Studies of shorebirds at Lindisfarne, Northumberland.

2. Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit

P. R. EVANS AND P. C. SMITH

Introduction

In a pioneer study on Canada Geese *Branta canadensis,* Hanson (1962) investigated possible parameters which could be used to evaluate the 'condition' of migrant waterfowl during the course of their annual cycle. He studied variations in total body weight, in weights of pectoral and tibiotarsal muscles, and in weights of liver and total body fat. He concluded that no parameter could measure 'condition' adequately, and, in particular, that it should not be assumed that the heaviest birds are in the best condition.

Since definitions of condition are lacking from most papers which have mentioned the subject, we begin with the assumption that condition is a measure of the chances of survival of an individual at a particular time of year, and/or of its potential for breeding successfully. It should, therefore, be quantifiable by examining the size of a bird's reserves of fat, protein and other groups of biologically important chemicals, in relation to the size of the demands likely to be made on these reserves at the particular time of year or stage in the annual cycle. In practice, the size of the demands may be hard to predict from armchair reasoning, but instead may be assessed by measuring the normal levels of reserves carried by birds at different times of year. These normal levels are presumed to have been selected during the course of evolution as those maximizing the chances of survival of the individual, or, indirectly, of its offspring. Condition, it should be stressed, is a relative measure, and no absolute value of a physiological or chemical parameter can indicate it. For example, a low level of body fat may indicate a bird in poor condition in midwinter (when fat reserves 'need' to be high as a safeguard against high energy demands or poor feeding conditions) but in good condition in mid-summer when high fat reserves are not needed.

This paper presents data on the body composition of 169 Bar-tailed Godwits *Limosa lapponica* collected at Lindisfarne, Northumberland, during the years 1970–1975 in connection with studies on food selection and heavy metal accumulation by this species. (Birds collected between February and August, inclusive, i.e. outside the official shooting season, were obtained under licence from the Nature Conservancy Council.) In this paper, we seek to establish the normal levels of fat and pectoral muscle in birds of different size at different times of year, and to identify those stages of the annual cycle or situations in which birds find it difficult to maintain good condition. We attempt to relate these to the feeding ecology and behaviour of the godwits, as described in part in an earlier paper (Smith & Evans, 1973) and in further detail here. The reader is referred to our earlier paper for a general description of the study area and its importance as a wintering area for godwits.

Bar-tailed Godwits vary considerably in size and weight, both within one sex and between sexes; smaller variations may occur with age. Data from small samples of birds collected on different days throughout the non-breeding season are thus inadequate to establish the patterns of weight change occurring within a whole population. Not surprisingly, therefore, our measurements from Lindisfarne godwits show no clear-cut trends in total body weight during the autumn, winter and spring. Similarly, data from the Wash, East Anglia, summarized by Minton (1973), suggest that there was no appreciable change in the mean weights of males or females between early autumn and winter —but winter samples were small. Even if true, important reciprocal changes could occur in the weights of certain body components, without changes in the total weight of a bird, and it is these which are explored in this paper.

Methods

Birds were collected during daylight hours, 1–2½ hours before the time of high tide, usually as they were flighting from their feeding grounds to their high tide roost. Since shorebirds feed at times mainly dictated by the tidal cycle and not by the alternation of day and night, the day-to-day condition of birds should be most comparable when considered at similar stages of the tide, rather than at the same hour of the day.

Immediately after collection, each bird was weighed and the gut removed and stored in 70% alcohol for subsequent analysis. Measurements were taken of the lengths of the bill and tarsus, and the sex was determined by dissection. The carcass was then stored in deep-freeze and eventually transported to Durham. While the carcass was thawing, the bird was aged by plumage characteristics (see later) and details of wing moult recorded. The breast muscles from the right side of the bird (the pectoralis, supracoracoideus and coracobrachialis) were excised after removal of any superficial covering of fat. They were then dried, weighed and extracted with petroleum ether (60°–80° b pt) in a Soxhlet extractor. The residual weight after further drying was taken to be the lean dry weight of the pectoral muscle. The liver was also removed and subjected to similar procedures, but the results are not discussed in this paper, since, as Hanson (1962) pointed out, the liver is an indicator of shifts in metabolic processes rather than of body condition.

The remainder of the carcass (i.e. minus gut, liver and one set of pectoral muscles) was also dried and fat was extracted from it by repeated washings in petroleum ether for three days. After further drying, the carcass was reweighed. The total weight of fat carried by the bird was then calculated, after due allowance had been made for fat extracted from liver and muscles. In the results discussed later, total body fat is expressed as a percentage of total body weight (including fat), termed the Lipid Index. This follows the usage of King & Farner (1966) and is the ratio appropriate for the calculation of potential flight range for a given quantity of fat (Pennycuick, 1969). It is not wholly appropriate for calculation of potential survival time, however, since this is a function of a bird's metabolic rate, which varies with body weight to the power of 3/4, i.e. large birds require less energy *per unit weight* to stay alive than do small birds. To survive a certain time, therefore, the larger female godwits require somewhat lower lipid indices than the smaller males. This difference may be enhanced further if the metabolic rate of females is lower than that of males of the same size, as has been claimed for certain other bird species (references in Hanson (1962)).

Lean dry weight of the pectoral muscles is expressed as an index related to the dimensions of the parts of the skeleton to which the muscles are attached. The area of attachment is determined by the areas of the keel and the bony raft of the sternum, together with the extension provided by the coracoid bone (Figure 1). Although an index of muscle size could be calculated by dividing muscle weight (which should be proportional to muscle volume) by the *area* of attachment, such an index would not be dimensionless, and so would be unsuitable for comparison of the conditions of muscles from birds of different size. Accordingly, muscle weight for each bird is expressed as a fraction of the volume of a muscle of *standard shape* attached to the appropriate area, as measured for that particular bird. The standard shape was chosen after examination of the pectoral muscles of several shorebird species, and so should have correspondingly wide applicability. The standard volume for the muscle, on either side of the bird, is given by the formula

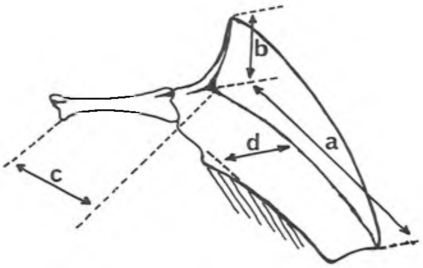


Figure 1. Skeletal measurements used to calculate the area of attachment of the pectoral muscles and hence a standard muscle volume. For further details, see text.

$$V = b\,(ad + 0{\cdot}433\,c^2)$$

where a = length of the sternum
b = height of the keel of the sternum
c = distance from the keel to the end of the coracoid
d = width of the bony raft of the sternum

These dimensions are illustrated in Figure 1.

Another muscle index is also used: the total lean dry weight of the pectoral muscles on both sides of the bird expressed as a proportion of the lean weight (total body weight minus fat) of the whole bird. (This index will not change if alterations in muscle size are accompanied by corresponding changes in water content of the body.)

It had been intended to present data also on the fat content of the pectoral muscles, but estimation of this quantity is unreliable when determined from whole muscles, since adhesion of even small quantities of superficial adipose tissue can produce unrealistically high values of the fat content of the muscle. Many of the determinations made on whole godwit muscles probably were free from this source of error, and in general the fat contents of muscle appeared to parallel closely the corresponding Lipid Indices for the whole birds, so they are not discussed further.

Age determination

The plumages of Bar-tailed Godwits were described in detail by Chapman (1907). Young birds arrive in August and September in warm brown 'speckled' plumage, with a strongly barred tail. Later they moult their body feathers to an ash-grey winter plumage of similar colour to that of adults. However, we noticed that they retain the finely-barred tail feathers, which differ markedly from the broadly-banded central tail feathers of the adults (Figure 2). By this feature, we were able to distinguish first-year birds from adults throughout the winter. In summer, according to Chapman, very few first-year birds acquire the red breast and belly feathers of the adults, so they may be distinguished also at this time of year.

The grey first-summer birds moult completely in late summer and early autumn, and then become indistinguishable from older birds in non-breeding plumage. At Lindisfarne, moult of the primary feathers usually was completed in late October or early November, but a few individuals were about to finish feather growth in mid-September in 1974. These may have been immature (first-summer) birds which had spent the summer months in England.

Figure 2. Central tail feathers of juvenile (barred) and adult (banded) Bar-tailed Godwits in midwinter. When spread, the tail feathers of adults show a terminal band.

Results

Lean weights

It had been hoped that, although total weights of godwits were very variable, even within one sex and age-class at any chosen time of year, lean weights might have been less variable, so that seasonal changes could have been detected. However, variability in body size is so great (about 15% on either side of the mean) that any trends in lean weight that might have been present were effectively swamped (Figure 3 and Appendix 1). On the

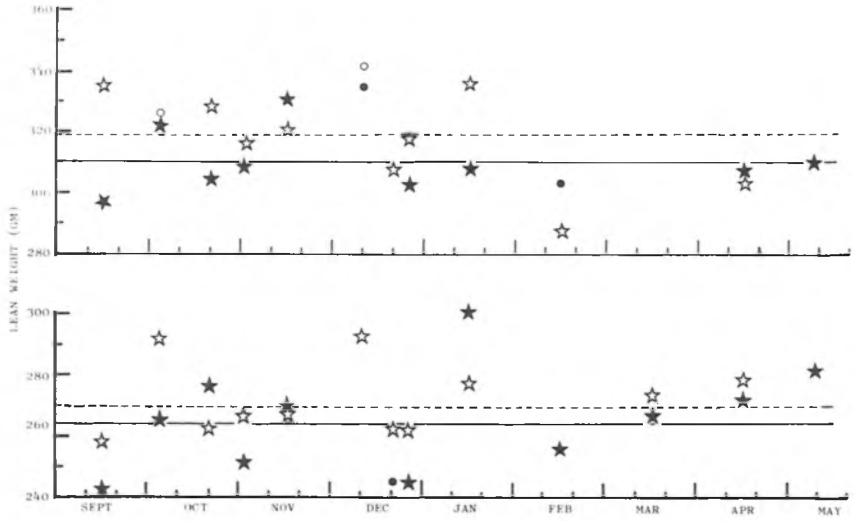


Figure 3. Average lean weights of female (upper panel) and male (lower panel) Bar-tailed Godwits throughout the non-breeding season at Lindisfarne. Filled symbols = juveniles, open symbols = adults, large stars = mean values, small circles = single observations. Trend lines: solid = juveniles, dashed = adults.

few occasions when weights differed significantly between one sampling period and the next, these differences resulted from size differences in the birds examined, rather than from true weight changes in the whole population from which the birds were sampled.

On average, females were about 20% heavier than males (mean weights throughout the non-breeding season: 319 g and 270 g for adults, and 311 g and 264 g for first-year birds, respectively).

Although lean weights apparently did not change with season or physiological state, the great variability in weights could mask underlying trends in the weights of components which together make up lean weight, namely muscle, water and skeleton. (The last-named is unlikely to alter much.) No direct measure was obtained of body water, since the gut of each bird was removed before the carcass was dried. However relative changes in the two muscle indicates enable changes in body water levels to be deduced, as will be shown later.

Normal patterns of change in lipid and muscle indices during the non-breeding season: birds in 'good condition'

Trends in the three indices are summarized in Figure 4 (a, b, c) and detailed in Appendix 2. In most instances, all values for a particular index at any chosen date or period of the year were similar, and approximately normally distributed about the mean value illustrated in the diagrams. (Differences between males and females, and between birds of different sizes, disappeared when the weights of fat and muscle were expressed as indices.) On a few occasions, exceptionally high or low values were recorded; these are shown separately in the diagrams and were excluded from calculations of the means given in Appendix 2. The trends in all years were similar, so data from several years have been combined for each period of the year.

As may be seen from Figure 4, the Lipid Indices of both adults and juveniles remained steady at about 5% during September and October, rose to a peak of just over 12% in mid-December but then fell again during the spring. By contrast, both of the pectoral muscle indices showed no change in adults throughout the winter, but a steady increase in juveniles from autumn to spring. For a juvenile of fixed skeletal size, its pectoral muscles increased in weight by about 25% between September and May, as the muscle index rose from about 0·25 to 0·31. In the same period, the proportion of the lean body weight formed by dry pectoral muscle rose

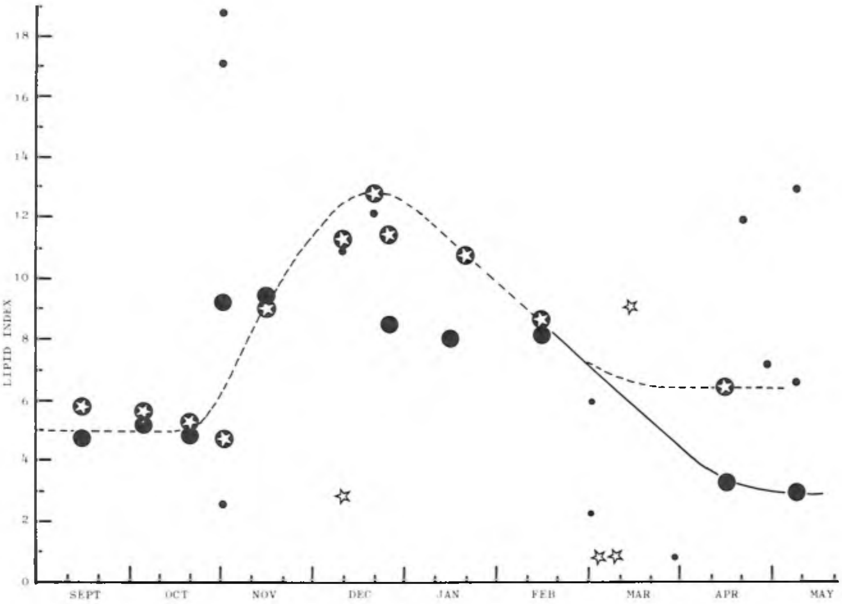
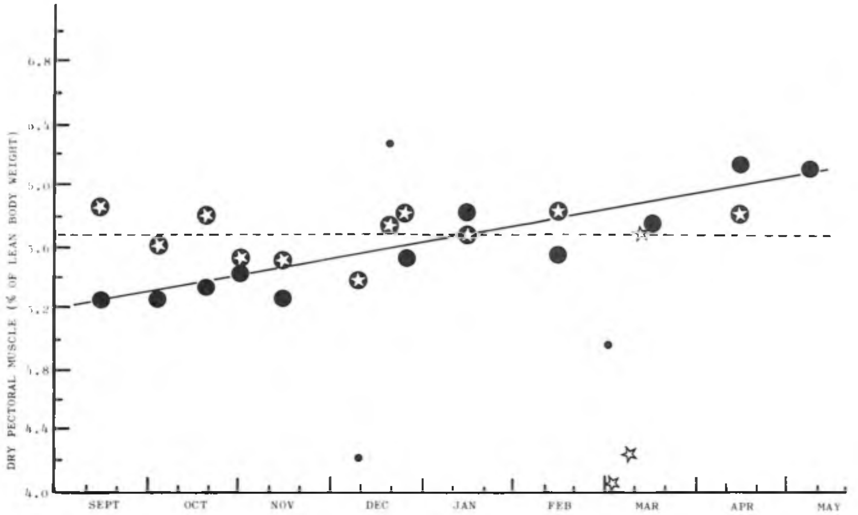
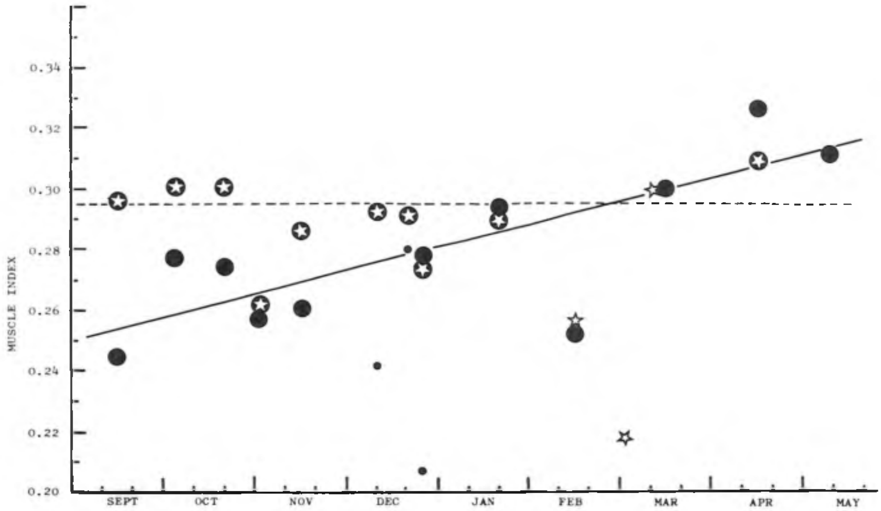


Figure 4 (a). Lipid Indices (fat as a percentage of total body weight) of juvenile and adult Bar-tailed Godwits at Lindisfarne. Trend lines (fitted by eye): solid = juveniles, dashed = adults. Symbols: filled circles = juveniles, circles with stars = adults. Small symbols indicate data from single birds.



(b). Pectoral muscle weight (as a percentage of lean weight) of juvenile and adult Bar-tailed Godwits at Lindisfarne. Key as in Figure 4(a).



(c). Pectoral muscle indices (measured in relation to standard muscle volume—see text) of juvenile and adult Bar-tailed Godwits at Lindisfarne. Key as in Figure 4(a).

from about 5·2 to 6·1%, a change of just over 17%. This lesser increase implies that the average lean weight of juveniles must also have increased slightly during their first winter of life.

The patterns outlined above may now be related to different events in the annual cycle.

(a) During moult

In most years, adult godwits do not return to Lindisfarne until late October, by which date they have almost finished moult of their primary feathers. For example, in 1970, a sample of birds collected on 1st November contained seven adults, all growing their outermost one or two primaries. In 1974, however, some adults returned to Lindisfarne unusually early and in full breeding plumage. By early September, some of these birds had almost finished wing moult, while others had renewed only half their primaries. (Chapman (1924) recorded the arrival in mid-August 1918 of adults in active wing-moult.) The fat levels of moulting birds varied very little amongst individuals, or with date, throughout September and October. Similarly, the pectoral muscle indices varied very little in moulting birds and were not significantly different from those of non-moulting adults at other times of year. This suggests that there was no marked increase in body water, including blood volume, during moult, since this should have led to a lower muscle index when expressed as a proportion of an increased body weight. Nor was there evidence of use of the pectoral muscles as a protein source for feather production, since this would have led to lower muscle indices, when expressed either as a proportion of lean body weight or in relation to skeletal size.

(b) During and after autumn migration

As mentioned above, in 1970 a sample of moulting adult godwits was collected on 1st November, within a few days of their arrival at Lindisfarne. These had a slightly, but not significantly, lower mean Lipid Index than moulting birds which had been at Lindisfarne for several months. This difference was attributable chiefly to one November bird with an index of only 2·7%, some two per cent below normal. After migration, the size of the pectoral muscles, measured in relation to skeletal size, was significantly lower ($p <$ 0·01, t-test) than in the other moulting birds. However, when expressed as a percentage of lean weight, the muscle index of the post-migratory birds was not significantly lower. These observations are consistent with the idea that some muscle protein is used during the migratory flight, together with an approximately equivalent percentage of body water, so that the ratio of muscle weight to total lean body weight remains almost unchanged. Comparison of the October and 1st November data indicate an average loss of some 13% in the weight of the pectoral muscles. Much of this loss was made good by mid-November, as indicated by the significant rise in muscle index during that month.

In the case of juveniles, there is less certainty that individuals were collected very soon after arrival at Lindisfarne. Nevertheless, the September data show pectoral muscle weights low in relation to skeletal size, but average in relation to lean body weight, just as found in the adults. By October, several weeks after the arrival of most of the juveniles, their muscle weights had risen considerably. Two juveniles collected on 1st November had very high Lipid Indices (Figure 4) similar to that (19·0%) of a juvenile held in captivity until mid-November. Presumably these birds would have migrated further. However, their muscle indices were lower than average.

(c) During winter

In most winters, godwit numbers at Lindisfarne remain steady from November to late January. The mean Lipid Indices of both adults and juveniles rise to a peak of about 12% in mid-December, when days are shortest, and decline thereafter as days lengthen. This lipid reserve can be used for either or both of two purposes: (i) to augment daily food intake when this is insufficient to meet daily maintenance costs, (ii) to provide fuel for flights to other areas. At worst, when the intertidal zone is completely frozen, godwits are unable to feed. Under these conditions, the fat reserves carried in mid-December, totalling between 30 and 40 gms (depending on the size and sex of the bird) would be sufficient to provide maintenance energy for about three days.

In contrast, no protein reserve appears to be laid down, at least in the pectoral muscles, to guard against temporary starvation in mid-winter. In adults, the two muscle indices are no higher in mid-December than during moult, when, as argued above, they might have been expected to be low. In juveniles, also, the rate of increase in both muscle indices between autumn and spring appears to be steady, with no mid-winter peak.

(d) Before and during spring migration

Most godwits which winter at Lindisfarne leave the area by late April. However, others arrive to take their place, some stopping only briefly before continuing migration northwards, a few hundred immatures remaining throughout the summer. As judged by direct observation, the Lindisfarne wintering population contains more short-billed males than long-billed females. In the September to March samples collected for this study 56% of the birds were males, 44%

females. By contrast, the sample of 13 one-year old birds collected on 8th May 1974 contained 70% females. This sample of passage migrant and/or potential summering birds contained only two individuals with fat levels sufficient to perform significant further migration. Possibly the rest had arrived only recently and so had not had time in which to prepare for further migration. Their Lipid Indices averaged only 3%, similar to the majority of juveniles in April. In both months the highest Lipid Indices recorded were 12–13%, comparable to mid-winter levels. No adults were examined in May; those collected in April had Lipid Indices averaging 6·5% and included no exceptionally fat individuals. Presumably the spring migration of godwits to Siberia takes place by a series of short flights from one refuelling area to another.

Both muscle indices of juvenile godwits reached their highest values in April and May. It might be supposed that this indicates growth of the pectoral muscles associated with preparation for migration, but this is not certain, since the muscle indices obtained were not significantly greater than those of adults in the following autumn. Furthermore, there was no statistically convincing evidence of muscle hypertrophy in adult godwits before their migration in April, although the index relating muscle weight to skeletal size in adults reached its highest mean value of the year in that month.

Departures from the normal patterns of change: birds in 'poor condition'

The inability of birds to maintain fat and muscle reserves at levels appropriate for the time of year must be the result of inadequate food intake. A number of possible situations can lead to this. Birds cannot feed during a migratory flight, may be unable to feed effectively during cold weather (for reasons to be discussed later) or may be injured.

It is well known that fat stored before migration is used as fuel during the flight; but little information is available on the levels of fat remaining at the end of the journey. Information presented earlier showed that only one of seven adults collected after arrival on 1st November 1970 had a Lipid Index notably below normal for the time of year. (One of nine juveniles collected on the same day had an equally low Lipid Index (2·6%), and possibly was a passage migrant.) These data suggest that the levels of fat accumulated before migration usually are more than sufficient for the flight, and allow a safety margin similar in quantity to the normal levels of fat carried by non-migrants at that time of year. By contrast, the muscle weights of adults after migration (measured against skeletal size) were lower in six of the seven birds examined than the *lowest* muscle weight recorded in non-migrants between September and early December. Using muscle as the criterion, therefore, most godwits were in 'poor' condition after migration, even though they carried adequate fat reserves.

The effects of a period of cold weather in restricting food intake are exemplified by the changes in body composition of samples of godwits taken on 20th and 25th December 1970. The average Lipid Index of adults fell from 12·8 to 11·5%, a non-significant drop, as the variation in Lipid Index about the mean was wide on both days. The lowest fat levels of individuals before and after the cold spell were 8·9 and 7·4% respectively. Thus, although apparently in poorer condition after five days of cold weather, adult godwits must have maintained daily energy intake almost at the levels needed to meet their daily requirements. Juveniles fared less well. At the end of the cold weather, their Lipid Indices averaged only 8·5%, significantly lower ($p = 0{\cdot}05$, t-test) than those of adults collected on the same day. Three of the eight juveniles carried fat levels lower than that of the adult in 'poorest condition'. The juvenile with least fat (5·0%) had one tarsus which had been broken but had healed subsequently. Muscle weights, measured against lean body weight, showed no change during the cold spell. However, when measured against skeletal size, the pectoral muscles of the sample of adults collected on 25th December, after the cold weather, were lighter than those of the sample collected on 20th December. As in the fall in Lipid Index, the change was nonsignificant, since the variation in muscle index around the mean was wide on both days. One adult had an index as low as 0·246, similar to the lowest values recorded in the birds collected after migration on 1st November. The mean muscle index of juveniles collected on 25th December was very similar to that of the adults, but this value is based on only seven of the eight juveniles, and omits one individual with an exceptionally low muscle index of 0·207. (This bird had a Lipid Index of 11·8%, well above average!) Although this juvenile was in 'poor condition', using the criterion of pectoral muscle weight, it should not be assumed that its chances of survival were very low, for its muscle index was identical with that of a healthy captive bird, in which the pectoral muscles had atrophied through disuse.

Exceptionally low fat levels for the time of year were obtained from two juvenile males in September/October 1974 and one adult male in March 1971. These birds had no noticeable deformities but were roosting or feeding singly. An adult male with a broken leg collected in early March 1971 also had an abnormally low Lipid Index. However, three other birds with bone damage which had healed—including one which had lost its right foot—had normal Lipid Indices, as did another carrying a heavy load of intestinal parasites. The muscle indices of the juveniles roosting alone were normal, but those of the adult males collected in March, while feeding solitarily, were very low.

It is not known why the solitary birds were feeding or roosting alone. We showed earlier (Smith & Evans, 1973) that godwits feeding singly had lower rates of prey capture than birds feeding in flocks. This could lead to loss of condition. Alternatively, birds which develop poor condition may then leave the feeding flocks.

Discussion

(i) *Are muscle and fat levels two independent criteria of condition?*

Hanson (1962) argued that during migration, food shortage or starvation, fat can be utilized as an energy source only with concurrent breakdown of protein. Fat is metabolized via the Krebs' cycle, provided that a supply of oxaloacetate, which can be derived only from carbohydrate or protein metabolism, is also available. During starvation, a bird's carbohydrate reserves are exhausted quickly; therefore, Hanson claimed, protein must be the source of the oxaloacetate: 'fat is burnt in the flame of protein'. We see no reason, however, why oxaloacetate, once provided, should be used up during fat catabolism, since it should be reformed (without loss) during the working of the 'Krebs' cycle'. Therefore we claim that protein breakdown is not necessary for fat utilization. However, all warm-blooded vertebrates have high rates of protein turnover in the liver and so require its continual intake. 'The primary function of protein food is to supply the amino-acids needed for the growth, repair and general maintenance of the structural and catalytic machinery of living cells' (Baldwin, 1967). Hence, during any period of inadequate protein intake, protein reserves within the body itself, e.g. the pectoral muscles (Kendall, Ward & Bacchus, 1973), will be utilized to provide the necessary amino-acids. During starvation, resulting either from food becoming unavailable, or from prolonged continuous migratory flight, a bird's muscles are likely to be used as the source of protein at the same time as its fat reserves are used as an energy source. During times of merely *shortage* of food, however, a situation could arise in which the daily protein intake was adequate, but the total energy intake insufficient, to meet the daily requirements. Under these conditions, a bird's fat reserves would decrease, but no change would be expected in the weight of its muscles. With less favourable feeding opportunities, but not complete starvation, both fat and muscle reserves would be used up, but fat more quickly than protein. Under total and prolonged starvation, at least in man, the daily use of fat reserves remains steady, but protein reserves are drawn upon progressively less heavily as the duration of the fast lengthens, as a result of reductions in enzyme activities in the liver.

The conclusions to be drawn from the arguments outlined above are that fat and muscle levels are independent measures of condition, but that they often vary in parallel, though not necessarily to the same extent. Insofar as the data from adult godwits collected on 20th and 25th December 1970 are representative of the population as a whole, fat levels were 10% lower but muscle weights only 6% lower after the period of cold weather. This could be interpreted as indicating a level of difficulty in obtaining food which was sufficient to reduce both daily protein intake and, more particularly, daily energy intake below daily requirements.

(ii) *Increases in muscle weight in birds: some general predictions*

As mentioned earlier, restriction of daily food intake will not necessarily lead to the depletion of protein reserves in a bird's body, whereas even temporary starvation must do so. One may predict, therefore, that those species which are likely to meet conditions in which food is made unavailable for several days, during predictable periods of the year when e.g. droughts or snow cover are likely to occur, will increase their protein reserves in anticipation. In contrast, those species which usually encounter merely reductions in food availability at certain times of year, but rarely complete absence of food, may well not increase their reserves in anticipation.

Shorebirds, feeding in the intertidal zone which rarely freezes for more than a few hours in normal British winters, would be expected to fall in the second category, and it will be noted that adult Bar-tailed Godwits did not increase their muscle levels in anticipation of cold weather in mid-winter at Lindisfarne.

With regard to migrants, most of which cannot feed on the wing, the use of body protein must increase approximately in proportion to the duration of non-stop flight. If the food types and availability at the destination do not permit rapid replacement of lost protein by a migrant species, then one may expect that species to prepare for migration by muscle hypertrophy before departure. The longer the flight to unfavourable feeding areas, the greater the extent of hypertrophy to be expected. If, on the other hand, migrants are travelling only short distances or to areas where feeding conditions are good, then hypertrophy need not occur. In the Bar-tailed Godwits at Lindisfarne, any increase in muscle weight which may have taken place before autumn migration was insufficient to provide the protein needed during the flight itself. Hence, on arrival in early November, birds had pectoral muscle weights below normal; but feeding conditions usually are good at that time of year and the losses were soon made up. In spring, pre-migratory fat deposits were relatively small, and the apparent (but not significant) increase in muscle weight was also small. Presumably, the flight to the arctic breeding grounds was not made directly from Lindisfarne, so the need for increased protein reserves before departure was lacking. It should be noted that small and medium-sized migrants do not need to acquire larger muscles to carry the extra fuel load during migration (Pennycuick, 1969).

Hypertrophy of the pectoral muscles before migration, and a reduction in muscle weight during migration, has been claimed for several passerine species, e.g. the Lesser Redpoll *Carduelis flammea* leaving Britain in autumn (Evans, 1969a) and the Yellow Wagtail *Motacilla flava* prior to crossing the Sahara while on northward migration in spring (Fry, Ferguson-Lees & Dowsett, 1972), though in neither case was it proven conclusively that the fattest birds, which had the highest pectoral muscle weights, were not merely the largest birds in terms of skeletal size.

(iii) *The functions and control of winter fattening in godwits*

The peak Lipid Index in godwits occurred in December, when days are shortest, rather than one month later, when the average daily temperature tends to be lowest. This suggests that increased fat reserves may be an adaptation to restricted hours of daylight feeding, as well as to increased metabolic needs at lower temperatures. Although godwits can feed by night as well as by day, they are more successful by day, when they hunt primarily by sight. Their preferred prey occur chiefly below mid-tidal level and so are available for less than 8 hours in every tidal cycle. When high tides occur in the middle of the day in mid-December, godwits at Lindisfarne are able to feed on their preferred prey for no more than three hours during daylight. By mid-January, with similar tidal conditions, the natural increase of daylength allows them another half-hour of daylight feeding, so it may be argued that they do not need to maintain such large fat reserves then to cope with any sudden onset of adverse conditions. Many wader species studied on the Wash also reach peak weights (and therefore very probably peak fatness) in December rather than January, as may be deduced from data summarized by Minton (1973). In contrast, several passerines, for example the Yellow Bunting *Emberiza citrinella,* reach peak fatness in mid-January (Evans, 1969b).

Unlike the winter fat deposits of passerines, those of godwits (and Oystercatchers *Haematopus ostralegus* (Dare, in prep.)) form a layer *over* the pectoral muscles, rather than being concentrated in the 'tracheal pit' (between the clavicles) and over the peritoneum. Hence winter fat in godwits may serve an insulative function, as well as acting as an energy reserve to be drawn upon if daily energy intake falls below requirements, or for hard-weather movements. If the distributions of winter and pre-migratory fat in waders are similar, problems might arise in dissipation of the heat produced by the pectoral muscles during migratory flights. It has been argued that passerine migrants used air-cooled 'engines' (Hart & Berger, 1972), so additional insulation over the pectoral muscles would seem a disadvantage. However, in godwits, presumed premigratory fat deposition in April and May was less extensive than in mid-winter, so that the muscles were rarely overlain by a thick layer of fat.

While the adaptive nature of winter fattening in godwits seems clear, its proximate control is unknown. Several passerines, e.g. the White-crowned Sparrow *Zonotrichia leucophrys* and the Bullfinch *Pyrrhula pyrrhula,* respond to sudden cold weather by increasing their fat reserves immediately

(King & Farner, 1966; Newton, 1969). However, the Yellow Bunting does not. The levels of its reserves are linked solely to the date and are unaffected by temperature (Evans, 1969b). In contrast, the Bar-tailed Godwit was unable to maintain its reserves during cold weather, but otherwise carried fat reserves linked to the date (Figure 4). These fat levels could have been regulated via an internal rhythm or by daylength. Differences in the proximate control of the fat reserve in waders and passerines are to be expected in view of the differences in its function. Passerines use fat as an overnight energy supply and to provide sufficient energy to enable them to fly from their roost to search for food next morning. Waders are able to feed by night, but their foods may be less available in cold weather, whereas those of granivorous passerines are unaffected by cold *per se*, though they may be made unavailable by snow cover.

(iv) *Body condition, food availability, and feeding behaviour*

The depressive effects of cold weather on body condition, as measured by fat and muscle indices, link neatly with data on the feeding behaviour of godwits at different temperatures (Smith, 1974 and in prep.). Their chief prey are lugworms *Arenicola marina,* which they detect and capture when the worms back up their U-shaped burrows to defaecate. When mud temperatures fall below 3°C, lugworms become progressively less active and the rate at which they are captured by godwits decreases. When mud temperatures fall below freezing point, godwits manage to take very few lugworms, and rely on finding other, smaller, polychaete worms. They then have difficulty in satisfying their daily food requirements—as happened, particularly to the juveniles, in late December 1970—and their lipid reserves are drawn upon.

Lugworms are less readily available to godwits also during periods of high winds, which dry the surface of the sand and reduce the frequency of defaecation by the worms. Gales also prevent godwits from feeding successfully at the tide-edge, as *Arenicola* casts are washed away as fast as they are formed (so depriving godwits of the clues they need to find the worms) and the water becomes turbid, thereby reducing visibility. In early autumn, godwits seem able to cope with this situation, provided that gales do not delay or prevent the ebbing tide from uncovering their preferred feeding areas. They obtain their daily food requirements by lengthening their period of feeding to compensate for lower rates of prey capture. Even juveniles manage to compensate in this way, for the average Lipid Index of the sample taken on 4th October 1974, after three days of northerly gales, was not significantly different from that of juveniles collected in September or later in October (means of 5·2 as against 4·8 and 4·9%, respectively). We have no information to indicate how seriously the onset of gales would aggravate an already bad feeding situation for godwits during cold weather in mid-winter, or during periods of midday high tides when daylight hours are short.

Acknowledgements

We are grateful to Professor D. Barker for allowing P.C.S. to use the facilities of the Zoology Department, Durham University; to the Nature Conservancy and the Lindisfarne Wildfowl Advisory Committee for allowing us to work on the Lindisfarne N.N.R. and to M. J. Hudson (Deputy Regional Officer) and E. F. Pithers and D. O'Connor (Chief Warden and Warden at Lindisfarne) for practical help. Financial support for P.C.S. was provided by the Frank Chapman Memorial Fund, American Museum of Natural History, and by the Research and Special Publications Fund of the British Ornithologists' Union, to whom grateful thanks are tendered.

For assistance in the collection of specimens during the official shooting season, we are particularly grateful to J. Brigham, T. Douglass, and the late 'T' Brigham.

For helpful comments on the first draft of this manuscript, we thank M. W. Pienkowski.

Summary

Body compositions have been determined of 169 Bar-tailed Godwits *Limosa lapponica,* collected at different times of year, between 1970 and 1975, at Lindisfarne, Northumberland. Normal trends in lipid and muscle indices are shown in Figure 4. The lipid index (weight of fat as a percentage of total body weight) of both adults and juveniles reaches a peak in December when daylight hours are shortest. Both muscle indices (lean dry weight of all the pectoral muscles (i) as a percentage of lean body weight (ii) in relation to skeletal size) remain unchanged in adults throughout the non-breeding season, but increase steadily in juveniles to reach adult levels by late winter. Slight hypertrophy of the pectoral muscles may occur before migration. Birds with lipid and/or muscle indices below normal for the time of year are considered to be in 'poor condition'; recovery of condition may be rapid, for example in adult godwits arriving at Lin-

disfarne with depleted muscles after autumn migration. During cold weather, lipid reserves are used to augment daily food intake if this is insufficient to meet daily energy requirements. At maximum, fat reserves alone could supply about three days' energy needs. Muscle may also be drawn upon as a protein reserve. Juveniles lose condition more rapidly than adults when food becomes less readily available in cold weather. Differences in the temporal pattern and functions of winter fattening in waders and passerines are discussed. Some predictions are made as to the likelihood of accumulation of protein reserves in winter or before migration in different bird species.

References

Baldwin, E. 1967. *Dynamic aspects of Biochemistry.* 5th Edition. Cambridge, University Press.

Chapman, A. 1907. *Bird life of the Borders.* 2nd Edition. London & Edinburgh, Gurney & Jackson.

Chapman, A. 1924. *The Borders and Beyond.* London & Edinburgh, Gurney & Jackson.

Evans, P. R. 1969a. Ecological aspects of migration, and pre-migratory fat deposition in the Lesser Redpoll. *Condor* 71: 316–30.

Evans, P. R. 1969b. Winter fat deposition and overnight survival in the Yellow Bunting. *J. Anim. Ecol.* 38: 415–23.

Fry, C. H., Ferguson-Lees, I. J. & Dowsett, R. J. 1972. Flight muscle hypertrophy and ecophysiological variation of Yellow Wagtail *Motacilla flava* races at Lake Chad. *J. Zool., Lond.* 167: 293–306.

Hanson, H. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. *Arctic Institute of N. America Technical Paper* No. 12.

Hart, J. S. & Berger, M. 1972. Energetics, water economy and temperature regulation during flight. *Proc. 15th Int. Orn. Congr.*: 189–99.

Kendall, M. D., Ward, P. & Bacchus, S. 1973. A protein reserve in the pectoralis major flight muscle of *Quelea quelea. Ibis* 115: 600–1.

King, J. R. & Farner, D. S. 1966. The adaptive role of winter fattening in the white-crowned sparrow, with comments on its regulation. *American Naturalist* 100: 403–18.

Minton, C. D. T. 1973. Seasonal variation in the weights of waders on the Wash. *Wash Wader Ringing Group Report* 1971/72 (mimeographed).

Newton, I. 1969. Winter fattening in the Bullfinch. *Physiol. Zool.* 42: 96–107.

Pennycuick, C. J. 1969. The mechanics of bird migration. *Ibis* 111: 525–56.

Smith, P. C. 1974. The feeding behaviour of the Bar-tailed Godwit. *Ibis* 116: 414.

Smith, P. C. & Evans, P. R. 1973. Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit. *Wildfowl* 24: 135–9.

Appendix 1. Lean body weights (gm) of Bar-tailed Godwits at Lindisfarne

Date Period		Juvenile Male	Adult Male	Juvenile Female	Adult Female
September	Mean	242	258	297	335
	S.E.	7·7	6·1	6·2	9·1
	n	8	6	4	6
4 October 1974	Mean	266	292	323	326
	S.E.	6·8	8·7	9·3	—
	n	7	3	3	1
17/23 October	Mean	277	263	305	329
	S.E.	11·0	0	17·6	12·7
	n	5	2	4	3
1 November	Mean	251	266	309	315
	S.E.	9·9	6·0	10·0	5·5
	n	5	2	4	5
November	Mean	270	269	331	321
	S.E.	3·9	5·8	17·0	49·5
	n	4	5	4	2
10/11 December	Mean	—	293	335	342
	S.E.	—	8·9	—	—
	n	—	3	1	1
20 December 1970	Mean	245	262	—	308
	S.E.	—	9·4	—	13·2
	n	1	4	—	3
25 December 1970	Mean	245	262	303	318
	S.E.	15·2	7·6	12·3	2·5
	n	3	5	5	2
14/16 January 1975	Mean	301	277	309	336
	S.E.	21·1	11·0	14·5	17·1
	n	3	2	3	4
late January/February	Mean	256	—	304	288
	S.E.	2·0	—	—	6·9
	n	2	—	1	4
March	Mean	267	274	—	—
	S.E.	10·4	0·7	—	—
	n	3	3	—	—
April	Mean	272	279	308	304
	S.E.	3·3	11·5	3·0	9·4
	n	3	3	2	3
8 May 1974	Mean	282	—	311	—
	S.E.	6·2	—	6·6	—
	n	4	—	9	—

Appendix 2. Fat and muscle indices of Bar-tailed Godwits at Lindisfarne

Date Period		Lipid Index (% of total body weight)		Muscle Index (% of lean body weight)		Muscle Index (related to skeletal size)	
		Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
September	Mean	4·8	5·8	5·26	5·88	0·245	0·296
	S.E.	0·88	0·42	0·150	0·104	0·007	0·0036
	n	12	12	12	12	12	12
4 October 1974	Mean	5·2	5·5	5·26	5·62	0·277	0·301
	S.E.	0·59	0·54	0·074	0·066	0·0040	0·0079
	n	10	4	10	4	10	4
17/23 October	Mean	4·9	5·2	5·34	5·82	0·275	0·301
	S.E.	0·25	0·48	0·082	0·092	0·0072	0·0049
	n	9	5	9	5	9	4
1 November 1970	Mean	10·3	4·7	5·44	5·54	0·259	0·261
	S.E.	1·78	0·39	0·130	0·152	0·0102	0·0069
	n	9	7	8	7	7	7
November	Mean	9·4	9·3	5·26	5·52	0·261	0·287
	S.E.	0·81	1·25	0·096	0·082	0·0086	0·0055
	n	7	7	6	7	7	8
10/11 December	Mean	11·0	11·3	4·22	5·40	0·242	0·293
	S.E.	—	1·38	—	0·108	—	0·0079
	n	1	3	1	4	1	4
20 December 1970	Mean	12·2	12·8	6·30	5·76	0·280	0·292
	S.E.	—	1·11	—	0·086	—	0·0099
	n	1	7	1	7	1	7
25 December 1970	Mean	8·5	11·5	5·54	5·84	0·277	0·275
	S.E.	1·03	1·13	0·118	0·114	0·0142	0·0062
	n	8	7	8	7	7	7
mid-January	Mean	8·0	10·8	5·84	5·70	0·294	0·290
	S.E.	0·93	1·09	0·136	0·110	0·0101	0·0081
	n	6	8	6	8	6	7
February	Mean	8·4	8·6	5·66	5·86	0·254	0·256
	S.E.	1·02	1·40	0·118	0·34	0·0024	—
	n	3	2	3	2	3	1
March	Mean	—	—	5·76	—	0·300	—
	S.E.	—	—	—	—	0·0027	—
	n	—	—	2	—	3	—
April	Mean	3·3	6·5	6·16	5·84	0·326	0·309
	S.E.	0·27	0·76	0·116	0·232	0·0141	0·0130
	n	3	6	5	6	5	6
8 May 1974	Mean	3·0	—	6·12	—	0·311	—
	S.E.	0·21	—	0·134	—	0·0090	—
	n	9	—	13	—	13	—

Dr P. R. Evans & P. C. Smith, Department of Zoology, Science Laboratories, South Road, Durham DH1 3LE.