THE BIOENERGETICS OF THE TUFTED DUCK
AYTHYA FULIGULA (L.)

by

KENNETH FRANK LAUGHLIN

A thesis submitted for the degree of Doctor of Philosophy

UNIVERSITY OF STIRLING
Department of Biology

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I wish to thank Dr I Newton for his encouragement and supervision of this research project in all its stages. I am indebted to Professor F G T Holliday for his advice and interest in this project. The Nature Conservancy and Sir David Montgomery gave permission to work at Loch Leven. Many fellow research students and colleagues in the Loch Leven IBP project have assisted in various ways but I owe a particular debt for the practical assistance and local knowledge so readily given to me by Allan Allison, the Reserve Warden and Colin Campbell of the Wildfowl Trust. Finally my thanks to my wife, Anne, for her encouragement and extreme patience during the course of this study.

ABSTRACT

This study formed part of the International Biological Programme project, to study the flow of energy through a freshwater ecosystem, at Loch Leven, Kinross, Scotland. The Tufted Duck Aythya fuligula was the only duck species which fed entirely from within the loch and was present throughout the year; 500-550 pairs nested annually and there were 2000-4000 birds in late summer, but fewer than 100 birds overwintered.

Chironomid larvae accounted for 60% of the food of the Tufted Duck at Loch Leven; other important foods were caddis larvae and molluscs (the latter were eaten during egg production). There was no competition for food with other diving ducks on the loch - Pochard Aythya ferina, Goldeneye Bucephala clangula, but diurnal and seasonal variations occurred in the availability of food organisms to the ducks.

Carcass analysis of 100 ducks taken throughout the year showed a pre-laying peak of reserves in the female, which provided all the fat and half the calcium for egg production. The remainder was obtained from food eaten during egg formation but reserves were the major determinant of clutch size. A similar amount of body reserves was retained by the female for use during incubation, but again reserves were supplemented by feeding and food availability during

incubation may be an important determinant of nesting success. Males were heaviest during winter but in all birds weight varied considerably in this season. Normal reserves were sufficient for at least 10d without food.

Liver and Pectoralis muscle analyses showed that, except in cases of starvation, they would not be good indicators of the bird's 'condition'. Liver weight varied diurnally in relation to feeding and in the long term with the overall plane of nutrition. Pectoralis muscle normally provided only a small protein reserve but in extreme starvation was considerably depleted. This was seen in Scaup _Aythya marila_ taken after an oil spillage, but many birds died of exposure before their reserves became exhausted.

The most important parameters in the energy budget were numbers and respiration energy. The annual consumption by Tufted Ducks was equivalent to less than 5% of the chironomid production and they are therefore unimportant as consumers, compared with Trout and Perch. Food availability, to the ducks, apparently limits clutch size(through the build up of reserves), nesting success and autumn and winter numbers of the Tufted Duck at Loch Leven.

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1 INTRODUCTION

The Tufted Duck Aythya fuligula was chosen as the subject of an energetics study, as part of the International Biological Programme (IBP) research at Loch Leven in East Central Scotland. This species is by far the commonest diving duck at Loch Leven, feeds almost entirely from within the Loch and is present throughout the year. It was, therefore, included in the IBP study of production and energy flow through the main food chains of the Loch.

My own study had as its primary aims the calculation of (a) the annual energy budget for the Tufted Duck population which could be incorporated into an energy budget for the Loch Leven ecosystem, and (b) an energy budget for individual ducks of both sexes throughout the year.

The International Biological Programme

From the late 19th century, Loch Leven has been the site of several isolated scientific studies. These involved microscopic and other small invertebrate animals (Scott, 1891), macrophytic plant life (West, 1910), phytoplankton (Rosenberg, 1937) and a study of the spawning of the Brown Trout Salmo trutta (Munro and Balmain, 1956). In 1963, after the appearance on the Loch of extensive algal blooms, regular and continuous observations on several aspects of the Loch's ecology were begun. In 1964 staff of the Freshwater Fisheries Laboratory (Pitlochry) and the Nature Conservancy (Edinburgh) met and proposed to carry out combined research on Loch Leven as part of the International Biological Programme. The first joint research was started in 1966 by these organisations, together with the Wildfowl Trust, and these three were later joined by scientists from several universities (N C Morgan, 1974).

The initial investigations showed that, at that time, the Loch was almost devoid of large plants and that the major primary production was by phytoplankton. Chironomid larvae dominated the bottom fauna, while Brown Trout and Perch Perca fluviatilis were the most important fish. These fish fed extensively on chironomids, as did the Tufted Ducks. Thus the main aim of the IBP project was to examine the production at different trophic levels and the flow of energy to the Trout, Perch and Tufted Duck. The project also included a bathymetric survey and investigations of the physical and chemical environment of the Loch. Twenty-five papers on all aspects of the Loch Leven IBP project were presented at a symposium in Stirling in 1973 and published in a special volume of the Proceedings of the Royal Society of Edinburgh (1974). They included one paper dealing with part of this thesis (Laughlin, 1974).

The Tufted Duck

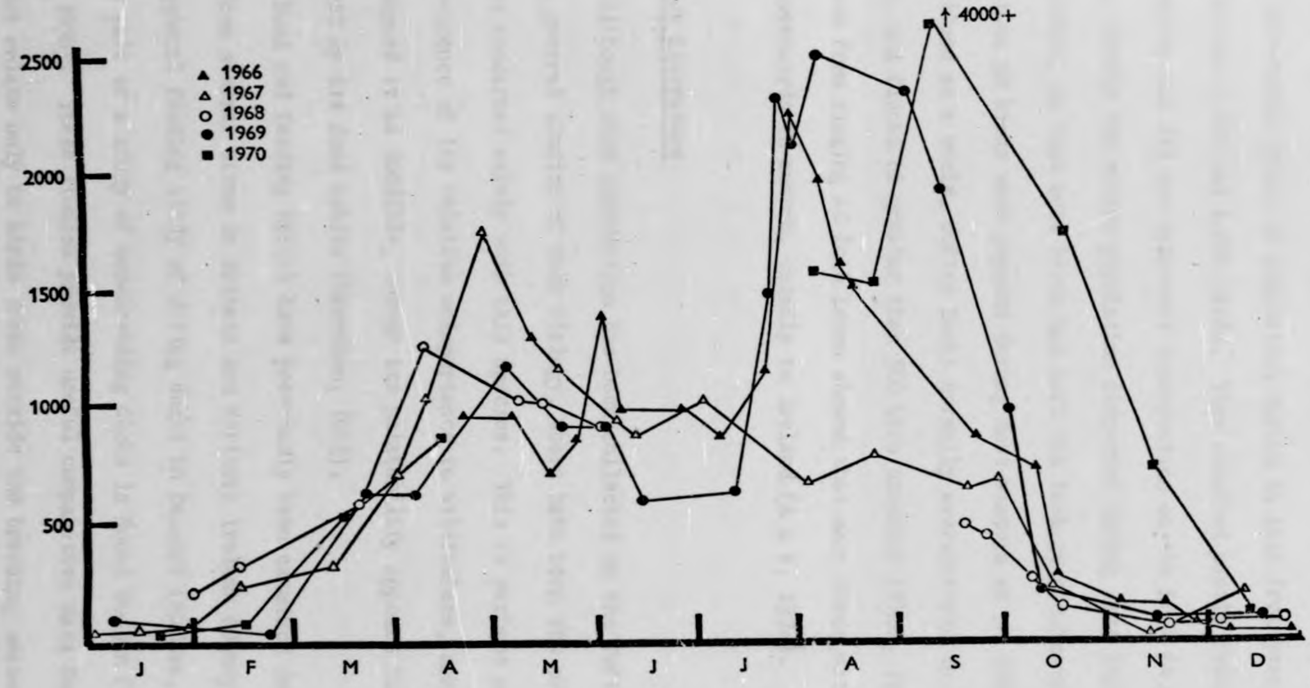
The Tufted Duck is the most common member of the tribe Aythyini (Pochards) in Britain. It is a relatively small duck, weighing 600 - 950g, which feeds by diving beneath the water surface in search of small invertebrates. It is not physically suited for life on land and, apart from the breeding season, spends most of its life on water. The male is a distinctive bird, almost entirely black, with white flanks and a long pendant crest. The female is a rich dark brown, with flanks striated light and dark brown, and crest short and truncated.

Tufted Ducks nest throughout Europe and Asia, roughly between latitudes 50° and 70° N; they winter south to 25° N in Europe and 12° N in Asia. At least since the late 19th century, the species has been increasing in numbers and expanding its range both in Britain and in Central and Western Europe. In Britain it is now one of the most abundant breeding wildfowl, with an estimated 1,500 - 2,000 pairs distributed throughout England and Central Scotland. (Yarker and Atkinson-Willes, 1971). Native birds have been estimated to comprise about 10% of the British wintering population of nearly 50,000 birds, which includes immigrants from Iceland, Northern and Central Europe.

Although the Tufted Duck was present in Central Scotland prior to 1850 (Jardine, 1843), it apparently began to breed in large numbers at Loch Leven only after that date. In 1880, Millais estimated that 100 broods were produced and that in late summer 300 - 1,000 birds were present (Harvie-Brown, 1906). This figure approaches the numbers found 1966 - 72 (Allison and Newton, 1974 - hereafter A & N) . During the latter period the Tufted was the commonest breeding duck at Loch Leven, with 500 - 600 pairs nesting annually. Various aspects of its biology, which complemented my own work, were studied first by Boyd and Campbell (1967) and then by Newton and Campbell (hereafter N & C, 1975), who were concerned chiefly with factors affecting nesting success.

The number of Tufted Ducks present on the Loch changed considerably throughout each year, but the pattern was consistent from year to year (Fig. 1). The main influx of breeding birds occurred during March and early April. The birds nested at high concentrations (up to 215 nests/ha), mainly on St Serf's Island, and egg-laying extended

FIGURE 1. Numbers of Tufted Ducks on Loch Leven, 1966 - 1970. The area under a curve fitted to these points was used to determine the number of bird days $\overline{N}T$ (Table 11), for calculation of the annual energy budget.



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from the first week in May to the third week in June (N & C, 1975). The ducks moulted from late June to October, the males beginning before the females, and were then found in large rafts offshore. The large late-summer peaks of population varied in size from year to year between 1,000 and 4,000 birds. They resulted partly from immigration and did not represent reproduction on the Loch (A & N, 1974). Nearly the entire population dispersed during late September and October, so that most birds had left the loch by mid-November and fewer then 50 birds were present during most winters up to 1969 - 70. In Scotland as a whole, Tufted Ducks normally overwintered in small groups, and flocks of greater than 500 were uncommon (Thom, 1969). Evidence from ringing at Loch Leven showed that many birds dispersed south-westwards in autumn, chiefly to Ireland (A & N, 1974).

Previous Literature

Although much information has been collected on the Tufted Duck during general studies of duck biology, there have been few previous studies concerned solely with this species. This is perhaps partly a consequence of its relative unimportance to wildfowlers, many of whom regard it as inedible, though its palatability appears to be governed by its food habits (Harrison, 1963).

Food and feeding habits have previously been examined in Tufted Duck from several sites in Britain and Northern Ireland (Olney, 1963), in a general feeding study of diving ducks in Denmark (Madsen, 1954), and as part of a study of non-breeding ducks in South Sweden (Nilsson, 1969; 1970). These studies provide useful comparative data for my own, but relate only to birds taken outside the breeding season.

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The post hatching development and growth of the Tufted Duck have been well described (Veselovsky, 1951; Kear, 1970), as have the associated changes in body composition (A J Evans, 1969). Another study of newly hatched ducklings included Tufted, and concerned their cold-hardiness (Koskimies and Lahti, 1964) in comparison with nine other species. The breeding biology and nesting success have been examined in some detail by Mikelsons *et al* (1968) in Latvia, Newton and Campbell (1975) at Loch Leven, and others elsewhere (refs. in the papers cited), while the migrations have been discussed by Allison, Newton and Campbell (1975).

In recent years a large amount of published data has accumulated on energy transformations and bioenergetics of birds, both individuals and populations, but few of these were on waterfowl. Such studies can be traced back to the observation of Odum and Perkinson (1951) that, although collectors had long been familiar with seasonal changes in the fat content of birds, there had at that time been no quantitative measurements made. Since then, much work has been published on the patterns of fat deposition in various birds (King and Farner, 1965; Odum, 1960). Initial interest centred on one of the more obvious energy demanding processes in a bird, its annual migrations. This subsequently led to studies of fat storage and body composition in general (Ward, 1969; Newton, 1969; King, 1970), but the major emphasis was on small birds (less than 100g) mostly passerines. Exceptions included a few studies of commercially important game birds, particularly the pheasant *Phasianus colchicus* (Breitenbach and Meyer, 1959; Gates and Woehler, 1968). Taken together, all these studies provided important information on the changes in carcass composition shown by various bird species and methods for their study.

One major study of the seasonal changes in body composition of a waterfowl was that of Hanson (1962) on the Canada Goose *Branta canadensis*. The bioenergetics of the Blue-winged Teal *Anas discors* were examined in captive birds (Owen, 1968) in an attempt to predict the energy requirements for growth of free living birds. Similar studies determined the energy requirements for growth and fledging of the Black Duck *Anas rubripes*, the American Coot *Fulica americana* (Penney and Bailey, 1970), and the Lesser Scaup *Aythya affinis* (Sugden and Harris, 1972).

So far as I know, my own study is the first attempt to construct an annual energy budget for any duck species in relation to its ecosystem and there are still relatively few bioenergetics studies of any birds heavier than 100g.

My Own Study

An outline of the requirements for the estimation of energy flow through bird populations was produced for the IBP programme (Buckner, 1967). These were " (a) an assessment of the population and its energy requirements from the study of individuals, (b) knowledge of the food habits of its members, and (c) an understanding of the ecology and dynamics of the study population."

Since the studies by the Wildfowl Trust and Nature Conservancy on the same population of ducks were concurrent with my own, I was able to participate in the overall programme. For the counts of population, I have relied entirely on data from the regular wildfowl counts in which I participated. Similarly, the study of Newton and Campbell (1975) provided some of the data necessary for my own. From the outline given above, I concentrated on (a) obtaining a knowledge of the food and feeding habits of the Tufted Duck, and (b) determining the energy requirements of the population from the study of individuals. I also compared the food and feeding habits of the Tufted Duck with those of other diving ducks at Loch Leven and with those of Tufted Duck at another site, Airthrey Loch. This water of 9 ha in area is in the grounds of Stirling University, about 32km west of Loch Leven.

The annual energy requirements of a population can be expressed in the form of an energy balance equation: $C = P + R + FU$, where C = consumption, P = production, R = respiration and FU = rejecta. In solving this equation, I concerned myself solely with the determination of P and made no attempt to measure the standard (basic) metabolic rate nor the existence energy requirements of the Tufted Duck. Not only would this have presented a considerable project in itself, but it was also felt to be unnecessary because the large amount of previous data, on the standard metabolic rate of birds of all sizes, has already been incorporated into a general equation relating standard metabolic rate to body weight (Lasiewski and Dawson, 1967). It is unlikely that a specific study of metabolism in the Tufted Duck could have provided a more accurate figure than this equation. Similarly, an estimation of the assimilation efficiency based on published evidence was deemed suitable for the determination of FU.

The annual production P was determined from three sources: (a) the biomass change (ΔB) of individual adult birds during their presence on the loch, (b) the production of eggs and (c) the production of young. Seasonal changes in the carcass composition of adult birds were investigated, paying particular attention to the female during the breeding season. I was unable to examine carcass composition during moult because of the impossibility of getting close enough to kill birds at this time. During December 1969 an oil slick in the Firth of Forth provided me with an unexpected bonus, a large number of the closely related Scaup *Aythya marila*, in various stages of exposure and starvation. These gave useful comparative data on the severe changes in body composition associated with starvation, which were not found in the Tufted Duck examined. Scaup taken from the same population for a feeding study (Player, 1970) during the month prior to the oil slick were available to determine the normal winter carcass condition of Scaup.

In all birds examined, the liver and pectoralis muscles were analysed separately from the rest of the carcass. The purpose was to determine to what extent, if at all, they could be used to indicate the condition of the whole bird. Previous authors have suggested that the liver should provide a good idea of body condition, while the state of the pectoral muscles (judged by feel) is often used for the same purpose by field workers. On average, in a wide range of bird species, the pectoralis muscles represented 15.5% of total body weight (Greenewalt, 1962), and being largely protein are a potential resource for feather growth and egg production, as well as an energy source in time of food shortage (Ward, 1969; Hanson, 1962; Gorman and Milne, 1971).

The annual egg production was calculated from data on clutch size taken from Newton and Campbell (1975) and from analyses of the composition of eggs. The opportunity was taken to examine variation in egg composition, within and between clutches throughout the laying season, and the relationship between egg composition and duckling composition.

As growth and body composition of young Tufted Duck from Loch Leven were investigated in detail by Kear (1970) and A J Evans (1969), this was not repeated. However juveniles around fledging were taken from the loch for carcass analysis to provide an estimate of the net production of young.

Study areas

Loch Leven

Loch Leven is the most important inland water body in Scotland, and one of the most important in Europe, for breeding, migratory and overwintering waterfowl. Primarily for this reason, it was declared a National Nature Reserve in 1964. The loch contains seven islands, all with a good growth of vegetation. The largest of these, St Serf's (42 ha) is especially important for nesting ducks, with more than 1,000 pairs, mainly Tufted Duck and Mallard *Anas platyrhynchos*, but with some Gadwall *Anas strepera*, Widgeon *A. penelope*, Teal *A. crecca*, Shoveler *A. clypeata* and Shelduck *Tadorna tadorna* (A & N, 1974; N & C, 1975).

The loch lies between the Firths of Forth and Tay on the plain of Kinross at an altitude of 107m, longitude 3°30' W and latitude 56°10' N. It is 13.3km^2 in area and has extensive areas of shallow water. The mean depth is 3.9m, and 50% of its area is less than 3m deep. In the shallows along the north-east shore the bottom is kept clear of mud by wave action, and consists mainly of sand and gravel which covers 45% of the total loch floor. Below three metres the sediment is soft organic mud.

The loch is now becoming increasingly eutrophic, mainly because of run-off of fertilisers from the surrounding farmland. In consequence, the flora and fauna have changed during this century, especially in the last 30 years (Morgan, 1970). In particular, the quality and species of rooted vegetation have declined greatly, and the emergent vegetation less so. West (1910) recorded abundant growth of 20 species of submerged plants, but these had declined to 12 species in 1972 and, whereas plant growth had extended to a depth of 4.5m at the beginning of the century, in 1972 it stopped at 1.5m (Jupp, Spence and Britton, 1974). Phytoplankton has increased; resulting in prolonged dense blooms, and at the same time the zooplankton changed in species composition. Since the survey of Scott (1891), Ephemeroptera and Odonata have disappeared, while Trichoptera have declined in numbers and species. *Gammarus pulex* (L.) has also declined, and only one of five species of *Planorbis* (Gastropoda) now remains (N C Morgan, 1974). During the period of the IBP study, there were large fluctuations in the numbers and species composition of the chironomids which now dominate the zoobenthos (Maitland and Hudspith, 1974).

In general, the variety of the flora and fauna of Loch Leven has become increasingly restricted and, during the course of my study, considerable changes in the relative importance of the remaining species were still taking place.

Airthrey Loch, Stirlingshire

This is a small loch (9.3 ha), with a greatest depth of 5m, but with more than half its area less than 1.5m. The edges of the loch had a good growth of plants, with *Polygonum* spp., *Typha* sp. and *Carex* spp. predominating. A small wooded island provided nesting cover for three or four pairs of Tufted Ducks and several pairs of Mallard. During the period of my study the loch was undergoing change, as the University was built around it.

In sharp contrast to Loch Leven, the peak numbers of Tufted Ducks (up to 300) occurred in November - March. Outside this period, the maximum number of birds on the loch was around forty. This was in late summer when the young birds produced on the loch supplemented the 3-4 breeding pairs and the non breeders. Tufted Ducks from Loch Leven, known by their wing tags, were seen in the winter flocks at Airthrey Loch. Such birds frequently commuted to Pendreich reservoir, 2km to the north in the Ochil Hills.

2 METHODS

Field Methods

Counts

Throughout the period of the Wildfowl Trust/Nature Conservancy studies, all duck species on Loch Leven were counted from a boat or raised vantage points on the shore at least once each month, except in the late spring and early summer (Allison and Newton, 1974).

The reliability of these counts depended on conditions. In view of the close association of Tufted Ducks with water, counts of this species did not suffer as much as those of other species which frequently moved to nearby land, ponds or ditches. Accurate counting of ducks in large flocks presented some difficulties, but checks between observers and repeated counts by the same observer did not reveal any major errors. The counts provided an order of magnitude for the populations, and for the Tufted Duck were probably accurate to within 10%. It was impossible for me alone to improve on these counts, because more than one observer was needed.

Breeding Success

During the duck breeding studies (N & C, 1975), the whole of St Serf's Island was searched, and known nests were checked, once or twice each week through the season. Each nest was numbered and marked with a bamboo cane placed a set distance and direction away. On each visit the status of the nest was noted, e.g. number of eggs, deserted, predated or hatched. At the first visit two of the eggs were candled from each clutch to find the approximate stage of incubation. All these data were collated on the nest record cards which were made available to me. From these were calculated the date that incubation commenced and, by assuming that one egg was laid per day (as indicated by many records), the date of first egg. The clutch size through the season was determined only from nests which were known to have been incubated and therefore had complete clutches. Clutches which were destroyed or deserted before incubation began were disregarded, although in some cases they provided data for determining date of first egg. Nest parasitism or "dump laying" affected up to 10% of nests in different years (N & C, 1975), and led to some abnormally large clutches. It was therefore necessary to decide upon a value above which clutches were to be regarded as the product of more than one female. I examined the distribution of clutch sizes in 856 nests, taken over three years, and decided that those of 15 and over should be regarded as the product of more than one hen. The analysis of Newton and Campbell (1975) included clutches up to 16 eggs and consequently their mean clutch sizes during the early periods of the season were higher than mine. An attempt was made to catch as many birds as possible on the nest, and some of these were weighed (to 5g) in the field on a spring balance.

Obtaining Birds and Eggs

A licence from the Nature Conservancy permitted the taking of a limited number of birds and eggs for analysis. Three methods were used to obtain birds:

1 Some were shot with a 12 bore shotgun or a .22 rifle, and when necessary carcasses were retrieved from open water using a dog. During the shooting season, I also obtained birds from the shooting parties which lease the wildfowling at Loch Leven. Four other birds,

shot at Loch Neagh (Northern Ireland) in December 1969, were given to me by R W Milleken.

2 Other birds were taken from the traps already in existence at Loch Leven and from a similar trap which was constructed at the start of the study and placed in Airthrey Loch. The traps, made of weldmesh, were 1.8m high and stood in about 1.2m of water on the bottom of the loch. In plan section they were kidney shaped, with a maximum diameter of 2.4m. The birds entered through a 300mm square hole at the bottom of the funnelled side, and usually remained in the trap feeding on the bait (barley) scattered on the bottom. To collect the birds a mesh door was placed over the entrance and they were caught in a long handled net introduced through a hatch in the top. When in use, the traps were visited in the early morning, as the birds usually entered them at night.

3 During the breeding studies, incubating females were caught on the nest using a net (600mm in diameter) on a long pole (2.5m). On approaching the nest site, the net was placed quickly over it, hopefully before the bird had time to leave.

Except in a few caught birds killed by cervical dislocation, most were given an intramuscular injection of 0.5ml of "Euthatal" (May and Baker, LTD.) in the thigh.

In 1970 a single egg was taken from each of 100 Tufted Duck nests before incubation had begun; these removals were spread throughout the normal laying season. In addition 20 females were taken from the nest with all their eggs. These nests were selected to give birds over a range of incubation states, and the female was used for carcass analysis. Three or four eggs from each clutch were analysed, and the remainder were incubated to hatching. Within six hours of hatch three or four ducklings from each clutch were killed for analysis.

All eggs were collected into egg boxes and transported to the laboratory in insulated containers. Eggs were incubated in Curfew Incubators (Western Incubators, Ltd) and maintained at 37.5°C and 60% relative humidity.

Laboratory Methods

Carcass analysis

Immediately on return to the laboratory, each bird was weighed (to 0.1g) on a top pan balance (Mettler, P1200). This weight was comparable with, but more accurate than, the field weight and was used as the body weight. In three birds the weight of food in the gut was such (@ 40g) that a correction was subsequently made for the body weight used in physiological calculations. Measurements were made of wing length, length of the first and tenth primary feathers, and length and width of the bill. The birds were then wrapped individually in polythene bags and stored at -20°C until further processing.

After thawing, the birds were weighed to determine any weight loss in the freezer, plucked and reweighed to determine the plumage weight (wet). This was found to be more practical than weighing the feathers themselves. The pectoralis muscle and the liver were dissected from the carcass for separate analysis. The lengths of the sternum and of the intestinal caeca were measured. The gonads were removed, measured and weighed, and their condition noted, before replacing them in the carcass. Ova from 7 gravid females were removed for separate analysis. After dissection the carcass was weighed and refrozen.

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As the carcass was too large to analyse completely, the following method was devised to get a representative sample. The frozen carcass was sawn into slices using a hacksaw or an electric bandsaw, and these slices were then split into pieces small enough for an electric mincer. The homogenate produced from the carcass was put through the mincer at least twice and then collected into weighed aluminium foil trays (200mm in diameter), weighed and refrozen. A cork borer (25mm) was used to take eight samples of the homogenate, which were selected at random using a numbered grid over the tray and random number tables. During my study a similar process for dealing with large carcasses was reported by Brisbin (1968).

My method was initially tested to ensure that it provided an accurate estimate of the carcass composition. Eight samples of approximately 12g each had a mean water content of 80.4%. The standard error of the mean estimate was 0.28% which indicated that the water content could be predicted to ± 0.5%. As a standard diameter tray was used, the amount of sample taken depended on the depth, and therefore the amount, of the homogenised carcass. It was usually around 10% which is slightly more than the 7-8% suggested by Brisbin (1968) to be adequate.

The following procedures were used for drying and fat extraction of the carcass samples, the pectoralis muscles, liver and eggs.

Water content was determined from the wet and dry weights of the samples. These were freeze dried to a constant weight, using a modified procedure for the drier (Edwards, EF2) which speeded the normal drying process. Samples were held in a rack in the drying chamber and, as drying proceeded, the trays were moved to the top. The insulation lid was not used on the drier, instead a 60 watt lamp in a reflector was held 100mm from the perspex lid of the chamber. This provided a radiant heat source to the samples on the top tray and increased the temperature gradient between the sample and the cooling coils. This procedure increased the speed and efficiency of water removal. Initially, repeated weighings during the drying process showed that a constant weight was achieved in all samples after 36 hours. All drying was therefore carried out over 48 hours which was more convenient for routine treatment.

After drying, the samples were put into weighed filter paper thimbles in Soxhlet extractors. The time needed for complete extraction of fat, using 60-80°C B.P. petroleum ether as solvent, was determined for various samples, and 12 h was found to be adequate and suitable for routine analysis. After fat extraction, the samples were dried to a constant weight at 60°C. This allowed calculation of the weight of fat removed from the sample and gave the lean dry weight of the sample. Lean dry material consisted of skeleton, protein and a negligible amount of carbohydrate from the bird's body; and dried food from the lower gut. Skeleton weight was determined in 3 samples of birds by boiling the lean dry material with 30% KOH which removed all but calcified skeleton (P R Evans, 1969).

Eggs

The length and maximum breadth of eggs were measured with vernier calipers, and weight was taken to the nearest 0.1g. Eggs for analysis were then hard boiled and the shells were removed, dried at 60°C and weighed. The contents were sliced and their composition determined as described above.

The volumes of 20 Tufted Duck eggs were measured by displacement in a eureka flask. These volumes were then used to determine the constant (k) in the regression of volume upon (Length x breadth^2). The value of k was 0.516 and the intercept of the regression did not differ significantly from y = 0. The volumes of all eggs subsequently collected were therefore determined from the equation

$$\mathrm{Vol} = 0.516.\mathrm{l}.\mathrm{b}^2$$

The term lipid includes, by circular definition, all the materials soluble in lipid solvents, and the term 'fat' may be restricted to neutral fats or triglycerides, but there is no general agreement on the use of these terms. I therefore used the term fat to describe the material extracted in the Soxhlet extractions in this study. In addition to using the absolute weights of the components when presenting data on carcass, organ or egg composition, I have used two other terms. The Water Index (WI) is the ratio of water to lean dry material and the Fat Index (FI) is the ratio of fat to lean dry material. These terms have been used in preference to expressing components as a percentage of the total weight. In the three component system into which I have divided the carcass, any one component expressed as a percentage of the whole can be affected by changes in either or both of the remaining components. The indices relate only two components and these can be examined in relation to the third.

Foods and Feeding

As already described, the gut contents of birds used for carcass analysis were obtained by dissection. I also obtained the gut contents of diving ducks killed by the shooting parties at Loch Leven. As these birds could not be mutilated, the food was removed by washing, as suggested by Pollard (1967). A tube attached to a wash bottle was inserted through the mouth down to the gizzard, and washing continued until no more food could be obtained. This procedure was not suitable for birds which had been shot through the digestive tract and these were discarded. In the laboratory the products of the washing were filtered and stored in 70% alcohol.

The stored samples were examined in a dish with a ring-shaped trough which could be rotated under a binocular microscope. This enabled rapid, sequential scanning of the whole sample. Individual items were removed for identification. Plant seeds were identified using a key and drawings (The Seeds and Fruits of Common Scottish Aquatic Plants - J T Swarbrick, unpublished; Martin, 1951; 1954). Animals were identified at least to Order and where possible to Genus and Species. Chironomids were identified specifically by Dr P S Maitland, Institute of Terrestrial Ecology. The barley in birds caught in traps was disregarded.

At the start of this study, the problem of quantifying the gut contents was considered in relation to the aim of the study, which was to determine the relative importance to the ducks of the foods available in the environment. Three measurements were possible; numbers of individual items, weight (wet or dry) and volume (wet and dry). Counts do not allow for differences in the size of individual food items. However, Madsen (1954) has pointed out that the volume or weight determinations can be used to advantage only for well filled stomachs. When the only contents are broken fragments of the calcareous or chitinous parts of animals, resulting from differential digestion between hard and soft parts, then weight or volumetric determinations provide little comparative data. I recorded the types of food in each bird in order to estimate the frequency of occurrence of food items. Then I made a subjective assessment of the 'main meal' in each bird where the quantity of food debris allowed this. This was not affected by volume of stomach contents e.g. one contained over 200 chironomid larva headshields of little volume or weight but clearly indicating a large chironomid meal. The persistence of hard materials in the gut was not an undue bias by this procedure, as all possible food items had some calcareous, chitinous or fibrous parts. In many of the birds the gut was completely empty suggesting that they either had not fed for a long time or, more likely, had cleared the gut rapidly. If very little or no food was found, then a main meal was not assigned, and if two items were equally numerous then both were termed $\frac{1}{2}$ main meals.

The feeding behaviour of Tufted Ducks was studied by observing several birds in a glass fibre tank (1.0 x .75 x .75m), which had one plate glass wall. The birds were hatched in the laboratory and allowed access to the tank from one day old. They were therefore quite practised at recovering barley and commercial food pellets from the bottom by the time they were observed at 5-6 weeks old.

A complete depth contour map of Airthrey Loch, prepared prior to the building of the University, enabled me to time birds diving to known depths. On several occasions, dives were timed at each of two places in the loch where there was a uniform depth over an area at least 15m in diameter.

In the statistical analysis the object has been to show trends in the data and I have therefore not attempted to fit complex mathematical expressions to the data, e.g. body weight and fat weight, body weight and pectoralis weight, since these could be misleading.

Regression analyses were used where it was appropriate or necessary to quantify relationships e.g. the daily weight loss during incubation.

The standard deviation (SD) or standard error of the mean (SE) are indicated on tables and the results of tests of significance denoted thus: $p<0.05$ - *; $p<0.01$ - **; $p<0.001$ - ***.

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3 FOOD AND FEEDING

To recapitulate, the initial aim of this feeding study was to determine the diet of the Tufted Duck at Loch Leven, but comparative data were also obtained from Airthrey Loch, and for other diving ducks (Goldeneye Bucephala clangula and Pochard Aythya ferina) at Loch Leven. Birds were collected at all seasons and not, as in previous published studies, just in the shooting season (September to January). There are few published data on how food is obtained by Tufted Duck, presumably as a consequence of its diving habits and of its predilection to feed at night. However, some information is available on feeding behaviour of the closely related Lesser Scaup in North America (Goodman and Fisher, 1962).

Structural features

The bill and tongue of the Tufted Duck form a complex feeding organ; the front half of the upper mandible is slightly expanded and overlaps the lower mandible by up to 4mm on either side (Fig. 2). No difference between males and females was apparent in culmen length, but they differed significantly ($p < 0.05$) in culmen width (Table 1). In the same birds sternum length and wing length showed highly significant differences ($p < 0.001$) between the sexes. There were no differences in bill structure between the sexes, and so no differences in feeding habits would be expected.

The opposing edges of each mandible have lamellae (A) along their full length (Fig. 2b). The sharp nail on the upper mandible (B) can oppose or pass the flat tip of the lower jaw (Fig. 2a) but is capable of only a weak bite due to poor mechanical advantage and weak

FIGURE 2. Bill of the Tufted Duck (a) from side to indicate overlap of the upper mandible - actual size: (b) from below to indicate overlap and gap between the upper and lower mandible when closed - x2.

(a)

(b)

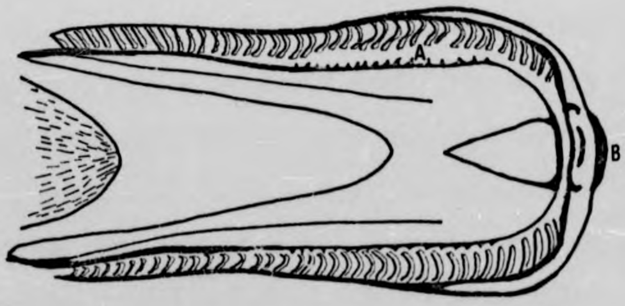

TABLE 1. Bill and body measurements, mean (SE), of male and female adult Tufted Ducks. Values which differed significantly between the sexes are indicated: * $p<0.05$, *** $p<0.001$.

	MALES (n=20)	SIGNIFICANCE	FEMALES (n=50)
Culmen length (mm)	38.83 (0.35)	N.S.	38.90 (0.20)
Culmen width (mm)	22.45 (0.16)	*	22.12 (0.10)
Sternum length (mm)	84.8 (0.50)	***	82.6 (0.25)
Wing length (mm)	209.8 (1.20)	***	204.1 (0.61)

adductor muscle. (This feature was also observed in the Lesser Scaup, which had considerable difficulty in removing the kernels of corn from a dry cob (Goodman and Fisher, 1962).) The tip of the tongue (C) is wedge shaped and flexible, and along the sides of the front half are a series of overlapping flaps (D) fringed with fine bristles (Fig. 3). The posterior half of the tongue has a muscular raised portion (E) with weak forward pointing bristles on the front edge and a double row of backward projecting spikes (G) on the rear edge, which cover the glottis when the tongue is retracted. Below this portion on each side are 4 strong projections (H) pointing upwards and outwards.

Feeding behaviour

The characteristic method of feeding in the Tufted Duck, as in other diving ducks, is by complete submergence to gather material from underwater. Observations on captive ducklings showed that from their first introduction to water at one day old, they could all dive to the bottom (750mm) of the tank, although at this stage they preferred to take food from the surface. This they did by swimming after and pecking at individual items. The feeding behaviour which I shall describe was of birds which were three-quarters grown. The tank was rather small for adult birds which could do little more than upend, and their attempts to maintain this position caused too much turbulence for any observations to be made. I have, however, no reason to believe that the juveniles studied were not already using the adult method of feeding.

While feeding, a bird maintained its position at 45° to the bottom by paddling its feet (Fig. 4). The bill was held about 20mm

FIGURE 3. Tongue of the Tufted Duck showing the suggested pathways of water during feeding. (a) Tongue from side - approx. x2 (b) Tongue from above - approx. x2

(1) First inspiration water enters bill tip below tongue.

(2) Water strained by flaps (D) at side of tongue on downstroke.

(3) Second inspiration forces water above tongue out of the sides of the bill.

Full explanation of lettering is in text.

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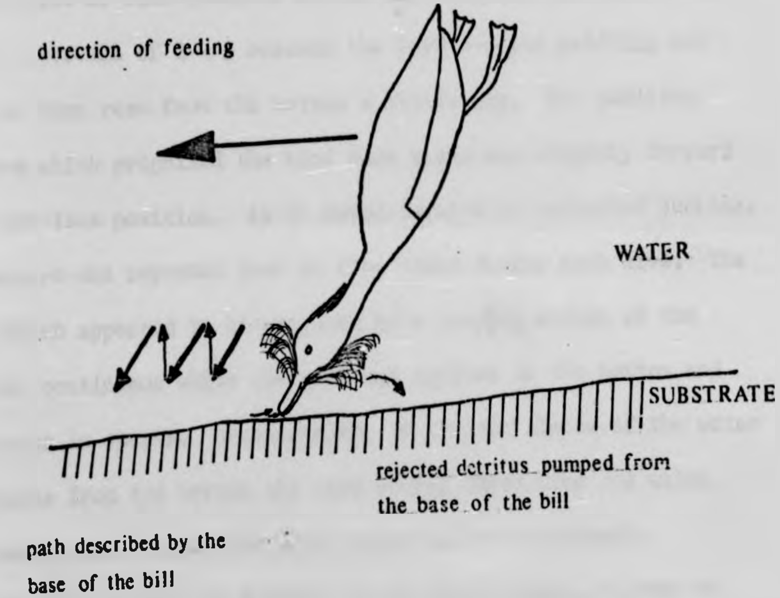
FIGURE 4. Feeding behaviour of a Tufted Duck during a dive.


direction of feeding
WATER
SUBSTRATE
rejected detritus pumped from the base of the bill
path described by the base of the bill

from the bottom and there was a continuous strong sucking action, which was indicated by the movement of grains of barley and other particles along the bottom of the tank and into the tip of the slightly open bill. In Lesser Scaup the bill opening mainly resulted from protraction of the upper mandible (Goodman and Fisher, 1962) and this was also the case in Tufted Duck. During feeding there was a continuous flow of fine detritus out of the sides of the bill at the back. At intervals of 2 - 3 seconds the bird stopped paddling and sucking; it then rose from the bottom a little way. The paddling recommenced which propelled the bird down again and slightly forward from its previous position. As it moved forward it restarted sucking. This procedure was repeated four or five times during each dive. The sucking, which appeared to be produced by a pumping action of the tongue, was continuous while the bill was applied to the bottom and did not occur in spurts. Occasionally, if the turbulence of the water lifted grains from the bottom the bird pecked these from the water column, turning its beak in whichever direction was necessary. However the Tufted Duck was similar to the Lesser Scaup, in that it appeared to prefer filtering to pecking.

The precise manner in which the complex structures of the bill and tongue were used to select and retain food could not be observed directly, but examination of the structures involved suggested a possible way in which they operate (Fig.3). As the tongue is raised water will enter the space below it through the tip of the bill (1). On the return stroke the lateral flaps will allow water to flow past the tongue (2), and at the same time retain large particles. During the next inspiration, water above the tongue will close the flaps and therefore be forced out of the rear of the mouth (3). Hence the apparently continuous stream of water which was observed entering and leaving the bill. From observations it was not clear when the bird swallowed, but presumably this occurred in the short period between bouts of paddling and sucking, during the dive.

By adjusting the size of the gape and the positions of the lateral flaps the duck could select and retain food items of a particular size. It was particularly noticeable when examining the stomach contents that most of the items in any one bird were of a similar size, but that this size varied from bird to bird. Even the grit in the gizzard was a uniform size and in this case, as when small plant seeds are eaten, the bird must be closing its gape to prevent entry of larger particles present on the bottom.

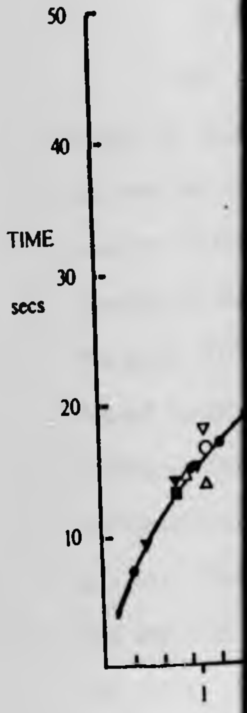
Feeding Depth

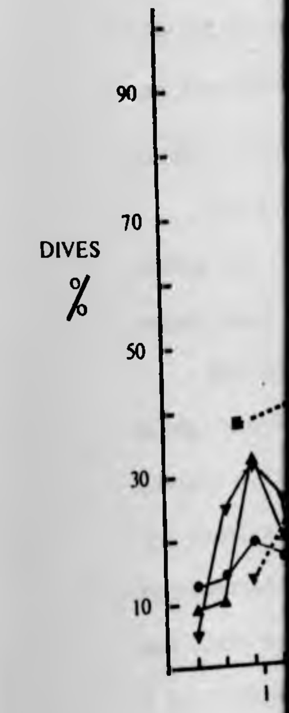
The depth to which the Tufted Duck can dive must presumably limit the feeding area available to it. Dewar (1924) investigated the diving ability of the Tufted and other diving duck species, by timing the periods of submergence in various depths of water, together with the intervals between dives. The few observations which I made were used to check Dewar's data. The average submergence times at Airthrey Loch were; 20.5 s (SD 1.1, n = 62) at six feet (1.83m) and 29.7 s (SD 1.4, n = 54) at 12 feet (3.66m). These two values are shown on figure 5 which was plotted from Dewar's data on several species. Also included in this figure are recent published figures for diving times of ducks. The data from all sources are similar and show that the relationship between diving time and water depth is consistent for the four species of diving ducks observed.

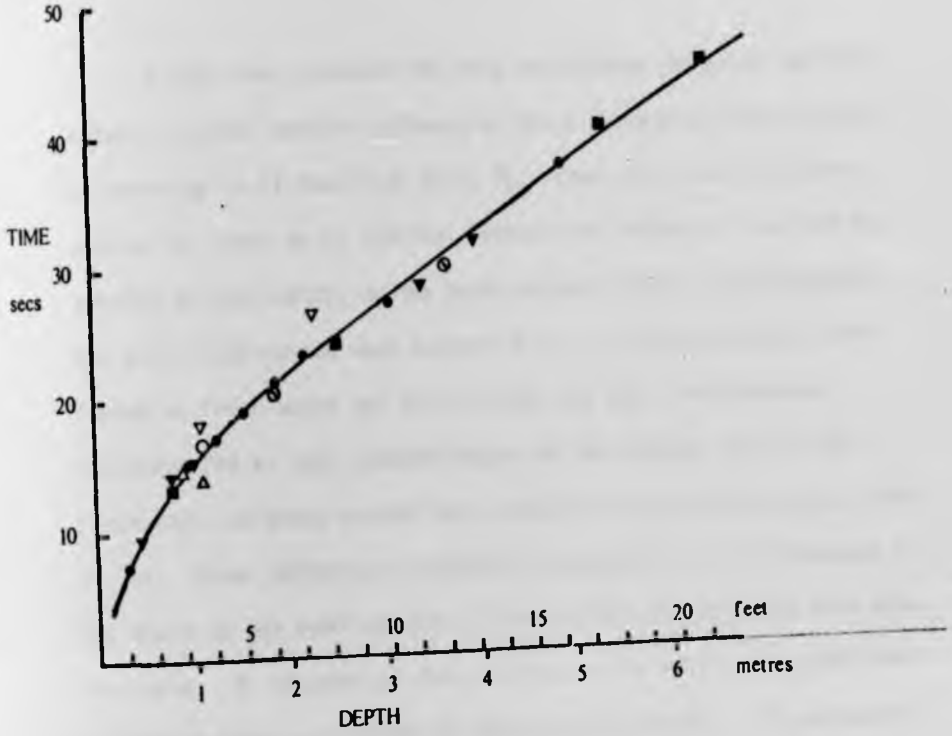
FIGURE 5. Relationship between depth and dive time in several species of diving ducks.

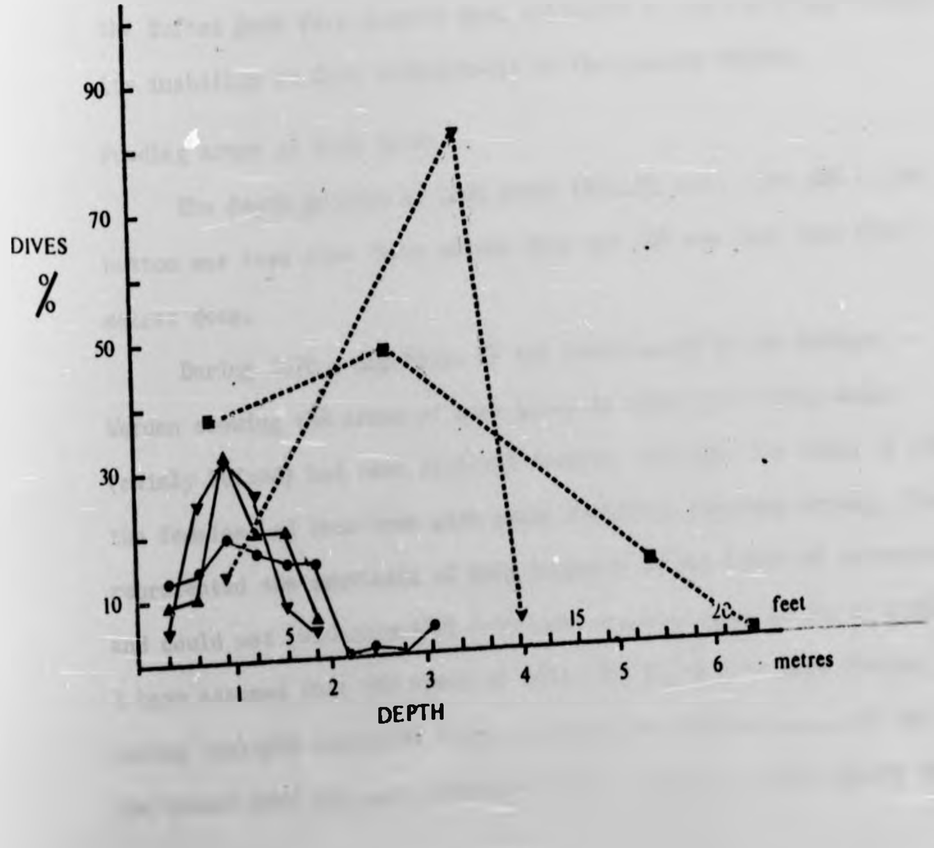
●	Tufted Duck	(Dewar, 1924)
⊖	Tufted Duck	(present author)
■	Scaup	(Dewar, 1924)
▼	Goldeneye	" "
▽	Goldeneye	(Nilsson, 1969)
△	Pochard	(Olney, 1969; Klima, 1966)

FIGURE 6. Percentage of dives to different depths by four duck species (drawn from data in Dewar, 1924). (●) Tufted Duck, (▼) Goldeneye, (▲) Pochard, (■) Scaup. Solid lines at freshwater site, dashed on the Forth Estuary.






50
40
TIME
secs
30
20
10
5
10
15
20
feet
1
2
3
4
5
6
metres
DEPTH


90
70
DIVES
%
50
30
10
5
15
20
feet
1
2
3
4
5
6
metres
DEPTH

I have also collated the data which Dewar presented on the extent to which species differed in their preferred diving depths, in water up to 21 feet (6m) (Fig. 6). These data were for three species in fresh water (Tufted, Pochard and Goldeneye) and for two species in salt water, on the Forth estuary (Scaup and Goldeneye). The major differences were between sites, all three species overlapped in fresh water and did not show any depth preferences. Goldeneye fed at much greater depths in the estuary than in the freshwater and Scaup ranged very widely in their feeding depth, from 1 - 6m. These differences presumably occurred due to differences in the depth of the food resource, which on the estuary would vary with the tides. It is possible that feeding on the estuary required the ability to dive efficiently to these greater depths. The absence of the Tufted Duck from Dewar's data collected on the Forth may indicate its inability to dive consistently to the greater depths.

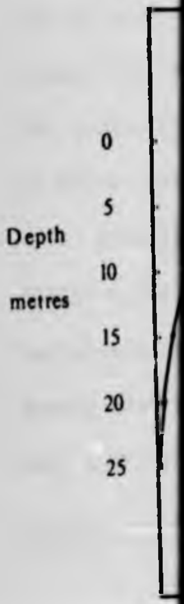
Feeding areas at Loch Leven

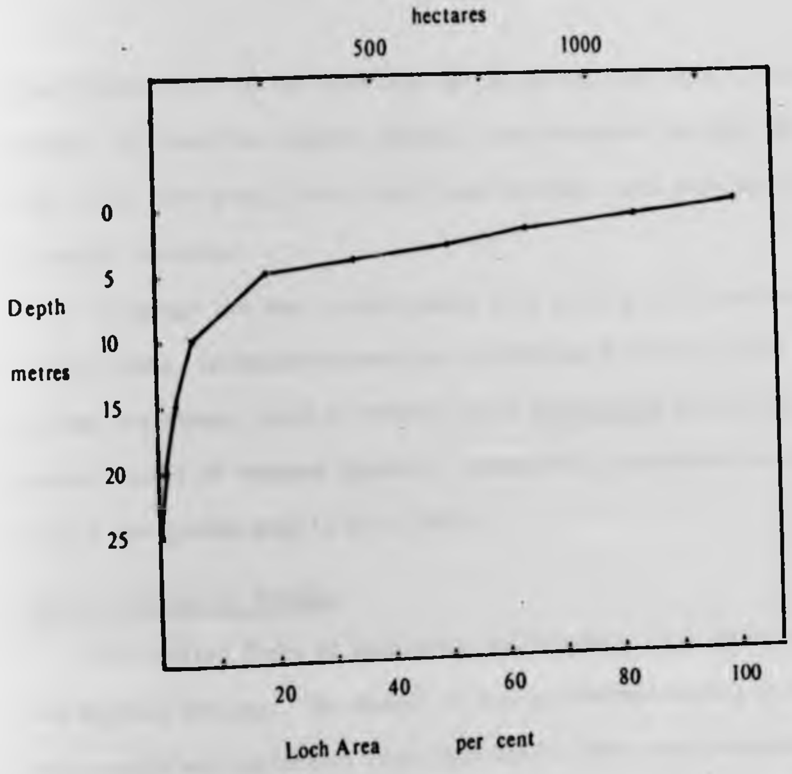
The depth profile at Loch Leven (Fig.7) shows that 50% of the bottom was less than three metres deep and 80% was less than five metres deep.

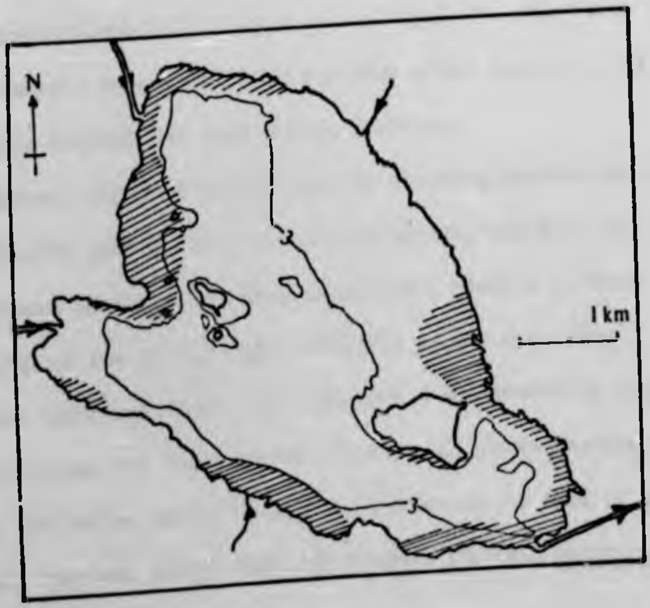
During 1970 a map (Fig. 8) was constructed by the Reserve Warden showing the areas of Loch Leven in which the diving ducks (mainly Tufted) had been observed feeding, and also the areas in which the females had been seen with young ducklings (nursery areas). This represented the synthesis of many hundreds of man-hours of observation and could not (economically) have been improved upon during my study. I have assumed that the areas in which the birds were seen feeding during daylight were also those in which they fed at night and that the latter were not more extensive. From this map, I calculated that

FIGURE 7. Area - depth curve for Loch Leven (from Smith, 1974)

FIGURE 8. Loch Leven showing 3m depth contour and the principal feeding areas of diving ducks (mainly Tufted).




hectares
500
1000
0
5
10
15
20
25
Depth
metres
20
40
60
80
100
Loch Area
per cent


N
1 km

the maximum area of the loch used by all diving duck species was around 35%, and that regular feeding areas extended to only 20% of the total loch area. Nearly all these feeding areas were within the 3m depth contour.

Although the same general areas were used by all species of diving ducks, Goldeneye showed some preference for areas where the bottom was stony. Also in 1970-72, when Potomageton grew well, the autumn flocks of Pochard grazed it extensively, sometimes in water only a few inches deep (A & N, 1974).

Diurnal rhythm of feeding

The Tufted Ducks at Loch Leven and Airthrey Loch spent most of the daytime resting. The amount of diving observed during daylight hours would not contribute significantly to their food requirements. However, at Airthrey Loch I observed considerable activity just before dawn, with most of the birds diving repeatedly. Further evidence that the study populations fed at night was that (a) the only birds that had full stomachs were shot within one hour after dawn and, (b) the birds usually entered the traps during darkness.

In winter, birds collected from the shooting parties had usually been shot in the late morning or early afternoon, and only 15% of the 20 Tufted Ducks involved contained significant amounts of food. In contrast, 70% of the 37 Goldeneye collected at the same time by the same parties contained food. This suggests a difference in diurnal activities between the two species, with the Goldeneye feeding mainly by day and the Tufted mainly by night. Little can be said of the other diving species, except that the Pochard that ate Potomageton fed at least partly by day.

Gut contents

The samples taken from Tufted Ducks were grouped according to date and place of origin:

(1) 127 birds taken from Loch Leven between October 1968 and January 1971. These included:

(a) 107 birds collected during the period April to October (summer) - 37 were taken by shooting, 38 in the diving trap and 32 from the nest.

(b) 20 shot in the period November to March (winter).

(2) 32 birds shot at Loch Leven between April and October in 1966 and 1967 (the material from a preliminary study in the IBP programme, before my own).

(3) 26 birds from Airthrey Loch between November and March over the years 1968-71. 18 were taken by shooting and 8 in the diving trap.

(4) 10 'downy' ducklings, from a creche, netted on the water at Loch Leven in July 1969.

The comparative gut material from other duck species was from 37 Goldeneye, 6 Pochard and 1 Scaup, all taken at Loch Leven during the 1968-1970 shooting season (September to January). The gut contents of the Scaup from Leith had all been removed.

The results are presented according to (a) the frequency of occurrence of different items (table 2) and (b) the proportion of birds which had taken each food item as a 'main meal' (table 3). The two studies carried out at Loch Leven during the period 1966-1971 showed no differences in the summer (April to October) foods from year to year; I have therefore considered the results together.

The food of the Tufted Duck from Loch Leven was almost entirely animal in origin. A variety of invertebrates was found, but chironomid larvae, of 4-16mm length, predominated. These larvae were also

TABLE 2. Numbers of birds in which specific food item occurred. Data were separated into summer and winter samples at Loch Leven. Only a winter sample was available at Airthrey.

	LOCH LEVEN.		AIRTHREY LOCH.
	Summer	Winter	Winter
TOTAL NUMBER	107	20	26
EMPTY	42 (40%)	6 (29%)	5 (19%)
Chironomid larvae	36	5	9
" pupae	6		
Dipteran adults	13		1
Trichoptera (Caddis)	15	2	1
Coleoptera	4		
Hymenoptera (Ants)	3		
Siphonaptera (Fleas)	2		
Arachnids	9		
Mollusca			
Valvata sp.	14	2	
Limnea sp.	1	1	
Planorbis sp.	2		
Pisidium sp.	7	1	
Crustacea			
Asellus		2	
Annelida			
Hirudinea (Leeches)	1	1	
Nematoda (Parasitic?)	10	3	4
Plant Debris	33	3	6
Seeds of			
Polygonum sp.	10	5	13
Potamogeton spp.	8	5	12
Hippuris sp.	3	1	9
Eleocharis sp.			1
Ranunculus sp.			1

TABLE 3. Numbers of birds in which food item formed the "main meal". In some birds the main meal was split between two items.

	LOCH LEVEN.		AIRTHREY LOCH.
	Summer	Winter	Winter
TOTAL	107	20	26
EMPTY	42	6	5
"MAIN MEAL" not obvious	20	11	6
Chironomid larvae	26	1	2½
Dipteran adults	3		
Trichoptera	7		1
Coleoptera	1		
Mollusca			
Valvata sp.	1		
Limnea sp.	1		
Crustacea			
Asellus sp.		1	
Plant debris	2	1	1½
Seeds			
Polygonum sp.	2		5
Potomageton sp.	2		4
Hippuris sp.			1

the most important food items found in the other diving ducks at Loch Leven; but plant foods predominated in the gut contents of Tufted Duck from Airthrey Loch.

In Tufted from Loch Leven, chironomid larvae were found in 55% of the stomachs containing food, and made up more than 50% of the food by volume or 'main meal'. Caddis larvae (Trichoptera) and molluscs were each found in 20% of birds. Caddis, however, were the more important on the basis of volume or 'main meal', forming up to 15% of the summer diet as against 4% for molluscs. None of the molluscs found in duck stomachs at Loch Leven were larger than 3mm across the longest axis.

Plant material was less important; in the 1967 study it comprised less than 25% of the gut contents by volume and in my own study only six birds (6%) were considered to have taken a 'main meal' of plant material. In many of the birds examined, the small plant fragments appeared to have been ingested incidentally as detritus with the food.

Birds taken during the summer from 1968-1971 included 32 females captured on the nest. In eight of these the gut was empty and a further nine contained only material of terrestrial origin, presumably picked off vegetation while the bird incubated. The remainder had only a few organisms in the gut, which lacked the normal muddy detritus and fine sand, suggesting infrequent feeding in water. Several birds had ingested down, presumably when plucking the breast to line the nest.

The two samples of birds collected during the winter, although small, showed distinct differences in the diet from the summer ones and between the two sites. As already mentioned, few of the Tufted Duck collected at Loch Leven in winter contained many food items, presumably because they were shot at the wrong time of day.

Plant and animal foods were of equal importance at Loch Leven in winter, but at Airthrey Loch plant foods predominated. Seeds occurred in 70% of the twenty-one stomachs and formed the main food in 47%. This difference between the sites reflects the relative scarcity of macrophytic vegetation at Loch Leven. Although chironomid larvae were found in birds from both sites in winter, they did not reach the same importance as at Loch Leven in summer.

Eleven of the 37 Goldeneye collected during winter were empty. The foods of the remaining 26 birds were predominantly animal: 88% of birds contained chironomid larvae, 27% caddis larvae and 23% Asellus sp. Plant debris occurred in negligible amounts and in only five birds, which suggested incidental rather than deliberate ingestion. Several birds contained enough material to determine main meals. Twelve (46%) were of chironomid larvae, 3 (12%) of Asellus sp. and one of caddis larvae.

Only one out of the six Pochard contained a significant amount of material, namely about 1000 chironomid larvae, 1 caddis, 2 molluscs and 2 leeches. The single Scaup contained 60 chironomid larvae and one Asellus sp. The significant point is that both individuals must have fed at Loch Leven or at another freshwater site, rather than on salt water, which is considered to be their main habitat in the Forth-Tay area in winter (Thom, 1969). They contained the same kinds of food as the Tufted Duck from Loch Leven.

The ten Tufted ducklings, all less than one week old, were taken between 07.00 and 08.00 hours. Chironomid larvae were present in seven, chironomid adults in five, while caddis, Hydracarina (mites) and Valvata sp. each occurred in only a single individual. No plant material was found in these ducklings and three were completely empty. The presence of chironomid adults suggests that the ducklings were feeding from the surface, as well as from beneath the water.

4 NUMBERS AND BREEDING SUCCESS

Seasonal and annual variations in numbers

Although the numbers of Tufted Duck at Loch Leven in any particular month varied between years (Fig. 1) the pattern was similar from year to year. In general, the overwintering population of less than 100 birds increased by late April to more than 1200. The apparent drop during the breeding season, May to mid-July, was due primarily to females being on nests and so missed during the counts. It was also possible that some birds which visited Loch Leven in spring then moved on to other waters. From mid-July the numbers increased, quite rapidly in some years (1966 and 1969), partly from breeding and partly from immigration, for many extra birds came to the loch to moult. The size and duration of this post-breeding peak varied from year to year. In 1967 no count after July exceeded 100 birds, but in 1966 and 1969 peak counts were around 2500 birds, and in 1969 the peak remained longer. In all years except 1970, the population had fallen below 250 by mid-October. The peak numbers in 1970 were exceptional (over 4000 birds in early September) and these birds remained on the loch for much longer than usual. Over 500 birds were counted in mid-November.

From five years of counts, I determined the average number of Tufted Ducks at Loch Leven in each month, excluding the months August to November 1970, which were treated separately. In May, June and July, allowance was made for incubating females on nests. These average population figures were used to calculate the number of bird-days, $\bar{N}T$, on the loch through the year. This figure was 314,000 in most years, but in 1970 an additional 124,500 bird-days were spent on the loch, an increase of 40% over the average for earlier years.

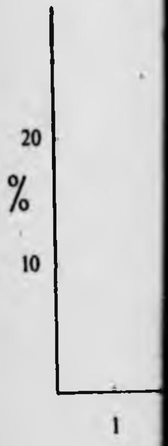
In 1969, when nest searches were most complete, 485 Tufted Duck nests were found on St Serf's Island. Allowing for nests on other islands and those not found on St Serf's, the breeding population of Tufted Duck at Loch Leven was assumed to be between 500 and 550 pairs. There was no evidence of any substantial changes during this study, so for subsequent calculations I have taken the figure as 525 nests.

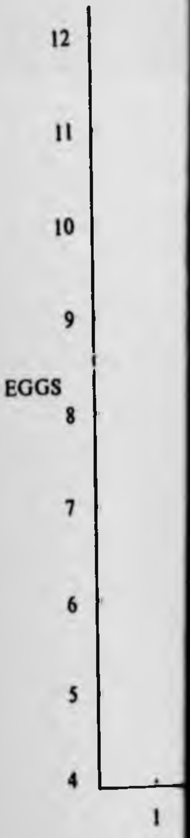
Laying season and seasonal trends

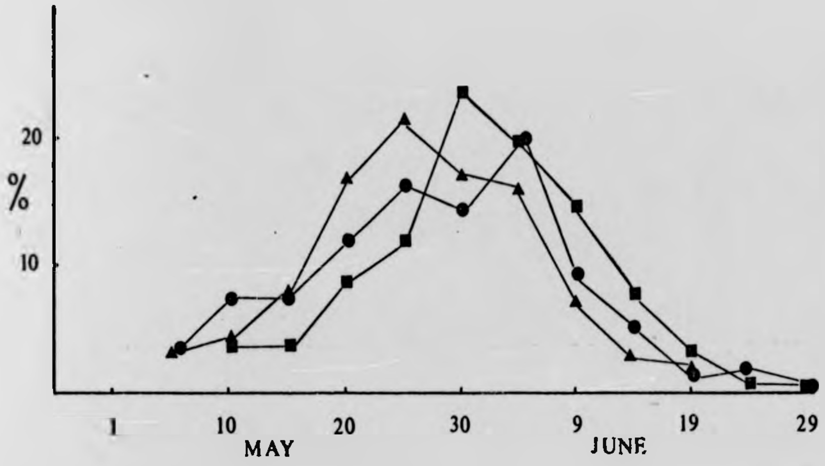
The first clutches were started in the period 1-5 May in 1968 and 1970, and in 6-10 May in 1969. The last clutches were started between 15-19 June in 1968 and 25-29 June in 1969 and 1970. Since incubation took 24 d, nests were active until well into July. The apparently shorter season in 1968 may have resulted from reduced efficiency of nest searching, since the total number of nests found in that year (177) was only about half the number found in subsequent years (315 and 395). In all three years, most birds (75%) started to lay between 16 May and 9 June, and the pattern of clutch initiation was similar from year to year (Fig. 9). Mean clutch size decreased through the season from 11 eggs at the start to 6 eggs at the end (Fig. 10 Table 4). The decline was slow in the first month (0.36 eggs per week) but more rapid in the second (0.90 eggs per week). The changes were similar in all years, the regressions of mean clutch size for each five day period in the season upon time in the season were not significantly different between years in either month, but the pooled data for all years gave significantly different regressions between months ($t = 2.77$, d.f.31; $p<0.01$) (Table 4). The mean clutch

FIGURE 9. Distribution of first egg laying in 5d periods – as % of total clutches started in each of three years.

FIGURE 10. Seasonal decline in mean clutch size for 3 years.







20
%
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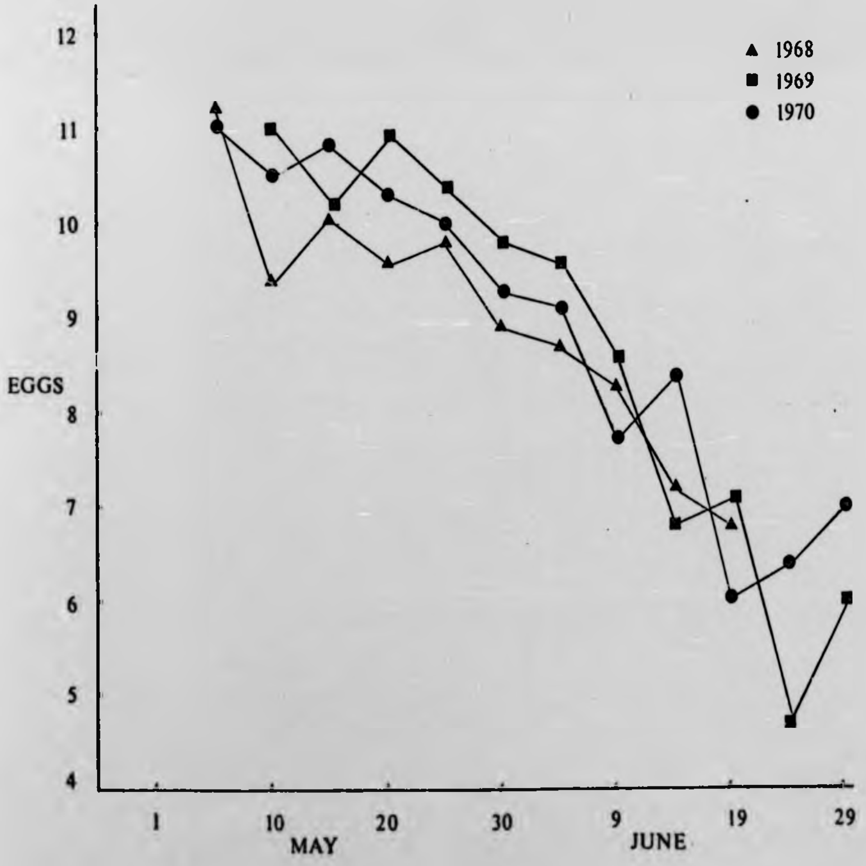
1
10
20
30
9
19
29
MAY
JUNE



▲ 1968
■ 1969
● 1970
12
11
10
9
EGGS
8
7
6
5
4
1
10
20
30
9
19
29
MAY
JUNE

TABLE 4. Mean clutch size in Tufted Ducks, and number (%) of clutches started in each 5 day period through 3 years.

					M A Y			:		J U N E			
		1–5	6–10	11–15	16–20	21–25	26–30	31–4	5–9	10–14	15–19	20–24	25–29
	No. of 5 day period, x	1	2	3	4	5	6	7	8	9	10	11	12
1968	MEAN CLUTCH SIZE – $\overline{y}$ (SE)	11.33 0.76	9.50 .35	10.14 0.49	9.57 0.29	9.79 0.34	8.90 0.31	8.72 0.29	8.25 0.29	7.20 0.33	6.75 0.38		
	NUMBER OF CLUTCHES STARTED (% of TOTAL CLUTCHES [n as %N])	6(3.5)	8(4.5)	14(8.0)	30(17.0)	38(21.5)	31(17.5)	29(16.0)	12(7.0)	5(3.0)	4(2.0)		
1969	$\overline{y}$ SE n (n as %N)		11.00 0.75 9(4.0)	10.22 0.72 9(4.0)	10.91 0.39 26(9.0)	10.43 0.35 30(12.0)	9.84 0.25 57(23.5)	9.458 0.31 48(20.0)	8.59 0.31 37(15.0)	6.84 0.33 19(8.0)	7.13 0.40 8(3.5)	4.60 0.88 3(-)	6.00 1.00 2(-)
1970	$\overline{y}$ SE n (n as %N)	11.0 0.53 9(3.4)	10.58 0.48 20(7.6)	10.89 0.49 19(7.2)	10.81 0.38 31(11.8)	10.00 0.26 42(16.0)	9.58 0.32 40(15.2)	9.09 0.21 53(20.2)	7.68 0.27 25(9.5)	8.38 0.24 13(4.9)	6.00 1.35 4(1.5)	6.4 0.68 5(1.9)	7.0 — 2(0.8)

In May: $\overline{y} = 11.21 - 0.2605\,x$; $r = .651$, SE of $b = 0.0783$, $n = 17$

June: $\overline{y} = 13.32 - 0.6412\,x$; $r = .834$, SE of $b = 0.1132$, $n = 16$

TABLE 5. Mean clutch size of Tufted Duck in 3 years, 1968 - 70.

YEAR	CLUTCH SIZE	SD	SE	N
1968	9.24	1.50	.11	177
1969	9.40	1.88	.11	248
1970	9.56	1.75	.10	261

size over the whole season was about the same in all years (Table 5) and for subsequent energy calculations an average of 9.5 was taken.

From the data on clutch size and initiation dates, the cumulative frequency distribution of egg laying through the season was calculated (Fig. 11). This method of presentation smoothed out the minor fluctuations between years and the time at which 50% of the eggs were laid can be seen to have varied by only 2.5 d over the three years. In the 25 d between 16 May and 9 June, 80% of all eggs were laid.

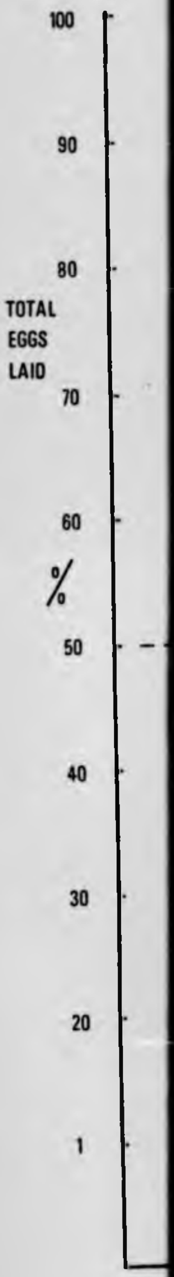
Breeding success and number of young produced

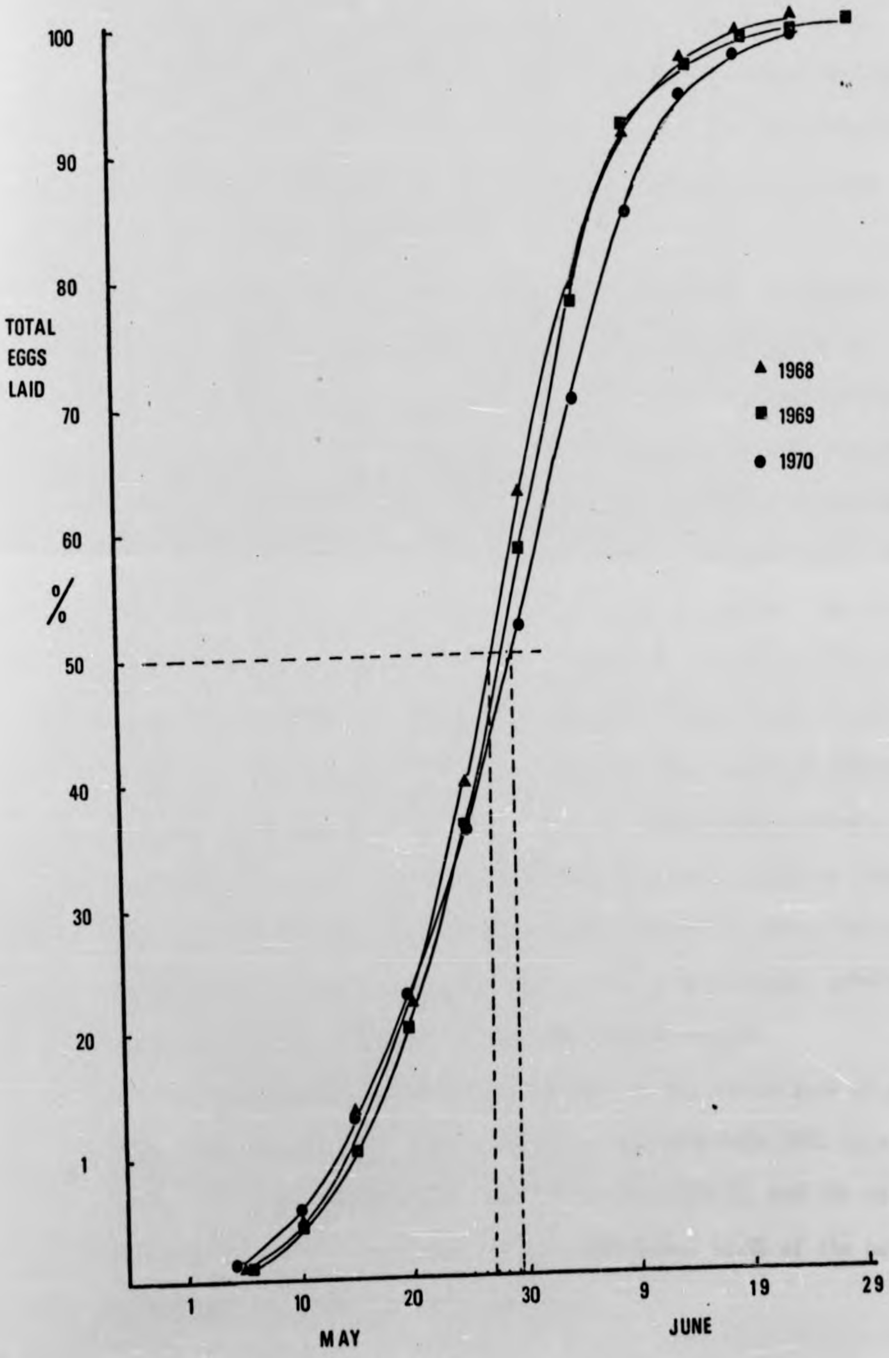
The main requirement of my study was an estimate of the number of young produced to fledging. It is appropriate, however, to include some data on breeding success and the nature of losses, because this is relevant to calculating an energy budget for the population and for an individual.

Assessment of nesting success at Loch Leven is complicated by the possible influence of the study programme itself, as discussed in considerable detail by Newton and Campbell (1975). Losses resulted from either desertion or predation. The main predators were Jackdaws Corvus monedula which, although unable to displace a duck from a nest, quickly took unguarded eggs whenever a duck left. Predation was therefore artificially increased when areas were searched during the study. Similarly, eggs left in the nest after hatch were quickly removed by predators and this precluded any determination of the proportion of eggs failing to hatch in successful nests.

In 1968-70, measured hatching success varied from 50% to 71% per annum, predation from 22% to 44% and desertion from 4% to 7%. The

FIGURE 11. Cumulative frequency distribution of eggs laid during each of three successive seasons. L_{50} = 50% of eggs laid. Spread of L_{50} only 2.5 days over three years.





100
90
80
70
60
50
40
30
20
1
TOTAL
EGGS
LAID
%
▲ 1968
■ 1969
● 1970
1
10
20
30
9
19
29
MAY
JUNE

average figures of six years of study, 1966-71 were 57% clutches hatched, 38% predated and 5% deserted (N & C, 1975). A general decline in success occurred through the season even though the human disturbance was constant. This seasonal decline was also observed in other duck species at Loch Leven and appeared to occur irrespective of predator numbers.

The sheer size of Loch Leven makes it difficult to assess duckling survival. In the early years, duckling production to fledging was thought to be very poor. Predation of young ducklings by Herring Gulls Larus argentatus was frequently observed, and predation by Pike Esox lucius was also seen occasionally. At the same time, large crèches of newly hatched ducklings were seen and at least once each year more than 500 of such young were counted. Too few birds were shot in winter to obtain meaningful age ratios, and in many years considerable immigration occurred, which would distort the figures on local production. An estimate of the number of ducklings fledged was necessary for calculating the overall energy budget; allowing for losses before fledging from the maximum numbers observed the figure taken was 350. Although this estimate is rather arbitrary, subsequent calculations showed that, at the levels likely, production of young was not important in the total energy budget.

In conclusion, total egg production by the Tufted Duck at Loch Leven was taken as 525 x 9.5 = 4987.5 or approximately 5000 eggs per year. Of these, on average, only 57% hatched (2840), and the estimated production of 350 fledged young represented 12.5% of the hatched ducklings, or 7% of the total eggs laid.

5 CARCASS COMPOSITION

This section concerns the changes in body composition which accompany changes in body weight. This information was necessary to determine changes in energy constant (ΔB) for calculating the energy budget of Tufted Duck. It is also of particular value in providing data on the use which the Tufted Duck makes of body reserves for breeding and for winter survival, and in the more general field of bird bioenergetics.

Data were obtained from 100 adult birds collected throughout the year, but I paid particular attention to breeding females.

Body weight

Body weights of adult Tufted Ducks taken in this study ranged from 500 to 970g (Fig. 12), the heaviest almost twice the weight of the lightest. Outside the breeding season weights in most months ranged over 200g. The heaviest males, up to 970g, were in December and January, although in the same months some birds weighed only 700g. In March the heaviest males were 850g, and no further decline in weight occurred until early May. Thereafter, the males lost weight quite rapidly, and in June most were around 700g. Outside the breeding season, the heaviest females, around 800g, also occurred in December and January. During the egg laying period some females exceeded 900g, but by the end of incubation, all were down to 500-650g. No significant differences in wing length occurred between winter and summer birds, indicating that these were not different sized birds (from different populations) present in mid Scotland at different seasons.

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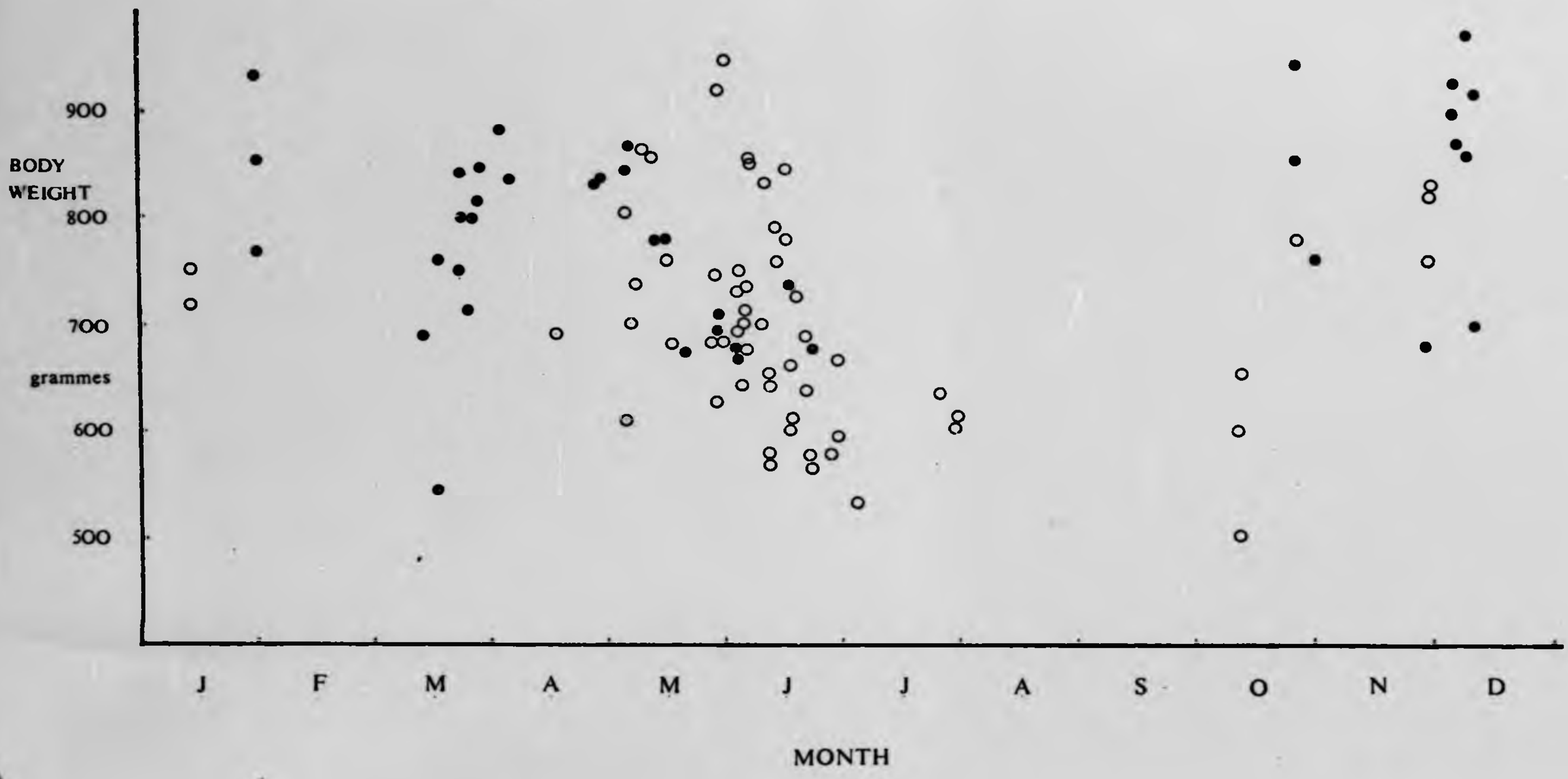
FIGURE 12. Body weight of adult Tufted Duck at different times of year

(● males, ○ females)


BODY
WEIGHT
grammes
900
800
700
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500
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F
M
A
M
J
J
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S
O
N
D
MONTH

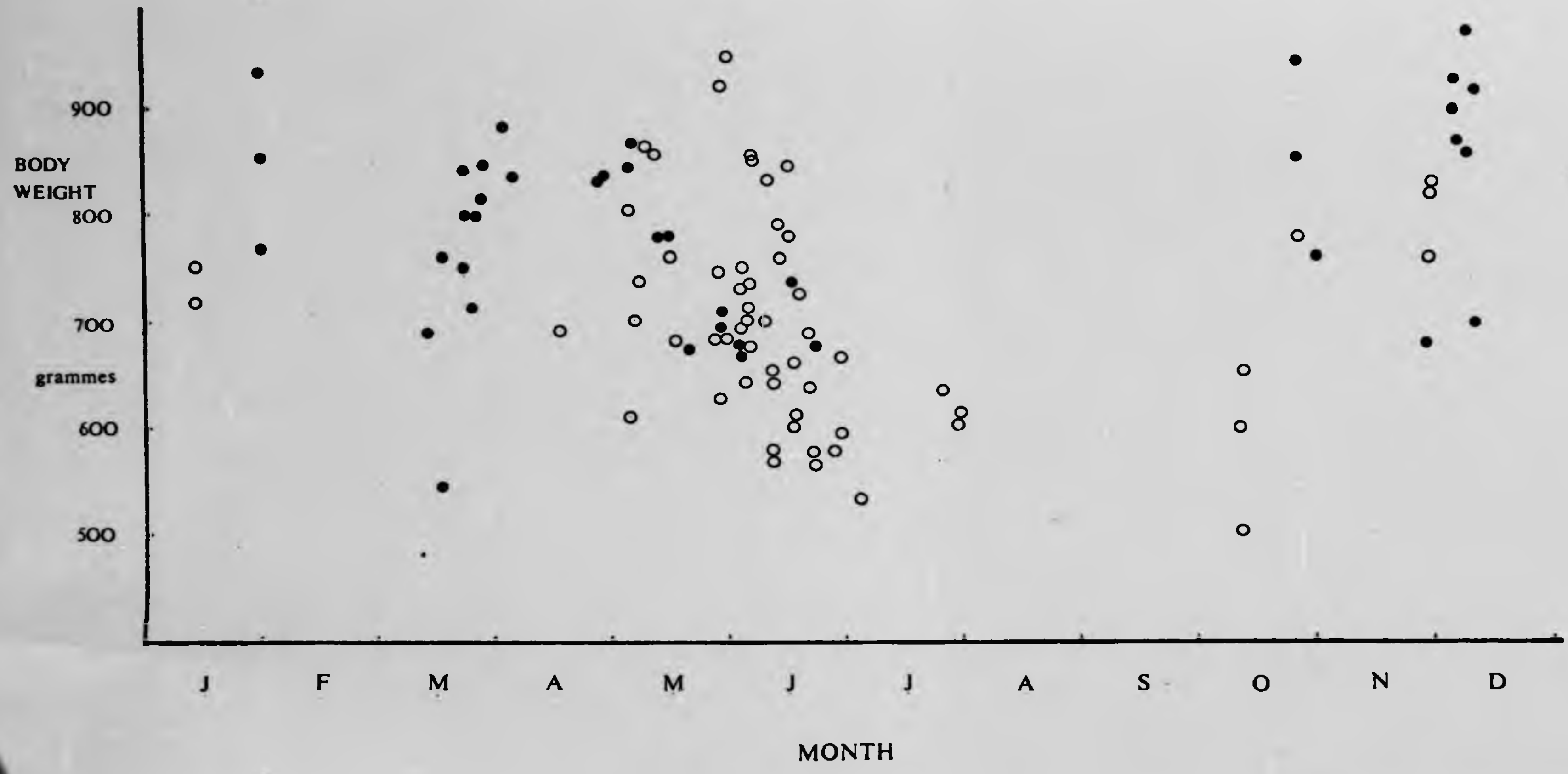

BODY WEIGHT grammes
900
800
700
600
500
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

TABLE 6. Weight loss during incubation calculated by regression analyses in female Tufted Duck.

	Weight at day 0 g	Wt. loss per day g	Correlation coefficient (r)	Number	Significance of r
Birds taken for analysis 1969 & 1970	739.7	6.03	0.607	29	***
Birds weighed in the field 1969					
HATCHED	720.9	6.15	0.640	27	***
FAILED	699.0	5.26	0.470	19	*
Birds weighed in the field 1970					
HATCHED	696.6	3.00	0.365	118	***

In 1969 enough birds were weighed both from nests which failed and from nests which hatched to allow separate analyses, but in 1970 insufficient birds from failed nests were weighed to allow separate analysis.

Weight changes during incubation were examined in four sets of data, three involving regression of weight against incubation time (Figs. 13, 15 and 16; Table 6) and the fourth from repeat weighings of individual birds. The data from birds weighed on the nest in 1969 were separated into two classes, those from nests which hatched successfully and those which failed (mainly from predation). The former lost 6.15g per day and the latter lost 5.25g per day, the two regressions were not significantly different ($t = 0.4726$) from each other or from that of birds taken for carcass analysis (6g per day). In 1970 only six nests from which females were weighed failed to hatch. The weight loss, calculated only from the successful nests, was only 3g per day and significantly different from the 1969 value ($t = 11.06$, $p < 0.001$). The initial weight of incubating females, predicted from the regression, varied between samples; those on nests which failed in 1969 (699g) were lighter than those on nests which hatched (721g), but in 1970 those on nests which hatched were even lighter (697g). During 1970 birds recaptured during incubation (40 pairs of weights) had a mean weight loss of 4g per day. In individual birds this change varied from - 18g to + 1.7g per day, the latter over only three days.

Apart from the post incubating females, two exceptionally light birds were taken at other times: a flightless female in moult, in early October, weighed only 502g, and a male shot in March weighed 550g but this bird had been previously wounded. These two birds provided useful information on the composition of low weight birds and helped to confirm that there was no difference between Tufted and Scaup in this respect.

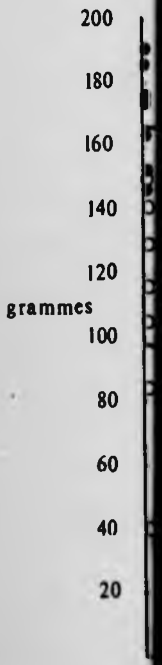
FIGURE 13. Body weight of female Tufted Duck in relation to stage of incubation.

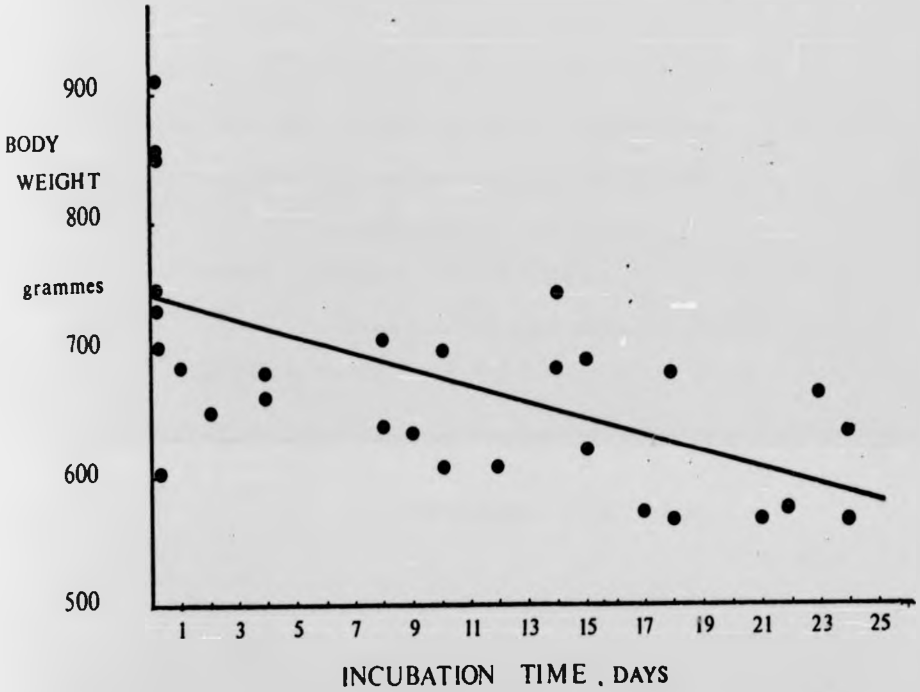
$W = 739.7 - 6.03d$ ($r = 0.607$)

FIGURE 14. Lean dry and fat components of the carcass of female Tufted Duck in relation to stage of incubation.

● Lean dry $W = 168.24 - 0.87d$ ($r = 0.508$)

○ Fat $W = 99.07 - 2.37d$ ($r = 0.557$)




900
BODY
WEIGHT
800
grammes
700
600
500
1
3
5
7
9
11
13
15
17
19
21
23
25
INCUBATION TIME . DAYS

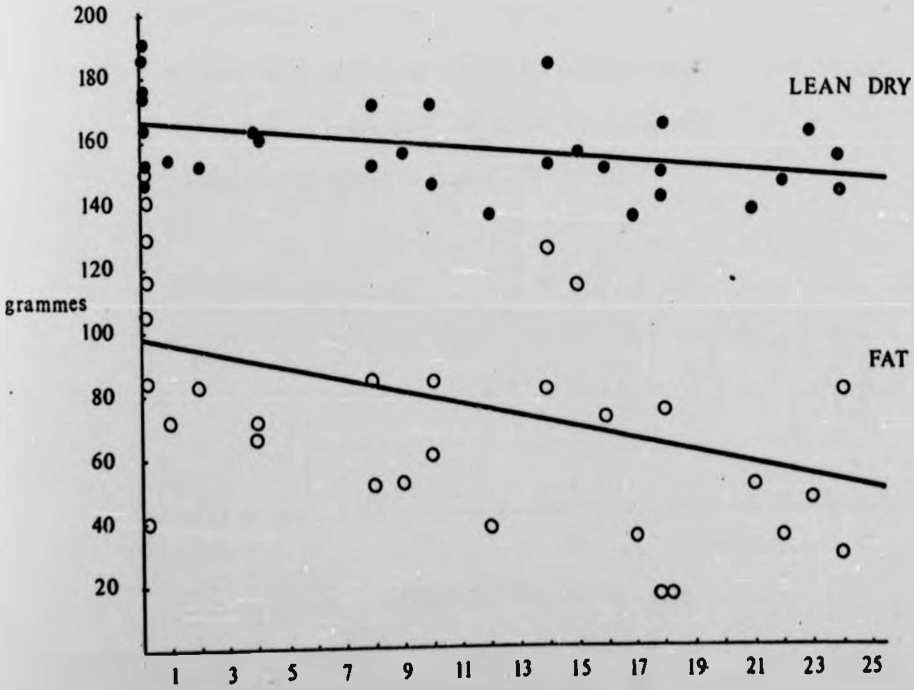

200
180
160
140
120
grammes
100
80
60
40
20
LEAN DRY
FAT
1
3
5
7
9
11
13
15
17
19
21
23
25

FIGURE 15. Body weights of captured Tufted Duck females in relation to stage of incubation - 1969.

o females from predated nests

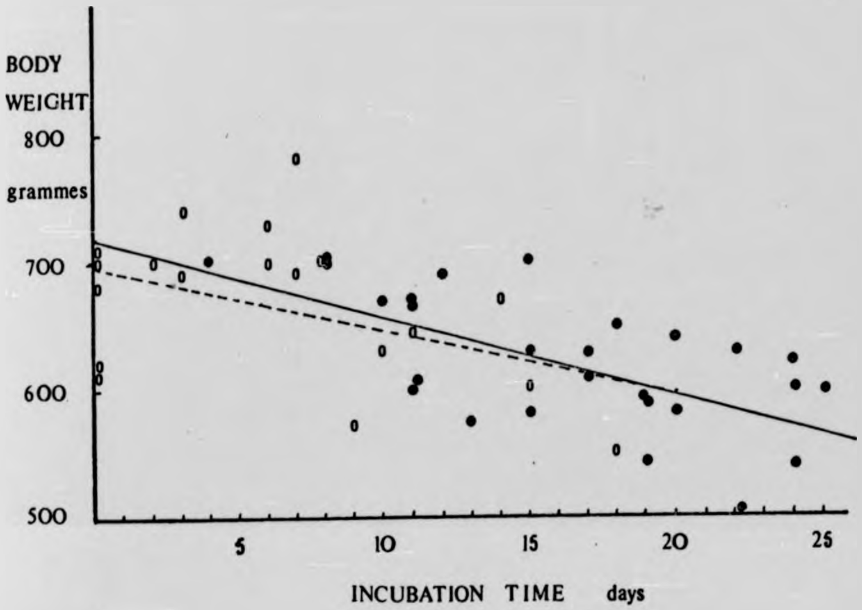
$$W = 699.0 - 5.26d \ (r = 0.470)$$

● females from hatched nests

$$W = 720.9 - 6.15d \ (r = 0.640)$$

FIGURE 16. Body weights of captured Tufted Duck females in relation to stage of incubation - 1970.

$$W = 696.6 - 3.00d \ (r = 0.365)$$


BODY
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grammes
800
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500
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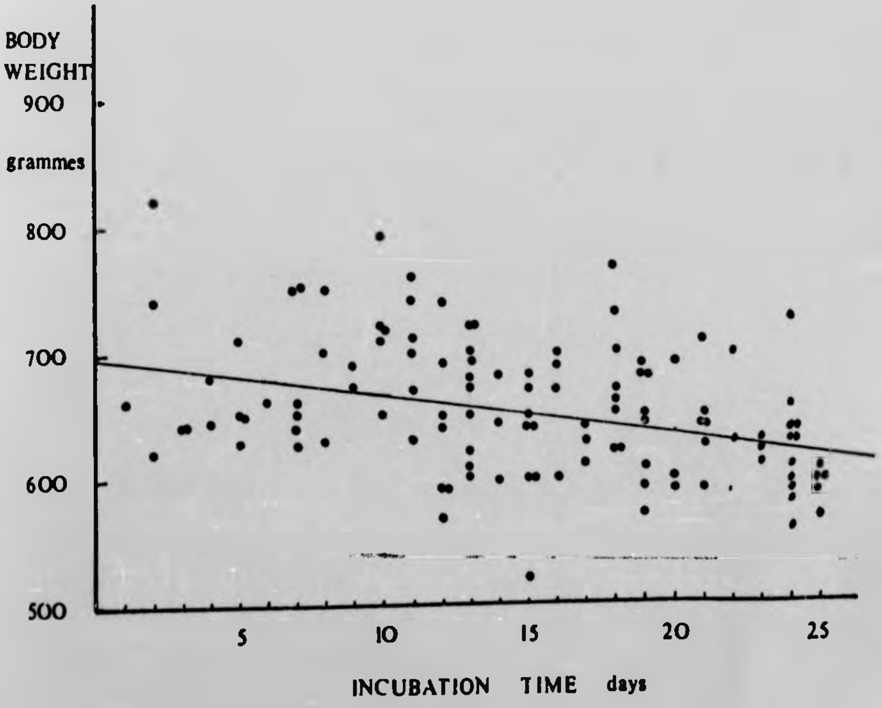
10
15
20
25
INCUBATION TIME days


BODY
WEIGHT
grammes
900
800
700
600
500
5
10
15
20
25
INCUBATION TIME days

The Scaup fell into three categories (Fig. 17). (1) Normal birds shot on the water weighed 1006-1435g, apart from a juvenile of 803g. (2) Birds found dead on the sea during the oiling incident weighed 471-1336g. (3) Birds which died at a rehabilitation centre through failure to feed weighed 406-758g. The smallest bird examined weighed 1000g less than the heaviest, only 28% of the latter's weight.

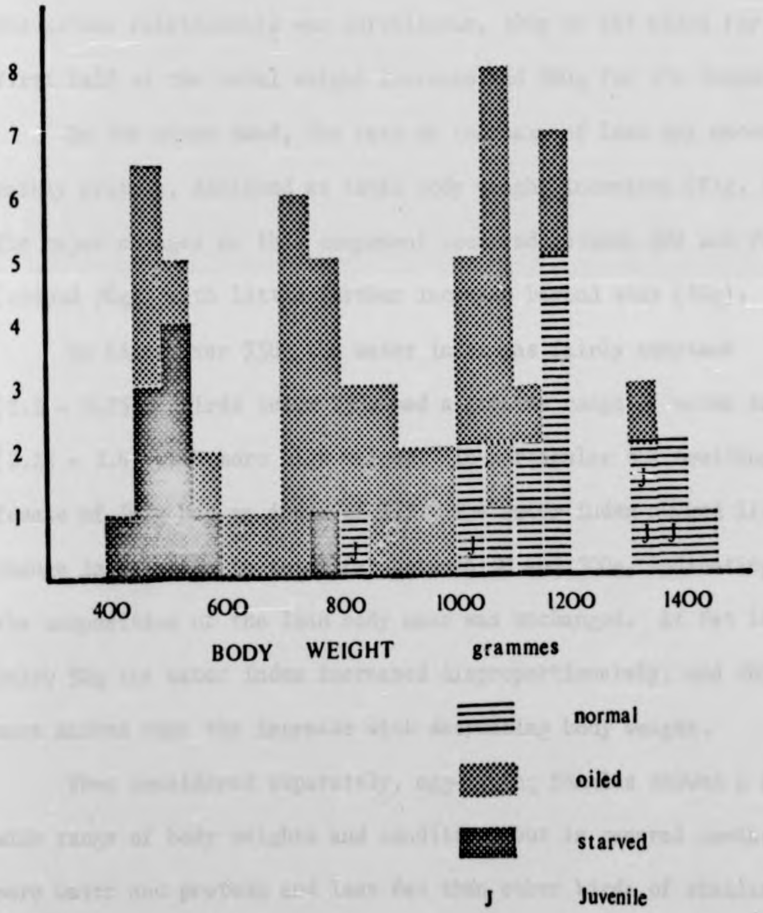
Carcass components

The plumage represented roughly 6% of total body weight but, since it did not change in relation to body weight, wide variations about this figure occurred. Data from small samples of birds showed that male breeding plumage in January to May (54.0g, SD 7.73, n = 9) was significantly heavier ($p < 0.001$) than the eclipse plumage (45.9g, SD 4.43, n = 9).

The lowest plumage weights were from females at the end of incubation. This resulted from the loss of down and breast feathers to expose the brood patches during incubation; this hormonally induced process is assisted in ducks by active removal of feathers to line the nest. In the moulting female which weighed only 502g, the plumage (55g) represented 11% of the total body weight. This was due partly to her low weight, but also to the high water content of the growing feathers.

In general, disregarding plumage, Tufted Ducks of similar weight had a similar carcass composition, irrespective of season (as was found in Bullfinches Pyrrhula pyrrhula by Newton (1969). Exceptions to this in Tufted Duck were the females taken during egg laying. These birds contained large ova and eggs which were removed and analysed separately, but the remaining carcass still had more water and lean dry material and less fat than other birds of comparable weight.

FIGURE 17. Distribution of weights of Scaup collected in this study.


8
7
6
5
4
3
2
1
400
600
800
1000
1200
1400
BODY WEIGHT grammes
J
J
J
J J
normal
oiled
starved
J Juvenile

Water accounted for half to two thirds of the total weight in Tufted Duck. The relationship between water and body weight (Fig. 18) appeared to be linear, although males exceeding 750g showed little further increase in water content.

The weight of fat and its proportion in the body increased from 10g (2%) in a 500g bird to 300g (31%) in a 970g one (Fig. 18). The actual relationship was curvilinear, 100g of fat added for the first half of the total weight increase and 200g for the second.

On the other hand, the rate of increase of lean dry material, mainly protein, declined as total body weight increased (Fig. 19). The major changes in this component occurred between 500 and 700g (around 70g), with little further increase beyond this (10g).

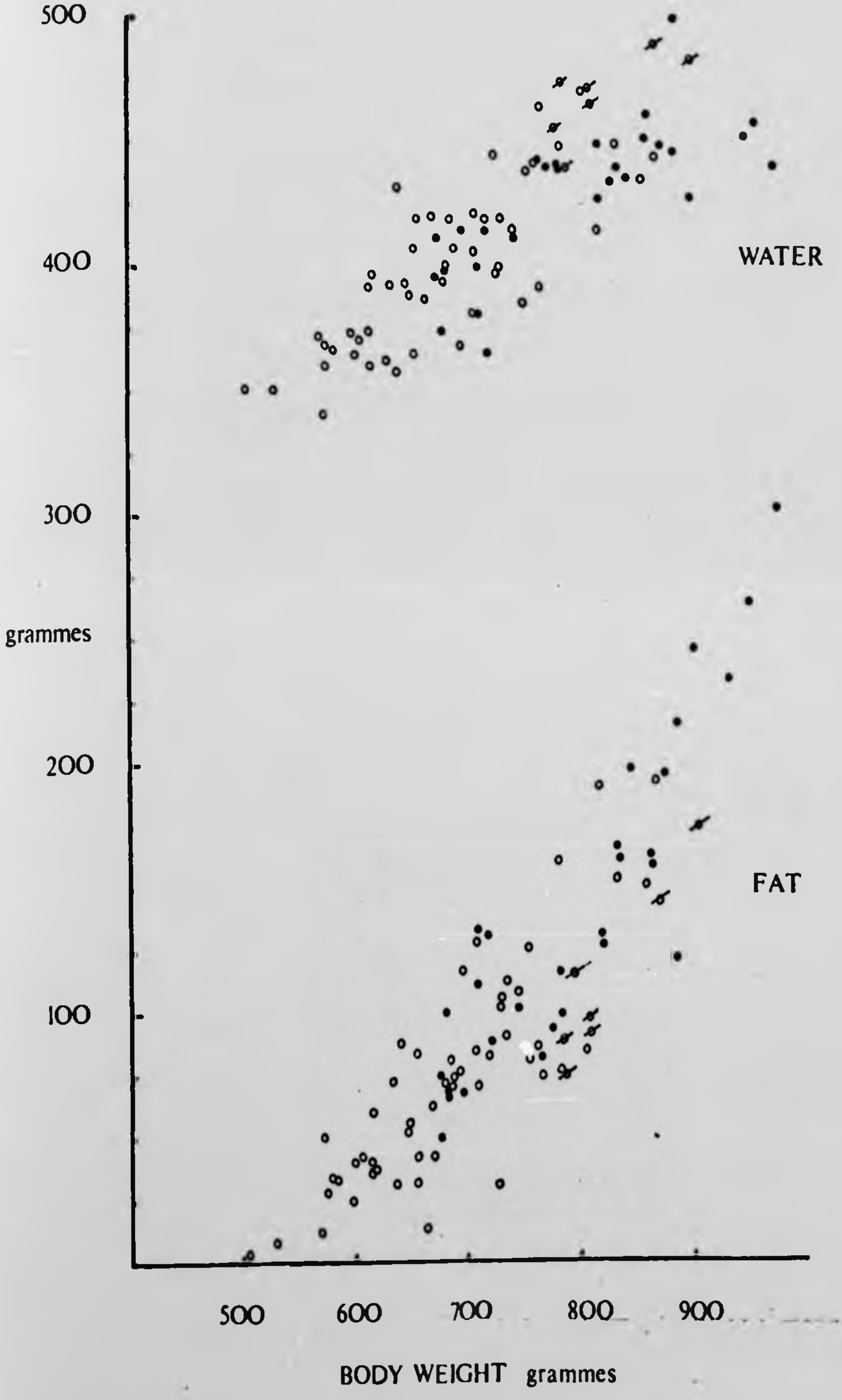
In birds over 750g the water index was fairly constant (2.3 - 2.75). Birds below 750g had a greater range of water index (2.25 - 2.9) with more high values. In particular the moulting female of 502g had an index of 3.7. The water index showed little change in relation to total fat between 50 and 300g, indicating that the composition of the lean body mass was unchanged. At fat levels below 50g the water index increased disproportionately, and this was more marked than the increase with decreasing body weight.

When considered separately, egg-laying females showed a fairly wide range of body weights and condition, but in general contained more water and protein and less fat than other birds of similar weight. The lean dry material was remarkably constant, with six of the seven birds having between 178 and 181g, and the seventh 193g. Despite the relatively high lean dry weights these birds also tended towards higher water indices than the average for their weight. The major

FIGURE 18. Relationship of water and fat components to total body weight in the adult Tufted Duck.

● males, ○ females, ∅ egglaying females.

tal

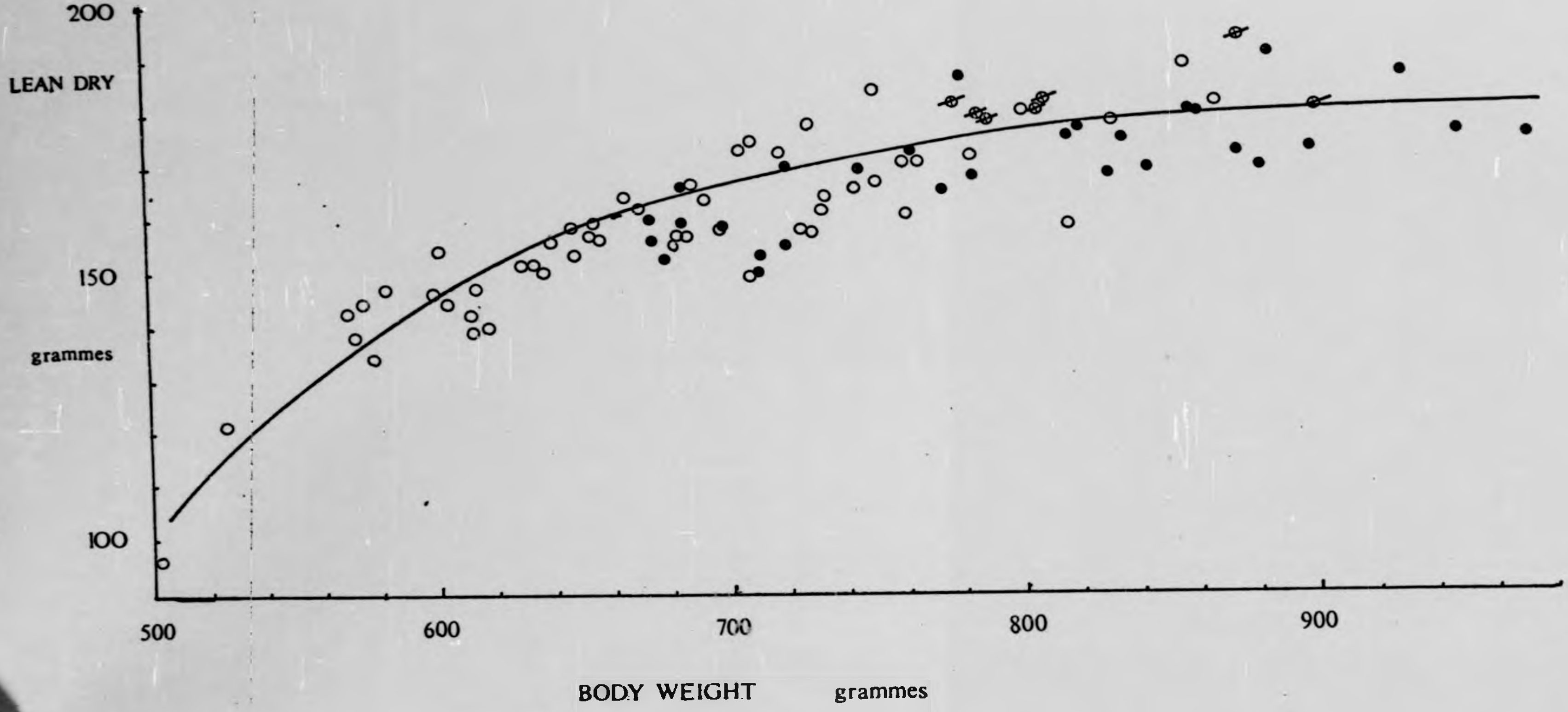


500
400
300
grammes
200
100
WATER
FAT
500
600
700
800
900
BODY WEIGHT grammes

FIGURE 19. Relationship between lean dry material and total body weight in adult Tufted Duck.

● males, ○ females, ø egglaying females.

total


200
LEAN DRY
150
grammes
100
500
600
700
800
900
BODY WEIGHT grammes

variation between the birds was in the amount of fat, a difference of 100g between extremes.

The 6g daily weight loss in incubating birds that were analysed was composed of 0.87g lean dry material, 2.37g of fat and 2.79g water (Fig. 14). These are mean figures calculated by regression for the period as a whole.

Pectoralis muscle

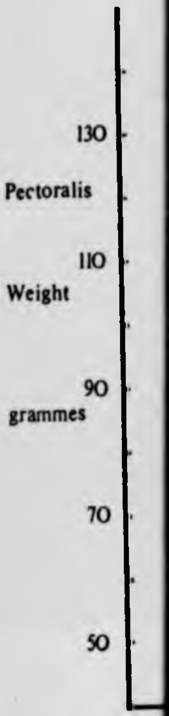
In considering the pectoralis muscle, I have examined its weight in respect to total body weight to find whether this relationship varies with the condition of the bird. Pectoralis weight and body weight were linearly related over the normal body weight range in adults of both sexes (Fig. 20), but the relationship with pectoralis as a percentage of body weight was negative; the pectoralis represented proportionately less of the total body weight in the heavier birds (Fig. 21). Three birds of low body weight had pectoralis weights below those which would be predicted by the trend in normal birds. During incubation females lost around 30g (wet weight) from the pectoralis but all maintained their pectoralis weight above the median for birds weighing less than 700g (Fig.20), and the muscle represented a relatively high proportion of body weight (around 18%) throughout incubation (Fig. 22). Thus although the muscle provided a small reserve (of protein) during incubation it was presumably an advantage to these birds to maintain their flying capabilities throughout the relatively vulnerable situation which incubation presents. The greatest variation in the proportionate weight of the pectoralis was among those birds taken from the nests during egg laying or at day 0 of incubation.

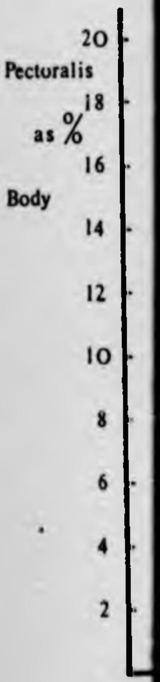
FIGURE 20. Pectoralis weight in relation to body weight in adult Tufted Ducks.

● males, □ females, ▣ incubating females.

FIGURE 21. Pectoralis weight as a proportion of body weight in relation to body weight in adult Tufted Ducks.

● males, □ females, ▣ incubating females.





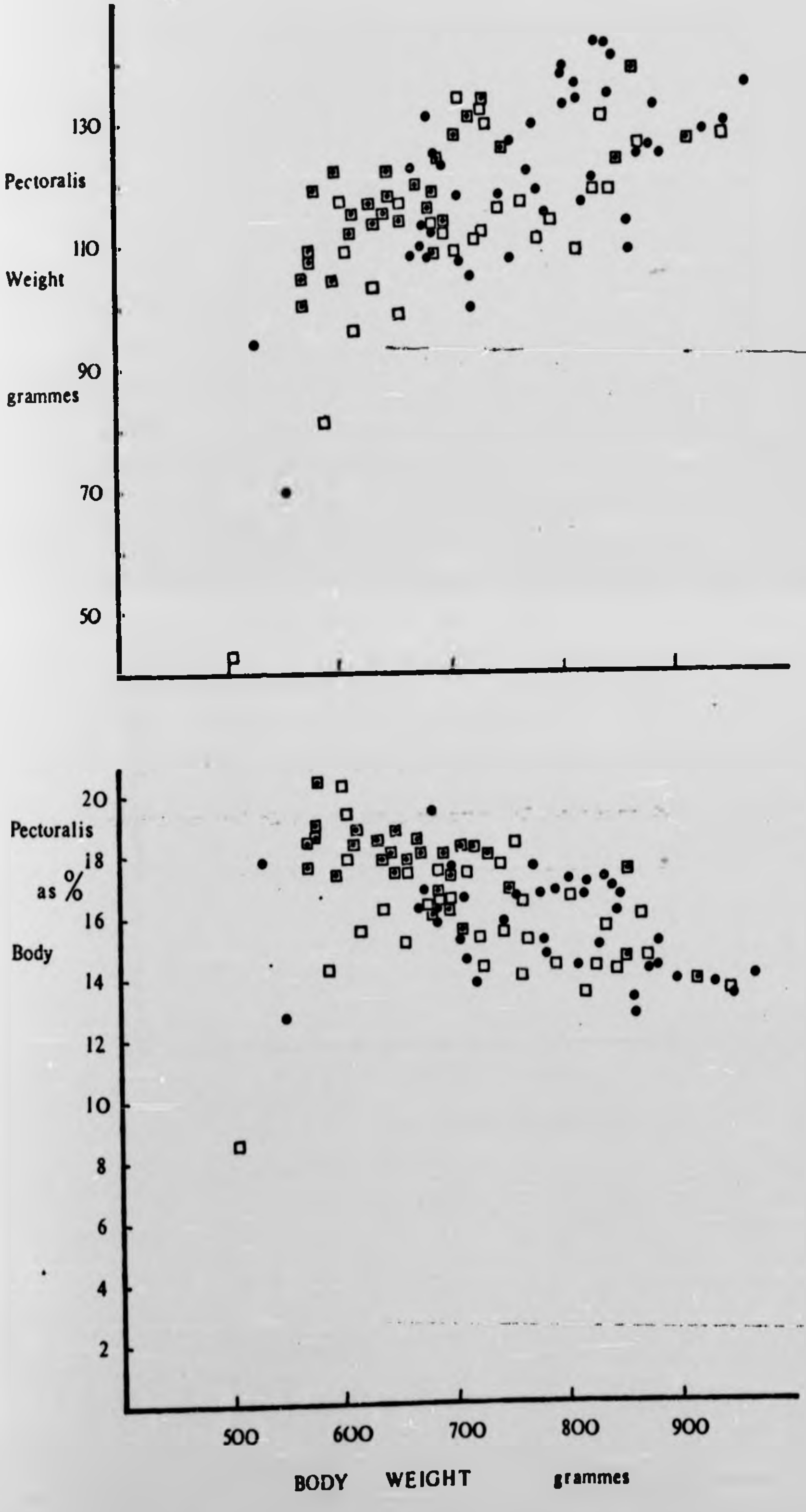
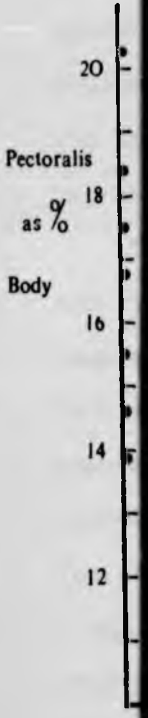
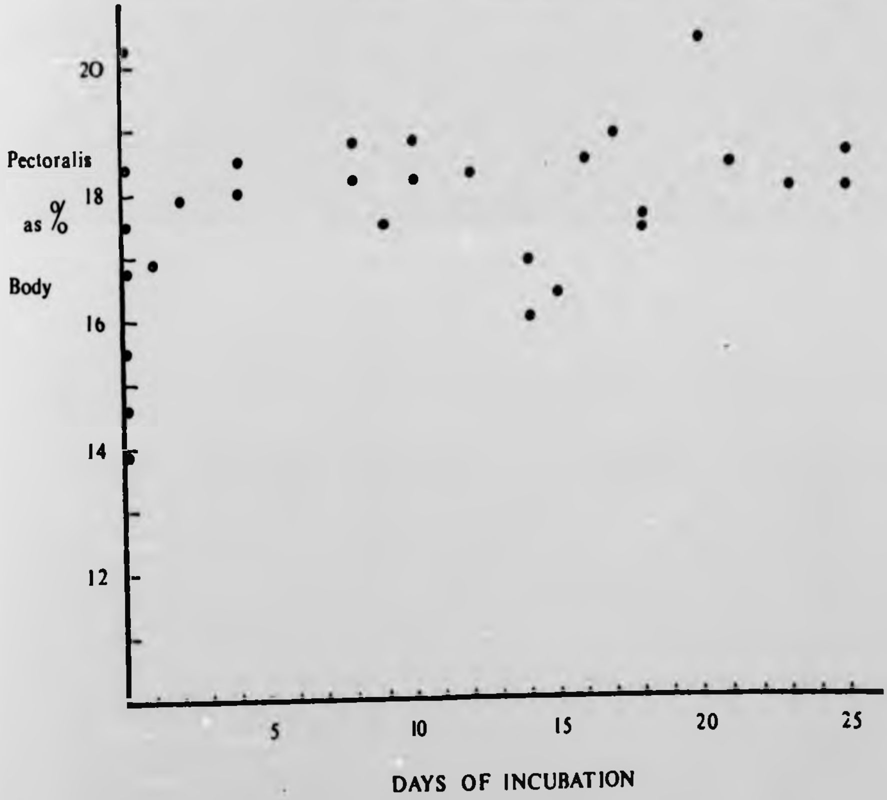

130
Pectoralis
110
Weight
90
grammes
70
50
20
Pectoralis
18
as %
16
Body
14
12
10
8
6
4
2
500
600
700
800
900
BODY WEIGHT
grammes

FIGURE 22. Pectoralis weight as a proportion of body weight in relation to stage of incubation in female Tufted Ducks.




Pectoralis
as %
Body
20
18
16
14
12
5
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15
20
25
DAYS OF INCUBATION

In Scaup, only one pectoralis muscle from each bird was analysed, but the results were then doubled to make them comparable with data from Tufted Ducks. The pectoralis in Scaup declined linearly with body weight down to 750g, but below this the decline became more rapid (Fig. 23). The change at this point was especially clear when pectoralis was expressed as a proportion of body weight (Fig. 24). Initially with declining body weight, ~~the~~ pectoralis proportion increased, then at weights less than 750g this proportion declined rapidly. The juveniles were identified separately since they increased the range of the data, though in other respects they were comparable with the adults (see later).

The water indices of all the pectoralis muscles examined in this study are shown in Fig. 25. In general there was a fairly narrow range of water index in the muscle of normal birds of both species. Both sexes of adult Tufted Ducks, including the incubating females, cover a similar range (2.3 - 3.3). The high value of 3.3 was from the injured male of 551g, while that of 3.5 was from a female taken dead from the diving trap. The female taken during primary moult also had a high water index of 4.3. Fully fledged juveniles covered a similar range to that of adults, but all the growing juveniles had higher water indices (2.7 - 5.2). To summarise, high water indices were associated with body or feather growth or with starvation, that is with accumulation of breakdown of protein tissue. This is borne out in Scaup, because those birds involved in the oiling had an increased proportion of water in the muscle. Water index increased markedly in birds below 750g, the same birds which showed a decrease in the proportion of the pectoralis relative to body weight.

FIGURE 23. Pectoralis weight in relation to body weight in Scaup.

● normal, □ oiled and starved.

ight in

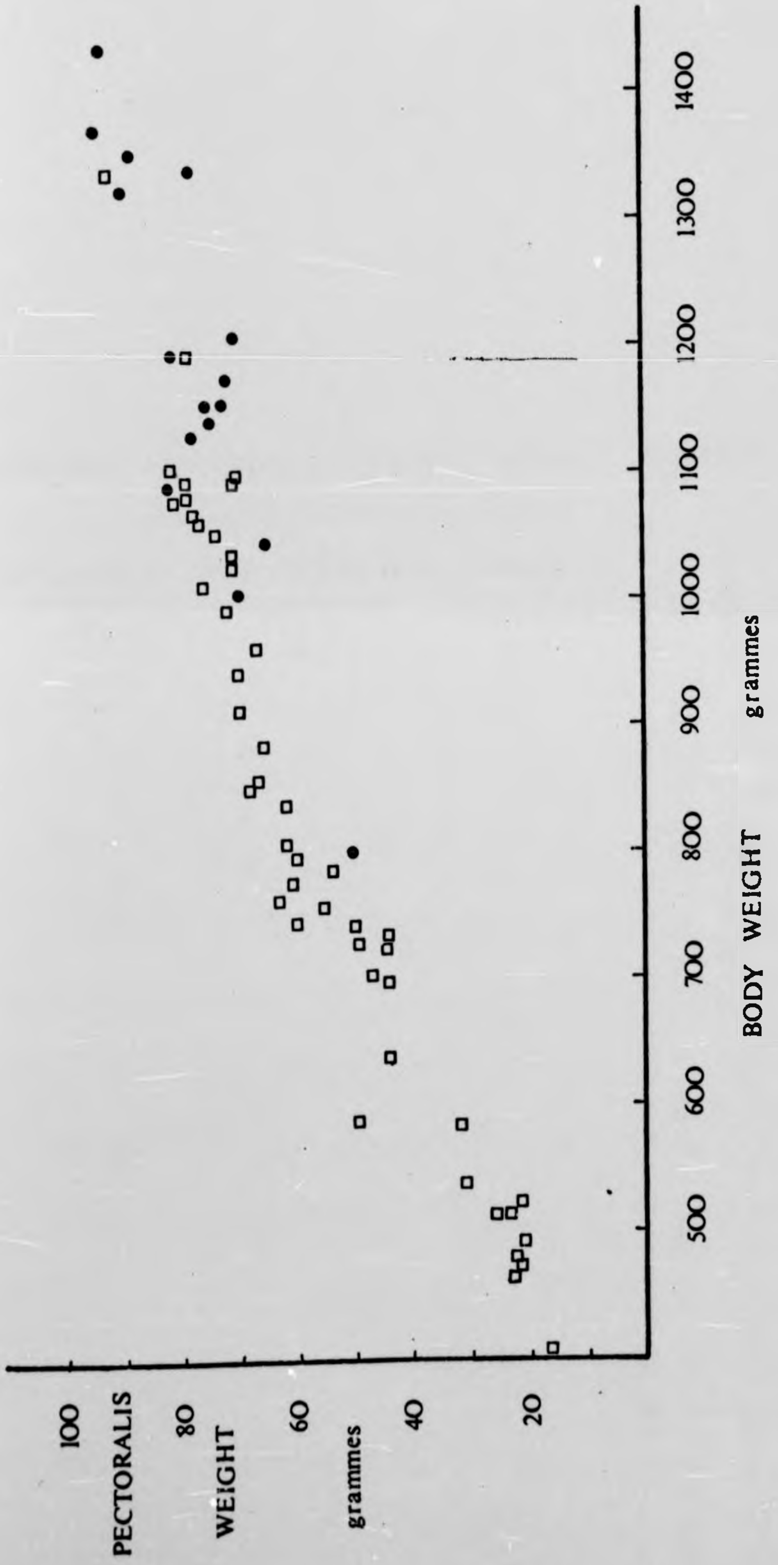

PECTORALIS WEIGHT grammes
100
80
60
40
20
BODY WEIGHT grammes
500
600
700
800
900
1000
1100
1200
1300
1400

FIGURE 24. Pectoralis weight as a proportion of body weight in relation to body weight in Scaup.

● normal, □ oiled and starved, J juveniles.

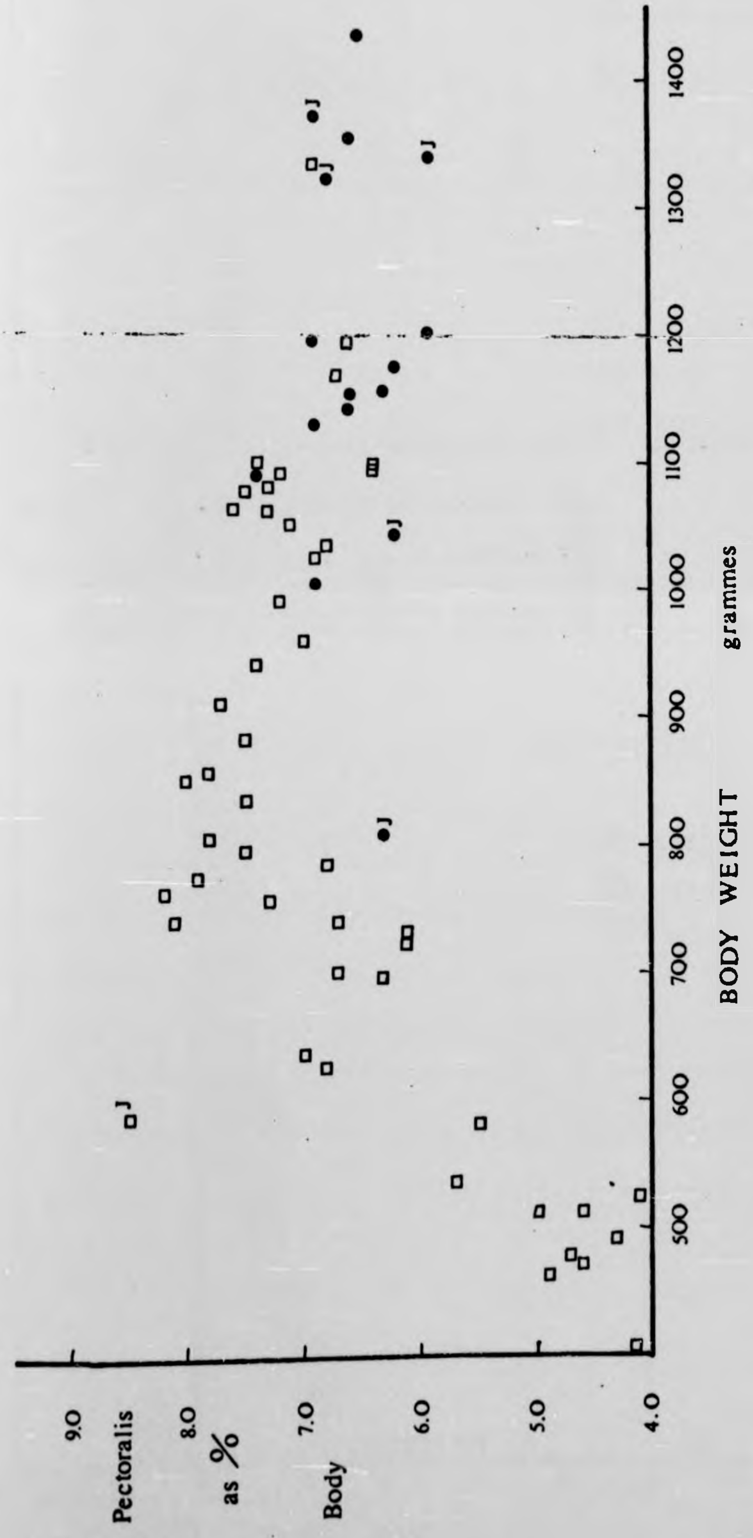
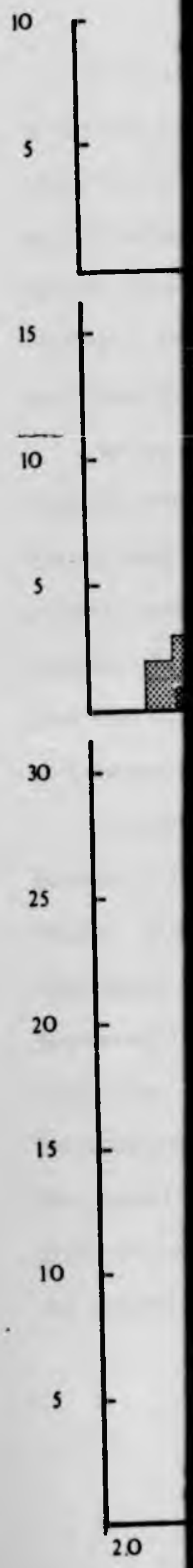
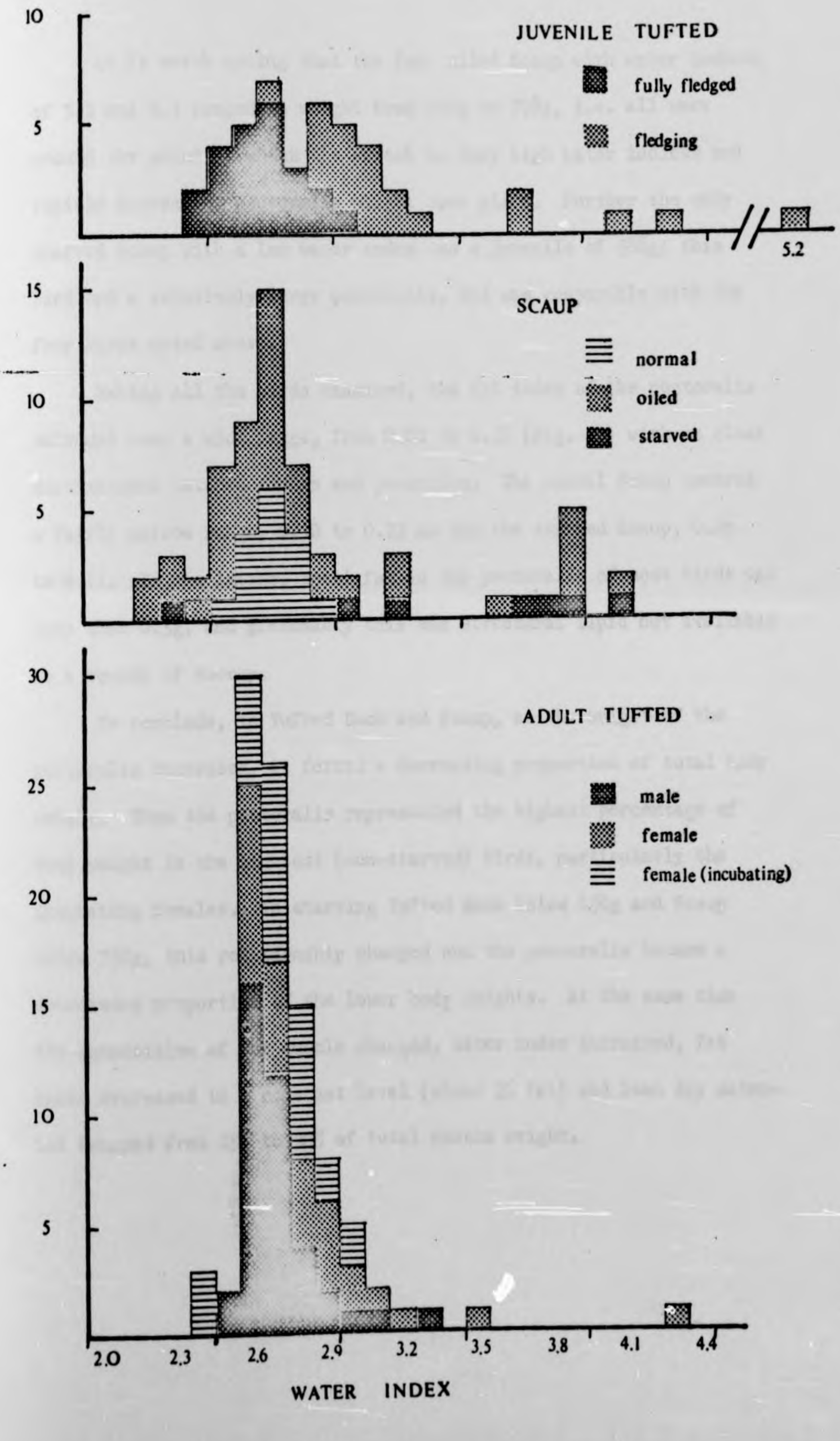

Pectoralis
as %
Body
9.0
8.0
7.0
6.0
5.0
4.0
500
600
700
800
900
1000
1100
1200
1300
1400
J
BODY WEIGHT
grammes

FIGURE 25. Water indices of pectoralis muscles in (a) Juvenile Tufted Duck (b) Scaup (c) Adult Tufted Duck.

(left axis indicates number in each class)




JUVENILE TUFTED
fully fledged
fledging
10
5
5.2
SCAUP
normal
oiled
starved
15
10
5
ADULT TUFTED
male
female
female (incubating)
30
25
20
15
10
5
2.0
2.3
2.6
2.9
3.2
3.5
3.8
4.1
4.4
WATER INDEX

It is worth noting that the four oiled Scaup with water indices of 2.2 and 2.3 ranged in weight from 725g to 798g, i.e. all were around the point at which the switch to very high water indices and rapidly decreasing pectoralis weight took place. Further the only starved Scaup with a low water index was a juvenile of 588g; this bird had a relatively large pectoralis, and was comparable with the four birds noted above.

Taking all the birds examined, the fat index of the pectoralis extended over a wide range, from 0.01 to 0.35 (Fig. 26) with no clear distinctions between adults and juveniles. The normal Scaup covered a fairly narrow range, 0.10 to 0.22 as did the starved Scaup, 0.06 to 0.11. In the latter, total fat in the pectoralis of most birds was less than 0.5g, and presumably this was structural lipid not available as a source of energy.

To conclude, in Tufted Duck and Scaup, as the weight of the pectoralis increased, it formed a decreasing proportion of total body weight. Thus the pectoralis represented the highest percentage of body weight in the lightest (non-starved) birds, particularly the incubating females. In starving Tufted Duck below 650g and Scaup below 750g, this relationship changed and the pectoralis became a decreasing proportion of the lower body weights. At the same time the composition of the muscle changed, water index increased, fat index decreased to a constant level (about 2% fat) and lean dry material dropped from 25% to 20% of total muscle weight.

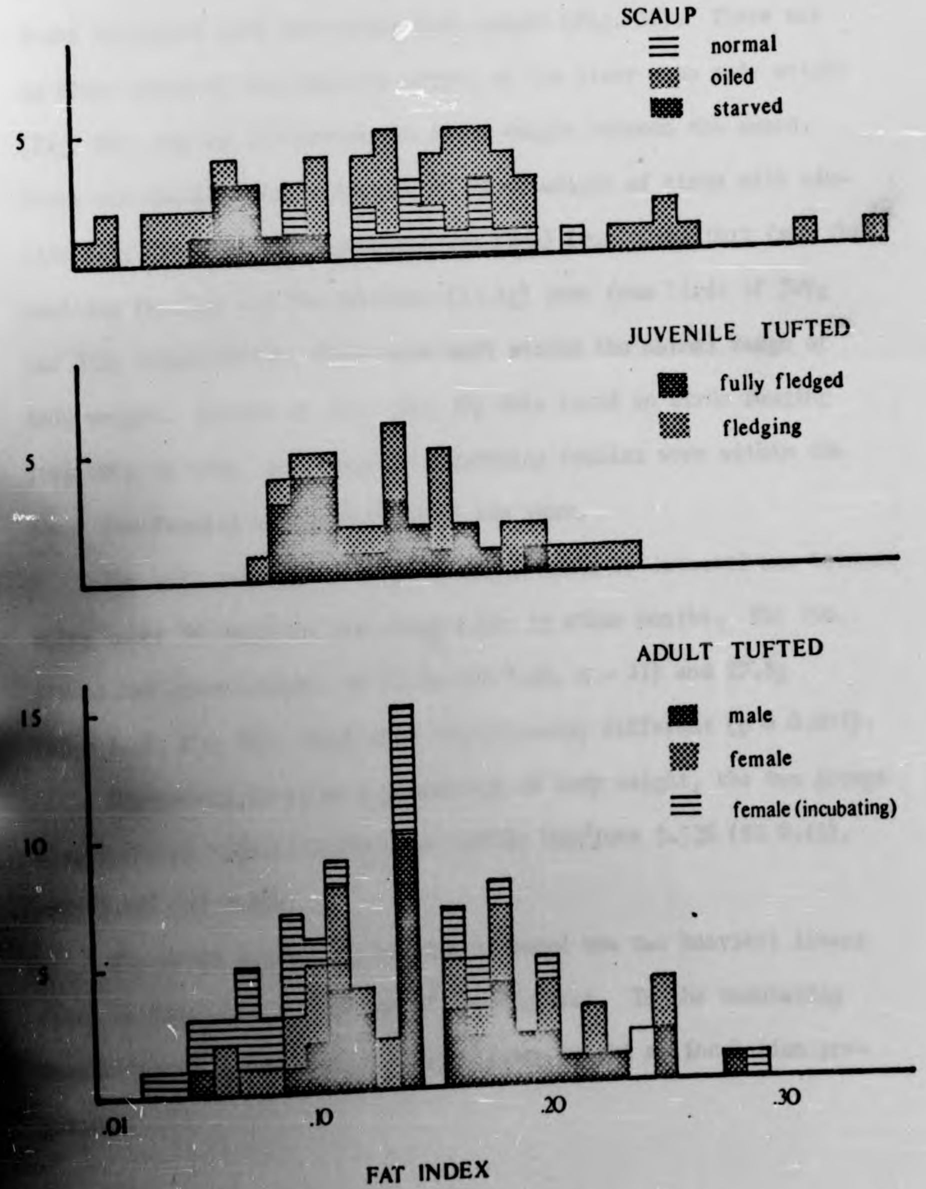
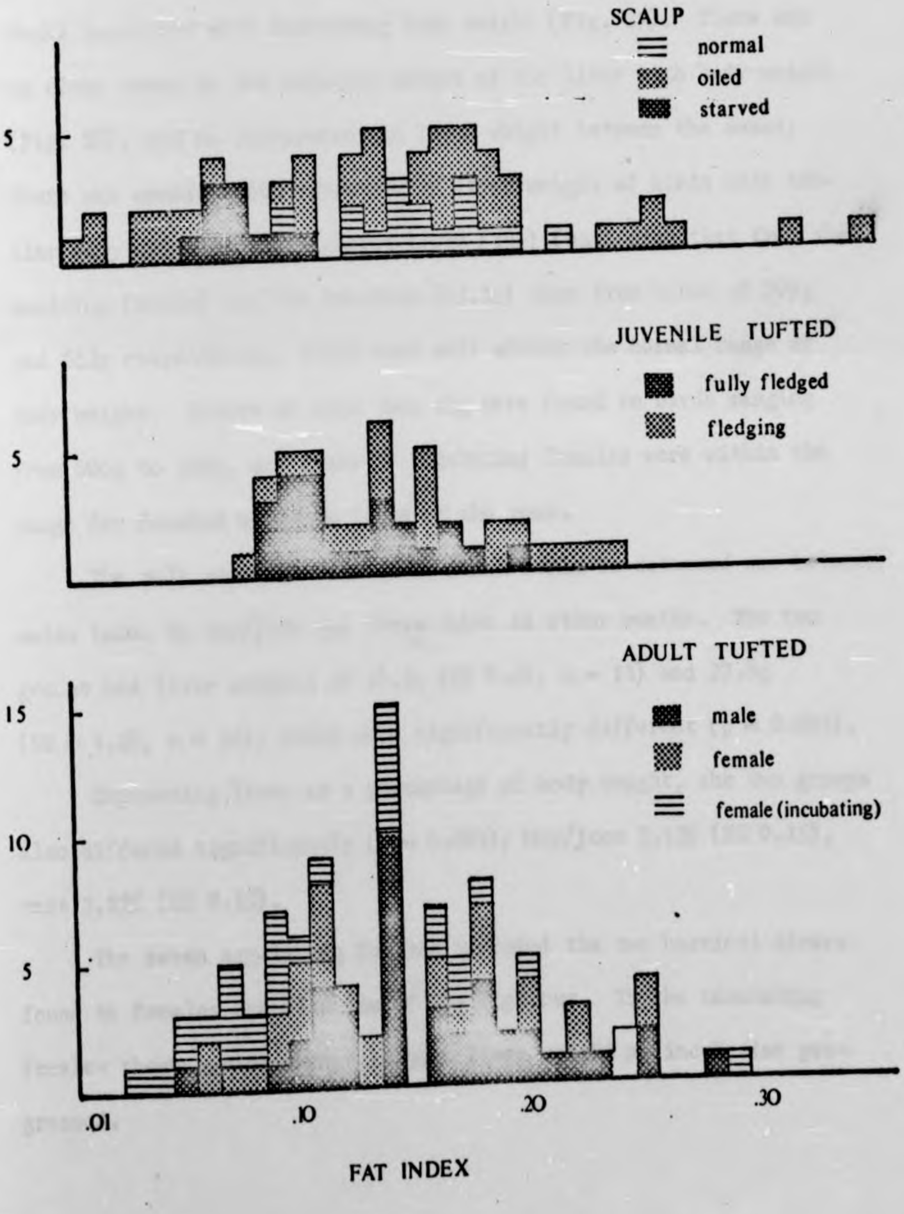

SCAUP
normal
oiled
starved
5
JUVENILE TUFTED
fully fledged
fledging
5
ADULT TUFTED
male
female
female (incubating)
15
10
5
.01
.10
.20
.30
FAT INDEX

FIGURE 26. Fat indices of pectoralis muscles in (a) Scaup (b) Juvenile Tufted Duck (c) Adult Tufted Duck. (left axis indicates number in each class)


SCAUP
normal
oiled
starved
5
JUVENILE TUFTED
fully fledged
fledging
5
ADULT TUFTED
male
female
female (incubating)
15
10
5
.01
.10
.20
.30
FAT INDEX

The liver

Changes in absolute weight of the liver were examined; also its weight as a percentage of body weight, in order to determine any relative changes. In general it was difficult to determine any pattern in the liver analyses, except that its weight in adult Tufted Ducks increased with increasing body weight (Fig. 27). There was no clear trend in the relative weight of the liver with body weight (Fig. 28), and no differences in liver weight between the sexes. There was considerable variation in liver weight of birds with similar body weights; the lightest liver (13g) (excluding that from the moulting female) and the heaviest (43.1g) came from birds of 709g and 842g respectively, which were well within the normal range of body weight. Livers of less than 16g were found in birds ranging from 600g to 940g, and those of incubating females were within the range for females at other times of the year.

The only seasonal difference which could be detected was between males taken in May/June and those taken in other months. The two groups had liver weights of 16.3g (SE 0.46, $n = 11$) and 27.8g (SE = 1.48, $n = 14$), which were significantly different ($p < 0.001$).

Expressing liver as a percentage of body weight, the two groups also differed significantly ($p < 0.001$); May/June 3.53% (SE 0.15), rest 2.27% (SE 0.15).

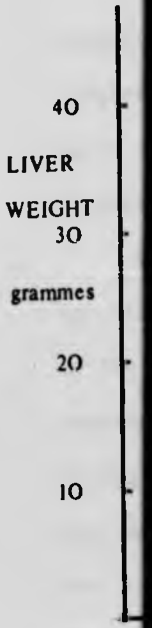
The seven egg-laying females included the two heaviest livers found in females and also one of the lightest. In the incubating females there was no change in mean liver weight as incubation progressed.

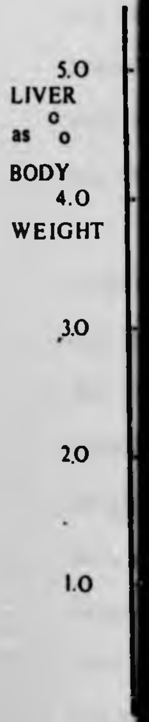
FIGURE 27. Liver weight in relation to body weight in adult Tufted Ducks.

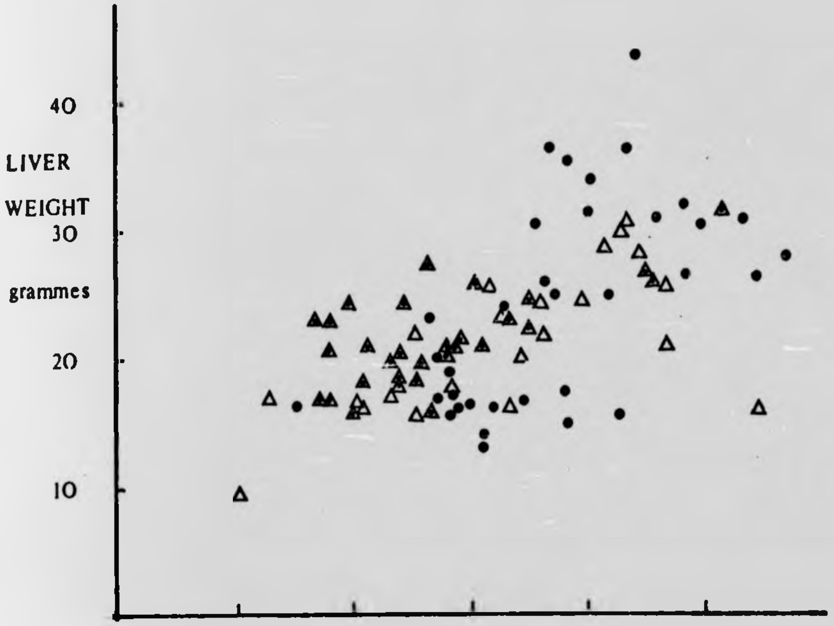
● male, △ female, ▲ incubating female.

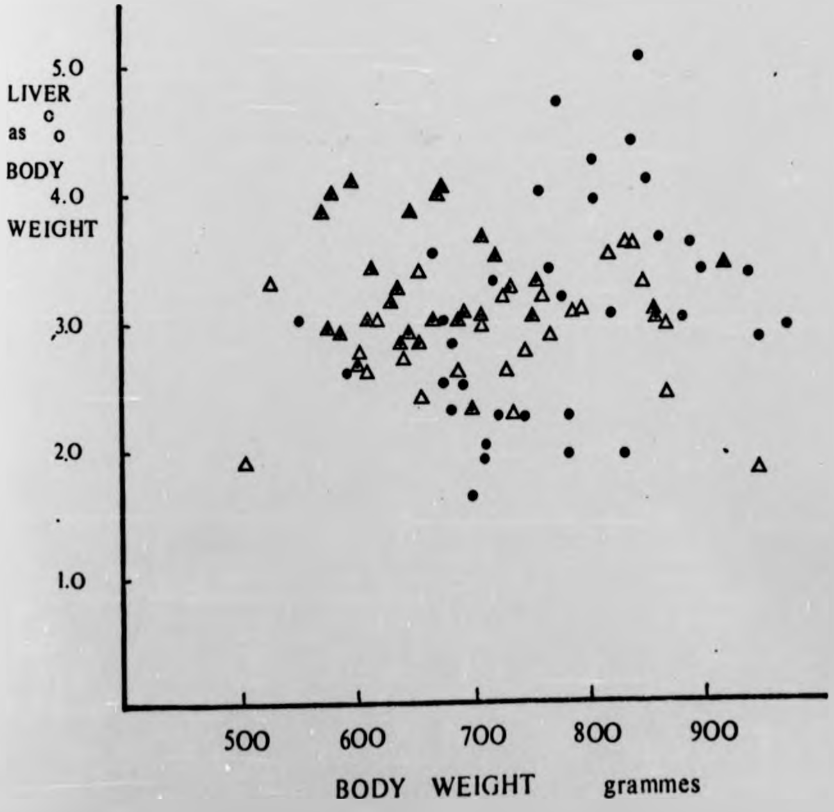
FIGURE 28. Scatter diagram showing liver weight as a proportion of body weight against body weight in adult Tufted Ducks.

● male, △ female, ▲ incubating female.






40
LIVER
WEIGHT
30
grammes
20
10

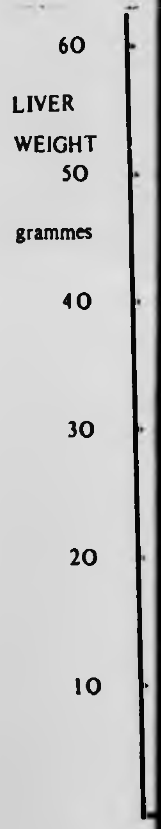

5.0
LIVER
as %
BODY
WEIGHT
4.0
3.0
2.0
1.0
500
600
700
800
900
BODY WEIGHT grammes

Over the wide range of body weights in Scaup, there was a good correlation between liver weight and body weight (Fig. 29). However a fairly wide range of liver weights among birds of normal weight was again evident. At body weights of less than 800g there was a sharp decrease in liver weight from 4-5% of the body weight to around 2%.

The water, fat and lean dry material in the liver did not show any clear changes in their relative proportions (FI and WI) in any of the groups of birds (Figs. 30 and 31). The fatty livers did not correlate with the heavy livers. Fat index in the livers of egg laying females ranged from 0.122 to 0.350. The water index, fat index and fat weight in the liver all varied over their total range throughout incubation. The distribution of fat indices in the adult Tufted Ducks was skewed towards those with low values (Fig. 30). Except for one egg laying female, all of the birds with a fat index greater than 2.5 were taken in the early morning (before 07.00) or while actively feeding. This is further evidence that they fed at night (see feeding section) as a fatty liver appears to be associated with recent feeding (Wilson and MacFarland, 1969).

The Scaup provided a wide range of liver weights, for which the proportions of the major components were determined (Fig. 32). Water and lean dry material increased linearly with total liver weight. The fat weight also increased but was extremely variable, and small absolute weights were involved. Evidently the major changes in liver weight resulted from changes in lean tissue. The fat in the liver accounted for a maximum of 10% of the total weight but was usually around 5%. There appeared to be an increased variation in the relative components of livers in the range 40-44g which was the weight below which its proportion of the body weight decreased.

FIGURE 29. Relationship between liver weight and body weight in Scaup.



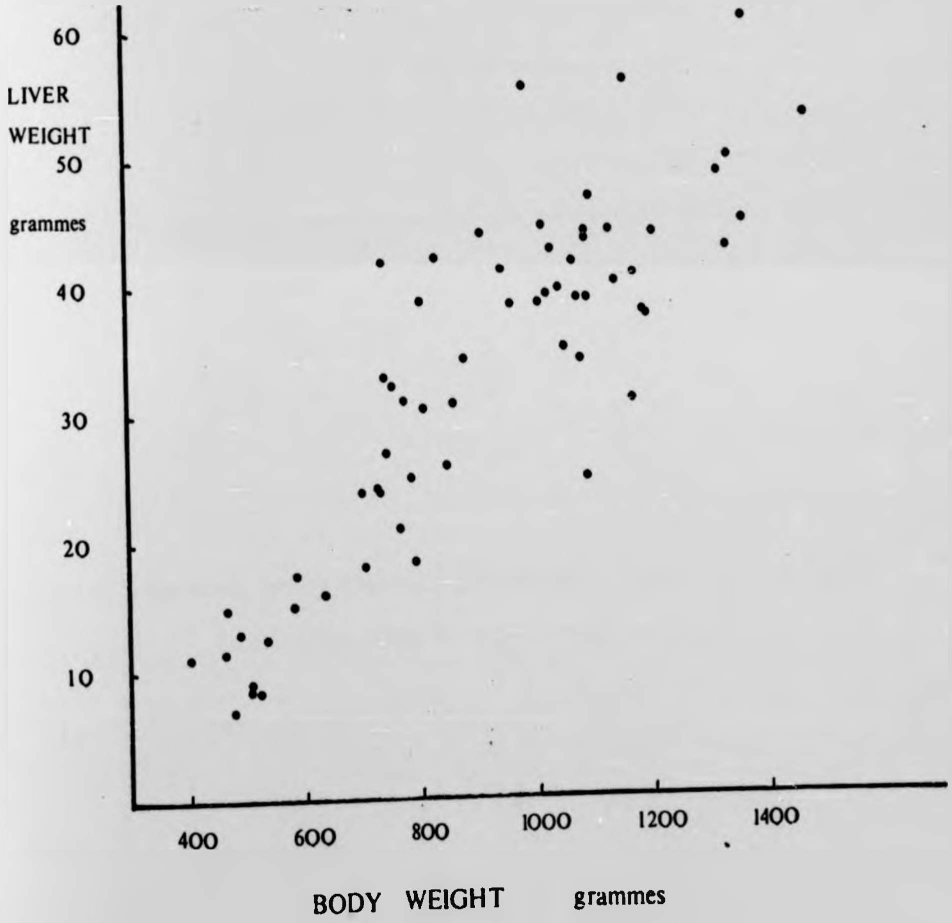

LIVER
WEIGHT
grammes
60
50
40
30
20
10
400
600
800
1000
1200
1400
BODY WEIGHT grammes

FIGURE 30. Scatter diagram showing liver fat index against total liver weight in adult Tufted Duck. Dashed line indicates index of 2.5.

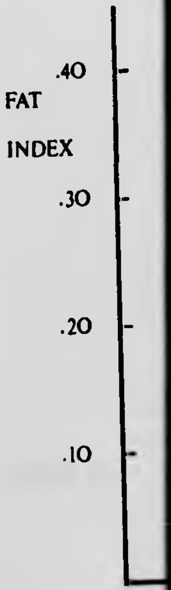


FIGURE 31. Scatter diagram showing liver water index against total liver weight in adult Tufted Duck.

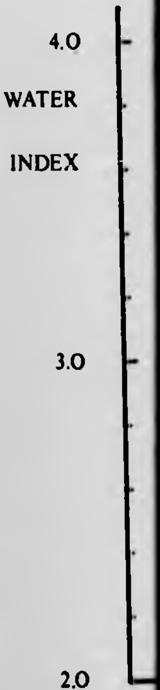


FIGURE 30. Scatter diagram showing liver fat index against total liver weight in adult Tufted Duck. Dashed line indicates index of 2.5.

FIGURE 31. Scatter diagram showing liver water index against total liver weight in adult Tufted Duck.

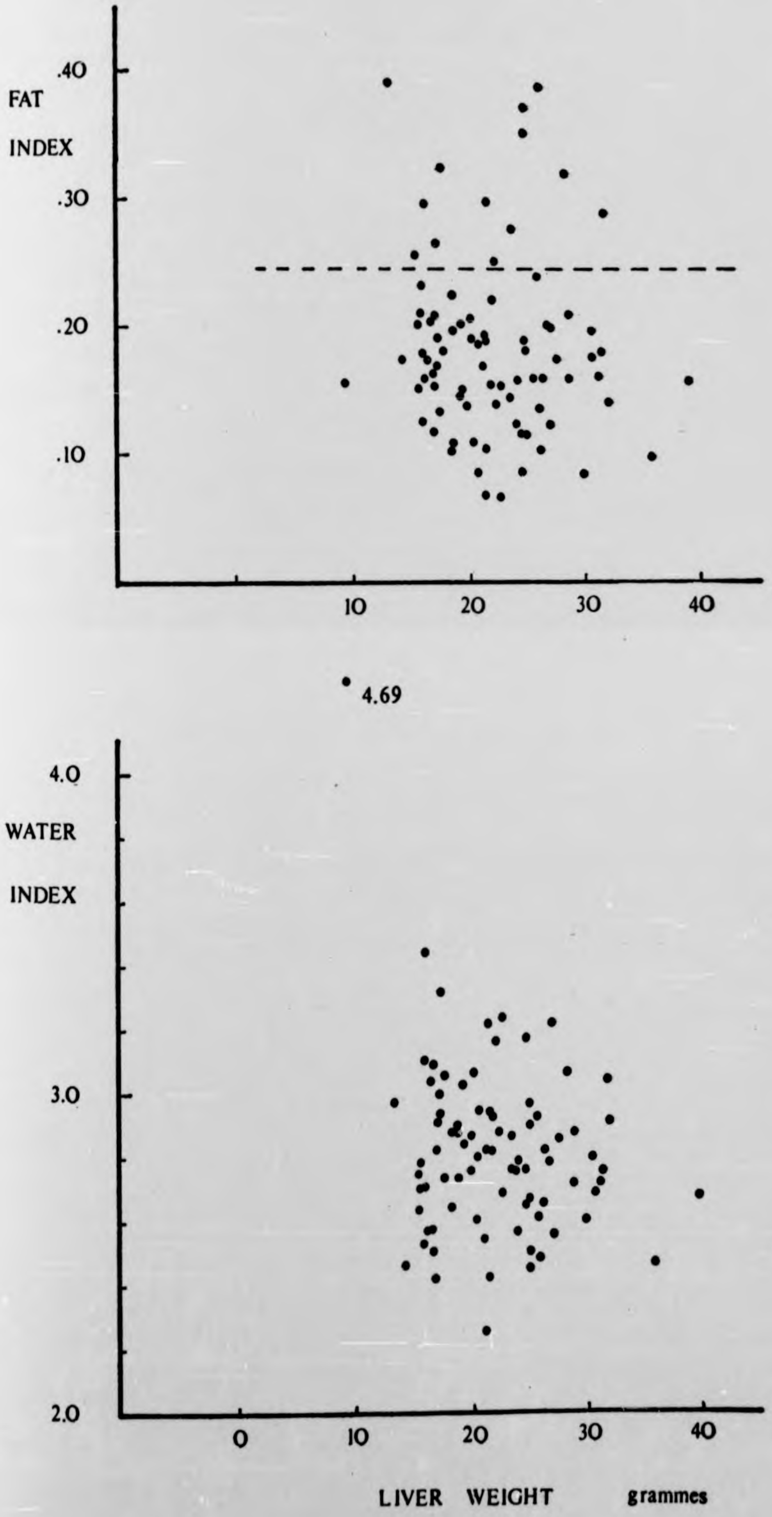
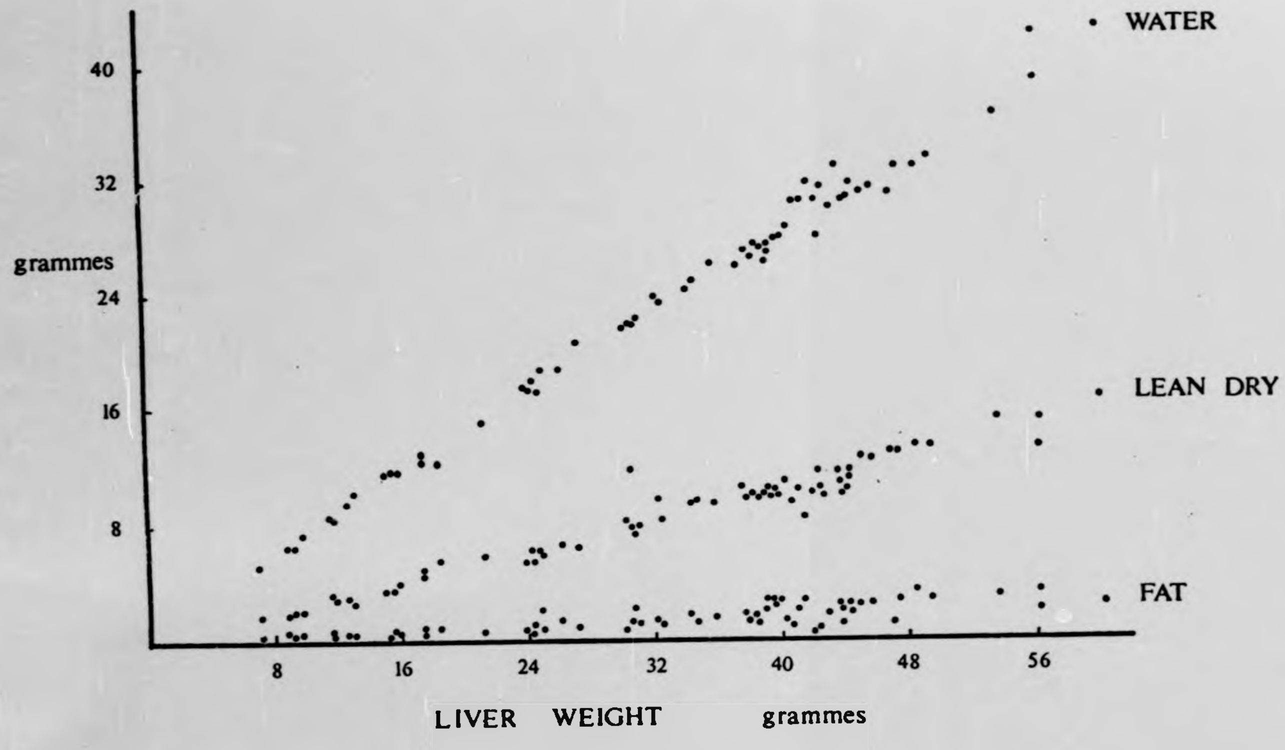

.40
FAT
INDEX
.30
.20
.10
10
20
30
40
4.69
4.0
WATER
INDEX
3.0
2.0
0
10
20
30
40
LIVER WEIGHT
grammes

FIGURE 32. Changes in the three components, water, lean dry material and fat with total weight in livers of Scaup.


WATER
LEAN DRY
FAT
grammes
40
32
24
16
8
8
16
24
32
40
48
56
LIVER WEIGHT
grammes

In general, liver weight in Tufted Duck increased with body weight, but the breeding females added considerable variation to this relationship. In winter Scaup, both sexes were similar and liver weight increased from 3% of body weight at 750g to 4.5% at 1100g. A similar pattern, in which the liver was proportionately larger in the heaviest birds occurred in the Wood Pigeon Columba palumbus (Ljungren, 1968).

The skeleton

Tufted Duck lay 6-12 eggs on consecutive days. The eggshell of the domestic fowl, which lays eggs of similar size, contains about 2g of calcium and therefore, by analogy, a duck requires 12 - 24g of calcium over 6 - 12 days. Apart from the food taken at the time, one possible source of calcium is the skeleton, which in birds contains 97-99% of all the calcium in the body (Common, 1938).

I determined the skeletal weight in three samples of birds: (1) males taken in April/May; (2) females taken just prior to or during egg laying, some of which had eggs in the oviduct; (3) incubating females which had completed their clutches. For each bird, I used sternum and wing length as an indication of the overall skeletal size (Table 7).

The skeletal weight of incubating females was significantly less ($p < 0.05$) than that of females prior to and during lay. In the latter birds skeletal weight did not differ from that in males which had significantly larger sternum and wing lengths ($p < 0.01$). Evidently, skeletal material was used during the laying period, and losses were recouped before laying in the next year. The amount of this loss (7g) is close to the total loss of lean dry material (8g) during egg laying, and about 20% of total skeletal material at start of lay.

TABLE 7. Skeletal weight, sternum and wing lengths (+SE) of pre- and post-laying female Tufted Ducks. Males in April and May are included for comparison. Significantly different values are marked;

* $p<0.05$, ** $p<0.01$.

	SKELETON WT. (g)	STERNUM LENGTH (mm)	WING LENGTH (mm)
MALES (n = 9)	30.0 (SE 2.85)	85.5 (1.08)	211.0 (1.71)
		*	**
FEMALES PRE-LAYING (9)	26.8 (2.38)	82.0 (0.69)	202.6 (1.50)
	*		
FEMALES POST-LAYING (8)	19.8 (1.60)	82.6 (0.94)	205.3 (1.71)

6 COMPOSITION OF EGGS AND DUCKLINGS

The main aims were to determine the composition of eggs laid by Tufted Duck at Loch Leven and of the fledged ducklings, as both sets of data were needed to calculate the overall energy budget. In addition I looked at egg composition through the season to see whether changes occurred, and the composition of eggs laid parasitically in the nests of other species, to determine whether these differed from eggs laid 'normally'. I also obtained information on the development of the ovum within the bird, and examined the relationship between the composition of the egg and that of the newly hatched duckling.

Egg composition

In 1970, one unincubated egg was taken at random from each of 96 nests, spread throughout the laying season. These eggs were used to determine the average composition of the eggs, and any variations in composition between eggs laid at different times during the season. Accidents and errors reduced the sample size.

The average fresh egg weighed 55.5g (SE 0.39, n = 82), comprising 5g (9%) shell, 7.9g (14%) lean dry material, 8.2g (15%) fat and 34.3 (62%) water (Table 8). The fat index was 0.963 (SE 0.089) and this did not change significantly with egg weight. Water index increased with egg weight, and the correlation between weights of water and lean dry material was highly significant ($p < 0.001$), and indicated an increase in water index from 4.00 at 7g lean dry weight to 4.32 at 9g. Thus the proportion of fat to lean dry material remained constant but the proportion of water increased in larger eggs. This is a different relationship to that found in body composition.

TABLE 8. Size and composition of eggs laid in Tufted Duck nests and of those laid parasitically (by Tufted Duck) in the nests of other species. (Mean ± SE).

	NORMAL (n=82)	Significance of difference	PARASITIC (n=13)
Weight (g)	55.45 (0.39)	*	52.96 (1.00)
Breadth (mm)	41.20 (0.10)	*	40.65 (0.25)
Shape index (b/l.100)	70.00 (0.29)	N.S.	69.59 (0.97)
Shell wt. (g)	5.05 (0.04)	N.S.	4.97 (0.11)
Lean dry wt. (g)	8.22 (0.06)	*	7.85 (0.13)
Water wt. (g)	34.32 (0.25)	**	32.52 (0.59)
Fat wt. (g)	7.94 (0.07)	N.S.	7.62 (0.26)
Water index	4.176 (0.022)	N.S.	4.142 (0.071)
Fat index	0.963 (0.009)	N.S.	0.963 (0.024)

TABLE 9. Egg size and composition in five 10 day periods of the 1970 egg laying season. One egg was taken from each clutch. Clutch size was taken from Table

	MAY			JUNE	
	11	21	31	10	20
NO. EGGS EXAMINED	20	21	19	14	5
EGG WT.	53.9 ± 0.74	55.1 ± 0.65	55.2 ± 0.79	57.0 ± 1.17	57.9 ± 1.23
EGG BREADTH	41.0 ± 0.17	41.0 ± 0.23	41.2 ± 0.18	41.3 ± 0.27	41.8 ± 0.49
SHAPE INDEX $\left(\frac{\text{Length}}{\text{Breadth}} \times 100\right)$	70.5 ± 0.66	70.0 ± 0.67	70.2 ± 0.45	68.9 ± 0.68	70.3 ± 1.51
WATER INDEX	4.16 ± 0.046	4.15 ± 0.053	4.25 ± 0.035	4.22 ± 0.041	4.27 ± 0.058
FAT INDEX	1.001 ± 0.017	0.938 ± 0.024	0.968 ± 0.014	0.985 ± 0.014	0.936 ± 0.011
‡CLUTCH SIZE (SE)	10.70 ± 0.26	10.83 ± 0.20	9.79 ± 0.15	8.62 ± 0.15	7.82 ± 0.37
* (n)	29	50	82	78	17

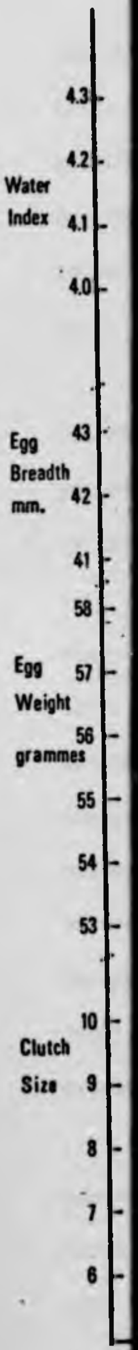
‡ For Whole Colony

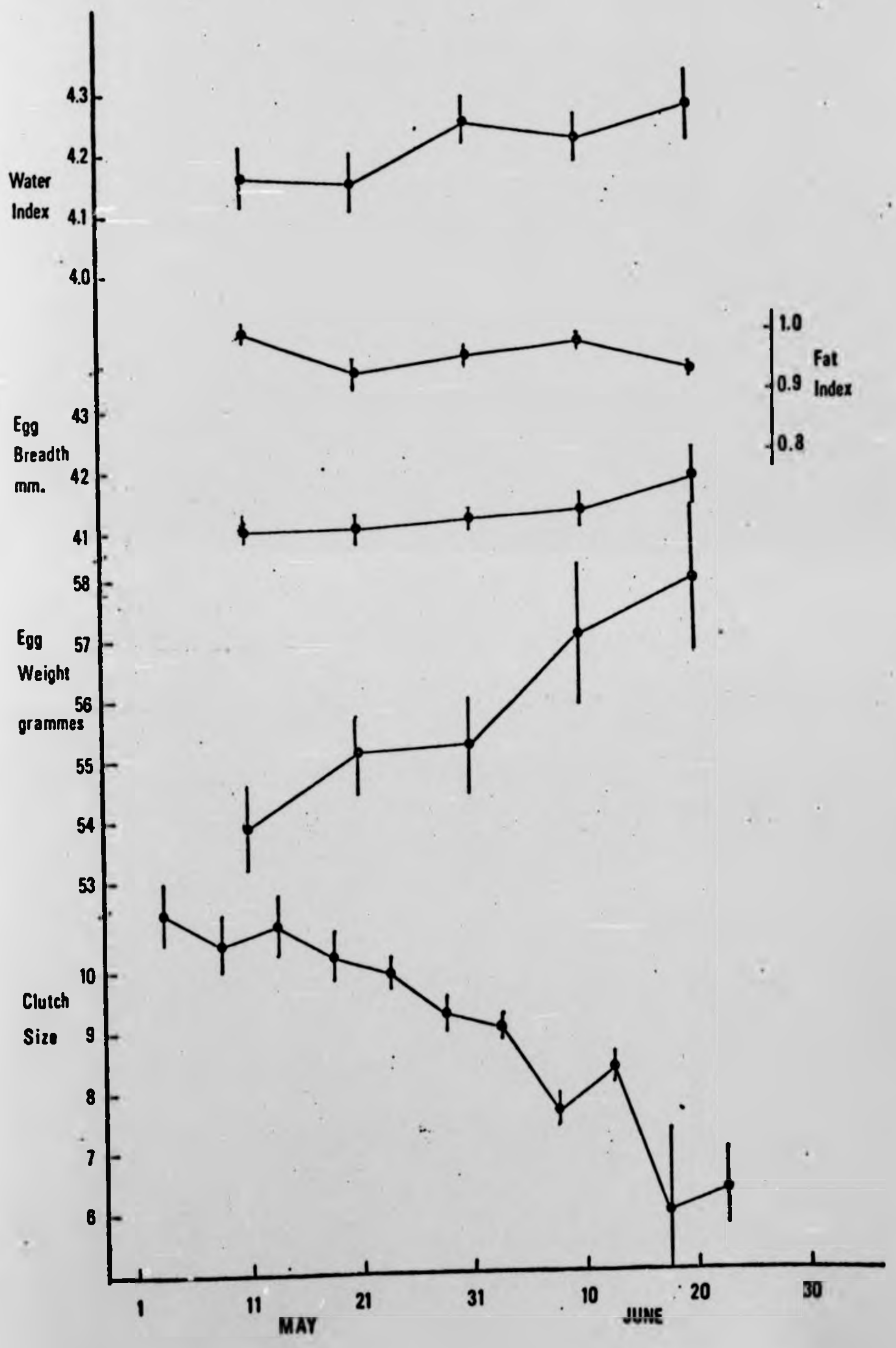
Regression equation for clutch size (y) upon egg weight (x)

$y = 52.73 - 0.774\, x$ $r = 0.947$ ($p < 0.01$)

SE of $b = 0.1512$

FIGURE 33. Trends in clutch size, egg size and egg composition through the season. Each point represents the mean of values for the preceding 5 or 10 d period.





Water Index
4.3
4.2
4.1
4.0
1.0
Fat Index
0.9
0.8
Egg Breadth mm.
43
42
41
Egg Weight grammes
58
57
56
55
54
53
Clutch Size
10
9
8
7
6
1
11
21
31
MAY
10
20
30
JUNE

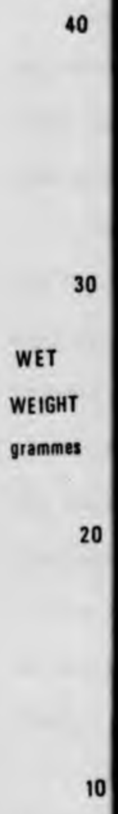
To find whether egg composition changed through the season, the data on egg composition were separated into five 10-day periods (Fig. 33, Table 9). Mean egg weight increased through the season and the negative correlation between mean clutch size (c) and mean egg weight (w) was highly significant ($p < 0.001$). The regression indicated an increase of just over 1g per egg reduction in clutch size.

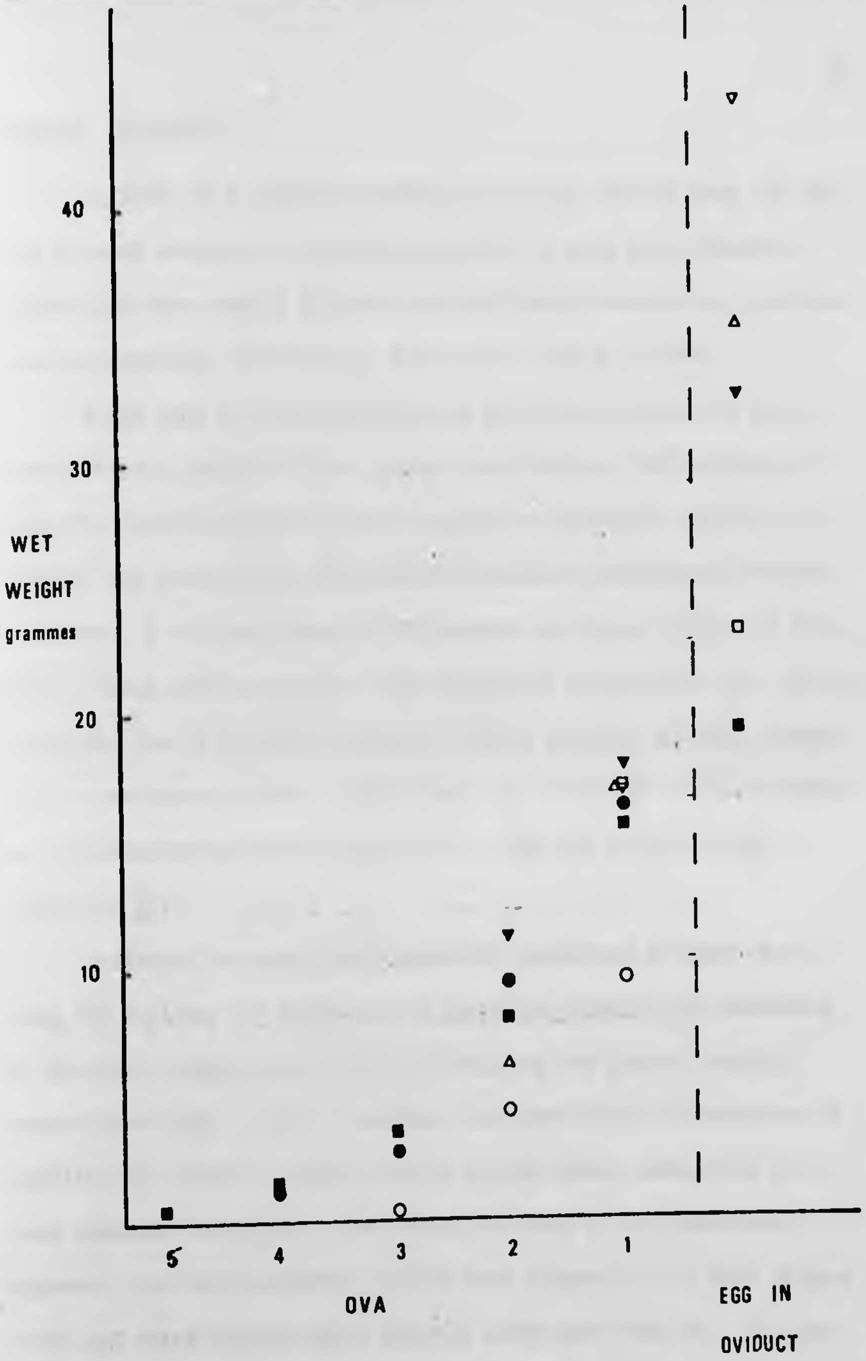
The fat index declined through the season, being higher in the first period, lower in the middle period and lowest in the last period (both differences were significant, t-test, $p < 0.01$). This is not incompatible with the earlier finding that fat index did not vary with egg weight, but implies that all eggs, irrespective of size, had relatively more fat in the earlier period than in the later one. The increases in water index and egg breadth through the season were not significant and the shape index of the eggs did not change. In respect to these two latter parameters, the Tufted Duck was unlike the Shag (Phalacrocorax aristotelis) for which egg breadth varied significantly during the laying season, and could be used to determine the age composition of the population (Coulson et al., 1969). A similar change in egg size and shape with age of the breeding birds was also demonstrated in the Kittiwake (Coulson, 1963).

As indicated elsewhere, 'dump-laying' by Tufted Ducks was quite common at Loch Leven, often in nests of other Tufted Ducks but sometimes in those of other species. In 1970, I found 13 Tufted Duck eggs laid in the nests of other species, where they were readily distinguishable from the host eggs. Nine of the 13 dumped eggs were laid between 26 May and 4 June and two each in 16-20 May and 10-14 June. They were therefore evenly distributed about the period of maximum egg laying. The mean weight of dumped eggs (52.96g SE 1.00) was significantly less than the mean weight of eggs laid normally through the season ($p < 0.05$). They were also significantly narrower ($p < 0.05$), but did not differ in any other respect (Table 8).

Seven females taken during the study for carcass analysis contained eggs or enlarged ova which were examined separately to determine the period and course of egg development. In examining the data I assumed that one egg was ovulated each day, and numbered the ova accordingly (Fig. 34). However the ova from different birds varied considerably and it was not possible to synchronise them with respect to ovulation time. Eggs in the oviduct provided little useful information as they had varying amounts of albumen or shell added. The largest ova in each bird had wet weights of 15.6 to 18.0g, except one (bird no. 148) in which it was only 9.5g. The second ova were more variable, ranging from 6.1 to 11.1g and again that of 148 was much smaller, 4.3g. In one bird five enlarged ova could be distinguished quite readily and in a second, four. Thus yolk material must be provided to at least five ova at a time. The difference in weight between successive ova showed that there was a progressive increase in the amount of yolk material deposited in the ovum each day. The maximum amount deposited by the bird in any day would not exceed the total amount of yolk in the largest egg produced by the bird, since this also is the sum of the daily increments, in one egg. Each day during egg laying albumen and shell for one egg must be laid down. Bird 148 was shot while feeding with a male and this would suggest that the small ova were just beginning to develop prior to egg laying.

FIGURE 34. Weight of ova and eggs dissected from 7 Tufted Ducks. Eggs in the oviduct varied considerably in the amounts of albumen and shell. The ova were numbered in descending order of size and the symbols represent individual ducks.





WET
WEIGHT
grammes
40
30
20
10
5
4
3
2
1
OVA
EGG IN
OVIDUCT

Duckling composition

In 1970, as a result to taking incubating females from the nest for carcass analysis, 18 complete clutches of eggs were obtained. These eggs were used to examine the relationship between egg composition and duckling composition, though five failed to hatch.

Since many of these clutches had been incubated by the duck, for differing lengths of time prior to collection, the analyses of eggs from each clutch were first examined to determine whether any changes had taken place, which would invalidate comparisons between clutches. A very wide range of fat indices was found (1.061 - 0.876), but no trend with incubation stage except for a low value in a clutch incubated for 21 d before analysis. Within clutches the eggs showed little variation in their composition, the ranges of the two extremes of fat index noted above being 1.049 - 1.085 and 0.823 - 0.923 (both n = 3).

Individual clutches were similarly consistent in their duckling fat indices; the highest mean clutch fat index 0.644 consisted of ducklings ranging from 0.616 - 0.691, and the lowest, 0.432, ranged from 0.383 - 0.453. However, the coefficient of variation of duckling fat index was twice that of egg fat index taken from the same clutches (Table 10). The reason for this is not immediately apparent, but it is unlikely to have been related to the time between hatch and being killed, since this was never more than 6h. In eggs and young of the Herring Gull *Larus argentatus*, incubated and hatched naturally, the correlations between egg volume and chick lipid ($r = 0.634$), and dry chick weight and chick lipid ($r = 0.623$) were much less than the correlation between egg weight and yolk lipid weight (0.810) (Parsons, 1970). This also suggests a greater variation in composition between chicks than between eggs of a clutch.

TABLE 10. Size and composition of eggs and ducklings. For each of 13 clutches, 3 or 4 eggs were analysed immediately after collection. The remainder were incubated and 3 or 4 ducklings were killed within 6h of hatch for analysis.

	EGGS (n = 35)				DUCKLINGS (n = 43)		
	$\bar{x}$	SD	COEFF. of VARIATION		$\bar{x}$	SD	C.V.
EGG VOLUME (ml)	50.50	2.998	5.9 %		51.40	2.72	5.3
				WEIGHT (g)	37.14	2.14	5.8
FAT WEIGHT (g)	7.66	0.719	9.4		4.38	0.679	15.5
LEAN DRY WEIGHT (g)	7.91	0.617	7.8		7.682	0.511	6.7
FAT INDEX	0.966	.0630	6.5		0.568	0.0708	12.5

When examining the differences between ducklings produced from different clutches I considered there to be an advantage of size *per se*, and also that fat index was a good estimate of duckling quality since it relates the energy reserves to the quantity of energy utilising tissue. There was a highly significant correlation ($r = 0.843$, $p < 0.001$) between mean egg volume and mean duckling weight (of each clutch) (Fig. 35). Mean egg volume was positively correlated with mean duckling fat index (Fig. 36; $p < 0.05$) and in general clutches with high egg fat indices gave ducklings with high fat indices (Fig. 37) but the correlation was not significant ($r = 0.162$). Thus the largest eggs produced the largest ducklings and also ducklings with high fat indices, however there was considerable variation in the fat index of ducklings from clutches having similar egg fat indices. There are two possible reasons for the variation in the condition of ducklings hatching from similar eggs: (1) the hatching process was not equally demanding in all cases or (2) the overall energy costs to the egg during incubation were not a constant proportion of the energy available to the egg. The former is possible, but all eggs within clutches were similar in their relationship to egg condition. The latter is also possible because, although all eggs of each clutch were subjected to the same incubation conditions, the length of artificial incubation varied between clutches.

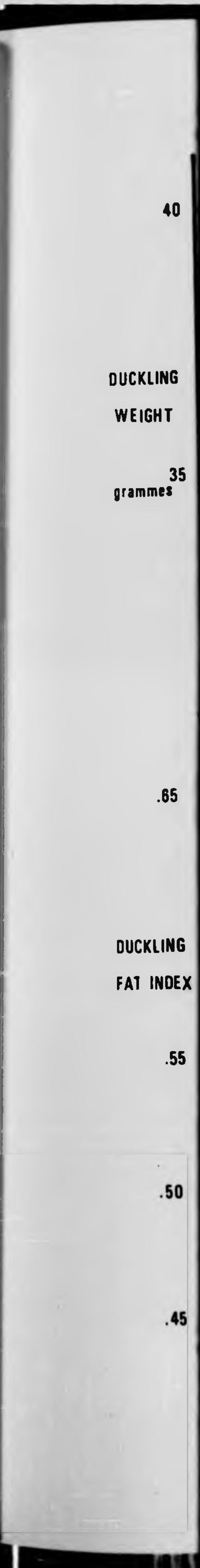
Using the data on egg fat weight and duckling fat weight, I calculated the average loss of fat during incubation at 3.28g (Table 10). This would provide 130kJ, which is 30% more than the energy used during incubation of chicken eggs of comparable size

FIGURE 35. Relationship between egg volume and duckling weight. Each point is the mean value for a clutch.

$$Y = 0.814\,X - 4.59 \;,\quad r = 0.843$$

FIGURE 36. Relationship between egg volume and duckling fat index. Each point is the mean for a clutch.

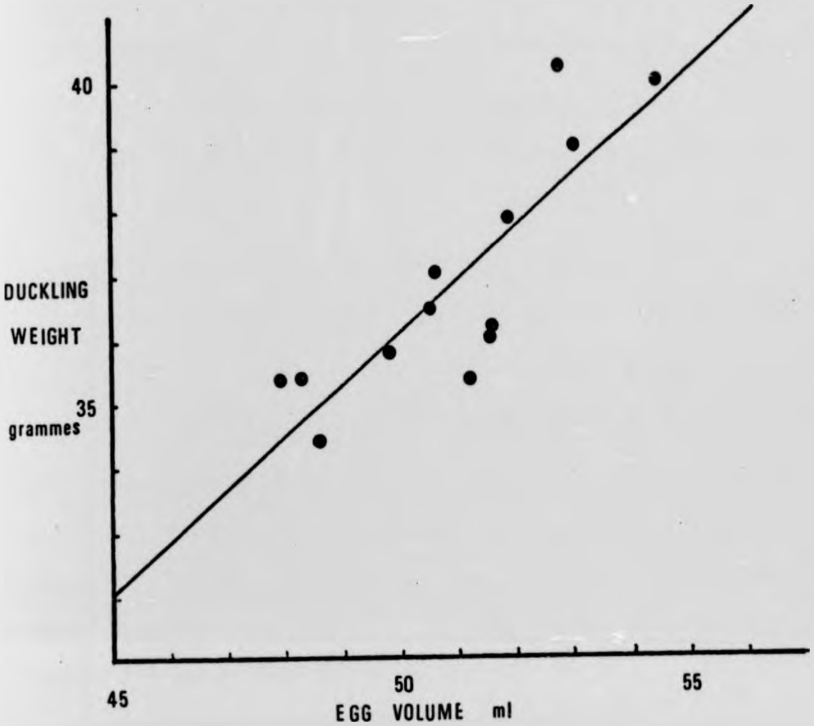
$$Y = 0.02\,X - 0.45 \;,\quad r = 0.567$$



g

clutch.

fat


40
DUCKLING
WEIGHT
35
grammes
45
50
55
EGG VOLUME ml

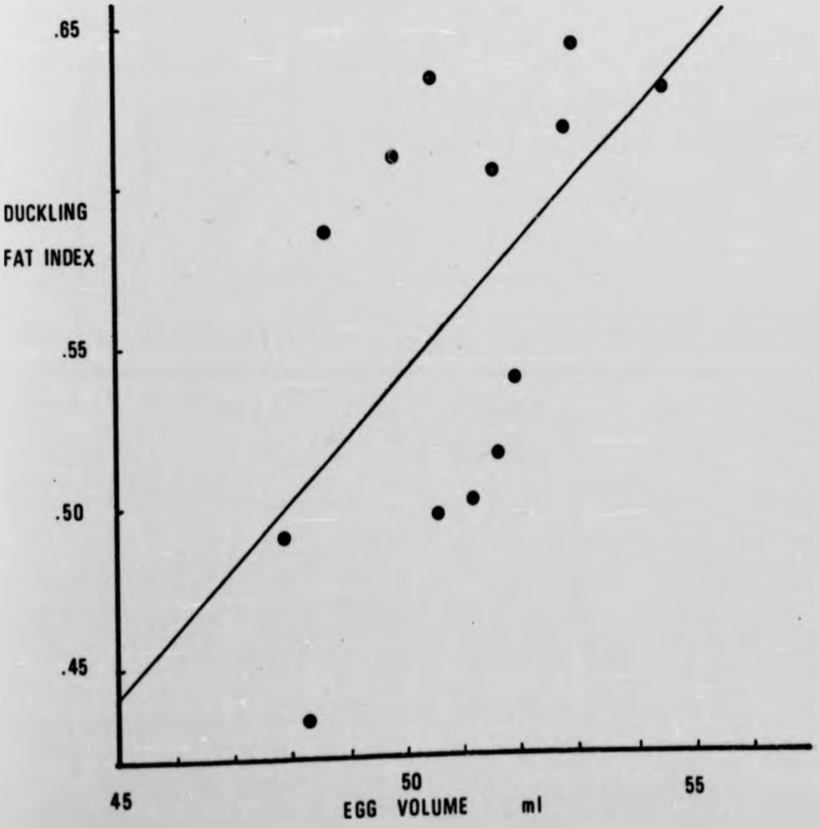
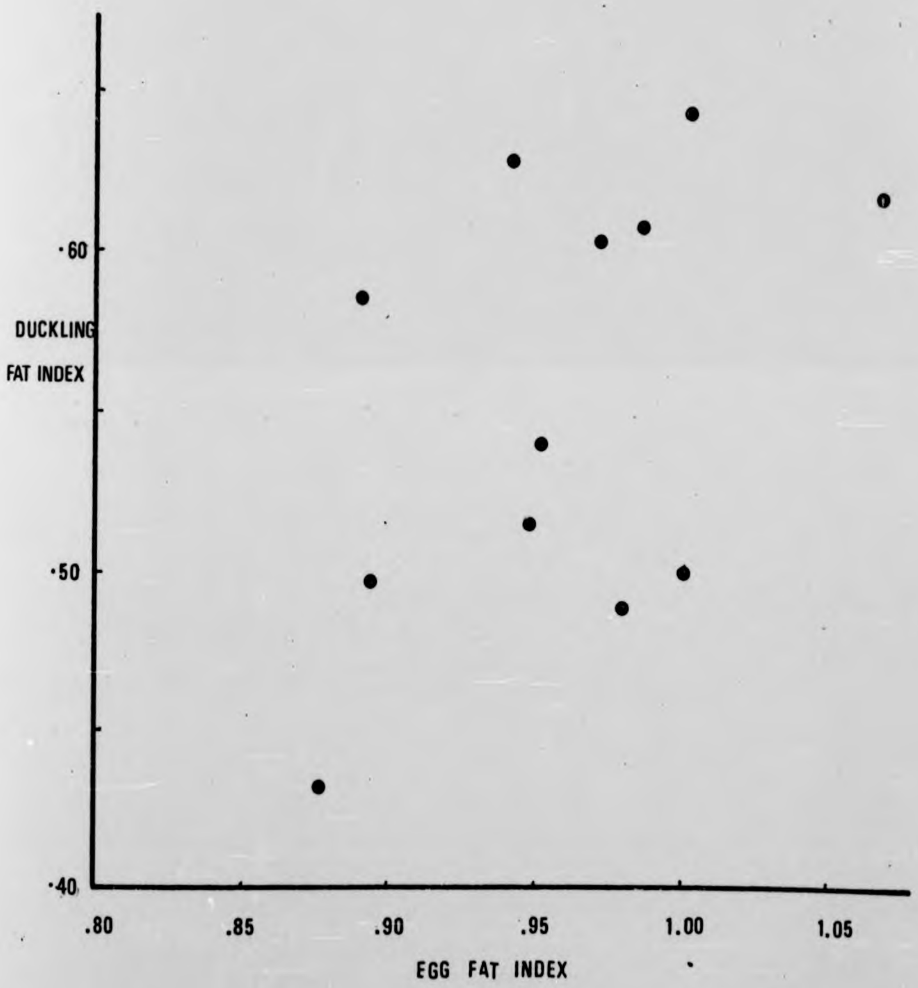

.65
DUCKLING
FAT INDEX
.55
.50
.45
45
50
55
EGG VOLUME ml

FIGURE 37. Plot of duckling fat index against egg fat index. Each point represents the mean for a clutch.



DUCKLING FAT INDEX
·60
·50
·40
.80
.85
.90
.95
1.00
1.05
EGG FAT INDEX

(Murray, 1925). In my study fat represented only 11.8% of the newly hatched duckling weight, which included the yolk sac, whereas Evans (1969) found 12.8% fat in ducklings from which the yolk sac had been removed, and since the latter contains mainly equal amounts of fat and lean dry material, ducklings containing the yolk sac would be expected to contain a higher proportion of fat than Evans' estimate. These two facts suggest the possibility that ducklings examined in the present study had lost an excessive amount of fat during incubation. This could occur if the incubation temperature, 37.5°C, was too high; since the embryo behaves as a poikilotherm and its metabolic rate is proportional to temperature (Barrott, 1937).

Juvenile Composition

The main aim was to determine the carcass composition and energy value of the fledged duckling; data were also obtained on first winter birds. This was possible since many birds retained the notched tail feathers until the spring after hatch, the latest these were found was 3 April.

In juveniles, weight increase is rapid up to fledging at eight weeks, then slows down. As it was not possible to put precise ages on birds taken in this study, I have related the weight to the wing length (Fig. 38), which allowed a comparison to be made with similar data from captive birds of known age and wing length. I have calculated the relationship between these two measurements given by Kear (1970) for birds hatched from eggs from Loch Leven and reared in captivity up to 10 weeks of age. The wild birds obtained prior to fledging were heavier at a given wing length than those reared in captivity. This implies either better feeding or food conversion

FIGURE 38. Relationship between wing length and body weight in juvenile Tufted Ducks. This shows a discontinuity around 500 - 600g body weight. The lines represent mean values calculated from Kear (1970); solid - males, dashed - females.

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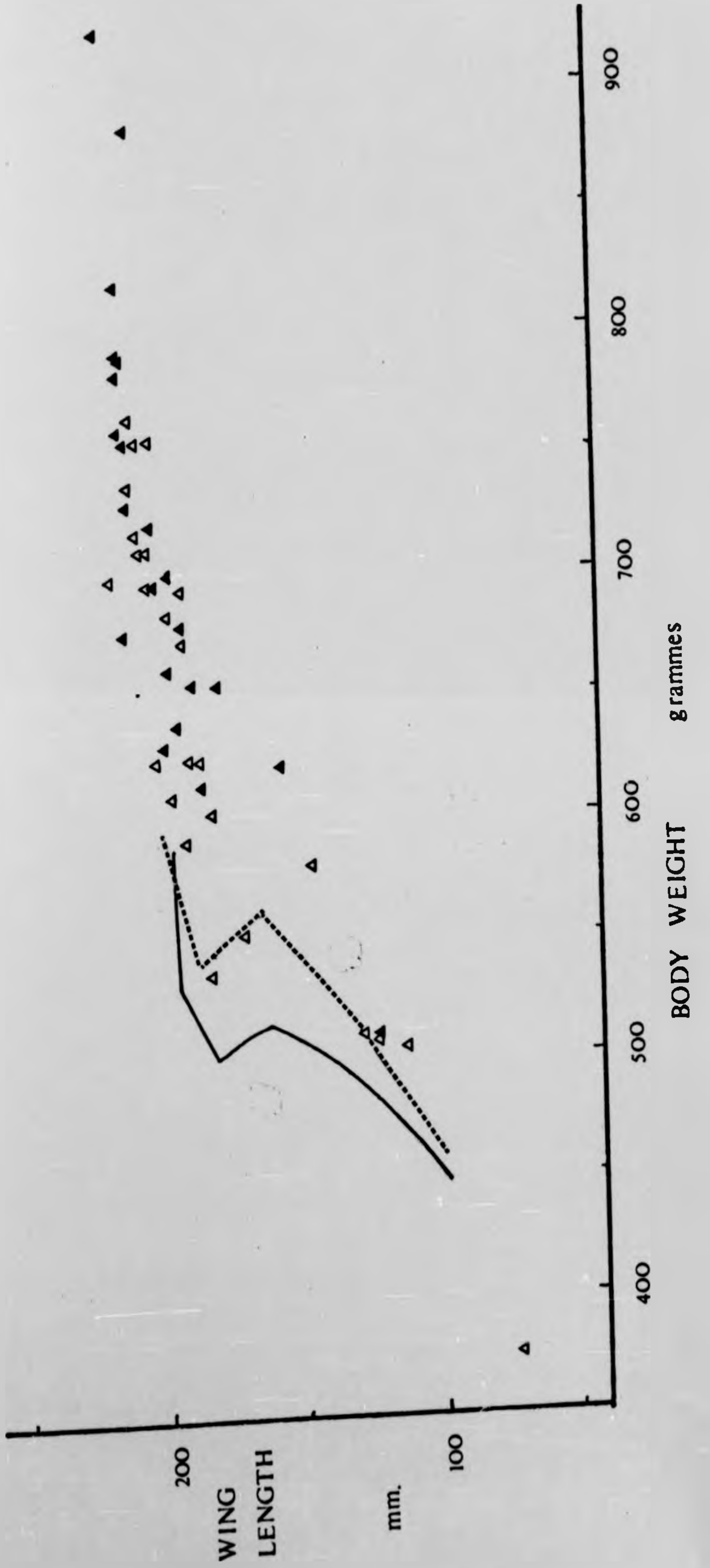
discon-
The lines
ar (1970);



efficiency in the wild birds, or that feather growth and fledging took longer in the wild and therefore birds were heavier when this occurred.

Most of the juveniles obtained in this study were fledged, so my data on body composition is mainly from post fledging birds. There was a steady increase in lean dry material with increasing body weight up to 160g at 700g (Fig. 39). Juveniles had lean dry weights lower than the mean for adults of the same body weight, but the relationship between fat content and body weight was similar in juveniles and adults (Fig. 40), with most of the fat increase occurring above 700g. Several juveniles had more fat than adults, particularly around 500g body weight, which was abnormally low for adults.

The water index is similarly distributed against body weight in juveniles and adults (Fig. 41). High water indices occurred at low body weights, a feature also noted in juvenile domestic and Tufted Ducks by Evans (1969) who suggested that the gradual decrease in water index during growth was part of the attainment of general 'chemical maturity' (Moulton, 1923).

A fledged Tufted Duck weighed on average 650g, which was composed of 470g (72%) water, 140g (22%) lean dry material and 40g (6%) fat.

There was a marked bimodal distribution in the pectoralis weights of juvenile Tufted Ducks (Fig. 42), which changed around 500-600g body weight. This change could be related to fledging, and the use of these muscles for flight. The pectoralis weights of pre-fledging birds represented only 2 - 6% of total body weight, but in

FIGURE 39. Relationship between lean dry material and body weight in juvenile Tufted Ducks. Line represents the median value for adults. ▲ males, △ females.

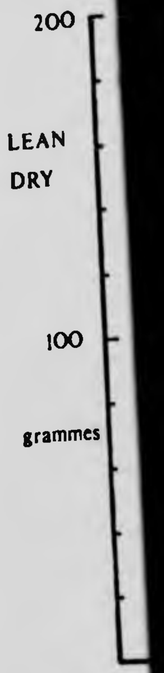


FIGURE 40. Relationship between fat and body weight in juvenile Tufted Ducks. Line would contain values for adult birds of this species (from figure 18) ▲ males, △ females.

body
resents
males.

alues
18)

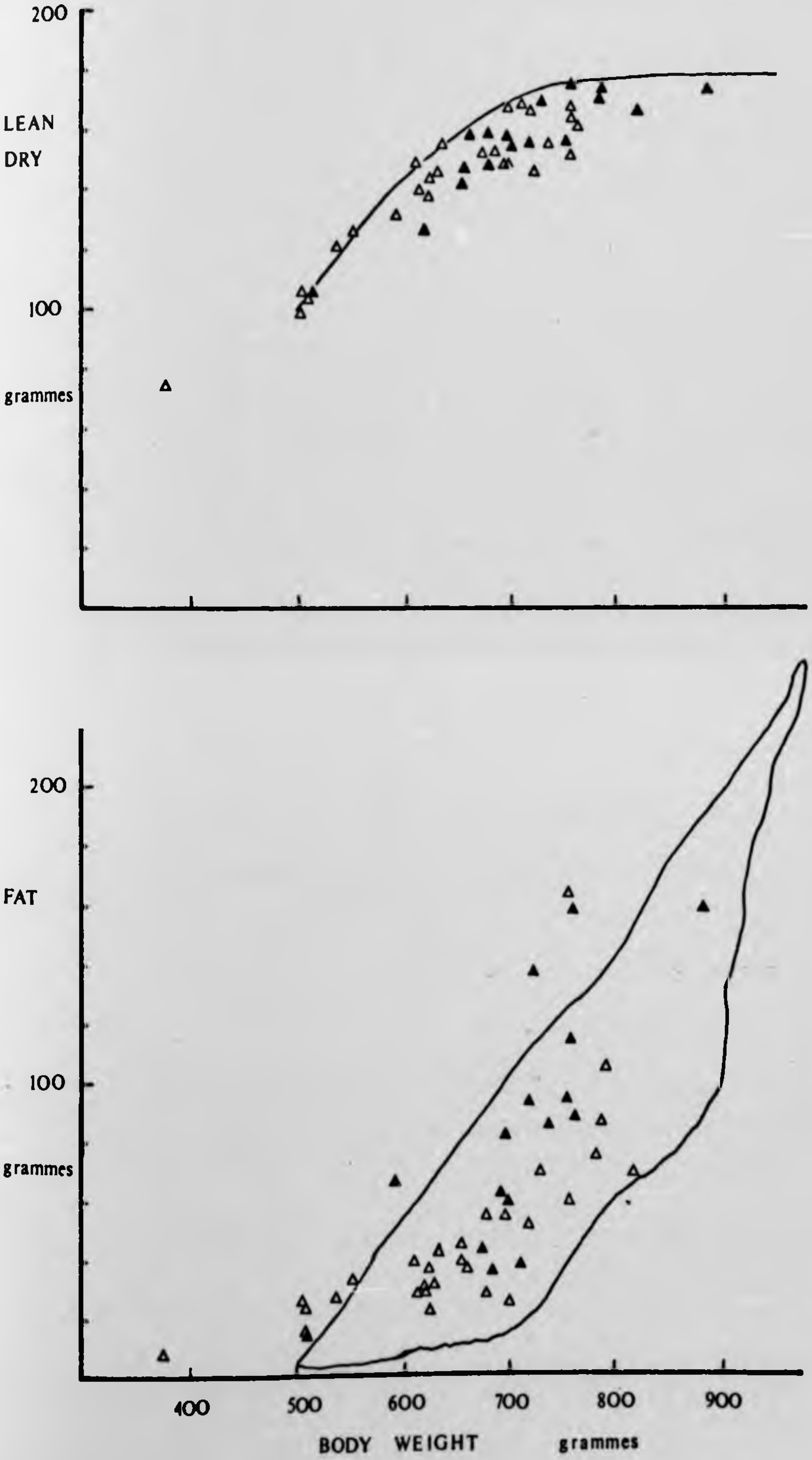


FIGURE 41. Plot showing water index against body weight in juvenile Tufted Ducks. The line would contain all values for adults of this species

▲ males, △ females.

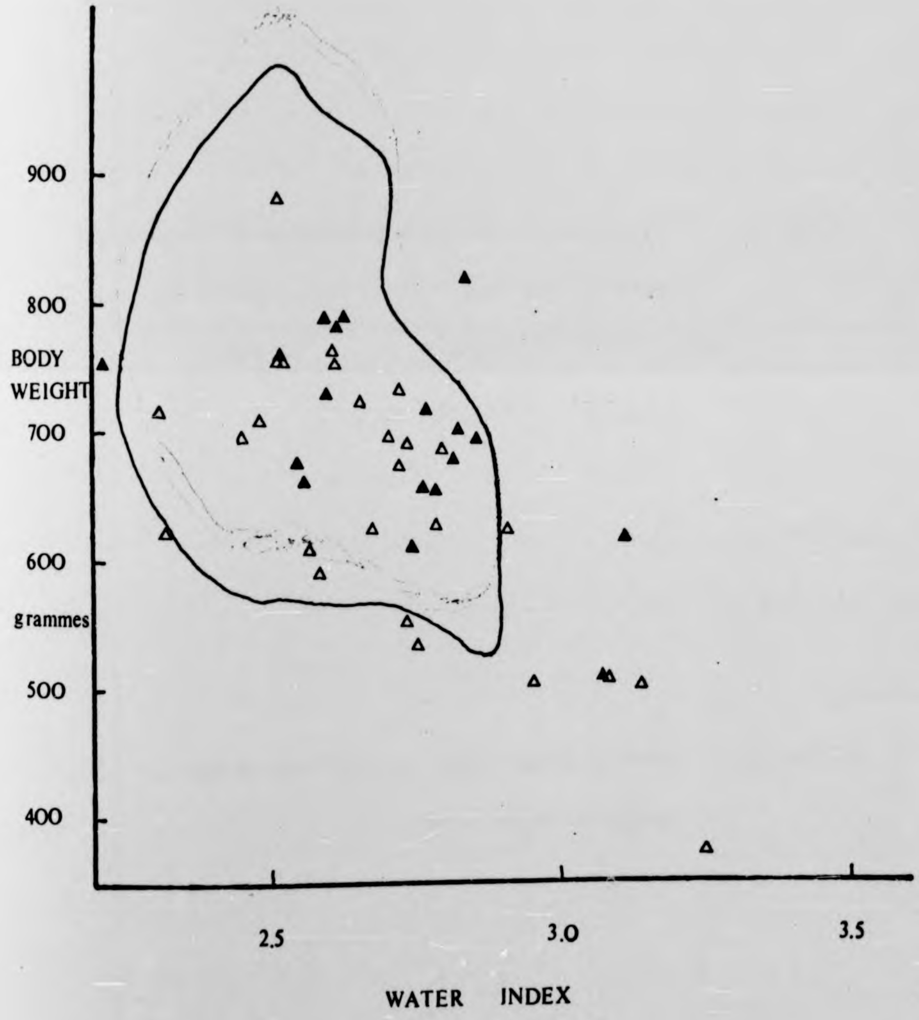

900
800
BODY
WEIGHT
700
600
grammes
500
400
2.5
3.0
3.5
WATER INDEX

FIGURE 42. Pectoralis weight as a proportion of body weight against body weight in juvenile Tufted Ducks. Sexes not separated.

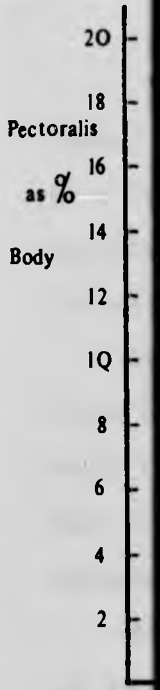
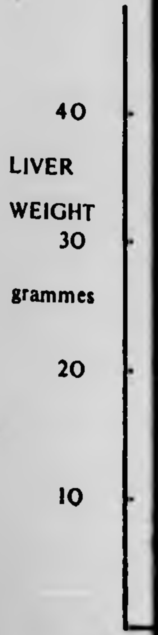
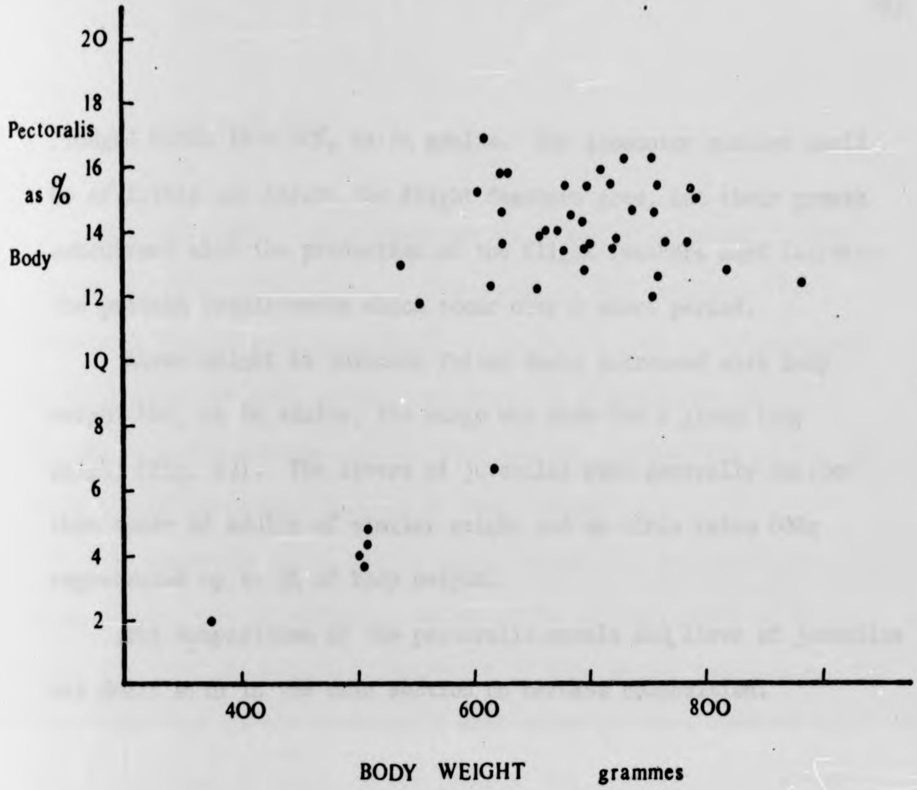
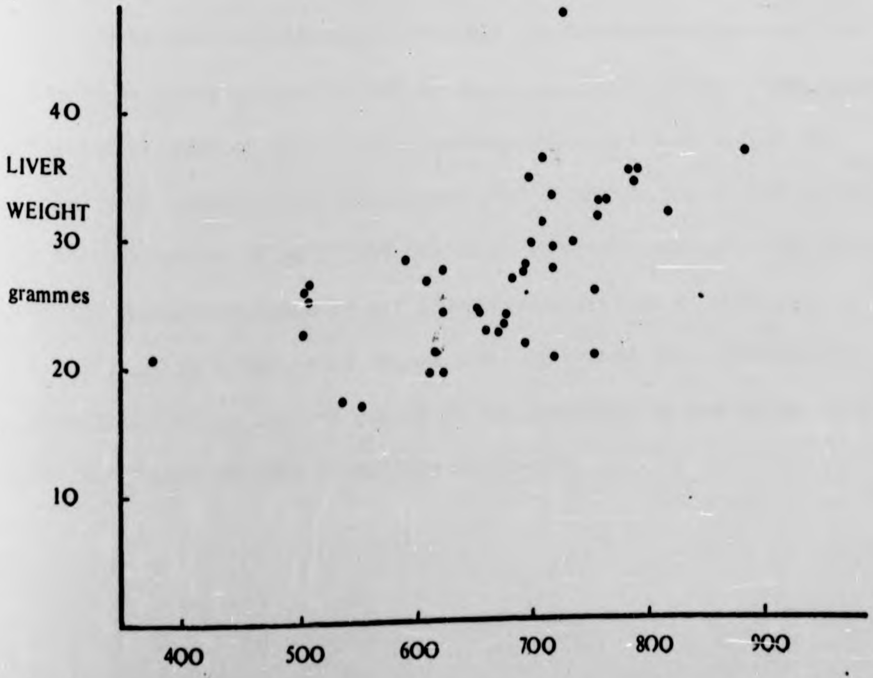


FIGURE 43. Plot of liver weight against body weight in juvenile Tufted Ducks.




20
18
Pectoralis
16
as %
14
Body
12
10
8
6
4
2
400
600
800
BODY WEIGHT grammes


40
LIVER
WEIGHT
30
grammes
20
10
400
500
600
700
800
900

fledged birds 12 - 16%, as in adults. The locomotor muscles would be of little use before the flight feathers grew, but their growth concurrent with the production of the flight feathers must increase the protein requirements which occur over a short period.

Liver weight in juvenile Tufted Ducks increased with body weight but, as in adults, the range was wide for a given body weight (Fig. 43). The livers of juveniles were generally heavier then those of adults of similar weight and in birds below 600g represented up to 5% of body weight.

The composition of the pectoralis muscle and liver of juveniles was dealt with in the main section on carcass composition.

7 THE ENERGY BUDGET

The main aim of this study was to construct an annual energy budget for the Tufted Ducks at Loch Leven, itself necessary to determine the role of these birds in the total Loch Leven ecosystem. Certain parts of this budget, considered in detail, for specific months or for individual birds, also provided information on how the duck itself copes with periods of heavy demand.

In constructing an annual energy budget for the population, the main concern was to determine values of the correct order of magnitude and thus the relative importance of the various components. For each parameter in the equation, a mean value was used, whether this was for numbers of birds on the loch, or for weight or body composition in a given month. No measure of spread was included, because this would become meaningless in calculations involving the products of several values. Where values were critical, for example in dealing with individual birds, the full range of figures was considered.

A population bioenergetics model was developed as part of the Grassland Biome project of IBP by Wiens and Innis (1974). They wrote: "In the absence of direct field measurements, one must couple the relatively scanty field information with values in the literature and a certain amount of sensitive guesswork to obtain realistic estimates of the population dynamics and bioenergetic demands of bird populations". In my study, many values were determined with considerable precision, but at several points it was necessary to use values from the literature or some "sensitive guesswork".

The definitions of the terms used in the classic energy-balance equation, C = R + P + FU, are: C = consumption, the total intake of food; R = respiration, that part of the food intake converted to heat and dissipated in life processes; P = production, the net balance of food transferred to the tissue of a population; FU = rejecta (faeces and urine), that part of the total intake not used for production or respiration (Petrusewicz and MacFadyen, 1970). I have dealt with each of these partitions in turn, and throughout the development of the energy budget, where relevant, I have compared my values with those estimated by the more complex model proposed by Wiens and Innis (1974). In many cases differences arose because their model was based on data from birds of less than 50g body weight, Dickcissels Spiza americana and Horned Larks Eremophila alpestris, whereas Tufted Duck weighed 500 to 1000g.

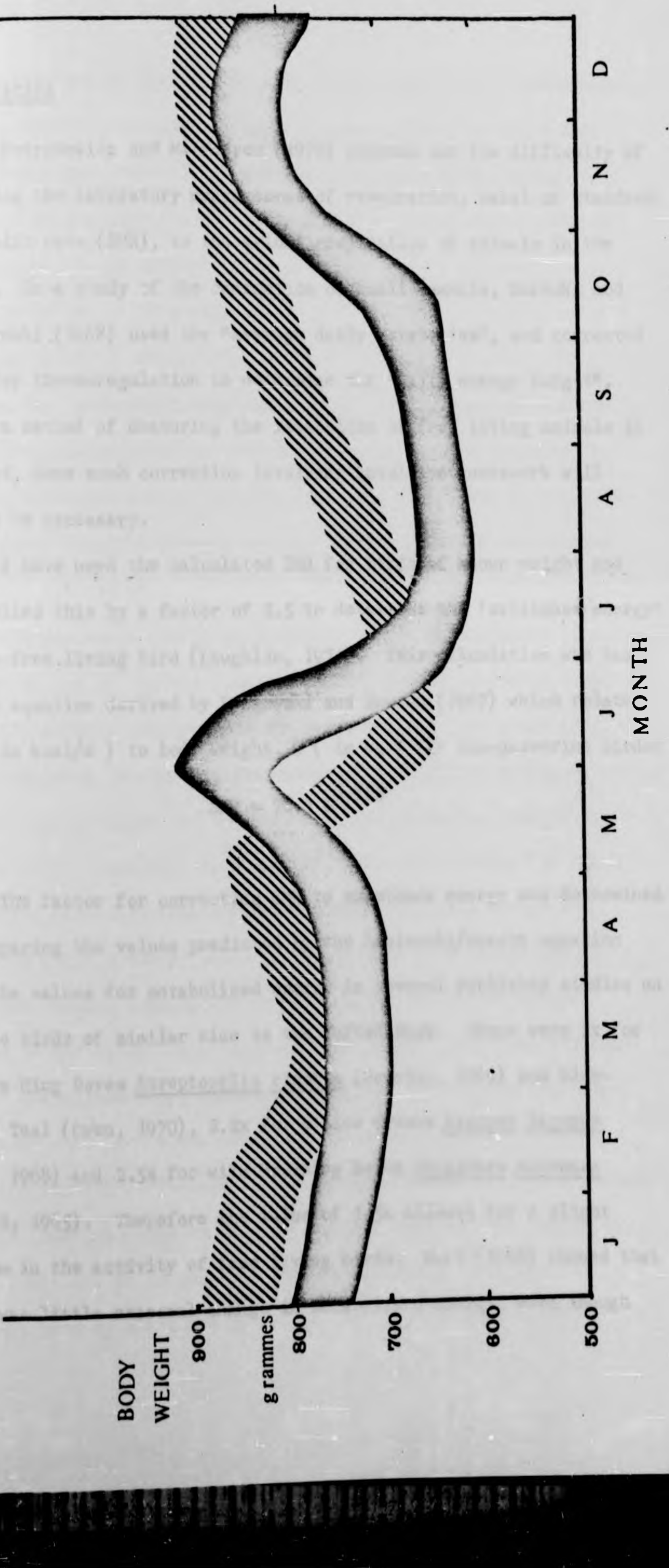
In autumn 1970 an abnormally high population of Tufted Ducks occurred at Loch Leven, and I therefore made a separate estimate for August to November in that year to determine the effect of the increase over normal years (Table 11).

It was necessary to have an estimate of body weight and composition in each month for both sexes to serve as the basis for determining the energy content of individuals (Fig.44). As no males were obtained between July and October, and no females between February and March, the weights in these periods were judged by extrapolation. These estimates may be subject to error for the months concerned, although the total budget will not be unduly altered.

TABLE 11. Monthly Totals for number of 'Bird days' ($\overline{N}$T) spent at Loch Leven by Tufted Ducks. Compiled from figure 1.

	av. popn.	$\overline{N}$T (rounded to 250)		
January	62.5	2000		
February	250	7000		
March	525	16250		
April	1270	38000		
May	1200	37250		
June	1200	36000		
July	1800	55750		
August	2250	69750	+ 500	+ 7000
September	1000	30000	+ 1500	+ 45000
October	500	15500	+ 1750	+ 52000
November	135	4000	+ 650	+ 20000
December	75	2300		
Total		318000		+124000

FIGURE 44. Diagram of seasonal changes in body weight used for calculation of the energy budget. Hatched - males, solid - females.


BODY WEIGHT
grammes
900
800
700
600
500
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

Respiration

Petrusewicz and MacFadyen (1970) pointed out the difficulty of relating the laboratory measurement of respiration, basal or standard metabolic rate (SMR), to the actual respiration of animals in the field. In a study of the energetics of small mammals, Gorecki and Grodzynski (1968) used the "average daily metabolism", and corrected this for thermoregulation to determine the "daily energy budget". Until a method of measuring the metabolism of free living animals is devised, some such correction involving intuitive guesswork will always be necessary.

I have used the calculated SMR for birds of known weight and multiplied this by a factor of 2.5 to determine the 'existence energy' of the free living bird (Laughlin, 1974). This calculation was based on the equation derived by Lasiewski and Dawson (1967) which related SMR (in kcal/d) to body weight, W (in kg) for non-passerine birds:

$$\text{SMR} = 78.3\ W^{0.723}$$

The factor for correcting SMR to existence energy was determined by comparing the values predicted by the Lasiewski/Dawson equation with the values for metabolised energy in several published studies on captive birds of similar size to the Tufted Duck. These were 2x for captive Ring Doves _Streptopelia_ _risoria_ (Brisbin, 1969) and Blue-winged Teal (Owen, 1970), 2.2x for Willow Grouse _Lagopus_ _lagopus_ (West, 1968) and 2.5x for wild Mourning Doves _Zenaidura_ _macroura_ (Schmid, 1965). Therefore the value of 2.5x allowed for a slight increase in the activity of free living birds. West (1968) showed that there was little seasonal change in metabolised energy, even though temperature varied over 50° C. The extra demands of thermoregulation in winter were balanced by increased activity in the summer.

Wiens and Innis (1974) determined R differently, using the equation of Kendeigh (1970) relating the existence energy, EE, to body weight, W, at different temperatures.

At 30° C $EE = 0.54\ W^{0.75}$

At 0° C $EE = 4.4337\ W^{0.53}$

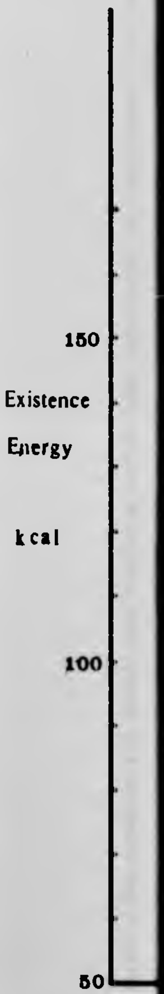
Whereas the Lasiewski/Dawson equation relates to birds at thermoneutrality, Kendeigh's equation incorporates ambient temperature, and his existence energy includes "the energy expended in standard metabolism, specific dynamic action, thermoregulation and limited locomotor activity."

The existence energy requirements can be extrapolated linearly through 0° and 30° C, and I determined the existence energy requirements for several weights over the range found in the study (Fig. 45). Wiens and Innis further modified Kendeigh's existence energy by a factor of 1.4x to "allow for activity over and above the limited locomotor activity permitted by Kendeigh". The calculations for Wiens and Innis' model are therefore more complicated than for my own.

The monthly energy costs of respiration were calculated for males and females (Tables 12a and 12b) using both these methods applied to the estimates of average body weight and population size. For the estimation using Kendeigh's equation the mean monthly air temperatures at Loch Leven were taken from Smith (1974).

The overall difference in the totals calculated by both methods was less than 10%; the monthly differences were largest during the winter (20%) but it is possible that the correction of 1.4x for activity, used by Wiens and Innis, is too high for Tufted Duck in

FIGURE 45. Relationship between existence energy and temperature, calculated for several body weights from Kendeigh (1970).



tempera-

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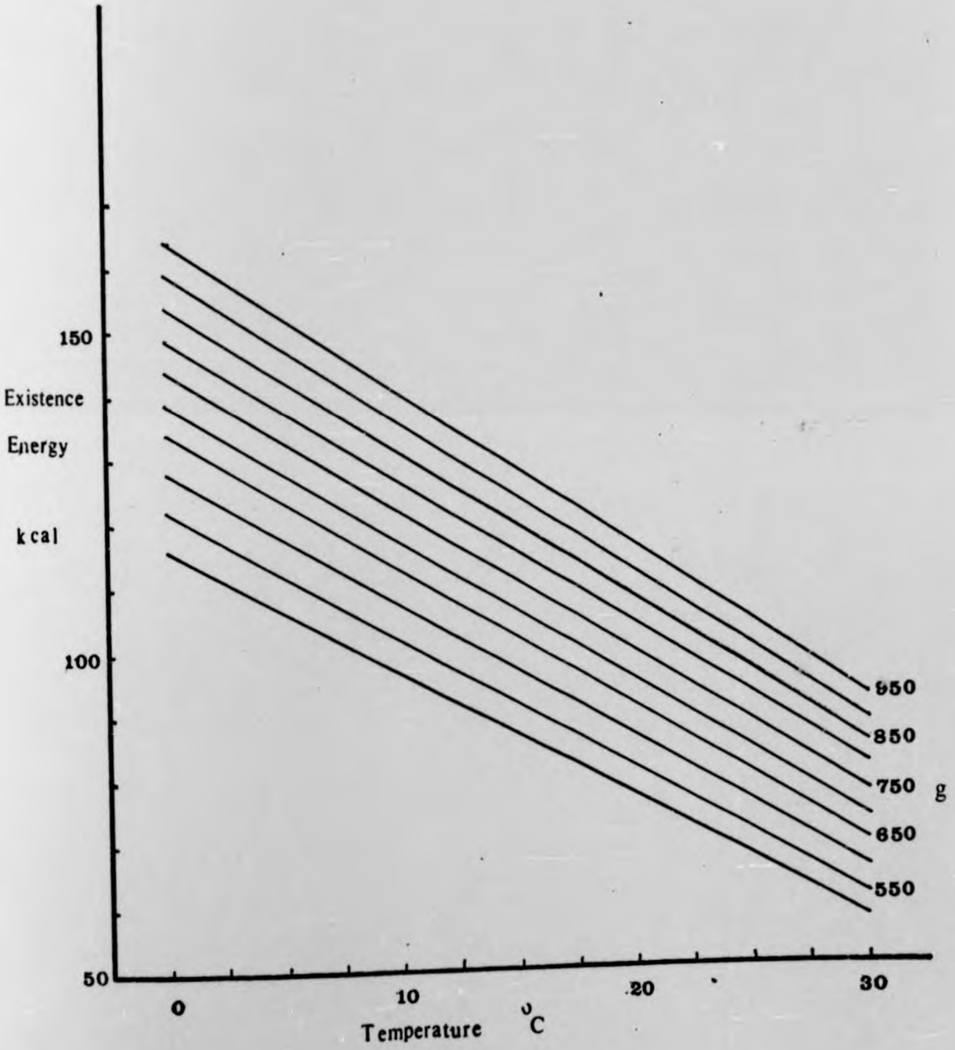


TABLE 12a. Calculation of the monthly Respiration (R) budget for the male Tufted Duck population at Loch Leven. For comparison calculations based on SMR x 2.5 and Existence energy (Kendeigh 1970) x 1.4 are both included. kJ = k cal x 4.1855

	Weight	SMR Lasiewski/ Dawson	Existence energy/bird (SMR x 2.5 x 4.1855)	Population Existence Energy (R)		Mean Temp at Loch Leven	Existence energy/bird (Kendeigh (1970) x 1.4)	Population Total (R')		% Error R' of R
	g	k cal	kJ	kJ x 10^3		°C	kJ	kJ x 10^3		
JAN	850	69.6	728	728		2	873	873		+20
FEB	825	68.1	713	2494		2	861	3014		+21
MAR	775	65.2	682	5543		3	820	6665		+18
APR	800	66.6	697	13241		5	803	15253		+15
MAY	800	66.6	697	12979		8	768	14297		+10
JUNE	675	59.0	617	11112		12	645	11602		+ 4
JULY	700	60.6	634	17675		13	645	17967		+ 2
AUG	720	61.8	647	22552	2263	13	656	22888	2297	+ 2
SEPT	775	65.2	682	10233	15350	11.5	703	10547	15821	+ 3
OCT	825	68.1	713	5523	17815	8.5	773	5994	19337	+ 8
NOV	850	69.6	728	1456	7283	5	832	1664	8321	+14
DEC	875	71.1	744	856		3	873	1004		
				104392	42711			111768	45776	
				147103				157544		+ 7

TABLE 12b. Calculation of the monthly Respiration (R) budget for the female Tufted Duck population at Loch Leven. For comparison calculations based on SMR x 2.5 and Existence energy (Kendeigh 1970) x 1.4 are both included. kJ = k cal x 4.1855

	Weight	SMR Lasiewski/ Dawson	Existence energy/bird (SMR x 2.5 x 4.1855)	Population Existence Energy (R)		Mean Temp. at Loch Leven	Existence energy/Bird (Kendeigh (1970) x 1.4)	Population Total (R')		% Error R' of R
	g	k cal	kJ	kJ x 10^3		°C	kJ	kJ x 10^3		
JAN	750	63.6	665	665		2	873	873		+20
FEB	725	62.0	649	2271		2	861	3014		+21
MAR	725	62.0	649	5271		3	820	6665		+18
APR	750	63.6	665	12644		5	803	15253		+15
MAY	800	66.6	697	12979		8	768	14297		+10
JUNE	775	65.2	682	12280		12	645	11602		+ 4
JULY	620	55.4	580	16159		13	645	17967		+ 2
AUG	640	56.6	592	20654	2073	13	656	22888	2297	+ 2
SEPT	675	57.3	600	9005	13508	11.5	703	10547	15821	+ 3
OCT	750	60.6	634	4918	15861	8.5	773	5994	19337	+ 8
NOV	800	66.6	697	1394	6969	5	832	1664	8321	+14
DEC	825	68.1	713	819		3	873	1004		+17
				99059	38411			111768	45776	
				137470				157544		+ 7

winter. My figures represent an increase of 20% on the Kendeigh existence energy estimate during winter. There does not appear to be any reason to change from the previous method (Laughlin, 1974) of determining R from 2.5x SMR and this estimate has been transferred to the total budget (Table 15).

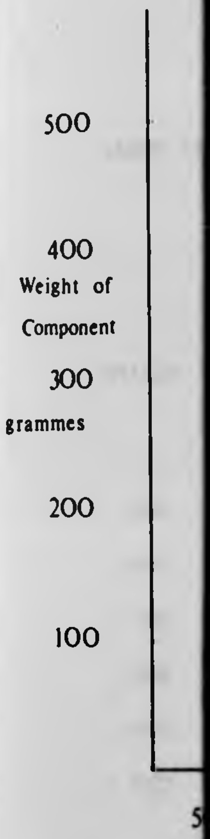
Production

The production (P) is made up of three components: (1) the net change in the biomass of the standing crop during its presence on the loch, ΔB, (2) the production of eggs, (3) the production of young to fledging.

Change in the Biomass, ΔB

It was necessary to convery data on body weight to energy terms. This was done by using a summary of the data on carcass composition described earlier (Fig. 46), calculating the energy content for birds of several weights (Table 13) and constructing a graph of body weight in relation to energy content (Fig. 47). Then by taking the average values of body weight in each month for each sex, the average energy values of the birds were read from the graph. This was plotted at the mid point of each month and the net change in each month read from the graph. These values were then converted to population biomass changes using the population counts. From March to August the pattern of monthly changes was quite different for the two sexes; females increased in weight from March to May and then lost heavily in June and July, during egg laying and incubation, while males lost most during May and June. The net annual increase in biomass of the Tufted Duck population during its presence on Loch Leven was 29×10^3 kJ. In the year of exceptional autumn numbers this increased to 5474×10^3 kJ (188x), though this was still only 2% of the annual budget for respiration. (Table 14.)

FIGURE 46. Carcass composition of Tufted Duck in relation to body weight, all birds except juveniles. Areas are shaded so as to enclose all individual values.



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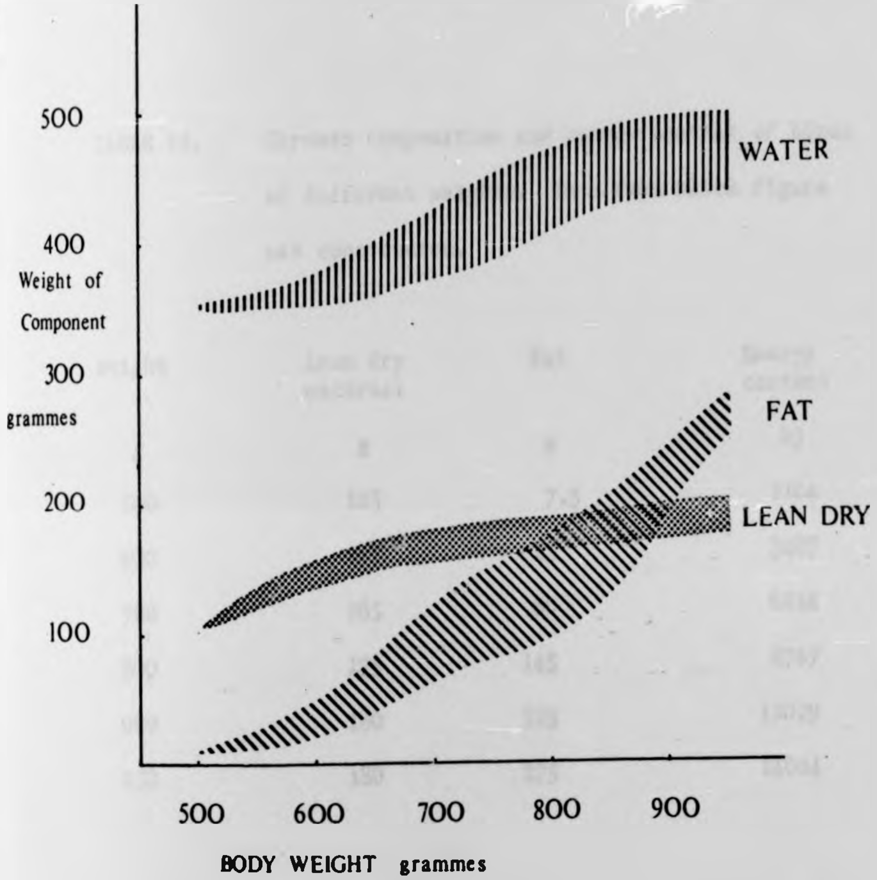
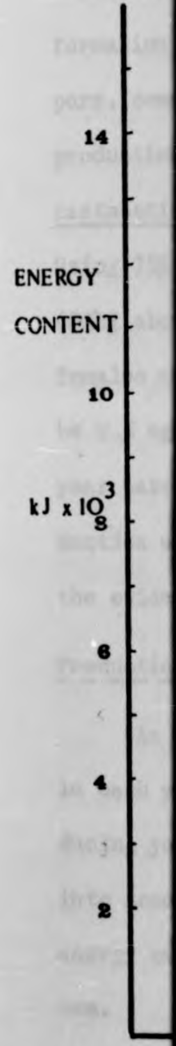


TABLE 13. Carcass composition and energy content of birds of different weights. Data from which figure was constructed.

Weight	Lean dry material	Fat	Energy content
g	g	g	kJ
500	105	7.5	2104
600	145	25	3487
700	165	80	6014
800	175	145	8767
900	180	225	12029
950	180	275	14014

FIGURE 47. Relationship between carcass energy content and body weight, used in calculating the energy budget.



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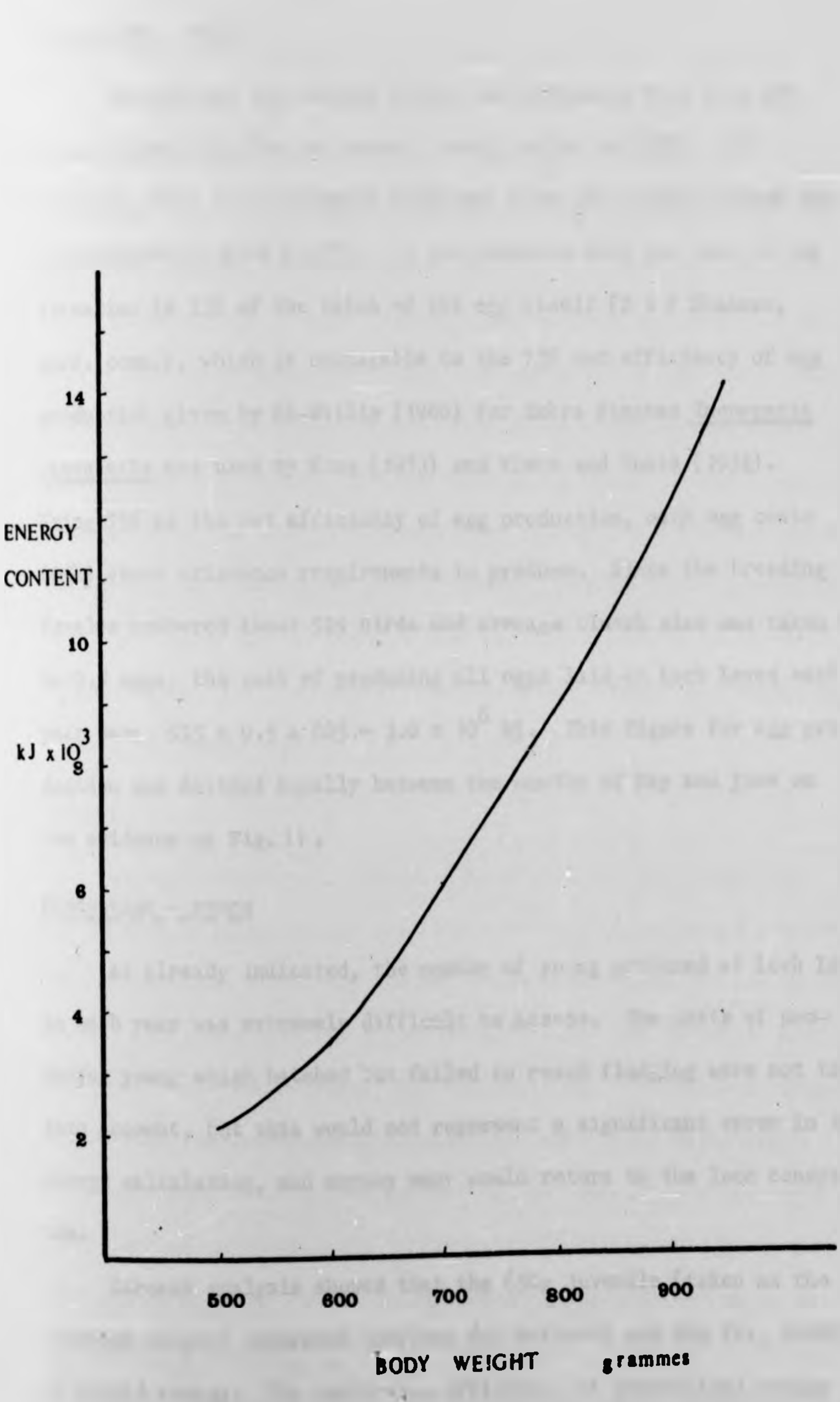
gy budget.



Production - eggs

The average egg weighed 55.5g, and contained 8.2g lean dry material and 7.9g fat, an overall energy value of 455kJ. At 8.20kJ/g, this is not greatly different from the 7.53kJ/g given for anseriformes by King (1973). In the domestic fowl the cost of egg formation is 33% of the value of the egg itself (D W F Shannon, pers. comm.), which is comparable to the 73% net efficiency of egg production given by El-Wailly (1966) for Zebra Finches *Taenopygia castanotis* and used by King (1973) and Wiens and Innis (1974). Using 75% as the net efficiency of egg production, each egg costs 605kJ above existence requirements to produce. Since the breeding females numbered about 525 birds and average clutch size was taken to be 9.5 eggs, the cost of producing all eggs laid at Loch Leven each year was: $525 \times 9.5 \times 605 = 3.0 \times 10^6$ kJ. This figure for egg production was divided equally between the months of May and June on the evidence of Fig. 11.

Production - young

As already indicated, the number of young produced at Loch Leven in each year was extremely difficult to assess. The costs of producing young which hatched but failed to reach fledging were not taken into account, but this would not represent a significant error in the energy calculation, and anyway many would return to the loch ecosystem.

Carcass analysis showed that the 650g juvenile (taken as the fledging weight) comprised 140glean dry material and 40g fat, 4000kJ of stored energy. The conversion efficiency of metabolised energy into body tissue during growth was taken to be 30%, as suggested in a recent review of growth in the domestic fowl (Fisher and Wilson, 1973). This includes the maintenance cost (R) during growth and therefore differs from the growth efficiency value used previously (Laughlin, 1974). The net energy cost of each fledged duckling was therefore 13,300kJ.

Assuming 350 fledged ducklings, as derived earlier, the total energy used in duckling production was 4.6×10^6 kJ per year. This cost had to be apportioned between the three months during which ducklings were growing. This was done by assuming the ducklings were produced with the same distribution as the eggs hatched, and multiplying this by a series of growth curves to estimate the population weight increase in each month. This was approximately in the ratio 1:5:4 in June, July and August, and the total energy expenditure was apportioned accordingly.

Rejecta

It was necessary to consider the efficiency with which the Tufted Duck obtained energy from its food but, as indicated earlier, the assimilation efficiency was not determined experimentally in this study. Published data for digestive efficiency was 70-80% in American Coots and Black Ducks (Penney and Bailey, 1970) and 70-75% in Blue-winged Teal, measured when production was zero. The digestive efficiency must vary between species and between foods eaten. For Trout feeding on chironomids a digestive efficiency of 80% was used (R I G Morgan, 1974), based on published digestibilities of up to 85% for Gammarus, Tubifex and housefly larvae. When considering grassland birds feeding on terrestrial insects and seeds, Wiens and Innis assumed that 70% of the energy intake was metabolically available.

I therefore have used 75% as the digestive efficiency of the Tufted Duck feeding at Loch Leven and this was applied to the net energy costs of respiration and production (Table 14).

The figures for respiration, production and rejecta gave the total energy consumption by Tufted Duck at Loch Leven (Table 15). This was then converted to a per m^2 basis over the loch as a whole in order that comparisons could be made with other values determined for the ecosystem. In the year with a large persistent population, the energy budget increased by 40% over the more normal year. The major cost in the budget (73%) was respiration; total production represented only 2% of the energy budget in normal years and 3% in 1970. In determining the annual energy budget in this way, the most important figures are the population data and the changes in body weight through the year, since these form the basis of the respiration value. The two different approaches to determining respiration did not lead to any major difference in the total budget. When considered in the context of the total budget, the figures for the production of eggs and young are relatively insignificant, but they are of considerable importance in the budget of individual birds.

Some details in the energy budget of individuals

Between March and July the female Tufted Duck built up her reserves, laid and incubated eggs and reared young. It was therefore of value to investigate the energy budget over this period in some detail.

The birds taken during egg formation averaged 865g with eggs and ova, and 820g when the latter were removed. It was difficult to

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TABLE 14. Calculation of the monthly Biomass change (ΔB) for the Tufted Duck population at Loch Leven.

	M A L E				:	F E M A L E				:	BOTH SEXES	
	Mean Wt.	Mean Energy Content	ΔB/birds. month	ΔB/population. month		Mean Wt.	Mean Energy Content	ΔB/birds. month	ΔB/population month		B	
	g	kJ	kJ	kJ x 10^3		g	kJ	kJ	kJ x 10^3		kJ x 10^3	
JAN	850	10400	-850	-27		750	7400	-1450	-47		-74	
FEB	825	9600	-1150	-144		725	6700	-350	-44		-188	
MAR	775	8100	-400	-105		725	6700	+350	+92		-13	
APR	800	8750	+300	+190		750	7400	+1050	+665		+855	
MAY	800	8750	-1750	-1050		800	8750	+300	+180		-870	
JUNE	675	5300	-1350	-810		775	8100	-2400	-1440		-2250	
JULY	700	6000	+600	+540		620	3850	-1900	-1708		-1168	
AUG	720	6550	+1100	+1237	+124	640	4300	+300	+337	+34	+1574	+158
SEPT	775	8100	+1550	+775	+1163	650	4600	+850	+425	+637	+1200	+1800
OCT	825	9600	+1100	+275	+887	700	6000	+2150	+538	+1734	+813	+2621
NOV	850	10400	+850	+57	+283	800	8750	+1750	+117	+583	+174	+866
DEC	875	11300	0	0		825	9600	-650	-24		-24	
				+938	+2457				-909	+2988	+29	+5445

assess the weight just before egg formation commenced, but 850g seemed a likely figure. Four estimates of body weight at the beginning of incubation were available from the four regressions (Table 6). These varied from 696g to 740g, and therefore 720g was used here, which gave a weight loss during egg formation of 130g. This comprised 94g fat, 8g lean dry material and the rest as water, roughly 3850kJ in all. An average clutch of eggs (9.5) contained 78g fat and 75g of lean dry material, and its production (assuming 75% efficiency) added 5748kJ to the energy budget of the female. Therefore the major requirement for the female during laying was 70g of the 78g lean dry material needed for egg production, since she evidently provides all the fat and over 65% of the energy requirements for egg production from her reserves.

The costs of egg production are distributed over the period from when the first ovum begins to enlarge to the laying of the last egg. Maximum production of egg material is reached in the 24h before the first egg is laid and begins to slow down 5d before the last egg is laid, when no new ova are enlarging. This maximum daily need will not be more than the cost of the largest egg, since it is the sum of the daily additions to each of the developing ova. If the ovum begins enlarging five days before the ovulation (or six days before oviposition) then the maximum production must be maintained for (clutch size -6) days. During this period the costs of daily egg production, 605kJ, represent an increase of 88% on the normal daily existence energy requirements (2.5 x SMR).

After egg laying the bird must retain sufficient reserves to allow her to successfully incubate the clutch. During incubation, weight loss was estimated at 6g per day, 2.37g fat and 0.87g lean dry material, which would provide 110kJ d^{-1}. The SMR of a 670g bird (the weight at 12d incubation predicted from the regression) is 245kJ and this must therefore represent the minimum requirements. Metabolism of body tissue would provide only 45% of this need and a smaller proportion of the actual metabolic costs of incubation. These costs are difficult to assess, but in the Zebra Finch metabolised energy increased by 10-15% during incubation over the pre-laying level (El-Wailly, 1966). Assuming some activity is essential for feeding, then the actual existence energy requirements during incubation could be as high as 1.5x SMR, 368kJ. The female would then need to collect 258kJ per day during incubation. Thus the female provided 30% of her energy requirements during incubation from body reserves and 70% from food eaten at the time, but the latter may be increased in years of good food supply.

I obtained little information on which to make estimates of energy costs for individual females after incubation was finished. Three of the four females taken in October still weighed less than 650g and one was still moulting her remiges. This would suggest that the females do not recover from breeding and moulting until well into autumn.

Turning now to the male, the most obvious feature in the energy budget is the rapid weight loss during May and June, around 125g or 3100kJ. It is not possible to say how much this loss resulted from reduced feeding and how much from increased activity during courtship. None of the males shot in June had begun their wing moult, so this did not contribute. Two of the three males shot in October were over 850g body weight indicating that they recovered before the females.

In the event of ice cover, it is relevant to assess how long Tufted Duck could last without food, given the weights I found. Since temperature is important in this situation I have used Kendeigh's estimate of existence energy requirements at 0°C, as this includes the costs of thermoregulation. Taking a 950g bird and assuming it could lose at least 200g without major distress; this weight loss would provide 6700kJ and the daily requirement of a bird of mean weight 850g is 640kJ. Thus this bird could last 10.5 days without food. A further reduction to the very low weight (in winter) of 650g would yield 2700kJ which with a new daily requirement of 580kJ would last a further 4.5 days. Thus the reserves become progressively less valuable as they are used up. This example is an extreme case, as many birds may be lighter to begin with and air temperatures may go below 0°C. It does however indicate that the birds could sit out long periods of ice cover, possibly by shifting to salt water (Thom, 1969). Even allowing for the increased energy expenditure of flying, these birds have adequate reserves to allow time to find open water in the event of cold weather and icing.

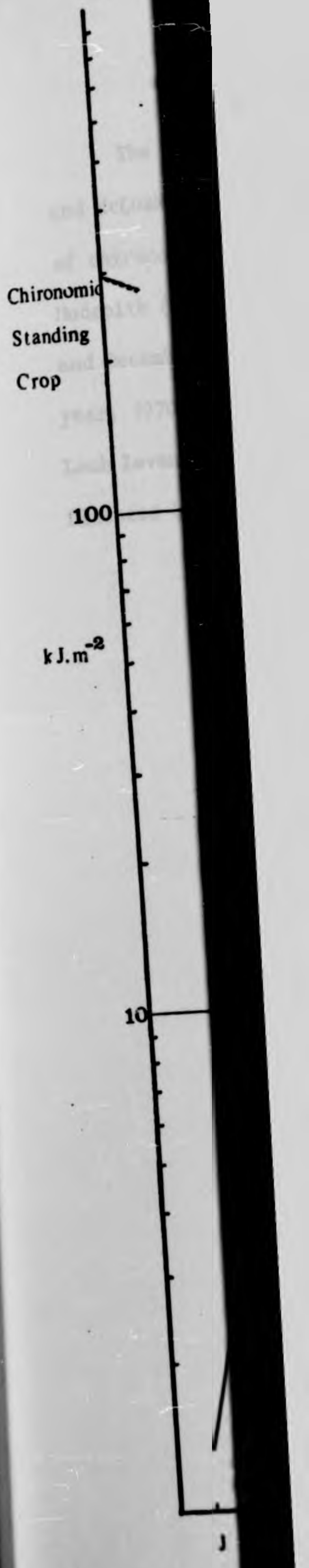
The food energy available in the ecosystem

Work on the zoobenthos in the IBP project at Loch Leven mainly concerned the estimation of production of larval chironomids (Maitland and Hudspith, 1974; Charles *et al*. 1974). From the data on numbers and dry weights of different species in different months, and those given by MacFarlane and McLusky (1974), I have produced a crude estimate of the monthly standing crop of the main chironomids at Loch Leven. The most complete sets of data were available for May 1970 - December 1971 and some figures were missing in certain months, but they still provide an indication of the seasonal changes in food supply (Fig. 48). On the figure, I have also shown the calculated requirements of the Tufted Duck at Loch Leven through the year.

The minimum standing crop of chironomids was in July in 1970 and June in 1971, and these were 10 - 100 times less than those in other months. Eggs were laid during the period of declining biomass of chironomid larvae and in 1971 some birds were still laying when the minimum occurred. This reduction in standing crop of the larvae was however associated with the emergence of adults, and they were abundant during much of this period. In June 1971 the standing crop of larvae, 3kJ m^{-2}, approached the monthly energy requirements of the Tufted Duck population, and in this month when most birds are incubating such a reduction in the food supply was critical, as the variety and abundance of alternative foods was limited (Maitland and Hudspith, 1974). Hatching success in 1971 (45%) was significantly worse than in 1970 (71%) (N & C, 1975).

In 1971 the main duckling hatch occurred during the period of minimum biomass of chironomid larvae but in 1970 the minimum occurred later and emerging adults and larvae would be available for many newly hatched ducklings. In both years the biomass of larval chironomids exceeded 100kJ/m^2 by August, at which time ducklings from the peak hatch would be one month old and growing rapidly.

FIGURE 48. Seasonal changes in the standing crop of the main species of chironomid larvae of the zoobenthos at Loch Leven (left scale) and the monthly energy consumption for the Tufted Duck population (right scale).



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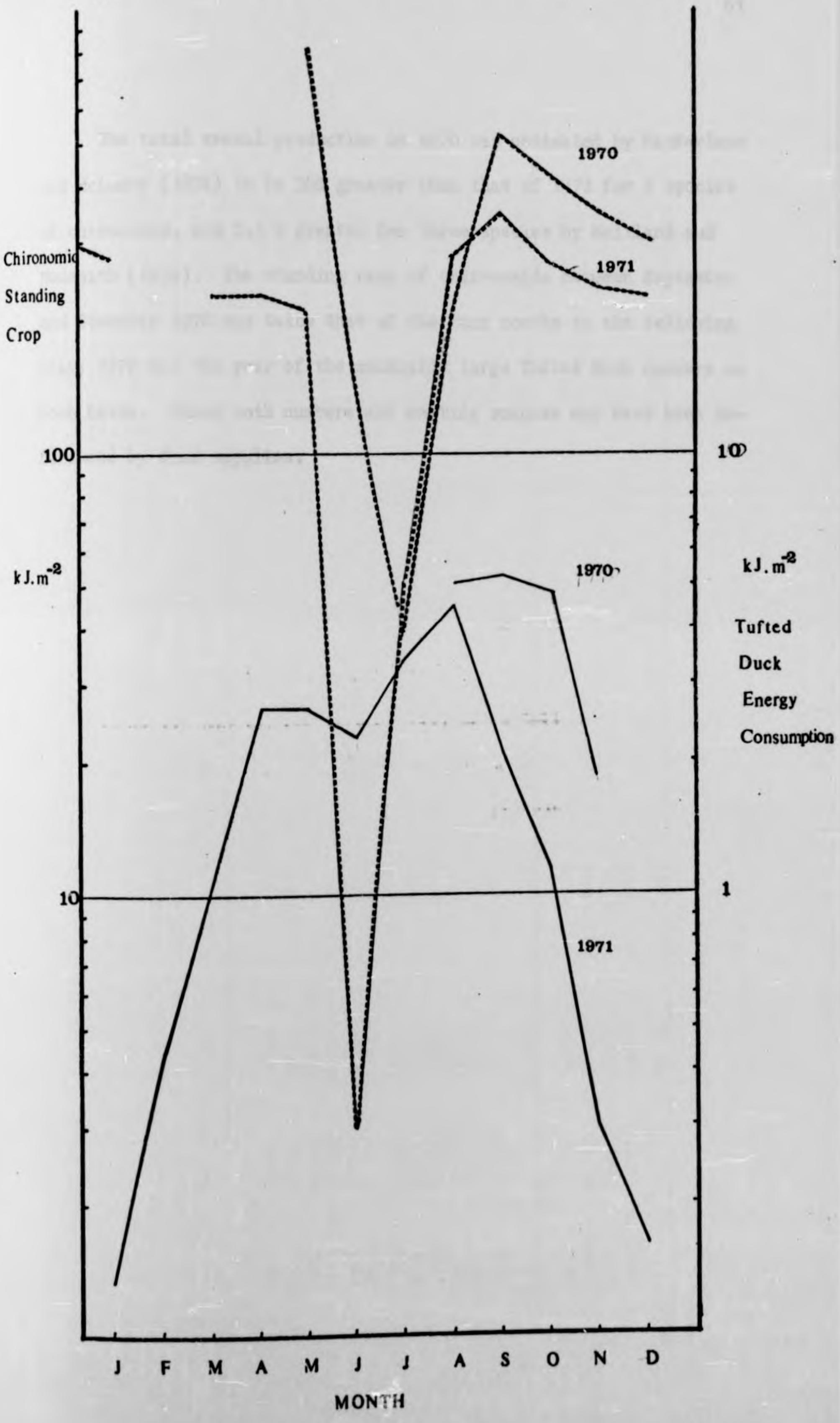

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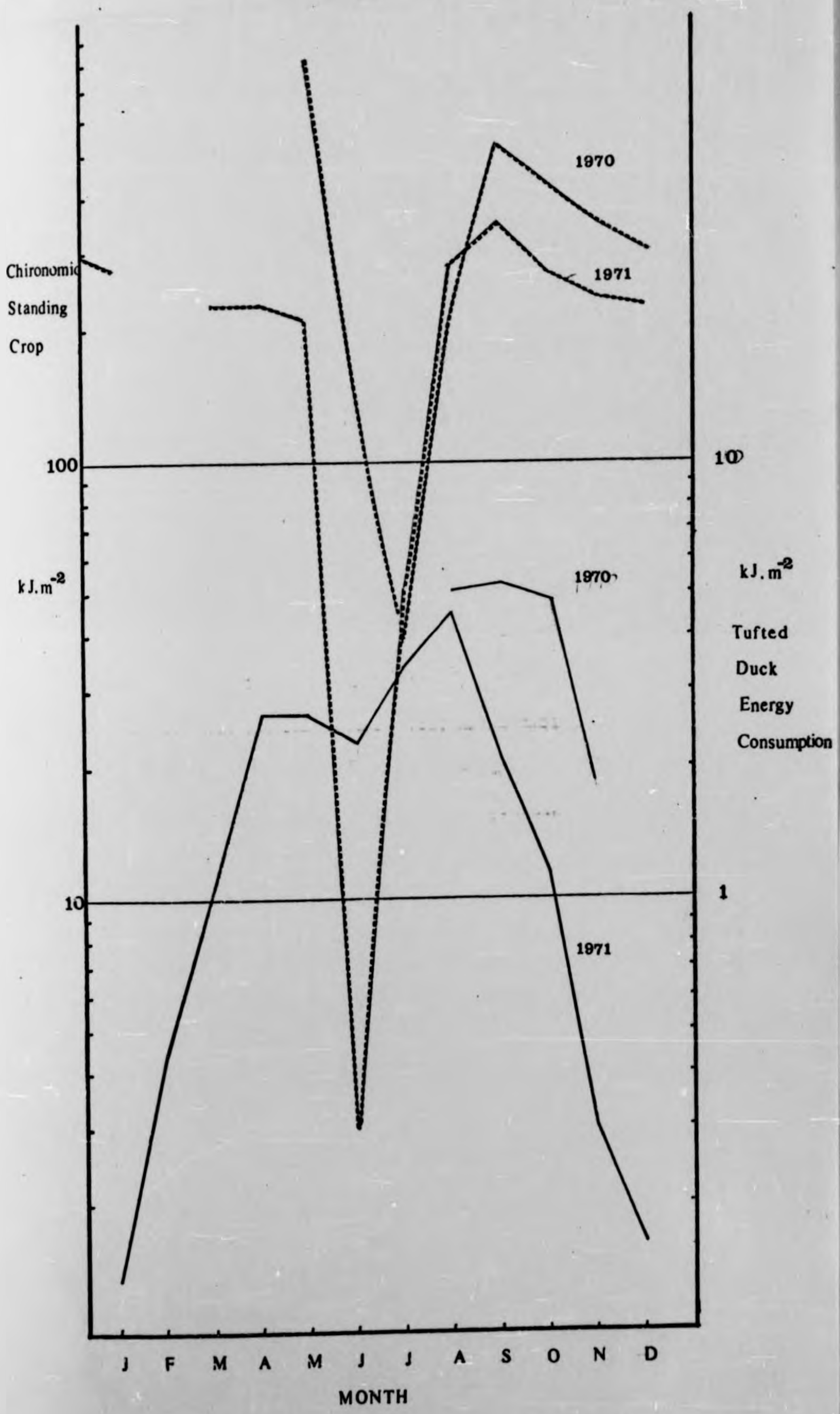

The total annual production in 1970 was estimated by MacFarlane and McLusky (1974) to be 36% greater than that of 1971 for 5 species of chironomid, and 2.5 x greater for three species by Maitland and Hudspith (1974). The standing crop of chironomids between September and December 1970 was twice that of the same months in the following year; 1970 was the year of the unusually large Tufted Duck numbers on Loch Leven. Hence both numbers and nesting success may have been influenced by food supplies.

TABLE 15. Total energy budget for Tufted Ducks at Loch Leven, month by month.

	No. of Ducks	Respiration	Biomass Change	Production (Eggs)	Production (Young)	Rejecta		Total Consumption
	$\overline{NT}$	R	ΔB	P(E)	P(Y)	FU	C	C
		←———	——— kJ x 10^3	———	———	———	———→	kJ/m^2 . month
JAN	2000	1393	-74			440	1759	0.1323
FEB	7000	4975	-188			1496	5982	0.4497
MAR	16250	10814	-13			3600	14401	1.0828
APR	38000	25885	+855			8913	35653	2.6806
MAY	37250	25958	-870	1500		8865	35461	2.6662
JUNE	36000	23392	-2250	1500	460	7617	30467	2.2908
JULY	55750	33834	-1168		2300	11272	45088	3.3900
AUG	69750	43206	+1574		1840	15233	60933	4.5810
SEPT	30000	19238	+1200			6812	27250	2.0489
OCT	15500	10441	+813			3751	15005	1.1282
NOV	4000	2850	+174			1008	4032	0.3032
DEC	2300	1675	-24			550	2200	0.1654
TOTAL		203361	+29	3000			278231	20.9196
AUG	7000	4336	+158			1498	5992	0.4505
SEPT	45000	28858	+1800			10219	40877	3.0735
OCT	50000	33676	+2621			12099	48396	3.6388
NOV	20000	14252	+866			5039	20157	1.5156
subTOTAL		81122	5445				115422	8.6784

8 DISCUSSION

Feeding Behaviour of Tufted and other Diving Ducks

Although Dewar (1924) collected many data on diving birds, he did not discuss their implications on feeding efficiency. The time taken for dives to any given depth was similar for the three species considered here and, at depths greater than one metre, the relationship between the depth and time was linear. This implies that if a bird travels through the water at constant speed it should spend a similar period on the bottom at all depths. This would be ten seconds at depths greater than one metre. The alternative explanation is that the bird accelerates during the dive and the return, and thereby spends progressively longer on the bottom at increasing depths. This explanation requires that the bird "knows" the depth, and times its foraging accordingly. I have assumed that the first explanation is the most likely.

Goldeneye diving more than 0.8m had dive: surface-pause ratios varying from 2.5 to 3; but this showed no clear trend with depth, and Nilsson (1969) concluded from this that the birds dived with equal economy in both deep and shallow water. Dewar's data indicated an increase in the dive: pause ratio from 2 to 3 as depth increased; i.e. the pause time increased with the dive time, although not proportionately. A dive and pause sequence took 25s at 1m and 40s at 3m. Therefore if unit time was spent on the bottom for each dive then feeding at 3m would be temporally less efficient than at 1m. Taking these values over a continuous feeding period of one hour, the number of dives at 1m and 3m would be 144 and 90 respectively. An increase in depth from 1m to 3m would therefore decrease the time spent in food gathering by 40%. To spend an equal period on the bottom at 3m would take a total feeding time of 1h 36min. Longer periods of feeding in greater depths presumably require the experditure of more energy and so, to feed efficiently, the bird must balance the amount of food available at various depths with the time required to gather it.

Possibly the potential feeding areas for Tufted Duck at Loch Leven are limited in the first instance by depth, since diving to greater depths becomes progressively less efficient. The deepest dive which Dewar (1924) recorded for the Tufted Duck was 4.5m, but few dives exceeded 3m. Masden (1954) stated "the species feeds mainly at smaller depths, 1-2m but may dive to 5m", and at an estuarine site in Sweden the 3m contour was regarded as the limit of the Tufted Duck feeding area (Nilsson, 1969; 1970). The areas used for feeding by the Tufted Duck at Loch Leven represent only 40% of the area less than 3m, so factors other than depth are also restricting. Tufted Duck do not appear to use the extensive shallow (sandy) area along the north east shore of the loch. Until 1950 this area was choked with an impenetrable growth of weeds, rendering it almost useless to bottom feeding ducks (A & N, 1974). This area now has a rich invertebrate fauna including chironomid larvae (Maitland and Hudspith, 1974), but was classified as 'wave dominated' by Smith (1974). Perhaps it is its exposure that makes it unsuitable for diving ducks, but shallowness combined with the wave action may also cause the benthic animals to burrow more deeply in the substrate, making them unavailable to ducks.

The Tufted Ducks at Loch Leven fed by night. This was also the case in southern Sweden (Nilsson, 1969; 1970), where birds were observed flighting from the resting areas about 40 minutes after sunset and arriving back before sunrise. At a second lake which was used both as a resting and a feeding site, Nilsson noted a general dispersion of the birds from the resting areas at dusk. During periods of cold weather, however, these birds fed during the daytime and the intensity of daytime activity was inversely correlated with the daily mean temperature.

There were no differences between the four duck species in the time taken for feeding at a given depth, nor in their preferences for feeding depth. This suggests that there were no species differences in the efficiency of feeding at a given depth. At a given site, different species dived to the same depth, and at different sites all 4 species showed different depth preferences (Dewar, 1924). It is therefore unlikely that differential diving depths would reduce any competition for food at Loch Leven between the four species of diving duck which occur there.

One possible advantage of night-time feeding to Tufted Duck is that certain species of chironomid larvae are more available then. At Loch Leven these larvae periodically leave the substrate and become planktonic (Davies, 1974), and during 24h studies of zooplankton, Walker (1970) collected chironomids from the water column only at night. A similar night-time peak of planktonic activity by larval chironomids was observed in certain Canadian lakes (Mundie, 1959; Hamilton, 1965). Thus animals which are normally unavailable to the Tufted Duck owing to their depth in the substrate may become available at its surface during this nocturnal migration and may partly explain the predilection for night-time feeding in the Tufted Ducks at Loch Leven. In view of the darkness, and from observations of feeding behaviour it is unlikely that the Tufted Duck would take the larvae from the water column.

One alternative possibility, that night-time feeding in the Tufted Duck could have been an anti-predator function is unlikely, since except when nesting, I know of no predators other than man and anyway similar pressures would apply to the Goldeneye, which fed by day. Nilsson (1969) also observed that Goldeneye in Sweden spent most of their day seeking food, while several authors (Breckenridge, 1953; King, 1961; Linsell, 1969) have noted evening gatherings to roost on open water.

In comparison, Pochard fed equally by day and by night (Klíma, 1966), and Olney (1970) suggested that since their foods were mainly vegetative and belonged to the benthos, they were little influenced by differences between light and dark. At Loch Leven feeding during darkness would be little different from during the daytime since for much of the year little light penetrated beyond 1m owing to the dense algal bloom (Bailey-Watts, 1974).

Thus the three species of diving ducks, which occur regularly at Loch Leven, differ in diurnal rhythm of feeding, probably according to diurnal availability of the respective foods, or to the total food needs of the birds themselves.

Food of the Tufted Ducks

An important feature of the food habits of the Tufted Duck almost everywhere that it has been studied is the predominance of a single food item. At Loch Leven chironomid larvae formed the main food during summer; and studies by Madsen (1954) in Denmark, Olney (1963) in various parts of Britain, and Nilsson (1969) in Sweden, on birds shot in the autumn, all reported molluscs to be of prime importance, though at one site Olney found the crustacean Asellus to predominate. In the only other studies of summer feeding, at Lake Myvatn, Iceland, chironomid larvae and the molluscs Limnea and Pisidium predominated (Bengtson, 1971).

A further common feature of Tufted Duck foods is that they all belong to the benthos; the plant seeds are presumed to lie on the bottom mud. When examining the gut contents of Tufted Ducks it was noticeable that all items from a single bird were usually of one type or, when more than one type was present, all were of a similar size. A possible method whereby the birds 'hoover' the substrate and select and retain items of a particular size was described earlier, and for feeding to be efficient the Tufted Duck probably requires a large number of densely aggregated food items of similar size.

In view of this conclusion, the importance of molluscs in the food studies of Madsen (1954) and Nilsson (1969) was probably a reflection of the importance of this group of animals in the estuarine benthic fauna. In fact seasonal changes in the food of ducks corresponded sufficiently well to the general composition of the fauna for Nilsson to determine a change in the feeding sites from a muddy bottom in autumn and spring to the Zostera marina meadows in deeper water during December. Olney suggested that at two sites where the diet included 30% plant material the varied diet occurred because no single food item was present in sufficient abundance.

In my own study the birds did not show any distinct food preference during winter, either at Loch Leven or at Airthrey Loch. Although individuals took a large meal of a single item, each took whatever food was available. Perhaps in winter there were no large aggregations of food items in these waters, although estimates of standing crop suggested that large numbers of chironomids were present at Loch Leven during the winter (Maitland and Hudspith, 1974; Charles _et al_., 1974). However, Davies (1974) did not record any planktonic activity by chironomid larvae between October and March. Therefore if this behaviour is important in making the chironomids available to Tufted Ducks, then its cessation during these months may explain the reduced numbers of birds on the loch during the same period. This indicates the importance of considering the availability of food to the predator, and not just its physical presence in the habitat.

Thom (1969) explained the small numbers of birds present on Loch Leven in winter on the basis of weather, in particular the threat of ice. However this rarely lasted more than two weeks (Smith, 1974), and birds on other waters of the Forth-Tay region remained until these waters froze over and then moved only to the nearest free water or onto the Forth estuary. Thus the departure of Tufted Duck from Loch Leven during the autumn is more likely to result from reduced food availability, especially in view of the larger autumn numbers in years of good total food supply.

Food of other diving duck species at Loch Leven

Most of the Goldeneye taken at Loch Leven during winter had eaten some chironomids, but more than a quarter took caddis larvae, and a similar number the crustacean Asellus. The latter was found only in birds taken in winter. One of the Tufted Ducks had taken a large number also, which indicated that at this time the diving ducks may be feeding in a different area possibly with a stoney substrate, of the loch, from that used in the summer.

The single Scaup examined had fed on chironomid larvae, but Scaup are rare visitors to Loch Leven. Pochard occur irregularly but then often in large numbers, e.g. peak numbers of several thousands occurred in June 1966, January, 1967 and October 1968 (A & N, 1974). My own studies gave little indication whether these birds fed on the loch or merely rested there. Pochard were known to feed on the Forth estuary and possibly one of their main reasons for visiting Loch Leven was to roost. The only bird examined which contained food had taken a large number of chironomid larvae. From data in a review of Pochard foods (Olney, 1970), I estimated that 90% were from plants. In recent years up to 1970, the macrophytic vegetation at Loch Leven was very restricted, and in 1966 no fruiting higher plants were found (Pollard, 1966). Therefore during this period if food attracted Pochard to Loch Leven it must have been animal, probably chironomid larvae, which have been recorded as foods elsewhere (Game Conservancy, 1971). From 1970-72 when Potomageton returned to the Loch, Pochard shot in the autumn had fed on the buds of these plants (A & N, 1974).

To summarise, there appeared to be little competition for food between the diving duck species at Loch Leven, mainly because they rarely occurred on the loch together in large numbers. Further, the Tufted Ducks and Goldeneye fed at different times in the 24 hours, and possibly in different areas (over different substrates) of the loch. The meagre data on Pochard suggested that they mainly fed on plant material except when large numbers of chironomid larvae were available.

Possible effects of food supply on Duck numbers.

Tufted Duck are particularly well adapted to gather foods which occur on the bottom in fairly dense aggregations at depths of less than 3m. These are just the sort of feeding opportunities which have increased in recent years, in both Britain and Europe, and may at least partly account for the increase and spread of Tufted Ducks. The many new reservoirs and flooded gravel pits are characterised by uniform depth and relatively simple ecosystems in which one or two benthic organisms predominate. Also in natural lakes, both in Britain and Europe, a loss of variety is associated with the widespread eutrophication, itself due to increasing nutrients draining from agricultural land (Morgan, 1970).

Food supply and Timing of breeding

The two main periods of food demand are during egg laying and duckling growth. At Loch Leven the peak of egg laying by Tufted Ducks occurred at a time of maximum biomass of chironomid larvae. This was followed by the emergence of adults, which reduced the biomass of larvae considerably. The timing of minimum biomass of chironomid larvae, in June/July varied by a month in the two years for which data were collected (McLusky and MacFarland, 1974). However in both years during this period of minimum benthic food supply small ducklings were on the loch.

In the laboratory, ducklings up to one week old pecked food from the water surface in preference to diving, but they occasionally took Daphnia sp. from the water column. The peak biomass of zooplankton at Loch Leven occurred in late June in 1969 (Walker,1970) and early June in 1972 (Johnson & Walker, 1974) whilst the peak hatch of ducklings in 1966-1970 occurred in every year between 24 June and 7 July. Therefore the two events coincided in at least one year, but the small sample of wild ducklings did not contain any evidence of zooplankton foods; the main foods of ducklings were the larvae and adults of chironomids. The food web drawn up for Loch Leven (Morgan and McLusky, 1974) does not reveal any other pathway from zooplankton to the diving ducks so peak zooplankton production and peak duckling hatch may be a coincidence, with no immediate benefit to the ducklings.

A situation similar to that at Loch Leven has been described in North America; at Delta Marsh the hatch of many species of ducklings, known from laboratory studies to be capable of feeding on daphnids, coincided with the peak population of Daphnia sp. (Collias and Collias, 1963). However, Bartonek and Hickey (1969) working at a different site, found that (as at Loch Leven), zooplanktonic cladocerans and copepods were conspicuously absent from the guts of North American diving ducks even though they were readily eaten by ducks fed under artificial conditions.

In conclusion, the food needs of the female, both prior to and during laying, are important in determining the timing of breeding. Female Tufted Ducks at Loch Leven build up their reserves after returning to the loch, but laying must take place before the emergence of adult chironomids reduces the number of larvae available as food. Chironomid adults were eaten by young ducklings and their availability may affect duckling survival, but their occurrence is irregular and varied from year to year, so it is unlikely that this would affect the timing of breeding.

Calcium Budget

Any breeding female needs enough calcium for egg shells. In domestic fowl, from about ten days before laying the amount of calcium retained from a given diet increases (Simkiss, 1967) and the amount excreted declines (Common, 1933; Taylor, 1965). This coincides with the deposition of medullary bone. In the Tufted Duck, skeletal weight during the egg laying period was greater than at the start of incubation. For a Tufted Duck laying 9 eggs this estimated loss of 7g from the skeleton represented 39% of the 18g of calcium required for eggshells. Estimations for the domestic fowl of the amount of calcium for eggshells which comes from the skeleton include 50% per egg (1.02g) (Mueller _et al._, 1964) 25-40% (Jowsey _et al._, 1956) and 65% (Driggers and Comar, 1949). Compartmental analysis of the skeleton (Solomon, 1960) indicated that 36% of the calcium entering the bloodstream in a laying fowl was derived from skeletal sources. Thus the proportionate use of skeletal calcium in the Tufted Duck was of the same order as in the domestic fowl, and at least half the calcium required for the eggs must have come from the diet on the day of laying.

Interestingly, although only 18 of the 127 birds taken at Loch Leven contained mollusc remains, 14 of these (9 females) were taken in May–June, when eggs were laid. Three of the seven birds which were taken with eggs in the oviduct had eaten 50-100 molluscs. These included two birds which had taken 'meals' of *Valvata* and *Limnea*. Hence, molluscs probably formed an important part of the diet during the egg laying period.

The energy value of Gastropod molluscs (total wet weight) is only 20% of the value of an equal weight of chironomid larvae (Cummins, 1969). Analyses of chironomid larvae taken from Loch Leven showed them to contain only 0.16% of the dry weight as calcium, or 0.03% of the wet weight. Thus to obtain 1g of calcium the Tufted Duck would need to collect 3.3kg of chironomids (wet weight). The birds must therefore search for the molluscs which occur in relatively small numbers (99mg m^{-2} for *Pisidium*; 125mg m^{-2} for Gastropoda; cf. 5 g m^{-2} for chironomids – Maitland and Hudspith, 1974), and take them in preference to the much more abundant and more energy-rich chironomids. Hughes and Wood-Gush (1971) have demonstrated a specific appetite for calcium in laying domestic fowl given a calcium-free diet, and female Arctic Sandpipers *Calidris* sp. eat Lemming bones as a source of calcium during egg laying (MacLean, 1974). Possibly the inability in some environments to find or to collect an adequate supply of molluscs, or other calcium rich foods, during the egg laying period may restrict the number of eggs laid by Tufted Ducks, since severe calcium restriction in the diet of the domestic fowl delays or stops egg production (Gilbert, 1972).

Seasonal changes in weight

It was extremely difficult to obtain regular large samples of Tufted Duck from a known population except during the breeding season; in winter they occurred in small groups on individual waters and moved around too much (Thom., 1969). The wide range of body weights and the seasonal distribution of the samples made it difficult to detect a clear seasonal pattern of weight change. Maximum weights occurred in both sexes in early winter and also in the female prior to egg laying while, in both sexes, minimum weights were near the end of incubation. In a study of Mallard throughout the year in Czechoslovakia (Folk _et al._, 1966), birds were heaviest in December with a second peak for the female at the beginning of the breeding season, and lightest immediately after the breeding season, similar to the pattern of Tufted Duck at Loch Leven. Most of the other previous studies on weights in ducks were restricted to the shooting season, September to January. Mallard and Pintail _Anas acuta_ (Bellrose and Hawkins, 1947) and Blue-winged Teal (Owen, 1969) are heaviest in late autumn.

The spring gain in weight of females simultaneous with the decline in males has been shown in the Eider (Gorman and Milne, 1971), several gallinaceous birds (Kirkpatrick, 1944) and in song birds (eg. finches; Newton, 1972). In the Eider, fat deposition in the female was due to hyperphagia, since the feeding rate of the female increased by 10% while that of the male decreased by 40%, from the normal winter rate, (Gorman and Milne, 1971). In this bird and in the gallinaceous birds (Kirkpatrick, 1944), the weight loss of the male has been attributed to the exigencies of the breeding period. Likewise the few Tufted Ducks which I observed feeding during the egg laying period were paired, and the males spent a considerable time protecting their mates from unpaired males. Loss of weight in the male Tufted Duck therefore appears to result from increased activity and reduced feeding whilst defending the mate and allowing her uninterrupted feeding; no measure was made of feeding rate, but the molluscs found in the stomach of males shows that they did feed at this time.

The wide range of body weights found in Tufted Ducks in winter may result from different energy demands and food supplies occurring in different groups of birds at particular times. By comparison, in some small birds (less than 50g) the seasonal changes in maximum daily weight occur in a predictable way and can be related to the specific demands of survival over one night, in low temperatures with no feeding (P.R. Evans, 1969; Newton, 1969). Such small birds could not last more than one day without food, but, as I have shown (page79), survival for a single night would not be limiting for a bird of around 800g. However the Tufted Duck may be prevented from feeding for several days and then have to move to other waters in search of food. Therefore although individual weights may vary according to local supplies and recent demands, the maximum reserves found in birds at any time may be related to the probability that a restriction in feeding will occur and also indicate the potential for birds that have experienced good feeding conditions.

Oiled birds and Starvation

Many of the Scaup killed in the oiling had considerable reserves and had presumably therefore died of exposure; the metabolic rate of the birds being insufficient to balance the heat loss, resulting in hypothermia and death. The metabolic rate of oiled ducks increases in proportion to the amount of oil on the plumage, since this reduces its insulating ability (Hartung, 1967). A heavily oiled bird at 15°C has a metabolic rate equivalent to a normal (fully feathered) bird at -20°C. In spite of this Hartung concluded that oiled ducks can survive extended periods at low temperatures as long as they have energy reserves, and death is therefore only indirectly due to exposure to cold; this is contrary to the evidence obtained in this study. Hartung's conclusion however, disregards the fact that in all his experiments the birds were in air, which has a thermal conductivity 0.04% of that of water, with which most oiled birds are in contact. The layer of boundary air around the experimental birds would further increase its insulation relative to water around a swimming duck. The heat loss (from birds) would therefore be considerably greater on water and, as my data show, birds may die directly from exposure while still having adequate reserves.

The starved Scaup in this study lost more weight (72%) before death than wild Mallard (55%) (Jordan, 1953) but this may be because they had more reserves to begin with or were kept warm artificially in the rehabilitation centre. The data on Mallard indicated that no birds survived a weight loss of more than 43%. Birds which did recover regained 80% of their normal weight in the first week. The food intakes for the three weeks of recovery were 278%, 246% and 154 of normal. This indicates the ability of these ducks to recover rapidly if an adequate food supply is available and is relevant to the rehabilitation of injured birds or the recovery of normal weight in wild birds subjected to food shortage or environmental stress.

Carcass composition

My study provided data which are relevant to published work on carcass composition in other species, and help to clarify one debated issue, namely homeostasis of the non-fat components. The hypothesis of homeostasis of the nonfat components of birds (Odum et al., 1964) has received considerable attention over the past ten years. A certain amount of confusion has arisen since this was variously interpreted to mean a constancy of weight of the nonfat components (Hicks, 1967; Helms et al., 1967; King and Farner, 1967) or a constancy of the proportion of the lean body components (Child and Marshall, 1969 ; Farrar, 1966; Johnston, 1968), and the original paper is not explicit. However, homeostasis is strictly a term which implies maintenance of the constancy of conditions in the internal environment (i.e. the proportions of the components and not their absolute amounts).

The heaviest Tufted Ducks contained the largest reserves of fat, and there was relatively little increase in lean material as birds increased from 750g to 950g. In this respect the Tufted duck was similar to those birds which show premigratory fat deposition with no associated change in the other components (Connell et al., 1960). However at body weights of less than 700g the Tufted Duck lost an increasing amount of lean dry material as body weight declined. A big variation in the lean dry material has been shown in the Bullfinch (Newton, 1968; Newton and Evans, 1966), and Bulbuls (Ward, 1968) which had small amounts of body fat (4½% of total weight) compared to migrants (up to 28%). Data in the present study cover birds with fat contents ranging from 2% to 31% of body weight and span the range of both groups of previous studies. Depending on the range of the fat contents it would be possible to draw different conclusions on the constancy of weight of the nonfat components in the species. In other words the differences found between species probably result from differences in the fat levels involved rather than inherent physiological mechanisms. Considering water index, which relates the water and the lean dry materials; in my data water index was fairly constant over the complete range of body weight in healthy adult Tufted Ducks. This implies true homeostasis of the nonfat components even though their absolute weight varied quite considerably during the initial stages of fat deposition. When considering a much larger bird, the Domestic Goose, Benedict and Lee (1937) concluded that "increases in body weight above the normal adult weight are chiefly additions of water and fat and are not associated with a corresponding increase in protein". A cursory examination of the summarised data on the carcass components in the Tufted Duck (Fig. 26) might lead to the same conclusion. However each unit of lean dry material (essentially protein) is associated with 2.5 units of water The latter therefore appears significant and the former insignificant in changes of total weight. The water is however just an essential accompaniment of changes in lean dry material, and the two maintain the same ratio as weight increases.

Much of the confusion over the homeostasis of lean dry material apparently arose from the different levels of fat in the carcasses of the birds studied, and uncertainty over the meaning of the term 'Homeostasis'.

In Tufted ducks of very low body weight (40% below normal), there was some evidence of increasing water index; and in Scaup there was a change in water balance of the muscle tissue during extreme weight loss (to 2[illegible]% of normal). High water indices similar to those of starving birds were found also in the pectoralis' of juvenile Tufted Ducks. In rats,water soluble proteins were lost from the muscle during fasting, but tissues showed no evidence of oedema (Hagan and Scow, 1957). In the King Salmon during migration,water index of the muscle increased from 3.7 to 5.8 in association with reduced body reserves (Greene, 1919). A high water content is known to be characteristic of newly formed tissues (Moulton, 1927; Kochakian 1950; Newton, 1968; A.J. Evans, 1969) but is apparently also associated with the catabolism of muscle protein in a wide range of animals. This may be necessary either for mobilisation of the water soluble proteins or to maintain tissue mass (or both).

The pectoralis muscle

The pectoralis major is not only the main locomotor muscle in birds, but may also be an important source of energy for flight (George and Jyoti, 1957), and of protein at times of protein deficiency

(Ward, 1969; Hanson, 1962; Kendall et al., 1973). By examining the seasonal changes in the weight and composition of the pectoralis muscle, I hoped to determine the importance of this muscle as an energy and protein reserve in the Tufted Duck, and its role in the annual cycle.

Considering first the energy content of the muscle in relation to flight, George and Naik (1960) suggested that the fat in the pectoralis muscle was a transient store for immediate use by the muscle, which was already known to be capable of using fat as a fuel for maintained activity (George and Scaria, 1956). A comparative study of 104 species showed that actively flying birds can be characterised by the high fat content of this muscle (5% of the wet weight) (Hartmann and Brownell, 1961). The Tufted Duck tended towards these higher fat levels but showed considerable variations. Scaup shot in this study represented the largest sample of similar birds, and had pectoralis fat contents varying from 3.3 to 5.3% of total weight, but possibly these relate to the activity of the bird just prior to shooting. Similar variations of 2-3% were seen in published data on a single species (George and Naik, 1960; Hartmann and Brownell, 1961).

Calder and King (1974) calculated that the average cost of flight in non-passerine birds was 9.6 x SMR. Thus for a Tufted Duck of 800g this would be 110kJ.h^{-1}. The same bird was found to have on average about 5g of fat in the muscle which, allowing for some structural lipids, would provide fuel for a flight of up to 1.5h. Therefore unless fat is replaced immediately it is used up, a flight of half an hour could reduce the muscle fat levels by at least one-third.

Only for flights over 1.5h would the bird need to mobilise fat from its other reserves during flight.

In extreme conditions, below 50% of maximum body weight, Scaup used the pectoralis muscle as a reserve, but incubating Tufted Ducks dropped to 60% without using using noticeable amounts of the pectoralis muscle. The latter may be linked to the greater need to retain their flying capability when on land during the relatively vulnerable conditions of incubation.

Some of the evidence collected in this study relates to the field assessment of pectoralis size as an index of the birds' condition. Although the absolute weight of the pectoralis muscle decreased with body weight, it did not do so proportionately over the normal weight range. Further, the loss of subcutaneous body fat during the initial stages of weight loss would affect the assessment of the muscle condition. In cases of starvation the sternum may protrude considerably, but then, and at other times, the weight of the bird relative to normal weights would give a better indication of condition. Therefore assessment of the pectoralis muscle is probably useful only in detecting cases of extreme starvation.

To conclude - the pectoralis muscle can provide a supply of energy for Tufted and Scaup ducks, but normally it is only important as a protein source and as a reservoir of fat for immediate use in flight. In extreme conditions, however, it may provide a significant proportion of the energy requirements of the bird.

The Liver

The liver functions in intermediary metabolism, in that all foodstuffs are absorbed by the liver after digestion, and from there are transported to other tissues. It is therefore likely that changes in the gross biochemical composition of the liver would reflect rate of metabolism rather than body condition, and the findings of this study tend to support this.

When considering the liver weight in Canada Geese, Hanson (1962) attributed the difference between the relative weight of 1-2% in this bird and that of 5% in the Starling Sturnus vulgaris (Stegman, 1952) to the higher metabolic rate of the smaller bird. But liver weight representing 2% and 5% occurred in different Tufted Ducks, showing that relative liver weight can vary over a similar range in one species.

The changes in the liver found in this study occurred both over the long and short term. Diurnal variations in liver weight were correlated with the predominance of night-time feeding, with the largest livers in the morning. Following the ingestion and absorption of food, the liver of Japanese quail Coturnix japonica assumed a tan colour characteristic of a fatty liver (Wilson and McFarland, 1969). In Redwinged Blackbirds Agelius phoeniceus Fisher and Bartlett (1957) also noted a striking difference in the colour of the liver, depending on the time the birds were killed (Presumably in relation to feeding activity.) Both these species also showed a diurnal rhythm in liver weight with up to 30% decrease overnight in Redwinged Blackbirds. However, in the Tufted Ducks the heaviest livers did not correlate with the highest fat indices.

The changing composition of the liver with size conforms with the role of the liver in respect to carbohydrates and amino-acids proposed by Shoemaker and Elwyn (1969). These authors suggested that the liver acts as a buffer for the diurnal supply of nutrients from the gut and also responds to the specific tissue requirements by varying the supply of nutrients to other tissues. In respect to lipids, this role is shared with the adipose tissue; the relative importance varies depending on size of the latter. In Scaup the large changes in liver weight were mainly accounted for by lean dry material and associated water. For an increase in total weight from 10g to 50g the fat weight increased by only 4g and no liver in Tufted Duck contained more than 2g of fat (8%). Similarly in Japanese Quail the changes in fat and glycogen levels accounted for only 19% and 1% respectively of the total changes in liver weight (Wilson and McFarland, 1969). Thus histological and visual evidence of fatty livers may give a disproportionate idea of the amount of fat present in the liver and thereby its importance. At all times, the amount of fat stored in the liver represents a small fraction of the total body fat.

Long term changes in liver weight were seen in this study and have been reported in other species. Hanson (1962) found low liver weights in incubating females and suggested that these reflected the stress of egg production on body reserves. Data collected in this study do not support this, as the incubating females had relatively high liver weights. However if liver weight is related to feeding activity the difference may reflect the fact that Canada Geese do not normally feed during incubation (Newton, in press) while Tufted Duck do (this study). In the male Tufted duck, liver weight was low in May and June, when the body weight also declined. If the latter decline resulted from a reduced food intake as well as increased activity, then the correlation between plane of nutrition and liver weight is seen here also. Similar situations have been described in the White Crowned Sparrow Zonotrichia leucophys gambeli (Oakson, 1956), in which liver weight declined as testis weight increased, and male Canada Geese which on the breeding grounds had higher body weights and lower liver weights than wintering birds (Hanson, 1962). The relatively large liver weights of growing juveniles (5% of body weight) probably reflected the high level of feeding associated with growth.

In conclusion, liver weight showed short term and long term variations, both of which could be related to intensity of feeding. The diurnal variations, related to specific bouts of feeding activity, could be of such magnitude that they masked the general trends; e.g. the incubating female with some of the heaviest and lightest livers. The seasonal trends were associated with seasonal changes in the overall plane of nutrition, e.g. the low liver weights of courting males. Therefore, unless large samples of birds could be taken at regular times with respect to feeding activity, the liver is unlikely to give any indication of the condition of the bird, since it mainly reflects dynamic and not static status. Nonetheless it is widely stated in the literature as reflecting the condition of the bird.

Weight loss and use of reserves by breeding females.

The lack of captures of birds during the first week of incubation may be explained partly by the greater wariness of birds at this stage, but more importantly because most nests were not found till then, and birds were not caught until the nests had been marked.

The large weight range of birds on unincubated eggs (600-915g) resulted from two factors. Firstly, a bird may have been taken on the nest at different stages of laying before incubation began. Although all birds were taken from nests containing at least 8 eggs, two had eggs in the oviduct plus one large ovum. These birds weighed 851g and 915g, corrected to 790g and 875g respectively after removal of the eggs and ova. These weights must approach the maximum weights for birds beginning incubation as each had then produced 8 eggs, and were forming 2 others, more than the average clutch size. Secondly, at the other extreme, birds weighing only 600g were taken from nests of unincubated eggs. These weights were very low for birds at the start of incubation and were as low as many birds taken at then end. Possibly these birds had previously incubated for some time at nests which had been destroyed, but still showed some 'incubation drive'. The most likely nests for such birds to usurp would be those left unattended by other birds between ovipositions. Evidence to support this comes also from three birds taken from unincubated eggs which had low plumage weights and bare brood patches. Loss of the breast feathers and down is normally a slow process occurring over several days after incubation has begun, and is therefore unlikely to be so far advanced in birds which were supposedly still laying.

The incubating female Tufted Duck lost 20% of her gross body weight, and the ratio of fat to lean dry material that was lost was 2.7:1. This compares with the ratio of 2:1 in the Eider, which loses

40% of its gross body weight (Gorman and Milne, 1971), and 2.4:1 in the domestic fowl, determined during periods of negative energy balance (Shannon and Brown, 1969). Metabolism of fat requires a supply of oxalo-acetate (Hanson, 1962: Gorman and Milne, 1971), which is normally available from carbohydrate metabolism. In a bird which is not feeding, carbohydrate reserves are used up within 24h (Benedict and Lee, 1937), and then oxalo-acetate must be obtained from glucogenic amino-acids derived from protein. Benedict and Lee (1937) suggested that the protein may represent 10% of total catabolism. This would result in a ratio of 9:1 if all the remainder were fat This is a considerably higher ratio than any noted above, and indicates that more protein is being used than just that required for oxalo-acetate production.

In the Tufted Duck both lean dry material and fat declined at a steady rate during incubation. The data presented by Gorman and Milne (1971) do not indicate whether fat and protein are used simultaneously and steadily in the Eider, since they are based on one sample prior to incubation and one after. Prior to egg laying the Tufted Duck female had 8g more lean dry material than at the start of incubation, which was equivalent to 40% of the lean dry loss during incubation (20g). The total lean dry weight loss from before egg laying to the end of incubation was less than 20% in the Tufted, but in the Eider total protein loss was 50%. Since the proportion of fat to protein in the total carcass is similar in both species prior to egg laying, the main difference is in the total amounts available and the greater use made of body protein by the Eider. Although the smaller Tufted Duck can lay down considerable reserves of fat, its reserves of protein must be supplemented during both egg laying and incubation. This difference between species may depend chiefly on their difference in body size.

Juvenile growth

The decrease in weight shown in the relationship between weight and wing length in the data calculated from Kear (1970), occurred at 8 weeks of age when the birds were fledging. Similar discontinuities in the growth curves are well documented for other Anatidae reared in captivity, Teal *Anas crecca*, Mallard, Gadwall, Shoveler *A. clypeata*, Pochard, Common White-eye *Aythya nyroca*, Tufted Duck (Veselovsky, 1953) and Redhead *Aythya americana* (Weller, 1957). Kear suggested that a drop in weight during fledging may occur in the wild in less than optimal conditions (presumably food shortage or low temperatures); and the wild birds collected in this study also displayed a step in the relationship between weight and wing length. It is difficult to say whether conditions were less than optimal at Loch Leven, but the weights of wild juveniles throughout growth were more than those of captive juveniles of similar wing length taken from the same parent population.

Clutch size and egg size

It is first worth considering the physiological changes which take place during follicular development and the mechanisms which control it. This information has been gathered in studies on the use made of body protein by the Eider. Although the smaller Tufted Duck can lay down considerable reserves of fat, its reserves of protein must be supplemented during both egg laying and incubation. This difference between species may depend chiefly on their difference in body size.

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The development of the oocyte occurs in three phases:

(1) and initial phase of slow growth when triglycerides are deposited, lasting months or even years;

(2) an intermediate phase, beginning 60d before egg laying and involving the addition of some yolk protein;

(3) the final phase of rapid growth from around 0.5g to 20g.

This takes place over the last 7-11 days before oviposition, and varies between individual birds and species, but is constant within an individual.

The amount of yolk material produced in the liver on any day will of course depend on body reserves and food supply, but the total amount deposited varies with the overall levels of follicle stimulating hormone (FSH). The differential rates of deposition of material in each of the follicles is under ovarian control, effected by the blood supply to the follicles.

In the domestic fowl control of the secretion levels of the pituitary hormones, including FSH, may involve calcium, because the production of a shelled egg affected the number of maturing follicles and also feeding low calcium diets terminated laying within a few days (Gilbert, 1969; 1972a).

It would be of value to know whether the smaller clutch sizes of late nesting ducks, as reported in this study, result from atresia of the developing follicles or because fewer follicles enter the period of rapid growth. The evidence on calcium reduction in the fowl, particularly the speed of its action, would indicate that, if a similar mechanism reduces clutch size in wild bird, then follicular atresia would occur.

In the three years for which I obtained detailed information, mean clutch size in the Tufted Duck at Loch Leven did not alter significantly, nor did the timing of laying. Constancy of clutch size between years has been noted in other duck species (Bengtson, 1971; Milne, 1974) but clutch-size can be reduced by extreme food shortage. At Lake Myvatn, Iceland, Bengtson (1971) studied eight duck species over nine years and found a significant reduction in clutch size in five species in only one year. Clutch size for Tufted Duck in his study averaged 10 eggs, but was reduced to 9 in a year when the food supply during the laying period was only an estimated 18% of the level in the preceding two years. Thus a very large reduction in food supply caused only a small decrease in clutch size; the laying season was not delayed. Unfortunately Bengtson did not give any data on egg size. In the Eider, significant reductions in clutch size occurred in only two of the 10 years studied by Milne (1974). These reductions of approximately 10% were apparently associated with low temperatures at the start of the normal laying period, and in these cases egg laying was delayed by up to two weeks and egg size was reduced, also by 10%. In both these species a major decrease in food supply or increase in food requirement was necessary to alter clutch size and the timing of laying. In contrast, the Greylag Goose *Anser anser* showed changes in the mean clutch size between years, during a five year study, which were equal in extent to the seasonal decline in any one year (Newton and Kerbes, 1974). There was also a range of 16d in the date on which the first eggs were laid over the five years. Egg production in these geese is apparently much more susceptible than that of diving ducks to the variations in food supply (or female reserves) between years. Newton (in press) has reviewed the data showing that in tundra nesting geese, egg production is totally dependent on the reserves collected on the wintering grounds. Apparently the extent of annual variations in clutch size of different species is linked with how much of the requirements come from reserves and how much from food eaten at the time. In Tufted Ducks food supplies do not usually vary sufficiently between years to produce differences.

The decline in clutch size through the season, found in Tufted Ducks, was also recorded in the four species of dabbling ducks at Loch Leven, and in all five species elsewhere (N and C, 1975). Although part of the decline in the dabblers could be accounted for by repeat nesting, it was already evident before much repeat nesting occurred, and in Tufted there was no evidence for repeat nesting. This seasonal decline has been reported in Eiders and other ducks (Milne, 1974), Greylag and other geese (Newton and Kerbes, 1974, Newton, in press), various seabirds (Coulson, 1963; Coulson *et al.*, 1969; Parsons, 1970), raptors (Cave, 1968; Newton, 1976), passerines (Klomp, 1970), and is evidently widespread in birds.

In at least three seabirds, egg size also declined through the laying season, varying in extent from 4.5% in the Kittiwake *Rissa tridactyla* to 11% in the Shag *Phalacrocorax aristotelis*, (clutch size was reduced more in the former than in the latter). Coulson *et al.* (1969) suggested that the decline in clutch size freed material to compensate egg volume, otherwise the decline in egg size would have been greater. Domestic fowl on restricted feeding reduced egg numbers but not egg weight (Heywang, 1940; Walter and Aitken, 1961), and in Ring-necked Pheasants eggs laid later in the season were not significantly lighter than those laid earlier (Labisky and Jackson, 1969). In the Great Tit *Parus major*, Perrins (1970) found an increase in egg weight during the laying season; which is similar to the situation which I found in the Tufted Duck. In the Herring Gull, egg size declined through the season at certain sites (Parsons, 1970) and in certain years (Davis, 1975), but not in other sites and other years (Davis, 1975), although clutch size invariably declined. Hence, whereas a decrease in clutch size through the season appears to be widespread in birds, seasonal changes in egg size vary between species, and in some species also between seasons and between localities.

In sea birds, the change in egg size has been partly attributed to the fact that older birds which lay larger eggs also nest earlier in the season (Coulson, 1963). Coulson *et al.* (1969) concluded that the seasonal decline in clutch size and egg size shown in Kittiwakes, Shag and Great Skua (*Stercorarius skua*) was unlikely to result from food shortage, but rather from individual differences in reproductive development, the earlier birds showing a "higher reproductive drive". However, Perrins (1970) attributed the larger eggs in later clutches of Great Tits to the increased food supply later in the season, and he suggested that a reduced clutch size in late season had evolved because small clutches laid then produced more offspring than large ones. This may operate because, by reducing the clutch size, the time of hatching would be advanced. This explanation is reasonable if the eggs are laid totally from food supplies at the time and if the food during the nestling period decreases. However, if the eggs are laid partly from the reserves of the bird, as in the Tufted Duck, then these reserves may influence egg numbers, while the immediate food supply influences egg size. This would be likely if the reserves provide materials that must go into every egg and cannot be quickly replaced, e.g. fat or calcium. The Tufted Duck provides mainly fat from reserves and most of the lean dry material of the egg (except shell) from food eaten at the time, while the calcium is apparently supplied equally from both sources. Although egg size increased through the season, fat index in the egg decreased and that this change was independent of egg size. Thus there is some evidence that the reserves (i.e. fat) were restricted in the later layers, but that egg size was maintained, and even increased, as a result of feeding. In the year in which these analyses were done, food supplies at Loch Leven were unusually good, and possibly in years of poor or decreasing food supply egg size may not increase. Similarly, the conflicting data on egg size in Herring Gulls may result from annual variations in food supply.

Lack (1967) examined the factors affecting clutch size in the Anatidae and it is pertinent to consider my data on a single species in relation to his conclusions. The inverse correlation between egg size and clutch size shown by Lack for all Anatidae was found also in Tufted Duck. Although Lack suggested that the average clutch size in each species evolved in relation to the average availability of food for the female around the time of laying, it has been suggested by Johnsgard (1974) that other factors may influence clutch size. The first of these was the efficient partitioning of energy between egg production and incubation. Ryder (1970) suggested that in Ross' Goose *Chen rossi* clutch size has evolved in relation to the food reserves accumulated by the female and that these are split between the eggs and the energy required for incubation. Recently, Newton (in press) showed that the situation described by Ryder is typical for all tundra nesting geese. My data suggest a similar situation in Tufted Duck, where a considerable reserve of energy was retained at the start of incubation; the amount of energy used in incubation was 70% of that used in egg production, but in both cases (unlike the geese) it was supplemented by feeding. In the Eider, whose eggs represented only 25% of gross body weight (compared with 60% in Tufted) many females incubate entirely without feeding. As indicated earlier these differences in the contribution made by reserves may relate to the absolute size of the birds.

Irrespective of the proportionate use of reserves in egg production if the reserves provide essential nutrients then their size may determine cluth size. Reynolds (1972) proposed a model to explain the decline in clutch size in the Mute Swan *Cygnus olor* through the season. In the model laying is initiated when food reserves reach a threshold value, which decreases with time and is set by some external factor. If clutch size is determined by food reserves, then the relationship between clutch size and date follows. I would suggest a modification of this model which does not involve an external change in the threshold. Rather, the threshold to which the bird responds would be a function of the rate of deposition of reserves which is itself a function of the food availability or feeding ability of the bird. Thus the birds which gather reserves quickly reach a higher level before laying is initiated (and then lay more eggs) compared with birds which gather reserves slowly and have therefore reached a lower peak (later) when laying is initiated. A difference in the rate of accumulating reserves is implied in Reynold's model. The average availability of food may therefore determine clutch size as suggested by Lack, but operate via the accumulation of reserves rather than directly on egg production. In this way the timing of laying would also be affected.

Johnsgard (1974) noted a decline in clutch size with the decreasing July isotherm and duck species nesting at high latitudes generally have smaller clutch sizes than those at middle latitudes (Lack, 1968). The mean clutch size at Loch Leven was less than that in Iceland, 10 (Bengtson, 1971) but more than the 8.5 eggs cited by Lack (1968). However since data are not available regarding the incidence of brood parasitism at these other sites, or the number of eggs assumed to be normal when clutch size was calculated, it cannot be determined whether the differences between sites are real.

Parasitic laying

In extreme years, up to 10% of Tufted Duck nests at Loch Leven contained eggs from more than one female. Tufted also regularly laid in the nests of other species. This 'parasitic' nesting behaviour has also been reported for Tufted Ducks at other nesting sites (Hilden, 1964; Fredrikson, 1968) and for other duck species (Friedmann, 1932; Weller, 1959; Vermeer, 1968; Morse and Wight, 1969). At Loch Leven the incidence of parasitic nesting was greatest at times and in places of greatest nesting density (N & C, 1975) but it is not known which birds lay parasitically. Tufted eggs found in the nests of other species were lighter and narrower than the average for the population. In some seabirds, the young birds lay lighter and narrower eggs than older birds but also lay nearer the end of the season (Coulson, 1963). At Loch Leven egg size in the Tufted Duck increased through the season; thus if younger birds lay late in the season, it is not possible (on the basis of egg size) also to implicate them in the parasitic laying.

The incidence of brood parasitism is so widespread in the Tufted and other ducks of the tribe Aythyini that it is difficult to believe that it results merely from reduced breeding drive. Rather, as Lack (1968) suggested for the evolution of brood parasitism in general it must be presumed that it leads to the individual concerned producing more offspring than they would otherwise have done. In ducks, body reserves are apportioned between egg production and incubation; so even though reserves could be saved by laying fewer eggs, the costs of incubation presumably vary little according to the clutch size, and are 'all-or-nothing'. Thus a duck with limited reserves before egg laying has only one chance of producing hatched young, to lay eggs in the nests of other birds. Any problem of asynchrony with the host eggs will be reduced by the fact that the nests of unincubated eggs are left unattended and are therefore most likely to be parasitised. Provided that the host can incubate some part of the increased clutch then this behaviour might be selected over an attempt at incubation by a female in poor condition.

Duckling size

In waterfowl egg size shows limited variation (Lack, 1968) and Lack (1967) concluded that a relatively large egg is of advantage to the newly hatched chick in providing it with a relatively large reserve of food. There were no geographical differences in the published data in egg weight of Tufted Ducks (Kear, 1970). (Except that eggs from captive birds of Loch Leven stock at the Wildfowl Trust were lighter than those from the wild population at Loch Leven. A similar difference in which newly hatched Mallard ducklings from southern Sweden were heavier than ducklings produced at the Wildfowl Trust was explained on the basis of latitude (Marcstrom, 1966).) Further evidence is available which suggests the importance of maintaining egg size, and hence the size of the neonate, in the Tufted Duck and other species. The Tufted duckling represents 4.2% of the adult female weight; this was the highest proportion found by Kear (1970) in any of the Northern *Aythya* species, which suggests that there is some advantage in a large duckling size. Milne (1974) suggested the possible advantage of size *per se* in the Eider duckling, since a larger animal would have better heat retention properties than a smaller one, simply on the ratio of surface to volume.

Parsons (1970) has demonstrated the importance to Herring Gulls of production of a large egg. Chick mortality was least in the young from large eggs, even when eggs with the same order in the clutch and the same date were compared. Davis (1975) also found a good correlation between hatching weight and survival to 14d in the Herring Gull. Parsons reported that the major cause of mortality in the Herring Gull was exposure, but the situation in this bird is slightly different from that in diving ducks since the latter can thermoregulate while the gull cannot (Koskimies and Lahti, 1964). Body temperature in the day old Herring Gull declined rapidly and immediately on exposure to a temperature of 8-10°C, while Eider and Tufted ducklings maintained their body temperature for at least 180min. Thus although the surface area law holds, the larger Herring Gull chick would be unable to make use of its greater reserves, since it apparently does not have the thermoregulatory mechanisms. In fact, the demonstrably cold-hardy Tufted Duckling had at hatching 36% of its dry weight as fat, while in the Herring Gull fat formed only 20% (Parsons, 1970). Most of the advantage of size in the latter species could be operating indirectly through the formation of a stronger parent-chick bond, which determines that the larger chick (with the stronger bond) receives more food (Parsons, 1970).

Cold-hardiness is apparently essential in young waterfowl, which obtain all their food from water and must maintain their body temperature during feeding; and the evidence from the Herring Gull indicates that temperature decline is immediate in a bird which does not have this thermoregulatory ability. In the thermoregulating bird, the surface area law is important, and hence there is a need to maintain egg size, and thereby duckling size and to provide adequate supplies of energy (fat) to supply the thermoregulatory mechanism. Cold hardiness of the duckling has a further advantage: it reduces the need for brooding by the female and this, coupled with crèche behaviour, frees the female to spend more time feeding to replace the considerable weight loss incurred during egg laying and incubation.

Nesting success

In contrast to the stability of clutch size and laying date between years in the Tufted Duck considerable variation was found in the proportion of clutches which hatched at Loch Leven (N & C, 1975). In 1966-71, this proportion varied from 64-86% in the undisturbed parts of the colony and 45-71% in the disturbed (intensively studied) ones. In general the two figures varied in parallel. Of particular relevance to my own study are the facts that (a) hatching success was significantly worse in 1969 (50%) and 1971 (45%) than in 1970 (71%) (X^2 test, $p>0.05$); (b) weight loss of incubating birds captured on the nest was significantly less in 1970 than in 1969; (c) gross food supply (estimated standing crop of chironomid larvae) was considerably greater in June 1970 than in June 1971.

As the reserves of the Tufted Duck are not adequate to supply the metabolic needs of incubation, some feeding must take place. The data on food supply suggest that the large food supplies in 1970 reduced the dependence of the incubating females on their reserves, and that these reserves were most important when food was not readily available. If food is readily available, then the female can presumably make fewer or shorter departures from the nest and thus reduce the chance that her eggs are taken by a predator. This may account for the differences in predation rates between years. If chironomid larvae are available, moreover, feeding may take place at night and reduce still further the risk of predation,since Jackdaws (the main predators) were not active then. However in years when chironomid larvae were not readily available during the incubation period, alternative foods, (possibly emerging adults) must be sought, and these would involve longer periods of feeding during daytime, thus increasing the risk of predation. Newton and Campbell, (1975) suggested that the decline in nesting success could be due to the late nesting birds being on average in poorer condition, and having to leave the nests exposed for longer. They supported this argument with the fact that the decline occurred at different dates in different species according to when they bred, and that in the Tufted, which did not renest, the decline was least marked. It is further possible that the Tufted normally rely to a greater extent on their body reserves than do the dabbling ducks and that in certain years, as suggested above, they can stay on their nests by day and feed by night. In all years, however, fewer chironomid larvae were available as the season progressed and this may partly explain why late nests were less successful.

Milne (1974) has suggested that the feeding efficiency of the female prior to laying is of crucial importance to the Eider in preparing to breed, and he indicated that the role of the male in keeping intruders away may be more important than the gross amount of food available. The considerable decline in weight of the male Tufted Duck during the egg laying period would sup ort this. A reduction in feeding in the male would, apart from allowing more time for defence, also reduce competition for food between the sexes; though evidence from the males which had eaten molluscs suggested that some feeding by males did take place.

To summarise - It is clear that many factors contribute to influence breeding success in the Tufted Duck. The reserves of the bird, collected prior to egg laying, provide much of the essential material for egg production and are therefore important in determing clutch size. Egg size may be modified by food availability during the egg laying period, and although some reserves are retained and used during incubation the food supply during this period is critical in determining nesting success; since the major factor affecting losses from nests is predation during the absence of the female from the nest. Little is known of the factors which affect duckling survival after the initial reserves are depleted but there are known to be large variations between years in the food available during the period of maximum duckling growth.

Energy budget of population

Calculation of the energy budget involved a certain amount of oversimplification and approximation of values. However in most cases these occurred at points in the calculation which would not greatly alter the total budget. For example, the estimation of the production of young at Loch Leven has presented a problem in all studies at this site, but an error of ± 100% on this figure would have altered the total annual budget by only ± 1%, and the total budget for any month by no more than ±2%. The most important contribution to the total budget was respiration (R), and this has been shown to be little affected by the precise method of its determination. The important requirements for the calculation of R are (a)an estimation of body weight and (b) population size. An error of 100g (over 10%) would alter the estimated daily metabolic rate figure by only 10%, and errors in the population would affect the result proportionately to the size of the error. Viewed retrospectively, it would have been possible to provide an estimate of the annual energy budget of the Tufted Duck population at Loch Leven accurate to within ±20% knowing only the population figures to ±10% and body weights to ±100g. Such an estimate would indicate that the Tufted Duck consumed less than 5% of the food available to it during the year, but would of course fail to explain any of the precise interactions between the duck and the loch ecosystem.

Considering only the data from the annual energy budget the requirements of Tufted Duck, 20.9 kJ m^{-2} represented 4% of the average (based on two years) net production chironomid larvae (Morgan and McLusky, 1974), compared with 144 kJ m^{-2} (28%) taken by Trout and 398 kJ m^{-2} (76%) by Perch which were the other two main vertebrate consumers. The Tufted Duck is apparently an unimportant predator of the benthic fauna at the loch in relation to the fish which must also be taking foods other than chironomids.

However certain constraints may be operating. . Roughly 50% of the loch is over 3m deep and, since Tufted Duck prefer feeding at depths less than 3m, the potential feeding areas may be reduced accordingly. The observed feeding areas at Loch Leven amounted to only 20% of the total area. If it is assumed that this restriction resulted from physical features (depth and exposure) rather than aggregation of the food (and that food is evenly distributed over the loch), then the Tufted duck takes 20% of the food 'available' and not 4%. Further, the work on chironomid larvae at Loch Leven has shown that they may be distributed through the bottom sediments to a depth of 100mm (Maitland et al., 1972). If they were evenly distributed in the substrate column and the feeding methods of the Tufted Duck limit it to the top 20mm, then the food 'available' would be reduced fivefold and the duck is now found to be taking all the food available to it. This exercise illustrates the value and limitations of a purely energetics approach which does not consider food availability. This study based on energetics has, however, determined the importance of body reserves to the energy demanding processes of egg laying, incubation and survival of food shortage in winter. It is clear that, in addition to gross energy reserves, specific nutrients must also be accumulated for egg laying, that during incubation birds are still dependant on food, and that body reserves may supplement poor feeding conditions in winter.

9. CONCLUSIONS

Chironomid larvae were the most important food of Tufted Ducks at Loch Leven. The annual energy requirements of the population, however, represented less than 5% of the chironomid production. The ducks are therefore relatively unimportant in the ecosystem in comprison with the other main consumers, Trout and Perch whose annual energy requirements were greater than chironomid production, but took other foods also. Food supply, and the ability of the ducks to collect it, may however, influence clutch size (indirectly through the reserves of the bird), hatching success and the autumn numbers of Tufted Duck at Loch Leven. Molluscs were essential foods of females during egg production and must then have been taken in preference to chironomid larvae.

Tufted Ducks are ideally suited to gather food items of similar size, occurring in dense aggregations on the substrate of shallow water bodies; this may explain the recent general increase in their numbers, with the increase in man-made shallow waters and of simple freshwater ecosystems resulting from eutrophication. Movements of chironomid larvae in the substrate, noted in other studies, indicated a possible advantage of night-time feeding, and the lack of such movements in winter may also explain the departure of the Tufted Duck from the loch then.

At least half of the loch area was not used for feeding by any of the diving ducks but there is unlikely to be competition for food between them, since they rarely occur in large numbers simultaneously and showed differences in the diurnal rhythm of feeding and the foods eaten.

There were large variations in weight between birds within any month; both sexes reached high body weights in December, but females were heaviest before egg laying. In winter, birds approaching peak weight would be able to survive at least ten days without feeding. Many oiled Scaup died of exposure before using all their reserves, but if body temperature was maintained artificially their weight was reduced to one third of normal before death.

At low body weights, fat free weight changed with total weight, but as the latter increased the major change was in proportion of fat in the carcass. At the lower weights, however, the water index of the tissues remained constant (except in starvation), confirming true homeostasis of the non-fat components. A high water index, known to be characteristic of growing birds, was found in juveniles and also in starving birds which were catabolising protein.

The pectoralis muscle is a protein reserve which is used mainly in extreme conditions e.g. starvation; it is used by incubating females, but then its proportion of body weight remains relatively high, presumably to maintain adequate flight powers. The muscle contains a small reservoir of fat for immediate use. An external assessment of pectoralis muscle conditions as an index of body condition is probably useful only in detecting cases of starvation.

Both long and short term changes in liver weight were found; the former in relation to the overall plane of nutrition and the latter to immediate feeding activity. In view of the affect of feeding, sampling of birds for liver examination must take into account diurnal feeding patterns. Major changes in liver weight were related to a change in lean tissue weight. Data on this organ would provide little information on the overall condition of the bird.

The reserves of the female prior to egg laying were used both for egg production and as an energy source during incubation. All the fat and about half the calcium for egg production came from reserves. During incubation the amount of body reserves used differed between years and apparently depended on food supply. In all years, however, food would be required to supplement reserves, and food supply during incubation was probably the major factor influencing hatching success (between years). Brood parasitism may have resulted from extreme cases in which the bird would have had insufficient reserves remaining after egg laying for successful incubation.

Egg size is important (for survival of the newly hatched Tufted Duck) and this did not decline, with declining clutch size, through the season; nor did it differ between breeding sites. Mean clutch size apparently differs between sites, though its determination may be affected by brood parasitism, and it shows little variation between years, except in response to extreme food shortage. The smaller clutches late in the season can be explained by the accumulation of fewer reserves (fat or calcium) by the females which lay then.

The most important parameters for estimating the energy budget of the Tufted Duck at Loch Leven were numbers of, and energy used for respiration by, the birds. The latter was estimated from a general equation relating standard metabolic rate to body weight in birds and then correcting this (by 2.5x) to give existence energy. A calculation using only these data would have indicated the relative importance of Tufted Ducks as consumers in the Loch Leven ecosystem. A bioenergetic study of the Tufted Duck indicated also the relative importance of carcass reserves and food for egg production, hatching success and winter survival of these birds.

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