Studies of the goosander Merqus merganser

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STUDIES OF THE GOOSANDER *Mergus merganser*

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No work contained in this thesis has been submitted elsewhere for another degree. Work carried out under contract to the Nature Conservancy Council is clearly defined and reports arising are quoted in the reference list.

ABSTRACT

This thesis describes a series of studies to investigate the predator-prey relationships between the Goosander *Mergus merganser*, a fish-eating duck, and populations of game fish in northern Britain.

The distribution and numbers of birds during the breeding season, in northern England and Scotland, were investigated and variations in density, between and within rivers, studied. Relationships between densities in spring and summer survey periods were also investigated. Possible biases in survey data are discussed.

Studies of the growth of ducklings reared in captivity allowed estimates to be made of food and energy requirements from hatching up to approximately the time of fledging, at c70 days. Seasonal changes in the body mass and body condition of adult and immature Goosanders were investigated and daily and seasonal food and energy requirements estimated.

Time-budget data were collected to investigate how birds partitioned their time between various behaviours. Of particular concern was the temporal and spatial distribution of foraging activities between and within broad habitat types, viz. rivers, standing waters known to be roost sites, and non-roost standing waters. Feeding behaviour was also recorded.

The species composition of the diet and the numbers of individual fish represented, were determined by the gut analysis of 54 birds received from various sources. Possible biases in this method are discussed. For salmonids, the size of individual prey items was investigated from regression equations of fork length on vertebrae length, based on a reference collection.

Conflicting evidence of damage to fisheries from other studies, chiefly in north America, is re-assessed in the light of current knowledge of the population dynamics of salmonids and of results presented here. The potential contribution of depredations by Goosanders to mortality at successive life stages of fish is considered.

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INTRODUCTION

This thesis describes a series of studies leading to estimates of the potential impact of depredation by a fish-eating duck, the European Goosander, *Mergus merganser merganser*, on game fish populations in several river systems of northern Britain.

The genus *Mergus*, of the tribe *Mergini*, family Anatidae (Delacour 1954), contains seven species and shows within it a gradation from the more generalised and typical 'duck' bill of the Smew *Mergus albellus*, through the elongated bill of the Hooded Merganser *Mergus cucullatus*, to the long, thin, tapering saw-bill, unique amongst waterfowl, of the larger and more specialised members of the genus.

The Goosander, the largest species, has a circumpolar distribution occurring as a breeding species throughout North America, Europe, and Asia. Over that range three distinct and non-overlapping subspecies are recognised;-

Mergus merganser merganser	European Goosander
Mergus merganser americanus	American Merganser
Mergus merganser orientalis	Asiatic Goosander

To avoid confusion due to nomenclature the European Goosander and the American Merganser will henceforth be termed 'Goosander'. 'Merganser' will be used only in reference to the Red-breasted Merganser *Mergus serrator*.

Background

Perhaps because its members were not considered as game/quarry species, the genus was the subject of little scientific study until the work of White (1936, 1937, 1939, 1957), Munro and Clemens (1937, 1939), and Elson (1950, 1962) in North America. These studies investigated diets, and focussed attention on the possible role of the Goosander, and Merganser, as predators of young salmonid fish (*Salmo* spp.). Results showed a wide variation in the percentage of all fish eaten that were salmonids, from 5% in the Nova Scotian rivers of the Bay of Fundy to 91% in the Cape Breton drainage system (White 1957). Findings are considered in detail in succeeding chapters.

In a supplement to his paper, Elson (1962) provided recommendations, based on studies made by the Fisheries Research Board of Canada and the Canadian Wildlife Service, on Goosander control. For Maritime streams with 'average' smolt production, "the maximum benefit [to smolt escapement] is likely to be obtained when [Goosanders] are reduced to a level of one bird per 15 miles of stream 10 yards wide." Whilst predator control has been shown to allow increased escapement of smolt (White 1937, Elson 1962), no increases in the number of returning adult fish from those cohorts has been reported attributable to predator control.

On the basis of their work in British Columbia, Munro and Clemens (1937) concluded that "A general reduction of [Goosanders], on the assumption that at some time or in some place they may cause losses of trout or salmon, is considered an unsound and unwarranted procedure." These, and other workers have stressed the need for each case to be examined independently since it is clear from a review of published studies that individual water courses show wide variation in the importance of salmonid species as constituents of the diet of the Goosander. This is a result of differences in the physical characteristics of the various areas where studies have been carried out which influence the diversity, abundance and availability of the fish species present.

The only detailed study of the diet of sawbill ducks to be carried out in Great Britain is that of Mills (1962a). He examined the gut contents of 147 Goosanders, and 148 Mergansers, from a range of Scottish rivers. He reported the percentage occurrence of salmonid remains as 86.1% and 75.2% respectively. In addition, bird densities, at least on the rivers Bran and Meig, were considered sufficiently high that control would result in increased smolt production. This has not been tested. Aside from that study little work has been published on the Goosander in Britain, with the exception of the results from various surveys (eg. Mills 1962b, Parslow 1967, Sharrock 1976, Lack 1986), and of a ringing programme in north-east England (Meek and Little 1977a, 1977b). These broadly delimit the incidence of Goosanders on inland waters.

Whilst many authors have shown overlap between the feeding and breeding areas of sawbills and areas where juvenile salmonids occurred, the relationship between the density of predator and prey were not investigated. Do these birds concentrate in areas of high prey availability, for example? During the course of the present study a series of papers was published which addressed this issue (Wood 1985a, 1985b, 1986, 1987a, 1987b, and Wood and Hand 1985). These reported the results of investigations to determine the daily, and seasonal, abundance of the Goosander on salmon producing waters of Vancouver Island, British Columbia, in relation to the density of both conspecifics and juvenile salmonids. Their findings are considered in detail in Chapter Five, but, in summary, showed that large feeding flocks occurred on streams where juvenile salmonid density was enhanced. Wood (1986) also showed that the estimated number of broods on a stream was highly correlated with both drainage area and juvenile salmon production, and postulated a "food assessment" hypothesis whereby breeding pairs chose a nesting area on the basis of prey availability during the nesting season. Similar analysis was carried out in this study for the Tweed system in 1984 (Carter and Evans 1985).

Aspects of breeding biology

The breeding biology of the Goosander is poorly studied and documented in Britain.

Birds typically return to breeding rivers in the early spring (late February/early March in Northumberland) when pair formation is usually complete (Cramp and Simmons 1977). However, communal courtship is commonplace from December until the beginning of the breeding season and has been observed in this study both on breeding rivers and standing water bodies where copulation has also been noted.

No territorial behaviour was noted in this study at any stage of the annual cycle. Cramp and Simmons (1977) report that females may be gregarious on the breeding grounds, both searching for nest sites together and nesting in the same tree. The absence of such behaviour in the study areas used here may be due to the low density of potential breeding pairs, although in areas of high density Geroudet (1985) reports competition for nest sites occurring but does not invoke territoriality.

The distribution of breeding pairs within a given waterway will be influenced by nest site availability and available food resources sufficient to support not only the nesting pair (principally the female) but also the brood. Disturbance must also be considered. Goosanders in north-east England, on the Tyne river system, were noticeably more wary than those in the north-west (River Lune), a feature which may be attributable to different levels of persecution. This is less evident on the latter river (Briggs pers.comm.).

It is likely therefore that the breeding density of Goosanders will vary between sites on a local, regional and national level. These aspects were examined using data collected during the 1984 Goosander and Merganser Survey of Scotland (Carter and Evans 1984), and during contract work undertaken in 1986 (Carter and Evans 1986). Results are presented in Chapter One.

Ringing and wing-tagging of flightless juvenile Goosanders caught at several sites in Northumberland in July and August annually since the late 1960's, have shown a general dispersion throughout the County and into the Border region and southern Scotland (Meek and Little 1977b). A similar pattern was shown by 71 recoveries from 623 Goosanders ringed on Cape Breton Island (1965-1968) (Erskine 1972). Few moved more than 50 miles from their natal streams in September and October, but subsequently were found to 'range somwewhat more widely' outside that landmass. Unfortunately the ages of the birds when recovered are not given to allow a direct comparison to be made with the work of Meek and Little (1977b).

Seasonal movements of females are largely unknown since the number that have been marked is small, and recoveries few. They are generaly considered to be fairly sedentary, however (Little pers.comm.).

Movements of adult males are better understood. In north-east England and the Borders region adult males typically leave the breeding rivers in May and congregate in a pre-moult assembly at Hoselaw Loch, near Coldstream. Up to 200 drakes, mainly adults assumed to have completed breeding activities, have been noted there in recent years although the timing and size of the peak count is dependent on the timing and spread of the breeding season. In a 'good' season, the flock steadily builds up to a peak in mid/late May, but in a 'late' season, such as 1983, no notable assembly occurs. In all years the site is vacant by mid-June.

Ringing recoveries from a cannon-net catch of 39 drakes in 1984 confirmed the existence of a moult migration to the Tana estuary in north Norway (Little and Furness 1985) which had previously only been suspected on the basis of a small number of unsexed recoveries from that area of birds ringed in Northumberland (Meek and Little 1977b). These birds return to Britain in October/November. Little and Furness (1985) consider this general pattern to hold true for all British Goosanders. Survey data presented here provide circumstantial evidence that this might be the case since the incidence of adult males in the summer is very low in Scotland. Tyler (1985) also records the departure of males from breeding rivers in May in Wales. More extensive ringing studies outside those being carried out in north-east England are needed.

In winter Goosanders occur to a much greater extent on standing water bodies of all types. Time-budget data, presented in Chapter Three, suggest that although the birds may be present for long periods on these waters, they do not feed extensively there and therefore probably regularly commute to river feeding sites. Data from Hoselaw Loch would suggest that the birds leave the 'roosting water' at, or before dawn, and return there in the late morning. A similar pattern is mentioned by Thom (1986).

Licencing and policy

In Great Britain the controversy surrounding the impact of sawbill ducks, in particular the Goosander, on populations of freshwater fish (specifically juvenile salmonids, Atlantic Salmon _Salmo salar_, and migratory (sea) trout _Salmo trutta_) is a relatively recent one, for it is little over a century ago that the Goosander was first confirmed to be breeding here. Full details of this colonisation are presented in Appendix One with an appraisal of population trends in the western Palearctic.

The Wild Bird Act (1954) afforded both this species and the Merganser, legal protection in England, Wales and Northern Ireland and required that anyone wishing to kill these species first had to provide evidence of 'damage to fisheries interests' on which the licencing authority could make a decision whether or not to issue a licence to kill. Since Scotland was outside the area of legislative protection, no licences were required to shoot Goosanders and Mergansers there and widespread "control" measures were taken. The situation remained unchanged until the introduction of the Wildlife and Countryside Act 1981 which gave the Goosander (and Merganser) protected status nationwide. Licences for control were then also required in Scotland.

Before a licence is issued the licencing authority should be convinced that the applicant has supplied adequate evidence of "serious" damage to fisheries interests in past seasons, or of anticipated "serious" damage in the current season to which the licence will apply. The nature of the evidence required and the term "serious damage" have not been defined and are therefore entirely subjective. The form titled "APPLICATION FOR LICENCE FOR THE CONTROL OF BIRDS HARMFUL TO FISHERIES IN SCOTLAND", prepared by the Department of Agriculture and Fisheries for Scotland (D.A.F.S.) provides less than three lines for this evidence to be presented.

Applications are submitted directly to the appropriate licencing authority who consider the evidence as presented. Before any decision is made on whether to grant the application, the authority has a statutory requirement to consult the Nature Conservancy Council (N.C.C.). This is the national governmental advisory body, basing its advice, with respect to individual licence applications, on current information on sawbill populations and distribution on that river, or in that region. The licencing authority is not, however, bound to accept recommendations made by N.C.C. as to the suitability and appropriateness of issuing a licence for a particular site, and it effectively remains, therefore, an autonomous organisation.

On the basis of information submitted on the appropriate forms no licences have been issued in England, Wales or Northern Ireland, although the number of applications has been small. In Scotland, however, licences have been granted annually by D.A.F.S. since 1981 to riparian owners and district Salmon Fishery Boards for the control of Goosanders, Red-breasted Mergansers and Cormorants (Phalacrocorax carbo).

In Scotland the licencing policy after 1981 was initially liberal, so that the situation as it stood prior to the Wildlife and Countryside Act 1981 was effectively maintained, although clearly this time with official sanction. In the absence of (a) a rigourous definition of "serious damage", (b) accurate data on the actual population size and distribution of sawbills in Scotland (and elsewhere in Great Britain), and (c) detailed studies of potential impact on fisheries, such a policy has "a large groundswell of opposition" (Mills 1987), having been widely and publicly criticised. Tighter controls on the issue of licences have been called for until such times as these data are available.

The current study

Against this background a three year study was carried out, between 1982 and 1985, of the feeding ecology and behaviour of the Goosander in the Border counties of northern England and southern Scotland. This was designed to investigate the predator-prey relationship between Goosanders and game fish, and to re-assess the conflicting evidence of damage to fisheries presented by White, Elson and others, in the light of current knowledge of salmonid population dynamics, and using data on predator ecology presented herein. The study was augmented by contracts from N.C.C. to conduct (a) the 1984 Goosander and Merganser Survey of Scotland (Carter and Evans 1984), (b) a desk study to integrate current knowledge of salmonid population dynamics with the number and distribution of sawbills in Scotland as shown by (a), (Carter and Evans 1985), and (c) a detailed study of sawbill populations and diet over the period of the smolt run (April to June) on the River North Esk, Tayside (Carter and Evans 1986).

This thesis therefore describes investigations of various aspects of the ecology of the Goosander by considering several factors which determine the potential impact of this predator on populations of its prey species, viz.

(i) the distribution and numbers of predators

(ii) the food requirements of the predator during growth and between seasons

(iii) the temporal and spatial distribution of its feeding activities

(iv) the composition of its diet

(v) the population dynamics of prey species.

These aspects are considered in the succeeding chapters, with overall conclusions finally drawn together to assess the potential impact of the Goosander on populations of commercially important game fish.

CHAPTER ONE ;

THE DISTRIBUTION AND NUMBERS OF THE GOOSANDER IN SCOTLAND

1.1.0 INTRODUCTION

A basic requirement for an accurate assessment of the potential impact of a predator on populations of its prey, is to know how both predator and prey are distributed in space and time, taking account, where appropriate, of age and sex differences.

From 1984-1986 I made attempts to determine both the numbers and distribution of Goosanders in Scotland during the breeding season, and to investigate between-river and within-river variations in bird density.

The numbers and distribution of both Goosanders and Mergansers were poorly known in Scotland until recently. Mills (1962b) used data collected from (a) published sources (Baxter and Rintoul (1922, 1953), Berry (1936, 1939), Venables and Venables (1955)), (b) the nest record scheme of the British Trust for Ornithology (B.T.O.), and (c) personal observations and those of friends and colleagues, to compile a map of the breeding distribution of both species in Scotland (for Goosander, see Figure 1.1). The publication in 1976 of "The Atlas of Breeding Birds in Britain and Ireland", (Sharrock 1976), provided the first comprehensive survey of the breeding distribution of Goosanders and Mergansers.

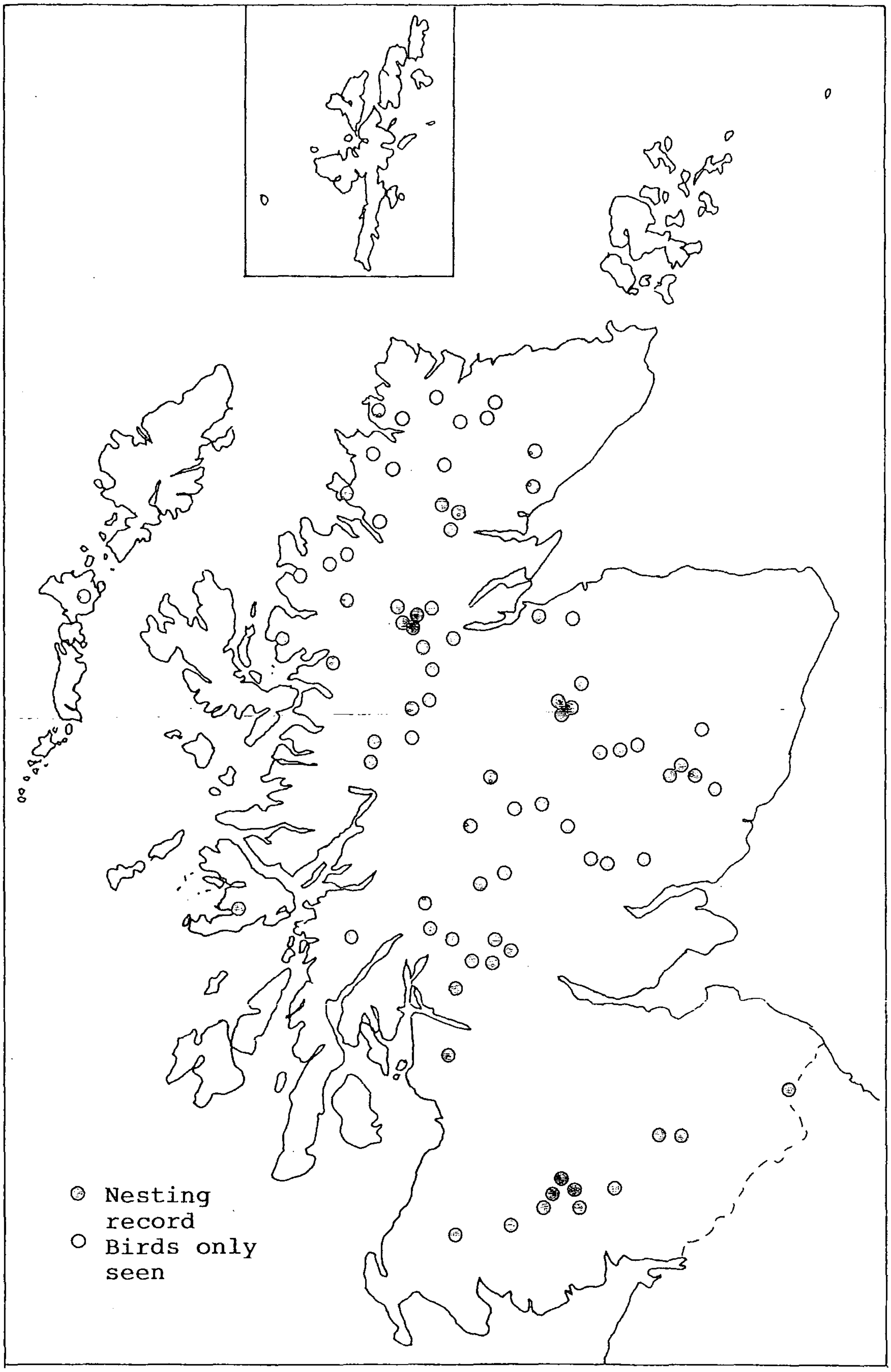


Figure 1.1 ; Breeding distribution of the Goosander in Scotland (Mills 1962a)

This was based on the results of fieldwork carried out across the country from 1968 to 1972, by amateur and professional ornithologists, using the 10km squares of the national grid as the basic geographical recording unit. From the total of 3,862 10km squares, all of which were surveyed, the Goosander was recorded in 412, and breeding was confirmed in 204 (Figure 1.2).

Since 1976 the range of the Goosander within Great Britain has continued to expand, particularly in north-west England and Wales. Populations within the latter principality have been studied by the Royal Society for the Protection of Birds (R.S.P.B.), and at least a 10 fold increase in the number of breeding pairs was found over the period 1977 to 1985 (Tyler 1986). See Appendix One for further information.

Against this background, the N.C.C. commissioned a Goosander and Merganser survey of selected rivers in Scotland in 1984 (Carter and Evans 1984), and further more detailed work in 1985 and 1986 (Carter and Evans 1985, 1986).

1.2.0 METHODS

Information on the numbers and breeding distribution of the Goosander was collected from published sources, and from detailed survey work conducted on selected river systems in Scotland in 1984 and 1986 by both amateur and professional ornithologists who

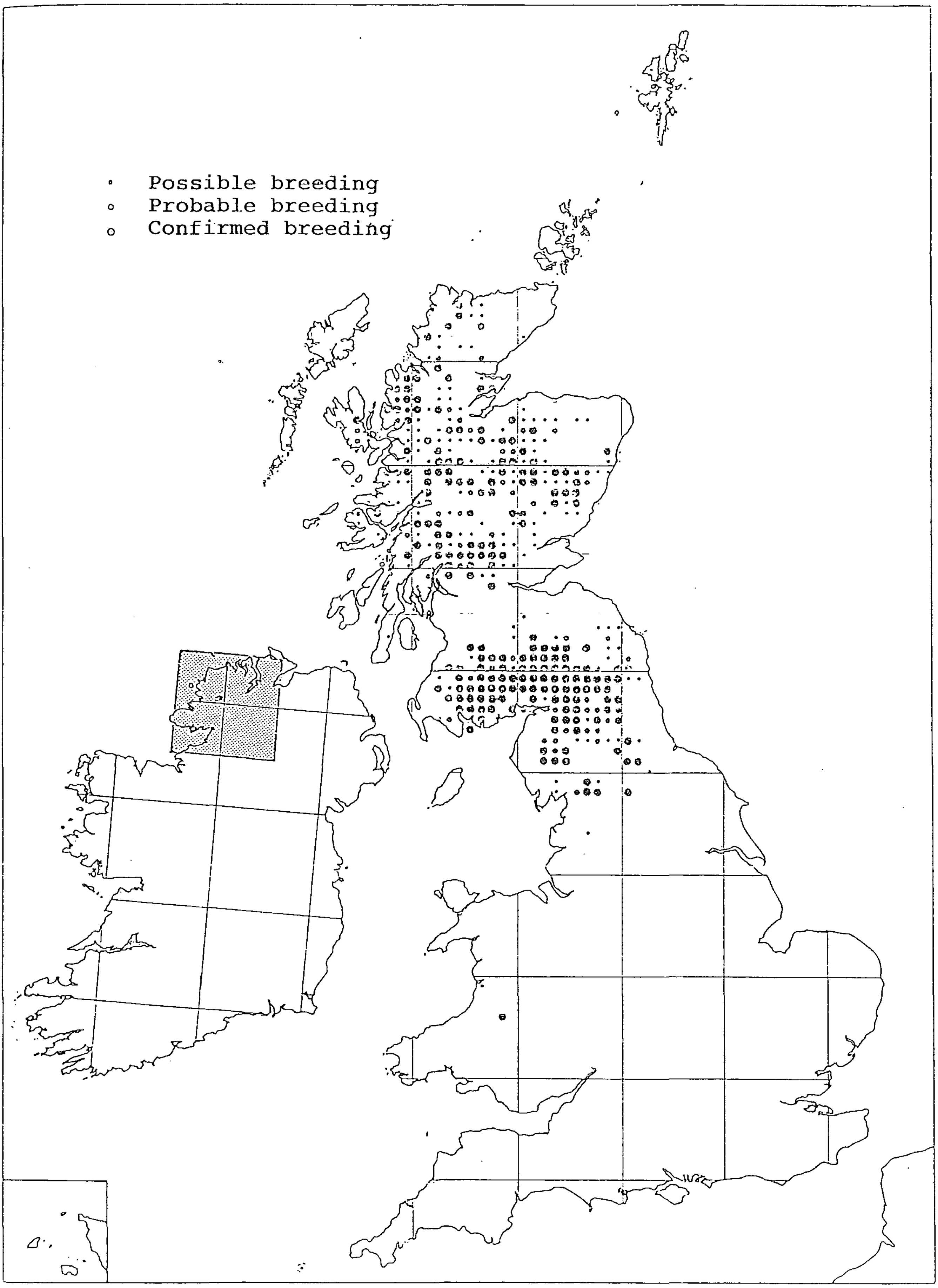


Figure 1.2 ; Breeding distribution of the Goosander in Britain and Ireland (Sharrock 1976)

used a standard methodology.

1.2.1 The 1984 Goosander and Merganser Survey of Scotland

This survey sought to determine the numbers and distribution of both sawbill species on selected river systems at two stages of the breeding season. Information was collected to provide data on between-river and within-river variations in bird density.

The survey was divided into two parts, each with a specific objective -

17-31st March 1984 - to give details of the number and distribution of potential breeding birds.

8-22nd July 1984 - to give estimates of the number and distribution of family parties as well as of other groups or individuals.

Observers were requested to achieve as great an overlap as possible in the stretches of river surveyed in the two periods. This enabled direct comparisons to be made between spring and summer counts.

Observers were instructed to survey (on foot) the maximum length of river they could cover during each of the two survey periods, rather than walking the same stretch several times. The length of river surveyed by each observer therefore differed at each site.

Goosander density was calculated as a mean value per km over the entire stretch.

To allow an assessment to be made of the accuracy of these single counts I made repeated counts of a section of the River Annan (Dumfries) during the March survey period, and a section of the River North Tyne (Northumberland) was counted several times by J.D. Uttley during the July survey.

During the March survey period, observers were asked to record separately the total number of (a) adult males, (b) immature males, and (c) 'redheads', in their survey stretch. (A 'redhead' is a bird showing no trace of male plumage; it will include adult and immature females and some immature males. See section 1.4.2.) In July, details were requested of the number of young in any broods noted and an estimate of the size of the ducklings in relation to the size of the female.

In addition to coverage carried out on foot in 1984, an aerial survey of the rivers Spey and Findhorn was undertaken at the end of the March survey period by R.H. Dennis (R.S.P.B.). The purpose of this was two-fold. Firstly, since these rivers are two of the longest in Scotland (c150 km and c90 km respectively) and flow through terrain difficult to cover on foot, it was considered that comprehensive ground counts were not feasible during a restricted time period. Secondly, an aerial count allowed, in conjunction with simultaneous ground counts of some limited stretches of each river, a comparison of aerial and ground survey methods in determining sawbill densities.

1.2.2 Survey work in Scotland in 1986

Survey work in 1986, intended to test the methodology for the 1987 B.T.O. national sawbill survey, had a more limited geographical scope than that conducted in 1984, and covered only the Tay, Tweed and North Esk river systems. More detailed recording than that used in 1984 was employed. This involved noting birds separately in each 1 km division of each survey stretch, as well as recording sex and age (where possible) as described above.

I carried out survey work on the Tweed between 24th January and 30th May with assistance from J. Richardson and others from the University of Durham, the Northumbria Ringing Group, Ray Murray, and local ornithologists, and on the North Esk from early April to the end of August, with the assistance of B. Hughes, J. Richardson, N. Atkinson and R. Goater. Data were received from coverage of the Tay in April carried out by local observers co-ordinated by R. E. Youngman.

1。3。0 RESULTS

1。3。1 The 1984 Goosander and Merganser Survey of Scotland

Figures 1。3 and 1。4 show the extent of rivers surveyed in both the spring and summer survey periods, and the mean density of Goosanders per km over each river section surveyed。 (The symbol is drawn at the centre of the section。)

1。3。1。1 Daily variation in the numbers of Goosanders recorded over the same river section

The total number of Goosanders recorded on a 16km section of the River Annan (Dumfries) during March 1984 for each of six repeat visits is shown in Table 1。1。 This shows an overall mean of 19。5 birds (SE=4。99), and demonstrates a more than five fold difference between minimum and maximum counts。

Weather over this period was generally stable but heavy rain and snow occurred between counts (3) and (4)。 Records collected by the Solway River Purification Board at Brydekirk Gauging Station (c5km dowmstream of the survey stretch) show that flow increased significantly (t=4。77) from a mean of 8。49 cubic metres per second (SE=0。37) for the days of counts (1)-(3), to 19。09 cubic metres per second (SE=2。19) for the days of counts (4)-(6)。 The mean numbers of birds recorded in the corresponding periods were

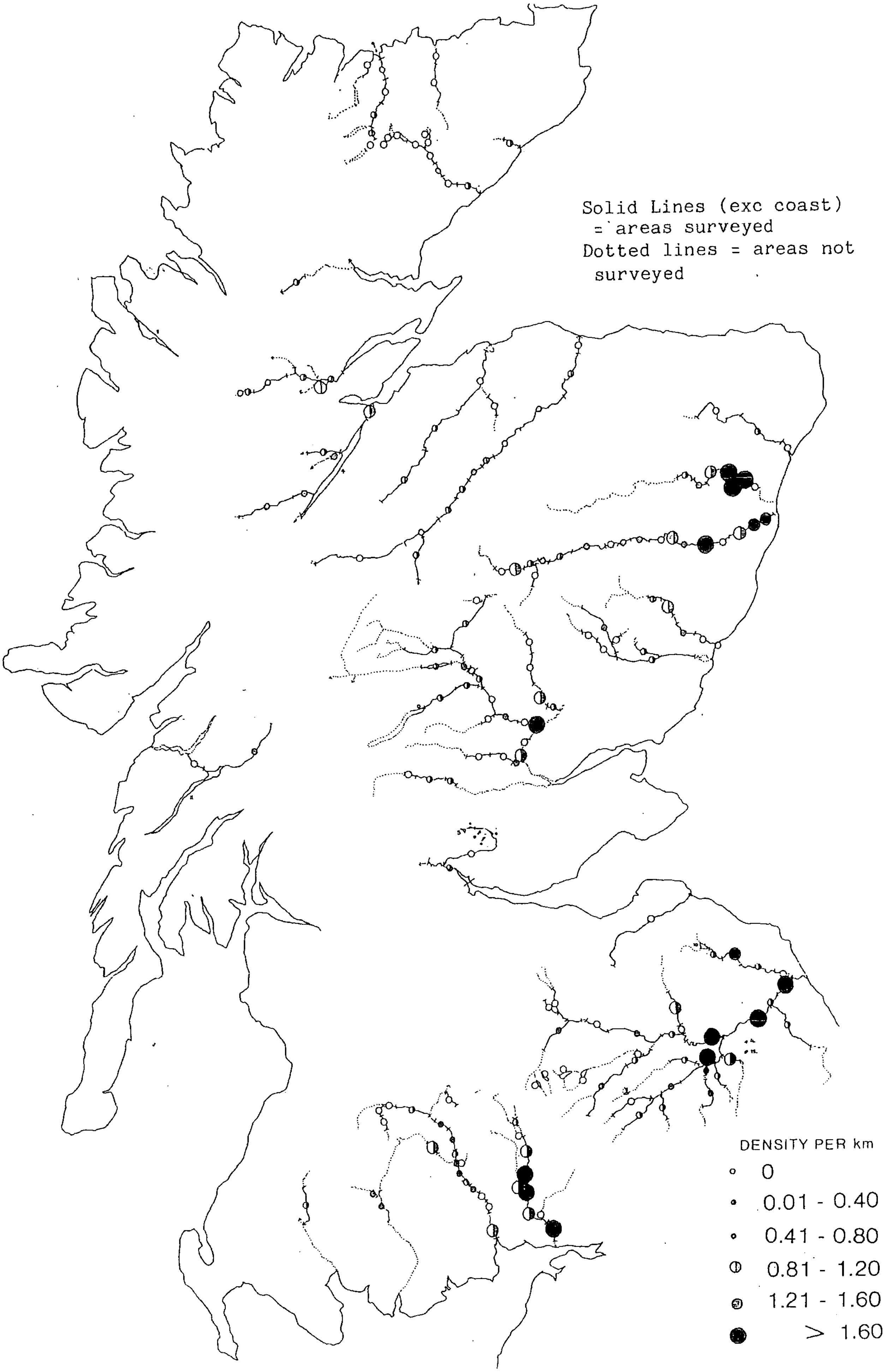


Figure 1.3 ; river areas surveyed in spring 1984 and observed Goosander densities per km

Figure 1.4 ; river areas surveyed in summer 1984 and observed numbers of Goosander broods per km

Table 1.1. Total numbers of Goosanders recorded on a 16 km section of the River Annan over the period 19th to 29th March 1984

Count number	Date	Total number seen
1	19th	42
2	21st	14
3	22nd	20
4	26th	8
5	28th	11
6	29th	22

25.3 (SE=8.51), and 13.7 (SE=4.26), respectively. Although the difference between these mean values is not statistically significant (df=4, t=1.22, p>0.05), the data suggest that increased river flow might lead to fewer sawbills on the river. Reasons to expect this are considered in section 1.4.4 below. However, the correlation between numbers of birds counted and river flow on the same day is also not significant (df=4, r=-0.55, p>0.05).

If, during the period covered by counts (1)-(3), the total number of Goosanders present on that stretch of river was constant at the maximum recorded, ie. 42, and that this figure was the actual number present, then by definition, 100% of birds were noted during count (1), 33.3% during (2) and 47.6% during (3). The mean percentage of birds observed on any single visit would thus have been 60.3%. Similarly, if during the period covered by counts (4)-(6), the actual number present was also constant but at the lower value of 22 (the maximum recorded), then the corresponding mean percentage of birds observed on any single visit would have been 62.1%.

During the summer survey period J.D. Uttley made repeat counts over three consecutive days of a section of the River North Tyne, Northumberland. These recorded three, two and two broods respectively. From the number of ducklings in each, and their size, it was estimated that at least four broods were present. The mean percentage of broods observed on each visit was calculated to be 58.3%.

It had been intended to use values for the mean percentage of birds/broods noted on any one site visit as crude correction factors for other survey data based on a single count. However, the validity of this approach is uncertain and analyses of survey data, presented below, are therefore based on uncorrected count values.

1.3.1.2 Aerial survey

The flight over the rivers Spey and Findhorn in 1984, was delayed due to adverse weather conditions and did not take place until 3rd April, 4-15 days after the ground counts. The results of ground and aerial counts are given in Figures 1.5a and 1.5b. It is clear from these that even assuming populations on the river remained constant between the dates of coverage by each method, no detailed comparison is possible because of the extremely poor level of ground coverage acheived. Nonetheless, R.H. Dennis (who carried out the aerial survey) considered it to be both successful and cost effective; birds were not disturbed into flight by the aircraft and were readily identified and counted along river sections where visibility to a ground observer would have been limited or impossible.

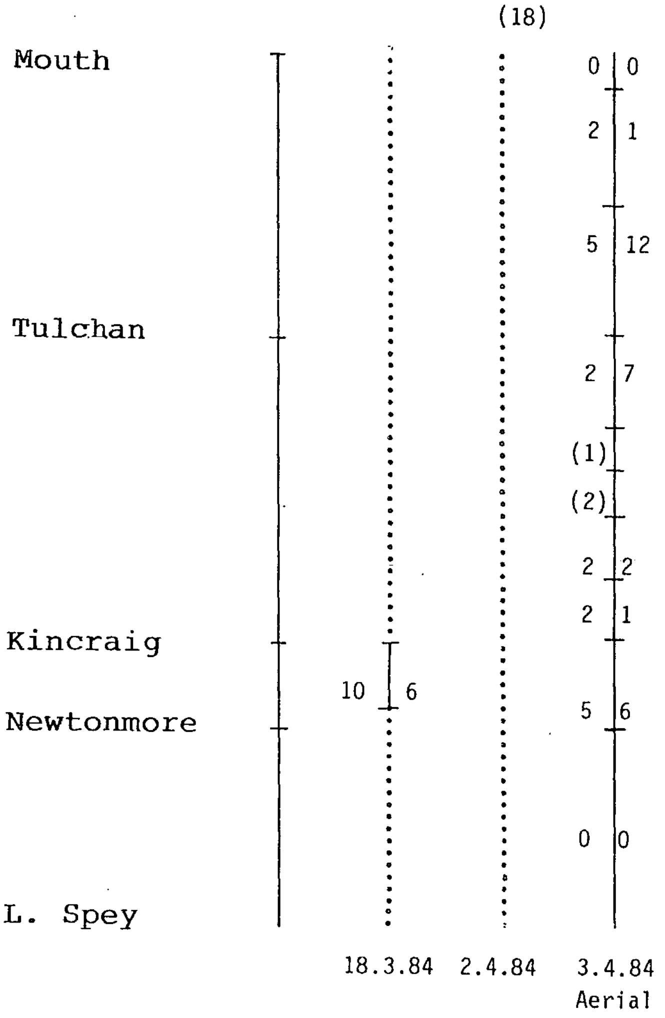


Figure 1.5a ; ground and aerial counts of the River Spey on 3 dates (dotted portion = not surveyed, values to left of line = no. adult males, values to right = no. 'redheads', values in parentheses = unidentified sawbills)

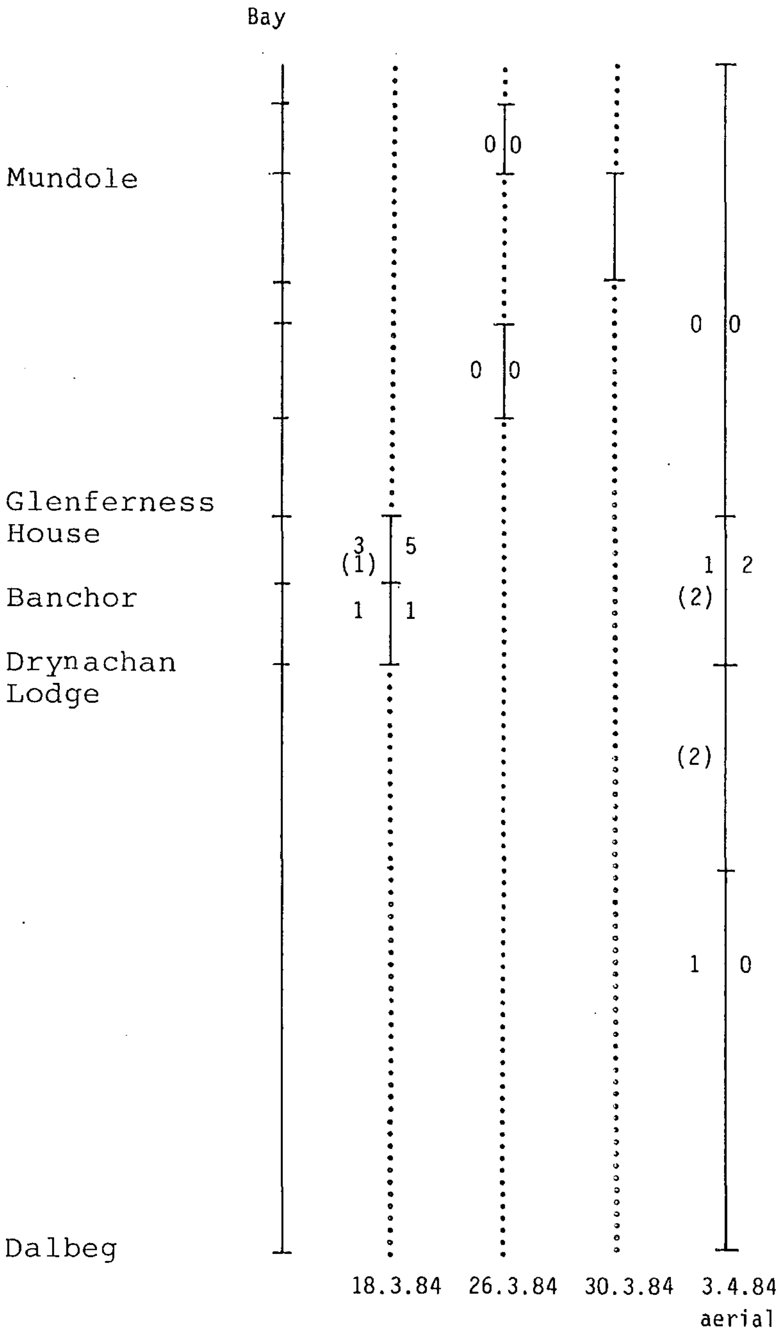


Figure 1.5b ; ground and aerial counts of the River Findhorn on 4 dates
(see legend on Figure 1.5a)

1.3.1.3 Full results of the 1984 Goosander and Merganser Survey of Scotland

Table 1.2 shows the total length of waterway surveyed in those river systems where coverage was undertaken, along with summary details of the Goosanders recorded there.

For March (Table 1.2a), the total number of Goosanders recorded is presented, together with the density per km of adult males, 'redheads' and total Goosanders. For July (Table 1.2b), the total number of birds recorded is given as well as the total number of ducklings, mean brood sizes, mean duckling size, and the density per km of adult males, 'redheads', broods and all birds (adults and ducklings).

Table 1.2c summarises all results. This shows an overall density of 0.42-0.47 Goosanders per km in spring, and 0.62 (including ducklings) in the summer. For adult males densities fell in the summer to c12% of their spring value. For immature males and 'redheads' the corresponding values are c11% and c45% respectively. This provides evidence in support of the suggestion by Little and Furness (1985) that, in general, male Goosanders undertake a moult migration from Britain to northern Scandinavia. This would involve adult males which had paired and copulated, immature birds, failed breeders and non-breeders. With the appearance of young of the year, typically in June, the overall density of Goosanders increases again. Numbers are further augmented in early autumn (ie. after the second survey period) by

Table 1.2a. Summary of coverage obtained in the spring survey period of the 1984 Goosander and Merganser Survey of Scotland (revised from Carter and Evans 1984)

Area	km	M	I	R	?	M_1	R_1	T_1
Dunbeath Wt.	6.0	1	0	1	0	0.17	0.17	0.33
Borgie	9.0	4	2	2	1	0.44	0.22	1.00
Halladale	19.0	0	0	0	0	0.00	0.00	0.00
Helmsdale	42.5	1	0	6	0	0.02	0.14	0.16
Naver	39.0	5	0	4	0	0.13	0.10	0.23
Gleann Mor	10.0	1	0	2	0	0.10	0.20	0.30
Conon	45.0	12	3	12	0	0.27	0.27	0.53
Ness	94.5	17	0	22	0	0.18	0.23	0.41
Findhorn (G)	25.0	5	0	7	1	0.20	0.28	0.52
Divie	7.0	0	0	0	0	0.00	0.00	0.00
Findhorn (A)	83.0	6	0	3	0	0.07	0.04	0.11
Spey (G)	30.0	11	0	6	0	0.37	0.00	0.57
Spey (A)	154.5	16	0	33	3	0.10	0.21	0.34
Ythan	54.0	4	0	5	0	0.07	0.09	0.17
Don	44.5	16	4	21	14	0.36	0.47	1.24
Dee	121.0	37	0	31	1	0.31	0.26	0.57
Clunie	10.0	0	0	0	0	0.00	0.00	0.00
N. Esk	33.0	7	0	7	0	0.21	0.21	0.42
S. Esk	92.0	12	1	8	0	0.13	0.09	0.23
Tay etc.	209.5	24	4	26	0	0.11	0.12	0.26
Earn	21.0	0	0	2	0	0.00	0.10	0.10
Devon/Forth	47.0	6	0	3	0	0.13	0.06	0.19
Tyne	42.0	0	0	0	0	0.00	0.00	0.00
Tweed etc.	427.5	83	18	147	35	0.19	0.34	0.66
Annan (+)	46.0	29	7	37	1	0.63	0.80	1.61
Annan (-)	46.0	12	5	21	0	0.26	0.46	0.83
Nith	93.5	10	0	14	3	0.11	0.15	0.29
Ken	16.5	5	0	5	0	0.30	0.30	0.61
Orchy/Awe	67.0	13	1	15	0	0.19	0.22	0.43

Key to column headings

M = no. adult males, M_1 = density of adult males per km
I = no. immature males
R = no. 'redheads', R_1 = density of 'redheads' per km
? = no. unidentified sawbills
T_1 = total density of Goosanders per km

(G) = based on spring ground count data
(A) = based on spring aerial count data

'+' = including spring aggregation (see text)
'-' = excluding spring aggregation (see text)

Table 1.2b. Summary of coverage obtained in the July survey period of the 1984 Goosander and Merganser Survey of Scotland (revised from Carter and Evans 1984)

Area	km	M	I	R	?	B	TD	MBS	MDS	M_1	R_1	B_1	T_1
Dunbeath Wt.	5.5	0	0	0	0	0	-	-	-	-	-	-	-
Borgie	8.0	0	0	0	0	0	-	-	-	-	-	-	-
Halladale	12.5	0	0	0	0	0	-	-	-	-	-	-	-
Strathay	3.0	0	0	0	0	0	-	-	-	-	-	-	-
Helmsdale	39.0	0	0	0	0	0	-	-	-	-	-	-	-
Naver	22.5	0	0	0	0	0	-	-	-	-	-	-	-
Vagastie	7.5	0	0	0	0	0	-	-	-	-	-	-	-
Ness	66.0	0	0	17	0	11	81	7.36	3.09	0.00	0.25	0.17	1.48
Findhorn	74.5	0	4	13	9	5	39	7.80	3.50	0.00	0.17	0.07	0.87
Spey	156.0	2	0	15	15	8	27	3.38	3.50	0.01	0.10	0.05	0.38
Ythan	27.0	0	0	0	0	0	-	-	-	-	-	-	-
Dee	73.5	8	1	28	17	10	78	7.80	3.00	0.11	0.38	0.14	1.80
N. Esk	45.0	3	0	2	0	3	16	5.33	3.50	0.07	0.04	0.07	0.47
S. Esk	76.0	0	0	10	0	8	54	6.75	3.43	0.00	0.13	0.11	0.84
Tay etc.	186.5	1	0	9	5	7	53	7.57	3.57	0.00	0.05	0.04	0.36
Earn	17.0	0	0	0	0	0	-	-	-	-	-	-	-
Tweed etc.	278.0	2	0	26	6	21	139	6.62	3.64	0.00	0.09	0.08	0.62
Annan	69.0	1	0	5	3	5	31	6.20	3.25	0.01	0.07	0.07	0.58
Nith	97.0	1	0	7	36	4	27	6.75	-	0.01	0.07	0.04	0.73
Stinchar	31.0	2	0	2	0	2	14	7.00	-	0.06	0.06	0.06	0.58
Orchy/Awe	57.5	1	0	7	0	5	32	6.40	3.40	0.02	0.12	0.09	0.70
Shin	5.0	0	0	0	0	0	-	-	-	-	-	-	-

Column headings as for Table 1.2a, but also,

TD = total number of ducklings recorded
MBS = mean brood size (B/TD)
MDS = mean duckling size code
B_1 = brood density per km

Table 1.2c. Summary of total coverage, and counts, obtained in the spring and summer survey periods of the 1984 Goosander and Merganser survey of Scotland

(i) Spring;

Total coverage;
ground only = 1651.5 km ; ground + aerial = 1834.0 km

Total count of -	M	I	R	?	T	M_1	I_1	R_1	T_1
Ground (Annan -)	286	38	367	55	746	0.17	0.02	0.22	0.45
Ground (Annan +)	303	39	383	56	781	0.18	0.02	0.23	0.47
Aerial (Annan -)	292	38	390	57	777	0.16	0.02	0.21	0.42
Aerial (Annan +)	309	39	406	58	812	0.17	0.02	0.22	0.44

(ii) Summer

Total coverage;
ground only = 1357.0 km

Total count of -	M	I	R	?	T	M_1	I_1	R_1	T_1
	21	5	141	91	258	0.02	0.00	0.10	0.19

Total count of ducklings = 591
Total brood count = 89
Mean brood size = 6.64

Total count of adults + ducklings = 849
Total density of adults + ducklings = 0.62

Column headings as in Table 1.2a

the return of birds from European moulting areas and by winter immigrants.

Two values are given for birds on the River Annan in Tables 1.2a and 1.2c. The first, marked (+), indicates a total count of 75 Goosanders, and the second, marked (-), the number of birds recorded if a large aggregation of 34 individuals is excluded. This concentration, noted on 19th March, was coincident with an apparent flux of birds through an adjacent stretch of river where I had made the repeat counts (see section 1.3.1.1). The exclusion of the numbers noted may therefore be justified since it is likely that those birds were on passage to breeding sites elsewhere.

Figure 1.6 shows the relationship between the spring density of (i) adult males, (ii) 'redheads', and (iii) the total number of Goosanders, and the density of broods in July using data from rivers/systems covered in both survey periods. This figure uses density values calculated from ground count data. Data for the rivers Spey and Findhorn are excluded due to the great disparity between lengths covered in the spring and summer. Data from the River Annan are shown both including and excluding the aforementioned aggregation. The dotted line on this figure indicates equivalence between the spring density of adult males, 'redheads' or all Goosanders, and the summer density of broods on the same river. All values except one fall below this line, ie. the density of broods was less than the spring densities of adult

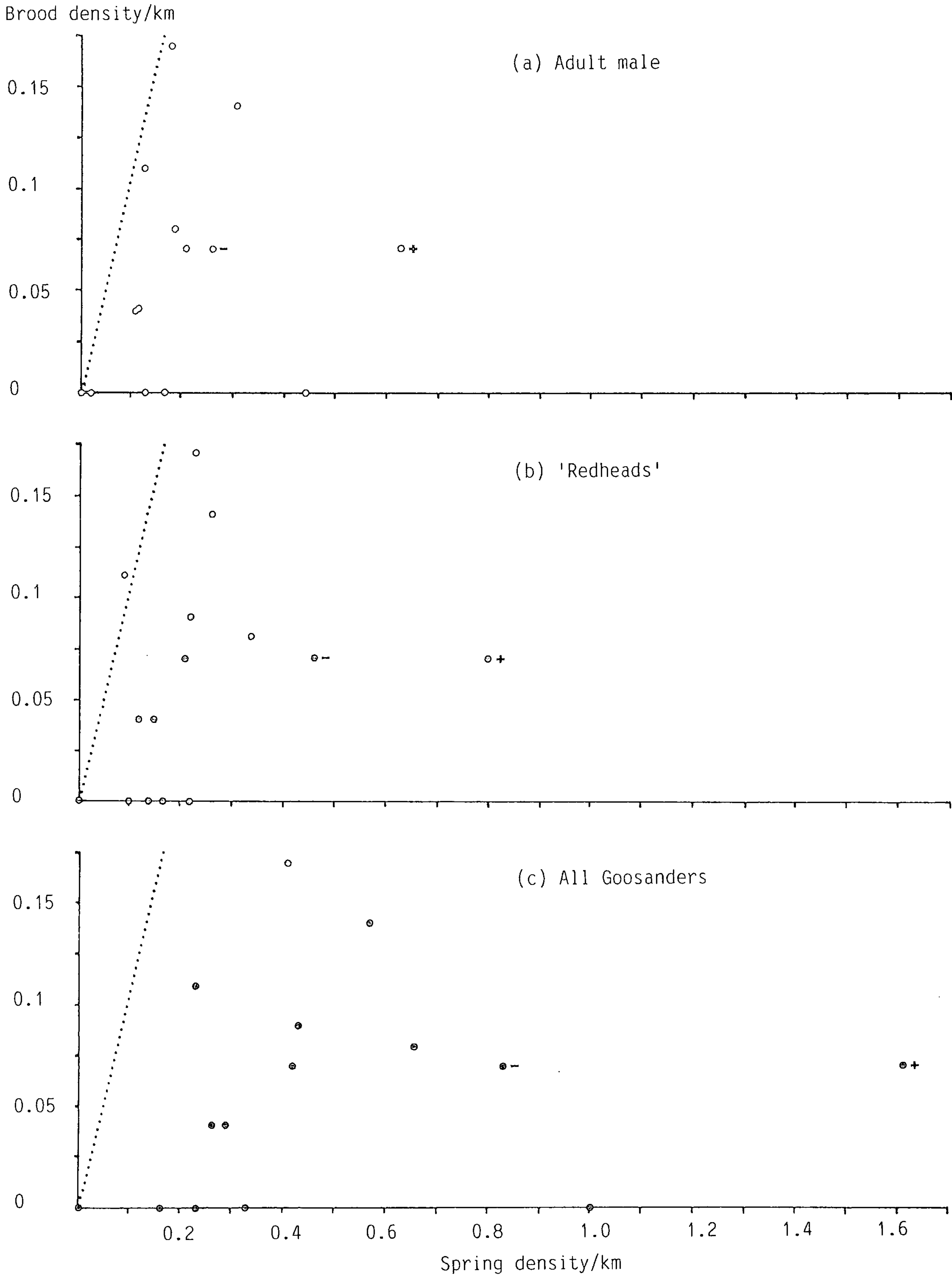


Figure 1.6: relationship between spring density of Goosanders and summer brood densities: dotted line is where spring density is equal to brood density, + = data for Annan excluding aggregation, - = Annan excluding aggregation.

males, 'redheads' or total Goosanders. The anomalous value mentioned above refers to the River South Esk, Tayside. Because the brood density there was greater than the spring density of 'redheads', some potential pairs must have been missed during the initial survey work. Although this could have occurred because of low observer efficiency, a more likely explanation is that the spring surveys were undertaken before all adult pairs had returned to the river. This would agree with the general impression of observers elsewhere in Scotland that spring survey work in 1984 was too early; but why this feature was noted only on the River South Esk is unclear.

The relationships between the spring density of adult birds and summer brood density are summarised in Table 1.3. These show that whether the Annan aggregation is included or not, and whether ground or aerial counts are used, there are no statistically significant relationships (at the 5% level) between the spring density of adults and summer brood density. Possible reasons for this are discussed in section 1.4.5 below.

Since the use of aerial count data does not increase the value of the correlation coefficient of spring density on brood density, ground counts can be assumed to provide at least as good an estimate of spring numbers. This is encouraging since aerial techniques are not widely available.

No statistically significant relationships were found between total Goosander density in the spring and total Goosander density in the summer.

Table 1.3. Relationships between spring densities of adult Goosanders and summer brood densities in 1984

'Y' variable = brood density

'X' variable;

	r	df	p
Ground counts (exc Annan aggregation)			
Adult male density	0.354	15	>0.05
'Redhead' density	0.452	15	>0.05
Total density	0.295	15	>0.05
Aerial counts (exc Annan aggregation)			
Adult male density	0.350	15	>0.05
'Redhead' density	0.443	15	>0.05
Total density	0.289	15	>0.05
Ground counts (inc Annan aggregation)			
Adult male density	0.303	15	>0.05
'Redhead' density	0.329	15	>0.05
Total density	0.247	15	>0.05
Aerial counts (inc Annan aggregation)			
Adult male density	0.299	15	>0.05
'Redhead' density	0.323	15	>0.05
Total density	0.243	15	>0.05

1.3.1.4 Regional variation in Goosander density

From spring counts, data from individual rivers (as given in Tables 1.2a and 1.2b) were grouped into eight geographical regions (see Table 1.4) and the mean total density per km length calculated for each. These data suggest that Goosander density decreases from south to north, with maximum values recorded in south-west Scotland and the Borders, and minimum values in highland areas and the extreme north-east. However, differences in density between regions were not statistically significant at the 5% level (Kruskal-Wallis, H=6.88, $X^2_{7df}=14.07$ at 5% level).

Allocating the data to one of the three Scottish EURING regions (EURING 1979) and repeating this analysis again showed no statistically significant differences in regional densities (H=1.74, $X^2_{2df}=5.99$ at 5% level).

Similar treatment of summer brood density values gave H values of 15.62 using data split between seven regions, and of 7.49 using EURING regions. Both of these results are statistically significant at the 5% level (for which $X^2_{6df}=12.59$ and $X^2_{2df}=5.99$ respectively) indicating a marked regional variation in brood density. In agreement with results from the spring, density was lowest in north-east Scotland but, in contrast to that period, brood density was greatest in the highland area to the east of the Great Glen.

Table 1.4. Regional and EURING groupings for examination of regional variations in Goosander in spring and summer 1984

a) Regional groupings; spring

Group 1 ; Dunbeath Water, Borgie, Halladale, Helmsdale, Naver, Gleann Mor, Conon.
Group 2 ; Ness, Findhorn, Divie, Spey
Group 3 ; Ythan, Don, Dee, Clunie, North Esk, South Esk
Group 4 ; Tay, Earn
Group 5 ; Devon, Tyne
Group 6 ; Tweed
Group 7 ; Annan, Nith, Ken
Group 8 ; Orchy/Awe

b) EURING groupings; spring

Group 1 ; Dunbeath Water, Borgie, Halladale, Helmsdale, Naver, Gleann Mor, Conon, Ness
Group 2 ; Findhorn, Divie, Spey, Ythan, Don, Dee, Clunie, North Esk, South Esk, Tay, Earn, Devon
Group 3 ; Tyne, Tweed, Annan, Nith, Ken, Orchy/Awe

c) Regional groupings: summer

Group 1 ; Dunbeath Water, Borgie, Halladale, Helmsdale, Naver, Gleann Mor, Strathay, Vagastie, Shin
Group 2 ; Ness, Findhorn, Spey
Group 3 ; Ythan, Dee, North Esk, South Esk
Group 4 ; Tay, Earn
Group 5 ; Tweed
Group 6 ; Annan, Nith, Stinchar
Group 7 ; Orchy/Awe

d) EURING groupings; summer

Group 1 ; Dunbeath Water, Borgie, Halladale, Helmsdale, Naver, Gleann Mor, Strathay, Vagastie, Shin, Ness
Group 2 ; Findhorn, Spey, Ythan, Don, Dee, Clunie, North Esk, South Esk, Tay, Earn
Group 3 ; Tweed, Annan, Nith, Stinchar, Orchy/Awe

1.3.1.5 Within-river variation in Goosander density

To investigate within-river variations in Goosander density data were used from those main rivers where coverage in 1984 was nearly complete (see Figures 1.3 and 1.4). For each of these rivers, sections surveyed were allocated to 'upper', 'middle' and 'lower' regions so that the total length covered in each was approximately equal. Details of rivers used, and of birds recorded thereon, are given in Table 1.5 for the spring period and Table 1.6 for the summer.

To test for differences between the three river regions, a Friedman two-way analysis of variance was performed (Siegel 1956) after ranking the data in Tables 1.5 and 1.6 according to the mean density per km of Goosanders in each region within each river such that rank 1 equals the greatest density. Ranked densities are presented in Table 1.7, and results in Table 1.8.

These show that in both spring and summer there were no significant differences between river regions in Goosander density, ie. birds were not significantly concentrated into either the 'upper', 'middle' or 'lower' reaches.

(Within-river variation in Goosander density is examined using 1986 data in section 1.3.2.1.)

Table 1.5. Number and density of Goosanders recorded in spring 1984 on the 'lower', 'middle' and 'upper' reaches of selected rivers.

'Lower'

	km	M	I	R	?	T	M_1	R_1	T_1
Helmsdale	9.0	0	0	1	0	1	0.00	0.11	0.11
Naver	13.0	1	0	2	0	3	0.08	0.15	0.23
Findhorn	30.0	0	0	0	0	0	0.00	0.00	0.00
Spey	50.5	7	0	13	0	20	0.14	0.26	0.40
Dee	42.5	20	0	19	0	39	0.47	0.45	0.92
N. Esk	11.0	0	0	0	0	0	0.00	0.00	0.00
Tweed	33.5	18	6	42	7	73	0.54	1.25	2.18
Nith	31.0	2	0	5	1	8	0.06	0.16	0.26
Annan (+)	9.0	9	5	7	0	21	1.00	0.78	2.33
Annan (-)	9.0	9	5	7	0	21	1.00	0.78	2.33

'Middle'

	km	M	I	R	?	T	M_1	R_1	T_1
Helmsdale	14.0	1	0	2	0	3	0.07	0.14	0.21
Naver	14.0	1	0	0	0	1	0.07	0.00	0.07
Findhorn	26.0	5	0	2	0	7	0.19	0.08	0.27
Spey	52.0	6	0	14	0	20	0.12	0.27	0.38
Dee	45.5	9	0	8	0	17	0.20	0.18	0.37
N. Esk	9.5	1	0	4	0	5	0.11	0.42	0.53
Tweed	44.0	14	4	27	10	55	0.32	0.61	1.25
Nith	22.0	1	0	1	0	2	0.05	0.05	0.09
Annan (+)	15.0	18	4	21	1	44	1.20	1.40	2.93
Annan (-)	15.0	1	4	5	0	10	0.07	0.33	0.67

'Upper'

	km	M	I	R	?	T	M_1	R_1	T_1
Helmsdale	12.5	0	0	1	0	1	0.00	0.08	0.08
Naver	12.0	1	0	1	0	2	0.08	0.08	0.17
Findhorn	27.0	1	0	0	0	1	0.04	0.00	0.04
Spey	52.0	5	0	6	0	11	0.10	0.12	0.21
Dee	33.0	8	0	4	1	13	0.24	0.12	0.39
N. Esk	12.5	6	0	3	0	9	0.48	0.24	0.72
Tweed	38.0	9	2	16	1	28	0.23	0.42	0.74
Nith	19.0	1	0	1	0	2	0.05	0.05	0.11
Annan (+)	14.5	5	0	7	0	12	0.34	0.48	0.83
Annan (-)	14.5	5	0	7	0	12	0.34	0.48	0.83

(Column headings as in Table 1.2a)

Table 1.6. Number and distribution of Goosanders recorded in July 1984 on the 'lower', 'middle' and 'upper' reaches of selected rivers

'Lower'

	km	M	I	R	?	B	T	M_1	R_1	B_1	T_1
Helmsdale	9.0	0	0	0	0	0	0	0.00	0.00	0.00	0.00
Findhorn	18.5	2	1	1	1	0	5	0.11	0.05	0.00	0.27
Spey	47.0	0	0	2	8	0	10	0.00	0.04	0.00	0.21
Dee	31.5	2	0	12	12	2	26	0.06	0.38	0.06	0.82
N. Esk	19.0	0	0	1	0	1	1	0.00	0.05	0.05	0.05
Nith	18.0	0	0	0	0	0	0	0.00	0.00	0.00	0.00

'Middle'

	km	M	I	R	?	B	T	M_1	R_1	B_1	T_1
Helmsdale	15.0	0	0	0	0	0	0	0.00	0.00	0.00	0.00
Findhorn	20.0	0	0	7	7	3	17	0.00	0.35	0.15	0.85
Spey	44.0	0	0	7	3	2	10	0.00	0.16	0.05	0.23
Dee	27.0	0	0	10	12	8	22	0.00	0.37	0.30	0.81
N. Esk	13.0	2	0	1	0	1	3	0.15	0.08	0.08	0.23
Nith	40.0	0	0	4	34	3	38	0.00	0.10	0.08	0.95

'Upper'

	km	M	I	R	?	B	T	M_1	R_1	B_1	T_1
Helmsdale	9.0	0	0	1	0	1	1	0.00	0.11	0.11	0.11
Findhorn	32.0	0	0	0	0	0	0	0.00	0.00	0.00	0.00
Spey	35.0	0	0	1	0	0	1	0.00	0.03	0.00	0.03
Dee	39.0	6	1	10	5	2	22	0.15	0.26	0.05	0.56
N. Esk	12.0	1	0	0	0	0	1	0.08	0.00	0.00	0.08
Nith	17.5	0	0	1	2	0	3	0.00	0.06	0.00	0.17

(Column headings as in Table 1.2a)

Table 1.7a. Ranked spring densities of (i) adult males, (ii) 'redheads' and (iii) total Goosander between river regions.
(Density values from Tables 1.5, rank 1 = highest density.)

(i) Adult male

	'Lower'	'Middle'	'Upper'
Helmsdale	2.5	1	2.5
Naver	1.5	3	1.5
Findhorn	3	1	2
Spey	1	2	3
Dee	1	3	2
N. Esk	3	2	1
Tweed	1	2	3
Nith	1	2.5	2.5

(ii) 'Redhead'

	'Lower'	'Middle'	'Upper'
Helmsdale	2	1	3
Naver	1	3	2
Findhorn	2.5	1	2.5
Spey	2	1	3
Dee	1	2	3
N. Esk	3	1	2
Tweed	1	2	3
Nith	1	2.5	2.5

(iii) Total Goosanders

	'Lower'	'Middle'	'Upper'
Helmsdale	2	1	3
Naver	1	3	2
Findhorn	3	1	2
Spey	1	2	3
Dee	1	3	2
N. Esk	3	2	1
Tweed	1	2	3
Nith	1	3	2

Table 1.7b. Ranked summer densities of (i) adult males, (ii) 'redheads' (iii) broods and (iv) total Goosander between river regions.
(Density values from Table 1.6, rank 1 = highest density.)

	(i) Adult male			(ii) 'Redhead'		
	'Lower'	'Middle'	'Upper'	'Lower'	'Middle'	'Upper'
Helmsdale	2	2	2	2.5	2.5	1
Findhorn	1	2.5	2.5	2	1	3
Spey	2	2	2	2	1	3
Dee	2	3	1	1	2	3
N. Esk	3	1	2	2	1	3
Nith	2	2	2	3	1	2

	(iii) Broods			(iv) Total Goosanders		
	'Lower'	'Middle'	'Upper'	'Lower'	'Middle'	'Upper'
Helmsdale	2.5	2.5	1	2.5	2.5	1
Findhorn	2.5	1	2.5	2	1	3
Spey	2.5	1	2.5	2	1	3
Dee	2	1	3	1	2	3
N. Esk	2	1	3	3	1	2
Nith	2.5	1	2.5	3	1	2

Table 1.8. X^2_r values for Friedman two-way analysis of variance between Goosander density and river region in spring and summer 1984

Spring;	X^2_r	df	p
Adult male	0.813	2	>0.05
Redhead	4.688	2	>0.05
Total	1.75	2	>0.05
Summer;			
Adult male	0.083	2	>0.05
Redhead	3.583	2	>0.05
Broods	5.083	2	>0.05
Total	3.083	2	>0.05

1.3.2 Detailed survey work in Scotland and the Borders in 1986

1.3.2.1 River Tweed

The main River Tweed from Berwick to Coldstream (see Figure 1.7) was surveyed on 10 dates between 24th January and 30th May. The number of Goosanders recorded per km on each date is shown in Figure 1.8, and the total numbers noted on each date in Figure 1.9. Figure 1.10 details the seasonal use by this species of two standing waters, Hoselaw Loch and the Hirsel, which lie close to the lower reaches of the river (see Figure 1.7).

Figures 1.8 and 1.9 suggest an influx of Goosanders near the river mouth during the cold weather of February 1986, and also that numbers declined through March. This may have been due to either (a) emigration of birds from the river system, (b) movement of birds to breeding sites elsewhere on the Tweed, or (c) a combination of (a) and (b).

Table 1.9 shows a progressive decline in the ratio of adult males to all females (which cannot be aged in the field) from late January to the end of May. Figure 1.9 indicates that this was attributable chiefly to a decrease in the number of adult males but that numbers of females also declined after mid-April, presumably as many settled to breed.

The decline in the number of males noted on the river from late

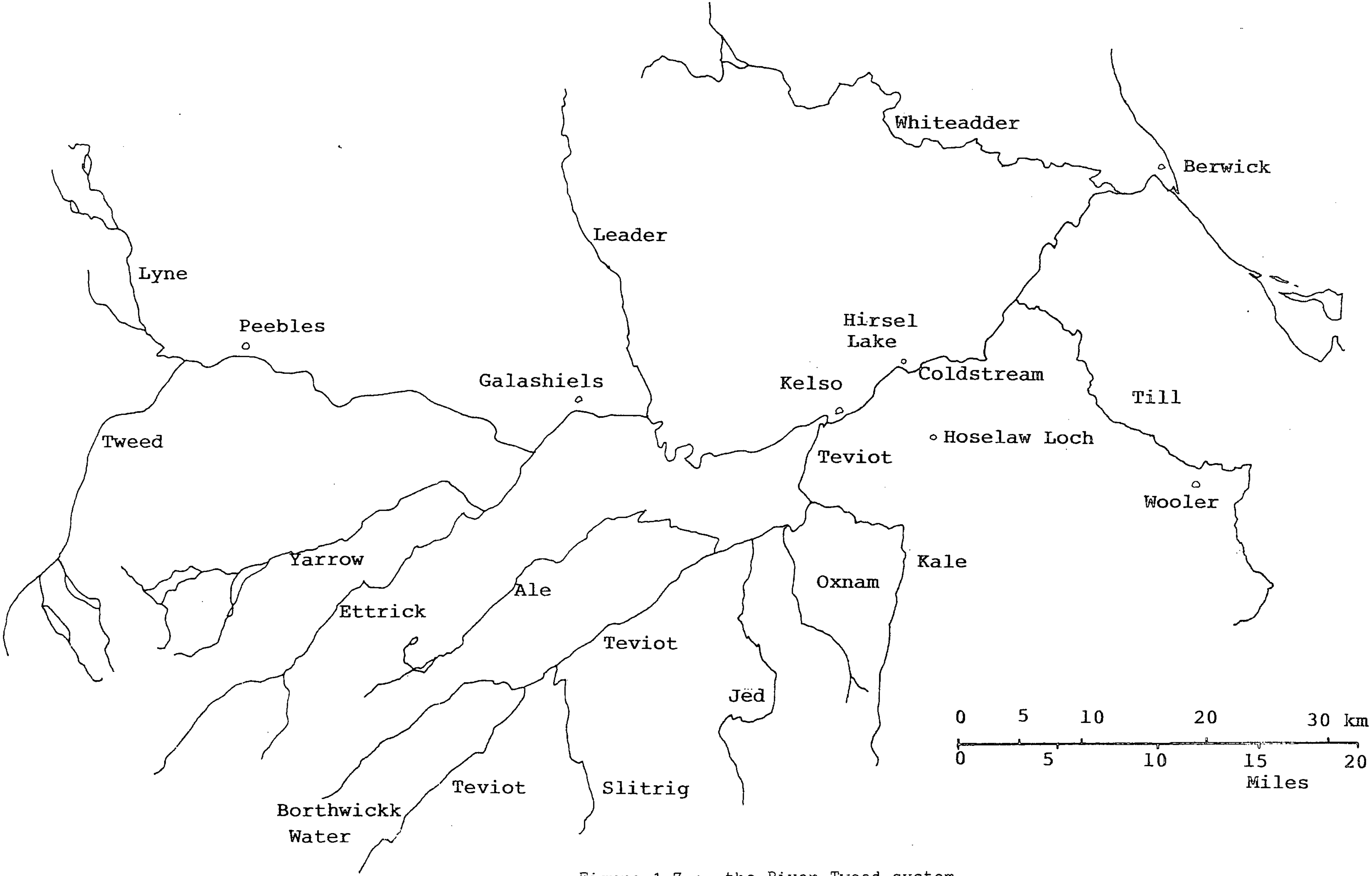


Figure 1.7 ; the River Tweed system

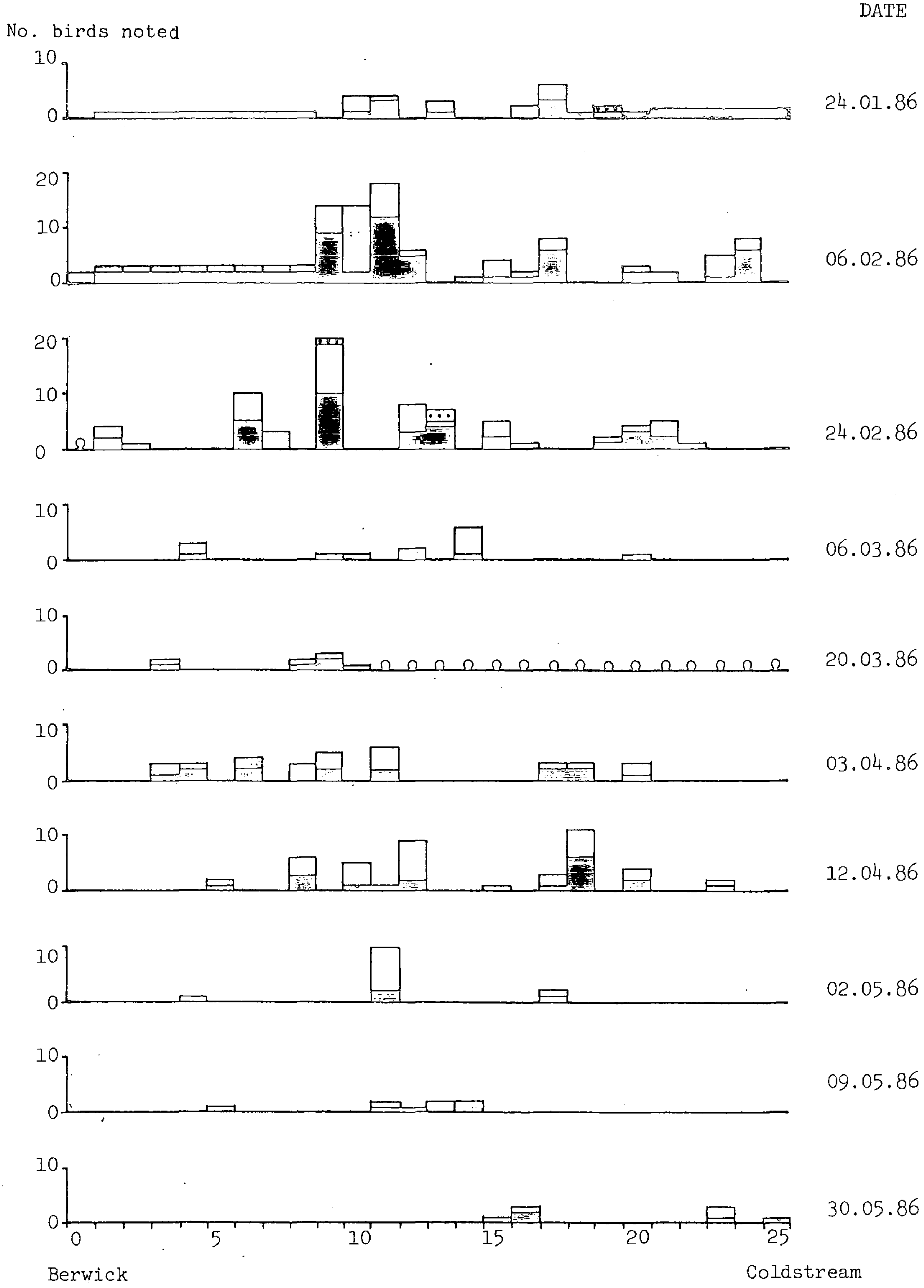


Figure 1.8 ; counts of Goosanders on the River Tweed, Berwick to Coldstream, January to May 1986

▨ adult male ☐ 'redhead'

∘∘∘∘ imm. male o not counted

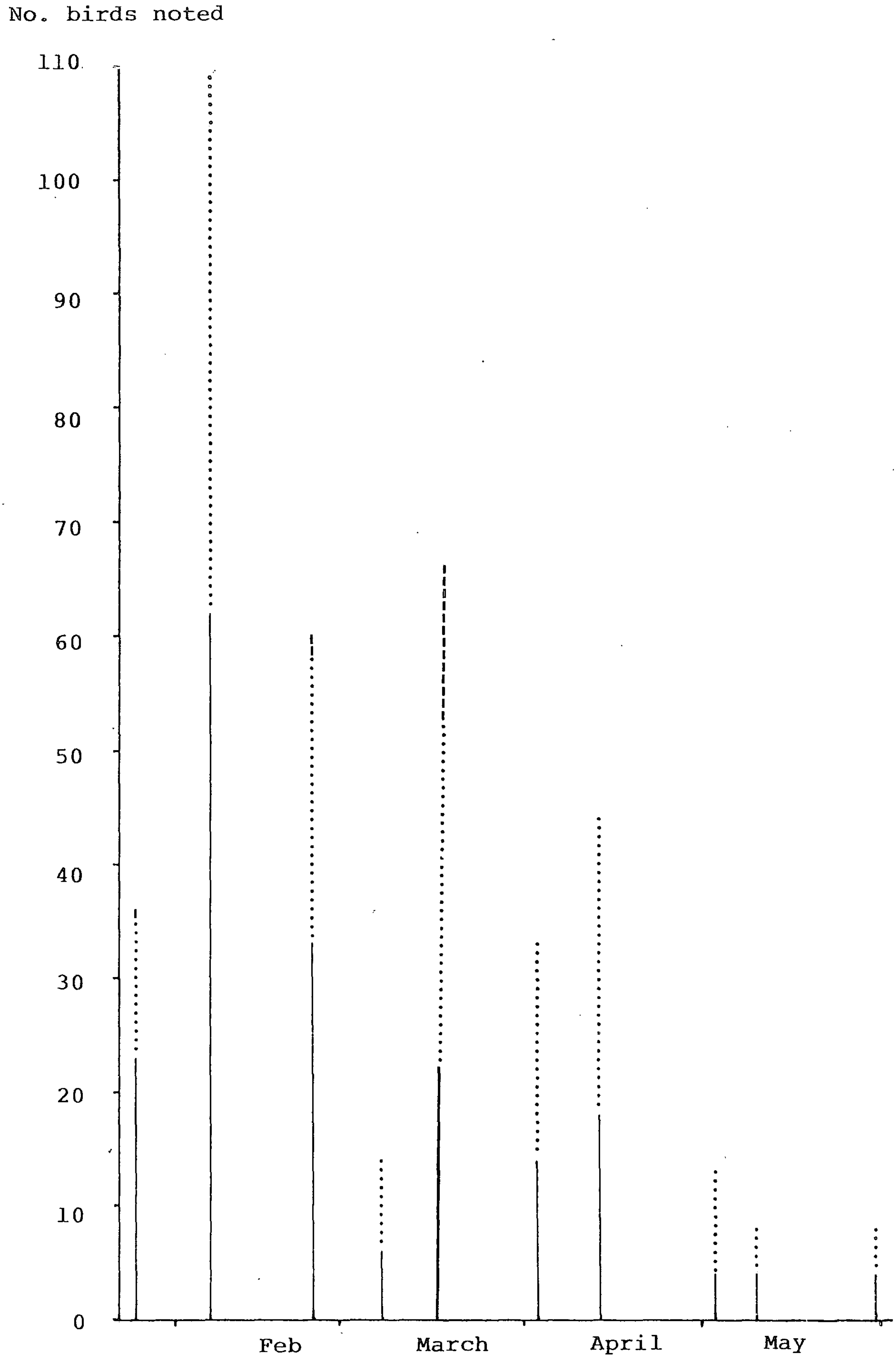


Figure 1.9 ; total numbers of Goosanders on the River Tweed, Berwick to Coldstream, January to May 1986
(——— adult male ...... 'redhead'
----- imm. male)

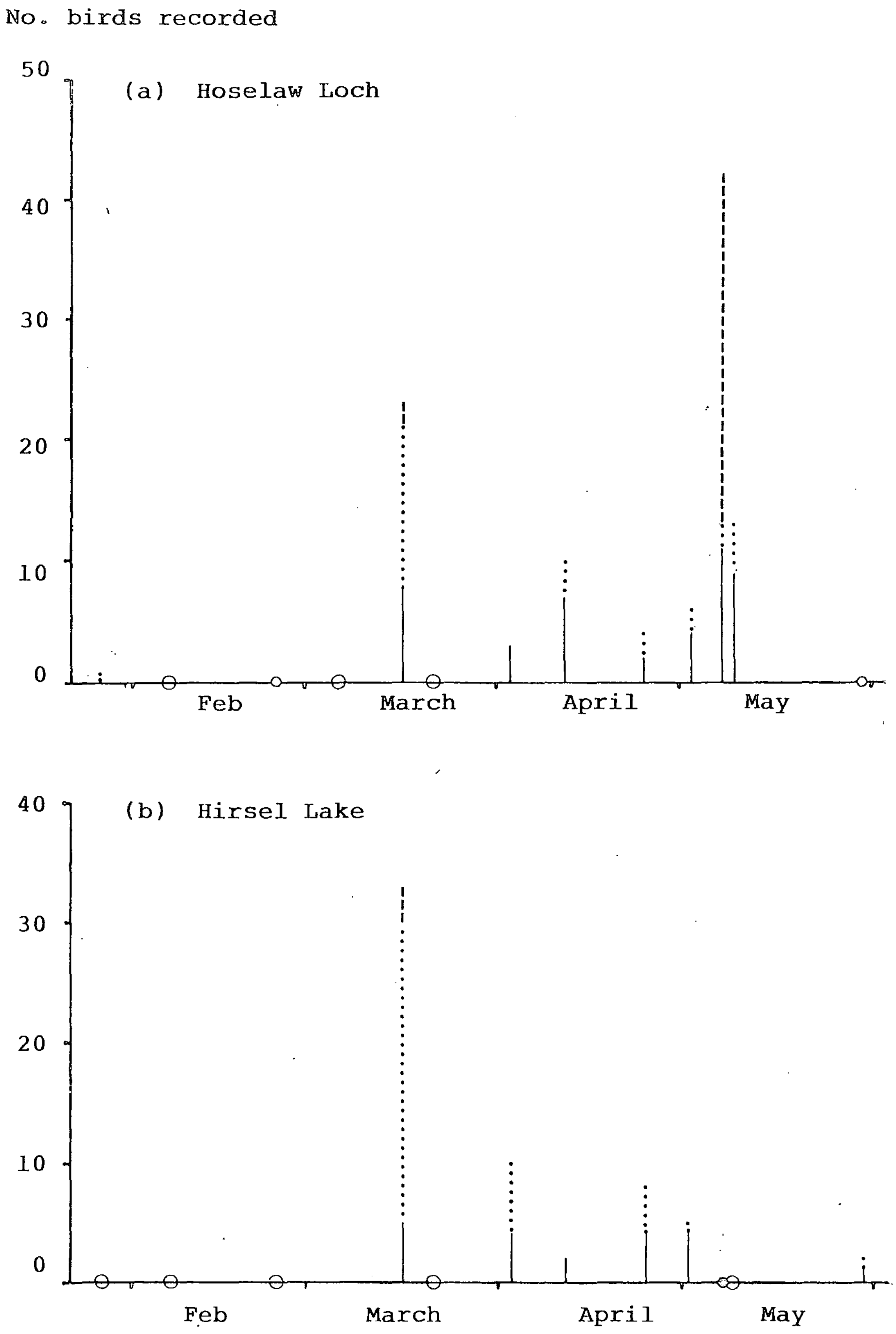


Figure 1.10 ; counts of Goosanders at Hoselaw Loch and Hirsel Lake, January to May 1986

——— adult male ······ 'redhead'
----- imm. male ○ not counted

Table 1.9. Sex ratios of adult males to all females on the lower Tweed between Berwick and Coldstream.

Date	Sex ratio	Total number of birds
24.01.86	1.92:1.00	35
06.02.86	1.32:1.00	109
24.02.86	0.94:1.00	68
06.03.86	0.75:1.00	14
16.03.86	0.76:1.00	51
03.04.86	0.74:1.00	33
12.04.86	0.69:1.00	42
02.05.86	0.44:1.00	13
09.05.86	1.00:1.00	8
30.05.86	1.00:1.00	8

February was coincident with an increase in numbers at Hoselaw Loch, which is used as an assembly site by males before their moult-migration to northern Scandinavia in May (Little and Furness 1985).

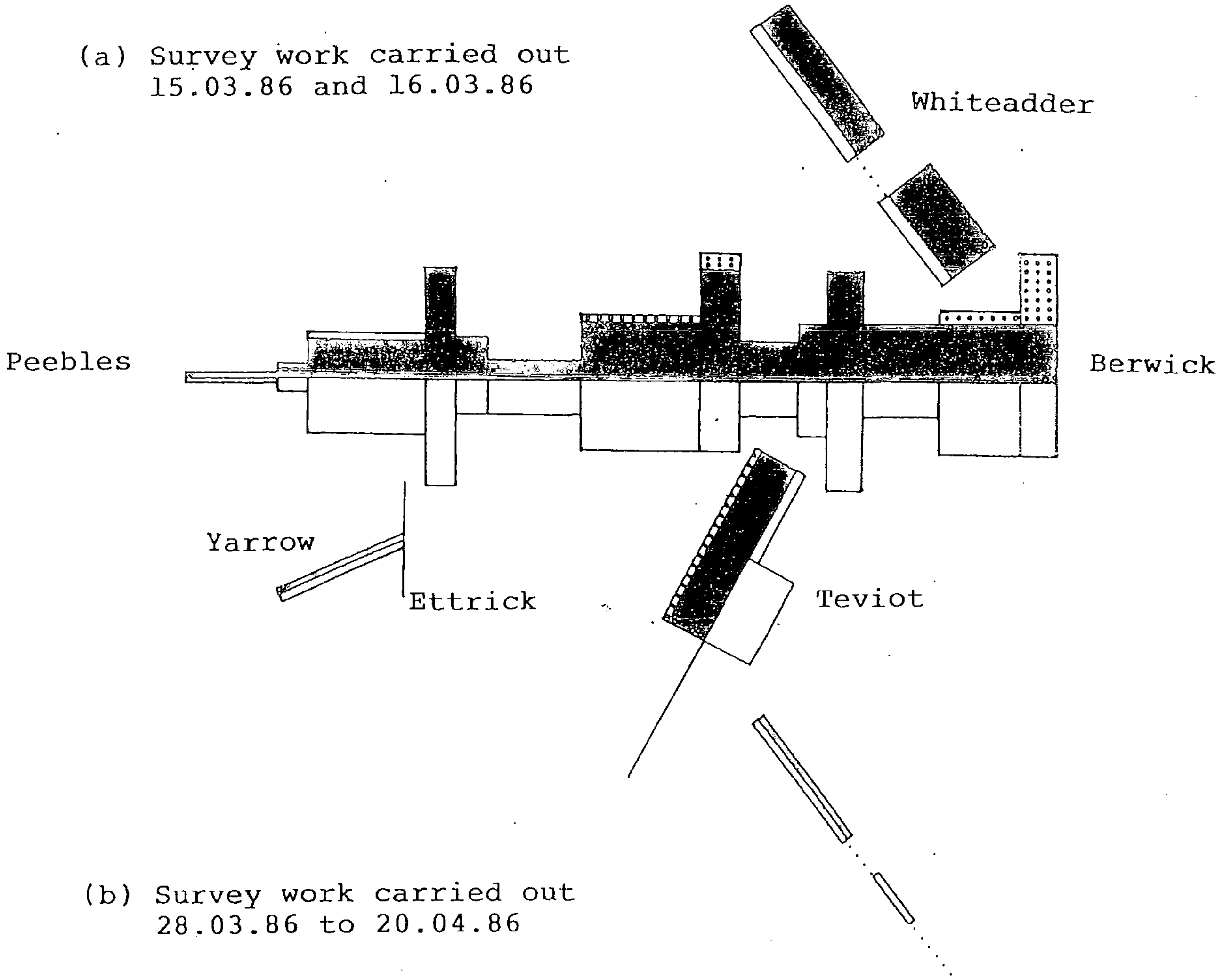
In addition to surveys of the lower Tweed as indicated above, Goosanders were surveyed on the main river from Berwick to Peebles, and on sections of the major tributaries (the Whiteadder, Till, Teviot, Ettrick and Yarrow) in mid-March. Subsequently c224 km of the main river and sections of the Whiteadder, Teviot, Ettrick and Yarrow were surveyed in early April.

Data from the March survey were provided by the Northumbria Ringing Group as totals (divided by age and sex where possible) for stretches of river of variable length. These results are presented diagrammatically in Figure 1.11a in the form of mean numbers per km over each section, as for the 1984 survey.

Data from the April surveys were submitted by observers as numbers on each km of river and are shown in detail in Figure 1.12, but also as mean numbers per km in Figure 1.11b, for direct comparison with the same stretches of river counted in mid-March. Totals for comparable stretches of river are given in Table 1.10.

The changes in distribution illustrated in Figure 1.11 between mid-March and April show an overall reduction in the density of birds on the Tweed between Peebles and Berwick, and on the

(a) Survey work carried out
15.03.86 and 16.03.86



(b) Survey work carried out
28.03.86 to 20.04.86

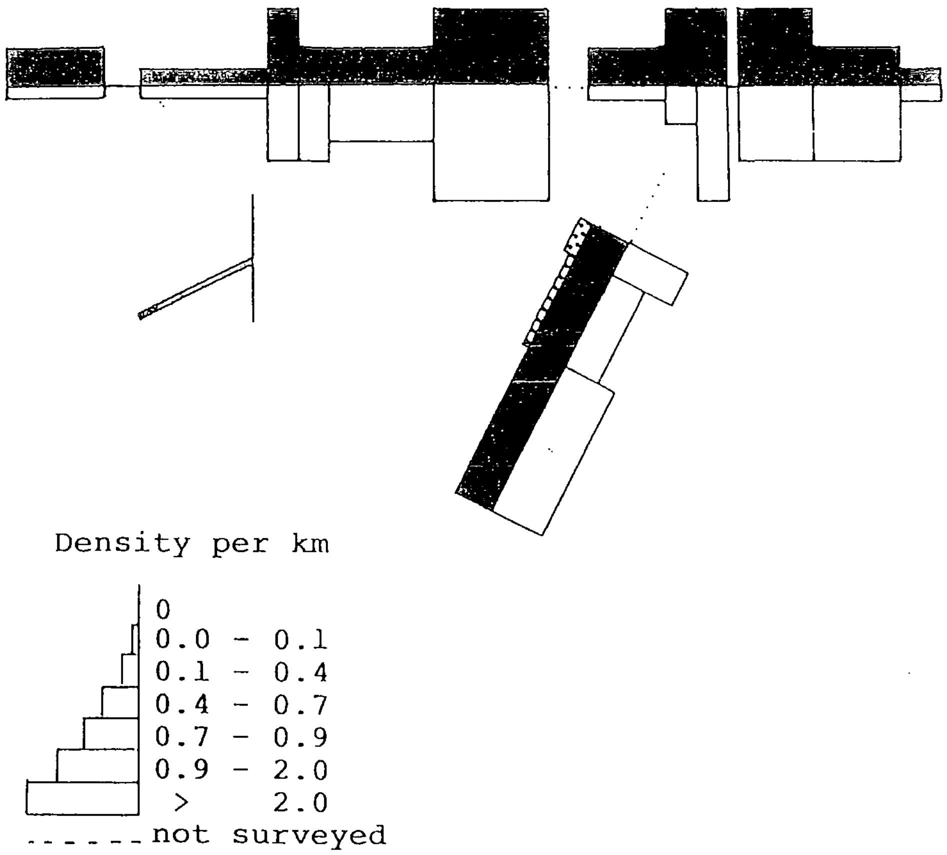


Figure 1.11 ; Diagrammatic summary of Goosander densities on the River Tweed in March and April 1986 (shading as in Figure 1.8)

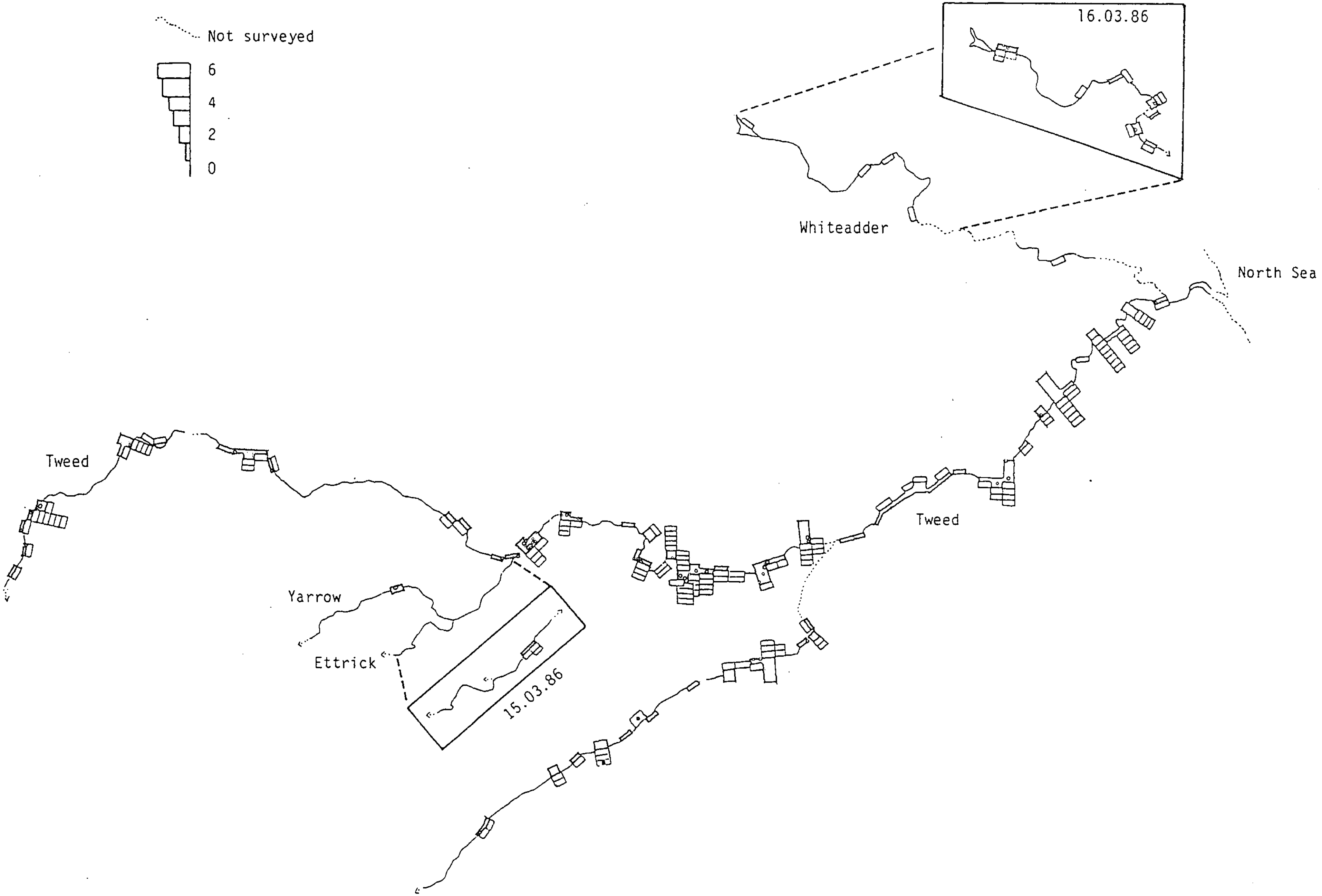


Figure 1.12 ; numbers of Goosanders per km on the River Tweed, 28th March to 20th April 1986

Table 1.10. Total counts of Goosanders on the Tweed and major tributaries in mid-March and April 1986

Section	mid-March	April
Tweed (Berwick to Peebles)	213	176
Teviot	32	52
Ettrick	0	0
Yarrow	2	2
Total	247	230

Whiteadder, and the disappearance of immature males from the tidal parts of the system. By mid-April birds were present further upstream along the Teviot, and the total numbers on that tributary had increased considerably. At the same time Goosander density increased on the lower reaches of the Teviot and for the first time birds were noted on the upper reaches of that tributary.

Table 1.11 shows that for the main river Tweed in mid-March, the 'upper' reaches had the lowest overall density and the 'lower' reaches the highest, but that by mid-April the trend had changed; densities remained lowest in the 'upper' reaches but the 'middle' reaches then held the greatest density of birds.

Using count data for individual kilometres surveyed, I calculated Chi-squared values (see Fowler and Cohen 1986) to test the goodness-of-fit of the observed distribution to a random distribution of birds on the main Tweed and on the Teviot, Ettrick/Yarrow and Whiteadder. The resulting X^2 and z values are given below. All results are highly significant indicating a strongly clumped distribution of Goosanders on each waterway.

	no. km	X^2	z	df	p
Tweed	121	405.69	12.99	119	<0.01
Teviot	39	122.04	6.91	37	<0.01
Ettrick/Yarrow	28	237.13	14.43	26	<0.01
Whiteadder	37	155.28	9.14	35	<0.01

Table 1.11. Comparison between Goosander density on the 'lower', 'middle' and 'upper' reaches of the main River Tweed in (a) mid-March and (b) mid-April 1986

'Lower' = Berwick to Carham,
'Middle' = Carham to Galafoot,
'Upper' = Galafoot to Peebles

(a) mid-March

	km	M	I	R	T	M_1	R_1	T_1
Berwick to Carham	30	38	13	43	94	1.27	1.43	3.13
Carham to Galafoot	35	35	2	40	87	1.00	1.14	2.48
Galafoot to Peebles	29	18	1	23	42	0.62	0.79	1.45

(b) mid-April

	km	M	I	R	T	M_1	R_1	T_1
Berwick to Carham	30	26	0	34	60	0.87	1.13	2.00
Carham to Galafoot	35	36	0	50	86	1.03	1.43	2.46
Galafoot to Peebles	29	12	2	16	30	0.41	0.55	1.03

(Column headings as in Table 1.2a)

1.3.2.2 River Tay

A total of c235 km of river throughout the Tay system was surveyed between 7th April and the beginning of May 1986 by local ornithologists co-ordinated by R.E. Youngman. The results are detailed in Figure 1.13.

1.3.2.3 River North Esk

The number of Goosanders in each km of the North Esk and its main tributary, the West Water, were recorded on five dates between 10th April and 29th August 1986. The results are presented in Figures 1.14 and 1.15. (Data collected during counts of part of each river on intermediate dates are presented in full in Carter and Evans (1986). Data on Merganser numbers on the river are also summarised therein).

Figures 1.14 and 1.15 show that Goosanders occurred at very low densities on both the River North Esk and the West Water; 0.11/km on the former and 0.30/km on the latter in spring 1986. Broods were noted on both rivers in mid-July. A small flock of both adult males and 'redheads', numbering nine at maximum, built up in late April/early May but were not noted after the 16th May.

It is suggested that these coincident events, ie. disappearance from the river and appearance at the estuary, can be best explained as follows ;-

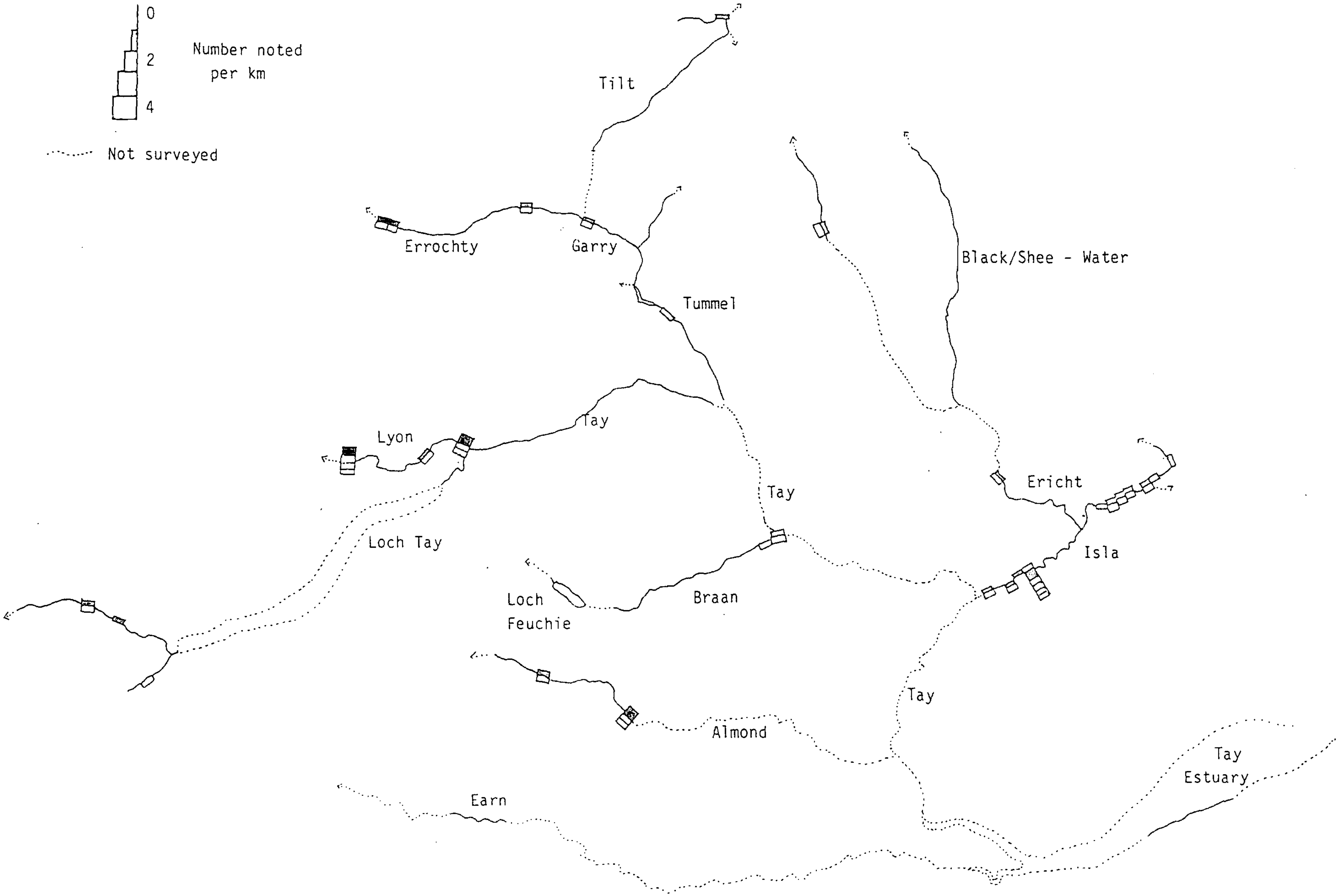


Figure 1.13 ; numbers of Goosanders per km on the River Tay system in April 1986
(shading as in Figure 1.8)

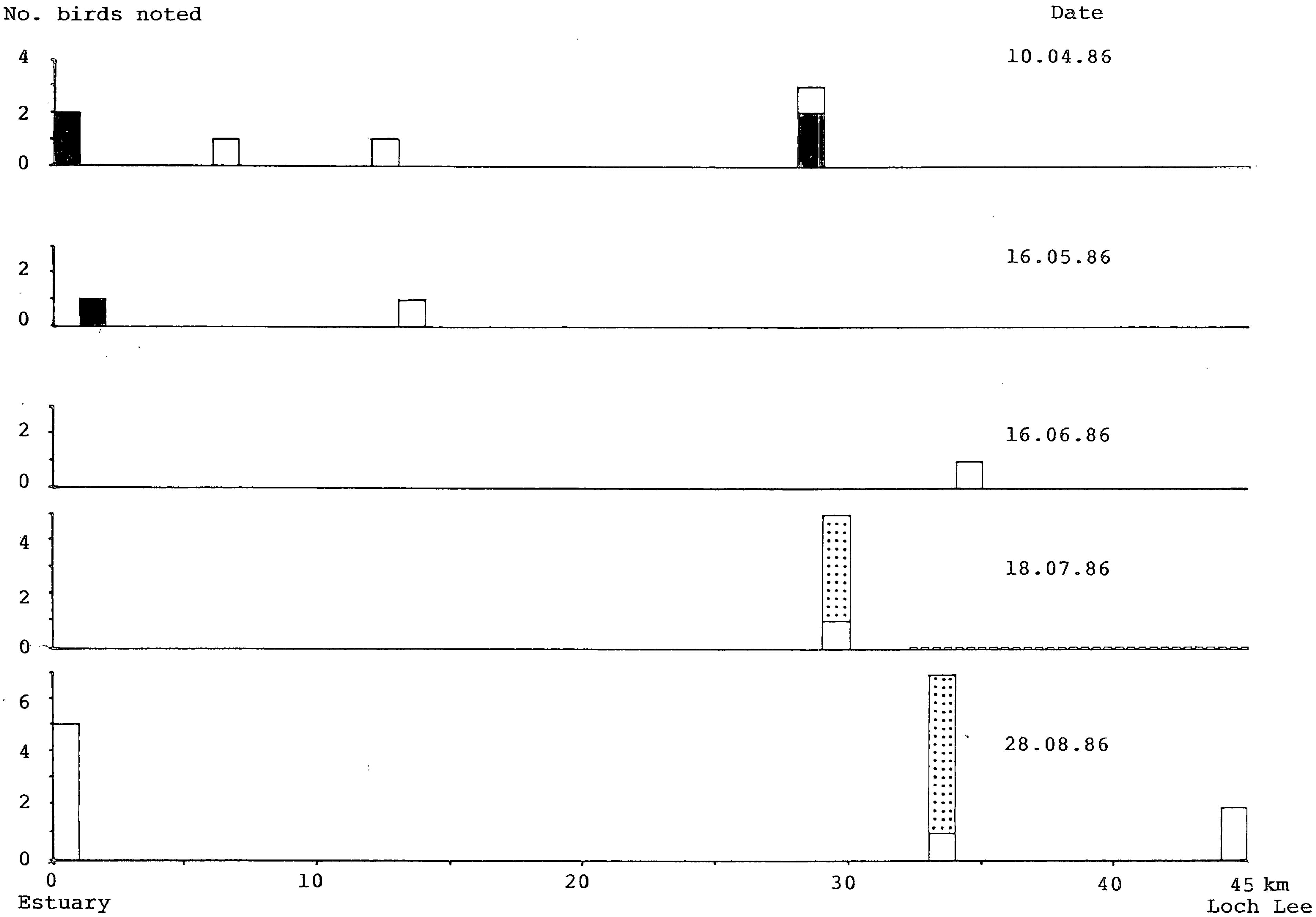


Figure 1.14 ; whole river counts of Goosander on the North Esk, Tayside, April to August 1986 (shading as in Figure 1.8, also ⁘ brood, ╌╌ not covered)

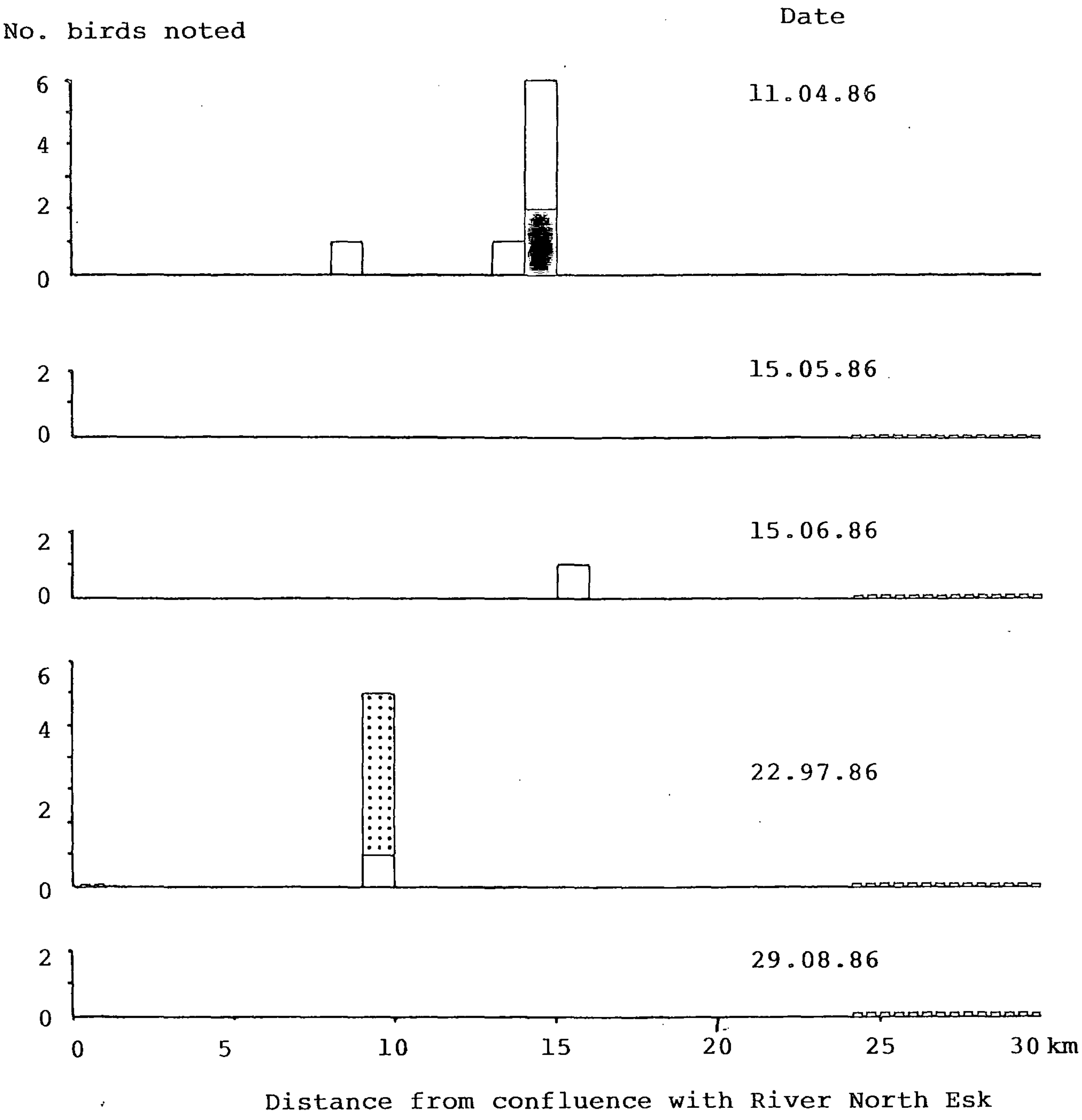


Figure 1.15 ; counts of Goosanders in the West Water, Tayside, April to August 1986 (shading as in Figures 1.8 and 1.14)

1. the birds counted on the river during spring survey work were potential breeding birds (and non-breeders),
2. birds 'disappeared' from the river when females began to incubate; the male of the pair, plus failed and non-breeders, departed to the estuary
3. the estuary flock represented a pre-moult assembly
4. this flock broke up as birds left either to undertake the moult migration, or to assemble elsewhere prior to such a movement.

1.3.3 Comparison between survey work carried out in 1984 and 1986

1.3.3.1 River Tweed

Table 1.12 contrasts the results of survey work carried out by the Northumbria Ringing Group along the main river over corresponding week-ends in mid-March of 1984 and 1986.

Three features can be noted:-

1. a more uniform distribution of birds in 1986 with a greater density along all reaches,
2. a greater incidence of paired Goosanders in 1986, with correspondingly fewer single adult males and females,

These features are consistent with the view, expressed by participants in 1984, that survey work in the spring of that year

Table 1.12. Counts of Goosanders on the main River Tweed from the sea (Berwick) to the upper reaches (Peebles) in mid-March 1984 and 1986

	1984					1986				
	P	M	I	R	T	P	M	I	R	T
Berwick to Norham	6	14	3	40	69	15	0	13	8	51
Norham to Coldstream	0	0	1	2	3	6	1	0	0	13
Coldstream to Wark	1	1	1	4	8	11	2	0	0	24
Wark to Carham	0	3	1	3	7	2	1	0	1	6
Carham to Sprouston	6	2	3	9	26	4	0	0	0	8
Sprouston to Kelso	0	3	0	1	4	9	3	1	0	22
Kelso to St. Boswells	3	7	1	15	29	12	3	1	6	34
St. Boswells to Melrose	0	0	0	2	2	2	0	0	5	9
Melrose to Gala Foot	1	0	0	0	2	2	0	0	0	4
Gala Foot to Ettrick mouth	0	0	0	0	0	6	2	0	2	16
Ettrick to Walkerburn	1	2	1	9	14	8	0	1	5	22
Walkerburn to Inverleithen	0	0	0	0	0	1	0	0	0	2
Inverleithen to Peebles	0	0	0	0	0	1	0	0	0	2
TOTAL	18	32	11	85	164	79	12	16	27	213

Key to columns;

P = number of pairs
M = number of unpaired males
I = number of immature males
R = number of unpaired redheads
T = total number of birds

was carried out too early, before many birds had reached their breeding areas.

Differences between these years may have been exaggerated as the first few months of 1986 were particularly cold, which could have resulted in numbers of wintering immigrants still being present on the river in mid-March, along with resident breeders. If these immigrants had been distributed along the length of the river, rather than concentrated in the lower reaches, the observed distribution would have resulted.

1.3.3.2 River Tay

From 17-31st March 1984 local ornithologists surveyed c240 km of the Tay system. Data were recorded as total counts over known distances of river, rather than as numbers per individual kilometre. To enable comparisons to be made with the 1986 data which were collected as counts per km (Figure 1.13), the 1986 data have been redrawn to cover stretches of river similar to those covered in 1984. These are presented in Figure 1.16. This figure shows that Goosanders were not seen in the estuary in either year (although coverage there was very limited), but that in April 1986 they were distributed more evenly along the middle reaches of the river, and were present at higher densities above the confluence of the Tay and Tummel, than in March 1984.

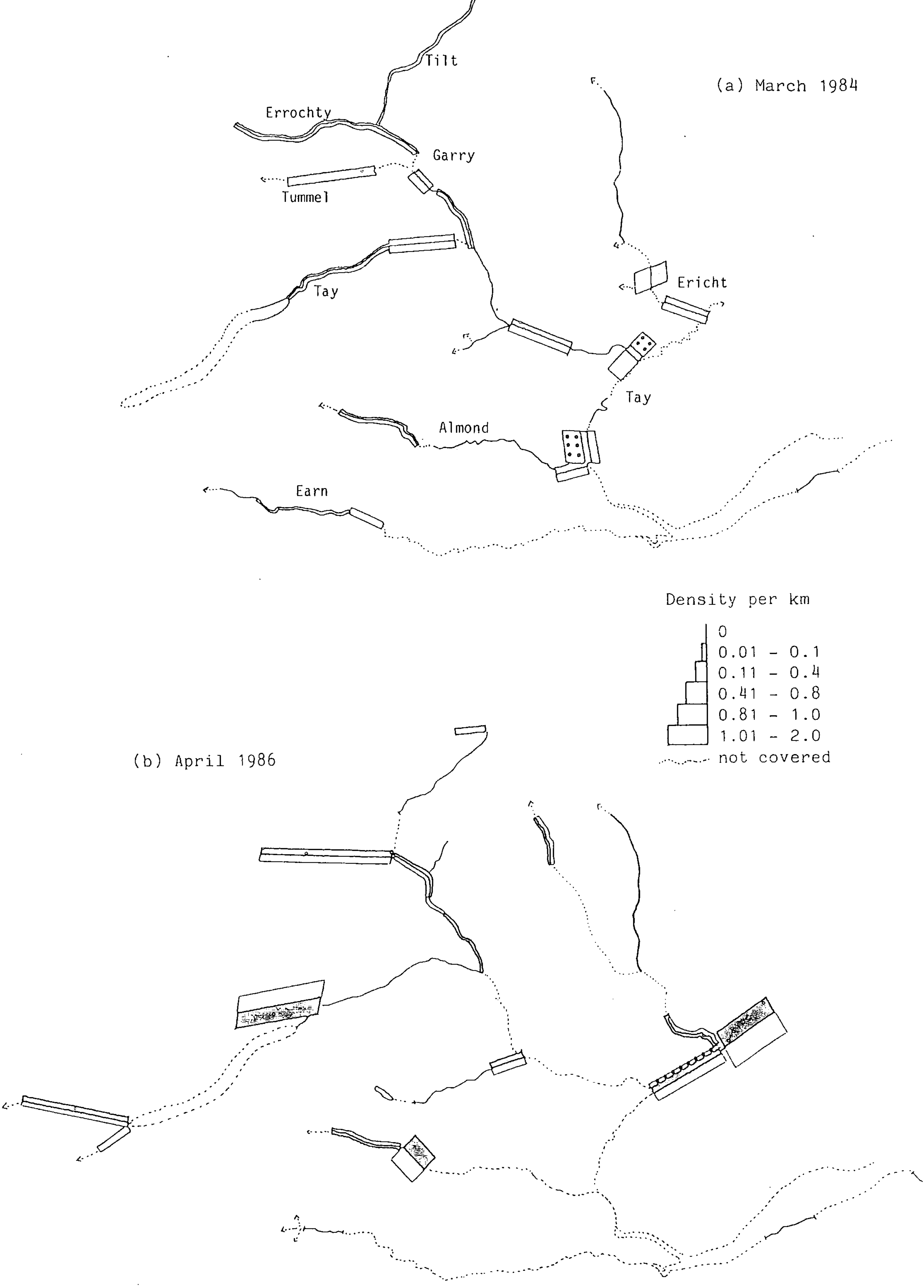


Figure 1.16 ; observed Goosander densities for river sections on the Tay system in 1984 and 1986 (shading as in Figure 1.8)

1.3.3.3 River North Esk

The density of Goosanders in each of six river sections of the North Esk above the estuary as recorded on 2nd April 1984 are presented in Figure 1.17a, and as recorded on 10th April 1986 in Figure 1.17b. These illustrate a very low density in both years, but the paucity of records prevents any comparison being made.

1.4.0 DISCUSSION

The Goosander is a relatively new addition to the list of British breeding birds, with the first confirmed nesting occurring as recently as 1871 in Perthshire. Its arrival in Britain is presumed to be a result of range extension, which took place more or less simultaneously in several parts of Europe, from a Scandinavian centre, perhaps as a result of long term climatic changes. The subsequent spread of the species in Great Britain throughout Scotland and into England, Wales and Northern Ireland, is covered in detail in Appendix One, which also contains an appraisal of current population trends in countries of the western Palearctic.

Survey data presented above provide a basis for the calculation of realistic predation pressures by Goosanders on fish populations. However, it is first necessary to assess the reliability of the results with respect to (a) the survey method

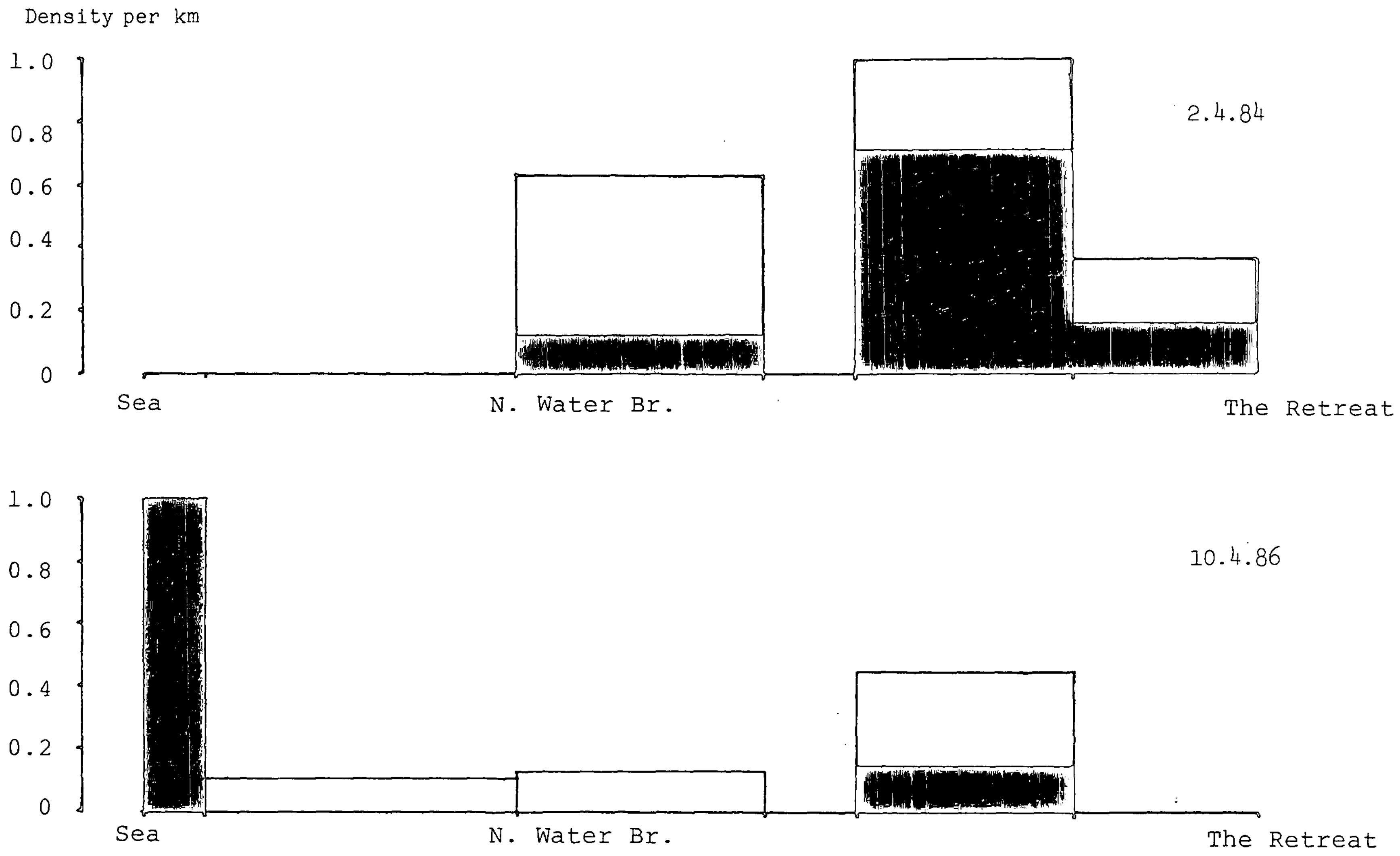


Figure 1.17 ; observed Goosander densities for sections of the River North Esk, Tayside, in 1984 and 1986
(shading as in Figure 1.8)

employed, and (b) the identification of sex/age classes of birds. This latter is important since male and female Goosanders differ markedly in size, and therefore also in potential food requirements.

1.4.1 Survey methodology

A survey methodology which was to be used by large numbers of volunteer observers needed to be devised which was (a) simple to use, and (b) required no specialist survey equipment. Instructing individuals to walk river sections, between up- and downstream limits chosen by themselves, was the only practical solution. Data collected in this way have limitations. No account could be taken of (a) variation in the ability of individual observers to accurately identify (and record) the target species, or (b) variation in the conspicuousness of birds in different habitat types, eg. sections with heavily wooded, steep banks compared to open reaches in arable areas. Variation in bird behaviour between sites is also important since the behaviour adopted will influence the probability of a bird being recorded. For example, on the River Coquet, females with broods swim up small tributaries to hide if disturbed on the main channel (Meek and Little 1977b), whereas on the rivers on which I have worked (principally the Tweed, North Tyne, Tyne, and Lune) broods either moved along the main river ahead of me or hid themselves under overhanging bankside vegetation. The effects of these various factors on counts were not quantified in the current study.

1.4.2 Species, sex and age determination

During both 1984 and 1986 survey work, observers were asked to record the occurrence of both Goosanders and Mergansers, since they have a broadly similar ecology, and in many areas are sympatric. To aid in the differentiation of these species, observers were supplied with notes on species, sex and age identification.

Correct field identification of adult male Goosanders and Mergansers during spring survey work is unlikely to have presented any problems to observers. The figures submitted are felt to provide an accurate estimate of the total population of adult males. Observers found it difficult, however, to distinguish females of the two species. In some cases this was indicated on the returned survey forms, but it is impossible for me to determine how many birds recorded as one species or the other were correctly or incorrectly identified. Similar difficulties arose with immature birds of each species.

With respect to the Goosander, another problem arose in spring survey work. At this time of year, the degree of development of the nuptial plumage of immature males is highly variable. The majority are intermediate between 'female-type' and 'adult male-type' plumages and can thus be readily assigned to the correct sex, but a small proportion are indistinguishable in the field from females. This has been established by cloacal examination of Goosanders caught for ringing at Hoselaw Loch (pers.obs.). Thus the figure for immature males obtained by summing the numbers given in the survey returns, will be an under-estimate of the actual number present. Conversely, the total for females will be an over-estimate of the actual number present.

Whereas the adult males observed were all potential breeding birds, the same cannot be said for individuals recorded as female since -

(i) a few may have been immature males incorrectly sexed

(ii) if correctly sexed, they may have been immature females which are indistinguishable in the field from adults.

The proportion of those Goosanders, of both sexes, present in breeding areas, which were capable of breeding but did not is unknown.

During the July survey period of 1984, both adult and immature male Goosanders would have been in eclipse plumage in which they superficially resemble the female. Since the eclipse plumage of adult and immature males is identical it is not possible to separate the total counts submitted into these age classes.

Additionally, confusion between males in eclipse plumage and females is likely to have occurred in some instances. However, since the incidence of males at this time of year is low (see Little and Furness 1985), incorrect recording of sex will have had little effect on total numbers. Size differences between the sexes are not obvious in the field. Nevertheless in July, the total figure for males is a minimum estimate whereas that for females is a maximum estimate.

1.4.3 Timing of survey work within the breeding season and population estimation

From changes in the observed sex ratio of birds, and observations of broods, Haapenen and Nilsson (1979) estimated the main laying periods for several waterfowl species in Sweden and suggested that since the laying dates of different females occurred over several weeks, there was no single date on which a pair-mapping technique was suitable to estimate the size of the breeding population. They also suggested that to survey immediately prior to, or during, the known main laying period for a given species was unsuitable for censusing the breeding population since small flocks of resting birds were easily confused with breeding conspecifics.

The ideal time for a census to be made, therefore, is after migratory flocks have left the breeding area and before pairs break up (Haapanen and Nilsson 1979). The interval between these events becomes shorter the further north the range of a species lies, due to compression of the season suitable for breeding at higher latitudes. Additionally, migratory flocks may move to their breeding areas at the same time as local pairs break up. For surveys conducted during the interval between these two events Haapenen and Nilsson (1979) considered that each male could be regarded as representing a breeding pair. This was similarly assumed by Poston (1974) for Shovelers (Anas clypeata) and by Dzubin (1969) for several species of dabbling duck.

The assumption that each adult male observed in the spring represents a breeding pair is valid only if the species concerned is monogamous and if non-breeding adults are absent or identifiable as such. Haapenen and Nilsson (1979) commented that in areas used by Goldeneyes Bucephala clangula and Goosanders as both moulting and breeding sites, counts of adult males in late May cannot be used to estimate the size of the breeding population. Adult male Goosanders leave breeding sites during the latter half of May and after this may be present at a site in order to complete moult rather than because they have been involved in a breeding attempt there.

In 1984, survey work to determine the number and distribution of potential breeding pairs was undertaken in the second half of March. It was anticipated that during that period, Goosanders would be present at breeding sites but that females would not have begun incubation, and males would still be in attendance.

However, many observers felt that work was carried out too early and that potential breeding sites were not fully occupied. Considering both the 1984 and 1986 data, Carter and Evans (1986) recommended that future survey work to record the breeding distribution of the Goosander (and Merganser) should be carried out in late March/early April.

Another problem affecting the accuracy of estimates of the breeding population of an area is the degree of movement of birds between adjacent suitable sites.

The summation of count data from several sites over a pre-determined survey period will provide an accurate estimate of the actual breeding population only if there is no interchange of individuals, or if all counts are done on a single day. If movement between sites has not been quantified then the accuracy of the population estimate can be improved only by making simultaneous counts at a greater number, or ideally, all, suitable sites. This could be done either with a network of observers on the ground or by the use of aerial survey techniques which, providing they do not disturb the target species into flight, will effectively (and efficiently) provide a 'simultaneous' count. As the duration of the survey period increases from zero (the simultaneous count), inaccuracies due to movement of birds between sites (if it occurs) are likely to increase.

During the aerial survey undertaken as part of this study, the Goosanders and Mergansers observed tended not to take flight at the approach of the aircraft (Dennis pers.comm.) Thus birds were neither frightened into nor out of view and their distribution on the river was not affected. Whereas the aerial survey undoubtedly located some birds in areas inaccessible to ground observers, it must have missed birds obscured beneath overhanging trees, for example, which would have been detected by a thorough ground count.

For a pre-breeding season census, the aerial survey conducted in 1984 was considered successful and cost-effective. Indeed for large rivers such as the Spey, Findhorn, Dee, Tay and Tweed, this method may be the most suitable. However, further detailed calibration with simultaneous ground counts is needed.

No aerial survey was attempted during the July survey period since growth of vegetation would have prevented any meaningful count from being conducted.

On waters where persecution is intense the presence of an observer almost invariably induces the birds to take flight but typically they return to alight on the river when out of sight of the observer. On rivers where the species is largely unpersecuted, birds tolerate a much closer approach by an observer and tend to swim away rather than take flight. This variation in behaviour has important implications. Where persecution occurs, in counts of contiguous stretches, there will be an increased probability of recording the same birds twice (or more) thereby over-estimating the actual number present. It is not possible, unfortunately, to assess the degree to which this occurs.

1.4.4 Daily and diurnal variation in Goosander density

For the spring survey period results presented in section 1.3.1.1 suggested, based on repeat visits to the same stretch, that on average, any single count recorded only about 60% of birds present. The corresponding figure for broods, based on three repeat visits, was also close to 60%. From count data presented by Tyler (1986) for three site visits to a stretch of the River Irfon (Powys) from 11-25th March, the mean percentage of Goosanders noted on any single date was 73%. For a stretch of the River Severn, counted five times between 27th March and 15th April, the corresponding value was 57%.

These percentage values assume that over the range of dates between first and last counts, the maximum number of birds recorded was the actual number present throughout that period. The longer the time period over which the repeat counts are made the greater the chance that this assumption is invalid. Additionally the greater the number of repeat counts made the greater the range between minimum and maximum values will become. If the basic assumption is true variation in the number of birds noted on repeat visits is the result of variation in survey efficiency. Standardisation of the time of day at which counts are made is likely to be important in reducing variation in the numbers of birds recorded over repeat visits. Data presented later (Chapter Four) suggest that birds move from morning feeding sites on rivers to standing water loafing or roosting sites in the afternoon at least during some seasons. Thus a river count made early in the day could be expected to record higher numbers of Goosanders than the same stretch surveyed at midday or in late afternoon.

Prevailing weather conditions may both directly and indirectly influence survey efficiency. Not only do windy and rainy conditions reduce visibility but they made birds generally more difficult to locate. Either they were absent from sites where they were otherwise regularly observed, or they tended to be found closer to river banks, under overhanging vegetation or in sheltered stream mouths. These effects were not quantified. Weather may indirectly affect Goosander numbers and distribution at a site through the effects of precipitation on river flow and river height. Murray (pers.comm.) noted from the River Whiteadder in 1986 that 'few birds are in evidence during spates'. My own observations agree with this.

Birds might be expected to leave a site if higher flows adversely affected feeding conditions, for example by increasing water turbidity, and/or causing prey species to seek more sheltered river bed stations, or to be displaced. Several studies support this suggestion. For example Ottoway and Clarke (1981) noted that the vulnerability of young salmon and trout to downstream displacement by high flows varied with the age of the fish. This was shown also for non-salmonids by Schlosser (1985) who found that changes in stream flow over time strongly influenced the structure of the fish community through an effect on the density, species richness and species composition of juvenile fish. More subtle effects of increased flow also occur. For example, increased water velocity leads to a reduction in both the size of the feeding territory of salmon and total fish density (Kalleberg 1958). However, Stradmeyer and Thorpe (1987) showed that feeding territory size increased, and presumably density decreased, on rainy days. Such changes can be related to flow mediated variation in the availability of drift particles.

1.4.5 Regional variations in Goosander density in 1984

The analyses presented above (section 1.3.1.4) showed clearly that although there was no statistically significant regional variation in Goosander density in the spring, there was a highly significant regional variation in brood density in the summer. Differences in regional distribution between spring and summer, however, were not statistically significant.

Several interpretations of this are possible. Firstly, spring coverage may not have accurately assessed the density of actual breeding birds even though the distribution and numbers of potential pairs were indicated. This is consistent with the results of analyses presented in section 1.3.3.1 which showed no statistically significant relationships between the spring density of adults and subsequent brood density.

If (a) all potential breeding pairs noted in the spring bred, ie. non-breeders (resident or migrant) were absent, (b) all birds present were recorded, ie. survey efficiency was 100%, (c) there were no losses of clutches and broods, and (d) no persecution occurred, then the number of broods observed should have equalled the spring estimate of the number of pairs, if spring coverage was carried out at the optimum time. Because none of these conditions is likely to have been met, however, the number of broods observed was expected to be less than the spring estimate of pairs, even if survey efficiency was comparable in both periods. This has already been shown (see section 1.3.1 and Figure 1.6).

Differences in regional variation between spring and summer will be affected by any regional variation in survey efficiency, the proportion of potential pairs which make a nesting attempt, nest success and persecution. These factors have not been quantified. Persecution in particular is likely to vary between the areas of authority of the various District Salmon Fishery Boards.

1.4.6 Within-river variation in Goosander density

The analyses performed in section 1.3.1.5 indicated that in 1984 there was no significant difference in the density per km of Goosanders betweem 'lower', 'middle' and 'upper' reaches of those main rivers where comprehensive data were available (Table 1.7a). This may be a reflection of the crude method employed to differentiate the reaches (simply on the basis, for each river, of a third of the total length surveyed). However, the data as they stand do not allow a more rigourous approach to be adopted. Results may be interpreted as indicating a random distribution of birds along the river in mid-March, perhaps because birds are able to find suitable breeding sites along the length of the main rivers considered, or because survey work was carried out too early in the year and recorded the distribution of resident (and migrant) Goosanders before they occupied nesting areas elsewhere. This cannot be tested using the 1984 data.

Results from coverage of the Tweed in mid-March and again in April 1986 suggest that birds moved away from the main river between these dates and that a large proportion of birds shifted to the Teviot, a major tributary (see section 1.3.2.1). Analysis of count values of Goosanders recorded in each individual kilometre surveyed in that year show a highly clumped distribution not only on the main river but also on the Teviot, Ettrick/Yarrow and Whiteadder. For the Tweed itself, the mean densities of birds amongst contiguous 10km stretches indicated a clumped distribution ($X^2=44.20$, $p<0.01$). This could have arisen for several reasons; variations in (i) habitat type, (ii) food availability and (iii) persecution.

Little detailed work on habitat selection by Goosanders has been carried out. Tyler (1986) collected values for mean river width, percentage of the site which was riffle habitat, the percentage of the river bed which was (a) rock, (b) mud or (c) gravel, and the percentage of deciduous cover on the banks, for 92 individual kilometre sections where Goosanders were recorded and 86 sections selected at random where birds were not recorded. Only the first of these habitat parameters showed any significant difference between the two groups of sites; sites with birds had a mean width of 19.0m (SE=1.11) and sites without birds had a mean width of 15.9m (SE=0.99). Such results may be entirely spurious however since Tyler (1986) pointed out that river sections surveyed were selected a priori for their suitability for Goosanders.

In addition to bird count data collected in 1987 during the B.T.O. national sawbill survey for approximately 10,000km of rivers, estimates were also made within each kilometre division of (a) mean river width, (b) predominant water type eg. riffle, and (c) the extent of bankside tree cover. These data have not yet been analysed (Carter in prep.).

Although Chapter Four shows that rivers are preferred feeding sites, data are not available to investigate habitat selection at a more detailed level. Observations suggest however that head-under-searches in shallow riffle areas are the preferred feeding method and location. If this is true then a greater incidence of Goosanders would be expected in individual km sections where riffle habitats predominated over other water types. Data to test this were collected during the B.T.O.'s national sawbill survey in the spring and summer of 1987, although results are not yet available (Carter in prep.).

The relationship between spatial variation in foraging behaviour and spatial variation in the fish population within a river (for example, as shown by Egglishaw and Shackley 1982) according to depth, micro-habitat, etc., has not been studied.

1.4.7 The use and value of density determinations

Calculation of bird density per km from data collected in 1986 necessarily produced much greater values for some individual km sections than if density had been determined over the entire stretch covered. This has important implications with respect to licencing policy for the shooting of Goosanders (see main 'INTRODUCTION'). If a threshold value of density above which damage to fish stocks is predicted to occur, has been set, then the unit over which it relates must be clearly defined.

Consider a hypothetical example of a river of 100km, surveyed completely, where 10 Goosander were recorded in km 15 (numbered from the source). Assume that the threshold value above which sawbill density is considered to cause significant damage to the fishery is 0.5 birds per km. If the unit over which densities are calculated is a 10km length, then the density of birds in the first section will be 0, in the second 1.0 and in the remainder, 0. If however, the units considered are 'upper', 'middle' and 'lower' river, each of equal length, then the density of birds in the first is 0.3, the second, 0, and the third, 0. For the river as a whole Goosander density is 0.1 per km, well below the threshold.

An alternative approach would be to calculate densities per unit area rather than per unit length of waterway since the predation pressure (and potential impact) of a given number of birds on a single kilometre section will be lower on a river of 30m wide than on a river 10m wide for example. This idea was adopted by Elson (1962) who suggested that the incidence of Goosanders should not exceed one bird per 20ha of water if "reasonably full smolt output is desired".

It is clearly important in view of these considerations that the correct unit of waterway is chosen. This could be complete tributaries, tributary systems or entire watersheds. However, it may be more meaningful, from the fisheries point of view, to divide the river into spawning, nursery and rearing areas and to determine predator density for each in turn. That such areas overlap would complicate this approach, however. In any case, it would not be possible to use the same threshold value for each area since the effect of depredations on final fish production, measured as smolt escapement for example, is dependent on the life stage of fish taken (see Chapter Six).

1.5.0 SUMMARY

An assessment was made of the distribution of the Goosander between and within selected rivers in Scotland and the Borders in 1984 and 1986.

A more detailed appraisal of results from simultaneous ground and aerial counts is needed to evaluate the cost-effectiveness of each technique.

Repeat counts of the same stretch of waterway suggested that the mean percentage of birds present there that were recorded on a single site visit was approximately 60%. Possible reasons for variations in the number of birds recorded at a site are considered.

In 1984, using ground count data, the overall density of adult males, immature males and 'redheads' was 0.17, 0.02 and 0.22 per km respectively. Corresponding values for the summer of that year were 0.02, 0.00 and 0.10 per km.

Data collected in 1984 showed no statistically significant differences in the regional densities of Goosanders in the spring, although data suggested that density declined from south to north. Significant differences between regions were noted for brood densities. These were least in north-east Scotland and greatest in the highland area to the east of the Great Glen. Using the same data set no statistically significant variation in the distribution of Goosanders between 'upper', 'middle', and 'lower' river sections was found in either the spring or summer. However, the method of subdivision of the data was probably too simple.

More detailed data collected in 1986 showed that on the Tweed river system in the spring Goosanders showed a strongly clumped distribution. Possible reasons for this are discussed.

Detailed information on the habitat characteristics of river stretches where Goosanders are noted and where they are recorded as absent may provide an insight into habitat selection. However, the distribution of birds is likely to be strongly influenced by disturbance and persecution. Apparently suitable areas may not support birds for this reason. Quantification of such factors has not been possible.

CHAPTER TWO ;

GROWTH, FOOD, AND ENERGY REQUIREMENTS OF CAPTIVE-REARED GOOSANDERS

2.1.0 INTRODUCTION

The determination of the daily food (and energy) requirements of a predator is central to an accurate assessment of its potential impact on populations of its prey species. Unfortunately it is not possible, under field conditions, to determine foraging success or food intake rate of wild Goosanders since all but the largest prey items are ingested underwater.

Measurements of captive birds provide an alternative approach which I used in this study. However, care needs to be taken in the interpretation of the results obtained from birds reared in captivity since the individuals will necessarily be held in an artificial and controlled environment where they will be protected (generally) from the most adverse weather conditions, and where they do not have to expend energy in extensive searches for food or to escape predation. Consequently energetic costs of maintenance (but not growth) will be reduced. The effect of confinement per se must also be considered. Prescott (1981) showed that the behaviour of Common Eiders (Somateria mollissima) was dramatically altered by 'spatial restriction'; in a large outdoor enclosure, locomotion and feeding were significantly more frequent than in a smaller indoor pen where resting predominated.

Such differences have important implications for energetic studies when extrapolations to the energy requirements of wild birds have to be made from measures made under captive conditions. The daily food (energy) intake of a captive bird must be regarded as a minimum value.

In this chapter I present the results of studies to estimate the changes in food consumption and energy requirements of Goosanders reared in captivity up to the time of fledging. These results are compared with similar studies carried out by White (1957), Latta and Sharkey (1966), and Wood (1987b) on the American subspecies of the Goosander, and by Atkinson and Hewitt (1978) on Red-breasted Mergansers.

2.2.0 METHODS

2.2.1 Egg collection and rearing Goosanders in captivity

Goosander eggs were collected under N.C.C. licence from sites in Northumberland and Cumbria during the springs of 1983 and 1984, and taken to the Wildfowl Trust, Washington, Tyne and Wear in an insulated box. Incubation was completed in a Schumacher 250 incubator.

In 1983, 16 eggs were collected from two sites, but of these, only three (from the same clutch) hatched successfully, a single duckling on 21st June and a further two on 22nd June. Initially the ducklings were maintained at the Wildfowl Trust in heated indoor quarters but subsequently were moved to an outdoor coop, and finally into a fenced grassed area with access to a small concrete pool and shelter.

In 1984 eggs were again collected from two sites, both in Northumberland. Four eggs from the first hatched on 15th June and three from the second on 16th June. Coincident with these hatchings the Wildfowl Trust received a brood of eight ducklings collected in the Tyne valley, where the female had been killed by traffic whilst leading them to water. Of these birds, which were estimated to have hatched on 11th June, four were placed with those hatched in captivity, and the remainder left for rearing at the Wildfowl Trust.

Thus in 1984 the 'brood' of ducklings available for study initially comprised four birds of wild origin estimated to have hatched on 11th June, four hatched in captivity on 15th June, and three hatched on 16th June. This 'brood' was maintained in heated indoor quarters at the University, and later transferred to an aviary with access to shelter and a small polythene lined pool. On occasions when birds could not be fed regularly there, they were returned temporarily to a holding pen at the Wildfowl Trust. They were transferred there permanently in early December 1984.

During both years ducklings were fed initially on a mixture of grated egg and poultry crumbs supplemented with mealworms. As the ducklings increased in size a range of fish species were presented (dead) as food either whole or chopped. These were whitebait, cod (Gadus morrhua), sand eel (Ammodytes spp.), saithe (Pollachius virens), sprat (Sprattus sprattus) and whiting (Merlangus merlangus). The species of fish presented on any given date was dependent largely on availability. Birds were fed ad libitum. The ducklings were fed at least twice daily, at approximately 0900 and 1800 hours. (For captive reared Red-breasted Merganser, Atkinson and Hewitt (1978) reported that the differences in food consumption recorded under either a fixed feeding, or ad libitum, feeding regime were negligible.)

Total body mass (measured to the nearest g), head plus bill, bill alone, and tarsus (all measured to the nearest 0.5 mm) were recorded regularly for the birds hatched in 1984. These data were also collected for the four Goosander ducklings of wild origin which were reared at the Wildfowl Trust. Only data on total body mass is available for the 1983 birds.

Food intake was measured only in 1984. The total wet weight of food presented at each feed was measured to the nearest g, and the food remaining at the time of the next feed was also weighed. Thus the total weight of food ingested per day by the entire brood could be determined. Mean intakes per bird were then calculated. To have measured the intake per individual would have necessitated isolating each from its conspecifics. This was tried but proved very stressful to the birds. Thus it was felt that average intake gave a better estimation of intake per bird than would the measured intake of an isolated stressed duckling.

For the purpose of subsequent analyses of food consumption, the brood was taken to comprise ducklings of the same average age hatched on 15th June.

2.2.2 Calorific values of food materials

Samples of each food material presented to the ducklings were retained and their calorific values determined using a ballistic bomb calorimeter (Gallenkamp model).

Sub-samples of wet fish of the species listed above, and of a sample of wild caught salmon parr collected by electrofishing in the River South Tyne, were dried in a vacuum oven at 50^{o} C. However, even at this low temperature it was discovered that some of the material lost lipid due to melting. Since a calorific value determination of the solid material remaining after such drying would have under-estimated the true value for that fish species, the method was modified and further sub-samples were vacuum oven-dried for several weeks at 30^{o} C. No exudation of melted lipid was observed to occur.

2.3.0 RESULTS

2.3.1 Calorific value of food

The calorific values of fish fed to captive Goosanders and of the sample of salmon parr are presented in Table 2.1.

2.3.2 Growth rates of captive ducklings

For Goosanders reared at the University, Figure 2.1 shows the number of ducklings alive at different ages.

Figure 2.2 shows the growth rate, in terms of total body mass of the single duckling reared in 1983. Figures 2.3-2.8 show the growth rates of all birds reared in 1984 with respect to (a) total body mass, (b) head plus bill length, (c) bill length, and (d) tarsus length.

For ducklings hatched in captivity, body mass decreased by between 4 and 8.5g (7.7-21.3% of initial body weight) up to an age of approximately five days. (These figures are derived from birds which recovered after the loss; many others did not and died at this stage.) A similar post-hatching weight loss was recorded for Ruddy Duck (Oxyura jamaciensis) by Siegfried (1973), and for Tufted Duck (Aythya fuligula) by Kear (1970).

Subsequent to this recession, weight increased rapidly up to days 66-78, ie. when the ducklings reached 9-11 weeks old. Data

Table 2.1 ; Calorific values of fish fed to captive Goosanders and of wild caught salmon parr.

Fish type	n	mean kcal/g dry weight	S.E.
Whitebait	6	5.67	0.15
Cod	12	5.31	0.13
Sand Eel	6	4.54	0.11
Saithe	8	5.83	0.11
Whiting	6	5.56	0.26
Sprat	6	6.48	0.26
Salmon	16	6.10	0.13

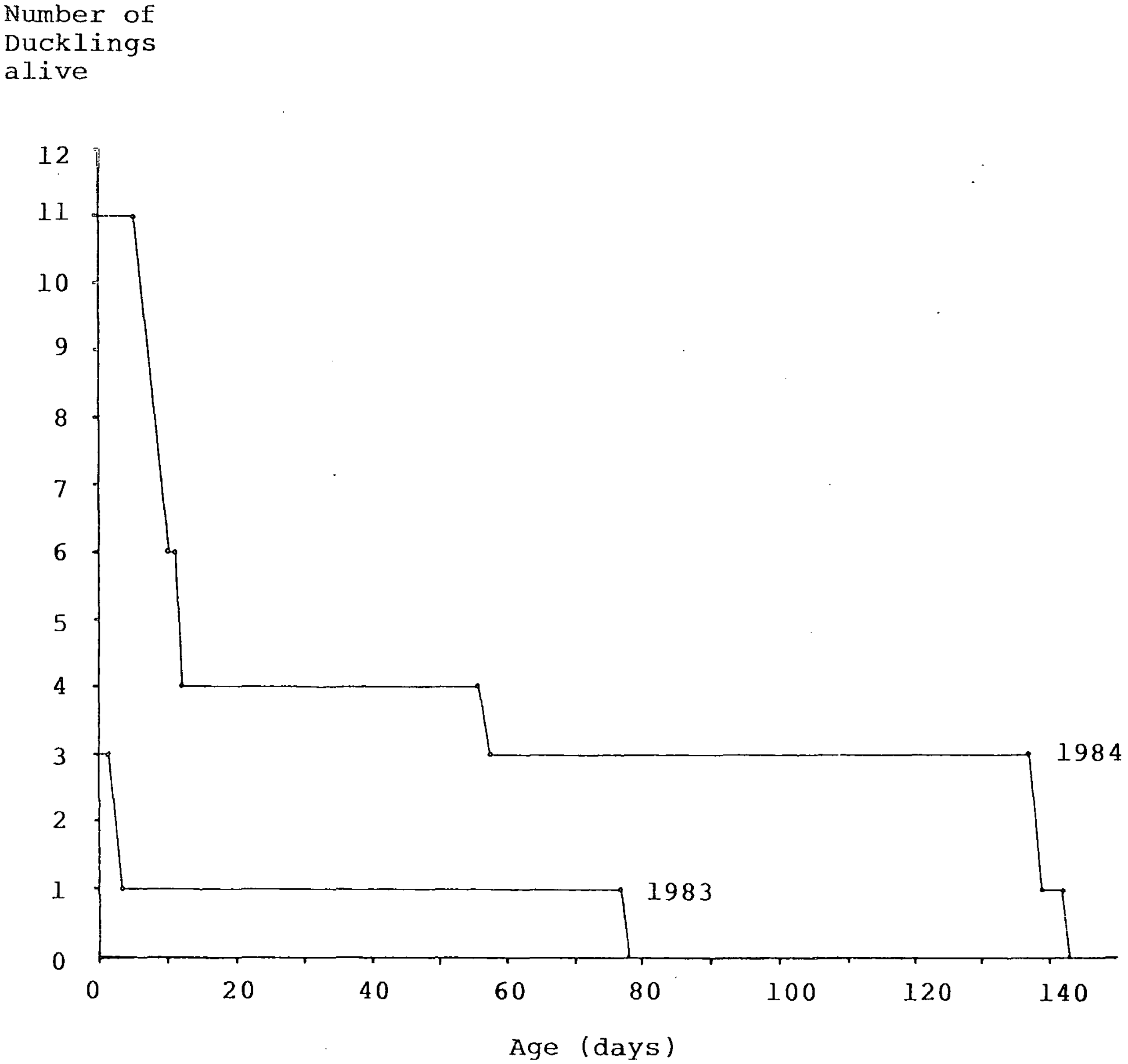


Figure 2.1 ; number of ducklings in captivity

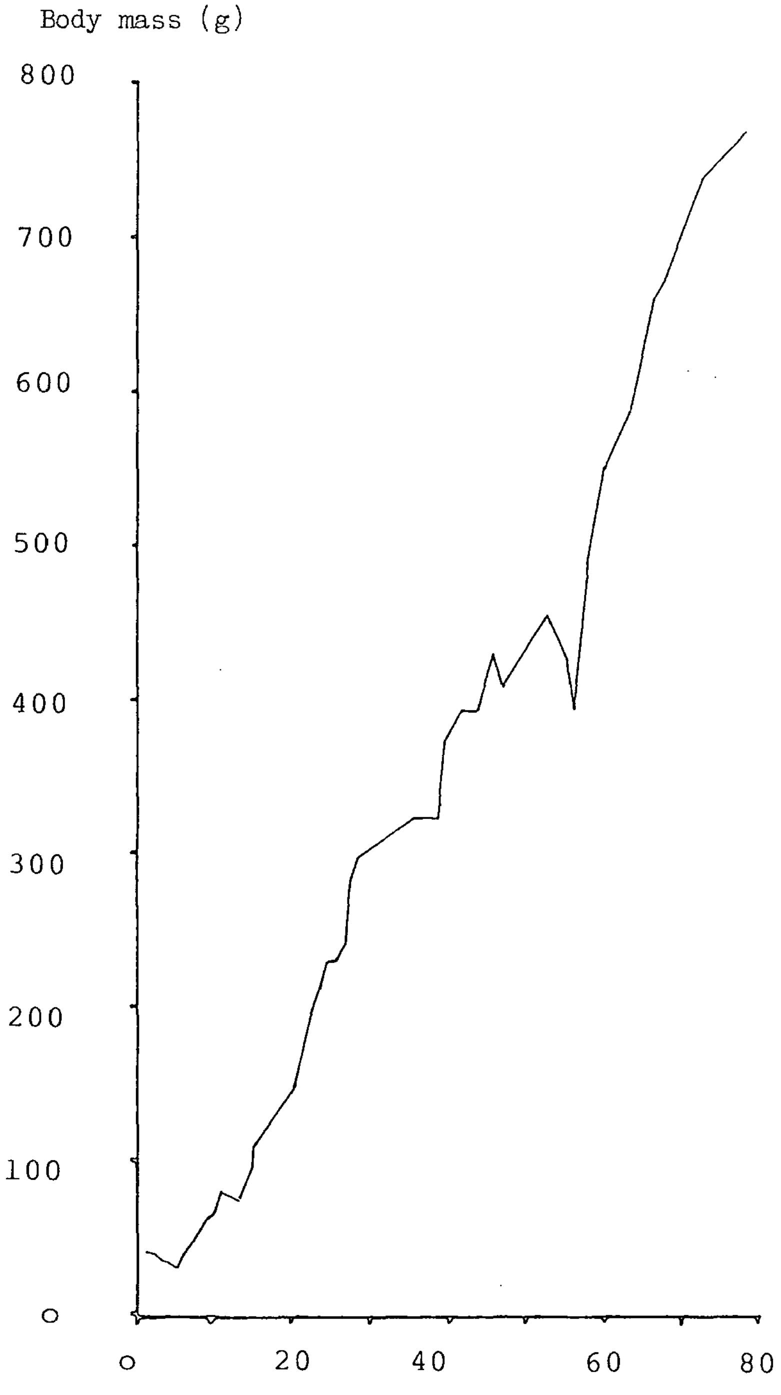


Figure 2.2 ; growth rate (total body mass) of a single Goosander duckling reared in 1983

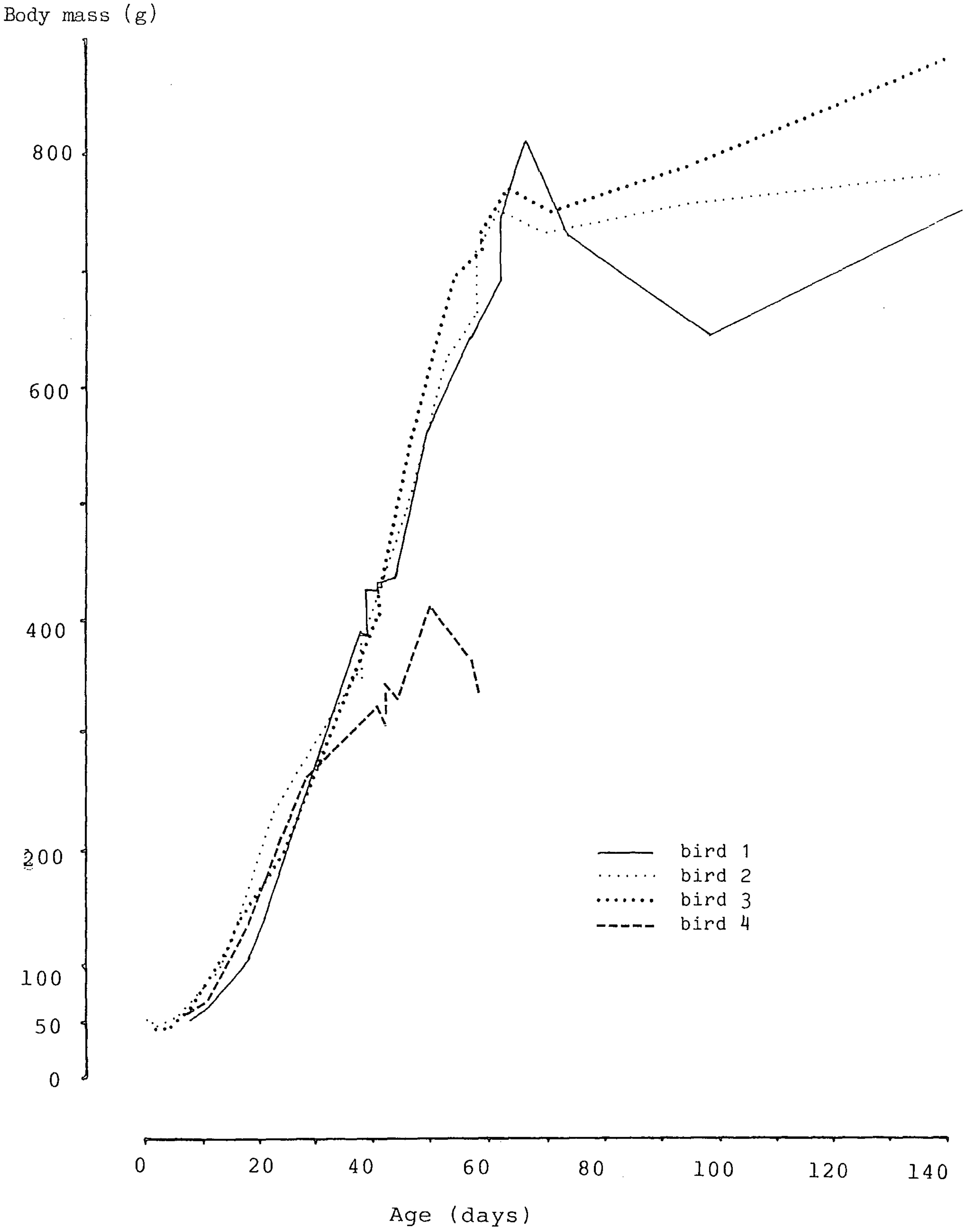


Figure 2.3 ; growth rate (total body mass) of Goosander ducklings reared in 1984

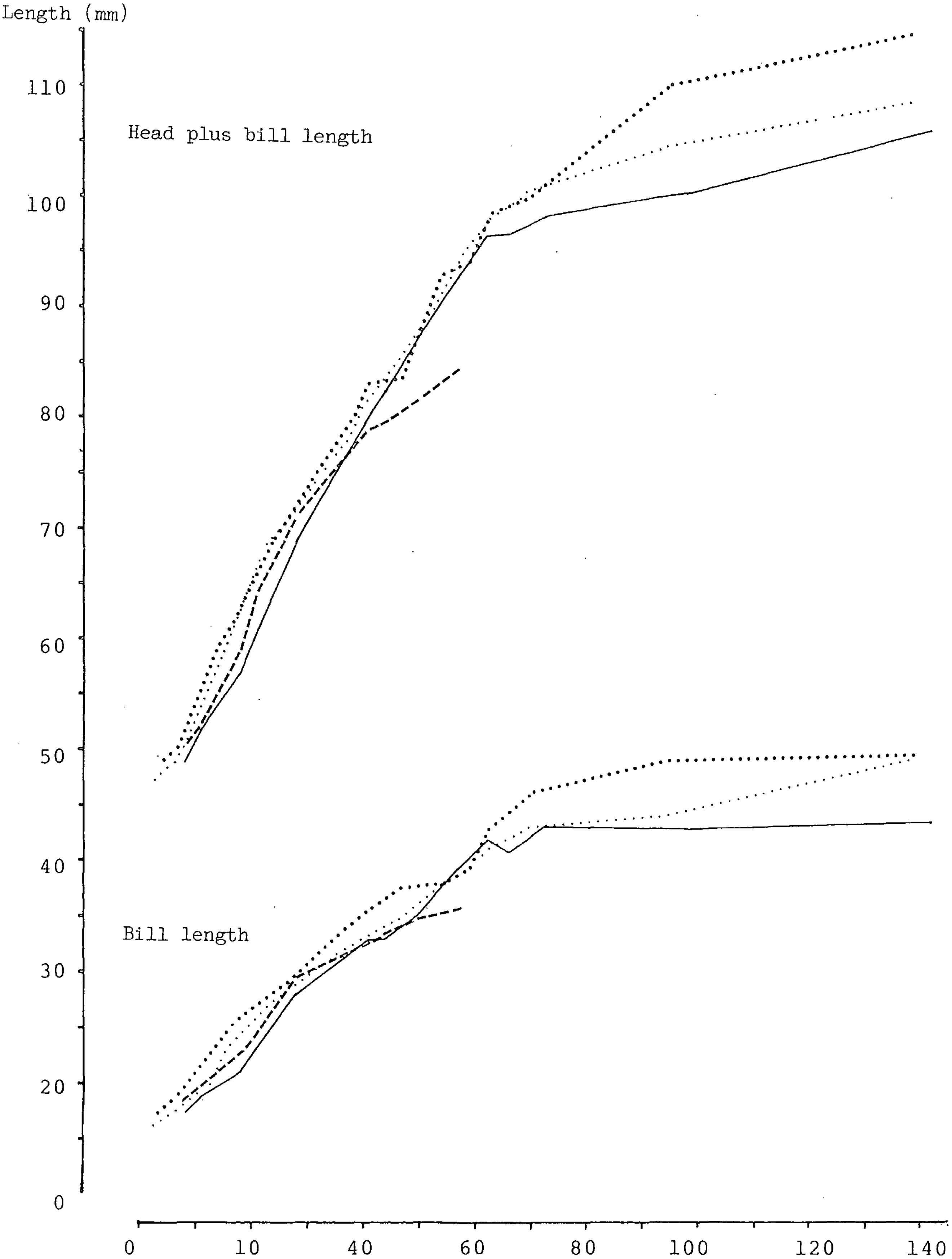


Figure 2.4 ; growth of head plus bill, and bill alone, of Goosander ducklings reared in 1984 (key as in Figure 2.3)

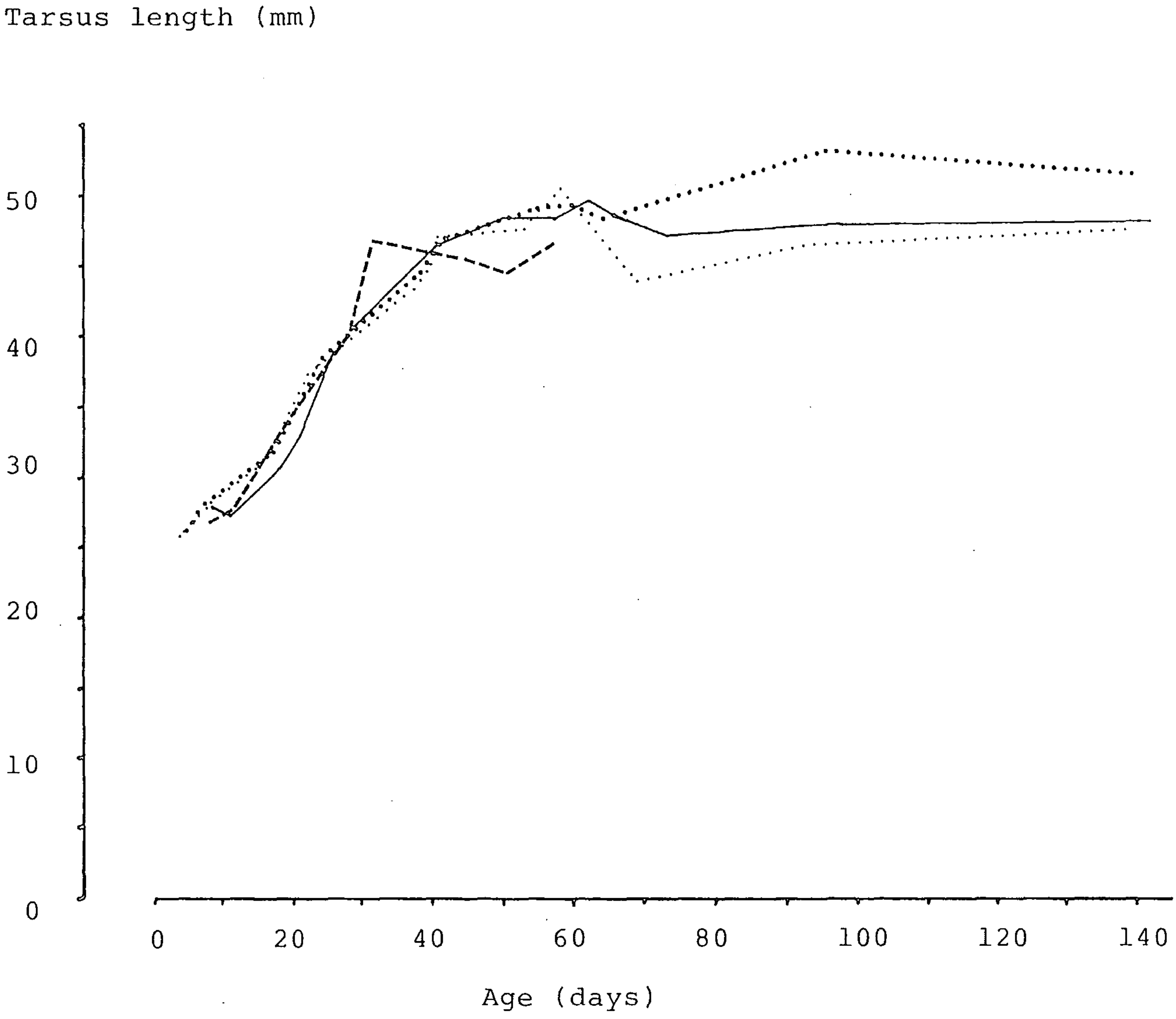


Figure 2.5 ; growth of tarsus of Goosander ducklings reared in 1984
(key as in Figure 2.3)

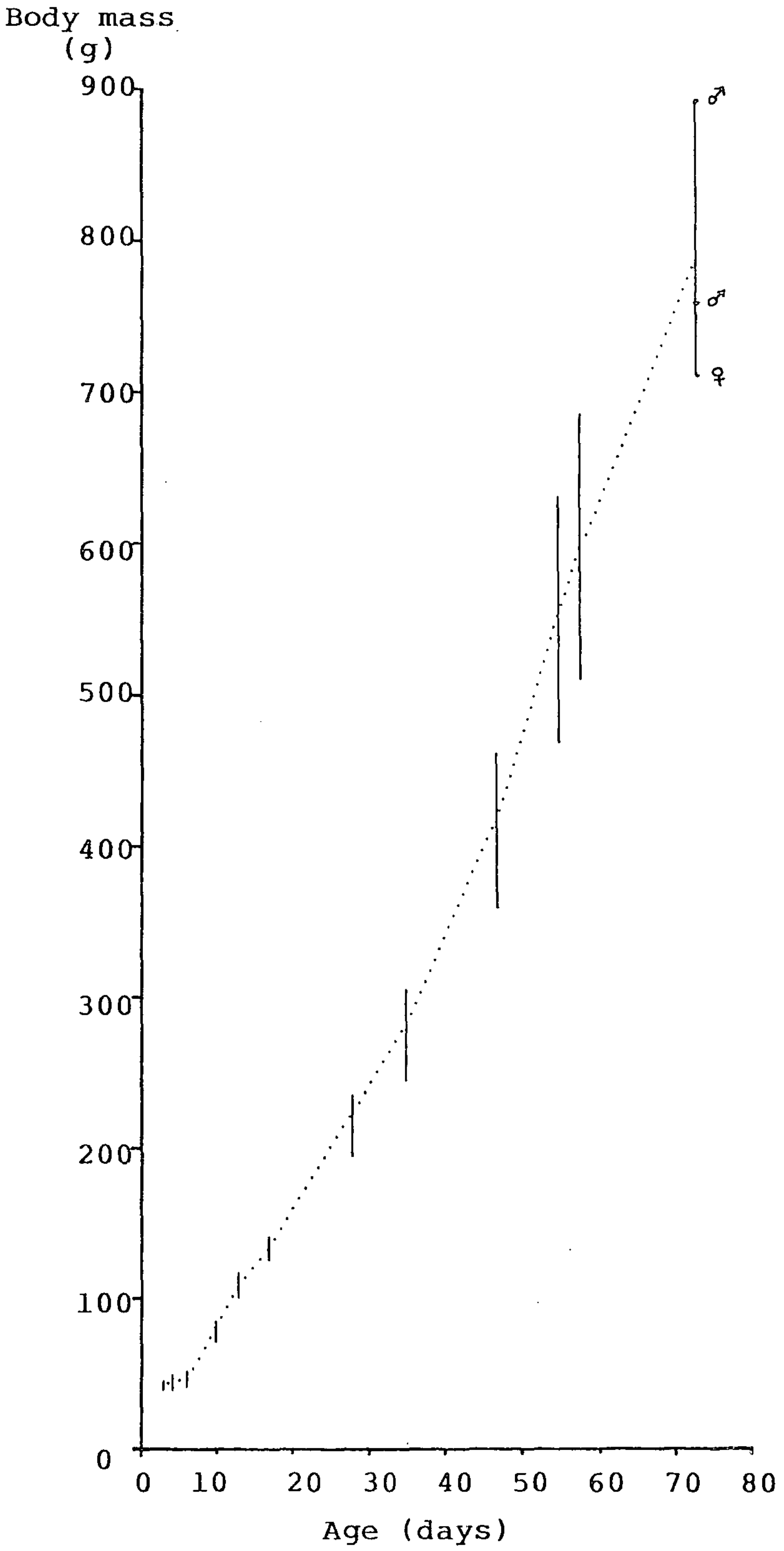


Figure 2.6 ; growth rate (total body mass) of Goosander ducklings reared by the Wildfowl Trust in 1984
(dotted line joins mean values, lines indicate observed range)

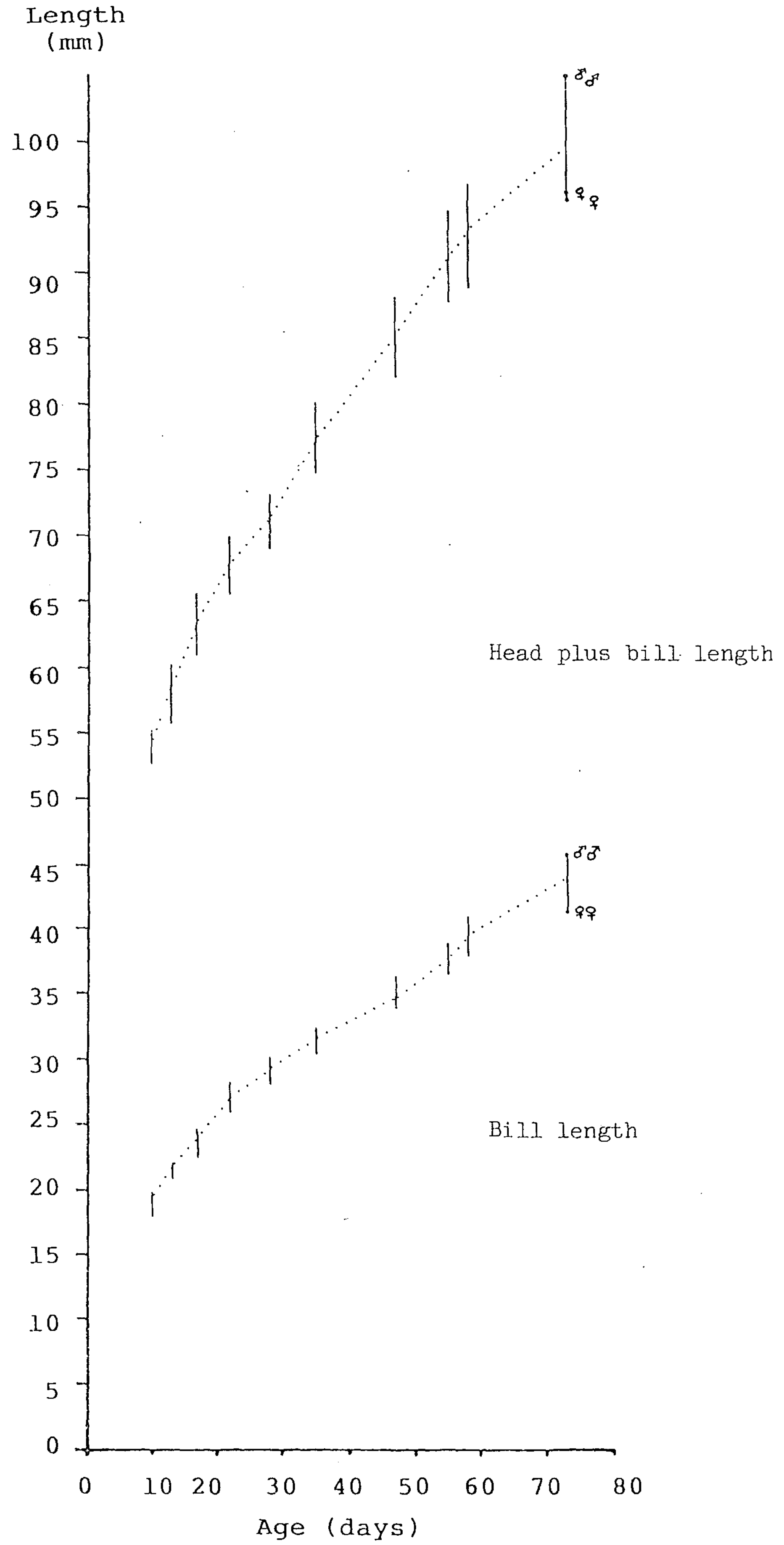


Figure 2.7 ; growth of head plus bill length, and bill alone, of Goosander ducklings reared in 1984 by the Wildfowl Trust

(see legend on Figure 2.6)

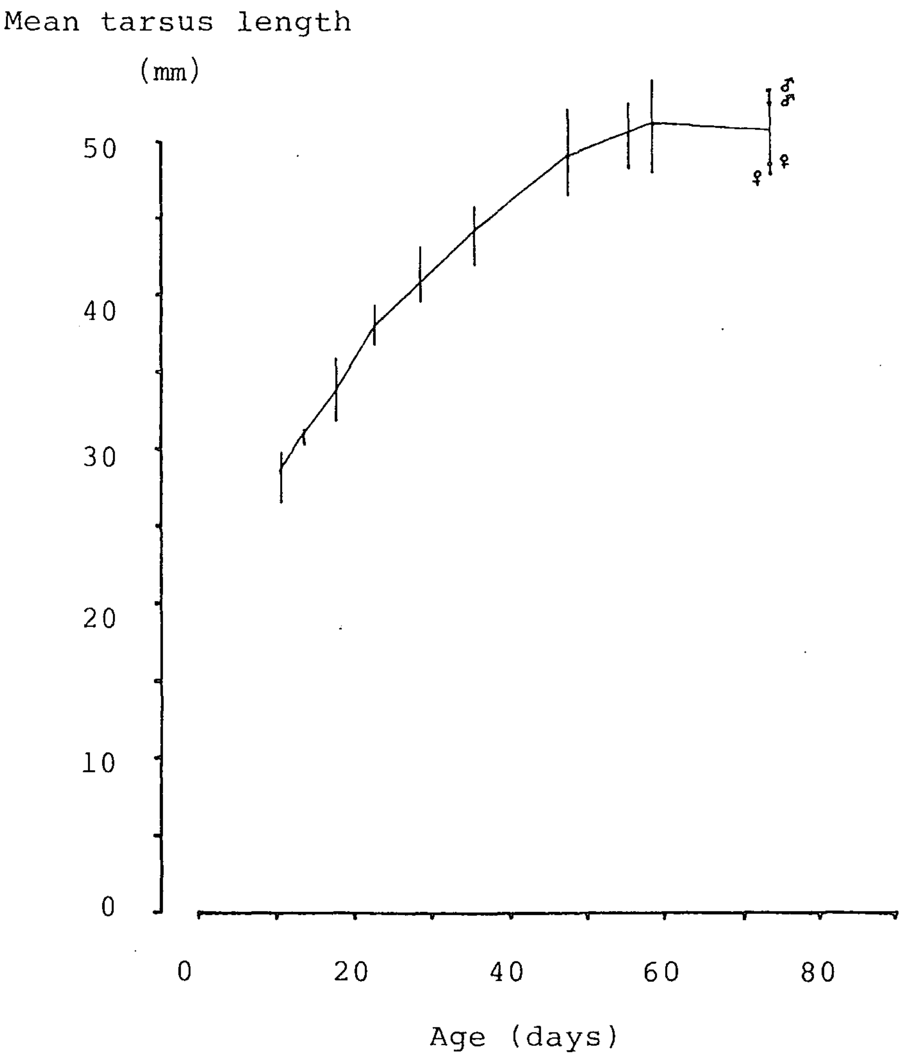


Figure 2.8 ; growth of tarsus of Goosander ducklings reared by the Wildfowl Trust in 1984

(see legend on Figure 2.6)

from 1984 indicate that this was followed in all three ducklings by a slight drop in weight but then by a further much shallower rate of increase. This weight recession is approximately coincident with fledging. A similar pattern was reported for captive reared Red-breasted Mergansers (Atkinson and Hewitt 1978). This is discussed in section 2.4.2 below. Data indicate a mean fledging weight of c800g which is approximately 61% of the autumn weight of adult females (see Table 3.7). This compares with 66% of adult weight attained by fledging Lesser Scaup (<u>Aythya affinis</u>) and 76% by fledging Canvasbacks (<u>Aythya vallisneria</u>) (Lightbody and Ankney 1984).

Growth of head plus bill occurred at a steady rate until approximately the time of fledging when it was approximately 80% of adult length. The rate of increase slowed thereafter. A similar pattern was shown by measurements of bill length alone which, by the time of fledging had attained approximately 86% of adult length. By contrast the tarsus had reached full adult length by this time.

Data from birds reared at the Wildfowl Trust show that the growth rates of males was greater than that of females and that, when two to three weeks old, the sexes could be distinguished on the basis of body weight and the biometrics used here.

2.3.3 Food consumption of Goosander ducklings during growth

(a) Change in daily intake with age

Figure 2.9 shows the mean wet weight of fish consumed per duckling on each day between 24th July and 9th December, and Figure 2.10 indicates the composition of the diet. Where data are lacking for a particular day (or days), the preceding and succeeding points on the graph are joined with a dotted rather than a solid line. Mean daily calorific intake (kcal) per duckling (using the values presented in Table 2.1) is also presented in Figure 2.9.

No data on food consumption are available before 24th July when the ducklings were approximately five weeks old.

As the mean weight of the ducklings increased up to mid-August, both the mean weight of food ingested/duckling/day and the mean energy ingested/duckling/day increased. In terms of biomass, food consumption increased from approximately 26% to almost 48% of mean body weight between 24th July and 17th August. After this there was a dramatic decline in both the daily wet weight of food consumed per bird and daily energy ingested. Figure 2.10 shows that this was associated with a shift from a diet of whitebait to one of whiting and sprat. With a further shift to saithe in early September, intake (wet weight and energy) increased. Ducklings were not weighed regularly over this period; the birds looked in poor condition and since they were maintained in a large pen at the Wildfowl Trust at that time, both capture and handling would

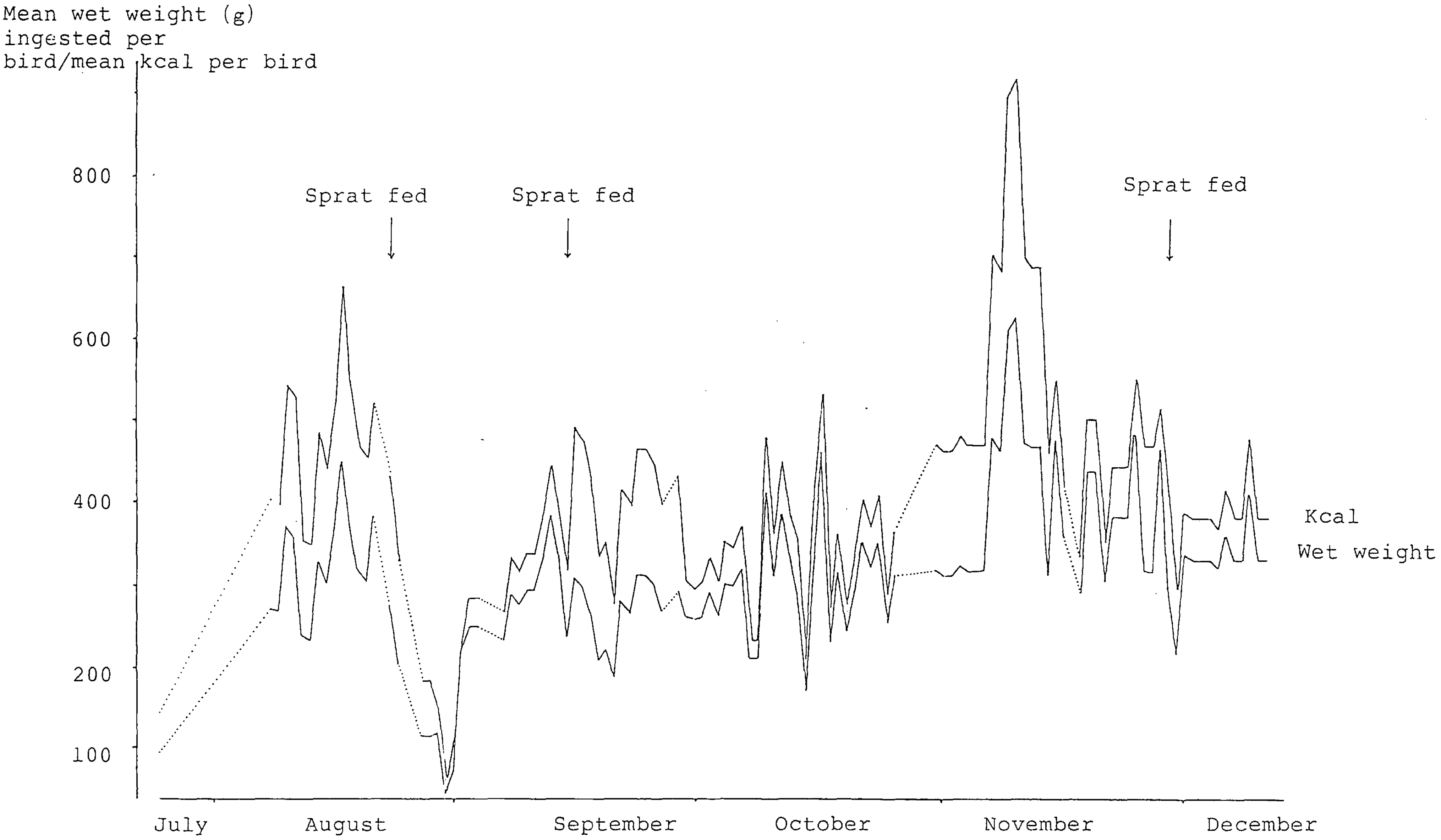


Figure 2. 9 ; food consumption (g wet wt/day) and energy intake (kcal/day) for ducklings reared in 1984

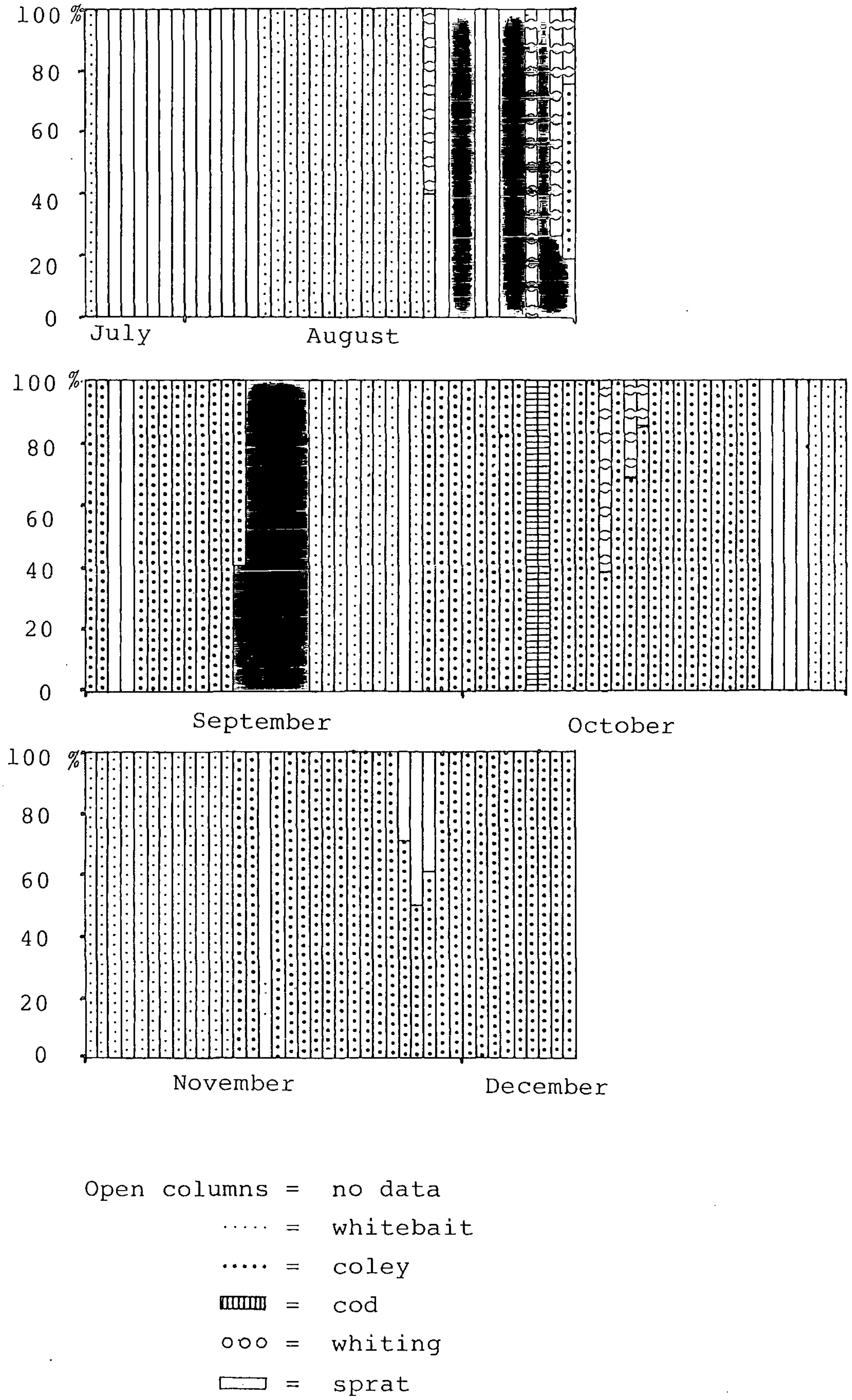


Figure 2.10 ; diet composition of Goosander ducklings reared in 1984

have been very stressful. The Goosanders reared from soon after hatching by the Wildfowl Trust similarly appeared in poor condition on a sprat diet.

From early September food (energy) intake fluctuated widely. Limited data suggest that daily food consumption, expressed as a percentage of body weight, decreased to 30-40%. On three occasions the 'troughs' in intake were associated with the presentation of sprat.

The relationship between mean body mass of ducklings and mean wet weight of fish ingested per bird can be compared for specific dates as shown in Table 2.2. Although values indicate a reduced intake, in terms of both biomass and energy, on a diet of sprat, it is not possible to determine if this was the result of the shift in type of food offered or to stress associated with a change in housing conditions.

(To test if food consumption at a given age (and mass) is affected by the calorific value or biomass of prey taken, or is independent of it, it would have been best to present different groups of ducklings (of the same age), with different prey types, assuming that the energetic demands of each group were the same. Data are inadequate to test this.)

(b) Change in biomass conversion rate with age

For the periods 8-13th August, and 14-17th August, data are complete enough to allow the biomass 'conversion rate' to be determined to enable comparisons to be made with other studies.

Table 2.2 ; Food consumption of captive Goosanders on selected dates

Date	Duckling age (days)	Mean weight (g)	Mean wet weight fish ingested (g)	% of body weight	Mean kcal ingested
24.07	39	366.25	96.5	26.35	142.09
08.08	54	580.00	270.0	46.55	397.58
13.08	59	691.67	330.0	47.71	485.92
17.08	63	776.67	370.0	47.64	544.83
18.09[1]	95	733.33	223.3	30.45	354.52
01.11	138	803.33	326.7	40.67	481.04

(1) Birds moved indoors previous day due to bad weather.

This is equal to weight increase per day x 100/ weight of food ingested per day. For the first of these periods the rate is 29.1% ((111.7 x 100)/ 383.94), and for the second is 22.8% ((84.9 x 100)/ 372.67). Despite the lack of accurate data later in the season, it is clear from Figure 2.9 that the conversion rate must decline further. Atkinson and Hewitt (1978) noted a progressive general decline in conversion rate for captive reared Red-breasted Merganser from hatching to 160 days. This indicates that, as the birds increase in size (and age), an increasingly greater proportion of ingested food (energy) is devoted to maintenance rather than to growth. White (1957) calculated a conversion efficiency for captive reared Goosanders as "the gain in weight [in ounces] for every 100 ounces of fish eaten". This showed a decline from 7.9% to 1.4% over the first four months of life. Similar declines in conversion rate with age have been reported for Black Ducks (Anas rubripes) and American Coots (Fulica americana) by Penney and Bailey (1970), and by Coulson and Pearson (1985) for four Guillemot chicks (Uria aalge) reared in captivity to approximately fledging age (20-25 days).

(c) Total food and energy intake during growth

Determination of the calorific value of each food type presented to captive birds allowed gross daily energy intake (GEI) to be estimated. From these values I estimated the daily energy budget (DEB, the total energy metabolised per day) by multiplying GEI by 0.85 which represents the mean assimilation efficiency by Double-crested Cormorants (Phalacrocorax auritus) of an exclusively fish diet (Dunn 1975). See section 2.4.3.

An alternative method of estimating DEB (and ultimately GEI) was also used, viz. application of an equation from Kendeigh et al. (1977) derived from growth data for the Black-bellied Tree Duck (Dendrocygna autumnalis) presented originally by Cain (1976). The equation was;

$$DEB = 1.638\ W^{0.7784} +/- 1.160$$

where DEB = kcal/bird/day and W = weight in g. Comparing estimates of DEB given by this equation (using body weights presented in Table 2.2) with estimates from observations (Table 2.2) showed that, on average, the observed value was 1.3 times greater than the calculated figure. See Table 2.3. This result is not surprising since the Tree Ducks on which the equation is based were maintained in metabolism cages at a constant high temperature (32°C) and photoperiod (15:9 L:D) throughout their period of growth, whereas in this study birds were kept in an outdoor enclosure (with a naturally varying photoperiod) where ambient temperatures were much lower. Monthly mean temperatures from July to October 1984 inclusive (as recorded by the Meteorological Office) were 15.7°C, 15.9°C, 12.7°C and 10.5°C respectively. The overall mean for the period was 13.7°C. A rough approximation of the difference in estimated GEI at 32°C and c14°C can be made from a study by Owen (1970) of the energetics of captive Blue-winged Teal (Anas discors). This indicated that GEI at the lower temperature should be 1.5-1.8 times the value at

Table 2.3 ; Comparison between observed and calculated estimates of DEB of captive-reared Goosanders on selected dates

Date	Calculated estimate of DEB(1)	Observed estimate of DEB(2)	Observed DEB divided by calculated DEB
24.07	161.0 - 163.3	120.78	0.75 - 0.74
08.08	230.8 - 233.1	337.94	1.46 - 1.45
13.08	264.8 - 267.2	413.03	1.56 - 1.55
17.08	290.0 - 292.3	463.11	1.60 - 1.58
18.09[3]	277.2 - 279.6	301.34	1.09 - 1.08
01.11	297.7 - 300.0	408.88	1.37 - 1.36
			Mean = 1.30

[1] Applying the equation from Kendeigh et al. (see text) to mean duckling weights from Table 2.2.

[2] Derived by multiplying mean kcal ingested (Table 2.2) by an estimated assimilation efficiency of 85% (Dunn 1975)

[3] Birds moved indoors previous day due to bad weather.

the higher value. The estimate derived above of observed DEB being 1.3 times greater than the calculated value is thus not unreasonable.

Using a regression equation (y=12.47x-86.19) for total body mass (g) on age (days) over the period 5-70 days, ie. from after the period of post-hatching weight loss to fledging, to estimate daily body mass, I calculated GEI by dividing the estimate of DEB given by the equation of Kendeigh <u>et al</u>. (1977) used earlier, by an estimated assimilation efficiency of 85% (Dunn 1975) and then multiplying the quotient by 1.3. (This assumed that assimilation efficiency remained constant. See section 2.4.3.) Energy requirments prior to this period over which the regression referred were calculated using a mean body weight of 51.6g. Cumulative energy needs were determined by addition. Results, given in Figure 2.11, indicate that approximately 16,600 kcal are required to rear a single female duckling to fledging (taken to occur at day 70, at weight 790g). If the diet consisted entirely of salmonids over this period then, given that the calorific value of this prey type is 1.137kcal/g wet weight, it can be estimated that to rear a female Goosander to age 70 days requires approximately 14.6 kg of salmon parr.

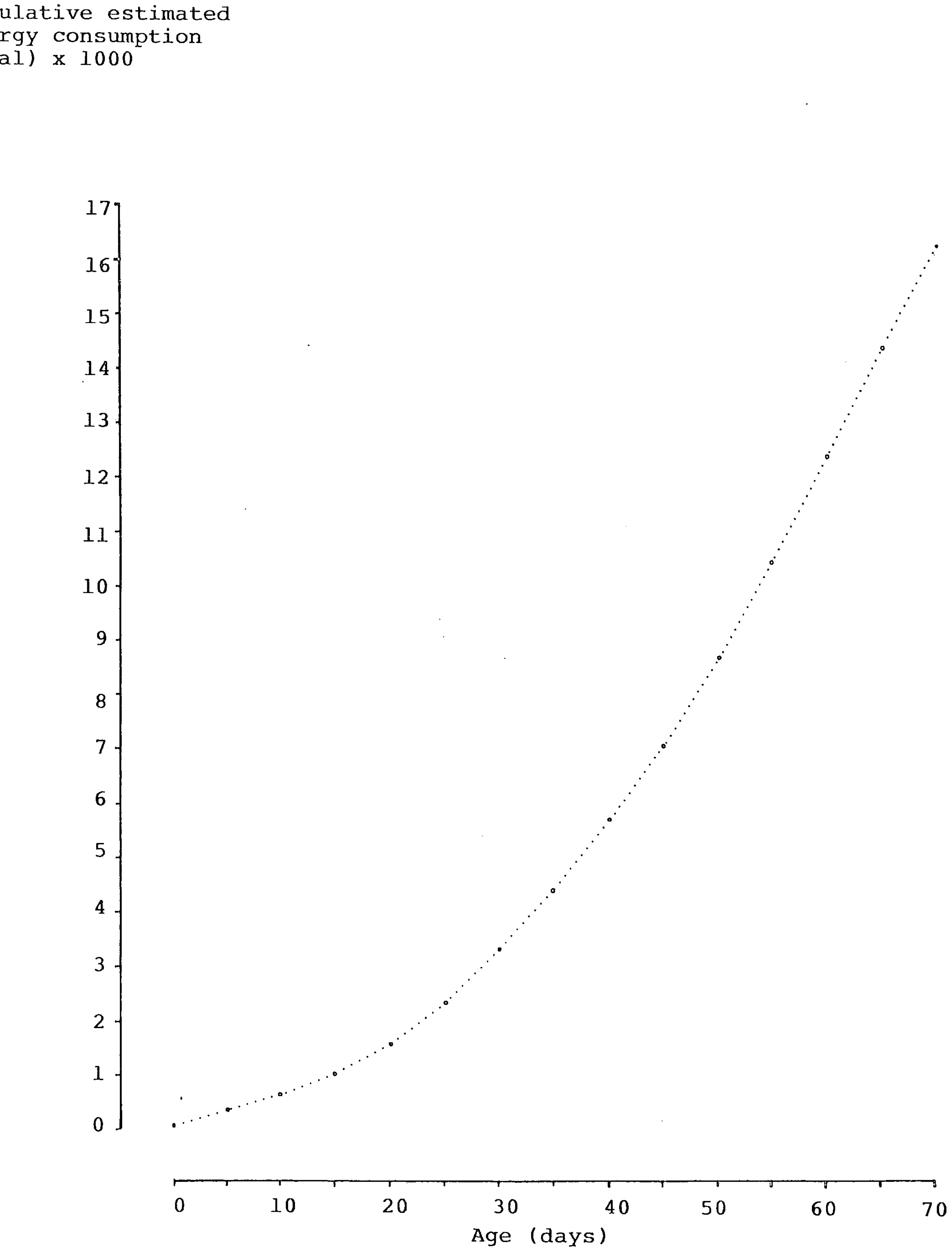


Figure 2.11 ; cumulative estimated energy consumption (kcal) of Goosander ducklings up to age 70 days

2.4.0 DISCUSSION

2.4.1 Growth of ducklings

Penney and Bailey (1970) suggested that there were three critical periods in the development of young Black Ducks and American Coots. These were, (1) the development of foraging behaviour, (2) the conversion of the digestive tract to absorb an adult diet, and (3) when the growing primary feathers break through their sheaths. For wild Goosanders, period (2) will occur during approximately the first fortnight of life as diet shifts from predominantly insect to almost exclusively fish (White 1957). In captivity, however, no comparable shift in diet occurred, and no expression of physiological stress was expected, or found, at this time. Weight losses did occur in this study coincident with critical periods (1) and (3), however.

Siegfried (1973) considered post-hatching weight loss to be normal in diving ducks, and related this to a delay in the onset of feeding activities and a need "to perfect more difficult feeding techniques than those employed by young dabblers". The food reserves of the yolk sac are utilised at that time with such resources being proportionately larger in Tufted Duck than Mallard (Anas platyrhynchos) (Kear 1970). This may be a general feature of diving ducks whose feeding methods are energetically relatively more expensive than those of dabbling ducks. For Goosanders, the proportional size of the yolk reserves in the egg/newly hatched young is unknown.

The long incubation period of the Goosander in relation to that of Aythya and Anas species probably allows greater pre-hatching development to occur to produce a more 'advanced' duckling able to dive and feed on active live prey. Associated with this is a prolonged growing period and a greater age at fledging. Figure 2.12 shows the nature of this relationship for waterfowl of the western Palearctic. This has been described by Lack (1967) who noted a positive correlation between the length of incubation and time to fledging which was characteristically different for each family of waders and seabirds he considered.

Erskine (1971), in a study of the growth rates of wild Goosanders in Nova Scotia, reported a fledging period of approximately 65 days but noted that many birds probably did not fledge until after 70 days. Cramp and Simmons (1977) support this and cite a fledging period of c65 days. The change in rate of weight gain, reported in section 2.3.2, was approximately coincident with this event in the birds I studied. However, it was also coincident with a move from a holding pen at the University to a similar pen at the Wildfowl Trust, and with a shift to a diet of sprat and whiting. Both of these factors are likely to have contributed the marked decline in daily food and energy intake which occurred and hence to weight loss, and it is not possible to partition the loss between them. A similar pattern of weight change, ie. a trough in the growth curve at the approximate time of fledging, was noted in Red-breasted Mergansers by Atkinson and Hewitt (1978), but again this coincided with disturbance in the rearing pen. However, other

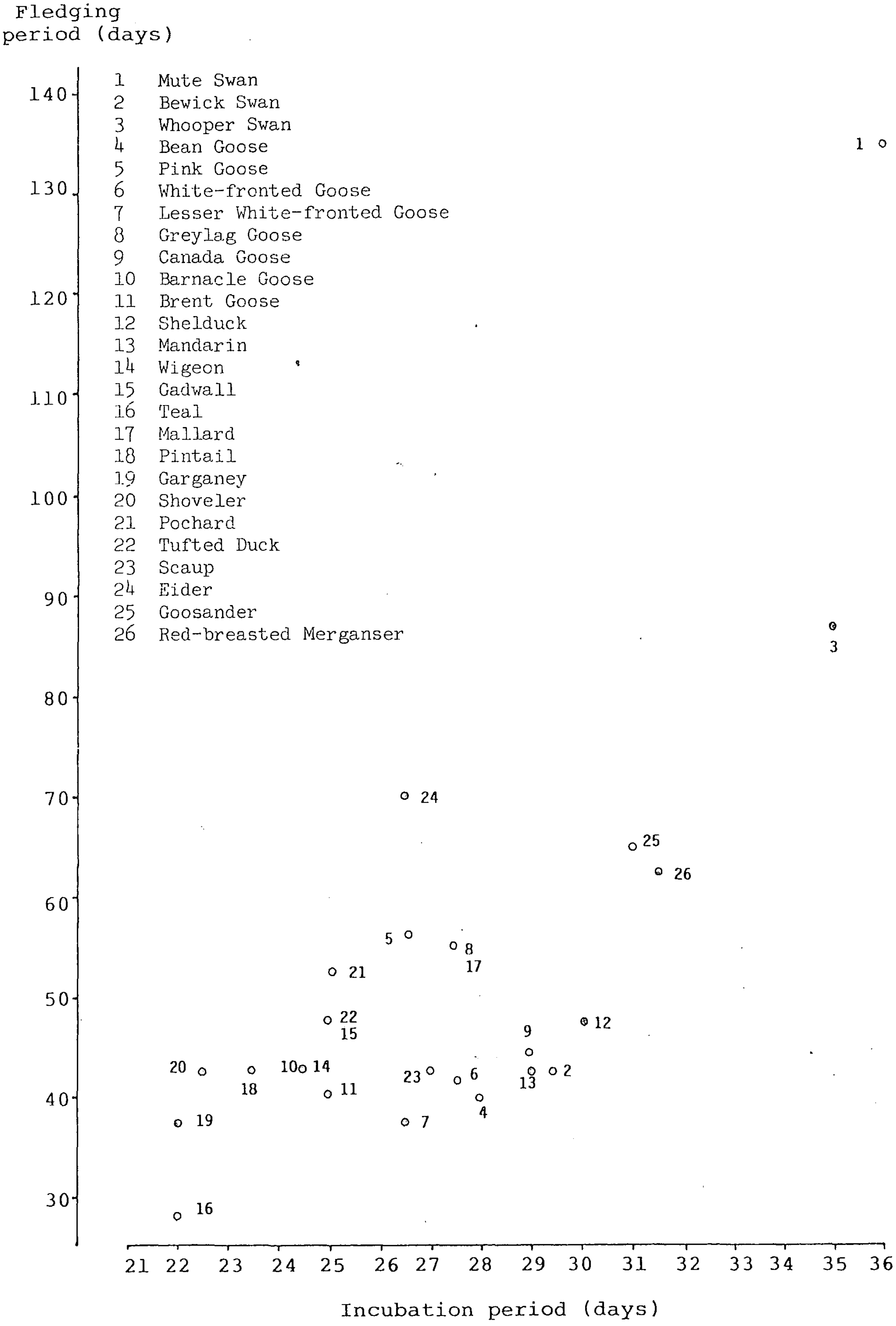


Figure 2.12 ; relationship between the length of incubation and fledging periods for European waterfowl

workers have noted weight recession at the approximate time of fledging in one species of Dendrocygna, seven Anas species, five Aythya species, one Cygnus species and one Melanitta species (Veselovsky 1953, Weller 1957, Brand 1961, Portman 1950, Penney and Bailey 1970, Kear 1970, Sugden and Harris 1972, Cain 1976, and Brown and Fredrickson 1983). The phenomenon is clearly widespread amongst waterfowl, and its possible significance is discussed in section 2.4.2 below.

In his Canadian study Erskine (1971) noted that the body weight of wild Goosanders increased at a constant rate up to about day 50 after hatching, and then slowed, with no evidence of weight recession at the time of fledging. The pattern of growth for both the bill and tarsus was similar to that noted in the present study although the latter appeared to reach full size by about day 40 in Erskine's study (cf day 60 here). Growth data presented by Cordonnier (1984) for three captive reared female Goosanders, agree closely with those of Erskine (1971) in that they do not show any weight recession around fledging. Tarsus growth is similar to that in the present study, however.

These data suggest that the growth rate of captive Goosanders may be slower than that for wild ducklings. From data collected in the maritime provinces of Canada, White (1957) found that by the autumn, captive reared Goosanders were approximately eight ounces (c227g) lighter than wild juveniles of the same age. However, the work of both White (1957) and Erskine (1971) is not directly comparable either with that of Cordonnier (1984) or that reported here since different subspecies were used. Comparative data to test for differences in the growth rates of wild and captive young Goosanders of the same subspecies are lacking.

The role of energetic or physiological constraints on growth were not specifically investigated.

2.4.1.1 Social facilitation

In feeding experiments with Black Ducks and American Coots, Penney and Bailey (1970) showed the importance of social facilitation in feeding. Birds in groups of four had a greater food consumption (and faster growth rate) than birds in groups of two. Atkinson and Hewitt (1978) suggested that the same was true for the Red-breasted Mergansers they reared in captivity, citing as evidence the fact that the growth curves of their three ducklings changed in synchrony. A more likely alternative explanation however, is that growth rates varied in all birds simultaneously as a result of external modifying factors (such as disturbance, temperature) which acted similarly on all birds.

Social facilitation in feeding was not specifically investigated in this study. However, data allow a comparison to be made between the growth curve of the single duckling reared in 1983 (Figure 2.2) and those of the birds reared in a 'brood' in 1984 (Figure 2.3). These figures suggest (a) a slower rate of growth, and (b) a later attainment of peak weight by the single 1983 bird. To investigate this more fully, regression lines were calculated of total body weight (g) on age (days) for the single bird in 1983, and the 'brood' in 1984 over the period 5-70 days of age (ie. after the period of post-hatching weight loss). These were; for 1983, $y=9.56x-15.18$, and for 1984, $y=12.47x-86.19$. A modified t-test (Sokal and Rohlf 1969) of the difference between the slopes of these lines was not statistically significant however ($t=0.81$).

More rigorous investigation of the effects of brood size on food and energy intake is required.

2.4.2 The adaptive significance of weight recession

Studies of moulting birds, where the beginning of the new flight period is analagous to fledging, provide additional information on the possible significance of the observed pattern of weight change noted above.

In waterfowl the flight feathers are lost simultaneously and there is therefore a period of flightlessness. Energy demands during feather replacement are high. For example, Owen (1980) estimated that 8g of fat per flightless day was needed by moulting Barnacle Geese (Branta leucopsis). Energy requirements can be met either by the mobilisation of body reserves accumulated prior to the onset of moult, by increasing energy intake rates during moult, or by a combination of the two.

Douthwaite (1976) considered that if Red-billed Teal (Anas erythrorhyncha) accumulated fat reserves prior to moult they would be (a) less vulnerable to food shortage, (b) be able to feed in areas less exposed to predation risk even if prey availability was not maximal, and (c) allow uninterrupted growth of new feathers. (The last point is not valid however, as fat cannot be used to synthesise feather proteins.) However, 'excess' weight would prolong the flightless period. Since flightless waterfowl have been shown to be more vulnerable to avian and mammalian predators than those capable of flight (eg., Gerell 1968, Oring 1963, Wishart et al. 1981), there is likely to be a strong selective advantage in reducing the length of the flightless period. An 11% pre-moult weight loss by male Red-billed Teal, and a 21% loss by females may therefore be adaptive in reducing the length of the flightless period, providing food resources are not limiting.

Geldenhuys (1983) reported a similar pattern for South African Shelducks (Tadorna cana). This species is sparsely distributed during the breeding season but during the moulting period large aggregations occur at favoured localities. These are typically large expanses of open water which afford good visibilty and provide a measure of security. Selection of sites appears to be on these criteria rather than on food availability since during the flightless period intake rates are drastically reduced. Concomitant with this is a reduction of 25.6% and 28.2% of pre-moult weight for male and female Shelducks, respectively, which begins as soon as the remiges are lost. In common with Red-billed Teal (Douthwaite 1976), Geldenhuys (1983) considered that weight loss may be due not to food shortage per se, but that it may be adaptive in allowing the birds to fly before their primary and secondary feathers are fully grown.

From studies of moulting Teal (Anas crecca) and Shoveler, Hongfa (pers.comm.) considered that body weight declined at the beginning of the new flight period (analagous to the fledging period), despite an increase in food intake, because of increased energy consumption associated with increased activity. Sugden and Harris (1972) ascribed weight loss at this time to 'feathering stress'.

Sjoberg (1988) similarly reported that over the course of the 21 day moulting period of Teal, the body weight of birds decreased by 10-19%. He argued that this was not due to nutritional stress, since prey availability was high, and therefore was likely to be adaptive. For arctic nesting waterfowl with a short breeding season, the ability to fly on incompletely developed pinions is also likely to be important in allowing migration before the onset of harsh winter conditions (Owen and Ogilvie 1979). This is in addition to an anti-predator function.

In eastern Canada, Erskine (1971) "noted excellent survival in broods of flightless [Goosanders] on Cape Breton Island", and suggested that, "selection is unlikely to favour reduction of the flightless period". The composite growth curves he presented for wild birds gave no indication of any weight recession at the time of fledging. Where such exists, as is suggested in the present study, it may be adaptive for birds to reduce the length of the flightless period, (a) to escape predation (this would be true if predation risk increased with duckling size), and (b) to move to areas of reduced feeding competition if food became limiting towards the time of fledging. It is not clear, however, why such factors would not operate in Erskine's study area.

2.4.3 Estimates of food and energy consumption of pre-fledging Goosanders.

Several authors have estimated changes in the food (energy) consumption of both altricial and precocial piscivorous birds during growth. For hand-reared White-breasted Cormorant Phalacrocorax lucidus, Reed Cormorant P. africanus, Wood Stork Mycteria americana, Darter Anhinga rufa, Grey Heron Ardea cinerea, and Goliath Heron A. goliath, du Plessis (1957), Kahl (1962) and Junor (1972) found that although daily food intake as a percentage of body weight fluctuated widely with increasing age (and weight) up to and beyond fledging, there was an overall marked decline. (Large day-to-day variations in the percentage of body weight consumed were also noted in this study (see Figure 2.9). They were considered by Kahl (1962) to be the result of a tendency to (a) overeat for one to two days when presented with a superabundant supply of food, and (b) to follow this period with one to two days where there was a "compensatory loss of appetite".)

Such measures of gross intake are an important aspect of energetic studies particularly when trying to assess the impact of a predator on populations of its prey. However, as highlighted above (section 2.3.3a) total daily food consumption may be affected by the calorific value of ingested food items, and also by variation in assimilation efficiency therewith. These factors, as commented by Dunn (1975), are "much neglected" in consumption studies and as a result values of proportional food intake cannot be compared directly between studies where the species of predator and presented prey differ. The energy metabolised per day (ie. DEB) is a better common currency but because the calorific values of ingested food, and assimilation efficiencies, are not always determined in each study, DEB must be estimated by extrapolation from the results of other investigations.

The most widely used equations for the estimation of metabolic rates are those given by Lasiewski and Dawson (1967), Aschoff and Pohl (1970) and Kendeigh et al. (1977). Most of these however, are not appropriate in the context of growing young since they are based on laboratory measures of the energy consumption of fully grown birds of different species of various, and at times unspecified nutritional status. Thus the derived equations for the relationship between BMR and body weight provide an uncertain approximation of actual energy demands.

This notwithstanding estimates of BMR derived from such equations may be used in ecological studies to estimate total daily food consumption if appropriate multiples thereof are used.

For passerines, Moreau (1972) reviewed published studies of the relationship between maintenance energy and "the needs for normal activity", and estimated that total energy requirements were 2.9 times maintenance costs. Ebbinge et al. (1975) repeated this approach for a range of wild non-passerines, and found that DEB was two to four times BMR. Additionally, Yom-Tov (1974) estimated the BMR of Carrion Crows (Corvus corone) from the equation of Lasiewski and Dawson (1967) and considered that to satisfy basal metabolism a bird weighing 0.5kg required c60g of fresh chick/day. Observed intake was approximately three times this value.

Estimation of "gross intake, the ecologically relevant parameter" (Ebbinge et al. 1975) from DEB values requires information on assimilation efficiency. In their review of avian energy metabolism King and Farner (1961) considered that assimilation efficiences ranged between 70% and 90% of gross energy intake "depending on the species of bird, the composition of the ration, and the environmental conditions". Although subsequent research has shown this range to be inadequate (eg. the assimilation efficiency of wild Barnacle Geese Branta leucopsis was determined by Ebbinge et al. (1975) as c34%), some authors, eg. Kahl (1962) and Wood (1987b), have chosen values from within it for use in their own studies. Without any justification of the reasons for this choice the results of such work must be viewed with caution. Additionally it is implicitly assumed that assimilation efficiencies remain constant. However, Dunn (1975) demonstrated an increase in this parameter from 79.9%

in 11-12 day old Double-crested Cormorants to 88.1% in birds of 20-21 days of age.

Wood (1987b) estimated the BMR of young Goosanders using the equation of Lasiewski and Dawson (1967) for non-passerines, and further estimated their total daily calorific requirements at various ages from hatching to 60 days by assuming (a) that 70% of the daylight period was spent in activities for which the energy expenditure was three to five times BMR (Yom-Tov 1974), and (b) an assimilation efficiency of 80% (King and Farner 1961). These estimates were converted to daily food consumption (using a value of 0.91 kcal/g wet weight of salmon fry), and the upper and lower limits of daily proportional intake plotted against age. This showed a decline in the percentage of body weight eaten per day from c45-70% at age 10 days to c20-30% at age 60 days. Direct estimates of gross intake from studies of both captive and wild Goosanders (White 1957, Latta and Sharkey 1966, Atkinson and Hewitt 1978, Wood 1987b, this study) are in broad agreement with estimates calculated as described above. This is encouraging in view of the compounding of errors of estimation that will have occurred at each stage of the calculation. This aside, values summarised by Wood (1987b) suggest that the consumption of birds less than 30 days old is underestimated by using the above procedure whereas at ages greater than this the method provides a better approximation to observed intake.

A similar approach was used in the current study to estimate the total calorific requirements of a Goosander from hatching to fledging (at 70 days). This used an equation from Kendeigh et al. (1977), modified as dexctibed above, to estimate DEB, assumed a constant assimilation efficiency of 85%, and further assumed that energetic requirements were met wholly by salmonid prey with a calorific value of 1.137kcal/g wet weight. The final estimate of approximately 14.6kg of salmonid prey needed to rear a female Goosander to fledging, compares well with White's (1957) estimate of 13-14 kg of 'fish' to rear a single duckling to 70 days old, and c12.75 kg wet weight of pelleted food, of unknown calorific value, required to rear a single Red-breasted Merganser to the same age (Atkinson and Hewitt 1978).

2.5.0 SUMMARY

Captive reared Goosanders showed a small post-hatching weight loss of c7-20%, followed by a period of rapid increase in body mass until age 60-70 days when a further recession, possibly associated with fledging, was evident. At this time the female ducklings used in this study had reached approximately 60% of adult weight. The possible adaptive significance of the observed weight recession coincident with fledging is discussed.

Growth of head plus bill occurred at a steady rate, reaching c80% of adult length by the time of fledging. Tarsus length increased more rapidly and had reached full adult length by this time. Estimates of the food consumed per day expressed as a percentage of body weight, ranged between 26 and 48%. Gross energy intake (GEI) during development was best predicted by extrapolating from an equation given by Kendeigh et al. (1977) derived from data presented by Cain (1976) for the metabolic rate of Black-bellied Tree Ducks kept at 32°C. For ducklings growing at a mean temperature of 14°C, appropriate equation is;

$$GEI = \frac{1.3\ ((1.638\ W^{0.7784}\ +/-\ 1.160)}{0.85}$$

where M = kcal/bird/day and W = weight in g. Using this equation it was estimated that c14.6kg of salmonids were required to rear a single female Goosander duckling to fledging.

CHAPTER THREE ;

BODY MASS, CONDITION AND ESTIMATED FOOD AND ENERGY REQUIREMENTS OF POST-FLEDGING GOOSANDERS

3.1.0 INTRODUCTION

Variation in the body mass and body condition both within and between individual birds will affect their energy and nutrient demands, and these factors need to be considered in any assessment of food/energy intake throughout the year.

A sample of wild post-fledging Goosanders was examined to investigate seasonal variation in body mass, and an attempt was made to assess body condition, in terms of both fat and protein reserves, using lipid indices for selected body components and carcass homogenates, and standard muscle indices for the breast and leg musculature.

Using these data I estimated annual cycles of weight and body condition of Goosanders and thus estimated the daily and annual food/energy requirements of fully grown birds.

3.2.0 METHODS

3.2.1 Estimates of body condition

Goosanders were received from several sources as listed in Table 5.1 of Chapter Five. Those from the rivers North Esk, South Esk, and Tweed were forwarded frozen by the Esk District Fishery Board, and Tweed Commissioners, respectively, whilst specimens of unknown origin, and the single bird from Kielder, were received as skinned carcasses from the Hancock Museum, Newcastle-upon-Tyne. Remaining birds were found by local ornithologists. Upon receipt all carcasses were placed in sealed polythene bags and deep-frozen.

Before analysis bodies were thawed overnight and body mass recorded to the nearest g. Birds were sexed and aged on the basis of plumage characteristics and examination of the gonads. Individuals were recorded as juvenile if the sternum was not completely ossified and as immatures if ossification was complete. With the bird placed on its back, total body length (from the tip of the bill to the tip of the tail) was recorded to the nearest 5mm division of the rule. More accurate measurement was not considered possible since the actual length depended on the degree of stretching of the body and the angle at which the head was positioned. Skull length, bill length, tarsus length and wing length were recorded to the nearest 0.1mm using dial calipers, as described in the Ringers Manual (BTO 1984).

The pectoralis major and supracoracoideus musculature from one side of the bird were removed to facilitate measurement of the keel and coracoid as described by Evans and Smith (1975). These authors presented an equation for the calculation of a standard muscle volume (SMV) for wading birds, included in which was a single constant derived from measurements of the sterna of the species with which they worked. Piersma et al. (1984) presented the derivation of both the formula and the constant. I therefore recorded additional morphometric data to derive a valid formula for the determination of standard muscle volume for Goosanders. This was $SMV = b(0.678c^2 + ad)$ where a = length of the sternum, b = height of the keel of the sternum, c = distance from keel to tip of coracoid, and d = minimum width of sternum raft. These measurements are illustrated in Figure 3.1. This volume will be referred to subsequently as SMV_m. An index of muscle size (SMI_m) was derived by dividing the lean dry mass of the pectoralis major and supracoracoideus by SMV_m.

The oesophagus and gizzard were removed and weighed separately, with care being taken to excise any associated fat deposits. Their contents were washed into petri dishes and the towel-dried empty organs re-weighed. Body mass minus the weight of the contents of the oesophagus, proventriculus and gizzard, was determined by subtraction. Food material was analysed as described in Chapter Five.

For 13 birds the leg musculature from one side was also removed, a = length of sternum

b = height of keel

c = distance from keel to end of coracoid

d = minimum width of raft

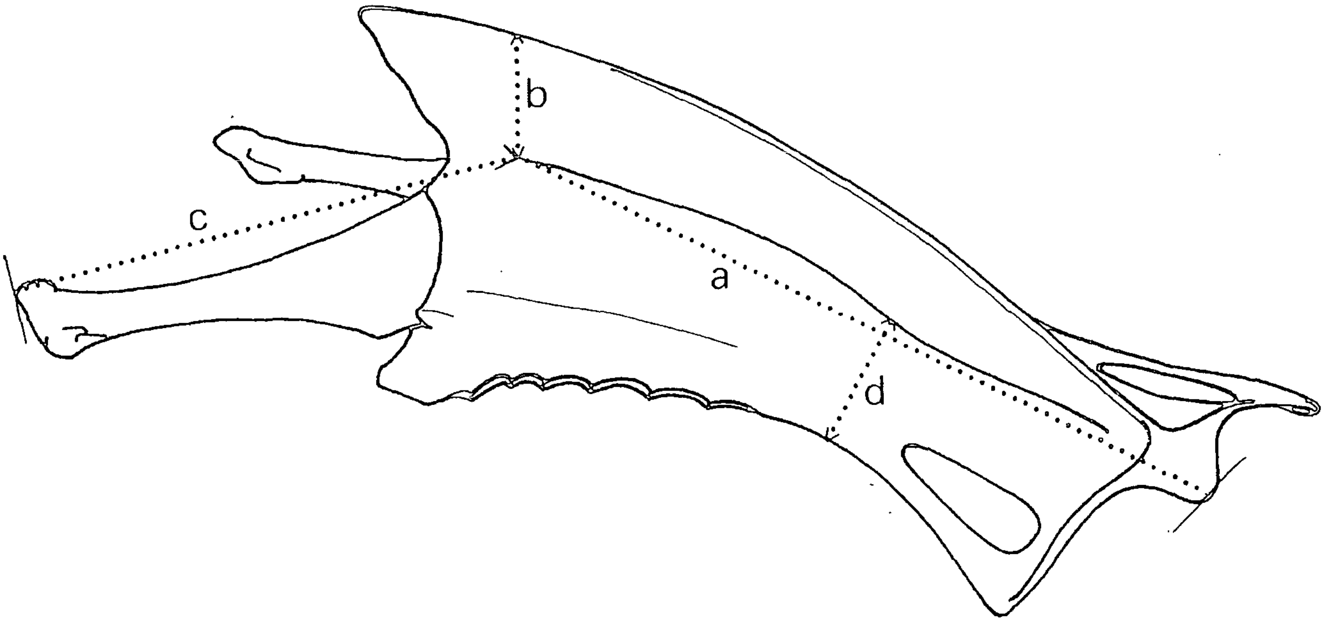


Figure 3.1 ; measurements of the keel used to calculate standard muscle volume, SMV_m

weighed and oven-dried as above. The total length of the attachment on the pelvic girdle, the mean width of attachment, the length of the femur, the length of the tibia and the width of the tibia at its base were measured as indicated in Figure 3.2. Treating the leg musculature as a cone, a standard volume, SMV_1, was determined on the basis of these biometrics. An index of muscle size, SMI_1, was calculated by dividing the lean dry mass of the leg musculature by SMV_1.

An attempt was made to find a short-cut method of estimating the total lipid content of individual birds, as a measure of body condition. For 11 specimens the lipid index (defined below) of selected body components was compared with the lipid index of the remaining homogenised carcass.

The following body components were used,

1. pectoralis major,
2. supracoracoideus,
3. gizzard,
4. musculature of one leg,
5. skin sample. This represented the skin overlying the pectoralis major on one side of the bird.

Carcasses, minus the body components listed above, were plucked, re-frozen and minced to produce a homogenate from which six samples, each of wet weight c30g, were taken for oven drying at 50° C. Dried samples were extracted with petroleum ether in a soxhlet extractor, with the residual weight (after additional a = maximum length of attachment on pelvis

b = maximum width of anterior area of attachment on pelvis

c = maximum width of posterior area of attachment on pelvis

d = length of femur

e = length of tibia to tendon

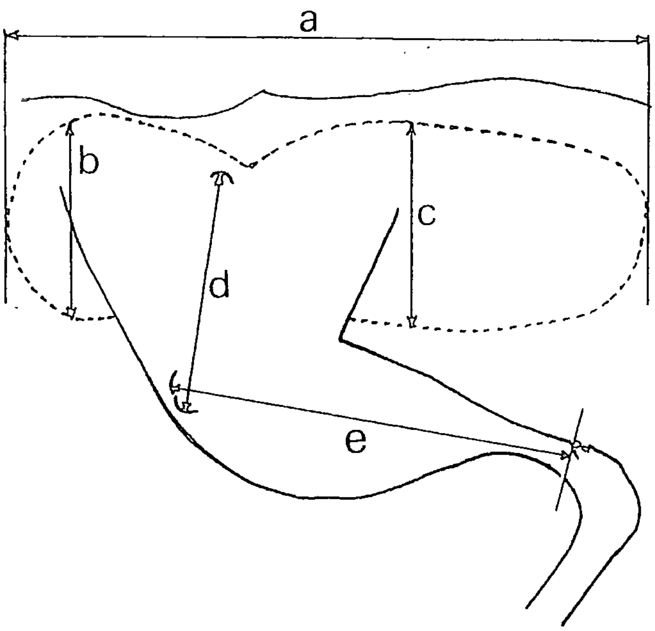


Figure 3.2 ; measurements of the leg and pelvic area used to calculate standard muscle volume, SMV_1

drying) taken to correspond to lean dry mass. A lipid index (LI) was calculated where;-

$$LI = \frac{(DW - LDW)}{LDW} \times 100$$

where DW = dry weight of organ before extraction, and

LDW = dry weight after fat extraction.

3.3.0 RESULTS

3.3.1 Measures of body condition

Three measures of body condition were determined, viz. lipid index (LI), standard muscle index for the breast muscles (SMI_m) and standard muscle index for the leg musculature (SMI_l). Results are discussed firstly by treating each as an independent measure, and secondly by considering relationships between them.

(i) Lipid index values

The results of the determination of LI values for selected body components and carcass homogenates are given in Table 3.1, and the results of regression analyses in Table 3.2. This demonstrates that the LI of the homogenate can be accurately predicted from the LI of the sample of skin overlying the

Table 3.1 ; Values for lipid index (LI) derived from selected body components and carcass homogenates.

Bird no.	Supra	Pect	Gizz	Leg	Skin	Homog
16	4.70	13.81	11.90	12.95	257.23	34.40
17	5.37	10.35	15.59	11.98	307.44	34.64
18	4.18	10.36	6.13	7.16	42.55	10.90
19	7.49	6.27	46.74	11.39	308.52	40.23
20	3.33	7.24	4.62	6.36	151.35	20.36
21	4.32	5.73	3.93	7.03	176.02	17.40
22	6.83	10.45	-	8.46	71.14	9.76
24	10.47	6.19	-	7.19	214.71	23.34
26	6.25	11.22	-	8.58	293.65	31.87
31	5.48	5.10	-	-	376.54	39.74
35	8.72	-	-	-	498.93	69.07

Table 3.2 ; Correlations between lipid indices of body components and of carcass homogenates

		n	df	r	p
Homog v	supra	11	9	0.254	ns
	pect	10	8	-0.198	ns
	gizz	6	4	0.651	ns
	leg	9	7	0.650	ns
	skin	11	9	0.963	<0.001

$$LI_{skin} = 7.62\ LI_{homogenate} + 15.50$$

pectoralis muscle, but that the LI's of other body components are poor predictors.

Table 3.3 details available LI_{skin} values. These data show a wide variation in the condition of individual birds, independent of body size (considering all Goosanders together). In Figure 3.3 LI_{skin} values are plotted against corrected body weight (ie. total body mass minus gut contents) for each sex and age class of birds regardless of the month of collection. These data suggest that at a given weight adult females have a greater LI_{skin} value than immature males which in turn have greater values, at a given weight, than adult males. An analysis of variance using general linear modelling within SAS (SAS 1985) showed no overall effect of age, sex or month of collection on LI_{skin} values however (see Appendix 2).

(ii) SMI_m

Available values of SMV_m and SMI_m are given in Table 3.3. This shows wide variation between individuals. Although data are scant there is the suggestion (see Figure 3.4) that at a given weight the SMI_m values of females are greater than those of males. This is in accord with the trend shown by LI_{skin} values above.

Table 3.3 ; Values of lipid index, standard muscle volumes and standard muscle indices

Code[1]	LI_{skin}	SMV_m	SMV_1	SMI_m	SMI_1
1 AM -	-	112.35	-	0.095	-
2 AM12 1733	-	116.71	492.05	0.336	0.025
3 JM	-	-	-	-	
4 JM	-	20.99	-	-	-
5 JF	-	26.55	363.86	0.372	0.057
6 AM 4	-	-	-	-	-
7 AM12 1660	-	113.40	609.00	0.337	0.039
8 AM 2 1465	-	91.87	-	0.303	-
9 AM 2 1437	64.79	100.27	587.71	0.333	0.038
10 IM 2 1621	457.08	93.48	479.79	0.379	0.044
11 AM 2 1698	469.80	102.51	493.08	0.192	0.041
12 AF 6 1080	-	-	-	-	-
13 IM 8 -	-	79.31	255.66	-	-
14 AF 2 1234	201.89	75.89	361.49	0.388	0.045
15 IM 9 1232	-	86.76	-	0.287	-
16 IM 9 1458	257.23	101.41	-	0.292	-
17 AF 9 1194	307.44	78.83	-	0.310	-
18 AF 6 1097	42.55	77.46	-	0.347	-
19 AF 9 1412	308.52	80.32	-	0.365	-
20 AF 9 -	151.35	83.02	-	0.319	-
21 JM 8 1303	176.02	81.80	-	0.339	-
22 IF 9 1016	71.14	72.18	-	0.277	-
23 AM 2 1691	371.43	106.51	-	-	-
24 JM 8 1057	214.71	25.76	-	0.196	-
25 AF 6 1116	-	78.14	-	-	-
26 JF 8 -	293.65	16.91	-	0.135	-
27 IM 2 1595	334.80	107.03	-	-	-
28 AM 4 1350	42.52	94.10	-	-	-
29 AF 2 1427	563.00	74.16	430.21	-	-
30 AM 2 1454	203.15	117.05	-	-	-
31 JF 8 902	376.54	18.30	384.20	0.265	0.047
32 AM 2 -	251.02	110.88	-	-	-
33 AM 2 1723	355.73	119.14	-	-	-
34 AM 5 1557	50.61	115.08	-	-	-
35 AF 2 1568	498.93	84.21	476.33	0.438	0.043
36 AF 5 1197	98.91	83.45	-	-	-
37 AM 2 1722	-	115.67	-	-	-
38 IF 9 1153	125.68	81.43	-	-	-
39 AM 2 1595	-	103.05	-	-	-
40 AM 2 1597	373.56	100.39	-	-	-
41 AM 2 1606	107.68	99.79	-	-	-
42 AM 2 1668	1.50	110.94	-	-	-
43 IM 2 1779	694.06	99.49	-	-	-
44 AM 2 1265	5.19	118.24	-	-	-
45 AM 4 1630	339.20	107.43	-	-	-

Table 3.3 cont.

Code^1	LI_{skin}	SMV_m	SMV_1	SMI_m	SMI_1
46 DM 7 -	-	-	-	-	-
47 DM 7 -	-	-	-	-	-
48 DF 7 -	-	-	104.12	-	-
49 DM 7 -	-	-	154.10	-	-
50 DM 7 -	-	-	-	-	-
51 DF 7 -	-	-	-	-	-
52 AM 5 1339	63.43	99.41	-	-	-
53 IF 2 -	258.54	77.43	-	-	-
54 IM - -	424.30	98.58	-	-	-

Code^1 ; A = adult, I = immature, J = juvenile, D = downy
M = male, F = female,
Succeeding numbers = month of collection and corrected body mass respectively

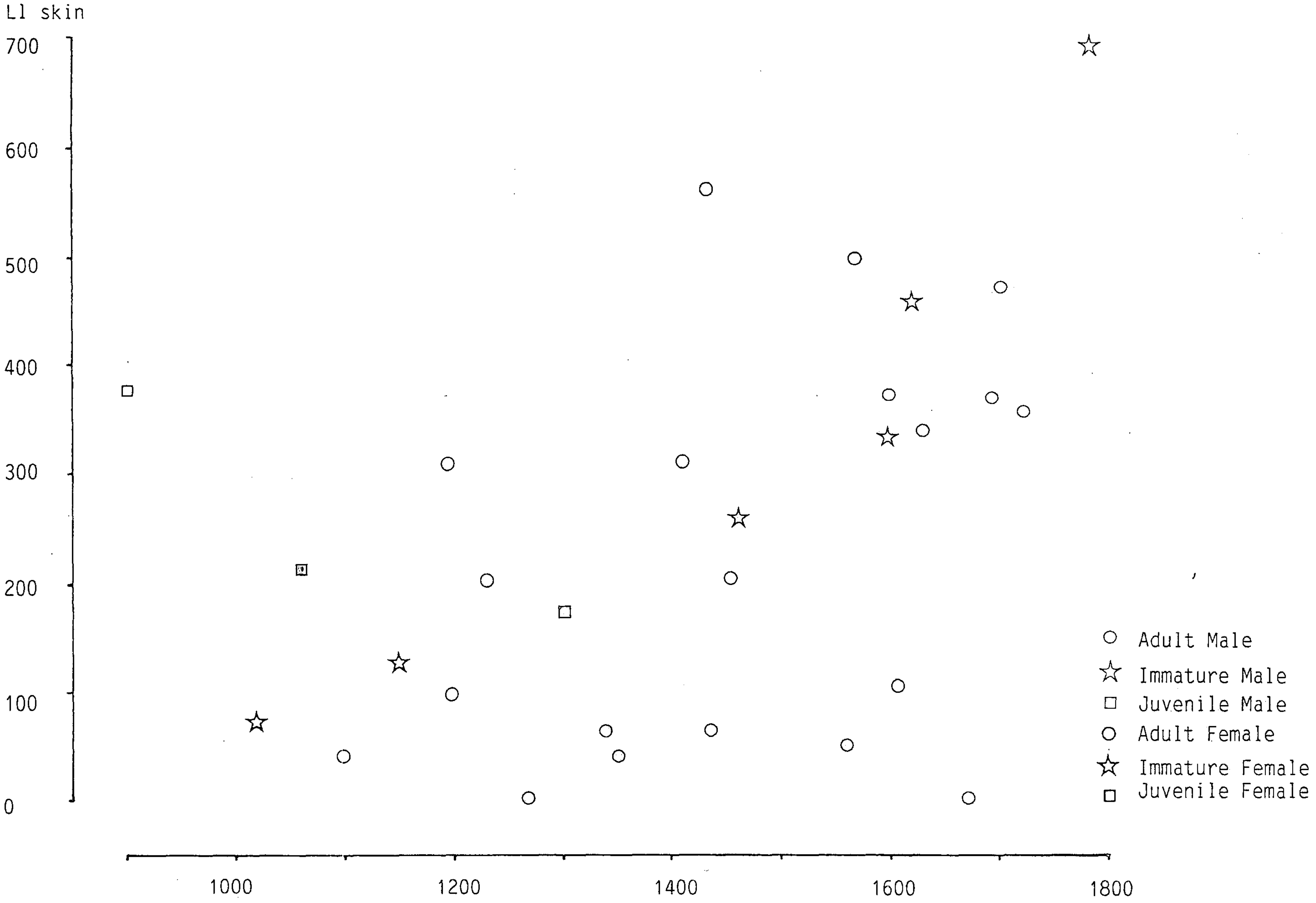


Figure 3.3; relationship between L1skin and corrected body mass (see text for derivation) of different age and sex classes of Goosander

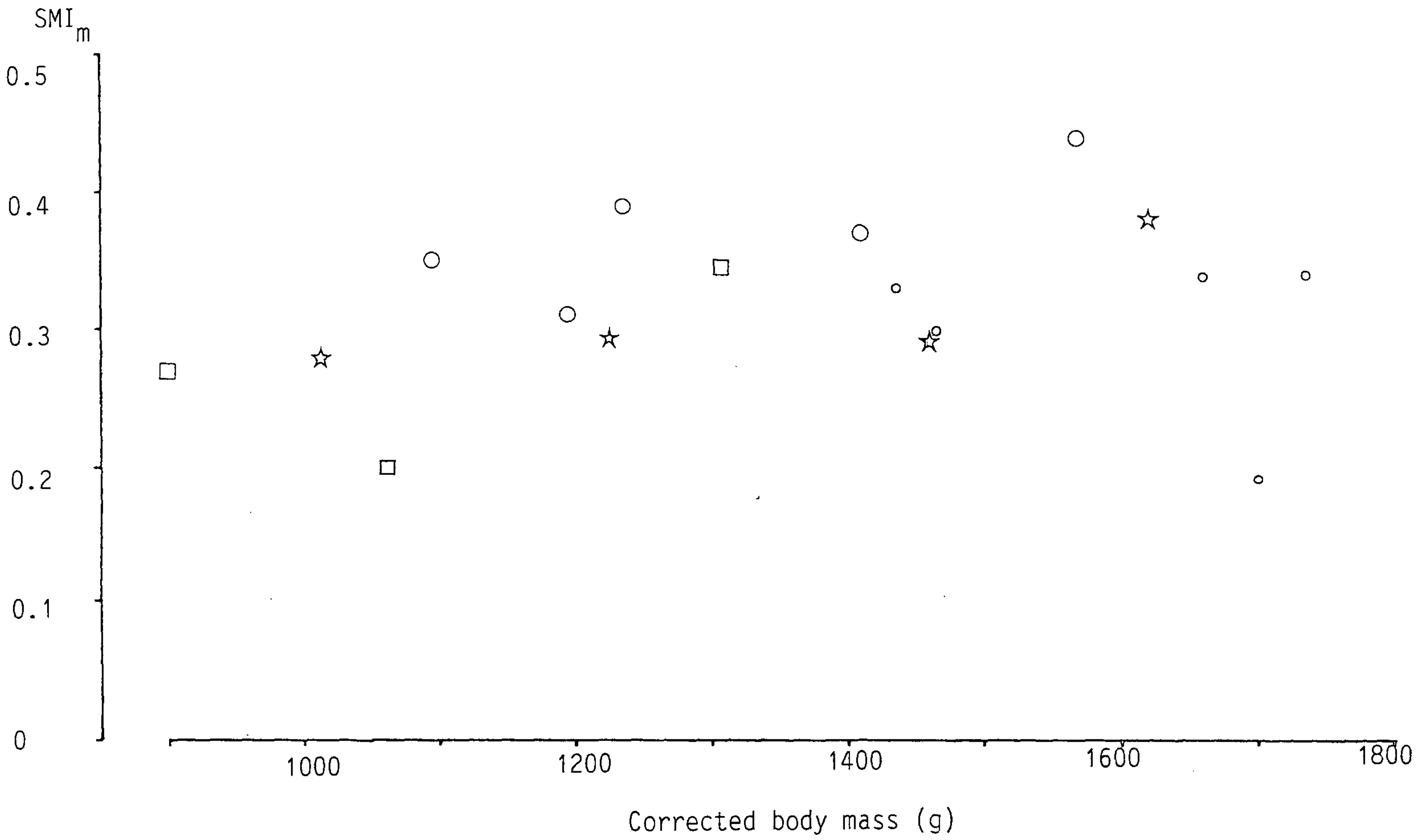


Figure 3.4: relationship between SMI$_m$ and corrected body mass (see text for derivation of different sex and age classes of Goosander. Key as in Figure 3.3.

(iii) SMI_1

Table 3.3 lists available values of SMV_1 and SMI_1. Data are too scant to draw any firm conclusions.

3.3.2 Estimates of body condition

Figure 3.5 shows the seasonal variation in corrected body mass (body mass minus the weight of the contents of the oesophagus, proventriculus and gizzard) in different sex/age classes of Goosanders. Data are summarised in Table 3.4.

The sample of birds from the River Tweed in February was the only sample large enough to investigate differences in body mass and condition between sex and age classes of Goosanders within a single month.

	n	Mean corrected body mass (g)	SE	n	Mean LI_{skin} value	SE
Adult male	12	1577	142.84	10	220.385	169.70
Immature male	3	1665	99.58	3	495.310	182.66
Adult female	3	1410	167.67	3	421.270	192.67

Data show that there were no significant differences between the mean corrected body mass of immature males and adult males ($t=0.507$, $df=13$), adult males and adult females ($t=0.759$, $df=13$), and immature males and adult females ($t=1.309$, $df=4$). The trend,

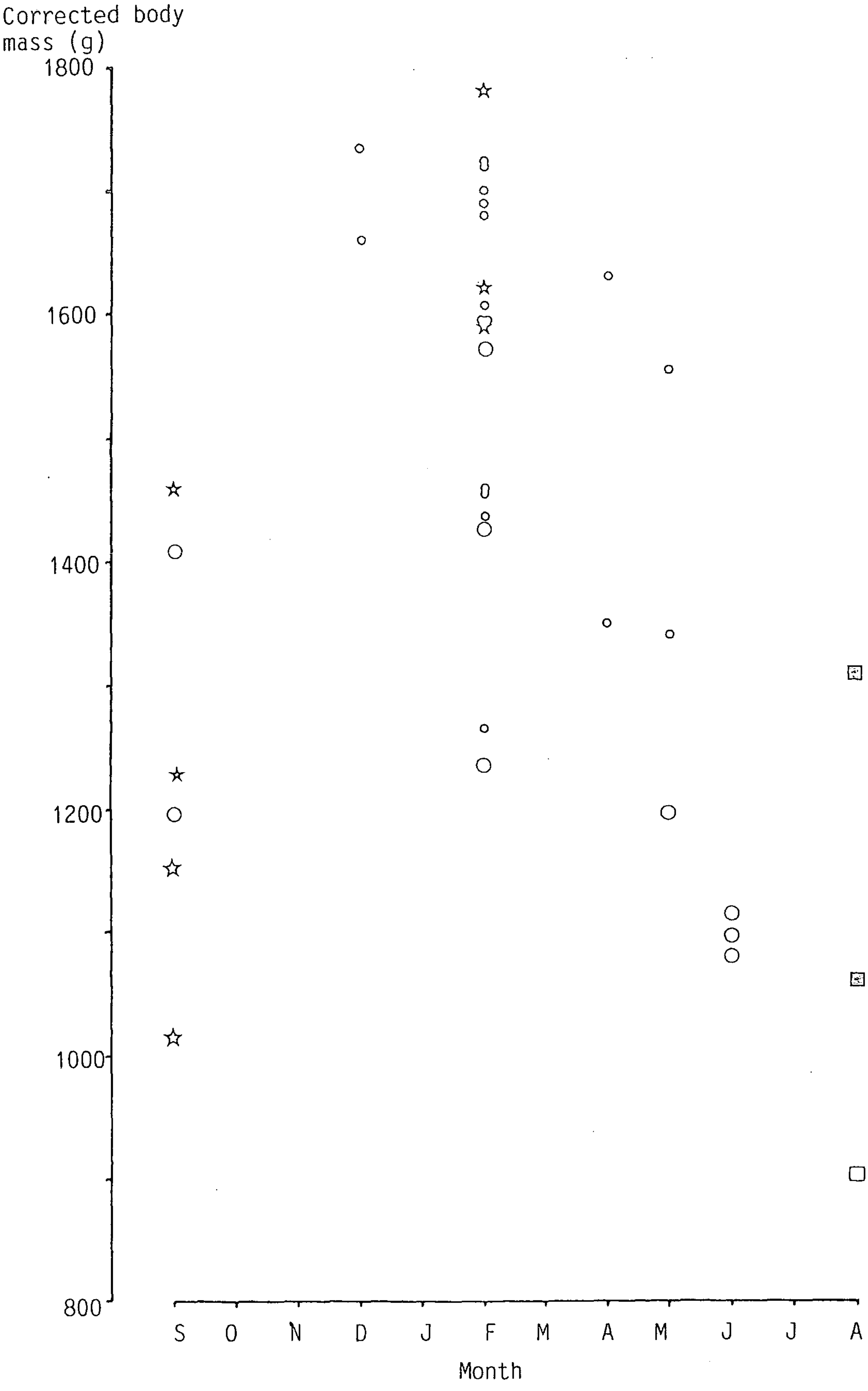


Figure 3.5; Seasonal variation in corrected body mass (see text for derivation) of different sex and age classes of Goosanders. Key as in Figure 3.3

Table 3.4 ; Corrected body masses[1] (g) of different sex/age classes of Goosanders in different months

	Adult male			Adult female		
	n	mean	SD	n	mean	SD
Jan	-			-		
Feb	12	1576.75	142.84	3	1409.667	167.67
Mar	-			-		
Apr	2	1490.00	197.99	-		
May	2	1448.00	154.15	1	1197	
Jun	-			3	1097.667	18.01
Jul	-			-		
Aug	-			-		
Sep	-			2	1303.000	154.15
Oct	-			-		
Nov	-			-		
Dec	2	1696.50	51.62	-		
Total	18	1566.11	146.51	9	1258.333	171.22

	Immature male			Immature female		
	n	mean	SD	n	mean	SD
Jan	-			-		
Feb	3	1665.00	99.579	-		
Mar	-			-		
Apr	-			-		
May	-			-		
Jun	-			-		
Jul	-			-		
Aug	-			-		
Sep	2	1345.00	159.81	2	1084.50	96.87
Oct	-			-		
Nov	-			-		
Dec	-			-		
Total	5	1537.00	205.091	2	1084.50	96.87

[1] - Total body mass minus the contents of the oesophagus and gizzard.

however, was for immature males to be heavier than adult males, which in turn were heavier than adult females. No immature females were collected. Mean lipid index values for skin samples (LI_{skin}) from these birds showed a different trend, being greatest for immature males and least for adult males (Table 3.5). However, LI_{skin} values of immature males were not significantly greater than those of adult males ($t=1.103$, $df=11$, $p<0.05$) and there were no significant differences between mean LI_{skin} values for immature males and adult females ($t=0.279$, $df=4$), or between adult males and adult females ($t=0.782$, $df=11$).

Data from all rivers combined suggest that adult males reach a maximum weight during December and fall to a minimum in late spring. LI_{skin} values show a similar trend, although unfortunately, none were available for the December sample. The same pattern was found by Milne (1976) for adult male Eiders; minimum weights occurred in the period June to September when males left the breeding area to moult offshore.

For adult male Goosanders, a minimum in May is surprising since it has already been noted (Chapter One) that the majority of this sex/age class in Britain undertake a moult migration to Fennoscandia in late May. It would be expected that following copulation, when involvement of the males in breeding ends, their reserves would be built up in anticipation of a long flight. That this was not found may be a result of very small sample sizes, but may also suggest that the individual males collected were not involved in the moult migration, or that fat deposition takes

Table 3.5 ; Lipid index values for skin samples of (a) adult males, (b) immature males, (c) adult females and (d) immature females in different months.

(a) adult males

	n	mean	S.D.
February	10	220.39	169.70
April	2	190.86	209.78
May	2	57.02	9.07

(b) immature males

	n	mean	S.D.
February	3	495.55	182.58
September	1	257.23	

(c) adult females

February	3	421.27	192.67
May	1	98.91	-
June	1	42.55	-
September	3	255.77	90.43

(d) immature females

September	2	98.41	38.57

place elsewhere and rapidly, for example, at a coastal site.

Data for seasonal changes in the body mass and body condition (in terms of LI_{skin}) of adult females are scant. They show, however, that both body weight and LI_{skin} values were high in February, immediately before the breeding season, declined over the brood rearing and moult period, and increased into early autumn. This pattern is consistent with females carrying large fat reserves for egg production, which are depleted over the course of breeding and moult, but which begin to be replenished prior to the onset of winter. Alternatively the accumulation of lipid reserves over winter could act as 'insurance' to augment daily energy intake during periods of reduced food availability such as during spate or freezing conditions. Such reserves (which are chiefly subcutaneous) may have an additional role in body insulation as has been suggested for Bar-tailed Godwit (Limosa lapponica) by Evans and Smith (1975).

For adult female Eiders, Milne (1976) found a trend in body weights and measures of body condition similar to that recorded here for female Goosanders. In the present study, only for a single bird, a female killed by traffic whilst leading her brood to water, was the breeding history in the year of death known. This bird had the lowest LI_{skin} value of all females examined. In the absence of further data it is not possible to determine how prospective breeding, or breeding females differ in condition from non-breeders. Females in poor condition may not be able to produce a clutch of eggs and/or sustain incubation, despite breaks for feeding.

3.4.0 DISCUSSION

3.4.1 Body condition

Several workers have attempted to calculate indices to estimate the body condition of individual birds, although the term 'condition' is defined in very few studies (see discussion by Evans and Smith 1975). It is used here in the sense used by Owen and Cook (1977), ie. to describe the fitness of a bird to cope with its present or future needs.

To fully describe condition, Piersma *et al*. (1984) argued that the size of both the fat and protein reserves must be measured since each has a different function; fat serves as an energy source and protein as a source of amino acids for catabolic processes. Most workers however, have based their studies of condition on estimates, or measures, of only fat/lipid reserves. This has occurred for three main reasons. Firstly, the estimation of fat reserves, by soxhlet extraction, is relatively straightforward; secondly almost all fat extracted is available as a reserve, and thirdly, fat is generally regarded as the most frequently limiting 'nutrient' throughout the annual cycle (Johnson *et al*. 1985).

Three broad types of condition indices are to found in the literature, viz. those based solely on external biometrics, those based solely on internal biometrics, and those utilising a combination of the two.

Total body weight has been shown to be a poor predictor of total fat reserves by several workers, eg. Bailey (1979), Wishart (1979) and Gauthier and Bedard (1985). This is perhaps not surprising since body weight has both a fixed structural component (the skeleton, associated musculature and internal organs) determined by the 'size' of the individual, and a variable component comprising fat, additional muscle and water. Wishart (1979), in a study of American Wigeon (Anas americana), noted that the heaviest bird was not necessarily in the best condition and that consideration must be given to variations in structural size. For live trapped birds he derived a body condition index equal to body weight divided by the sum of body length and wing length ($r=0.64$). Such a correction for body/structural size is important in allowing valid comparisons between the condition, however estimated, of different individuals or groups.

Several authors have found statistically significant positive relationships between the size of total body fat reserves (determined by soxhlet extraction) and the size of the abdominal fat depot in water birds. For example, Woodall (1978) for Red-billed Teal, $r^2=0.91$, Gauthier and Bedard (1985) for Greater Snow Geese (Anser caerulescens atlanticus), $r^2=0.86$, Piersma

(1984) for Great Crested Grebes (Podiceps cristatus), $r^2=0.85$, Bailey (1979) for the Redhead (Aythya americana), $r^2=0.83$, Wishart (1979) for American Wigeon, $r^2=0.83$. For a sample of 14 Goosanders, Platteeuw (cited "in press" by Piersma 1984) also found the size of the abdominal fat depot to be a good indicator of total body fat; 57% of the variation in total body fat was accounted for by variation in the size of the abdominal fat depot. In the present study fat deposition in this area was seen in only two birds and was not considered to be useful in estimating condition.

Estimation of total fat reserves using measures of the abdominal fat depot can only be used on dead birds. To avoid killing, and to increase the sample sizes of birds available for analysis, it is desirable to derive non-destructive condition indices based on body mass in conjuction with external biometrics. These use various measures, most commonly body weight, bill length, keel length, and wing length (eg. Owen and Cook 1977). Although Johnson et al. (1985) point out that the validity of such indices is untested, this approach has been attempted by some workers. For example, Woodall (1978) derived a condition index for Red-billed Teal from body weight, bill length, keel length and wing length which gave a positive significant correlation with total body fat. Gauthier and Bedard (1985) evaluated several 'external' condition indices in Greater Snow Geese, and found that although morphometric data were poorer predictors of total fat reserves than internal measures, a satisfactory index for use on live birds was given by the sum of the thickness of subcutaneous fat (measured by an adiposimeter) and total body weight (r=0.65).

In the present study, significant relationships were found between corrected body mass (total body mass minus the contents of the gizzard and oesophagus) and LI_{skin} (as a measure of condition) for adult males and adult females separately which explained 46% and 74% of variation in fat load respectively. Significant relationships were also found between LI_{skin} and two simple indices of body size; (i) corrected body mass divided by wing length, and (ii) corrected body length divided by the cube of wing length. For adult males these respectively explained 46% and 37% of fat load, for immature males, 96% and 81%, and for adult females 78% and 81%.

Restriction of estimates of condition to evaluation of fat loads, and ignoring protein reserves, does not diminish the usefulness of these indices. Evans and Smith (1975) concluded that "fat and muscle levels are independent measures of condition" and they noted that these need not vary in parallel. In cases where ingested food is adequate to satisfy protein demands, but insufficient to meet energy needs, protein reserves would be maintained but fat reserves depleted.

Indices of protein reserve size most commonly use measures of the size of individual muscle blocks, viz. sternal muscles, leg muscles and gizzard, and of areas of muscle attachment (eg. Ankney 1977, Wishart 1979, Bailey 1985, Gauthier et al. 1984, Piersma 1984, Davidson et al. 1986). In the present study, standard muscle volumes (Evans and Smith 1975, Piersma et al. 1984), for both the sternal and leg musculature, were calculated and standard muscle indices derived by dividing the lean dry mass of each of these blocks by their calculated volumes. This excluded the effects of variations in body size and allowed valid comparisons between sex/age classes of Goosanders to be made.

3.4.2 Annual cycles of weight and body condition

Data presented above (section 3.3.4) are consistent with the hypothesis that the total body mass of adult males reaches a peak in early winter (December), declines to a minimum in late spring (May) in the absence of preparation for moult migration, remains 'low' during the summer months, and increases again in the autumn. This is in accord with the annual cycle reported by Erskine (1971) for Goosanders (if his data from single males in September and December are excluded).

Similarly, data for adult females are consistent with the view that body mass is greatest in late winter (February), declines to a midsummer low and increases in the autumn. This agrees with the data of Erskine (1971) for adult females although he gives no indication of the breeding status of birds in his sample. It is not known how this pattern differs between non-breeding and breeding females.

Body condition, as estimated by LI_{skin} values, appears to follow a similar pattern, for both adult males and females, to changes in body mass.

3.4.3 Estimates of daily and seasonal food/energy requirements

Changes in both body mass and body condition have important implications in that variations in either or both of these factors both between and within individuals will result in variation in daily energy demands, and therefore in food consumption. Thus the energy requirements of an adult male in winter (when body mass and LI_{skin} values are greatest, and ambient temperatures are low) will be greater than its requirements in late spring (when it has a lower body weight, lower LI_{skin} values, and ambient temperatures are higher). This will occur despite gonadal growth which requires little energy (King 1973). However, individual males will need to build up reserves if they are to undertake a moult migration, and in such cases energy demands will be increased.

Data from Table 3.3 were used to provide estimates of the corrected body mass of adult males and females between seasons. Using equation 5.5 of Kendeigh et al. (1977), estimates of basal metabolic rates were made from mean seasonal weights. The seasons used, and results, are given in Table 3.6. Assuming that total daily energy requirements are three times BMR (Moreau 1972, Yom-Tov 1974, Ebbinge et al. 1975, this study (see Chapter Two,

Table 3.6 ; Corrected body masses (g) of adult male and adult female Goosanders and estimates of their basal metabolic rates and energy needs

(a) adult males

	n	mean body mass	SD	Estimated BMR[1] (kcal/bird/day)	Energy needs; daily (kcals)	seasonal (kcals)
Winter[2]	14	1594	139.14	117.726	415	37395
Spring[3]	4	1469	146.89	110.870	391	36000
Summer[4]	0	-	-	(110.870)[6]	391	36000
Autumn[5]	0	-	-	(114.313)[7]	403	36715

[1] - using equation 5.5 of Kendeigh *et al.* (1977)
[2] - Winter = Dec, Jan, Feb
[3] - Spring = Mar, Apr, May
[4] - Summer = Jun, Jul, Aug
[5] - Autumn = Sep, Oct, Nov
[6] - assuming same mean body mass in summer as in spring
[7] - assuming mean body mass is mean of winter and spring values

(b) adult females

	n	mean body mass	SD	Estimated BMR (kcal/bird/day)	Energy needs; daily (kcals)	seasonal (kcals)
Winter	3	1410	167.673	107.581	380	34173
Spring	1	1197	-	95.385	337	30972
Summer	3	1098	18.009	89.523	316	29069
Autumn	2	1303	154.149	101.520	358	32606

section 2.4.3)), and that the assimilation efficiency is 85% (Dunn 1975), daily, and total, energy intake in each season can also be estimated. Values are given in Table 3.6. Derived annual energy requirements for single adult male and adult female Goosanders are 146,110 kcal, and 126,820 kcal respectively. Such values are at best crude estimates since the increased energy demands of moulting, migrating and breeding have not been taken into account.

Food consumption, in terms of g wet weight of fish/day was estimated from these values as follows.

Assuming a value of 1.137 kcal/g/wet weight as the calorific value of salmonids (see section 2.3.3), the required daily wet weight of prey (further assuming that all prey is salmonid) ranges between 344g and 365g for adult males, and 278g to 334g for adult females. This is equivalent to 23% of body weight for males, and 23-25% for females. See Table 3.7.

An additional method was presented by Nilsson and Nilsson (1976). These authors derived an equation for the estimation of the daily consumption of fish-eating birds based on estimates of food consumption from other studies (Cormorant, van Dobben 1952, Pied Kingfisher Ceryle rudis, Tjomlid 1973, Pink-backed Pelican Pelecanus rufescens, Din and Eltringham 1974, White Pelican Pelecanus onocrotalus, Din and Eltringham 1974). Using their equation ($\log F = -0.293 + 0.85 \log W$, where F = g of fish/day, and W = weight of bird in g), adult male Goosanders required

Table 3.7 ; Estimates of daily food consumption of adult male and female Goosanders in different seasons

	(a) adult males				(b) adult females			
	wt[1]	%[2]	wt[3]	%[4]	wt[1]	%[2]	wt[3]	%[4]
Winter	365	23	269	17	334	23	242	17
Spring	344	23	251	17	296	25	211	18
Summer	344	23	251	17	278	25	196	18
Autumn	354	23	260	17	315	24	226	17

[1] = calculated by dividing estimated daily energy needs (Table 2.11) by the calorific value of juvenile salmonids determined, as 1.137 kcal/g wet weight

[2] = wt[1] as a percentage of body weight (Table 3.6)

[3] = calculated from the equation of Nilsson and Nilsson (1976)

[4] = wt[3] as a percentage of body weight (Table 3.6)

(See Table 3.6 for details of seasons)

251-269g of fish per day (17% of body weight), and adult females required 196-242g per day (17-18% of body weight). See Table 3.7. The explanation of why these estimates are less than 75% of the values derived from the energetic calculations lies in the derivation of the equation of Nilsson and Nilsson (1976). Of the four studies on which they based their method (see above), only one was carried out in the temperate zone (van Dobben 1952); the others were undertaken in Uganda and Zambia. The equation of Nilsson and Nilsson (1976) is thus probably of greatest value in estimating consumption under tropical conditions, and has little direct value in other climatic zones without a correction being applied.

From data in Pearce and Smith (1984) I calculated the mean annual temperatures for Britain (based on six sites throughout England , Scotland and Wales), Uganda (Entebbe), and Zambia (Lusaka) as 9.4°C, 21.6°C and 20.5°C respectively. From information presented by Owen (1970) I estimated that for males gross energy intake at approximately 21°C is about 72% of intake at approximately 9°C. For females the corresponding value is 82%. Assuming that estimates of 17% of body weight consumed per day by adult male Goosanders, and 17-18% by females given by the equation of Nilsson and Nilsson (1976), refer to consumption at approximately 21°C, proportional intake at approximately 9°C would be 24% for adult males and 21-22% for females. These values are in good agreement with those estimated from energetic calculations.

3.5.0 SUMMARY

Several measures of the structural size and body condition of a sample of wild Goosanders were made to investigate variations (a) both between and within sex/age classes and (b) between seasons. For adult males data suggested that maximum body mass occurred during December and declined thereafter to a spring low. Using the lipid index (mass of fat divided by lean dry mass) of a standard skin sample as a measure of condition, showed a similar trend. For adult females body mass was highest during the winter, declined over spring and summer and began to increase in the autumn. Measures of condition show a similar trend and data are consistent with females carrying large fat reserves for egg production which are depleted over the course of breeding and moult, but which begin to be replenished before the onset of winter.

Data on seasonal changes in body mass allowed an estimate to be made of the daily food requirements of adult birds. This used an equation of Kendeigh _et al._ (1977) to estimate BMR and assumed that (a) total energy needs were three times BMR, (b) all energy needs were met by salmonid prey of mean calorific value 1.137kcal/g wet weight, and (c) a constant assimilation efficiency of 85%. Using this method indicated that adult males required 344-365g (23% of body weight), and adult females required 278-334g (23-25% of body weight). A second method of estimating total food consumption, using an equation of Nilsson and Nilsson (1976), indicated that adult males required 251-269g of fish/day (17% of body weight), with adult females needing 196-242g/day (17-18% of body weight). Reasons for the difference between these estimates are discussed.

CHAPTER FOUR ;

TIME-BUDGETS

4.1.0 INTRODUCTION

Many attempts have been made in recent years to estimate how various bird species partition their time between different activities. Such time-budget studies have, in some cases, concentrated on a particular activity, or group of activities, (eg. Dzinbal and Jarvis 1984, Minot 1980), whilst others have been more comprehensive investigations of time allocation over a wide spectrum of behaviours on a daily, seasonal, or annual basis (eg. Brodsky and Weatherhead 1984, 1985a and 1985b, Geroux et al. 1986, Lo and Fordham 1986, Nilsson 1974, Rushforth Guinn and Batt 1985, Seymour and Titman 1979). In this context the only detailed work on the Goosander was published by Sjoberg (1985) although this was a study of foraging activity patterns rather than of time-budgets.

I made time-budget studies of Goosanders to collect quantitative information, at different periods of the annual cycle, on the activities during daylight hours of birds present on river and lake habitats. The intention was to identify periods and areas where foraging activities were concentrated.

4.2.0 METHODS

Observations were made of birds on both running and standing waters within the study area using a 15-60 x 60 telescope, 10x50 binoculars, and a Modulux 130 image intensifier fitted with a 600mm lens. Sites were classified as,

(a) 'roost river' (running water site known to hold evening roost of Goosanders),
(b) 'non-roost river' (running water site not known to hold roost),
(c) 'roost lake' (standing water site known to hold evening roost), or
(d) 'non-roost lake' (standing water site not recorded as holding an evening roost),

where a roost site was defined as a site where 'loafing' dominated the time budgets of birds when collectively considering all records from that site. A limitation of this broad site classification is that it ignores any differences which may exist between the behaviour of birds on different sub-divisions of each site type such as 'stream', 'upper river', 'lower river' etc, or 'reservoir', 'upland loch', 'tarn' etc. Unfortunately data are not adequate to make such detailed investigations.

The location and classification of sites where data were collected are shown in Figure 4.1. The monthly distribution of field visits is shown in Table 4.1.

Focal animal sampling was the preferred sampling method and was used wherever possible, but in cases where a given individual

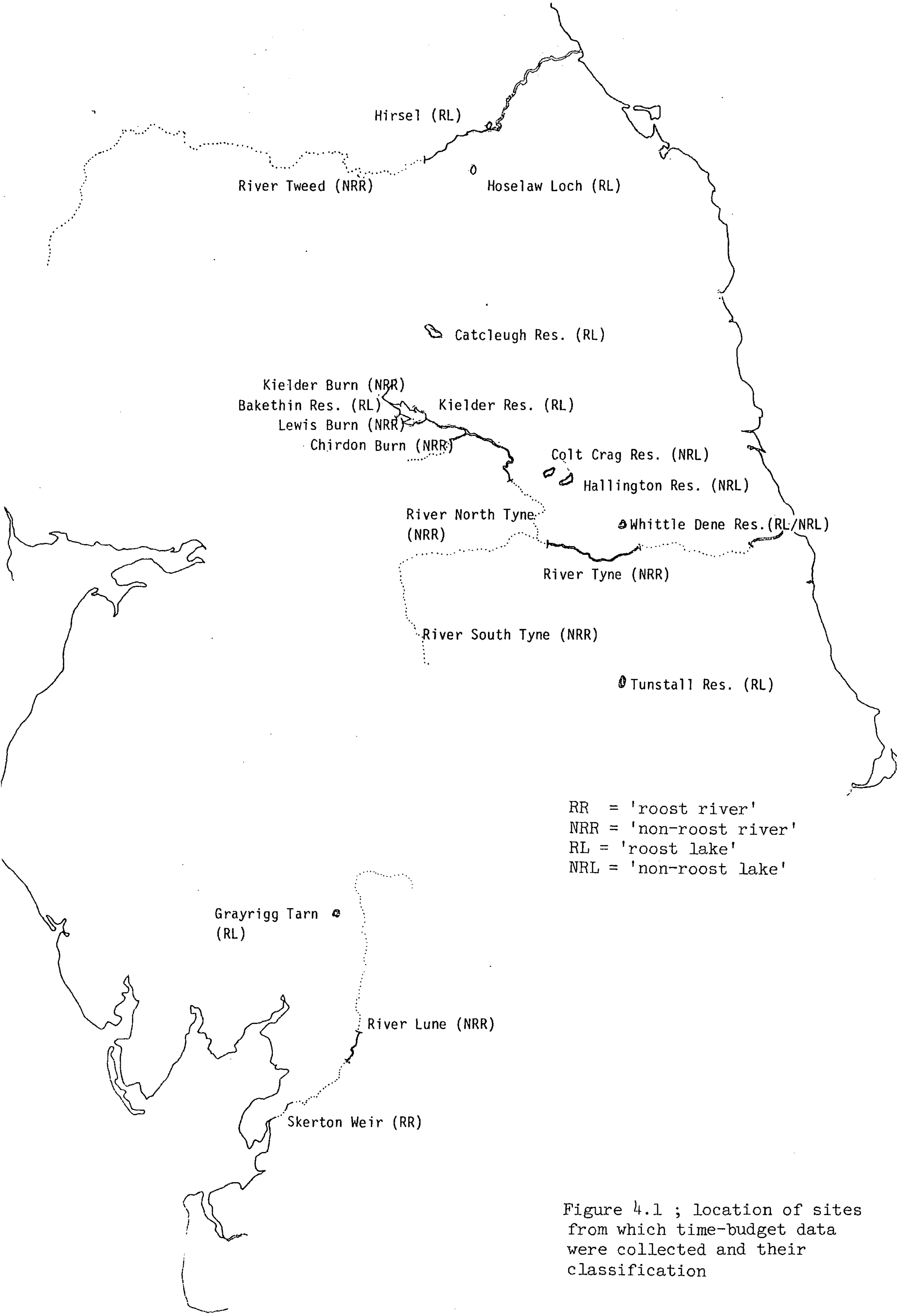


Figure 4.1 ; location of sites from which time-budget data were collected and their classification

Table 4.1 ; Monthly distribution of field visits

Month	Total no. visits
Mar	4
Apr	13
May	6
Jun	4
Jul	2
Aug	4
Sep	1
Oct	4
Nov	5
Dec	10
Jan	6
Feb	4

could not be recognised, eg. when with a conspecific or when within a group, a scan sampling method was employed (Altmann 1974). For small groups of birds in which individuals could not be distinguished from one another, scans of the group were made at one minute intervals and the behaviour of each bird assigned to a particular category (see below).

Activities were recorded as one of the following categories ;-

1. foraging - diving or head-under-searches (see Chapter Five for an account of feeding behaviour), including handling and swallowing times, and time between dives,
2. preening - all comfort movements,
3. sleeping - positioned with bill tucked into back, eyes closed,
4. loafing - resting, 'doing nothing',
5. swimming - purposeful movement,
6. display - courtship activities and copulation,
7. flying
8. aggression

These observations were used to derive estimates of the percentage of time spent in various activities, and to determine how these estimates varied with respect to site type, season, time of day, sex, and status (paired or unpaired).

4.3.0 RESULTS

A total of 1723 minutes of continuous observations from focal animal sampling were collected in addition to 6452 'Goosander minutes' from scan sampling. The distribution of observation periods divided by observation method, month, site type, sex and time of day (see Table 4.2) shows several important points. Firstly, observations were concentrated over the winter months November to February. This contrasts with the distribution of fieldwork effort (Table 4.1) and is a result of the relative difficulty in locating birds in different months. The lack of observations of brood activities and movements is unfortunate, and this is clearly an area, important in the context of interactions with fisheries, where future effort could profitably be concentrated. Secondly, Table 4.2 shows the dominance of focal animal observations at river sites and scan sample observations at lake sites. This could lead to a bias in comparisons of the time-budget of birds between types of site if the two sampling methods are not comparable. This possibility is examined below (section 4.3.1). Thirdly, few data were collected from 'roost river' sites. Indeed such data derive from a single site, Skerton Weir, on the River Lune, Lancaster, visited only in January 1983. This prevents any conclusions being drawn about activity at this site type. Fourthly, Table 4.2 shows that observations were not uniformly distributed throughout the day, with none available before 0900 and after 2000 hours. The absence of early morning and late evening observation periods would be particularly crucial if specific activities were concentrated into that part of the day, for example dawn or dusk feeding bouts.

Table 4.2 ; The distribution of time-budget observation periods according to method (a, focal animal and b, scan sampling), month, site type (1 = 'non-roost rivers', 2 = 'roost rivers', 3 = 'non-roost lakes, and 4 = 'roost lakes'), time period of day and sex (M = adult male, I = immature male and R = redhead). Numbers are numbers of observation periods in each category. '-' indicates no available data.

(a) Focal animal sampling

		Time period																	
		09-11			11-13			13-15			15-17			17-19			19-21		
		M	I	R	M	I	R	M	I	R	M	I	R	M	I	R	M	I	R
Jan	1	-	-	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	1	-	3	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Feb	1	-	-	1	1	-	1	-	-	-	-	-	-	1	-	1	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mar	1	2	-	1	2	-	2	1	-	1	2	-	2	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apr		no data																	
May	1	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Jun		no data																	
Jul		no data																	
Aug		no data																	
Sep		no data																	
Oct		no data																	
Nov	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dec	1	2	-	4	1	-	1	-	-	3	-	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-

(b) Scan sampling

		Time period																	
		09-11			11-13			13-15			15-17			17-19			19-21		
		M	I	R	M	I	R	M	I	R	M	I	R	M	I	R	M	I	R
Jan	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	3	-	3	-	-	-	-	-	-
Feb	1	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	3	-	3	-	-	-	1	-	1	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mar	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apr	1	-	-	-	1	-	1	-	-	-	-	-	-	1	-	1	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
May	1	-	-	-	-	-	-	-	-	-	-	-	2	1	-	3	1	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	1	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Jun		no data																	
Jul	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aug	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Sep		no data																	
Oct		no data																	
Nov	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	1	1	1	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
Dec	1	2	-	1	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

4.3.1 Comparison between sampling methods of estimates of time spent in various activities

The allocation of time between each behavioural category, irrespective of site type, month, time of day, sex and age, is given in Table 4.3 for each sampling method. This shows that for 'loaf', 'feed' and 'swim' there were statistically significant differences between the estimates of the overall percentage of time spent in each of these behaviours between each method. These differences could result either from differences in the times of year or day at which the samples were collected by each of the observational methods or from the fact (as noted in section 4.3.0 above) that scan samples were the dominant method at lake sites, with focal animal records dominating at river sites. However, it is also possible that the different methods would give different estimates if applied to the same birds. I tested this latter possibility as follows.

Using data from periods of continuous observation of a focal animal I extracted the activity recorded at time 0, 1 minute, 2 minute etc. These data were then treated as a scan sample. The same observation period thus yielded two comparable estimates of the percentage of time spent in each behaviour category. For each activity t-tests were performed to examine differences between these paired estimates using arcsin transformed values of percentages (see Table 4.4). For none of the activities were the estimates significantly different.

Table 4.3 ; Percentage of time spent in each behaviour as estimated by (a) focal animal sampling, (b) scan sampling, and (c) both methods combined, using all observations made during the study. The results of a t-test of differences between each method in estimates of time in each behavioural category are shown. Asterisks show values significant at the 5% level.
(Percentage values have been arcsin transformed.)

	(a) Focal animal sampling (n=49)		(b) Scan sampling (n=68)			(c) both methods combined (n=117)	
	mean	SD	mean	SD	t	mean	SD
Loaf	26.3	26.2	54.8	31.2	5.36*	42.9	32.4
Feed	38.5	28.4	14.7	23.0	4.83*	24.7	27.9
Preen	18.5	18.5	7.8	11.9	1.64	12.3	15.8
Sleep	5.2	12.4	10.0	20.7	1.56	8.0	17.8
Swim	12.4	13.0	6.6	12.1	2.45*	9.0	12.8
Alert	2.3	5.4	2.5	6.0	0.19	2.4	5.7
Display	0.8	2.8	2.8	10.3	1.52	2.0	8.1
Fly	0.2	1.1	1.6	5.8	1.94	1.0	4.5
Aggression	0.1	0.4	0.1	0.7	0.00	0.1	0.6

Table 4.4 ; Comparison between focal-animal and scan sampling of the estimated percentage of time spent in each behavioural category, using arcsin transformed values from 19 observation periods.

Activity	Mean %; focal animal	scan	Mean difference	SE of difference	t
Loaf	36.1	35.0	1.03	1.48	0.70
Sleep	5.7	5.6	0.17	0.21	0.81
Feed	28.1	29.0	-0.85	0.96	0.89
Swim	12.5	12.7	-0.14	0.69	0.20
Preen	23.5	24.8	-1.22	1.01	1.21
Aggression	0.1	0.0	0.14	0.13	1.08
Alert	3.3	4.0	-0.74	0.84	0.89
Display	2.2	2.3	-0.17	0.35	0.49
Fly	0.0	0.0	0.0	-	-

These results indicate that differences other than observational method must account for the observed differences in the overall time allocated to each behaviour. In subsequent analyses therefore, data collected by each of these methods were combined.

4.3.2 The relationship between site type, month, time of day, sex and the percentage of time spent in each activity category

To examine the relationship between site type, month, time of day, and sex, and the percentage of time allocated to each activity category, a four-way analysis of variance was performed using a general linear model facility within the SAS system (SAS 1985) which allows analysis where cell totals are unequal. The classes used in these analyses for each independent variable were as follows;

Site classification

Classes used are as defined above but data from 'roost rivers' were excluded (see section 4.2.0).

Season

Since data are not adequate to investigate differences between individual months in the percentage of time allocated to specific behaviours, values were combined into 'seasonal' groups as follows;-

(1) late winter - January and February (total no. obs. = 32)
(2) spring - March, April and May (total no. obs. = 44)
(3) early winter - November and December (total no. obs. = 41)

This grouping minimised the variation in the number of observation periods between groups.

Time of day

Other workers (eg. Sjoberg 1985, Timken and Anderson 1969) have described diel variations in the activity of Goosanders. Rather than use a broad division of the day ('morning') and 'afternoon', which may have masked the existence (or otherwise) of 'early' and 'late' activity peaks, data were combined into time periods as follows;

Time period 1 = 0900 - 1100 hours
2 = 1101 - 1300
3 = 1301 - 1500
4 = 1501 - 1700
5 = 1701 - 2000

Sex

Data were combined into two sex categories, 'male' and 'redhead'. Adult male Goosanders are readily identifiable but immature males vary enormously, at any given time of the year, in their degree of development of adult plumage. Some are obviously intermediate in overall appearance between adult males and females and can thus be assigned readily to the correct sex, but an unknown proportion of immature males are indistinguishable in the field from adult females. Cloacal examination of birds caught at Hoselaw Loch (see Chapter One) has confirmed this. Thus the occurrence of immature males will be under-estimated. Perhaps as a result of this, the incidence of birds identified as immature males during the study (and in the wider ranging survey work) was low and insufficient time-budget data were collected to treat immature males as a separate category. Data were therefore combined with those of adult males.

The 'redhead' category includes all birds not identified as either adult or immature males. This will necessarily be a more heterogeneous group than the 'male' category since it will contain not only adult and immature females (which are impossible to distinguish under most field conditions and hence cannot be given separate sex/age categories), but also a proportion of immature males.

Table 4.5 presents the results of the overall test of the effects of site type, season, time of day and sex; significant effects were shown on the percentage of time allocated to 'loaf', 'sleep', 'feed', 'preen' and 'display' behaviours. Detailed tests on these behaviours are shown in Table 4.6 and the results discussed in the following sections.

Table 4.5 ; Results of a four-way analysis of variance to investigate the effect of site type, sex, season and time period of day on the percentage of time allocated to each behaviour: test of overall effects. (F = variance ratio.)
Degrees of freedom = 116 for all behaviour categories.

Activity	r^2	F	p
Loaf	0.739	3.60	0.0001
Sleep	0.577	1.74	0.02
Feed	0.554	1.58	0.04
Swim	0.438	0.99	0.51
Preen	0.676	2.66	0.0001
Aggression	0.237	0.40	1.00
Alert	0.539	1.49	0.07
Display	0.789	4.77	0.0001
Fly	0.457	1.07	0.39

Table 4.6 ; Detailed tests from a four-way analysis of variance for behaviours on which there was a significant overall effect (Table 3.5) of the independent variables.
\+ marks effects significant at the 5% level.

Loaf	F	df	p
+Site	27.22	2	0.0001
Season	1.77	2	0.18
Sex	0.37	1	0.55
Time	0.40	4	0.81
Site * season	2.07	2	0.13
Site * sex	1.09	2	0.34
Site * time	1.23	6	0.31
Site * season * sex	0.00	1	0.98
Season * time	1.75	6	0.12
Site * season * time	0.76	3	0.52
Sex * time	0.33	4	0.86
Site * sex * time	0.49	5	0.78
Season * sex * time	0.62	6	0.71
Site * season * sex * time	0.05	1	0.83

Feed	F	df	p
+Site	9.62	2	0.0002
Season	0.73	2	0.49
Sex	0.18	1	0.67
Time	0.81	4	0.52
Site * season	0.93	2	0.40
Site * sex	0.10	2	0.91
Site * time	0.28	6	0.94
Site * season * sex	0.01	1	0.90
Season * time	1.50	6	0.19
Site * season * time	0.23	3	0.88
Sex * time	0.56	4	0.69
Site * sex * time	0.23	5	0.95
Season * sex * time	0.14	6	0.99
Site * season * sex * time	0.04	1	0.84

Preen	F	df	p
Site	2.56	2	0.09
+Season	3.32	2	0.04
Sex	0.03	1	0.86
+Time	4.74	4	0.002
Site * season	1.62	2	0.21
Site * sex	0.40	2	0.67
+Site * time	5.77	6	0.0001
Site * season * sex	0.29	1	0.59
Season * time	2.05	6	0.07
Site * season * time	0.71	3	0.55

Table 4.6 cont.

Preen cont.	F	df	p
Sex * time	0.16	4	0.96
Site * sex * time	0.49	5	0.78
Season * sex * time	0.38	6	0.89
Site * season * sex * time	0.01	1	0.91

Display	F	df	p
+Site	3.96	2	0.02
+Season	9.09	2	0.0003
Sex	0.00	1	0.97
+Time	13.32	4	0.0001
+Site * season	19.15	2	0.0001
Site * sex	0.30	2	0.74
+Site * time	11.04	6	0.0001
Site * season * sex	0.00	1	0.96
+Season * time	5.98	6	0.0001
+Site * season * time	11.94	3	0.0001
Sex * time	0.36	4	0.84
Site * sex * time	0.50	5	0.78
Season * sex * time	0.52	6	0.79
Site * season * sex * time	0.30	1	0.58

Sleep	F	df	p
+Site	5.79	2	0.005
+Season	11.50	2	0.0001
Sex	0.04	1	0.85
+Time	4.34	4	0.004
Site * season	0.74	2	0.48
Site * sex	0.14	2	0.87
Site * time	1.64	6	0.15
Site * season * sex	1.12	1	0.29
Season * time	1.59	6	0.16
Site * season * time	1.17	3	0.33
Sex * time	0.25	4	0.91
Site * sex * time	0.48	5	0.79
Season * sex * time	0.21	6	0.97
Site * season * sex * time	0.00	1	0.97

4.3.3 Loaf

Table 4.6 shows that at the 5% level of significance the only independent variable to show a significant effect when acting alone was 'site'. The mean percentage of time spent loafing on each site type (with sample sizes and standard errors) was;

'non-roost river'	30.0%	n=73	SE=2.85
'non-roost lakes'	35.4%	n=16	SE=7.13
'roost lakes'	80.8%	n=28	SE=4.15

Differences in the percentage of time spent loafing between 'non-roost river' and 'non-roost lake' sites were not statistically significant ($t=0.703$, $df=87$, $p>0.05$), but the mean values for each of these were significantly lower than that derived from observations at 'roost lake' sites ($t=10.09$, $df=99$, $p<0.01$, and $t=5.50$, $df=42$, $p<0.01$ respectively). See Figure 4.2.

Table 4.6 also shows that no other combination of independent variables had any statistically significant effect on the percentage of time allocated to loafing activities.

4.3.4 Feed

Of all the independent variables acting alone or in combination with each other, only 'site' showed a significant effect on foraging (see Table 4.6). The mean percentage of time spent foraging at each site type (with sample sizes and standard

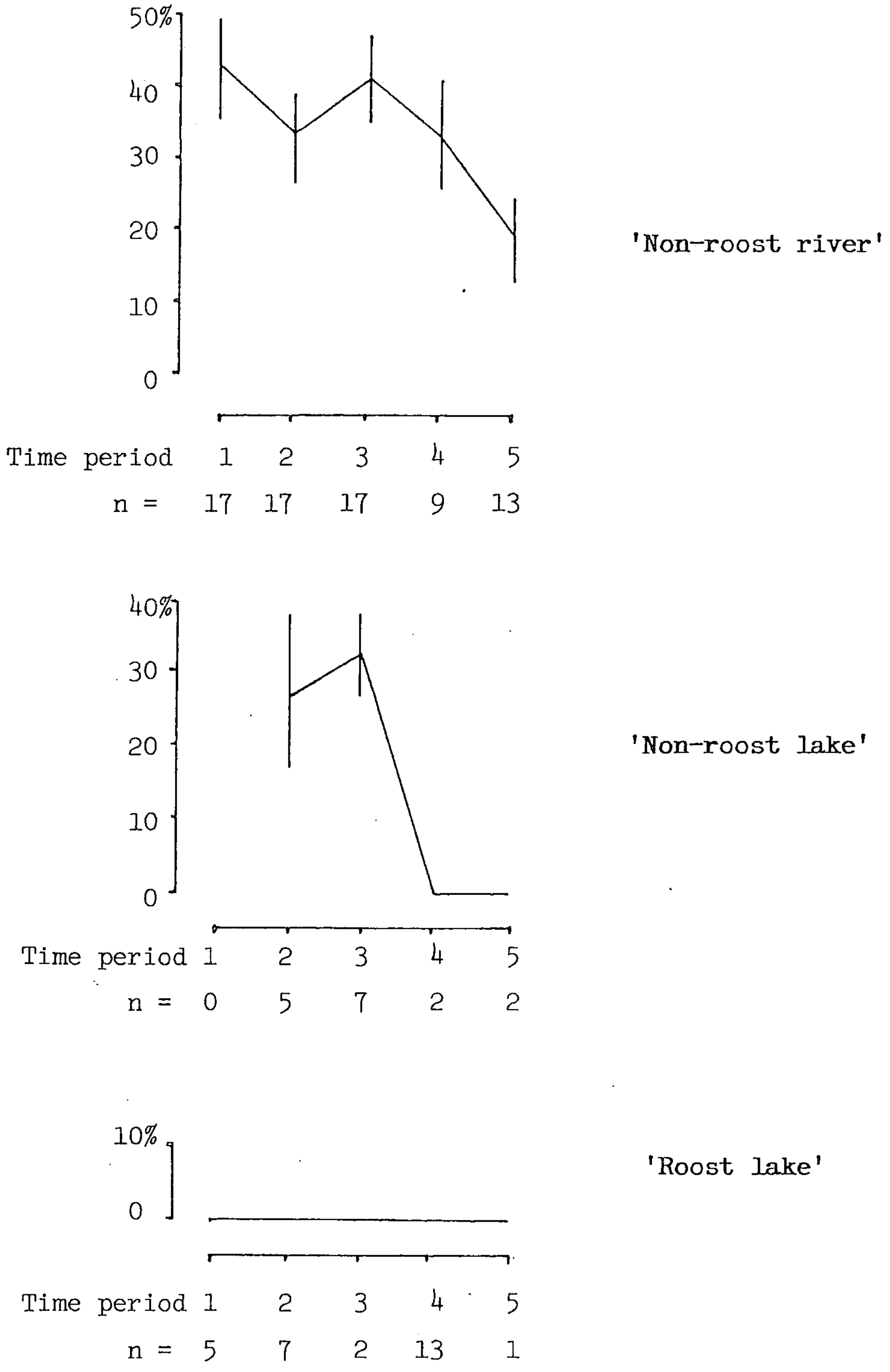


Figure 4.2 ; Relationship between the percentage of time spent foraging and site type and time period of day
(Mean values are shown +/- 1SE, n = no. observation periods)

errors) was;

'non-roost river'	34.5%	n=73	SE=3.35
'non-roost lake'	23.2%	n=16	SE=5.56
'roost lake'	0.0%	n=28	

Differences between 'non-roost river' and 'non-roost lake' sites in the percentage of time spent foraging were not statistically significant (t=1.74, df=87, p>0.05). 'Roost lake' sites are clearly not important for feeding.

4.3.5 Preen

Table 4.6 shows both season and time acting singly, and site and time together, had statistically significant effects (at the 5% level) on the percentage of time spent preening.

The mean percentage of time spent preening during each season (with sample sizes and standard error) was;

early winter	16.4%	n=41	SE=2.69
late winter	4.9%	n=32	SE=1.42
spring	13.7%	n=44	SE=2.59

The percentage of time observed in display and courtship activities shows the reverse pattern (see section 4.3.6). This suggests that changes in the estimates of time allocated to preening are not related to these other behaviours but to variation in self-maintenance activities per se.

The effect of time alone on the percentage of time spent preening (with sample sizes and standard errors) was;

Time period	1	7.0%	n=22	SE=2.22
	2	15.2%	n=29	SE=3.35
	3	13.0%	n=26	SE=2.83
	4	8.4%	n=24	SE=2.40
	5	18.7%	n=16	SE=5.59

Analyses show a significant combined effect of site and time on the percentage of time allocated to preening. For 'non-roost rivers' values suggest a morning 'low' (0900-1100) but thereafter a generally constant allocation of 15-20% of time to preening. For 'non-roost lakes' no data are available for the first time period but in periods 2 to 4 allocation of time to this activity is similar to that on 'non-roost rivers'. However no preening activities were noted at 'non-roost lake' sites after 1700 hours. Time allocated to preening on 'roost lakes' shows a different pattern. The percentage of time allocated to preening there was significantly lower than on 'non-roost rivers' (mean percentage 'roost lakes' = 5.3%, SE=3.3, n=28, mean percentage 'non-roost rivers' = 14.8%, SE=1.8, n=73, t=2.558, df=99, $p<0.01$), although there was no significant difference between the percentage of time spent preening on 'roost' and 'non-roost lakes' (mean percentage 'non-roost lakes'=12.8%, SE=3.3, n=16, t=1.633, df=42, $p>0.10$). If however the outlying single observation for 'roost lakes' in time period 5 is excluded (this derives from a single adult male Goosander noted on the Hirsel), the mean percentage of time spent preening at this site type is 0.0%. See Figure 4.3.

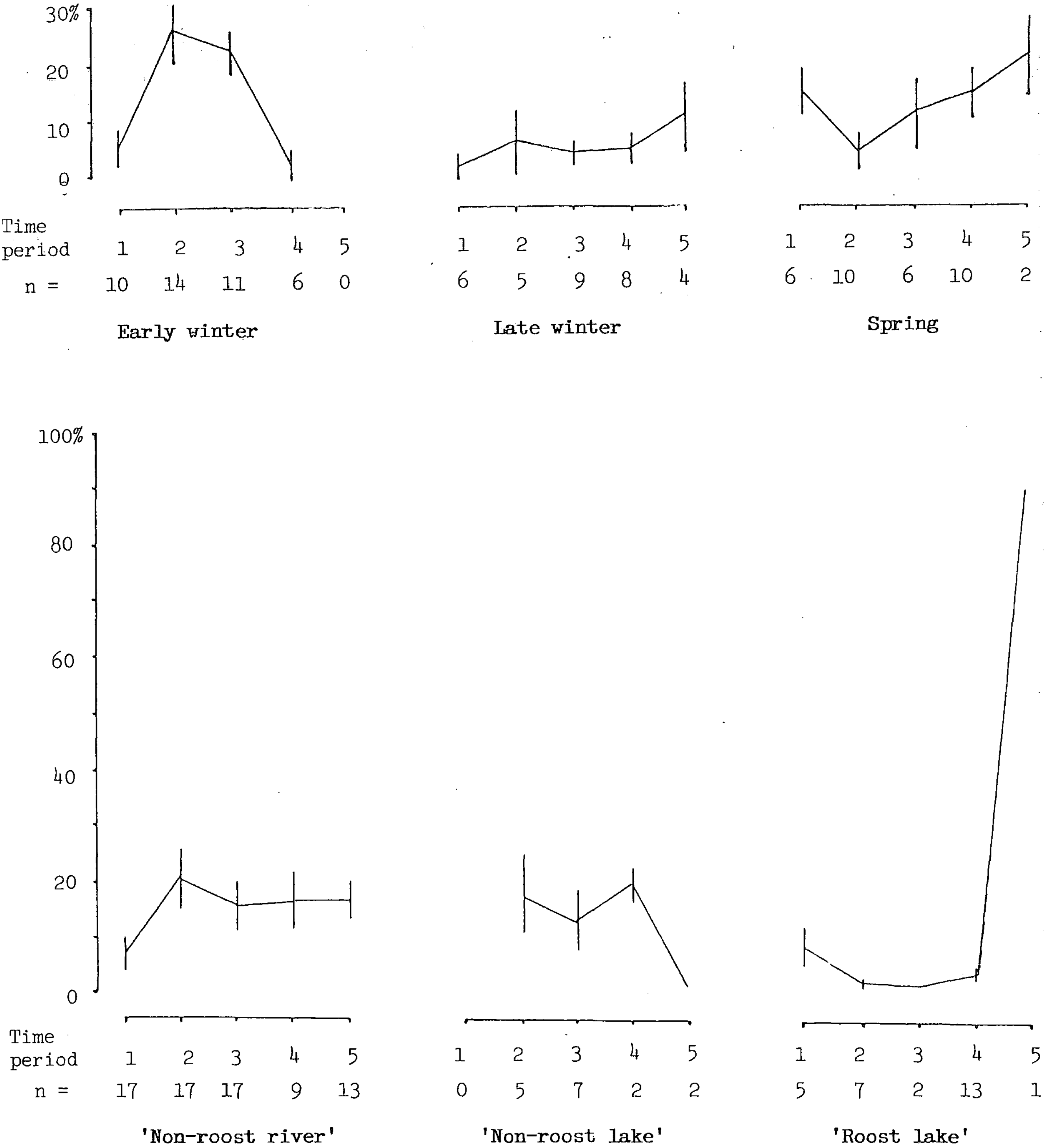


Figure 4.3 ; Relationship between the percentage of time spent preening and season, site type and time period of the day

(Mean values are shown +/- 1SE, n = no. obsrevation periods)

4.3.6 Display

Table 4.6 shows the specific effects of site, season and time acting singly and in combination with each other on time spent in this behaviour. These are illustrated in Figures 4.4a-d.

Data show that display and courtship activities were not recorded at 'roost lake' sites. Combining all observations indicates that this suite of behaviours was concentrated into the early part of the day irrespective of season or site type, and that the focus for these activities shifted from 'non-roost lakes' in the late winter period (January and February), to 'non-roost rivers' in the spring (March to May), where they occupied a lower percentage of time. (The difference was not statistically significant at the 5% level of significance; t=1.38, df=97).

4.3.7 Sleep

Table 4.6 indicates that acting alone, 'site', 'season' and 'time' had significant effects (at the 5% level) on the percentage of time spent sleeping.

Mean percentages for each site type (with sample size and standard error) were;

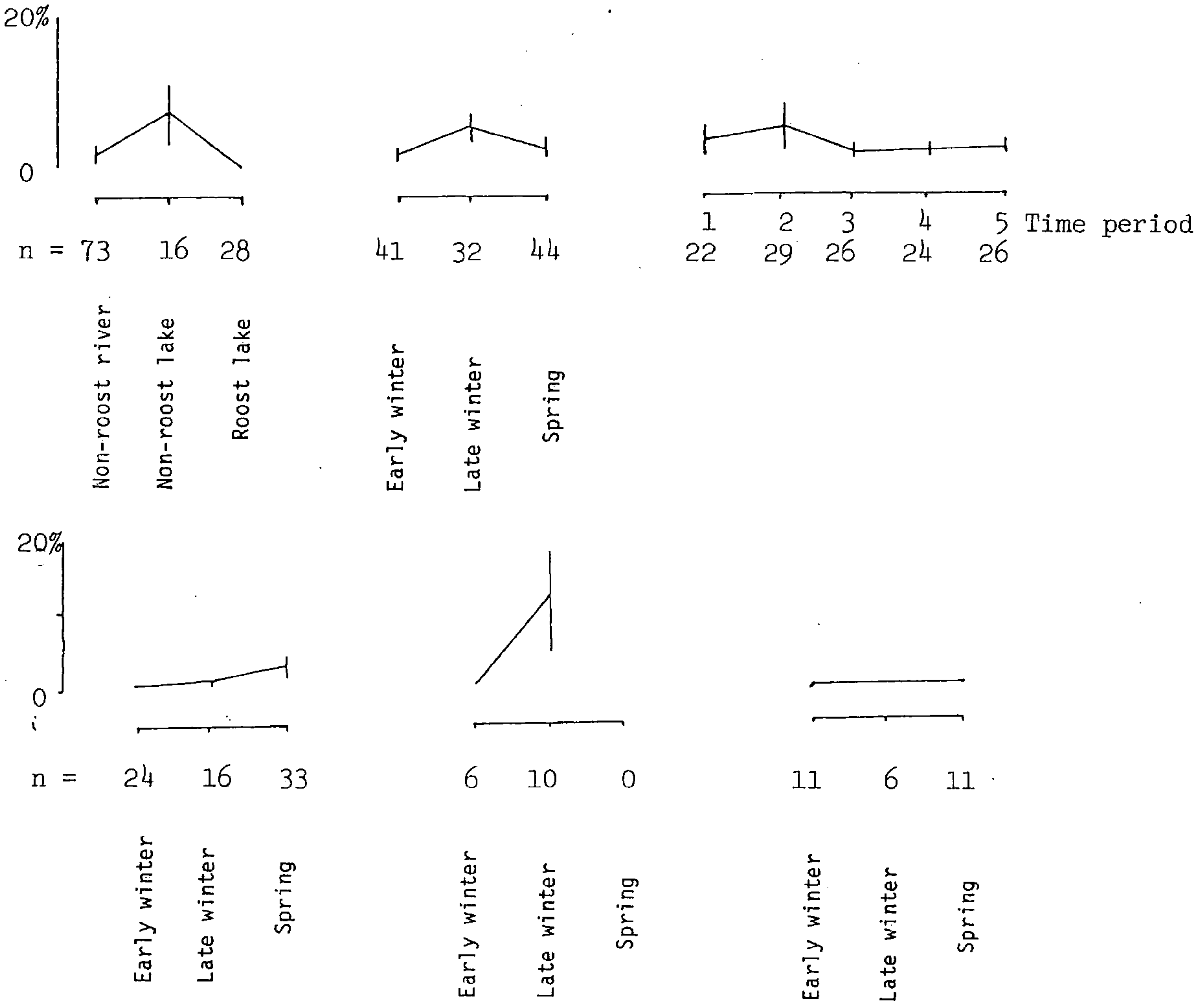


Figure 4.4 ; Relationship between the percentage of time spent in display and site type, season and time period of day

(Mean values are shown +/- 1SE, n = no. observation periods)

'non-roost rivers'	8.8%	n=73	SE=2.23
'non-roost lakes'	8.9%	n=16	SE=4.77
'roost lakes'	5.4%	n=28	SE=2.56

Differences between site types were not statistically significant at the 5% level.

For each season the mean percentages of time spent sleeping (with sample size and standard error) were;

early winter	2.5%	n=44	SE=1.3
late winter	3.4%	n=32	SE=2.4
spring	16.4%	n=44	SE=3.5

The mean percentages of time spent sleeping for each time period (with sample size and standard error) were;

Time period 1	7.6%	n=22	SE=3.4
2	2.2%	n=29	SE=1.1
3	4.8%	n=26	SE=3.0
4	11.2%	n=24	SE=3.7
5	19.2%	n=16	SE=7.5

See Figure 4.5.

4.3.8 Other activities

Swim

None of the independent variables used in analyses showed a significant overall effect on the percentage of time spent swimming (see Table 4.5).

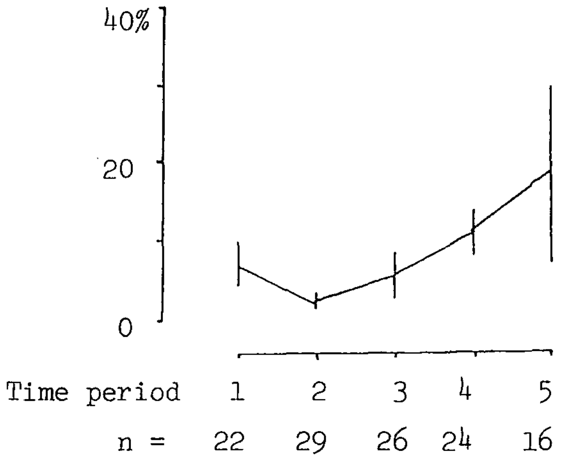


Figure 4.5 ; Relationship between the percentage of time spent sleeping and time period of the day (Mean values are shown +/- 1SE, n = no. observation periods)

'Alert', 'aggression' and 'fly'

Collectively these activities accounted for less than 2.5% of the overall time-budget (as estimated from scan and focal-animal sampling combined). Data collection targetted at these particular activities is needed to study the effects of the independent variables considered in section 4.3.3.

4.3.9 Comparison of the time-budgets of paired and unpaired Goosanders

Comparisons of behavioural differences between paired and unpaired birds were restricted to the 'winter' (November to February) and 'spring' (March to May) periods, and to 'non-roost rivers', by the availability of data. The seasonal distribution of observation periods is shown in Table 4.7.

Analyses of these data were made using general linear modelling as before, with status (paired or unpaired), season, and sex as the independent variables and the estimate of the percentage of time spent in each behaviour category, as the dependent variable. No significant effects were detected, although sample sizes were small.

Table 4.7 ; Distribution of observation periods used in the comparison of the time-budgets of paired and unpaired Goosanders

	a) males		b) redheads	
season	paired	unpaired	paired	unpaired
winter	5	9	4	13
spring	9	7	4	9

4.4.0 DISCUSSION

4.4.1 Possible biases within the data

The majority of data were collected from a vehicle at vantage points on road bridges or adjacent roads. Almost invariably the bird(s) would take flight or swim out of view if an attempt was made to approach on foot, so the vehicle served as a mobile hide, the presence of which did not appear to disturb the birds. Although birds often showed alert behaviour when a vehicle stopped (behaviour not elicited by moving traffic), by the time activity recording commenced, some 2-3 minutes later, they always appeared to have resumed normal activities.

Although data collected in this way could be biased in favour of those individuals which are tolerant of vehicular disturbance, such bias would be restricted to birds on rivers and small standing water bodies with a roadside perimeter, rather than to those on large areas of water observed from some distance away. The bias could not be quantified, since observation of birds away from roadside or bridge viewpoints was extremely difficult because the birds were so much more wary of an approaching human than of a vehicle. This was especially true on the River Tyne system as compared to the Tweed and Lune, the other major river systems covered.

Activities which involved movement were likely to take the bird out of the field of view and thus bias estimates of the amount of time spent in those activities. The 'easiest' birds to observe for long periods were those involved in static activities such as preening, sleeping or loafing and it is possible that the contribution of these activities to the overall time-budget was over-estimated, and the amount of time spent in 'active' behaviours such as flying and foraging under-estimated. This is likely to be a greater problem on river sites where birds were more frequently lost from view under vegetation, around bends, etc. than on open reservoir and loch sites. Correction for this bias could be made only if observations were made from the moment a bird flew into the site to the moment it flew out. Since these data are not available here possible biases of this type could not be investigated.

The absence of observation periods both early and late in the day would introduce a major bias into results if specific activities were concentrated into either or both of these periods. The extent of such bias might vary through the year with changes in daylength, being more important during the summer when the observed portion of the day was a lower proportion of total daylight hours.

This may explain the absence of any significant diurnal variation in time spent foraging. Other workers have noted marked morning and evening peaks in Goosander feeding (eg. Sjoberg 1985, Timken and Anderson 1969), although Wood (1987a) found that foraging activity was not correlated with time of day.

4.4.2 Habitat use

The two activities which dominate the time-budgets of Goosanders are 'loaf' and 'feed'; time spent in one or other of these activities accounted for over two-thirds of all observations (based on scan and focal-animal sampling data combined).

The percentage of time allocated to loafing was significantly greater on 'roost lakes' than on both 'non-roost lake', and 'non-roost river' sites. By contrast the percentage of time allocated to foraging may have been greater on 'non-roost river' sites than on 'non-roost lakes' (although the difference was not significant), and no feeding was observed on 'roost lakes'. However, since 'loaf' and 'feed' dominate the overall time budgets of Goosanders (see Table 4.3), and roost sites were defined as sites where loafing was the predominant activity, these results are not surprising. Such differences suggest a broad dichotomy in habitat use by Goosanders; standing waters as loaf sites, flowing waters as centres for foraging.

The distribution of other activities, showing that river sites were also more important for 'preen', 'display', and 'swim' behaviours, is consistent with this hypothesis, reinforcing the view that overall 'roost lakes' are unimportant for all but loafing.

If this is true then shifts in habitat use on a daily basis should be evident. Circumstantial evidence to support this suggestion is provided by data collected at Hoselaw Loch, a known 'roost lake', on 19th May 1983. Figure 4.6 shows the results of counts made there at five minute intervals from 0920 to 1340, 1425 to 1445, 1515, and 1545 to 1610 hours. Dividing the day into 'am' and 'pm' periods shows that for the 33 morning counts, the mean number of birds noted was 18.6 +/- 1.5 (95% confidence limits), whereas for the 32 afternoon counts the mean number was 25.3 +/- 2.1. The difference is significant at the 1% level (t=5.07, df=63). Since the birds remained on the same part of the Loch and did not move to other areas where they may have become more, or less, visible, this result indicates that more Goosanders came to Hoselaw Loch to loaf and roost during the afternoon.

Assuming that, during that single day the local population remained of constant size, it follows that the Loch held a greater proportion of the total number of birds present in the area during the afternoon. However, on the date concerned, 19th May, this assumption may not be valid since numbers of Goosander using the Loch increase during May and June as birds move through the Borders region using a small network of sites (of which Hoselaw is one) as pre-moult migration assembly points (Murray 1986, Little and Furness 1985). Non-systematic observations made by myself and other local ornithologists on other days at this time of year, would suggest that Goosander numbers are indeed greater at Hoselaw Loch in the afternoon, because birds have shifted away from foraging sites on the River Tweed. Data from river counts coincident with the Loch counts are lacking,

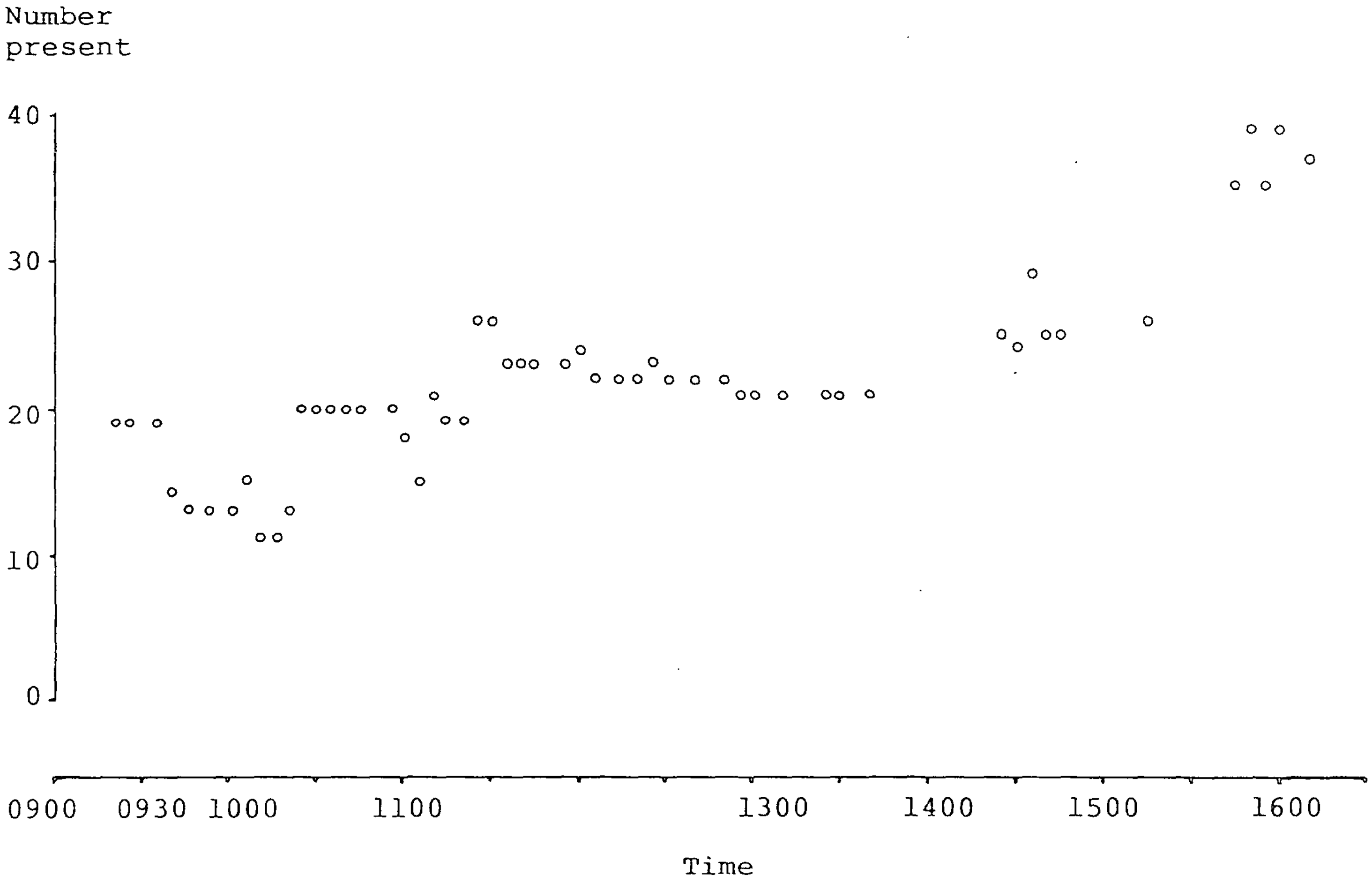


Figure 4.6 ; counts of Goosanders on Hoselaw Loch, 19th May 1983, between 0920 and 1620 hours

however。

Unfortunately detailed time-budget information for birds on both 'roost' and 'non-roost lakes' in spring is scant (section 4。3。4) and the results of the analyses of variance presented in sections 4。3。2 and 4。3。3 are unable to provide firm support (or otherwise) to the suggested pattern of habitat use。 However, data do indicate that in the spring birds on 'non-roost river' sites spent more time foraging in time periods 1-3 (0900-1500 hours) than thereafter。

Other workers have noted differential use of separate habitats for Mergus species。 For wintering Goosanders in the Tweed basin, Murray (1986) noted that "a small number of lochs hold the birds overnight that are seen on the surrounding rivers during the day", and Smaldon (1982) showed that roosting wintering Goosanders at Burrator Reservoir, Devon, spent the day on adjacent river feeding areas, leaving the roost site at around dawn and returned during mid- to late afternoon。 In Scotland Thom (1986) noted the importance of freshwater sites as roosts with "the birds dispersing to nearby rivers during the day"。 For Goosanders on the Missouri River, Timken and Anderson (1969) reported that non-feeding birds were present on large sandbars downriver from the feeding areas to which they would fly。 Although the distance separating these two areas is not given, their work clearly shows segregation of habitat。 Similarly, Sjoberg (1985) noted a flight of both Goosanders and Red-breasted

Mergansers from coastal areas into river foraging sites on the Ricklea River in northern Sweden; and for an inland area in northern Germany, Rehfeldt (1986) recorded 'periodical flights' of up to 15km by Red-breasted Mergansers between river feeding habitats and lake/gravel pit breeding sites.

The separation in space of foraging and roost sites is well documented for many species of waterfowl, waders, gulls and other birds (see, for example, Owen 1980, Prater 1981, Feare 1984). The factors governing roost site selection are likely to be common to most cases ie. a site free from disturbance, providing good opportunities for the detection of approaching predators, and affording a degree of shelter. Since foraging is not an important activity at such sites, food availability is unlikely to be a factor in site selection. Indeed one of the more important Goosander loafing and roosting sites used in this study, the Hirsel, near Coldstream, is reported not to support a fish population.

Goosanders make extensive use of loafing and roosting sites and may be present for a large part of the day. This is possible because daily energy and nutrient requirements can be satisfied by a relatively short period of diurnal foraging activity.

There was no indication from the present study of nocturnal foraging activities. However, Sjoberg (1985) found evidence for this in his study on the Ricklea River, Sweden; there the pattern of foraging activities, chiefly of adult and immature males, shifted from a day to night time peak as the activity of their principal prey, the river lamprey (Lampetra fluviatilis) changed to predominantly nocturnal. The author suggested that night time foraging by Goosanders was only possible there because of "favourable [although low] light conditions" and a "specialised feeding technique". (See Chapter Five.)

Data presented here suggest that rivers are preferred feeding sites. But is foraging there more profitable than at lake sites? To test this suggestion would require accurate data on the energetic costs of foraging methods (see Chapter Five) and estimates of foraging success. The latter would be influenced by prey availability, itself a function of water transparency, prey density, and the distribution of prey in both space and time, as affected by habitat structure, flow rate, and temperature, for example.

4.4.3 Sexual differences in time-budgets

The absence of significant differences associated with sex and status in the time-budget study reported here may be a product of small sample sizes. Such differences have been demonstrated for several waterfowl species (eg. Afton 1979, Krapu 1981, Goodburn 1984, Seymour and Titman 1979). For Mallard, Krapu (1981) and Goodburn (1984) both noted that during the period of egg formation male attentivesness to the female increased. This was considered by Asplund (1981) to be "of great importance in allowing undisturbed feeding by the female", but it also serves to prevent sexual harrassment during the period when she is most sexually receptive. Thus mate guarding may be viewed as the 'protection of parenthood' as hypothesised by Mineau and Cooke (1979) in their study of Greater Snow Geese.

Implicit in this suggestion is that males are more vigilant than females during their period of association. This was confirmed by Lendrem (1983) who showed that the 'peeking' rate (number of momentary eye openings by sleeping birds) was significantly greater for male Mallard than female and for paired against unpaired males.

The need for increased attentiveness of the male Goosander to his female especially during the critical period of egg formation, to prevent sexual harrassment and to protect 'parenthood', is obviated by the low breeding density of birds and the absence of territoriality (see Chapter One). Break up of wintering flocks and dispersion to breeding areas will have occurred before the female becomes reproductively receptive and when she attains this condition, in the vicinity of the breeding site, her mate will be the only male in attendance (contrast the high breeding densities of many dabbling and diving ducks, and colonial nesting geese).

Increased vigilance to allow the female to extend the time available for foraging may be important however. This was illustrated by observation of a pair of Goosander on the Kielder Burn, Northumberland on 7th April 1983. The pair were first noted at the head of a small weir pool, moving slowly upstream the male alert and the female feeding. They were lost from view almost immediately but were relocated further upstream where the female was noted either feeding or sleeping whilst the male typically remained alert. Over a total observation period of c12 minutes the female spent c41% of her time feeding, 33% sleeping and the remainder swimming. In contrast the male was alert for almost 60% of the time, fed for almost 17% and was swimming for the remainder.

Considerably more data are required for paired and unpaired birds of both sexes to further investigate this feature. However, the collection of data during the breeding season is much more difficult for dispersed breeding pairs than for aggregated individuals at other seasons.

4.5.0 SUMMARY

This study, based on scan and focal-animal sampling, showed that loafing and feeding activities dominated the time-budgets of Goosanders, together accounting for almost two-thirds of time. Possible biases within the data are considered.

A four-way analysis of variance was performed to investigate the effect of site type, season, time of day and sex on the percentage of time allocated to each behaviour. This revealed significant overall effects on 'loaf', 'sleep', 'feed', 'preen', and 'display' behaviours. Detailed effects of the independent variables are discussed.

Overall, data suggest that the broad habitat types distinguished here are important to Goosanders for different reasons; lakes as loafing and roosting sites, and rivers as feeding sites. Movements of birds between loaf/roost and feeding sites are discussed.

CHAPTER FIVE ;

FEEDING BEHAVIOUR AND DIET

5.1.0 INTRODUCTION

Observations of feeding behaviour were collected during the course of time-budget observations (see Chapter Four) at both river and lake sites. The infrequency with which prey items were noted to be brought to the surface provided circumstantial evidence, confirming the work of Lindroth and Bergstrom (1959), that Goosanders "could catch and swallow many fishes in succession during one dive". A practical consequence of this was that diet, and foraging success, could not be determined in the field. Since the birds have not been recorded to produce pellets, and their faeces do not contain solid remains, information on diet was collected in this study from the examination of the gut contents of dead birds. All other studies of the diet of Goosanders (eg. White 1937, 1957, Elson 1962, Munro and Clemens 1937) have used this method to investigate the species and size composition of the diet. The nature of possible biases in this methodology have not been addressed, and there remains no general agreement on whether prey is taken in proportion to its abundance (or availability), or whether particular species (or sizes) of fish are selected above others. A further source of difficulty in comparing between studies is that some authors have expressed their findings as percentages of birds examined that contained particular prey species, whilst others have estimated the percentage composition from the sum of all prey items identified from all birds. Both approaches are used in the present study, although the latter is more relevant to questions of the impact of Goosanders on fish populations.

The use of emetics or stomach pumps could not be tested as no birds could be caught whilst feeding.

An attempt was made to determine the diet of the Goosander in terms of (a) the species taken, (b) the number of each species taken, and (c) the age class composition of ingested prey. (Considerations of these results with respect to interactions with fisheries, in particular salmonid population dynamics, are presented in Chapter Six.)

5.2.0 METHODS

5.2.1 Feeding behaviour

Observations of feeding behaviour were recorded during the collection of time-budget data at both river and standing water sites (see Chapter Four). The equipment, and methods used are as described therein.

5.2.2 Gut analyses

Goosander carcasses were obtained principally from the Esk District Salmon Fishery Board, Tayside, and the Tweed Commissioners, under licence from D.A.F.S.. Details of the origin of the 54 Goosanders received are given in Table 5.1.

Analyses were carried out after the recording of biometrics etc. as described in Chapter Three. For 10 birds the entire alimentary canal, from the anterior end of the oesophagus to the cloaca, was examined for 'hard' remains. Since none were found posterior to the gizzard further analyses were restricted to the contents of the oesophagus, proventriculus and gizzard.

The alimentary canal from the anterior end of the oesophagus to the posterior exit of the gizzard was removed intact, towel-dried, weighed, and the contents flushed into petri-dishes. The weight of the empty towel-dried organs was recorded and the weight of the contents determined by subtraction.

Complete fish, or fragments thereof, were removed and stored separately. The vertebral column was threaded onto wire and cleaned, along with other bones, by gentle boiling in a weak solution of hydrogen peroxide. Bones and other solid remains were air-dried at room temperature.

Any parasitic organisms, eg. nematodes, cestodes, were removed and preserved in 70% alcohol.

Whole fish, and incomplete sections, were identified on external features and, where possible, fork length (tip of snout to inner

Table 5.1 ; Sex, age and origin of Goosanders received for gut analysis.

Bird no.	Sex	Age	Place of origin	Date of collection
1	M	A	Unknown[1]	Unknown
2	M	A	Tweed (Berwick)	Dec 82
3	M	J	Unknown	Unknown
4	M	J	Unknown	Unknown
5	F	J	Unknown	Unknown
6	M	A	Kielder	Apr 79
7	M	A	Rawthey (Lancs)	Dec 83
8	M	A	Tweed	Feb 84
9	M	A	Tweed	Feb 84
10	M	I	Mid-Tweed	Feb 84
11	M	A	Upper Tweed	Feb 84
12	F	A	(Shrewsbury)[2]	Jun 84
13	M	I	Unknown	Unknown
14	F	A	Tweed	Feb 84
15	M	I	S. Esk, Tayside	Sep 84
16	M	I	S. Esk, Tayside	Sep 84
17	F	A	S. Esk, Tayside	Sep 84
18	F	A	S. Esk, Tayside	Jun 84
19	F	A	S. Esk, Tayside	Sep 84
20	F	A	S. Esk, Tayside	Sep 84
21	M	J	S. Esk, Tayside	Aug 84
22	F	I	S. Esk, Tayside	Sep 84
23	M	A	Mid-Tweed	Feb 84
24	M	J	S. Esk, Tayside	Aug 84
25	F	A	S. Esk, Tayside	Jun 84
26	F	J	S. Esk, Tayside	Aug 84
27	M	I	Mid-Tweed	Feb 84
28	M	A	S. Esk, Tayside	Apr 84
29	F	A	Mid-Tweed	Feb 84
30	M	A	Tweed	Feb 84
31	F	J	S. Esk, Tayside	Aug 84
32	M	A	Tweed	Feb 84
33	M	A	Tweed	Feb 84
34	M	A	S. Esk, Tayside	May 84
35	F	A	Tweed	Feb 84
36	F	A	S. Esk, Tayside	May 84
37	M	A	Mid-Tweed	Feb 84
38	F	I	S. Esk, Tayside	Sep 84
39	M	A	Upper Tweed	Feb 84
40	M	A	Upper Tweed	Feb 84
41	M	A	Mid-Tweed	Feb 84
42	M	A	Mid-Tweed	Feb 84
43	M	I	Mid-Tweed	Feb 84
44	M	A	Tweed	Feb 84
45	M	A	S. Esk, Tayside	Apr 84

Table 5.1 cont.

Bird no.	Sex	Age	Place of origin	Date of collection
46	M	D	Feshie	Jun 85
47	M	D	S. Esk, Tayside	Jul 84
48	F	D	S. Esk, Tayside	Jul 84
49	M	D	S. Esk, Tayside	Jul 84
50	M	D	S. Esk, Tayside	Jul 84
51	F	D	S. Esk, Tayside	Jul 84
52	M	A	N. Esk, Tayside	May 86
53	F	I	S. Esk, Tayside	Feb 85
54	M	I	N/S. Esk, Tayside	(84)

[1] = received from Hancock Museum, Newcastle-on-Tyne
[2] = killed on road with brood. Forwarded by Wildfowl Trust.

point of tail fork) was measured to the nearest mm. Vertebrae and other bones were identified to species level where possible using published keys and a small reference collection. In some cases identification beyond the family or genus was not possible.

Of the hard remains from salmonid prey, only the atlas vertebrae can be used to differentiate salmon and trout (Feltham and Marquiss 1989). However, of the total of 236 salmonid atlas vertebrae found in gut analyses only 146 (62%) could be reliably assigned to particular species. It is assumed that atlas vertebrae which could be identified were representative, in terms of species and size, of all such bones. Non-identified salmonid atlas vertebrae, and all non-atlas salmonid bone remains, were recorded as non-identified salmonid.

All vertebrae and other bones, chiefly jaws, were examined and measured, using a binocular microscope, to determine the species and size composition of the diet. Graticule eye-piece divisions allowed measurement to the nearest 0.03mm. Although both length and width of vertebrae have been used by other workers in this context, I preferred length since this could be measured more accurately. In addition, Wise (1980) found that variation in the lengths of individual vertebrae along the vertebral column was less than variations in width.

5.2.2.1 Estimation of the number, and size, of prey fish

Estimation of the number of fish present was made by White's (1953) method. This compares the frequency of individual types of vertebrae in the sample to their expected frequency in a single fish of that species. For example, a salmonid has a single atlas vertebra and the presence of 'n' of this type of bone in the sample indicates that the remains derive from a minimum of 'n' individuals. However, the method works accurately only where the expected frequency per fish is unity since it takes no account of the sizes of the bones being considered. For instance, five salmonid thoracic vertebrae could derive from a single fish or from up to five different individuals depending on their sizes. The method provides a minimum estimate of number of prey items, however, irrespective of expected frequencies.

To estimate the minimum number of fish more accurately where the expected frequency of a particular bone type is greater than one, the sizes of fish from which individual bones were derived needed first to be estimated. Casteel (1976) discussed, and compared on the basis of accuracy and parsimony, five methods for such 'reconstruction' and concluded that the 'best' was the so-called single regression method. This allows "the prediction of fish size directly from some criterion of bone size by means of a single regression equation".

This method was adopted in the present study. For salmonids, regression equations were calculated from a small reference collection of 30 fish of known fork length, for the prediction of fork length (y) from length of vertebra in mm (x);-

(i) mean length of atlas vertebrae; $y=12.881 + 63.895x$,

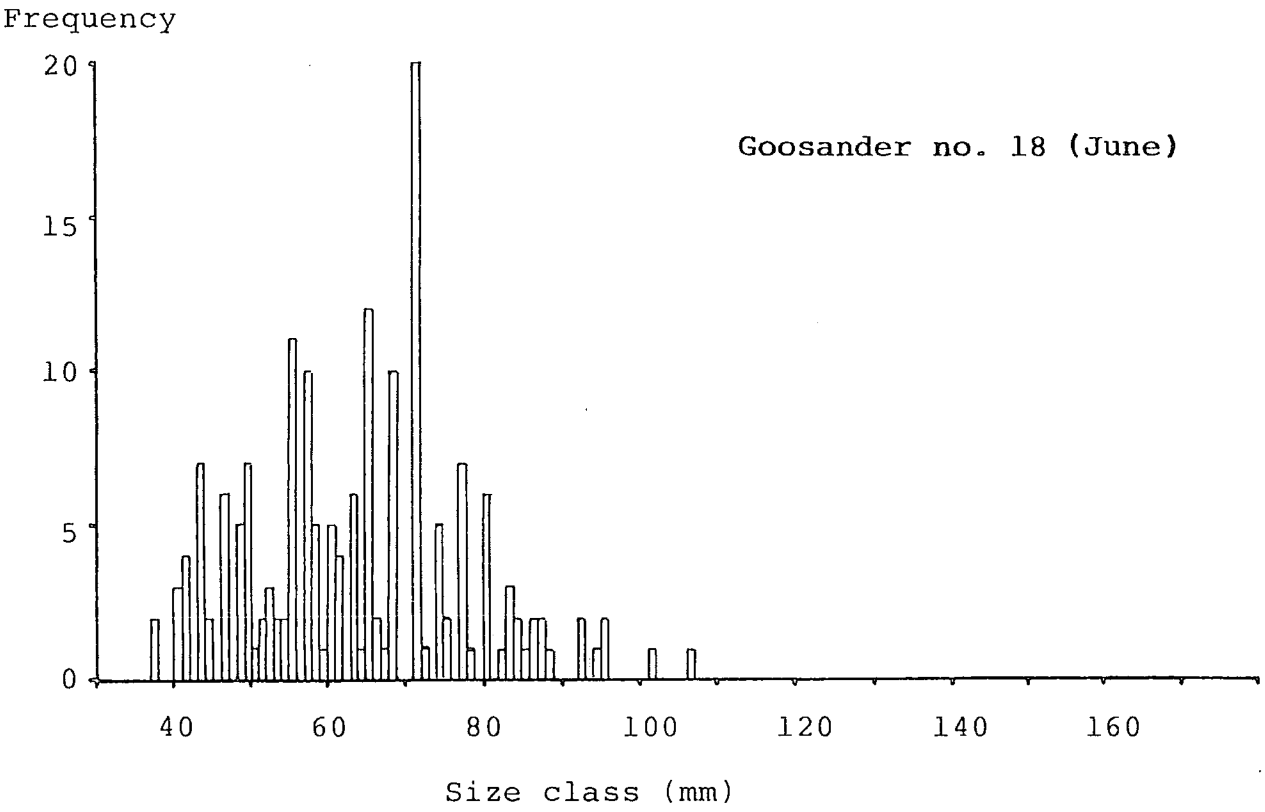
(ii) mean length of thoracic vertebrae; $y=14.404 + 46.203x$,

(iii) mean length of caudal vertebrae; $y=5.938 + 42.555x$,

(A separate regression for salmon and trout atlas vertebrae was not calculated because of small sample sizes. However, Feltham and Marquiss (1989) found that regression lines for these species were not significantly different from each other.)

The measured lengths of individual vertebrae were used to estimate the fork length of the fish from which they derived, with 95% confidence limits (calculated using formulae presented in Fowler and Cohen 1986). For each gut sample, the frequency distribution of estimates were determined in 1mm size classes. Because of the wide confidence limits associated with each estimate of size it was, in most cases, not possible to determine, from the size-frequency plots, the size/age composition of the diet. However, such plots were valuable in identifying individual fish which were not recorded by White's method. Examples are given in Figure 5.1.

The size/age composition of salmonids in the diet was determined using the regression equation calculated for atlas length on fork length. Egglishaw and Shackley (1977) presented data on the mean



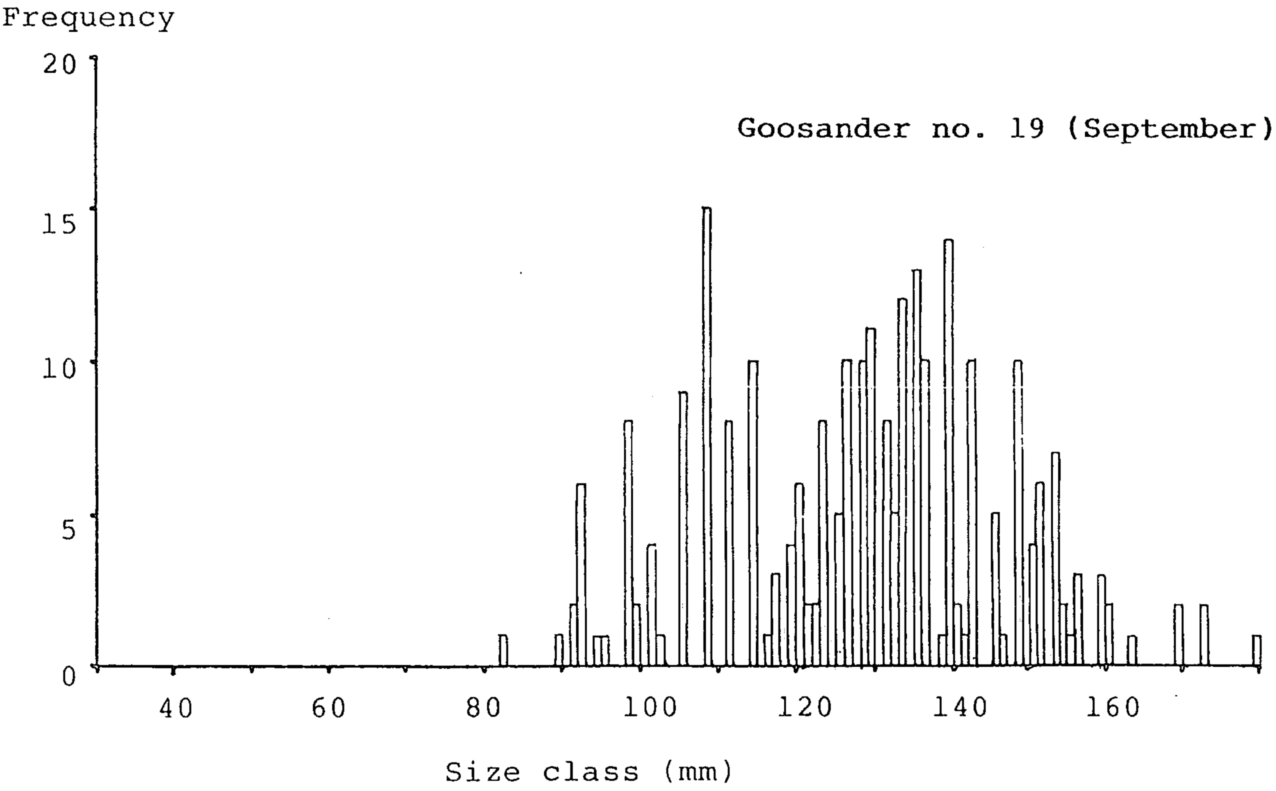


Figure 5.1 ; frequency distribution, in 1mm size classes, of salmonid prey in Goosanders no. 18 and 19

Perthshire, at the end of the growing season (September). Using these values and accounting for the time of year at which the fish were eaten, the age class composition of the diet of individual Goosanders was estimated.

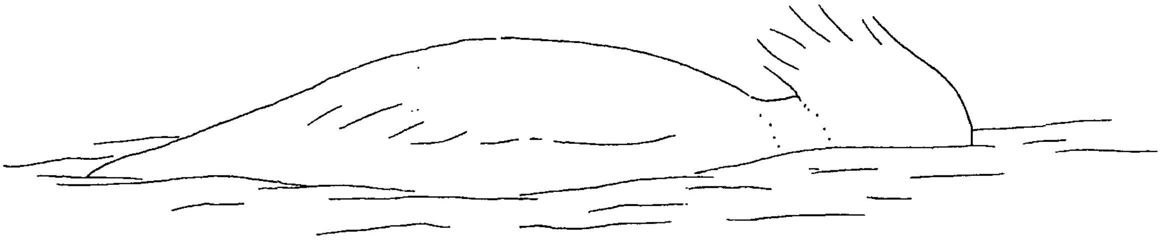
5.3.0 RESULTS

5.3.1 Feeding behaviour

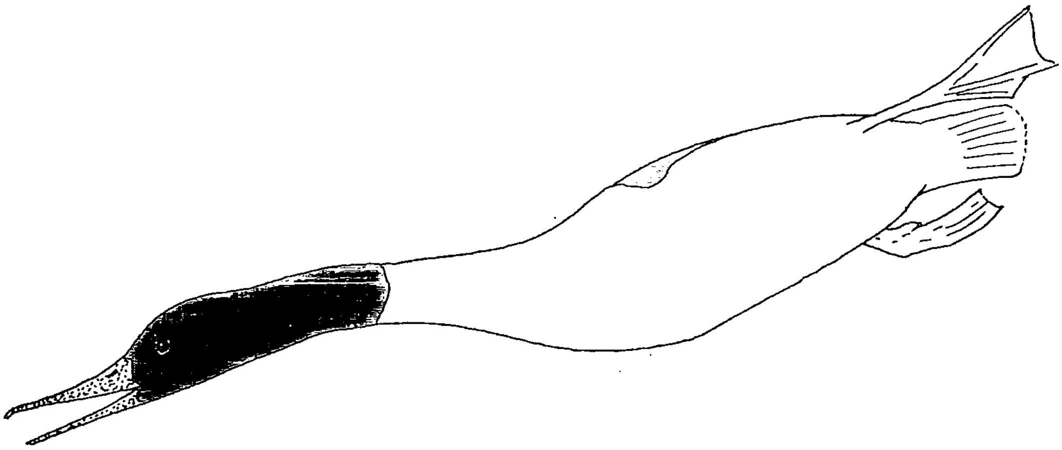
Two basic feeding techniques are used. The first, 'head-under-searches' (HUS henceforth), involves the bird swimming with the front part of the head and eyes submerged as illustrated in Figure 5.2. The second is diving.

Following location by HUS, prey may be captured either with the bird remaining on the surface or, if prey is noted at a depth greater than that which can be reached from the surface, the Goosander will dive in pursuit.

Prey located during a foraging dive (in contrast to a pursuit dive which necessarily succeeds prey location) will be chased and captured underwater. Lindroth and Bergstrom (1959) reported that captive reared Goosanders "could catch and swallow many fishes in succession during one dive", but there is likely to be an upper size limit to fish that can be swallowed in this way, with prey larger than this critical value being taken to the surface. On



head-under-searches (HUS)



diving

Figure 5.2 ; foraging methods of Goosanders only 10 occasions during observations of birds in HUS or diving, were prey visible to me and in none of these cases could items be positively identified.

During periods of continuous observation on both rivers and lakes the duration of dives was recorded using a hand held stopwatch. Dive duration was significantly greater for males than for females when data collected for both sexes in the same habitat are compared; for lakes, $t=4.06$, $df=27$, $p<0.01$, and for rivers $t=3.86$, $df=359$, $p<0.01$. These results are shown in Table 5.2. Dive duration of neither sex differed significantly between habitats, however; for males $t=0.95$, $df=156$, for females $t=1.85$, $df=230$. This is not surprising since it would be expected that the major factor influencing choice of feeding behaviour would be water depth.

5.3.2 Gut analyses

Over 10,000 individual vertebrae and other bones were identified to species, genus or family level, and measured. Qualitative results are presented in Table 5.3. This shows that the percentage occurrence, ie. the percentage of guts examined which contained a particular species, genus etc., was 48% for salmon, 56% for trout, 70% for non-identified salmonid, 35% for cyprinid, 30% for eel <u>Anguilla anguilla</u>, 15% for 3-spined stickleback <u>Gasterosteus aculeatus</u>, and 2% for each of stone loach

Table 5.2 ; Comparison of dive duration between habitat and sex

	Lake		River	
	male	female	male	female
n	12	17	146	215
mean length of dive (s)	21.25	15.44	19.94	16.90
SD	3.31	4.09	7.73	6.73
t	4.06		3.86	
df	27		359	
p	<0.001		<0.001	

Table 5.3 ; Occurrence of prey items in individual Goosanders (Numbers in parentheses in the final column refer to notes at the bottom of the table.)

Bird no	Sal	Tro	Non	Cyp	Eel	Sti	Ins	Pla	Grit	Other
1	-	-	-	-	-	-	-	-	-	
2	-	-	*	*	*	-	*	-	*	
3	-	-	*	*	*	-	-	*	*	
4	-	-	-	*	-	-	-	*	-	
5	-	-	*	*	-	*	-	*	*	Loa, Bul
6	-	-	*	-	*	-	-	*	*	
7	-	-	*	-	-	-	-	-	*	(1)
8	-	*	-	-	*	-	-	*	*	
9	*	*	*	-	*	-	-	*	*	(2)
10	-	-	*	*	*	-	-	*	*	
11	-	*	*	*	*	-	-	-	*	
12	-	-	-	-	-	-	-	-	*	
13	-	-	-	-	-	-	-	-	-	
14	*	*	*	-	-	-	-	-	-	(3)
15	*	-	*	-	-	-	-	*	*	(4)
16	*	*	-	-	-	-	-	-	-	
17	*	*	*	-	-	-	*	*	*	
18	*	*	*	-	-	*	*	*	-	
19	*	*	*	-	-	-	-	-	*	(5)
20	-	*	-	-	-	-	-	-	*	
21	*	*	*	-	-	-	*	*	*	
22	*	*	*	-	-	-	-	*	*	(6)
23	*	*	*	-	*	-	-	-	*	
24	*	*	*	-	-	-	-	*	*	(7)
25	*	-	*	*	*	*	*	-	*	
26	*	*	-	-	-	-	-	*	*	
27	-	-	-	-	*	-	-	*	*	
28	-	-	-	-	-	-	*	*	*	(8)
29	*	*	-	-	*	-	-	*	*	
30	*	-	-	-	*	-	-	*	*	(9)
31	-	-	*	-	-	-	-	*	-	(10)
32	-	*	*	*	*	-	-	*	*	
33	*	*	*	-	-	-	-	*	-	
34	-	*	-	-	-	*	-	*	-	(11)
35	*	*	*	-	*	-	-	-	*	
36	-	*	*	*	-	*	-	-	*	
37	-	-	-	-	*	-	-	*	*	
38	*	*	*	-	-	-	-	*	*	
39	-	-	*	-	-	-	-	-	*	Per, (12)
40	*	*	*	*	-	-	-	-	*	
41	-	*	*	*	-	-	-	-	*	
42	*	*	-	-	-	-	-	-	*	
43	*	*	*	*	-	-	-	-	*	
44	-	*	*	*	-	*	-	-	*	Ple, (13)
45	-	-	*	-	-	-	*	*	*	(14)

Table 5.3 cont.

Bird no	Sal	Tro	Non	Cyp	Eel	Sti	Ins	Pla	Grit	Other
46	-	-	-	-	-	-	*	-	-	
47	*	-	*	*	-	-	*	*	*	
48	*	*	*	*	-	-	-	*	*	
49	*	-	*	*	-	-	-	*	*	
50	-	*	*	*	-	-	-	*	*	
51	-	*	*	*	-	-	*	*	*	
52	*	-	*	-	-	*	-	-	-	(15)
53	*	*	*	*	*	-	-	-	-	
54	-	-	*	-	-	*	-	-	-	

Notes;

1 - fishing line, 25 salmonid eggs
2 - fragments of plastic
3 - small piece of metal
4 - a single 'pea'
5 - fragment of plastic
6 - small piece of metal
7 - silver paper
8 - single smolt tag
9 - fishing line
10 - a single 'pea'
11 - fishing line and hook, silver paper
12 - fish hook, amphibian bones
13 - fishing line and lead shot
14 - 2 smolt tags
15 - single smolt tag, fish hook

Key to column headings and other codes;

Sal = salmon
Tro = trout
Non = non-identified salmonid
Cyp = <u>Cyprinidae</u>
Sti = Three-spined Stickleback
Loa = Stone Loach
Bul = Bullhead
Per = <u>Percidae</u>
Ple = <u>Pleuronectidae</u>
Ins = insect
Pla = Plant

Noemacheilus barbatulus, bullhead Cottus gobio, Percidae, and Pleuronectidae. A single bird contained salmonid eggs, another the remains of an amphibian, three contained smolt tags and four contained unidentified remains. The high incidence of non-animal remains is also illustrated. There was no significant difference (at the 5% level) between the percentage occurrence of prey in adult males and females ($X^2=1.20$, df=3).

Table 5.4 contrasts the estimates of the numbers of salmonid fish present in each bird using White's method applied to (a) lower jaw, (b) atlas vertebrae, (c) caudal vertebrae, (d) thoracic vertebrae, (e) ligular teeth, and (f) the vomer. If it is assumed that the maximum number of fish estimated by any of these indicators is the actual number from which all remains found in the gut derive, the lower jaws correctly estimate this figure in 30.2% of birds, the ligular teeth in 22.6%, the vomer in 17.0%, the atlas in 58.5%, the thoracic vertebrae in 45.3% and the caudal vertebrae in 47.2%. These differences may arise from differential rates of digestion/erosion of each bone type as a result of differences in size and structure.

Using the maximum value obtained above for the number of salmonids present, and applying White's method to the other fish species present, allowed the total number of fish of all species present to be estimated. Results, given in Table 5.5, show that c78% of all fish ingested were salmonid, 12% were cyprinid, 5% eel, 3% stickleback and less than 1% for each of the other

Table 5.4 ; Estimates of the number of salmonids present per bird using White's (1953) method

Bird	Results from White's method using;						Assumed
no.	jaws	atlas	caudal	thoracic	lig	vomer	max no.
1	0	0	0	0	0	0	0
2	1	1	1	1	1	1	1
3	0	1	0	0	0	0	1
4	0	0	0	0	0	0	0
5	2	2	3	3	1	0	3
6	4	1	0	0	2	2	4
7	1	1	2	1	1	1	2
8	1	1	1	1	0	1	1
9	6	17	-	-	7	6	17
10	1	0	0	1	1	0	1
11	11	6	-	-	7	5	11
12	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0
14	5	6	7	7	4	6	7
15	3	4	4	4	2	2	4
16	1	4	3	3	2	1	4
17	5	15	6	7	9	1	15
18	5	10	3	4	3	1	10
19	5	4	6	5	4	4	6
20	2	5	7	6	3	3	7
21	2	5	2	2	2	1	5
22	12	25	18	19	17	7	25
23	3	5	5	4	1	2	5
24	6	13	6	8	3	3	13
25	1	3	2	3	0	2	3
26	1	3	3	3	1	0	3
27	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0
29	6	2	3	3	1	1	6
30	0	1	1	1	0	0	1
31	1	2	2	2	1	0	2
32	2	4	4	4	3	2	4
33	6	9	5	6	3	4	9
34	1	1	2	2	1	0	2
35	6	4	5	7	2	3	7
36	3	2	2	3	2	0	3
37	0	0	0	0	0	0	0
38	8	14	9	13	9	6	14
39	3	4	-	-	3	2	4
40	4	4	-	-	5	3	5
41	7	4	-	-	4	4	7
42	2	2	2	2	2	1	2
43	9	14	6	5	8	4	14
44	1	3	2	2	3	0	3
45	0	0	0	1	0	0	1

Table 5.4 cont.

Bird no.	Results from White's method using; jaws	atlas	caudal	thoracic	lig	vomer	Assumed max no.
46	0	0	0	0	0	0	0
47	0	3	3	2	1	0	3
48	2	5	5	7	4	1	7
49	3	3	4	4	0	1	4
50	1	2	5	3	0	1	5
51	4	3	3	5	1	1	5
52	0	4	0	0	1	0	4
53	4	14	-	-	12	3	14
54	1	0	0	1	0	0	1

Table 5.5 ; Estimated numbers of each fish species, genera etc. per bird

Bird no.	Sal	Tro	Non	Cyp	Eel	Sti	Loa	Bul	Per	Ple	Total
1	0	0	0	0	0	0	0	0	0	0	0
2	0	0	1	2	1	0	0	0	0	0	4
3	0	0	1	1	1	0	0	0	0	0	3
4	0	0	0	1	0	0	0	0	0	0	1
5	0	0	3	5	0	1	1	1	0	0	11
6	0	0	4	0	1	0	0	0	0	0	5
7	0	0	2	0	0	0	0	0	0	0	2
8	0	1	0	0	2	0	0	0	0	0	3
9	5	6	6	0	1	0	0	0	0	0	18
10	0	0	1	2	1	0	0	0	0	0	4
11	0	1	10	3	1	0	0	0	0	0	15
12	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0
14	2	3	2	0	0	0	0	0	0	0	7
15	1	0	3	0	0	0	0	0	0	0	4
16	1	3	0	0	0	0	0	0	0	0	4
17	4	1	10	0	0	0	0	0	0	0	15
18	4	1	5	0	0	1	0	0	0	0	11
19	1	2	3	0	0	0	0	0	0	0	6
20	0	5	2	0	0	0	0	0	0	0	7
21	2	2	1	0	0	0	0	0	0	0	5
22	7	11	7	0	0	0	0	0	0	0	25
23	1	3	1	0	1	0	0	0	0	0	6
24	5	2	6	0	0	0	0	0	0	0	13
25	1	0	2	1	1	1	0	0	0	0	6
26	1	2	0	0	0	0	0	0	0	0	3
27	0	0	0	0	1	0	0	0	0	0	1
28	0	0	0	0	0	0	0	0	0	0	0
29	1	1	4	0	1	0	0	0	0	0	7
30	1	0	0	0	2	0	0	0	0	0	3
31	0	0	2	0	0	0	0	0	0	0	2
32	0	1	3	1	1	0	0	0	0	0	6
33	3	4	2	0	0	0	0	0	0	0	9
34	0	1	1	0	0	1	0	0	0	0	3
35	2	1	4	0	1	0	0	0	0	0	8
36	0	1	2	6	0	3	0	0	0	0	12
37	0	0	0	0	1	0	0	0	0	0	1
38	6	7	1	0	0	0	0	0	0	0	14
39	0	0	4	0	0	0	0	0	1	0	5
40	1	1	3	1	0	0	0	0	0	0	6
41	0	3	4	1	0	0	0	0	0	0	8
42	1	1	0	0	0	0	0	0	0	0	2
43	3	3	8	1	0	0	0	0	0	0	15
44	0	2	1	6	0	1	0	0	0	2	12
45	0	0	1	0	0	0	0	0	0	0	1

Table 5.5 cont.

Bird no.	Sal	Tro	Non	Cyp	Eel	Sti	Loa	Bul	Per	Ple	Total
46	0	0	0	0	0	0	0	0	0	0	0
47	2	0	1	1	0	0	0	0	0	0	4
48	1	2	4	3	0	0	0	0	0	0	10
49	2	0	2	4	0	0	0	0	0	0	8
50	0	1	4	1	0	0	0	0	0	0	6
51	0	1	4	1	0	0	0	0	0	0	6
52	3	0	1	0	0	1	0	0	0	0	5
53	7	5	2	1	1	0	0	0	0	0	16
54	0	0	1	0	0	1	0	0	0	0	2
Totals	68	78	129	42	18	10	1	1	1	2	350
%	19.4	22.3	36.9	12.0	5.1	2.9	0.3	0.3	0.3	0.6	

(Fish species, genera codes etc. as in Table 5.3.)

species.

Figure 5.3a shows a size frequency distribution in 1mm size classes for estimates of salmonid size derived from the atlas vertebrae of salmon, trout and non-identified salmonid. This not only demonstrates that fish of a wide range of sizes are taken but, because the distribution is essentially bimodal, also that some size classes (with approximate means of 77mm and 120mm) are ingested more frequently than others. For all atlas vertebrae the mean size of salmonid prey was estimated as 106mm. Considering individual species showed that the estimated mean size of salmon was 79.07mm (SE=2.66), and for trout was 114.27mm (SE=3.53). The difference between the estimated mean sizes of salmon and trout was highly statistically significant (t=7.969).

Figure 5.3b shows the frequency distribution of estimates of the sizes of salmonids from birds shot on the River Tweed in a cull in February 1984. Peaks at fish lengths of c77mm and c120mm correspond to 0+ and 1+ salmonids respectively, although the tail of the distribution of the larger size class will also contain 2+ and older fish. The estimated mean size of salmon in this data set, 88.55mm (SE=4.527), is highly significantly lower than the estimated mean size of trout (127.35mm, SE=5.92, t=5.206). Similarity in the form of the distribution of Figures 5.3a and 5.3b is striking.

Differences in estimates of the sizes of salmon, trout and

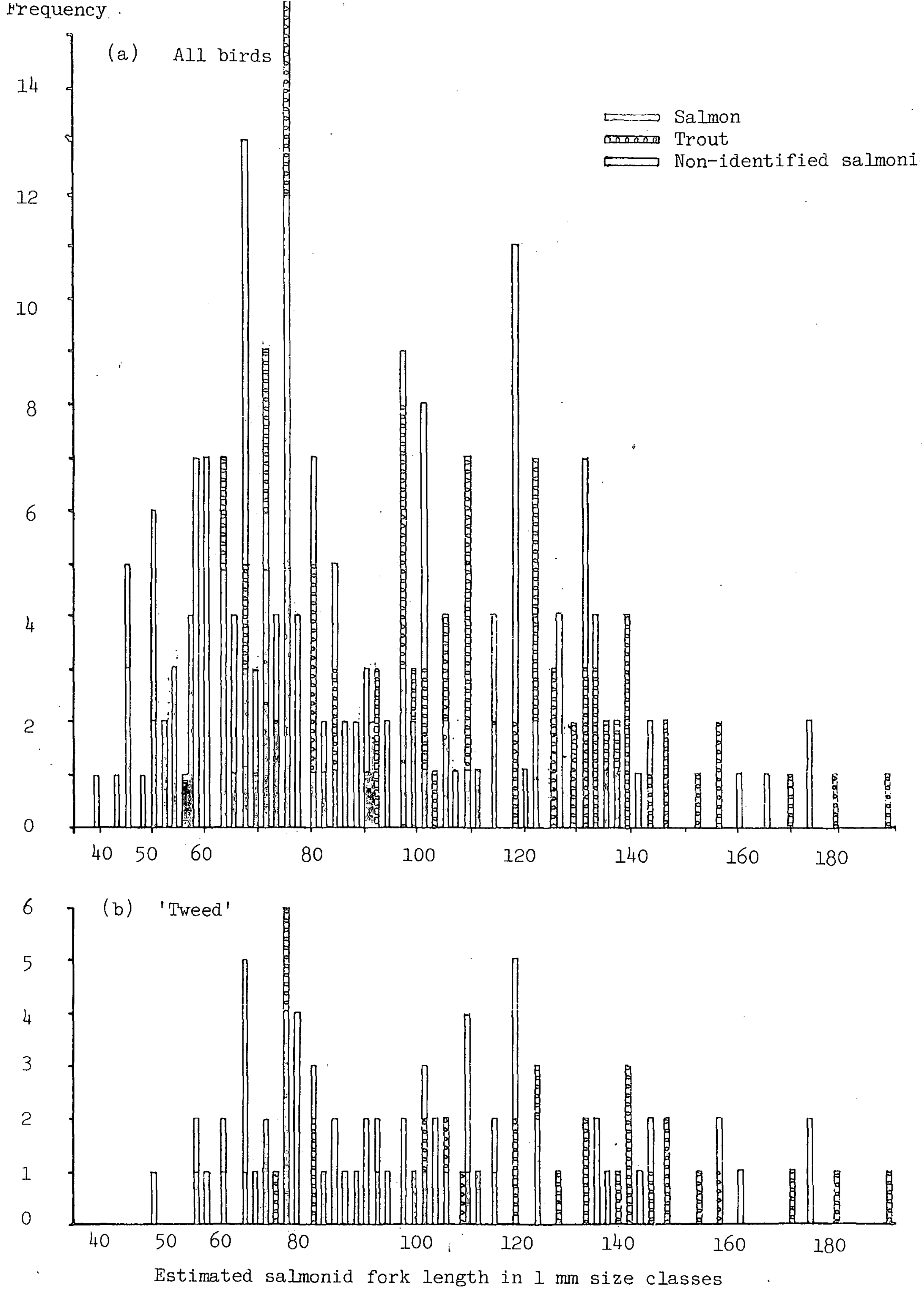


Figure 5.3 ; frequency distribution, in 1mm size classes, of salmonid prey in Goosanders

non-identified salmonids taken by adult male and female Goosanders was investigated using a three-way analysis of variance (SAS 1985). Results demonstrate a highly significant effect of sex, season and species on prey size, as estimated from measurements of the atlas vertebrae, with c35% of variation in estimated prey size explained by these factors. Table 5.6 shows the result of additional analyses. These demonstrate that the estimated prey size of adult males was significanty greater than that of females (110.92mm and 98.38mm respectively, t=2.09) when considering all salmonid prey together. For non-identified salmonid and trout there was no significant difference between the sexes with respect to prey size (t=1.862, df=48, p>0.05, and t=0.057, df=37, p>0.05 respectively). However, estimates of the size of salmon prey were significantly greater (at the 5% level) for adult males than for females (t=2.239, df=28). To investigate whether these results were a consequence of seasonal differences, estimates of mean prey size for salmon, trout and non-identified salmonid for each sex were compared within seasons. Unfortunately this was only possible for the late winter period (December-February). Results confirmed those obtained previously, ie. no significant difference between the sexes in the estimated size of non-identified and trout prey (t=1.67, df=27, p>0.05 and t=0.043, df=26, p>0.05 respectively), but significantly larger salmon in males (t=2.612, df=15).

Seasonal differences were themselves statistically significant, and indicated that the size of individual prey items (salmon, trout and non-identified salmonid) was greatest in the autumn and

Table 5.6 ; Estimated sizes of salmonid prey (mm) between sexes and seasons, based on the regression of atlas vertebrae length on total fork length

	Male			Female			Seasonal	
	n	mean	S.D.	n	mean	S.D.	mean	S.D.
Winter	62	112.37	31.87	12	98.08	33.87	110.05	32.40
Spring	5	92.97	24.17	2	122.57	4.52	101.43	24.53
Summer	0			13	73.50	13.66	73.50	13.66
Autumn	0			23	110.49	33.00	110.49	33.00
Sex	67	110.92	31.63	50	98.38	32.40		
						Overall =	105.56	28.88

winter, and declined through spring to reach a summer low.

Table 5.7a shows the estimated age class composition of salmonid prey from adult Goosanders using the regression of atlas vertebrae size on fish fork length and with reference to Egglishaw (1970). The frequency distribution of age classes of salmon and trout is significantly different ($X^2=19.59$, df=4, $p<0.01$); more 0+ and 1+ salmon and more 2+ trout occur than expected. Estimates of the age class composition of the prey of non-adult birds (Table 5.7b) also shows a significant difference between salmon and trout: $X^2=14.00$, df=2, $p<0.01$). Here 0+ salmon, and 1+ and 2+ trout occurred more frequently than expected.

The diet of birds 18 and 19 provide an interesting comparison. Both birds were shot on the River South Esk, the first in June and the second in September. Estimates of the size of fish from which the gut remains derive (based on estimates from atlas, thoracic and caudal vertebrae) are normally distributed in each case and show a clear shift from a mean of 75.1mm in June to 137.3mm in September. See Figure 5.1. From growth curves for salmon and trout, presented by Egglishaw (1970), reproduced in Figure 5.4, this represents depredations of 1+ and 2+ parr respectively rather than of a single year class.

Table 5.3 shows that insects had a high percentage occurrence (18.5%). However, it was not clear if these were actively

Table 5.7a ; Estimated age class composition of salmonid prey in the diet of adult Goosanders

	Age class						
	0+	0-1	1+	1-2	2+	>2+	
Salmon	8	3	16	0	2	0	29 (25%)
Trout	2	3	10	6	14	0	35 (35%)
Non-identified salmonid	6	6	27	5	9	0	53 (45%)
Total	16	12	53	11	25	0	117
%	14	10	45	9	21	0	

Table 5.7b ; Estimated age class composition of salmonid prey in the diet of non-adult Goosanders

	Age class						
	0+	0-1	1+	1-2	2+	>2+	
Salmon	19	3	10	0	1	0	33 (28%)
Trout	6	2	19	2	7	0	36 (31%)
Non-identified salmonid	26	6	14	1	1	0	48 (41%)
Total	51	11	43	3	9	0	117
%	44	9	37	3	8	0	

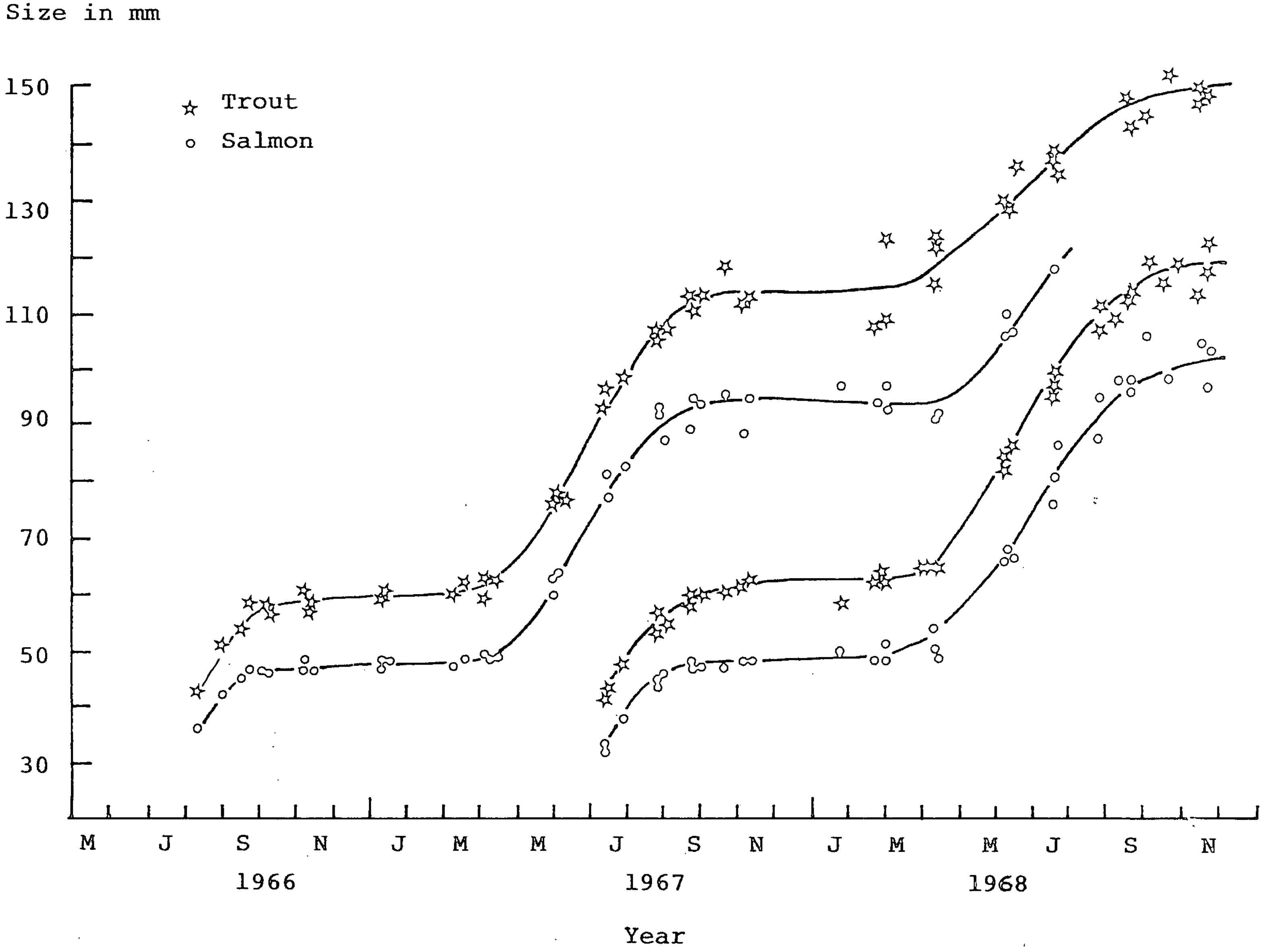


Figure 5.4 ; growth curves for salmon and trout in the Shelligan Burn (Egglishaw 1970)

ingested or originated as food items in the guts of prey fish. Since in some cases this latter was certainly true, it is not possible to assess the dietary importance of insect prey. The occurence of plant material in more than one half of the birds examined may be similarly explained.

The fish hooks, line, plastic, metal and silver paper found were also considered to have been ingested passively, probably as the bird picked up gravel to aid digestion. A single female was observed in the spring at Hoselaw Loch, stabbing at an exposed earth bank. Unfortunately the site could not be later investigated, and in the absence of this it is assumed that she was ingesting gravel/stones, or perhaps oligochaete prey. With such behaviour it is clearly possible for individuals to 'consume' plant material and other extraneous materials.

Three birds contained a total of four smolt tags originating from fish tagged at the stationery trap operated on Kinnaber Mill Lade, River North Esk, by D.A.F.S.. Goosander no. 28 was shot at Merulzie on the River South Esk, on 20th April 1984 and contained a single tag which had been attached to a smolt in May 1981. Similarly, Goosander no.45, shot at Cortachy on the River South Esk, on 10th April 1984, contained tags from 2 smolt marked in May 1981. These tags were complete and their details clearly readable, suggesting that they had been recently ingested. This could have occurred whilst feeding on flesh of the dead adults, or they could have been picked up 'loose' from the stream bed with gravel. Carrion feeding was found in only one bird in this study. The single tag recovered from Goosander no.52, shot on the estuary of the River North Esk in May 1986, had been attached to a smolt 15 days earlier.

5.4.0 DISCUSSION

5.4.1 Feeding behaviour

Choices between HUS and diving as the primary methods of prey location will be influenced firstly by habitat selection and secondly by water depth, transparency and food availability. Data are presented elsewhere (Chapter Four) which indicate that rivers are preferred feeding sites. Typically birds utilise HUS in shallow riffle areas where these are available. Such behaviour is less 'energy expensive' than diving but data are inadequate to investigate the relationship between the energetics of foraging methods and habitat selection.

Eriksson (1985) classified Goosanders as 'pursuit divers' (cf 'surface plungers' such as terns and piscivorous raptors), and constructed a model to demonstrate how changes in prey density and water transparency affected prey encounter rates. He concluded that high fish density was more important in habitat selection than water transparancy for Goosanders in south-west Sweden in April/May, but considered that they may be compensated for reduced densities by increases in transparency. Such changes occur in the acidification of freshwater biotopes.

The mechanisms of prey location under conditions of low visibility, due to low light intensities and/or high water turbidities, are unclear. Birds have been noted in this study, and by Sjoberg (1985) feeding in rapids (white water), under overhanging vegetation and on spate river flows where light conditions are poor. The success rate of feeding in these areas could not be assessed since, as described above, a proportion of prey is swallowed underwater with only the larger items brought to the surface. It is not known if prey can be both located and captured in the total absence of visual cues. However, Heard and Curd (1959) speculated that "perhaps they [Goosanders] perceive the presence of fish, particularly fish moving in schools such as the gizzard shad (Dorosoma cepedianum), in turbid water situations by hypersensitivity to motion in water". Working with captive Goosander in a stream tank, Lindroth and Bergstom (1959) reported that birds fed by random probing amongst gravel and stones and that "hiding fish were promptly seized and swallowed". The importance of tactile senses was confirmed by Sjoberg (1988) who showed that the birds were able to catch hidden prey found during random searches of streambed cavities. The influence of light intensity on this behaviour, and on capture rates for prey, was unfortunately not investigated.

Mean dive durations were reported in section 5.3.1 as 19.94 seconds for males and 16.90 seconds for females on rivers, and 21.25 seconds and 15.44 seconds respectively on lakes. These values compare with means of 20.35 seconds in coastal waters 1-2 m deep, 23.50 seconds in depths of 2-3m, and 27.5 seconds in depths of 4-5m (Nilsson 1970). Unfortunately the sex composition of these data were not presented.

Statistically significant differences in the mean duration of dives between the sexes could occur for several reasons.

Firstly, maximum dive times will be set by physiological constraints viz. the volume of air (oxygen) stored in the body at the start of the dive, the capacity for those reserves to be mobilised, and utilised, and the rate of oxygen consumption of the tissues. Butler and Jones (1982) pointed out that "it is the largest animals that seem to excel in diving performance, whether a comparison is made between diving species or within a single species". Since males are larger than females (1670g and 1535g respectively (Todd 1979)) females may be restricted to shorter dives than males.

Another factor to consider is buoyancy which increases with size. Males will be more buoyant than females and a dive of given duration will therefore be energetically more expensive, in absolute terms, for them than for females. This absolute difference will be accentuated because the dive duration of males is significantly greater. However, relative to body size this difference may be less pronounced.

If males were less efficient than females in terms of prey location and capture then males would need to stay submerged longer, or dive at a faster rate, to ingest the same number of fish as a female. Similarly if males select larger, scarcer prey which take longer to locate and capture, or select a higher proportion of benthic species than females a greater dive duration would be expected. Comparisons between the diet of each sex, presented in section 5.3.2 above, showed that the mean estimated length of salmonids taken by adult males was not significantly greater than the mean for females. Also, no differences in diet composition (as indicated by percentage occurrence) were found. In a study of the diet of Mergansers on Lake Myvatn, Iceland, Bengston (1971) found no differences in the composition of the diet between males and females; both fed predominantly on sticklebacks in shallow waters.

5.4.2 Possible biases in gut analyses

Data on diet composition obtained by the methods used in this study will accurately represent the actual diet only if;

(i) all prey items are digested at the same rate,

(ii) retention in the stomach is non-selective with respect to the size or structure of remains,

(iii) all retained remains are identifiable, and

(iv) no remains are lost, eg. due to regurgitation, prior to analyses.

Carter and Evans (1986) noted that the relative 'hardness' of the bones of fish species is likely to vary both between and within species (in relation to size, sex, etc.), and thus that the results of analyses based solely on the recovery and identification of fragments of bones from the gizzard will not provide an unbiased estimate of the composition of the diet. They commented that recovery of items from the oesophagus before digestive processes have begun, would give more reliable information. Lifjeld (1983) also emphasised the importance of considering differential rates of digestion of prey species in dietary studies. He found that dipteran larvae and mites were recognisable in the gut of force fed Dunlin (Calidris alpina) for 40 and 20 minutes respectively, whereas most enchytraeid oligochaetes were digested within a minute.

In the context of the present study, the presence of soft bodied invertebrate prey, eg. oligochaetes, polychaetes, and soft boned vertebrate prey, most notably lamprey (Petromyzon marinus and Lampetra spp.), would be under-estimated. In a study of the diet of sawbills on the rivers North and South Esk, Tayside, Carter and Evans (1986) examined a total of seven Goosanders and 39 Mergansers, and found lamprey remains only in the oesophagus. Although this prey was almost certainly present in the gizzard of these and other birds examined, no remains were detected. The deployment of ELISA (enzyme-linked immunosorbent assay) techniques as described by Giles and Phillips (1985) and Walter (1986) for the identification of 'soft' remains would provide a highly sensitive method of producing a complete qualitative picture of diet. They could not, however, supply quantitative information.

Differential rates of digestion of fish of different sizes are also likely to occur. For example, salmon fry are likely to be much more rapidly digested than smolt and thus their contribution to the diet would be under-estimated. This could be tested experimentally by feeding a controlled diet of fish of different sizes and examining gut contents at regular time intervals, either with the use of emetics, stomach pumps or by sacrificing individuals. Due to the small number of captive birds used in the study (see Chapter Two) this was not attempted here.

5.4.3 Diet composition

Several studies have been made in various regions of north America of the diet composition of the Goosander during both the breeding and non-breeding seasons.

The first detailed studies were made by White (1936, 1937, 1939, 1957) in the maritime provinces of Canada. From a total of 28 birds shot in the summer of 1935 on the Margaree River, Nova Scotia, White (1936) found salmon to constitute 82.2% of all fish found therein, trout 6.3% and 'other' fish 11.5%. He concluded that the composition of the diet roughly reflected that of the available prey populations, and that where these birds were sympatric with nursery areas of salmon and trout "considerable depletion" of these fish could occur. The results of further analyses (White 1937) on young birds confirmed these results and reinforced the earlier subjective impression that young salmonids were common where sawbills were not, and vice versa.

Further work on other river systems in that region, based on the analysis of 887 birds collected during the breeding season, showed wide variation between major drainage basins in the percentage of fish identified in the guts which were salmon (White 1957); values ranged from 5% in the Bay of Fundy systems to 91% in Cape Breton, with a mean of 43%. The percentage occurrence showed less variation, ranging from 45% on the Petitcodiac system to 96% in parts of the Gulf mainland drainages. The mean percentage occurrence was 71%. Similarly, from a sample of 332 birds collected on a range of salmonid and non-salmonid waters in 'cold' water wintering areas of Michigan, Sayler and Lagler (1940) found wide variation in the percentage occurrence of salmonids from 0% on marginal waters to 79.9% in hatchery areas.

Timken and Anderson (1969) collected a sample of 220 Goosanders from the north-central United States during the non-breeding seasons of 1966 to 1968. Only 67 of these contained food remains however, and of these 13% (by number) were game fish. They suggested that the Goosander was largely opportunistic in its feeding habits, concentrating, for example, downstream of hydroelectric installations to feed on stunned fish, or on shoals of forage fish over-wintering in areas of reduced river flow. The availability of year-round open water was also considered an important factor.

In contrast, on 'warm water' wintering areas diets showed a general predominance of non-game fish. Alcorn (1953) in Nevada, and Heard and Curd (1959) in Oklahoma found that 76% and 81% respectively (by number) of the Goosanders diet comprised non-game species. However, the results of each of these studies must be treated with caution since the first excluded a number of birds which "contained fish remains that were digested beyond identification" (see section 5.4.2), and the second considered only "gross stomach contents" without defining what this actually represented. Huntingdon and Roberts (1959) reported similar findings from two reservoir sites in New Mexico (89% and 95% of the diet was gizzard shad), but at a third site game fish were more important (chiefly sunfish Lepomis spp., crappie Pomoxis nigromaculatus, and largemouth bass Micropterus salmoides).

Contemporaneous to White's early work Munro and Clemens (1937) carried out gut analyses of 402 Goosanders collected throughout the year in British Columbia. In terms of both percentage occurrence and percentage of total volume of each food type the freshwater sculpin Cottus asper was the most frequently occurring item which constituted the greatest percentage volume. This is important since these authors also showed that this fish was itself an important predator on salmon and trout fry. The second most frequently occurring item was salmon eggs (25% occurrence, 22% of volume), followed by salmonidae (20% occurrence, 13% of volume), sticklebacks (11% occurrence, 5% of volume), coarse fish (13% occurrence, 9% of volume), and marine fish (10% occurrence, 8% of volume). Evidence for feeding on carrion fish was recorded from 19 birds. Marked seasonal variations in diet, associated with annual cycles in prey availability, were found. For example, the availability of salmon eggs peaked in autumn during the spawning period and this was reflected in the observation that in some areas the diet was exclusively eggs at that time. Since only uncovered eggs are ingested (ie. the birds do not dig for them), the only opportunity the birds have to take viable eggs is during the actual spawning process. Although the authors indicate that a proportion of eggs may be taken in this way, the majority were taken either drifting in the water column or from redds uncovered by gravel erosion. In each case the eggs would not have been viable and their consumption did not therefore represent "a drain upon salmon production" (Munro and Clemens 1937).

In Europe little work has been published on the diet, and relationship to fisheries of sawbill ducks.

From a sample of 23 Goosanders collected in Finland, Bagge *et al.* (1970) found the 3-spined Stickleback to be the single most important prey species, and in Sweden Sjoberg (1974) analysed the gut contents of 46 Goosanders collected on salmon rivers between April and October but found no salmonid remains at all. Adult river lamprey (*Lampetra fluviatilis*) and bullheads were the most common prey species although there were marked differences between rivers.

In Great Britain, the 'classic' study of the diet of the

Goosander (and Merganser) was that of Mills (1962a) who examined the gut contents of 147 Goosanders (and 148 Mergansers) from several Scottish rivers. Unfortunately the seasonal distribution of the sample was not presented, although it is stated that "young salmon were found to be present in the diets of Goosanders practically the whole year round". For Goosanders, analysis gave the percentage occurrence of salmon as 57.2%, trout 9.7%, non-identified salmonid 19.2%, eels 14.5%, perch (*Perca fluviatilis*) 9.7%, insects 6.4%, cyprinids 4.8%, pike *Esox lucius* 2.4%, and 0.8% for each of bullhead, 'birds' and 'mammals' (Water Shrew, *Neomys fodiens*). In a sample of the stomachs examined Mills determined the frequency of each prey type and calculated the percentage that each constituted of the total number. Salmon comprised 71% of all fish, perch 9.4%, trout 9.1%, eel 7.9%, cyprinid 2.1%, pike 0.9% and bullhead 0.3%. Whilst calculation of these values is a valuable approach it is not clear how the sample used in this determination was chosen, although it is intimated that it was those where "it was possible . . to count the number of fish eaten". This creates a clear bias in the results which must be considered, but which here cannot be quantified.

The results of the current study for the percentage occurrence of salmonids (salmon, trout and non-identified salmonids) are within the limits found by other workers, but considering individual species are strikingly different to the findings of Mills (1962a) in Scotland. Whilst the value in the present study for the percentage occurrence of salmon is broadly similar to his results, the value for trout is more than six times his result. For cyprinids the percentage occurrence recorded here is approximately nine times that found by Mills (1962a), and for eels is c2 times his figure. Sticklebacks were not reported as Goosander prey in his work (although they were recorded from Mergansers), yet occurred in 15% of guts examined here. By contrast the occurrence of perch is lower here and I did not record pike in the diet. Such differences could arise for several reasons each related to variations in prey availability in space and time. Firstly, birds were collected from a different range of river systems in the two studies. Additionally actual river areas where birds were collected were not reported by Mills (1962a), and for most birds examined here such details were rarely forthcoming. In the absence of such data accurate comparison between the results of these two studies cannot be made. Secondly, the seasonal distribution of birds examined is likely to have differed between the studies; Mills (1962a) did not provide these details. The time of day of bird collection may also have an effect as a result of diurnal patterns of foraging behaviour (see Chapter Four).

5.4.4 Species and size selection

Examination of the gut contents of Goosanders allows the species and size composition of the diet to be estimated. However, these data alone cannot be used to investigate prey selection. To attempt this requires additional information on the species and size composition of the fish population in the area where the predator was active, together with an assessment of prey availability. This latter will be a function not only of density, but also of habitat selection and behaviour. Few studies have attempted this.

The first to do so was White (1957) who compared the results of surveys of the fish population with the results from gut analyses of birds shot on an experimental section of the Pollett River, New Brunswick. For each of the four dominant fish species (in both the diet and the stream) he divided the percentage it constituted in the diet by the percentage it represented of the total fish population. The resulting values were 3.7 for salmon, 2.0 for suckers (Catostomus spp.), 0.3 for chub and 0.4 for blacknose dace (Rhinichthys atratulus). As he pointed out however, this need not indicate positive selection for salmon, but may simply reflect greater availability of this species over others. For instance, salmon parr exhibit territorial behaviour in favoured riffle areas (eg. Stradmeyer and Thorpe 1987) and tend to occupy slower flowing areas and frequently school.

Huntington and Roberts (1959) compared the fish population of several 'warm' waters in New Mexico (assessed using seine and gill nets, and rotenone), with the results of gut analyses of birds shot there. This suggested that some selection for carp and shad may have occurred but that in general "availability is one of the most important factors in determining the species of fish upon which they [Goosanders] feed". A similar conclusion was reached by Bagge et al. (1970) in Finland. However, their data indicated that the 10-spined Stickleback (Pungitius pungitius) was selected against.

The absence of any salmonid remains from Goosanders collected by Sjoberg (1974) from salmon waters in northern Sweden over the course of the smolt migration, and the dominance of lamprey and bullhead, was explained in terms of the differing availability of each species. Lamprey undertake the first stage of their spawning migration in autumn when they move up river, and when they are typically nocturnal. However, during the spawning period beginning in June, they shift to 24 hour activity, although the peak remains during the night (Sjoberg 1985). Their occurrence in large numbers, attached to stones in the same riffle areas as those preferred by juvenile salmonids and feeding sawbills, results in a higher availability than at other times. Sjoberg (1974) considered they had an important role as a 'buffer' species. Indeed, if the composition of the diet reflects availability, the factor determining the numbers and sizes of salmonids taken will be dependent on the nature of the total fish population.

Habitat segregation between different fish species and different size/age classes is well documented. Kennedy and Strange (1982) studied the distribution of 0+, 1+ and 2+ salmon and trout in the River Bush, Northern Ireland. This showed that fry of both species were significantly more abundant in water less than 20cm than older fish, and that as fish age increased deeper waters were selected. These authors suggested that this was size, rather than age, related, however, since larger 1+ parr were found in deeper water than smaller members of the same year class. Data presented by Jones (1975) support this suggestion. He demonstrated a partial segregation of species, with 0+ salmon, bullheads and lampreys predominating in riffles, 1+ salmon, 0+ trout and stone loach predominating in riffles and runs, 1+ trout in runs and pools and 2+ trout, older trout, minnows and gudgeon (Gobio gobio) in pools. Trout appeared to be limited in their distribution to areas of 'lower' flow. Since water depth and gradient are significantly negatively correlated there was an apparent preference of trout for slightly deeper habitats than equivalent year classes of salmon. Unfortunately the time of year of these studies was not reported.

Observed differences in prey size between male and female Goosanders may be related to differences in habitat selection by different size/age classes of these two fish species (see above), and to possible preferences of one or other sex of Goosander for particular, specific, feeding locations. Differences in dive duration (see 5.4.1) may be important in this connection.

Observations did not indicate segregation of the sexes between feeding areas, and assuming this to be true, gut analyses suggest that male Goosanders select larger (older) salmon than females but similar sizes (and ages) of trout. This could arise if females showed a preference for probing amongst stones on the stream bed for prey whilst males foraged more within the water column. Why depredated trout do not show a size difference between the sexes is unclear but may be related to these fish occupying slightly deeper waters than salmon (see above). This assumes that the sample of Goosanders available for gut analyses did not show any bias towards particular river areas for particular sexes of bird. Unfortunately this cannot be tested.)

The dominance of game fish in the diet of a sample of Goosanders on both trout and non-trout waters, reported by Sayler and Lagler (1940) was suggested to be a result of a preference for 'large' prey items. The mean length of 357 trout, taken from the guts of shot birds, was 5.8 inches. This, commented the authors was "evidently much greater than the average size of 547 forage fishes". Thus they considered that "in most waters, but especially in trout streams, this preference has a direct bearing on the kinds of fishes taken for the fishes of larger average sizes are for the most part game species".

Latta and Sharkey (1966) specifically investigated species and size selection in captive Goosanders. They showed that when presented with live trout 4-8 inches long, in a gravel bottomed tank, birds selected the smaller trout in preference. Further work indicated that girth, rather than length, determined the upper limit of prey size, and that there was a positive relationship between the size of the predator and the size of prey it was able to ingest. Their largest Goosander (60 ounces) could consume trout up to 6.2 inches girth. Presentation of equal numbers of sculpin, chub and brook trout (Salvelinus fontinalis) of similar size showed that equal numbers of 'mobile' prey (chub and trout) were consumed, but fewer benthic fish (sculpin). Selection for smaller fish was also shown by Sjoberg (1988) when satiated (rather than hungry) sawbills were presented with two size classes of salmon and minnow (Phoxinus phoxinus) (40-60mm, and 80-100mm) in a 'neutral' tank affording no shelter. When his birds were hungry, however, fish of the larger size class were selected. White (1957) reported that for his captive Goosanders "when there was a choice of sizes at any particular time, tended to take the larger fish up to the limit of a size which they could readily swallow".

In enclosures with known densities of coho salmon (Oncorhynchus kisutch) smolt and fry , Wood and Hand (1985) found that smolt were selected over fry, but that the foraging success of Goosanders was affected by previous exposure of the fish to this predator ('naive' fish were more vulnerable), and by available cover.

In addition to demonstrating the influence of nutritional status on size selection of prey, Sjoberg (1988) also showed variation in species selection. He presented combinations of 2-7 fish species, of similar size (10-12cm), to both hungry and satiated hand-reared Goosanders and Mergansers. In a 'neutral' tank offering no cover, when all prey were "easily and equally" available, no preferences in species selection was shown by hungry birds. However, if satiated birds were used an order of preference was noted from salmon (most preferred), through brown trout, minnow, whitefish Coregonus lavaretus, sculpin Cottus gobio, burbot Lota lota, and river lamprey (least referred). Repeating the experiment with hungry birds in a stream tank which offered "unlimited shelter" showed selection for open-water species rather than for salmonids which maintained station on the streambed.

Seasonal differences in the estimated size of salmonid prey, which were shown above to be statistically significant, may result from changes in the availability of salmonids of different size classes. Prey size was least in the summer (June-August) when the mean size of all stream salmonids would be lower than at other seasons because of the appearance of a new year class. Changes in estimated mean prey size between autumn/winter and spring/summer may also be partly attributable to changes in prey availability as a result of season and size related changes in micro-habitat selection within waterways. This has been investigated by Rimmer et al. (1983, 1984, 1985) in New Brunswick. They found that at a temperature threshold of c10°C there was an apparent population decline for young salmon of 92-98% which was caused by fish moving from their stations above the stream bed to sheltered chambers beneath stones. This was shown to be related to a decline in point-holding performance below 8°C (Rimmer et al. 1985). Considering 0+, 1+ and 2+ fish separately showed that 1+ parr moved from pools to runs, ie. habitat choice differed between summer and autumn, whereas pools tended to be occupied year-round by 2+ fish.

Growth curves presented by Egglishaw (1970) indicate that for all age classes of salmon and trout, growth slows in September and that little increase then occurs until the following March. Thus the size class composition should remain similar between autumn (September-November) and winter (December-February). This is supported by data collected here.

5.5.0 SUMMARY

Two foraging methods are used by Goosanders; head-under-searches (HUS) and diving. Choice of foraging method appears to be related to water depth. The dive duration of males was found to be significantly greater than that of females, but no differences between habitats were noted.

The results of gut analyses show that in terms both of percentage occurrence, and frequency of occurrence, salmonid fish are the most important food items of Goosanders; the percentage occurrence of salmon was 48%, trout 56% and non-identified salmonid 70%, and c78% of all prey items were salmonid. However, other fish, notably cyprinids, eels and sticklebacks are also important. The overall mean size of salmonids taken, estimated from a regression of the length of the atlas vertebra on fork length, was 106mm (SD=28.88). All age classes, from 0+ fish to 2+ fish were represented. Data are not adequate to test for species and/or size selection since fisheries information was not available to compliment the results of gut analysis.

CHAPTER SIX ;

GENERAL DISCUSSION; THE SIGNIFICANCE OF GOOSANDER PREDATION TO SALMONID FISHERIES

6.1.0 INTRODUCTION

The potential impact of any predator on populations of its prey species is affected by a variety of factors. Of these, the distribution and numbers of predators present, their energy requirements, the temporal and spatial distribution of their feeding activities, and their diet, as estimated from gut analyses, have been the subjects of previous chapters. Attributes of prey populations must also be considered viz. the distribution of prey species between and within rivers, patterns of diel and seasonal activity, mechanisms of population regulation, and, for anadromous species, the relationship between the numbers of young fish descending to the sea and the number of adult returning. It is also important to evaluate interactions between prey species.

In this chapter I attempt to integrate the results from previous chapters with information on fish population dynamics, to provide an assessment of the relationship of the Goosander to fisheries interests in general, and game fish interests in particular. Of especial concern is the effect depredations by sawbills on populations of juvenile salmon and migratory (sea) trout, has on the numbers of adult fish returning to the spawning river.

The number of native adult fish returning to spawn in a given river will be the product of the number of eggs deposited, total survival during early river and marine life, and the proportion of adult spawners returning to their native waters. Total mortality can be partitioned into mortalities occurring during successive life stages: egg, alevin, fry, parr, smolt and the marine phase. Fishing mortality must also be considered.

Since mortality due to depredations by sawbills occurs only during the juvenile, non-marine, stages of the life history of salmon and migratory (sea) trout, it is appropriate to consider the potential contribution of sawbills to the mortalities of eggs, alevins, parr and smolt, within the population dynamics of these fish.

6.2.0 POPULATION DYNAMICS OF SALMONIDS

6.2.1 Mortality of eggs, alevins, fry and 0+ parr

The only evidence found in this study for consumption of salmonid ova by Goosanders was from a single adult male, shot on the River Rawthey, Lancashire in December 1983; approximately 25 eggs were present in the proventriculus (see Chapter 5). Mills (1962a) did not find salmonid eggs in any of the 147 Goosanders, or 148 Mergansers, he examined from various Scottish waters.

However his sample may not have included birds taken in salmonid spawning areas at, or around, the time of egg deposition.

Although predation on ova has been reported, both from the literature (Munro and Clemens 1937) and a questionnaire survey of district salmon fishery boards in Scotland (Carter and Evans 1985), we questioned whether predation on viable ova occurred to any significant extent. To exploit viable ova as a food resource would necessitate the Goosander (or Merganser) either (a) removing eggs from the redd in the presence of the spawners, between the time of fertilization and their being covered by the female, or (b) digging in the redd to expose the eggs which are buried c10-30cm below the gravel surface, depending on the size of the spawning female and the fish species considered. In British Columbia Munro and Clemens (1937) considered that a proportion of the eggs they found in the guts of Goosanders had been taken directly from the redd during spawning. Digging for ova is not reported in the literature and was not recorded throughout this study. Carter and Evans (1985) therefore considered that any eggs ingested would originate either from a redd exposed by erosion, or from loose eggs found otherwise on the gravel surface. For migratory (sea) trout in Black Brows Beck, Lake District, Elliott (1984a) estimated that up to 2% of eggs were lost from the redd during the spawning process, being carried downstream by the current. In numerical terms, for a female of 40-50cms, this represented up to c40 eggs lost. Since exposed eggs do not remain viable, their consumption does not represent a loss of potential fish.

Using key-factor analysis, Elliott (1985a) found strong density dependent mortality of young migratory (sea) trout in Black Brows Beck, Lake District, during their first spring and summer, which accounted for at least 90% of losses. To examine factors other than density which could have affected survival, he investigated the relationship between loss rate and water temperature, rainfall, density of older trout and the density of other fish species (chiefly bullhead and eel). Results indicated no significant effects. He subsequently showed (Elliott 1986) that the high losses reported were due to mortality rather than emigration or predation, and that approximately 81% of fry emerging from redds were moribund and in poor condition. These fish, whose numbers were directly proportional to the number of fry per redd, drifted downstream chiefly at night and died. This drift occurred throughout the summer period, but Elliott (1986) found that c73% of those estimated to have died in situ were not recovered from a trap at the stream mouth. This authors treatment of causes of this mortality (Elliott 1985a) was superficial. He commented only that young parr were not eaten by other fish present and that "herons fished the stream and probably accounted for some trout losses". Elliott (1986) argued that the downstream drift of moribund fry had adaptive value; fish emerging in poor condition would be at a disadvantage in competition with siblings for food and space but could enhance their survival probability by moving downstream and perhaps finding an area of lower density. This idea was supported by a study of juvenile salmon and trout in the River Bush, Northern Ireland (Kennedy and Strange 1982) which concluded that competition for space between fry/0+ parr and 1+ parr was probably a critical factor affecting salmon fry survival.

In contrast to Black Brows Beck, Elliott (1987) found no evidence of density dependent regulation in a non-migratory population of trout in nearby Wilfin Beck. He concluded that this supported Haldane's (1956) hypothesis that changes in population density will be largely due to density dependent factors in areas of high density (favourable areas) and to density independent factors in areas of low density (unfavourable areas). The low density of trout in Wilfin Beck compared to Black Brows was considered below the level at which density dependent regulation would occur, and was prevented from increasing by irregular spate and drought conditions.

Losses of 0+ fish over their first winter were not density dependent; data suggested proportionate survival with 41% (95% CL 38-45%) of autumn 0+ parr surviving to the spring (Elliott 1985a). However, losses were attributable to both mortality and migration, with fish moving from shallow fast-flowing sections of the stream to deeper pools (Elliott 1986). Such habitat shifts will be considered below.

Gardiner and Geddes (1980) suggested that "nutritional insufficiency" was a major factor in determining the observed pattern of mortality of 0+ salmon parr in the Shelligan Burn, Perthshire (Egglishaw 1970) and Egglishaw and Shackley 1977), but commented that the causes of mortality of young fish were not well understood. Also for salmon, Mills (1964) reported the survival of planted unfed fry to 1+ fish in the River Bran, Ross-shire, to be only 2.6% but that subsequent mortality up to smolt age was slight. He concluded that although predators exerted an effect during all life stages, some distinction could be made between the effect of predation during downstream migration (the smolt run) and at earlier stages. During the fry and parr stages, he identified trout and goosanders as the main predators, but felt that their combined effect may not have been important since the proportion of planted unfed fry surviving to the late parr or smolt stage was not unusually low for a river of that type.

6.2.2 Mortality of 1+ and older parr

Mortality of migratory (sea) trout older than 0+ was not found by Elliott (1985a) to be density dependent, and could be estimated from mean values over a number of years (excluding drought years). This exclusion was necessary since for 1+ parr Elliott (1985a) showed a significant positive relationship between losses of 1+ parr and summer drought. Whether these findings are applicable to waters where sawbills occur is not known.

6.2.3 Mortality of smolt

Less than 10% of the estimated smolt production of the River Bran was shown by Mills (1964) to reach Luichart Dam 13 miles from the sea. This was attributed to the fact that during dowmstream migration the fish were exposed to a greater spectrum of predators. Pike, confined chiefly to loch areas, were estimated to have consumed c10% of the 1959 and 1961 smolt runs; and 28% of trout examined contained smolt. Of the avian predators, Goosanders were considered the most serious but their contribution to smolt mortality was not evaluated. More recently, Mills (1980) stated that "Although the named birds [Goosander, Merganser, Cormorant and Shag (<u>Phalacrocorax aristotelis</u>)] undoubtedly eat young salmon, their low numerical density on any one river precludes them from being a serious threat to salmon stocks in Scotland."

A large proportion of the reported losses of smolt in Mills earlier study could be attributed to the effects of damage during passage over the Dam which occurs either via the fish lift or shute pools. Such losses may not be entirely independent of predator density however, since both piscine and avian predators may congregate in settling pools etc. below dams to feed on stunned fish (Timken and Anderson 1969).

On the River Lule, Sweden, Larsson (1985) also found high mortality of migrating smolts with 50-70% estimated not to reach marine waters. Pike, perch and burbot were important predators during this movement with the latter removing up to 26% of released smolt (Larsson and Larsson 1975). The relative importance of other predators was unclear. Larsson and Larsson (1975), Piggins (1958) and Hvidsten and Mokkelgjerd (1987) reported a tendency for predatory fish to congregate at smolt release sites following the first introduction and suggested that this was an adaptation to the exploitation of a predictable resource. The presence of saithe, pollack (Pollachius pollachius), bass (Dicentrarchus labrax) and freshwater eels in inshore and estuarine waters, was suggested by Wheeler and Gardner (1974) to pose a serious threat to migrating smolt. This has not been studied.

Hvidsten and Mokkelgjerd (1987) studied predation by fish predators on post-smolts stocked in the River Surna, Norway in 1984 and 1985. They found that cod were the main predator, accounting for an estimated 24.8% of total smolt mortality in a restricted areas of the estuary. The importance of estuarine predation was demonstrated by further experiments which showed that smolt stocking at sea resulted in recovery rates of adult salmon up to three times better than those from river stocking. Similarly, Hansen (1982) found that the mean recapture rate of fish stocked in the upper and lower reaches of the River Glomma, was 0.8 and 3.8% respectively.

In relation to the Scottish salmonid fisheries, predation on smolts by other fish species will vary from area to area depending on which other species are present. Burbot are absent and pike confined chiefly to lochs in Scotland (Maitland 1972), whilst perch were found not to be an important predator on the River Bran system (Mills 1964). In nutrient poor rivers, which tend to support only salmon and trout, adults of the migratory form of the latter (as distinct from the resident Brown Trout) are potential predators of smolt. However, these may not feed on their ascent to spawning gravels if the distance from the estuary is short. Migratory (sea) trout in Black Brows Beck travel the 8km between the estuary and the spawning areas overnight and return as spent fish the following day without having fed (Elliott pers.comm.).

Levels of predation on smolt by all potential predators will be affected markedly by river conditions during the period of the smolt run. In spate years feeding opportunities for predators which locate prey visually will be greatly reduced due to high flows and turbidity, but in years of low river discharge when fish become concentrated in narrower reaches, greater feeding opportunities will be afforded to sawbills, Grey Herons, and gulls, eg. Mills (1964). Fluctuating water levels in the River Nidelva, Norway were shown by Hvidsten (1985) to lead to large losses of 0+ salmon and trout due to stranding during periods of water drop.

From a literature survey, Wheeler and Gardner (1974) concluded that "very little is known about the fish predators of the Atlantic salmon in the sea".

6.2.4 Timing of smolt migration

Several types of activity cycles exist in wild fish, related to tidal, diel and seasonal cycles (Hoar and Randall 1978).

For salmonids the most marked seasonal cycles within rivers are the downstream movements of smolt in late spring/early summer, and the upstream movements, in autumn, of adult spawners. In general, Bakshtanskiy et al. (1980) considered that downstream migration would be most intensive under conditions in which the hunting efficiency of predators was decreased. The timing of movements within the diel cycle is suggested therefore to be related to the feeding behaviours of the predators to which the fish are exposed. It is generally assumed however, that smolt movements occur during the hours of darkness. Whilst this has been shown by several authors, eg. Thorpe and Morgan (1978), pers.obs., Bakshtanskiy et al. (1980) reported that a large proportion of young salmon migrated downstream in bright sunlight in the Little Por'ya River which flows into the White Sea. This was because under such conditions, bright spots from the light ripple served as camouflage for the fish and reduced the field of view of pike, their chief predator.

Larsson (1985) suggested that because the timing of the smolt migration coincided with the spawning of two important predators, pike and perch, it might have a high survival value. In the context of predation by sawbills the same hypothesis could be made in that at the time of the smolt run the number of Goosanders present on rivers and estuarine waters is falling rapidly. During this period adult males and immatures leave the breeding areas for moulting sites in northern Scandinavia (Little and Furness 1985), and although ducklings of this species are present then they are too small to handle prey as large as smolt. This they could not do until c2-3 months old ie. late August/September.

The most critical time for migrating smolt was considered by Tytler et al. (1978) to occur in the transition from fresh to salt water. Using ultrasonic tags, they showed that the rate of progress of fish through an estuary was the result of the outcome of two conflicting needs. Firstly, the need to leave quickly to reduce the risk of predation, and secondly the need to prolong residency to orientate and adjust osmoregulatory mechanisms. Implicit in this is the suggestion of increased risk of predation in the estuary compared to offshore areas. Evidence to test this is lacking. For hatchery reared smolt released into a wedge flow, partially mixed estuary (the River Eden, Lomond) movement was dominated by the influence of tide on the direction of water flow; all fish had left the estuary on an ebb tide within a single tidal cycle. By contrast, the downstream movement of wild smolt in a two-layered estuary (the River North Esk, Tayside) occurred in short steps separated by long pauses. No fish escaped within one tidal cycle and many remained for periods of up to 108 hours.

If predators congregate in estuaries to take advantage of downstream migrating fish then the potential impact of a given number of predators on smolt escapement may be related to estuary type. On the estuary of the River North Esk, Mergansers, chiefly males and immatures, occur in moulting flocks, which begin to assemble in early June and reach peak size, by mid-July. These birds fed both within estuary limits and offshore (Carter and Evans 1986). It cannot be determined if the Mergansers congregated there primarily to exploit smolt or because the geography of the site afforded good all round visibility and good hauling out/loafing sites. On the basis of survey work and diet studies carried out on this river, Carter and Evans (1986) estimated that 10-25% of the smolt run may be lost to sawbill predation. On Vancouver Island, Wood (1985b) estimated the maximum mortality rate attributable to Goosanders did not exceed 10% over the period of the smolt run.

The responses of Goosanders to variations in prey density was studied by Wood (1985a, 1985b), on Vancouver Island. He found that birds congregated on streams where salmon populations had been enhanced by hatchery plantings etc.. Using experimental enclosures stocked with various densities of coho salmon smolt and fry he showed that the abundance of Goosanders increased from less than three birds to more than 10 birds within 1km of the enclosures, within one week of stocking with smolt (Wood 1985b). Further, the distribution of breeding pairs on eight coastal streams was shown to be highly correlated with both drainage area and juvenile salmon production (r=0.95), and Wood (1986) postulated a food assessment hypothesis whereby a pair chose a nesting stream on the basis of prey availability during the nesting season. Using data from the 1984 Goosander and Merganser Survey of Scotland (Carter and Evans 1984, see Chapter 1), and data presented by Mills and Tomison (1985), the relationship between the July density of birds and autumn fish density, on the River Tweed system, was investigated (Carter and Evans 1985). This was not significant at the 5% level (r=0.551, df=9), with only c30% of variation in bird density being accounted for by variations in fish density.

6.2.5 Return rates

The relationship between numbers of salmon smolt entering the sea and the number of adult returning cannot be accurately predicted from present information. Rates vary widely between years, and there may be significant differences between river stocks depending on river type, mean smolt age and mean smolt size (Ministry of Agriculture, Food and Fisheries, MAFF, pers.comm.)

Return rates for salmon of the River North Esk, reported by Shearer (1984a) and Shearer et al. (1987), to range between 13.9% and 46.3% (see Figure 6.1a), are much greater than values for salmonids from other studies (eg. 1-4% Hansen 1980, 1982, 2-9% Isaksson 1982, less than 2% Struthers 1984, and c10% MAFF pers.comm.). Reasons for this are unclear.

Data presented by Shearer (1984a) and Shearer et al. (1987), suggested that increasing smolt escapement may be beneficial in terms of increasing numbers of adult fish returning (Figure 6.1a). Using data in Shearer et al. (1987) there is a significant positive relationship between the size of a smolt run and the number of adults returning from that cohort ($r=0.557$, $df=12$, $0.02<p<0.05$). However, there is no indication of a plateau or maximum value of adult returns from a given smolt run, above or at a certain level of smolt escapement, respectively.

There are many difficulties surrounding the interpretation of estimates of smolt survival. These stem initially from uncertainties about the accuracy of estimates of smolt production from the River North Esk , derived by mark-recapture analyses, as a result of changes in trap efficiency with variations in river flow. These effects remain to be quantified. A further problem arises from the unquantifiable, and variable impact, from year to year, of commercial fisheries in Greenland and the Faeroes, and of illegal netting off the Scottish and English east coasts.

In contrast to the number of adult fish returning, the

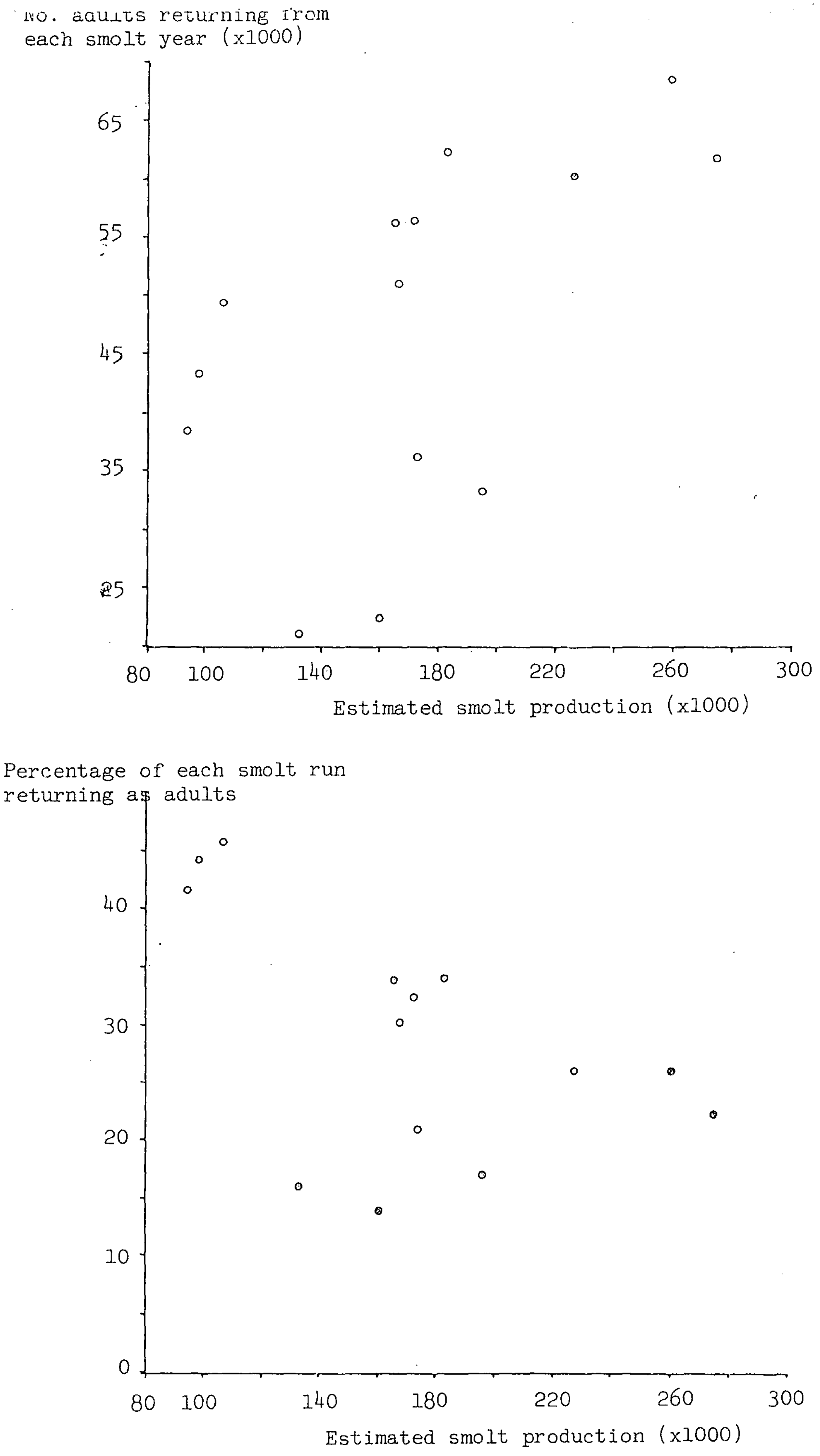


Figure 6.1 ; Relationship between estimated smolt production of the River North Esk, Tayside and (a) the number of adults returning from each smolt year, and (b) the percentage of each smolt run returning as adults

percentage returning from a given smolt run falls with increasing size of that run, although the relationship is not significant using linear regression ($r=0.516$, $df=12$, $p>0.05$). See Figure 6.1b. This could arise because of density dependent mortality at sea which Peterman (1980) identified as an underlying assumption of salmon enhancement programs. For Pacific salmonids he concluded that "there is reason to doubt the prevailing belief that marine survival of salmon is not density dependent". The mechanisms by which such a process may occur is unclear but competition for food, increased predation and transmission of parasites/disease organisms are obvious possibilities.

Although the possible density dependent mortality at sea of North Esk salmon cannot be taken as proven (Shearer et al. 1987), partially compensatory mortality of that type has been found in Sockeye Salmon (Onchorynchus nerka) by Foerster (1954). This relationship is explained, at least in part, by the finding that percentage survival at sea is positively related to mean body size of smolts at escapement, and that the larger the number of smolts escaping, the smaller their average size (Foerster 1954, Ricker 1962). Data for migratory (sea) trout, Elliott (pers.comm.) supported the suggestion that larger individual smolts have a higher probability of survival during their marine life, but found that there was no relationship between mean body size of juvenile fish and population density during the freshwater phase of the life cycle (Elliott 1985b). This suggested that food was not a limiting factor for that population (Elliott 1984b). For Sockeye Salmon in the Gulf of Alaska, Peterman (1984) found that enhanced smolt escapement from rivers led to lower growth rates (and hence smaller final body size) during early ocean life probably as a result of feeding competition in the Gulf where the entire phase of marine life was spent. It is not known whether the mean body size of smolts escaping from the River North Esk is related to, or is independent of, the number escaping. Hence even if density dependent mortality at sea was to be confirmed by further studies, it is not known whether size/density relationships would be relevant.

6.2.6 Commercial catches and exploitation

Estimates of the natural mortality at sea of salmonids based on the return rate of adults marked as descending smolt (eg. Shearer 1984a, Shearer et al. 1987) will be strongly affected by changes in the exploitation rate by the high seas and inshore commercial fisheries. Knowledge of the movements of post-smolt, and of fish of increasing sea age, is needed as well as information on their age class contribution to catches of, for example, the Faeroese and Greenland fisheries.

These data are largely lacking although from recaptures of smolt tagged on the River North Esk, Shearer (1984b) showed that fish from that river were not exploited in the Faeroese fishery until after their second winter at sea. Thus there was no fishing mortality from this source on grilse.

For the period 1952-1981, Shearer and Clarke (1983) examined the proportion of the total salmon catch in Scotland which comprised grilse, spring salmon and summer salmon. In all regions there was an increase in the grilse component and a general decline in spring catches. This was explained by earlier maturation in recent years, and was consistent with the observation that growth rates in the first sea year have generally increased over the same period. If growth at sea is density dependent then these changes may have occurred as a result of reduced densities of older fish, perhaps as a result of increased fishing mortality.

6.3.0 PREDATION PRESSURE

A convenient unit in which to measure predator pressure is the 'Goosander-day', where the number of Goosander-days is the product of the number of birds present and the duration (in days) of their presence at the site. Using values presented elsewhere on the daily energy requirements of individuals, and on the mean percentage contribution made to the diet by individual species, or genera, of prey, the accuracy of this measure could be improved. However, because of variation both between and within rivers with respect to fish diversity, relative abundance and availability, such an estimate may have little or no validity outside the areas where the original data were collected. Several authors have emphasised this point, and highlighted the need for each case to be examined individually. Nonetheless such a crude method will provide a useful first indication of the potential impact of the Goosander on fish populations at a given site.

The potential daily food consumption of adult Goosanders, in terms of the numbers of individual salmonids taken, is shown in Table 6.1 and Figure 6.2 over a range of 15-50% of body weight consumed per day. Values are based on (a) mean weight of adult males of 1556g, mean weight of adult females of 1258g (Table 3.5), (b) 78% of prey items being salmonid (Table 5.5), and (c) mean weight of salmonid prey of 12g. (This latter is estimated from $y = 0.194x-8.637$, where y = wet weight in g, and x = fork length in mm (derived from the reference collection), using 106mm as the mean length of salmonid prey (Table 5.6).) For food consumption equivalent to 25% of body weight, the daily food requirements of an adult male are 26 salmonids of mean length 106mm, and for adult females, 21 salmonids.

Shearer et al. (1987) developed a steady state model to examine the effect of predation by sawbills on the number of adult salmon returning to the River North Esk, Tayside, and particularly to estimate how the proportion of adults returning to the river is affected by reducing sawbill predation on smolts. The model was;

$$A_r = N_o \exp(-k_1 -k_2 -k_3)$$

where A_r = number of adults returning,

Table 6.1 ; Potential consumption of salmonids by (a) adult male, and (b) adult female Goosanders

% of body wt consumed	(a) adult males wt food[1]	 wt salmo[2]	 no. salmo[3]	(b) adult females wt food	 wt salmo	 no. salmo
15	235	186	15	189	149	12
20	313	247	21	252	199	17
25	392	310	26	315	249	21
30	470	371	31	377	298	25
35	548	432	36	440	348	29
40	626	495	41	503	397	33
45	705	557	46	566	447	37
50	783	619	52	629	497	41

[1] = calculated using mean body weight for adult males of 1566g, and 1258g for adult females (Table 3.4)

[2] = calculated as 79% of total food (Table 5.3)

[3] = using mean weight of salmonid prey of 12g (see text)

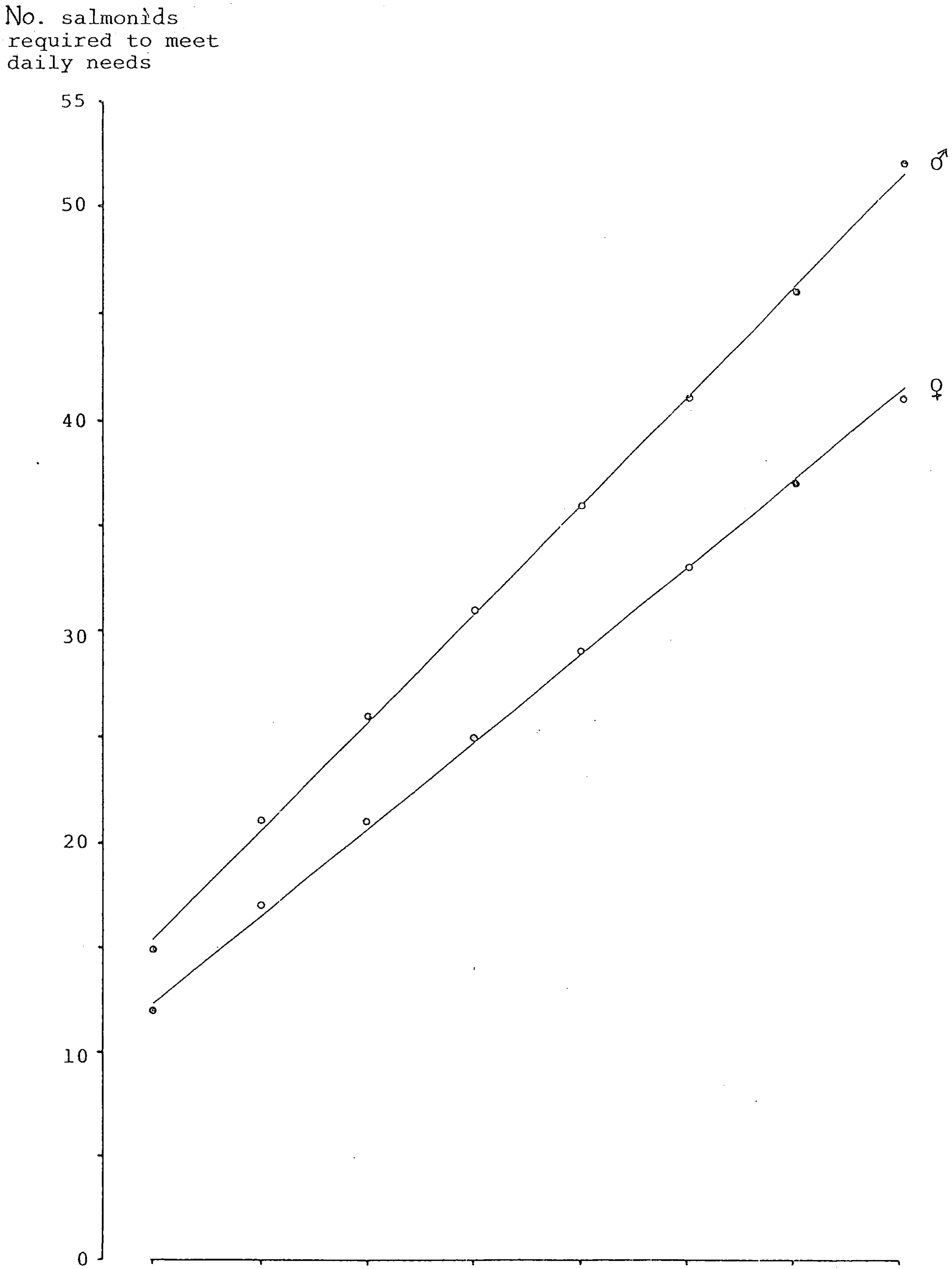


Figure 6.2 ; potential consumption of salmonids by Goosanders

N_o = smolt population before any mortality,

k_1 = smolt mortality due to sawbills,

k_2 = other smolt mortality, and

k_3 = total mortality at sea

Estimates of the coefficient of density dependence, b, although not statistically significant, were included in term k_3, but the authors recognised that this value, and estimates of mortality due to sawbills (k_1) were "uncertain". Output from the model was therefore given for two values of b and a range of values of k_1. This indicated that the greatest benefit from reducing k_1 would be a 35% increase in the numbers of returning adults in the absence of density dependent survival of adults. If k_1 was small (less than 0.1) and adult survival was density dependent, then the maximum gain if all predators were removed would be less than 5%. The authors pointed out however, that benefits are likely to be less than calculated values.

6.4.0 THE VALUE OF PREDATOR CONTROL

It is assumed (a) that the aims of salmonid fisheries are (i) to increase the absolute numbers of adult fish returning to each river and associated coastal areas, and (ii) to increase the size of the adult fish returning, and (b) that sufficient control can be applied to the intensity of harvesting by the commercial and sport fisheries to ensure that spawning escapement is adequate to attain the carrying capacity of each water for juvenile salmonids.

Predator control to increase smolt escapement is of value to the commercial and sport fisheries only if it can be shown that it increases the number of adult fish returning to spawn, given that the original assumptions above, relating to the aims of the fishery, are correct.

White (1939) reported the first experiment to test the effect of controlling the numbers of fish-eating birds (sawbills and Belted Kingfisher, Megaceryle alcyon), on salmon production. On Forest Glen Brook, Nova Scotia, 1834 smolt descended in spring 1937 following years of "unrestricted feeding by the birds". Control measures were then introduced and the smolt run of the following spring was determined as 4065 fish, an increase of over 120%. The incidence of large trout, predators themselves on young salmon, also increased. The results of this experiment, which had only one control year and one experimental year, cannot be regarded as conclusive. The observed increase in smolt escapement found on Forest Glen Brook between 1937 and 1938 could lie within the range of natural variation, although White took no account of this. The extent of annual variation in estimated smolt production was shown by Shearer et al. (1987) for the River North Esk, Tayside; this ranged between 93,000 and 275,000 between 1964 and 1982.

In a subsequent study, also carried out in the maritime provinces of Canada, Elson (1962) determined the mean annual production of the Pollett River, Nova Scotia, from 1942-1946 (following mean annual plantings of c69,250 hatchery reared underyearlings) as c2,000 sea-ward migrating smolt. Following the control of Goosander and Belted Kingfisher numbers between 1947 and 1950, and mean annual plantings of c249,250 underyearling, mean annual smolt production was estimated as c19,750. However, his data show that survival of fish from planted underyearlings to smolt was not significantly different between the periods 1942-1946 and 1947-1950; respective mean survival was 5.7% and 7.9%, $t=1.08$, $df=7$, $p>0.05$). The value of predator control is thus not proven. The effect of the observed increase in smolt production during Elson's experimental period on the numbers, or percentage, of fish returning as adults was not investigated, and thus no benefit to the commercial or sport fisheries attributable to predator control was demonstrated.

In a supplement to his paper, Elson (1962) provided recommendations, based on studies made by the Fisheries Research Board of Canada and the Canadian Wildlife Service, on sawbill control. For Maritime streams with 'average' smolt production, "control which reduces [Goosanders] to a density of 3 birds per 15 miles length and 10 yards width is unlikely to give a noticeable increase of smolts over the uncontrolled situation; but as the birds are reduced below this level, larger and larger benefits will be obtained," adding that, " the maximum benefit is likely to be obtained when [Goosanders] are reduced to a level of 1 bird per 15 miles of stream 10 yards wide." On the basis of these results a Goosander density of 2-3 birds per 10 mile of water, 20 yards wide on the rivers Bran and Meig in Scotland, noted by Mills (1962a), was suggested to be at a level where control should have an effect on smolt production.

In contrast to the results obtained by White and Elson, Munro and Clemens (1937) reported that in British Columbia, the Goosander did not adversely affect salmon and trout production appreciably because it occurred at low densities and its food consisted largely of coarse and "undesirable" fish. They found the freshwater sculpin, a salmon predator, to be the most frequently occurring fish in the diet.

Coldwell (1939), Lindroth (1955) and Peterson (1956) also found large numbers of predatory fish, eg. eels and bullheads in the stomachs of Goosanders, and suggested that "the birds should be given credit for killing these fish, which were detrimental to salmonids." Munro and Clemens (1937) further conclude that "A general reduction [of Goosanders], on the assumption that at some time or in some place they may cause losses of trout or salmon, is considered an unsound and unwarranted procedure." These, and other workers stress the need for each case to be examined independently since it is clear from this general review of published literature that individual water courses show variation in the importance of salmonid species as constituents of the diet of the Goosander. This is a result of differences in the physical characteristics of the various areas where studies have been carried out which will influence the diversity, abundance and availability of the fish species present.

In general, Draulans (1987) pointed out that it had not been demonstrated that the control of fish-eating birds increased fish production. Although both White (1939) and Elson (1962) showed increases in smolt escapement when bird depredations were reduced, their experiments were flawed (see above). Even if increases in the number of smolt entering the sea were shown to result from predator control, for predator control to be of value to sports fisheries increases in the number of returning adults attributable to that control, would need to be demonstrated. In particular, to date it has not been shown to what extent the shooting of sawbills in Scotland increases smolt escapement and, as has been illustrated, the effect of increasing smolt escapement on the numbers and size of returning adult fish has not been fully quantified.

APPENDIX ONE ;

COLONISATION BY THE GOOSANDER OF THE UNITED KINGDOM AND ITS CURRENT STATUS IN THE WESTERN PALEARCTIC

A.1.0 Colonisation of the United Kingdom

A.1.1 (i) Scotland

The first reported breeding of the Goosander in the United Kingdom was cited by Gray (1871) from near Loch Maddy, North Uist in 1840, and followed several years when summering birds had been present (Harvie-Brown and Buckley 1892). However, Harvie-Brown (in Buchanan 1879) and Harvie-Brown and Buckley (1888), did not consider the breeding record properly authenticated and suggested that it was probably the nest of a Red-breasted Merganser. Doubt also exists over a nest found on Loch Assynt (Sutherland) in 1865. Harvie-Brown (1878) considered that this possibly belonged to a Goosander but thought that Goldeneye was more likely, whilst Evans (1922) considered that the nest was almost certainly that of a Goosander. Although Harvie-Brown (1880) subsequently reported that he knew of a locality in Perthshire where Goosanders had bred since 1864, the first well documented, and undisputed, breeding record was not forthcoming until 1871 on Loch Ericht. This again followed years when summering birds had been recorded (Harvie-Brown and Buckley 1895). Although breeding had almost certainly occurred at the same site in the previous year (1870), this record, along with that of a female and brood on Loch Awe, Argyllshire in the same year, is usually taken as the first fully authenticated breeding of the Goosander in the United Kingdom (Meek and Little 1977a, Sharrock 1976, Cramp and Simmons 1977).

For the period up to the early 1870's Berry (1939) commented that "on the whole [the Goosander was] a scarce winter visitor to Scotland." To explain the gradual spread of the species from that time he suggested the existence of a drift migration, presumably from a Scandinavian centre. This movement, he continued, "amounted to a mass emigration" by the autumn and winter of 1875/76 with the birds remaining in Scotland thereafter. This he felt explained the apparently simultaneous colonisation of "the areas of Argyll, the North-west Highlands, the Moray Basin and Tay", by the turn of the century, a feature previously commented on by Baxter and Rintoul (1922). By the early 1900's therefore, the Goosander was well established as a breeding species in these areas. Further west, on the Outer Hebrides, and further north in Caithness, it remained an uncommon winter visitor or migrant with no confirmation of breeding confirmed, as on Orkney and Shetland (Baxter and Rintoul 1922, Berry 1939).

During the early part of this century the breeding distribution of the species spread gradually in areas north of the Highland Boundary Fault, including Aberdeenshire where the first confirmed nesting on the Dee was recorded in 1922. The Central Lowlands, the belt of land running east-west between the Highland Boundary

Fault and the Southern Upland Fault, appear to have been largely bypassed as breeding areas in favour of the western portion of the Southern Uplands. This trend is clearly demonstrated in the distribution maps presented by Mills (1962a) and by Sharrock (1976). Breeding was first recorded on the Annan, Dumfries-shire in 1926 with up to two pairs (British Birds 1926-27, vol.20, page 252).

Bolam (1912) described the Goosander on the Tweed as a winter visitor which was "often numerous, particularly during early spring, and appears also, more or less regularly, on most of its larger tributaries, sometimes following their course till they are little more than mere mountain burns..." Baxter and Rintoul (1922) simply record the species as a winter visitor on this river system. Breeding was first confirmed in 1930 with three or four pairs on the Ettrick (British Birds 1930-31, vol. 24, page 111), one of the Tweed's major tributaries. From here the species spread into northern England.

A.1.2 (ii) England

Chapman (1924) described the Goosander in central Northumberland as abundant from October to April with numbers being greater "whenever the highland lochs froze over." Although summering birds were occasionally present by the late 1920's, there was no suggestion of breeding during that period (Meek and Little 1977a). It was not until 1941 that breeding was first confirmed south of the Scottish border in upper Coquetdale (Meek and Little

1977a). Temperley (1951) reported breeding to be annual thereafter on that river, and noted that the colonisation of north Tynedale occurred in 1945. Meek and Little (1977a), however, stated that the first nest in Tynedale was not until 1956, and that the range of the species had further extended to south Tynedale by the end of that decade. Macfarlane (1971) suggested a total breeding population for Northumberland of 35 pairs for 1967/68 (based on survey work by the Tyneside Bird Club), and Meek and Little (1977a) estimated 90 pairs in 1973, and 130-150 pairs in 1975. Meek and Little (1980) reported that the population appeared to have stabilised in Northumberland at this latter value. This still appears to hold true (Little pers.comm.).

Of the status of the species in Durham, Hutchinson (1840) says "The Goosander seldom makes its appearance in the County except in winters of more than usual severity, when small flocks of from 6-12 are found on rivers". Atkinson-Willes (1963) included Durham in his assessment of the breeding distribution of the species in north-east England, but this would appear to be incorrect since (although suspected earlier), breeding was not confirmed there until 1967 when a pair nested on the Tees. The first breeding record for the Wear was made in 1971, and the 1975 population estimate for the County was 10-20 pairs (Meek and Little 1977a).

In north-west England the first definite breeding records were (1) a pair on the Eden near Brampton (Cumberland) in 1950, (2) a pair on Coniston Water (Lancashire) in 1961, and (3) a pair on Windermere (Lancashire/Westmorland) in 1961. For north-west England the breeding distribution was given by Atkinson-Willes (1963) as Cumberland and Lancashire, and by the BOU (1971) as Cumberland, Westmorland and north Lancashire. Numbers continued to increase throughout these areas in the 1970's although, despite the lack of good survey data, the rate at which this increase has occurred appears not to have been as great as in the north-eastern counties of Northumberland and Durham. The 1975 population was estimated at 35-115 pairs for the north-west, compared to 140-170 pairs for the north-east.

For Yorkshire, Mather (1986) reports that the first breeding record was of two pairs on the Tees near Barnard Castle in 1969. Further south, the first confirmed nesting in Wensleydale (River Ure) was in 1972. On both of these rivers numbers have increased subsequently. By 1980 the breeding range had extended to include the rivers Ribble and Wharfe where nesting was described as 'regular'. For the county as a whole at least 14 pairs bred in 1983.

Elsewhere in England the most recently documented southern extension of range has been into Devon. The species was regarded as an uncommon winter visitor, but in 1980 a pair bred successfully on the Dart. Since then breeding has been sporadic but at least two pairs nested in 1985.

A.1.3 (iii) Wales

Lovegrove (1978) provided the first review of the colonisation and breeding status of Goosanders in Wales. He considered it almost certain that the species first bred on the Afon Dyfi in 1968, although the first fully authenticated record was at an upland reservoir site in Montgomery in 1970 (Meek and Little 1977a). By 1977, five (probably six) pairs were breeding in Montgomery, four in Radnor and one in Gwent, giving a minimum total population size of 10 pairs. Survey work by the RSPB (unpub.) in 1981 on 11 selected rivers, or parts thereof, throughout Wales, concluded that the rapid extension of the Goosander population that had occurred there until at least 1977, had slowed and that there was no clear evidence of the colonisation of 'new' rivers, or of increased densities on known waters.

A more complete survey (Tyler 1986) during both the winter of 1984/85 and the subsequent breeding season, suggested a spring population of c100 pairs. Although the 1985 survey was more extensive than the 1981 survey (1981: 482 km on 11 rivers; 1985: 666 km on 29 rivers), comparison of populations on those waters covered during both years demonstrates a clear increase in population size. See Table A.1.

A.1.4.(iv) Ireland

The first known breeding record for the Goosander in Ireland was of a pair which successfully nested in Donegal, within the Glenveagh National Park, in 1969 (Sheppard 1978). A single pair bred there annually over the next 'ten years or so, but then left, apparently because they were disturbed,' (O'Keeffe pers.comm.). At the present time no Goosander are therefore known to breed in Ireland.

A.2.0 The status of the Goosander in the western Palearctic

A.2.1 Methods

Information on the breeding status of the Goosander in the countries of the western Palearctic was collected from published sources and national governmental/private organisations. Organisations listed in the "International Directory" of the Birdwatchers Yearbook 1986 (Pemberton 1985) were circulated with a request for information on (a) the numbers and distribution of the Goosander within their country/region, and (b) any documented changes therein.

A.2.1 Results

Information on Goosander numbers and population trends in the countries of the western palearctic are presented in Table A.2. It is clear from this that the Goosander is essentially a species of northern latitudes. The major centre of population lies in the countries north of the Baltic, with Sweden the most important of those with known population size.

In areas bordering the Baltic the population generally appears to be stable or increasing slightly, as a result of both legislative protection and the provision of nest-boxes. Population trends for western Russia (excluding Latvia and Estonia) are unknown.

In both Norway and Denmark in contrast, the Goosander appears to be becoming increasingly uncommon. Hansen (1980) has suggested that in southern Norway, where this reduction is most apparent, it may be the result of acidification of freshwater biotopes, whereas in the north, intensive hunting may be a major contributing factor. The changing status of the Goosander in recent historical times in the Baltic states is unknown.

In the late nineteenth century the distribution of the Goosander on a European scale began to change. Colonisation of the United Kingdom occurred in 1871, and the current population estimate is of 1-2,000 breeding pairs (Sharrock 1976). As indicated above data suggest that range expansion is still continuing.

At approximately the same time as the Goosander population was rapidly expanding throughout Scotland, sporadic breeding was noted elsewhere outside the main breeding range at at least two sites in Yugoslavia. At that time the species also showed a slight increase in abundance on Lake Geneva, Switzerland. Here Poncy and Meylan (1930) estimated 8-10 breeding pairs to be present by the early part of the century. Although considered rare on the Lake until the Second World War, the relaxation of shooting pressure during that six year period appears to have allowed the population to expand. Subsequent restrictions on hunting (from 1962) and total protection (from 1972), as well as the provision of nest-boxes, are considered to be the major factors responsible for a marked increase in abundance. In 1984 Geroudet (1985) estimated 700 potential breeding pairs on the Lake but Plessix (pers.comm. 1985) considers this figure too high and suggests 350 as a more realistic value.

Geroudet (1985) noted the occurrence of what he termed "over-population" on the western part of Lake Geneva, citing high competition for nest sites, laying by several females in the same nest, and a high proportion of non-breeders, as evidence. He further commented that "peripheral radiation and occupation of new breeding waters" proceeded "only slowly or reluctantly", and concluded that the Goosander was "strongly conservative and not a good coloniser." This is in contrast to the situation further north in Europe (cf United Kingdom), and may lend support to the suggestion made by Yeatman (1971) that this southern population, which, as indicated, lies outside the main breeding range, is a relic from the last Ice Age. Because of the probable absence both of winter migrants from the Baltic states and of any movement of the Swiss birds, this population may well be discrete and possess different characteristics from those further north.

Bauer and Glutz (1969) indicate that several other areas in Switzerland also support breeding Goosanders, as also do a small number of sites in Bavaria. The species also occurs in the French provinces adjacent to the Swiss border, but is there considered very rare (Yeatman 1976).

Both Cramp and Simmons (1977) and Geroudet (1985) make reference to a small population of Goosanders breeding in the Balkans but detailed information on numbers and status is not available. This 'population' would appear to be of recent origin however, and may therefore represent a further permanant range extension. Cramp and Simmons (1977) imply that these birds may derive from wintering populations originating further from the east in western Siberia, rather than from the central European population which is principally resident but may be pushed into southern France and northern Italy by severe weather conditions.

Details of a 'colony' of Goosanders on Lake Sevan, Armenia (Dementiev and Gladkov 1952) are lacking. Cramp and Simmons (1977) reported that breeding no longer occurred there.

Table A.1; A comparison of counts of adult and young Goosanders made in July 1981 and July 1985 (from Tyler 1986)

	1981	1985
WYE	17	99
IRFON	12-15	33
DEE	2	42
DYFI	-	14
YSTWYTH	-	3
TWYI	5	53

Table A.2 : Current populations and trends in the western Palearctic

Country/ region	Population trend	No. breeding pairs	Reference
France			
Lake Geneva	Unknown	'very rare'	Yeatman 1976
Switzerland	Increasing	200	Schifferli et al 1980
Lake Geneva	Increasing	700	Geroudet (1985)
		350	Plessix (pers.comm.)
Austria	Unknown	5-10	Prokop (pers.comm.)
Poland	Increasing	scarce	Tomialojc (pers.comm.)
East Germany	Decreasing	50	[Rutschke 1968]
West Germany	Increasing		
Bavaria		52-56	[Bauer and Zintle 1974]
Sch.-Holstein		35+	[Bauer and Glutz 1969]
Sch.-Holstein		50-60	Schmidt 1980
Denmark	Increasing?		Hansen 1981
	Stable	25	Joensen (pers.comm)
Norway	Decreasing	scarce	Hansen 1976
Sweden	Increasing		Andersson et al 1978
		18,000	Andersson (pers.comm.)
		20,000	[Ulfstrand and Hogstedt 1976]
Finland	Increasing	5-10,000	Niittyla 1980
Estonia	Decreasing	2,000	Kumari (pers.comm.)
Latvia	Decreasing 1970's	50-70	Viksne 1983
	Unknown	70-100	[Mednis in litt.]
Lithuania	Unknown	rare	[Kumari et al 1968]
Iceland	Stable?	100	[Fjeldsa pers.comm.]

References in square brackets '[ ]' are as cited in Hansen (1980)

APPENDIX TWO ;

ILLUSTRATION OF STATISTICAL METHODS

To illustrate the statistical techniques used in this thesis additional analyses are presented here to investigate the relationship between the lipid index values of skin samples (LI_{skin}), the age and sex of the bird from which they derive, and the month during which the bird was collected. These data, summarised from Table 3.3, are given below. Data for juvenile Goosanders are not included since these birds had not completed growth.

The null hypothesis that the three independent variables being considered had no effect on LI_{skin} values was investigated using general linear modelling (GLM) within the SAS system (SAS 1985). The analysis of variance procedure of SAS (ANOVA) is not suitable for this investigation because each sub-group contains different numbers of observations; ANOVA is only applicable to such unbalanced data sets where there is a single independent variable. GLM tests how well the model (constructed using the independent variables) accounts for variation in the single dependent variable being considered, as well as giving details of the effect of each independent variable acting singly or in paired combination.

For data given below GLM shows that although age, sex and month together explained approximately 53% of the observed variation in LI_{skin} values their combined effect was not statistically significant at the 5% level; F = 1.72, df = 10, 15, p = 0.17. Further analysis showed that at the 5% level of significance none of the independent variables acting singly or in paired combination showed any significant effect on LI_{skin} values. On the basis of these result the null hypothesis cannot be rejected.

* * * * *

Age/sex	Month of collection	Corrected body weight (g)	LI_{skin}
AM	2	1437	64.79
IM	2	1621	457.08
AM	2	1698	469.80
AF	2	1234	201.89
IM	9	1458	257.23
AF	9	1194	307.44
AF	6	1097	42.55
AF	9	1412	308.52
IF	9	1016	71.14
AM	2	1691	371.43
IM	2	1595	334.80
AM	4	1350	42.52
AF	4	1427	563.00
AM	2	1454	203.15
AM	2	1723	355.73
AM	5	1557	50.61
AF	2	1568	498.93
AF	5	1197	98.91
IF	9	1153	125.68
AM	2	1597	373.56
AM	2	1606	107.68
AM	2	1668	1.50
IM	2	1779	694.06
AM	2	1265	5.19
AM	4	1630	339.20
AM	5	1339	63.43

where AM = adult male, IM = immature male,
AF = adult female, and IF = immature female.
Corrected body weight is defined as total body mass minus gut contents.

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