WINTER HABITAT USE BY TRUMPETER SWANS (CYGNUS BUCCINATOR) IN THE FRASER DELTA, BRITISH COLUMBIA

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ABSTRACT

Abundance patterns over two winters (1993/94 and 1994/95), and the possible role of habitat quality in governing upland habitat use, were investigated in a population of Trumpeter swans (*Cygnus buccinator*) in the Fraser delta.

Apart from displacements due to cold weather, and brief influxes of transients, abundance on upland habitat remained constant between fall and spring migrations in both winters. Movement to and from the marsh not associated with diurnal migration was minimal. These observations, in conjunction with evidence for site fidelity provided by marked individuals, suggest that the swans using upland habitat may comprise a closed population.

Seasonal changes in habitat quality on potato and early- and late-planted winter wheat fields were represented proximally via indices of biomass, protein and fiber. According to these indices, habitat quality differed significantly among habitats, and relative habitat quality changed over time. Temporal changes in relative habitat quality were examined using principal components analysis. PC2 was interpreted as "overall nutrient quality" due to the strong and opposite effects of protein and fiber, and the weak effect of biomass. PC1 had no obvious interpretation, but showed a strong negative effect of biomass, and slightly weaker positive effects of protein and fiber.

Swans showed significant preferences relative to availability for late planted winter wheat in the first third of both winters (this preference extended into the second third in 1993/94), for potatoes in the second third, and for winter wheat (early planted in 1993/94 and late planted in 1994/95) in the final third. These shifts may have reflected a preference for high nutrient quality prior to significant biomass depletion, followed by preference for high biomass as high-nutrient-quality habitat became depleted, followed by a preference for the best combination of biomass and nutrient quality when both were limiting.

Field size confounded the interpretation of preference. There was a weak tendency for swans to initiate the use of smaller fields later in the winter, but individual small fields accounted for preferences in the last third of both winters.

Differences in preference were observed between families and non-families. The possible role of juveniles in benefiting and constraining adult habitat use is discussed.

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Chapter 1

General Introduction

1.1 Introduction

The functional relationship between habitat characteristics and the demographic and distributional phenomena exhibited in wildlife species and populations has been the subject of considerable research, but has seen comparatively little application in the area of conservation biology. For migratory species, required habitat can include a diverse array of breeding, staging and wintering areas for which the relative importance to the population may not be readily apparent.

Until relatively recently, breeding habitat was the principal focus of research on waterfowl habitat (Stewart et al. 1988). This was due to the intuitive connection between breeding habitat and population effects such as reproduction and survival, as well as the view that the reproductive period was a limiting stage for migratory species (Anderson and Batt 1983). There has, however, been a dramatic increase in the attention paid to wintering habitat and its effects on components of waterfowl life cycles and the evolution of life history strategies. There are 2 main reasons: (1) the realization that wintering habitat may be as important, and in some cases more important than breeding habitat in maintaining waterfowl populations, and (2) it is predominantly winter habitat which is being lost to development and urban encroachment.

The importance of winter habitat to migratory waterfowl has frequently been demonstrated. Pair formation and maintenance (Anderson et al. 1988, Black and Owen 1988), the unity of family groups (Johnson and Raveling 1988), and the acquisition of resources, which subsequently effect survival and reproductive success (Davies and Cooke 1983, Boudewijn 1984), are all related to some extent to winter habitat quality.

Some life history "decisions" are thought to be made on the basis of physiological "condition", or nutrient status, which results in part from habitat characteristics (for example, food availability and quality, disturbance and competition) which limit resource acquisition. Body condition on arrival at the breeding grounds has been found in geese to control clutch size (Ankney and MacInnes 1978, Findlay and Cooke 1982), and affects the decision of whether to lay or feed (Ganter 1994, Raveling 1979). Further, Gauthier et al. 1984 found that fat reserves accumulated by Greater Snow Geese (*Anser caerulescens atlantica*) varied markedly between two different staging habitats, and speculated that it would be quite unlikely that this disparity would disappear before the geese reached their nesting grounds. This implies that the resources available for reproduction may differ depending on the staging habitat selected. McLandress and Raveling 1981 state that reserves accumulated prior to migration and reproduction are "critical in affecting clutch size" in geese, and Ankney and MacInnes 1978 conclude that incubating females must have sufficient reserves to meet daily energy requirements, in addition to those used for egg production, in order to reproduce successfully.

Clearly, then, the alteration or loss of winter habitat has the potential to profoundly affect waterfowl populations, particularly by affecting resource acquisition and the deposition of nutrients essential for survival, migration and reproduction.

1.2 The Study of Habitat Use

Habitat management and conservation requires, at least to some extent, the documentation and understanding of patterns of habitat use. This aids in the assessment of habitat requirements for the population (Owen and Williams 1976, Korschgen et al. 1988), in protecting the habitat against overuse, and in predicting the location and severity of potential wildlife/agricultural land use conflict (see McKelvey and Verbeek 1988, Earnst 1994). Ideally, it would be possible to estimate habitat requirements, and predict the effects on habitat use (and hence access to resources) of different hypothetical management strategies prior to their implementation. Toward this end, conceptual and analytical tools have been acquiring greater sophistication (for example, predictive distributional/demographic models by Pulliam and Danielson 1991), though as is usually the case, field studies require the careful and artful adaptation of these ideas.

An important concept in the study of habitat use is that of "habitat selection", defined as the "differential use of habitats relative to availability" (Kaminski et al. 1988). This concept is important because it implies that there are attributes of habitat which serve as cues in foraging decisions, and which can therefore illuminate possible causes of habitat choice. Habitat selection is synonymous with habitat preference (the use of preferred habitat is more intensive than would be predicted by random habitat choice). An empirical test for habitat selection requires only a measure of habitat use, and a means of distinguishing between habitats. The significance attached to a positive conclusion of habitat selection is contingent upon the way in which "availability" is defined, on the temporal scale used to represent habitat use, and on the spatial scale and specific attributes used to define habitat types.

The array of attributes which might conceivably be used to distinguish among habitats is infinite. A theoretical measure of habitat quality is found in "profitability", which is defined as "the gain of energy per unit of time spent handling and searching for food in a particular habitat" (Guillemette et al. 1992). This is clearly a composite measure, incorporating such elements as resource availability and quality, nutrient acquisition and assimilation rates, and costs associated with disturbance and competitive interaction. In other words, it is the ultimate measure of how "good" habitat is in specific circumstances at enabling an organism to survive and reproduce. Profitability is realized from the perspective of an organism as the "payoff" achieved, which is ultimately measured by fitness, and may in some cases be equal among habitats differing markedly in food quality. Profitability is considered to be a good correlate of habitat quality when predation risk is constant, but when predation risk is variable a tradeoff between these two factors arises (Guillemette et al. 1992).

Profitability can be defined reasonably well in controlled experiments, particularly in cases where fitness components can be measured. It is virtually impossible to measure profitability directly in the wild. However, just as inferences about fitness can be made on the basis of proximate measures which we call fitness components (Ganter 1994), profitability can be represented indirectly by means of proximate measures. For example, though the array of possible attributes which collectively make up "habitat quality" is infinite, proximate measures such as food biomass and nutrient content, which are components of habitat quality and therefore profitability, can be used to draw comparisons between habitats.

Developing a complete picture of profitability, or the relative payoff afforded by different habitats, is not a trivial task, even using proximate measures. Without attempting to measure fitness components (such as survival and reproductive propensity), derived proximate measures can be grouped into three general areas: measurements of physical and biological attributes of the habitat itself, such as food biomass and quality (see Earnst 1994, McKay et al. 1994, Owen 1973, 1976); measurements of behavioural traits, particularly those used in calculating activity budgets and in estimating the energetic cost of nutrient acquisition (which includes such things as the costs of disturbance, competition, and searching for and handling food) (Gauthier and Bedard 1984, Belanger and Bedard 1990, Goss-Custard et al. 1995); and measurements of physiological attributes of the study organism, such as those associated with digestion and fat deposition (McLandress and Reveling 1981, Kehoe et al. 1988, Heitmeyer 1988, Bowler 1994). Similar groupings have been arrived at by other researchers (for example, Korschgen et al. 1988, King and Murphy 1985). It is usually not feasible to address all of these general areas in a single study.

In the remaining chapters, the ability for habitat quality, as described by simple proximate measures, to provide an interpretation of habitat use will be investigated in a population of Trumpeter Swans in the Fraser delta.

1.3 The Trumpeter Swan: Background Information

The Trumpeter Swan (*Cygnus buccinator*) once nested throughout boreal North America (Banko 1960). By the early 1900's, however, over-harvesting had so reduced its numbers that it was feared by many ornithologists to be near extinction. Banko 1960, Anderson 1993, the Trumpeter Swan Society and others provide details of the recovery of the species and the management efforts involved, which include aviculture and reintroduction, full protection from harvest, and the establishment of Trumpeter swan refuges. As with other swans, Trumpeters are monogamous and long-lived, and juveniles remain with their parents through their first winter (Banko, 1960).

Trumpeter Swans are popularly divided into three sub-populations (Subcommittee on Pacific Coast Trumpeter Swans 1993). The Rocky Mountain Population consists of a migratory sub-population which breeds in central Alberta, the Northwest Territories and possibly northeastern B.C. and southeastern Yukon Territory, and winters in Idaho, Montana and Wyoming, and a non migratory sub-population which winters and breeds in Idaho, Montana and Wyoming. The Pacific Coast Population breeds in southern Alaska and winters on the Pacific coast from the Alaska panhandle to northern California.

The Pacific Coast Population of Trumpeter Swans has been growing at an exponential rate of approximately 7% per year since the 1970's (Boyd 1994); the trend toward increasing populations is mirrored in many other waterfowl populations around the world (see Moser and Kalden 1991). Trumpeter Swans in British Columbia have increased at a rate similar to that of the Pacific Coast Population, with the greatest accumulations of swans occurring in areas having significant agricultural activity in the vicinity of the marine foreshore (see McKelvey 1991). Swan numbers in the Fraser delta, B.C., have grown from 50 in the early 1970s to close to 1300 in 1996-1997, a rate of approximately 15% per year (Boyd 1994, and unpublished data). In the Skagit valley, Washington, and Comox valley, Vancouver island, the numbers of wintering Trumpeter

Swans have also grown rapidly (McKelvey 1991). In each of these areas, population growth has been accompanied by a shift in habitat use from the marine foreshore to upland (farmland) habitat.

This population growth is theorized to have been facilitated both by breeding range expansion back into historically occupied areas (Subcommittee on Pacific Coast Trumpeter Swans 1993, McKelvey et al. 1988) and by the acquisition of field grazing habits enabling the consumption of higher-quality foods. The present investigation is motivated by the population growth among Trumpeter Swans in general, by the potential for conflict with agriculture, and by the increased demands placed on ever-decreasing habitat in the Fraser delta.

1.4 Purpose

The primary objectives of this study are to quantify upland habitat use by Trumpeter Swans wintering on the Fraser River delta west of Ladner, B.C., and to interpret patterns of upland habitat use in terms of habitat quality. Swan abundance on upland habitat, and possible causes of variability in abundance, are discussed in Appendix 1. Chapter 2 gives simple proximate descriptions of changes in relative upland habitat quality over the winter, and compares these to temporal changes in preference. Chapter 3 discusses the possible contributions of additional factors (field size and social status) to habitat preference.

1.5 Study Area

The Fraser delta (Figure 1.1) is the largest estuary on Canada's Pacific coast, and provides habitat for as many as 300,000 to 750,000 waterfowl over the course of the year (Vermeer et al. 1994). Physical and vegetational characteristics of the Fraser delta are summarized by Vermeer et al. 1994, and discussed in detail in references contained therein. Habitats used by Trumpeter swans can be divided into two general categories:

(1) marine foreshore habitats, consisting of alluvial deposits, sands, silts and clays, and vegetated primarily by three-square bulrush *Scirpus americanus*, sea bulrush *S. maritimus*, Lyngby's sedge *Carex lyngbyei*, and cattail *Typha latifolia* (Hutchinson 1982), and (2) upland agricultural habitat, which has been reclaimed through dyking and draining.

Trumpeters share the foreshore habitat with a host of other waterfowl species over the fall and winter, but the only species with which they actually compete for food to a significant degree on this habitat is the Lesser Snow Goose (*Anser caerulescens caerulescens*). Boyd 1994 estimated that swans and geese currently account for 6-8% and 92-94% respectively of the grubbing impact on rhizomes of *Scirpus americanus*.

Farmland on the Fraser delta is among the most productive in B.C. Even as early as the 1950s, however, loss of farmland habitat to urban encroachment, a trend which continues to this day, resulted in the intensive use of localized areas by waterfowl (Duynstee 1992). This intensity of use has necessitated the more recent development of the Greenfields Project (Duynstee 1992). The Greenfields Project provides forage to waterfowl, in the form of cover crops, in compensation for the loss of traditional habitat. In addition, by distributing waterfowl over a larger area, reducing soil compaction, and providing green manure in the spring, cover cropping enhances the productivity of farmland. The most commonly planted cover crops are winter wheat *Triticum aestivum* and fall rye *Secale cereale*. Winter wheat has become the most popular, due to its resistance to winter kill and to its potential as a feed crop for livestock (Duynstee 1992).

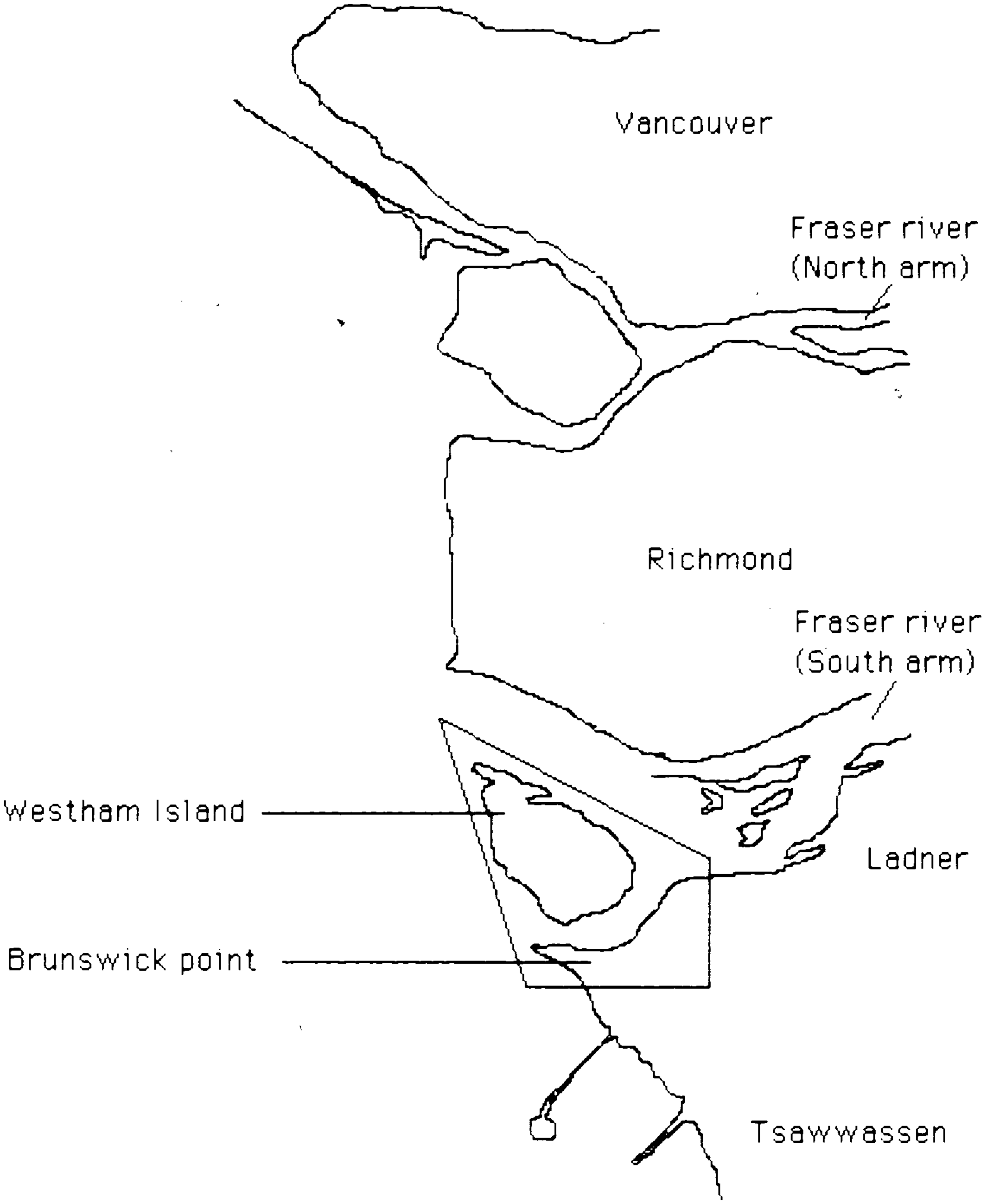
Trumpeter Swans use two general upland habitat types: potato fields (from which the swans obtain waste potatoes lying on the surface of the ground early in the winter, and buried potatoes after these are depleted), and fields seeded with winter cover crops (primarily winter wheat). The winter wheat fields are for the purposes of this study further classified into early (mid to late August) and late (September to early October) planted fields, since crop age has a marked effect on the subsequent characteristics of habitat (Duynstee 1992).

Trumpeter Swans share agricultural land with a variety of other waterfowl species, particularly American Wigeon (*Anas americanus*), Mallard (*Anas platyrhynchos*), Pintail (*Anas acuta*), Lesser snow geese and Tundra swans (*Cygnus columbianus*). Of these, Wigeon, Snow Geese and Mallard occur in significant numbers on swan habitat at various times over the fall and winter. Since these are all hunted species, while the swans are not, their spatial and temporal patterns of habitat use differ markedly. Snow geese are almost entirely excluded from fields outside the Alaksen National Wildlife Area during hunting season, while Wigeon and Mallard use fields almost exclusively at night during the hunting season. However, when their distributions overlap with those of swans, these species (particularly Wigeon) can have a profound affect on the amount of food available to swans (Duynstee 1992), and presumably therefore on swan habitat use.

1.6 Management Concerns

Currently there is little concern among farmers in the Fraser delta over field use by swans, although this could change as more land is turned over to livestock grazing (McKelvey, pers comm.) and as swan numbers on the delta continue to grow. There is at present a need to quantify swan abundance and distribution over the winter in order to identify important habitats, and to achieve some understanding of the causes of habitat choice, particularly in the interest of predicting future habitat use (see Vickery et al. 1995). This would serve three purposes: (1) help to minimize the potential for conflict between swans and farmers; (2) identify potential threats to habitat stability which may result from concentrating swans on small areas; and (3) help to determine habitat requirements of the population, particularly in light of the potential for exploitative competition with Snow Geese and for habitat loss.

Figure 1.1. Map of the Fraser River delta. Surveys were conducted within the study area marked. Swan abundance data are presented for upland areas only.


Vancouver
Fraser river
(North arm)
Richmond
Fraser river
(South arm)
Westham Island
Ladner
Brunswick point
Tsawwassen

Chapter 2

Habitat Quality and Habitat Preference

2.1 Introduction

This chapter asks whether Trumpeter Swans using upland habitat in the Fraser delta show habitat preferences, and, if so, whether and in what way preferences change over time. The chapter concludes by investigating the possible effect of habitat quality in governing habitat preference. Chapter 3 discusses some of the additional factors (apart from habitat quality) which may contribute to observed preferences.

There are numerous examples in the wild of habitat preference (non-random habitat choice, or habitat selection). For example, in gregarious species, habitat choice is largely based on the presence of conspecifics (see Drent and Swierstra 1977). Differences in predation risk can also result in habitat preferences (see Laing and Raveling 1993), as can differences in habitat quality. The sequence of shifts in preference over time and their relationship to habitat quality (in particular the availability and quality of food) has been the focus of numerous studies of wintering waterfowl (see Madsen 1985, Dirksen et al. 1991, Vickery et al. 1995).

Habitat quality is potentially comprised of a wide array of environmental factors. An approach to defining habitat quality based on some simple energetic principles is used here.

Daily energy expenditure (Ricklefs 1994, Mooij 1992) sets a minimum level of energy acquisition required for a bird to remain in energy balance. Net energy acquisition is a function of intake (feeding), food energy content, and assimilation efficiency, or digestion (Nagy and Haufler 1980). The concentration of food in the environment, its energy density and content of specific nutrients (i.e. protein), are measurable attributes of habitat quality which limit net energy acquisition and therefore affect a bird's ability to remain in energy balance.

Structural carbohydrate (cellulose), generically referred to as fiber, reduces the digestibility of food (Nagy and Haufler 1980, Buchsbaum et al. 1986), thereby inhibiting the uptake of nutrients such as protein, fat and simple carbohydrates. Fiber and lignin concentrations increase (with subsequent decreases in digestible energy) with plant maturation (Wilmshurst et al. 1995). The presence of plant secondary chemicals, such as phenolics, also reduces digestibility and palatability (Buchsbaum et al. 1984, Karasov 1990). Variability in food availability, energy density and digestibility among habitats and food types has been shown to have physiological consequences to the consumer (giving rise, for example, to variable weight gain and fat deposition) (see Gauthier et al. 1984, Coleman and Boag 1987). Because of this functional relationship to energy balance, these factors can provide indices, or proximate measures, of habitat quality.

Because profitability is a function of habitat quality, and because "optimally foraging" individuals (see Begon et al. 1986) will presumably maximize profitability, it would be expected that the intensity of habitat use exhibited by a population would be to some extent predicted by habitat quality (Wilmshurst et al. 1995). To this end, numerous studies have attempted (some successfully) to relate non-random distributions and food choice in waterfowl to habitat quality as represented through the use of proximate indices.

Coleman and Boag 1987 found that of three food plant types, the one with the lowest fiber and highest total non-structural carbohydrate content was preferred by staging Canada Geese (*Branta canadensis*), while that with the highest fiber and lowest non-structural carbohydrate was least preferred. Mayes 1991 used an index of "organic matter digestibility" to compare the profitability of different food types in an attempt to explain the use by Greenland White-fronted Geese (*Anser albifrons fravirostris*) of low-availability food types. Boudewijn 1984 compared assimilation efficiencies in captive birds to explain habitat selection in wild Brent Geese (*Branta bernicla bernicla*).

The weight of food per area of habitat (biomass) also provides a commonly-used index of relative habitat quality, and is a particularly useful descriptor in habitats which undergo biomass depletion over time (see Owen 1971). Summers et al. 1993 found that biomass depletion in a salt marsh, while not attributable to grazing by Brent Geese (*Branta bernicla bernicla*), did coincide with their switch to higher-biomass inland habitats. Ydenberg and Prins 1981 found a positive relationship between the rate of biomass accumulation (from plant growth) and the intensity of habitat use by Barnacle Geese (*Branta leucopsis*).

Additional indices of habitat quality which have been used in studies of habitat use include the moisture content of food (Gauthier and Bedard 1991), and the presence and amount of standing water (Hirst and Easthope 1981). Two or more factors are generally used in conjunction to predict habitat preference (for example, Earnst 1994 used an index of sago pondweed (*Potamogeton pectinatus*) presence, extent of open water and wetland size to predict Tundra Swan habitat preference).

Interspecific competition can have a significant effect on the availability of food, and subsequently on habitat choice. Sutherland and Allport 1994 modeled predicted habitat preferences of wintering Bean Geese (*Anser fabalis*) in relation to stock grazing regime and Wigeon numbers, and found that observed preferences varied in the manner predicted by the model. Madsen 1985 found that exploitative competition between Pink-footed Geese (*Anser brachyrhynchus*) and Greylag Geese (*Anser anser*) resulted in shifts in habitat preference. In the present system, Wigeon distributions significantly overlap those of swans, and Wigeon can have considerable grazing impact, particularly on cover crops (Duynstee 1992). While it might in theory be possible to employ methods similar to those of Sutherland and Allport 1992 and include the effects of Wigeon grazing in a systematic interpretation of swan habitat preference, it was beyond the scope of the present study to quantify Wigeon abundance and grazing impact. It must therefore be acknowledged that Wigeon present a confounding factor to the present investigation.

If habitat use is non-random, there are two premises which must be established before it can be determined if preferences, and changes in preference, are related to habitat quality. First, habitat quality must actually differ among habitat types. This can be ascertained by means of appropriate indices of habitat quality, such as those given above. Second, habitat quality and relative habitat quality must change over time.

The objective of this chapter is to use measurements of fiber, protein and biomass, as proximate indices of habitat quality, to establish whether the three upland habitat types (early planted winter wheat, late planted winter wheat and potatoes) differ, and whether they change relative to each other over time. Habitat preference is evaluated by comparing observed habitat use to that expected under the null hypothesis of random habitat choice, and the ability for habitat quality to explain habitat preference is examined.

2.2 Methods

2.2.1 Swan Abundance and Distribution

The wintering population of swans in the Fraser valley consists primarily of Trumpeter Swans, although between 50 and 150 Tundra Swans winter in the same area (pers obs., Boyd 1994). Efforts were made to discriminate between the two species, but this was not always possible, particularly at distances of over 100 meters or in inclement weather conditions, since the morphological traits used in species identification are subtle.

In the present study, Trumpeter and Tundra Swans were distinguished by means of the following traits: bill shape (the culmen profile is straight in Trumpeters and concave in Tundras), lore shape (the lore surrounds the eye in Trumpeters, but not in

Tundras), and the presence (in Tundras) or absence (in Trumpeters) of a yellow lore spot (Hansen et al. 1971, Mitchell 1994, Patten and Heindel 1994). The greater neck/body length ratio and greater overall structural size in Trumpeters (Mitchell 1994) were occasionally used when other traits were indistinct.

Surveys were conducted between early November and early March during the winters of 1993-1994 and 1994-1995 (referred to from here on as 1993/94 and 1994/95), at a frequency of once per week in 1993/94, and two to three times per week in 1994/95. The study area included Westham island and Brunswick point, as marked on Figure 1.1. Only upland habitat was surveyed in 1993/94, and all habitat (upland and marsh) was surveyed in 1994/95. Most surveys started in the morning, at least one hour after sunrise, and were always concluded at least an hour prior to sunset (since efforts were made to avoid conducting swan counts during diurnal migration, which occurred from the marsh to upland habitat within half an hour of sunrise, and from upland habitat back to the marsh within half an hour of sunset (pers. obs.)). The order in which the study area was covered was altered from survey to survey. Surveys took 3 to 5 hours to complete.

Observations in the first half of 1993/94 were made through a fixed 15X spotting scope, and observations in the latter half of 1993/94, and in 1994/95, were made through a variable 25X-45X spotting scope. Neck collar codes were only visible through the more powerful scope. Weather conditions and distance problems resulted in some inconsistency in the quality of observations, particularly in the identification of species and of juveniles.

Total numbers of adults and juveniles for both Trumpeter and Tundra swans were recorded at each field (or marsh location) during surveys in 1994/95, but only total numbers of each species were consistently recorded in 1993/94. Tundra swan numbers were eliminated from the data presented here. During surveys in 1994/95, a 15-minute continuous observation was made at each field (or marsh location), in which all arrivals and departures were recorded. Since these observations occurred between sunrise- and sunset-migrations (diurnal migrations), arrivals and departures were assumed not to be part of regular diurnal movement. 5 neck-collared swans (4 Trumpeters and 1 Tundra) were observed on several occasions in 1993/94; no individually marked swans were seen in 1994/95 in spite of increased observer effort.

Daily minimum temperatures (according to observations made by Environment Canada) were recorded for each day in the study period.

2.2.2 Habitat Quality

Habitat sampling was done in 1994/95 only. It is assumed in the discussion which follows that the general description of habitat quality derived from these data is applicable to both years. Two early planted and two late planted winter wheat fields and one potato field were selected for regular sampling. Samples were also collected incidentally, as time permitted, from 2 other early planted winter wheat fields and 1 other late planted winter wheat field.

Fields 128, 168, 60 and 65 (winter wheat) were sampled using stratified random sampling methods (Krebs 1989). The centers of these fields were intensively grazed while the edges were not, so high-biomass zones at the field edges and low-biomass zones in the field centers developed over time. Unstratified random sampling methods were used in the case of the remaining winter wheat fields (33, 45, and 21), since high- and low-biomass zones did not emerge and stratification was deemed unnecessary. A 25 cm. X 25 cm. quadrat was used for all sampling, and a survey chain was used to measure the dimensions of each field and of each stratum. Stratum weights were calculated as the stratum area divided by the field area. Plant stalks were clipped to within 1 cm. of ground level, and frozen for later analysis.

Potato samples were collected using unstratified random sampling methods. Buried potatoes were excavated to a depth of 7 cm., which was the maximum depth observed for grub-marks left by swans prospecting for buried potatoes (pers. obs.).

In the lab, samples were washed in cold water, placed in preweighed polystyrene weighing boats, and dried to constant weight (taking approximately 48 hours) in a drying oven at 60-70 degrees Celsius. Samples were then weighed, ground in a Wiley mill with a 20 mesh screen, and stored in plastic scintillation vials. Analyses for percent acid detergent fiber (ADF) and percent crude protein were carried out by Norwest Labs, using standard techniques.

Standard stratified estimates (Krebs 1989) (or, in the case of unstratified fields, regular means) for biomass, ADF and protein were calculated for each winter wheat field on each sampling date. Mean biomass was presented in grams per sample. Because of small sample sizes, degrees of freedom calculated for stratified estimates using Cochran's formula (Krebs 1989) were consistently less than 1, so true 95% confidence intervals were not calculable. Confidence intervals for these fields were therefore calculated using n-1 degrees of freedom (where n is the total number of samples in all strata), rather than simply reporting the mean plus or minus one standard deviation, in order to provide some representation of sample size in the estimate of variability around the mean. It must be noted however that these confidence intervals underestimate the width of true 95% confidence intervals. Confidence intervals reported for fields 33, 45, and 21 are true 95% confidence intervals.

Regular (unstratified) means for the same parameters were calculated for the potato field, and confidence intervals reported are true 95% confidence intervals.

2.2.3 Statistical treatment of data

Multivariate analysis of variance (PROC GLM in SAS, with a "manova" statement and multiple dependent variables (biomass, fiber and protein)) was used to determine whether habitat types differed significantly, and whether the relationship between them changed over time.

Partial correlations (PROC CORR in SAS, with a "partial" statement) were computed for all possible combinations of protein, fiber, and biomass, in order to assess the degree of interrelatedness among proximate measures.

Principal components analysis (PROC PRINCOMP in SAS) was applied to the habitat quality data. A simple description of changes in relative habitat quality within and among habitats over time was achieved by plotting the output principal components separately for each third of the study period.

Null hypotheses of random habitat choice were tested by means of chi-squared tests (Alldredge and Ratti 1986). Rejection of the null hypothesis was taken as evidence in favor of habitat selection (preference). To maintain a temporal component in the analysis, the test was subdivided so that comparisons of habitat use and availability were made in each third of each winter. Observed use was represented as the intensity of habitat use (in swan-days), calculated as the area under the abundance/time curve using the "trapezoidal rule" for integration (Swokowski 1984). A straight line was assumed between consecutive data points. Expected values in the chi-squared tests were calculated by multiplying total swan-days in a given period by the ratio of the total area in a given habitat type over the total area of all habitats.

A critical assumption of this statistical technique (and, for that matter, alternative methods of identifying preference such as multiple regression) is that all observations are independent (Alldredge and Ratti 1986). This is clearly violated in the present instance, given that swans are aggregated. Apparent significance must therefore be viewed with skepticism. In addition, the probability of incorrectly rejecting the null hypothesis increases with the number of simultaneous tests (Rice 1989), though this problem may be overcome through the use of the sequential

Bonferroni test. Since six tests are made simultaneously, there is a considerable probability that one or more will incorrectly reject the null hypothesis.

2.3 Results

A total of 29 fields (414.2 hectares) were used by swans in 1993/94, and 33 fields (422 hectares) were used in 1994/95 (Table 2.1).

2.3.1 Coverage achieved by habitat sampling regime

Before presenting habitat quality data, it seemed pertinent to indicate to what extent the sampling regime matched habitat use by swans. Fields 128, 168, 33, 45 and 75 were intensively sampled (Table 2.2, Appendix 2), while fields 21, 60, and 65 were each sampled only twice (once at the beginning of the season and again after field use was initiated). Total use of upland habitat amounted to 34315 swan-days in 1994/95, and the fields sampled received 61.7% of this. The intensively sampled fields received 49% of total upland habitat usage. Among potato fields, field 75 received 45% of total usage, and among winter wheat fields (i.e. excluding potato fields), the fields which were sampled received 80% of total usage, while intensively sampled fields received 46%.

2.3.2 Biomass, Protein and Fiber

Measurements of biomass, protein and fiber are summarized in Appendix 2 (Figures A.2.1-A.2.8). It is important to note that day 80 in the study period is the approximate point in both years at which swans on potato fields made the pronounced shift from feeding on potatoes lying on the surface of the ground to grubbing for subsurface potatoes. This point was defined based on observations of foraging behavior, which showed a marked change in the predominant foraging strategy (from no grubbing to almost all grubbing behavior) at around this time in both years (pers. obs.).

The potato field (Figure A.2.8) contained the highest biomass, which subsequently underwent the greatest decline over the course of the season. Protein and fiber concentrations remained more or less constant. Most of the reduction in biomass was attributable to feeding by Trumpeter swans, though Mallard and Snow Geese contributed to a lesser extent. Tundra Swans were almost never observed on potato fields.

In general, because of the shorter elapsed time between planting-and sampling, late planted winter wheat started with lower biomass, lower fiber concentrations and higher protein concentrations than early planted winter wheat (see Appendix 2, Figures A.2.1-A.2.8). Biomass declined more quickly on late planted fields. If there was any regrowth on either early or late planted fields, it was negligible in comparison to depletion due to grazing. Protein concentrations declined while fiber concentrations increased on both early and late planted winter wheat.

Multivariate analysis of variance

Results of multivariate analysis of variance (Table 2.3) give an indication of the significance of apparent differences among habitat types. Univariate results test, for each proximate measure (biomass, protein and fiber), whether there are differences among habitat types, whether there are differences over time, and whether the relationship among types differs over time (the date*type interaction). Multivariate results test the overall significance of changes in the relationship among habitats over time (the overall significance of the date*type interaction).

All test statistics in the multivariate results show a significant overall date*type effect (in other words, the relationship among habitat types differs over time).

Correlation Analyses

Partial correlation analyses (Table 2.4) evaluate the interrelatedness of individual proximate measures. Numbers given are Pearson partial correlation coefficients, and P values refer to the probability that correlations of this strength would be observed under the null hypothesis of zero correlation (Prob > |R| under Ho: Partial Rho = 0). Values for P of less than 0.05 are considered significant.

All of the correlations are significant, with the exception of that between fiber and biomass, with constant protein, for early planted winter wheat.

Principal Components Analysis

Summary results of principal components analyses of habitat quality are given in Tables 2.5 and 2.6. Principal components 1 (PC1) and 2 (PC2) explain most (90%) of the original variability in the data (Table 2.5), so these will be used in the description of habitat quality. PC1 (which explains 61% of the original variability) shows a strong negative effect of biomass and strong positive effects of both protein and fiber (Table 2.6). PC2 (which explains 29% of the original variability) shows a strong negative effect of protein, a very weak positive effect of biomass, and a strong positive effect of fiber. PC3 (10% of the original variability) shows strong positive effects of all three variables.

Arbitrary ellipses (these are not confidence ellipses) drawn around the data point clusters in the plot of PC2 against PC1 (Figure 2.1) give a concise visual representation of the relative quality of habitats in each third of the study interval. All three habitat types differ in periods 1 and 2, but in period 3 early and late planted winter wheat are indistinguishable, while potatoes remain distinct but approach similarity to the other two habitats. In periods 1 and 2, early and late planted winter wheat differ along the horizontal axis (PC2) but not along the vertical axis (PC1), while in period 3 they don't differ on either axis. Potatoes fall more or less in the middle of early and late planted winter wheat on the horizontal axis (PC2) throughout the season, but differ along the vertical axis (PC1). The range of values for PC1 shown in potatoes decreases between periods 2 and 3, with values in period 3 differing less from those of early or late planted winter wheat than in either of the other two periods.

2.3.3 Habitat Preference

Abundance patterns on each upland habitat type do not appear to be similar between years. A large-scale shift in habitat use from late planted winter wheat to potatoes to early planted winter wheat is observed in 1993/94 (Figure 2.2), but not in 1994/95 (Figure 2.3). However, comparisons between observed habitat use and expected use under the null hypothesis that habitat use is in proportion to availability (Figure 2.4) indicate that preferences are roughly similar between years. Both show preferences for late planted winter wheat in the first third of the study interval, for potatoes in the second third, and for winter wheat (early planted in 1993/94 and late planted in 1994/95) in the last third. Differences are observed in the strong preference for late planted winter wheat in the second third of 1993/94, and in the weak preferences for late planted winter wheat in the last third of 1993/94 and for early planted winter wheat in the first third of 1994/95. Null hypotheses are rejected in each case (values for chi squared range from 358.8 to 10320.3 (df=2; $p << 0.001$)), meaning that in each instance the differential use of habitat relative to availability is significant (recall, however, the limitations imposed by the violation of the assumption of independence).

2.4 Discussion

The importance of spatial and temporal scale to the interpretation of habitat use has been well illustrated (see Orians and Wittenberger,1991). Studies (for example, Anderson 1993) which pool habitat use data over an entire season may identify overall habitat preferences, but in the process lose information on changes in habitat preference over time. With a suite of habitats which change significantly over time, the interpretation of changing preferences (habitat switching) may provide valuable insight into the general process of habitat choice.

Habitat quality, as measured proximally by protein, fiber and biomass, differs among the three upland habitat types, and relative habitat quality changes over time. Abundance on each upland habitat type in 1993/94 seems to suggest a process of habitat switching, in that there is an apparent shift from late planted winter wheat to potatoes to early planted winter wheat over the course of the season (Figure 2.2). This is demonstrated further by the comparison of observed to expected habitat use, which shows changes in habitat preference relative to availability following the same order (Figure 2.4), a pattern which is more or less reiterated in the second year.

Thus the assumptions upon which the interpretation of habitat use as a function of habitat quality is based (that habitat quality differs, that relative habitat quality changes over time, and that preference changes over time) are satisfied. It must by noted, however, that without the experimental manipulation of habitat quality, no specific hypotheses can be tested, so any inferences about the relationship between habitat use and habitat quality are at this point speculative.

The investigation of preference is grounded in the assumption that abundance patterns on upland habitat reflect individual foraging decisions, which in turn assumes that the study population consists of individuals which show high site fidelity to the study area over the winter. The validity of this assumption is discussed in Appendix 1, which also provides data on overall abundance on upland habitat.

2.4.1 Habitat quality

As noted above, it was beyond the scope of this study to monitor Wigeon grazing. However, Wigeon have generally been observed to graze late planted crops intensively, possibly due to the better nutritional characteristics and lower sward height, and tend to avoid early planted crops (Duynstee 1992). Sutherland and Allport 1994 also showed an avoidance by Wigeon of both high and low biomass areas, and speculated that the avoidance of high biomass areas may result from the inaccessibility and age structure of the sward, and from increased predation risk. Wigeon grazing possibly accounts for most of the reduction in biomass on the larger late planted fields (such as fields 33 and 45), while most of the reduction in biomass on the early planted fields (such as fields 128 and 168) may be attributable to grazing by swans.

Univariate analysis of variance results (Table 2.3) show that biomass, protein and fiber all differ among habitats. Multivariate results show that in general the difference among habitats changes over time. This means that there are significant differences in habitat quality among habitats, and that the three habitat types described are in fact unique. It also means that relative habitat quality changes over time, and therefore provides the basis for an expectation of changes in habitat preference.

Partial correlation results (Table 2.4) show that biomass, fiber.and protein are not independent descriptors of habitat quality, and can therefore not be treated as such in the interpretation of habitat use. This problem is overcome by the use of principal components analysis, since the principal components, which are composite variables derived from the original measurements, are by definition uncorrelated.

PC2 might be described as "overall nutrient quality" given the strong negative effect of protein, the strong positive effect of fiber, and the very weak effect of biomass (Table 2.6). In other words, high and low values of PC2 correspond to similar values of biomass. Protein (a desirable attribute of food) and fiber (an undesirable attribute) have strong and opposite contributions, in that a high value for component 2 corresponds to relatively low protein content and relatively high fiber content, and a low value corresponds to high protein content and low fiber content.

A simple definition for PC1 is unclear. Biomass has the strongest effect (negative), so low values of this component are associated with high biomass. However, protein and fiber also have strong effects (positive), so high values correspond to low concentrations of both protein and fiber.

The general conclusions drawn from analysis of variance (that habitat types differ and that relative habitat quality differs over time) are illustrated by the separation of the three habitat types on the principal component axes (Figure 2.1).

If it is reasonable to describe PC2 as "overall nutrient quality", then in periods 1 and 2 late planted winter wheat, which has the lowest values of this component, would have the highest overall nutrient quality. Early planted winter wheat would have the lowest overall nutrient quality, with potatoes falling in between. Early and late planted winter wheat would have equal overall nutrient quality in period 3.

Potatoes show the lowest values for PC1, and show a relative increase over time (which is expected, given the strong negative effect of biomass on PC1, which is highest on potato fields and undergoes the greatest decrease over time). Early and late planted winter wheat have similar values for PC1, and show less change over time than potatoes. This is probably because the differences in biomass between early and late planted winter wheat are insignificant compared to the differences between these two and potatoes, and because the reduction in biomass on winter wheat fields is also insignificant in comparison to that on potato fields.

A slight decrease is seen in values of PC1 over time for early and late planted winter wheat, mostly between periods 2 and 3, which corresponds to a relative increase in biomass. This does not appear to be related to regrowth on intensively grazed fields, but reflects the swans' shift to fields which were not previously utilized (and which were then reintroduced to the sampling regime), which retained higher biomass reserves.

2.4.2 Habitat preference

Swans show an obvious shift in habitat use in 1993/94 from late planted winter wheat to potatoes to early planted winter wheat (Figure 2.2). No such easily discerned pattern appears in 1994/95 (Figure 2.3).

Habitat preferences relative to availability, and changes in preference over time, are clearly shown by the comparison of observed habitat use to expected use under the assumption of random habitat choice (Figure 2.4), and chi-squared values indicate that preferences are significant in each case.

Habitat preferences are fairly similar between years. Shifts from strong preferences for late planted winter wheat in period 1 to preferences for potatoes in period 2 back to strong preferences for winter wheat in period 3 are seen in both years. Differences arise in period 3 in that the strong preference is for early planted winter wheat in 1993/94 and for late planted winter wheat in 1994/95. In addition, the strong preference for late planted winter wheat in period 1 of 1993/94 carries over into period 2 (the large-scale shift in abundance spans these periods (Figure 2.2)), and the preference for potatoes is weak relative to availability. There are also minor differences, in that a weak preference for early planted winter wheat occurs in period 1 of 1994/95, and a weak preference for late planted winter wheat occurs in 1993/94.

It must be noted that in some instances usage which defines habitat preference does not amount to the highest usage in a given period. For example, in period 3 of 1994/95 preference relative to availability was identified for late planted winter wheat, which actually received the lowest overall usage in that period. It is preference, rather than overall use, which is of interest in the interpretations which follow.

2.4.3 Does habitat quality explain habitat preference?

Recall that the results of principal components analysis supplied a simple proximate description of habitat quality. PC2 was interpreted as "overall nutrient quality", while PC1 was dominated by biomass but lacked a simple definition. In periods 1 and 2, late planted winter wheat showed the highest overall nutrient quality, early planted winter wheat the lowest, with potatoes in between. In period 3 early and late planted winter wheat showed equivalent nutrient quality, while potatoes remained the same as previously, with intermediate values. Potatoes showed the lowest values of PC1 (corresponding to high biomass), which declined over time, particularly between periods 2 and 3. Early and late planted winter wheat showed similar (high) values for PC1 (corresponding to low biomass relative to potatoes), with a slight decrease over time, mostly between periods 2 and 3.

Since no experimental manipulation of habitat quality was attempted, it is not possible to test hypotheses concerning the relationship between habitat quality and habitat preference. As such, the discussion which follows, while based on logical expectations, is purely speculative.

At the beginning of the season, there are biomass reserves present on all fields, so presumably biomass is not limiting. It is therefore reasonable to speculate that preferences would be shown for habitat with the highest nutrient quality (specifically, the lowest fiber concentrations and highest protein concentrations). As biomass reserves become depleted on the highest nutrient quality habitat, it might be expected that nutrient quality would be sacrificed in return for ease of foraging, with preferences shifting to high biomass habitats. When both biomass and nutrient quality are reduced (and possibly limiting), preferences might be expected to reflect the best combination of factors, with tradeoffs being made resulting in the acceptance of intermediate quantities of both (for example, Wilmshurst et al. 1995 experimentally tested models which predicted that herbivores would optimize energy gain by selecting patches of intermediate biomass, because the use of high-biomass patches would result in a constraint in digestive capacity while the use of low-biomass patches would constrain the short-term rate of food intake).

The first expectation appears to be met in both years of the study, in the strong preferences in period 1 for late planted winter wheat (Figure 2.3), which had the highest overall nutrient quality as demonstrated by low values for PC2 (Figure 2.1). The weak preference for early planted winter wheat in period 1 of 1994/95 may also fit this expectation, given that there is some overlap in values of PC2 between early and late planted winter wheat.

The second expectation also appears to be met in both years, in the shift to preferences in period 2 for potatoes, which continue to show low values for PC1 and intermediate values for PC2. The change in PC1 on winter wheat fields is not pronounced, but it must be remembered that it is scaled relative to potatoes, and even the complete loss of biomass on late planted fields results in a change which is only a small fraction of potato biomass.

The strong preference for late planted winter wheat in period 2 of 1993/94, reflective of the fact that the shift from late planted winter wheat to potatoes spanned periods 1 and 2 (Figure 2.2), may have been because there was a larger total area of late planted winter wheat in 1993/94 than 1994/95, so that it took longer for biomass depletion to make biomass limiting.

The transition from period 2 to 3 is important in the regard that non-buried potatoes were depleted by this point, leaving only buried potatoes. Thus even though values for PC1 remain lowest on potato fields (corresponding to the highest biomass), and values for PC2 remain approximately the same (in fact, if anything they are equivalent to the best values among winter wheat), there may be significant energetic costs associated with grubbing for buried potatoes which account for the fact that no preferences for potatoes are observed in period 3.

It is not clear whether the third expectation is met or not. This is because it is not possible to determine what the best combination of PC1 and PC2 might be. In addition, the three upland habitat types (particularly early and late planted winter wheat) approach similarity in both of these traits in period 3, as indicated by the overlapping values for PC1 and PC2 for early and late planted winter wheat, and the nearness of the values for potatoes to those of early and late planted winter wheat in comparison to the other periods. The interpretation is additionally confounded by the fact that most of the habitat use which accounts for observed preferences in period 3 occurs on fields which were unused in the first two periods. This lag in field use initiation likely results from factors which are outside the current definition of habitat quality, or are not components of habitat quality. Chapter 3 discusses some of these additional factors, and the effect they may have on preference.

2.4.4 The effects of scale and the definition of availability on preference

Different temporal scales will result in the observation of different habitat preferences. For example, lumping data over the whole season for 1994/95 shows a strong general preference relative to availability for late planted winter wheat (6615 swan-days observed compared to 3637 expected), a near perfect match for early planted winter wheat (12341 observed compared to 12388 expected) and an underutilization of potatoes (15359 observed compared to 18290 expected). Dividing the season into smaller time blocks than those used will also show a different set of preferences than those described. Given the descriptive resolution afforded by the available habitat quality data, the temporal scale used was deemed appropriate for attempting to illustrate a possible relationship between habitat quality and preference.

Depending on how "availability" is defined, different (and possibly more accurate) expectations for habitat use, assuming a null hypothesis that habitat use is in proportion to availability, may be generated, and this would affect the determination of preference. For example, discounting availability according to field size, or including biomass in the definition of availability, might change whether habitat preference was concluded.

2.4.5 Other factors

As noted in the introduction, habitat quality is not the only thing which may contribute to habitat preference. Such things as disturbance, predation risk, and social status (for instance, the role of juveniles in dictating habitat choice) may also affect preference. These factors will be considered in greater detail in the following chapter.

2.5 Conclusions

Habitat quality was shown, via multivariate analysis of variance and via principal components analysis, to differ among habitats, and relative habitat quality to change over time.

Swans showed significant habitat preference relative to availability in each third of each winter. In 1993/94 preferences were shown, in period 1, for late planted winter wheat, in period 2, for late planted winter wheat (strong) and potatoes (weak), and in period 3 for early planted winter wheat (strong) and late planted winter wheat. In 1994/95 preferences were shown, in period 1, for late planted winter wheat (strong) and early planted winter wheat, in period 2, for potatoes, and in period 3 for late planted winter wheat (strong) and early planted winter wheat.

Changes in preference over time suggest that swans may be selecting habitat which maximizes energetic payoff (i.e. preference is first for the highest nutrient quality when biomass is not limiting, then for the highest biomass (as biomass becomes limiting on the highest nutrient quality fields), and then for the best combination of quality and biomass when both are limiting). Strong preferences late in the season result from a tendency for swans to concentrate on a few fields which retain high biomass due to the lack of early-season use.

Table 2.1. Summary of physical characteristics for the three main upland habitat types (Wl = late planted winter wheat; Po = potatoes; We = early planted winter wheat) in each year of the study. Ha = Hectares.

Year	Type	Number of fields	Average field size (Ha) (+/- 95% C.I.)	Total area (Ha)
1993/94	Wl	7	11.3 (+/- 4.6)	78.6
	Po	12	15.8 (+/- 5.0)	190.0
	We	10	14.6 (+/- 4.2)	145.6
1994/95	Wl	5	10.2 (+/- 4.4)	49.0
	Po	17	13.3 (+/- 4.1)	225.5
	We	11	13.4 (+/- 3.8)	145.6

Table 2.2. Intensity of swan use sustained by fields included in the habitat sampling regime (1994/95). Values (in swan-days) were calculated as the area under the abundance/date curves for each field. Proportions of total upland habitat use are the ratios of these values over total swan-days' use of upland habitat in 1994/95. We = early planted winter wheat, Wl = late planted winter wheat, Po = potatoes.

Field	Type	Swan-days use (% of total)
128	We	1798 (5.2%)
168	We	4111 (12.0%)
21	We	1148 (3.3%)
65	We	1116 (3.3%)
33	Wl	1684 (4.9%)
45	Wl	1154 (3.4%)
60	Wl	3216 (9.4%)
75	Po	6944 (20.2%)

Table 2.3. (A) Univariate and (B) multivariate results from multivariate analysis of variance (PROC GLM in SAS, with "manova" statement and multiple independent variables (biomass, fiber and protein)). Type = habitat type; Date = days after Nov. 1; df = degrees of freedom (Num df = numerator df; Den df = denominator df); Type 3 SS = Type 3 Sums of Squares; MS = Mean Square; F = F ratio; P = probability (values of less than 0.05 are considered significant). Multivariate results test the null hypothesis of no overall Date*Type effect.

(A) Univariate Results

Source	df	Type 3 SS	MS	F	P
Biomass					
Type	2	5837.5	2918.7	60.95	< <0.01
Date	1	121.5	121.5	2.54	0.11
Date*Type	2	124.9	62.5	1.30	0.27
Protein					
Type	2	3154.8	1577.4	196.02	< <0.01
Date	1	185.5	185.5	23.05	< <0.01
Date*Type	2	137.9	68.9	8.57	< <0.01
Fiber					
Type	2	3207.2	1603.6	79.83	< <0.01
Date	1	17.4	17.4	0.86	0.35
Date*Type	2	712.2	356.1	17.73	< <0.01

(B) Multivariate Results

Statistic	Value	F	Num df	Den df	P
Wilk's Lambda	0.769	9.63	6	412	< <0.01

Table 2.4. Partial correlation results for habitat quality data (PROC CORR with "partial" statement in SAS). Values are Pearson partial correlation coefficients, and P values refer to the probability that correlations of this strength would be observed under the null hypothesis of zero correlation. Values for P of less than 0.05 are considered significant. Po = potato, We = early planted winter wheat, Wl = late planted winter wheat.

Habitat Type	Correlation	Correlation coefficient	P
	Constant Biomass		
Po	Fiber-Protein	0.436	<<0.01
We	Fiber-Protein	-0.688	<<0.01
Wl	Fiber-Protein	-0.738	<<0.01
	Constant Fiber		
Po	Biomass-Protein	-0.576	<<0.01
We	Biomass-Protein	0.439	<<0.01
Wl	Biomass-Protein	-0.485	<<0.01
	Constant Protein		
Po	Fiber-Biomass	0.173	0.02
We	Fiber-Biomass	-0.073	0.47
Wl	Fiber-Biomass	-0.899	<<0.01

Table 2.5. Eigenvalues of the correlation matrix, derived from principal components analysis of the habitat quality data (PROC PRINCOMP in SAS). Principal components 1 and 2 (PC1 and PC2) explain most (90%) of the original variability in the data, and are therefore used to describe habitat quality.

Principal Component	Eigenvalue	Difference	Proportion	Cumulative
PC1	1.84	0.98	0.61	0.61
PC2	0.87	0.58	0.29	0.90
PC3	0.29	--	0.10	1.00

Table 2.6. Eigenvectors derived from principal components analysis. Principal component 1 (PC1) shows a strong negative effect of biomass, and strong positive effects of both protein and fiber. Principal component 2 (PC2) shows a strong negative effect of protein, a strong positive effect of fiber, and a negligible effect of biomass. PC2 is interpreted as "overall nutrient quality".

Variable	PC1	PC2	PC3
Biomass	-0.68	0.03	0.74
Protein	0.55	-0.64	0.53
Fiber	0.49	0.77	0.42

Figure 2.1. Relationship between principal component 2 (PC2) and principal component 1 (PC1), derived from principal components analysis of habitat quality data. PC2 is interpreted as "overall nutrient quality"; low values correspond to high proportional representations of protein and low proportional representations of fiber per dry weight. PC1 lacks a simple interpretation; low values correspond to relatively high biomass, and to low concentrations of both protein and fiber. Components are plotted separately for each third of the study interval (period 1 = 1 to 40 days after Nov. 1; period 2 = 41 to 80 days after Nov. 1; period 3 = 81 to 120 days after Nov. 1). Ellipses are arbitrary (they are not confidence ellipses), and serve only to simplify the visual representation of relative habitat quality. Wl = late planted winter wheat, We = early planted winter wheat, Po = potatoes.

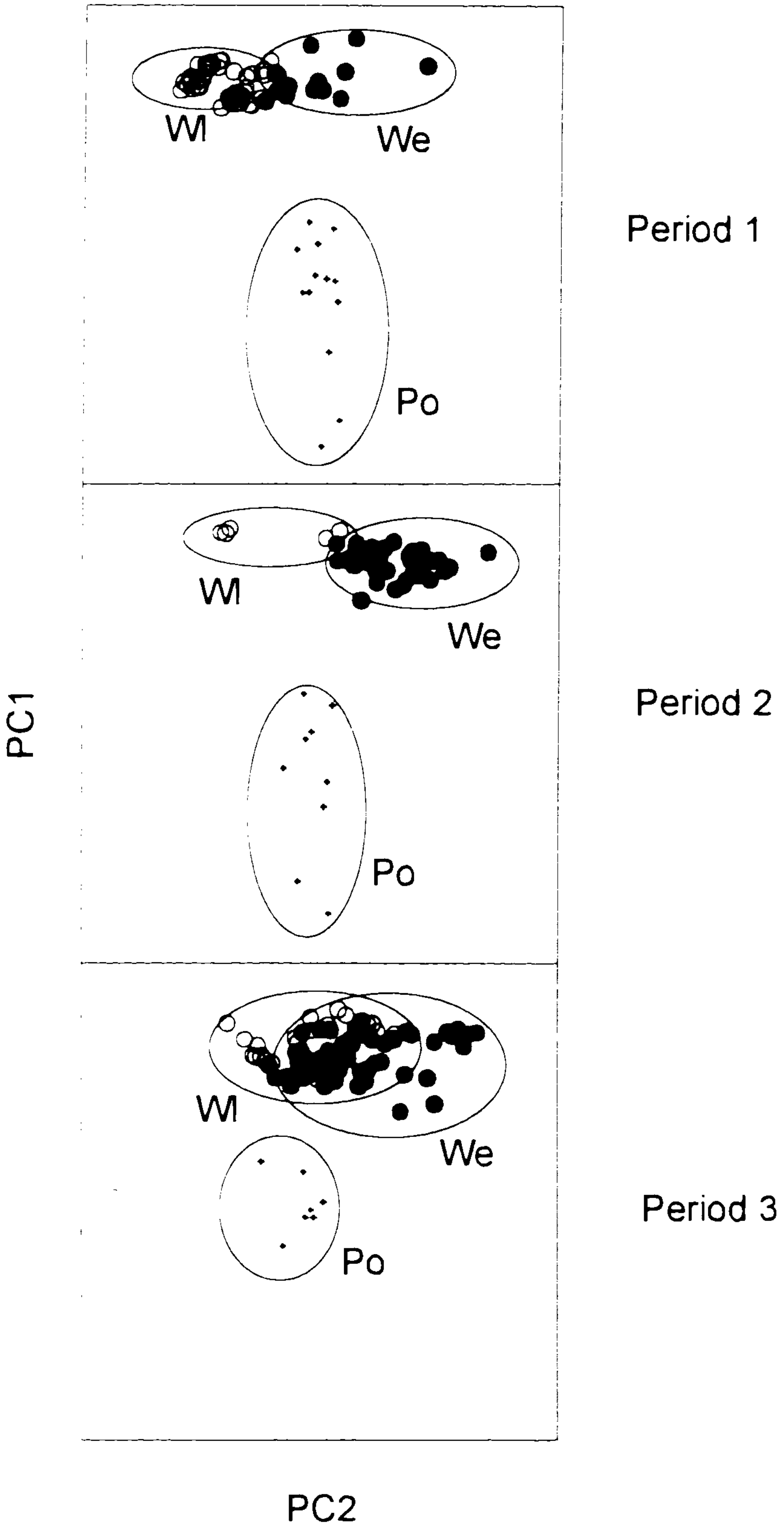

Wl
We
Po
Period 1
Wl
We
Po
Period 2
Wl
We
Po
Period 3
PC1
PC2

Figure 2.2. Trumpeter Swan abundance on each of the three main upland habitat types (late planted winter wheat, potatoes, and early planted winter wheat) in 1993/94. Open triangles correspond to days with low temperatures below freezing, and closed circles to days with low temperatures above freezing.

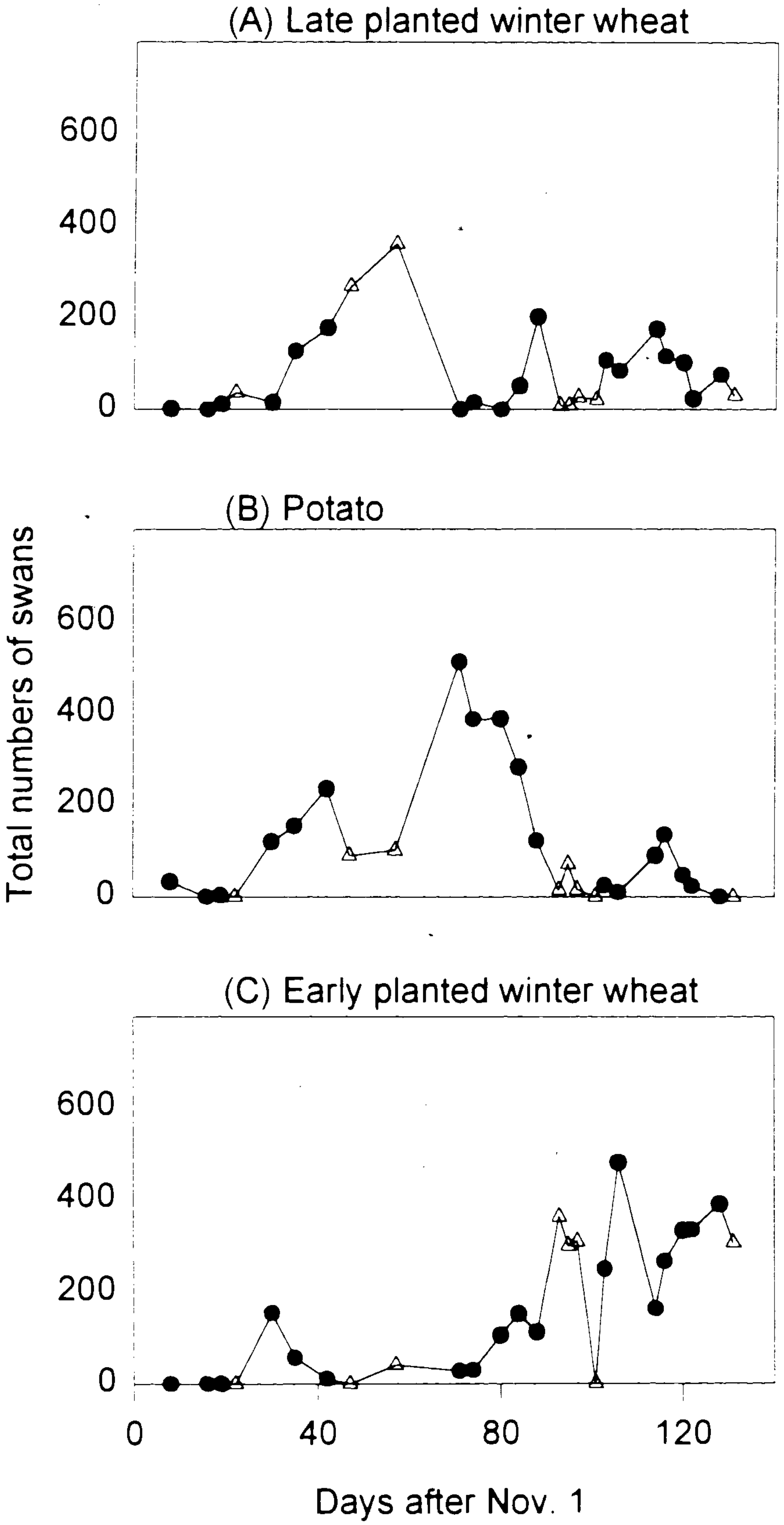

(A) Late planted winter wheat
600
400
200
0
(B) Potato
Total numbers of swans
600
400
200
0
(C) Early planted winter wheat
600
400
200
0
0
40
80
120
Days after Nov. 1

Figure 2.3. Trumpeter Swan abundance on each of the three main upland habitat types (late planted winter wheat, potatoes, and early planted winter wheat) in 1994/95. Open triangles correspond to days with low temperatures below freezing, open circles to days with accumulated snow in addition to freezing temperatures, and closed circles to days with low temperatures above freezing.

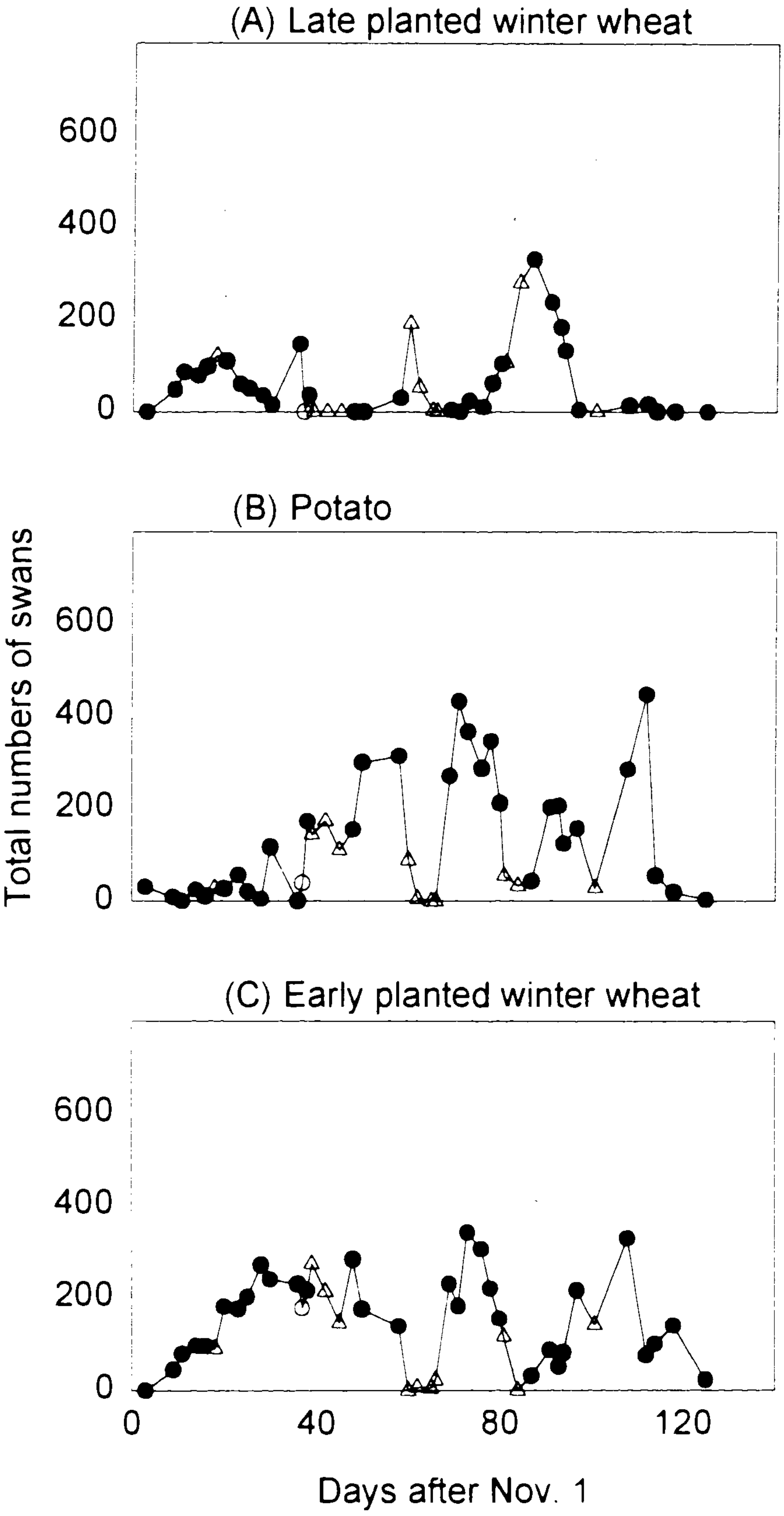
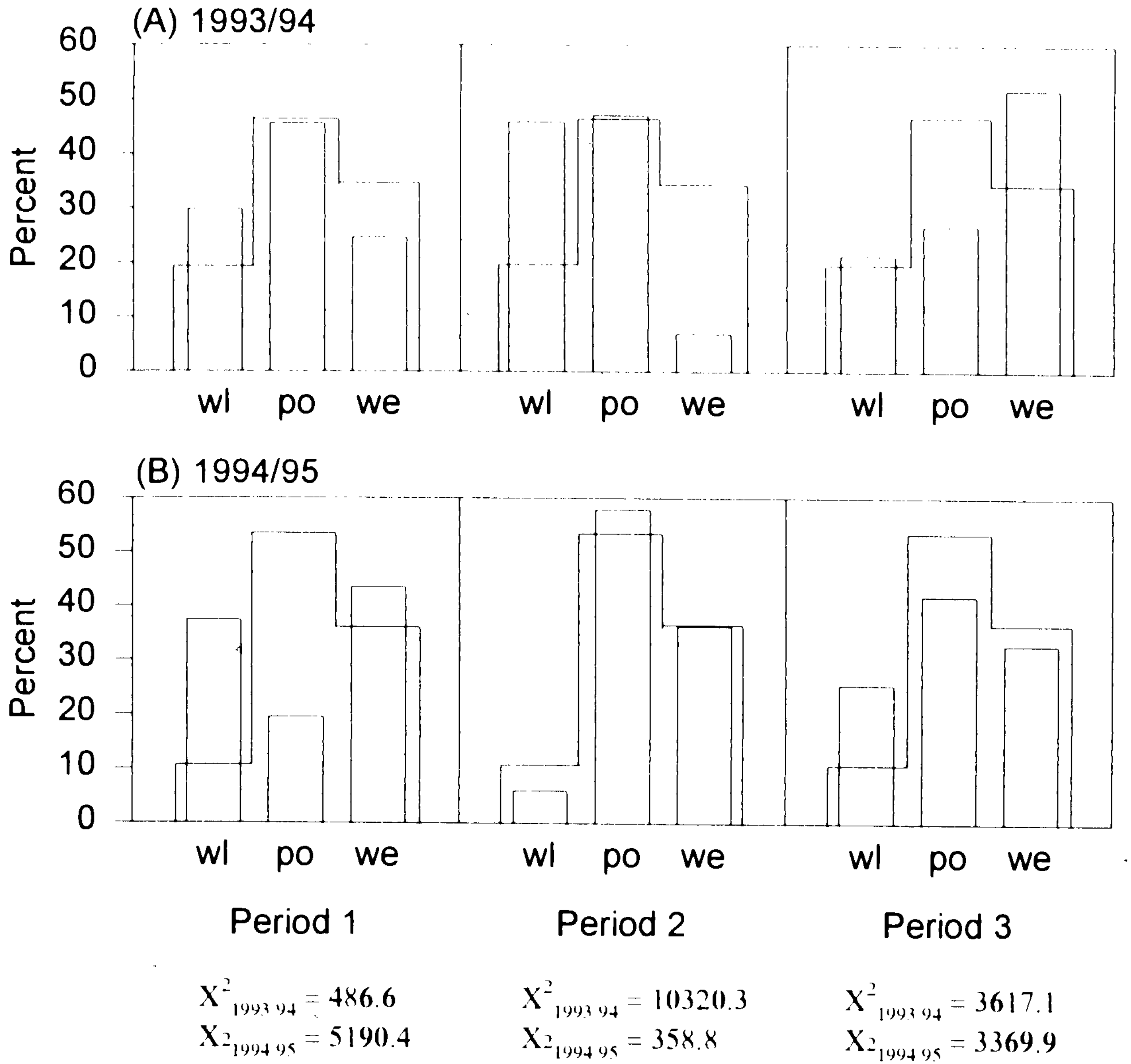

(A) Late planted winter wheat
(B) Potato
(C) Early planted winter wheat
Total numbers of swans
Days after Nov. 1
0
200
400
600
0
40
80
120

Figure 2.4. Comparisons of observed habitat use and expected habitat use under the null hypothesis that habitat use is in proportion to availability, for the two years of the study (1993/94 and 1994/95). Observed values were calculated for each habitat type as the area under the abundance/date curve within each third of the study interval; values for each habitat type were converted to percentages of total usage, and are represented by histograms. Expected values (represented by superimposed plots) reflect the proportion of total usage within each third of the study interval which would be expected if habitat use is in proportion to the availability (area) of habitat. Comparisons were made for each third of the study interval (period 1 = 1 to 40 days after Nov. 1; period 2 = 41 to 80 days after Nov. 1; period 3 = 81 to 120 days after Nov. 1). Chi-squared values (subscripts refer to year) evaluate the significance of observed preferences, and are significant in all cases ($p << 0.001$). Chi-squared values were calculated using the original units (swan-days) rather than the percentages represented in the figure.


(A) 1993/94
Percent
60
50
40
30
20
10
0
wl
po
we
wl
po
we
wl
po
we
(B) 1994/95
Percent
60
50
40
30
20
10
0
wl
po
we
wl
po
we
wl
po
we
Period 1
Period 2
Period 3
$X^2_{1993\ 94} = 486.6$
$X2_{1994\ 95} = 5190.4$
$X^2_{1993\ 94} = 10320.3$
$X2_{1994\ 95} = 358.8$
$X^2_{1993\ 94} = 3617.1$
$X2_{1994\ 95} = 3369.9$

Chapter 3

Other Factors Governing Habitat Preference

3.1 Introduction

It was shown in the previous chapter that simple habitat availability does not predict habitat use (since there were clear preferences relative to availability). Speculation was then made on the possible role of habitat quality in determining preference. This chapter addresses factors other than habitat quality which may also contribute to habitat preference.

Given that survival and reproductive success are contingent upon body condition, it seems likely that physiological demands may affect winter habitat choice. Madsen 1985 speculated that shifts from pasture to grain feeding in Pink-footed Geese (*Anser brachyrhynchus*) resulted from high initial demands for protein, followed by demands for carbohydrates necessary to build up fat reserves for reproduction. Physiological constraints may similarly regulate habitat use, particularly those which limit digestive efficiency (for example, development of gizzard musculature (Alisauskas 1988)). Interaction with other species, social status, physical features of habitat (such as patch size), and disturbance may also affect habitat use (Norriss and Wilson 1993, Sutherland and Allport 1994, Belanger and Bedard 1990, Owen 1973).

3.1.1 Patch size

A considerable body of literature exists surrounding the effect of resource heterogeneity, or patchiness, on foraging behaviour (see Begon et al. 1986). Patch size can affect resource acquisition in a variety of ways. Under equivalent feeding intensity, smaller patches become depleted more quickly than larger ones. Smaller patches also have a proportionally higher "edge effect" relative to area, which means that on average the distance from any arbitrarily chosen point to the edge of the patch decreases with decreasing patch size. Predation risk is often higher at patch edges (Cody 1985), and consequently increases with decreasing patch size. Other effects such as disturbance, which are associated with patch edges, also increase in intensity with decreasing patch size.

In the present study, the heterogeneous environment which comprises the study area consists of a number of patches (fields), each of which contains a comparatively homogeneous distribution of resources, and which tend to be separated by physical features such as roads, hedges and buildings. For swans, which in flight gain altitude slowly (pers. obs.), obstructions at field edges such as power lines, hedges and trees may make small fields unattractive because of the navigational difficulties posed (Sean Boyd, pers. comm.). Given the urban setting, houses, roads and human activity at field edges may also result in a considerable disturbance factor, again making smaller fields less attractive. Following from these points, it is reasonable to predict the general avoidance of small fields relative to large.

3.1.2 Social status

A number of studies have shown that habitat use within a population of waterfowl varies according to social status. Because swan and goose families remain together through the winter, the presence of offspring may constrain parents' habitat use in comparison to that of adults without young, while in some cases the presence of offspring may be advantageous. Differences in habitat use depending on the presence or absence of offspring may provide insight into the possible causes of habitat choice in general, and indicate possible effects of variation in productivity (the representation of juveniles in the population) on habitat choice (see Scott 1980, Raveling and Zezulak 1991).

Juvenile swans and geese often pioneer into new habitats (Black et al. 1991), possibly as a process of experimentation (see Kear 1963, Anderson 1993). The exposure to new habitats may be advantageous to parents. In addition, differences in competitive ability often exist between families and non-families (Black and Owen 1989, Earnst and Bart 1991, Black et al. 1992, Goss-Custard et al. 1995). Larger families are often better at maintaining territory in preferred habitat than smaller ones, and families are generally better than single or paired adults. Again, the presence of offspring may be advantageous to parents. However, it is also possible in some instances that adults without young are simply "poorer" individuals, and would have lower competitive ability regardless.

Juveniles spend less time engaged in vigilant or aggressive behavior than adults (Black and Owen 1989), and so are less likely to respond to factors which contribute to these behaviors when choosing habitat (for example, Jozkowicz and Walasz 1991 found higher concentrations of juvenile Mute Swans (*Cygnus olor*) in urban wintering sites than rural ones, possibly because juveniles suffer less of an energetic cost due to disturbance). Juveniles may also select habitat according to different criteria than adults (Raveling and Zezulak 1991, Cresswell 1994). Because of these factors the presence of offspring may pose an energetic cost to parents, through the demands of increased vigilance, and through the acceptance of what may be for parents nutritionally sub-optimal habitat.

It was noted incidentally in the first year of the present study that juveniles seemed to have a lot of difficulty eating potatoes early in the season, possibly owing to the firmness of the potatoes at that time of the year. It was also noted in the last third of the study period that there was a considerable investment of time required in grubbing for buried potatoes, and that juveniles appeared to have lower success rates at finding potatoes than adults. In light of these observations, one might predict that, if juveniles dictate habitat choice for the family, families would avoid potato fields in comparison to non-families. Differences in habitat use would also be expected if families and non-families possess different competitive abilities, and if juveniles show a stronger tendency to seek out specific nutrients than adults (for example, if juveniles have a stronger tendency to maximize protein intake).

This chapter considers the possible effects of field size and social status (families versus non-families) on habitat use. It is beyond the scope of this study to address other factors mentioned in the introduction, although their potential importance, both individually and interactively, is noted.

3.2 Methods

3.2.1 Field Size

The effect of field size on habitat use was investigated by comparing the date of field use initiation (drawn from the survey data) to field size, by means of regression analysis. Data for both years were pooled.

3.2.2 Social Status

Juvenile numbers were recorded consistently in 1994/95 only, so the discussion of social status is restricted to that year. The total intensity of habitat use in each third of the study interval was separated into that attributable to families and non-families. The number of swan-days attributable to families was calculated by taking juvenile swan-days, and for each (X) juvenile swan-days (where (X) is the average number of juveniles in a family) two swan-days were subtracted from adult swan-days and added to juvenile swan-days. The remaining adult swan-days therefore represent non-families.

Family sizes were recorded throughout 1994/95. Only those families which were unambiguously identified were included in the calculation of average family size. Families observed arriving at or departing from a field, or in flight, were assumed to contain all family members.

Habitat preferences in families and non-families in each third of the study period were investigated by (as in chapter 2) comparing the observed intensity of use to that expected under the null hypothesis that habitat use is in proportion to availability. Chi-squared tests were again used to assess significance.

3.3 Results

3.3.1 Field Size

Slopes of the regression lines for field size versus date of first use are negative for each habitat type (Figure 3.1), indicating a tendency for smaller fields to be used later in the season. However, the relationship is fairly weak, as indicated by the low r-squared values (r-squared ranges from 0.26 to 0.50).

3.3.2 Social Status

The average number of juveniles in a family in 1994/95 was 2.5 (95% confidence intervals = +/- 0.13).

Preferences relative to availability for families and non-families were generally similar (Figure 3.2). Both showed preferences for late planted winter wheat and early planted winter wheat in period 1, and for late planted winter wheat in period 3. Differences were observed in that families showed a preference for late planted winter wheat in period 2, while non-families show a preference for potatoes, and in that the strength of preference differed somewhat between these classes. For example, families showed a slightly stronger preference relative to availability in period 1 for late planted winter wheat than non-families (the ratio of observed to expected was 3.7 for families and 3.4 for non-families), while non-families showed a stronger preference for late planted winter wheat in period 3 (the ratio of observed to expected was 2.8 for non-families and 1.9 for families).

The strength of habitat avoidance also differed somewhat between families and non-families. For example, families showed a stronger avoidance for potatoes in period 1 (the ratio of observed to expected was 0.3 for families and 0.4 for non-families), and a weaker avoidance in period 3 (the ratio of observed to expected was 0.9 for families and 0.7 for non-families).

3.4 Discussion

The evidence presented suggests that patch size and social status are both important in determining habitat preference, and temporal changes in preference. However, it is only possible at this time to speculate on the particular mechanisms (such as disturbance, competitive interaction and physiological and developmental constraints) through which these factors act. The general similarity in preference exhibited by families and non-families suggests that the underlying criteria for shifting between habitats may be similar, and the differences suggest that responses to changes in these criteria may vary in intensity according to social status.

3.4.1 Field Size

The order in which fields are used is to some extent a function of field size (Figure 3.1), with a tendency on all habitat types for swans to initiate use of smaller fields later in the season. Any or all of the mechanisms noted above (predation risk, navigational difficulty and disturbance) may contribute to the avoidance of smaller fields, though it is not possible from present data to distinguish between them.

Goss-Custard et al. 1992, using multiple regression analysis, eliminated patch size as a predictive variable for foraging Oystercatcher density. Anderson 1993, also using multiple regression analysis, found that field size was not an important predictor of Trumpeter Swan abundance in the Skagit delta. It is possible that these results arose not because patch size has no effect on habitat choice, but perhaps because the relationship is non-linear.

In the present study, the tendency for swans to avoid small fields early in the season confounds the interpretation of preference because, first of all, the tendency is weak (note the small r-squared values), and secondly because once use is initiated it can account for most of the total use of that habitat type. For example, in 1994/95 field 60 (6.3 hectares) was unused until period 3, but once use was initiated it accounted for 3216 of the 3640 swan-days total use of late planted winter wheat in that period. Because this field was ungrazed up to period 3, the biomass reserves it possessed probably accounted for the intensive use it sustained. Thus the preference for late planted winter wheat observed in period 3 is not only attributable almost entirely to one field, but the very unattractiveness of the field early in the season likely resulted in its attractiveness late in the season.

3.4.2 Social Status

Social status appears to affect habitat preference, as indicated by the differences in preference (particularly in the intensity of preference) exhibited by families and non-families. It is not possible from the present data to distinguish between such potential causes of these differences as pioneering by juveniles, differences in selective criteria between families and non-families, and learning and developmental effects, but some speculation on how these may be operating is offered for selected instances.

Non-families show a weaker preference for late planted winter wheat and a weaker avoidance of potatoes in period 1 than families, and show a preference for potatoes in period 2 which is not seen in families. Swan and goose families often possess a competitive advantage in that they are better able to hold territory in preferred habitat (see references given in the introduction). If late planted winter wheat is the preferred habitat in period 1 (which is conceivably the case, given the favourable combination of biomass and nutrient characteristics), then it is possible (though at this point untestable) that non-families are to some extent displaced off this habitat by families. This would simultaneously account for the weaker preference for late planted winter wheat, and for the weaker avoidance of potatoes, which might receive displaced swans. A similar effect may extend into period 2, resulting in the preference among non-families for potatoes.

An alternate, though by no means mutually-exclusive explanation for these differences in preference could be supplied by differences in nutrient demand between adults and juveniles. A stronger tendency in juveniles to maximize protein uptake might also produce a stronger preference for late planted winter wheat and a weaker preference for potatoes in families. Juveniles may also lack sufficient physiological development (for example, bill musculature) to cope with the mechanical difficulties of eating potatoes, and this would also contribute to a stronger avoidance of potatoes in families. Again, these are only some of the possible hypothesis which are consistent with the present data, and there is currently no way of eliminating or selecting among them.

As a final example (there are of course others, but since this discussion is purely speculative it seemed injudicious to belabor the point), families show a weaker avoidance of potatoes in period 3 than non-families. Based on preliminary observations in the first field season, it appeared as though foraging on potatoes this late in the season would entail considerable search costs, since non-buried potatoes were effectively used up by the end of period 2. In particular, it seemed likely that there would be a considerable learning component to effective foraging, as juveniles appeared to have low success rates at locating buried potatoes (pers. obs.).

Attempts at quantifying components of foraging behavior suggested that (1) juveniles covered smaller areas per unit of time while foraging than adults, (2) tested fewer spots, and (3) spent more time grubbing in non-productive spots (pers. obs.). It was speculated that these differences in behavior would give rise to the apparently lower success rates at locating buried potatoes. In light of this, it might be construed as counter-intuitive that families would actually show weaker avoidance of potato fields than non-families in period 3. Though it is not possible to satisfactorily account for this difference (or for that matter establish whether or not it is indeed counter-intuitive), it is interesting to note that parents were observed on numerous occasions in effect provisioning their offspring, by giving up potatoes and productive spots (buried potatoes tended to be in clumps (pers. obs.), so a spot which yielded one potato was likely to have more). Similar behavior has been documented in geese feeding on buried rhizomes (Turcotte and Bedard 1989), and in Tundra Swans feeding on buried and submerged clams (Earnst and Bart 1991).

The differences in potato field use by families and non-families is contrary to what might be expected on the basis of the requirements for learning in order to achieve efficient foraging. However, one might say that provisioning helped to facilitate the use of this habitat, and therefore helped to account for the weaker avoidance of potatoes by families than by non-families. Alternatively, if juveniles dictate habitat choice, this effect may arise from constraints on learning, and the slower response in juveniles than adults to changing habitat conditions (see Bernstein et al. 1991).

3.5 Conclusions

In addition to habitat quality, there are a number of contributors to habitat preference which may act simultaneously and interactively. While only two of these (field size and social status) are discussed here, the likelihood that others (for example, metabolic constraints and demands, and interaction with other species) are also acting is acknowledged.

Field size is related to the timing of field use initiation, and is therefore a relevant factor to preference. However, though there is a tendency for smaller fields to be used later in the season, the relationship is weak. The biomass reserves which are, as a result of the lack of early season use, retained on some of these small fields, allow for very intensive use late in the season, with the result that a single small field can account for most of the use observed on a given habitat type late in the season. Field size is therefore considered a relevant but confounding factor with regard to habitat preference.

Differences in habitat preference are observed between families and non-families. Social status is therefore also concluded to be a relevant factor with regard to preference. There are a number of non-mutually-exclusive hypotheses which may be consistent with the observed differences in preference between families and non-families, though these hypotheses are currently untestable.

Figure 3.1. Comparisons between the date of first observed use and field size, for each upland habitat type. Data for both years (1993/94 and 1994/95) are pooled. Low r-squared values indicate that the tendency for swans to initiate the use of smaller fields later in the season (as indicated by the negative slopes for each regression line) is weak.

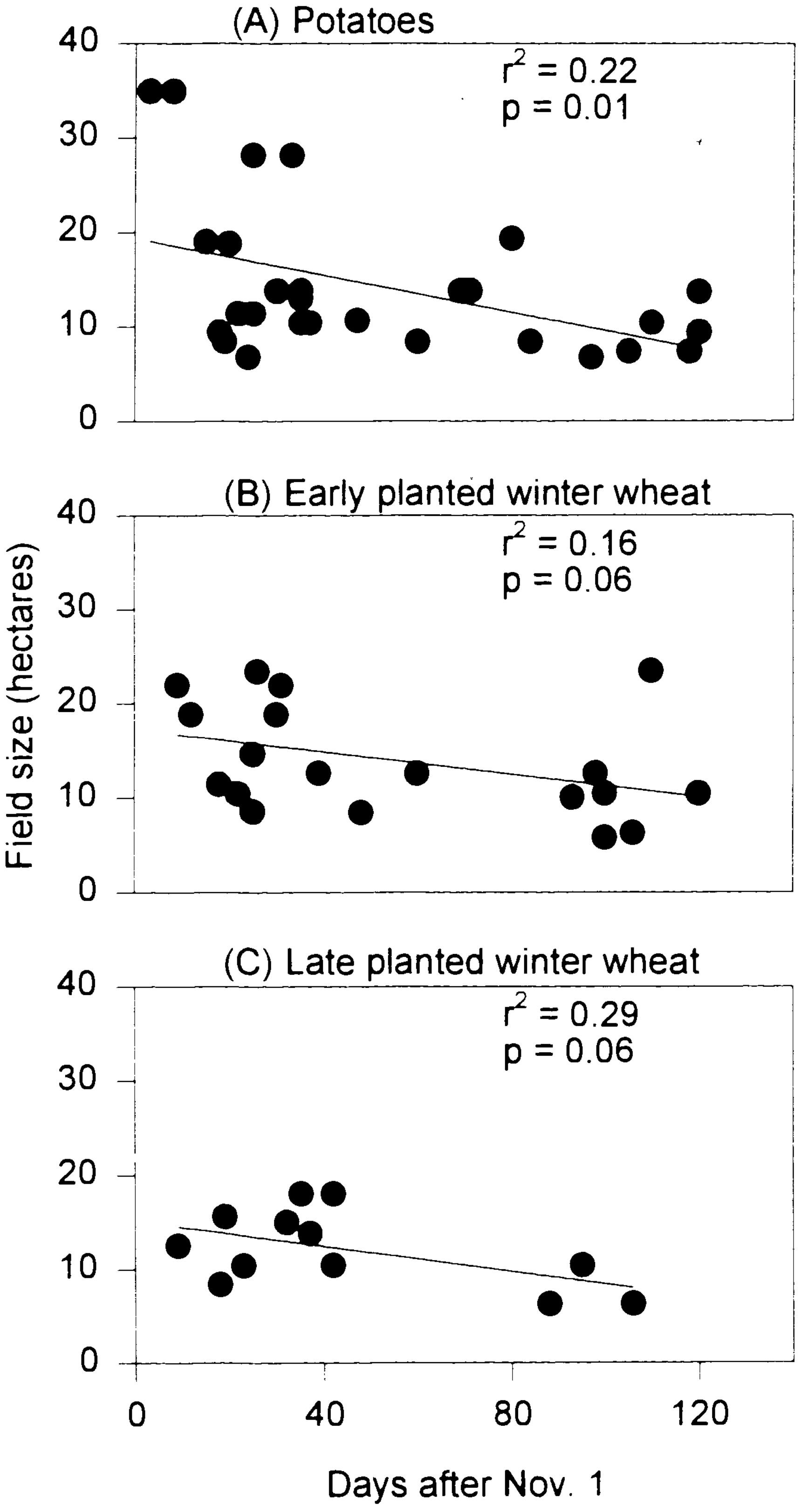
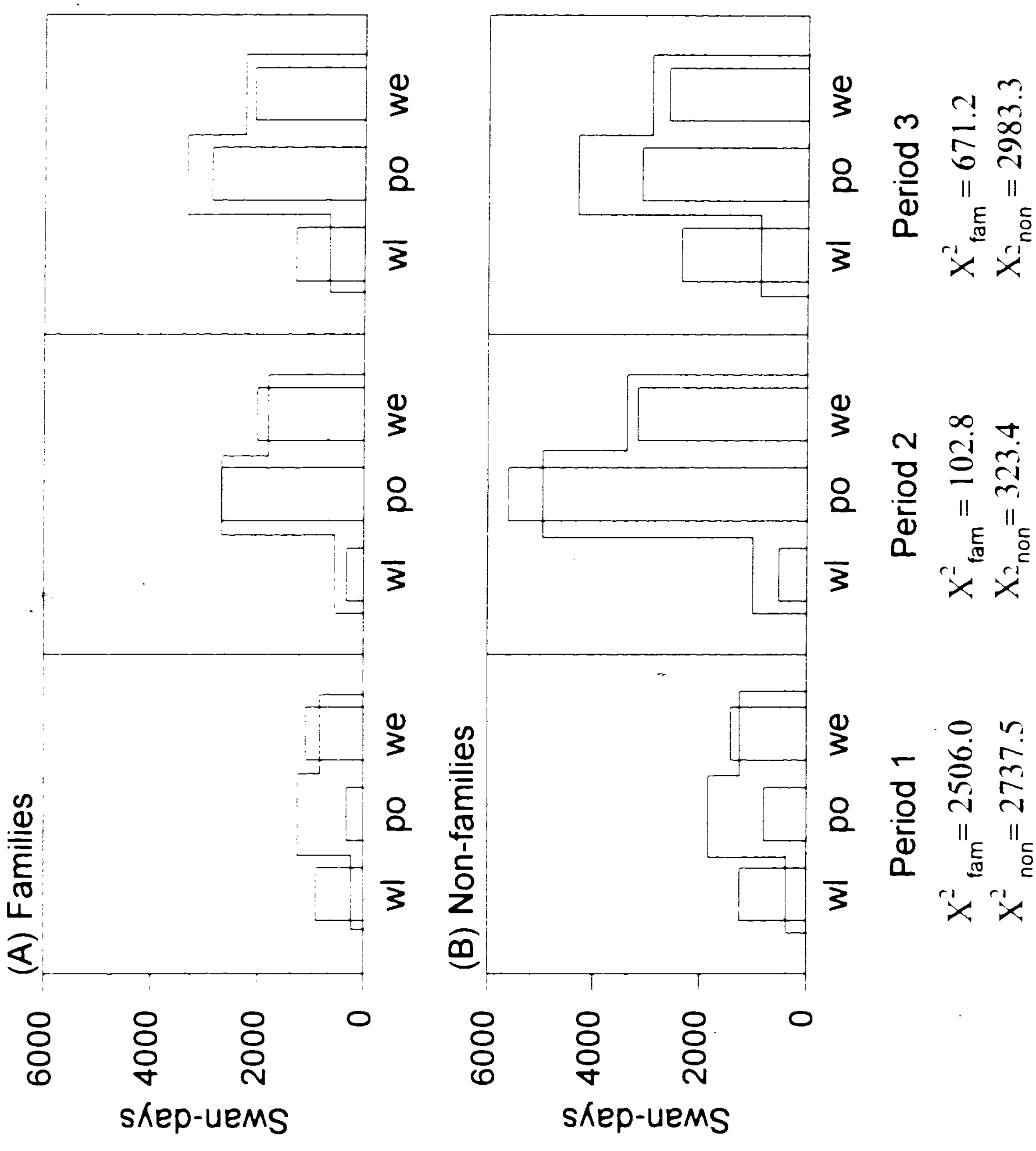

(A) Potatoes
$r^2 = 0.22$
$p = 0.01$
(B) Early planted winter wheat
$r^2 = 0.16$
$p = 0.06$
(C) Late planted winter wheat
$r^2 = 0.29$
$p = 0.06$
Field size (hectares)
0
10
20
30
40
Days after Nov. 1
0
40
80
120

Figure 3.2. Comparisons of observed habitat use and expected habitat use under the null hypothesis that habitat use is in proportion to availability. Comparisons are for families and non-families in each third of 1994/95 only. Observed values (represented with histograms) were calculated using average family size to separate total usage (in swan-days) into that attributable to families and non-families. Expected values (represented with superimposed plots) were calculated assuming that habitat use is in proportion to the availability (area) of each habitat type. Chi-squared values (subscript "fam" refers to families, and "non" to non-families) evaluate the significance of observed preferences, and are significant in all cases ($p << 0.001$). Period 1 = 1 to 40 days after Nov. 1; period 2 = 41 to 80 days after Nov. 1; period 3 = 81 to 120 days after Nov. 1.


(A) Families
(B) Non-families
Swan-days
6000
4000
2000
0
wl
po
we
Period 1
Period 2
Period 3
X^2_{fam}= 2506.0
X^2_{non}= 2737.5
X^2_{fam} = 102.8
$X2_{non}$= 323.4
X^2_{fam} = 671.2
$X2_{non}$ = 2983.3

Chapter 4

Summary and Conclusions

4.1 Introduction

Winter habitat choice in waterfowl can have important implications to seasonal nutrient status, to survival and reproductive success, and ultimately to population dynamics contingent on these (McLandress and Raveling 1981, Boudewijn 1984, Huey 1991). In light of this, an understanding of the processes of winter habitat choice is important to the conservation and management of waterfowl, particularly in its capacity to predict future habitat use (Vickery et al. 1995). This study sought to quantify the winter abundance and distribution of Trumpeter Swans using upland habitat on the Fraser delta, and to identify possible causes of habitat preference.

4.2 Population and Abundance

Since the way in which a population distributes itself among habitats is ultimately the result of individual foraging decisions, it is important, before considering the possible causes of habitat preference, to identify in some way the individuals about which inferences are to be made. In particular, do significant numbers of individuals move into and out of the study area over time, or do abundance patterns reflect foraging decisions made by the same individuals over time? The latter is referred to as a closed population.

It was shown (see Appendix 1) that after the end of fall migration, sharp drops in Trumpeter Swan abundance on upland habitat in both years could be attributed to temporary displacement resulting from cold weather, and that sharp increases in abundance could be attributed to brief influxes of transients. Apart from these instances, total numbers remained fairly constant. Movement rates to and from the marsh which were not associated with'diurnal migration were low (particularly in comparison to those on upland habitat), possibly indicating strong individual fidelity to upland habitat. Sightings of marked individuals provided some further support for this inference. It was concluded from this evidence that swans using upland habitat may represent a closed population. This conclusion is further supported by air count data (S. Boyd, unpubl. data) for the years 1987/88 to 1991/92, which suggest that within each winter the total population in the Fraser delta may be closed.

4.3 Habitat Quality and Preference

Habitat preference gives a description of habitat use which, since it is defined as non-random habitat choice, implies a functional relationship to attributes of habitat. Because of this, the interpretation of habitat preference can serve as the basis for the prediction of habitat use. Relative habitat quality likely changes over time among different habitat types which undergo rapid seasonal change. If preference is related to habitat quality, it likely changes over time as well.

It was shown in chapter 2, via proximate measures of habitat quality, that the upland habitat types (late planted winter wheat, potatoes, and early planted winter wheat) differed significantly, and that relative habitat quality changed over time. It was also shown that swans demonstrated habitat preferences in each third of each winter, and that these preferences changed over time. The general similarity between years (shifts in preference from late planted winter wheat to potatoes to early and late planted winter wheat (in 1993/94) and late planted winter wheat (in 1994/95)) suggest an underlying similarity in the general process of habitat choice in both years.

The inability to control for habitat quality made it impossible to test hypotheses concerning the relationship between preference and habitat quality. However, it was speculated that the shifts in preference might reflect (1) preference for high nutrient quality (high protein and low fiber concentrations) when biomass was not limiting, (2) as biomass declined, and became limiting on high-nutrient-quality fields, preference for the highest biomass (which necessitated the acceptance of intermediate nutrient quality), and (3) preference for the best combination of biomass and nutrient quality when both were limiting on all habitats.

4.4 Other Factors related to Preference

Besides habitat quality, there are a number of other factors which may affect preference. For example, patch size is known to affect the suitability of habitat through a variety of mechanisms. Differences in preference have also been shown according to social status, particularly (among swans and geese) as determined by the presence or absence of offspring (see Dirksen et al. 1991).

Field size was shown in chapter 3 to have an effect on habitat use, in that there was a weak tendency for swans to initiate the use of smaller fields later in the season. However, the rules governing the avoidance of small fields apparently change over the season, since some small fields which were avoided early in the season received very intensive use late in the season, possibly as a result of the food reserves they retained.

Social status was also shown to have an effect on preference. While families and non-families showed general similarities, their preferences differed in the second third of the study interval (non-families showed a preference for potatoes, while families showed a preference for early planted winter wheat), and the intensity of preference differed throughout the season. It was not possible with the present data to test hypotheses concerning these differences, though speculation on possible factors was offered. Among the hypotheses which may be consistent with observed preferences are: that physiological development in juveniles may have constrained feeding on potatoes early in the season; that families may have a competitive advantage over non-families; and that the learning requirements for efficient foraging for sub-surface potatoes late in the season may act as a constraint on juveniles (though this may be offset by provisioning).

4.5 Management Implications

In numerous instances, decreases in natural habitat and increases in farmland have resulted in large-scale shifts in swan habitat use to agricultural crops (Earnst 1994), and in some cases this has led to conflict (see Van Roomen and Madsen (eds.) 1991, Patterson 1991). The loss of agricultural crops, through urbanization or through changes in planting regime, could result in an increasing dependency on traditional food sources (Anderson 1993, Boyd 1995). In the Fraser delta, the potential impact on the marsh, and the subsequent implications to swan and goose life cycles, should be considered before making changes to the availability of preferred agricultural crops. At the same time, action should be taken to mitigate the impact of swan grazing on agricultural land.

In 1993, a strategic plan for the securement of wildlife habitat in the Fraser delta was drafted (anon. 1993). The goal of this plan was "to provide sufficient upland habitat in the vicinity of the Fraser River Delta of British Columbia to meet the regional contribution to established goals for migratory bird populations". The established goal for Pacific Coast Trumpeter Swan populations, in the absence of location-specific objectives or clearly defined criteria, can be taken as that prescribed by the Subcommittee on Pacific Coast Trumpeter Swans (1993), namely to at least maintain existing populations. It is in general recommended that where and to what extent possible, the implementation of the wildlife habitat securement plan should continue. More specifically, efforts should continue to be made to incorporate lands into the securement strategy, and secured lands should be managed "to develop wildlife habitat potential", through the improvement and enhancement of carrying capacity (anon. 1993).

Given these objectives, an effective management and conservation program in the Fraser delta should strive to realize the following:

1. At least maintain current Trumpeter Swan populations. This can be achieved in part through the continuation of cover-cropping programs such as the Greenfields project, through the continued securement of wildlife habitat, and through public education about the necessity for conservation of agricultural land and wetlands. Opportunities for the development of swan refuges should be examined.

2. Minimize impact on farmland. This can be achieved through the use of cover crops and hazing methods to regulate the order, duration and intensity of field utilization by swans. (Moser and Kalden (1991) note that it is in general not the total size of waterfowl populations which pose a problem to agriculture, but rather the spatial and temporal distribution across the wintering range). Distributing preferred crops types over as wide an area as possible may reduce the likelihood of localized high-intensity field use which tends to occur late in the season. Information on the habitat preferences of Wigeon (for example, preferences related to crop age and sward height) may be useful in this regard, in that differential sward depletion due to Wigeon grazing (which denudes some fields but leaves considerable food resources on others) may currently account for much of the high-intensity field use by swans.

There may be a tradeoff inherent in the choice of cover crop planting date, since anecdotal evidence suggests that Wigeon and swans show preferences for crops of different ages. Wigeon tend to prefer younger crops, which are often completely denuded (resulting in little swan use), while avoiding older crops (which as a result persist and retain food reserves later into the winter, which attracts more intensive swan use). More information is required to determine what the relative effects on field productivity later in the growing season are of soil compaction and cover crop loss in the winter, and to determine the best crop planting regime to minimize the impact of grazing by waterfowl. For example, one problem which may be considered is whether the loss of cover crop biomass from intensive Wigeon grazing is more or less deleterious to field productivity than the soil compaction which may result from intensive swan use, and whether the soil compaction which results from swan use is significant compared to that which results from heavy rain on bare or denuded fields.

3. Evaluate the potential impact on the marsh, and the subsequent impact on swan and goose life cycles, of causing significant shifts in swan habitat use away from upland habitat and onto the marsh. Again, the interaction between swans and Wigeon on upland habitat should be considered, and efforts made on secured lands to provide cover crops of different ages, in particular so that swans are not displaced from upland habitat through exploitative competition with Wigeon. At some point, as utilization of the marsh increases (which will occur at an accelerated rate if swans are displaced from upland habitat), density-dependent processes will take effect (Boyd 1995); the long-term demographic consequences of this should be taken into account in any instance which threatens to reduce the availability of upland habitat and food reserves.

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Appendix 1. Description and definition of the study population.

I present data here on overall Trumpeter Swan abundance on upland habitat, including a brief discussion of some of the possible causes of variability in abundance. I then present data on movement rates within the study area and on sightings of marked individuals, followed by a brief discussion of the assumptions on which inferences about habitat choice are based.

Total numbers of swans (of which the majority were Trumpeters) using upland habitat were roughly similar between years (Figure A.1.1). Abundance on upland habitat increased steadily in both years up to around day 30, which may be taken as the end of fall migration.

Sharp decreases in abundance tended to be associated with frozen conditions, which probably displaced swans by making food unpalatable or inaccessible. Cold weather did not always result in displacement, and the complete abandonment of upland habitat was restricted to periods in which there were several consecutive days of below-freezing weather. Ground-level ambient temperatures would probably give a better prediction of food availability and field use. Daily minimum temperatures (Figure A.1.2) show that cold weather was generally more intense and of longer duration in 1994/95 than 1993/94. Cold-weather abandonment of upland habitat was more prominent in 1994/95 than in 1993/94, probably due to the more intense and longer cold spells.

Sharp increases in abundance occurred immediately after the intense cold spell (around day 75) and late in the season (around day 100) in 1994/95 (Figure A.1.1). The late-season increase was possibly due to the movement of swans from more southerly wintering areas into the study area at the onset of spring migration. The mid-season increase was possibly the result of a brief influx of swans from small populations which winter further east in the Fraser valley (Sean Boyd pers. comm.) and migrate out to the coast when the lakes and marshes they normally winter on begin to freeze over.

Average arrival and departure rates (in swans/hour) were much lower on the marsh than on upland habitat (Figure A.1.3). This indicates that rates of movement between the marsh and upland habitat not accounted for by diurnal migration were low. The relatively high arrival and departure rates on upland habitat probably reflected movement between different upland habitats. Some of the variability in total numbers recorded on upland habitat may have resulted from this movement.

Five neck-collared swans (four Trumpeters and one Tundra) were observed in 1993/94 (Table A.1.1); no individually marked swans were seen in 1994/95. Individual 25T is the offspring of individual 42AK. Four of the five marked swans showed strong site fidelity to specific upland locations (when they were sighted, they tended to be on the same fields). Three of the five showed, at least within a given month, a tendency to use upland habitat on a consistent basis. It is not possible to determine if, for the rest of the observations, the apparent lack of such a tendency was a reflection of lower "sightability", or of lower fidelity to upland habitat. Large flocks, rain, poor lighting and large distances were not conducive to spotting marked individuals, and some or all of these conditions predominated during observations. Given that mortality rates are low in Trumpeter Swans (Anderson et al. 1991), the fact that none of the marked swans observed in the first year of the study showed up in the second year may indicate very weak wintering site fidelity between years.

For management purposes, and when drawing inferences about a population, it is important to define the population of interest. In particular, it is important to know whether or not the population is closed. Vickery et al. 1995 described distributional patterns in Brent Geese as a process of habitat switching, which implied that individuals were moving between habitats over time. This in turn implicitly assumed a closed population, though support for the acceptance of this premise was not offered.

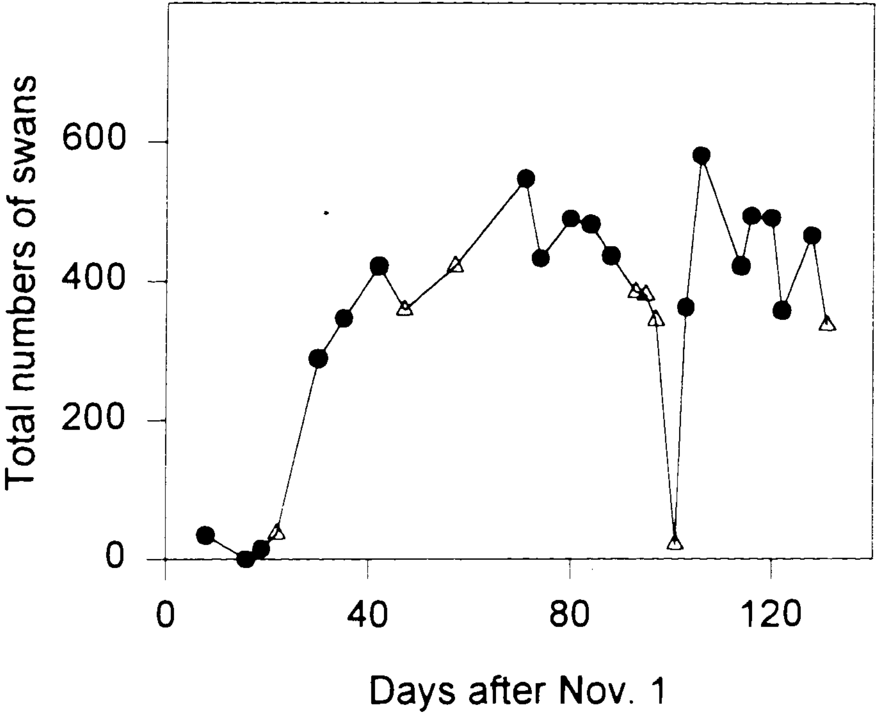
Whether or not a population is closed can only be established through the empirical measurement of immigration and emigration rates, requiring marked individuals. In the present instance, since habitat use is diurnal and the investigation is restricted to upland habitat, these effects would actually be interpreted as measurements of day-time fidelity to upland habitat.

Total numbers of swans using upland habitat remained reasonably constant over the course of each winter. Deviations from constancy were brief in duration (Figure A.1.1) and could be attributed either to displacement from upland habitat (in the case of cold temperatures), or to the influx of what may be considered transients (as a result of cold-weather migration and the onset of spring migration). It can be inferred from the low arrival and departure rates on the marsh that day-time movement (that which is not attributable to diurnal migration) between the marsh and upland habitat was minimal (Figure A.1.3). These observations, in combination with anecdotal evidence from sightings of marked swans (Table A.1.1), suggest that there may be a strong tendency for the same individuals to return to upland habitat on a regular basis. It is therefore possible, though currently untestable, that swans using upland habitat may be interpreted as a closed population.

Air count data (which give highly accurate measurements of abundance due to the rapidity of the surveys and the low probability of missing swans) for the years 1987/88 to 1991/92 (S. Boyd, unpubl. data) show reasonable constancy in total numbers of swans in the Fraser delta within each winter. Some of the variability in total numbers is possibly the result of "edge effect" in the surveys (S. Boyd, pers. comm.). Abundance patterns on upland and marsh habitats form almost perfect mirror images of each other. These observations suggest that swans in the Fraser delta in general may comprise a closed population, and because most of the variability in total numbers on each habitat probably occurred during cold weather, this supports the conclusion that swans using upland habitat may comprise a closed population as well.

Figure A.1.1. Trumpeter Swan abundance on upland habitat over the two winters of the study (1993/94 and 1994/95). Open triangles correspond to days with low temperatures below freezing, open circles to days with accumulated snow in addition to freezing temperatures, and closed circles to days with low temperatures above freezing.

(A) 1993/94



(B) 1994/95

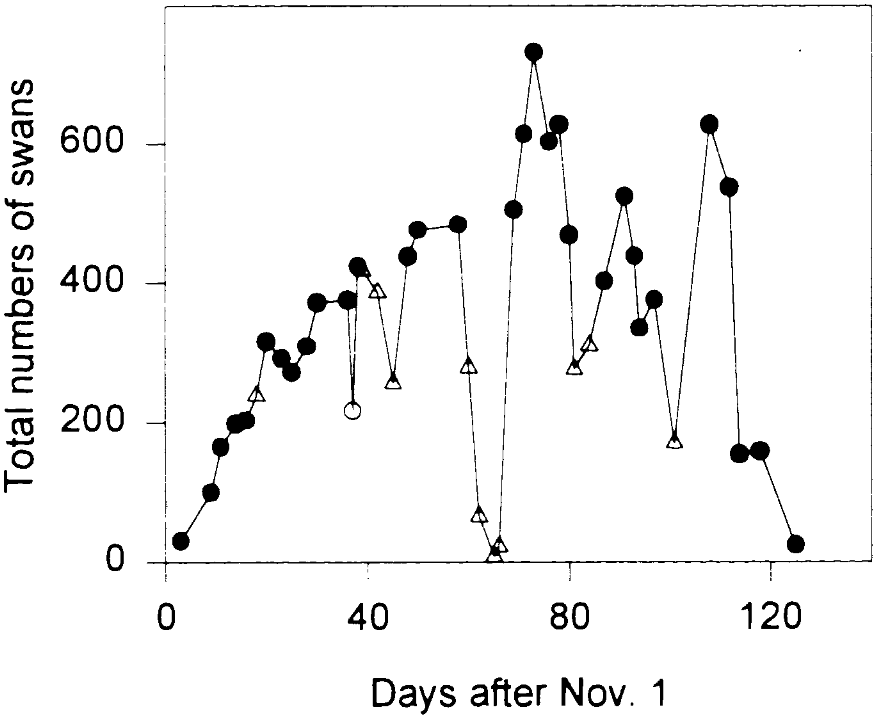


Figure A.1.2. Daily minimum temperatures (in degrees Celsius) over the two winters of the study (1993/94 and 1994/95).

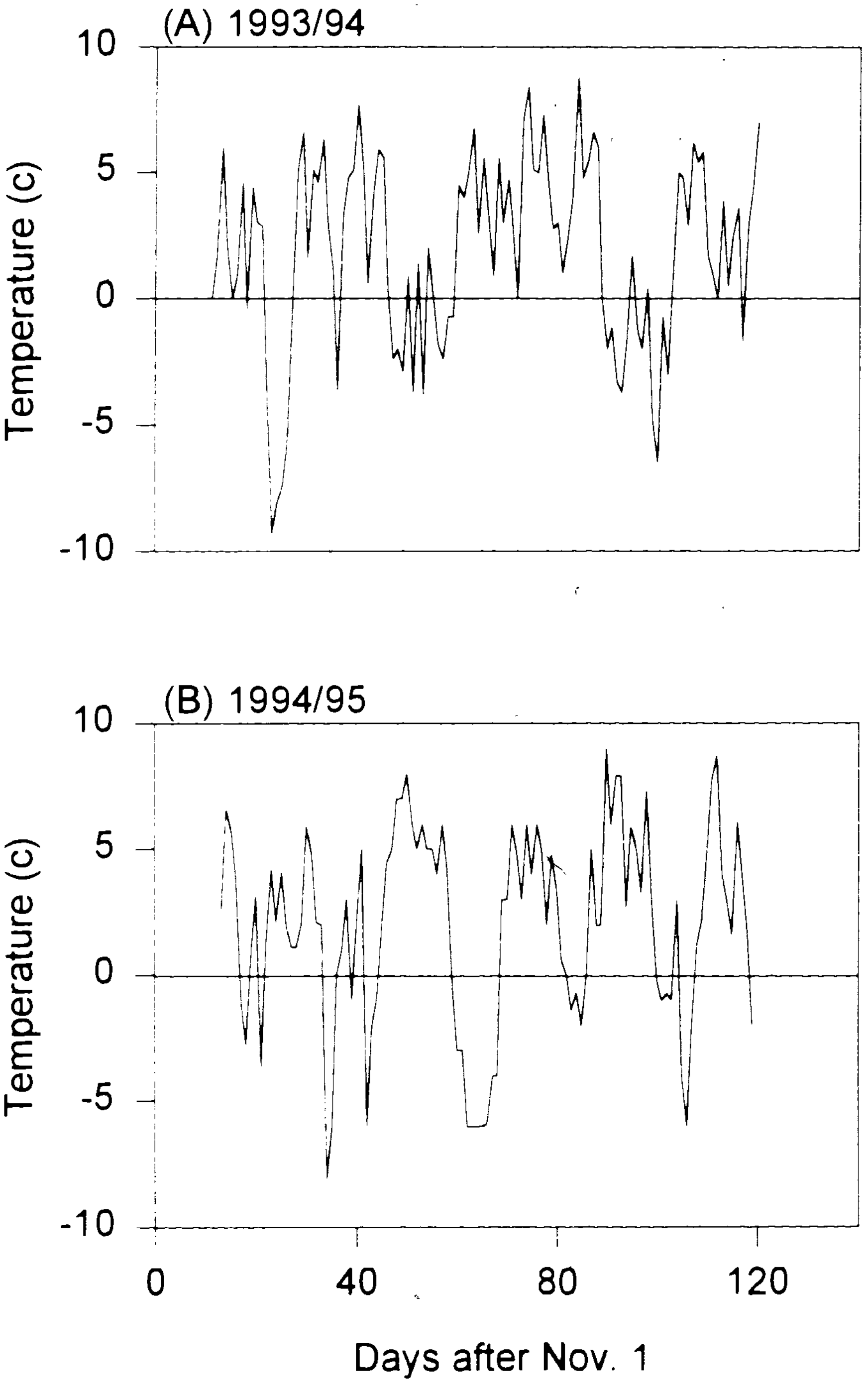
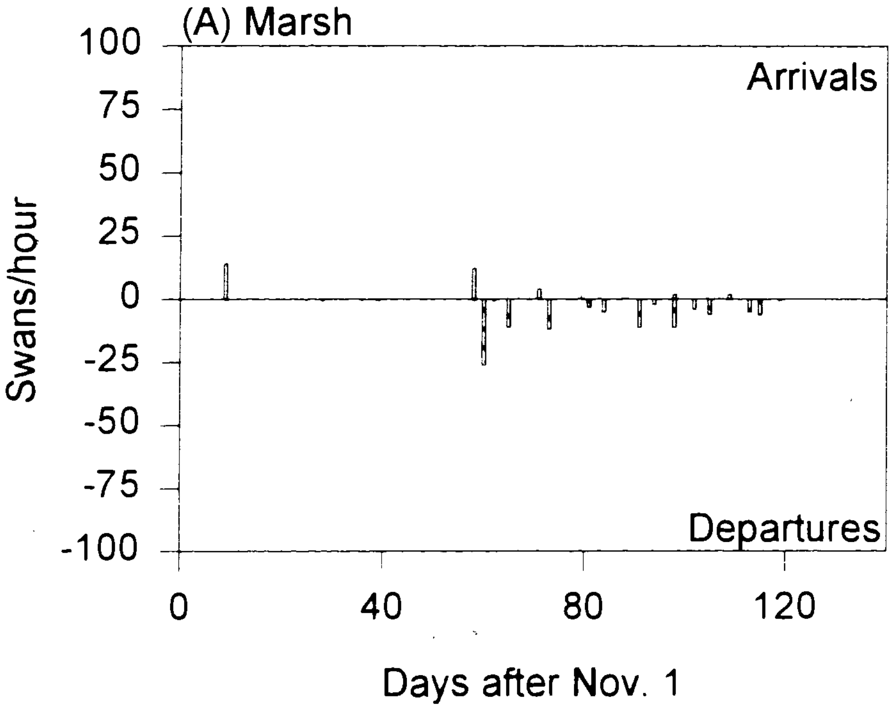

(A) 1993/94
Temperature (c)
10
5
0
-5
-10
(B) 1994/95
Temperature (c)
10
5
0
-5
-10
0
40
80
120
Days after Nov. 1

Figure A.1.3. Average arrival and departure rates on marsh and upland habitats (1994/95). Values were derived from 15-minute daytime observation bouts, and represent movement which is not attributable to diurnal migration.


(A) Marsh
Arrivals
Departures
Swans/hour
100
75
50
25
0
-25
-50
-75
-100
0
40
80
120
Days after Nov. 1

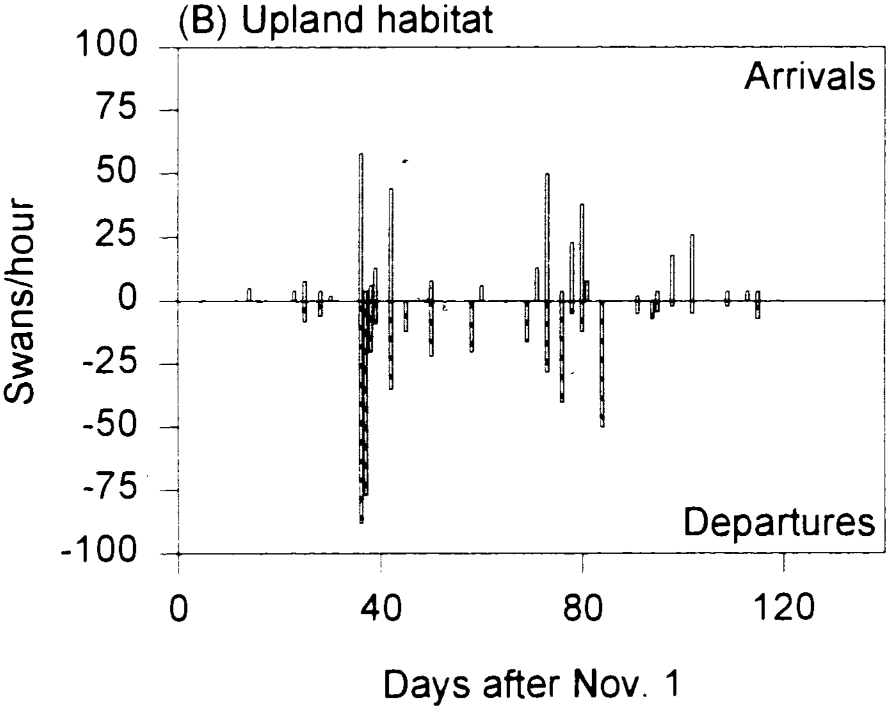

(B) Upland habitat
Arrivals
Departures
Swans/hour
100
75
50
25
0
-25
-50
-75
-100
0
40
80
120
Days after Nov. 1

Table A.1.1. Sightings of individually marked swans, 1994. Codes were read from neck collars. Individual 25T is the offspring of individual 42AK.

Individual	**Sighting date**	**Field**
KO23 (Tundra adult)	Jan.13	212
	Jan. 23	99
	Feb. 3	31
	Feb. 15	60
25T (Trumpeter juvenile)	Jan. 13	31
	Jan. 19	99
	Jan. 23	99
	Jan. 27	31
	Jan. 31	31
	Feb. 3	31
	Feb. 15	31
	Feb. 16	31
	Feb. 17	33
	Feb. 22	31
	Feb. 24	33
	Feb. 28	31
	Mar. 2	31
42AK (Trumpeter adult)	Jan. 13	31
	Jan. 23	99
	Jan. 27	31
	Jan. 31	31
	Feb. 3	31
	Feb. 14	33
	Feb. 15	31
	Feb. 16	31
	Feb. 17	33
	Feb. 22	31
	Feb 24	33
	Feb. 28	31
	Mar. 2	31
24PN (Trumpeter adult)	Jan. 19	31
	Feb. 3	60
	Feb. 14	31
	Feb. 16	31

	Feb. 17	33
	Feb. 24	35
	Feb. 28	38
	Mar. 8	640
2C4 (Trumpeter adult)	Jan. 31	31
	Feb. 3	33
	Feb. 22	31
	Feb. 24	33
	Feb. 28	38

Appendix 2. Proximate measures of habitat quality.

Figures A.2.1 to A.2.8 summarize measurements of percent protein, percent fiber, and biomass for fields sampled in 1994/95. Field numbers and crop types are indicated on individual figures. Field 128, 168, 60 and 65 were sampled using stratified random sampling methods; confidence intervals reported are not true 95% confidence intervals. Fields 33, 45, 21, and 75 were sampled using regular random sampling methods; true 95% confidence intervals are reported. Note that a different y-axis scale is used in the representation of biomass for potatoes (Figure A.2.8), because of the much higher initial values in comparison to the other fields. The dotted line on the biomass figure reflects the observation that surface potatoes were depleted by approximately day 80, prompting the switch to feeding on sub-surface potatoes.

Figure A.2.1. Field 128 (early planted winter wheat)

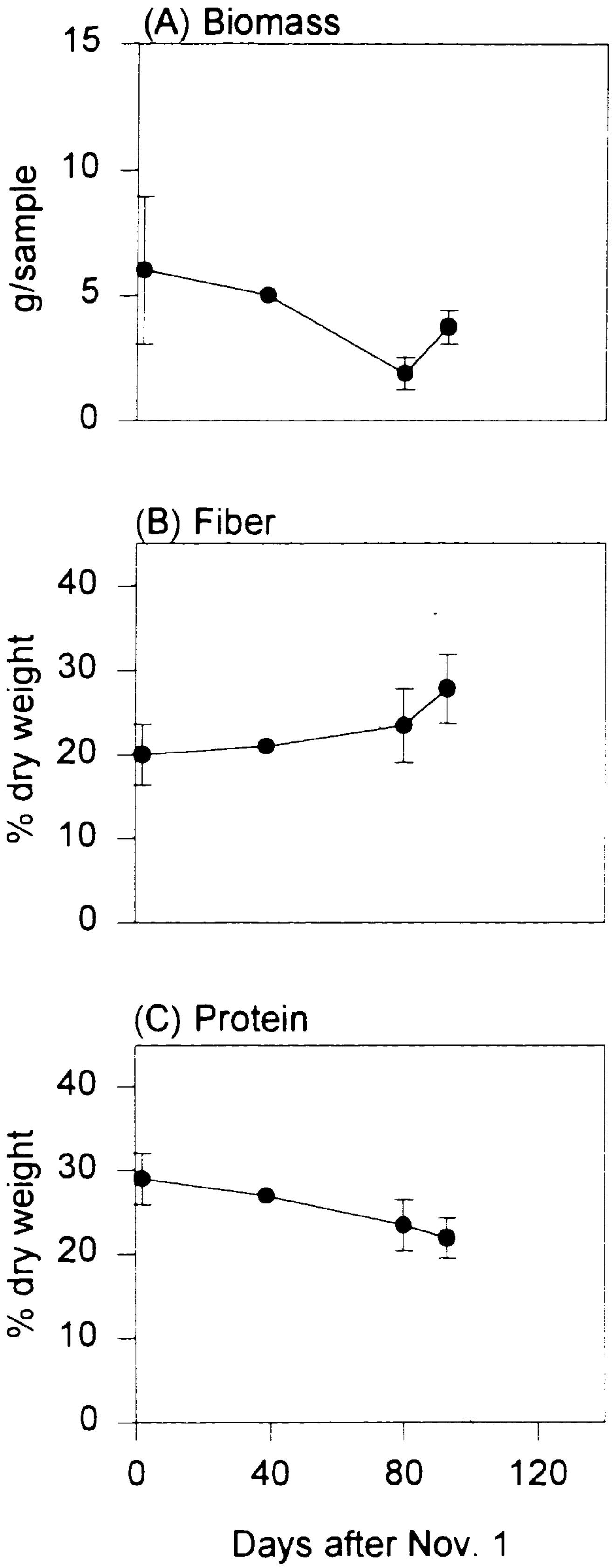


Figure A.2.2. Field 168 (early planted winter wheat)

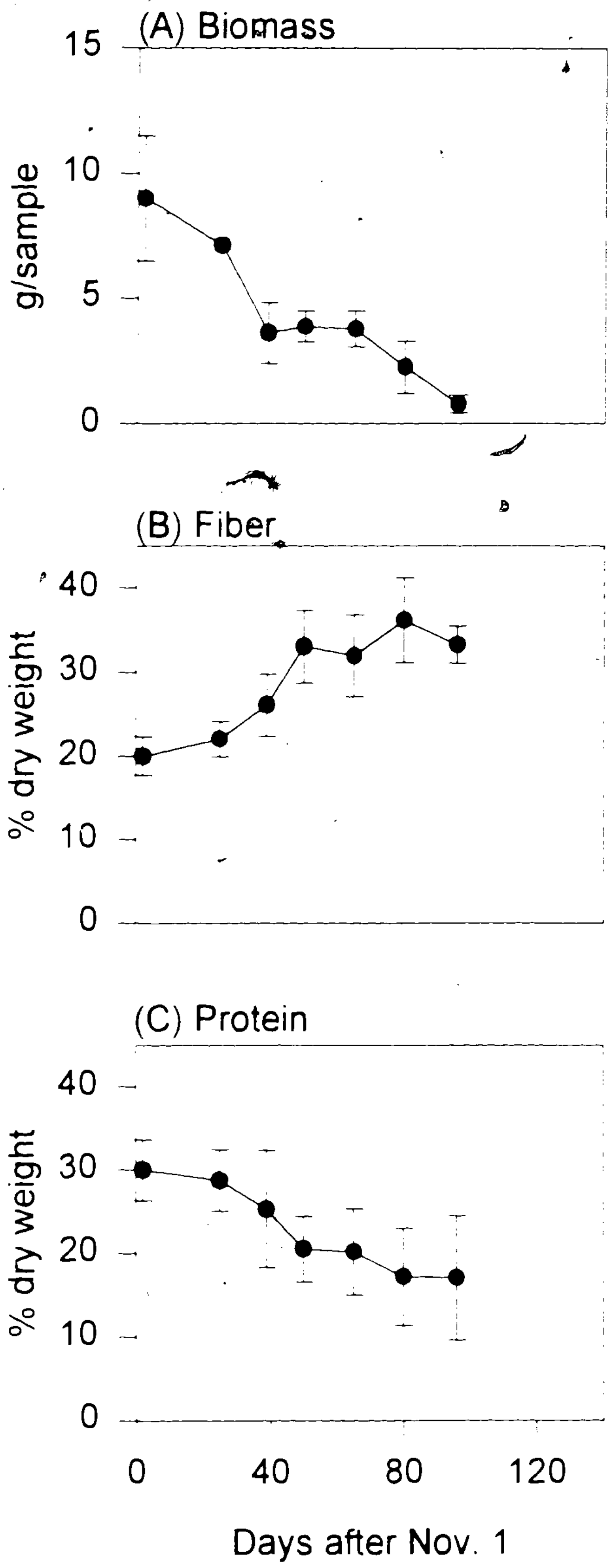


Figure A.2.3. Field 33 (late planted winter wheat)

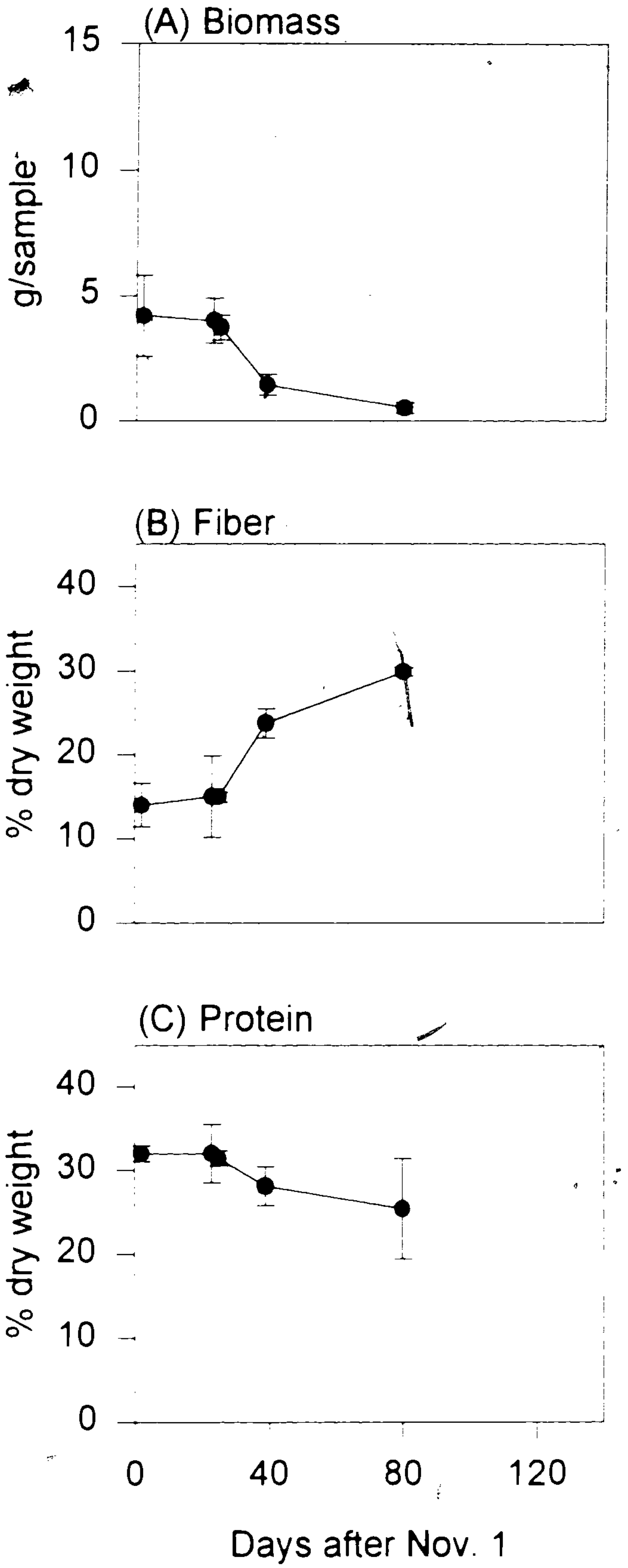


Figure A.2.4. Field 45 (late planted winter wheat)

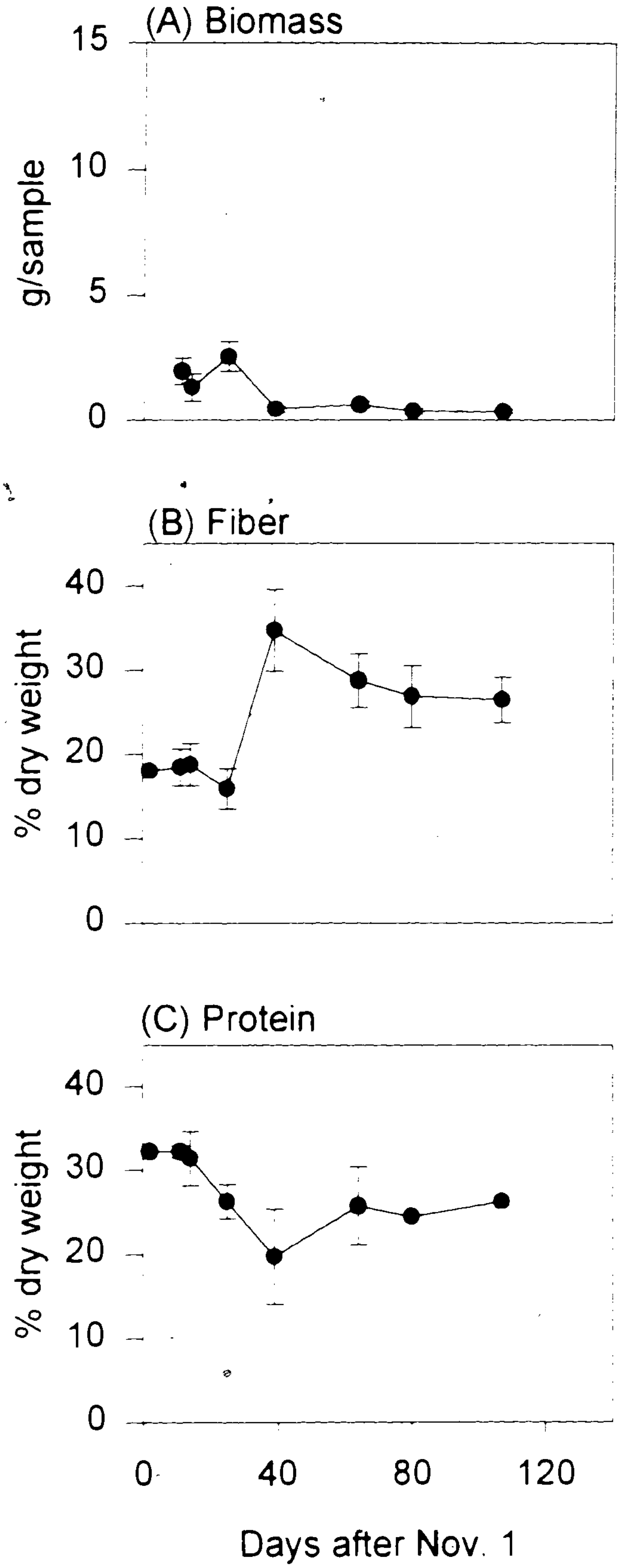


Figure A.2.5. Field 21 (early planted winter wheat)

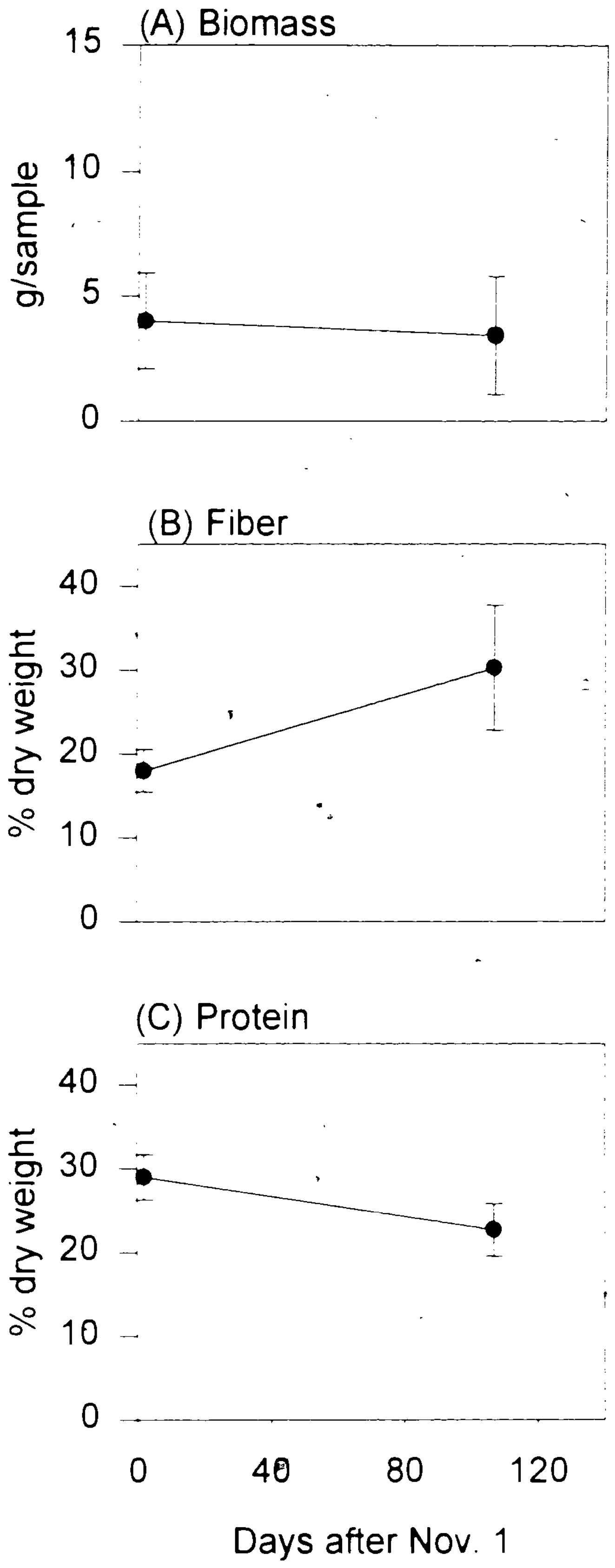


Figure A.2.6. Field 60 (late planted winter wheat).

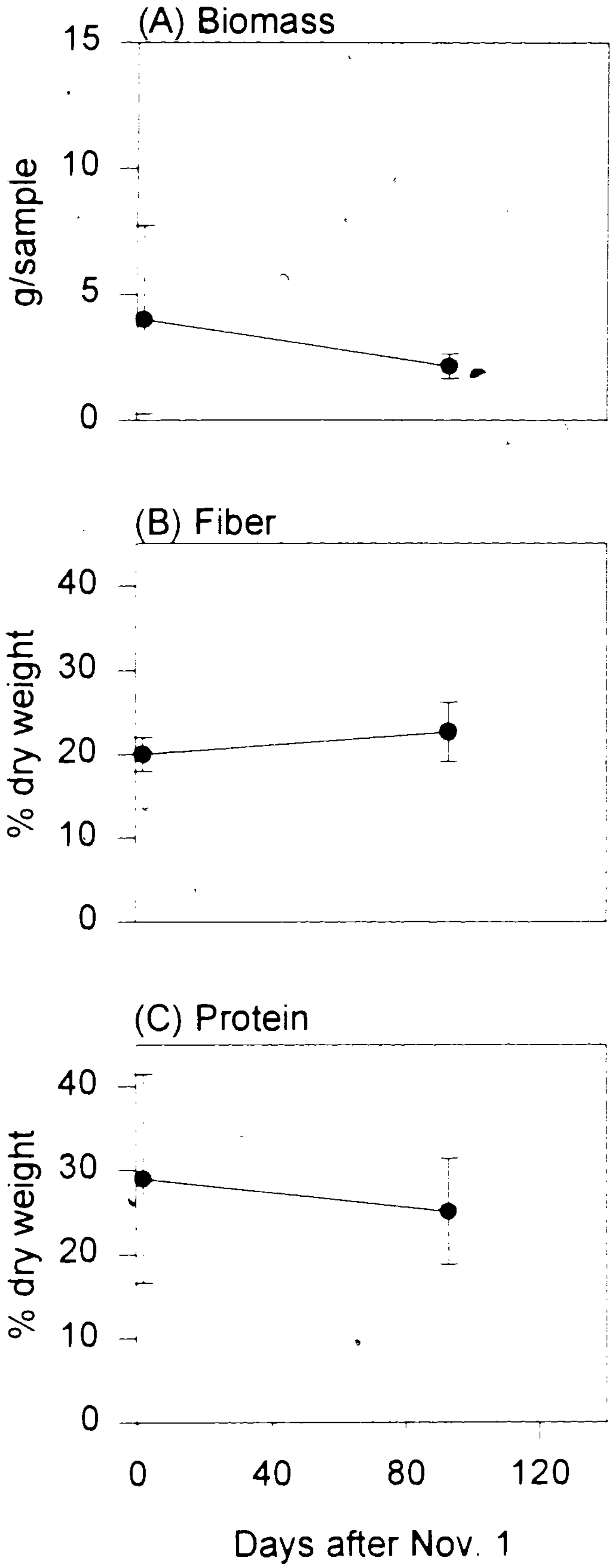


Figure A.2.7. Field 65 (early planted winter wheat).

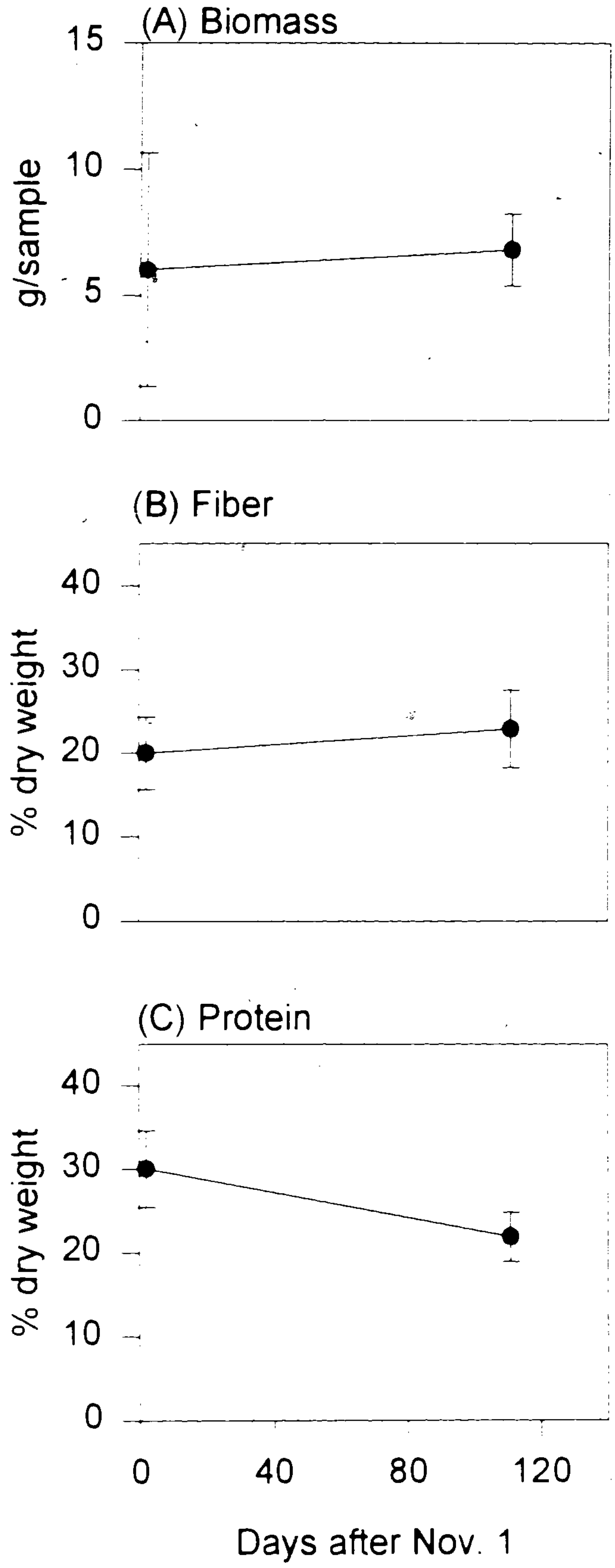
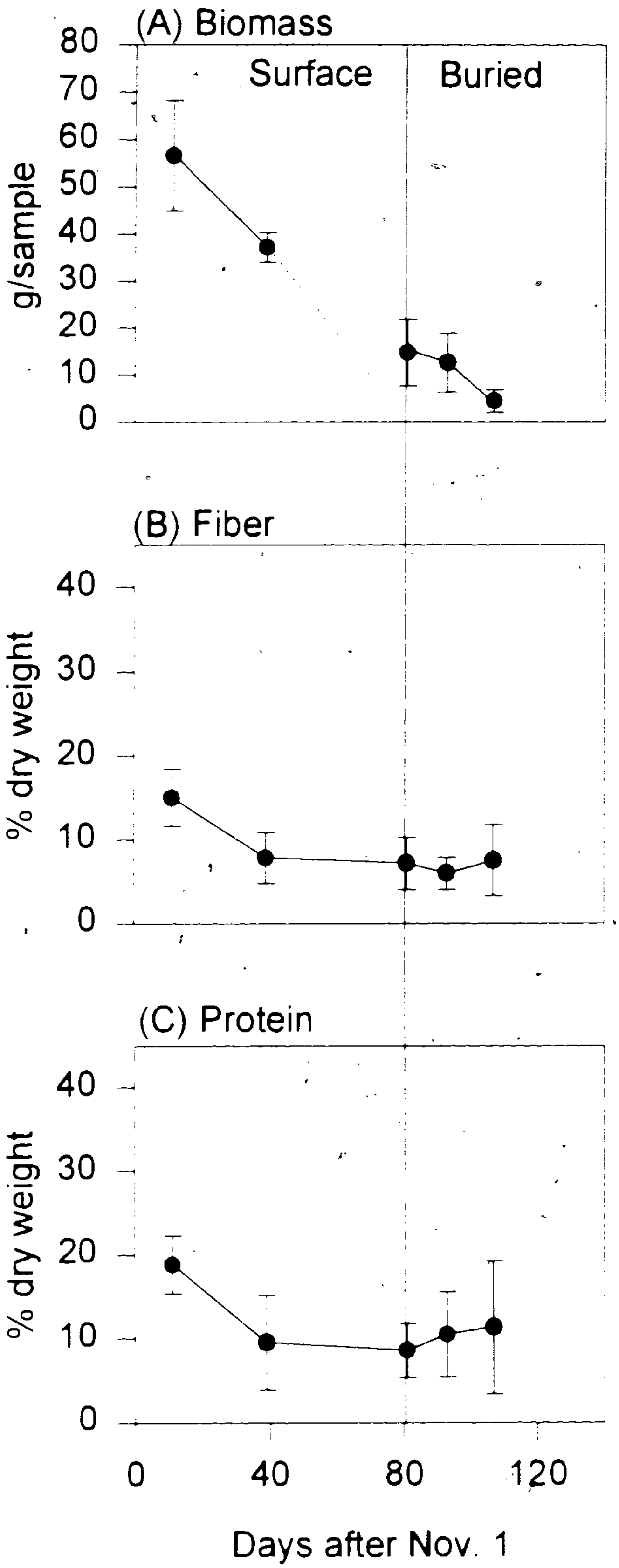


Figure A.2.8. Field 75 (potato).



Allemande

Dedicated to PJ Fairfield-Carter

B. Fairfield-Carter