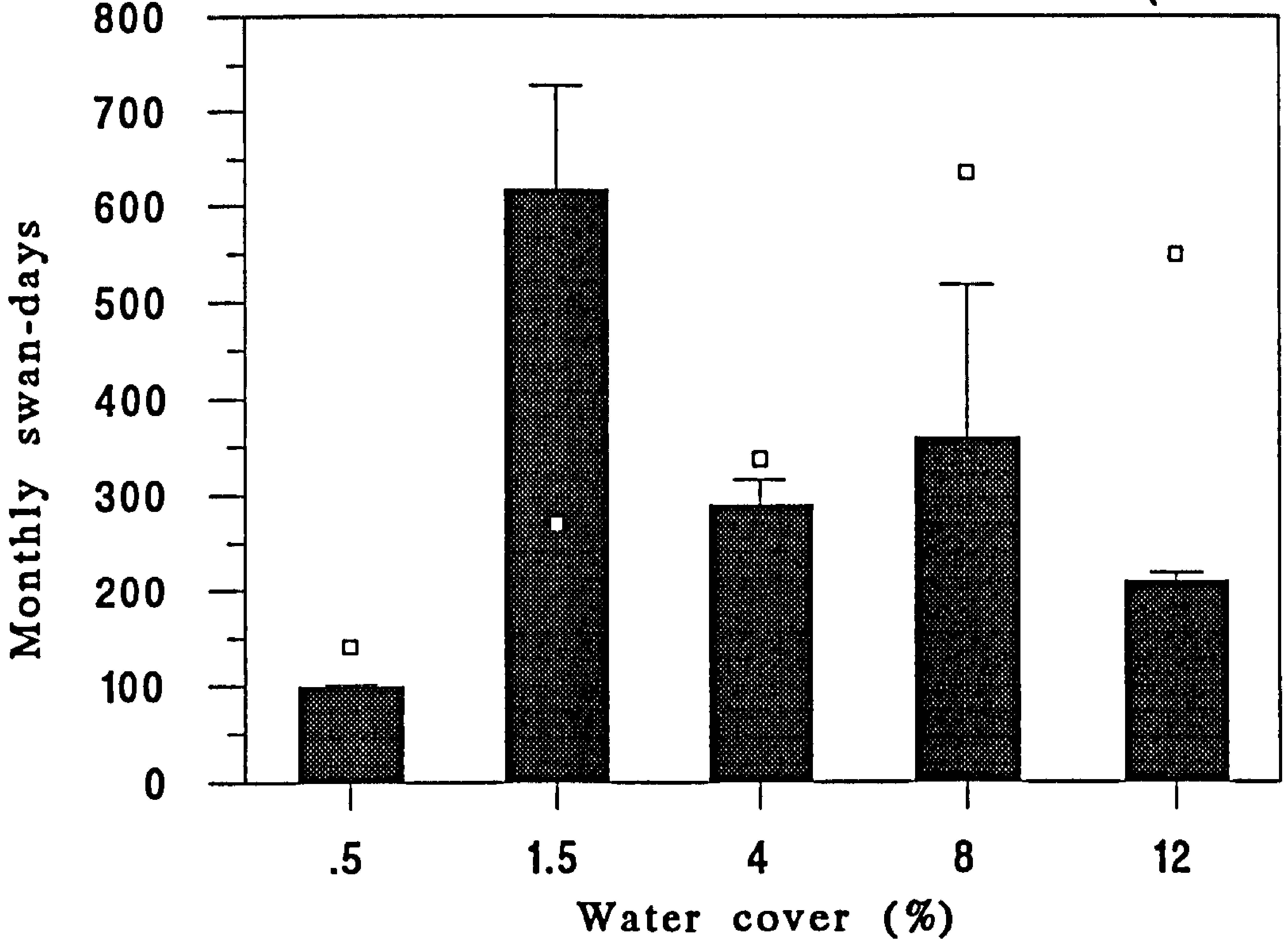


Fig. 4.19. Monthly swan-days in relation to wigeon-days in the previous month at the feeding sites (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 160).

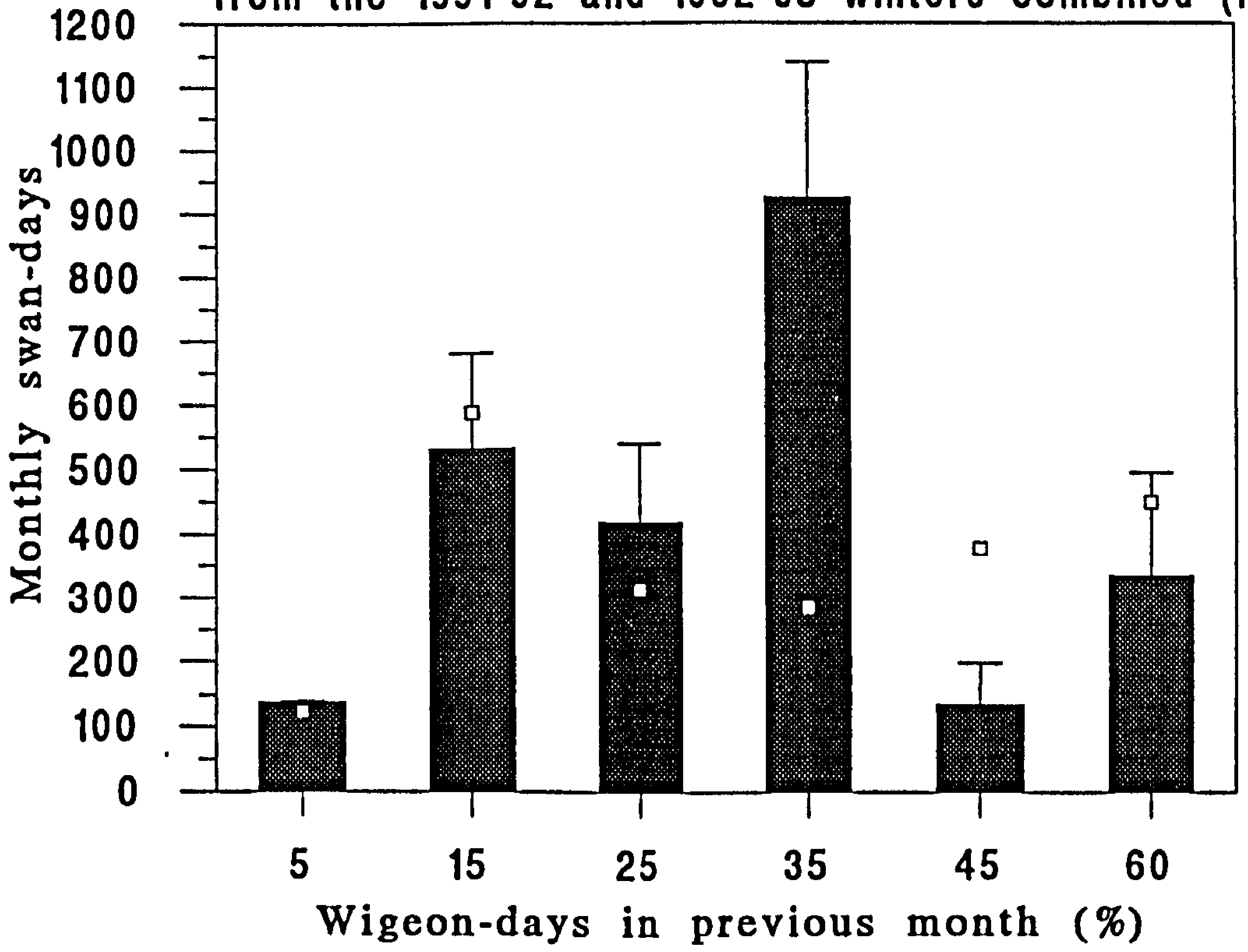


Fig. 4.20. The number of Rushy Pen units identified per field with distance from roost-site (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 99).

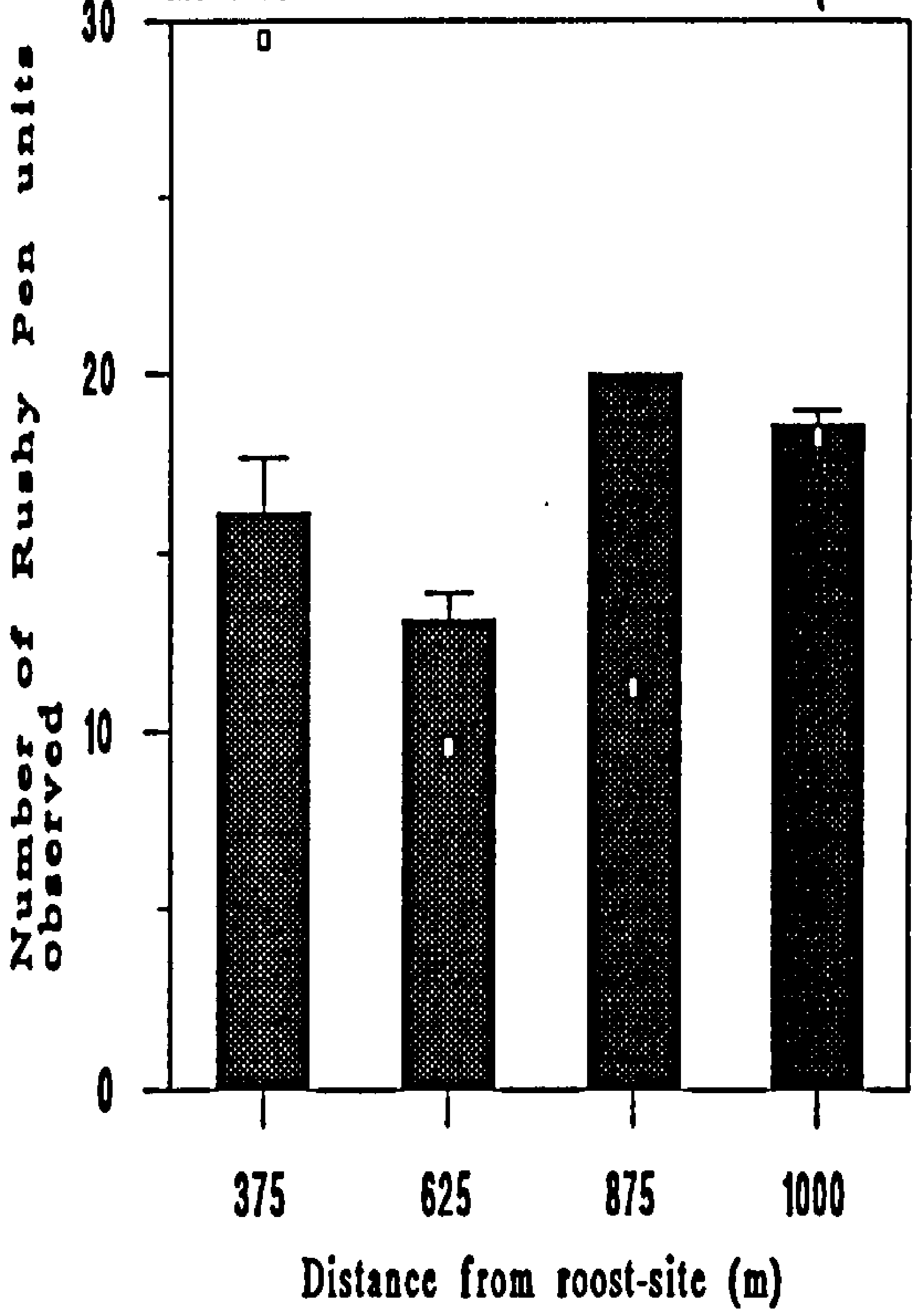


Fig. 4.21. The number of Rushy Pen units observed per field in relation to water cover (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 88).

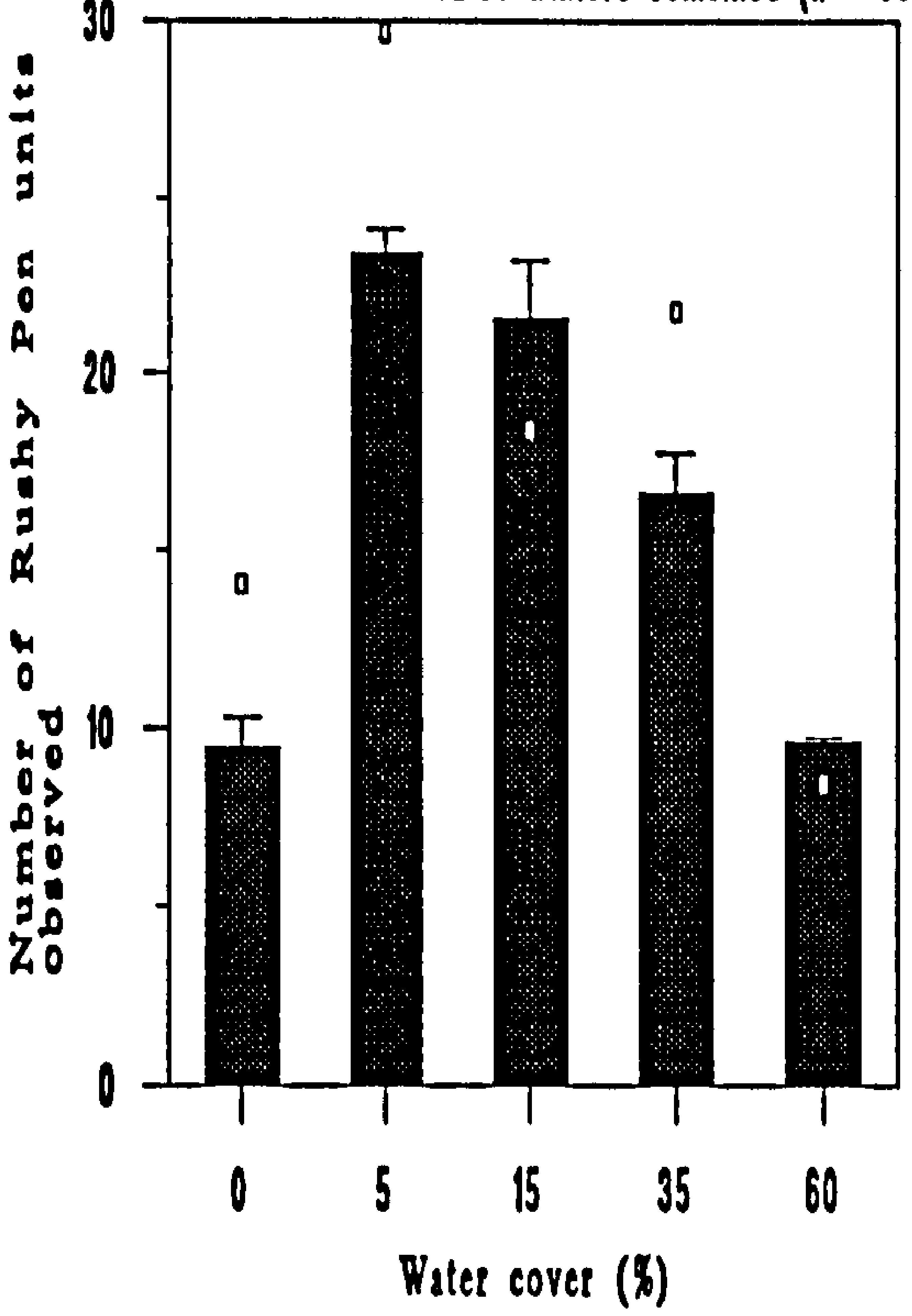


Fig. 4.22. The number of Rushy Pen units observed per field in relation to the protein content of the grass sward (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 70).

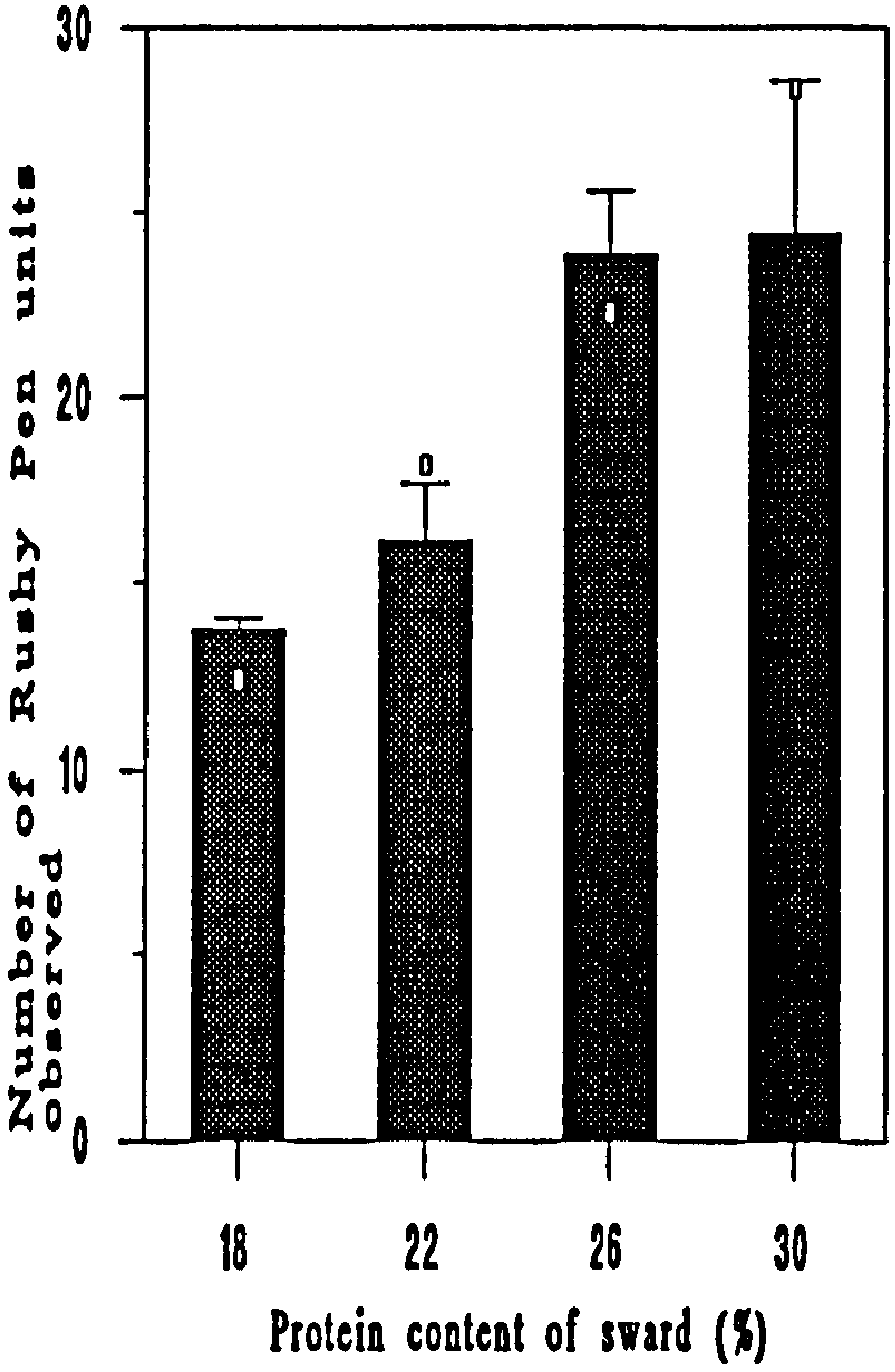


Fig. 4.23 The number of Grounds units observed per field with distance from roost-site (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 99).

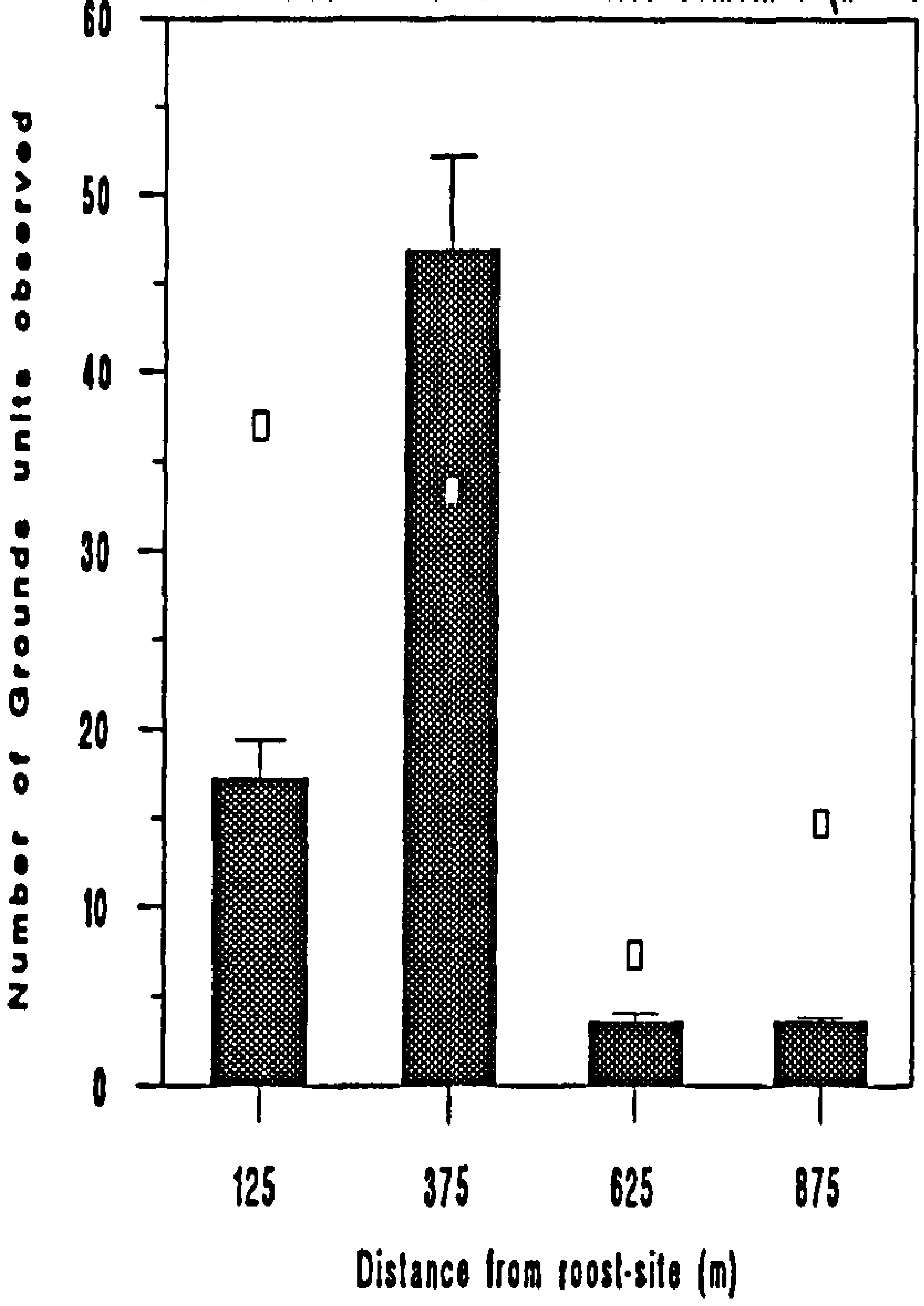


Fig. 4.24. The number of Grounds units observed per field in relation to biomass of grass sward (histogram and S.E. bar) plus predicted values from generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 75).

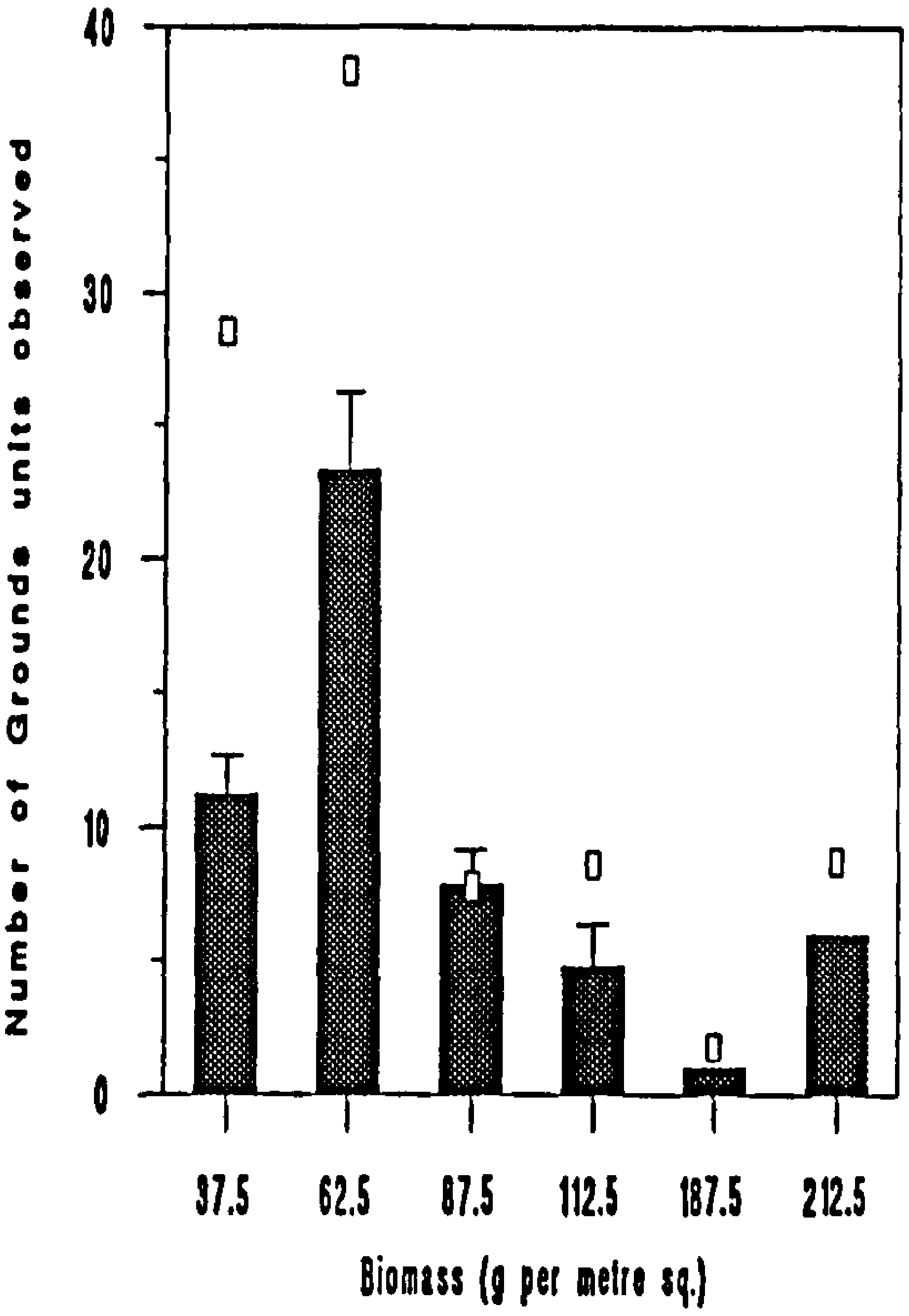
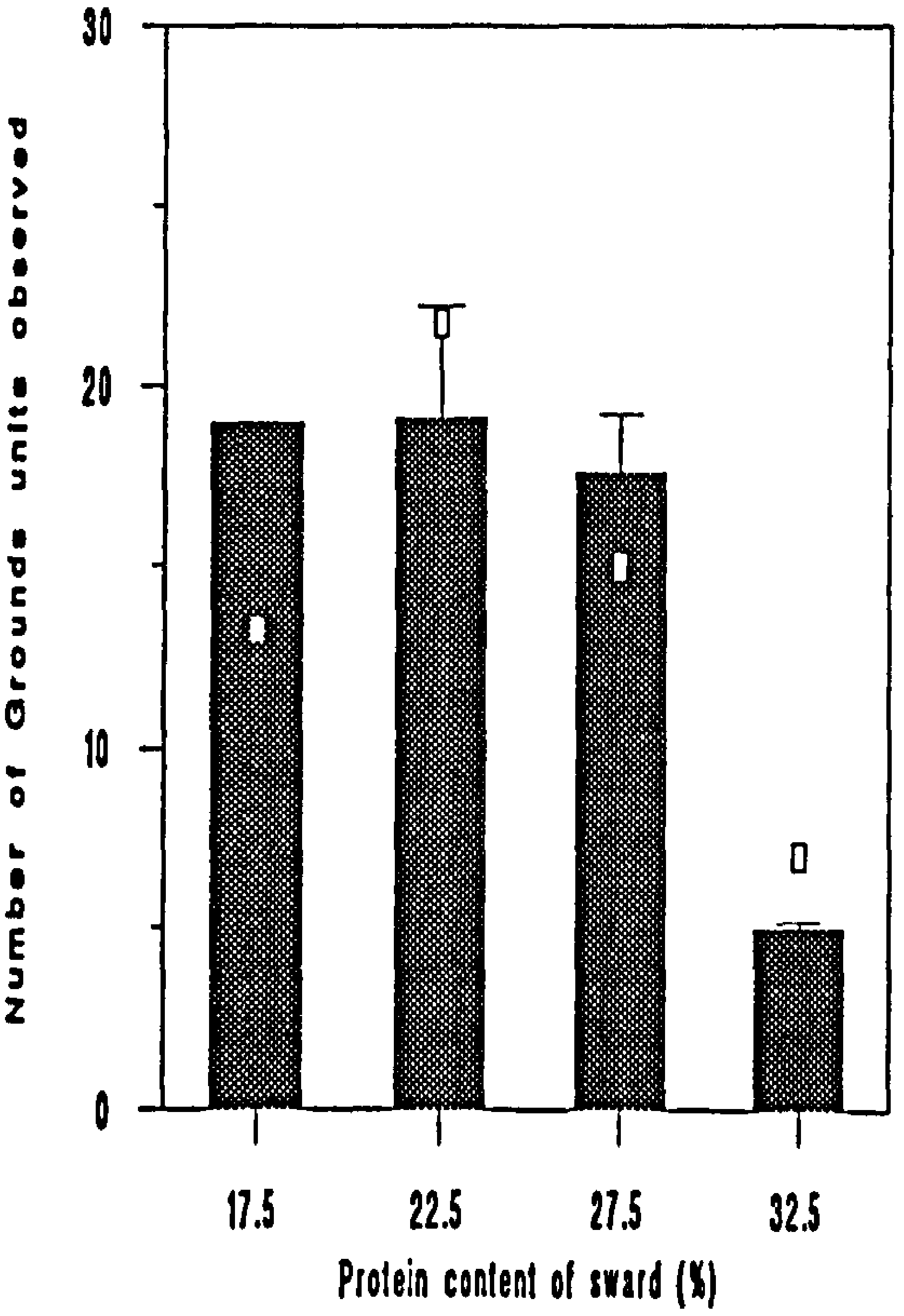


Fig. 4.25. The number of Grounds units observed per field in relation to protein content of the grass sward (histogram and S.E. bar) plus predicted values from a generalised linear model. Data from the 1991-92 and 1992-93 winters combined (n = 70).



CHAPTER 5 ACTIVITY PATTERNS OF THE SWANS AT THE FEEDING SITES

5.1 INTRODUCTION

Having established that the diurnal pattern of swan distribution on the Slimbridge fields is affected by habitat variables, the diurnal activities of the swans were investigated to test further theories concerning field selection and foraging routines.

Wildfowl feeding on land are mainly diurnal feeders because of the risk of predation after dark and because they rely on sight for feeding (Owen & Cadbury 1975). Time available for foraging is therefore short, particularly with reduced day-length during the mid-winter period, and birds will feed on nights with strong moonlight, particularly when feeding from water. Day-length increases again in spring but this is a period of peak energy and nutrients demands since, like Arctic-nesting geese, the birds have to accumulate body reserves in preparation for the migration to the breeding grounds (Prop et al. in prep). Herbivorous wildfowl which feed on terrestrial habitats have rather inefficient digestive systems compared with other grazers (review in Owen & Black 1990). In addition they deplete their food supply whose quality also declines in winter (Owen et al. 1992). Under normal conditions food quality and quantity do not increase until spring. Individuals should therefore adopt foraging regimes which aim to optimise their time at the feeding sites throughout the winter period.

Amongst several species of geese it has been shown that the annual cycle is adapted to variation in food quality e.g. amongst Canada Geese (Sedinger & Raveling 1984), Barnacle Geese (Prins & Ydenberg 1985, Owen & Black 1989), Brent Geese (Summers & Critchley 1990), Pink-footed Geese (Madsen 1985), and Nene Branta sandvicensis (Black et al. 1994), so that the phases of the life cycle that are most demanding for energy or specific nutrients are tuned to the availability of high quality foods (Prop et al. in prep). Owen et al. (1992) estimated the energy intake and expenditure of Barnacle Geese wintering in southwest Scotland and showed that the birds achieved a net energy surplus in October and November when most food was available, a net deficit in December and January when biomass and food quality were lowest, and a net surplus again in February as grass began to grow once more. The authors argued that the loss of mass by birds in midwinter was enforced by the limited feeding opportunity and declining food supply, rather than evolving as a balance between the likelihood of body reserves being needed, for instance during spells of inclement weather, and the disadvantages of carrying unnecessary weight (e.g.

increased predation risk), as has been suggested by other authors (e.g. Pienkowski et al. 1979).

Herbivorous grazing birds may be able to compensate to some extent for declining food stocks in winter by:

a) pecking more rapidly e.g. Barnacle Geese wintering in south west Scotland (Owen et al. 1992).

b) increasing the proportion of time spent feeding e.g. Greylag Geese wintering in southwest Spain during drought conditions (Amat 1986a).

c) by changing feeding patch or diet if better quality areas are available e.g. amongst Pink-footed Geese at spring staging areas in Denmark (Madsen 1985), and Barnacle Geese at spring staging areas in the Netherlands (Ydenberg & Prins 1985) and Norway (Black et al. 1991).

d) dispersing into smaller groups to make use of a wider range of feeding sites.

e) reducing energy expenditure.

The biomass and the quality (protein content and digestibility) of food is crucial to the net energy a bird obtains per unit of foraging time (Prop & Deerenberg 1991). Barnacle Geese wintering in the Netherlands had to consume a larger amount of grass to meet the energy requirements than to fulfil the protein needs. However, since the metabolizable energy and the protein content of the grass were positively related, selection for plants containing a high proportion of protein was favourable for the energy budget as well (Prop et al. in prep).

This chapter investigates the activities of the swans at the feeding sites in an attempt to answer the following questions:

1) Do the activity budgets of adults and cygnets differ at the feeding sites. Owen (1972a) for example, showed that vigilance afforded by parent Greater White-fronted Geese, permitted their offspring to spend less time alert and more time feeding on the wintering grounds.

2) Do the swans alter their activity patterns during the winter, and if so, how does this relate to the quantity and quality of the food supply at the feeding sites. Is there evidence that they attempt to compensate for declining food stocks during the winter.

3) Do the activity budgets of swans from the two roost groups differ at the feeding sites. This might be expected because birds from the Grounds roost generally had lower AP scores than those from the Rushy Pen roost group and were less critical in their selection of feeding sites (Chapters 3 & 4).

5.2 METHODS

a) Activities

The activity of swans at the feeding sites was monitored on a near-daily basis on the fields of the Slimbridge refuge and on adjacent farmland throughout the study period (1990-91 to 1992-93 winters inclusive), and at Walmore Common when swans were known to be present at this more distant site (see Fig. 3.3). The activity patterns of swans at the feeding sites were monitored by conducting flock scans at regular intervals (15 - 30 minutes), in which all birds in the flock were checked systematically, working through the flock from one side to the other (generally left to right). During a flock scan, the activity of each bird in the flock, when first observed, was recorded. It was not possible to identify individual birds during each scan (focal bird studies were carried out to investigate differences in activity patterns between individuals, see Chapter 6), but birds were recorded either as adults (including yearlings) or cygnets, and results from the two groups were investigated separately. Scans of small flocks were recorded directly into a notebook but those of larger flocks (> 25 birds) were recorded by dictaphone on to a cassette tape, which was subsequently transcribed, in order to reduce the duration of each scan.

Activities were placed into seven main categories:

1) Feeding - including grazing, surface dabbling, head-under, up-ending and pecking (at potatoes or fodder beet).
2) Resting - birds sitting on land or water with eyes open or closed, and not engaged in other activities (including sleeping and 'loafing').
3) Comfort activities - including preening, washing and scratching (see McKinney 1965).
4) Vigilant - including 'head-up watching' and extreme 'head-up watching'.
5) Movement - including swimming, walking and flying.
6) Social interactions - including aggression (neck-stretching, head-low threats, physical combat, triumph displays) and non-aggressive interactions (calling, greeting displays, head-pumping prior to take-off).
7) Drinking.

The activities of adults and cygnets were considered separately since Owen (1972a) demonstrated that the activity patterns of Greater White-fronted Geese in their first winter were significantly different from those of adults. The number of individuals performing each activity for each of the two age classes, was ascertained for each scan and expressed as a percentage of the total number of birds in the flock for each age class. Since scans which were close together in time may have recorded the same activity for an individual bird, mean scans were calculated for each 60 minute sampling period per field in order to reduce the problem of pseudoreplication. Hurlbert (1984) defined pseudoreplication as testing for treatment effects with an error term inappropriate to the hypothesis being tested, and demonstrated that in many behavioural studies, the appropriate units for testing were not the individual records but rather the mean per individual. Flock scans which were interrupted by an unexpected event, such as the passage of a low-flying jet aircraft or the sudden appearance of someone walking a dog in the field, and which caused a marked change in the activity of the swans (generally a marked reduction in the number of feeding birds and an increase in vigilance), were removed from analysis. Similarly scans collected during very severe weather e.g. heavy thunderstorms or blustery squalls (which resulted in fewer swans feeding and an increase in rest/sleep activity), were also removed prior to analysis.

b) Statistical analyses

Data for the two age classes were compared in order to see if the activities of adults and cygnets at the feeding sites differed significantly. Since evidence was found to suggest that this was the case, subsequent analyses were conducted separately upon data from the two age classes. The effect of the independent variables in influencing the activity patterns of the swans at the feeding sites was determined by co-variate analysis, using GLIM (NAG 1986). Co-variate analysis was chosen in order to identify explanatory variables from a number of variables which were thought likely to be inter-correlated. The first five variables to be examined were considered since they might explain variation in the hourly flock scan data throughout the winter: year, half-month, hour, flock-size and field. Year and field were treated as factors. A binomial error distribution was used, in which the number of birds from an age class recorded in a particular activity were divided by the total number of birds of the same age class in the scan (the binomial denominator). This distribution was used since both the number of birds engaged, and not engaged, in a given activity were known in each case. By not using the percentage activity as the response variable, information concerning the size of the sample could be retained. Over-dispersion of the data was compensated for, as before, by the use of the WILLS.MAC programme (Crawley 1993, see Chapter 4). The number of combined effects entered into the initial model was reduced by first determining which of the five variables were significant. Variables proving to be significant or near-significant were investigated further in the main model together with their interaction terms. The statistical significance of the explanatory variables and their interactions, was then determined by fitting the full model and inspecting the changes in deviance with respect to the change in the degrees of freedom. The most non-significant ($P > 0.05$) variables were then progressively removed from the model. The final model was thus the most parsimonious (see Crawley 1993).

Since field identity (included as a categorical variable) was found to be a significant factor in all twelve of the initial models (Tables 5.2 & 5.3), the association between field identity and the swans' activities was investigated further. The models were run again, omitting the field variable but including habitat variables pertaining to the field(s) in question for the 1991-92 and 1992-93 winter seasons (see Chapter 4): mean sward-length (mm), biomass of the grass sward (g per m^2), protein content of the grass (%) and water cover on the field (%), in order to investigate their effect upon the activities of the swans. The variables of flock-size, year and the time of day were retained in the models, whilst the variable half-month was changed to month, since sward-length, biomass and protein content were collected only once a month. One further variable, the proportion of the total number of swan units identified in the flock from the Rushy Pen roost group (see Chapter 3), was also added to the model, in order to investigate differences in activity patterns between swans from the two main roost-groups. These differences are not clear-cut since activities were not assigned to known individuals (and thus to roost groups) during the flock scans. All variables were considered initially in the models and the most parsimonious models were derived as before.

5.3 RESULTS

A total of 3755 uninterrupted flock scans were conducted during the study period at 28 different feeding sites (see Fig. 3.4), from which 1028 mean hourly scans were calculated. A summary of the frequency of activities observed for adult swans and cygnets are given in Table 5.1. On average, adult birds spent a third of the time actually feeding at the feeding sites, a third resting (sleeping and loafing), and a third in other activities, mostly comfort (preening and washing), movement and vigilance behaviour. Social interactions (mostly aggressive encounters) and drinking amounted to only 2.1% of time spent at the feeding sites. The activities recorded for cygnets differed significantly from those of the adults (Chi-sq. = 152.1, df = 6, $\underline{P} < 0.001$, see Table 5.1b). Cygnets were significantly more often seen feeding, preening/washing, and moving than adults, and significantly less often seen resting, being vigilant or involved in social interactions.

a) Initial model - excluding habitat variables

Feeding

Variation in the proportion of adult swans in flocks in the fields recorded as feeding was associated with field identity, half-month and the time of day (Table 5.2). There was also a significant interaction between field and half-month, indicating that field identity may be more important in some months than in others. Amongst cygnets, variation in the proportion recorded feeding was associated with field identity, half-month and the time of day (Table 5.3). There were also significant interactions between field, the time of day and half-month, indicating that the time of day may be more important at different stages of the season, and for some fields more than others.

The number of adult swans feeding in the flocks generally tended to increase during the day but there were feeding peaks both at the start and end of the day (Fig. 5.1). During the winter season, both the number of feeding adults and cygnets tended to increase up until the second half of December, with the exception of a sharp increase in the first half of February, and then subsequently declined (Figs. 5.2 & 5.17). This same general pattern was noted in all three seasons of the study (as indicated by the small standard errors in Figs. 5.2 & 5.17). The number of cygnets feeding in the flocks varied during the day, but as with the adults there were pronounced feeding peaks at both the start and end of the day (Fig. 5.16).

Resting

Variation in the proportion of adult swans recorded resting in flocks in the fields was associated with field identity, half-month, the time of day and year (Table 5.2). Amongst cygnets, variation in the proportion recorded resting was associated with field identity, half-month and the time of day (Table 5.3). There were no significant interactions between any of these variables.

The number of adult swans resting in the flocks was higher in the 1992-93 winter than in the previous two winters (Fig. 5.3). There was a marked increase in the number of both adults and cygnets seen resting each half-month as the winter progressed (Figs. 5.4 & 5.18). During the day the number of adults and cygnets recorded resting was highest during the midday period (10.00-14.00 hrs) and was lower both in the early morning and later in the afternoon (Figs. 5.5 & 5.19).

Comfort

Variation in the proportion of adult swans engaged in comfort activity in flocks in the fields was associated with field identity, half-month and flock-size (Table 5.2). There was a significant interaction between field and half-month indicating that field identity may be more important in some months than in others. Amongst cygnets, the proportion recorded in comfort activity was associated with field identity and half-month (Table 5.3). There were no significant interactions between these two variables.

The number of adult swans engaged in comfort activity on the fields increased both with flock-size (Fig. 5.6), and half-month (Fig. 5.7) with numbers increasing steadily throughout the season from October to the end of February. Although flock-size and half-month were closely correlated (Spearman's rank correlation $r_s = 0.199$, $P < 0.001$, $n = 1028$) both had a significant effect upon the proportion of swans in the flocks that were engaged in comfort activity. There was also a steady increase in the number of cygnets engaged in comfort activity as the season progressed, with markedly lower numbers washing/preening in the period October to December, than in January to March (Fig. 5.20).

Vigilance

Variation in the proportion of adult swans engaged in vigilance activity in flocks in the fields was associated with field identity, half-month and the time of day (Table 5.2). There was a significant interaction between the time of day and half-month, indicating that half-month affected diurnal vigilance activity. Amongst cygnets, variation in the proportion engaged in vigilance activity was associated with field identity, half-month, the time of day and flock-size (Table 5.3). There were significant interactions between the time of day, half-month and flock-size indicating that both the time of day and flock-size were more important in some half-months than in others.

The amount of adult vigilance activity generally increased as the season progressed (Fig. 5.8) with a distinct peak in the first half of February. Adult vigilance levels also tended to increase during the day, especially after 14.00 hrs (Fig. 5.9). Amongst cygnets, the proportion engaged in vigilance activity at the feeding sites tended to increase with flock-size although this relationship may be biased by the sudden increase in the number of vigilant cygnets in the very largest flocks (Fig. 5.21). There was also a tendency for the number of cygnets engaged in vigilance activity to increase during the season, although there were distinct peaks in both the second half of October and the first half of February (Fig. 5.22). Numbers of cygnets engaged in vigilance activity during the day showed pronounced peaks in the early morning and late afternoon with lower numbers during the midday period (Fig. 5.23).

Movement

Variation in the proportion of adult swans engaged in active movement in flocks in the fields was associated with field identity, year, half-month and the time of day (Table 5.2). There was a significant interaction between field identity and the time of day indicating that the time of day was more important on some fields than on others. Amongst cygnets, variation in the proportion recorded swimming, walking or flying was associated with field identity, the time of day and flock-size (Table 5.3). As with the adults, there was a significant interaction between field and time of day indicating that the time of day was more important on some fields than others.

The number of adult swans recorded swimming, walking and flying varied between winters (Fig. 5.10). There was also a significant increase in the number of adults engaged in active movement during the course of the season (Fig. 5.11), and during the course of the day (Fig. 5.12) with most movement occurring after 14.00 hrs. Active movement by cygnets at the field feeding sites increased steadily with flock-size (Fig. 5.24), indicating that the proportion of cygnets walking/swimming/flying increased as flock-size increased. During the course of the day, there were two distinct peaks in the levels of movement activity amongst cygnets; one in the early morning and one in the late afternoon, with distinctly fewer cygnets seeming active during the midday period (Fig. 5.25).

Social interaction

Variation in the proportion of adult swans engaged in social interactions in flocks in the fields was associated with field identity, year, the time of day and flock-size (Table 5.2). There was also a significant interaction between year and the time of day indicating that diurnal variation in social interactions in the flocks differed between years. Amongst cygnets, variation in the proportion engaged in social interactions was associated with field identity, year, half-month and the time of day (Table 5.3). There were significant interactions between field identity, year, half-month and the time of day indicating that the importance of field identity varied between years, and that the importance of the time of day varied both with half-month and year.

The number of adult swans engaged in social interactions in flocks in the fields increased almost exponentially with flock-size (Fig. 5.13), indicating that the proportion of birds engaged in social interactions increased as flock-size increased. However, there were also significant differences between years (Fig. 5.14). There was also a tendency for the number of adults engaged in social interactions to increase during the course of the day, with a peak during the late afternoon (Fig. 5.15). This late afternoon peak was due, in part, to an increase in pre-flight signalling prior to departure to the roost sites, but also related to an increase in aggressive encounters amongst swans regrouping before take-off. The number of cygnets engaged in social interactions at the feeding sites decreased each winter during the study period (Fig. 5.26) as a result of annual variation in the proportion of juveniles in the herd (see Chapter 7). The number of cygnets engaged in social interactions tended to increase during the course of the winter (Fig. 5.27). During the day, there were two distinct peaks; one in the morning and one in the late afternoon, with distinctly fewer social interactions during the midday period (Fig. 5.28).

Activity patterns recorded for both adults and cygnets were significantly affected by the fields being used by the birds. This inter-field variation was investigated further by the removal of the categorical variable field and the inclusion of habitat variables, used to describe conditions in the fields, in the second series of models, together with the proportion of birds present in each feeding flock from the Rushy Pen roost group.

b) Second model - habitat variables included

Feeding

Variation in the proportion of adult swans seen feeding in flocks in the fields was associated with month, protein levels (measured as the percentage of protein in the sward) and the extent of flooding (measured as the percentage water cover of the field) (Table 5.4). The time of day was no longer associated with the proportion of adults seen feeding when the habitat variables were also considered. There was a significant interaction between protein levels and the extent of flooding, indicating that protein levels may be more important to feeding swans under some flooding regimes than others. Amongst cygnets, variation in the proportion recorded feeding was associated with month and the time of day, as in the initial model, together with the extent of flooding, protein levels and the proportion of swan units present from the Rushy Pen roost (Table 5.5). There were also significant interactions between the time of day, half-month, the extent of flooding and the proportion of swan units present from the Rushy Pen roost, indicating that effect of time of day may be more important; a) in some months than in others, b) under different flooding regimes and c) when different proportions of swan units from the Rushy Pen roost were present in the flocks.

The number of adult swans feeding in the flocks generally increased with both the protein levels in the sward (Fig. 5.29) and with the extent of flooding on the field (Fig. 5.30). Highest numbers of feeding swans were seen on extensively flooded pasture with a high protein content; lowest numbers were seen on dry pasture with a low protein content. The number of cygnets feeding in the flocks tended to increase with the protein content of the sward, although the results were less clear-cut than for the adults possibly due to the smaller numbers involved (Fig. 5.40). There was a pronounced increase in the number of cygnets feeding as the proportion of swan units present from the Rushy Pen roost increased (Fig. 5.41), whilst the number of cygnets feeding tended to decrease as the extent of flooding increased on the fields (Fig. 5.42).

Resting

Variation in the proportion of adult swans recorded resting in flocks in the fields was associated with month, the time of day, protein levels and the biomass of the sward (measured as g/m^2) (Table 5.4). Year was no longer associated with the proportion of adults seen resting when the habitat variables were also considered. In addition there was a significant interaction between month and biomass, indicating that the effects of biomass on the proportion of adults resting were more important in some months than in others. Amongst cygnets, variation in the proportion recorded resting was associated with month and the time of day, as in the initial model, together with the extent of flooding and biomass of the sward (Table 5.5). There were significant interactions between these variables, indicating that the time of day was more important in some months than in others, and under different flooding regimes.

The number of adult swans resting in the flocks tended to increase with protein levels in the sward (Fig. 5.31). Increasing biomass of the sward caused a steady decrease in the number of both adults and cygnets recorded resting in the flocks (Figs. 5.32 & 5.43). In addition, the number of cygnets recorded resting decreased steadily as the extent of flooding increased on the fields (Fig. 5.44).

Comfort

Variation in the proportion of adult swans engaged in comfort activity in flocks in the fields was associated with year, month, flock-size, extent of flooding and the proportion of swan units present from the Rushy Pen roost (Table 5.4). The association between year and the proportion of adults in comfort activity became apparent when the habitat variables were also considered. There was a significant interaction between year and the proportion of units from the Rushy Pen roost indicating that the effect of roost group upon the proportion of adults seen washing/preening was more important in some years than in others. Amongst cygnets, variation in the proportion recorded in comfort activity was associated with month, the time of day, flock-size and protein levels in the sward (Table 5.5). The associations between the proportion of cygnets seen in comfort activity and both the time of day and flock-size, became apparent when the habitat variables were also considered. There were significant interactions between these variables, indicating that both the time of day and flock-size may be more important at some stages of the season than others, and that flock-size may be more important at certain levels of protein in the sward than in others.

The number of adult swans engaged in comfort activity tended to increase with the extent of flooding on the field although the trend was rather variable (Fig. 5.33), and to decrease with the proportion of swan units present from the Rushy Pen roost (Fig. 5.34), although again the trend was not uniform. The number of cygnets engaged in comfort activity increased steadily with increasing flock-size (Fig. 5.45), and generally decreased with increasing protein levels in the sward, although the relationship was rather variable (Fig. 5.46).

Vigilance

Variation in the proportion of adult swans engaged in vigilance activity in flocks in the fields was associated with month, the time of day, biomass of the sward and the proportion of swan units present from the Rushy Pen roost (Table 5.4). Flock-size was no longer associated with the proportion of adults seen in vigilance activity when the habitat variables were also considered. There were significant interactions between time of day, month and biomass, indicating that both the time of day and the biomass of the sward may be more important in some months than in others. Amongst cygnets, variation in the proportion seen in vigilance activity was associated with month, the time of day, and flock-size, as in the initial model, together with the proportion of swan units present from the Rushy Pen roost and protein levels in the sward (Table 5.5). There were significant interactions between the time of day, month, the proportion of swan units present from the Rushy Pen roost and protein levels in the sward, indicating that the time of day may be more important; a) in some months than in others, and b) at certain levels of protein in the sward than in others, and that the level of protein in the sward may be more important when different proportions of swan units from the Rushy Pen roost were present in the flocks.

The number of adult swans engaged in vigilance activity in flocks in the fields generally decreased as the biomass of the sward increased (Fig. 5.35), and increased as the proportion of swan units present from the Rushy Pen roost increased (Fig. 5.36). The number of cygnets engaged in vigilance activity tended to decrease as protein levels increased in the sward (Fig. 5.47) and to increase as the proportion of swan units present from the Rushy Pen roost increased (Fig. 5.48), although peaking when the ratio was roughly 50:50.

Movement

Variation in the proportion of adult swans in flocks in the fields recorded in active movement was associated with year, flock-size and biomass of the sward (Table 5.4). The time of day was no longer associated with the proportion of adults recorded in active movement when the habitat variables were also considered, whilst the association with month became apparent. There were significant interactions between year and flock-size, and also between year and biomass, indicating that the associations between the active movement by adults in the flocks with flock-size and also with biomass, varied between years. Amongst cygnets, variation in the proportion recorded walking, swimming or flying during the flock scans was not reduced significantly by any of the terms entered into the model.

The number of adult swans engaged in active movement at the feeding sites showed a rather variable relationship with biomass of the sward, with no obvious trend apparent (Fig. 5.37).

Social interaction

Variation in the proportion of adult swans engaged in social interactions in flocks in the fields was associated with the time of day, flock-size, the extent of flooding and proportion of swan units present from the Rushy Pen roost (Table 5.4). The time of day and year were no longer associated with the proportion of adults recorded in social interactions when the habitat variables were also considered, whilst the association with flock-size became apparent. There were significant interactions between the time of day, flock-size and the extent of flooding, indicating that flock-size may be more important at different times of the day and under different flooding regimes. Amongst cygnets, variation in the proportion engaged in social interactions was associated with month, the time of day, the proportion of swan units present from the Rushy Pen roost and protein levels in the sward (Table 5.5). Year was no longer associated with the proportion of cygnets seen in vigilance activity when the habitat variables were also considered. There were significant interactions between the time of day, the proportion of swan units present from the Rushy Pen roost and protein levels in the sward, indicating that the time of day was more important; a) at certain levels of protein in the sward than in others and b) when different proportions of swan units from the Rushy Pen roost were present, and that protein levels in the sward may be more important when different proportions of swan units from the

Rushy Pen roost were present in the flock. These results differ significantly from those for the adults and may be less meaningful since the numbers involved were considerably smaller.

The number of adult swans engaged in social interactions at the feeding sites tended to increase with the extent of flooding of the field (Fig. 5.38). There was a distinct peak in the frequency of social interactions amongst flocks containing roughly 50% swan units from the Rushy Pen roost and (therefore) 50% swan units from the Grounds roost group (Fig. 5.39). The number of adults engaged in social interactions tended to increase with the proportion of swan units present from the Rushy Pen roost (Fig. 5.39), and the number of adults engaged in social interactions in flocks dominated by Rushy Pen birds (> =75%) was significantly higher than in flocks dominated by Grounds birds (Mann-Whitney U comparison, $W = 44051$, $P < 0.025$, df = 1, $n = 221$ and 162 respectively). The number of cygnets engaged in social interactions increased as the protein levels increased in the sward (Fig. 5.49). As with the adults, the highest frequency of social interactions occurred amongst flocks containing roughly 50% swan units from the Rushy Pen roost (Fig. 5.50).

5.4 DISCUSSION

During the winter adult swans spent, on average, approximately one third (32.8%) of their time feeding when they were on the fields, whilst cygnets spent significantly longer feeding (nearer 40%). This difference may stem from the protection from feeding competition (in terms of both vigilance and aggression) afforded to the cygnets by their parents (Scott 1980b), since cygnets were less often recorded in the activities of vigilance and social interaction than adults. Although the bone measurements of swans in their first winter indicate that they are close to adult size, they are still only 85-88% of adult weight (Evans & Kear 1978) and would therefore need to feed more frequently than adults in order to sustain growth. These results concur with those of Owen (1972a) who found that the vigilance afforded by parents to Greater White-fronted Geese in their first winter, permitted the young birds to spend less time alert and more time feeding and resting. In the current study, parental protection also, apparently, allowed cygnets to spend less time in vigilance and social interactions, and more time in comfort activities. Parental protection is investigated in greater detail in Chapter 6. The higher frequency of movement amongst the cygnets was probably linked to the high level of feeding activity, since feeding bouts were frequently interspersed with periods of walking/ swimming as the birds selected food items.

The proportion of birds in the flock engaged in a given activity at any one time will reflect the proportion engaged in other activities. In general, higher levels of feeding activity led to an increase in not only movement, but also vigilance and social interactions, whilst higher levels of resting activity were associated with a decrease in vigilance and social interactions, and an increase in preening/washing. The level of feeding activity in turn will depend on the time of day, the time of year, food supply and the extent of flooding on the fields.

Assuming an average arrival time at the feeding sites of 10.00 hrs and an average departure time of 16.00 hrs (these times are connected to the timing of the supplementary feeds at the roost-sites and varied little during the winter, despite the effect of change in day-length), swans spent six hours at the feeding sites a day of which 2.0 hrs and 2.4 hrs were spent feeding by adult swans and cygnets respectively. In addition swans spent a small but variable amount of time feeding on the provisioned grain at the roost sites (see Chapter 6); for example just 10.2% of swans in the Rushy Pen were recorded feeding during flock scans in a previous study (Rees & Bowler 1991). These figures are similar to those from studies of Mute Swans feeding predominantly on water bodies, for example 42% feeding in the Slimbridge area (Ryley & Bowler 1994), 36% feeding at Cork Lough, Ireland (Keane & O'Halloran 1992), 30% feeding at Caerlaverock, Dumfries (Black & Rees 1984), 22% in the Thames Valley (Sears 1989), and 40% of Whooper Swans feeding at Rostellan Lake, Co. Cork (O'Donoghue & O'Halloran 1994), but are considerably lower than those recorded in an earlier study at Slimbridge (Rees & Bowler 1991), when on average 54.3% of the swans in the fields were recorded as feeding during flock scans. This latter difference may result from variation due to weather variables which were not specifically controlled for in either study and/or to a difference in the precise definition of the activities included in the feeding class. In the current study, swans were only recorded as feeding if they were actually grazing or pecking in head-down behaviour, or if they were obviously ingesting food items which they had just collected. Swans which were observed walking or swimming in search of another feeding site were placed in the active movement category, whilst birds which were sitting or standing in a relaxed head-up posture and possibly digesting food items which they had already collected were coded as 'loafing' and placed in the resting category. This difference likewise may account for the apparently small proportion of the day that the swans in the current study actually spent feeding when compared to studies of other grazing Anatidae in winter: Greater White-fronted Geese about 90% (Owen 1972a), Pink-footed Geese 70% (Giroux & Patterson 1995), Barnacle Geese 75 to 85% (Ebbinge et al. 1975), Eurasian Wigeon 74% (Mayhew 1988) and Gadwall Anas strepera 60% (Paulus 1984).

The activities of the swans at the feeding sites were influenced by a range of interacting variables. Flock size had a positive effect upon the proportion of adult swans engaged in comfort activities and in social interactions, and upon the proportion of cygnets engaged in comfort, vigilance and movement activities. The increased security inherent amongst larger flocks (Lazarus 1978) permitted more time to be spent in comfort activities, although there was also an increase in the number of cygnets in vigilance behaviour, possibly because of increasing numbers of competitive encounters for food items with increasing flock size, as demonstrated amongst Common Cranes Grus grus in their first winter (Alonso & Alonso 1993). Aggression has also been shown to increase with flock-size amongst Black Swans Cygnus atratus (Tingay 1974), although flock density rather than total numbers may be the relevant factor. There was no apparent relationship between flock-size and the proportion of adults in vigilance activity, although studies amongst other grazing Anatidae species have shown that as flock size increases the percentage of birds vigilant at any one time decreases (Lazarus 1978, Drent & Swiestra

1977, Mayhew 1987). The edge effect is important in these cases, with peripheral birds in the flock being more vigilant to watch for potential predators, than central ones. As flock size increases, the relative perimeter area of the flock decreases so that there will be proportionally less birds on the perimeter, and hence the average level of vigilance in an individual will also decrease (Drent & Swiestra 1977). However, since individuals in swan flocks tend to be much more randomly distributed than in goose flocks, the periphery of the flock is less well defined. This may explain the lack of a negative relationship between flock size and vigilance levels amongst swans in this and other studies (e.g. O'Donoghue & O'Halloran 1994). Moreover, vigilance serves several functions other than watching for predators (Lazarus & Inglis 1978), such as looking for food, or looking for conspecifics to avoid interference during feeding. As flock size increases, the need for an individual to watch for predators may decrease because of the increased number of vigilant swans within the group, but the need to watch for conspecifics, to avoid interference during feeding, may increase, as suggested in the current study by increased rates of social interaction. Thus levels of vigilance overall may not necessarily show a direct relationship with flock size. In species where vigilance to watch for predators is thought to be more important than to avoid intra-specific competition for food, e.g in Eurasian Wigeon, individual vigilance rates decrease exponentially with flock size (Mayhew 1987).

The number of adults and cygnets recorded feeding, resting and in vigilance and comfort activities generally increased during the winter season. This may relate to the increased number of birds at the site later in the season, although flock-size only had a significant effect on the proportion of time spent by adults on comfort activities and social interactions, and by cygnets on vigilance and movement. The proportion of birds feeding in flock scans in an earlier study was found to be lower in the second half of the winter (Rees & Bowler 1991) which was attributed to increased foraging upon arrival in the wintering grounds to replenish their nutrient reserves following the energetic demands of the autumn migration. A similar suggestion was put forward to account for high levels of feeding amongst Whooper Swans upon arrival at a wintering site in Ireland (O'Donoghue & O'Halloran 1994). In the current study, numbers of feeding swans were extremely high in the first half of February in all years (Figs. 5.2 & 5.17), when food supply was low and climatic conditions were at their most harsh (see Fig. 5.51), suggesting that the swans were attempting to compensate for the declining food stocks and increased energy demands by increasing the proportion of time spent feeding, as has been demonstrated for geese (Owen et al. 1992, Giroux & Patterson 1995). The increase in vigilance during the season was probably associated with the increase in feeding activity, since in general swans which were 'resting' were less vigilant than those feeding. The proportion of adult birds engaged in vigilance behaviour was positively correlated with the proportion feeding in the flock (Spearman's Rank correlation $r_s = 0.130$, $P < 0.01$, $n = 1028$), and negatively correlated with the proportion resting in the flock ($r_s = -0.372$, $P < 0.01$, $n = 1028$). Feeding birds would need to be vigilant to look for a new food patch, to watch out for predators, and to avoid interference from conspecifics; resting birds would not need to look for food and the risk of interference from conspecifics (normally competition for food resources) would also be reduced. The remaining low levels of vigilance shown by resting birds therefore would mostly be for the detection of predators. The frequency of vigilance was highest in the first half of February when numbers of swans feeding at the feeding sites were also at their maximum. There was no indication that the frequency of social interactions changed during the season, although Scott (1988) showed that in Norfolk, levels of aggression were highest in Bewick's Swans upon arrival in autumn when birds were sorting out their position in the dominance hierarchy.

Although the swans tended to be more active as the day progressed (i.e. the frequency of feeding, vigilance, movement and social interaction increased), there was distinct bimodality in these activity patterns. Numbers of feeding birds peaked in both the early morning and late afternoon, with a lull during the midday period when there was an increase in the number of birds resting. Similar bimodality in the number of birds recorded as vigilant, moving or in social interactions again indicated that these activities were more common in flocks where the birds were otherwise 'feeding' rather than resting. Aggression has also been found to be more prevalent amongst Black Swans when they are feeding (Tingay 1974). Since there was generally little change in flock size or flock density during the day, the increase in aggression amongst feeding swans may relate to direct competition for food. Bimodality in the diurnal feeding pattern is common amongst northern geese including Barnacle Geese (Ebbinge et al. 1975), Greylag Geese (Amat 1986a), Greater White-fronted Geese (Owen 1972a), Bean Geese (Mooij 1992), and Blue Geese (Davis et al. 1989) and has also been noted amongst Bewick's Swans feeding on fenland at the Ouse Washes (Owen & Cadbury 1975), Whooper Swans (O'Donoghue & O'Halloran 1994) and Eurasian Wigeon (Mayhew 1988). Despite this bimodality, the feeding activity of swans on water tended to increase significantly during the day as has also been shown amongst Whooper Swans (O'Donoghue & O'Halloran 1994) with up to 87% feeding at six hours after sunrise amongst Bewick's Swans on the Ouse Washes (Owen & Cadbury 1975). An increase in feeding rate towards the end of the day may allow the birds to accumulate food in their crops, enabling them effectively to lengthen their feeding day. For example, increased ingestion rates towards evening amongst Greater White-fronted Geese have been shown to effectively increase their grazing day by 5-10% (Owen 1972a), an important addition during the short day-lengths of mid-winter. Such a trend was also inferred in the current study, since the proportion of adult birds feeding tended to increase both with time of day and with water cover on the field. Birds feeding from water use touch to a greater extent than sight to select their food (Owen & Kear 1972) and being safe from land predators (Owen & Cadbury 1975) can afford to spend less time being vigilant and more time feeding. Moreover the ability to ingest wet grass and to drink between individual foraging bouts may improve digestive efficiency, since water increases the ease with which vegetation is broken up in the gizzard (Owen et al. 1977). By way of a contrast, the proportion of cygnets feeding tended to decrease as water cover on the fields increased. This may be because they were less skilled at feeding from water or because the reduced vigilance of their parents caused them to select other behaviours (mostly preening and washing).

Increasing water cover led to an increase both in the frequency of social interactions, and in the level of comfort activities recorded amongst adults. The increase in social interactions may be associated with the increased feeding activity. In addition, crowding may have resulted on deeply flooded fields since birds would concentrate at favoured shallow edges of the flood in order to be able to reach the food. The increasingly limited area of accessible food would lead to a reduction of individual space and a consequent increase in aggressive interaction (Tingay 1974). Increasing water cover on the fields resulted in higher levels of washing and preening, since swans were able to bathe in the deeper water, but as a consequence, levels of resting were reduced.

The proportion of swans feeding on the fields increased as the percentage protein content of the sward increased, suggesting that the swans were selecting protein-rich grass when available. Since protein levels in the grass were highest in spring (see Fig. 4.10), and the number of birds feeding increased during the season, this indicated that feeding was particularly concentrated on protein-rich swards at the end of the winter season, prior to the start of the return migration to the breeding grounds. This effect was most marked in February when birds on poorer fields spent considerably less time feeding than those on better pasture, suggesting that protein levels were driving feeding rate. These findings concur with those of Prop et al. (in prep.) working on Barnacle Geese who demonstrated that although geese had to consume a larger amount of grasses to meet their energy requirements than to fulfil their protein needs, selection for plants containing a high proportion of protein was advantageous since the metabolizable energy and protein content of the grasses were positively correlated. Towards the end of the winter, the swans would need to metabolize a large amount of energy per day, in order to store some in body reserves to fuel the spring migration. Increased feeding prior to spring migration has also been noted in similar studies on migratory geese, for example, amongst Blue Geese wintering in the Middle Missouri River valley (Davis et al. 1989) and Greater White-fronted Geese wintering in California (Ely 1992).

The proportion of adults resting on the fields also increased with the protein content of the sward suggesting that the increased feeding on protein-rich swards may have necessitated increased rest periods for food digestion, since Bewick's Swans have relatively poor digestive efficiency (Scott 1972). There was also an increase in movement and social interactions amongst cygnets with increasing protein content and a consequent decrease in comfort and vigilance activities, perhaps relating to increased aggression between families to gain access to the best feeding areas. This point is considered further in Chapter 6.

There was no relationship between biomass of the sward and the proportion of birds seen feeding in the flock scans. However there was evidence to suggest that adults spent less time resting and being vigilant, and more time moving, when on fields of higher biomass. Since biomass levels were highest at the end of the winter and a higher frequency of movement was noted amongst birds which are otherwise feeding, these results also suggest that the swans were again optimising their time on the better food resources prior to departure on spring migration.

Mean sward-length was not a relevant factor in determining the activities of swans at the feeding sites. Although biomass and sward-length were positively correlated (see Chapter 4), biomass and protein content would appear to be better indicators of grass quantity and quality, respectively, and the inclusion of biomass in the models masked the weaker effects that sward-length had on its own.

The proportion of birds present from the roost-sites had a significant effect on activity patterns at the feeding sites. An increasing proportion of swans from the Rushy Pen roost led to increased vigilance amongst birds in the flock, and an increase in social encounters, which supports the hypothesis put forward in Chapter 3, that one advantage of being a member of the smaller Grounds roost group may be that the presence of a higher proportion of related individuals could lead to reduced levels of aggression. Moreover, levels of social interaction were highest in flocks where the proportion of swans from the two roost groups was roughly equal, suggesting that the presence of many unfamiliar birds led to increased levels of interaction. This concurs with D'Eath (in litt.) who demonstrated that recognition of conspecifics amongst domestic hens played an important role in the formation of peck orders; hens discriminated between familiar and unfamiliar conspecifics, and more readily approached and began feeding near a familiar bird.

There was also evidence for an increase in the proportion of swans feeding at the feeding sites as the proportion of Rushy Pen units increased, at least amongst cygnets. This agrees with the findings from Chapter 4, in that swans from the two roost groups were using the fields differently; Grounds birds relied more heavily upon the supplementary feeds of grain at the roost-sites, whilst Rushy Pen birds selected fields more judiciously for feeding purposes.

5.5 SUMMARY

This chapter investigated the activities of Bewick's Swans at the feeding sites during the winter in the Slimbridge area from 1028 mean hourly flock scans, in order to elucidate the factors that influenced the observed activity patterns. Non-habitat variables investigated included: year (winter season), time in season (half-month), the time of day (hour), flock size and the proportion of birds present in flock from the two roost groups. Habitat variables investigated included: water cover on the field (%), biomass of the sward (g/m^2), protein content of the sward (%) and mean sward-length.

1) Adult swans spent, on average, one third of their time feeding at the feeding sites, one third resting, and one third in other activities, mostly comfort, movement and vigilance. The time spent feeding was low compared to other diurnal studies of swans and geese grazing on terrestrial vegetation, but similar to other figures from studies of swans feeding predominantly on water bodies. Reasons for this difference are discussed.

2) The activity patterns of adults and cygnets at the feeding sites were significantly different. Cygnets were more frequently encountered feeding, preening/washing, and walking/swimming than adults, and less often resting, being vigilant and in social interactions. Parental protection of the cygnets thus enabled them to spend more time feeding and in comfort activities.

3) The frequency of adult swans engaged in comfort activities and social interactions, and of cygnets engaged in comfort, movement and vigilance activities increased with flock-size. There was no direct relationship between adult vigilance and flock size.

4) The frequency of swans (both adults and cygnets) engaged in feeding, resting, vigilance and comfort activities increased during the season. Feeding activity peaked in early February when food availability was low and climatic conditions were at their worst. This suggested that the swans were attempting to compensate for declining food stocks and the increased energy demands of laying down fat reserves during cold conditions in February, by increasing the proportion of time spent feeding. Vigilance was also most frequent in early February since, in general, 'feeding' birds were more vigilant than those engaged in other activities.

5) The frequency of feeding swans showed two distinct peaks during the day; in early morning and late afternoon, with a recess during the midday period when more birds were seen resting. This bimodal feeding pattern also occurs in geese. The frequency with which swans engaged in vigilance, movement and social interaction also peaked in the early morning and late afternoon, indicating that these activities were associated with feeding

activity rather than resting. Feeding birds showed higher levels of vigilance than resting birds, suggesting that vigilance functions both in the avoidance of grazing competition from conspecifics and in the detection of potential predators. There was an indication that the frequency of feeding amongst adults on water, showed a different distribution to that of grazing adults on land, and instead tended to continue to increase during the day.

6) Increasing water cover led to an increase in the frequency of feeding, comfort activities and social interactions. The increase in feeding and comfort may have resulted from the increased protection afforded by the water cover from land predators. The increased frequency of social interaction may be consequent upon the increased frequency of feeding, although there may also have been a crowding effect amongst the feeding birds, since the area of food available to the swans decreased when water cover was high.

7) Increasing protein levels in the sward at the end of the winter season led to an increase in the number of swans seen feeding, perhaps because the swans were developing fat reserves to fuel their spring migration. There was also an increase in the number of swans resting, suggesting that the increased feeding on protein-rich swards necessitated increased rest periods for food digestion.

8) There was no significant relationship between the biomass of the grass in the field and the number of swans seen feeding. Resting and vigilance activity declined with increasing biomass however, and active movement (walking/swimming/flying) increased, suggesting that the swans spent more time looking for food on the swards of higher biomass at the end of the winter season prior to departure on spring migration.

9) Mean sward-length was not found to be a relevant factor in determining the activities of swans at the feeding sites. Biomass and protein content were better indicators of grass quantity and quality, respectively. The effects of sward-length were masked by the inclusion of biomass in the models.

10) An increase in the proportion of swans from the Rushy Pen roost present in the feeding flocks led to increased levels of vigilance and social interaction. Levels of social interaction were highest amongst flocks where the proportion of swan units from the two roost groups were roughly equal. In addition, an increase in the proportion of swans present from the Rushy Pen roost led to increased levels of feeding amongst cygnets. This concurs with the findings of Chapter 3, in that the use made of the fields by the two roost groups differed, with Rushy Pen birds selecting fields more judiciously than Grounds birds, for feeding purposes.

Table 5.1. Summary table of activity of Bewick's Swans on fields in the Slimbridge area from 3755 flock scans conducted during daylight hours (1990-91 to 1992-93 winters inclusive).

a) Adults. Number of mean hourly flock scans = 1028.

Activity	Percent of records Mean	S.D.	n
Feed	32.77	26.09	1028
Rest	32.56	24.15	1028
Comfort	16.56	14.36	1028
Alert	8.81	9.26	1028
Move	7.19	7.46	1028
Interact	1.45	3.27	1028
Drink	0.66	1.85	1028

b) Cygnets. Number of mean hourly flock scans = 815.

	Percent of records			Chi-square comparisons. (Using original count data from mean flock scans) Adults v cygnets		
Activity	Mean	S.D.	n	Chi-sq.	P	
Feed	39.29	32.34	815	35.41	<0.001	+
Rest	28.28	27.96	815	52.68	<0.001	-
Comfort	17.55	20.79	815	26.29	<0.001	+
Alert	5.73	10.73	815	37.48	<0.001	-
Move	7.63	12.51	815	11.78	<0.001	+
Interact	0.85	3.37	815	23.88	<0.001	-
Drink	0.67	2.87	815	1.92	>0.1	N.S.

Note; + indicates a higher percentage of cygnets engaged in an activity; - indicates a lower percentage of cygnets engaged in an activity; N.S. = not significant

Table 5.2. Linear models using maximum likelihood estimates fitted to the number of adult swans recorded in the different activities during flock-scans conducted on fields in the Slimbridge area (1990-91 to 1992-93 winters inclusive). Habitat variables excluded. Note: * P < 0.05, ** P < 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

ACTIVITY

	Feeding			Resting			Comfort		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Field	21.41	27,1024	***	13.05	27,1023	***	12.94	27,1024	***
Half-month	58.31	1, 998	***	89.08	1, 997	***	8.79	1, 998	**
Time (hrs)	19.55	1, 998	**	87.61	1, 997	***	-	-	-
Year	-	-	-	10.78	2, 998	***	-	-	-
Flock size	-	-	-	-	-	-	6.90	1, 998	**
Field * half-month	13.05	1, 998	***	-	-	-	4.41	1, 998	*
Final model:									
Deviance		1008.9			1077.3			1032.3	
df		997			996			997	

(con)

ACTIVITY

	Vigilance			Moving			Social interaction		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Field	4.19	27,1024	***	5.54	27,1022	***	3.77	27,1022	***
Half-month	24.42	1, 998	***	17.54	1, 996	***	-	-	-
Time (hrs)	2.78	1, 998	NS	18.42	1, 996	***	0.06	1, 996	NS
Year	-	-	-	4.92	2, 997	**	8.33	2, 997	***
Flock size	-	-	-	-	-	-	6.73	1, 996	**
Time * half-month	19.77	1, 998	***	-	-	-	4.41	1, 998	*
Time * field	-	-	-	8.47	1, 996	**	-	-	-
Time * year	-	-	-	-	-	-	6.51	1, 996	*
Final model:									
Deviance		918.1			946.7			623.6	
df		997			995			995	

Table 5.3. Linear models using maximum likelihood estimates fitted to the number of cygnets recorded in the different activities during flock-scans conducted on fields in the Slimbridge area (1990-91 to 1992-93 winters inclusive). Habitat variables excluded. Note: * P < 0.05, ** P < 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

	ACTIVITY								
	Feeding			Resting			Comfort		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Field	14.44	26, 810	***	7.47	26, 812	***	9.00	26, 813	***
Half-month	5.10	1, 785	*	14.46	1, 787	***	8.60	1, 788	**
Time (hrs)	5.25	1, 785	*	37.69	1, 787	***	-	-	-
Year	-	-	-	-	-	-	-	-	-
Flock size	-	-	-	-	-	-	-	-	-
Field * time	3.86	1, 785	*	-	-	-	-	-	-
Half-month * time	8.66	1, 785	**	-	-	-	-	-	-
Final model:									
Deviance		814.6			882.8			825.0	
df		784			786			787	

(con)

	ACTIVITY								
	Vigilance			Moving			Social interaction		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Field	3.14	26, 809	***	3.32	26, 811	***	3.04	26, 807	***
Half-month	20.13	1, 784	***	-	-	-	5.98	1, 782	*
Time (hrs)	6.67	1, 784	**	9.17	1, 786	**	11.50	1, 782	***
Year	-	-	-	-	-	-	5.57	2, 783	**
Flock size	12.82	1, 784	***	5.47	1, 786	*	-	-	-
Time * half-month	11.83	1, 784	***	-	-	-	-	-	-
Flock size * half month	17.30	1, 784	***	-	-	-	-	-	-
Time * year	-	-	-	-	-	-	18.98	1, 782	***
Time * field	-	-	-	4.84	1, 786	*	-	-	-
Field * year	-	-	-	-	-	-	6.37	1, 782	*
Time * half month	-	-	-	-	-	-	4.64	1, 782	*
Final model:									
Deviance		692.7			690.6			402.0	
df		783			785			781	

Table 5.4. Linear models using maximum likelihood estimates fitted to the number of adult swans recorded in the different activities during flock-scans conducted on fields in the Slimbridge area (1990-91 to 1992-93 winters inclusive). Habitat variables (mean sward-length, biomass, % protein content of sward, % water cover on field) included, plus % of birds present from the Rushy Pen roost. Note: * P < 0.05, ** P < 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

ACTIVITY

	Feeding			Resting			Comfort		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Month	30.30	1, 240	***	3.27	1, 249	NS	5.49	1, 295	*
Time (hrs)	-	-	-	16.29	1, 249	***	-	-	-
Year	-	-	-	-	-	-	14.29	1, 295	***
Flock size	-	-	-	-	-	-	6.81	1, 295	**
Sward-length	-	-	-	-	-	-	-	-	-
Biomass	-	-	-	14.13	1, 249	***	-	-	-
Protein	49.24	1, 240	***	43.11	1, 249	***	-	-	-
Water cover	23.57	1, 240	***	-	-	-	5.15	1, 295	*
Rushy Pen	-	-	-	-	-	-	17.39	1, 295	***
Biomass * month	-	-	-	6.12	1, 249	*	-	-	-
Protein * water cover	20.59	1, 240	***	-	-	-	-	-	-
Year * Rushy Pen	-	-	-	-	-	-	5.84	1, 295	*
Final model:									
Deviance		259.6			263.2			306.3	
df		239			248			294	

Table 5.4 (con.)

	ACTIVITY								
	Vigilance			Moving			Social interaction		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Month	10.77	1, 255	**	13.77	1, 268	***	0.05	1, 295	NS
Time (hrs)	0.74	1, 255	NS	-	-	-	-	-	-
Year	-	-	-	-	-	-	-	-	-
Flock size	-	-	-	7.44	1, 268	**	6.23	1, 295	*
Sward-length	-	-	-	-	-	-	-	-	-
Biomass	41.08	1, 255	***	4.70	1, 268	*	-	-	-
Protein	-	-	-	-	-	-	-	-	-
Water cover	-	-	-	-	-	-	0.11	1, 295	NS
Rushy Pen	11.29	1, 255	***	-	-	-	3.97	1, 295	*
Month * time	5.21	1, 255	*	-	-	-	-	-	-
Biomass * month	23.34	1, 255	***	-	-	-	-	-	-
Year * flock size	-	-	-	5.93	1, 268	*	-	-	-
Year * biomass	-	-	-	8.70	1, 268	**	5.84	1, 295	*
Time * flock size	-	-	-	-	-	-	7.42	1, 295	**
Flock size * water cover	-	-	-	-	-	-	6.88	1, 295	**
Final model:									
Deviance		221.0			251.7			238.8	
df		254			267			294	

Table 5.5. Linear models using maximum likelihood estimates fitted to the number of cygnets recorded in the different activities during flock-scans conducted on fields in the Slimbridge area (1990-91 to 1992-93 winters inclusive). Habitat variables (mean sward-length, biomass, % protein content of sward, % water cover on field) included, plus % of birds present from the Rushy Pen roost. Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS not significant, - variable removed from final model (see methods).

	ACTIVITY								
	Feeding			Resting			Comfort		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Month	16.14	1, 149	***	2.60	1, 169	NS	6.72	1, 153	**
Time (hrs)	11.88	1, 149	***	7.29	1, 169	**	7.19	1, 153	**
Year	-	-	-	-	-	-	-	-	-
Flock size	-	-	-	-	-	-	0.00	1, 153	NS
Sward-length	-	-	-	-	-	-	-	-	-
Biomass	-	-	-	6.48	1, 169	*	-	-	-
Protein	17.48	1, 149	***	-	-	-	8.45	1, 153	**
Water cover	12.37	1, 149	***	3.22	1, 169	NS	-	-	-
Rushy Pen	6.29	1, 149	*	-	-	-	-	-	-
Month * time	20.06	1, 149	***	3.91	1, 169	*	10.38	1, 153	**
Month * flock size	-	-	-	-	-	-	5.06	1, 153	*
Time * water cover	12.70	1, 149	***	3.92	1, 169	*	-	-	-
Time * Rushy Pen	7.18	1, 149	**	-	-	-	-	-	-
Flock size * protein	-	-	-	-	-	-	4.30	1, 153	*
Final model:									
Deviance		176.8			184.7			161.3	
df		148			168			152	

Table 5.5 (con.)

ACTIVITY

	Vigilance			Social interaction		
Variable	F ratio	d.f.	P	F ratio	d.f.	P
Month	22.09	1, 149	***	14.62	1, 150	***
Time (hrs)	17.37	1, 149	***	23.90	1, 150	***
Year	-	-	-	-	-	-
Flock size	25.86	1, 149	***	-	-	-
Sward-length	-	-	-	-	-	-
Biomass	-	-	-	-	-	-
Protein	17.29	1, 149	***	7.57	1, 150	**
Water cover	-	-	-	-	-	-
Rushy Pen	12.16	1, 149	***	20.63	1, 150	***
Month * time	18.88	1, 149	***	-	-	-
Month * Rushy Pen	-	-	-	16.46	1, 150	***
Time * protein	11.65	1, 149	***	15.54	1, 150	***
Rushy Pen * protein	13.73	1, 149	***	8.12	1, 150	**
Final model:						
Deviance		49.3			36.7	
df		148			149	

Fig. 5.1. The number of adult swans recorded feeding at the feeding sites by hour (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

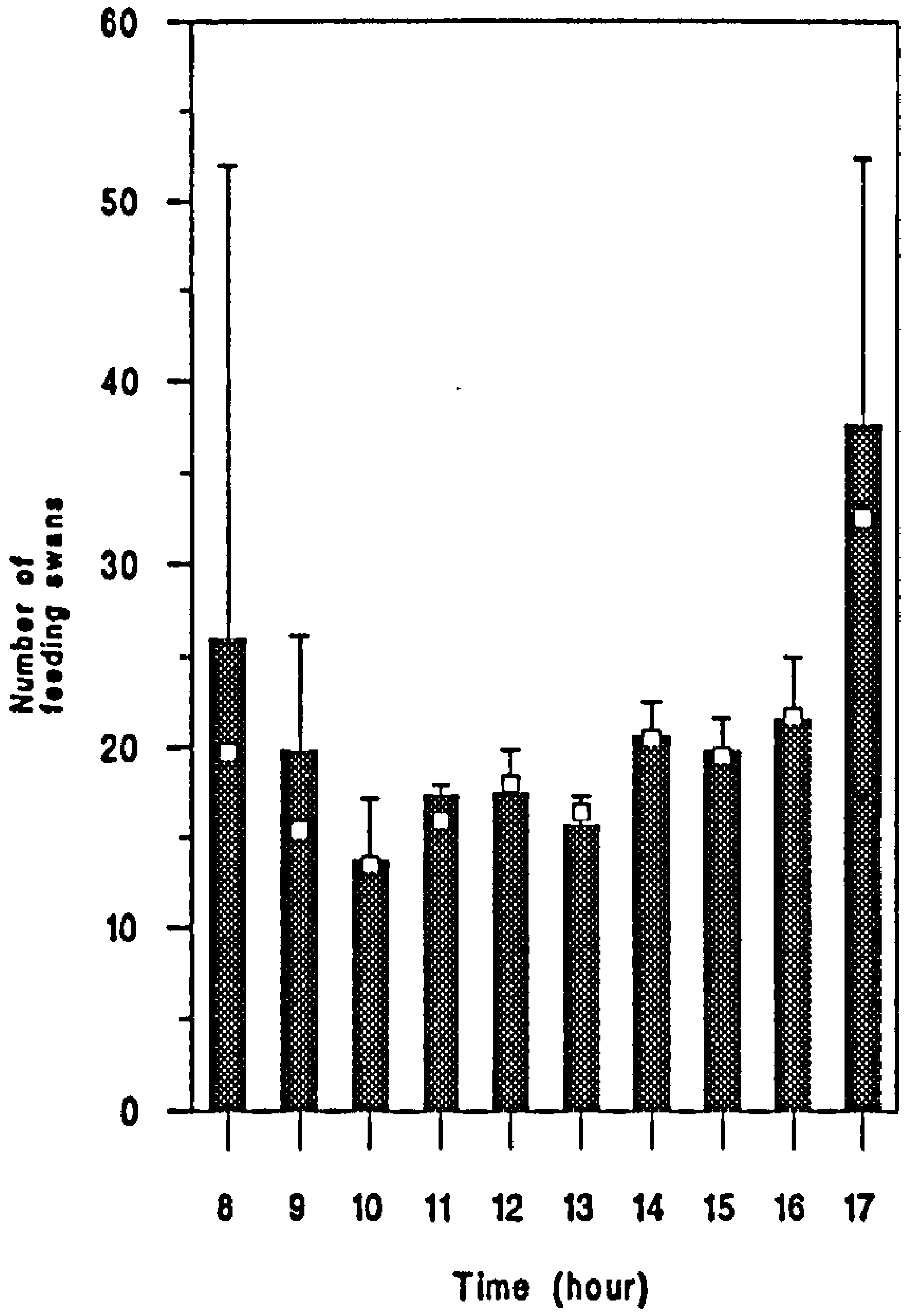


Fig. 5.2. The number of adult swans recorded feeding at the feeding sites by half-month (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

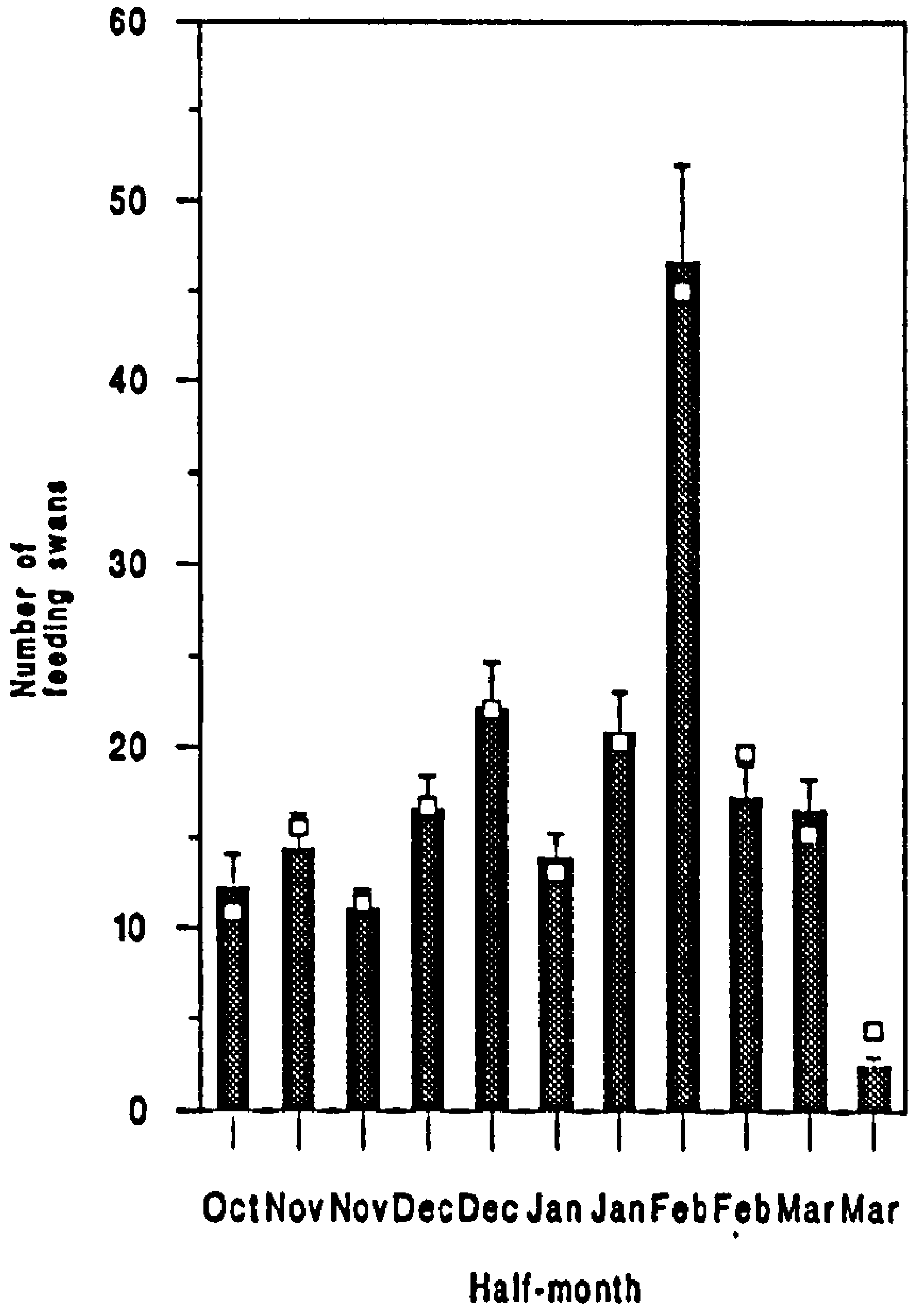


Fig. 5.3. The number of adult swans recorded resting at the feeding sites by winter (mean per flock scan and S.E. bar, n=1028) plus predicted values from generalised linear model.

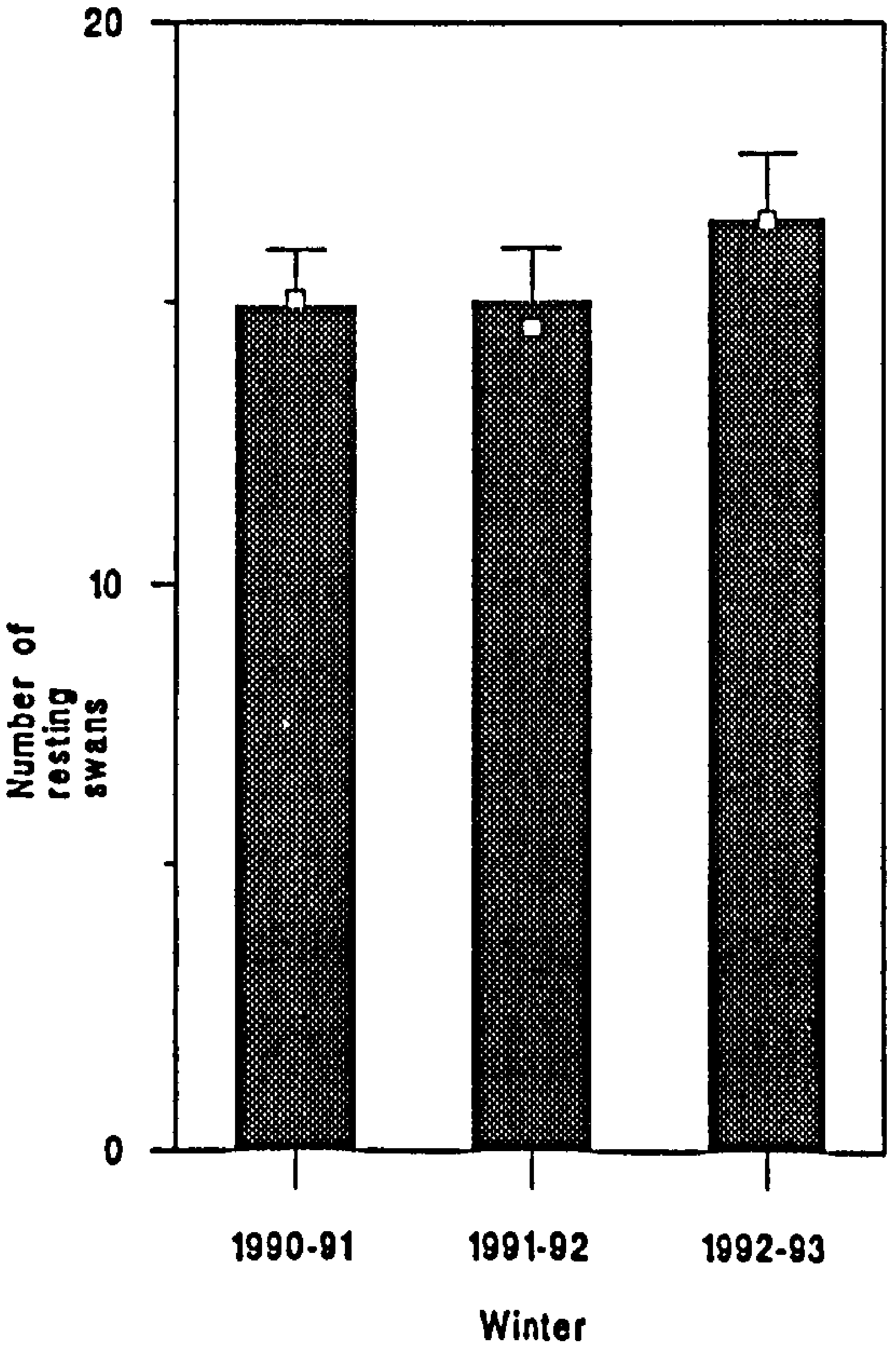


Fig. 5.4. The number of adult swans recorded resting at the feeding sites by half-month (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

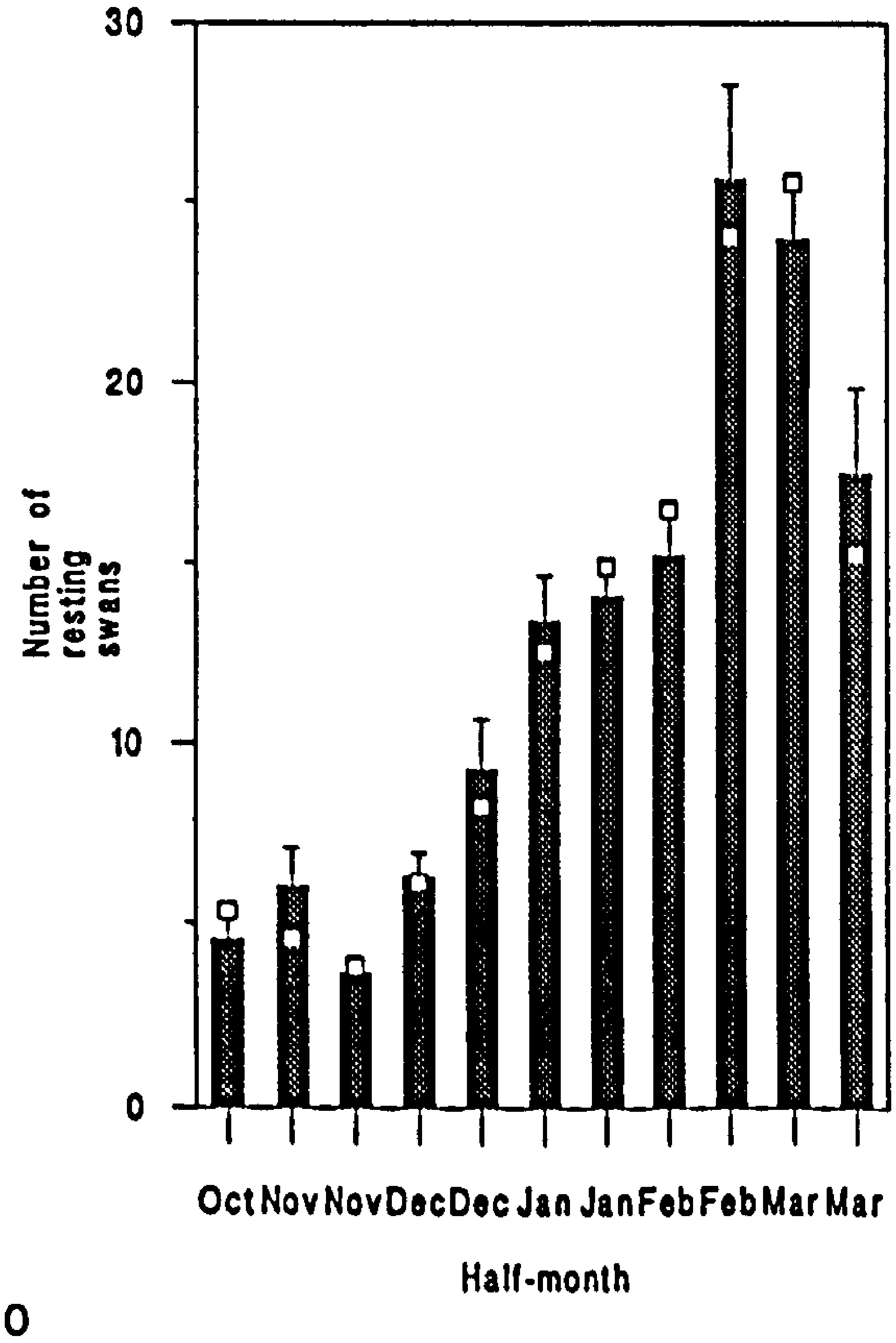


Fig. 5.5. The number of adult swans recorded resting at the feeding sites by hour (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

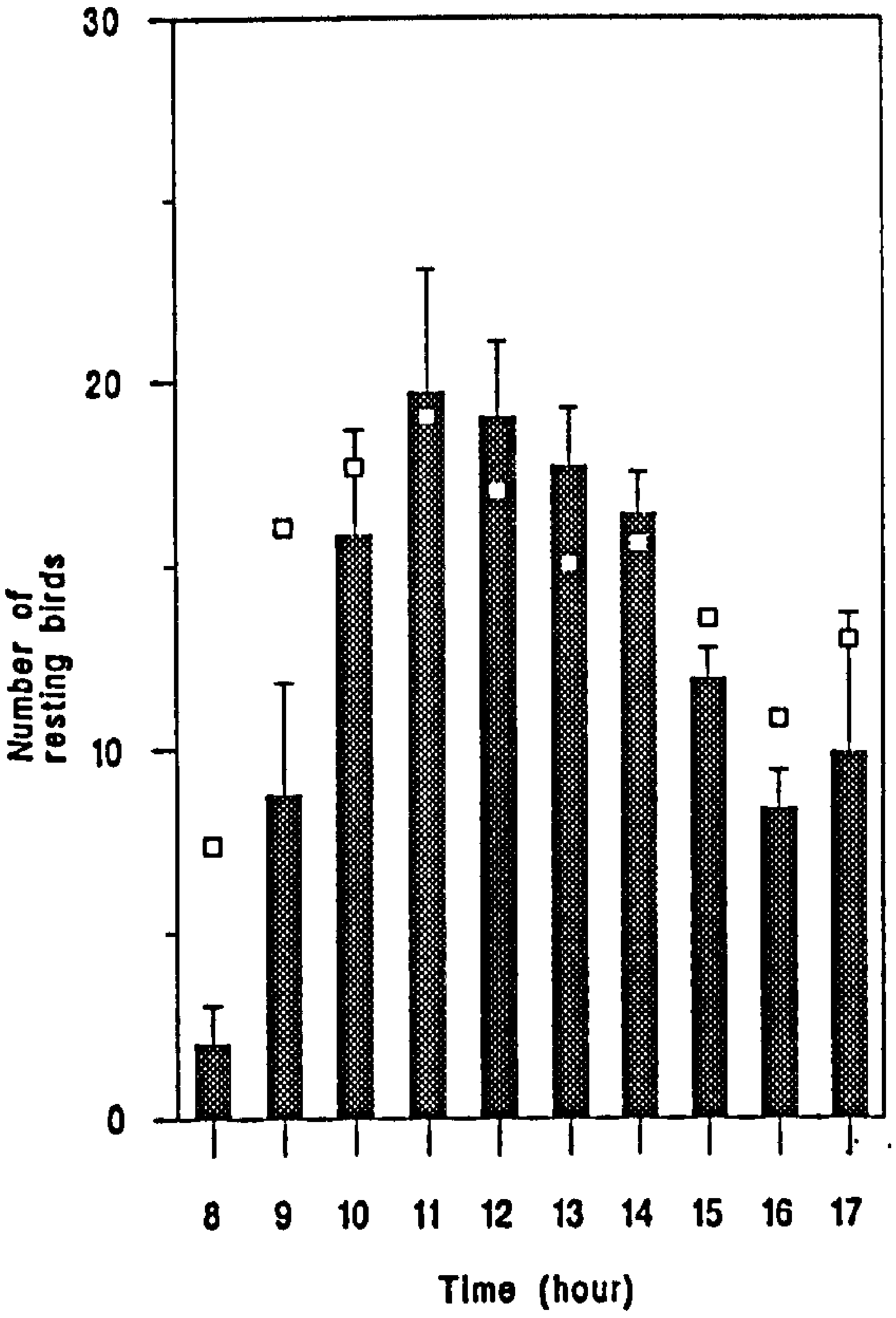


Fig. 5.6. The number of adult swans recorded in comfort activity at the feeding sites with flock-size (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

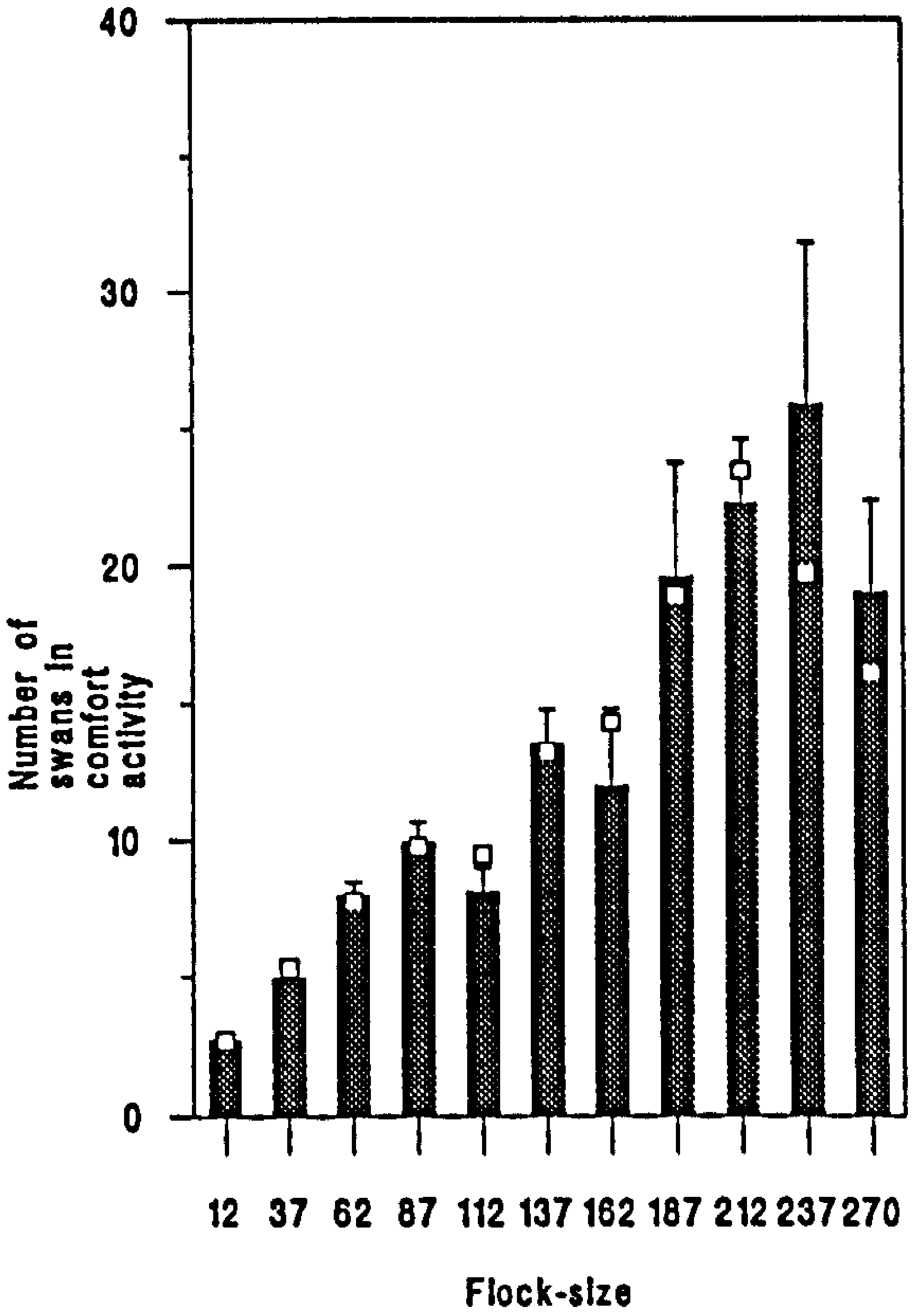


Fig. 5.7. The number of adult swans recorded in comfort activity at the feeding sites by half-month (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

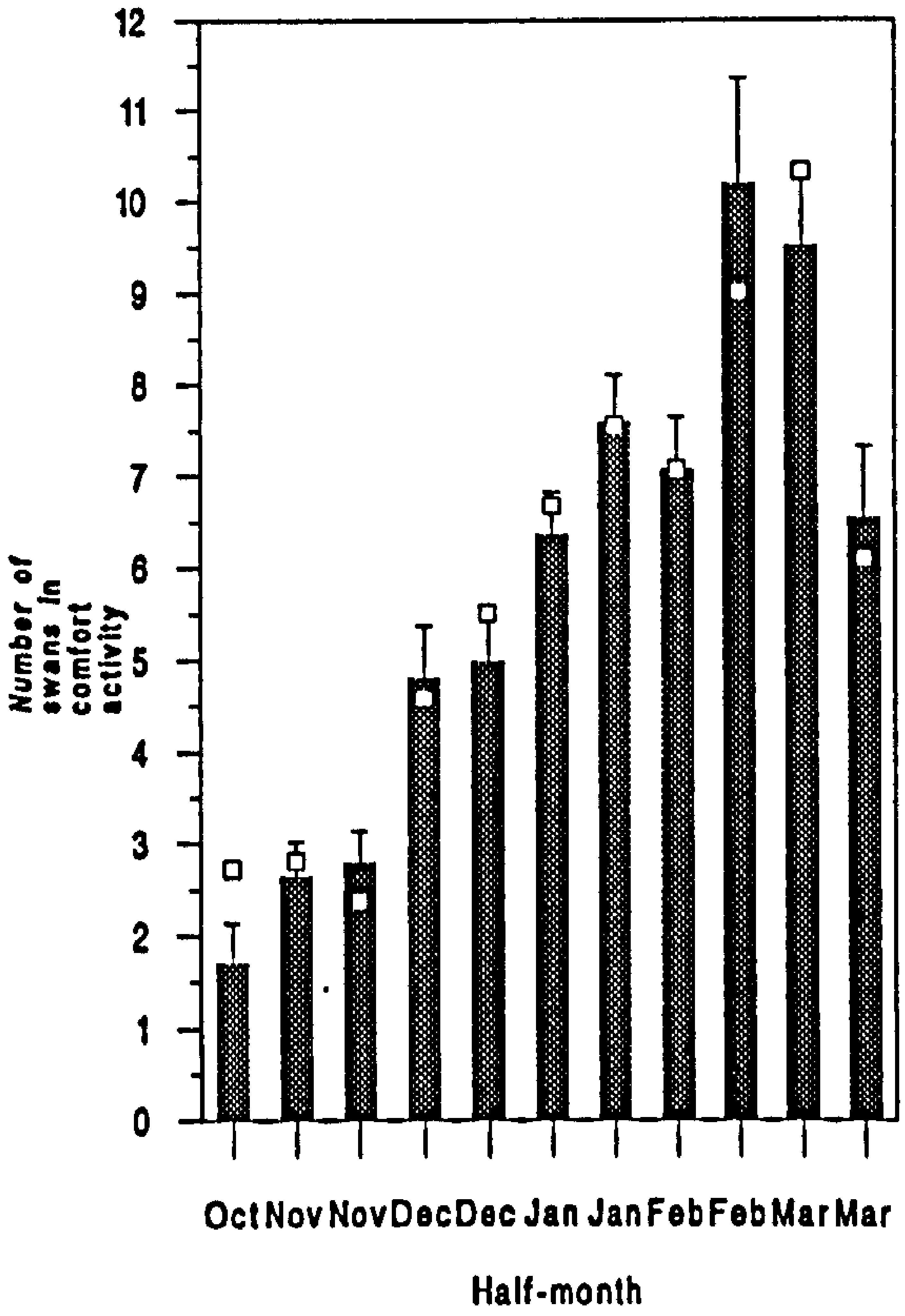


Fig. 5.8. The number of adult swans recorded in alert activity at the feeding sites by half-month (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

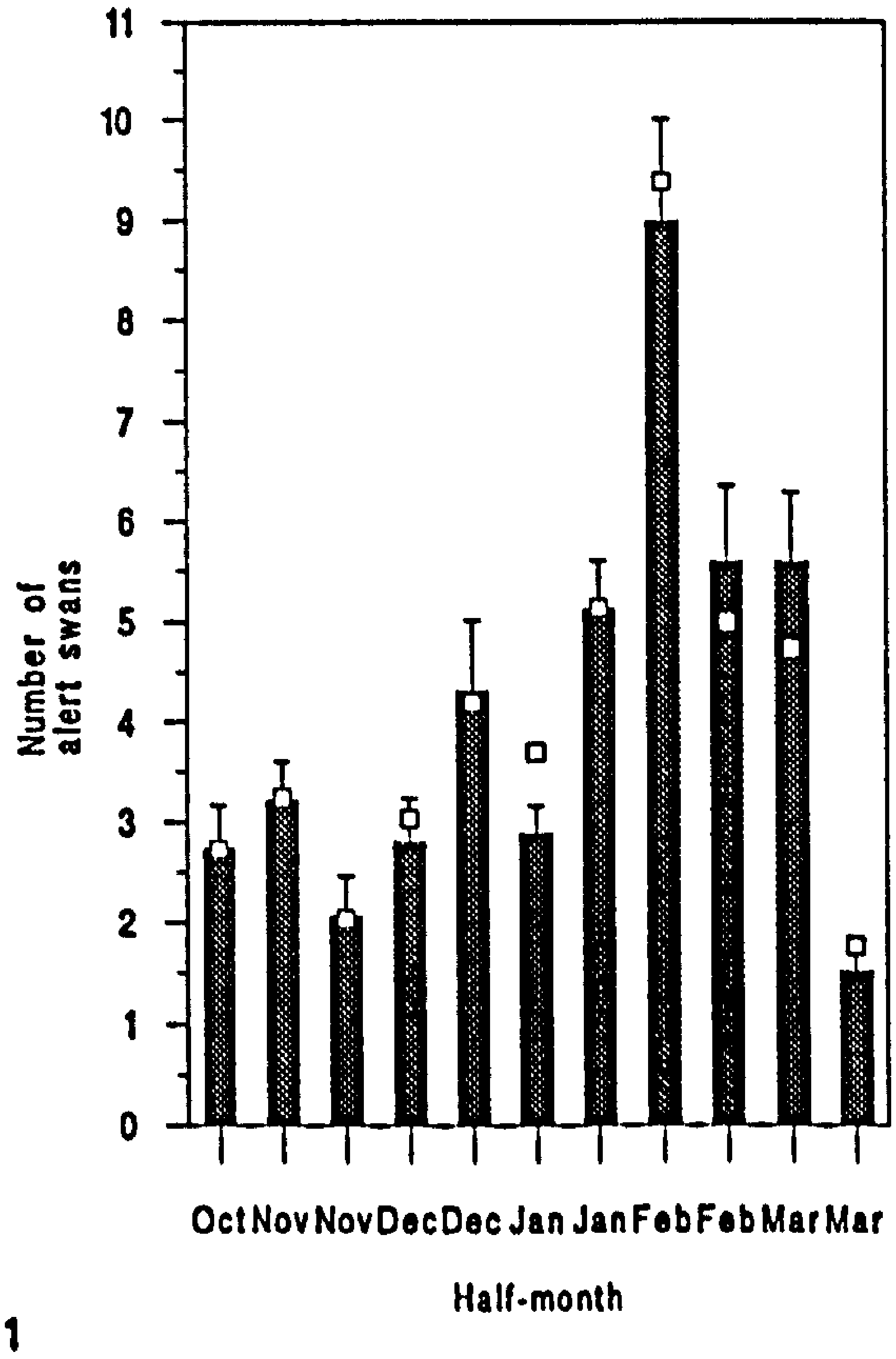


Fig. 5.9. The number of adult swans recorded in alert activity at the feeding sites by hour (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

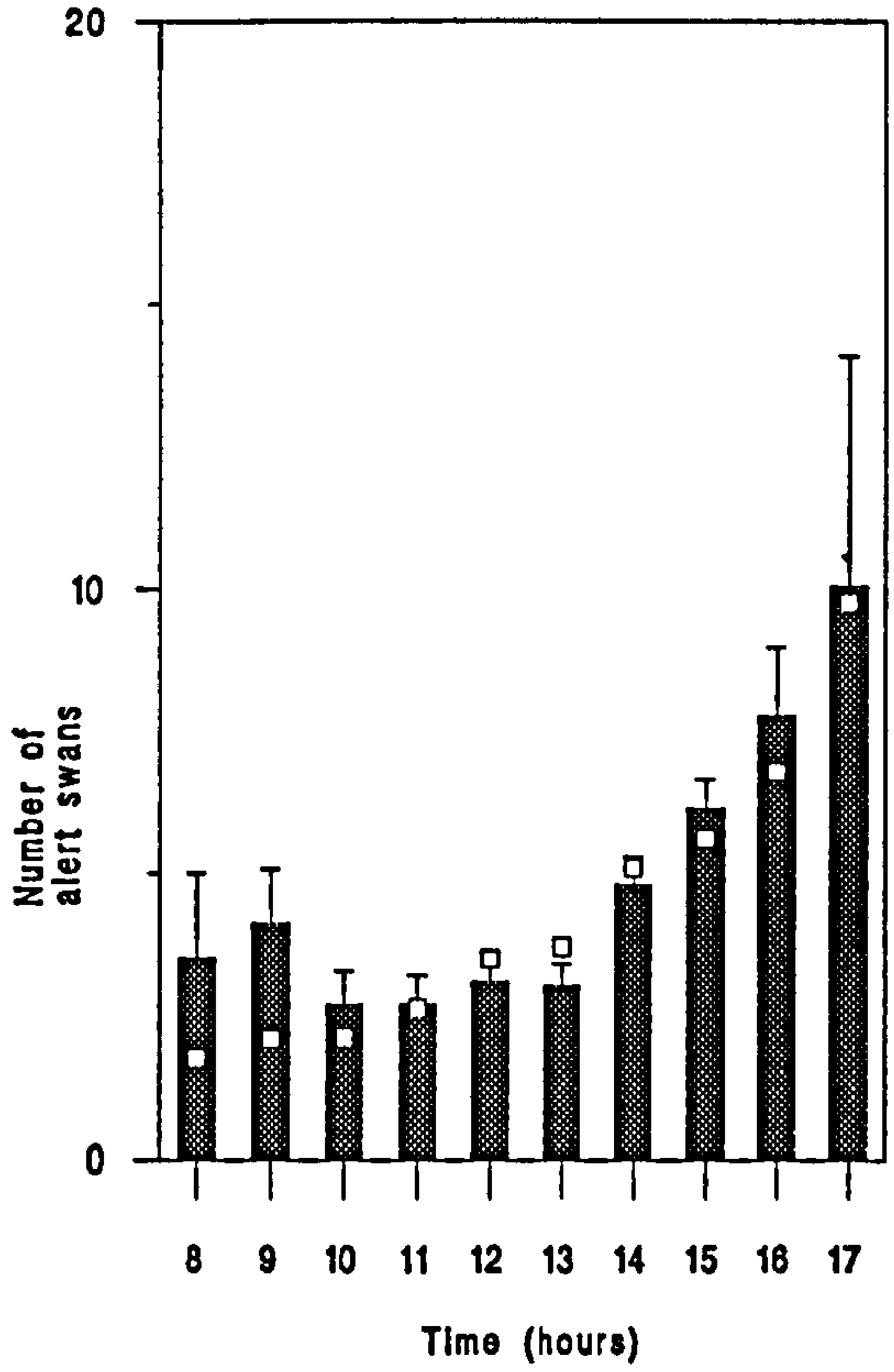


Fig. 5.10. The number of adult swans recorded in the activity of movement at the feeding sites by winter (mean per flock scan and S.E. bar, n=1028), plus predicted values from a generalised linear model.

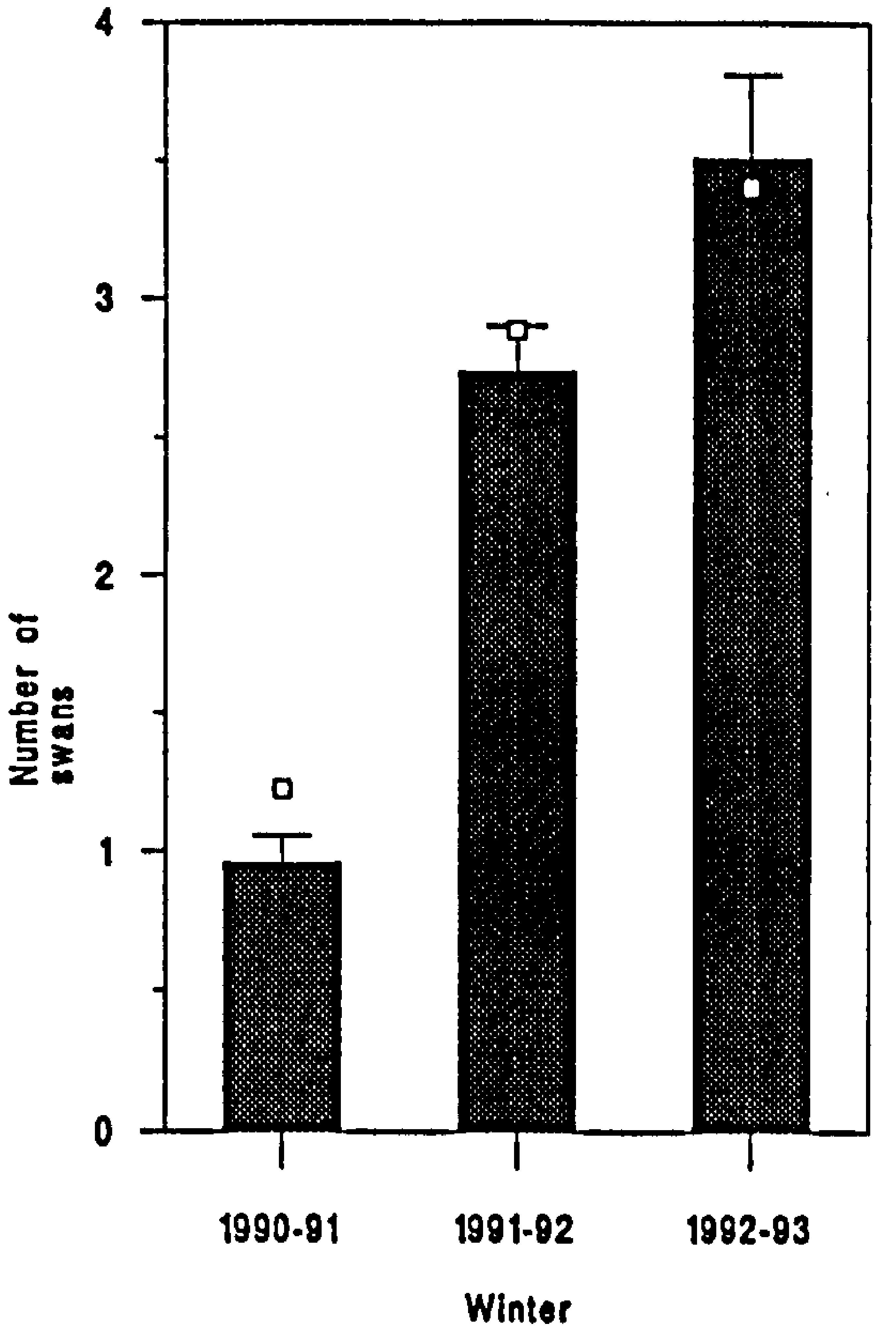


Fig. 5.11. The number of adult swans recorded in the activity of movement at the feeding sites by half-month (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

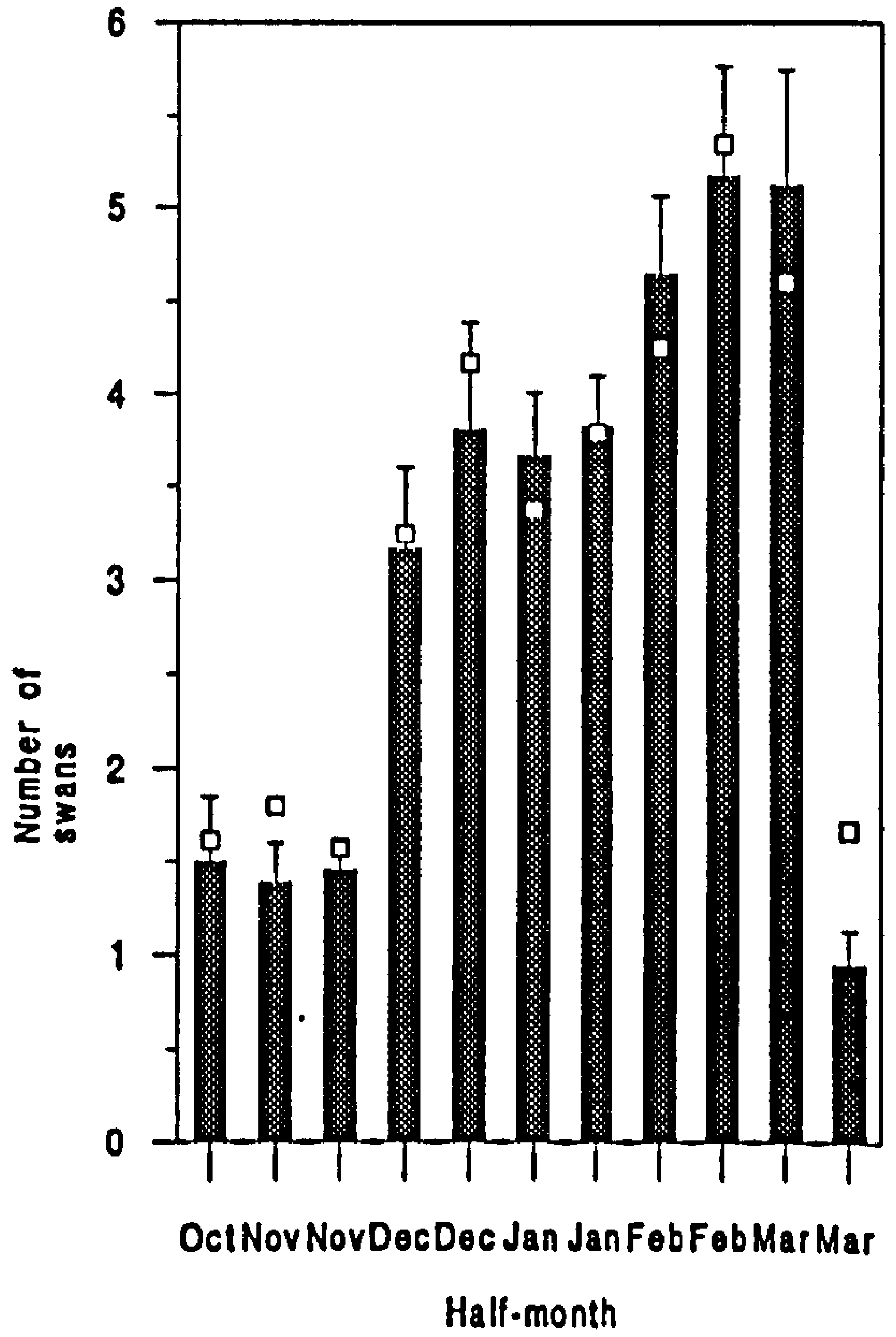


Fig. 5.12. The number of adult swans recorded in the activity of movement at the feeding sites by hour (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from generalised linear model.

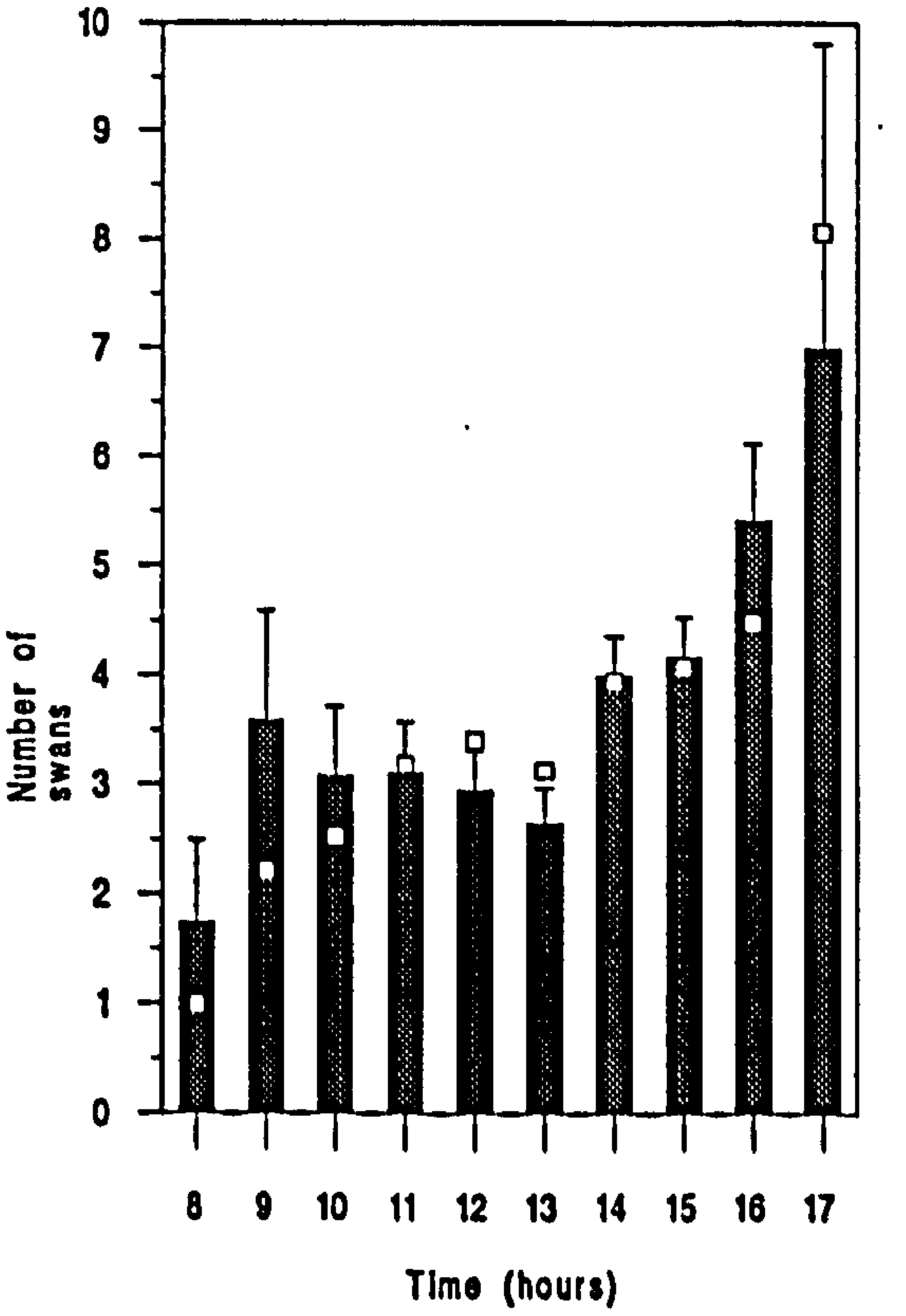


Fig. 5.13. The number of adult swans recorded in social interactions at the feeding sites with flock-size (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028), plus predicted values from a generalised linear model.

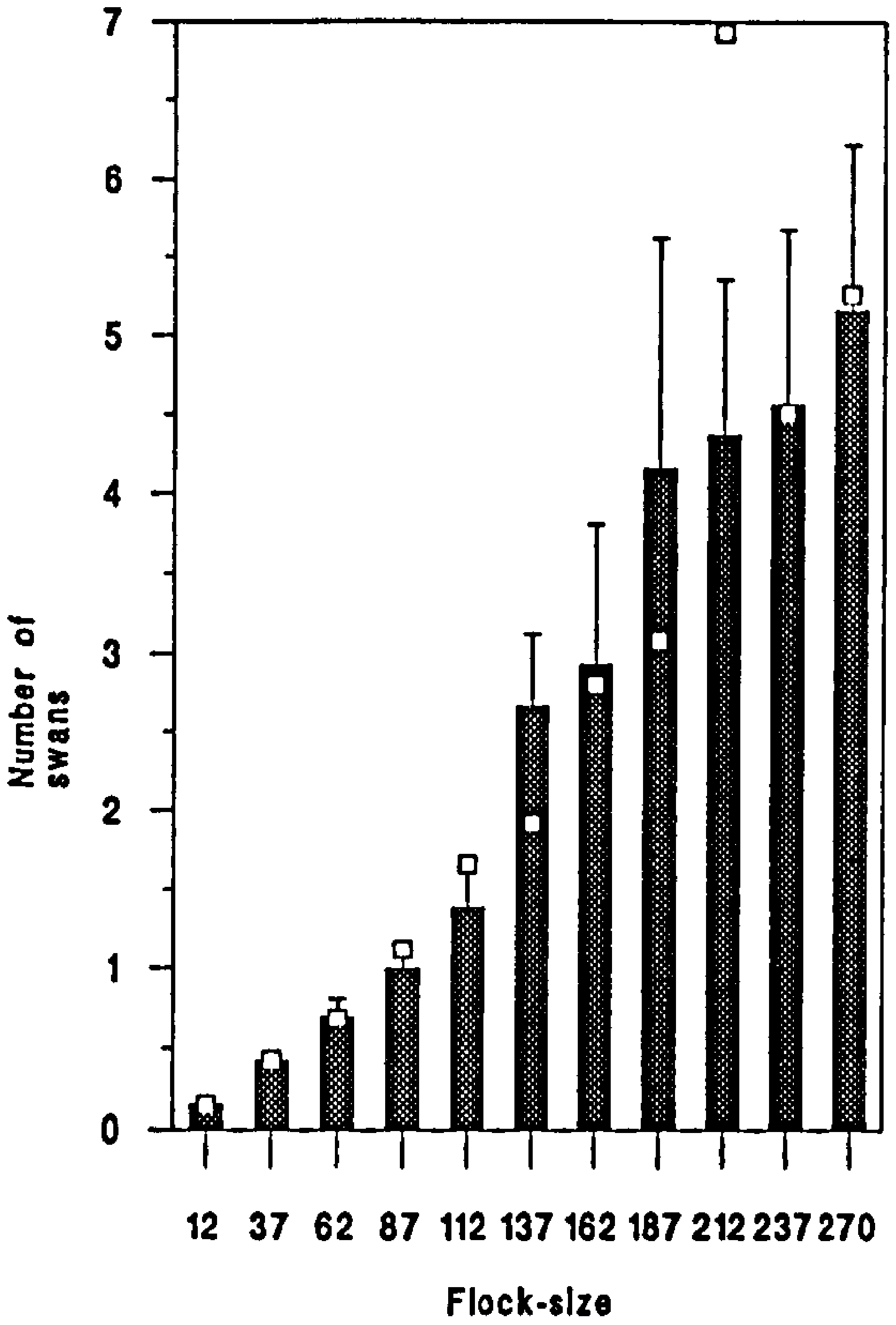


Fig. 5.14. The number of adult swans recorded in social interactions at the feeding sites by winter (mean per flock scan and S.E. bar, n=1028), plus predicted values from a generalised linear model.

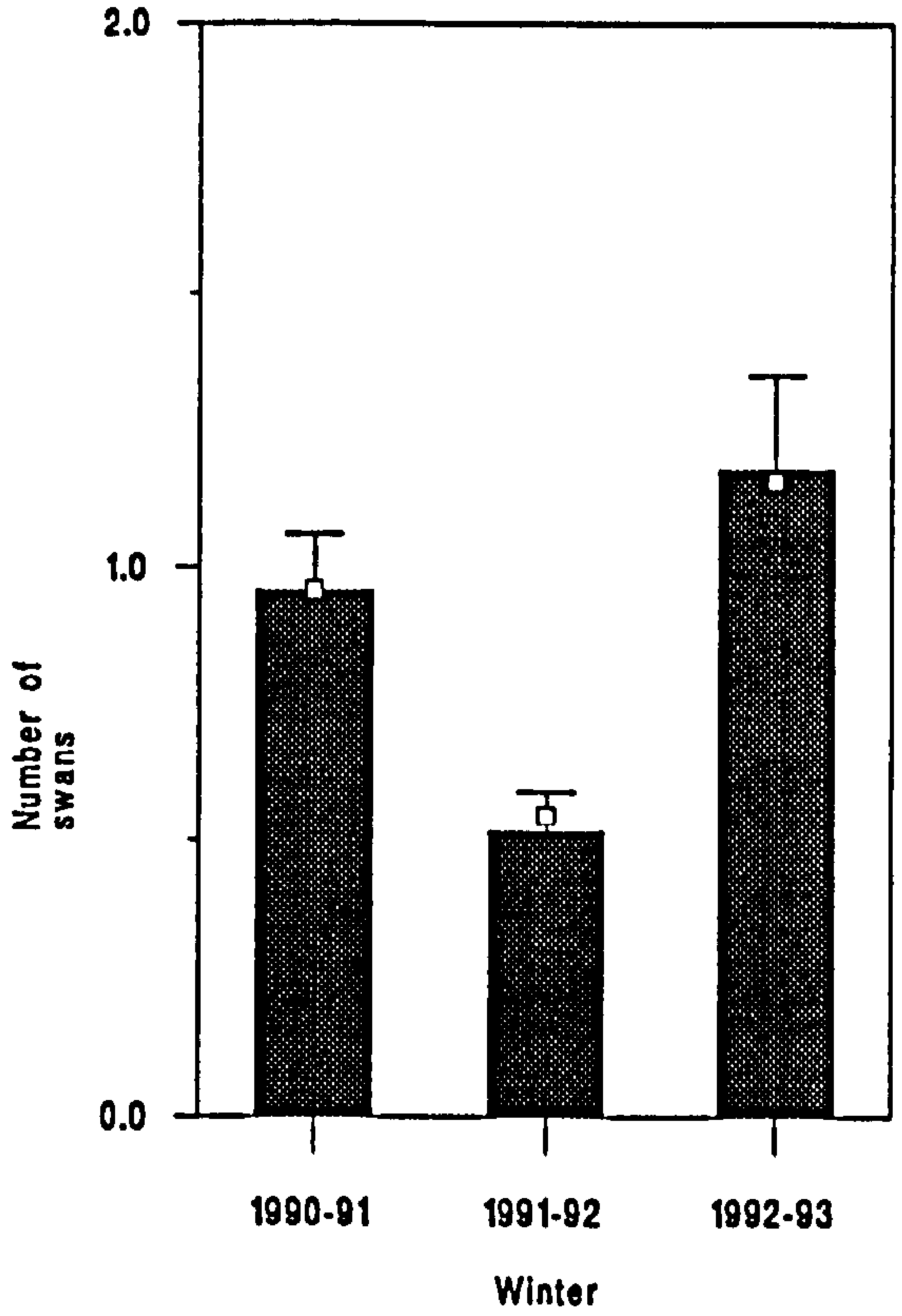


Fig. 5.15. The number of adult swans recorded in social interactions at the feeding sites during the day (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=1028) plus predicted values from a generalised linear model.

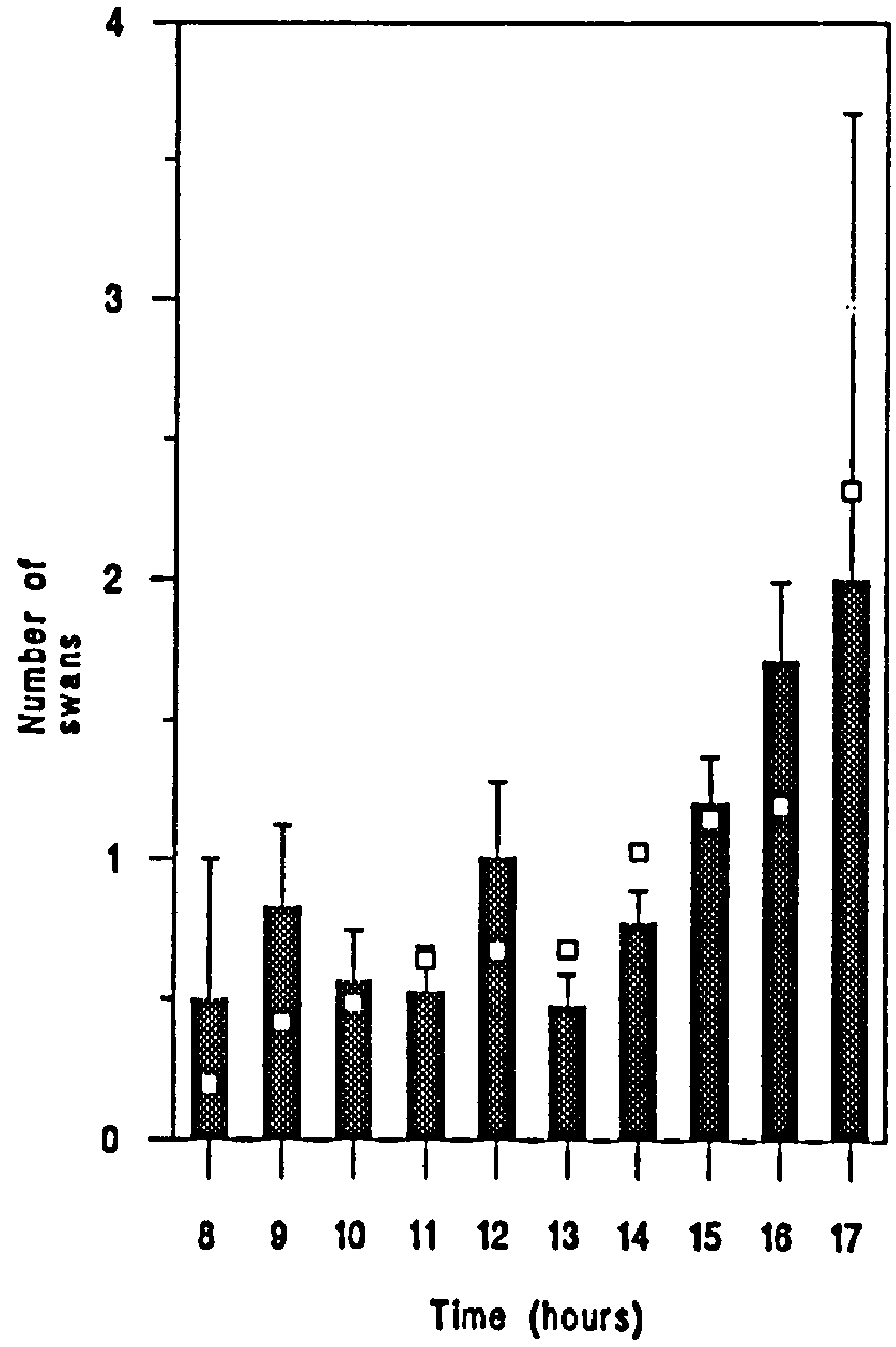


Fig. 5.16. The number of cygnets recorded feeding at the feeding sites by hour (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=815) plus predicted values from a generalised linear model.

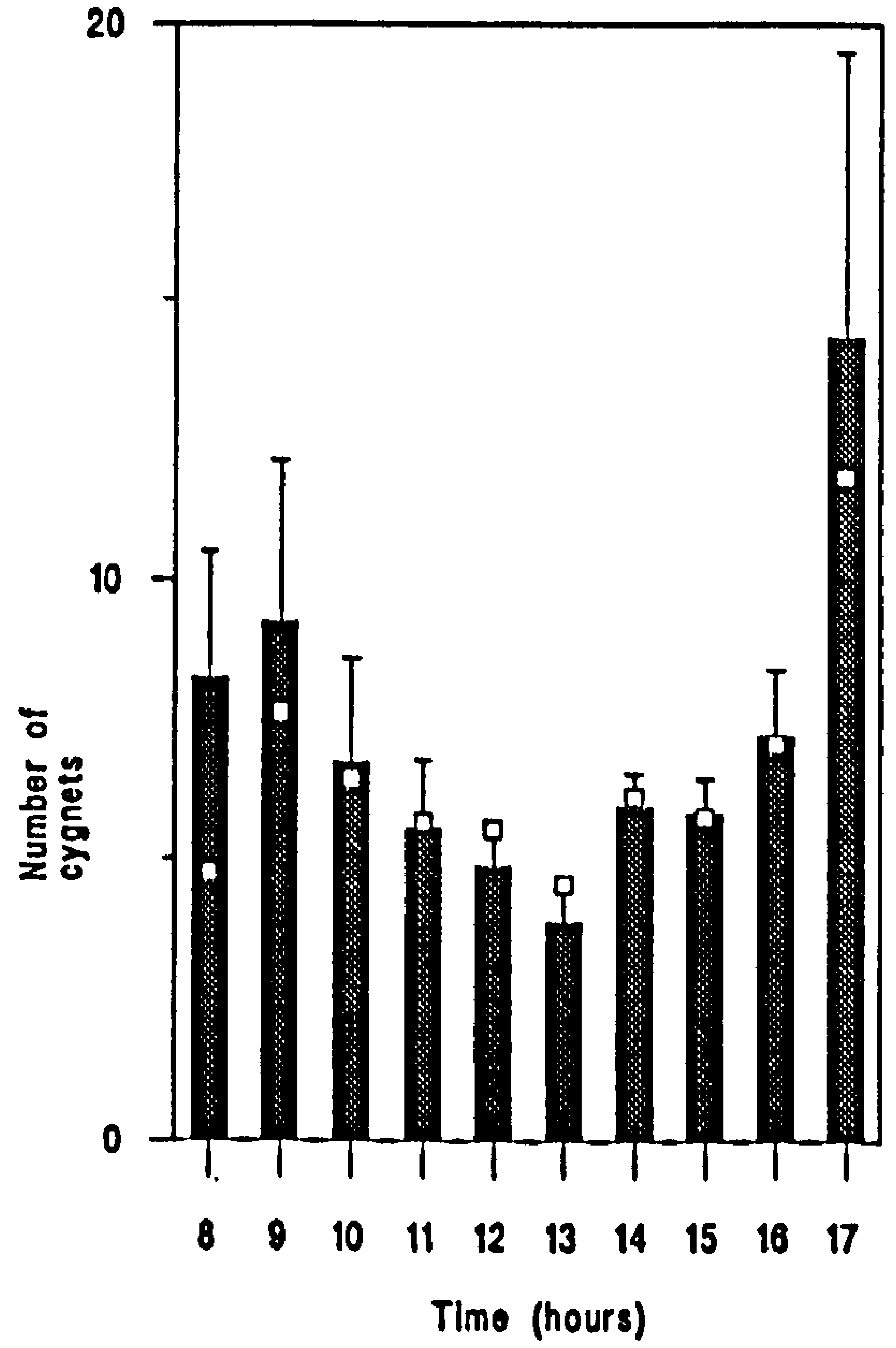


Fig. 5.17. The number of cygnets recorded feeding at the feeding sites by half-month (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=815) and predicted values from a generalised linear model.

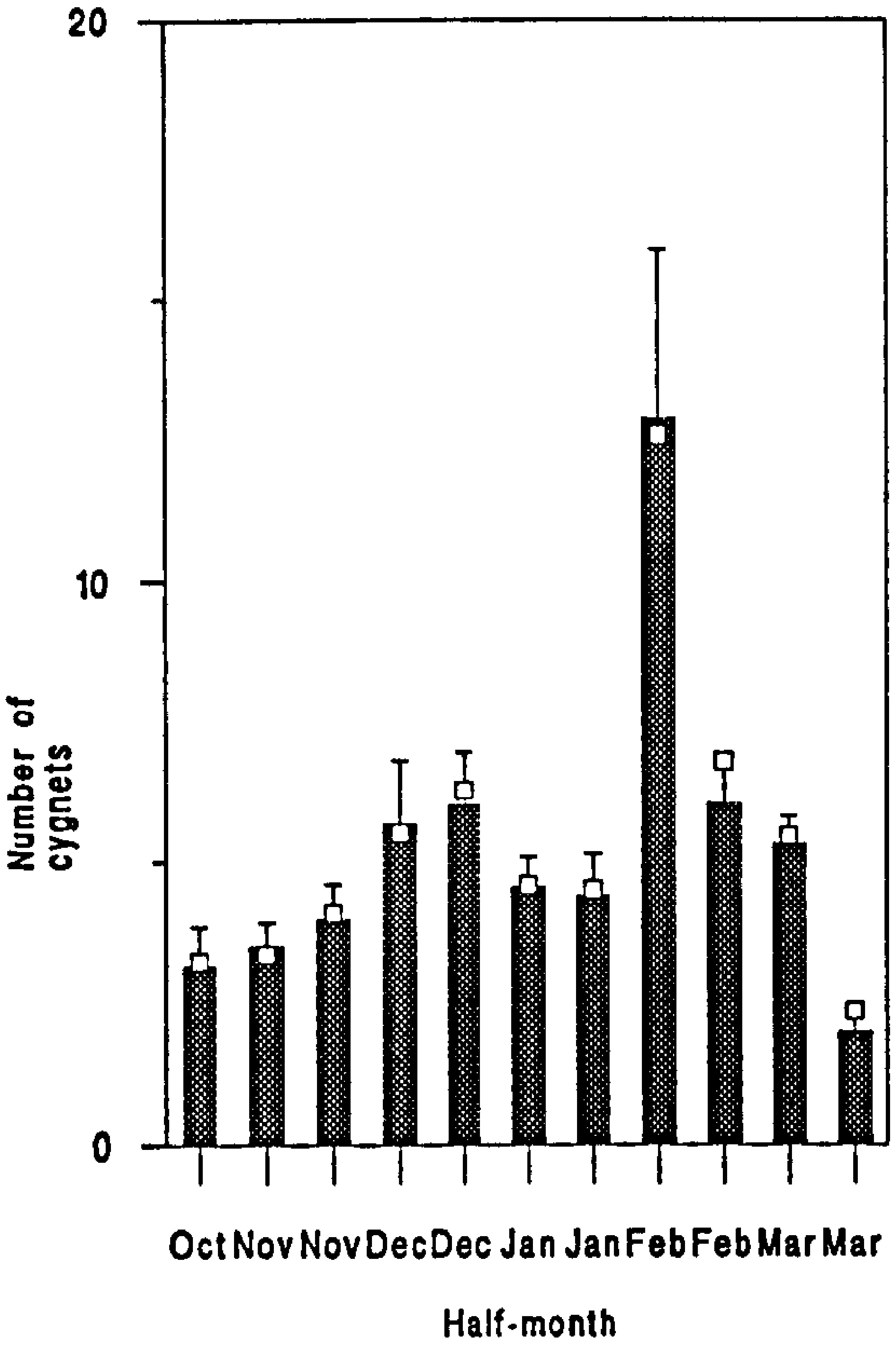


Fig. 5.18. The number of cygnets recorded resting at feeding sites by half-month (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

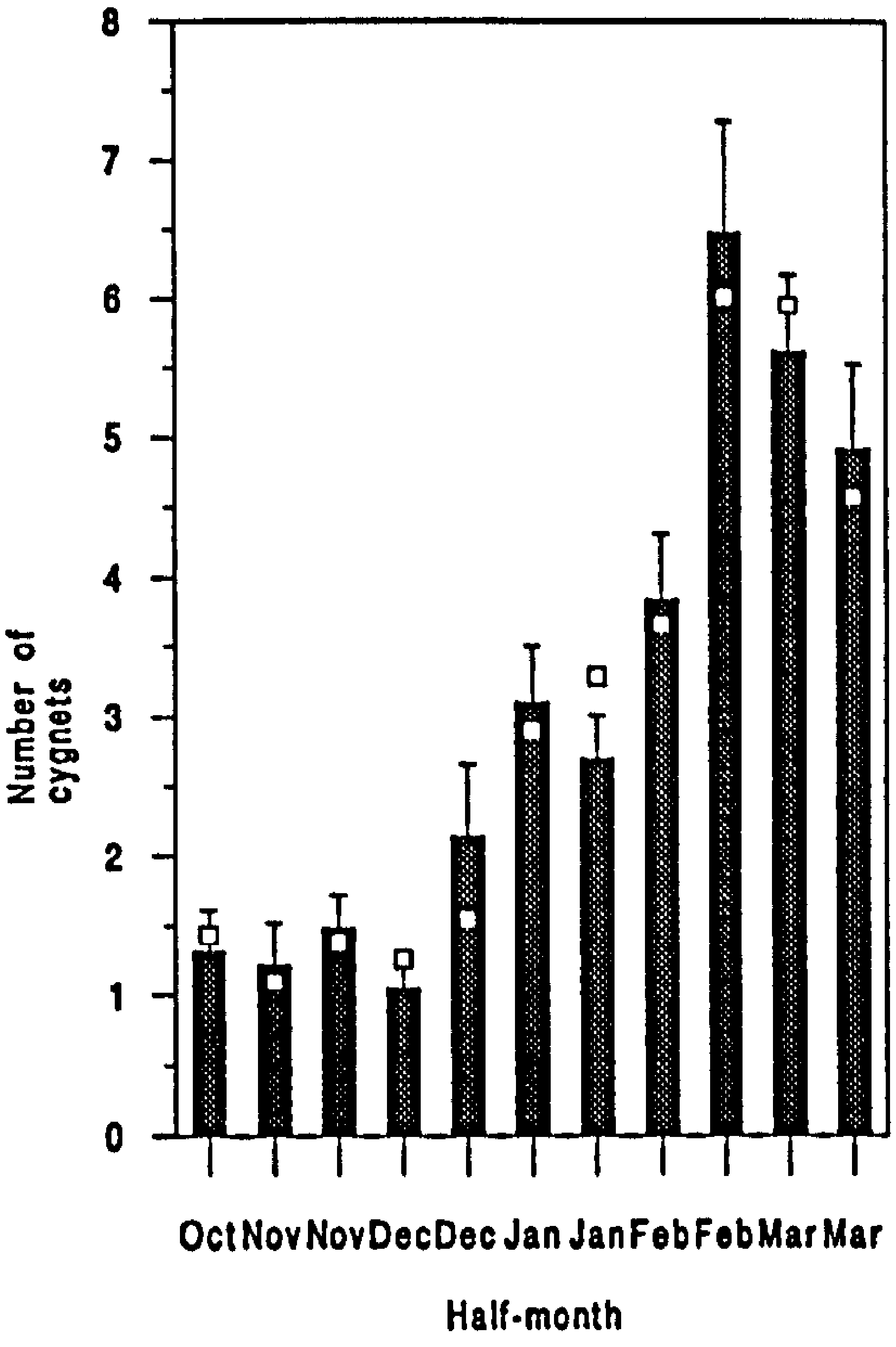


Fig. 5.19. The number of cygnets recorded in comfort activity at the feeding sites by hour (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

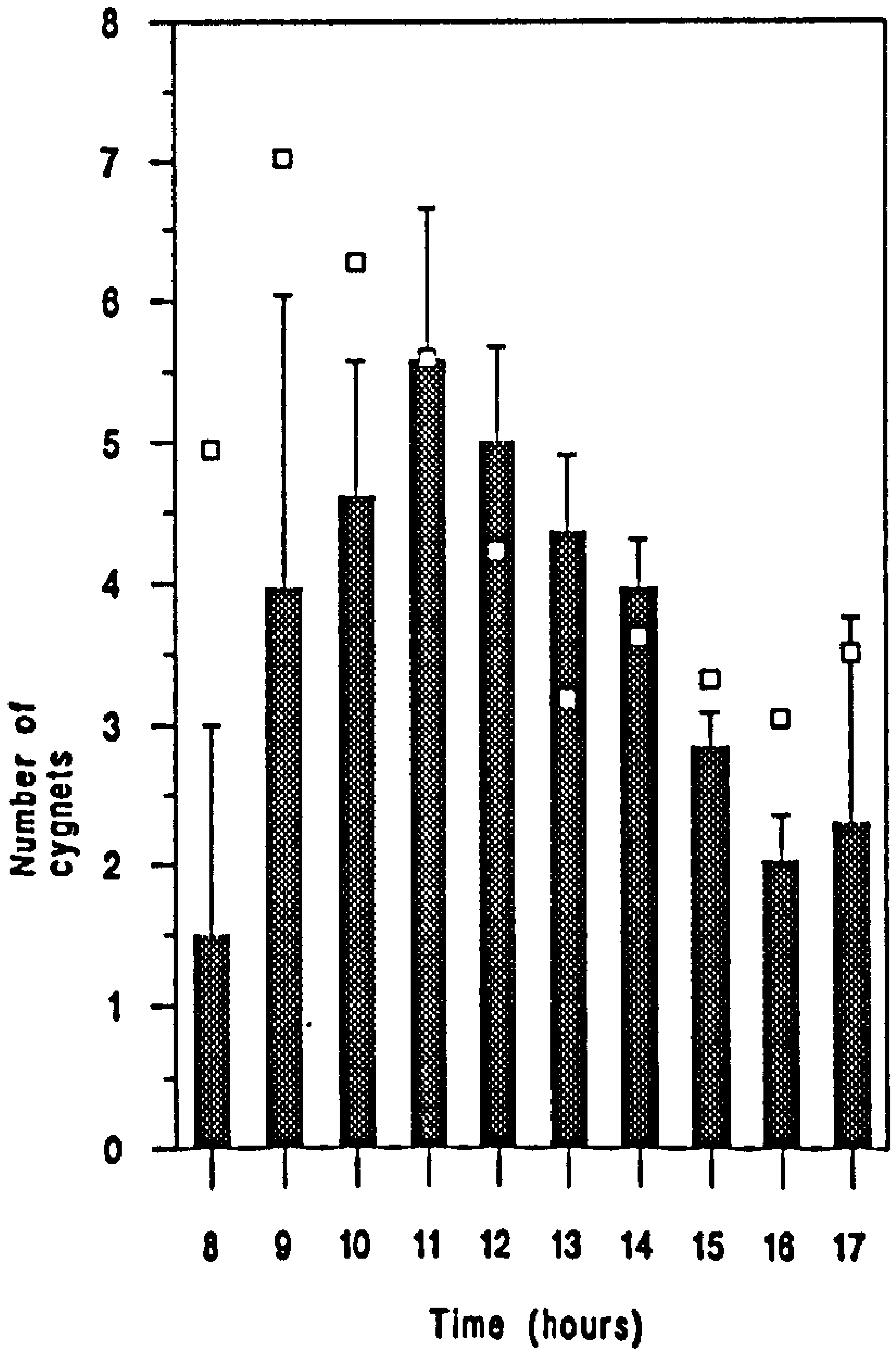


Fig. 5.20. The number of cygnets recorded in comfort activity at the feeding sites by half-month (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

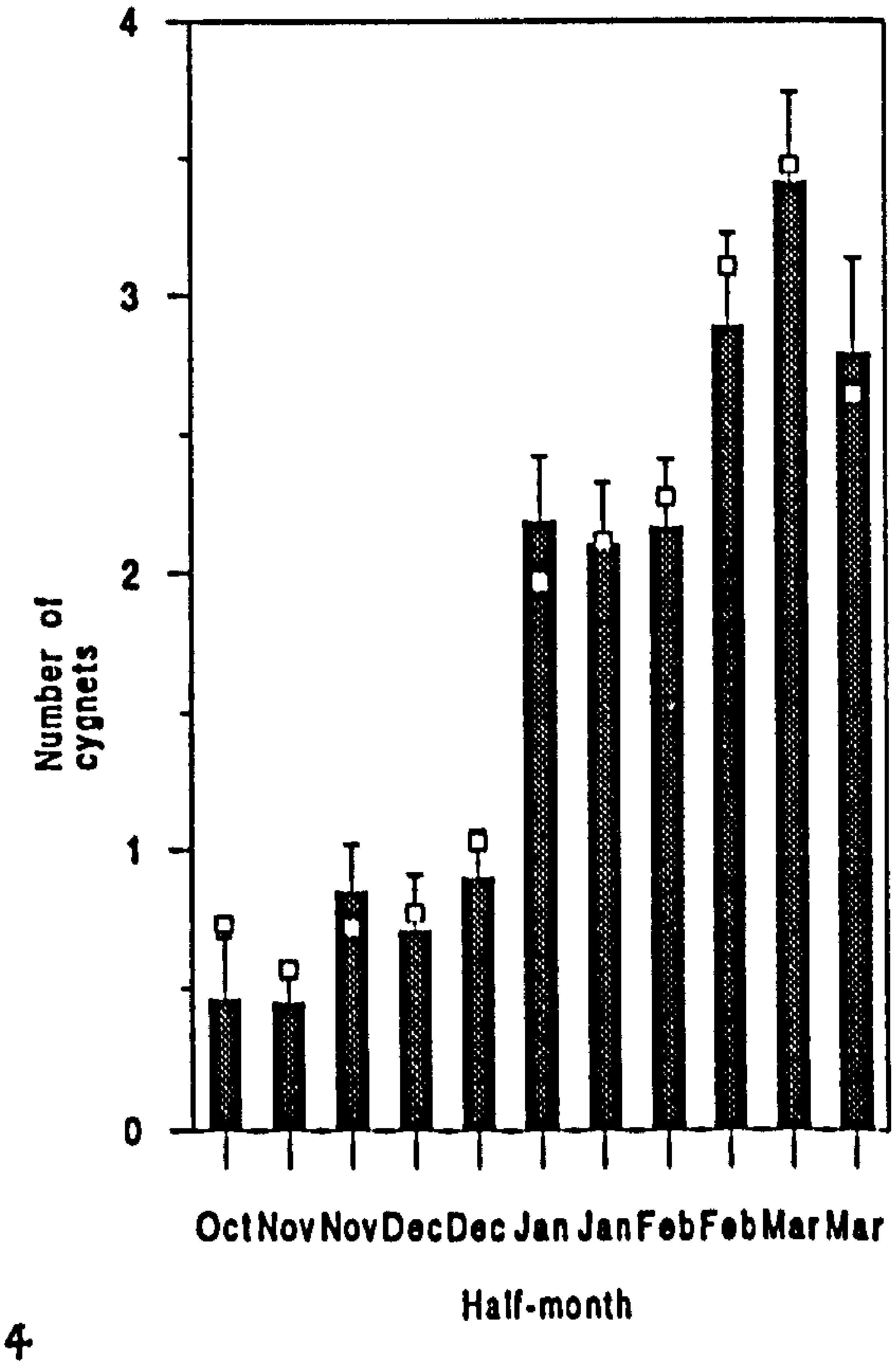


Fig. 5.21. The number of cygnets recorded in alert activity at the feeding sites with flock-size (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

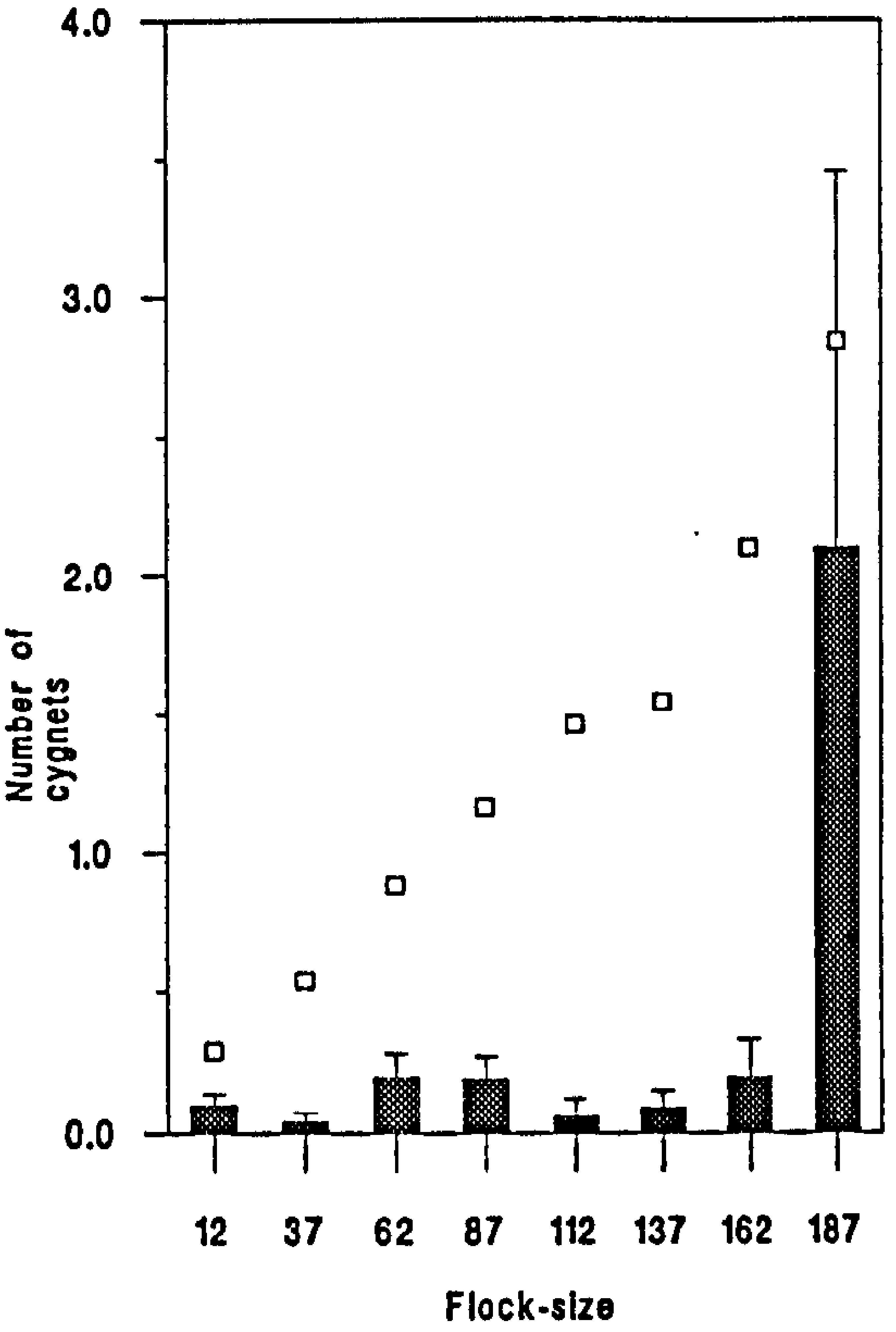


Fig. 5.22. The number of cygnets recorded in alert activity at the feeding sites by half-month (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

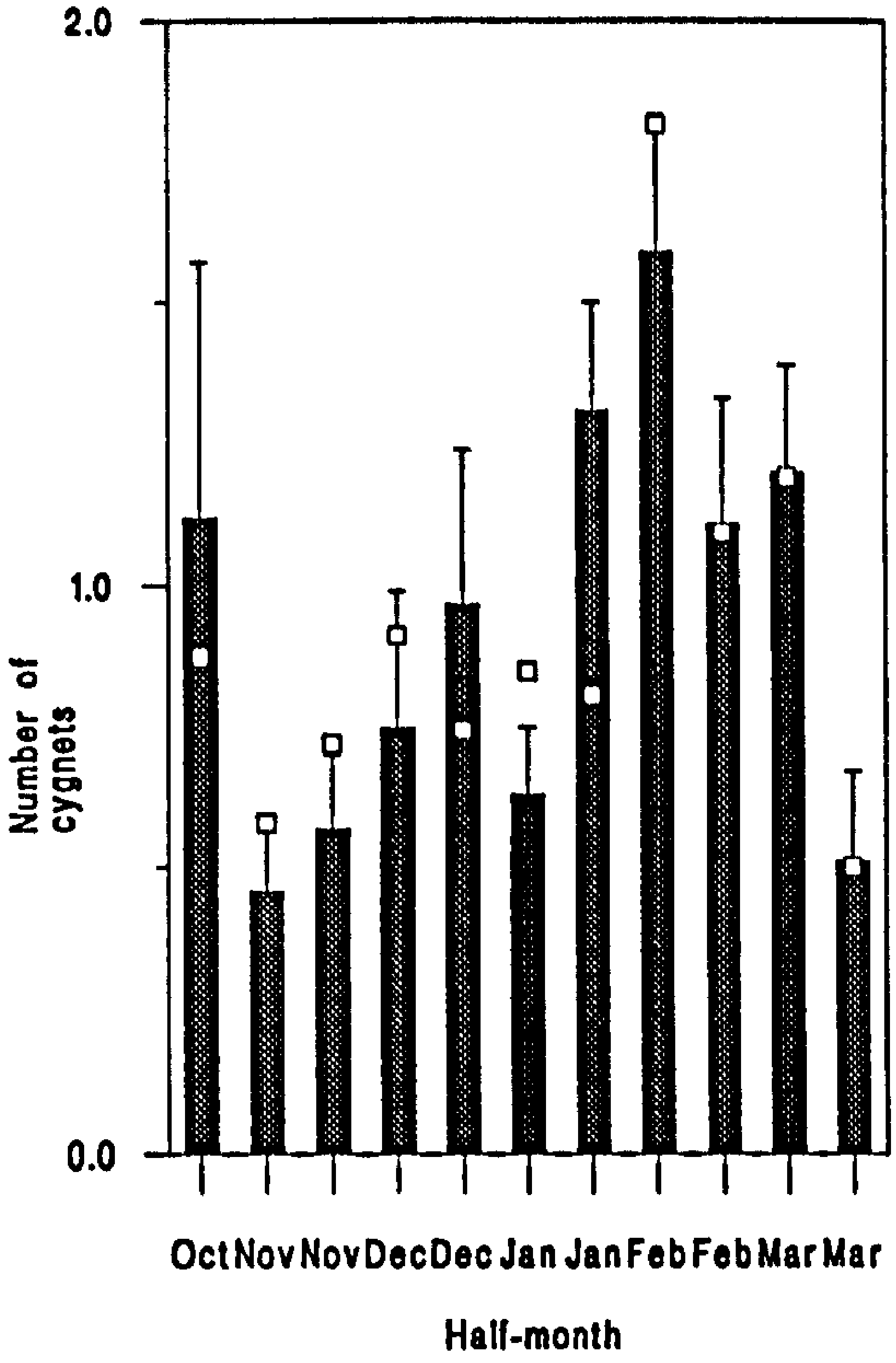


Fig. 5.23. The number of cygnets recorded in alert activity at the feeding sites by hour (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

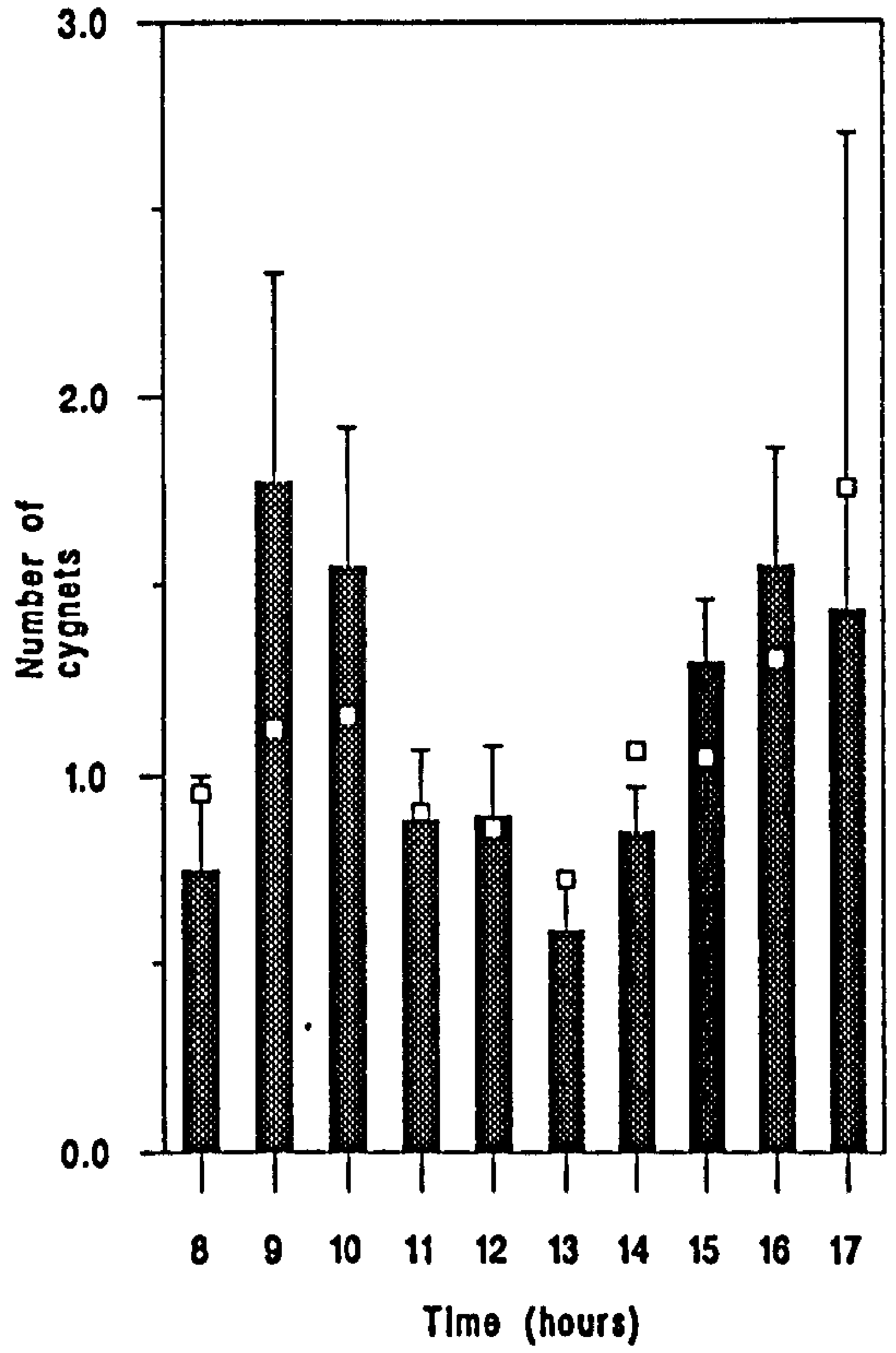


Fig. 5.24. The number of cygnets recorded in the activity of movement at the feeding sites (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

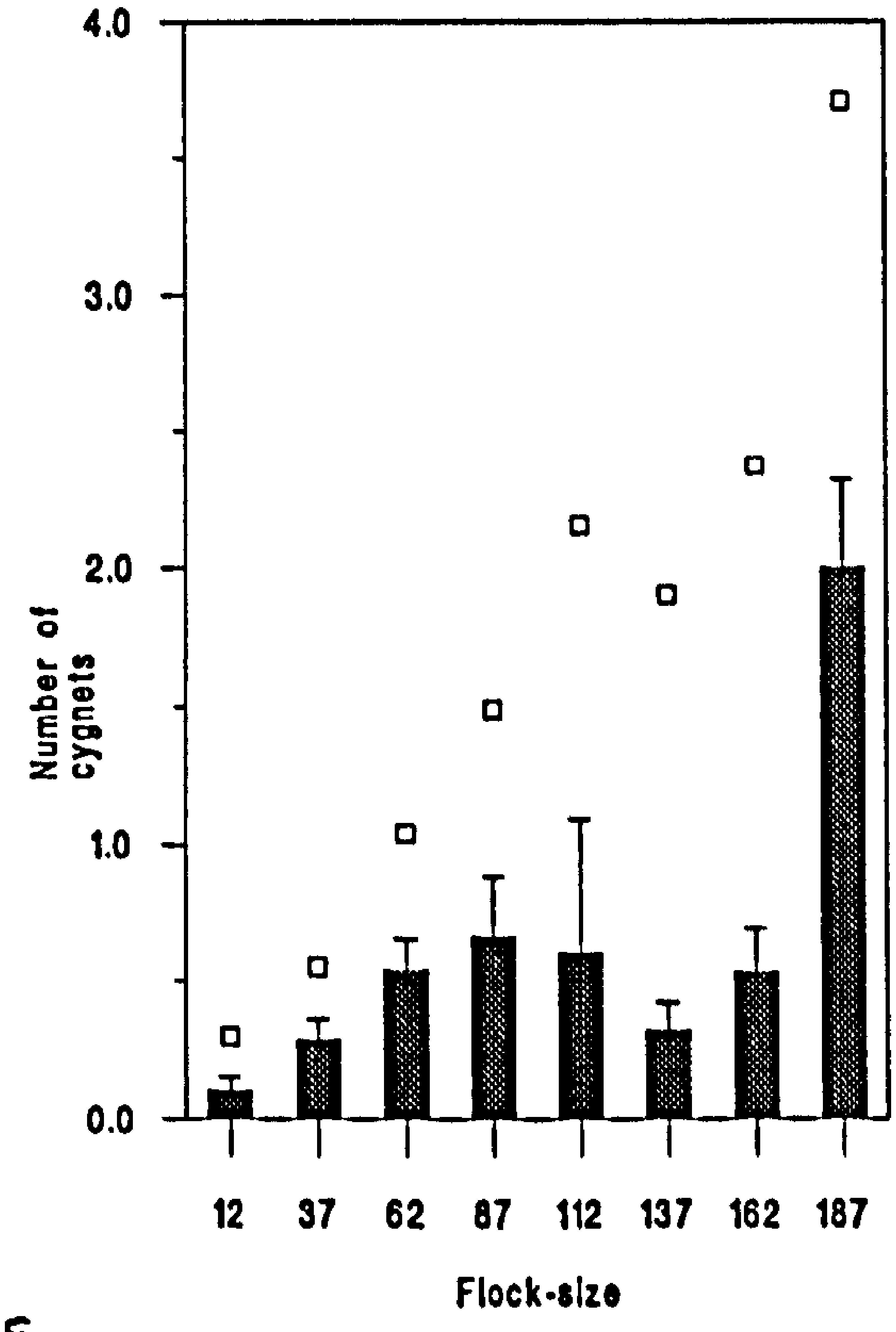


Fig. 5.25. The number of cygnets recorded in the activity of movement at the feeding sites by hour (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

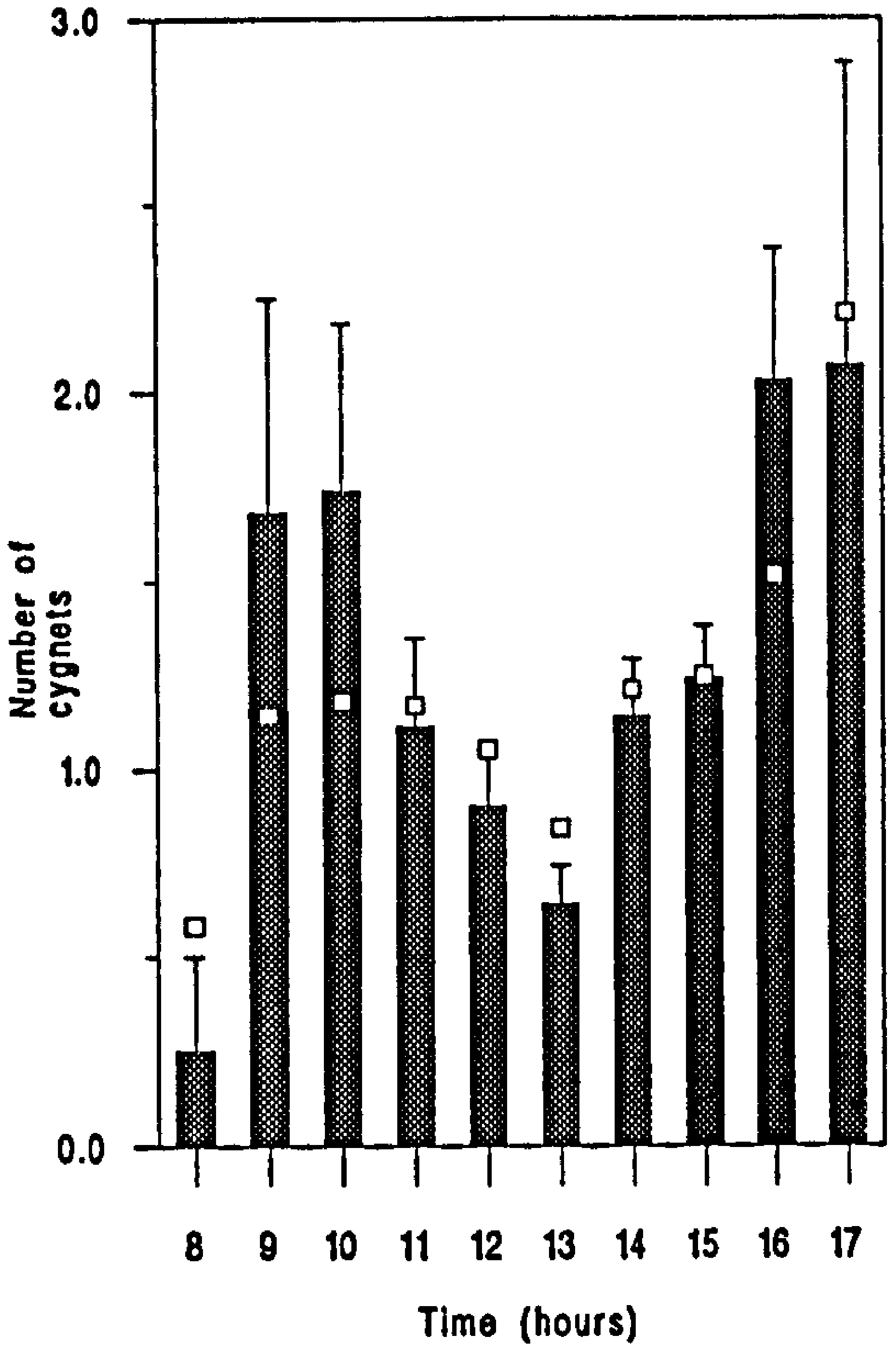


Fig. 5.26. The number of cygnets recorded in social interactions at the feeding sites by winter (mean per flock scan and S.E. bar, n=815), plus predicted values from a generalised linear model.

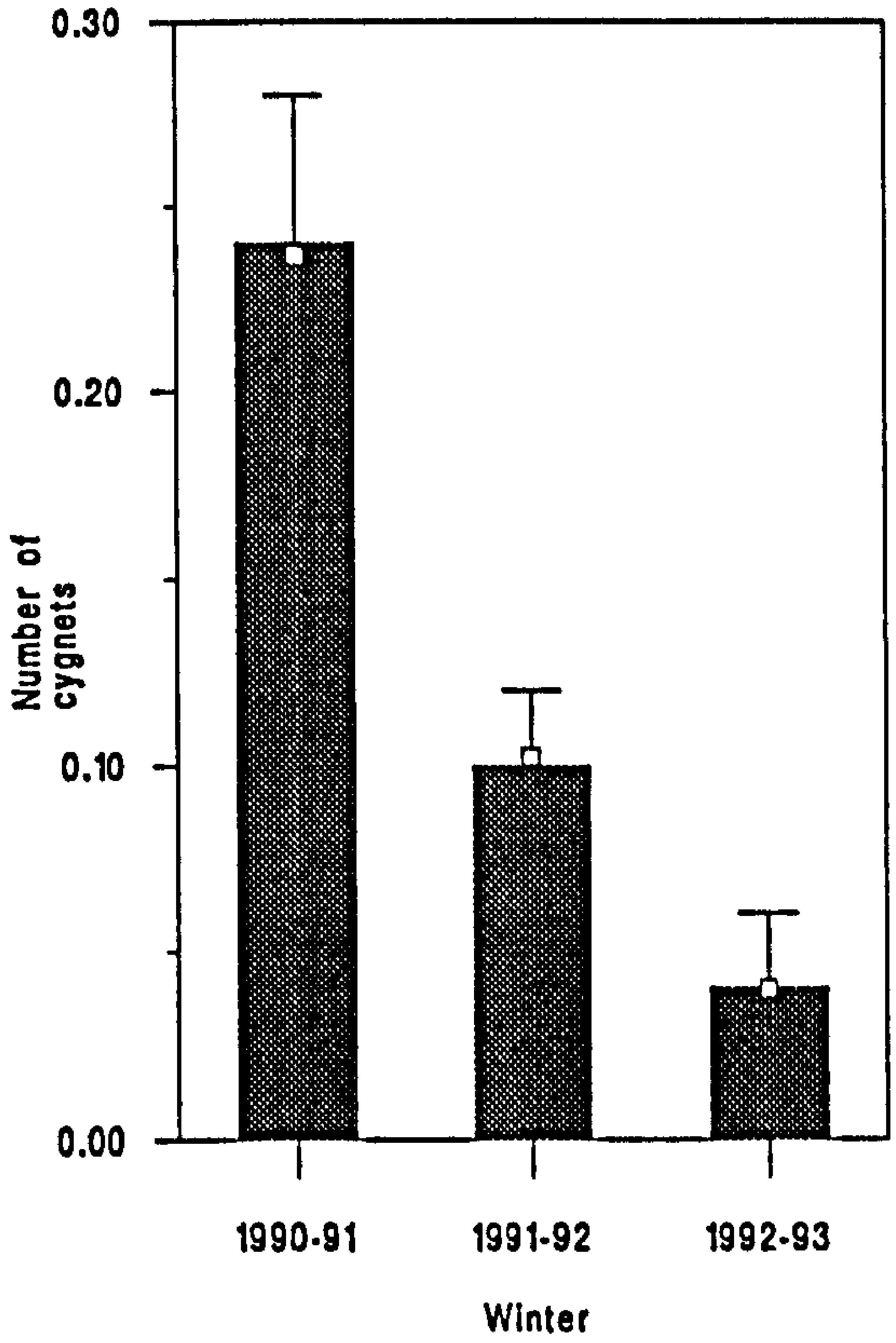


Fig. 5.27. The number of cygnets recorded in social interactions at the feeding sites by half-month (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

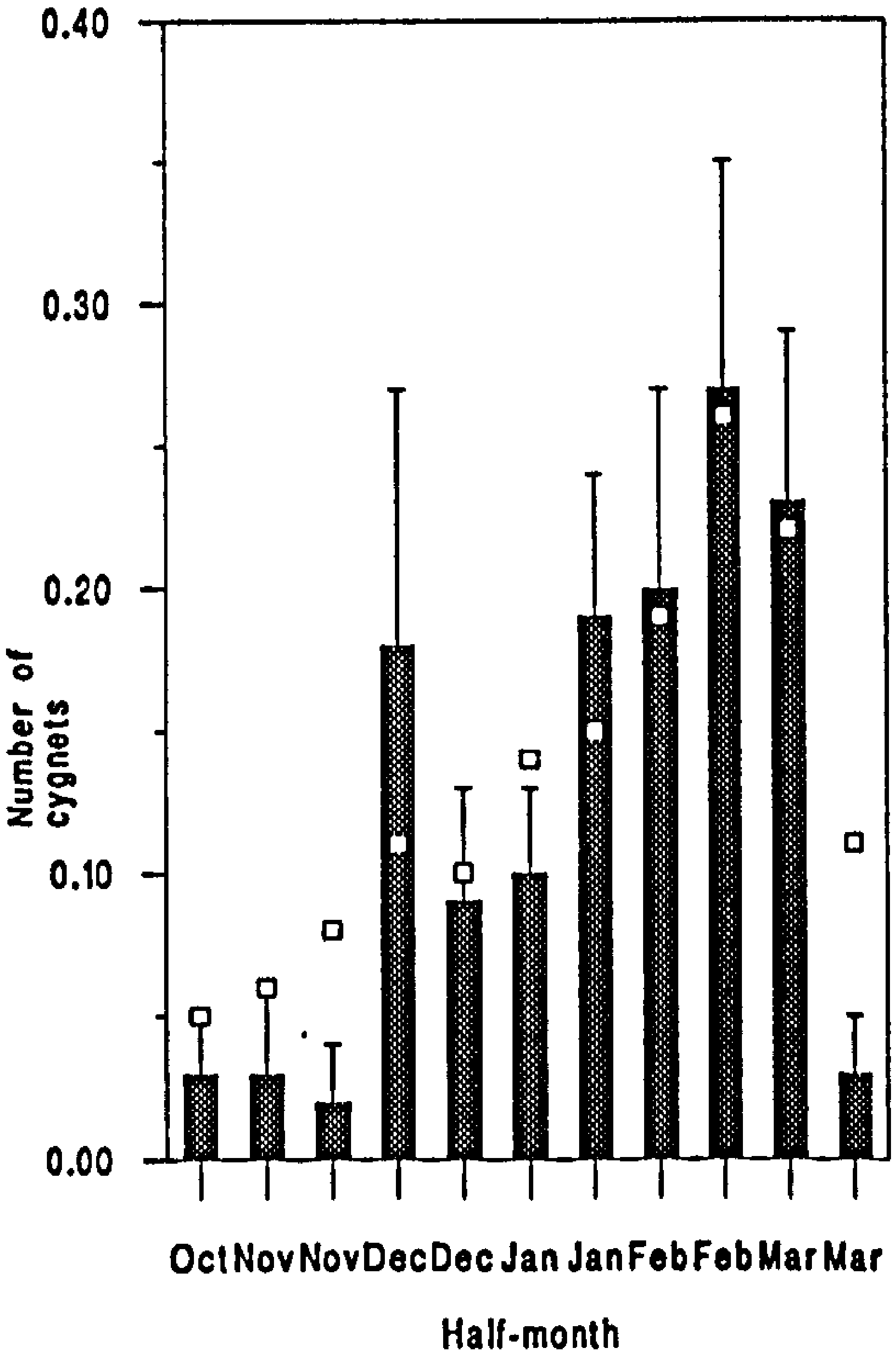


Fig. 5.28. The number of cygnets recorded in social interactions at the feeding sites by hour (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=815), plus predicted values from a generalised linear model.

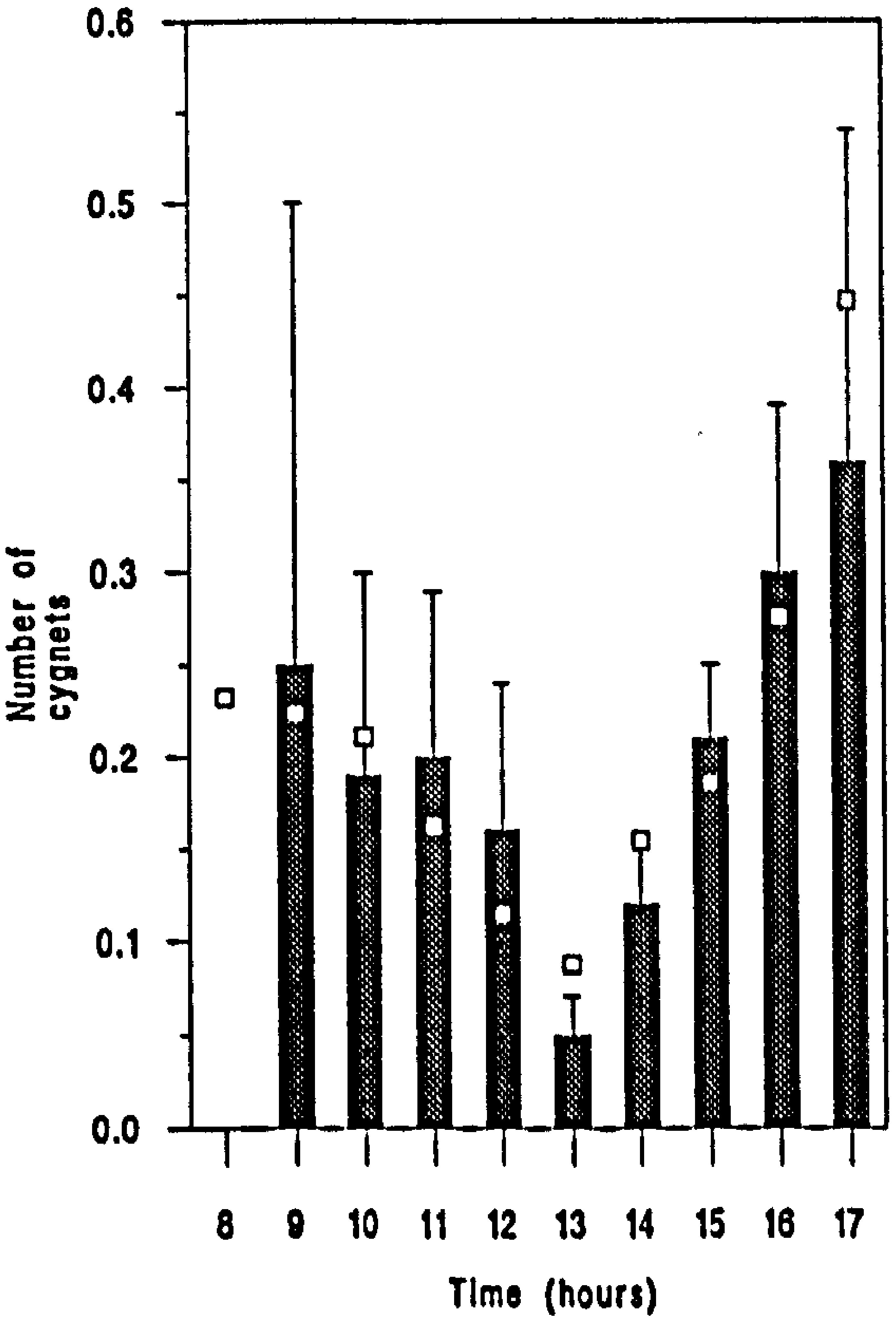


Fig. 5.29. The number of adult swans recorded feeding at the feeding sites with percentage protein content of the sward (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=375), plus predicted values from a generalised linear model.

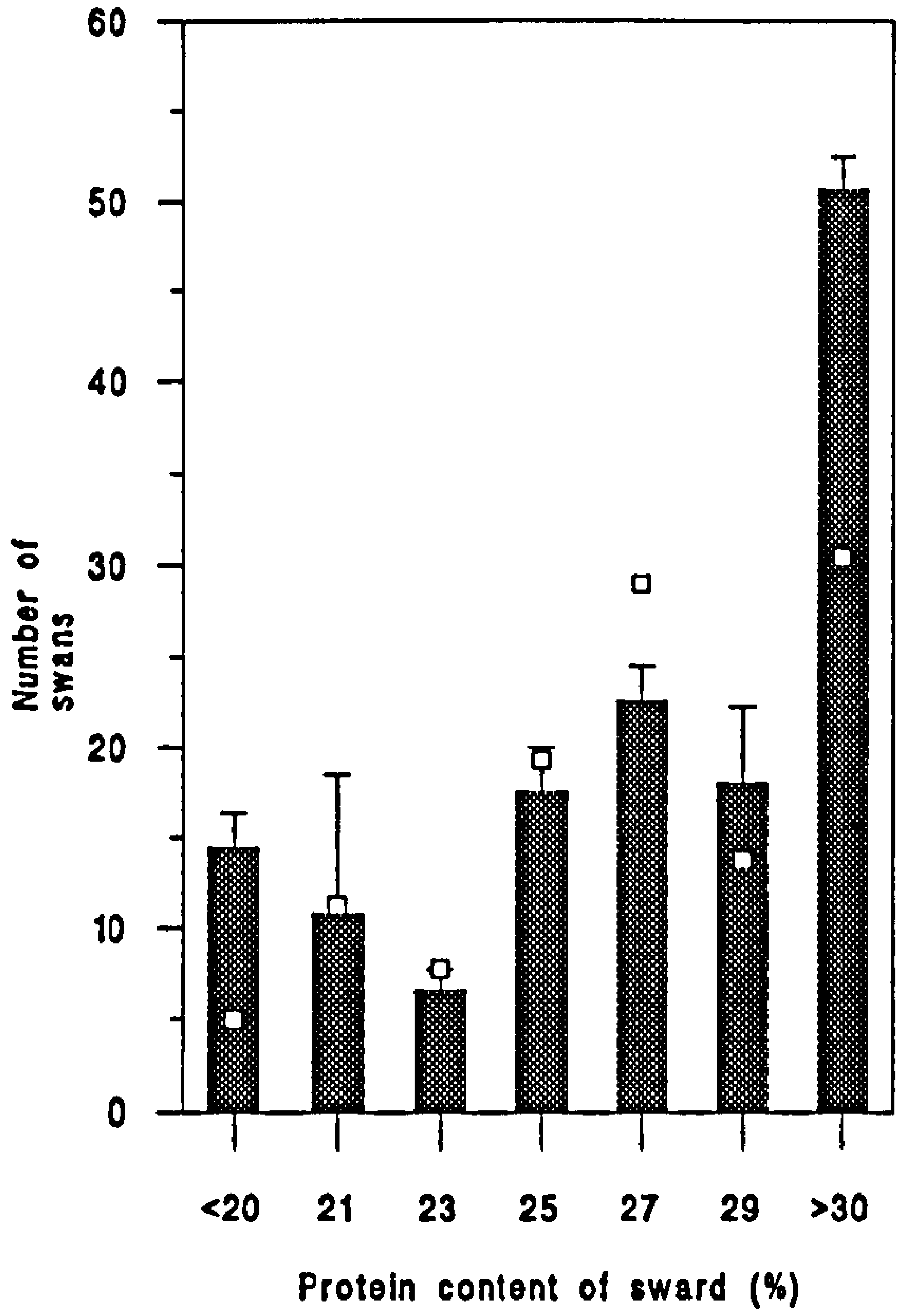


Fig. 5.30. The number of adult swans recorded feeding at the feeding sites with the percentage water cover of the fields (mean per flock scan for 1990-91 to 1992-93 winters combined & S.E. bar, n=413), plus predicted values from a generalised linear model.

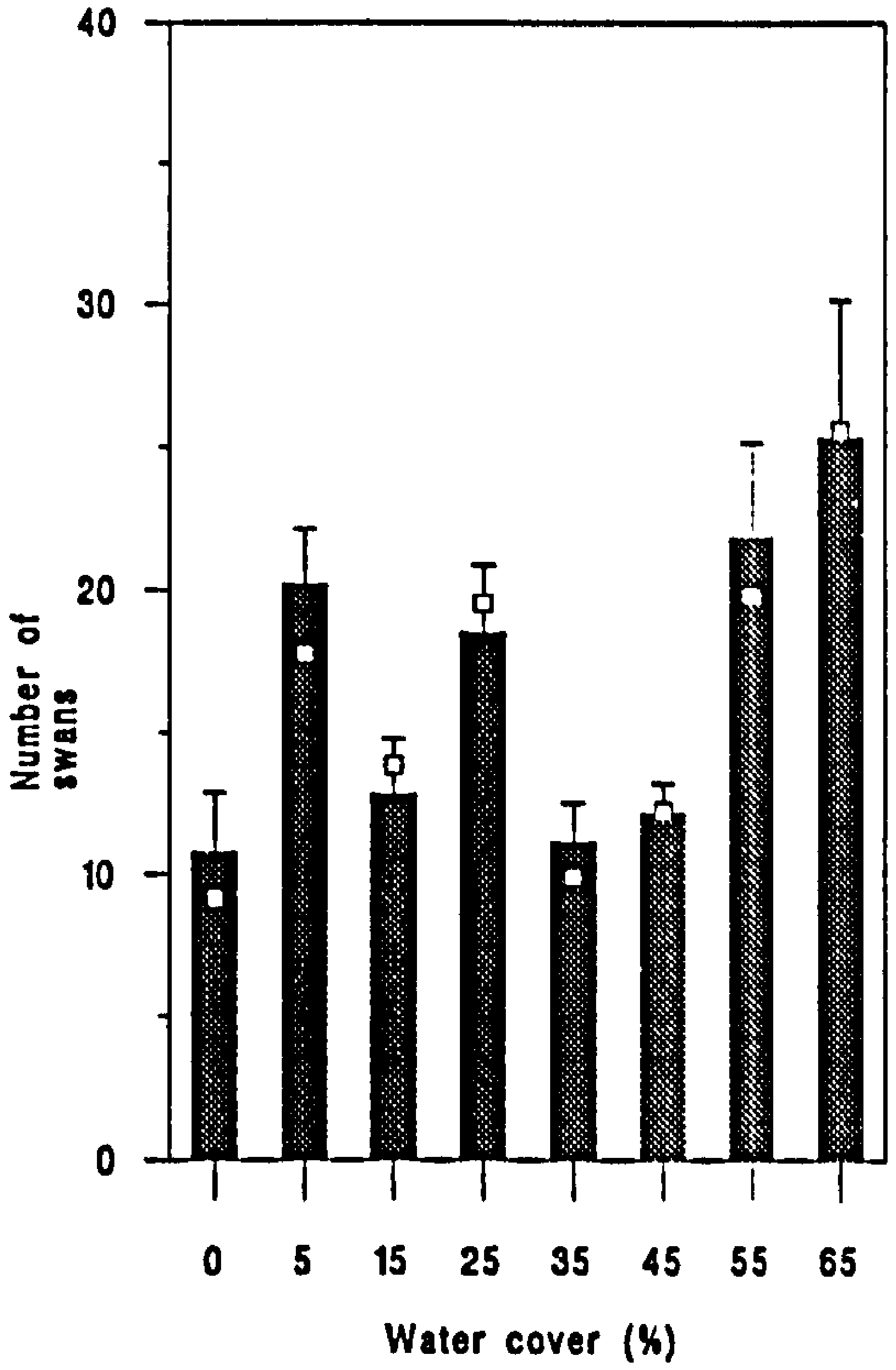


Fig. 5.31. The number of adult swans recorded resting at the feeding sites with percentage protein content of the sward (mean per flock scan for 1990-91 to 1992-93 winters combined & S.E. bar, n=375), plus predicted values from a generalised linear model.

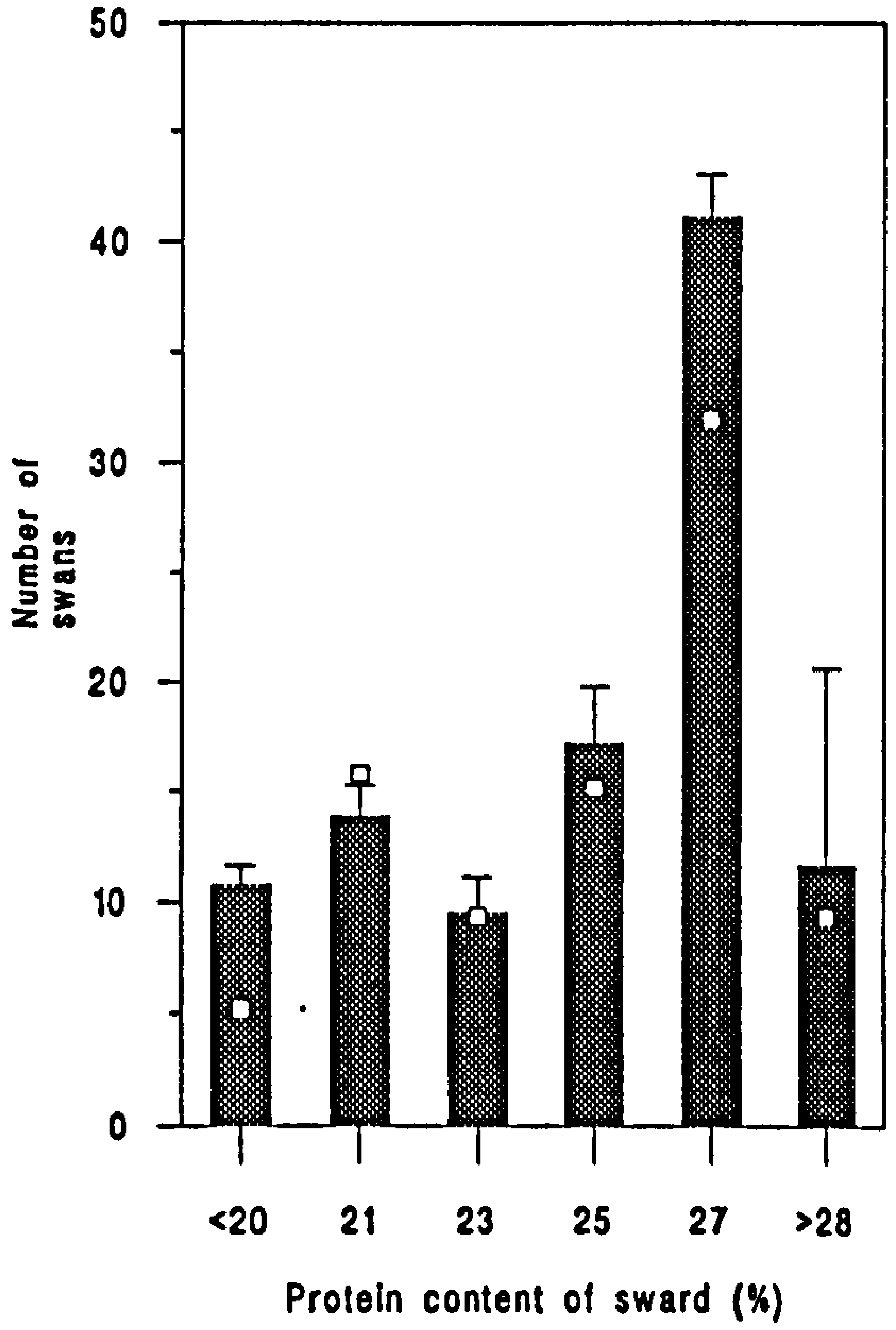


Fig. 5.32. The number of adult swans recorded resting at the feeding sites with biomass of the sward (mean per flock scan for 1990-91 to 1992-93 winters combined & S.E. bar, n=375), plus predicted values from a generalised linear model.

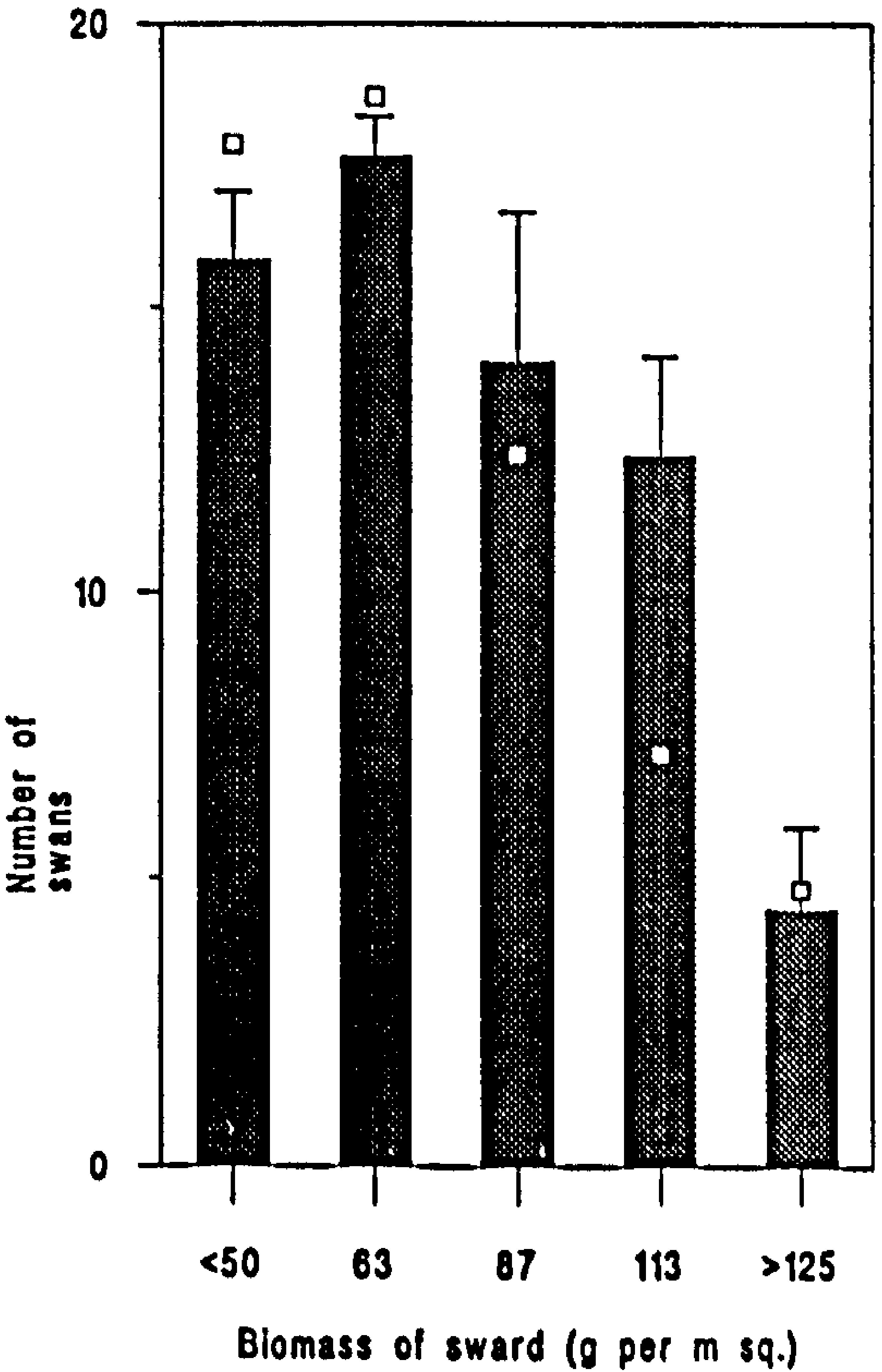


Fig. 5.33. The number of adult swans in comfort activity at the feeding sites with percentage water cover of the fields (mean per flock scan for 1990-91 to 1992-93 winters combined & S.E. bar, n=413), plus predicted values from a generalised linear model.

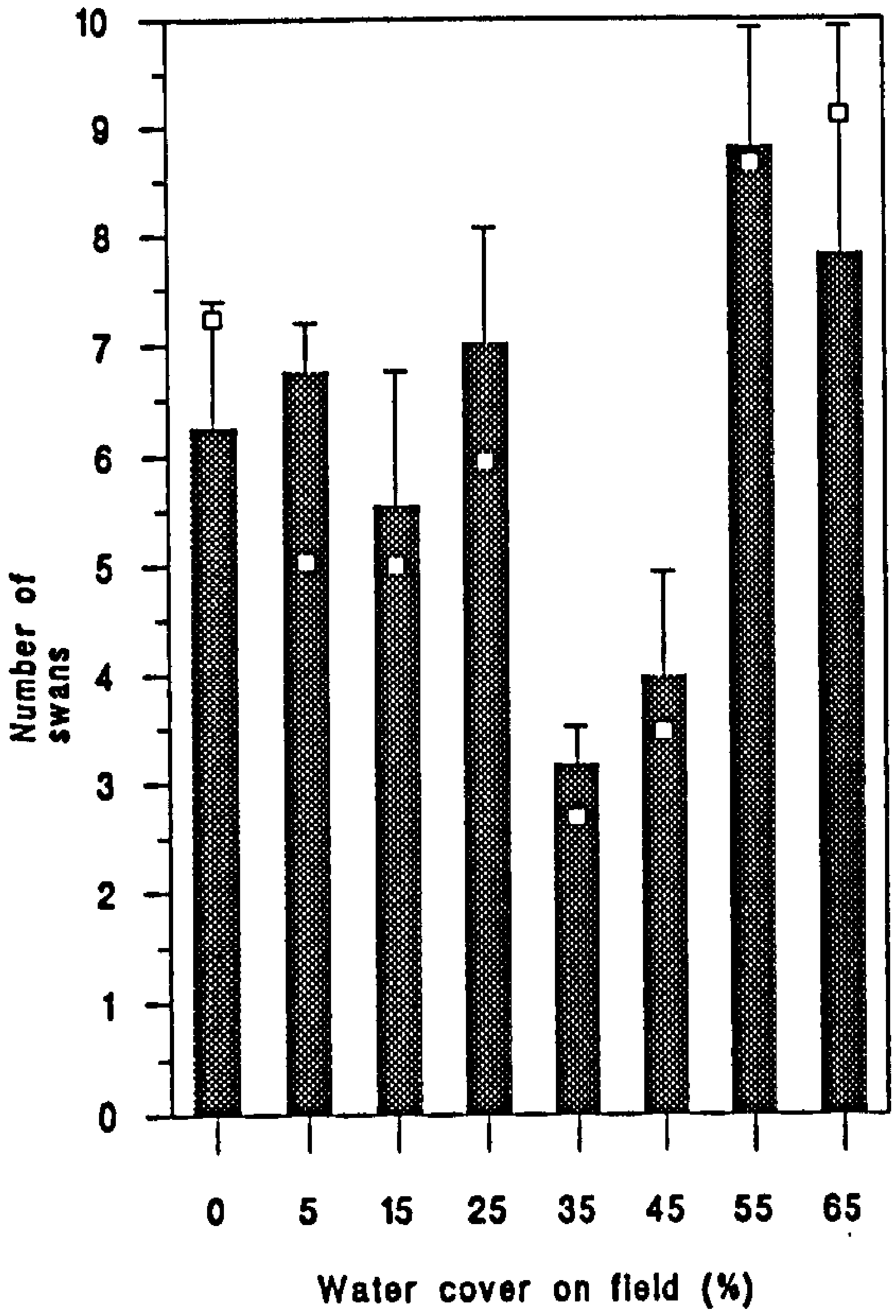


Fig. 5.34. Number of adult swans in comfort activity at the feeding sites with the proportion of swan units present from the Rushy Pen roost (1990-91 to 1992-93 winters combined mean & S.E.bar, n=413), plus predicted values from a generalised linear model.

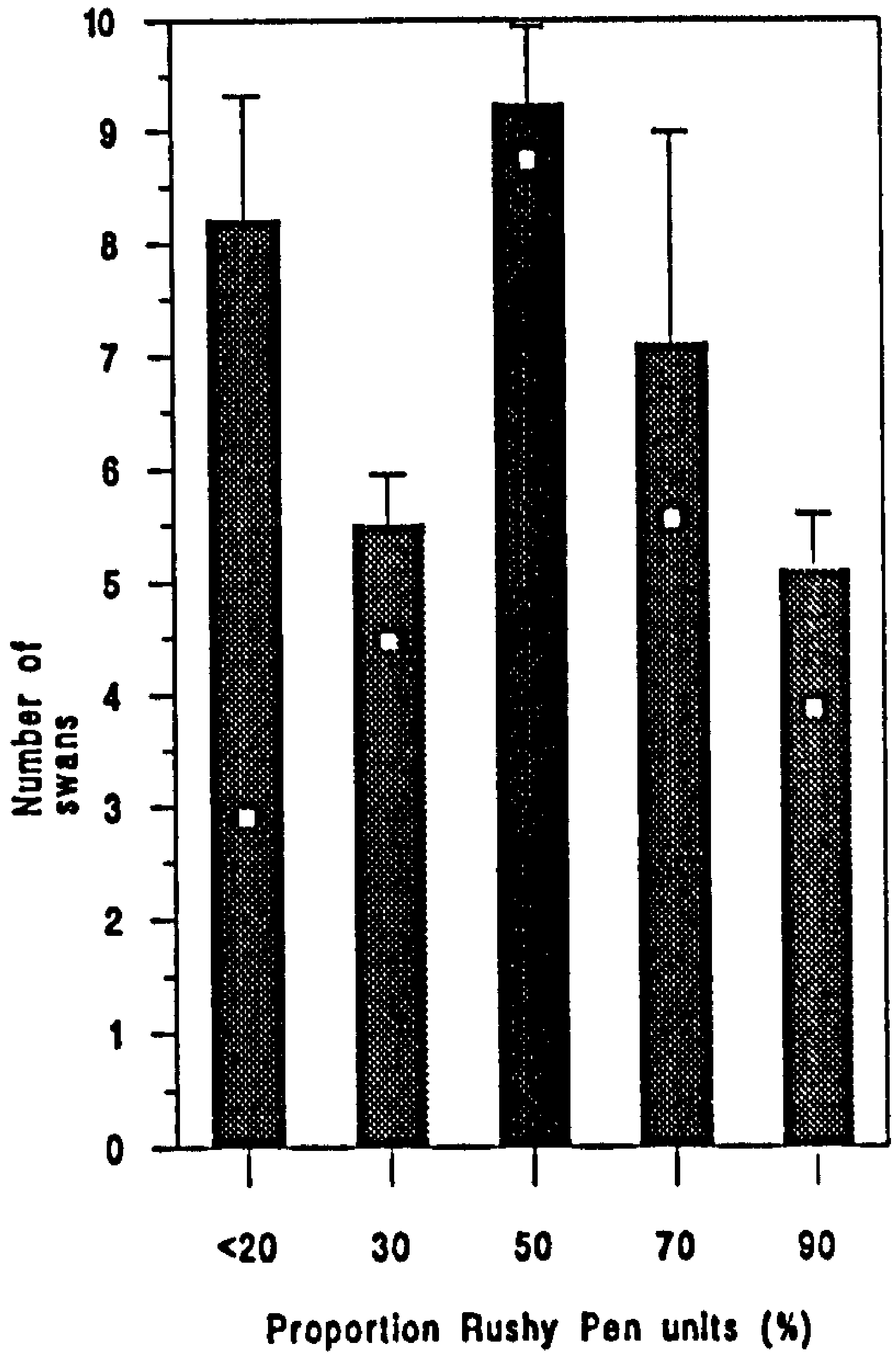


Fig. 5.35. The number of adult swans recorded in alert activity at the feeding sites with biomass of the sward (mean per flock scan for 1990-91 to 1992-93 winters combined and S.E. bar, n=375), plus predicted values from a generalised linear model.

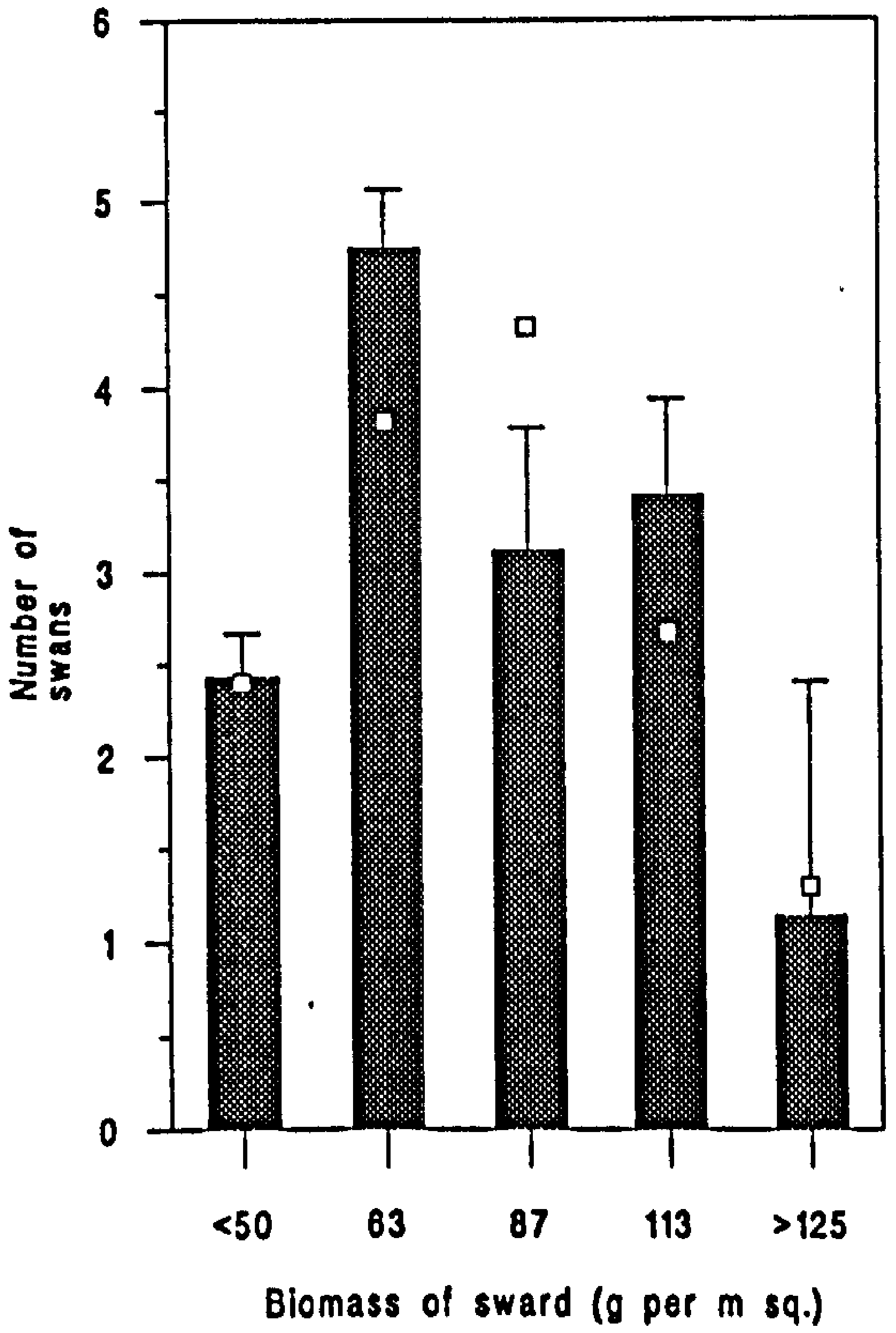


Fig. 5.36. Number of adult swans in alert activity at the feeding sites with the proportion of Rushy Pen units present (mean per flock scan for 1990-91 to 1992-93 winters combined & S.E. bar, n=413), plus predicted values from a generalised linear model.

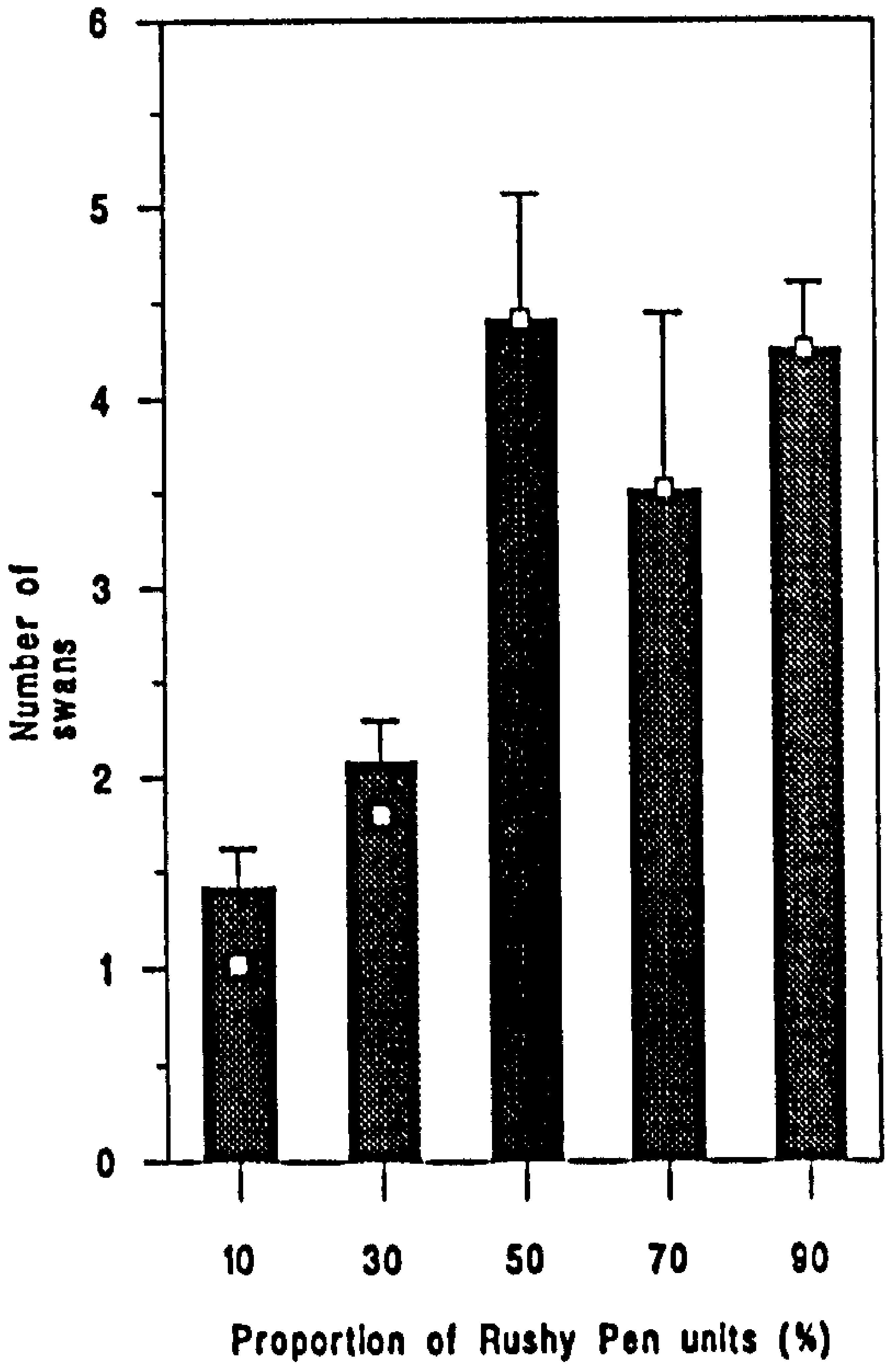


Fig. 5.37. The number of adult swans in the activity of movement at the feeding sites with the biomass of the sward (mean per flock scan for 1990-91 to 1992-93 winters combined & S.E. bar, n=375) plus predicted values from a generalised linear model.

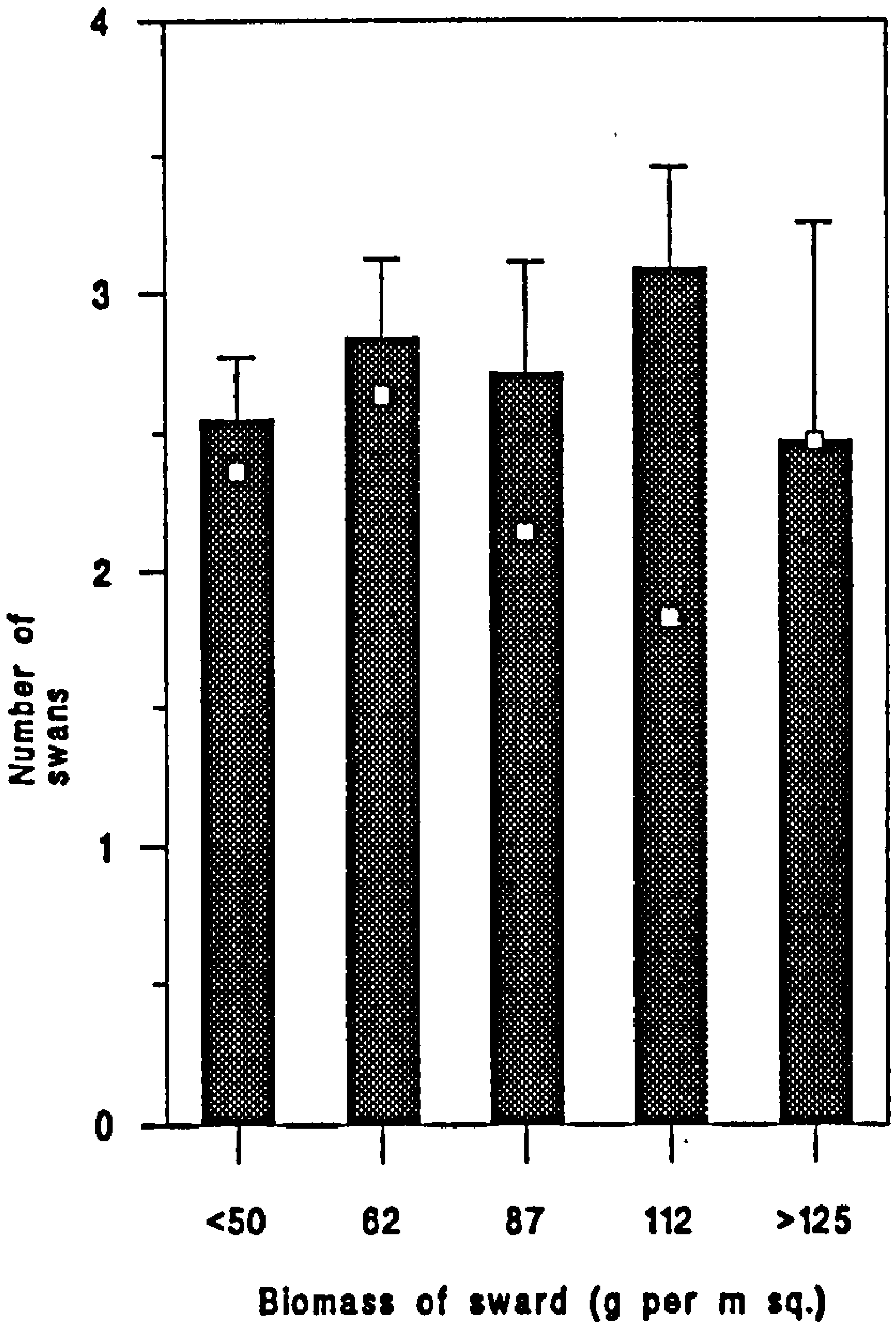


Fig. 5.38. The number of adult swans in social interactions at the feeding sites with percentage water cover of field (mean per flock scan for 1990-91 to 1992-93 winters combined & S.E. bar, n=413), plus predicted values from a generalised linear model.

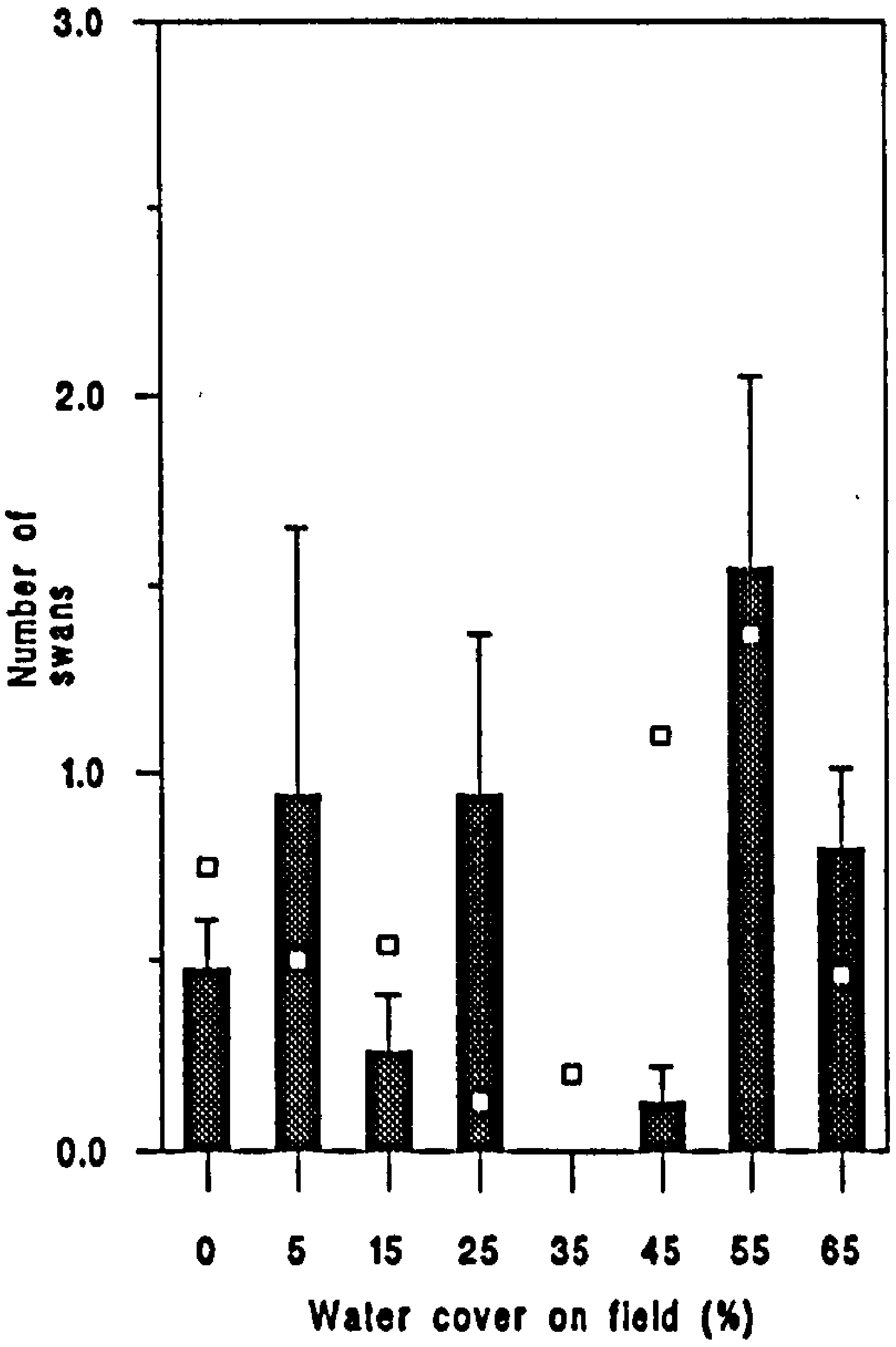


Fig.5.39. Number of adult swans in social interaction with the proportion of swans present in the flock from the Rushy Pen roost (mean per flock scan 1990-91 to 1992-93 winters combined & S.E.bar,n=413)plus predicted values from a generalised linear model.

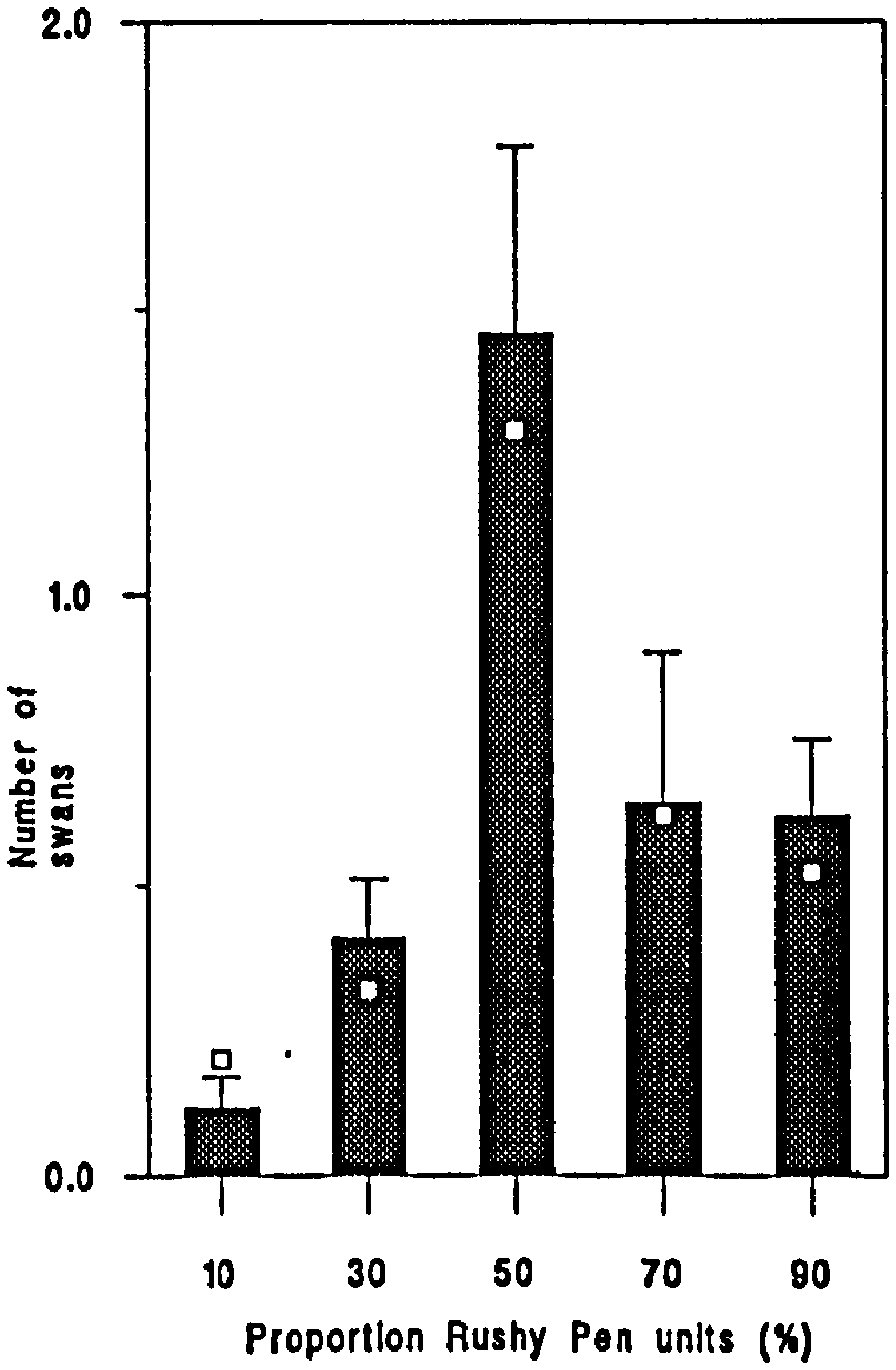


Fig. 5.40. The number of cygnets recorded feeding at the feeding sites with percentage protein content of the sward (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=228), plus predicted values from a generalised linear model.

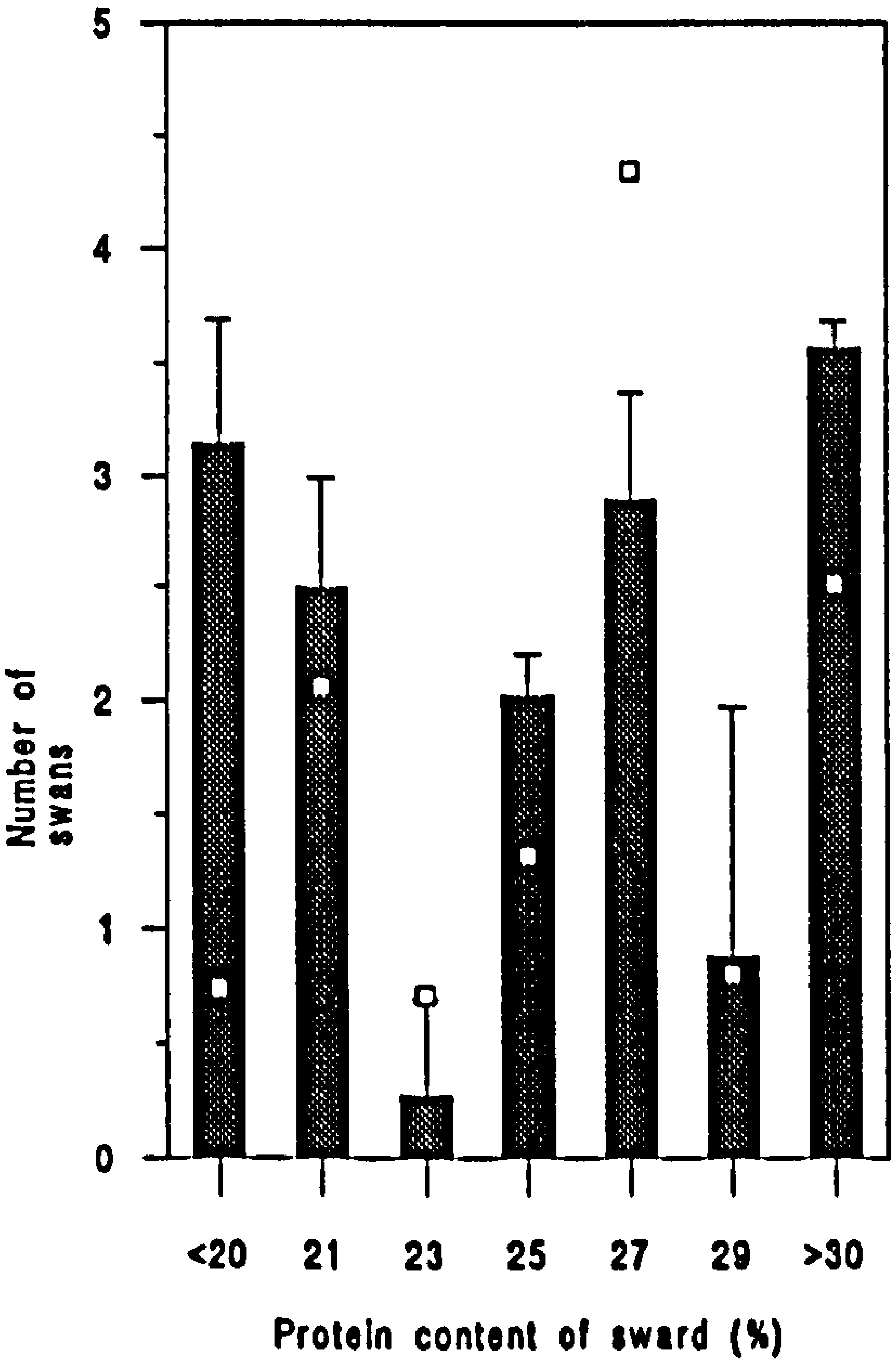


Fig. 5.41. The number of cygnets feeding on the fields with the proportion of swan units present from the Rushy Pen roost (mean per flock scan 1990-91 to 1992-93 winters combined & S.E. bar, n=228), plus predicted values from a generalised linear model.

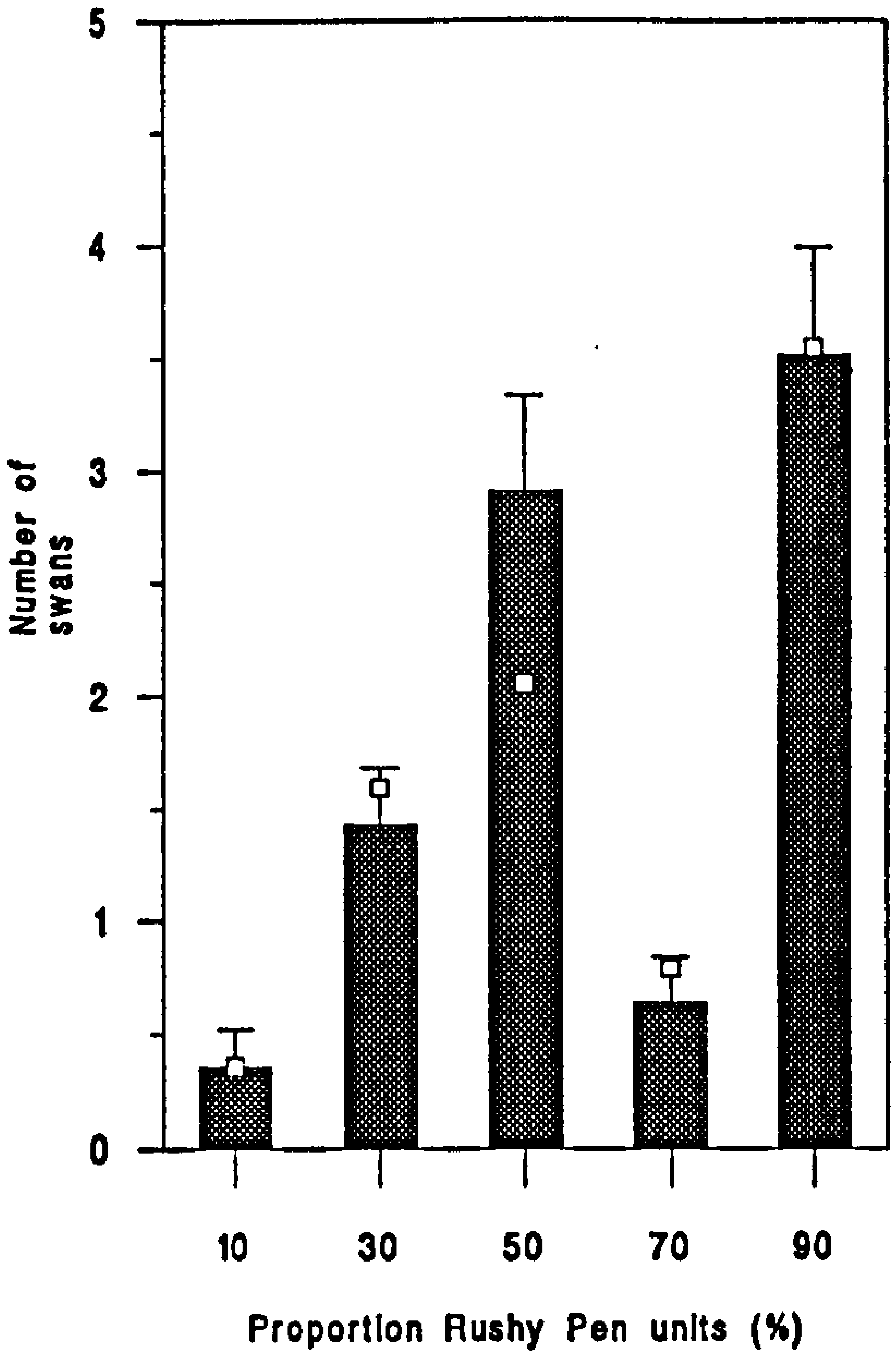


Fig. 5.42. The number of cygnets recorded feeding at the feeding sites with percentage water cover (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=228), plus predicted values from a generalised linear model.

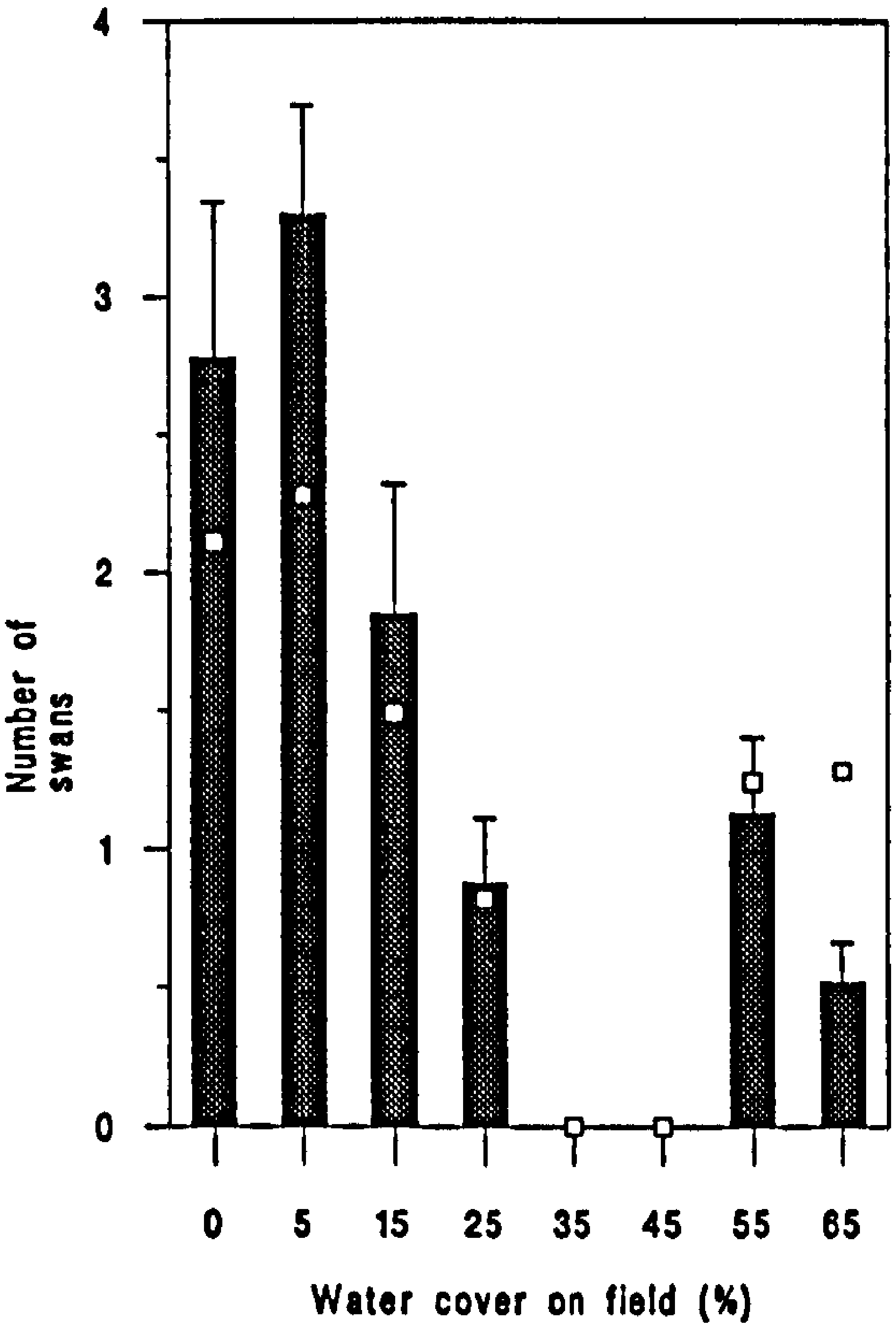


Fig. 5.43. The number of cygnets recorded resting at the feeding sites with biomass of sward (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=228), plus predicted values from a generalised linear model.

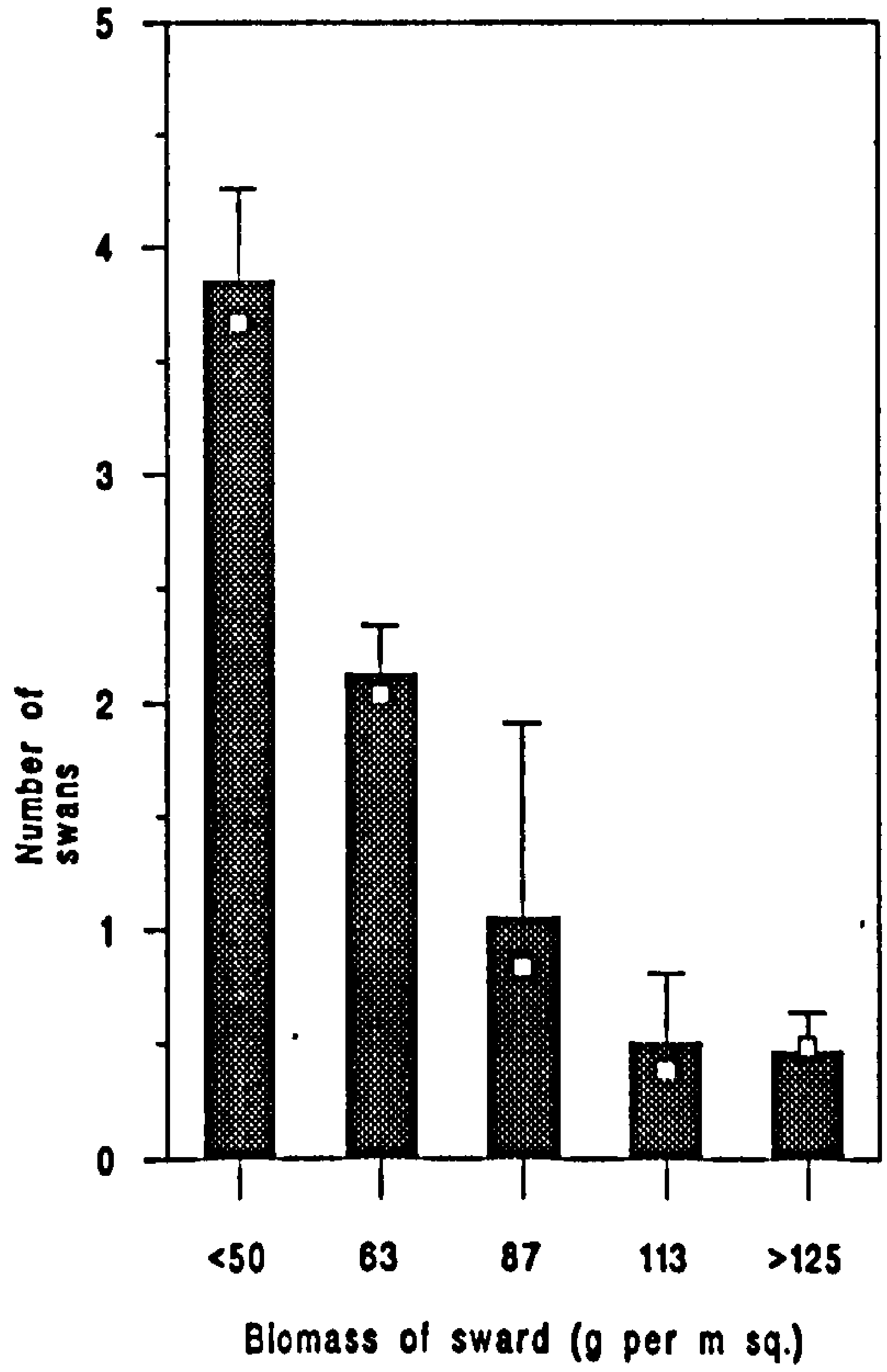


Fig. 5.44. The number of cygnets resting at the feeding sites with percentage water cover (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=228), plus predicted values from a generalised linear model.

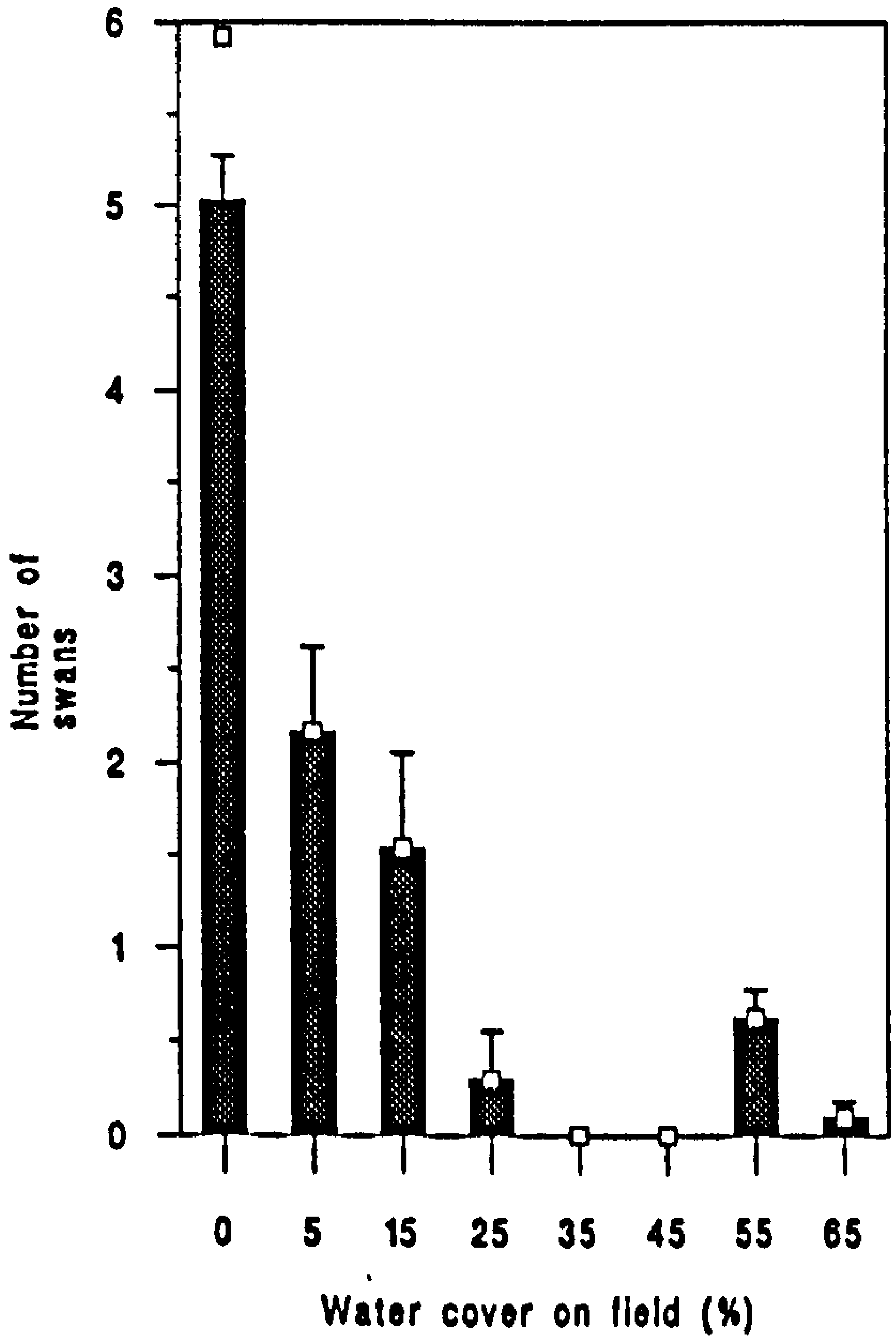


Fig. 5.45. The number of cygnets recorded in comfort activity at the feeding sites with flock size (mean per flock scan 1990-91 to 1992-93 winters combined and S.E. bar, n=228), plus predicted values from a generalised linear model.

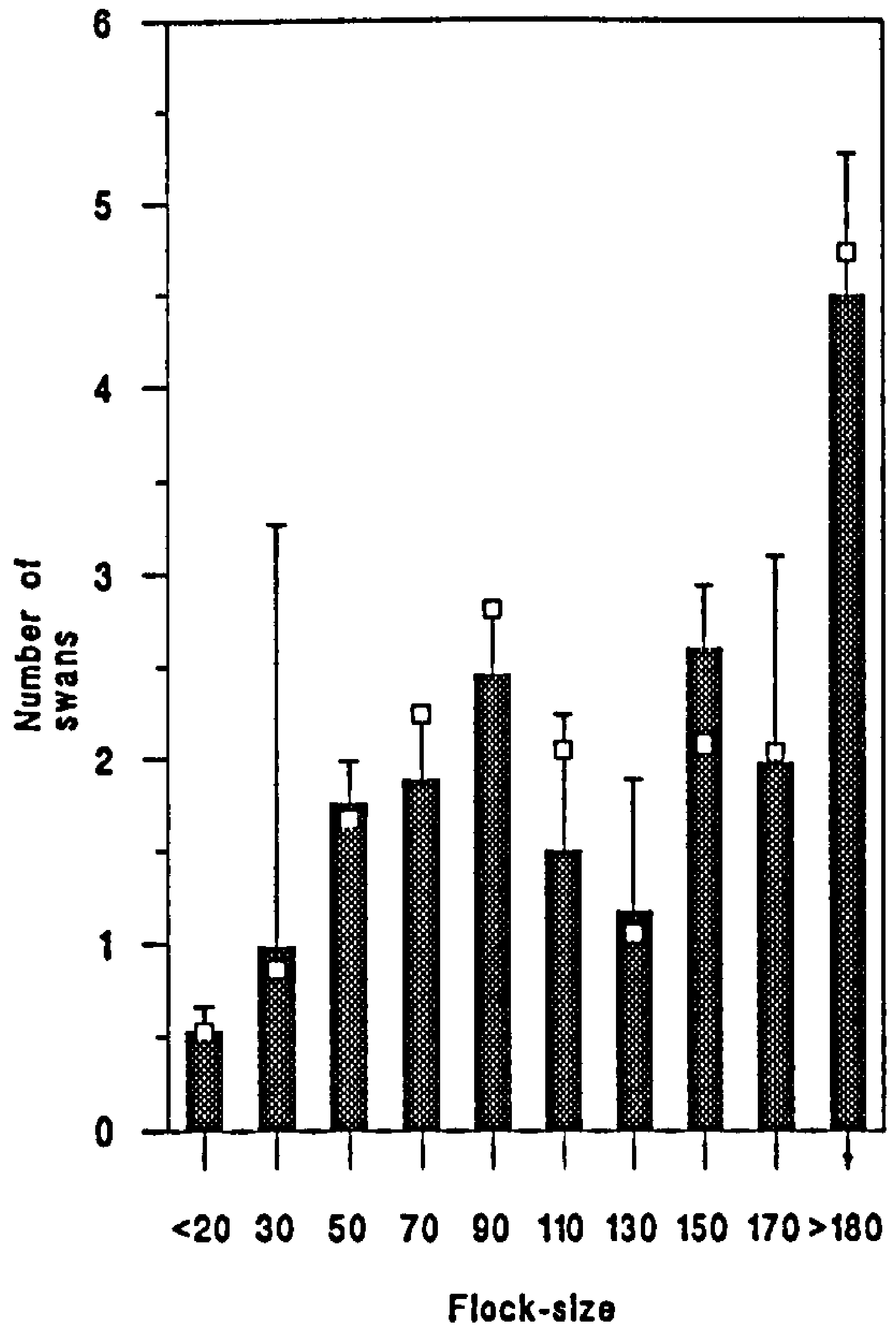


Fig. 5.46. The number of cygnets recorded in comfort activity at the feeding sites with percentage protein content of the sward (mean per flock scan 1990-91 to 1992-93 winters combined & S.E.bar,n=228),plus predicted values from a generalised linear model.

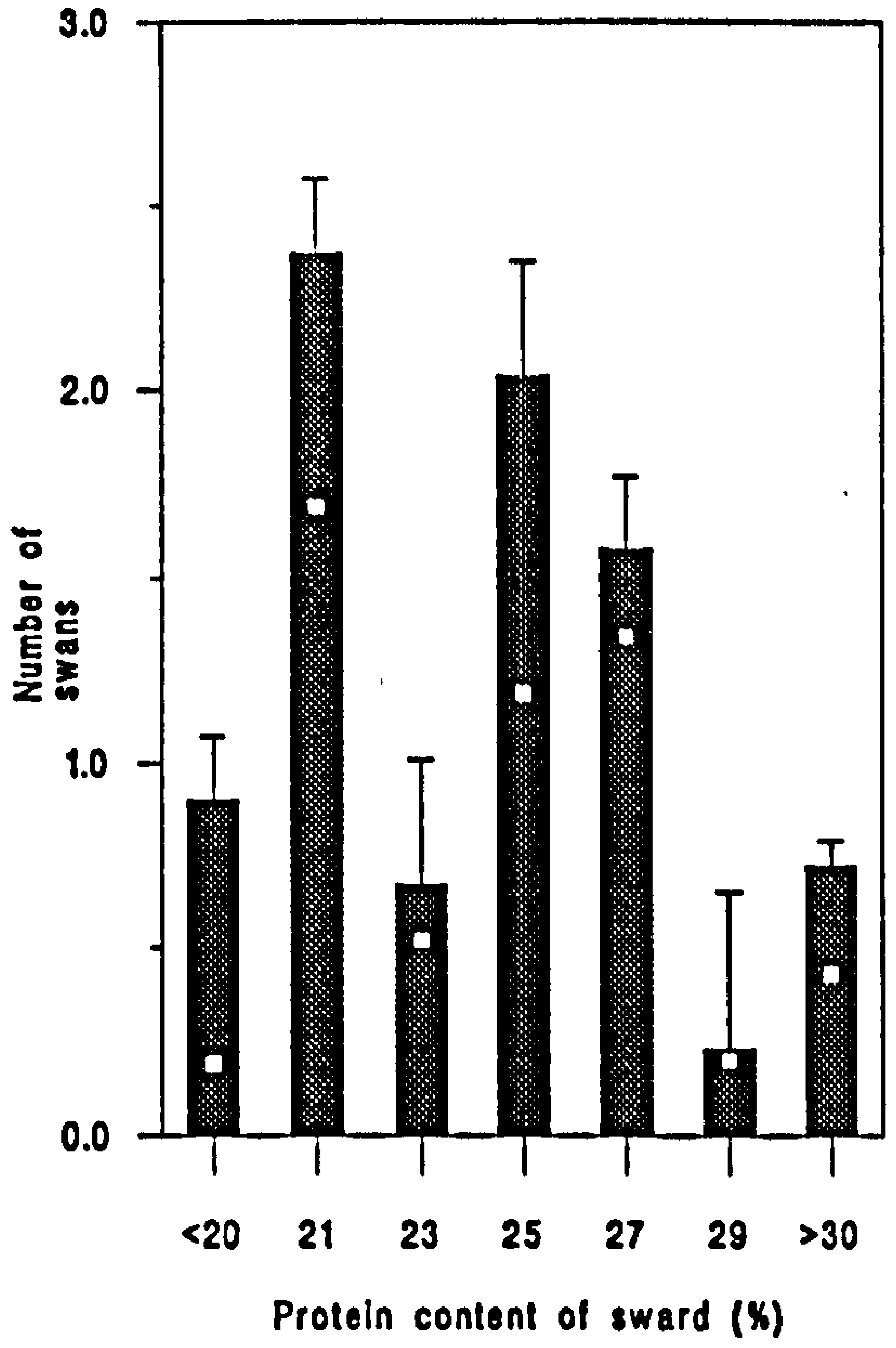


Fig. 5.47. The number of cygnets recorded in alert activity at the feeding sites with percentage protein content of the sward (mean per flock scan 1990-91 to 1992-93 winters combined & S.E.bar, n=228), plus predicted values from a generalised linear model.

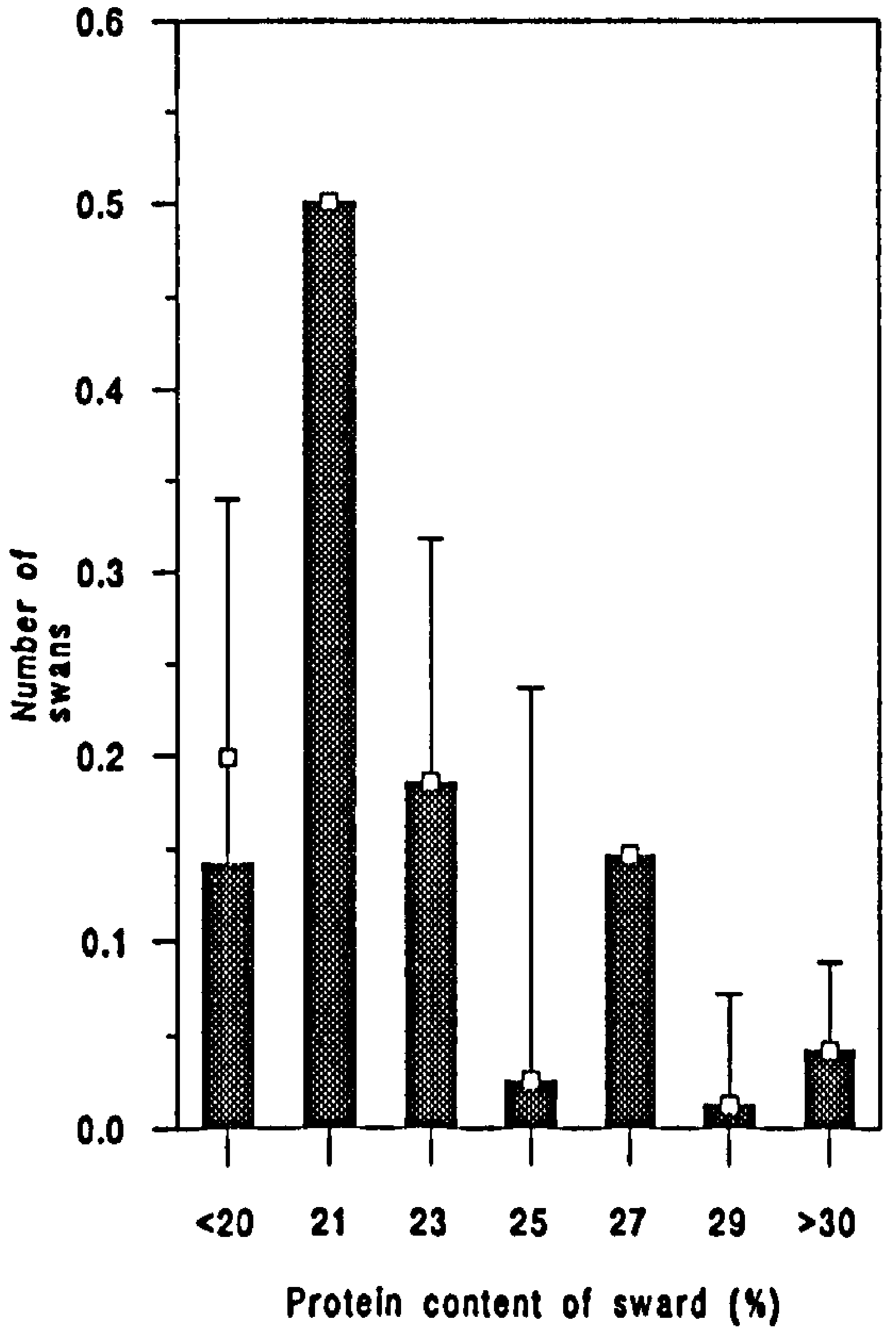


Fig. 5.48. Number of cygnets alert at the feeding sites with the proportion of swan units present from the Rushy Pen roost (mean per flock scan 1990-91 to 1992-93 winters combined & S.E.bar,n=228), plus predicted values from a generalised linear model.

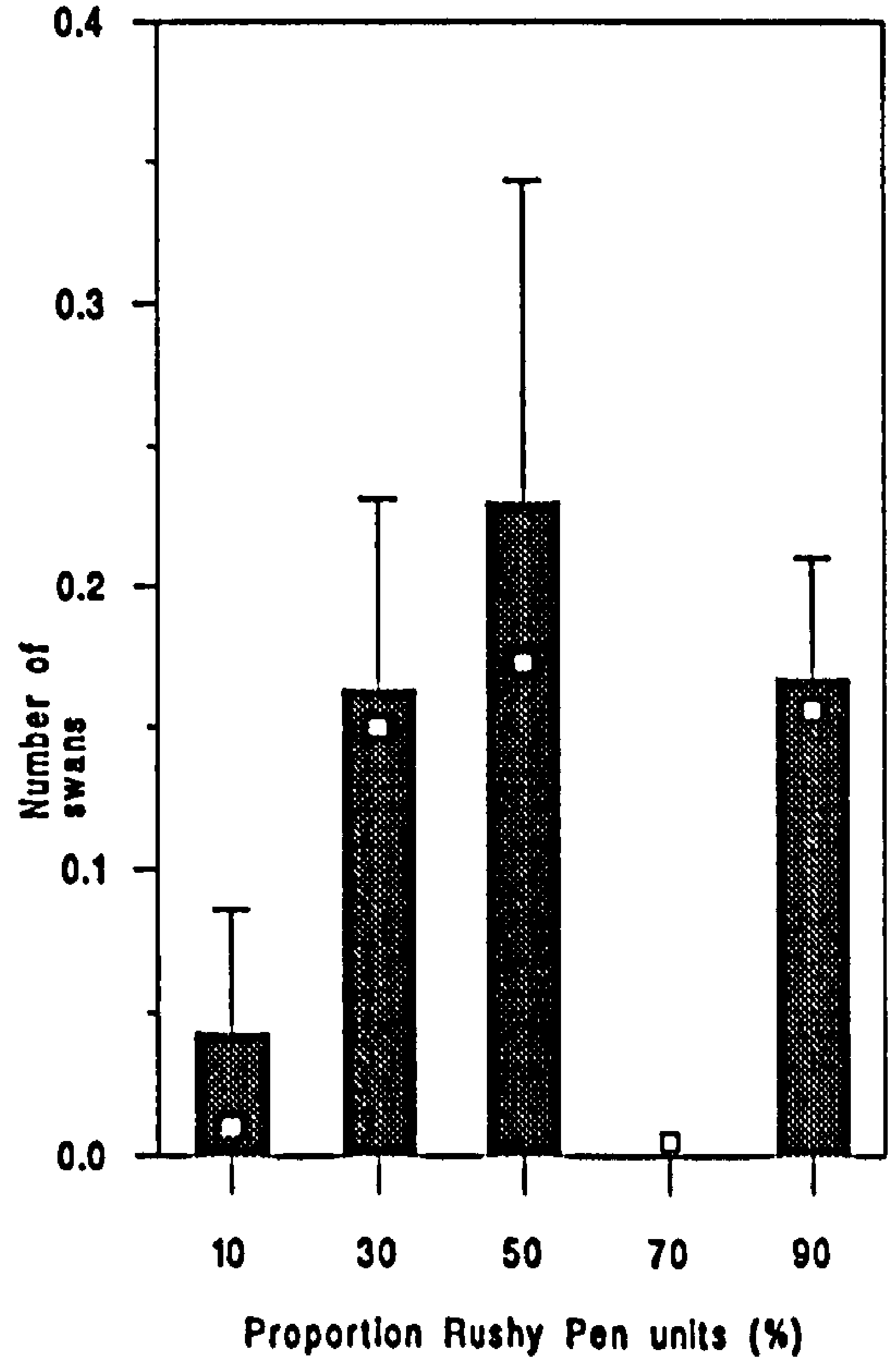


Fig. 5.49. Number of cygnets recorded in social interaction at the feeding sites with percentage protein content of the sward (mean per flock scan 1990-91 to 1992-93 winters combined & S.E. bar,n=228), plus predicted values from a generalised linear model.

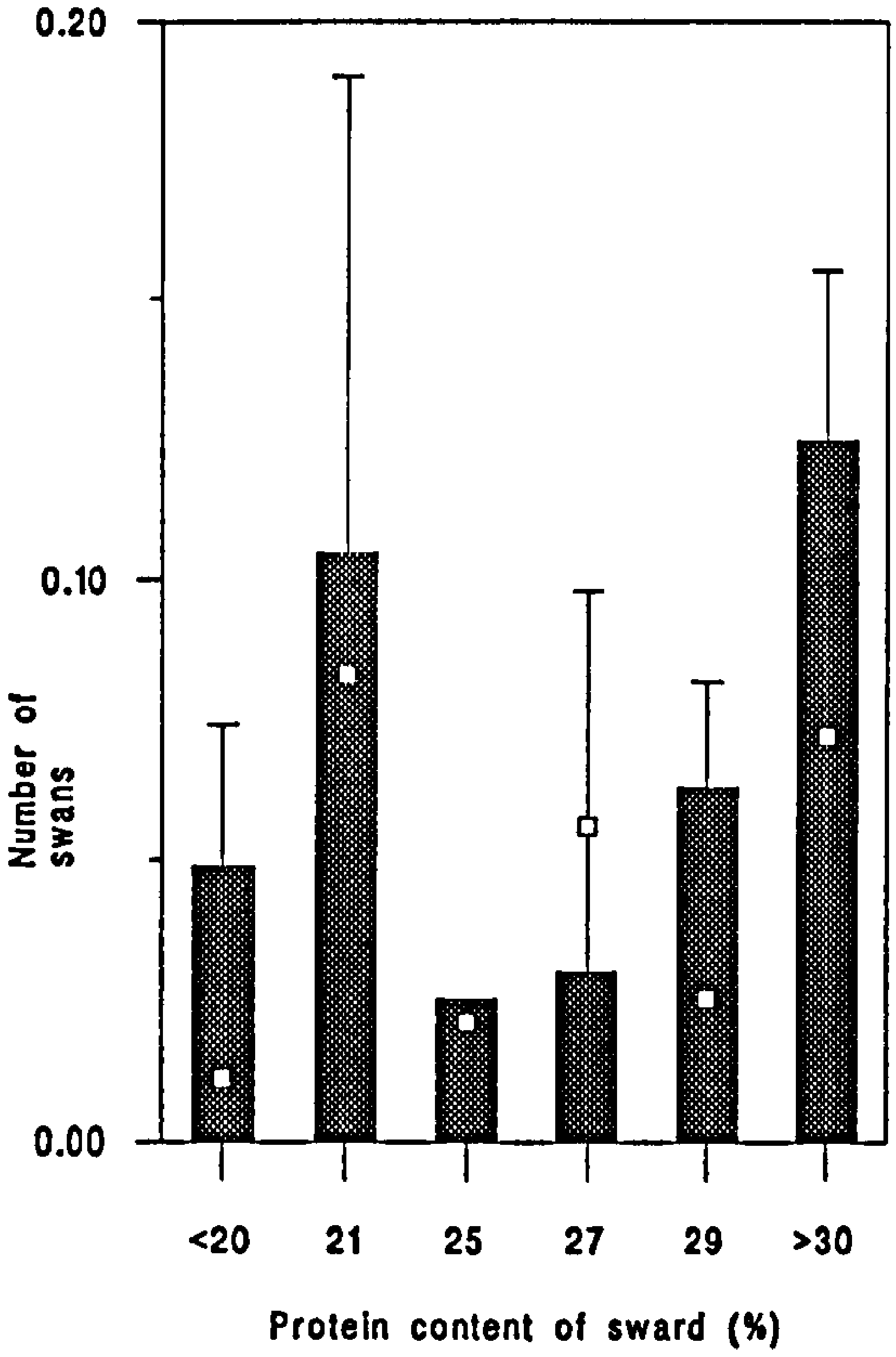


Fig. 5.50. The number of cygnets in social interaction with the proportion of swan units present from the Rushy Pen roost (mean per flock scan 1990-91 to 1992-93 winters combined & S.E.bar, n=228), plus predicted values from a generalised linear model.

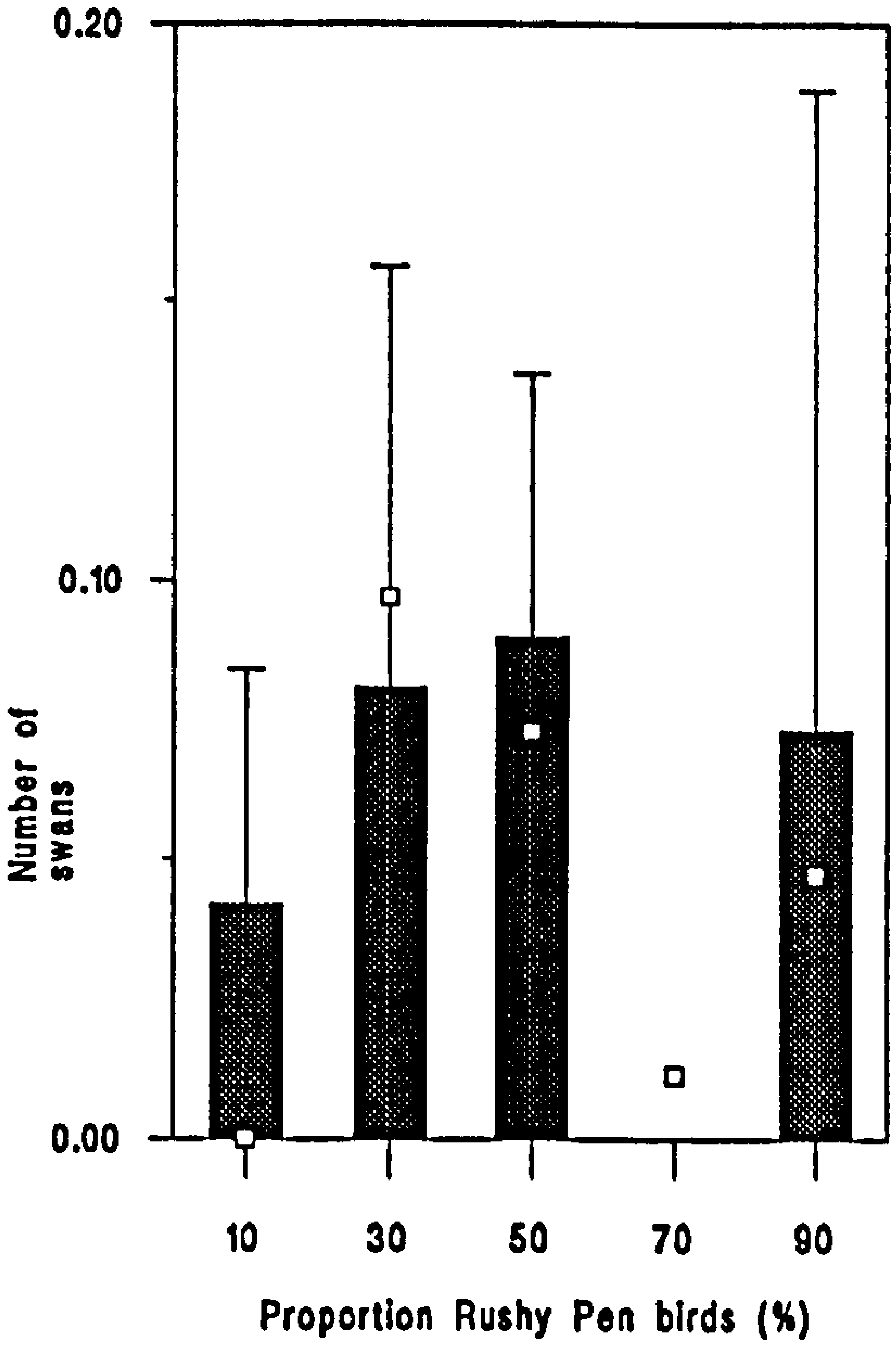
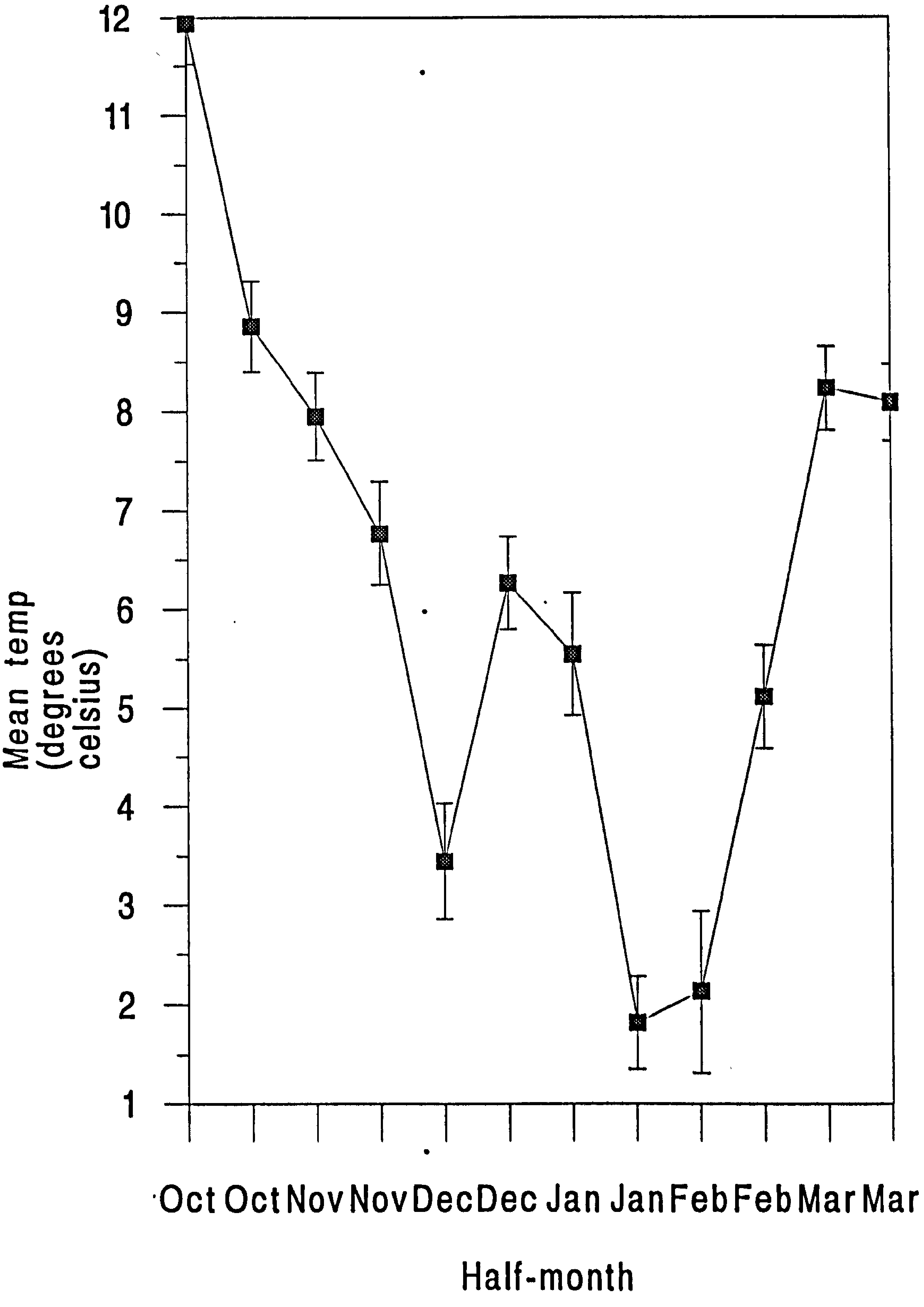


Fig. 5.51. Daily mean temperatures (and S.E. bar) recorded at the Slimbridge meteorological station by half-month for the 1990-91 to 1992-93 winters combined. N.B. daily mean = (daily max - daily min)/2, n = 422, data not complete for all half-months.



CHAPTER 6 FORAGING PERFORMANCE OF INDIVIDUAL SWANS

6.1 INTRODUCTION

Having established reasons for the observed distribution of swans at the feeding sites (Chapter 4) and the swans' activity patterns at those sites (Chapter 5), this chapter aims to investigate the foraging performance employed by individual swans. According to the ideal free distribution theory (Fretwell & Lucas 1970) individuals should distribute themselves around patches of a particular resource such that each receives equal benefit. At low population densities individuals should exploit the best quality patches of the resource, but as the population density increases on a patch, the gain in resources to each individual should decrease to a point at which lower quality patches may become equally attractive. The theory assumes that individuals should move if they can achieve greater benefits elsewhere, so that each experiences the same level of benefit. Individuals may differ in competitive ability however, so that low-ranking individuals may suffer from strong competition from high-ranking individuals at the best patches and may move to poorer patches (Sutherland & Parker 1985).

Monaghan (1980) for example, showed that amongst Herring Gulls Larus argentatus, dominant adult males tended to use the higher quality feeding sites, where they had higher feeding rates, whilst less dominant adult female and immature gulls changed their feeding sites more frequently and tended to use secondary feeding sites. Similarly, Bautista et al. (1995) showed that the average daily food intake of Common Cranes was positively correlated with both the quality of the foraging zone and the dominance rank of the bird, and that dominant cranes tended to feed in zones with highest food densities, although both dominant and subordinate birds occurred in all foraging zones. Harper (1982), showed that the distribution of Mallards between food patches was influenced by the distribution of despotic individuals whose behaviour resulted in unequal pay-offs between individual ducks. He suggested that the frequency of supply of food items was used initially by the ducks to assess the profitability of a patch but that over a longer time scale, other cues such as the avoidance of damaging fights could also be used. Milinski et al. (1995) demonstrated experimentally amongst Mute Swans Cygnus olor that adult birds were more successful than sub-adults in obtaining food at a patch in which much food was provided in a small area ('clumped') but were similarly successful at a patch where food was scattered over a wider area. When given the option of both a clumped and a scattered patch, sub-adult swans preferred the scattered patch whilst adults tended to prefer the clumped patch, and the two age-classes showed partial separation in their distribution. Foraging success of dominant individuals, may not always improve when food is clumped. Amongst wild Brown Hares Lepus europaeus for example, dominants attempt to monopolise small defendable food patches. However as group size increases on a clumped food resource, there are more aggressive encounters and feeding rates decline, such that when more than two hares are present, all individuals perform less well than when food is more evenly spaced (Monaghan & Metcalfe 1985). The selective advantages of living in a group (e.g. increased protection from predators and increased likelihood of finding food) must be weighed against the costs (e.g. increased conspicuousness to predators and competition for food) such that group size may reflect a compromise between the selective advantages and costs of group size (Pulliam & Caraco 1984, Krebs & Davies 1987). In addition, since individuals in a group may attain different pay-offs and have different optima, group sizes which are a compromise between the optima for different individuals may not be optimal for any one individual, whilst optimal-sized groups may be unstable because they tend to be joined by individuals from smaller groups (Krebs & Davies 1987).

Prop & Loonen (1988) showed that, in grazing Brent Geese, the first birds to arrive at a plot of vegetation had a higher intake rate and made a different selection from the plants available than birds further back in the flock. Differences between 'early' and 'late' individuals in their intake rate and diet may relate directly to their subsequent body condition (Prop & Loonen 1988), to the extent that individuals at the rear end of a Brent Goose flock at a spring staging area had a much lower probability of returning with offspring the next autumn, than those at the front of the flock (Teunissen et al. 1985). The latter finding may reflect the distribution of birds of different social rank within the flock; in Barnacle Geese, the dominant families tend to occupy and actively monopolize, the leading edge of foraging flocks (Black & Owen 1989, Black et al. 1992). Since the green biomass of vegetation was highest at the leading edge of a flock, the families secured access to the best resources whilst less dominant birds further back in the flock fed on an already depleted sward. In addition, birds on the edge of the flock pecked faster and gained more food per peck as a result of the higher biomass.

Wintering flocks of diving ducks often show a great disparity in sex ratio with males of some species predominating in the northern parts of their winter ranges (e.g. Owen & Dix 1986). Males are thought to dominate and exclude females from limited food resources, forcing the females to migrate further south (see Sutherland & Parker 1985, for discussion). Choudhury & Black (1991) demonstrated that male Common Pochard Aythya ferina dominated females under manipulated feeding conditions to the extent that females would only feed after the requirements of the males were fulfilled. Given their reduced foraging opportunities, the subordinate females might be expected to move on to alternative feeding sites where competition from males may be less. However, amongst low-ranking birds, the benefits of being in a large flock containing more dominant individuals (e.g. reduced predation risk or increased group vigilance, Bustnes 1993) may outweigh the costs of poorer quality foraging, and movement to another site may only be profitable at times of low food availability. Duration and timing of low food availability may also influence the decision to move on. For example, Greenland White-fronted Geese feeding on semi-natural grassland lost condition rapidly following periods of freezing weather in January, when they were temporarily unable to probe for roots and stolons (Mayes 1991). However, instead of moving to improved/arable farmland where other individuals of the same species were buffered against loss of condition by the presence of highly digestible root crops and stubble grains, the birds remained on the semi-natural grassland and regained condition as temperatures and day-length increased in February and March.

Depletion of the food supply has been shown to be a relevant problem in optimal-foraging theory in investigations of time spent by an individual in a habitat patch in many studies of herbivorous wildfowl including Barnacle Geese (e.g. Drent & Swierstra 1977, Black & Owen 1989, Owen et al. 1992), Brent Geese (Prop & Loonen 1988), White-fronted Geese (Owen 1971 & 1972a, Mayes 1991), Bean Geese (Sutherland & Allport 1994), Greylag Geese (Amat 1986a,b), Eurasian Wigeon (Mayhew & Houston 1989) and Bewick's Swans (Rees 1990 and results of this study), particularly during the winter when grass growth may be restricted by cold temperatures. In the current study, the swans attempted to compensate for declining food stocks in February by feeding more frequently (Chapter 5).

This chapter investigates the foraging activities of individual swans at the feeding sites in an attempt to answer the following questions:

1) Do males and females differ in foraging performance at the feeding sites. Males with a mate and/or cygnets, may be more vigilant than females and spend more time in aggressive interactions in order to reduced intra-specific feeding competition for their families, and consequently spend less time feeding themselves (Scott 1980c, Mayhew 1987, Sedinger & Raveling 1990, Johnson & Sibly 1990, Williams et al. 1994, Sedinger et al. 1995).

2) Do social class and dominance rank affect foraging performance. Swans from the high-

ranking family class for example, might be expected to have higher foraging efficiency than low-ranking singletons by monopolizing the best food resources (Black et al. 1992, Bautista et al. 1995).

3) Do foraging routines vary during the course of the day. Does the provision of high quality food at the roost sites preclude the need for a peak in feeding rate on the fields prior to departure for the roost which has been observed in Greater White-fronted Geese at Slimbridge (Owen 1972a).

4) How does flock size affect foraging performance. Are the effects positive, for example through increased group vigilance (Pulliam 1973), or negative through increased intra-specific competition for food (Lazarus & Inglis 1978).

5) Do swans from the two roost groups differ in foraging performance at the field feeding sites, and if so, how does this difference relate to the amount of grain they receive at the roost sites.

6) How does the foraging performance of individual swans vary throughout the winter period and do individuals differ in their response to changes in the quantity and quality of the food supply. Do males for example, spend more time protecting their family from intra-specific foraging competition when food supply is low and/or of low quality, and less time when food is abundant and/or of high quality.

6.2 METHODS

a) Monitoring foraging ecology

Simultaneous monitoring of two or more members of a swan unit proved to be problematic in the field and instead, three methods were used to assess the foraging patterns of individual swans:

i) Focal bird scans

The foraging patterns of individual swans, identified by bill pattern or leg ring at the feeding sites, were monitored to investigate differences in the individuals' feeding activity in relation to changes in the quantity and quality of the food supply. Five minute activity scans were conducted of actively feeding birds, selected at random (first actively feeding bird encountered) from within the flock. Scans were made during the day of swans using fields in the Slimbridge area, and also at Walmore Common when there were birds present, in each year of the study (1990-91 to 1992-93 winters inclusive). Each focal bird was observed continuously, usually for five minutes, and its activities dictated to a tape-recorder. Activities were placed into the same seven categories as used in Chapter 5: Feeding, Resting, Comfort, Vigilance, Movement, Social Interaction (mostly aggressive encounters) and Drinking. A typical scan of foraging behaviour included bouts of food ingestion (feeding) interspersed by generally much shorter periods of movement (between food patches), vigilance, drinking, social interaction, comfort and rest. Scans of birds which stopped feeding within three minutes and became engaged in a lengthy bout of rest or comfort activity, or were interrupted by disturbance to the flock, were removed from analysis. For scans in which the bird stopped feeding during the last two minutes, the first part of the scan (i.e. the feeding behaviour) was retained for analysis. No individuals were selected more than once on a field in an hour, to reduce pseudoreplication (Hurlbert 1984). Scans were not made during extremely wet or windy weather conditions, thus controlling for any effect of severe weather upon the foraging behaviour of the swans.

Each scan was timed using a stop-watch. The data collected on audio-tape were subsequently transcribed using the EVENT4.BAS (basic) event recorder programme written by Carl Mitchell (WWT). This programme translated the activity patterns into a character code, and summed the length of time that each activity occurred during the scan. The resultant figures were adjusted by the factor LS/LE, where LS = true length of scan (secs) and LE = length of event recorder scan (secs), since the cassette recorder did not always record at a standard speed (depending on the age of the batteries).

ii) Peck rates

The peck rates of individually-recognised swans grazing on grass swards were investigated in order to compare individual foraging performance. Peck rate was calculated by recording the length of time taken to achieve fifty pecks of grass by a swan selected at random (see Owen 1972a). The data were then expressed as pecks per unit time. Pecks per five seconds were used for analysis, rather than pecks per minute as used by Owen (1972a), since many scans lasted for less than one minute. Times were recorded to the nearest second with a stop-watch. In addition, for each scan, the number and duration of 'head-up' watchful periods were recorded on a second stop-watch, together with the number of steps taken to achieve the fifty pecks. Up to five samples were taken for an individual per hour on a field and means were then calculated for each 60 minute sampling period, per bird, per field, in order to reduce the problem of pseudoreplication (Hurlbert 1984). Peck rate samples which were interrupted by a disturbance event were not included in the analysis. In addition, no samples were collected during extremely wet or windy conditions. Ringed cygnets were chosen for study in preference to unringed cygnets, since cygnets could not be sexed in the field.

iii) Grain feeds

The use made by swans of the supplementary feeds of grain at the roost-sites was investigated in order to compare the relative intake rates of birds of differing competitive ability. This was monitored by following the activities of individually-recognised birds during the distribution of grain at the late afternoon and early evening feeds (16.00-18.30 hrs). The swans typically arrived on the pens prior to the feeds and waited at the back or centre of the pen for the feeder to arrive. The feeders distributed grain along the 'near' edges of the pens and the swans followed in behind as the grain was dispersed. Feeding bouts were intense but brief, and the swans generally returned to the centre or back of the pen, to preen, bathe and drink, upon completion of a feeding bout. Following an individual swan through the feed was therefore feasible, although the rapid movement of birds through the feeding melee frequently resulted in the focal bird being lost from view and termination of the scan. Around one scan in three was carried through to completion. It was not possible to monitor the number of individual items of grain ingested by the birds as demonstrated amongst Whooper Swans Cygnus cygnus at Caerlaverock by Black (1988), since the grain for the swans was distributed in the shallow but murky margins of the collection pools (>0.5 m deep). Instead, for each focal bird, the number and duration of head-under periods in the areas receiving grain were recorded during the grain distribution, in order to provide a comparative estimate of the amount of grain consumed by individuals. In addition the total length of time that the bird spent in the feeding areas was recorded together with the number of times that the focal bird i) attacked other swans and ii) was attacked by other swans. Data concerning the number of scoops of grain thrown into the pens by the feeders were collected, both in the individual pools of the Grounds roost (see Fig 1.1) and in the Rushy Pen, where more detailed data were collected on grain distribution in the four separate feeding areas of the main pool (see Fig. 6.54). The foraging time spent by individuals in each feeding area was corrected for by the known density of grain in order to make the results from different areas more directly comparable (as in Black 1988).

b) Statistical analyses

The effect of the independent variables in influencing the foraging patterns of the swans was determined by co-variate analysis using GLIM (NAG 1986). Co-variate analysis was chosen in order to identify explanatory variables with a significant effect, from a number of variables which were thought likely to be inter-correlated. Ten variables were examined initially in relation to foraging activity in each of the three data sets, since it was thought that they might explain variation in the activity data: sex, social class, dominance rank, abdominal profile, roost-group, year, half-month, hour, flock-size, and feeding site (field identity for the focal bird scans and peck rates, roosting pen for the grain feeds). The two sexes were investigated separately since initial inspection of the data suggested differences in foraging activity between males and females. Social class, roost-group, year and feeding site were treated as factors. For the focal bird (five-minute scan data) a binomial error distribution was used in which the amount of time (secs) spent by an individual in a particular activity was divided by the total length of the scan (the binomial denominator). This distribution was used since both the amount of time engaged, and not engaged, in a given activity by an individual were known in each case. By not using the percentage activity as the response variable, information concerning the size of the sample could be retained. Over-dispersion of the data was compensated for, as previously, by the use of the WILLS.MAC programme (Crawley 1993, see Chapter 4). For both the peck rate and the focal grain feed data-sets a normal error distribution was used since the data distributions for both sexes were approximately normal.

The number of combined effects entered into the initial model in each case, was reduced by first determining which of the ten variables were significant. Variables proving to be significant or near-significant were investigated further in the main model together with their interaction terms. The statistical significance of the explanatory variables and their interactions, was then determined by fitting the full model and inspecting the changes in deviance with respect to the change in the degrees of freedom. The most non-significant ($P > 0.05$) variables were then progressively removed from the model. The final model was thus the most parsimonious (see Crawley 1993).

Since field identity, was found to be a significant factor in all ten of the initial models involving the focal five-minute scan data (Tables 6.2 to 6.5), the influence of field identity upon activity patterns was investigated further. This inter-field variation was investigated further by substituting the categorical variable used to describe each field with the habitat variables recorded in the same fields during the 1991-92 and 1992-93 winter seasons (for methods see Chapter 4) in terms of: i) food quantity i.e. mean sward-length (mm) and biomass of the grass sward (g per m^2), ii) food quality i.e. protein content of the grass (%) and iii) water cover on the field (%), in order to investigate their effect upon the foraging activities of the swans. The variables sex, social class, dominance rank, abdominal profile, roost-group, flock-size, year and time of day were retained in the models, whilst the variable half-month was changed to month, since sward-length, biomass and protein content were collected only once a month. All variables were considered initially in the models and the most parsimonious models were derived as before. For the peck rate data, all variables including the detailed habitat variables (rather than field identity) were included in the initial model since it was assumed that the condition of the sward would have a significant effect upon foraging activity.

6.3 RESULTS

a) Focal bird scans

A total of 347 focal bird scans were conducted during the study period at 15 different feeding sites, involving 137 males, 133 females and 77 birds of unknown sex. A summary of the percentage frequency of activities observed for the swans during the focal scans are given in Table 6.1. During feeding bouts on the fields, birds spent on average 71.9% of their time actually feeding, 17.0% with the head up being watchful (including extreme head-up), 7.8% moving between feeding patches and 3.3% in other activities including comfort, social interactions, drinking and loafing. Females spent a significantly higher percentage of time actually feeding than males during the scans (Mann-Whitney U comparison, $W = 17212$, $P = 0.035$, $n = 137$ for males and $n = 133$ for females), and the two sexes were therefore treated separately in the subsequent analyses.

i) Initial model - excluding habitat variables

Feeding

Variation in the proportion of time that male swans spent feeding during focal scans at the feeding sites was associated with field identity and year only (Table 6.2). There was no significant interaction between these two variables. The proportion of time spent feeding by male swans feeding in the flocks was lowest in the 1990-91 winter and higher in the subsequent two winters.

Variation in the proportion of time that female swans spent feeding during focal scans at the feeding sites was associated with field identity, time (hour) and flock-size (Table 6.3). There were no significant interactions between any of these variables. The proportion of time spent feeding by female swans in the flocks during the day was rather variable (Fig. 6.1). There was evidence for peaks of feeding in the early morning, at midday and mid-afternoon although there was no clear overall trend. The proportion of time spent feeding by female swans generally tended to decrease as flock-size increased (Fig. 6.2) although the predicted values were rather variable. Fields with high proportions of feeding males and females included JBs field, Pylon B field and fields at Walmore Common, whilst fields with low proportions of feeding males and females included the Top New Piece, Pylon A field and the South Middle field (for location of fields see Figs 3.3 & 3.4).

Total head-up (including extreme head-up)

Variation in the proportion of time that male swans spent with their head up during focal scans at the feeding sites was associated with field identity and social class (Table 6.2). There was no significant interaction between these two variables, indicating that the observed variation between social classes did not vary significantly between fields. Amongst males, breeding adults spent proportionately the largest amount of time, and family cygnets (i.e. with parents), the smallest amount of time, with their heads up during feeding bouts (Fig. 6.3); paired adults, single adults, single yearlings and paired yearlings spent an intermediate proportion of their time with their heads up.

Variation in the proportion of time that female swans spent with their head up during focal scans at the feeding sites was associated with field identity, time (hour) and flock size (Table 6.3). There were no significant interactions between any of these variables. The proportion of time spent with head up by females tended to decrease during the day (Fig. 6.4) and to increase as flock size increased (Fig. 6.5).

Alert (extreme head up)

Variation in the proportion of time spent by male swans in alert activity during focal scans at the feeding sites was associated with field identity, year, social class and abdominal profile (Table 6.2). There were no significant interactions between any of these variables. Amongst males breeding adults spent proportionately the largest amount of time, and family cygnets (i.e. with parents), the smallest amount of time engaged in alert activity during feeding bouts (Fig. 6.6). Single yearlings spent a larger proportion of time than single adults in alert activity; paired adults and paired yearlings (probably siblings) spent an intermediate proportion of their time in alert activity (Fig. 6.6). The proportion of time spent in alert activity generally decreased as abdominal profile increased (Fig. 6.7). The proportion of time spent by male swans engaged in alert activity at the feeding sites was largest in the 1991-92 winter and smallest in the 1992-93 winter. This probably reflected differences in breeding success between years (lowest in 1992, see Table 4.2), since breeding males spent more time in alert activity than males from other social classes. There was no correlation between the proportion of time spent alert by male swans and the number of cygnets in their families (Spearman's rank correlation r_s = -0.269, $P > 0.1$, n = 22).

Variation in the proportion of time spent by female swans in alert activity during focal scans at the feeding sites was associated with field identity, time (hour), social class and dominance rank (Table 6.3). There were significant interactions between time of day, social class, field and dominance rank, indicating that the time of day was more important for some social classes than others, and that dominance rank was more important in some fields than in others. Amongst females, single yearlings spent proportionately the largest amount of time, and paired adults, the shortest amount of time engaged in alert activity during feeding bouts (Fig. 6.8). Breeding adults spent a larger proportion of time in alert activity than paired adults without cygnets; single adults, family cygnets and trio yearlings spent an intermediate proportion of their time in alert activity (Fig. 6.8). There was no correlation between the proportion of time spent alert by female swans and the number of cygnets in their families (Spearman's rank correlation $\underline{r}_s = 0.167$, $\underline{P} > 0.1$, $n = 28$). The proportion of time spent in alert activity by female swans generally increased during the day (Fig. 6.9), and decreased as dominance rank of the bird concerned increased (Fig. 6.10) although the latter relationship was less clear-cut. Fields with high proportions of both males and females in alert activity included the South Middle Field and the Seventeen Acre field, whilst those with low proportions engaged in alert activity included the Dumbles, the Tack Piece and the Pylon B field (for location of fields, see Fig. 3.4).

Movement

Variation in the proportion of time spent by male swans in active movement during focal scans at the feeding sites was associated with field identity and year only (Table 6.2). There was no significant interaction between these two variables. The proportion of time spent in active movement by male swans was highest during the 1990-91 winter and lowest during the 1992-93 winter.

Variation in the proportion of time spent by female swans in active movement during focal scans at the feeding sites was associated with field identity, time (hour), social class and dominance rank (Table 6.3). There were significant interactions between time of day, social class, field and dominance rank, indicating that the time of day was more important for some social classes than others, and that dominance rank was more important in some fields than in others. Amongst females, single yearlings spent the largest proportion of time, and paired adults the smallest proportion of time, in active movement during feeding bouts (Fig. 6.11); breeding adults, single adults, family cygnets and trio yearlings spent an intermediate proportion of time engaged in active movement. The proportion of time spent in active movement by female swans generally decreased during the course of the day although there was a distinct drop in the middle of the day (Fig. 6.12). The proportion of time spent in active movement also tended to decrease as the dominance rank of the bird concerned increased (Fig. 6.13).

Social interaction

Variation in the proportion of time spent by male swans in social interaction during focal scans at the feeding sites was associated with field identity, year, time (hour), social class, dominance rank and abdominal profile (Table 6.2). There were significant interactions between social class, dominance rank, time (hour), field and abdominal profile, indicating that both dominance rank and the time of day were more important amongst some social classes than others, and that abdominal profile was more important in some fields than in others. Amongst males, breeding adults spent the largest, and paired adults the smallest, amount of time in social interactions (Fig. 6.14); single adults, single and paired yearlings, and family cygnets spent an intermediate proportion of time engaged in social interactions. The proportion of time spent by male swans in social interaction at the feeding sites was extremely high upon arrival at the feeding sites in the morning and was much lower for the rest of the day, increasing again slightly in the late afternoon, prior to departure for the roosts (Fig. 6.15). The proportion of time spent by male swans in social interaction generally increased as abdominal profile increased (Fig. 6.16), and decreased as the dominance rank of the bird concerned increased (Fig. 6.17), although there was a peak amongst birds of moderately high dominance rank (0.60-0.79).

Variation in the proportion of time spent by female swans in social interaction during focal scans at the feeding sites was associated with field identity, year, social class, roost group and dominance rank (Table 6.3). There were significant interactions between social class, field, and dominance rank, indicating that both social class and dominance rank were more important in some fields than in others. Amongst females, single yearlings and family cygnets spent a larger proportion of time in social interaction than adults of all classes (Fig. 6.18). The proportion of time spent by female swans in social interaction generally increased as flock size increased (Fig 6.19), and was significantly higher for birds from the Rushy Pen roost than from the Grounds roost (Fig 6.20.). The proportion of time spent by female swans in social interaction at the feeding sites was lowest for birds of intermediate rank and was higher for both high and low ranking birds (Fig 6.21).

ii) Second model - habitat variables included

Detailed habitat data were only collected in the 1991-92 and 1992-93 winters; their inclusion led to a marked reduction in the degrees of freedom in each of the models considered and in many cases the loss of 'year' as a significant factor.

Feeding

Variation in the proportion of time that male swans spent feeding during focal scans at the feeding sites was associated with protein levels in the sward only (Table 6.4). Year was no longer associated with the proportion of time spent feeding by males when the habitat variables were also considered. The proportion of time spent feeding by male swans feeding in the flocks increased as protein levels increased in the sward (Fig. 6.22).

Variation in the proportion of time that female swans spent feeding during focal scans at the feeding sites was not associated with any of the habitat variables considered.

Total head-up (including extreme head-up)

Variation in the proportion of time that male swans spent with their head up during focal scans at the feeding sites was associated with protein levels in the sward only (Table 6.4). Social class was no longer associated with the proportion of time spent with the head up by males when the habitat variables were also considered. The proportion of time spent by male swans with their head up at the feeding sites tended to decrease as protein levels increased in the sward (Fig 6.23).

Variation in the proportion of time that female swans spent with their head up during focal scans at the feeding sites was not associated with any of the habitat variables considered.

Alert (extreme head up)

Variation in the proportion of time spent by male swans in alert activity during focal scans at the feeding sites was associated with protein levels in the sward only (Table 6.4). Year, social class and abdominal profile were no longer associated with the proportion of time spent alert by males when the habitat variables were also considered. The proportion of time spent in alert activity generally tended to decrease as protein levels increased in the sward (Fig. 6.24).

Variation in the proportion of time spent by female swans in alert activity during focal scans at the feeding sites was associated with time (hour) and protein levels in the sward (Table 6.5). Social class and dominance rank were no longer associated with the proportion of time spent alert by females when the habitat variables were also considered. There was a significant interaction between the time of day and the protein levels indicating that the time of day was more important at some protein levels than others. The proportion of time spent in alert activity by female swans tended to decrease as protein levels increased in the sward (Fig. 6.25).

Movement

Variation in the proportion of time spent by male swans in active movement during focal scans at the feeding sites was associated with protein levels in the sward only (Table 6.4). Year was no longer associated with the proportion of time spent in active movement by males when the habitat variables were also considered. The proportion of time spent in active movement by male swans tended to decrease as protein levels increased in the sward (Fig. 6.26).

Variation in the proportion of time spent by female swans in active movement during focal scans at the feeding sites was not associated with any of the habitat variables considered.

Social interaction

Variation in the proportion of time spent by both male and female swans in social interaction during focal scans at the feeding sites was not associated with any of the habitat variables considered.

b) Peck rates on grass swards

Peck rate data were collected during a total of 2669 scans at 19 different feeding sites. Means per individual bird, per hour, per field, per day were calculated giving rise to 1680 values which were retained for further analysis. These data pertained to 607 males, 686 females and 387 birds of unknown sex. A summary of the peck rate, step rate and head up time data for swans during the focal peck rate scans are given in Table 6.6. During grazing bouts on grass swards, birds pecked the grass on average 65 times a minute, walked 9.5 steps a minute and spent 5.8 secs per fifty pecks with the head up being watchful (including extreme head-up). Females generally had faster peck rates and slower step rates than males (Kruskal-Wallis Chi-sq. = 32.524 and 77.386 respectively, *P* < 0.001, df = 1 in both cases), and spent less time in head-up vigilance activity (Kruskal-Wallis Chi-sq. = 20.589, *P* < 0.001, df = 1). The two sexes were therefore treated separately in the subsequent analysis.

Peck rates

Variation in the peck rate of male swans during grazing bouts at the feeding sites was associated with social class, year, abdominal profile, flock size, the extent of flooding and mean sward-length (Table 6.7). There were significant interactions between year, abdominal profile, mean sward-length and the extent of flooding, indicating that abdominal profile was more important in some years than others, and that sward-length was more important under some flooding regimes than others. Amongst male swans, single adults and family cygnets had the fastest peck rates whilst trio yearlings and breeding adults had the lowest peck rates (Fig. 6.27); paired adults and single yearlings had intermediate to high peck rates. Mean male peck rates were higher in the 1992-93 winter than in the 1991-92 winter, and tended to increase with flock size (Fig. 6.28), although peck rates were slower amongst very large flocks (>250). Male peck rates generally increased as abdominal profile increased from AP score 2 to 5, although birds in the lowest AP category (1) had the fastest mean peck rate (Fig. 6.29). Male peck rates tended to decrease as sward-length increased (Fig. 6.30), and to increase as the extent of flooding increased (Fig. 6.31), although at higher levels of water cover (>10% of field) peck rate began to decrease.

Variation in the peck rate of female swans during grazing bouts at the feeding sites was associated with social class, year, flock size, the extent of flooding and mean sward-length (Table 6.8). There were significant interactions between flock size, mean sward-length, and the extent of flooding, indicating that sward-length was more important; a) at some flock sizes than others, and b) under some flooding regimes than others. Amongst female swans, family cygnets, paired adults and family yearlings had the fastest peck rates whilst lone yearlings had the slowest peck rate although differences between classes were less obvious than for the males (Fig. 6.32); single adults and breeding adults had intermediate peck rates. Mean female peck rate was faster in the 1992-93 winter than in the 1991-92 winter, and tended to increase with flock size (Fig. 6.33), although peck rate was slower amongst very large flocks (>250). Female peck rate generally increased as abdominal profile increased (Fig. 6.34). Female peck rate tended to decrease as sward-length increased (Fig. 6.35), although the rate increased again on fields with sward-lengths above 150 mm. In addition female peck rate tended to increase as the extent of flooding increased (Fig. 6.36), although as with the males, peck rate began to decrease at higher levels of water cover (>10% of field).

Variation in the amount of time spent by male swans with their head up during the time taken to achieve fifty pecks at the feeding sites was associated with social class, month, flock size, the extent of flooding and mean biomass of the sward (Table 6.7). There were significant interactions between month, flock size, and the extent of flooding, indicating that both flock size and the extent of flooding were more important in some months than in others. Amongst male swans, breeding adults and family yearlings (i.e. yearlings associating with their parents) spent the most time with their heads up during feeding bouts (Fig. 6.37); paired adults spent an intermediate amount of time with their heads up, whilst single adults, trio, paired and single yearlings, and family cygnets spent the least time with their heads up during the time taken to achieve fifty pecks (Fig. 6.37). Time spent with the head up during feeding bouts by male swans was high during the early and late winter periods, and lowest in mid-winter during the months of December and January (Fig. 6.38). Time spent with the head up by male swans during feeding bouts generally decreased as flock size increased, except amongst very large flocks (>200) when it increased again (Fig. 6.39). In addition, time spent with the head up by male swans during feeding bouts tended to increase as mean biomass of the sward increased (Fig. 6.40), and to vary rather irregularly with the extent of flooding (Fig. 6.41); at first increasing (up to 3% water cover) and then decreasing.

Variation in the amount of time spent by female swans with their head up during the time taken to achieve fifty pecks at the feeding sites was associated with social class, the extent of flooding and mean sward-length (Table 6.8). There were no significant interactions between any of these three variables. Amongst female swans, single cygnets (i.e. without parents), breeding adults and single yearlings spent the most time, and family cygnets and paired adults spent the least time, with their heads up during the time taken to achieve fifty pecks (Fig. 6.42); single, family and trio yearlings spent an intermediate amount of time with their heads up during feeding bouts. Time spent with the head up during feeding bouts by female swans tended to decrease as mean sward-length increased, although the predicted values from the model did show this pattern (Fig 6.43), and to vary rather irregularly with the extent of flooding (Fig. 6.44); at first increasing (up to 4% water cover) and then decreasing.

Variation in the step rate of male swans during grazing bouts at the feeding sites was associated with social class, roost group, abdominal profile and the extent of flooding (Table 6.7). There was a significant interaction between roost group and the extent of flooding. Amongst male swans, yearlings in general had the fastest step rates, whilst family cygnets had the slowest step rate (Fig. 6.45); breeding, paired and single adults all had similar intermediate step rates. Males from the two main roost groups (the Rushy Pen and Grounds) had a slower step rate than males from the third group of birds using alternative roost sites (see Chapter 3) (Fig. 6.46). Male step rate tended to decrease as abdominal profile increased (Fig. 6.47), and to decrease as the extent of flooding increased (Fig. 6.48).

Variation in the step rate of female swans during grazing bouts at the feeding sites was associated with social class, roost group, abdominal profile, percentage water cover of the field and mean sward-length (Table 6.8). There were significant interactions between social class, roost group, the extent of flooding and mean sward-length, indicating that sward-length was more important: a) under some flooding regimes than others (there was some evidence to suggest that flooding may have had an enhancing effect on sward-length since the two were weakly correlated, Spearman's rank correlation, $r_s = 0.145$, $P < 0.2$, $n = 81$) and b) for some social classes than others, and that the extent of flooding was more important for swans from some roost groups than from others. Amongst female swans, trio and single yearlings had the fastest step rates, whilst family yearlings and breeding adults had the slowest step rates (Fig. 6.49); paired and single adults, single yearlings and family cygnets had intermediate step rates. Females from the two main roost groups (the Rushy Pen and Grounds) had a slower step rate than females from the third roost group using alternative roost sites (see Chapter 3) (Fig. 6.50). Female step rate tended to decrease as abdominal profile increased (Fig. 6.51). In addition female step rate tended to increase as mean sward-length increased (Fig. 6.52), and to increase as the extent of flooding increased (Fig. 6.53).

c) Grain feeds

A total of 77 focal birds were followed through the grain feed during the study period. On average, each bird spent 518 seconds at the feed of which 157 seconds (30.3%) were spent actually searching for food or feeding, with the head under water. In the Rushy Pen the swans generally followed the feeder closely, feeding in most/all of the feeding sites just after the grain had been distributed and leaving shortly afterwards to preen at the back of the pen. The average number of head-under bouts per bird during a feed was 26.7 and the average length of a head-under bout was 6.0 seconds. Swans were attacked on average 2.47 times during a feed and initiated attacks on average 1.45 times.

Densities of grain (scoops per metre of pool frontage) distributed at the feeds was found to be broadly similar both between the Rushy Pen and pens in the Grounds and within the Rushy Pen (Table 6.9). Only the 'kitchen' section of the Rushy Pen had a markedly lower grain density (see Fig 6.54) and data concerning time spent by swans feeding in this area was multiplied by a correction factor of 2/3 in order to make it more directly comparable (in terms of potential ingestion rates of grain) with the other areas.

Variation in the corrected amount of time spent feeding head-under during the distribution of grain by male swans was associated with flock size only (Table 6.10). The amount of time spent feeding by male swans during the grain feeds increased as flock size decreased (Fig. 6.55).

Variation in the corrected amount of time spent feeding head-under during the distribution of grain by female swans was associated with dominance rank only (Table 6.10). The amount of time spent feeding by female swans during the grain feeds increased as the dominance rank of the swan unit increased (Fig. 6.56).

Although sample sizes were generally too small to permit meaningful analysis, the behaviour of individuals at the swan feeds varied considerably between social class, within the two sexes (see Figs. 6.57 - 6.60). Amongst adult males, time spent feeding at the feeds was highest for singletons and lowest for breeding birds although not significantly so (Mann-Whitney U test, $\underline{W} = 85.0$, $\underline{P} < 0.7$, n = 10, 7 respectively) whilst amongst adult females, time spent feeding was lowest for singletons and highest for breeding birds ($\underline{W} = 71.0$, $\underline{P} < 0.1$, n = 7, 8 respectively, see Fig. 6.57). The mean length of a head-under bout for both adult males and females, was longest for breeding birds and shortest for singletons ($W = 95.0$, $P < 0.7$, $n = 10, 7$ respectively for males and $W = 74.0$, $P < 0.05$, $n = 7, 8$ respectively for females, see Fig. 6.58). Aggression during the feed was initiated mostly by males and was more frequently initiated by parents than by singletons (Fig. 6.59). Amongst both males and females, singletons were the most frequently attacked group during the feed, whilst breeding birds were the least frequently attacked (Fig. 6.60). Cygnets had the longest mean head-under bouts and similarly spent a long time feeding during the grain feeds (Figs. 6.57 & 6.58). Yearlings spent less time feeding at the grain feeds than all classes except single adult females and similarly had a short mean head-under bout time (Figs. 6.57 & 6.58). In addition single yearlings were the most frequently attacked class during the feed and they rarely initiated attacks (Figs. 6.59 & 6.60).

6.4 DISCUSSION

Foraging patterns of individual swans varied significantly at the feeding sites and were influenced by a range of interacting variables. There were significant differences between the sexes; males generally spent less time actually feeding during 'feeding bouts' than females and had a slower peck rate, a faster step rate and spent more time with their head up being vigilant and initiating attacks upon conspecifics. These findings are consistent with those of other studies of grazing Anatidae. Mayhew (1987) for example, showed that amongst grazing flocks of Eurasian Wigeon in winter, males were generally more vigilant than females. Johnson & Sibly (1990) showed that in Canada Goose pairs feeding in flocks prior to nesting, males spent less time feeding than females, and more time in vigilance and aggressive encounters. Similarly during the post-hatching period, both Cackling Geese Branta canadensis minima and Black Brant Branta bernicla nigricans, males spend more time in alert and aggressive behaviour than the females which spend more time foraging in order to restore depleted nutrient reserves (Sedinger & Raveling 1990, Sedinger et al. 1995). Data for the two sexes in this study were therefore investigated separately.

At the feeding sites, breeding males had a slow peck rate and spent more time being vigilant in the head-up and extreme head-up positions, and in social interactions than other males. This was reflected in their generally low AP scores (Chapter 2) and suggests that they were investing in their mate and offspring by protecting them from conspecific feeding competition and/or predation at the cost to themselves of increased participation in aggressive encounters, reduced food intake and reduced body condition. Scott (1980c) also showed that amongst Bewick's Swans wintering at the Ouse Washes, parents spent more time in vigilance and threat behaviours, and less time feeding than pairs without offspring, but the author did not find differences between the two sexes. Johnson & Sibly (1990) however, found that male Canada Geese spent more time than their mates in vigilance and in aggressive encounters and less time feeding, whilst feeding in flocks prior to the nesting season, and suggested that protection by the male enabled the female to spend more time feeding, allowing her to gain the reserves of fat and protein necessary for breeding. In the current study, there was no difference in the step rates recorded for breeding, paired and single adult males. However, females with offspring, cygnets, and to a lesser extent paired females, had lower step rates, faster peck rates and spent less time in social interactions, which may be attributed to protection from interference during feeding by the presence of their mate.

Breeding females were more vigilant than paired females when feeding on grass swards (Fig. 6.42) suggesting that they also shared in the protection of their offspring, and yet were still able to achieve high AP scores (Chapter 2). This suggests that the families may have been monopolizing the best food resources, as demonstrated for Barnacle Geese in winter by Black et al. (1992). It has already been shown (Chapter 3) that families tend to use fields close to the roost in order to minimise the energetic costs of flight between the feeding and roost sites. The results from the more experimental conditions of the grain feeds concur with this theory, since breeding females and family cygnets spent the most time feeding on the limited, but high-quality grain, and breeding females had the longest mean head-under bouts. Breeding males spent less time feeding on the grain than paired males without cygnets, and vigorously defended the area around their feeding families, initiating attacks more frequently than any other class. The negative correlation amongst males between dominance rank and AP score (Chapter 3) may result from the burden of protecting both a mate and an increasing number of offspring amongst the family class (since dominance rank increases linearly with family size - Chapter 2), and the subsequent reduction in time spent feeding by the males.

Cygnets benefitted from the protection afforded by their parents by spending less time being vigilant in the head-up and extreme head-up behaviours, having a fast peck rate and a slow step rate and spending much time feeding on the provisioned grain (second only to breeding females), resulting in generally high AP scores (Chapter 2). Juvenile Greater White-fronted Geese have also been found to have a faster peck rate than their parents (Owen 1972a) and ate 6-7% more material per unit time than birds over one year old. Such high intake rates may be necessary to permit continued growth during the winter, since swans in their first winter are typically only 85-87 % of adult weight, and yet continue to increase in weight during the winter (Evans & Kear 1978). Faster peck rates may also be at the expense of food selection, since there is less time for selecting each mouthful, and it may be that the cygnets, which are less experienced at grazing than the adults, are compensating for their lower feeding efficiency by increasing their food intake rate. The slow step rates of cygnets in this study differ from those of juvenile Greater White-fronted Geese which were found to walk significantly faster than adults (Owen 1972a). Flocks of geese grazing on land tend to be more tightly packed than swans, and faster step rates may serve to keep goose families at the edge of the flock where they have a competitive advantage. Amongst the looser swan flocks there may be less to be gained from being on the edge, and the slow step rates of the cygnets may allow them to concentrate their foraging in more profitable areas, as shown for Brent Geese feeding on experimentally enhanced vegetation at a spring staging area in the Netherlands (Teunissen et al. 1985), and amongst Blue Geese broods feeding on high-biomass food patches (Mulder et al. 1995). Since the AP scores of cygnets increased with the dominance rank of the family (Chapter 2), which in turn reflects the fighting ability of the male parent, male dominance rank can be seen to have a direct effect upon the extent to which its offspring can build up fat reserves during their first winter. This may have important repercussions upon the survivorship of the cygnets during the winter and also during their first spring migration (see Chapter 7).

Yearlings of both sexes which were not associating with their parents had intermediate to high peck rates and high step rates indicating that they were attempting to feed rapidly but that they may have been grazing on poorer quality grass and therefore had to move more frequently between feeding patches.

The effect of dominance rank differed between the two sexes. Amongst females, both the time spent alert and moving during feeding bouts decreased with dominance rank, whilst time spent feeding at the grain feeds increased with dominance rank, agreeing with the findings of other studies which have shown that average daily food intake is positively correlated with dominance rank e.g. amongst Common Cranes (Bautista et al. 1995) and Willow Tits Parus montanus (Koivula et al. 1995). Since female rank is a function of the dominance rank of its mate, these results reflect the increased protection afforded by a dominant male. Amongst pairs, the rank of the male therefore directly affects the amount of time spent feeding by its mate and the extent to which it can build up fat reserves, as reflected in its AP score (Chapter 2), necessary both for the spring migration to the breeding grounds and for nesting. Amongst both males and females, the effect of dominance rank upon time spent in social interactions was less clear cut, with low and high ranking birds generally showing higher rates of social interaction than those of intermediate rank. This pattern may reflect the observations from the grain feeds where amongst both males and females, birds from the high-ranking family class were the most frequent to initiate attacks upon conspecifics (Fig. 6.59) whilst low-ranking single yearlings were the most frequently attacked class (Fig. 6.60). In addition larger broods (of highest rank), may occupy a larger area and therefore both initiate and elicit attacks at higher frequency (Mendenhall & Milne 1985).

The effect of abdominal profile upon activity patterns will reflect to some extent the effects of social class and dominance rank already discussed, which are closely linked to the AP score of an individual (Chapter 2). Amongst males, time spent alert decreased with abdominal profile reflecting the higher vigilance burden of both breeding adults and single yearlings (Fig 6.6) which have the lowest AP scores amongst males (Chapter 2). Time spent by males in social interactions increased with abdominal profile (Fig. 6.16). The reason for this very neat relationship is not clear. The peck rate of males generally increased as AP score increased above AP score 2, reflecting the faster food intake of single adults (with higher AP scores) and the slower peck rates of breeding adults (with lower AP scores). Male peck rate did not increase as AP scores increased during the winter, since half-month did not have a significant effect upon the peck rate of male swans. Male swans with the lowest AP score (1) had the fastest peck rates, suggesting that they were attempting to replenish their fat reserves through increased food ingestion rates.

Foraging routines did not vary greatly with time of day amongst the birds monitored during the five minute focal observations. The general daily pattern in foraging activity of the swans as described in Chapter 4 was not seen because only actively feeding birds were chosen in the sample. Nevertheless, amongst feeding females there was some evidence for a decline in feeding intensity during the course of the day (Fig. 6.1), and declines in the amounts of time spent with their heads-up being vigilant and in active movement. This may possibly reflect the need to fill the gizzard and stomach with grass early in the morning in order to maximise the amount of food processed during the day. Time spent in extreme head-up alert activity however generally increased during the day. Time of day had no significant effect upon feeding intensity amongst males, or any other activity except social interactions which were most frequent as birds arrived on the feeding grounds in the morning but then dropped to much lower levels once most members of the feeding flock were present and the social hierarchy of the units present had become established. This contrasts with some work on geese. Owen (1972a) for instance, showed that the peck rate of Greater White-fronted Geese feeding on salt-marsh at Slimbridge in winter increased linearly during the course of the day reaching a maximum just before departure to the roost, whilst Ebbinge et al. (1975) showed that the peck rate of Barnacle Geese feeding on pasture in the northern Netherlands in the winter shared a parallel bimodal distribution to feeding frequency, with peaks in the morning and late afternoon. The absence of an obvious increase in food intake before departure for the roost sites may in part be explained by the provision of supplementary feeds of grain at the Slimbridge roost sites during the late afternoon which allowed birds the chance to ingest high-quality food prior to roosting for the night.

Flock size affected activity patterns of individuals at the feeding sites in several ways. Amongst females, time spent feeding tended to decline as flock size increased (Fig. 6.2) whilst time spent with the head-up being vigilant, and in social interactions, correspondingly increased, suggesting that the potential for feeding competition from conspecifics may increase as flock size (and presumably flock density) increased. Peck rates of both male and females however, tended to increase with flock size, whilst time spent with the head-up by male birds tended to decrease, suggesting that the increased vigilance against predators provided by additional birds (see Pulliam 1973), permitted more rapid intake rates of food. Beyond a flock size of around 225 birds however, peck rates of both and females began to decline and the time spent head-up by males increased, suggesting that in flocks above this size, the increased potential of intra-specific competition for food may begin to outweigh the advantages of increased protection from predators. Total time spent feeding at the grain feeds by male swans decreased significantly with flock size, suggesting that both intra-specific competition, and vigilance/social interactions necessary to reduce intra-specific competition for the mate and/or offspring increased as flock size (and density) increased. In general, total time spent feeding by all swans at the grain feeds declined as numbers increased, possibly simply due to the crush of birds attempting to feed. Since densities of distributed grain were very similar between the pens of the Grounds roost and the Rushy Pen (Table 6.10), but mean flock size in each of the individual Grounds pens was generally much smaller than on the Rushy Pen, males feeding in the Grounds Pens were not only able to feed for longer, but also had access to more grain per swan than in the Rushy Pen.

Females from the Grounds roost group spent significantly less time in social interactions during feeding bouts on the fields than those from the Rushy Pen roost (Fig. 6.20), again illustrating the reduced rates of interaction amongst the Grounds units as described in Chapter 5. The activity patterns of birds from the two roost groups when feeding on the fields did not otherwise differ, suggesting that although the amount of time spent feeding by the Grounds birds on the fields was less than that for Rushy Pen birds (Chapter 5), the intensity of feeding (i.e peck-rates, step-rates and time spent actively feeding) within a feeding bout did not differ significantly. Male swans from the third roost group which used alternative roost sites, had a significantly faster step rate than those from the two main roost groups. This difference reflects the fact that the males in the sample from the third roost group were mostly yearlings, which tend to have a faster step rate than adult males (Fig. 6.45 and see above).

Habitat variables exerted a considerable effect upon the swans' activity patterns at the feeding sites. Amongst males, the amount of time spent feeding increased and the time spent in movement, and in general vigilance (head-up) and alert behaviour (extreme head-up) decreased, as protein content of the sward increased. Time spent feeding by female swans did not vary significantly with the protein content of the sward; but time spent in alert behaviour decreased as the protein levels decreased. These results suggest that the importance of male vigilance to reduce feeding competition from conspecifics may decrease as food quality increases. The males fed most intensively during conditions of high food quality and appear to invest most effort into protecting their mates and/or offspring from intra-specific feeding competition when food quality is low. The decrease in alert behaviour amongst females at 'poorer quality' sites may reflect their need to spend more time foraging when protein levels were low. This agrees with the findings of Reed (1993), who showed that inter-brood aggression amongst winter flocks of Brent Geese was generally rare except when feeding on a patchily distributed food resource. The female and offspring would benefit most from male protection when food supply was both low and patchily distributed. This finding may help to explain the absence of a difference in feeding and vigilance rates between paired male and female Bewick's Swans recorded grazing on abundant beds of Chara at a spring migratory site in Estonia (Rees & Bowler 1991). Rates of aggressive interactions amongst feeding migratory swans have been found to be higher at supplementary feeds of grain than at field sites (Scott 1980c, Black & Rees 1984, and results from this study). This may reflect increased aggression on a patchily distributed food source, although flock density and its effect on the rate of conspecific interference amongst feeding birds may also be relevant. The amount of time spent each year in vigilance by adult Black Brant during the post-hatching period decreased and time spent feeding increased, as the size of a breeding colony in Alaska, increased and food supplies declined (Sedinger et al. 1995). These findings contrast with those in the current study, and presumably resulted from strong density-dependent effects operating on both juvenile and adult survival, and again suggest that food supply was not limiting for the swans at Slimbridge.

The peck rates of both male and female swans decreased as sward-length increased. This agrees with the findings of other authors working on geese e.g. Owen (1972a), Drent & Swierstra (1977), Black et al. (1992). Assuming bite size increases with sward-length (Owen 1972a, Drent & Swierstra 1977) this suggests that handling time increases with the size of individual food items. The time spent in head-up behaviour by males tended to decrease with the mean biomass of the sward but then increased again at higher levels of biomass. Since biomass and sward-length were closely correlated (Chapter 4), the increased handling time of food items on taller swards may have allowed the males to spend more time being vigilant, whilst continuing to ingest food. Time spent by females with their head-up, on the other hand, tended to decrease as sward-length increased, possibly because of the increased vigilance of the males on fields with high biomass (and hence high sward-length).

The peck rates of both male and female swans tended to increase as the percentage water cover on the field increased, suggesting that water may aid the speed at which the swans' can ingest and process individual food items, despite the fact that sward-length tended to increase with water cover. At higher levels of water cover (>10%) however, peck rates declined, indicating that the selection and/or handling time of individual food items may increase on more heavily flooded swards. Time spent in head-up behaviour by both male and female swans tended to increase at first as water cover of the field increased, but then decreased on more heavily flooded swards, perhaps reflecting the decreasing burden of anti-predator vigilance on deeper water. The water cover on the field affected the step rates of the two sexes differently, with the step rates of male swans decreasing and the step rates of females increasing as water cover increased. This may reflect differences in foraging strategies by the two sexes. With reduced vigilance and an increased food handling time on more heavily flooded fields, males with mates and/or offspring, may reduce their step rate in order to maximise their own intake rate. Females with mates and/or offspring on the other hand, may increase their step rate in order to search for more profitable food patches, in terms of one, or a combination, of the following habitat variables: water cover, sward-length, biomass and protein content, since the dietary needs of the female may differ from those of the male particularly prior to departure to the breeding grounds. Sward-length may be important since the step rates of females (and not males) tended to increase as sward-length increased (Fig. 6.52). This relationship is the opposite to that shown by Barnacle Geese (Black et al. 1992), and is unexpected since the larger bite sizes expected on taller swards would increase handling time of individual food items. This suggests that on fields with a high mean sward-length, females may be selectively grazing on patches of shorter grass. This suggestion is also supported by the fact that although the peck rates of females on pasture were always higher than those of males, this difference was greatest on fields with the highest sward-length (Figs. 6.30 & 6.35). Since females have significantly shorter bill-lengths than males (3.5% shorter in adults, Evans & Kear 1978), they may not be able to handle larger items of food as efficiently, and thus seek shorter swards in the field.

6.5 SUMMARY

This chapter investigates the activities of individual Bewick's Swans from 347 five minute focal scans of feeding birds and 1645 sets of peck rate data collected at the feeding sites during the day, and from 77 focal scans conducted at the roost sites during the late afternoon /early evening supplementary feeds of grain. Generalised linear models were fitted in order to elucidate the factors that influenced the swans' activity patterns. Non-habitat variables investigated included: year, time in season (half-month and month), time of day (hour), feeding site identity, flock-size, sex of the individual, its' social class, roost group membership, abdominal profile and dominance rank. Habitat variables investigated included: area of flooding, biomass of sward, protein content of sward and sward-length.

1) During feeding bouts on the fields, swans spent on average 71.9% of their time with their heads down feeding, 17% with the head up being vigilant, 7.8% moving between feeding patches and 3.3% in other activities including comfort, social interactions, drinking and loafing. Females spent a significantly higher proportion of time actually feeding than males during feeding bouts. In addition they had faster peck rates and slower step rates than males, and spent less time in vigilance, movement, comfort and social interaction. The two sexes were treated separately in subsequent analyses.

2) Breeding males had slow peck rates and spent more time in vigilance and social interactions than other males, suggesting that they were protecting their mate and offspring from conspecific feeding competition and/or predation at the cost to themselves of increased participation in aggressive encounters and reduced food intake. Breeding females and their cygnets, and to a lesser degree paired females (without cygnets), benefitted from the protection afforded by their mates, which enabled them to have faster peck rates, slower step rates and to spend less time in social interactions and vigilance. These differences were reflected in the swans' AP scores. Breeding females were more vigilant than paired females (without cygnets) indicating that they shared in the protection of their offspring.

3) Families monopolized the most profitable food resources. The slow step rates, and fast peck rates, of the breeding females and cygnets may have allowed them to concentrate their foraging in the most profitable areas, helping them to build up fat reserves important for growth and survival amongst the cygnets, and for successful breeding amongst the adult females. The dominance rank of the pair directly affected the amount of time that the female spent in vigilance and movement during feeding bouts on the fields (decreased with dominance rank), and the time spent feeding during the grain feeds (increased with

dominance rank), and hence the extent to which it could build up fat reserves as reflected in its AP score (see Chapter 2).

4) Amongst both sexes, parents most frequently initiated attacks upon conspecifics during the grain feeds, whilst single yearlings were the most frequently attacked social class.

5) The foraging routines of feeding males did not vary greatly with time of day, although there was some evidence that amongst females, feeding intensity during feeding bouts declined during the course of the day. Social interactions amongst males were most frequent immediately upon arrival at the feeding grounds and subsequently declined to much lower levels for the rest of the day.

6) Peck rates increased, and male vigilance decreased, with increasing flock size, suggesting that the presence of more birds increased group vigilance against predators and permitted more rapid intake rates of food. Beyond a flock size of around 225 birds however, peck rates declined and male vigilance increased, suggesting that the increased potential of intra-specific competition for food (possibly as a result of increased bird density in the flock), may have outweighed the advantages of increased protection from predators in flocks above this size.

7) There was no difference between birds from the two main roost groups in terms of feeding intensity during feeding bouts on the fields, although females from the Grounds roost were less frequently engaged in social encounters than females from the Rushy Pen roost, again highlighting the reduced levels of aggression exhibited by birds from the Grounds roost. Total time spent feeding at the grain feeds by male swans decreased as flock size increased and this reflected the location of the feed, since mean flock size in each of the individual Grounds pens was generally much smaller than on the Rushy Pen. Males feeding in the Grounds pens were not only able to feed for longer, but also had access to more grain per swan than those in the Rushy Pen.

8) Males spent less time being vigilant, and fed more intensively, when grazing on swards with a high protein content. They invested more effort into protecting their mates and/or offspring from intra-specific feeding competition when food quality (in terms of protein levels in the sward) was low.

9) The peck rates of both male and female swans decreased as sward-length increased. Assuming bite size increases with sward-length, this suggests that handling time i.e. chewing and swallowing, increased as the volume of food ingested increased.

10) Peck rates increased as percentage water cover on the field increased until around 10 % of the field was covered in water, possibly because water aids the speed at which swans can ingest and process food items. Peck rates on fields with higher percentage water cover (above 10 %) subsequently declined, suggesting that selection and/or handling

time of food items increased on more heavily flooded swards. Male step rates decreased as water cover on the field increased, whilst female step rates increased, indicating that females were grazing more selectively than males. Unexpectedly, the step rates of female swans (and not males) also increased as sward-length increased, suggesting that they may have been selectively grazing on patches of shorter grass. This theory is given added weight by the fact that although the peck rates of females were always faster than those of the males, the difference between the sexes was most marked on fields with the highest mean sward-length.

Table 6.1. Summary table of activity of Bewick's Swans by sex, on fields in the Slimbridge area from focal bird scans conducted during daylight hours (1990-91 to 1992-93 winters inclusive).

	Male (n=137)		Female (n=133)		Unknown sex (n=77)		All (n=347)	
	mean	S.D.	mean	S.D.	mean	S.D.	mean	S.D.
Feed	68.12	21.78	73.93	17.60	74.94	19.06	71.86	19.85
Head-up	18.27	14.28	16.56	12.33	15.64	10.06	17.04	12.71
Movement	9.01	11.96	7.32	9.99	6.28	9.25	7.75	10.69
Comfort	1.87	5.86	0.85	2.03	1.59	4.02	1.42	4.34
Interaction	1.16	3.14	0.80	1.71	0.65	1.92	0.91	2.42
Drink	0.74	3.26	0.57	2.13	0.15	0.70	0.53	2.46
Loaf	0.32	1.20	0.42	1.93	0.55	2.20	0.41	1.75

Table 6.2. Linear models using maximum likelihood estimates fitted to the time spent in the different activities during five-minute focal bird scans, by male swans recorded feeding on fields in the Slimbridge area (1990-91 to 1992-93 winters inclusive). Habitat variables excluded. Note: * P < 0.05, ** P < 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

	ACTIVITY								
	Feeding			Head-up (inc. alert)			Alert		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Field	1.67	13, 134	*	2.44	13, 130	**	2.86	9, 86	**
Half-month	-	-	-	-	-	-	-	-	-
Time (hrs)	-	-	-	-	-	-	-	-	-
Year	9.44	2, 123	***	-	-	-	4.31	1, 78	*
Flock size	-	-	-	-	-	-	-	-	-
Social class	-	-	-	2.73	6, 123	**	3.72	6, 83	**
Abdominal profile (AP)	-	-	-	-	-	-	4.11	1, 78	*
Dominance rank	-	-	-	-	-	-	-	-	-
Roost group	-	-	-	-	-	-	-	-	-
Final model:									
Deviance	126.1			121.8			80.3		
df	121			117			77		

Table 6.2 (con) ACTIVITY

	Movement			Social interactions		
Variable	F ratio	d.f.	P	F ratio	d.f.	P
Field	2.25	13, 134	**	5.24	13, 107	***
Half-month	-	-	-	-	-	-
Time (hrs)	-	-	-	19.88	1, 95	***
Year	11.46	2, 123	***	5.08	2, 96	**
Flock size	-	-	-	-	-	-
Social class	-	-	-	3.35	6, 100	**
Abdominal profile (AP)	-	-	-	21.77	1, 95	***
Dominance rank	-	-	-	0.26	1, 95	NS
Roost group	-	-	-	-	-	-
Social class * dom. rank	-	-	-	4.06	1, 95	*
Social class * time (hour)	-	-	-	8.41	1, 95	**
Field * AP	-	-	-	31.25	1, 95	***
Final model:						
Deviance		115.1			64.7	
df		121			94	

Table 6.3. Linear models using maximum likelihood estimates fitted to the time spent in the different activities during five-minute focal bird scans, by female swans recorded feeding on fields in the Slimbridge area (1990-91 to 1992-93 winters inclusive). Habitat variables excluded. Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS not significant, - variable removed from final model (see methods).

	ACTIVITY								
	Feeding			Head-up (inc. alert)			Alert		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Field	2.43	13, 130	**	3.64	13, 130	***	4.34	10, 82	***
Half-month	-	-	-	-	-	-	-	-	-
Time (hrs)	4.88	1, 118	*	3.97	1, 118	*	3.12	1, 73	NS
Year	-	-	-	-	-	-	-	-	-
Flock size	11.42	1, 118	***	10.60	1, 118	**	-	-	-
Social class	-	-	-	-	-	-	3.43	1, 73	NS
Abdominal profile	-	-	-	-	-	-	-	-	-
Dominance rank	-	-	-	-	-	-	4.52	1, 73	*
Roost group	-	-	-	-	-	-	-	-	-
Time * social class	-	-	-	-	-	-	9.48	1, 73	**
Field * dom. rank	-	-	-	-	-	-	7.34	1, 73	*
Final model:									
Deviance		127.4			119.1			47.0	
df		117			117			72	

Table 6.3 (con) ACTIVITY

Variable	Movement F ratio	Movement d.f.	Movement P	Social interactions F ratio	Social interactions d.f.	Social interactions P
Field	4.00	13, 107	***	2.42	13, 104	**
Half-month	-	-	-	-	-	-
Time (hrs)	8.66	1, 95	**	-	-	-
Year	-	-	-	4.91	2, 93	**
Flock size	-	-	-	-	-	-
Social class	4.36	6, 100	***	2.20	6, 97	*
Abdominal profile (AP)	-	-	-	21.77	1, 95	***
Dominance rank	13.69	1, 95	***	6.09	1, 92	*
Roost group	-	-	-	5.66	1, 92	*
Social class * time	6.48	1, 95	*	-	-	-
Social class * field	-	-	-	6.93	1, 92	**
Field * dom. rank	3.98	1, 95	*	4.25	1, 92	*
Final model:						
Deviance		93.5			65.2	
df		94			91	

Table 6.4. Linear models using maximum likelihood estimates fitted to the time spent in the different activities during five-minute focal bird scans, by male swans recorded feeding on fields in the Slimbridge area (1990-91 to 1992-93 winters inclusive). Habitat variables (mean sward-length, biomass, % protein content of sward, % water cover on field) included. Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS not significant, - variable removed from final model (see methods).

	ACTIVITY								
	Feeding			Head-up (inc. alert)			Alert		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Month	-	-	-	-	-	-	-	-	-
Time (hrs)	-	-	-	-	-	-	-	-	-
Year	-	-	-	-	-	-	-	-	-
Flock size	-	-	-	-	-	-	-	-	-
Social class	-	-	-	-	-	-	-	-	-
Abdominal profile (AP)	-	-	-	-	-	-	-	-	-
Dominance rank	-	-	-	-	-	-	-	-	-
Roost group	-	-	-	-	-	-	-	-	-
Sward-length	-	-	-	-	-	-	-	-	-
Biomass	-	-	-	-	-	-	-	-	-
Protein	10.69	1, 33	**	6.24	1, 33	*	15.28	1, 33	***
Water cover	-	-	-	-	-	-	-	-	-
Final model:									
Deviance		33.4			32.7			29.6	
df		32			32			32	

Table 6.4 (con)

ACTIVITY

Movement

Variable	F ratio	d.f.	P
Month	-	-	-
Time (hrs)	-	-	-
Year	-	-	-
Flock size	-	-	-
Social class	-	-	-
Abdominal profile (AP)	-	-	-
Dominance rank	-	-	-
Roost group	-	-	-
Sward-length	-	-	-
Biomass	-	-	-
Protein	4.93	1, 33	*
Water cover	-	-	-

Final model:

Deviance	23.9
df	32

Table 6.5. Linear models using maximum likelihood estimates fitted to the time spent in the different activities during five-minute focal bird scans, by female swans recorded feeding on fields in the Slimbridge area (1990-91 to 1992-93 winters inclusive). Habitat variables (mean sward-length, biomass, % protein content of sward, % water cover on field) included. Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS not significant, - variable removed from final model (see methods).

	ACTIVITY		
	Alert		
Variable	F ratio	d.f.	P
Month	-	-	-
Time (hrs)	7.70	1, 32	**
Year	-	-	-
Flock size	-	-	-
Social class	-	-	-
Abdominal profile (AP)	-	-	-
Dominance rank	-	-	-
Roost group	-	-	-
Sward-length	-	-	-
Biomass	-	-	-
Protein	8.14	1, 32	**
Water cover	-	-	-
Protein * time	7.07	1, 32	*
Final model:			
Deviance		21.3	
df		31	

Table 6.6. Peck rates, step rates and time spent with head up of swans by sex, feeding on grass swards in the Slimbridge area during focal bird observations 1989-90 to 1992-93 winters inclusive.

	Peck rate (pecks/min.)			Step rate (steps/min.)			Time spent with head up (per 50 pecks)		
Sex	mean	S.D.	n	mean	S.D.	n	mean	S.D.	n
Male	60.85	17.65	607	10.79	8.27	458	7.60	7.48	593
Female	66.71	19.20	686	8.59	6.92	489	5.04	5.74	660
Unknown	68.42	19.64	387	9.09	6.74	261	4.33	4.46	386
Total	64.99	19.02	1680	9.53	7.56	1208	5.79	6.59	1645

Table 6.7. Linear models using maximum likelihood estimates fitted to the peck-rate (pecks per five seconds), step-rate (steps per 50 pecks) and time spent head-up (per 50 pecks) of male swans recorded feeding on grass pasture in the Slimbridge area (1991-92 and 1992-93 winters only). Habitat variables (mean sward-length, biomass, % protein content of sward, % water cover on field) included. Note: * P < 0.05, ** P < 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

	ACTIVITY								
	Peck-rate			Head-up (inc. alert)			Step-rate		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Month	-	-	-	0.48	1, 328	NS	-	-	-
Time (hrs)	-	-	-	-	-	-	-	-	-
Year	5.14	1, 325	*	-	-	-	-	-	-
Flock size	25.68	1, 325	***	7.28	1, 328	**	-	-	-
Social class	6.82	7, 331	***	8.53	7, 334	***	2.16	6, 348	*
Abdominal profile (AP)	4.16	1, 325	*	-	-	-	4.57	1, 343	*
Dominance rank	-	-	-	-	-	-	-	-	-
Roost group	-	-	-	-	-	-	15.09	2, 344	***
Sward-length	1.17	1, 325	NS	-	-	-	-	-	-
Biomass	-	-	-	5.55	1, 328	*	-	-	-
Protein	-	-	-	-	-	-	-	-	-
Water cover	30.02	1, 325	***	6.35	1, 328	*	10.22	1, 343	**
Year * AP	5.83	1, 325	*	-	-	-	-	-	-
Sward-length * water	23.67	1, 325	***	-	-	-	-	-	-
Month * flock-size	-	-	-	6.01	1, 328	*	-	-	-
Month * water	-	-	-	5.71	1, 328	*	-	-	-
Roost group * water	-	-	-	-	-	-	19.67	1, 343	***
Final model:									
Deviance		440.2			372.1			20926	
df		324			327			342	

Table 6.8. Linear models using maximum likelihood estimates fitted to the peck-rate (pecks per five seconds), step-rate (steps per 50 pecks) and time spent head-up (per 50 pecks) of female swans recorded feeding on grass pasture in the Slimbridge area (1991-92 and 1992-93 winters only). Habitat variables (mean sward-length, biomass, % protein content of sward, % water cover on field) included. Note: * P < 0.05, ** P < 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

	ACTIVITY								
	Peck-rate			Head-up (inc. alert)			Step-rate		
Variable	F ratio	d.f.	P	F ratio	d.f.	P	F ratio	d.f.	P
Month	-	-	-	-	-	-	-	-	-
Time (hrs)	-	-	-	-	-	-	-	-	-
Year	13.67	1, 363	***	-	-	-	-	-	-
Flock size	19.87	1, 363	***	-	-	-	-	-	-
Social class	3.05	7, 369	**	6.12	7, 373	***	3.83	7, 365	*
Abdominal profile (AP)	-	-	-	-	-	-	12.84	1, 359	***
Dominance rank	-	-	-	-	-	-	-	-	-
Roost group	-	-	-	-	-	-	28.81	2, 360	***
Sward-length	0.93	1, 363	NS	6.12	1, 367	*	6.29	1, 359	*
Biomass	-	-	-	-	-	-	-	-	-
Protein	-	-	-	-	-	-	-	-	-
Water cover	11.46	1, 363	***	4.14	1, 367	*	24.05	1, 359	***
Sward-length * water	6.84	1, 363	**	-	-	-	35.83	1, 359	***
Sward-length * flock-size	6.80	1, 363	**	-	-	-	-	-	-
Sward-length* social class	-	-	-	-	-	-	9.58	1, 359	**
Roost group * water	-	-	-	-	-	-	35.83	1, 359	***
Final model:									
Deviance		564.9			402.9			14150	
df		362			366			358	

Table 6.9. The distribution of grain in pens used by Bewick's Swans for feeding and roosting within the collection at Slimbridge.

a) Grounds Pens

	Pen				
	Asian	European	Tundra	Big	African
No. of scoops					
mean	17.20	9.40	8.60	23.90	18.40
S.D.	3.08	1.96	2.63	3.31	2.37
n	10	10	10	10	10
Length of feeding front (m)	28	16	15	45	32
Scoops per m of feeding front	0.61	0.59	0.57	0.53	0.58

b) Rushy Pen

	Section (see Fig. 6.54)			
	Hostel	Backs	Studio	Kitchen
No. of scoops				
mean	17.00	23.31	17.15	6.69
S.D.	7.39	5.63	6.31	4.19
n	13	13	13	13
Length of feeding front (m)	25	36	27	16
Scoops per m of feeding front	0.68	0.65	0.64	0.42

Table 6.10. Linear models using maximum likelihood estimates fitted to the time spent by male and female swans feeding 'head-under' during the distribution of grain in the pens (1990-91, 1991-92 and 1992-93 winters). Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS not significant, - variable removed from final model (see methods).

TIME SPENT FEEDING
WITH HEAD-UNDER WATER

	Males			Females		
Variable	F ratio	d.f.	P	F ratio	d.f.	P
Pen identity	-	-	-	-	-	-
Half-month	-	-	-	-	-	-
Time (hrs)	-	-	-	-	-	-
Year	-	-	-	-	-	-
Flock size	4.40	1, 35	*	-	-	-
Social class	-	-	-	-	-	-
Abdominal profile (AP)	-	-	-	-	-	-
Dominance rank	-	-	-	5.99	1, 31	*
Final model:						
Deviance		4171607			351970	
df		34			30	

Fig. 6.1. Time spent feeding by female Bewick's Swans during five minute focal scans at the feeding sites with time of day (mean and S.E. bar, n=133), plus predicted values from a generalised linear model.

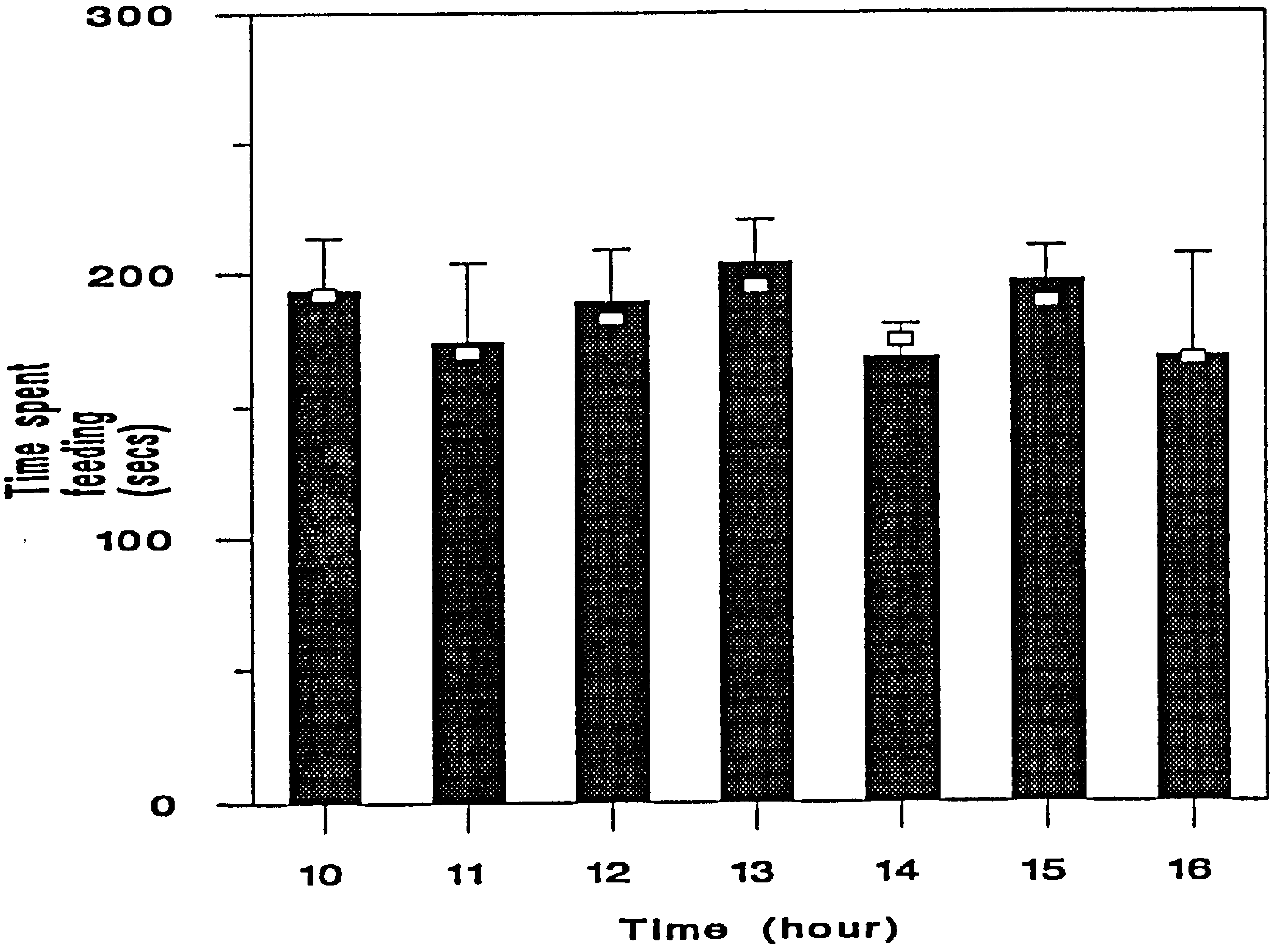


Fig. 6.2. Time spent feeding during five-minute focal scans of female swans at the feeding sites with flock size (mean and S.E. bar, n=133) plus predicted values from a generalised linear model.

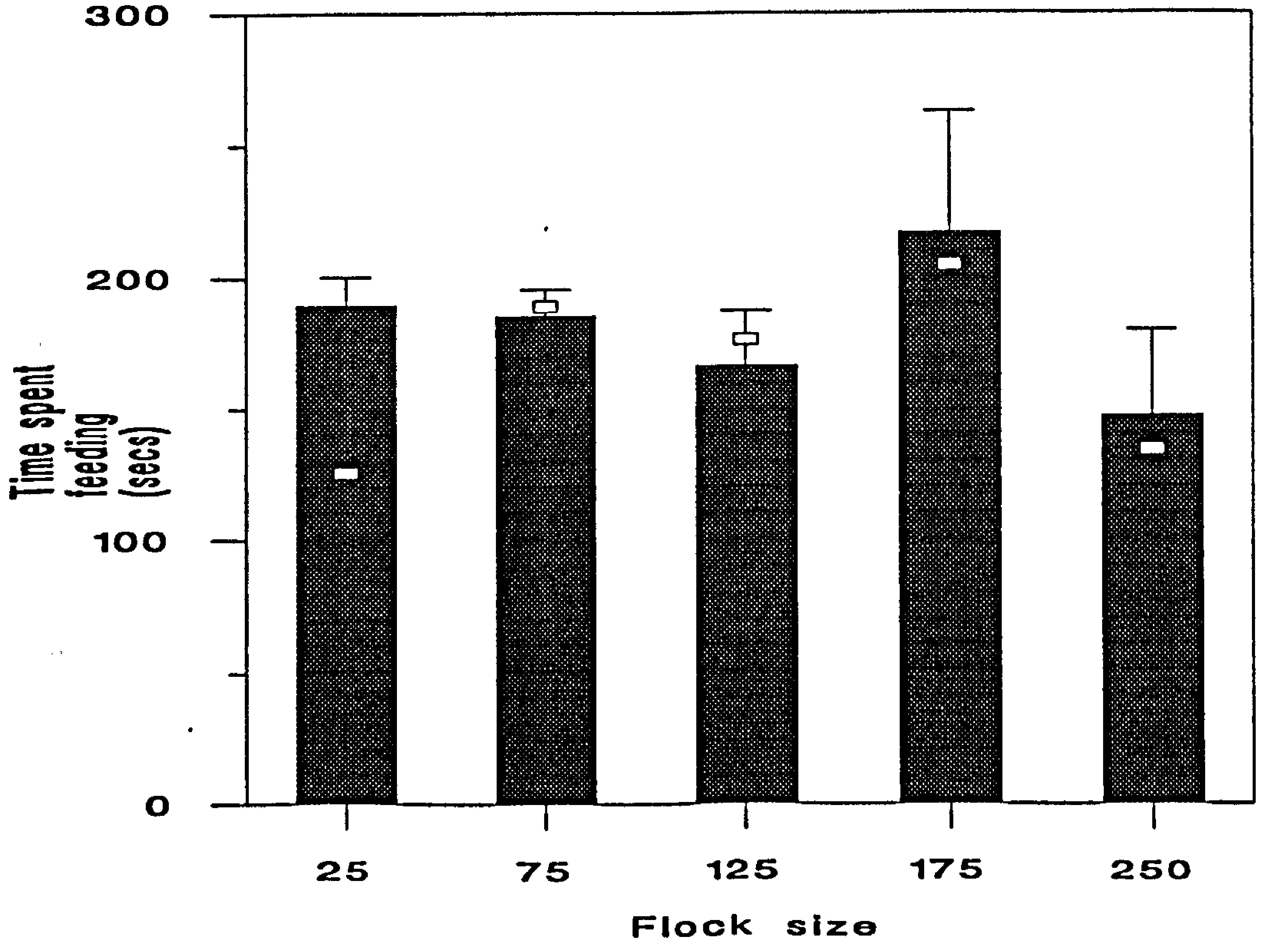


Fig. 6.3 Time spent with head up by male Bewick's Swans during five-minute focal scans with social class (mean and S.E. bar,n=133) plus predicted values from a generalised linear model (A=adult,Y=yearling,C=cygnet,B=breeding, P=paired, S=single, F=family).

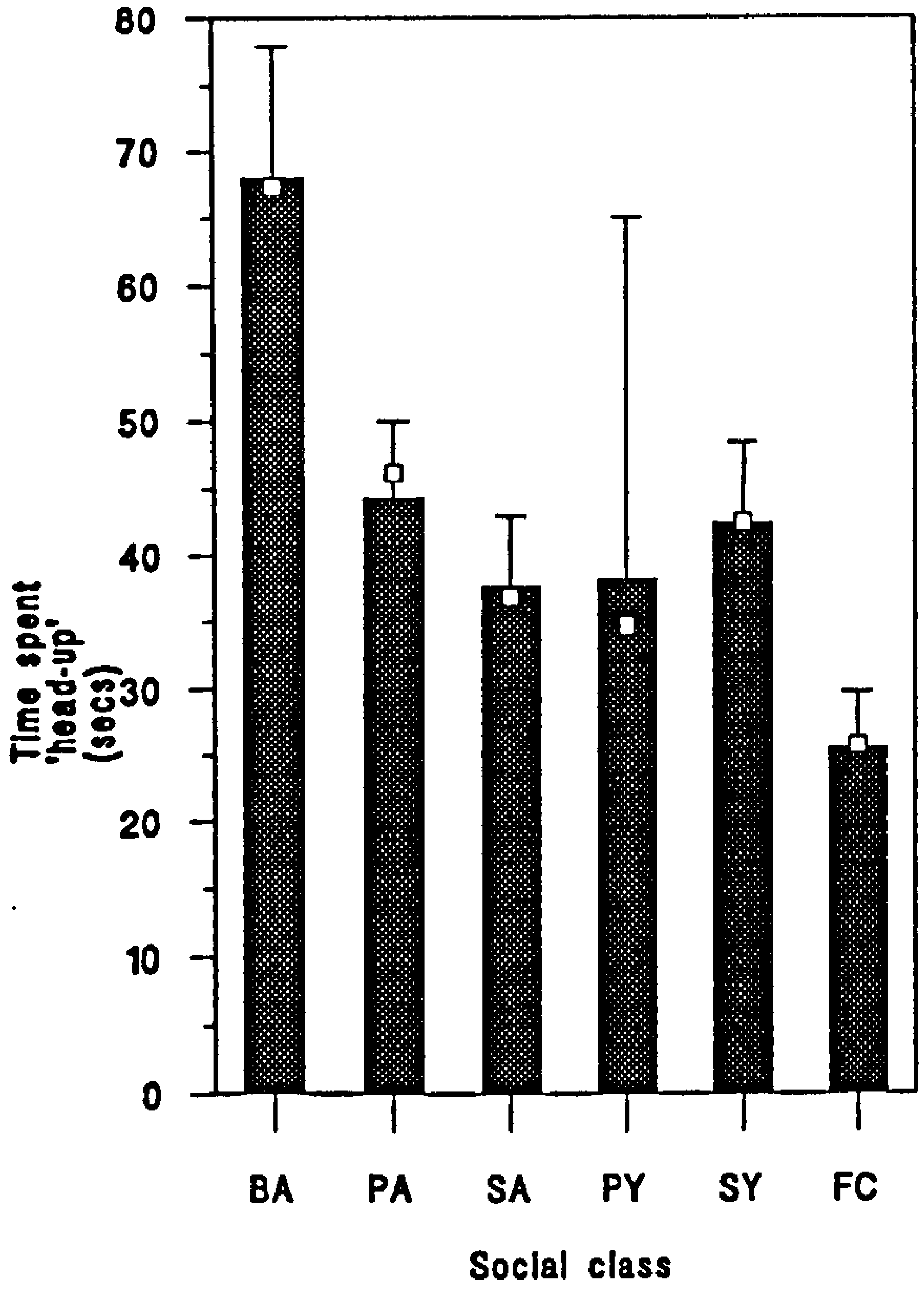


Fig. 6.4. Time spent with head up by female Bewick's Swans during five-minute focal scans at the feeding sites with time of day (mean and S.E. bar, n=133), plus predicted values from a generalised linear model.

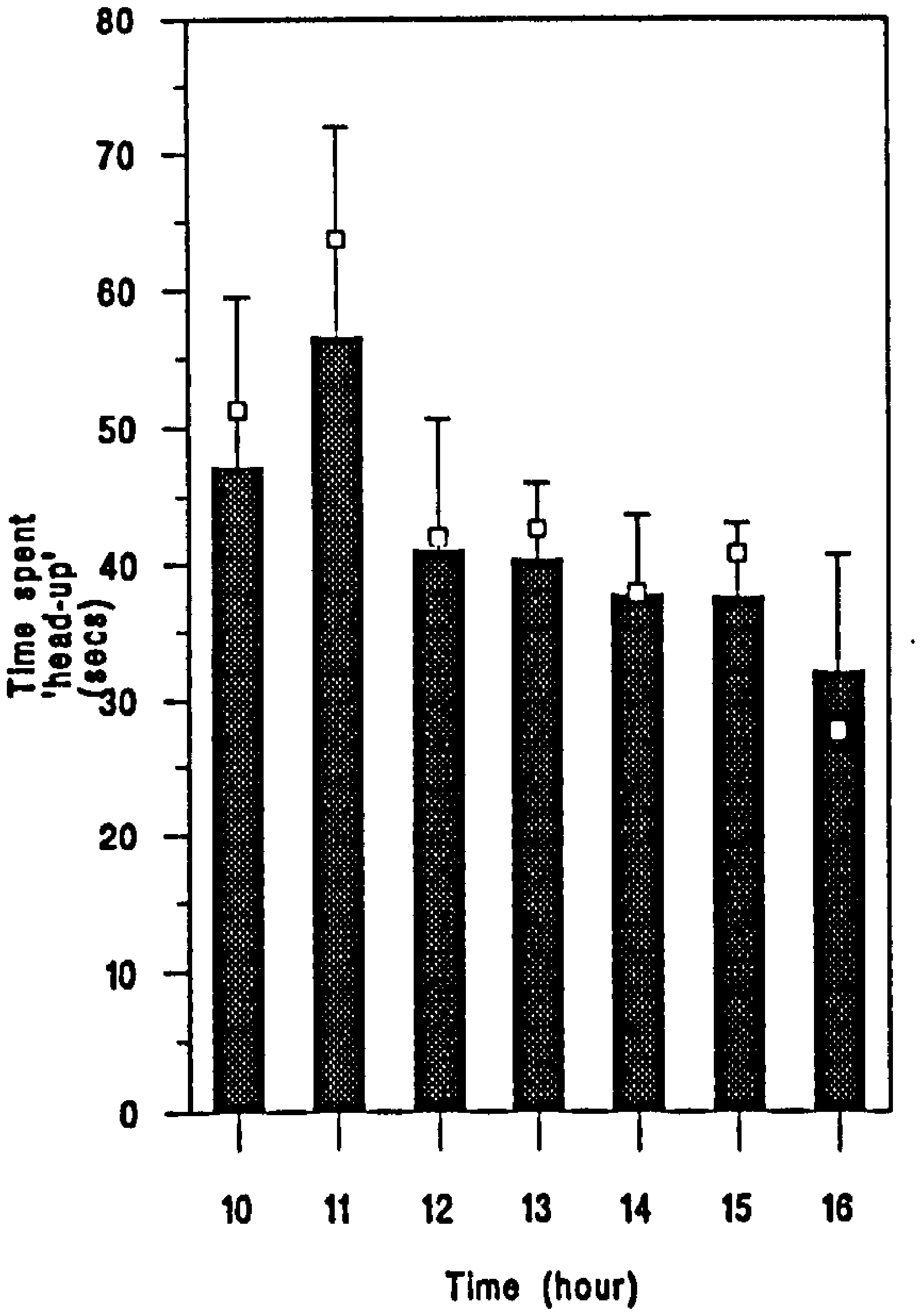


Fig. 6.5 Time spent with head up by female Bewick's Swans during five-minute focal scans at the feeding sites with flock size (mean and S.E. bar, n=133), plus predicted values from a generalised linear model.

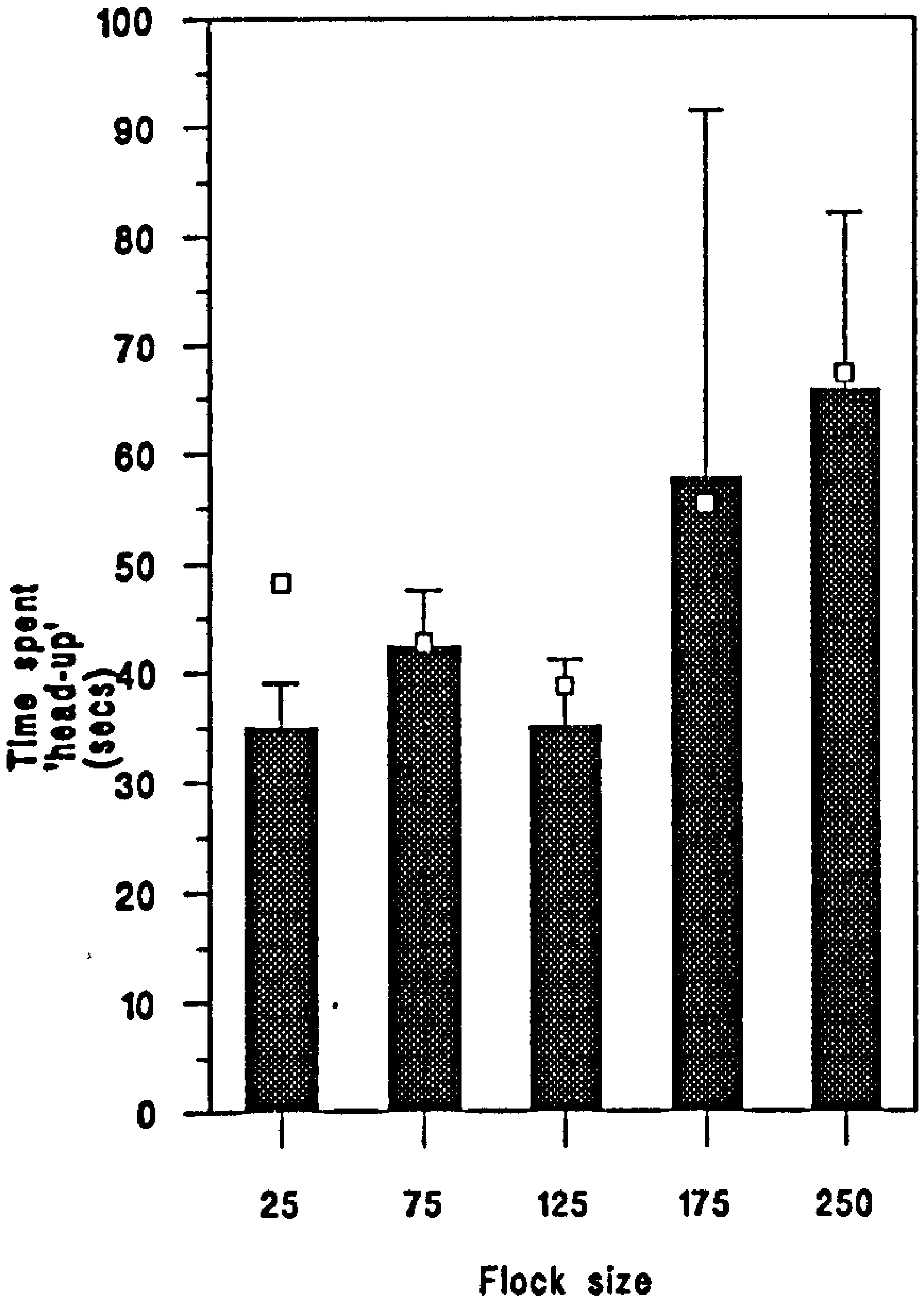


Fig. 6.6 Time spent alert by male Bewick's Swans during focal scans at the feeding sites with social class (mean and S.E. bar,n=95), plus predicted values from a generalised linear model (A=adult,Y=yearling,C=cygnet,B=breeding,P=paired,S=single,F=family).

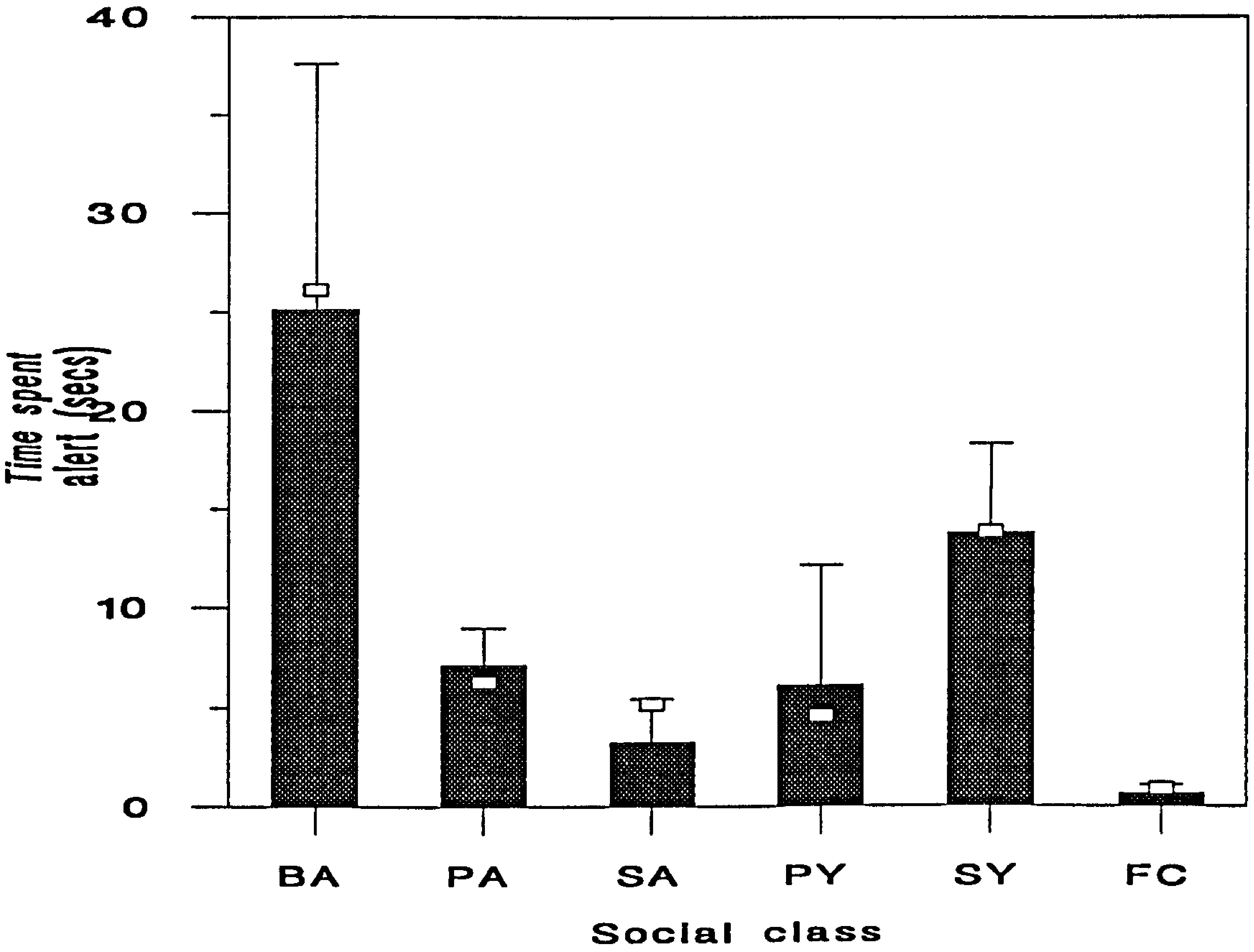


Fig. 6.7 Time spent alert by male Bewick's Swans during five-minute focal scans at the feeding sites with abdominal profile (mean and S.E. bar, n=95), plus predicted values from a generalised linear model.

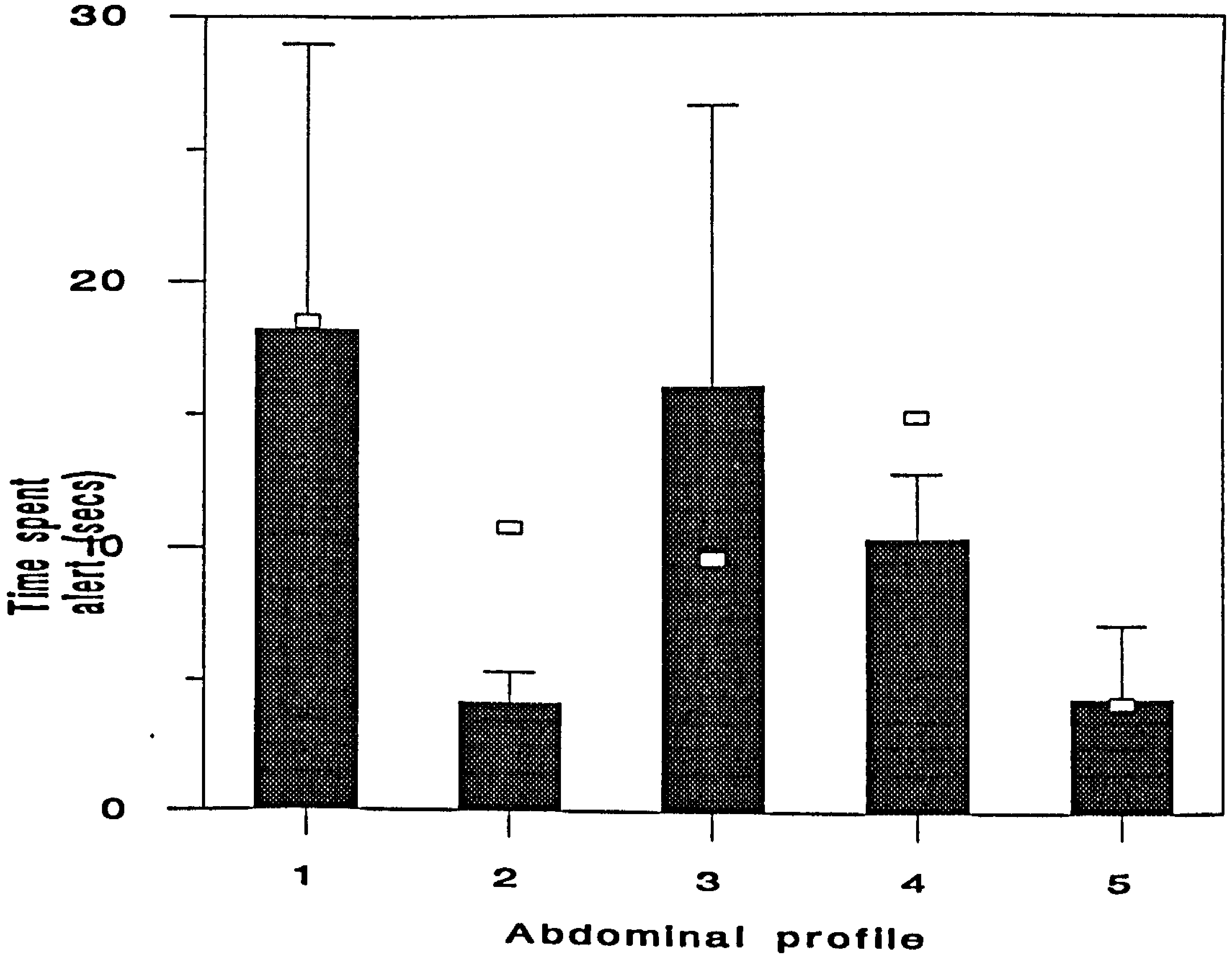


Fig. 6.8. Time spent alert by female Bewick's Swans during 5-min. focal scans with social class (mean and S.E. bar, n=93), plus predicted values from a generalised linear model. (A=adult,Y=yearling,C=cygnet,B=breeding, P=paired,S=single,F=family,T=trio).

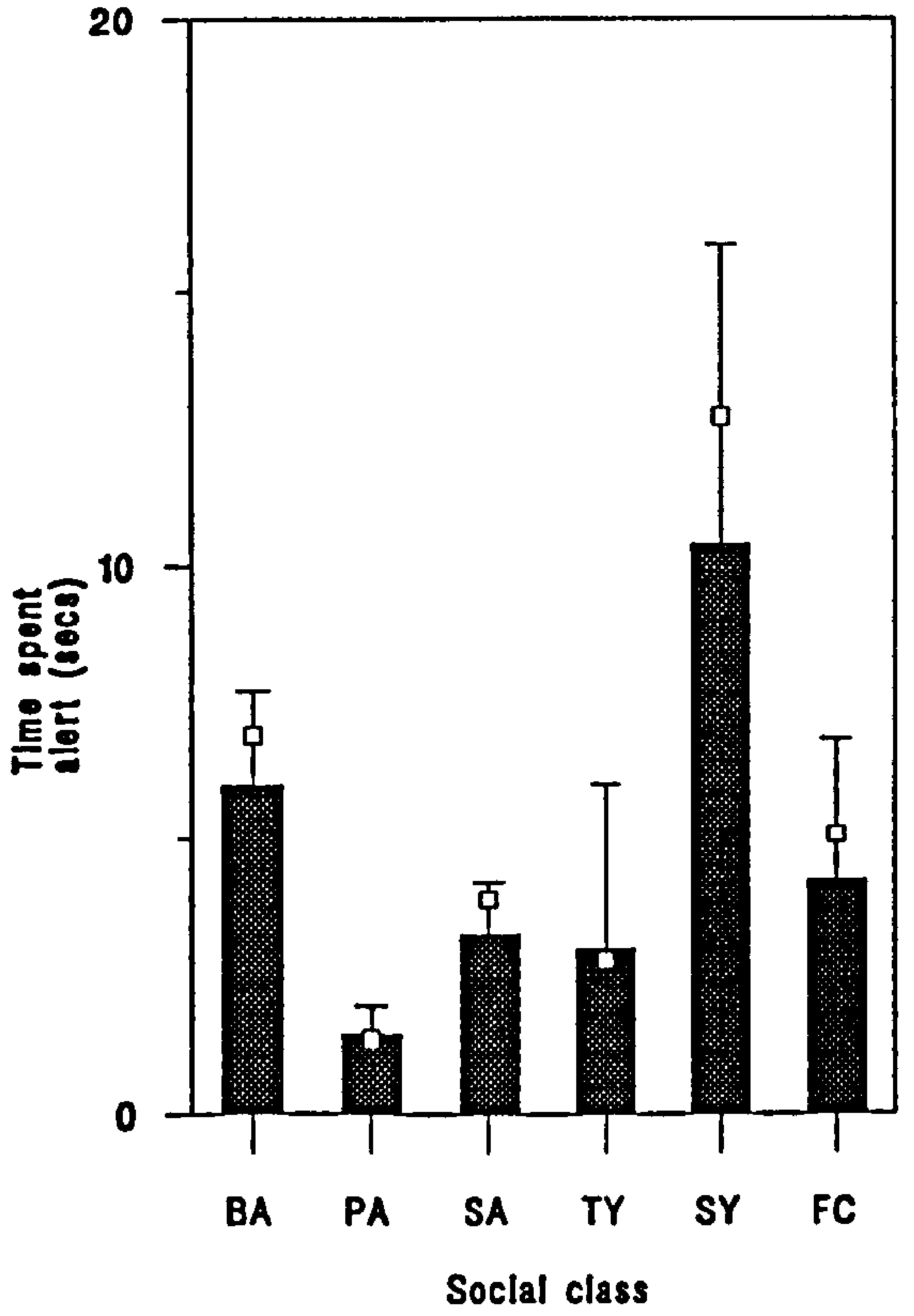


Fig. 6.9. Time spent alert by female Bewick's Swans during 5-minute focal scans at the feeding sites with time of day (mean and S.E. bar, n=93), plus predicted values from a generalised linear model.

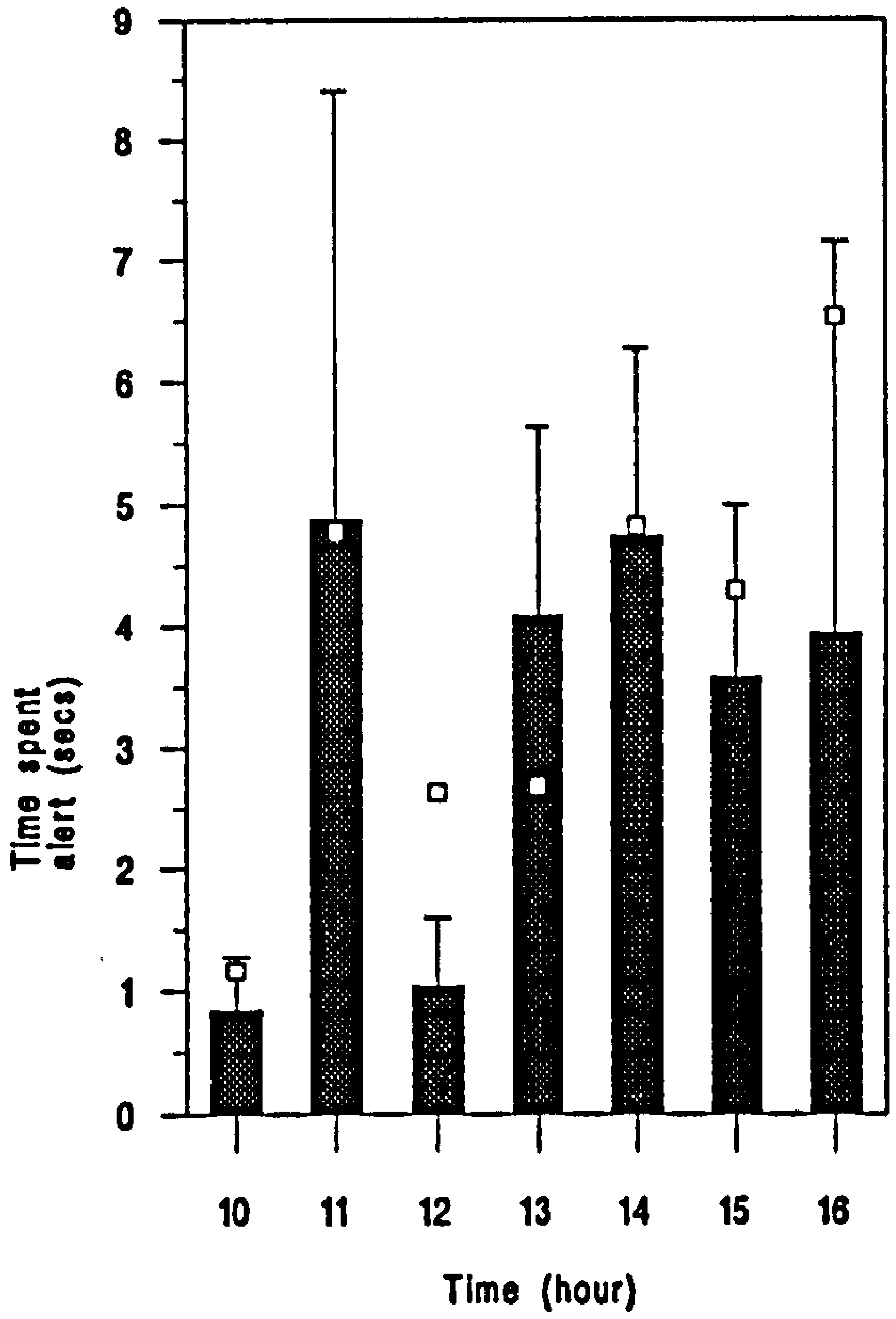


Fig. 6.10. Time spent alert by female Bewick's Swans during 5-minute focal scans at the feeding sites with dominance-rank (mean and S.E. bar, n=93), plus predicted values from a generalised linear model.

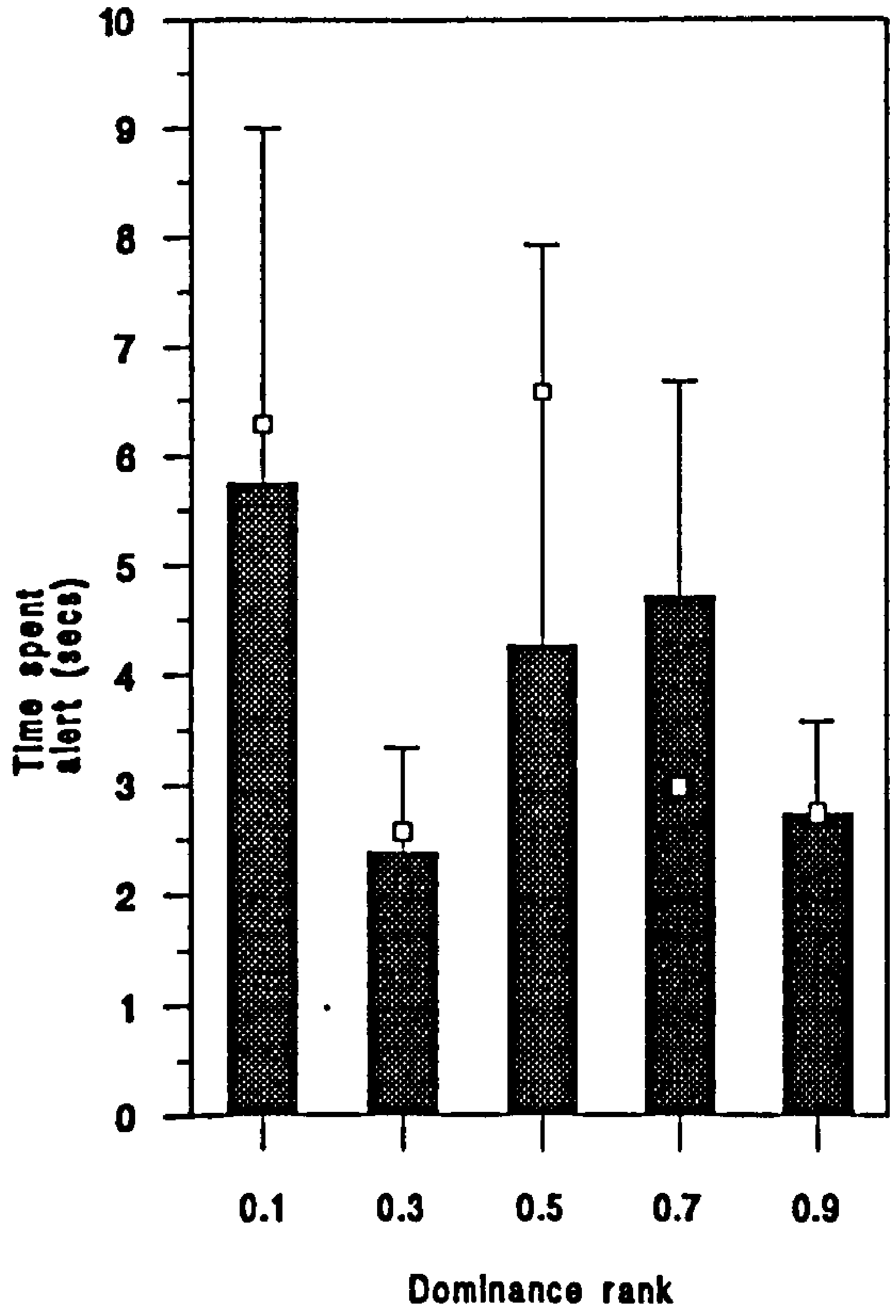


Fig. 6.11. Time spent moving by female Bewick's Swans during 5-min. focal scans with social class (mean and S.E. bar, n=118), plus predicted values from a generalised linear model. (A=adult,Y=yearling,C=cygnet,B=breeding,P=paired,S=single,F=family,T=trio).

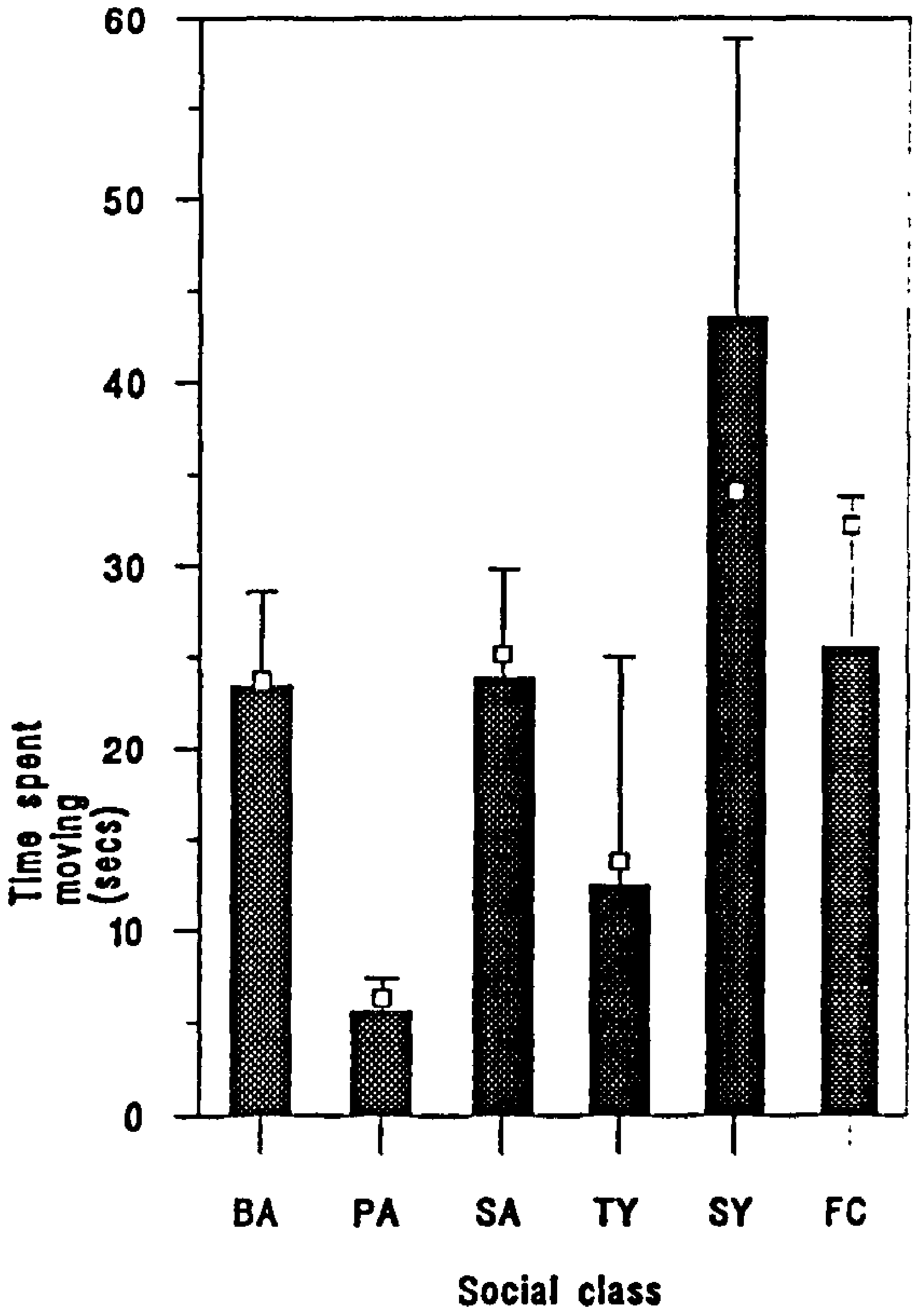


Fig. 6.12. Time spent moving by female Bewick's Swans during 5-minute focal scans at the feeding sites with time of day (mean and S.E. bar, n=118), plus predicted values from a generalised linear model.

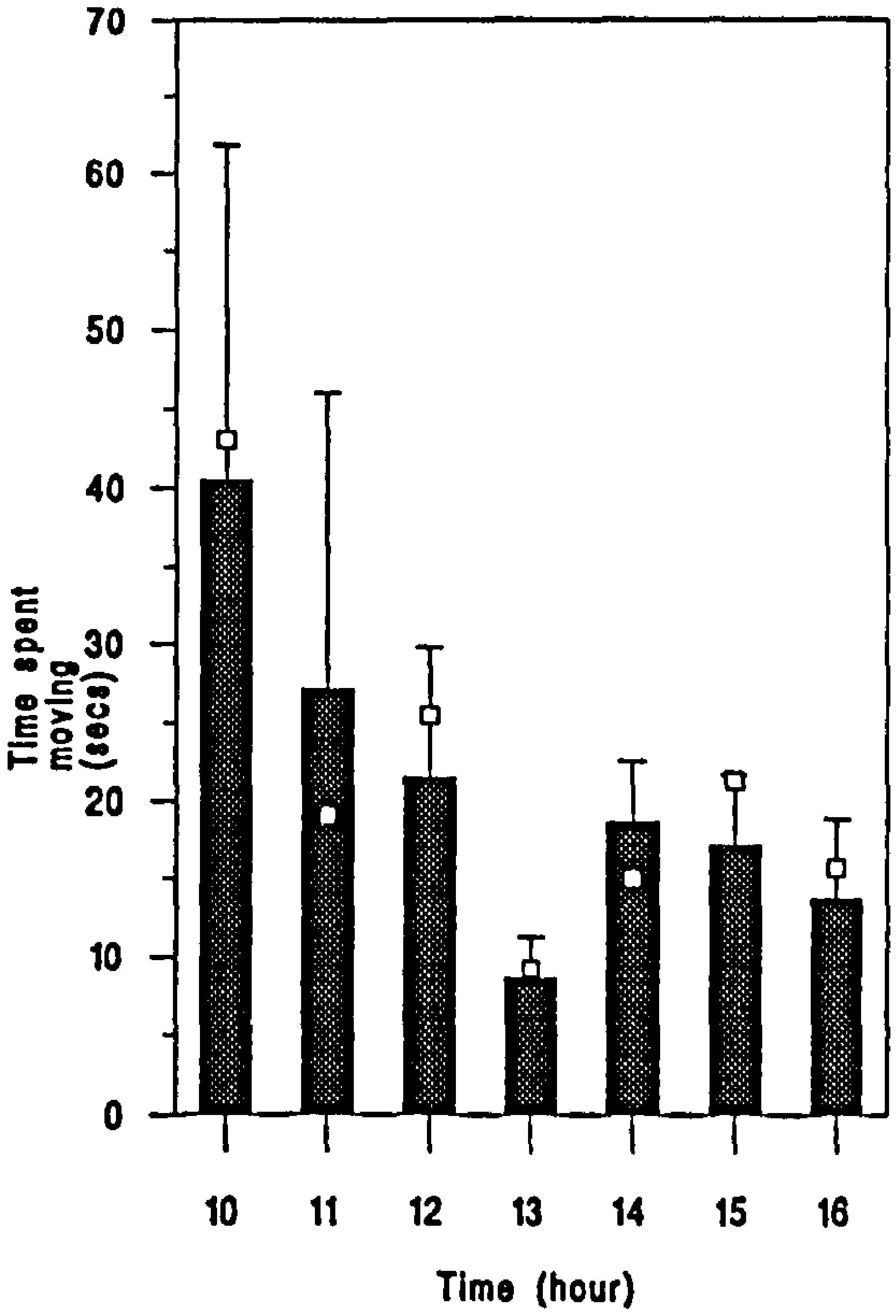


Fig. 6.13. Time spent moving by female Bewick's Swans during 5-minute focal scans at the feeding sites with dominance rank (mean and S.E. bar, n=118), plus predicted values from a generalised linear model.

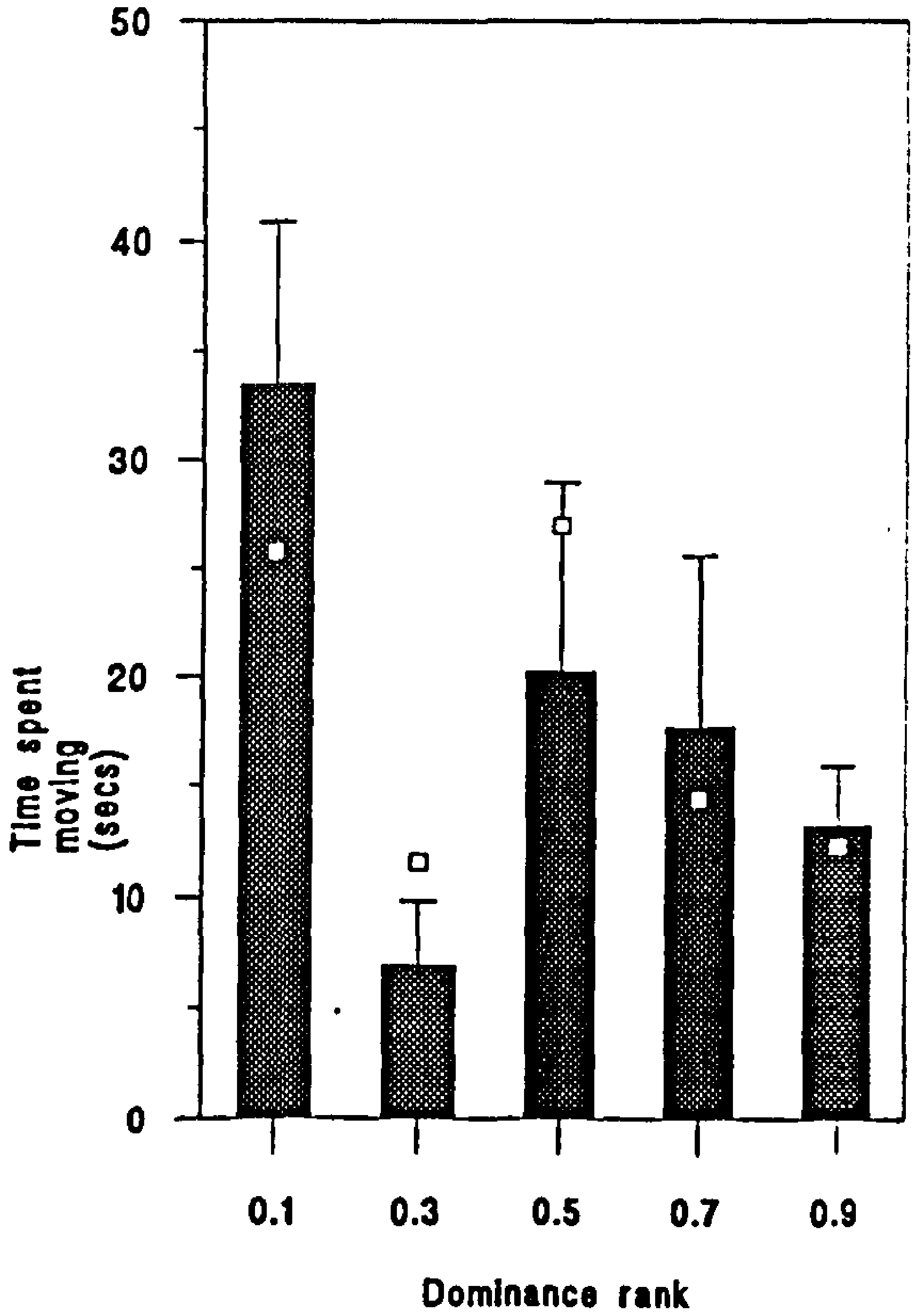


Fig. 6.14. Time spent in social interaction by male Bewick's Swans during 5-min. focal scans with social class (mean & S.E.bar,n=122) plus predicted values from a generalised linear model(A=adult,Y=yearling,C=cygnet,B=breeding,P=paired,S=single,F=family).

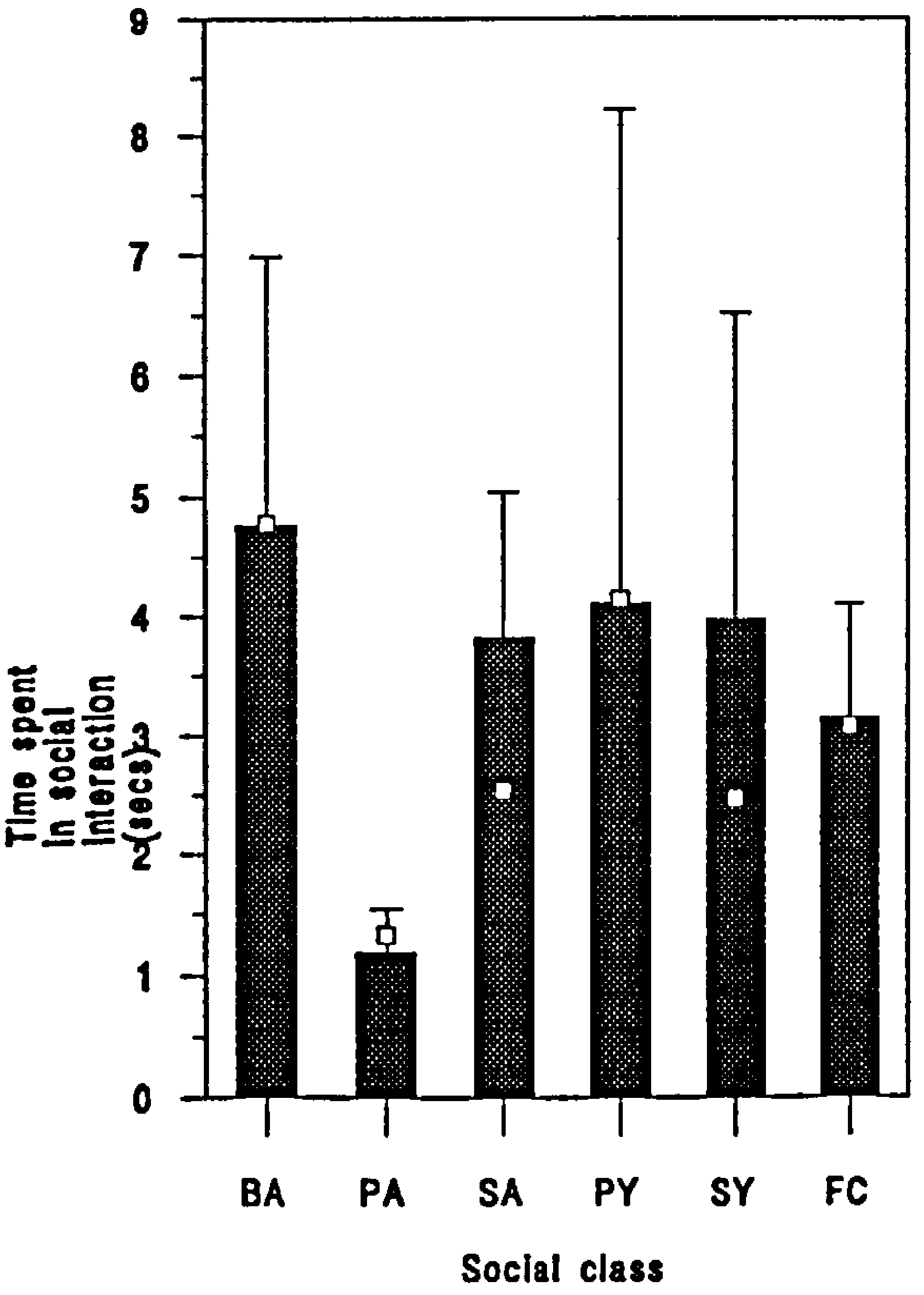


Fig. 6.15. Time spent in social interaction by male Bewick's Swans during five-minute focal scans at the feeding sites by hour (mean and S.E. bar, n=122), plus predicted values from a generalised linear model.

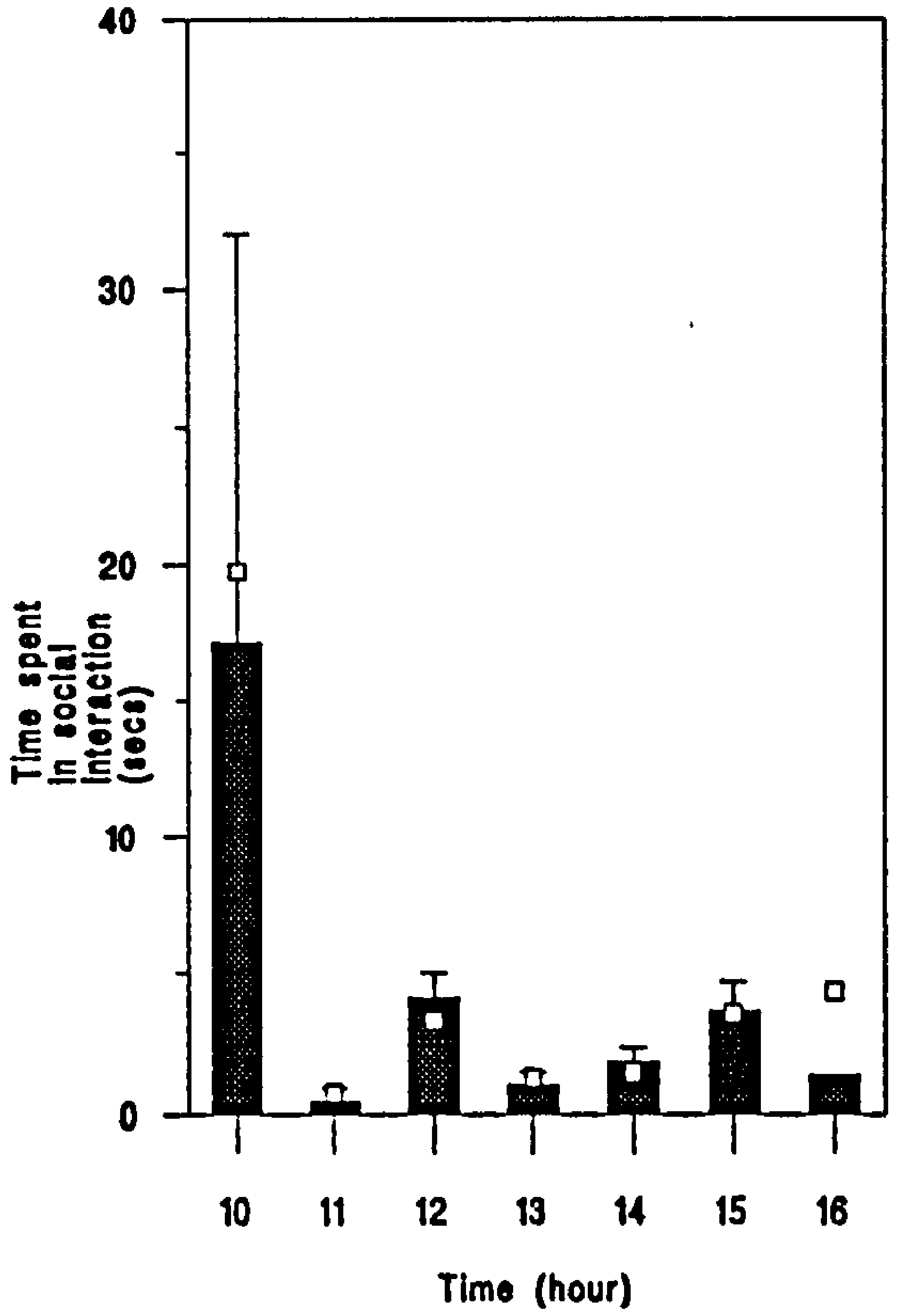


Fig. 6.16. Time spent in social interaction by male Bewick's Swans during five-minute focal scans at the feeding sites with abdominal profile (mean and S.E. bar, n=122), plus predicted values from a generalised linear model.

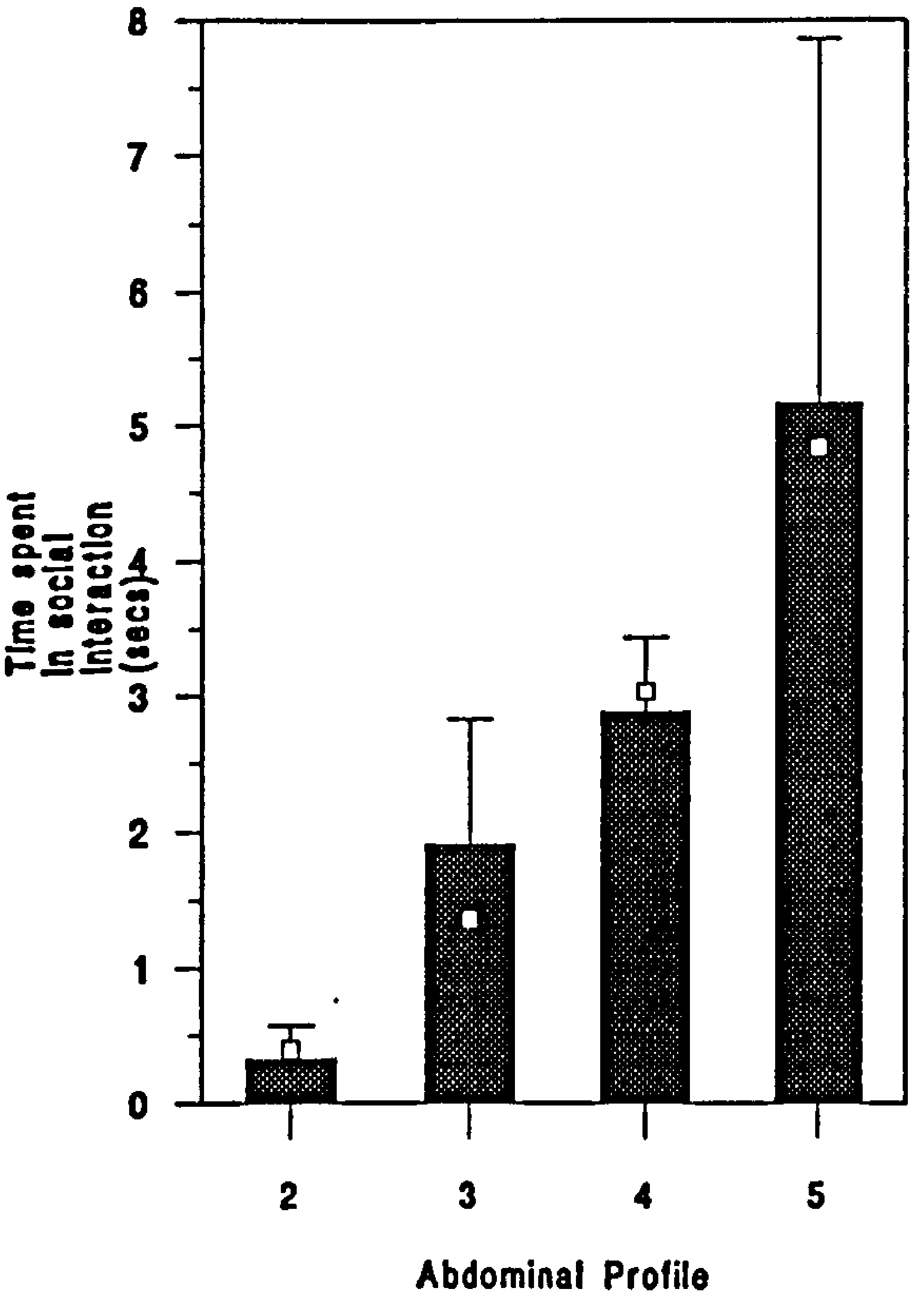


Fig. 6.17. Time spent in social interaction by male Bewick's Swans during five-minute focal scans at the feeding sites with dominance-rank (mean and S.E. bar, n=122), plus predicted values from a generalised linear model.

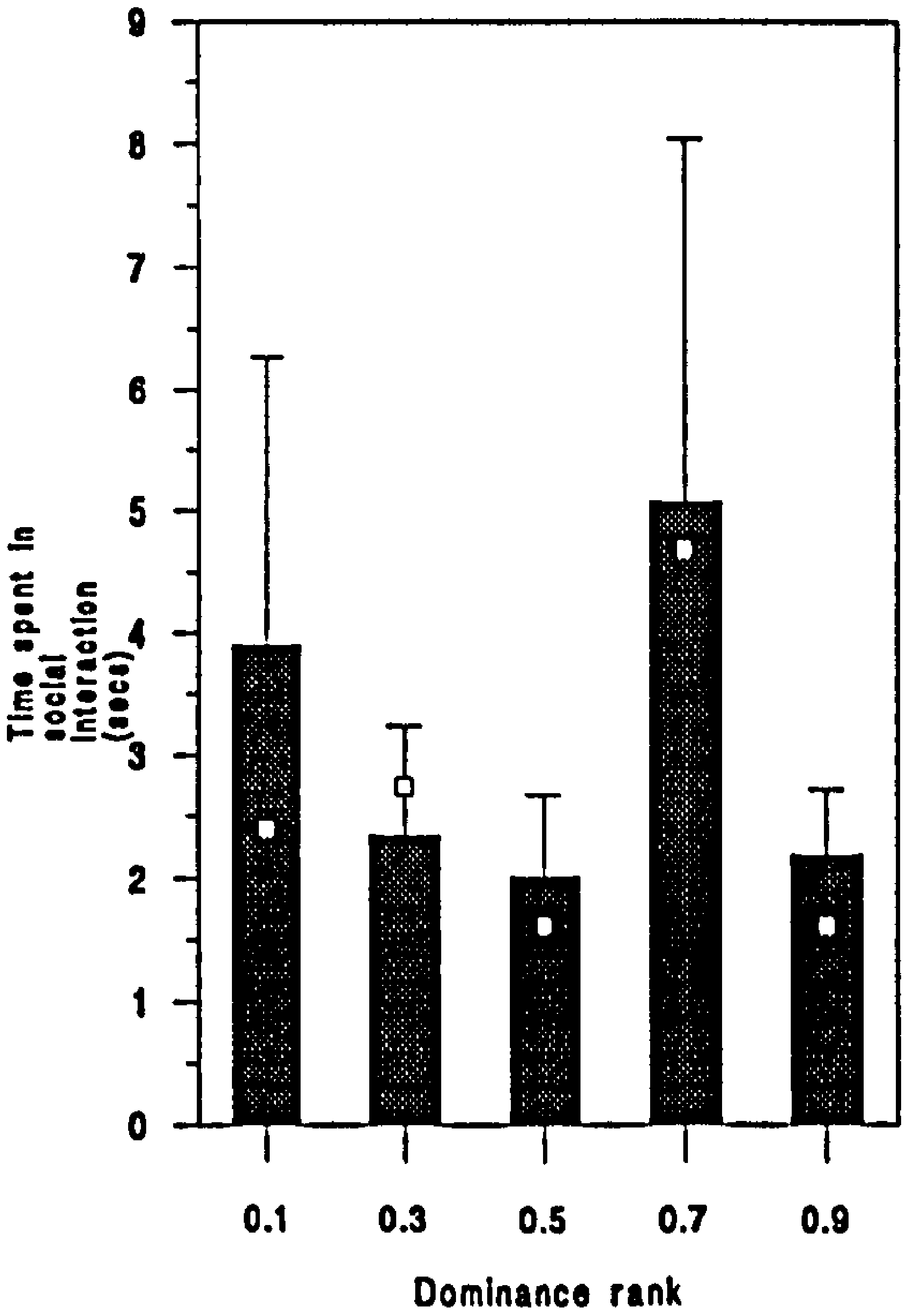


Fig.6.18. Time spent in social interaction by female Bewick's Swans during 5-min focal scans with social class (mean & S.E.bar,n=118),plus predicted values from a generalised linear model. (A=adult,Y=yearling,C=cygnet,B=breeding,P=paired,S=single,F=family)

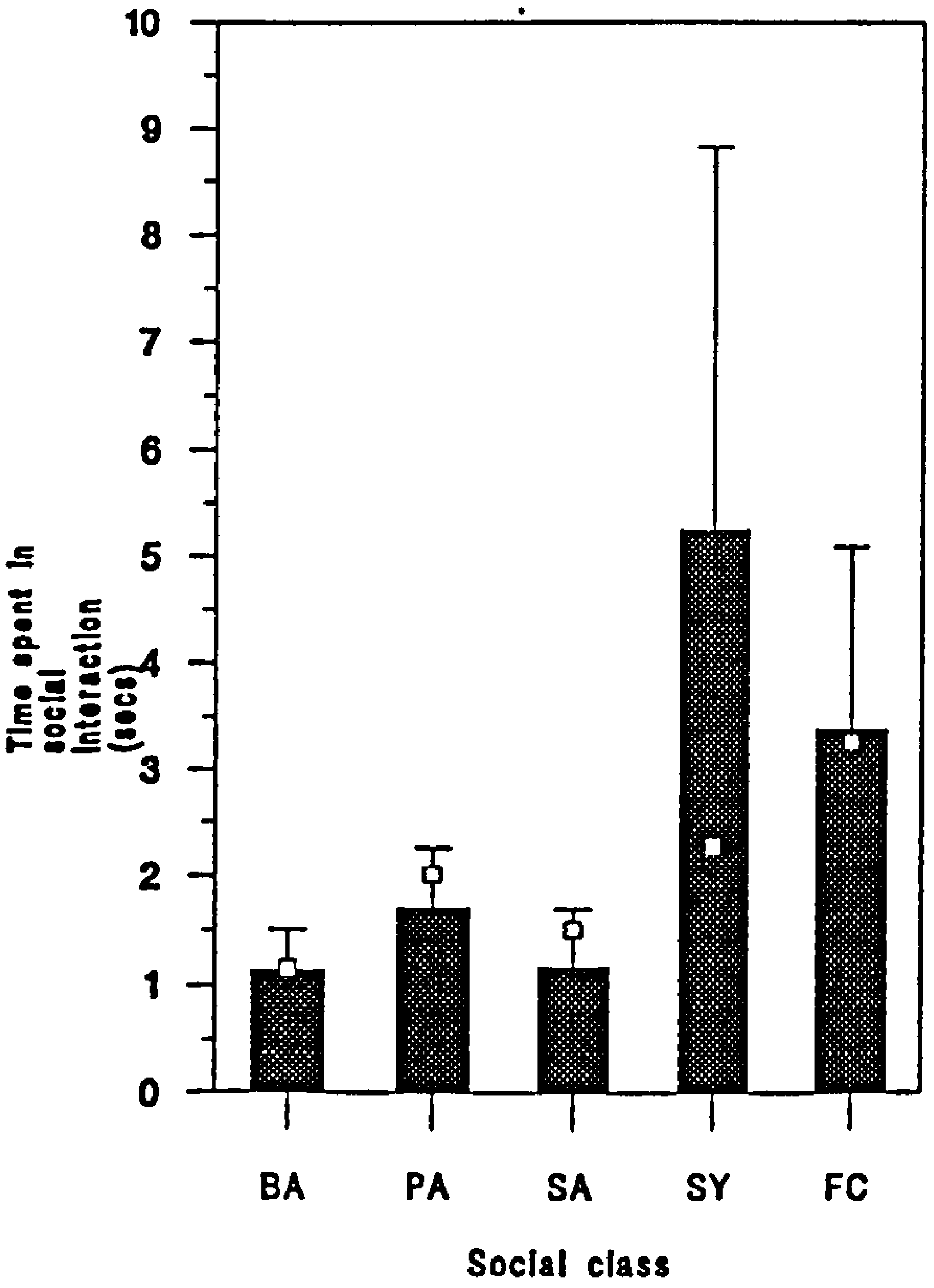


Fig. 6.19. Time spent in social interaction by female Bewick's Swans during five-minute focal scans at the feeding sites with flock size (mean and S.E. bar, n=118), plus predicted values from a generalised linear model.

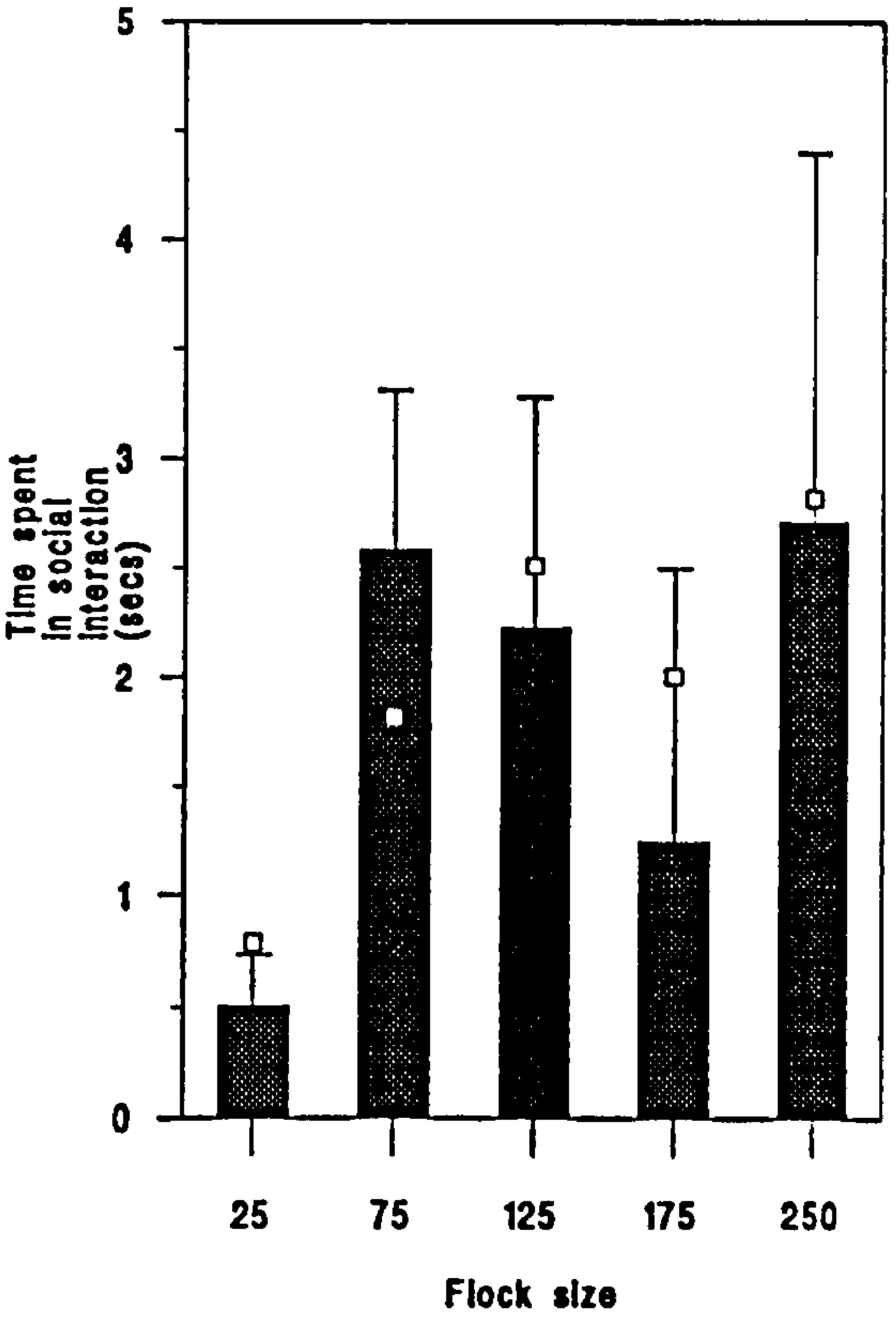


Fig. 6.20. Time spent in social interaction by female Bewick's Swans during five-minute focal scans at the feeding sites by roost group (mean and S.E. bar, n=118), plus predicted values from a generalised linear model.

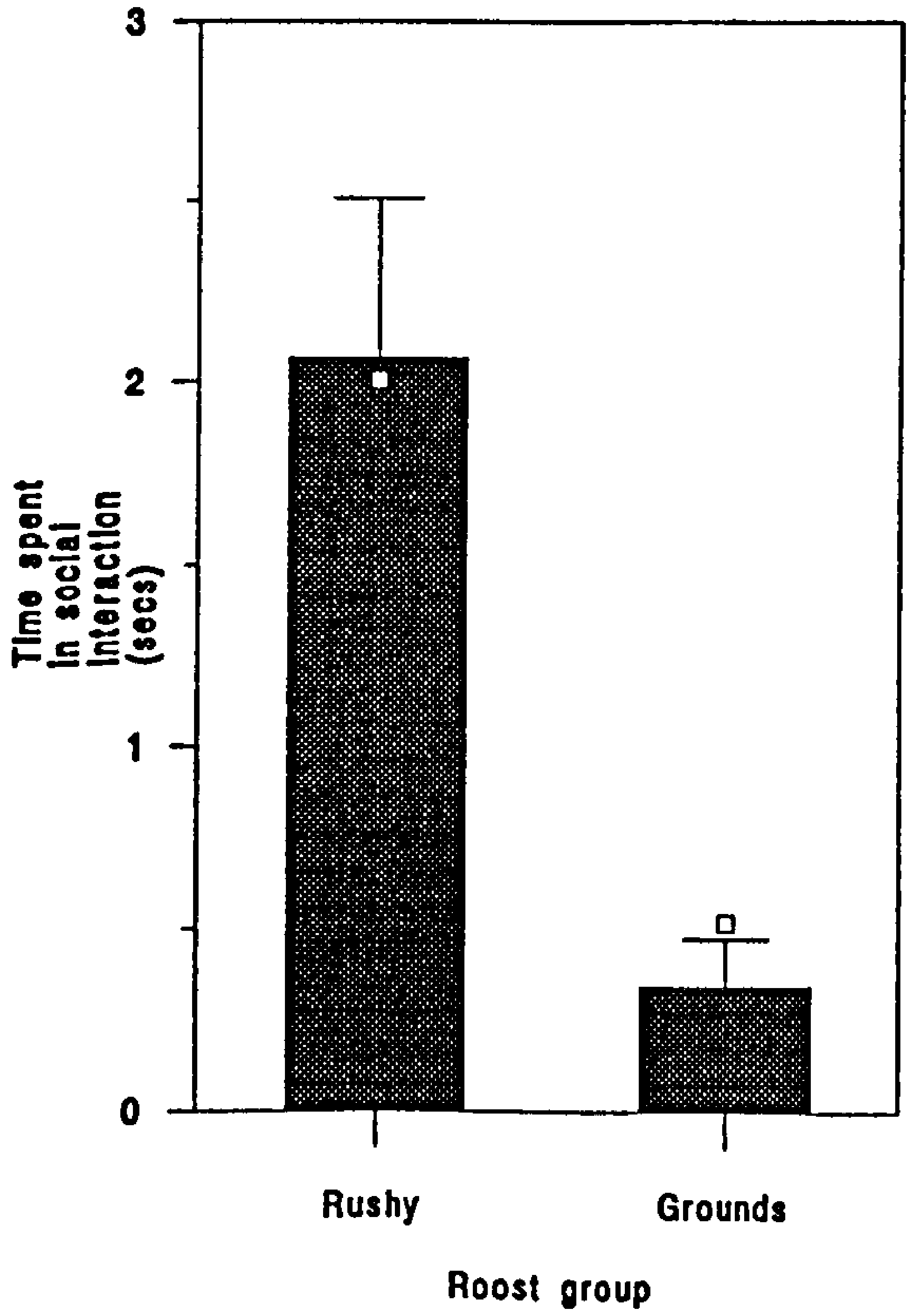


Fig. 6.21. Time spent by female Bewick's Swans in social interaction during five-minute focal scans at the feeding sites with dominance rank (mean and S.E. bar, n=118), plus predicted values from a generalised linear model.

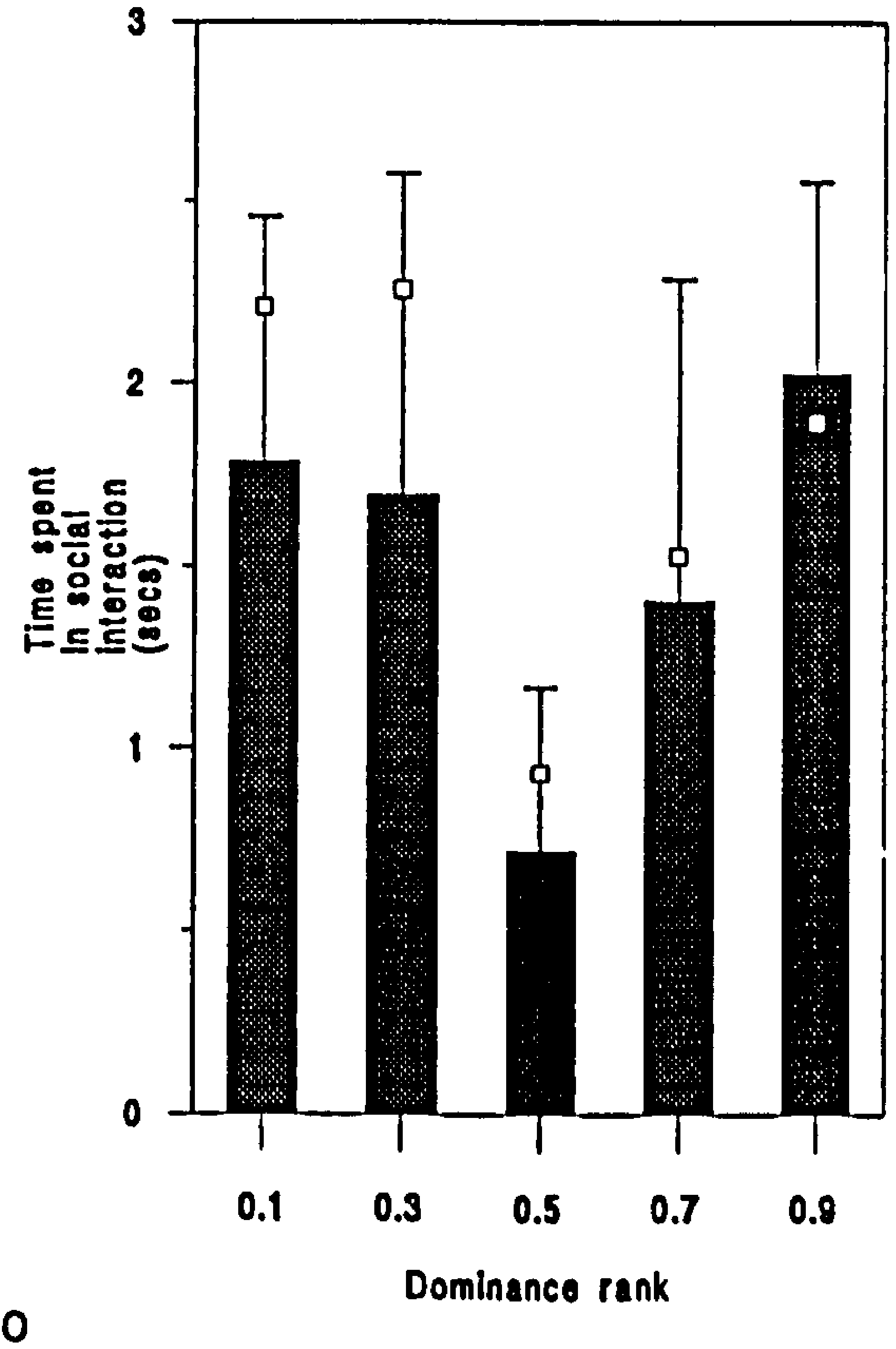


Fig. 6.22. Time spent feeding by male Bewick's Swans during five-minute focal scans at the feeding sites with percentage protein content of the sward (mean and S.E. bar, n=33), plus predicted values from a generalised linear model.

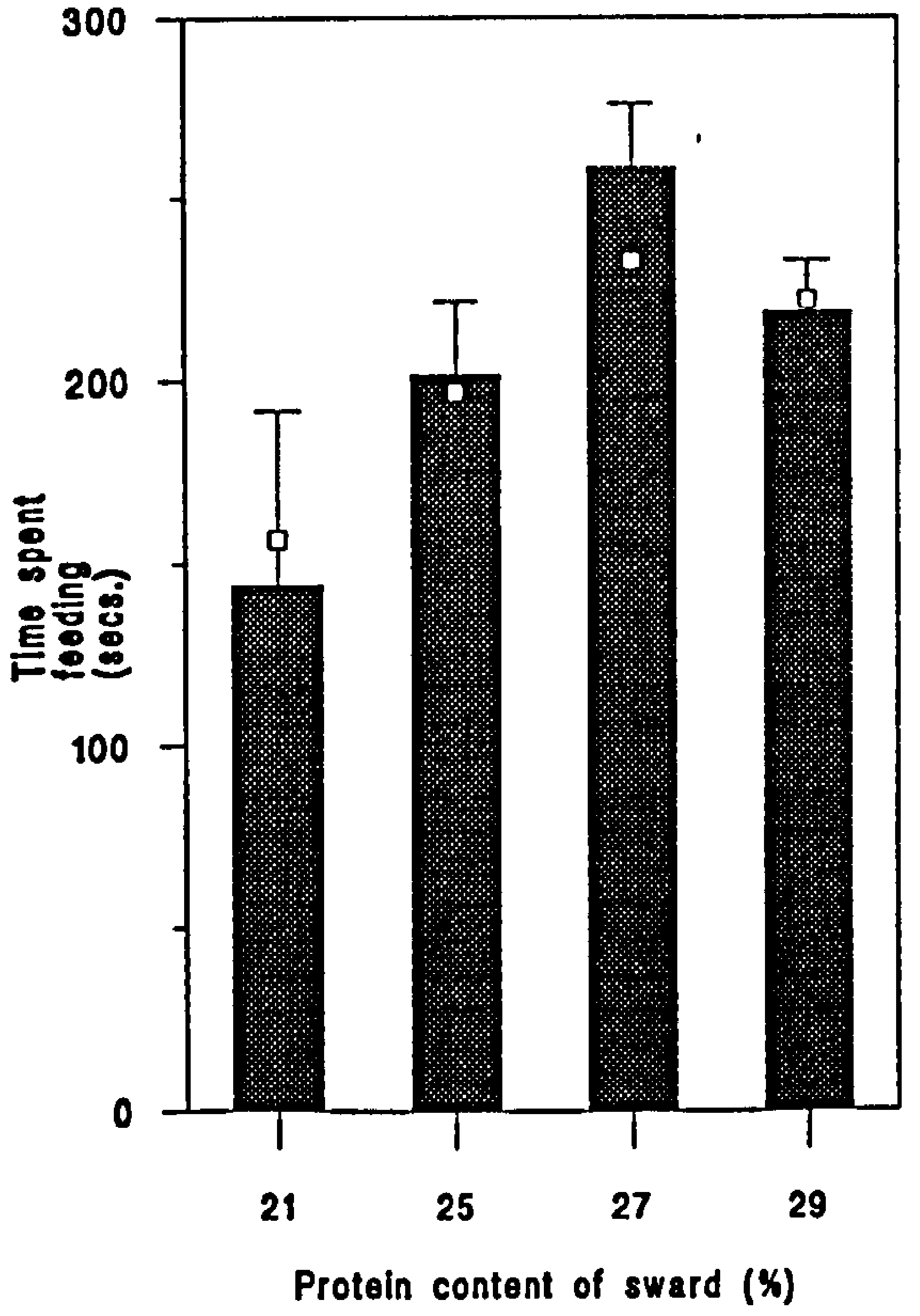


Fig. 6.23. Time spent with head up by male Bewick's Swans during five-minute focal scans at the feeding sites with the percentage protein content of the sward (mean and S.E. bar, n=34), plus predicted values from a generalised linear model.

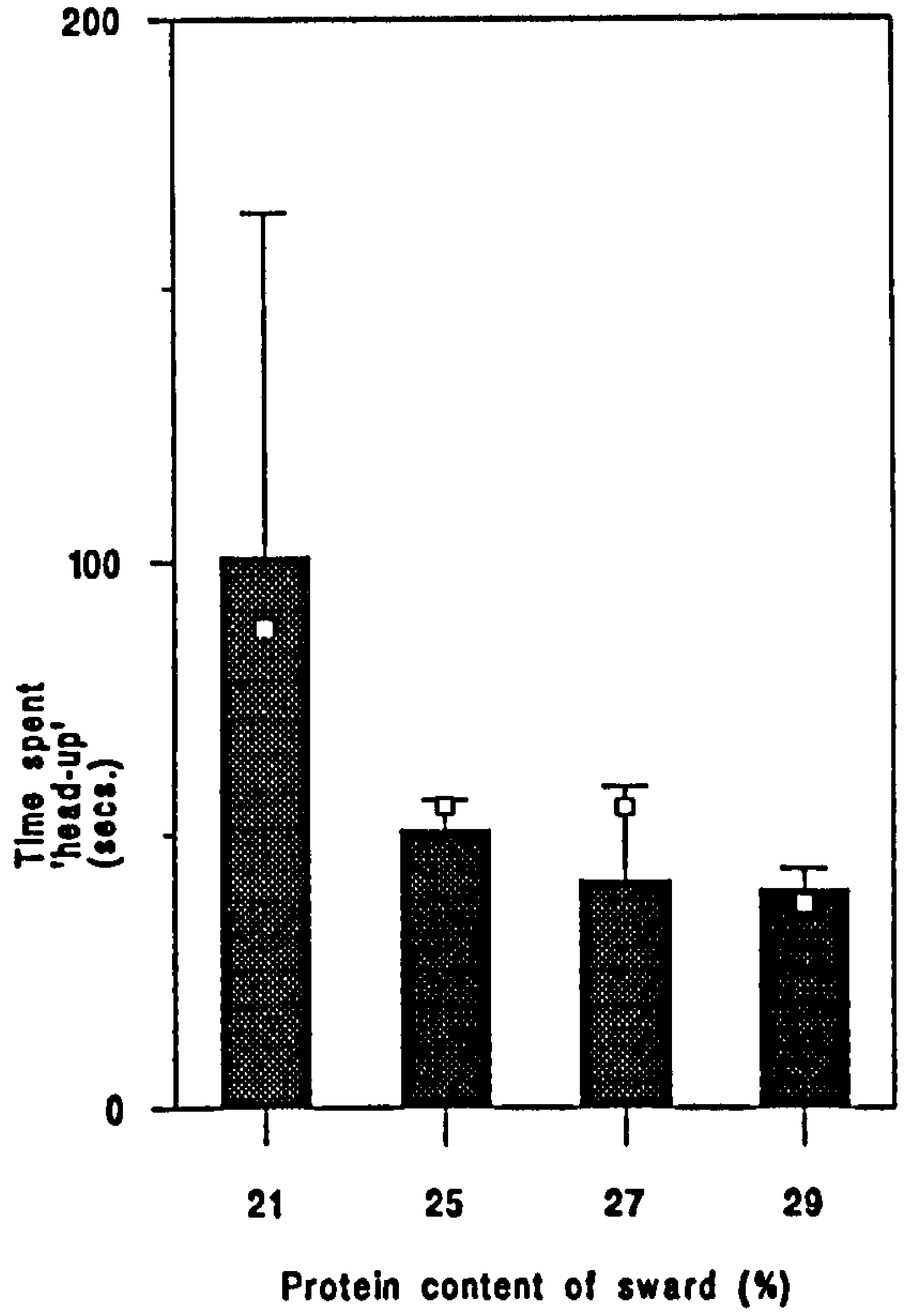


Fig. 6.24. Time spent alert by male Bewick's Swans during five-minute focal scans at the feeding sites with percentage protein content of the sward (mean and S.E. bar, n=34), plus predicted values from a generalised linear model.

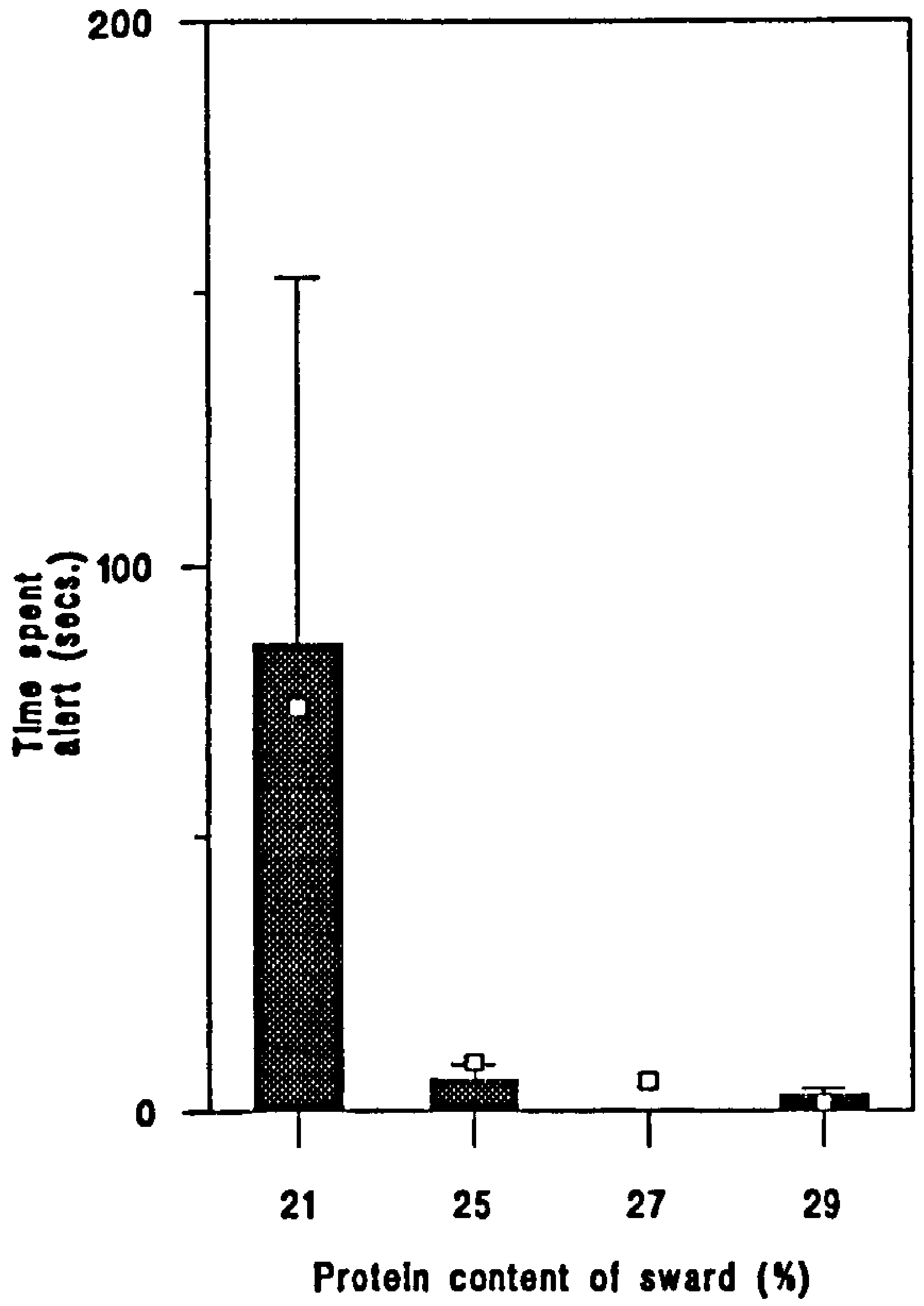


Fig. 6.25. Time spent alert by female Bewick's Swans during five-minute focal scans at the feeding sites with percentage protein content of the sward (mean and S.E. bar, n=35), plus predicted values from a generalised linear model.

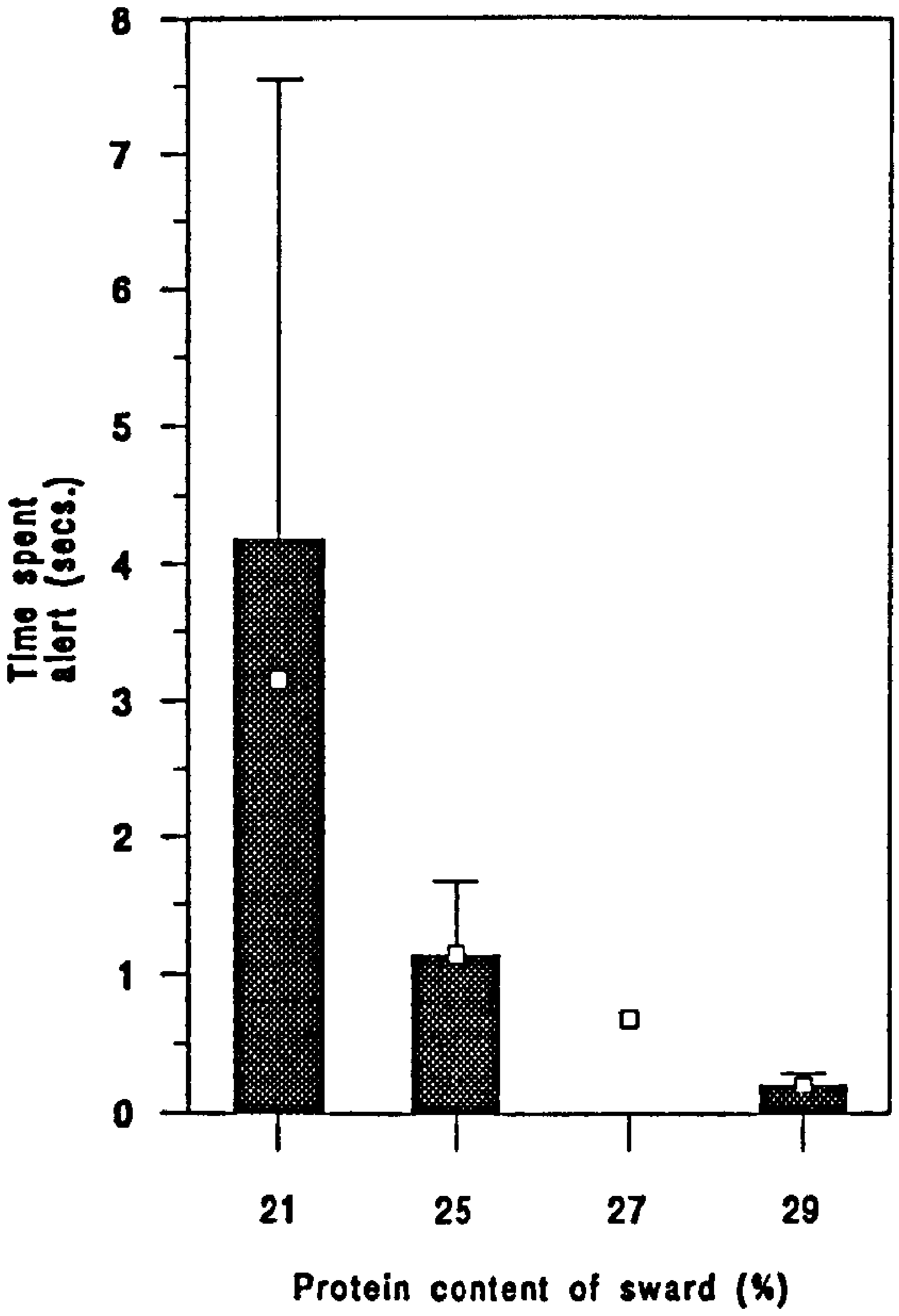
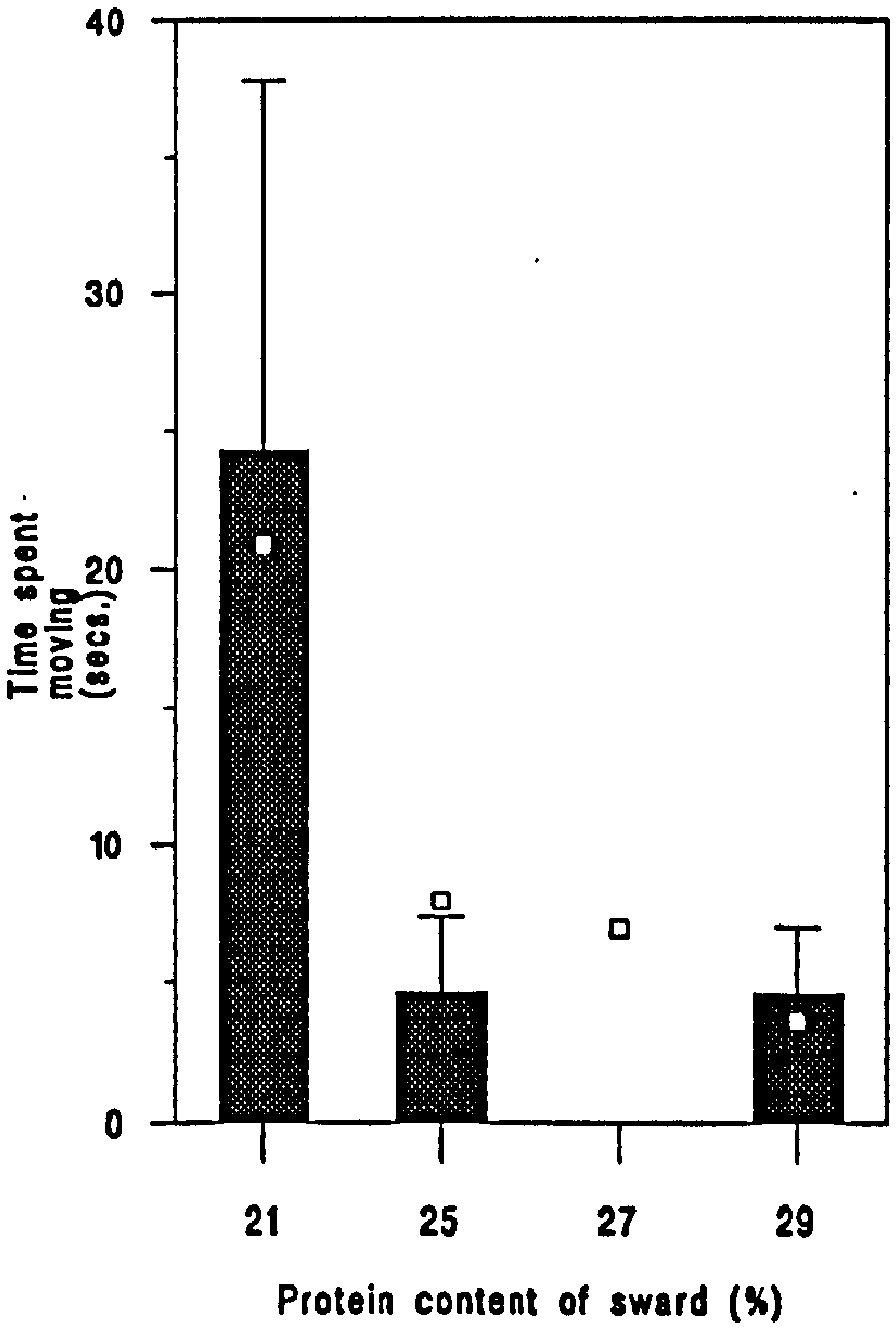


Fig. 6.26. Time spent moving by male Bewick's Swans during five-minute focal scans at the feeding sites (mean and S.E. bar, n=34), plus predicted values from a generalised linear model.



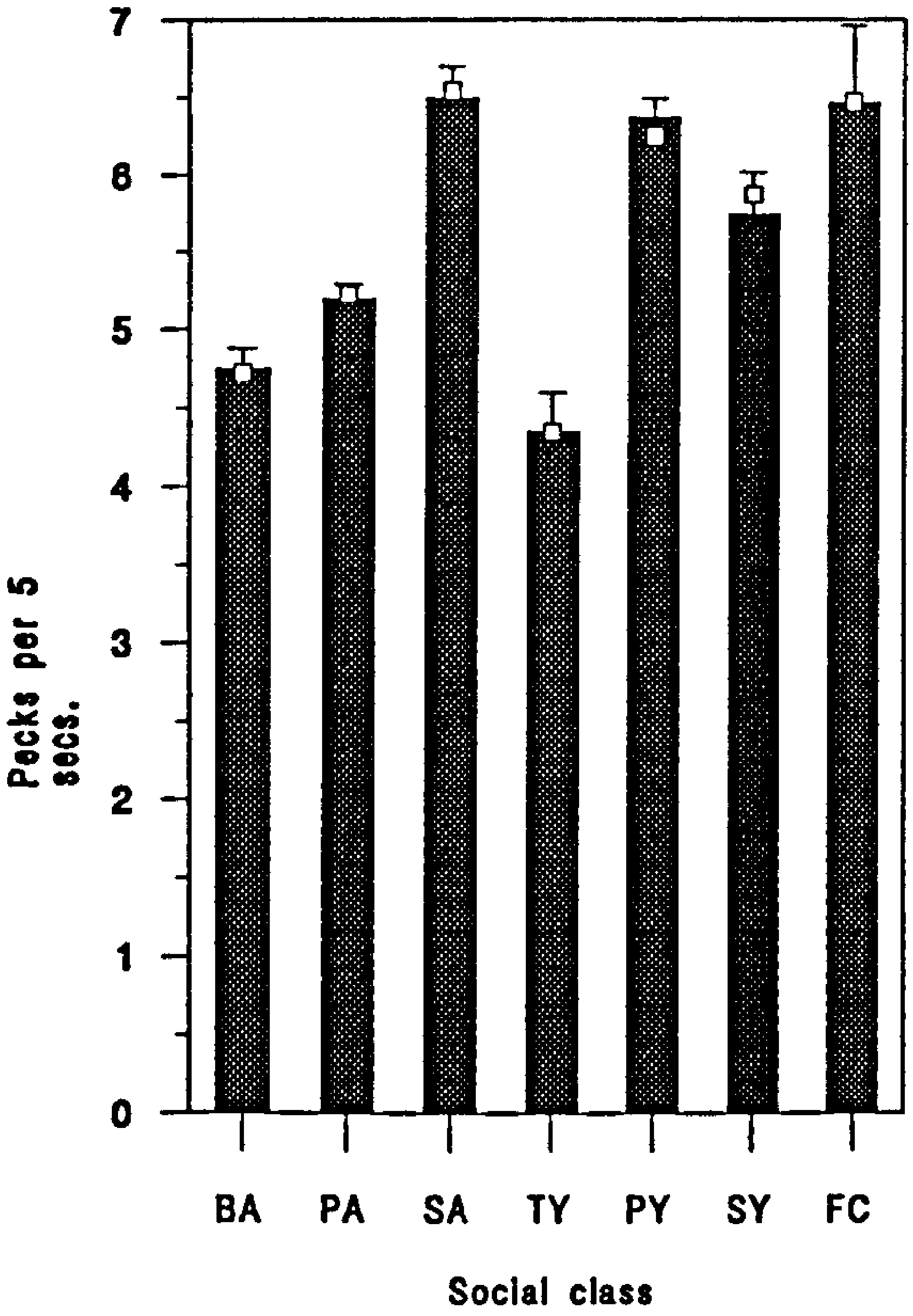


Fig. 6.27. Peck rates of male Bewick's Swans feeding on grass swards according to social class (mean and S.E. bar, n=607) plus predicted values from a generalised linear model. (A=adult,Y=yearling,C=cygnet,B=breeding,P=paired,S=singleton,T=trio,F=family).

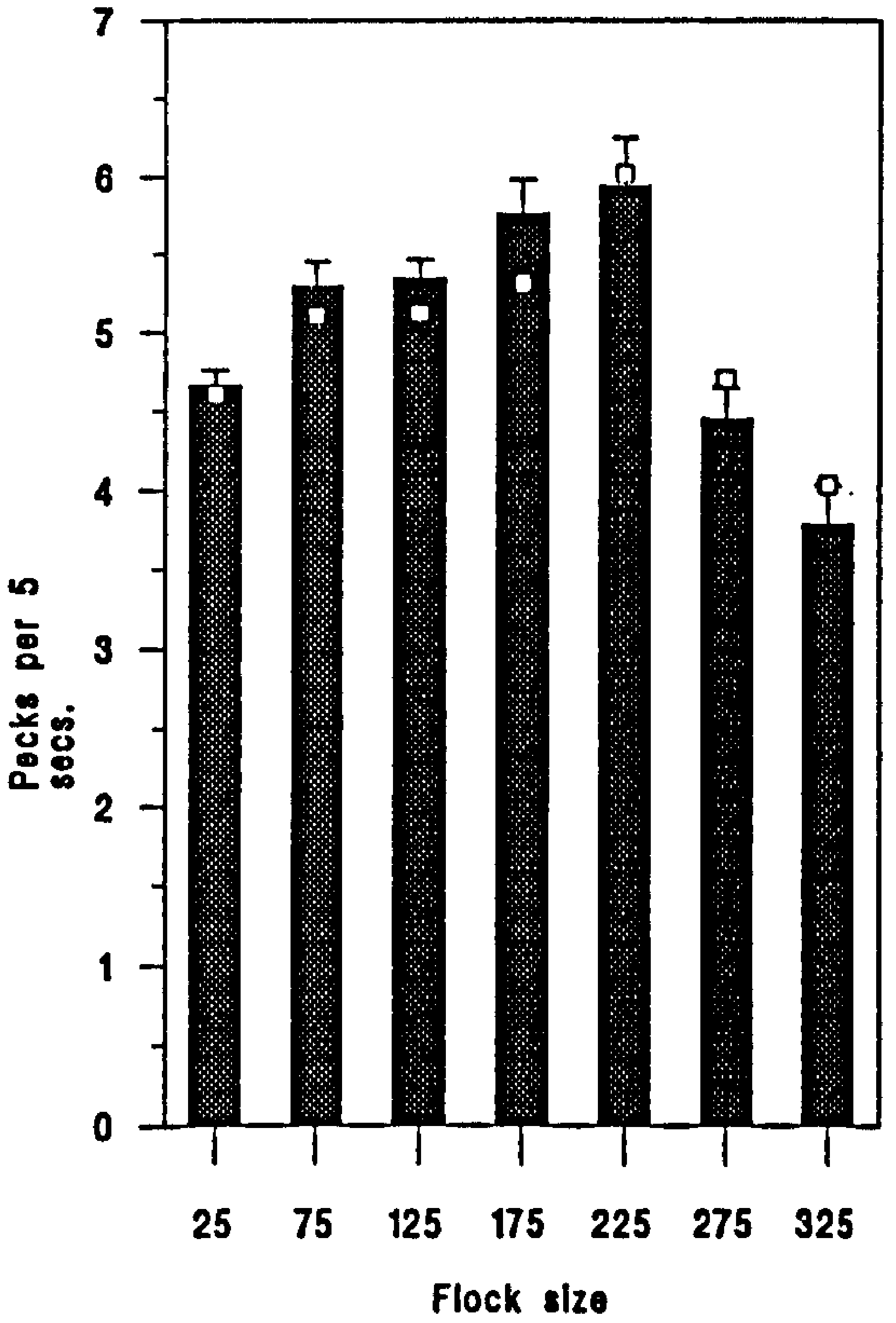


Fig.6.28. Peck rates of male Bewick's Swans feeding on grass swards with flock size (mean plus S.E. bar, n = 607), plus predicted values from a generalised linear model.

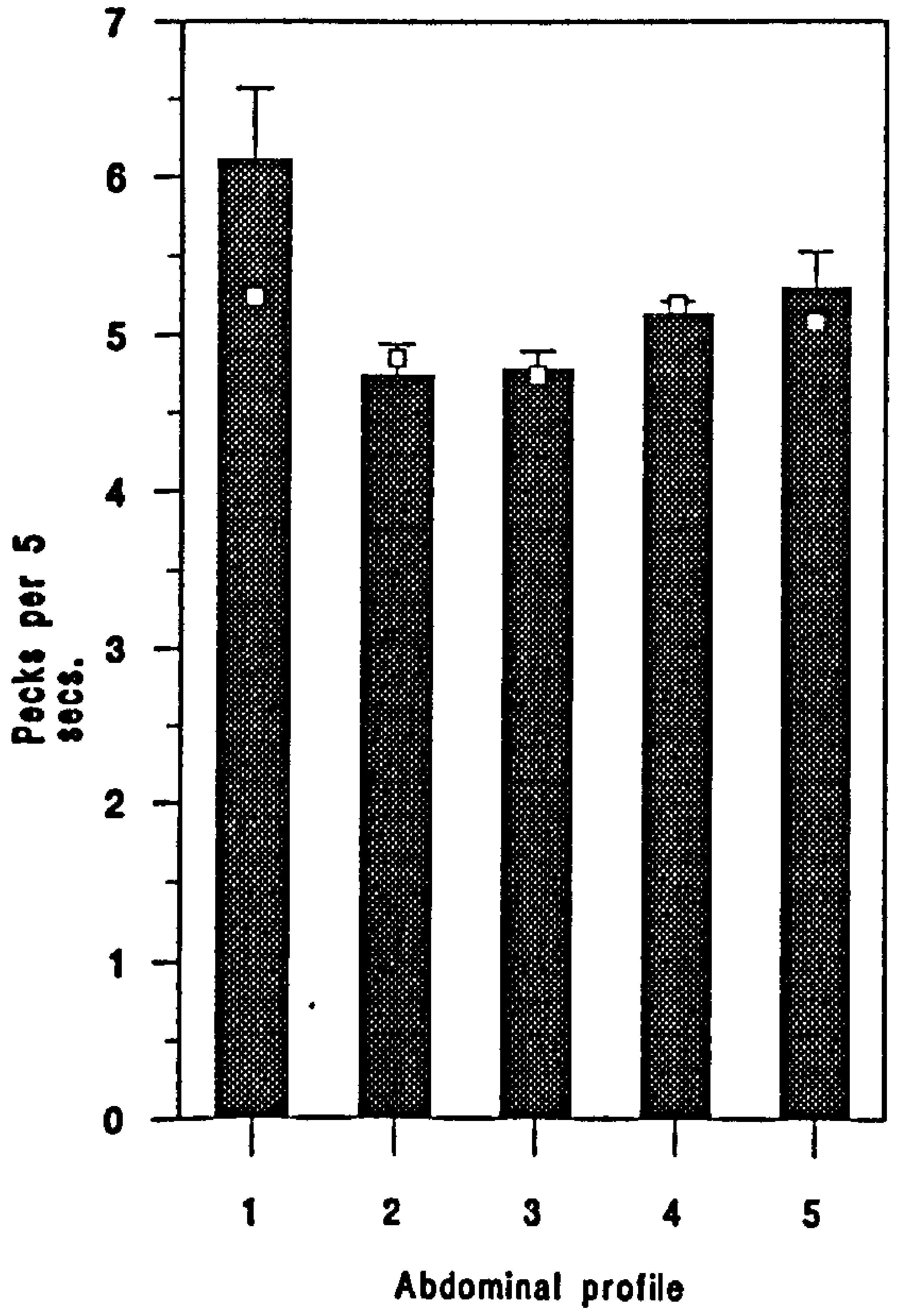


Fig. 6.29. Peck rates of male Bewick's Swans feeding on grass swards with abdominal profile (mean plus S.E. bar, n = 603), plus predicted values from a generalised linear model.

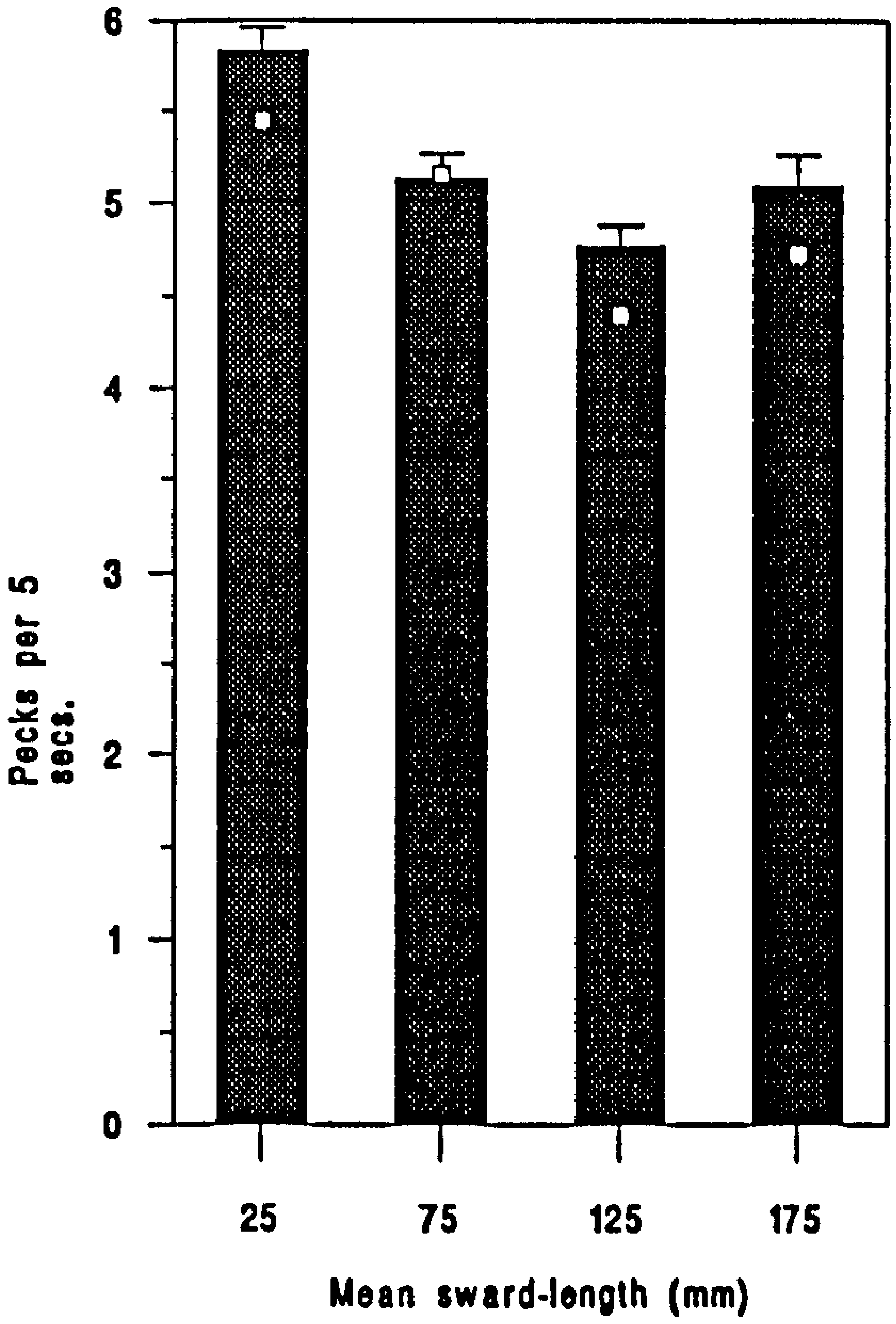


Fig. 6.30. Peck-rates of male Bewick's Swans feeding on grass pasture with mean sward-length (mean plus S.E. bar, n=397), plus predicted values from a generalised linear model.

Fig. 6.31. Peck rates of male Bewick's Swans feeding on grass pasture with water cover of field (mean and S.E. bar, n=397), plus predicted values from a generalised linear model.

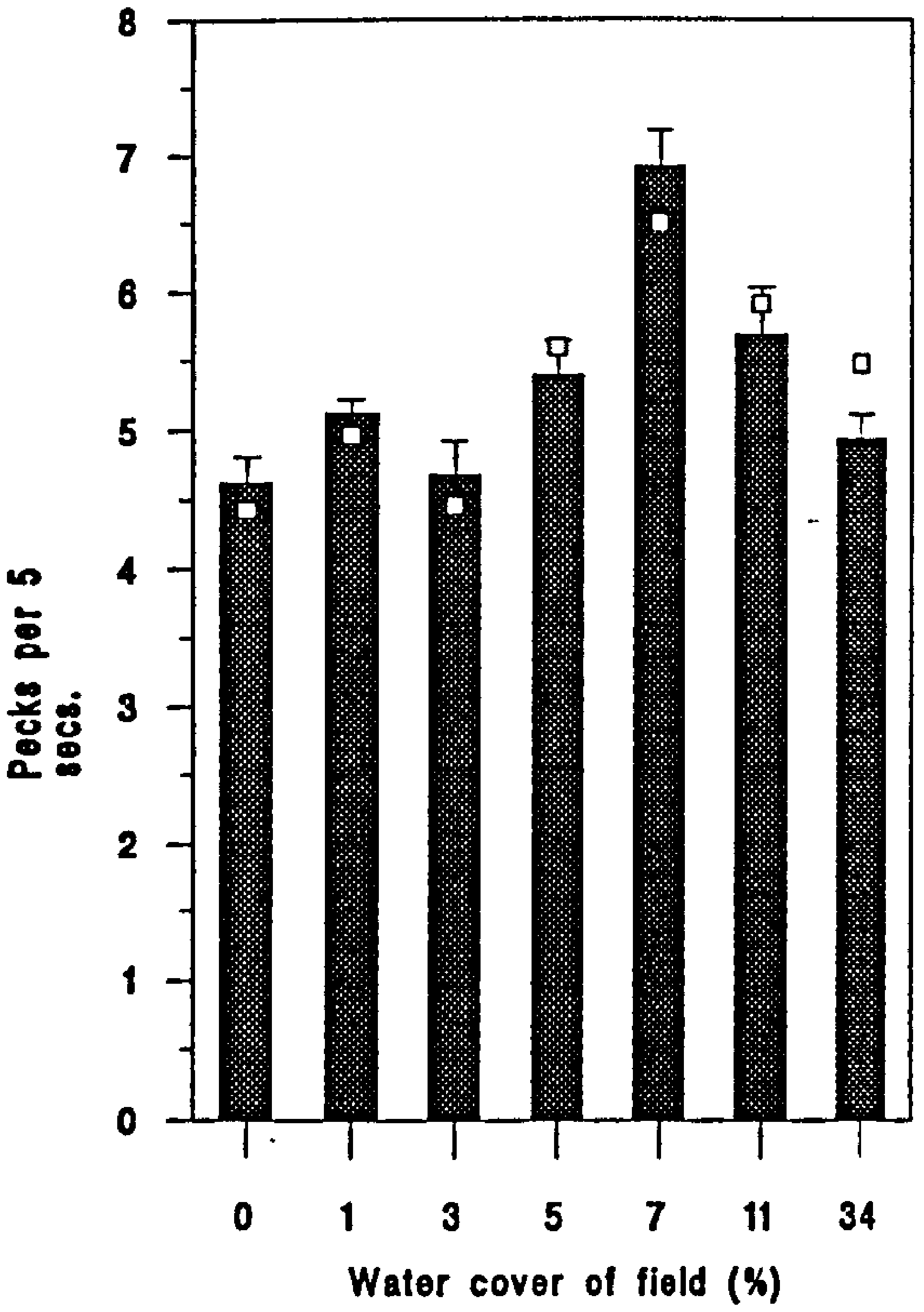


Fig. 6.32. Peck rates of female Bewick's Swans feeding on grass swards according to social class (mean and S.E. bar, n=682), plus predicted values from a generalised linear model(A=adult,Y=yearling,C=cygnet,B=breeding,P=paired,S=singleton,T=trio,F=family).

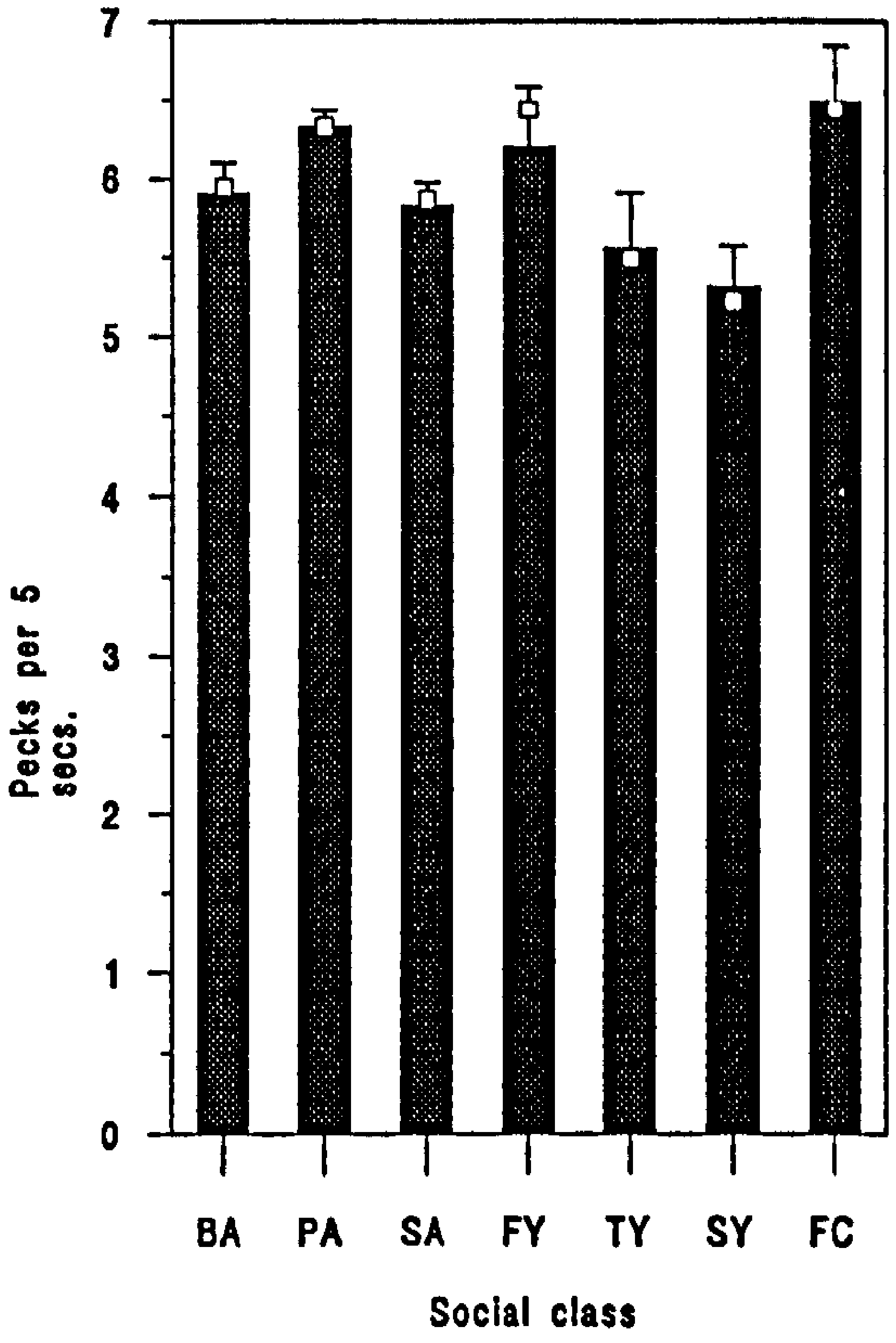


Fig. 6.33. Peck-rates of female Bewick's Swans feeding on grass swards with flock size (mean plus S.E. bar, n=686), plus predicted values from a generalised linear model.

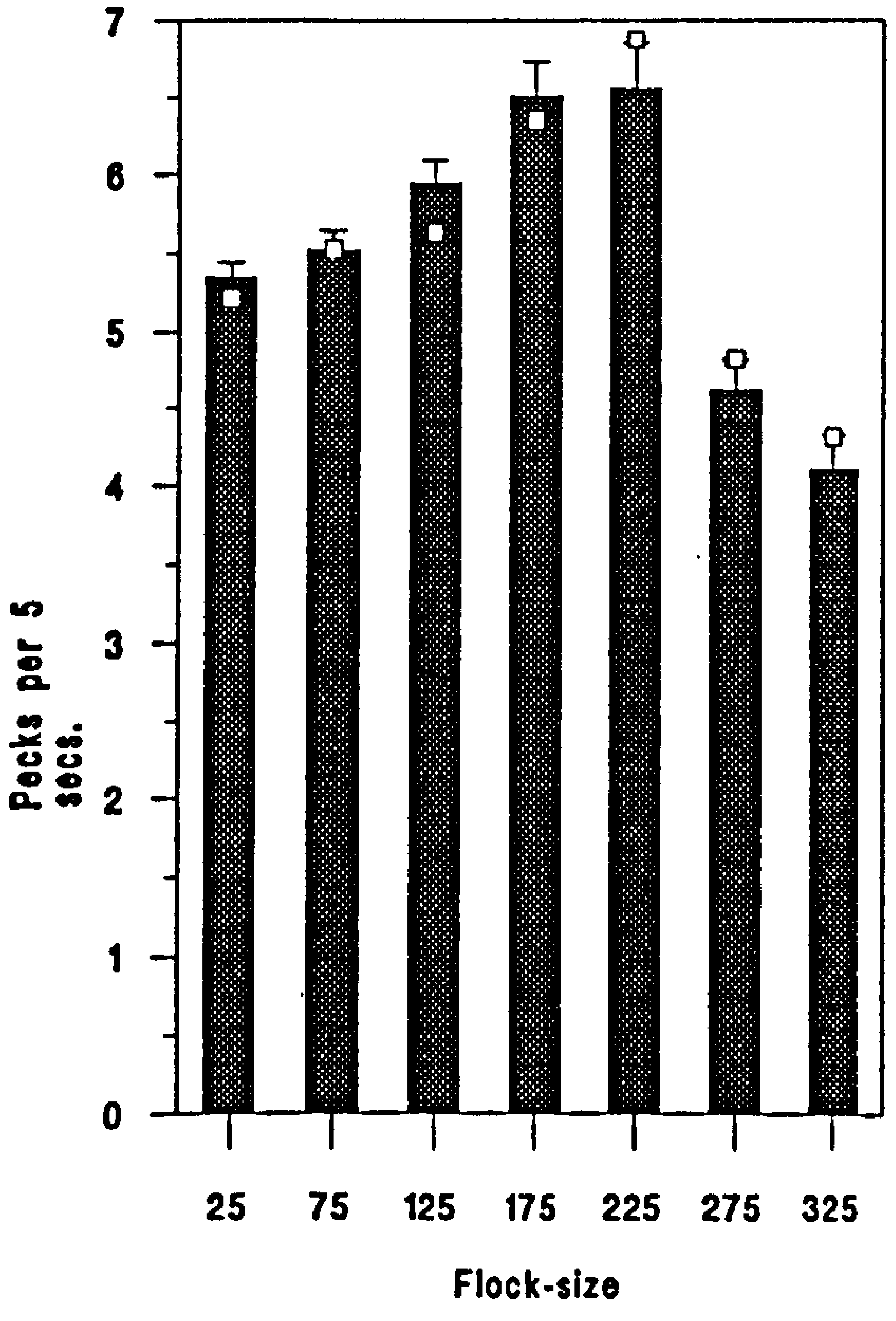


Fig. 6.34. Peck rates of female Bewick's Swans feeding on grass swards with abdominal profile (mean plus S.E. bar, n = 682), plus predicted values from a generalised linear model.

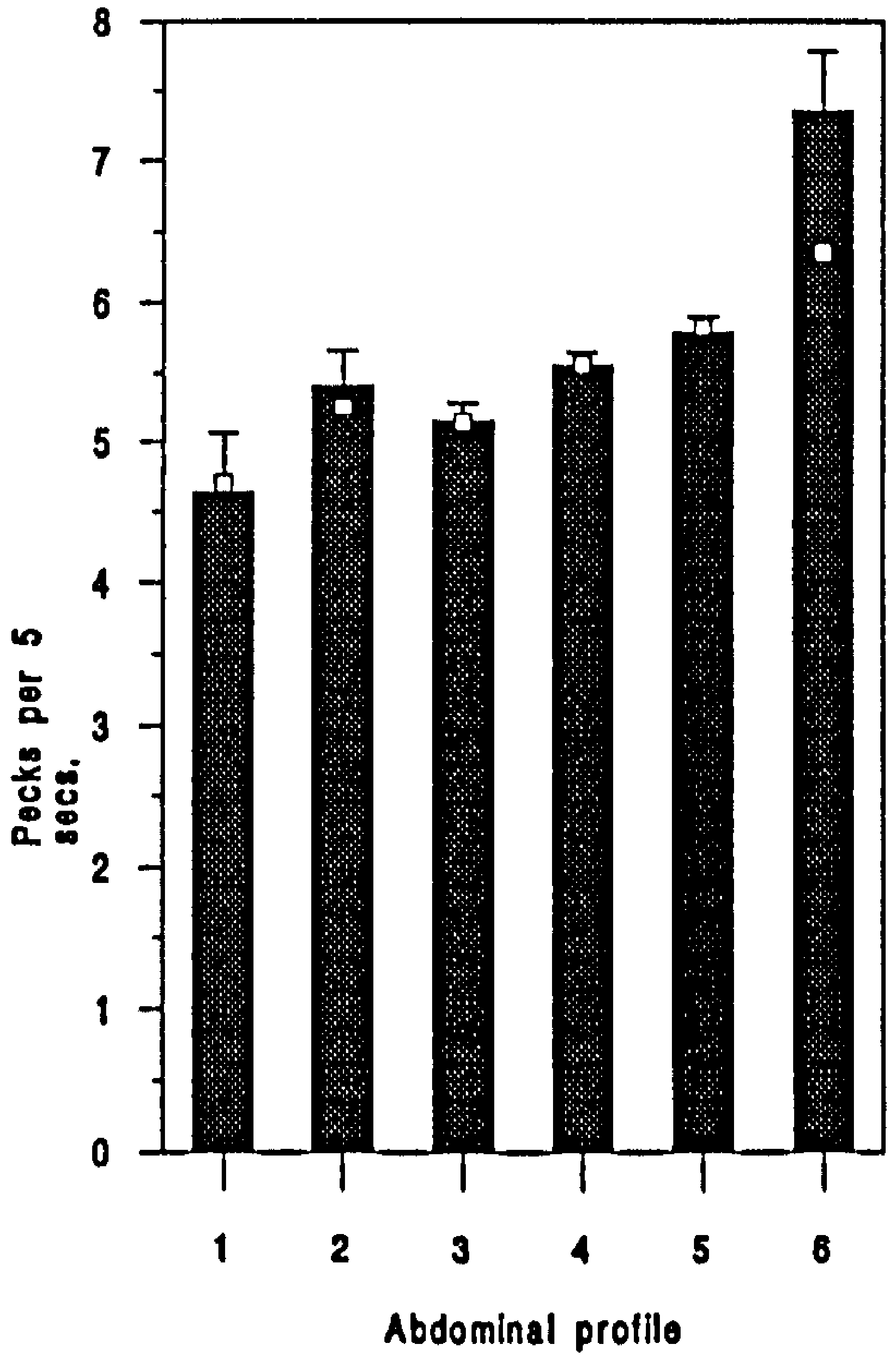


Fig. 6.35. Peck-rates of female Bewick's Swans feeding on grass swards with mean sward-length (mean plus S.E. bar, n=386), plus predicted values from a generalised linear model.

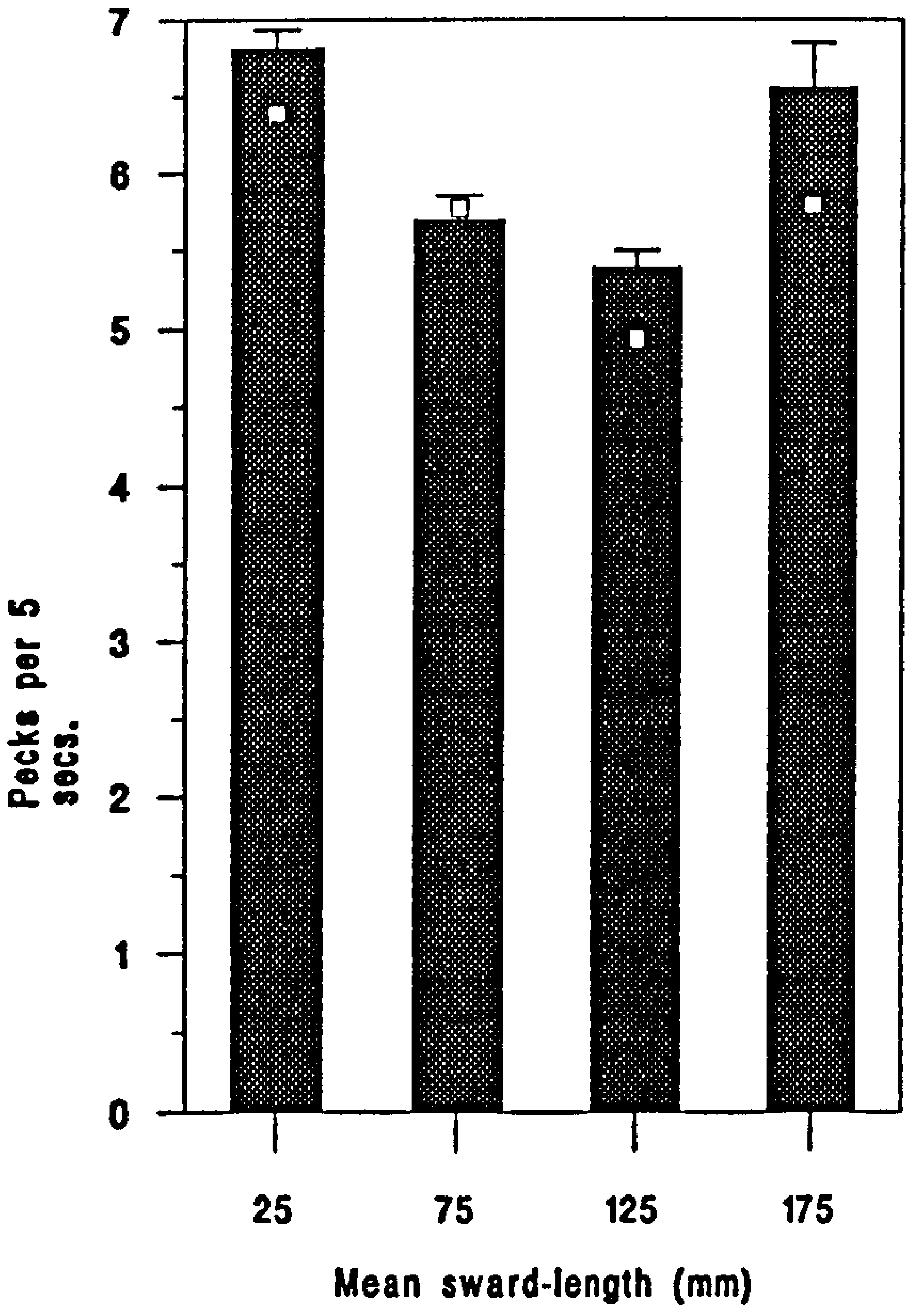


Fig. 6.36. Peck rates of female Bewick's Swans feeding on grass pasture with water cover of field (mean and S.E. bar, n=386), plus predicted values from a generalised linear model.

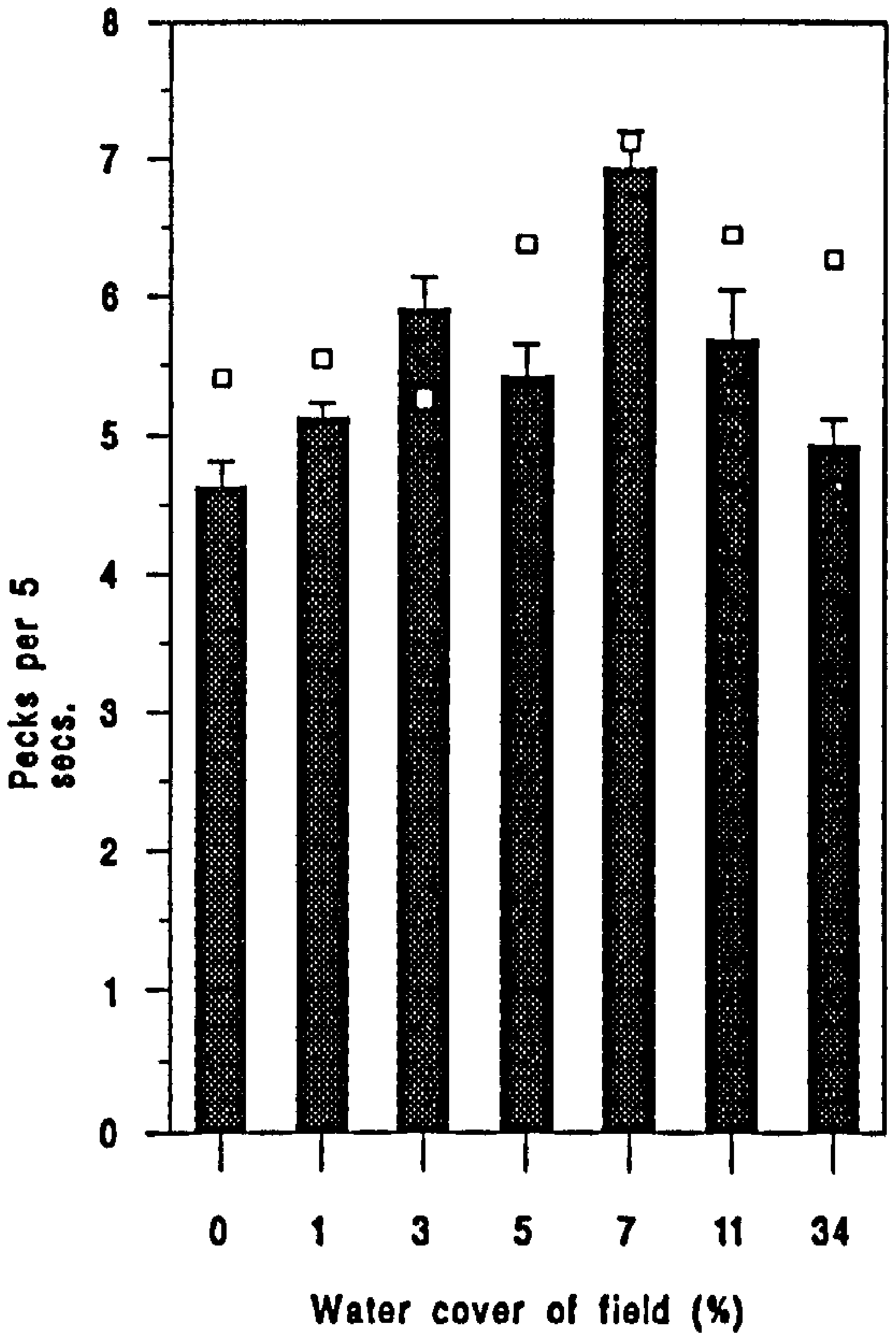


Fig.6.37. Time spent with head-up per 50 pecks amongst male Bewick's Swans feeding on grass swards (mean plus S.E. bar, n=593), plus predicted values from a generalised linear model (B=breeding,P=paired,S=single,A=adult,Y=yearlingC=cygnet,T=trio,F=family).

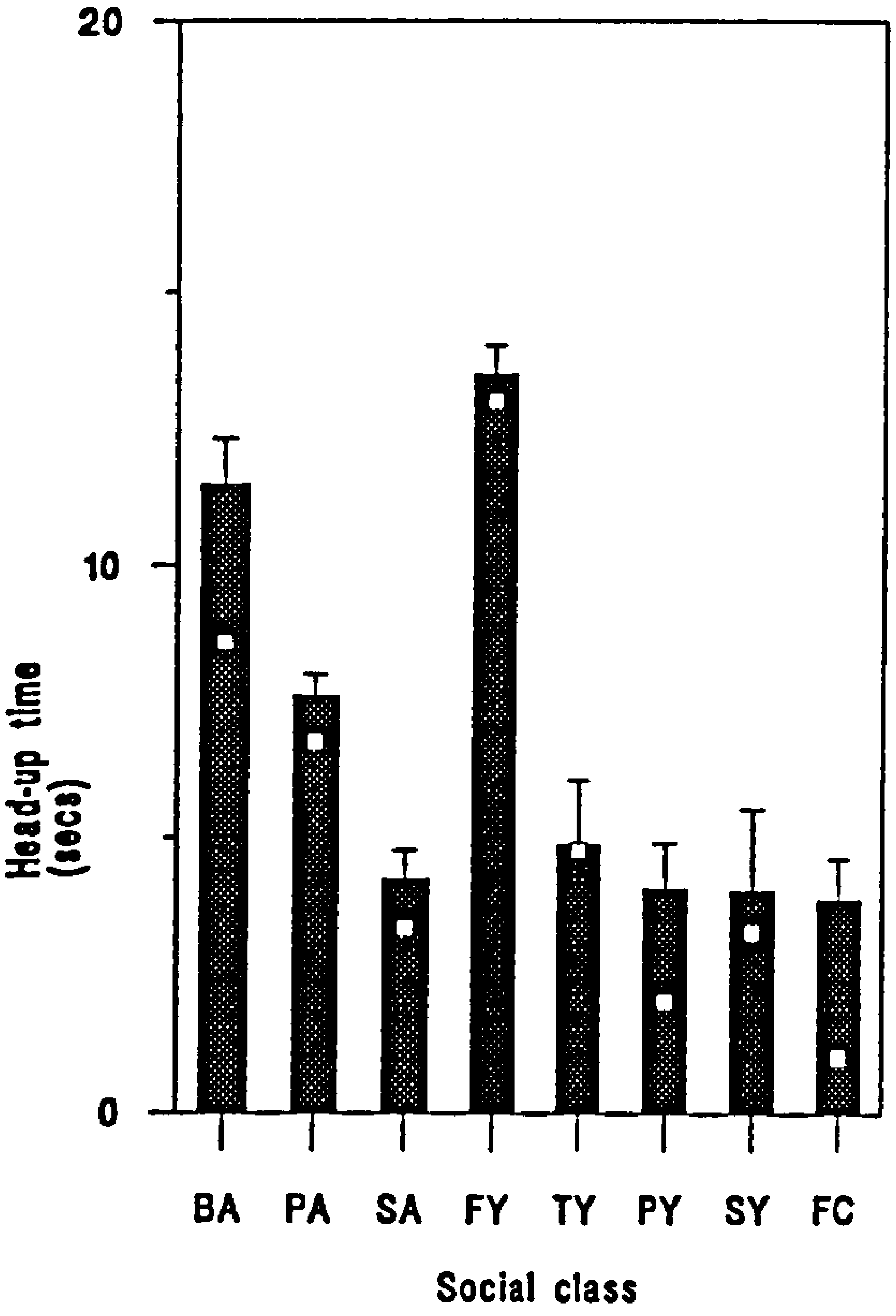


Fig. 6.38. Time spent with head-up per 50 pecks by male Bewick's Swans feeding on grass swards with month (mean and S.E. bar, n=593) plus predicted values from a generalised linear model.

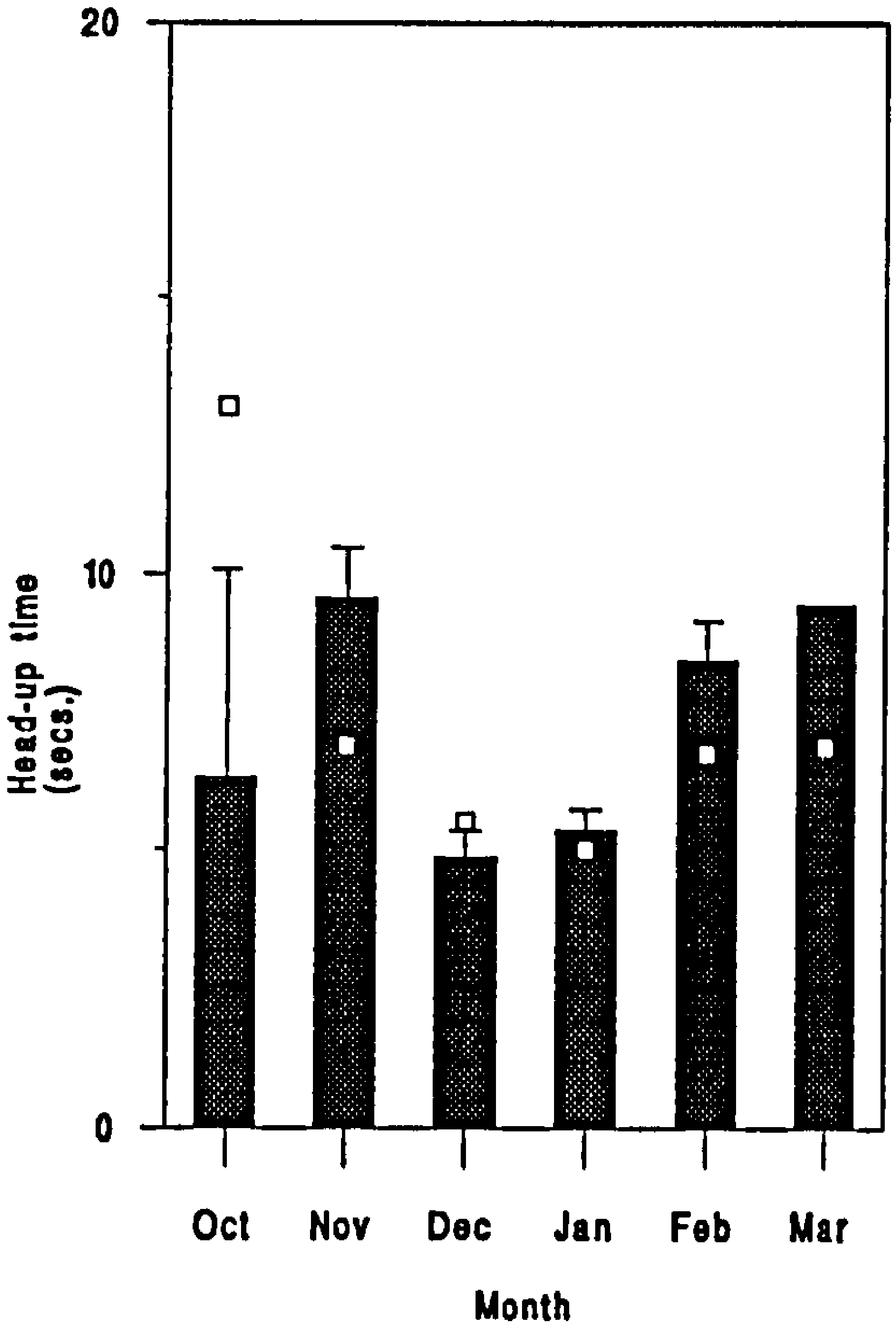


Fig. 6.39. Time spent with head-up during fifty pecks by male Bewick's Swans feeding on grass pasture with flock size (mean and S.E. bar, n=593), plus predicted values from a generalised linear model.

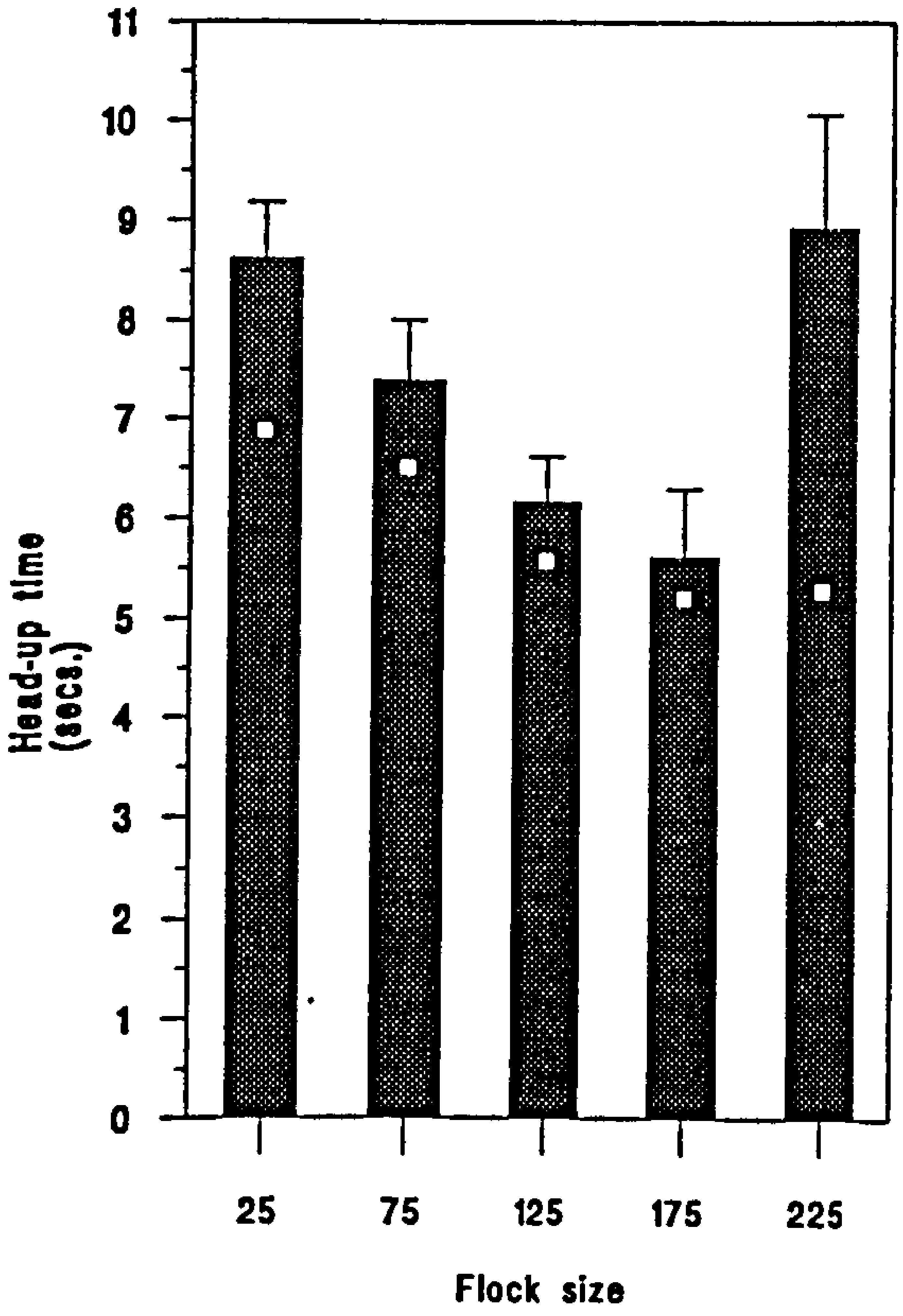


Fig. 6.40. Time spent with head-up per fifty pecks by male Bewick's Swans feeding on grass pasture with biomass of sward (mean and S.E. bar, n=358), plus predicted values from a generalised model.

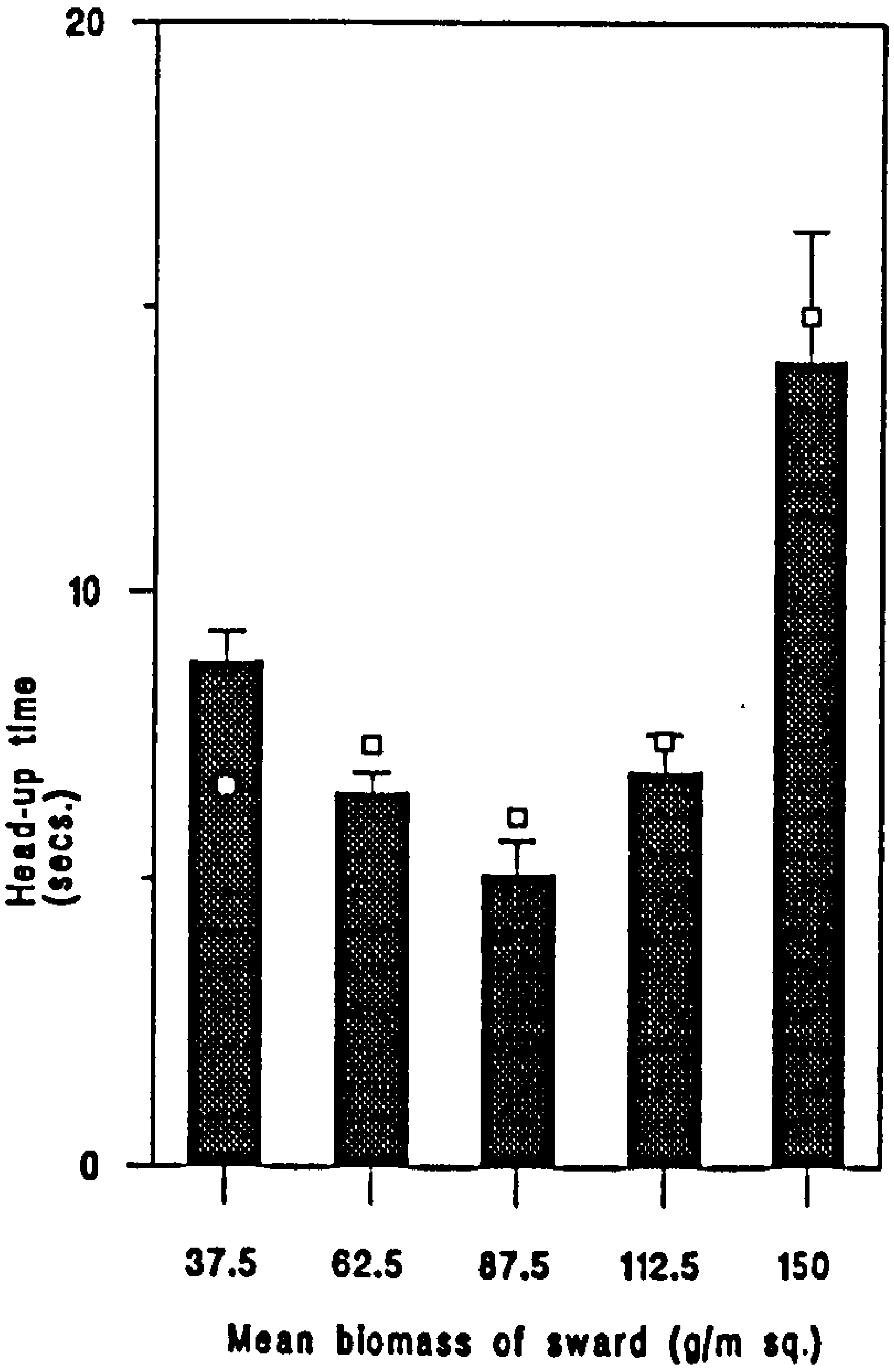


Fig. 6.41. Time spent with head-up during fifty pecks by male Bewick's Swans feeding on grass pasture with water cover on field (mean and S.E. bar, n=358), plus predicted values from a generalised linear model.

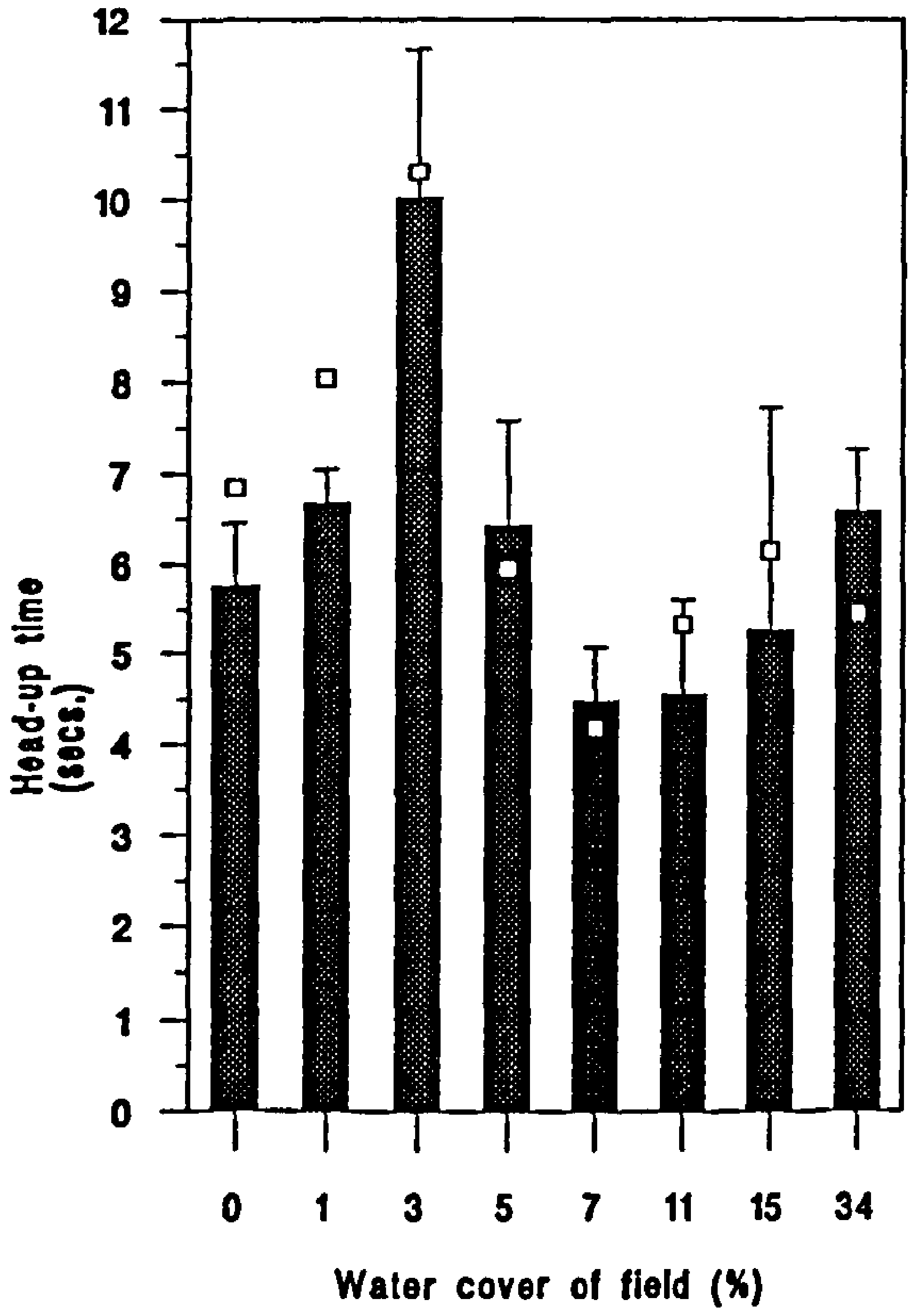


Fig. 6.42. Time spent with head-up during fifty pecks by female Bewick's Swans according to social class (mean and S.E. bar, n=665), plus predicted values from a generalised linear model (codes as before).

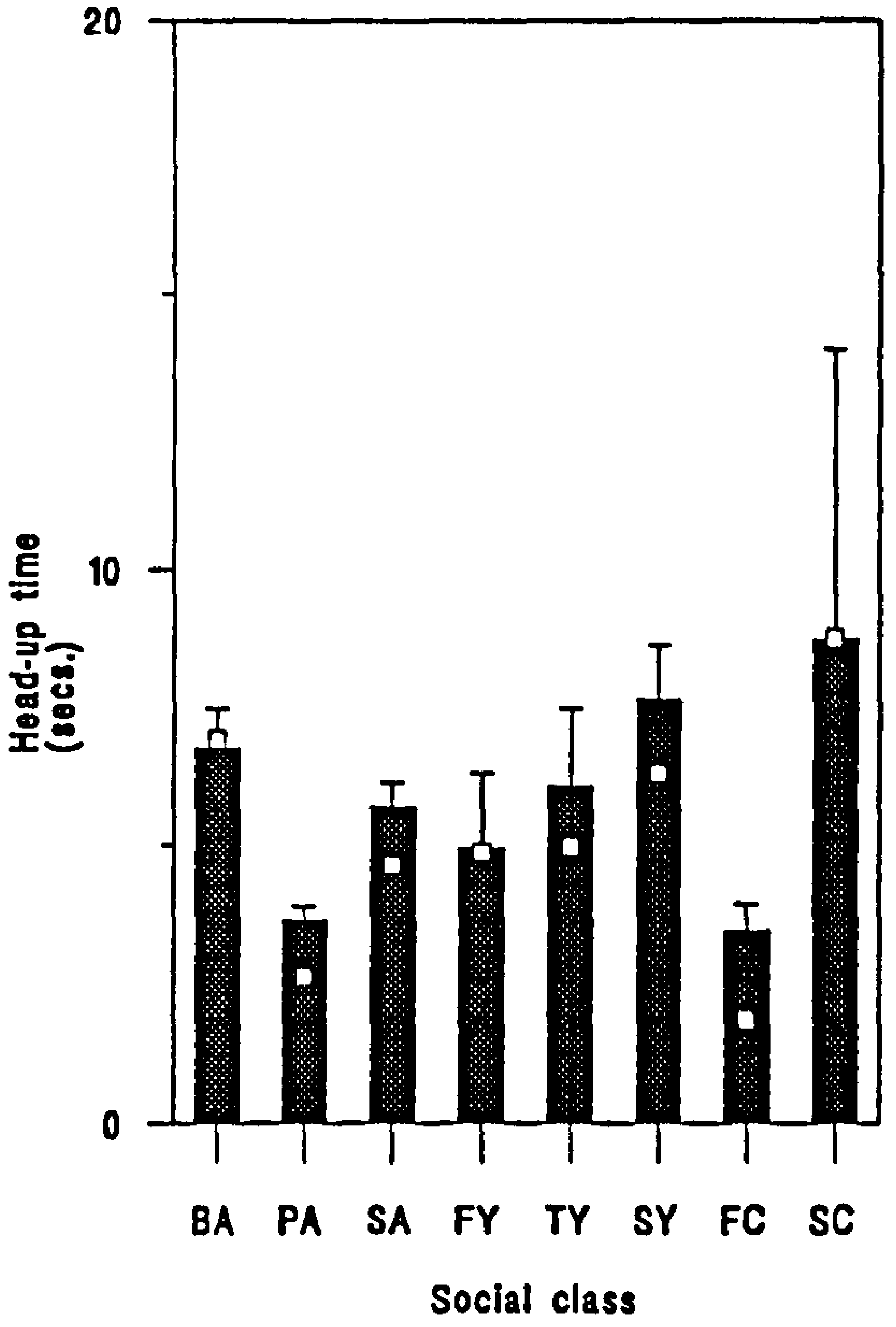


Fig. 6.43. Time spent head-up during fifty pecks by female Bewick's Swans feeding on grass pasture with mean sward-length (mean and S.E. bar, n=376), plus predicted values from a generalised linear model.

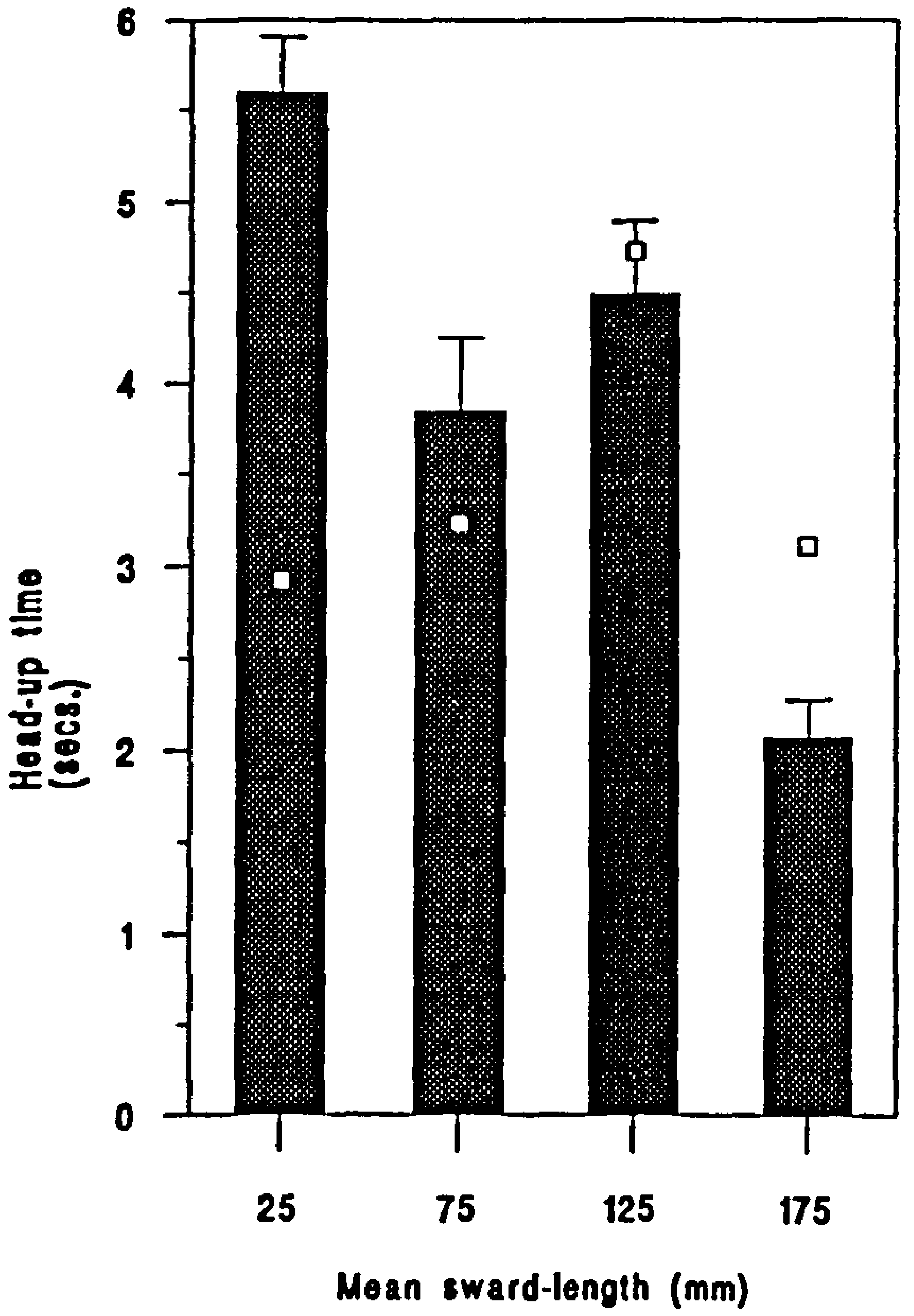


Fig. 6.44. Time spent head-up during fifty pecks by female Bewick's Swans feeding on grass pasture with water cover of field (mean and S.E. bar, n=391), plus predicted values from a generalised linear model.

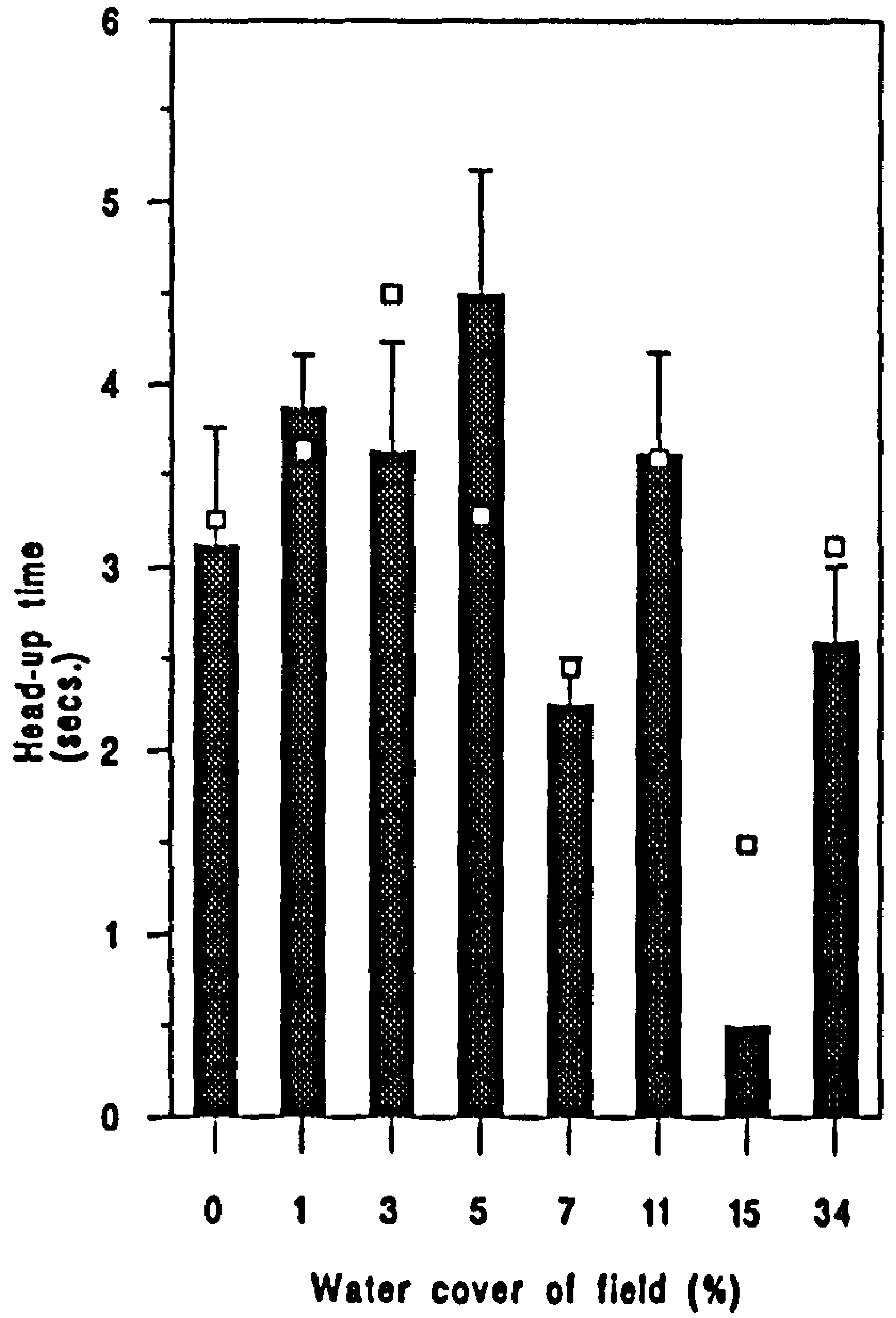


Fig. 6.45. Step rates of male Bewick's Swans feeding on grass pasture with social class (mean and S.E. bar, n=457), plus predicted values from a generalised linear model (B=breeding, P=paired, S=single, A=adult, Yearling, C=cygnet, T=trio, F=family).

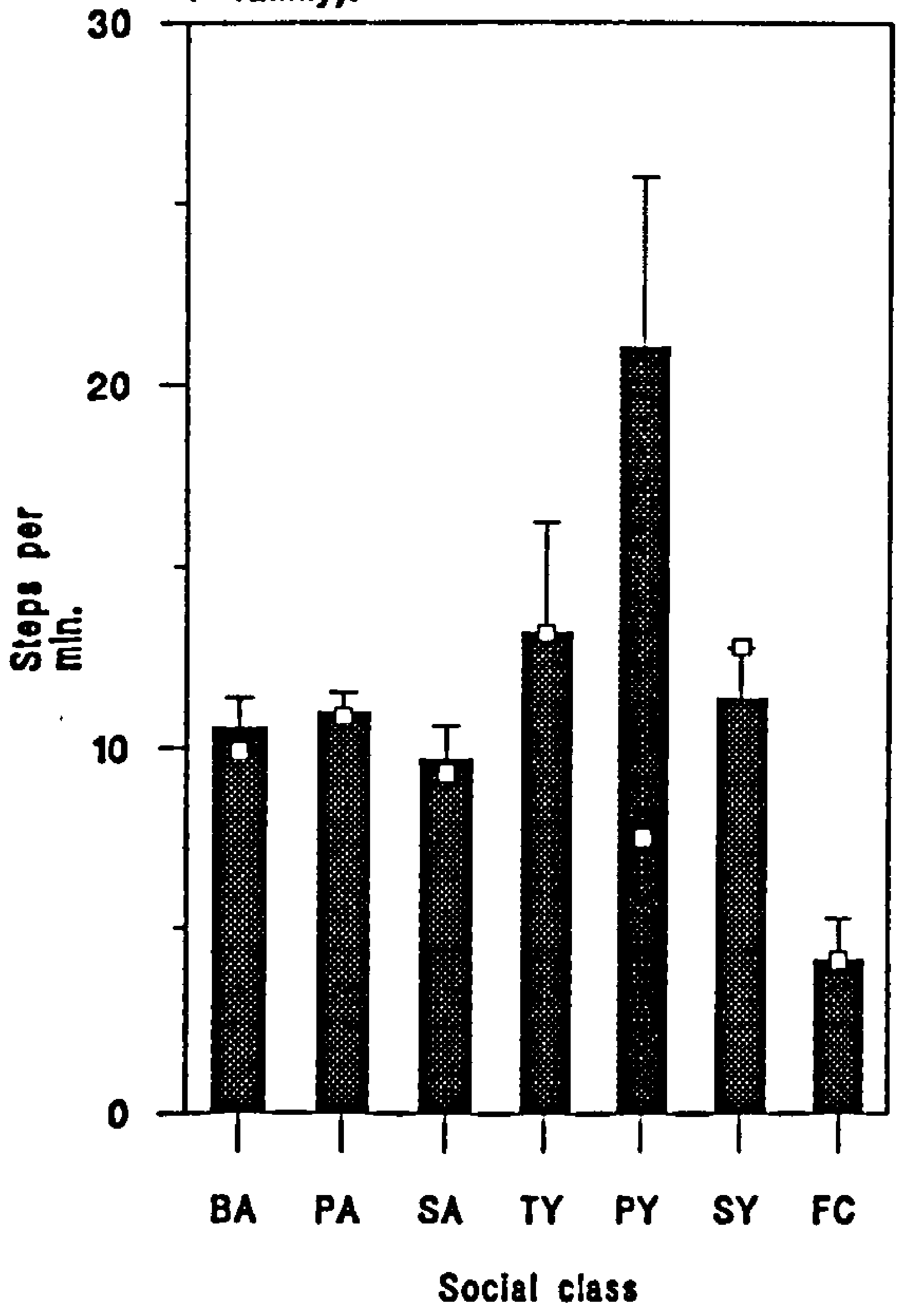


Fig. 6.46. Step rates of male Bewick's Swans feeding on grass pasture by roost group (mean and S.E. bar, n=457), plus predicted values from a generalised linear model.

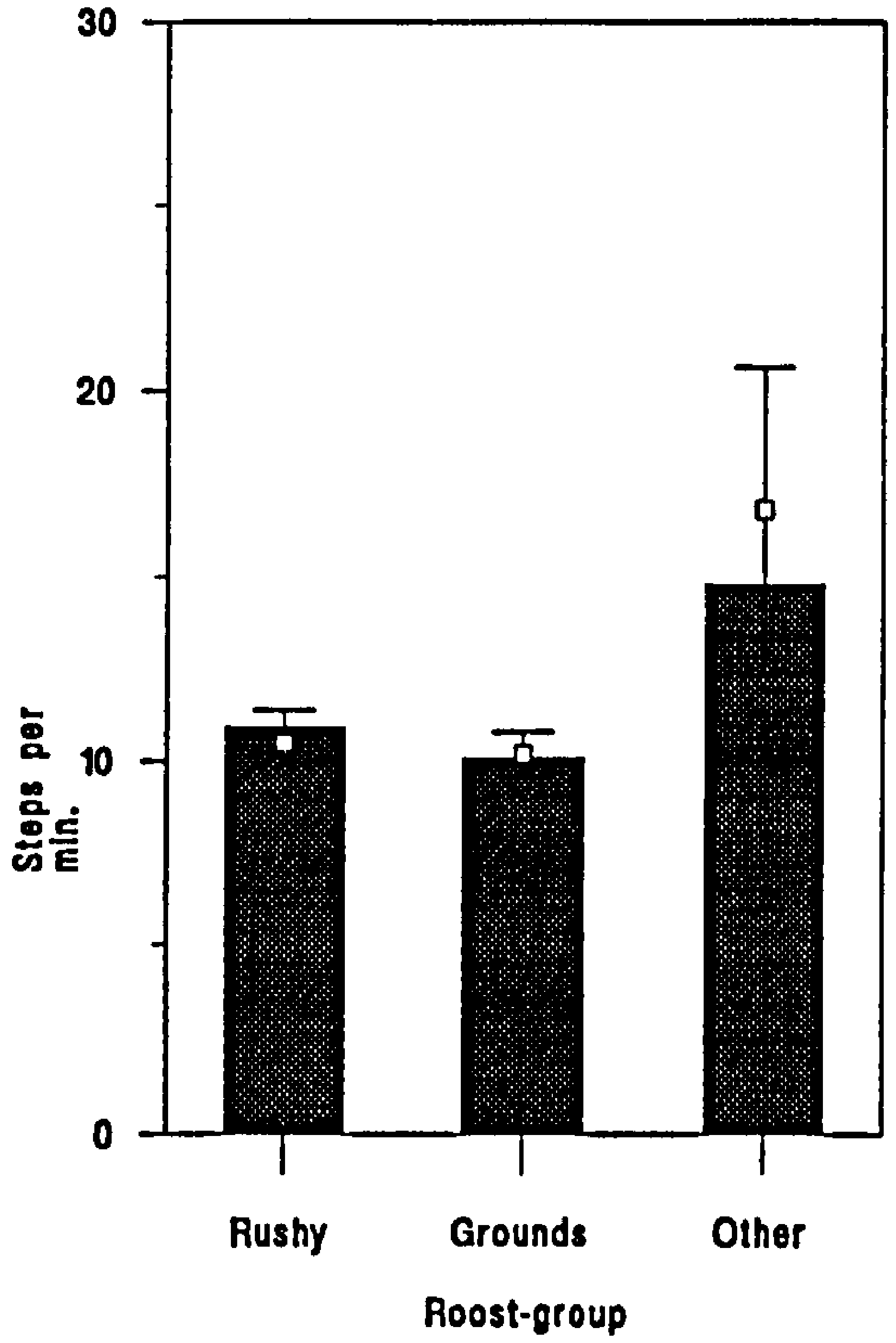


Fig. 6.47. Step rates of male Bewick's Swans feeding on grass pasture with abdominal profile (mean and S.E. bar, n=455), plus predicted values from a generalised linear model.

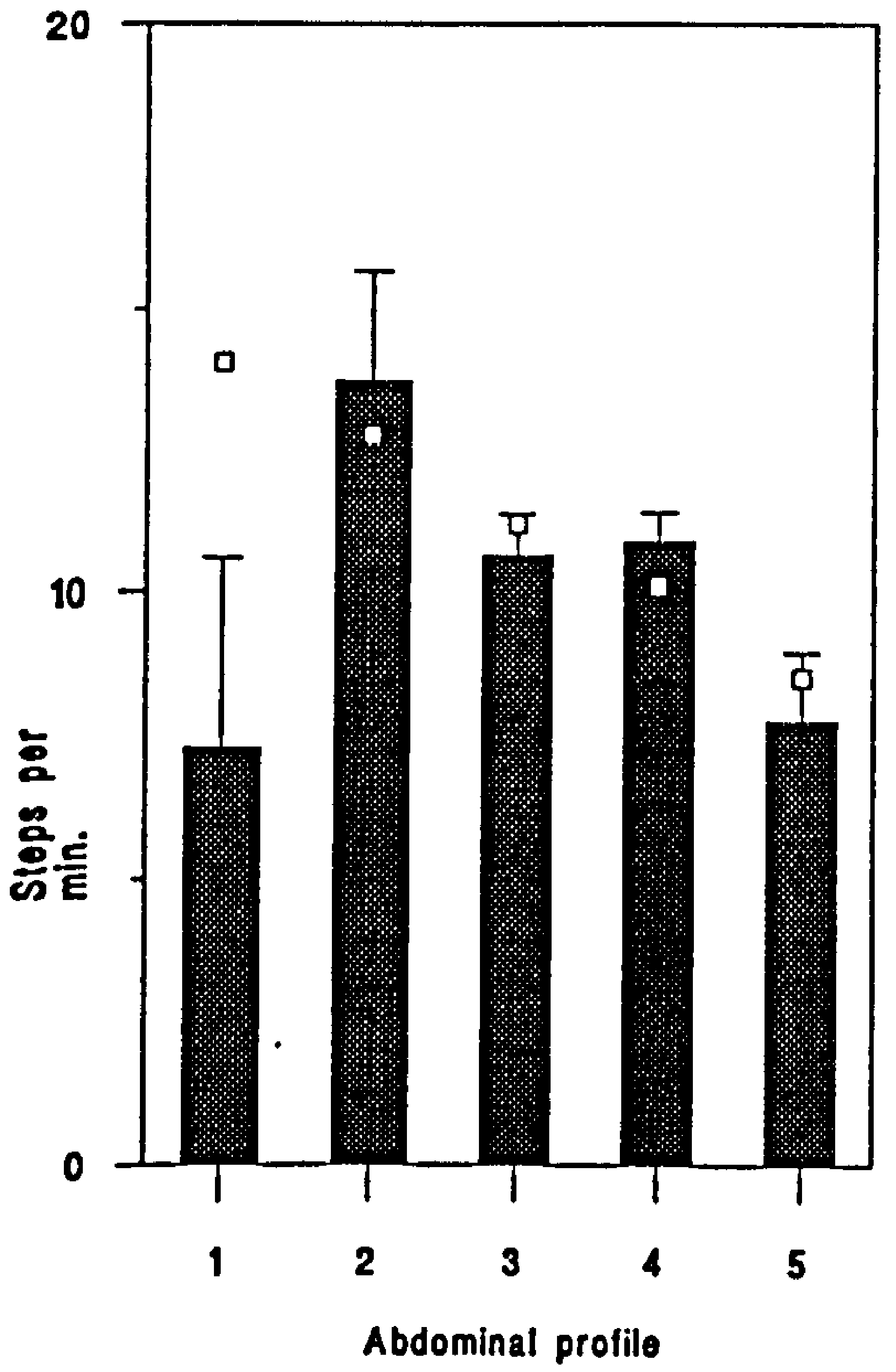


Fig. 6.48. Step rates of male Bewick's swans feeding on grass pasture with water cover of field (mean and S.E. bar, n=354) plus predicted values from a generalised linear model.

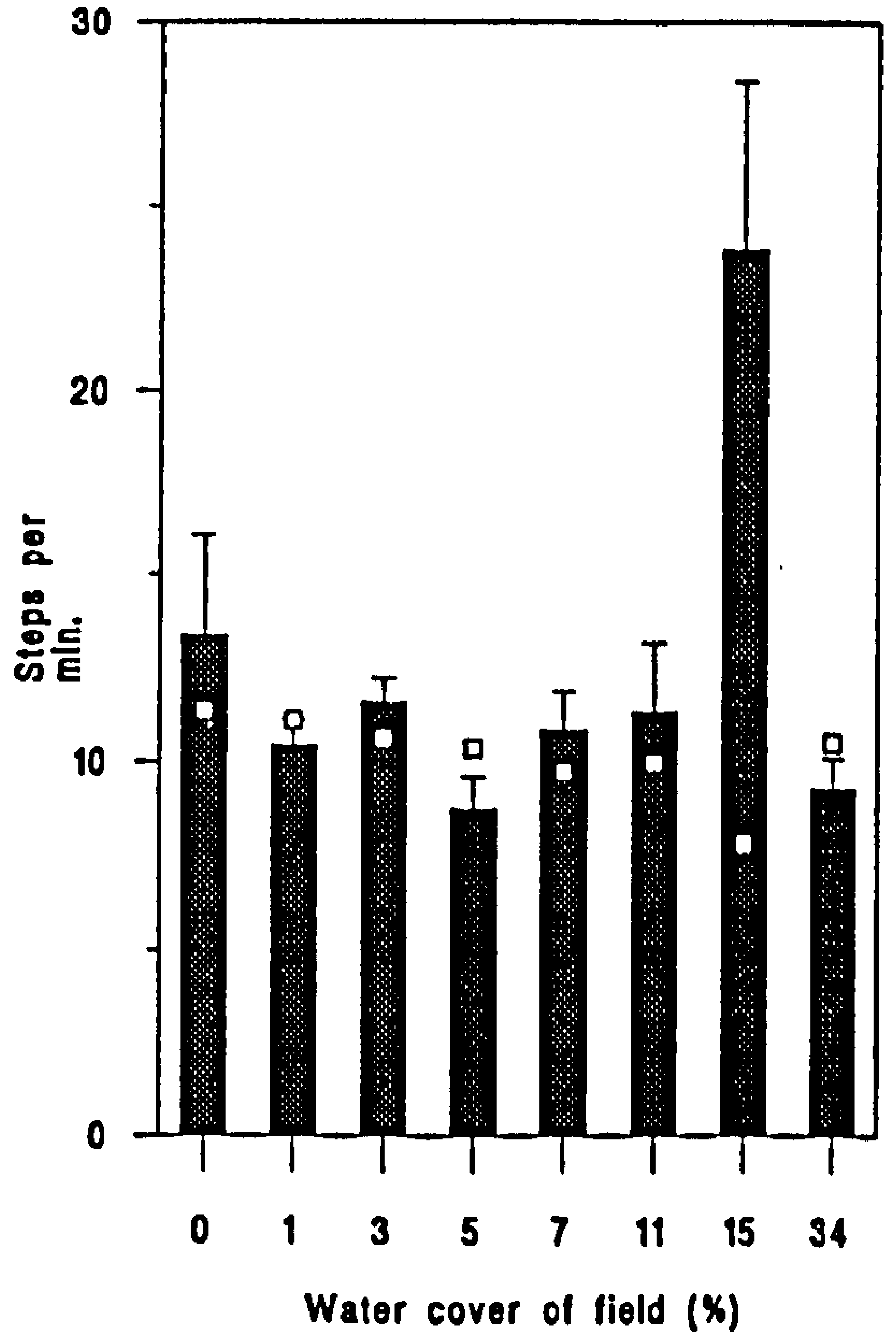


Fig. 6.49. Step rates of female Bewick's Swans feeding on grass pasture according to social class (mean and S.E. bar, n=487), plus predicted values from a generalised linear model. (B=breeding,P=paired,S=single,A=adult,Y=yearling,C=cygnet,T=trio,F=family).

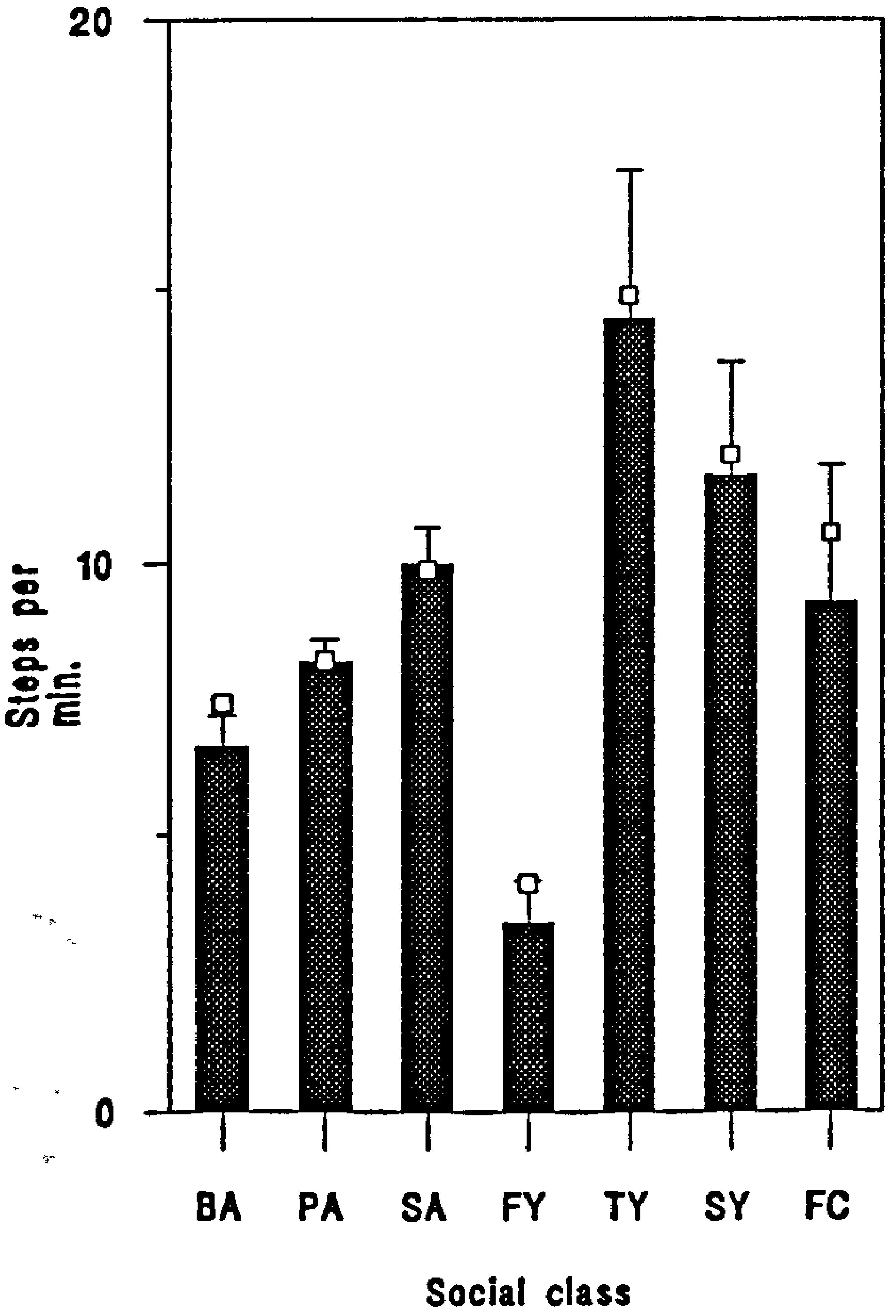


Fig. 6.50. Step rates of female Bewick's Swans feeding on grass pasture by roost-group (mean and S.E. bar, n=488), plus predicted values from a generalised linear model.

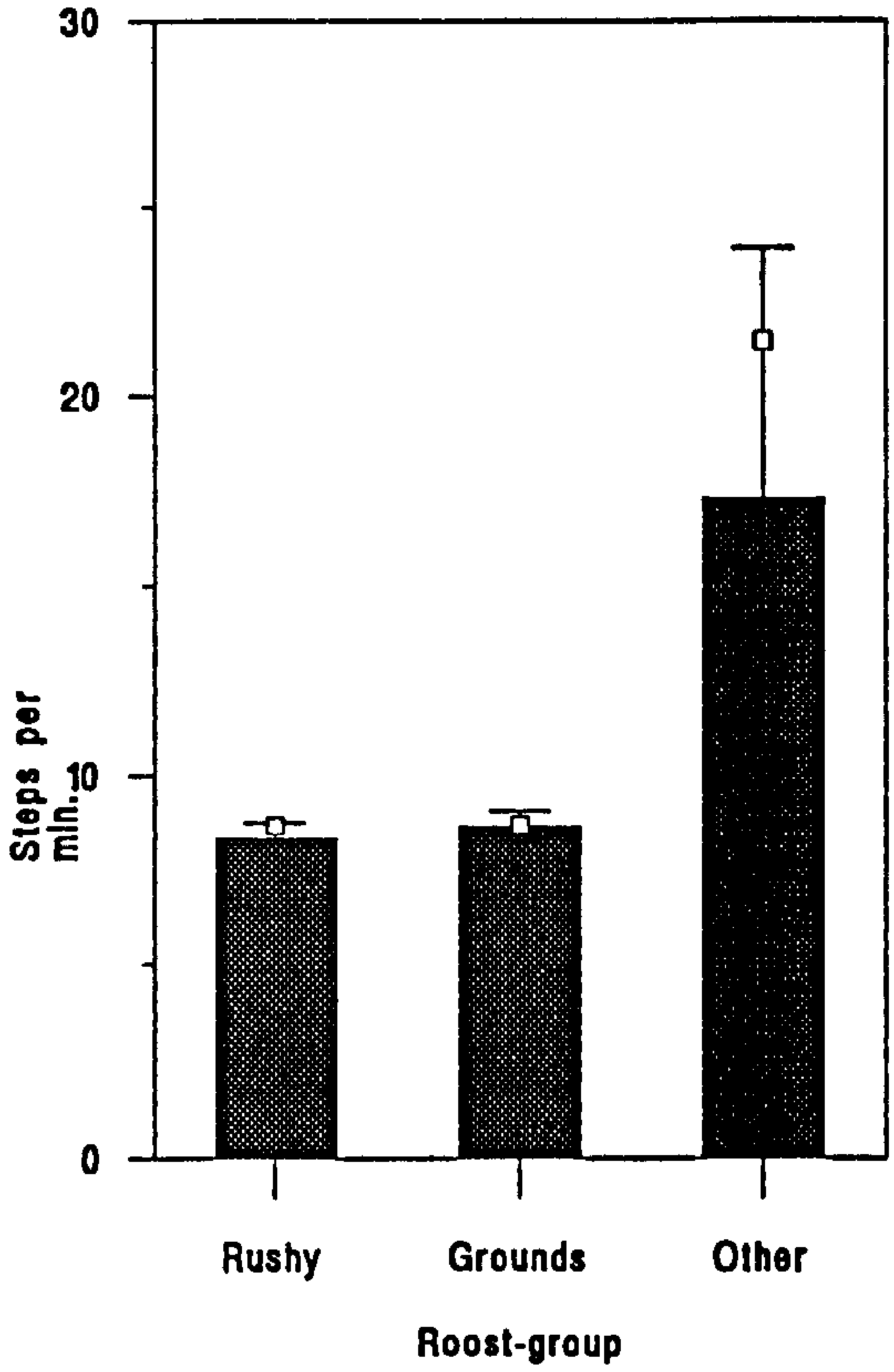


Fig. 6.51. Step rates of female Bewick's Swans feeding on grass pasture with abdominal profile (mean and S.E. bar, n=485), plus predicted values from a generalised linear model.

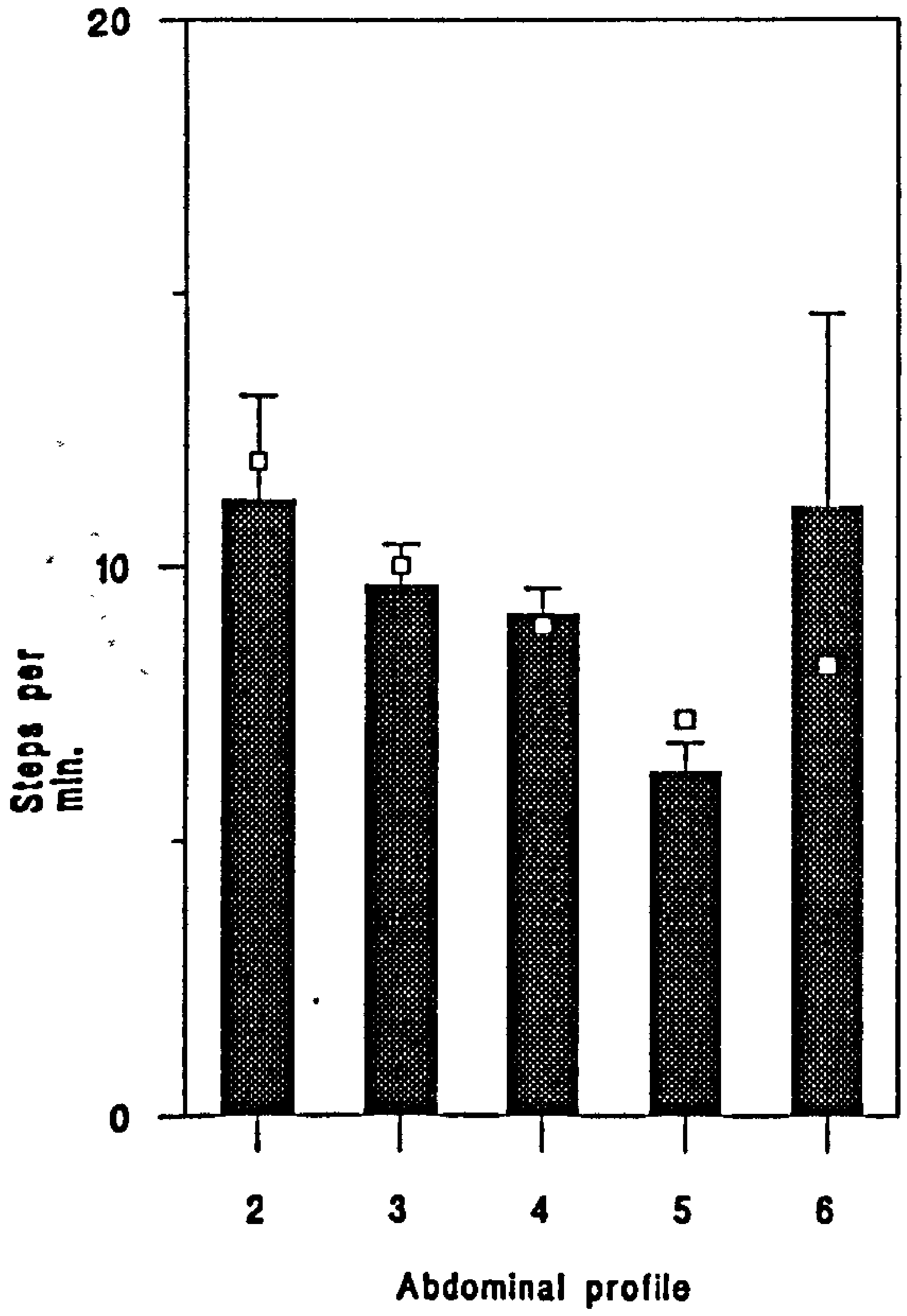


Fig. 6.52. Step rates of female Bewick's Swans feeding on grass pasture with mean sward-length on field (mean and S.E. bar, n=375), plus predicted values from a generalised linear model.

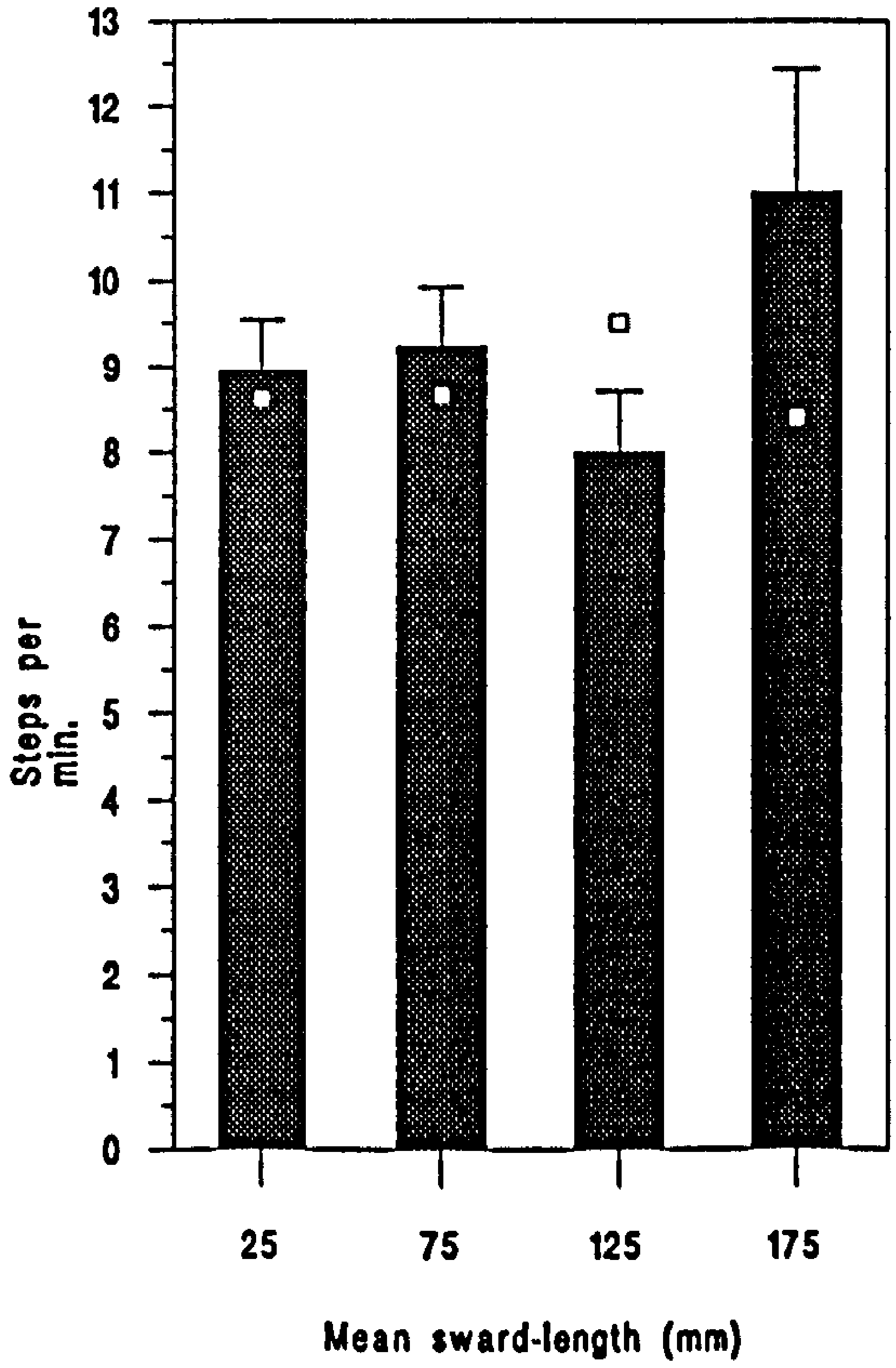
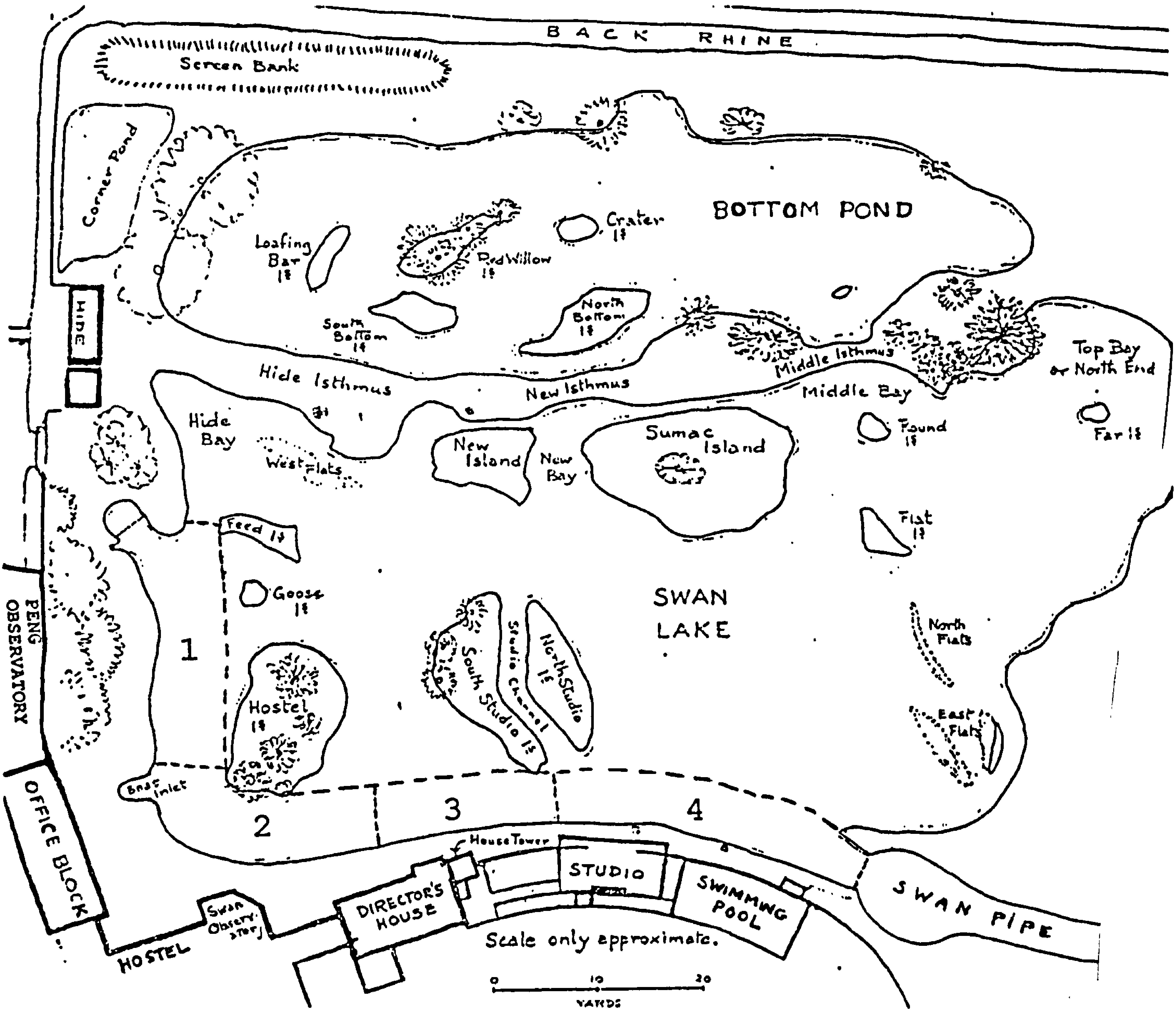


Fig. 6.54. Sketch map of the Rushy Pen at Slimbridge showing the main feeding areas on Swan Lake where grain is distributed daily during the winter to feed the wildfowl present (adapted from a sketch by Sir Peter Scott).



Key to feeding areas:

1 The Backs
2 The Hostel
3 The Kitchen
4 The Studio

Fig. 6.53. Step rates of female Bewick's Swans feeding on grass pasture with water cover of field (mean and S.E. bar, n=374), plus predicted values from a generalised linear model.

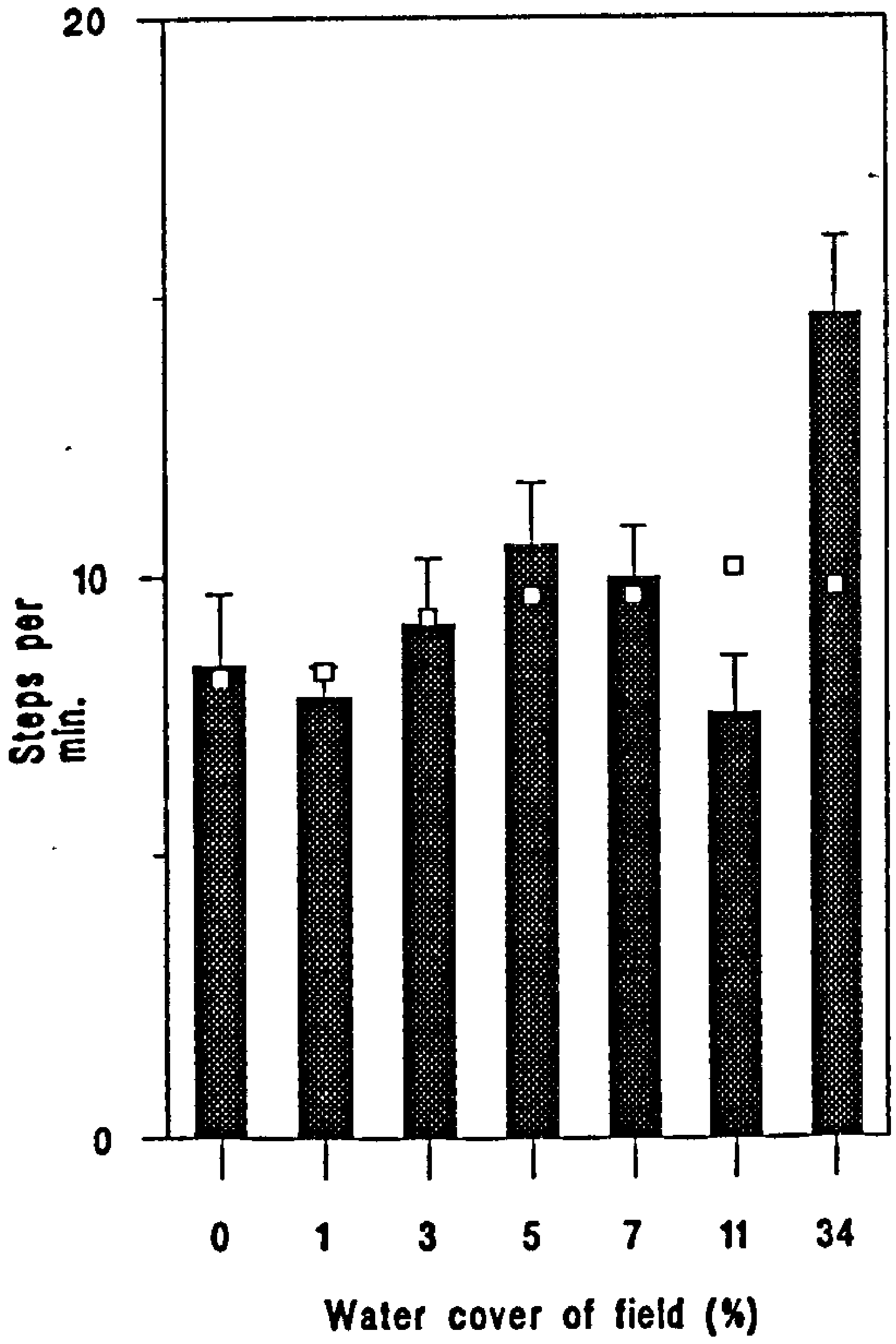


Fig. 6.55. Total time spent foraging with head under water by male Bewick's Swans during grain feeds at the roost sites with flock size (mean and S.E. bar, n=36), plus predicted values from a generalised linear model.

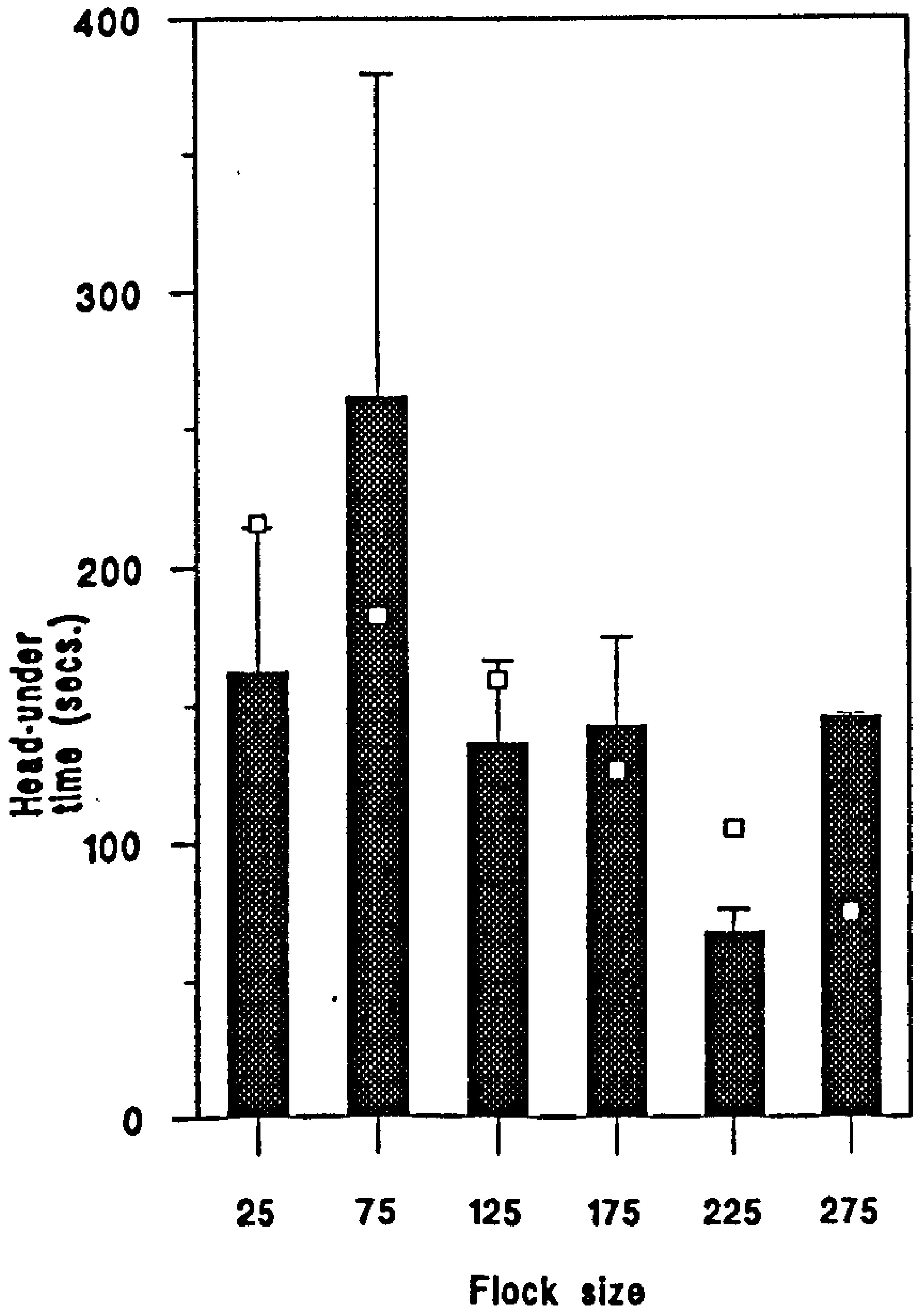


Fig. 6.56. Total time spent foraging with head under by female Bewick's Swans during grain feeds at the roost sites with dominance rank (mean and S.E. bar, n=32), plus predicted values from a generalised linear model.

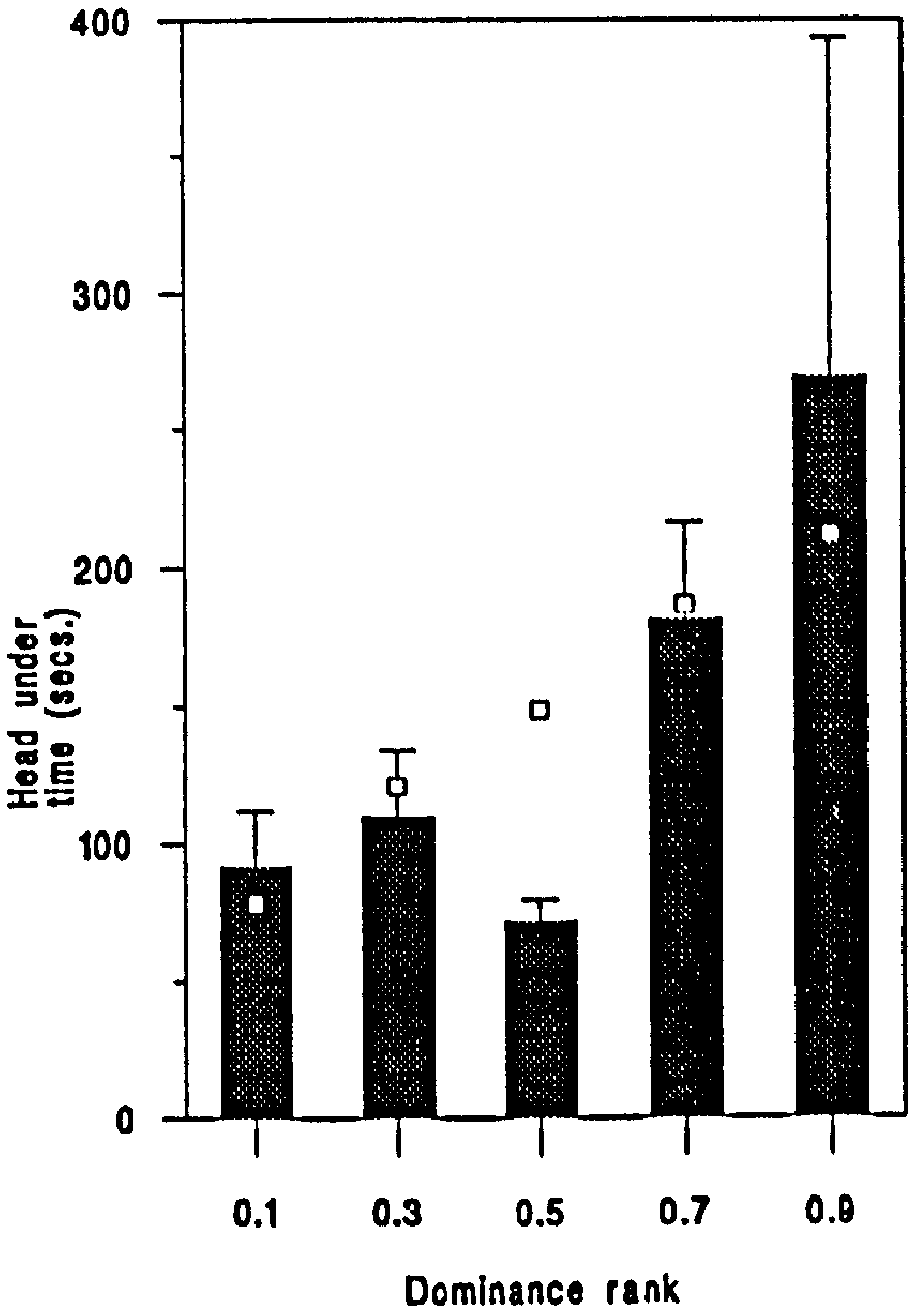


Fig. 6.57. Total time spent with head under water by Bewick's swans foraging during grain feeds at the roost sites with social class (mean and S.E. bar,n=69).(FC=family cygnet,A=adult, Y=yearling,B=breeding,P=paired,S=single,M=male,F=female).

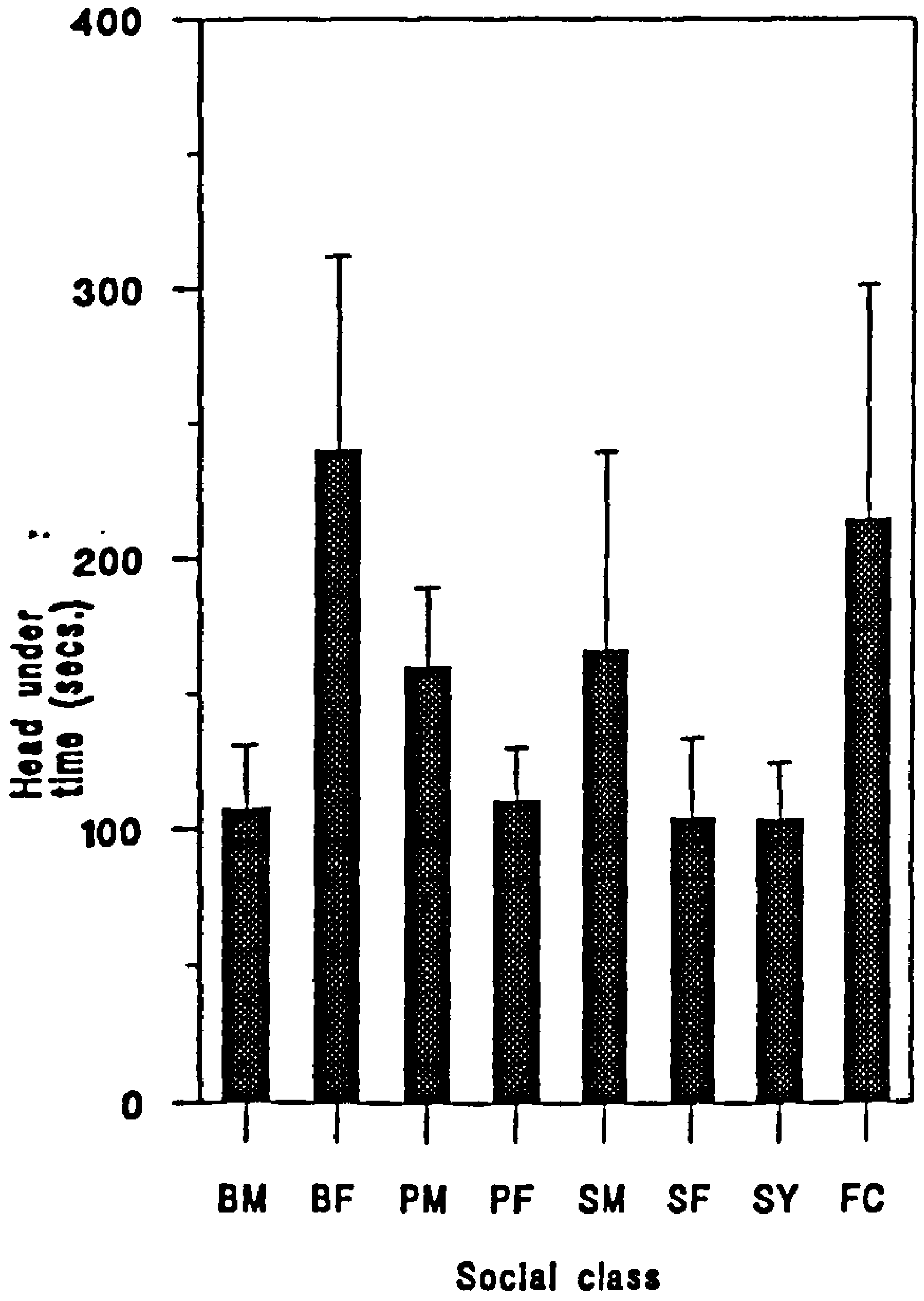


Fig. 6.58. Length of individual head-under foraging bouts by Bewick's Swans during grain feeds at the roost sites with social class (mean of average values per swan per feed and S.E. bar, n=69, codes as before).

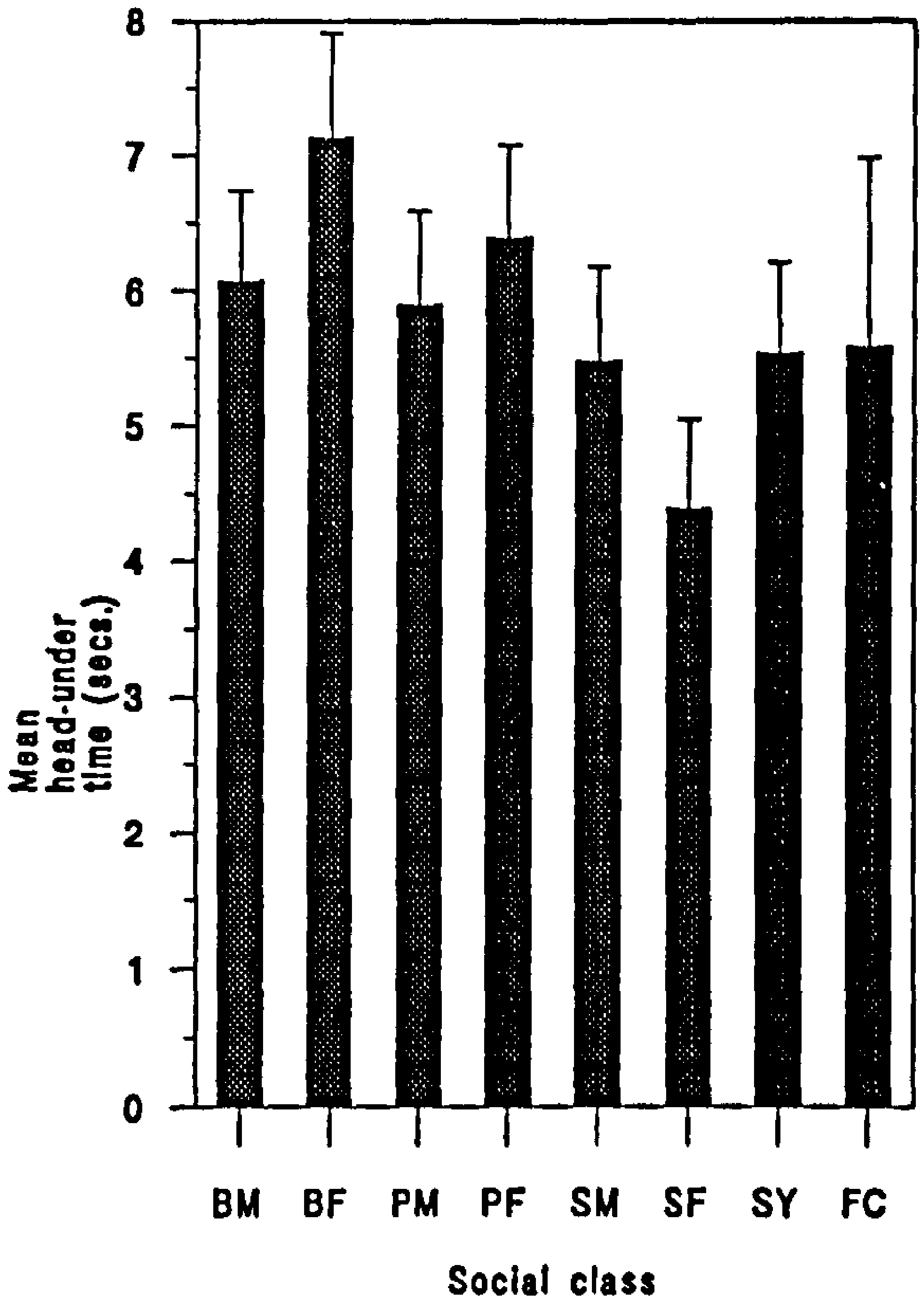


Fig. 6.59. The rate at which Bewick's Swans initiated attacks upon conspecifics during grain feeds at the roost sites with social class (mean and S.E. bar, n=56, FC=family cygnet,Y=yearling, B=breeding,P=paired,S=single,M=male,F=female).

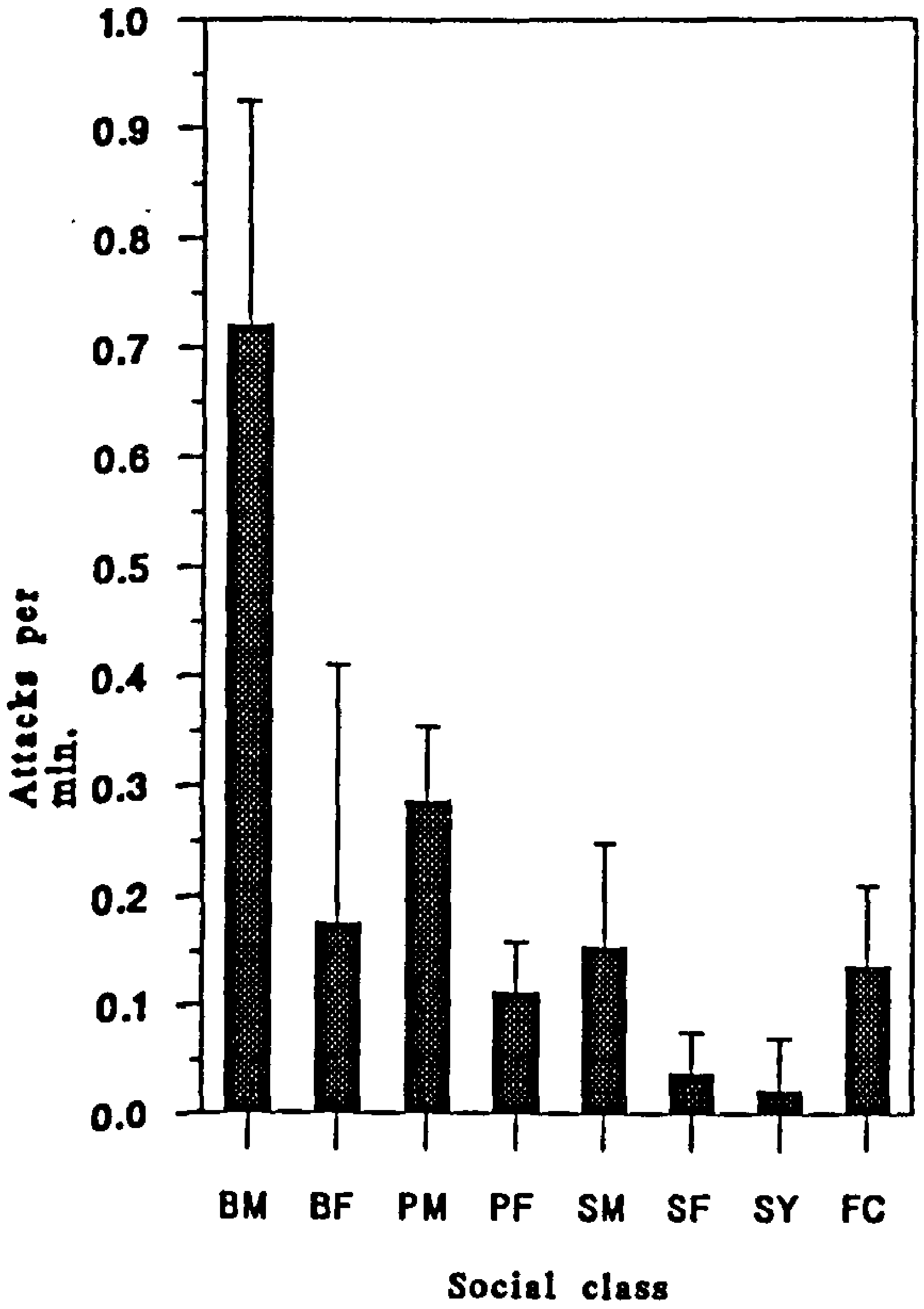
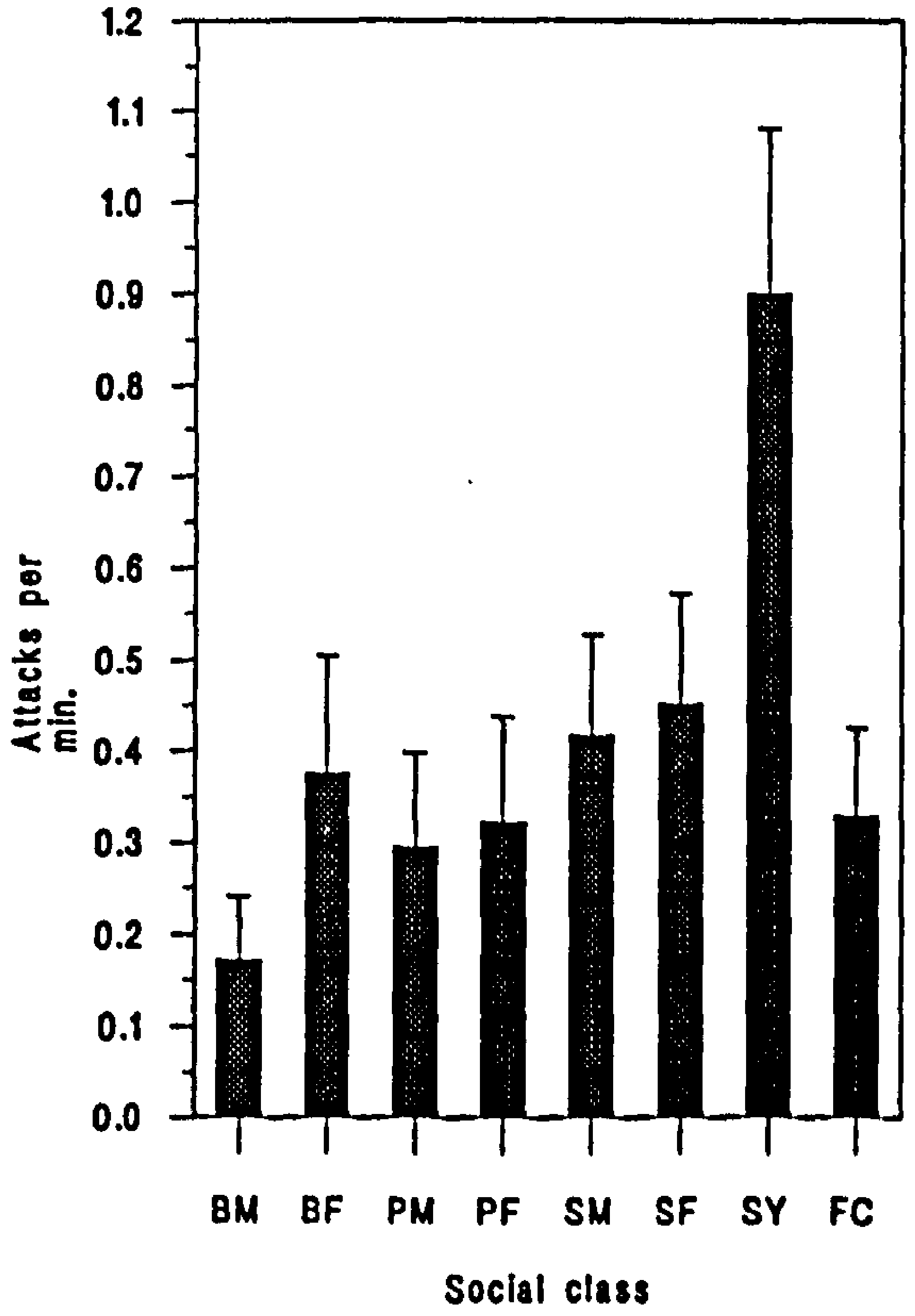


Fig. 6.60. The rate at which Bewick's Swans were attacked by conspecifics during grain feeds at the roost sites with social class (mean and S.E. bar, n=56, FC=family cygnet, Y=yearling, B=breeding, P=paired, S=single, M=male, F=female).



CHAPTER 7 RETURN RATES AND BREEDING SUCCESS

7.1 INTRODUCTION

The current study aimed to investigate the feeding strategies of individual Bewick's Swans in winter, in order to determine how this affected their body condition, which in turn might affect their subsequent return rates and breeding success. The Slimbridge wintering flock was found to consist of three sub-populations which used different roost sites (Chapter 3): two large and well established roosts - the Rushy Pen roost, and the Grounds roost respectively, and a third, smaller more ephemeral group which rarely visited the two main roost-sites but roosted instead on a range of water-bodies beyond the Trust's enclosures. Swans from the two main roost groups made very different uses of the food resources available at Slimbridge (Chapter 4). Birds from the Rushy Pen roost group selected fields more critically than those from the Grounds roost, favouring flooded fields with swards containing high protein levels, in line with conventional optimal foraging theory which states that individuals should select the most profitable food items involving the least feeding effort (e.g. Parker & Stuart 1976), whilst Grounds birds tended to select fields with swards of low biomass containing low levels of protein which were close to the roost site. These differences reflected differences in rates of food intake. At their roosts, Grounds birds were able to feed for longer, and on larger amounts of provisioned grain per swan, than the Rushy Pen birds (Chapter 6), which compensated for their lower food intake by devoting more time to feeding on the fields (Chapter 5).

Low AP scores during the winter and early spring may reduce subsequent breeding success, since it has been shown amongst Mute Swans that birds which went on to breed were heavier at the end of the winter than non-breeders (Reynolds 1972). It is possible that a self-perpetuating situation exists in which parental birds achieve dominance, have better body condition because of their access to the best resources and are therefore again better able to breed, such that a 'super-class' of birds may exist which breed each year. Collias et al. (1994) for example, showed that dominance rank was the most important factor affecting lifetime reproductive success in female Red Junglefowl Gallus gallus, and that the most dominant birds added a disproportionate number of offspring in to the population. Female Barnacle Geese returning to the wintering grounds with goslings were heavier than those that had nested (brood patch present) but had no young in the winter (Owen & Black 1989), suggesting that dominant birds not only had higher breeding success but that they also had better access to food resources. Amongst both temperate and arctic nesting geese, the quantity of fat reserves stored by the female has been shown to directly affect breeding success (Ankney & MacInnes 1978, Drent & Daan 1980, Aldrich & Raveling 1983, Johnson & Sibly 1993, Ebbinge & Spaans 1995). In the current study food intake correlated with AP score (Chapter 6), and female parents achieved the highest AP scores prior to migration, suggesting that they would be more likely to breed successfully again than paired females without cygnets.

The different foraging strategies employed by the two roost groups may not have been equally profitable for individual swans, since in general birds from the Grounds roost had lower AP scores than those of similar social rank from the Rushy Pen roost, particularly towards the end of the winter (Chapter 3). In addition there was a preponderance of high-ranking pairs without cygnets in the Grounds roost (Chapter 3), suggesting that some good quality pairs from the Grounds roost were failing to breed successfully.

This chapter set out to test the hypotheses that:

a) birds which performed well during a particular winter (i.e. high dominance rank, high AP score, Rushy Pen roost group) were more likely to return than those which performed less well.

b) female AP score in the spring prior to departure was correlated with subsequent breeding success. This has been noted amongst arctic-nesting geese (Ankney & MacInnes 1978, Drent & Daan 1980).

c) there was a difference in breeding success between swans from the two main roost groups. Swans from the Grounds roost might be predicted to suffer lower breeding success, since they selected feeding sites less critically than those from the Rushy Pen (Chapter 4) and in general had lower AP scores (Chapter 3).

7.2 METHODS

The effect of the independent variables in influencing a) whether or not an individual swan returned in the subsequent winter and b) the swans' subsequent breeding success (assessed by the presence/absence of cygnets upon returning the next winter), was determined by co-variate analysis using GLIM (NAG 1986). Co-variate analysis was chosen in order to identify explanatory variables with a significant effect, from a number of variables which were thought likely to be inter-correlated. Eight variables were examined initially, since it was thought that they might explain variation in the return/breeding success data: sex, social class, dominance rank, previous experience of site (years), pair duration (years), AP score upon departure in the spring (February and March departures only), roost group, and year. Social class, roost group and year were treated as factors. The two sexes were treated separately for two reasons:

1) initial investigation of the data indicated differences between males and females in terms of return rates (males were more likely to return than females, as in Rees 1987)

2) this removed the problem of duplicate data if both members of a pair were included.

For all analyses, a binomial error distribution was used in which return/reproductive success in the subsequent year was each coded as 1 and failure to return/failure to breed was coded as 0, this was divided by 1 in each case (the binomial denominator). This distribution was used since there were only two possible outcomes for each analysis: returned/did not return, and bred/did not breed. Unringed cygnets were omitted from the return rate analysis since the bill patterns of cygnets are not fully developed; these birds could not be reliably identified by bill pattern when they returned as yearlings the following winter (Evans 1979b). Only birds from the paired and breeding classes were included in the breeding success analysis, whilst data concerning birds which lost and/or replaced their mates between successive winters were excluded. In addition, individuals which were known (by ring sightings) to have wintered elsewhere were not included, since the presence of cygnets was frequently not recorded.

The number of variables included in the main model was reduced by first determining which of the seven variables were significant when considered separately without their interaction terms. Variables which were significant or near-significant were then investigated further, together with their interaction terms. The statistical significance of the explanatory variables and their interactions, was determined as before (see Chapter 2).

7.3 RESULTS

a) Return rates of individual birds from one year to the next

During the study period (1989-90 to 1992-93 winters, and including birds returning in 1993-94) the mean return rate of swans for which sex was known, was 65.9% (SE = 1.6, n = 885 swan years, where one swan year = an individual returning from one year to the next).

i) Males

The likelihood of male birds returning from one year to the next varied with year and social class only (Table 7.1). There was no significant interaction between these two variables, indicating that social class was not more important in years when fewer birds visited the site. Amongst males, the return rate of swans from one winter to the next was highest for birds which had been present in the 1990-91 winter (81.0% returned in 1991-92) and lowest for swans present in the 1992-93 winter (56.4% returned in 1993-94, see Fig. 7.1). Birds seen with a mate and/or cygnets were more likely to return in the following winter, whilst family yearlings (i.e. yearlings which were associating with their parents), single yearlings (i.e. not associating with their parents or other birds) and cygnets were less likely to return (see Fig. 7.2). Single adults had intermediate return rates.

ii) Females

Variation in the likelihood of females returning from one year to the next was associated with roost group and social class only (Table 7.1). There was no significant interaction between these two variables, indicating that the observed variation between social classes was not affected by the roost group to which the birds belonged. Amongst females, return rates for swans from the Grounds roost group were higher than for the Rushy Pen roost group (Fig. 7.3). Return rates for females were highest for birds seen with a mate and/or cygnets, and for family yearlings, and family adults, and lowest amongst cygnets and single yearlings (Fig. 7.4). Single adults had intermediate return rates.

b) Breeding success of individual birds from one year to the next

Variation in the subsequent breeding success of males and females (from the paired and breeding classes) was associated with year, roost group, and dominance rank, whilst experience was also relevant for females only (Table 7.2). There were significant interactions between year, roost group and experience indicating that roost group was more important; a) in some years than in others and b) for females with a certain number of years of previous experience at the site than for others. The proportion of pairs from the two roost groups returning in the following year with cygnets was similar for the 1989-90 and 1992-93 winters, but lower for pairs from the Grounds roost in the 1990-91 winter and markedly lower in the 1991-92 winter (Fig 7.5). None of the Grounds pairs from the 1991-92 winter returned with cygnets in 1992-93. Subsequent breeding success for males and females was highest for birds from the 1989-90 and 1990-91 winters and lowest for birds from the 1991-92 winter (Figs. 7.6 & 7.9), reflecting variation in the reproductive success of the European wintering population (see discussion). Subsequent breeding success was higher for birds from the Rushy Pen roost group than from the Grounds roost group (Figs. 7.7 & 7.10), and increased with the dominance rank of the pair (Figs. 7.8 & 7.11). Subsequent breeding success also increased with the females' experience of the site (number of years previously recorded at Slimbridge, see Fig. 7.12). There was some evidence that breeding success reached a plateau amongst the most experienced birds (>20 years previous experience, see Fig. 7.12).

c) Breeding success of pairs from one year to the next

In order to elucidate the individual characteristics of the members of each pair which had a significant influence upon breeding success, measured in the following winter by the presence/absence of cygnets, the analysis was run again including the following nine variables: year, roost group, social class (i.e. pair without cygnets, or breeding pair), dominance rank of pair, experience of male, experience of female, pair duration, AP score of male upon departure in the spring, AP score of female upon departure in the spring.

Variation in the subsequent breeding success of pairs was associated with year, social class, roost group, and the AP score of the female bird upon leaving Slimbridge in the spring (Table 7.3). There were significant interactions between year, social class, roost group, and AP score of the female upon departure, indicating that social class was more important in some years than in others, and that AP score of the female upon departure was more important for some roost groups than others. As in the two previous analyses, subsequent breeding success (in the following year) was highest for pairs from the 1989-90 and 1990-91 winters, and lowest for pairs from the 1991-92 winter (Fig. 7.13). Pairs which bred successfully in one year were more likely to breed successfully again in the following year than those which had been unsuccessful (Fig. 7.14). This was most marked in the very poor breeding year of 1992 when the only successful breeding birds were pairs that had also bred successfully in 1991. Pairs from the Rushy Pen roost group were more likely to breed successfully than those from the Grounds roost group (Fig. 7.15), whilst the breeding success of pairs tended to increase with the AP score of the female upon departure in the spring (Fig. 7.16). Although mean female AP score in spring was higher for birds from the Rushy Pen than from the Grounds in all years (e.g. spring 1992, Mann-Whitney U test, $W = 1314$, $P < 0.18$, $n = 43$, 14 for Rushy Pen and Grounds females respectively), the difference was not significant in any one year, possibly because sample sizes were small.

7.4 DISCUSSION

Male swans were more likely to return to Slimbridge from one year to the next than females, as shown previously by Rees (1987). Amongst males, but not females, return rates also varied between years. The reason for this difference may be linked to differences between the sexes in the return rates of birds of different social class (particularly amongst singletons, since paired birds tend to move together), and to annual variation in the proportion of birds from those classes. Amongst both males and females, birds from the breeding and paired classes had higher return rates than singletons. Single birds have been shown to be less predictable in their choice of roost sites than pairs and families (Raveling 1969, and results of this study - see Chapter 3); their low return rates suggest that they are also less predictable in their choice of wintering site. Singletons are of low dominance rank (Chapter 2) and their use of different wintering sites may represent exploratory dispersal which allows them to assess which wintering site suits them best in terms of the availability of resources (e.g. food and roost sites) and their ability to compete for them. Alternatively, the results may suggest that the survivorship of adult singletons was lower than that for paired birds. This seems unlikely for male singletons which were able to achieve high AP scores by the end of the winter (Chapter 2), but may be plausible for female singletons which in general achieved rather low AP scores. However, there was no significant difference between the return rates of adult male and female singletons (Mann-Whitney U comparison, $\underline{W} = 4160$, $\underline{P} > 0.86$, $\underline{n} = 64, 64$), so differences in survivorship between singletons and pairs seem unlikely. In addition females are more likely than males to change their winter site upon (re-)pairing (Rees 1987), so a significant result would not have been conclusive.

Cygnets and single yearlings of both sexes had lower return rates than adults. This may reflect the higher mortality rates of young age classes (see Evans 1979b, Scott 1988) but also indicates the tendency for young birds to investigate alternative sites prior to establishing a regular wintering site, as shown for other long-lived migratory wildfowl such as Pink-footed Geese (Boyd 1955). Rees & Bacon (in press) found that single Bewick's Swans used more sites than paired birds during migration, and suggested that this represented exploratory dispersal and habitat assessment by birds which were not constrained by the food requirements of a mate and/or cygnets. Single adult males, for example, spend less time in vigilance and aggressive interaction than males with a mate and/or cygnets, and have higher food intake rates allowing them to achieve high AP scores (Chapters 2 and 6). In addition young singletons have low dominance ranks which may result in them having reduced food intake amongst flocks at the best feeding areas (or, indeed, elsewhere) and make them more likely to explore alternative sites. This would agree with the ideal free model proposed by Parker & Sutherland (1986) concerning the distribution of individuals of differing competitive ability on a resource, which predicts that the better competitors should go to the patch where they gain most from their competitive superiority and the poorer competitors should choose the patch where they suffer least from their inferiority. Bautista et al. (1995) showed that the average daily food intake of Common Cranes was positively correlated with both the quality of the foraging zone and the dominance rank of the bird, and as a consequence, when numbers of cranes were high at the study site, dominant birds preferred to feed in areas of highest food density. Similarly Milinski et al. (1995) demonstrated experimentally that adult Mute Swans were more successful than sub-adults in obtaining food at a 'clumped' patch and showed a distinct preference for the clumped patch over a scattered patch where adults and sub-adults were similarly successful. In the current study, single yearlings were less successful than birds with a mate and/or cygnets at obtaining food during the grain feeds at the roost sites (Chapter 6), and as a consequence were less predictable in their choice of roost site during the course of a winter (Chapter 3).

Yearling males still associating with their parents had low return rates whilst yearling females still associating with their parents had high return rates the following year. This difference between the sexes suggests that female yearlings may benefit from returning to a known wintering site, with the prospect of other related birds being present, whilst for male yearlings this advantage is either smaller and/or the advantage of finding an alternative winter site is greater than for females. The fact that females from the Grounds roost were more likely to return than females from the Rushy Pen roost also supports this theory, since the levels of social interaction are lower between birds in the Grounds (Chapter 5), which may be due to a higher proportion of related individuals in the roost. The difference in return rates may also result from the differences between the sexes in fighting ability. Female singletons have lower dominance ranks than male singletons of the same age (Chapter 2), and may therefore be less likely than males to improve their foraging performance at unfamiliar alternative sites away from the presence of related individuals.

Return rates of cygnets in the following winter as yearlings were low (around 50%). There was no difference in the dominance rank of cygnets which did and did not return the following year (Mann Whitney U comparison, $W = 1688$, $P > 0.5$, $n = 53, 36$

respectively), suggesting that there was no difference in the return rates of cygnets from high and low- ranking families.

Breeding success, measured as whether or not cygnets were associating with a pair upon arrival at Slimbridge, varied considerably between years. This reflected annual variation in the breeding success of the European Bewick's Swan population as a whole, estimated from the percentage of cygnets in swan herds at Wildfowl & Wetlands Trust Reserves. For example, the very low breeding success of birds leaving Slimbridge at the end of the 1991-92 winter, was due to 1992 being an exceptionally poor breeding season; estimates of 3-5% juveniles in the population, were the lowest on record (Bowler et al. 1993). Breeding success in 1990 and 1991 was higher at 11% (reaching 23% at Slimbridge) and 10% (23% at Slimbridge) respectively (estimates from Rees et al. 1991 and Bowler et al. 1992), and low at 7% (14% at Slimbridge) in 1993 (Bowler et al. 1994), fitting in neatly with the annual patterns of individual breeding success documented here. The actual percentage of juveniles in the Slimbridge population was consistently higher than that recorded at other sites in Britain within a winter, suggesting a bias in the distribution of families throughout the wintering grounds (see also Dirksen & Beekman 1991, Rees et al. in press).

The likelihood of a pair returning with cygnets in the following winter, correlated positively with the AP score of the female member of the pair upon departure in the spring. This agrees with the findings of other authors working on migratory arctic-nesting geese (e.g. Ankney & MacInnes 1978, Drent & Daan 1980, Ebbinge & Spaans 1995), who showed that the quantity of fat reserves stored by the females directly affected breeding success. The AP score of the female in spring is connected to the dominance rank of the pair, and may therefore reflect, to some extent, their ability to gain access to food at migratory sites and on the breeding grounds, as well as during the winter. However since the swans do exhibit pronounced pre-migratory fattening, and snow cover may severely reduce the availability of food on the breeding grounds during the pre-nesting period (pers. obs.), the quantity of fat reserves stored by the female during the winter is likely to have a direct effect upon breeding success. The protection afforded by dominant males during the winter, allowed females from high-ranking pairs to monopolise the best food resources, where they had higher feeding rates (Chapter 6), and were able to achieve the highest AP scores prior to departure in spring. Dominant males may be able to compensate for their low AP scores at the end of the winter (Chapter 2), by increased feeding activity at the migratory sites on route to the breeding grounds. This seems likely since swans at a spring migratory site in Estonia spent a larger proportion of time feeding than in the winter, whilst paired males and females had similar feeding rates (Rees & Bowler 1991). Moreover, paired birds spent less time being vigilant than singletons, even though cygnets continued to associate with their parents, suggesting that protection of the mate and /or cygnets was less important than in the winter.

The breeding success of swans from the Rushy Pen roost group was higher than that for swans from the Grounds roost group (omitting singletons from the analysis). This confirmed the hypothesis put forward in Chapter 3, that the higher dominance rank of pairs without cygnets in the Ground Pens, compared to those in the Rushy Pen, was a result of the lower breeding success of high-ranking Grounds pairs (Chapter 3). The importance of roost group upon breeding success varied considerably between years however (Fig 7.5), with a marked difference occurring in the very poor breeding season of 1992, such that none of the Grounds pairs from the 1991-92 winter returned with cygnets in 1992-93. Since female AP score prior to departure in the spring was positively correlated with subsequent breeding success, and the AP scores of paired females, both with and without cygnets, from the Grounds roost were significantly lower than those from the Rushy Pen roost in all years, the lower breeding success of Grounds pairs seems likely to have resulted from less successful foraging performance. The Grounds birds' foraging strategy of relying more heavily on the supplementary feeds of grain and selecting fields less critically in terms of food quality than Rushy Pen birds, resulted in similar AP scores early in the winter when food supply was high but in lower AP scores later in the winter when food supply was lower (Chapter 3), and ultimately to reduced breeding success, particularly during a year (1992) when breeding success in the European population as a whole was very low. Breeding success amongst Canada Geese has also been shown to be strongly influenced by condition (assessed by abdominal profile), which in turn reflected the amount of time spent feeding by the female during the pre-breeding period (Johnson & Sibly 1993). The reason for the Grounds swans adopting these less successful foraging strategies is not clear. The transfer of birds with low AP scores from the Grounds roost to the Rushy Pen roost, and their subsequent change in field selection during January and February when grass biomass was lowest, indicated that the birds were capable of detecting, and attempting to improve upon, poor foraging performance. The inferred presence of a higher proportion of related individuals in the Grounds pens may have conferred other advantages, including reduced levels of social interaction (Chapter 5), possibly of greater benefit to female swans, which showed higher rates of return to the Grounds roost group than to the Rushy Pen. In addition there was a tendency in all years for Grounds birds to leave later in the spring than those from the Rushy Pen. This may have been because they were generally in poorer condition, or possibly because they originate from a different part of the breeding range (i.e. closer to Britain than the Rushy Pen birds) and consequently have a different migration threshold (Rees 1989). If the latter theory is correct then the breeding failure of the Grounds pairs in 1992 could also have resulted from differences in conditions (e.g. predator levels, climatic conditions, food availability) experienced on the breeding grounds.

Social class (i.e whether a bird had bred or not in the previous year), was not significantly associated with subsequent breeding success when males and females were investigated separately. However breeding success was positively correlated with dominance rank in the previous winter, and since families were generally dominant over pairs (Chapter 2), dominance rank may have masked any effect of social class alone. The positive correlation between dominance rank and breeding success in this study agrees with Scott (1988) and with the findings of other studies on reproductive success in birds. For example Henderson & Hart (1995) showed that amongst Jackdaws, dominance rank was positively correlated with the more efficient provisioning of offspring and the raising of larger annual broods. Females from dominant pairs in the current study were able to monopolise the best food resources, where they had higher intake rates (Chapter 6), and were able to achieve the highest AP scores prior to departure for the breeding grounds in the spring. When the characteristics of individual swan pairs were investigated, social class became significant i.e. pairs which bred successfully in one year were more likely to breed successfully again in the following year, than those which had been unsuccessful, reinforcing the view that a relatively small number of good breeding pairs are responsible for recruitment to the population. There was variation between years in the effect that social class had upon subsequent breeding success, reflecting in part the disastrous breeding year of 1992, when the only pairs to raise young successfully were those which had also been successful in the previous year. Reproductive success has been shown to increase with pair duration amongst Bewick's Swans (Rees et al. 1996). However, the effect of pair duration is more pronounced in some years than others, and the run of data in the current study may have been too short to reveal this trend.

7.5 SUMMARY

This chapter considered the findings of the previous chapters in relation to observed return rates and breeding success for individual birds.

1) The return rate of 885 birds for which sex was known, from one year to the next was 65.9%. The sex of the bird had a significant effect upon the likelihood of its returning the following winter; the two sexes were therefore investigated separately.

2) Single adults (irrespective of sex) had lower return rates than birds from the paired and breeding classes, whilst cygnets and yearlings had the lowest return rates. Young singletons may investigate alternative sites prior to pairing and breeding. This may be partly because they are not constrained by the food requirements of dependents, but may also reflect their low dominance ranks which reduced their foraging performance amongst flocks at the best feeding areas, and made them more likely to explore alternative sites. There was no difference in the return rates of cygnets from high and low-ranking families.

3) Females from the Grounds roost had higher return rates than those from the Rushy Pen. Moreover, female yearlings which had associated with their parents were more likely to return to Slimbridge in the following winter than males. These results suggested that females, which are generally lower-ranking than male swans, found some advantage (e.g. reduced levels of social interaction and improved foraging performance), in returning to a familiar site where the proportion of related individuals was likely to be high.

4) Individual breeding success varied considerably between years, in line with fluctuations in the breeding success of the European population as a whole. The proportion of cygnets recorded at Slimbridge was generally higher than at other sites in Britain within a winter, suggesting a bias in the distribution of family parties throughout the wintering grounds.

5) When males and females were investigated separately, dominance rank had a significant positive effect upon subsequent breeding success, regardless of whether the swans were accompanied by cygnets or not, in the previous winter. The protection from intra-specific feeding competition afforded by a dominant male upon its mate, permitted females from high-ranking pairs to monopolise the best food resources, where they had higher feeding rates (Chapter 6), and were able to achieve the highest AP scores prior to departure for the breeding grounds in spring (Chapter 2).

6) Female AP score at the end of the winter had a positive effect upon breeding success the following summer. The lower AP scores of paired and breeding females in the Grounds roost compared to those in the Rushy Pen were a product of less successful foraging strategies and resulted in reduced breeding success, particularly during a year when breeding success in the European population as a whole was very low. It should be noted

however that the proportion of juveniles recorded during the study period amongst swans wintering at Slimbridge was generally much higher than at other sites in Britain.

Table 7.1. Linear model using maximum likelihood estimates fitted to the return rates of male and female Bewick's Swans at Slimbridge from one winter to the next (1989-90 to 1992-93 winters inclusive). Note: * P < 0.05, ** P< 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

	Males			Females		
Variable	F ratio	d.f.	P	F ratio	d.f.	P
Year	4.09	3, 436	**	-	-	-
Social class	2.01	8, 441	*	2.16	8, 437	*
Experience	-	-	-	-	-	-
AP in spring	-	-	-	-	-	-
Dominance rank	-	-	-	-	-	-
Roost group	-	-	-	3.60	2, 431	*
Final model:						
Deviance		532.2			548.3	
df		433			429	

Table 7.2. Linear model using maximum likelihood estimates fitted to the breeding success of male and female Bewick's Swans returning to Slimbridge from one winter to the next (1989-90 to 1992-93 winters inclusive. Swans without a partner and data concerning swans which lost and/or replaced their mate between successive winters excluded from analysis). Note: * P < 0.05, ** P< 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

	Males			Females		
Variable	F ratio	d.f.	P	F ratio	d.f.	P
Year	0.00	1, 183	NS	0.00	1, 174	NS
Social class	-	-	-	-	-	-
Experience	-	-	-	2.42	1, 174	NS
Pair duration	-	-	-	-	-	-
AP in spring	-	-	-	-	-	-
Dominance rank	4.36	1, 183	*	3.90	1, 174	*
Roost group	0.00	1, 183	NS	0.00	1, 174	NS
Roost group * year	3.43	7, 189	**	3.76	7, 180	***
Roost group * experience	-	-	-	4.38	1, 174	*
Final model:						
Deviance		213.3			187.7	
df		182			173	

Table 7.3. Linear model using maximum likelihood estimates fitted to the breeding success of Bewick's Swan pairs returning to Slimbridge from one winter to the next (1989-90 to 1992-93 winters inclusive. Data concerning swans which lost and/or replaced their mate between successive winters excluded from analysis). Note: * P < 0.05, ** P< 0.01, *** P < 0.001, NS not significant, - variable removed from final model (see methods).

Variable	F ratio	d.f.	P
Year	0.00	1, 144	NS
Social class	0.00	1, 144	NS
Roost group	4.15	1, 144	*
Dominance rank	-	-	-
Male experience	-	-	-
Female experience	-	-	-
Pair duration	-	-	-
AP of male in spring	-	-	-
AP of female in spring	3.58	1, 144	NS
Year * social class	5.47	5, 148	***
Roost group * AP of female in spring	3.86	1, 144	*
Final model:			
Deviance		143.9	
df		143	

Fig. 7.1. Return rates of male Bewick's Swans from one winter to the next at Slimbridge (mean and S.E. bar per winter, n = 445), plus predicted values from a generalised linear model.

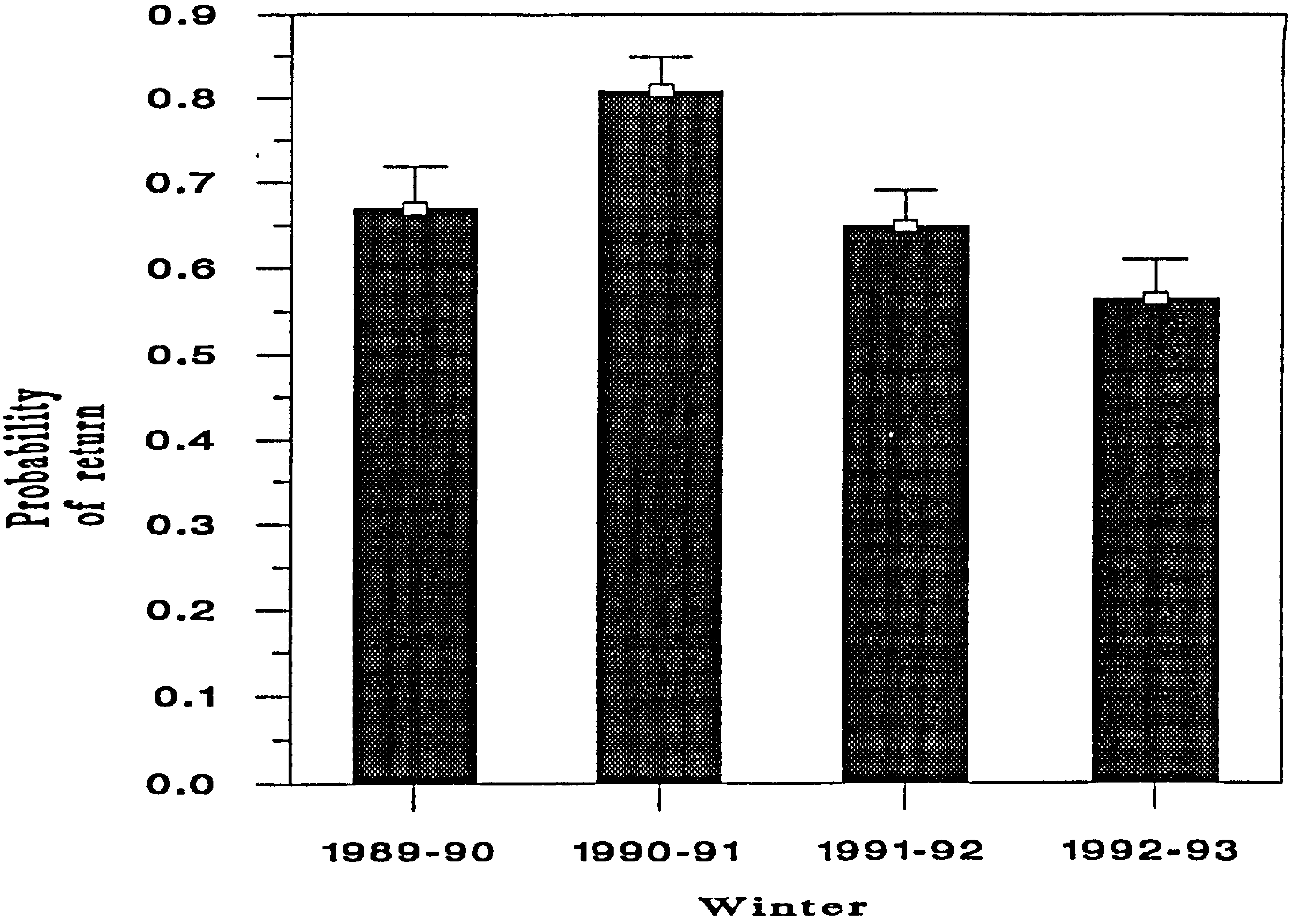


Fig. 7.2. Proportion of male swans which returned to Slimbridge from one winter to the next by social class (mean & S.E.bar,n=445), plus predicted values from a generalised linear model (S=single,P=paired,B=breeding,F=family,A=adult,Y=yearling,C=cygnet).

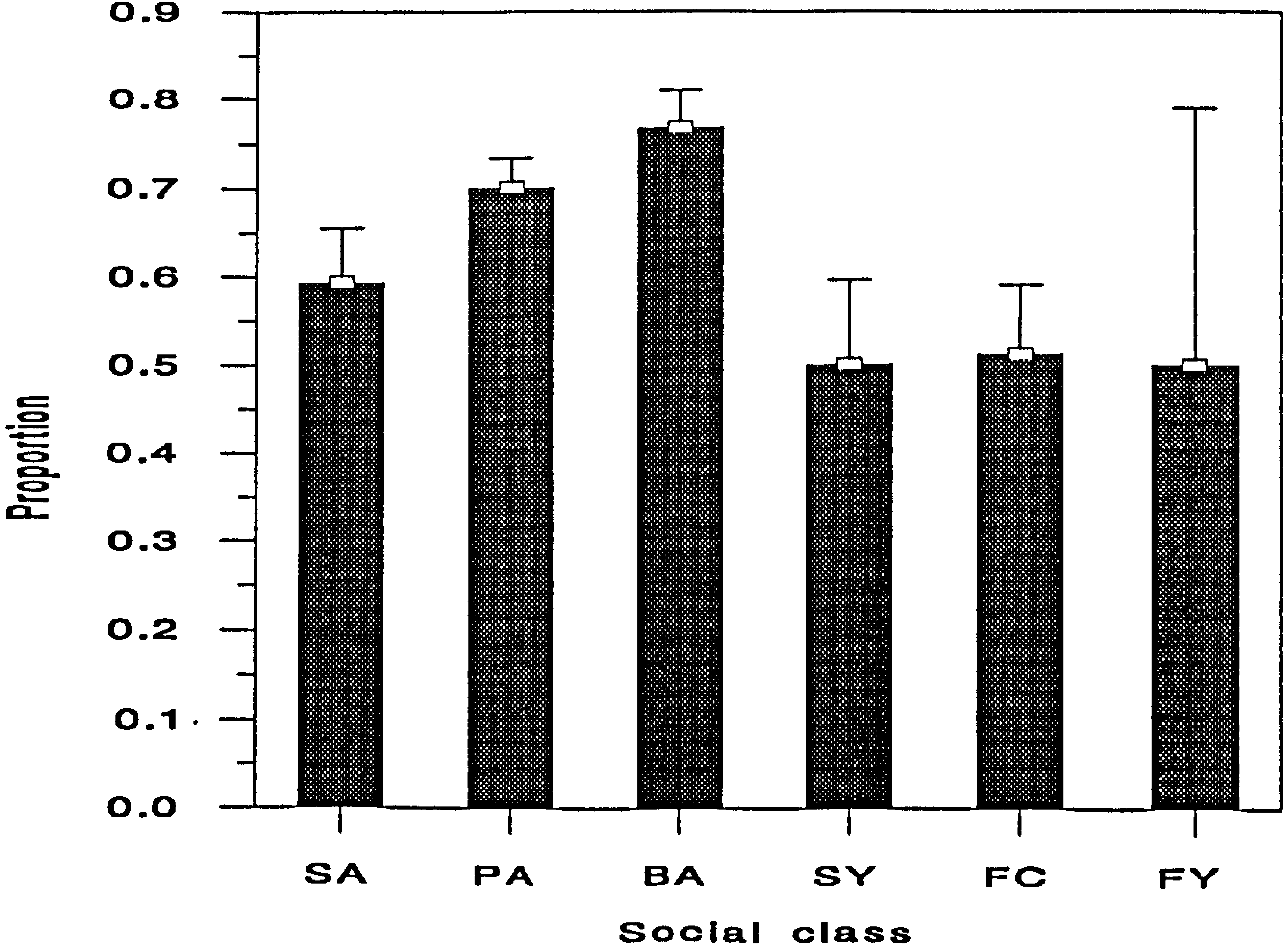


Fig. 7.3. The proportion of female Bewick's Swans returning to Slimbridge from one year to the next by roost group (mean and S.E. bar, n=329 and 110 for the Rushy Pen and Grounds roosts respectively), plus predicted values from a generalised linear model.

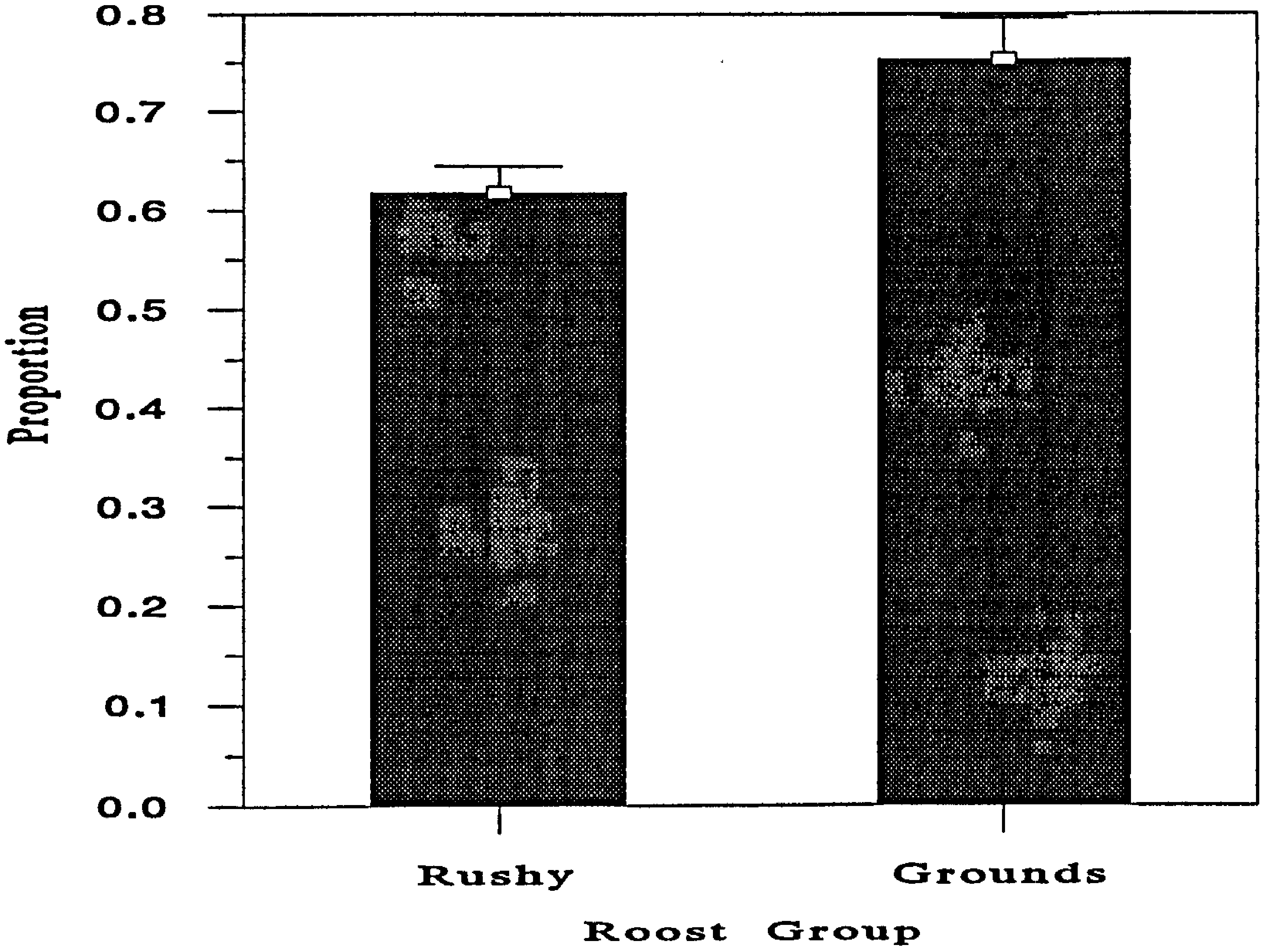


Fig. 7.4 Proportion of female swans which returned to Slimbridge from one winter to the next by social class (mean & S.E.bar, n=440), plus predicted values from a generalised linear model (S=single,P=paired,B=breeding,F=family,A=adult,Y=yearling,C=cygnet).

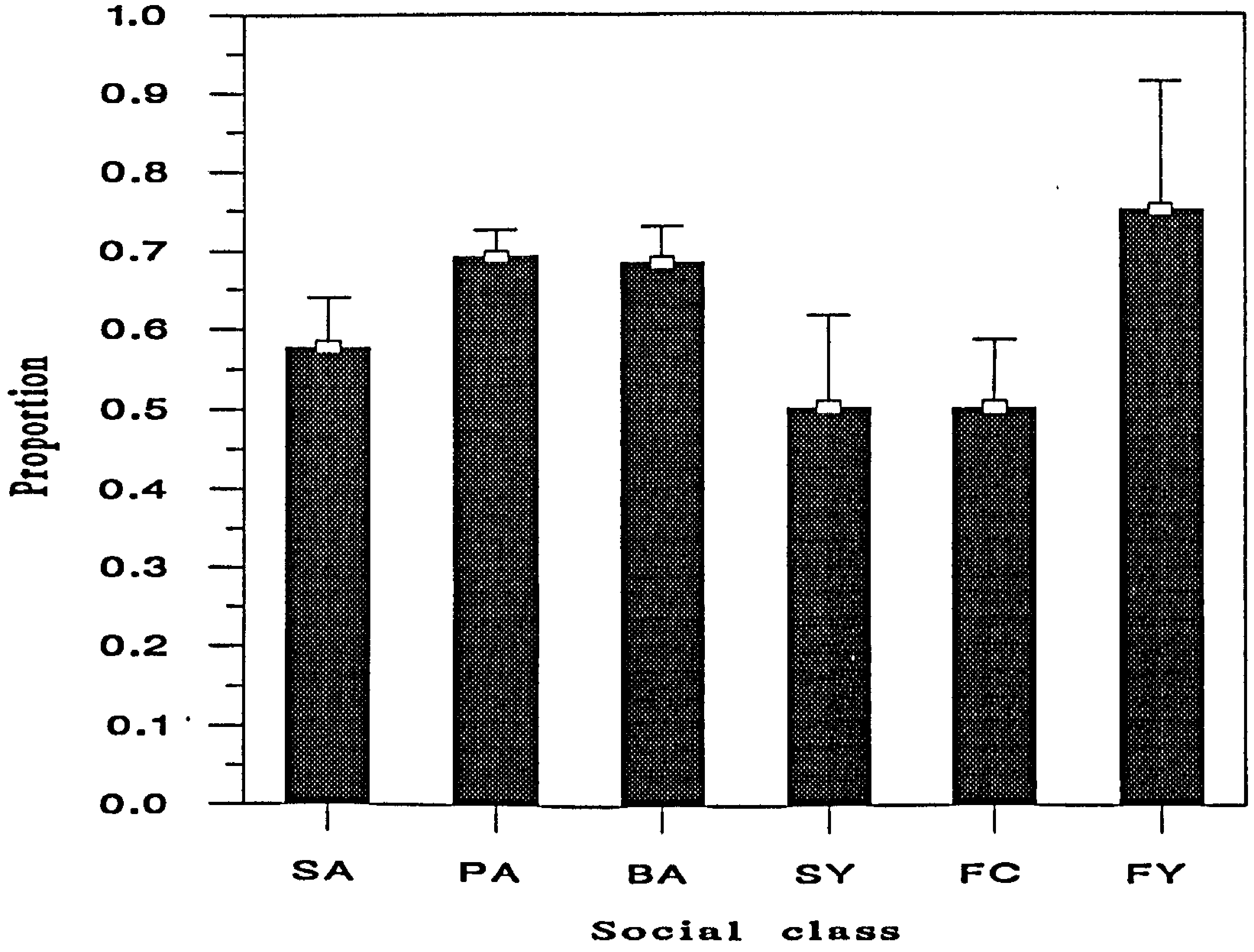


Fig. 7.5. The proportion of paired Bewick's Swans from the two roost groups at Slimbridge (R = Rushy Pen, G = Grounds Pens) which returned in the following winter with cygnets, by winter (n = 54,61,61,45 for the four winters respectively).

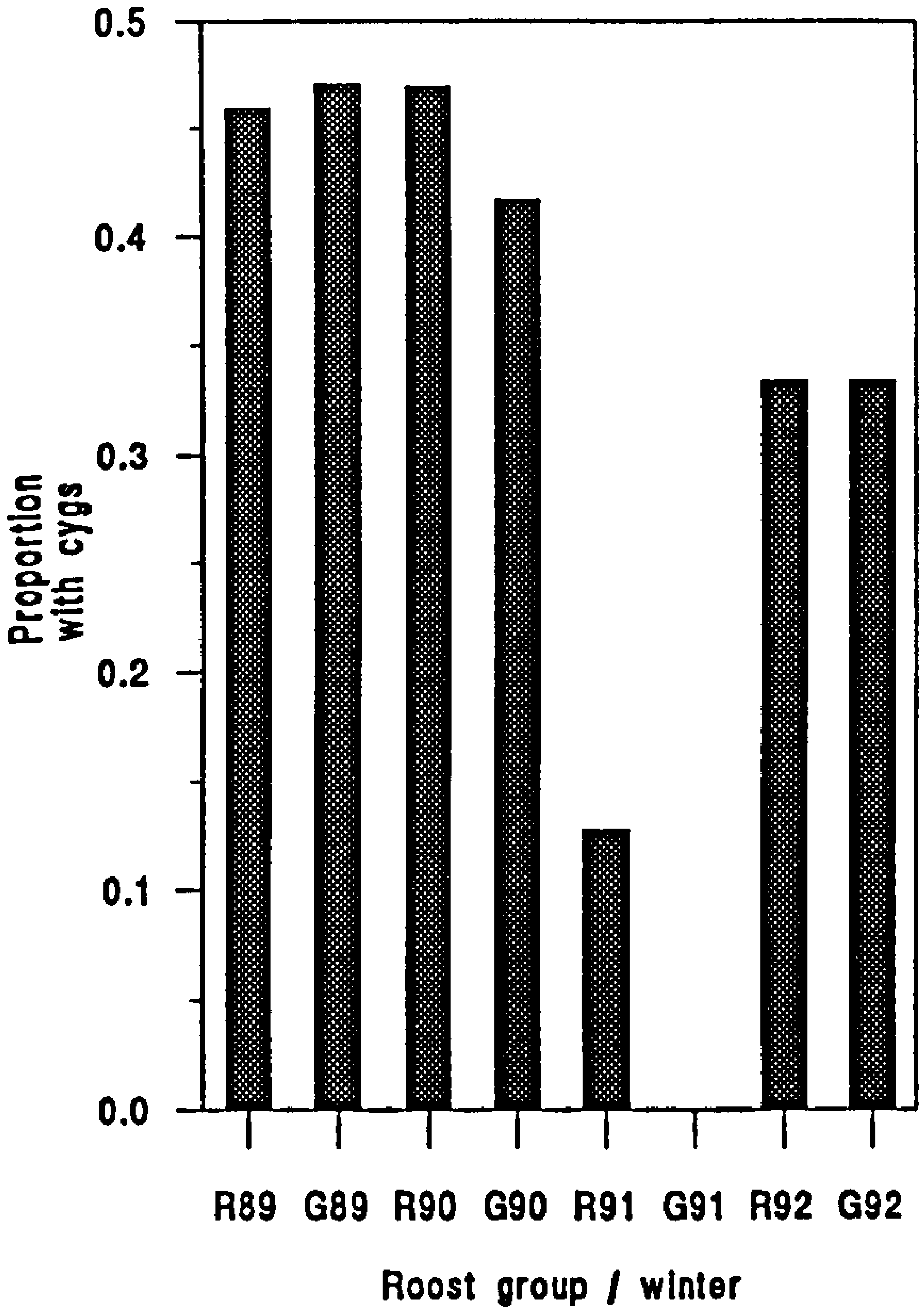


Fig. 7.6. The proportion of paired male Bewick's Swans at Slimbridge which returned in the following winter with cygnets, by winter (mean and S.E. bar per winter, n = 54,61,61,45 for the four winters), plus predicted values from a generalised linear model.

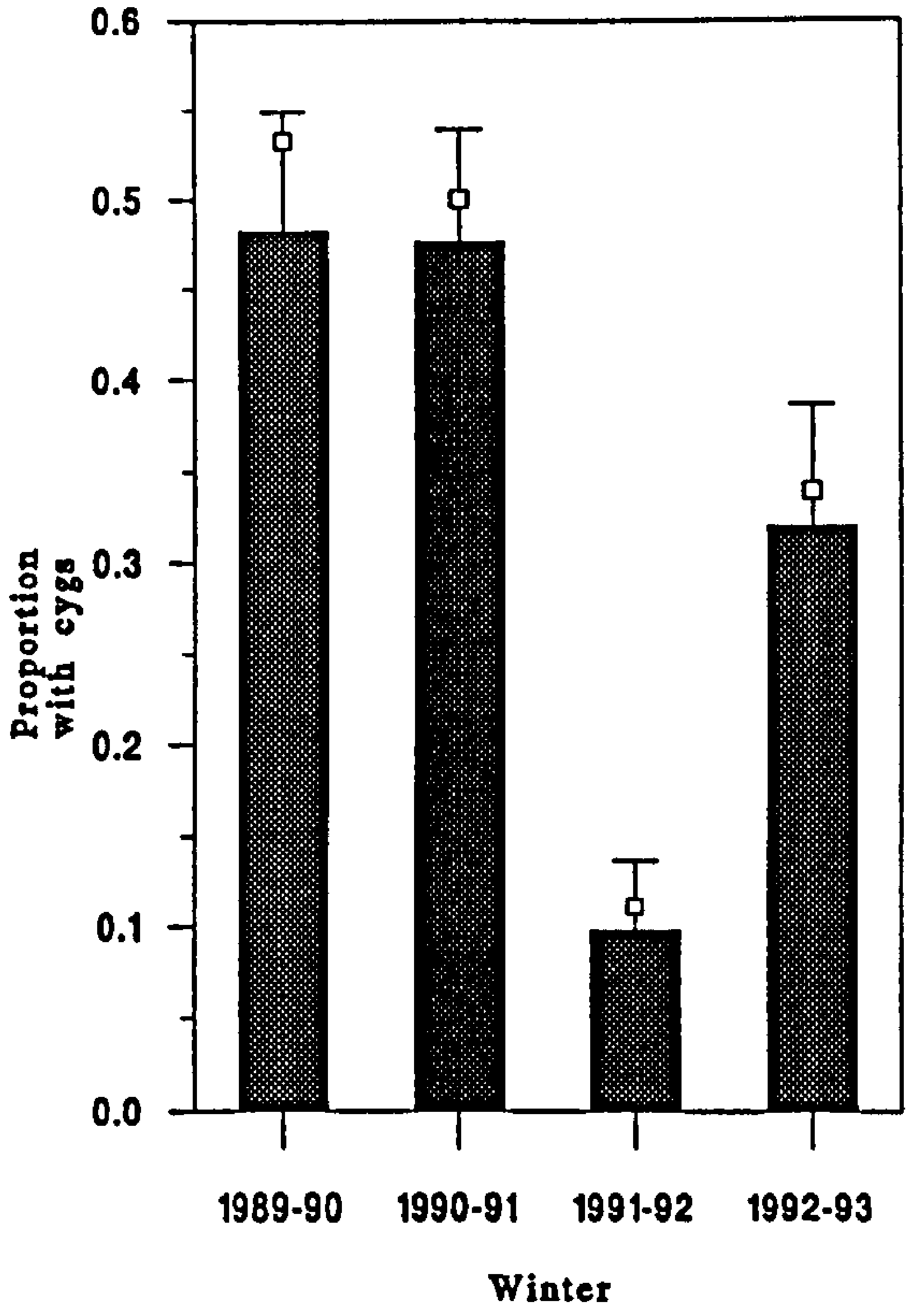


Fig. 7.7. Proportion of paired male Bewick's Swans at Slimbridge which returned in the following winter with cygnets, by roost group (mean & S.E.bar, n=173 and 61 for Rushy Pen & Grounds respectively), plus predicted values from a generalised linear model.

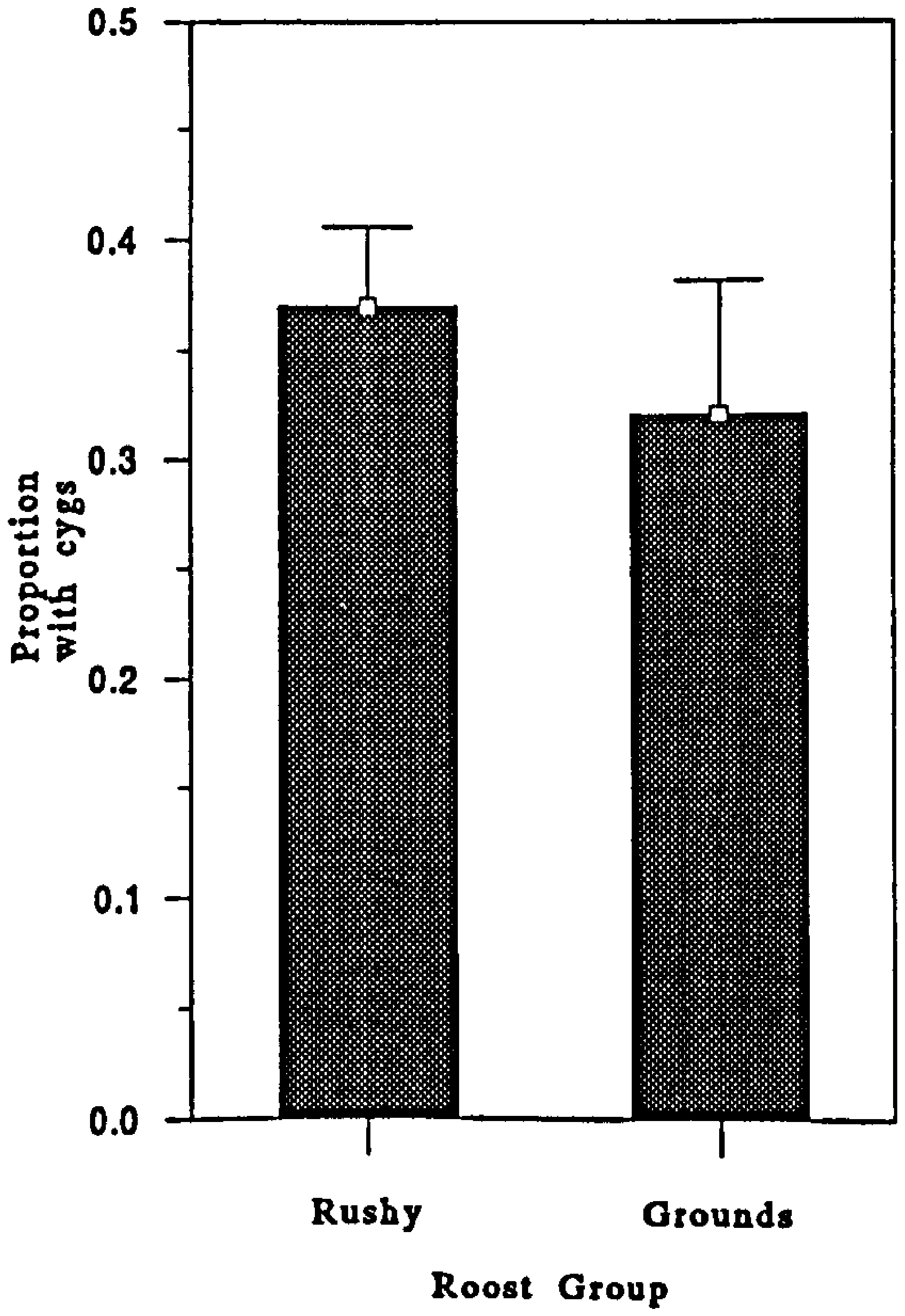


Fig. 7.8. Proportion of paired male Bewick's Swans returning to Slimbridge with cygnets, by dominance rank in the previous winter (mean and S.E. bar, n=234), plus predicted values from a generalised linear model.

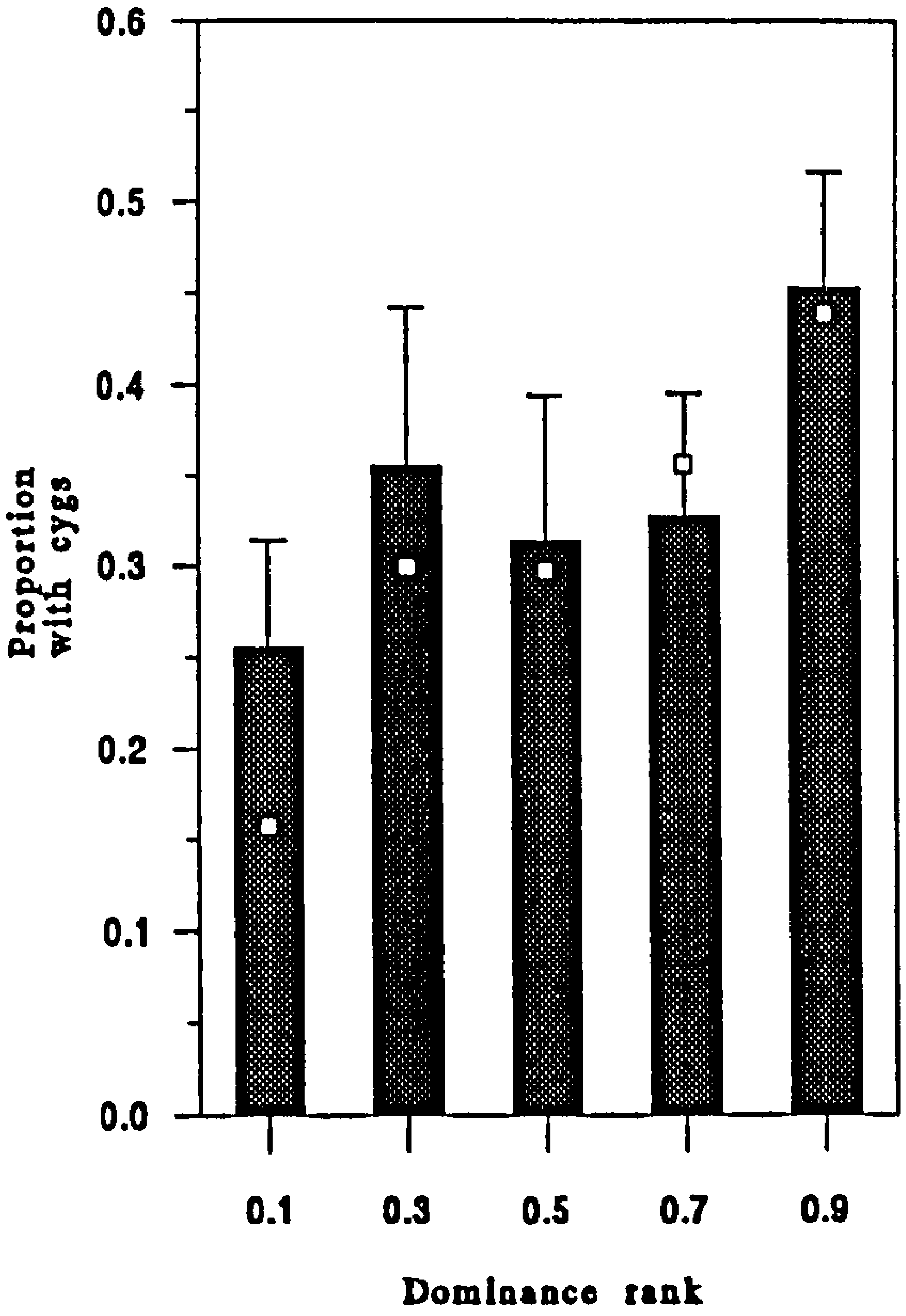


Fig. 7.9. The proportion of paired female Bewick's Swans which returned to Slimbridge in the following winter with cygnets, by winter (mean and S.E. bar, n = 223), plus predicted values from a generalised linear model.

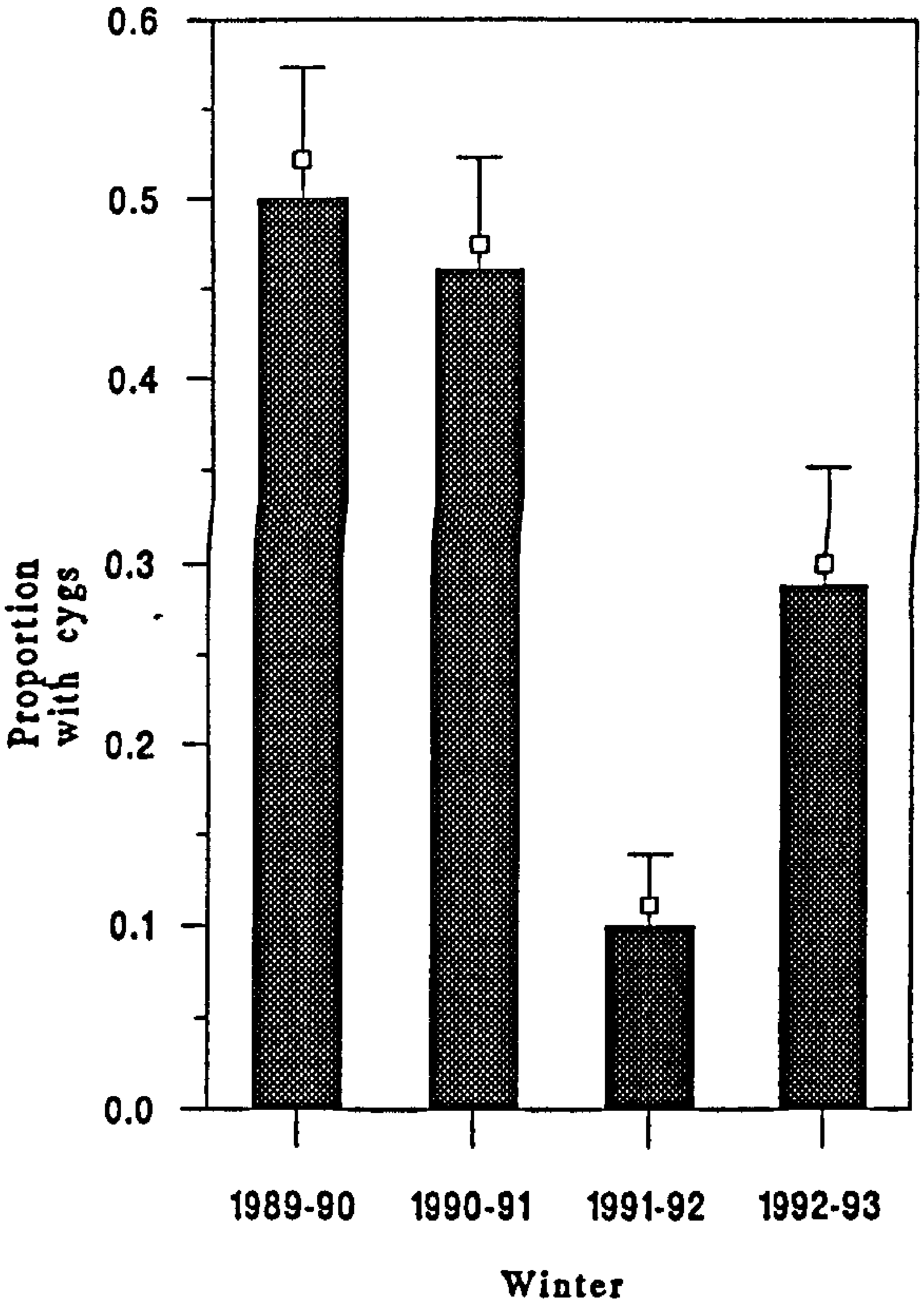


Fig. 7.10. The proportion of paired female Bewick's Swans which returned to Slimbridge from one year to the next, by roost group (mean & S.E.bar,n = 160, 63 for Rushy Pen and Grounds respectively), plus predicted values from a generalised linear model.

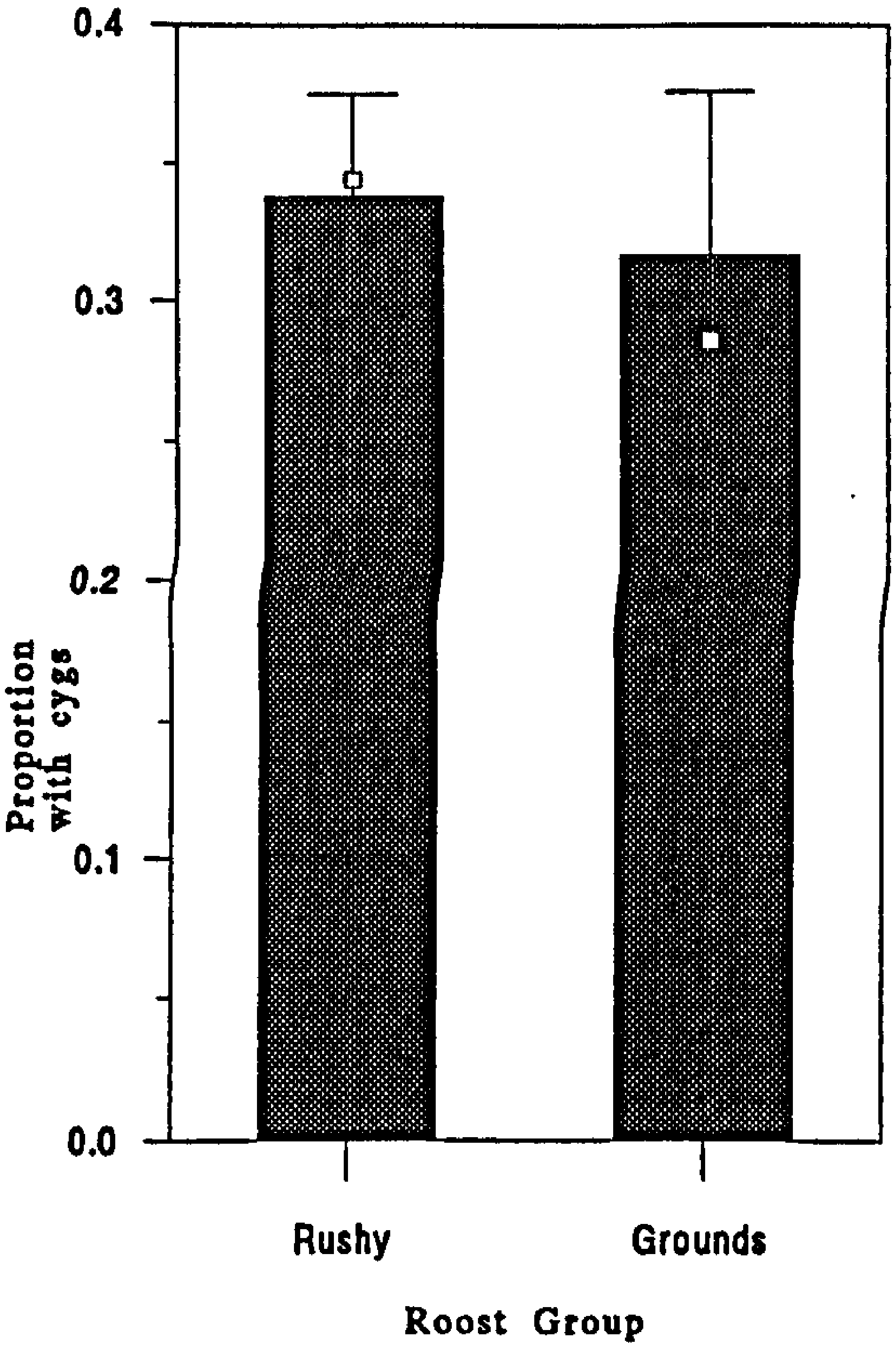


Fig. 7.11. The proportion of paired female Bewick's Swans which returned to Slimbridge with cygnets from one winter to the next, with dominance rank in the previous winter (mean and S.E. bar, n=223), plus predicted values from a generalised linear model.

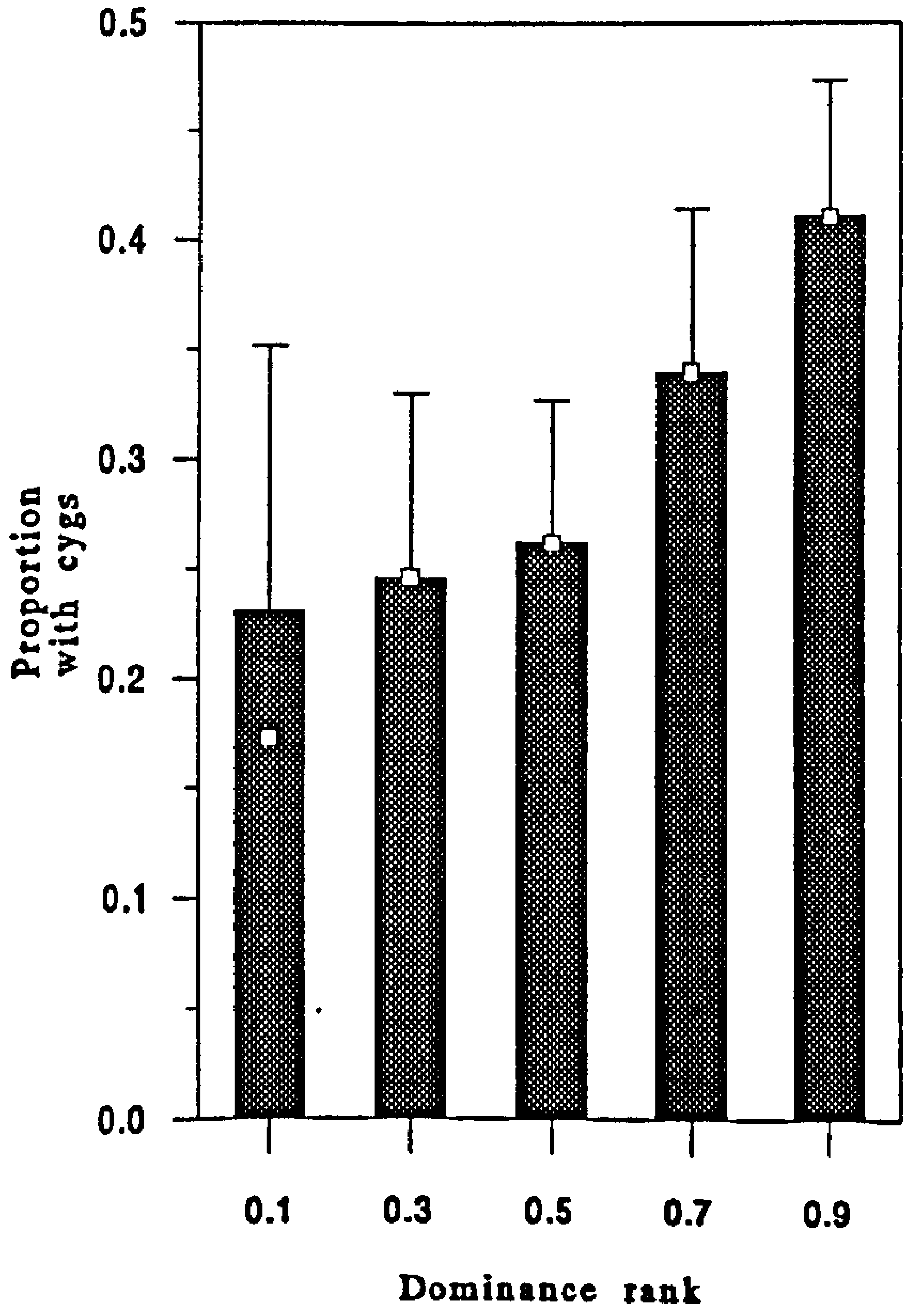


Fig. 7.12. The proportion of paired female Bewick's Swans which returned to Slimbridge with cygnets from one winter to the next, with previous experience of the site in years (mean and S.E. bar,n=223), plus predicted values from a generalised linear model.

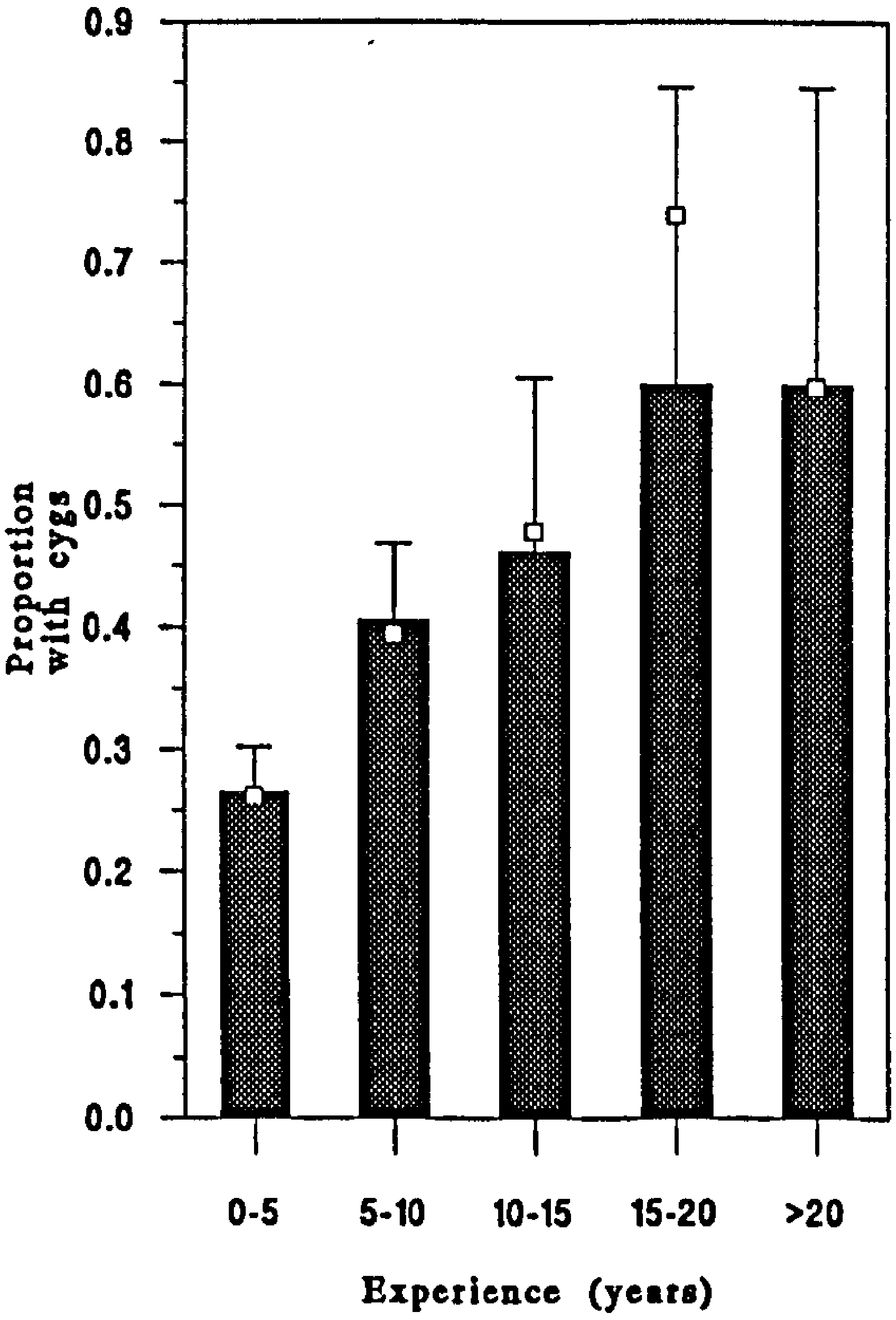


Fig. 7.13. The proportion of Bewick's Swan pairs at Slimbridge which returned in the following winter with cygnets, by winter (mean and S.E. bar, n = 221), plus predicted values from a generalised linear model.

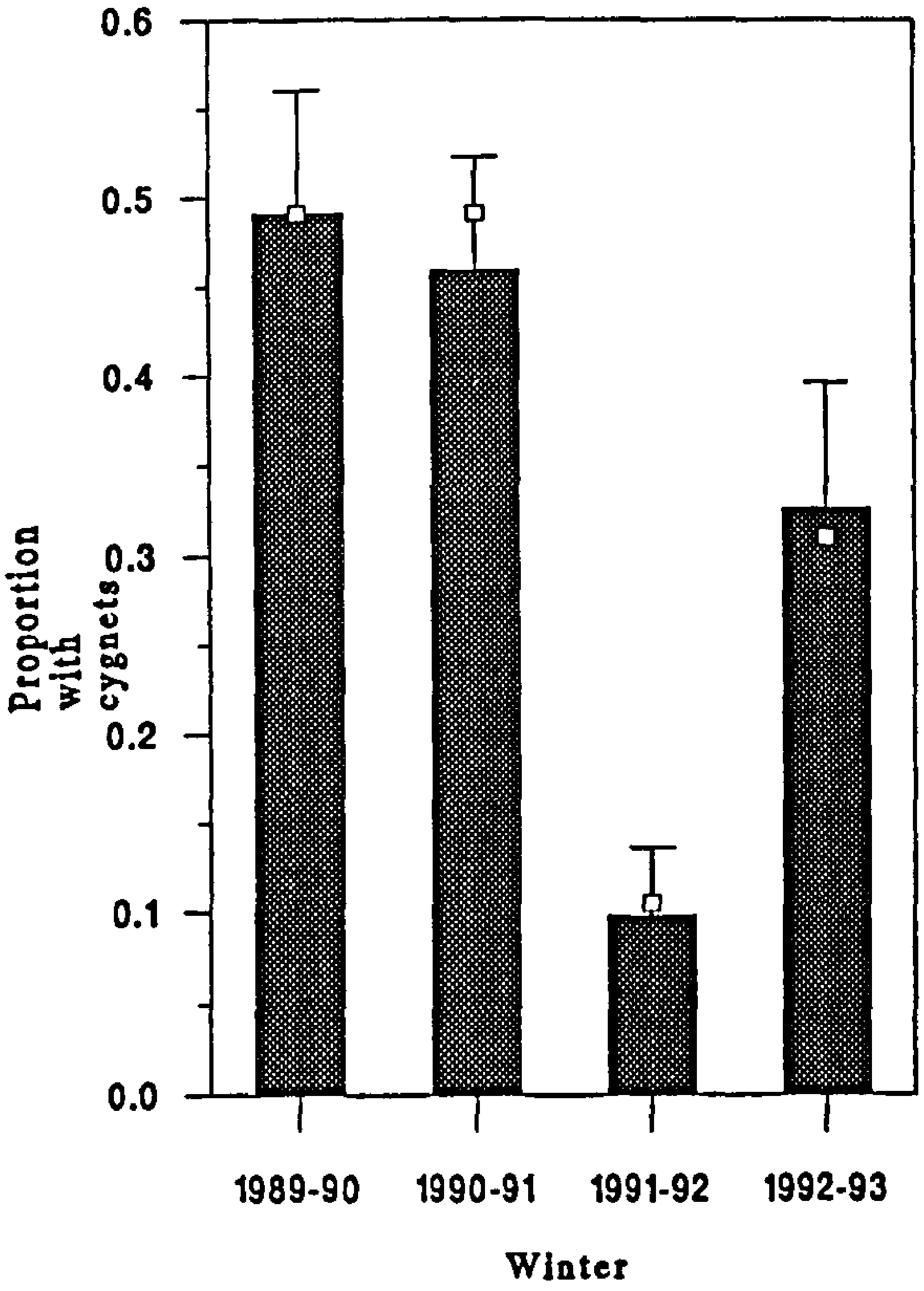


Fig. 7.14. The proportion of Bewick's Swan pairs which returned to Slimbridge with cygnets, with breeding success in the previous year (mean and S.E. bar, n=221), plus predicted values from a generalised linear model.

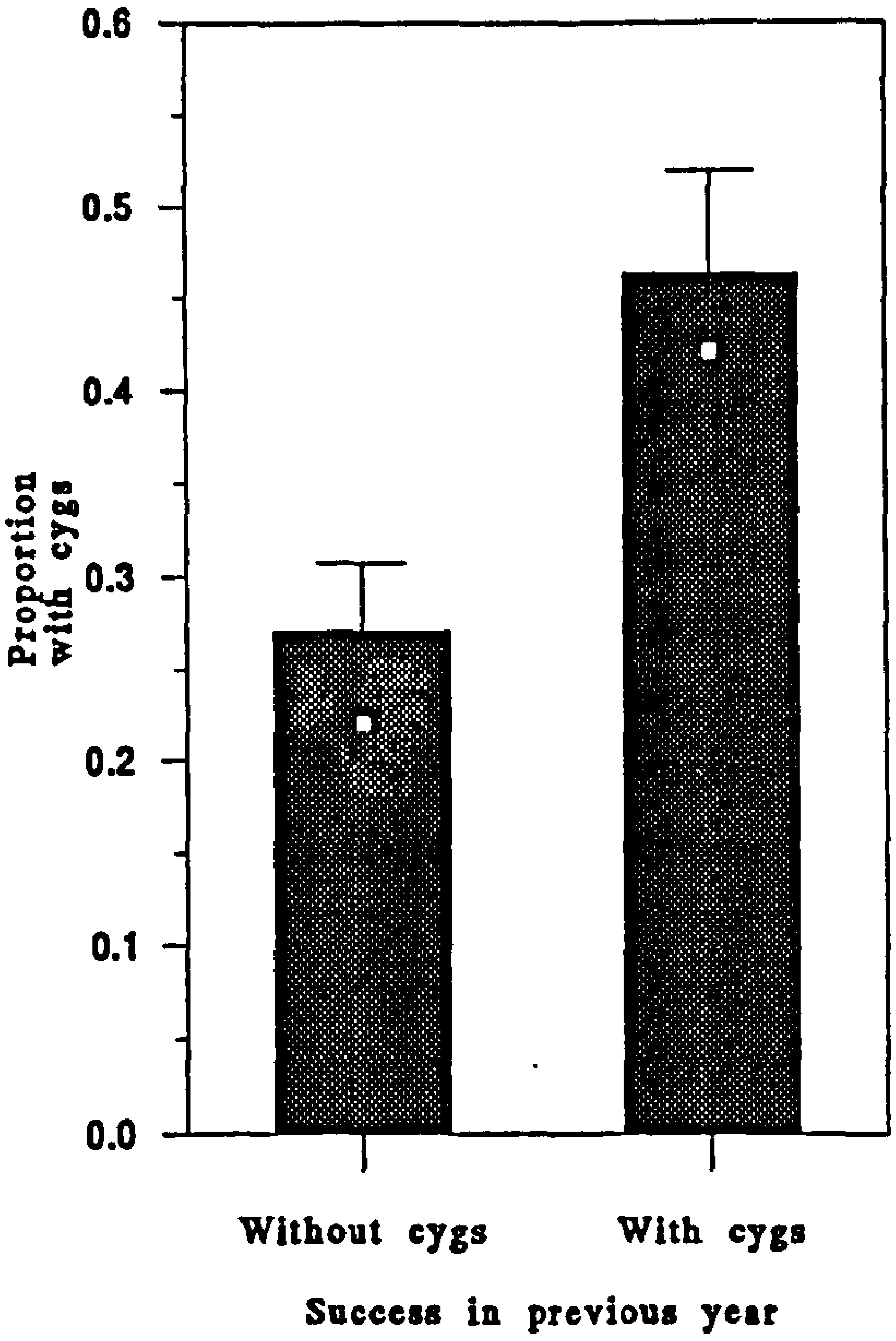


Fig. 7.15 The proportion of Bewick's Swan pairs which returned to Slimbridge with cygnets from one winter to the next by roost group (mean & S.E.bar,n=163, 58, for Rushy Pen and Grounds respectively), plus predicted values from a generalised linear model.

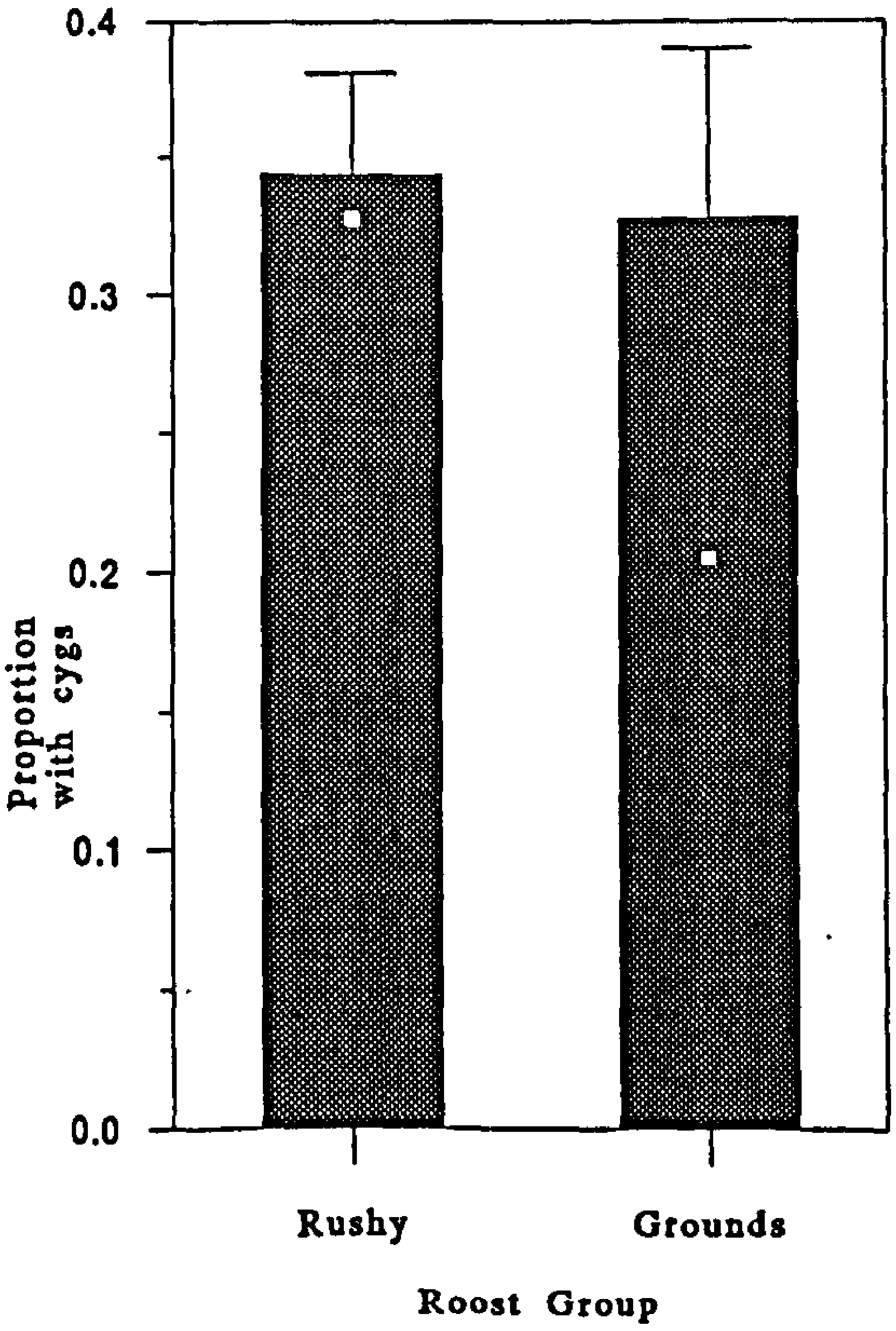
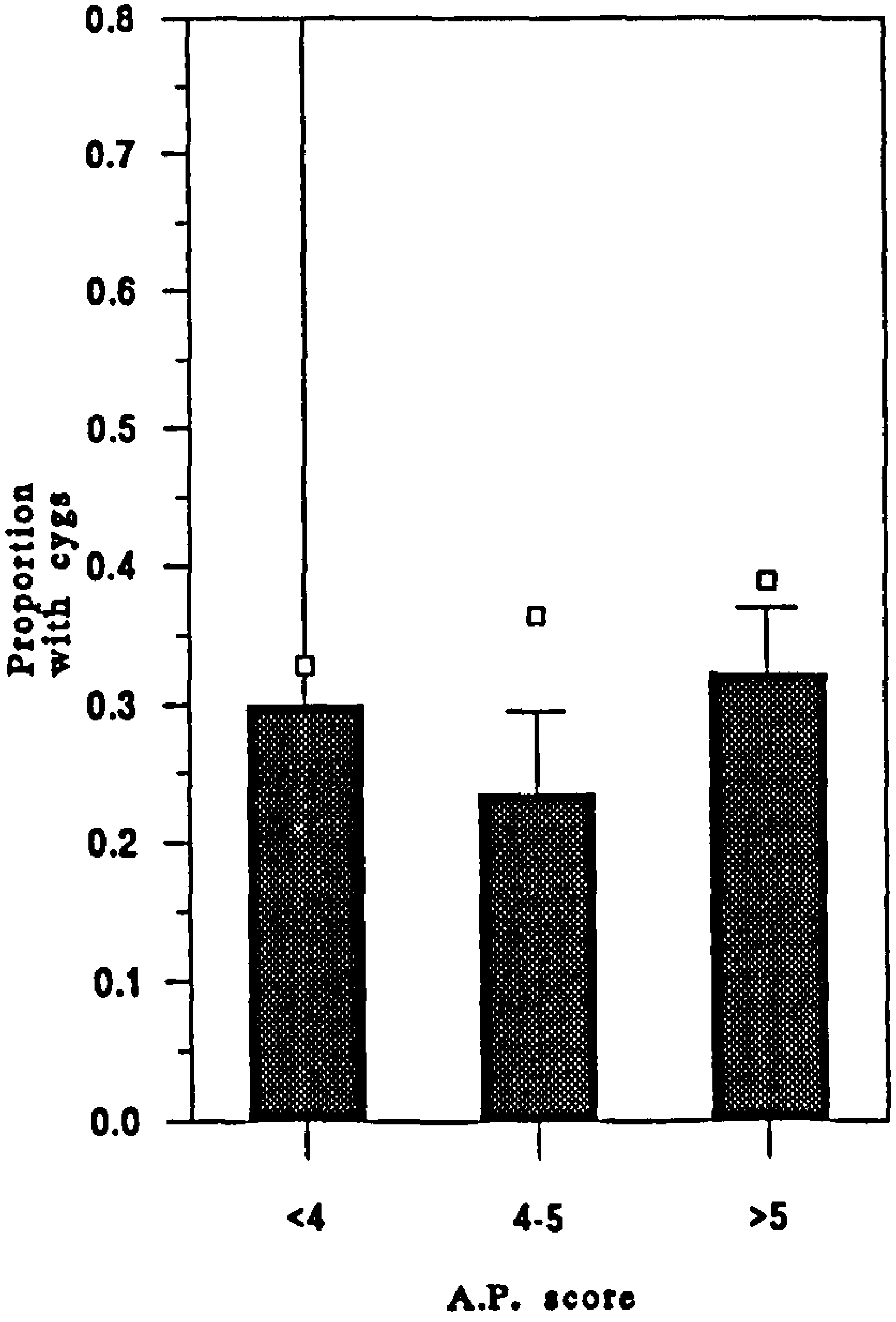


Fig. 7.16. The proportion of Bewick's Swan pairs which returned to Slimbridge from one winter to the next with cygnets, with the AP score of the female in the previous spring (mean and S.E.bar,n=221), plus predicted values from a generalised linear model.



CHAPTER 8 GENERAL DISCUSSION

The initial aim of this thesis was to determine whether individual Bewick's Swans wintering in Gloucestershire modified their feeding strategies in response to changes in the food supply, and whether feeding performance during the winter affected their likelihood of returning to the site and their subsequent breeding success. This chapter reviews the findings of the previous chapters in relation to current foraging theory and the extent to which they have advanced our understanding of the winter feeding ecology of Bewick's Swans.

8.1 Feeding strategies employed by individual swans during the winter

According to the ideal-free distribution (Fretwell & Lucas 1970), individuals are free to feed anywhere and will distribute themselves on a given resource such that there are equal pay-offs to all. Variation in both the quality and quantity of the food supply, and in the competitive ability of individuals will modify the distribution however, since the relative pay-offs for individuals may differ between patches, depending on the food supply, and the number and competitive ability of others already present (Sutherland & Parker 1985).

Although food may ultimately not have been limiting for the swans during the winter at Slimbridge, there was both temporal and spatial variation in the quantity and quality of food supply, and in the extent of flooding on the fields (Chapter 4). Swans responded to changes in the food supply in two ways: a) by selecting different feeding sites and b) by altering their feeding rates.

a) Site selection

Bewick's Swans were observed to use 41 different feeding sites in Gloucestershire during the course of the study. Swans were concentrated at a relatively small number of feeding sites upon arrival in October, and used a greater number of fields later in the winter. However, since flock size did not decrease during the winter, the increase in the number of feeding sites used, may have reflected the overall increase in numbers of swans at Slimbridge as the winter progressed. There was a direct linear relationship between the number of fields used by the swans and the monthly swan-day total, suggesting that dispersal increased as the number of swans increased (numbers were highest during the mid-winter period), perhaps in relation to optimal flock size and density, rather than as a direct response to a decline in food supply as suspected by Rees (1990), but not borne out by the results of this study.

The daily distribution of Bewick's Swans wintering at Slimbridge was determined primarily by the extent of flooding at the feeding sites; swan use of a field increased as water cover increased. Rees (1990) also showed that Bewick's Swans mainly fed on flooded pasture, although the precise depth of flooding was not found to have a significant effect upon site selection (the extent of flooding was not considered in the study). The presence of water at the feeding sites may improve foraging efficiency in two ways: i) it aids the digestive process by increasing the ease with which food is broken up in the gizzard, thereby controlling the availability of nutrients to the bird (Owen et al. 1977).
ii) it reduces time spent in activities other than feeding (Owen 1972a) and removes the need for energetically expensive flights (see Mooij 1992) to water-bodies during the day for drinking and bathing. Swan use declined on heavily flooded fields however, presumably because deep water reduced the amount of grazing available to the swans (Owen & Cadbury 1975).

The presence of other wildfowl on the fields also affected the extent to which the swans used each site. The number of swan-days recorded on a field declined as the number of goose-days (mostly Greater White-fronted Geese and Canada Geese) increased. This agrees with similar findings by Rees (1990) who found a strong negative correlation between swan use and the use of the fields by other grazing wildfowl. Heavy usage by geese significantly depleted the biomass of vegetation and swans occurred most frequently and in greatest numbers at sites where the highest biomass of green grass was available (Rees 1990). Grass biomass did not have a significant positive effect in the current study however, and this may have resulted from reduced variation in biomass during the relatively mild winters of 1991-92 and 1992-93, differences in statistical analysis and/or differences in the other habitat variables considered such as the duration of flooding causing vegetation die-back, and the protein profiles of the sward which were markedly different in the two studies.

The use made by the swans of an invertebrate food source on the River Severn was the first to be documented for Bewick's Swans on the wintering grounds. Macro-invertebrates are rich in protein which can be digested rapidly (Swanson & Bartonek 1970), and by feeding on estuarine invertebrates in March, the swans may have been attempting to increase their intake of protein-rich food prior to departure on spring migration. This concurs with work conducted on Blue Geese, which have been shown to require higher amounts of protein in the early stages of spring migration (Alisaukas & Ankney 1992). Protein may be required in larger amounts during the energetically stressful period of migration, whilst endogenous protein is used in small but possibly important amounts during laying in northerly breeding Northern Pintail Anas acuta (Mann & Sedinger 1993, Esler & Grand 1994).

b) Feeding rates

In a previous study, Rees & Bowler (1991) demonstrated that the proportion of Bewick's Swans feeding in flocks during the 1986-87 winter was higher in the first half of the winter than in the second half. This was attributed to increased foraging by the swans upon arrival in the wintering grounds, in order to replenish their nutrient reserves following the energetic demands of the autumn migration. Brent Geese in Sussex were thought to maximise dietary protein early in the winter by concentrating their feeding on protein-rich winter cereals, in order to replace that lost during migration. The geese subsequently switched to feeding on grass pasture for the rest of the winter, possibly to maximise water soluble carbohydrates (McKay et al. 1994). The protein levels recorded in grass swards at Slimbridge in 1986-87, declined after December (Rees 1988), suggesting that the increased feeding shown by the swans upon arrival may also have been to replace protein lost during migration. Such a trend was not observed in the current study however, and indeed the proportion of feeding swans was highest in the first half of February. The swans may not have increased their feeding rates upon arrival because protein levels in the sward in the 1991-92 and 1992-93 winters were actually lowest in November and increased during the winter reaching a peak in March. This also contrasts with protein levels recorded in winter cereals in the Sussex Brent Geese study, which were relatively constant during the 1991-92 winter and were always significantly higher than in grass swards (McKay et al. 1994). In addition, annual variation in the food supply at autumn staging areas in the Netherlands may also be a relevant factor in both studies.

Grass biomass and sward-length were highest when the swans arrived in October and their lower frequencies of feeding at this time may have resulted, in part, from improved foraging efficiency on the abundant food, since bite size increases with sward-length (Owen 1972a, Drent & Swierstra 1977). Certainly the swans were able to rapidly replace fat lost during migration, since their AP scores increased steadily over the winter with the most marked increase occurring between the second half of October and the first half of November.

The swans increased their frequency of feeding in February when protein levels in the sward were increasing, but biomass was still low and climatic conditions were at their most harsh (Chapter 5). This suggested that they were attempting to compensate for the declining food stocks by increasing the proportion of time spent feeding, as has been demonstrated amongst Barnacle and Pink-footed Geese in winter (Owen et al. 1992, Giroux & Patterson 1995). Although the swans lost condition at this time, both in terms of AP score and weight (Evans & Kear 1978), they were able to regain lost fat quickly in order to achieve their highest AP scores of the winter, prior to departure in late March. The swans' ability to quickly regain mass lost during cold spells, supports the hypothesis that fat reserves form an insurance against the risk of future inclement conditions, and that with increasing day-length the benefit of reserves becomes diminished (as the risk of severe weather declines) compared with the costs of carrying unnecessary weight (Pienkowski et al. 1979).

The proportion of swans feeding on the fields increased as the percentage protein content of the sward increased. Feeding was particularly concentrated on protein-rich swards at the end of the winter season, prior to the start of the return migration to the breeding grounds (Chapter 5). This effect was most marked in February, when birds on poorer fields spent considerably less time feeding than those on better pasture, suggesting that protein levels were influencing both feeding rate and site selection. Selection for plants containing a high proportion of protein has also been found to be advantageous for the energy budget of Barnacle Geese since the metabolizable energy and protein content of the grasses were positively correlated (Prop et al. in prep.), and this would be particularly important prior to migration when the swans would need to metabolize a large amount of energy per day, in order to store some in body reserves to fuel the spring migration. Moreover, since protein digestion occurs rapidly, optimizing protein intake (by high turnover rates) is probably more important than increasing the efficiency of carbohydrate digestion (by retaining food for longer periods of time) (Buchsbaum et al. 1986). Increased feeding prior to spring migration has also been noted in similar studies on migratory geese, for example, amongst Blue Geese in the Missouri River valley (Davis et al. 1989) and Greater White-fronted Geese in California (Ely 1992).

8.2 Variation in feeding strategies by *different categories of swans*

In the ideal-free distribution of Fretwell & Lucas (1970), individuals should have an equal intake rate wherever they go. In social birds such as Bewick's Swans however, feeding strategies will vary between individuals, reflecting differences in both competitive ability and foraging efficiency. Low-ranking individuals may suffer strong competition from high-ranking individuals at the best food patches and may move to poorer patches in order to improve their relative pay-offs (Sutherland & Parker 1985). Perfect separation of phenotypes is unlikely to occur in natural situations however, since this would be observed only after a vast number of 'rounds' of learning among the same competitors, with no further input of naive individuals, whilst the resulting distribution will also depend on the number of birds present of the different phenotypes, the range of competitive abilities present within those phenotypes, and the ability of individuals to re-adjust decisions about where to forage (Parker & Sutherland 1986, Milinski et al. 1995). Broad separation of good and poor competitors between food patches which provided different relative pay-offs has been observed in Common Cranes in Spain (Bautista et al. 1995) and demonstrated experimentally amongst Mute Swans in Switzerland (Milinski et al. 1995).

There is a well ordered social hierarchy amongst the Bewick's Swans at Slimbridge. Families are dominant over pairs which in turn are dominant over singletons (Scott 1980b, and this study). Moreover, dominance rank increases linearly with family size, and with age amongst male singletons (Chapter 2). Swan units within the Slimbridge herd therefore exhibit a range of competitive abilities which may have a strong effect upon their observed foraging strategies. Individual foraging strategies may differ with respect to a) social class and b) roost group.

a) Social class

Swans from the three main social classes differed in their use of feeding sites. Families tended to use the fields closest to the roosts whilst singletons used more distant fields (Chapter 4). Giroux & Patterson (1995) found a similar distribution amongst unpaired singletons and families of Pink-footed Geese, flying out to feeding sites from roosting lochs in Scotland. The results suggested that high-ranking families could dominate their preferred feeding sites, close to the roost, whilst low-ranking singletons were forced to travel further afield, spending more time in the energetically-costly activity of flight (Mooij 1992), and that some separation of phenotypes was occurring at the feeding sites. Moreover, the proportion of cygnets in the feeding flocks decreased with flock size, as has been found during the winter in both the conspecific Whistling Swan (Bart et al. 1991) and in the Whooper Swan (Hewson 1964, Salmon & Black 1986). This suggests that families may have been able to dominate their preferred food resources, as has been demonstrated for Brent and Barnacle Geese in winter (Lambeck 1990, Black et al. 1992), and experimentally amongst pre-fledging broods of Blue Geese (Mulder et al. 1995).

Breeding males had slow peck rates and spent more time in vigilance and social interactions than other males, indicating that they were protecting *their mate and offspring* from conspecific feeding competition and/or predation (Chapter 6). These findings are consistent with those from other studies of grazing Anatidae including Eurasian Wigeon (Mayhew 1987), Canada Geese (Sedinger & Raveling 1990, Johnson & Sibly 1990) and Black Brant (Sedinger et al. 1995). Scott (1980c) demonstrated amongst Bewick's Swans wintering at the Ouse Washes, that parents spent more time in vigilance and social interactions than pairs without offspring, but did not find differences between the two sexes. Breeding males in the current study spent less time feeding and were in poorer body condition, in terms of AP score, than males of lower social class. The females and offspring benefitted from the protection afforded by their mates, which enabled them to spend more time feeding, have faster peck rates, slower step rates and to spend less time in vigilance and social interactions. This was reflected in their high AP scores. Time spent feeding by the females under the more experimental conditions of the grain feeds, increased with the dominance rank of the pair whilst time spent in vigilance and in movement decreased with dominance rank, and hence the extent to which they could build up fat reserves as reflected in their AP scores. Other studies have also shown that average daily food intake is positively correlated with dominance rank, for example amongst Common Cranes (Bautista et al. 1995) and Willow Tits (Koivula et al. 1995). The uniqueness of the results of the current study are that female feeding performance was correlated with the dominance rank of its social unit (rather than its own dominance rank), which is largely a function of the fighting ability of the male, since single females have very low dominance rank. These results demonstrate how the fighting ability of the male influences the foraging performance of its mate, which may have important consequences upon subsequent return rates and breeding success.

Improved foraging success by females from dominant pairs is to the detriment of male foraging success, since much of the male's time is taken up in vigilance and aggressive encounters in order to protect the female, and male AP scores tended to decrease with dominance rank. One way in which males improved their foraging performance was to spend less time in vigilance and to feed more intensively on grass swards with a high protein content. They invested most effort into protecting their mate and/or offspring from intra-specific feeding competition when food quality was low. Females also spent less time being vigilant at poorer quality sites suggesting that they needed to spend more time foraging when food quality was low. This agrees with Reed (1993), who showed that inter-brood aggression amongst winter flocks of Brent Geese was generally rare, except when they were feeding on a patchily distributed food resource. The female and offspring would benefit most from male protection when food supply was both low and patchily distributed. Dominant males may also be able to improve upon their late winter AP scores, by increased foraging activity at spring migratory sites on route to the breeding areas. For example, Rees & Bowler (1991) showed that swans at a migratory site in Estonia spent a larger proportion of their time feeding than in the winter, whilst paired males and females had similar feeding rates. Moreover, paired birds spent less time being vigilant than singletons, even though cygnets continued to associate with their parents, suggesting that protection of the mate and/or cygnets was less important than in the winter.

The peck rates of both male and female swans decreased as sward-length increased, agreeing with similar findings for grazing geese (e.g. Owen 1972a, Drent & Swierstra 1977, Black et al. 1992). Assuming bite size increases with sward-length, these results suggest that handling time increases with the size of individual food items. However the step rates of females (and not males) also increased with sward-length. This unexpected relationship is the opposite to that shown by Barnacle Geese (Black et al. 1992), and suggests that on fields with a high mean sward-length, females may be selectively grazing on patches of shorter grass, particularly since they also pecked more rapidly on swards of longer grass. The idea is further supported by the fact that although the peck rates of females on pasture were always higher than those of males, this difference was greatest on fields with highest sward-length. Selection for shorter grass may be favourable for the females, since their smaller bills (Evans & Kear 1978) may result in less efficient handling of larger food items. The difference in food selection may also reflect differences in dietary needs between the sexes, particularly prior to departure for the breeding grounds; shorter grass for example, may have higher relative growth rates and be proportionately richer in protein than longer grass (Ydenberg & Prins 1981). Protein is considered by some authors to be the most limiting nutrient to reproduction in arctic-nesting geese (e.g. Raveling 1979b, Davies & Cooke 1983).

b) Roost group

Swans from the two main roost sites at Slimbridge made very different use of the feeding sites. Distance from the roost site was the most important variable affecting distribution of swans from the two roost-sites on the fields; the number of Rushy Pen units identified increased with distance from the roost, whilst the number of Grounds Pen units identified decreased. Swans from the Rushy Pen selected fields on the basis of high protein content, and extensive water cover, seemingly in line with conventional optimal foraging theory, which suggests that birds should tend to select the most profitable food items, giving them the greatest yield of nutrients or energy per unit of search /handling effort (Parker & Stuart 1976, Pyke et al. 1977). Feeding sites chosen by the Grounds roost tended to have swards of low biomass and low protein content; a short flight and the presence of water appeared to be the overriding factors affecting their field choice. A tendency for birds to select fields closer to the roost-site than expected given the habitat distribution, has also been demonstrated for Red-breasted Geese in Bulgaria (Sutherland & Crockford 1993) and amongst Common Cranes in Spain, particularly when numbers at the roost site were low (Bautista et al. 1995). The energetic costs of flight to and from more distant feeding sites may be high (Mooij 1992), and the use of such sites may only be advantageous when larger flock sizes on the fields permit a sufficiently reduced proportion of time spent by individual birds in vigilance, and a consequently increased proportion of time spent feeding.

Differences in the selection of field sites by swans from the two roost-sites can be explained by differences in their foraging behaviour. Swans from the Rushy Pen spent less time feeding on provisioned grain at the roost-site, where there was greater competition for food from other swans, geese and ducks, than those in the pens of the Grounds roost-site, and spent more time feeding on the fields (Chapters 4 & 6). The selection of feeding sites was therefore more critical for swans roosting in the Rushy Pen than those roosting in the Grounds. The provision of supplementary high-quality feeds of grain at the roost-sites may also help to explain the absence of an obvious increase in food intake on the fields prior to departure to the roosts, which has been shown to effectively lengthen the feeding day in Greater White-fronted and Barnacle Geese (Owen 1972a, Ebbinge et al. 1975).

Swans from the Grounds roost spent less time feeding at the feeding sites during the day than those from the Rushy Pen, although there was no difference between the two groups in terms of feeding intensity (ie. peck-rates, step-rates and time spent actively feeding) within a feeding bout. This suggested that swans from the Grounds roost were not inherently less successful foragers, and reinforced the view that differences in site selection between the two roost groups reflected differences in food availability at the roost-sites. The different foraging strategies may not have been equally profitable for individual swans however, since in general birds from the Grounds roost had lower AP scores than those of similar rank from the Rushy Pen and as a consequence they suffered reduced breeding success, particularly in a year when breeding success in the European population as a whole was very low.

The transfer of birds with low AP scores from the Grounds roost to the Rushy Pen roost, and their subsequent change in field selection during January and February when grass biomass was lowest, indicated that the birds were capable of detecting, and attempting to improve upon, poor foraging performance. These results also inferred that some form of information transfer may have been occurring at the roost, for example by comparison of the AP scores of similar ranked birds (see Chapter 3). The inferred presence of a higher proportion of related individuals in the Grounds pens may have conferred other advantages, including reduced levels of social interaction within the roost group, whilst Raveling (1979a) suggested that the local stratification caused by the assemblage of related Canada Geese helped to maximise acquisition of the most desirable roost locations.

8.3 Effect of foraging success on return rates

Swans of high social status were more likely to return to Slimbridge than those of lower social status (Chapter 7). Males for instance, which in general have higher dominance ranks than females because of their greater fighting ability (Scott 1980a), had higher return rates than females, agreeing with the findings of Rees (1987). Similarly, cygnets and single yearlings had lower return rates than both adult singletons, and birds from the paired and breeding classes. Young singletons (< 2 years old) are of lowest dominance rank and their use of different wintering sites may represent exploratory dispersal, as demonstrated amongst Pink-footed Geese (Boyd 1955). Such dispersal may allow the birds to assess which site suits them best in terms of the availability of resources such as food and roost sites, and their ability to compete for them. Yearlings of both sexes, which were not associating with their parents, had high peck rates indicating that they were attempting to feed rapidly. However, yearlings also had high step rates suggesting that they may have been grazing on poorer quality grass, and therefore had to move more frequently between feeding patches. In addition, they were the most frequently attacked class, and as a result of their poor foraging performance they had lower than average AP scores.

Adult singletons also had low return rates. However, although single adult males are of low dominance rank they were able to achieve higher AP scores than males with a mate and/or cygnets because they lacked dependent birds to protect and could therefore spend less time in vigilance and aggressive encounters, and more time feeding. Rees & Bacon (in press) found that single Bewick's Swans used more sites than paired birds during migration, and suggested that this represented exploratory dispersal and habitat assessment by birds which were not constrained by the food requirements of a mate and/or cygnets. Since singletons have low dominance ranks they may suffer from reduced food intake, particularly at the best feeding areas such as the grain feeds (see Chapter 6), and make them more likely to explore alternative sites. This would therefore agree with Parker & Sutherland's (1986) modified ideal free distribution in which the better competitors should go to the food patch where they gain most from their competitive superiority, and the poorer competitors should attempt to choose the patch where they suffer least from their inferiority. Swans with a mate and/or cygnets have a higher dominance rank than singletons, are potentially able to obtain better access to the resources and consequently had higher return rates. Return rates did not relate directly to foraging performance of individual adult swans (as estimated by AP score at the end of the winter), since males which have mates and/or cygnets to protect, spent less time feeding.

Instead for paired birds, it is the dominance rank of the male and its effect upon the foraging performance of the female, which seem likely to influence the likelihood of a pair returning to Slimbridge. This suggestion is supported by the fact that the return rates of breeding females (which are generally of high rank) were higher than for females from unsuccessful pairs (which are generally of lower rank).

Return rates of female swans varied significantly between the two roost groups; those from the Grounds roost were more likely to return to Slimbridge than those from the Rushy Pen roost, despite their poorer foraging success, due to the higher return rate of yearling and single females to the Grounds roost. This difference was most marked for yearlings and suggests that low-ranking female singletons may benefit from returning to a known wintering site, with the prospect of other related birds being present and consequently reduced levels of social interaction. Female singletons have lower dominance ranks than male singletons of the same age, and may be less able to improve their foraging performance at unfamiliar alternative sites away from the presence of related individuals.

Return rates of cygnets in the following winter as yearlings were low (around 50%). There was no difference in the return rates of cygnets from low and high-ranking families, suggesting that foraging performance during their first winter did not influence their subsequent return rate as yearlings. Amongst the cygnets that did return as yearlings, there was no evidence to suggest that dominance (and therefore access to resources) was inherited, although sample sizes were small.

8.4 Effect of foraging success on breeding success

Female condition in spring prior to migration as assessed by its AP score, reflected the dominance rank of the male, and had a positive effect upon breeding success the following summer (Chapter 7). This agrees with similar work on high arctic-nesting geese, where breeding success was found to be correlated with the condition of the female in spring (e.g. Ankney & MacInnes 1978, Drent & Daan 1980, Ebbinge et al. 1982, Ebbinge & Spaans 1995), and suggests that fat reserves collected during the winter have an important effect upon breeding success. More recently it has been shown that female Dusky Canada Geese nesting in the low arctic (c60°N) could feed at all stages of the breeding cycle and that exogenous sources accounted for 100% of estimated daily energy requirements during pre-laying and 24% during incubation (Bromley & Jarvis 1993). However, Bewick's Swans breeding at higher latitudes (c 68° 30'N) may begin nesting when the breeding grounds are still almost entirely covered with snow (pers. obs.), hence endogenous reserves are likely to be important at least for egg production and for the early stages of incubation. Although males do not incubate, they usually sit on the eggs whenever the females are absent, helping to reduce heat loss from the eggs (Hawkins 1986) and protecting them from predators, whilst allowing the females to feed during incubation.

Female AP score in the spring, prior to migration, reflects foraging performance during the winter, which in turn is a function of feeding site selection together with the protection from conspecific feeding competition and predation, afforded to the female by its mate. The protection afforded by dominant males during the winter allowed females from high-ranking pairs to monopolise the best food resources, where they had higher feeding rates. Female AP score was correlated with the dominance rank of the pair (Chapter 2) which in turn was correlated with the time spent feeding by the female at the grain feeds. This agrees with Scott (1988) who demonstrated that breeding success in Bewick's Swans was correlated with dominance rank. The findings of other studies on reproductive success in birds demonstrate ways in which high dominance rank may influence success. Henderson & Hart (1995) for example, showed that amongst Jackdaws, dominance rank was positively correlated with the more efficient provisioning of offspring and therefore the raising of larger annual broods. Mulder et al. (1995), showed that the parents of dominant broods of Blue Geese 'defended' experimental plots of high vegetation biomass, which allowed the brood to feed for longer and to have higher intake rates, and in addition helped to reduce the energetic costs of foraging by reducing the step rate of the offspring.

8.5 SUMMARY

The study has shown that Bewick's Swans are capable of altering their feeding strategies in relation to changes in the quantity and quality of the food supply. Bewick's Swans favour protein-rich swards that are partially flooded, and increase their intake of protein by increasing feeding rate and/or by changing feeding site, particularly when food supply is low and prior to migration in spring. The swans' requirement for protein-rich pasture that is partially flooded, has important implications for habitat management at other grassland wintering sites in Britain. The distribution of individual swans of differing competitive ability at the feeding sites during the winter, broadly followed that predicted by Sutherland & Parker's (1985) modified ideal-free distribution, agreeing with the findings of studies of other socially-feeding birds. Swans of high social status were more likely to return to Slimbridge than those of lower social status, whilst the return rates of pairs was influenced by the dominance rank of the pair and its effect upon the foraging performance of the female. Both findings agree with the predictions of the modified ideal-free distribution.

The current study also showed for the first time, that the mass of a bird can be predicted from its' AP score *recorded in the field, without* the need for repeated capture. This finding is directly relevant to similar studies of grazing geese, and has been published in a paper (see Appendix 1). Moreover, female AP score at the end of the winter correlated with subsequent breeding success, indicating that fat reserves built up by the female during the winter may have a direct effect upon breeding success. This is the first time that such a correlation has been found in migratory swans, but agrees with similar findings amongst geese nesting in the high Arctic, where food supply upon arrival at the breeding grounds was unpredictable. Maintenance of suitable feeding and roosting conditions on the wintering grounds (and perhaps also at spring migratory sites) which permit breeding females to achieve good condition prior to breeding, has important consequences for the breeding success, and ultimately long-term conservation, of high-arctic nesting waterfowl.

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THE CONDITION OF BEWICK'S SWANS *Cygnus columbianus bewickii* IN WINTER AS ASSESSED BY THEIR ABDOMINAL PROFILES

JONATHAN M. BOWLER

ABSTRACT An Abdominal Profile (*AP*) scale was developed to assess body condition of Bewick's Swans in the field. Change in *AP* score for individual birds correlated significantly with change in their body mass: moreover *AP* was significantly correlated with condition indices that were designed to remove the potential confounding effects of variation in size between individuals. This demonstrates, for the first time, that mass can be predicted from *AP*. There was considerable overlap between the values of adjacent profiles however, indicating that predictions for single birds may not be very precise. Generalised linear models were used to examine the variation in *AP* between birds; variables which statistically accounted for some of the variation included month, year, sex, status, dominance-rank and the multiple effects of month × year, and month × status. Females had significantly higher *AP* scores than males throughout the winter. The effect of social dominance upon *AP* was opposite for the two sexes; low-ranking single males had higher *AP* scores than higher-ranking paired males, whilst low-ranking single females had lower *AP* scores than higher-ranking paired females.

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INTRODUCTION

The Bewick's Swan *Cygnus columbianus bewickii* is a wholly migratory species that breeds on the arctic tundra of Russia. Swans from the western part of the breeding range winter in Europe, primarily in The Netherlands and Britain, with smaller numbers in Germany, Denmark and Ireland (Ogilvie 1972a). The study site at Slimbridge, Gloucestershire, England (51°44'N, 02°25'W) lies towards the western edge of the winter range, and has been used regularly by Bewick's Swans since the 1950s. Choice of wintering site is important since the fat reserves developed by the birds prior to the spring migration serve to fuel the c4,500 km return flight to the summer breeding grounds and may also affect condition upon arrival at the nest sites. Snow cover may severely reduce the availability of food during the pre-nesting period (pers. obs.) so the quantity of stored fat reserves could directly affect egg production in females, territorial defence activity in males, and therefore ultimately breeding success (Harvey 1971) as has been demonstrated in other arctic nesting species (Ankney & MacInnes 1978, Drent & Daan 1980).

The current study investigates the acquisition of fat reserves by individual swans whilst overwintering at Slimbridge as assessed by their abdominal profile (*AP*). Fat content is a good indicator of 'condition', defined as the fitness of a bird to cope with its present and future needs (Owen 1981). The mass of the abdominal fat has been found to be a good predictor of total body fat in Lesser Snow Geese *Anser c. caerulescens* and Canada Geese *Branta canadensis* (Thomas & Mainguy 1983). The use of *AP* as a technique for assessing condition is well established amongst *Branta* geese (Owen 1981, Owen & Black 1989, Johnson & Sibly 1993) and has also been applied to grey geese (Loonen *et al.* 1991, Van Eerden *et al.* 1991, Warren 1990, and Mayes 1991). Of the three species of swan that occur naturally in Europe the Bewick's Swan is most akin to geese in size. Moreover, the relatively short distance between the tail and the lowest point of the belly

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causes fat accumulation in this area (as revealed by the dissection of swans that had died by colliding with power-lines) to produce similar profiles to those seen in geese. An *AP* scale similar to the one described by Owen (1981) was developed for the study. The validity of using this method is assessed by comparing biometric data recorded upon catching swans for ringing, with abdominal profiles made during observations of the same individuals in the field. A number of variables are likely to affect *AP* and correlates of *AP* were investigated in relation to time, year, social status (recorded as single, paired, or paired with cygnets), dominance-rank and sex.

MATERIALS & METHODS

Field observations of Swans

During the winters 1990-91, 1991-92 and 1992-93 the condition of individual swans at Slimbridge, identified both by their unique bill markings (see Scott 1978 and Rees 1981) and coded leg rings, (Ogilvie 1972b) was assessed by recording their *AP* on a near-daily basis from arrival in mid-October to departure at the end of March. Because of the effect of food intake on *AP* (Loonen *et al.* 1991), records were taken only in the afternoon at feeding sites and at the evening roost, in order to ensure that all swans had had the opportunity to feed, prior to having their *AP* scored. All birds were scored by the same observer in order to reduce variability. An *AP* scale reflecting the shape of the belly between the tail and legs with scores from 1 to 6 was developed from photographs and observations taken in the 1989-90 winter (see Fig. 1).

Biometric data recorded for birds caught during the winters were compared to their *AP* scores obtained within two days of the catch date. Measurements taken included weight, tarsus length, skull length and wing length (maximum chord). Condition indices were calculated based on the mass divided by a) wing-length, b) skull-length c) tarsus length, to account for differences in the overall size of the individual (Owen & Cook 1977). The cube of these three measurements was also calculated in order to investigate the relationship between mass and volume as in Fox *et al.* (1992), but these transformations compounded sampling variance, so the results using linear measurements only are presented here.

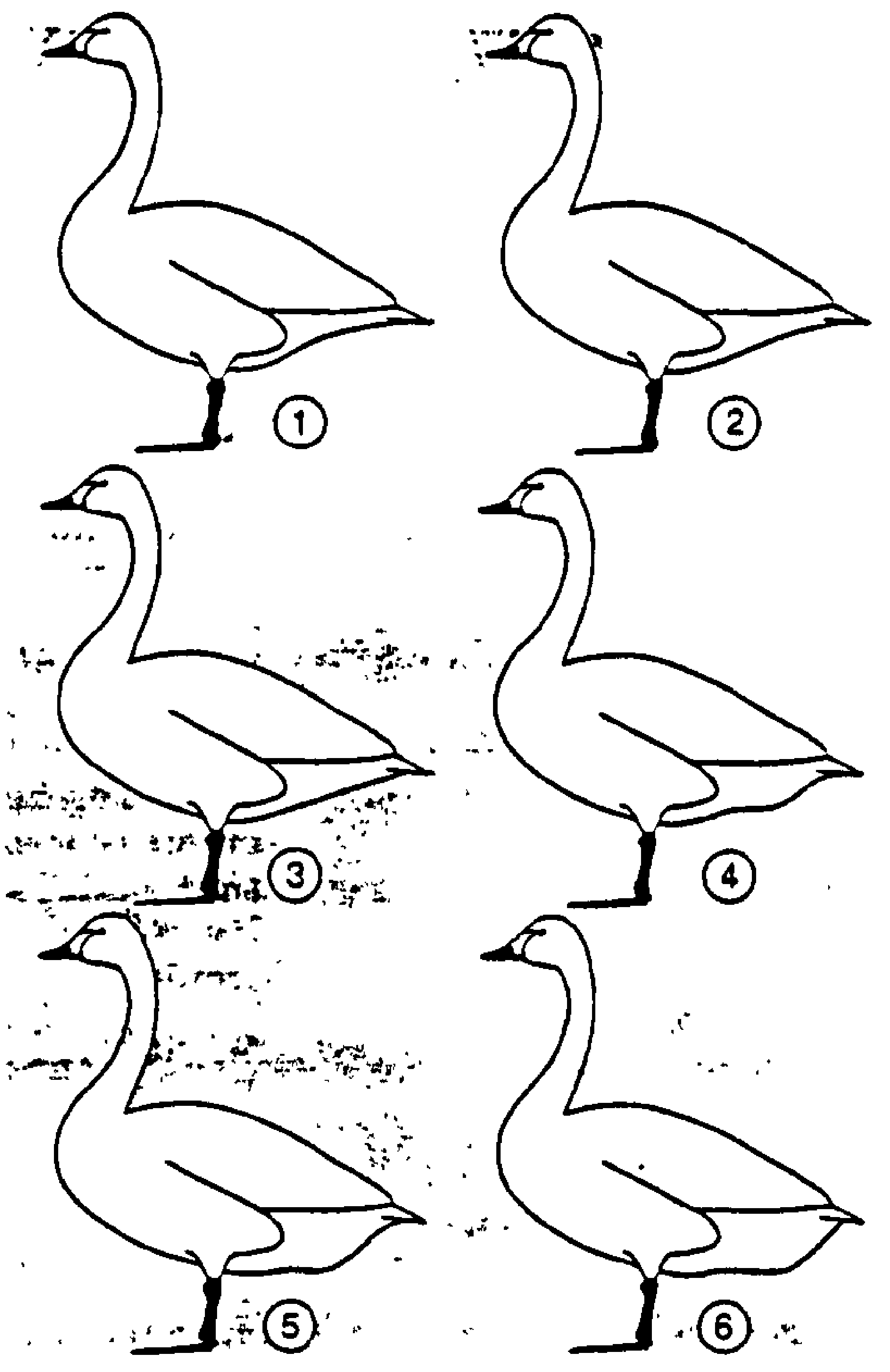

Fig. 1 Classification point values (1-6) of abdominal profiles of Bewick's Swans used for assessing body condition in the field.
1 Very concave, 2 Concave, 3 Straight, 4 Convex, 5 Very convex, 6 Sagging.

Swans were sexed both by cloacal examination and in the field by observing the behaviour of paired birds. Age was determined by the extent of grey feathering remaining on an individual (see Cramp & Simmons 1977). Social class was recorded by daily observation of individual swans in order to discern presence / absence of a mate, associate and / or cygnets. The social status of each swan was calculated from a combination of its age and social class, giving rise to eleven different categories.

Dominance-rank was measured by monitoring the outcome of aggressive interactions between swan units (families, pairs and singletons). A simple value of dominance was calculated by dividing the number of successful encounters for a given unit by the total number of encounters in which it was seen to be involved. An augmented dominance value was then derived by the addition of a) units that beat other birds dominant to the focal unit and b) units that were beaten by subordinate swans, as used by Scott (1978) and Rees (1988). The augmented values are considered preferable to the original ratio in that they take into account the "quality" of the opposition. Dominance values recorded for units involving fewer than five encounters or ten augmented encounters were omitted from the analyses.

Statistical analyses

Correlates of Abdominal Profile score For each individual a weighted median *AP* score for each half-month period was taken to prevent bias for frequently resighted birds. Weighted medians as devised by Owen & Black (1989) were used for the analyses instead of means, since a 'mean' profile assumes that the intervals between the index values are equal, which is not necessarily true.

Co-variate analysis of the data was performed initially using the PROC GLM command in the SAS statistical package to fit a generalized linear model and then investigated further using GLIM (NAG 1986). Four variables were examined in relation to abdominal profile since it was thought that they might explain the variation between individuals: time (coded by half-month), year, social status and dominance-rank. Male and female birds were treated separately because of their differences in size (Evans & Kear 1978) and to monitor sex differences in condition during the winter. The interactions between all six pairs of the above variables were also added to the model. Sex, year and status were treated as factors. In order to assess the statistical significance of the explanatory variables and their interactions, a full model was initially fitted and the Type III sums of squares inspected (SAS/STAT 1990). The least non-significant ($P > 0.05$) variables were then progressively removed from the model. The final model was thus the most parsimonious (see Crawley 1993).

RESULTS

Comparisons with biometric data

There was a significant positive correlation between change in *AP* and change in mass for individual swans caught in December 1990 and again in January 1991 (Pearson's correlation test $r = 0.645$, $n = 48$, $P < 0.01$). The condition indices (morphometric measurement / mass) based on skull-length and tarsus-length correlated positively with *AP* (Pearson's correlation tests $r = 0.321$, $n = 68$, $P < 0.01$ for males and $r = 0.461$, $n = 58$, $P < 0.01$ for females; $r = 0.323$, $n = 68$, $P < 0.01$ for males and $r = 0.521$, $n = 58$, $P < 0.01$ for females respectively. Regressions were fitted to these datasets (see Fig. 2) and the following predictive formulae were derived:

(a) males:

$M/T = 47.17 + 3.17{\cdot}AP \ (F = 7.69, P < 0.007, df = 67)$

$M/S = 32.50 + 1.94{\cdot}AP \ (F = 7.58, P < 0.007, df = 67)$

(b) females:

$M/T = 35.70 + 4.90{\cdot}AP \ (F = 20.88, P < 0.001, df = 57)$

$M/S = 25.60 + 2.73{\cdot}AP \ (F = 15.13, P < 0.001, df = 57)$

where M = mass (g), T = tarsus length (mm) and S = skull length (mm)

The condition index based on wing-length was not significantly correlated with *AP*.

Correlates of Abdominal Profile

The *AP* of males and females were analysed

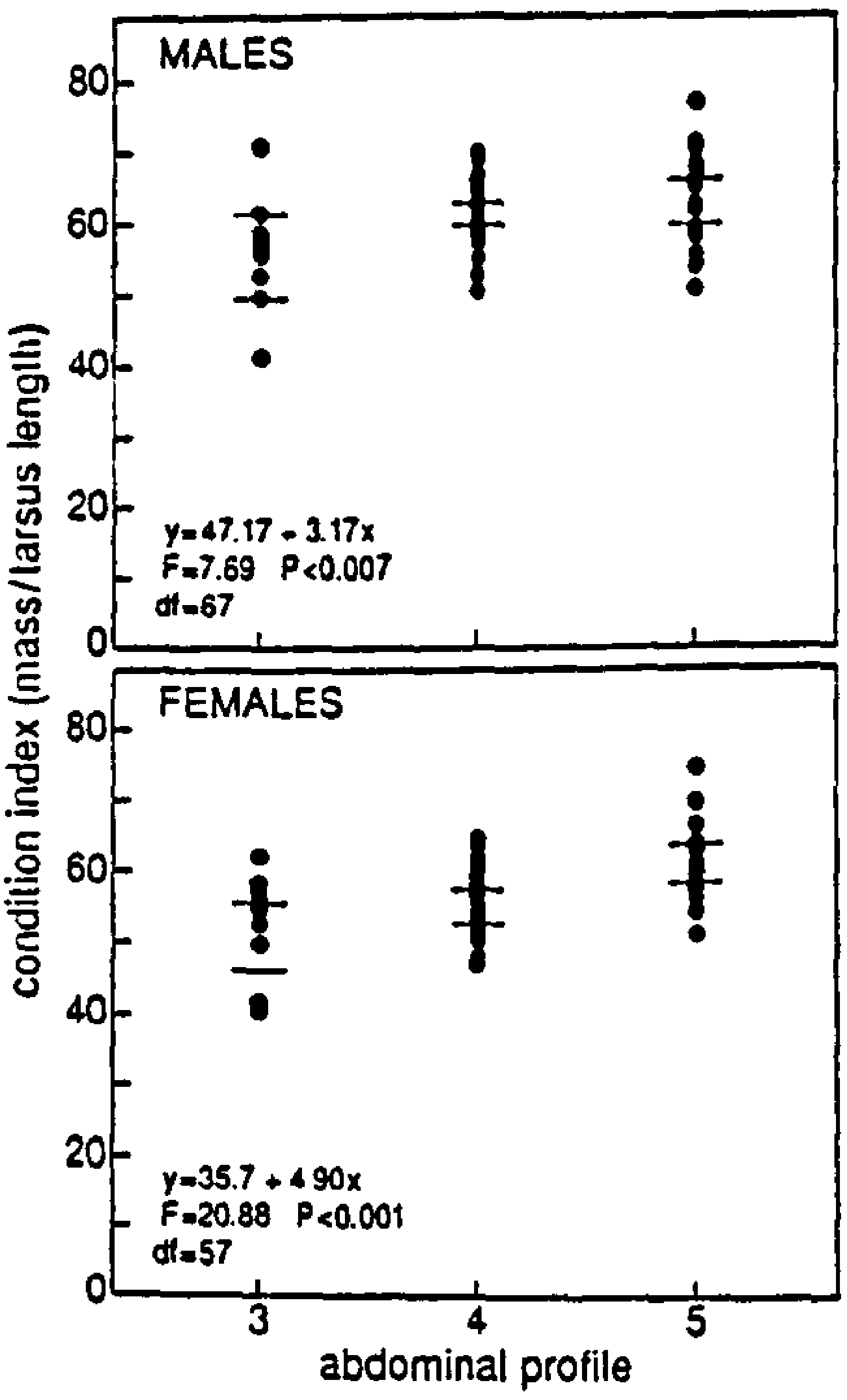

Fig. 2 Condition index values, mass/tarsus length, plotted against Abdominal profile. All data points plotted plus 95% confidence limits of the mean value for each profile score.

separately, and for both sexes the variation in the observed *AP* was significantly reduced by the addition of the explanatory variables year (factor) and time in half-month intervals, as well as the social status of the individual and, for females only, its dominance-rank (Table 1). In addition there were significant interactions between year, month, and status, indicating that *AP* varied between years and month, and status and month.

Seasonal variation Time of year had a significant positive effect on *AP* (Table 1) with *AP* scores generally increasing during the winter period, and differing little from the expected values of the linear model except in October. For both sexes, profiles reached a peak in the second half of January and then again in March. The slight reduction in profiles in February occurred in all three winters.

Table 1. Linear model using maximum likelihood estimates fitted to abdominal profile. Sexes treated separately.

a) Males

Variable	*F* ration	*d.f.*	*P*
Half-month	26.64	1,1545	<0.001
Year	44.98	2,1546	<0.001
Status	2.32	8.1562	< 0.02
Month × year	14.65	2.1546	<0.001
Month × status	6.69	8.1562	<0.001

b) Females

Variable	*F* ration	*d.f.*	*P*
Half-month	74.85	1,1359	<0.001
Year	17.79	2,1360	<0.001
Status	5.81	8,1366	< 0.001
Dominance	18.56	1,1359	<0.001
Month × year	7.04	2,1360	<0.001
Month × status	3.71	8,1366	<0.001

Gain in *AP* was most marked between the second half of October and the first half of November with birds on average increasing one half-score. *AP* gain was steady and more gradual over the rest of the winter.

Year Year had a significant effect on *AP* (Table 1). The pattern of increase in *AP* varied significantly between the three winters for both males and females with *AP* scores in the 1991/92 and 1992/93 winters generally rising more slowly than in the 1990/91 winter. The pattern of increase for each winter, however, was similar between the two sexes. Mean *AP* upon arrival in October differed significantly between winters for both sexes (Kruskal-Wallis χ^2 approximation test, $\chi^2 = 7.355$, $P = 0.025$, $df = 2$, $n = 24$ for males and $\chi^2 = 8.384$, $P = 0.015$, $df = 2$, $n = 21$ for females) but profiles prior to departure in late March did not differ significantly between years ($\chi^2 = 3.510$, $P = 0.187$, $df = 2$, $n = 73$ for males and $\chi^2 = 1.651$, $P = 0.438$, $df = 2$, $n = 75$ for females).

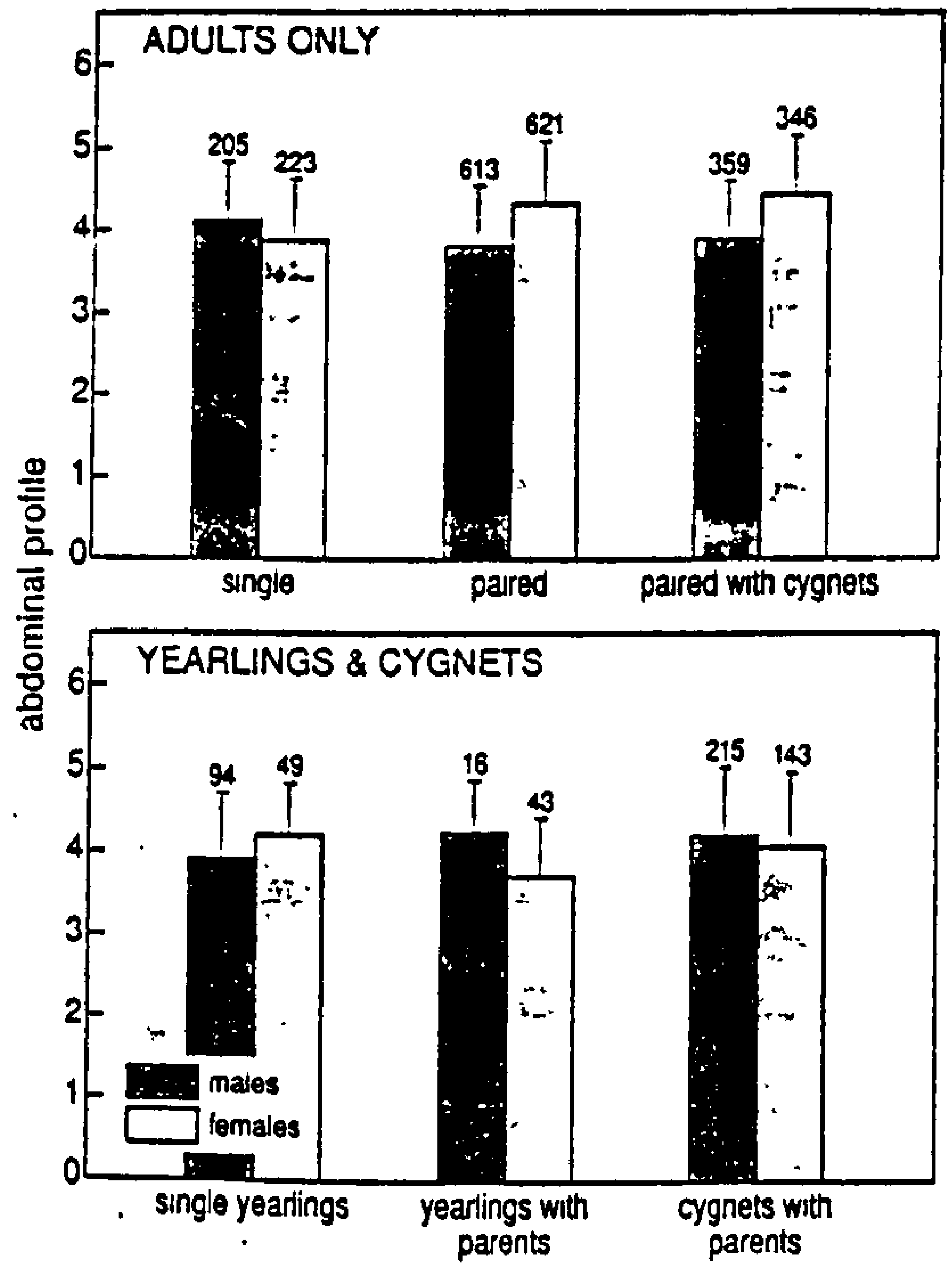

Fig. 3. Mean Abdominal Profile score plotted against social class (histogram plus SD) and the fitted values from a linear model (see text). The number of individuals involved in each category is given above each histogram.

Status Status had a significant effect upon *AP* (Table 1), with mean *AP* scores varying significantly between different social classes (Fig. 3). Because the mean *AP* of swans in the adult classes did not differ significantly from the predicted class means, differences between theses classes were investigated further using the Kruskal-Wallis χ^2 approximation test ($df = 1$ for all comparisons). Data for paired birds, and for birds with a mate plus cygnets, were combined in order to investigate the effect of presence of a mate. Amongst males, birds with a mate had a significantly lower *AP* score than those without a mate ($\chi^2 = 38.166$, $P < 0.001$, $n = 972$ and 205 respectively), whilst amongst females, birds with a mate had significantly higher *AP* scores than those without a mate ($\chi^2 = 85.712$, $P < 0.001$, $n = 967$ and 223 respectively). In addition male birds with a mate had a significantly lower *AP* score than females with a mate ($\chi^2 = 252.83$, $P < 0.001$, $n = 972$ and 967 respectively). Amongst male yearlings, there was no significant difference in *AP* between birds associating with their parents and singletons ($\chi^2 = 1.992$, $P = 0.158$, $n = 16$ and 94 respectively). Amongst female yearlings however, birds associating with their parents had significantly lower *AP* scores than singletons ($\chi^2 = 10.212$, $P < 0.001$, $n = 43$ and 49 respectively). The interaction term status × month also had a significant effect upon *AP* (Table 1), and this was particularly marked for cygnets.

Dominance-rank The effect of dominance-rank upon *AP* differed markedly between the two sexes. When data from all social classes were lumped together, *AP* for females increased significantly with dominance-rank (Table 1), whilst for males *AP* tended to decrease with dominance-rank although this relationship did not reach significance and this factor was therefore removed from the generalised linear model.

There was a significant negative correlation between *AP* and dominance-rank for males with a mate (Pearson's correlation $r = -0.092$, $P < 0.01$, $n = 948$), and a significant positive correlation for females with a mate (Pearson's correlation $r = 0.110$, $P < 0.001$, $n = 940$).

Amongst cygnets *AP* increased significantly with increasing dominance-rank (Pearson's correlation $r = 0.106$, $P < 0.002$, $n = 908$).

Sex Female *AP* scores were consistently higher than male scores throughout the winter and this difference was significant when all data were tested together (Kruskal-Wallis χ^2 approximation, $\chi^2 = 113.06$, $df = 1$, $P < 0.001$. Mean = 3.931, $SD = 0.744$, $n = 1545$ for males and mean = 4.203, $SD = 0.789$, $n = 1457$ for females). However amongst adults, single males had a significantly higher *AP* score than single females ($\chi^2 = 19.465$, $P < 0.001$, $n = 205$ and 223 respectively).

DISCUSSION

The strong significant positive correlations observed between the *AP* index developed in this study with both change in mass of individual swans and condition indices involving mass/tarsus and mass/skull, indicate the suitability of this technique for assessing the body condition of Bewick's Swans in the field. Moreover they indicate for the first time that it is possible to predict mass from the *AP* of known individuals for which biometric data is available, thereby precluding the need for repeated capture to monitor body condition. The considerable overlap between values of adjacent profiles indicates however, that predictions may not be very precise.

The change in *AP* recorded over the winter is similar to graphs plotted of change in mass of swans wintering at the site in previous winters (-Evans and Kear 1978). Mass was lowest upon arrival and rose quickly to reach a maximum in late December/early January. Similarly *AP* scores were lowest on their arrival and peaked in January. The drop in *AP* recorded between late January and early February is supported by a decrease in mass amongst birds caught during the second half of the winter (Evans & Kear 1978). As with a number of other wildfowl species including Canada Geese (Elder 1946), Greylag Geese *Anser anser* (Matthews & Campbell 1969), Mallard (Owen & Cook 1977), Teal *Anas crecca* (Fox *et al.* 1992) and diving duck (Ryan 1972), the gain in mass in Bewick's Swans increases to mid-winter and then declines. The increase in *AP* prior to migration at the end of March found in the present study agrees with the increase in mass amongst some age classes of Bewick's Swans at Slimbridge (Evans & Kear 1978). However the full weight gain prior to departure was not known since catching immediately prior to departure is discouraged to minimize possible disturbance. The high *AP* scores achieved prior to the start of migration to the breeding grounds mirrors similar gains recorded amongst Greenland White-fronted Geese *Anser albifrons flavirostris* in Ireland (Warren 1990 and Mayes 1991). Pre-migratory fattening was not evident amongst Teal caught and weighed at Abberton Reservoir in Essex indicating that they were able to gain weight at sites en route to nesting areas in order to improve body condition in readiness for reproduction (Fox *et al.* 1992). The fact that Bewick's Swans exhibit marked pre-migratory fattening suggests that either they are unable to gain weight sufficiently at migratory sites to achieve the necessary body condition for nesting upon arrival at the nesting areas or that, being much heavier, they require proportionately larger fat reserves to fuel their migratory flights. In either case the level of fat accumulation prior to migration is likely to be important; it has been shown to influence both migration survival in Barnacle Geese *Branta leucopsis* (Owen & Black 1989) and breeding success in Lesser Snow Geese (Ankney & MacInnes 1978).

There was little variation between the mean *AP* scores of different social classes within each sex category (Fig. 5). Only cygnets differed significantly (negatively) from the null model. The statusxtime effect for cygnets however was strongly positive indicating a greater than predicted increase in *AP* during the winter. Cygnets are also known to put on weight more rapidly than other age categories (Evans & Kear 1978) suggesting that parental care may permit increased food intake.

Male birds had a significantly lower mean *AP* score than females when all classes were treated together and this difference is most marked prior to migration. Studies on geese have suggested that males protect their mates during the prebreeding season (e.g. Hanson 1953, Inglis 1976, Fox & Madsen 1981, Johnson & Sibly 1990) thereby allowing them to acquire more food and ultimately to breed more successfully. Since females with a mate had a significantly higher mean *AP* score than males with a mate this would also appear to be true for Bewick's Swans during the pre-migratory fattening stage. Moreover, males with a mate had a significantly lower mean *AP* score than single males, implying that the protection of their female partners incurs the cost of a reduction in their own intake of food. The relationship between *AP* and dominance-rank for the two sexes is a function of the differences already described between social classes since, in general, singletons are subordinate to pairs which in turn are subordinate to families (Scott 1978). Low-ranking single males have higher mean *AP* scores than higher ranking males with a mate, whilst low-ranking single females lacking the protection of a mate have lower mean *AP* scores than higher-ranking females with a mate. Moreover the *AP* of females with a mate increases with the dominance-rank of the pair. This is consistent with the observation that the dominance-rank of a pair is related to the size of the male (Scott 1978). Conversely the *AP* of males with a mate decreases with increasing dominance-rank of the pair, highlighting the cost to the male of maintaining a high dominance level, to the benefit of its mate. The positive correlation between *AP* and dominance-rank amongst cygnets implies that they also benefit from the increased protection afforded by a dominant male parent, since the dominance of family units is also related to the size of the male parent. There was no evidence, in terms of increased *AP*, to suggest that yearlings benefit by associating with their parents during the winter since yearlings remaining with their parents did not have significantly higher *AP* scores than single yearlings.

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SAMENVATING

Om de conditie van Kleine Zwanen te kunnen beoordelen werd de de mate van bolling van de buik (abdominaal profiel, *AP*) als maat genomen (Fig. 1). Veranderingen in de score voor deze maat bij individuele vogels bleek inderdaad duidelijk te correleren met lichaamsgewicht en nog duidelijker met relatieve maten waarin ook de lichaamsgrootte betrokken werd (Fig. 2).

Omgekeerd kan nu dus ook, maar helaas nog niet met een erg grote nauwkeurigheid, het gewicht voorspeld worden aan de hand van het abdominale profiel.

Het abdominale profiel, en dus de conditie, hangt samen met diverse factoren, waaronder de tijd in het seizoen, het jaar (wellicht de klimatologische omstandigheden), sekse, sociale status (Fig. 3) en dominantie (Tabel 1) het meest in het oog springen. Wijfjes hebben gedurende de winter een hogere score (meer vet) dan mannetjes. Wijfjes die laag in rang zijn en alleen zijn hebben een lagere score dan gepaarde wijfjes van een hoge rang. Echter, mannetjes die laag in rang zijn en alleen, hebben een hogere score dan gepaarde mannetjes van hoge rang. Kennelijk zijn er voor mannetjes kosten verbonden aan het gepaard zijn (verdediging partner), terwijl voor wijfjes de baten overwegen.

JvR

APPENDIX 2. MANAGEMENT IMPLICATIONS

The results concerning habitat selection by Bewick's Swans wintering in the Severn Valley, can be applied to the management of sites used by swans in order to improve foraging performance and hence aid survivorship and subsequent breeding success.

Bimodality in foraging activity during the day is the norm amongst Anatidae grazing on dry pasture (e.g. Owen 1972a, Ebbinge et al. 1975, Owen & Cadbury 1975, Amat 1986b, Mayhew 1988, Moiij 1992, O'Donoghue & O'Halloran 1994, and results of this study). The swans in the current study spent more time resting during the midday period and would normally fly to a water source before returning for further grazing in the afternoon. Swans grazing on flooded fields did not show bimodality in their feeding regime, however; instead the number of birds seen feeding increased throughout the day (see also Owen & Cadbury 1975, O'Donoghue & O'Halloran 1994), suggesting that the presence of water at the feeding sites improved foraging efficiency. Water aids the digestive process by increasing the ease with which food is broken up in the gizzard, thereby controlling the availability of nutrients to the bird (Owen et al. 1977). Water ingested during or between feeding bouts therefore enabled swans feeding on flooded fields to continue grazing throughout the day.

Traditionally, Bewick's Swans in the Netherlands in winter fed mainly on rhizomes of pondweeds Potamogeton pectinatus and P. perfoliatus, and on other aquatic plants including Zostera in brackish tidal areas (Brouwer & Tinbergen 1939, Bauer & Glutz 1968). Depletion of submerged macrophytes through water pollution, drainage and land reclamation encouraged a shift to grass leys and semi-natural grassland after 1968 and subsequently to cereals and root crops (Poorter 1991). Bimodality in feeding regimes on dry pasture therefore may reflect the digestive ability of a species which is best suited to aquatic feeding. The swans feed frequently in the morning in order to fill the crop, gizzard and stomach with protein-rich but dry grass, and then need to fly to a water source in order to drink, and then rest for a substantial period (presumably to allow digestion) before feeding again to refill the crop, gizzard and stomach prior to roosting for the night. The foraging efficiency of swans grazing on dry protein-rich swards therefore could be improved in the following ways:

1) Provision of water-filled scrapes on the fields to reduce distance travelled (and therefore energy expenditure) in the search for water to aid digestion.

2) Periodic flooding of fields in order to allow foraging birds to ingest wet grass and to drink in between individual foraging bouts. Depending on the grading of the land and the extent of water cover, very heavy flooding may be of less value as deep water reduces the amount of grass available to the swans. However, periodic extensive flooding may be useful at more distant sites (e.g. Walmore Common), since the safety afforded by deeper water can allow swans to roost at the feeding site, thereby removing the high energetic costs of flying to and from a more distant roost-site.

3) Constant deep flooding of fields is less effective since grass that is under water for too long will begin to degenerate and lose nutritive value.

More generally:

4) Provision of protein-rich (i.e. improved), moderately grazed swards close to the roost site, from which the stock has been removed. Swans select fields with protein-rich swards, possibly by perceiving the greeness of the grass (as has been suggested for Brent Geese Summers & Critchley 1990), but will avoid fields containing stock. Sheep may even physically chase swans from a field (pers. obs).

5) Provision of additional food e.g. potatoes, sugar beet, and grain, particularly during January/February when the biomass of grass is lowest and the percentage protein content of swards is still increasing.