# Studies in Willow Grouse *Lagopus lagopus* of some possible measures of condition in birds

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Size measurements, body and breast muscle weight and fat content were studied in 256 Willow Grouse, collected in western central Sweden. Protein content was estimated in 51 of the birds. In all age and breeding categories breast muscle lean dry weight was a good predictor of protein. Pectoral fat was an acceptable predictor of body fat only in part-grown birds, but the difference between dry body weight and the lean dry body weight extrapolated from breast muscle lean dry weight was a fairly good predictor of body fat in the other birds as well. Significant relationships between sternal length and breast muscle lean dry weight were used to correct for variation in body size in estimating energy reserves. Although the Willow Grouse fat content never exceeded 7 % of wet weight, fat accounted for more of the variation in total energy reserves than protein. Since the fat and protein levels were not strongly correlated, both must be studied to assess condition adequately in Willow Grouse. The utilizable energy reserves averaged 309 kcal, with a maximum of 627 kcal, enough to keep the birds alive for only a few days without feeding.

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## Introduction

A number of authors have related bird nutritional condition to extent of migration (Odum & Connell 1956, Nisbet et al. 1963, Evans 1969a), reproductive success (Cave 1968, Moss et al. 1974, Jones & Ward 1976), survival during food shortage (Nice 1938, Baldwin & Kendeigh 1938, Murton et al. 1971) or avoidance of predators (Kenward 1978). Most often body weight has been used as an index of condition, but more detailed investigations have measured fat and protein reserves independently. In some species body weight is a relatively good index of fat and protein reserves, but this is not always so. Moreover, the extent of fat reserves relative to protein varies between species, and can differ between seasons within the same species. Studies using indices of condition should therefore involve assessment of the variation in fat and protein reserves in the species concerned.

Since determination of total protein and fat content in large birds is time-consuming, several authors have used indices to represent these measurements. The fresh or lean dry weight of the breast muscle is sometimes used to indicate protein reserves (e.g. Hanson 1962, Evans & Smith 1975, Houston 1977), although little work has been done to determine the validity of these predictions. Baker (1975), Coleman & Robson (1975) and Woodall (1978) have found close correlations between the discrete fat deposits adjacent to the viscera and total fat in Oystercatchers *Haematopus ostralegus*, Starlings *Sturnus vulgaris*, and Redbilled Teal *Anas erythrorhyncha*. However,

TABLE 1. Measurements and weights of Swedish Willow Grouse. Mean ± *SD*.

| | *N* | Wet body weight (g) | Wing length (mm) | Sternal length (cm) |
|---|---|---|---|---|
| Full-grown males | 144 | 557±39 | 206±5 | 9.15±0.26 |
| Full-grown females | 44 | 489±32 | 192±5 | 8.67±0.23 |
| Egg-layers | 30 | 569±43 | 195±5 | 8.66±0.23 |
| Part-grown males | 20 | 498±60 | 197±12 | 8.82±0.65 |
| Part-grown females | 18 | 407±68 | 182±11 | 8.13±0.66 |

Willow Grouse usually have insignificant visceral fat deposits. In Goshawks *Accipiter gentilis* pectoral fat is a good predictor of total fat (Marcström & Kenward 1981), and this also applies to Woodpigeon *Columba palumbus* and Japanese Quail *Coturnix coturnix* (Brittas unpubl.). The object of this paper is to assess the value of pectoral fat and protein as indices of total protein and fat in Willow Grouse in different age and sex classes, and to show how measures of Willow Grouse condition may be corrected for variation in body size. Attention is paid to energy storage in the Willow Grouse and its ecological significance.

## Material and methods

In a mountainous area of western central Sweden (62°N, 13°E), described by Höglund (1967, 1970), 256 Willow Grouse were shot or snared between August and May 1973—79. The birds were divided into three categories: 30 "egg-laying" (EL) females killed in May, which were in breeding condition with well-developed gonads; "part-grown" (PG) juveniles collected in August-September (20 males and 18 females); and a group of "full-grown" (FG) birds (144 males and 44 females), which included juveniles taken later in the winter and not differing in weight from adults. The unequal sex-ratio in the third category results from sex-segregation during winter, when there is a low proportion of females in the study area (Höglund 1975, 1980), and from the exclusion of females in breeding condition.

For financial reasons, protein estimations were made for only 46 full-grown birds (22 males and 24 females) and 5 egg-layers.

All the birds were sealed in plastic bags soon after being killed and kept frozen until analysis. Each carcass was then weighed without the crop contents; wing length was measured from the flexed wrist to the end of the longest primary with a curved ruler fitting the natural curvature of the wing. The bird was then plucked and both breast muscle sets *(pectoralis major* and *minor)* were excised, care being taken not to include any extramuscular fat; the gizzard contents were removed; the sternum length was measured; and the sex was determined by gonad inspection. The wet and dry body weight values do not include the weight of the feathers, crop contents or gizzard contents. A one-gram sample for Kjeldahl nitrogen determination was cut from the left *pectoralis major* and refrozen.

The right breast muscle set and the remainder of the carcass (i.e. minus feathers, both sets of breast muscles, crop and gizzard contents) were homogenized separately, using a commercial food mincer, and freeze dried to constant weight. Lipid content was determined on the breast muscle homogenate and on two one-quarter samples of the "carcass" homogenate by 24-hour Soxhlet extraction with ether/ethanol (3:1) and weighing after vaporization of the solvent.

Kjeldahl nitrogen was determined, by the National Swedish Laboratory of Agricultural Chemistry, for two one-gram samples of the "carcass" homogenate (which was minced to

TABLE 2. Correlation coefficients from regression of different breast muscle measures on total protein in Swedish Willow Grouse.

| | | Breast muscle protein weight (g) | Breast muscle lean dry weight (g) | Breast muscle dry weight (g) | Breast muscle wet weight (g) |
|---|---|---|---|---|---|
| Total protein weight (g) | FG♂ *N*=22 | 0.948 | 0.921 | 0.927 | 0.934 |
| | FG♀ *N*=24 | 0.916 | 0.913 | 0.914 | 0.911 |

TABLE 3. Protein contents of featherless body and pectoral muscle in Swedish Willow Grouse. Mean ± *SD*.

| | *N* | Total protein (% of wet wt) | Total protein (% of dry wt) | Breast muscle protein (% of wet wt) | Breast muscle protein (% of dry wt) |
|---|---|---|---|---|---|
| Full-grown males | 22 | 20.7±0.5 | 82.0±0.5 | 24.9±0.6 | 99.0±2.3 |
| Full-grown females | 24 | 20.2±0.7 | 82.9±1.8 | 24.1±0.8 | 97.2±2.5 |
| Egg-layers | 5 | 19.6±0.3 | 81.8±0.9 | 24.5±0.7 | 100.0±1.9 |

a fine powder and carefully blended after freeze-drying), and the *pectoralis major* sample. A conversion factor of 6.25 was used in estimating protein from Kjeldahl nitrogen. The protein content of *pectoralis minor* was assumed to be similar to that of *pectoralis major*.

Calorific contents were calculated using the constants 4.4 kcal/g protein and 9.3 kcal/g fat (see Dargolts 1973).

Data were processed at Uppsala Data Centre, using the Biomedical Computer Programs P-series (Dixon & Brown 1977). Parametric statistics were used in all calculations.

## Results

*Body weight and body composition.* Wet body weight showed considerable inter-sex overlap, but males were significantly heavier ($P<0.001$) than females in both full-grown and part-grown birds (Table 1). Egg-layers were significantly ($P<0.001$) heavier than the rest of the females, which is consistent with the general tendency of avian species to gain weight prior to egg-laying. In fact, the egg-layers had a higher mean body weight than the full-grown males, although this difference was not significant.

In both full-grown birds and egg-layers breast muscle lean dry weight (B) was strongly correlated with the estimated total protein weight (P) ($r_{FG♂}=0.921$ ($P<0.001$), $r_{FG♀}=0.913$ ($P<0.001$), $r_{EL}=0.922$ ($P<0.05$) (Fig. 1). The relationship did not differ significantly between sexes, but in females the B-to-P ratio tended to be higher than in males, and the difference might be significant with larger samples. Correcting for this difference, and combining the data, we obtain the equation

$$P♂ = 4.04B + 32.88 \quad (I)$$

($P♀ = P♂ - 5.70$ and $r_{FG♂+♀} = 0.934$ ($P<0.001$)), which could be used to predict total protein levels from breast muscle lean dry weight. In the egg-layers, which had large reproductive organs and fat deposits, the breast muscles were relatively lighter than among the other full-grown females and males ($P<0.001$). The corresponding equation for egg-layers was:

$$P_{EL} = 3.57B + 45.02 \quad (II).$$

Breast muscle wet weight and dry weight are about as good as breast muscle lean dry weight as predictors of protein reserves (Table 2).

The linear correlations between breast muscle lean dry weight and lean dry body weight (Fig. 2, Table 4) were strongly significant ($P<0.001$) for full-grown ($r_♂=0.911$, $r_♀=0.890$), part-grown ($r_♂=0.989$, $r_♀=0.922$) and egg-laying ($r=0.833$) grouse. In full-grown birds females had relatively heavier lean dry breast muscles than males ($P<0.001$), while egg-layers had lighter breast muscles than other full-grown females ($P<0.001$).

Protein levels (Table 3) showed small variability. Among full-grown males the estimated total protein

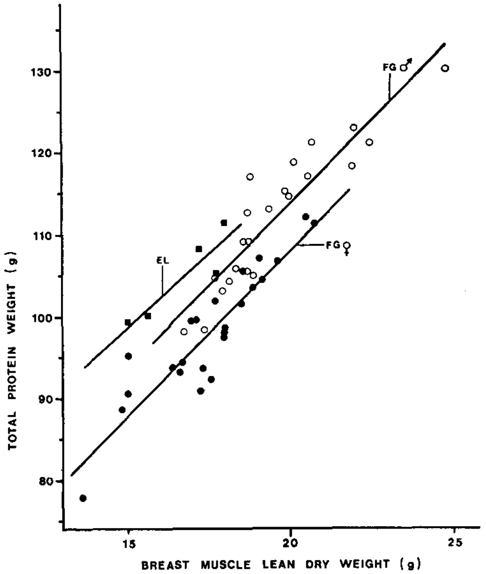


FIG. 1. Total protein weight as a function of breast muscle lean dry weight in Swedish Willow Grouse. O = full-grown males, ● = non-breeding full-grown females, ■ = egg-layers.

content averaged 82.0 ± 1.6 % of lean dry weight. The estimated breast muscle protein content averaged 99.0 ± 2.3 % of lean dry weight in males and slightly less (97.2 ± 2.5 %) ($P<0.05$) in full-grown females.

There were significant correlations between breast muscle fat and total fat in all age and breeding categories (FG and PG: $P<0.001$, EL: $P<0.05$). However, the variation in breast muscle fat accounted for only 13 % of the total fat variation in egg-laying females, compared with 27 % in other full-grown females and 16 % in full-grown males. In part-grown birds the two fat measurements were correlated more strongly: the variation in one accounted for 65 % (♂) and 61 % (♀) of the variation in the other. Hence, intramuscular pectoral fat was an acceptable predictor of total fat only in part-grown birds.

However, the difference between the dry body weight and the lean dry body weight extrapolated from breast muscle lean dry weight using the relationships presented in Fig. 2 and Table 4, could be used as a fairly reliable fat measure when estimates of total fat have not been made. Fat weight calculated in this way explained 58 % (♀) to 70 % (♂) of the variation in estimated total fat weight among full-grown birds, while the corresponding values among the other categories were: 73 % in part-grown males and 85 % in part-grown and egg-laying females. The regression lines also fitted relatively well with the 1:1 relationship (Fig. 3), although there is a tendency to overestimate high fat levels and underestimate low levels in egg-layers.

TABLE 4. Regression equations ($y = ax + b$) and correlation coefficients for the relationship between breast muscle lean dry weight (x) and lean dry body weight (y) in different age and breeding categories of Swedish Willow Grouse.

| | *N* | Regression coefficient (a) | Intercept (b) | Correlation coefficient (*r*) |
|---|---|---|---|---|
| Full-grown males | 144 | 4.56 | 47.48 | 0.911 |
| Full-grown females | 44 | 4.57 | 39.16 | 0.890 |
| Egg-layers | 30 | 4.24 | 59.77 | 0.833 |
| Part-grown males | 20 | 5.62 | 26.87 | 0.989 |
| Part-grown females | 18 | 5.37 | 25.81 | 0.992 |

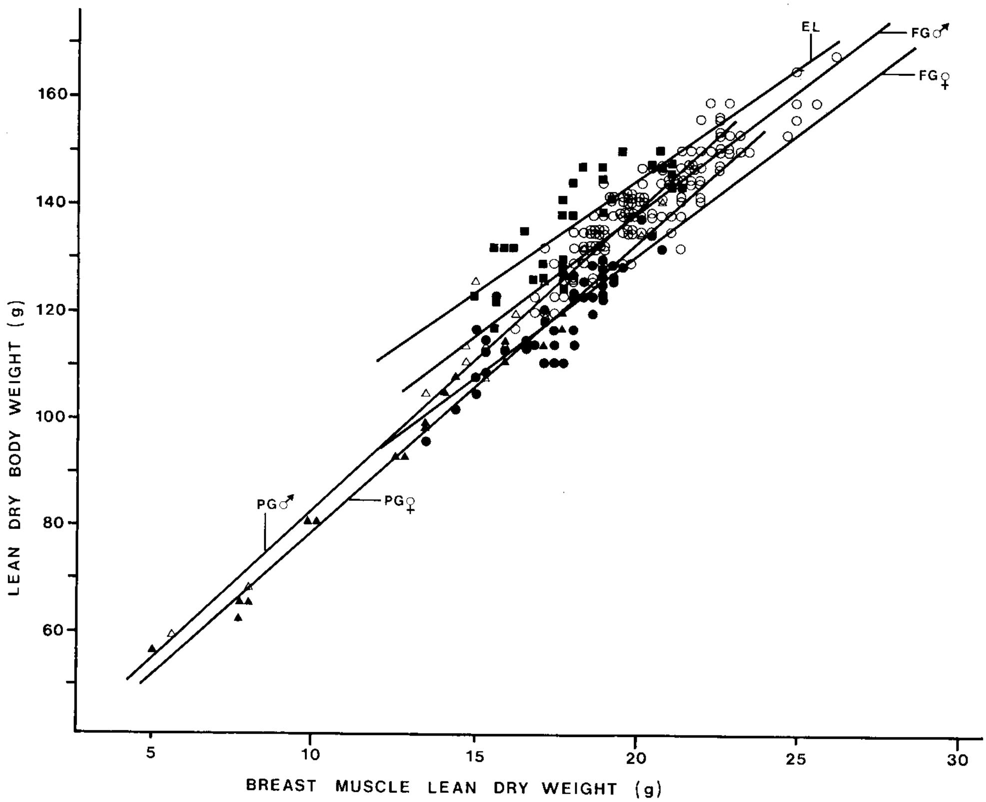


FIG. 2. Lean dry body weight as a function of breast muscle lean dry weight in Swedish Willow Grouse. O = full-grown males, ● = non-breeding full-grown females, ■ = egg-layers, △ = part-grown males, ▲ = part-grown females.

The total fat content averaged 3.9 ± 0.9 % of wet weight and 13.6 ± 2.9 % of dry weight in full-grown males and did not differ significantly between full-grown and part-grown birds or between sexes (Table 5). However, egg-layers had a significantly ($P<0.05$) higher fat content than the other groups. Breast muscle fat, which showed smaller variability than total fat, averaged 7.0 ± 0.9 % of dry weight in full-grown males and a somewhat higher value (7.4 %) in full-grown females ($P<0.05$). Despite their higher total fat content, egg-layers had a significantly ($P<0.01$) lower breast muscle fat content than other full-grown females. The water content was significantly ($P<0.001$) higher in part-grown birds than in the other categories.

*Body size.* Both wing length and sternal lenght showed between-sex overlap, but males were significantly larger than females ($P<0.001$) (Table 1). Both wing length (FG and PG: $P<0.001$, EL: $P<0.05$) and sternal length were significantly correlated with wet body weight, (FG and PG: $P<0.001$, EL: $P<0.01$), but the

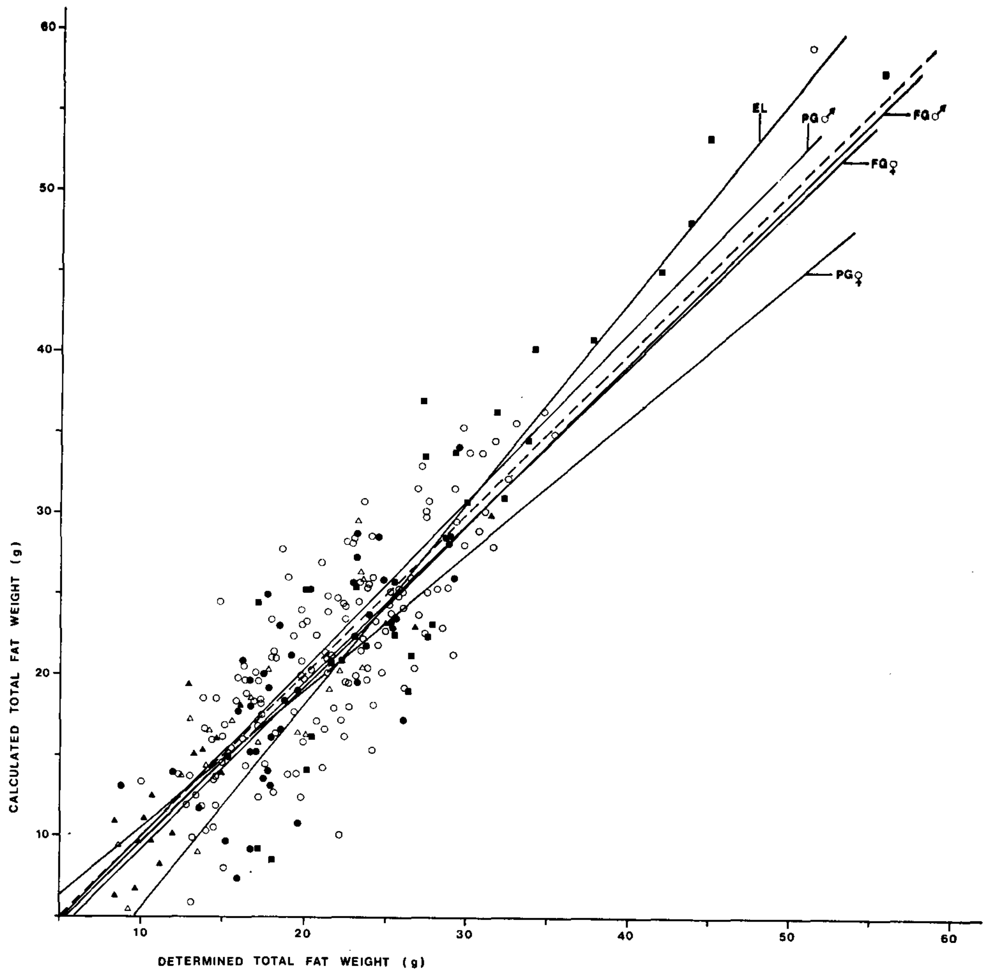


FIG. 3. Calculated total fat weight (dry body weight — lean dry body weight extrapolated from breast muscle lean dry weight) as a function of total fat weight in Swedish Willow Grouse. The broken line indicates the 1:1 relationship.

former size measure generally explained the weight variation less well than sternal length. Except for egg-layers, the correlation between sternal length and wing length was significant ($P<$ 0.001), but in full-grown birds the variation in one accounted for only 14 % (♂) to 31 % (♀) of the variation in the other.

Sternal length and breast muscle lean dry weight were significantly correlated in all three categories (FG and PG: $P<0.001$, EL: $P<0.05$) (Fig. 4). The relationship did not differ significantly between sexes or between full-grown birds and egg-layers. However, part-grown birds had significantly ($P<0.05$) lighter lean dry breast muscles in relation to sternal length, than full-grown birds and egg-layers; the slope of the regression line showed no significant difference between the groups. Variation in this measure of body size explained 28 (♂) — 34 (♀) % of the lean dry breast muscle weight variation in full-grown birds, 84 (♂) — 87 (♀) % in part-grown birds and 17 % in egg-layers. Total fat was significantly correlated with sternal length only in part-grown birds ($r_{PG♂} = 0.590$, $r_{PG♀} = 0.618$). However, there is some evidence that sternal length (L) is more strongly correlated with the logarithm of total fat (LF) ($r_{PG♂} = 0.665$, $r_{PG♀} = 0.732$), although the differences are not significant. Since this relationship did not differ significantly between sexes, the data for part-grown males and females could be combined, giving the equation:

$$LF = 0.159L - 0.172 \quad \text{(III)}$$
$$(r_{PG♂+♀} = 0.735).$$

Breast muscle lean dry weight and total fat weight were also plotted against the third power (Bailey 1968) of sternal length in the three different categories and in the combined materials of full-grown and part-grown males and females. The correlation coefficients were never significantly greater than those for the linear functions, being usually equal or lower in value.

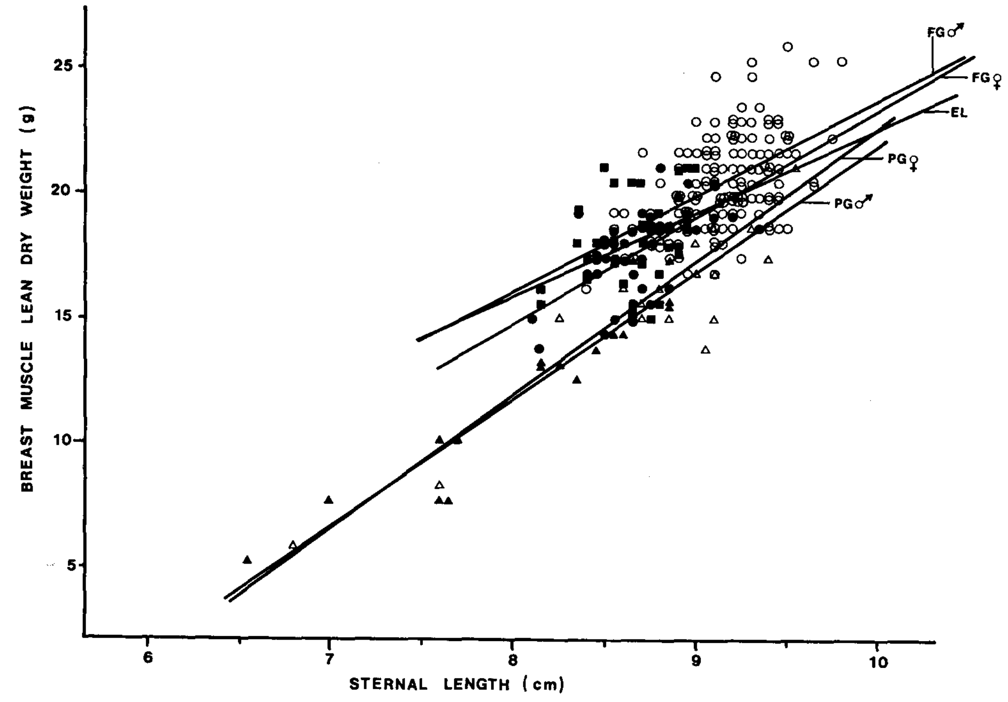


FIG. 4. Breast muscle lean dry weight as a function of sternal length in Swedish Willow Grouse.

TABLE 5. Fat and water contents in Swedish Willow Grouse. Mean ± *SD*.

| | *N* | Total fat (% of wet wt) | Total fat (% of dry wt) | Breast muscle fat (% of wet wt) | Breast muscle fat (% of dry wt) | Body water (% of wet wt) |
|---|---|---|---|---|---|---|
| Full-grown males | 144 | 3.9 ± 0.9 | 13.4 ± 2.9 | 1.9 ± 0.2 | 7.0 ± 0.9 | 70.9 ± 0.8 |
| Full-grown females | 44 | 4.1 ± 0.9 | 14.3 ± 2.8 | 2.0 ± 0.2 | 7.4 ± 0.9 | 71.3 ± 1.1 |
| Egg-layers | 30 | 4.8 ± 1.4 | 16.5 ± 3.9 | 1.8 ± 0.2 | 6.8 ± 0.7 | 71.1 ± 1.2 |
| Part-grown males | 20 | 3.6 ± 0.7 | 12.9 ± 2.0 | 2.0 ± 0.3 | 7.6 ± 1.1 | 72.4 ± 1.1 |
| Part-grown females | 18 | 3.5 ± 1.1 | 13.0 ± 3.1 | 1.9 ± 0.3 | 7.2 ± 1.0 | 73.0 ± 1.6 |

*Calorific content.* Equation I was used for calculation of total protein in the complete material of full-grown birds (Table 6). In males the average protein weight was 115 ± 8g while the average fat weight was 22 ± 6g. Table 6 also includes data for two full-grown males which were captured in winter with foot-snares (Höglund 1968) and starved to death in an enclosure (which gave little or no protection against winter weather with temperatures varying between —5 and —25°C). These birds contained on average 80 g protein (according to Kjeldahl analysis) and 5 g fat, with sternal lengths slightly below average at 8.8 cm. The difference between the average calorific contents in full-grown males and in the two starved males was 152 kcal for protein and 157 kcal for fat, which can be considered a rough estimate of the available energy reserve. In the bird with the largest calorific content 626 kcal appeared to be available.

## Discussion

There must be a systematic error in the protein or lipid estimations, since protein appears to average 97—100 % of the lean dry breast muscle, yet the ash content in breast muscles from captive Willow Grouse is about 5 % of dry weight (Grammeltvedt 1978). This difference may partly result from the extraction of some lipoprotein by alcohol in the solvent used for fat extraction (Mascher & Marcström 1976). Another possible explanation is that 6.25 was too high a conversion factor for estimating protein from nitrogen. This constant bias will not have influenced the correlations between protein and the other variables, but will produce slightly too high calorific values.

The relatively light breast muscles found in egg-laying females (Fig. 2) probably result from a smaller prebreeding weight increase of the breast muscles than of other body constituents (e.g. reproductive organs and the intestines with contents (Brittas in prep.)). The relatively heavier breast muscles in non-breeding full-grown females than in males are more difficult to explain. When the square of wing length is used as an index of wing surface area, males and females appear to have approximately equal wing loading, so that the relative difference in breast muscle weight indicates a somewhat larger flying capacity among the slightly smaller females. The relatively large breast muscles might make it easier for the females to carry the extra weight due to development of the gonads and other organs in the breeding season.

The weak correlation between total fat and intramuscular pectoral fat makes the latter a poor fat index. This contrasts with data from Woodpigeon, Japanese Quail (Brittas unpubl.) and Spitzbergen Rock Ptarmigan *Lagopus mutus hyperboreus* (Grammeltvedt & Steen 1978), but is consistent with data from captive Willow Grouse, in which the pectoral fat was not markedly affected by fasting, although fat deposits were heavily utilized (Grammeltvedt 1978). Pectoral fat, including the intramuscular lipid and overlying deposits was a good predictor of total fat in Goshawks (Marcström & Kenward 1981), but the overlying pectoral fat deposits in Willow Grouse are small. The fact that egg-layers had a relatively lower pectoral fat level than other full-grown females, probably reflects withdrawal of lipids from the breast muscles during egg-development (Jones & Ward 1976).

Since the combined length of the intestines is longer during the winter (Brittas in prep.), the weight of the intestines and their contents varies seasonally. Therefore the value calculated for total fat (dry body weight — lean dry body weight extrapolated from lean dry breast muscle weight) would probably have correlated somewhat better with the total fat weight if the intestinal contents had been excluded from the rest of the carcass before analysis. Despite this bias the calculated fat weight, is a fairly good measure and requires considerably less work to obtain than total fat estimates.

Wing length is frequently used as a measure of size in birds, although some authors have pointed out that it is not an accurate size index since the length of the primaries is subject to seasonal changes due to abrasion and moult (Van Balen 1967, Evans 1969b). Other authors have used a variety of thoracic skeletal measurements (Evans & Smith 1975, Modafferi 1975, Myrberget & Skar 1976, Kenward 1977), and Marcström & Kenward (1981) have shown that sternal length is a better measure of size than wing length among Goshawks. This is also the case in Willow Grouse, and sternal length is parti-

TABLE 6. Total protein, total fat and calorific contents in Swedish Willow Grouse.

| | | Total protein | | Total fat | | calorific ct. |
|---|---|---|---|---|---|---|
| | | weight (g) | calorific ct. (kcal) | weight (g) | calorific ct. (kcal) | calorific ct. (kcal) |
| Full-grown males $N=144$ | Mean: | 115.1 | 507 | 21.8 | 203 | 709 |
| | *SD*: | 7.6 | 33 | 5.9 | 55 | 76 |
| | Range: | 98.8—138.1 | 435—608 | 10.0—51.2 | 93—476 | 569—1027 |
| Full-grown females $N=44$ | Mean: | 98.1 | 432 | 20.2 | 188 | 620 |
| | *SD*: | 6.9 | 30 | 4.8 | 45 | 61 |
| | Range: | 82.1—111.1 | 361—489 | 8.8—29.4 | 82—274 | 474—730 |
| Starved males $N=2$ | Mean: | 80.6 | 355 | 5.0 | 46 | 401 |
| | Range: | 80.0—81.2 | 352—357 | 4.7—5.2 | 44—48 | 396—405 |

cularly appropriate when breast muscle weight is used as an index of protein content.

In contrast to the weight-length relationships in Cottontail Rabbits *Silvilagus floridanus* (Bailey 1968) and Pheasants *Phasianus colchicus* (Kenward 1977), the breast muscle lean dry weight was not better fitted by regression on the third power of a length measure than by regression on the first. This is similar to data from Oystercatchers, indicating that increasing mass is compensated for by a linear increase in wing length (Baker 1975). However, in samples with large variation in body size, for example when specimens at all stages of growth are included, curvilinear weight-length relationships are probably more common.

Sternal length (L) explained up to 34 % of the variability in breast muscle lean dry weight (B). Since the relationship between these measures (Fig. 4) did not differ significantly between full-grown males and females, or between egg-layers and other full-grown birds, body size-related variation in breast muscle lean dry weight can be taken into account with the equation:

$$B = 4.39L - 20.0 \quad (IV).$$

For part-grown birds the corresponding equation is:

$$B = 5.14L - 29.3 \quad (V).$$

However, since the relationship between breast muscle lean dry weight and total protein weight differed somewhat between sex and breeding groups, among full-grown birds, equation (IV) should be combined with equation (I) or (II) when the protein reserve is compared between groups.

In full-grown birds and egg-layers total fat (F) was not significantly correlated with sternal length. Nevertheless, when sample size is small it seems suitable to relate fat to a standardized protein level; fat may be assumed to increase at the same rate as protein with increase in body size, whereas the percentage of body weight is not appropriate due to the large variability of the protein reserve. This gives the "Lipid Index" (LI) equations:

$$LI = \frac{F}{4.39L - 20.0} \quad (VI)$$

for full-grown birds and egg-layers, and:

$$LI_{PG} = \frac{F}{5.14L - 29.3} \quad (VII)$$

for part-grown birds. In the latter category, however, an alternative LI is obtained by extraction of the regression coefficient from equation (III):

$$LI_{PG} = \frac{LF + 0.172}{L} \quad (VIII),$$

where LF = log(total fat weight). Among the part-grown birds the two indices (VII and VIII) are strongly correlated ($r_{PG\,♂+♀} = 0.971$, $P < 0.001$). This supports the assumption that fat increases at the same rate as protein with increase in body size.

In full-grown males the minimum and maximum breast muscle values correspond to a total protein weight of 101 and 133 g, respectively, in a bird of average size (i.e. sternal length being 9.15 cm). The corresponding fat values are 10 and 53 g. Thus both the main energy reserves show considerable variation, although variation in fat reserves accounts for more of the variation in energy reserves (400 kcal) than variation in protein (141 kcal). This will be true even if Willow Grouse can obtain slightly more than 4.4 kcal/g from protein, by metabolizing a large part of their nitrogen to ammonia as in Red Grouse *Lagopus*

*lagopus scoticus* and Rock Ptarmigan *Lagopus mutus* (Moss & Parkinson 1972, 1975). Since the two reserves are not strongly correlated in Willow Grouse, they must both be taken into consideration to assess condition in this species adequately.

The observed average (4 %) and maximal (7 %) lipid levels do not deviate markedly from data obtained in Norwegian (Myrberget & Skar 1976) and Alaskan (West & Meng 1968) Willow Grouse, but are low compared with the levels in several other herbivorous birds of about equal size. Thus the dissectable fat deposits of autumnal Spitzbergen Ptarmigan averaged 14 % of body weight (Grammeltvedt & Steen 1978), while in Polish Partridges *Perdix perdix* (Szwykowska 1969) they averaged 7—8 % over the year with a maximum winter mean of about 10 %.

The protein and fat levels differed little between the two starved specimens, which indicates that the average given is reliable although the sample size is small. The lipid level (1.1 % of body weight) in these birds was similar to figures obtained for the Goshawk (1 %) (Marcström & Kenward 1981) and Lapwing *Vanellus vanellus* (1.3—1.4 %) (Marcström & Mascher 1979).

The protein and fat levels in the starved birds were markedly lower than the lowest levels recorded in the population. This may indicate either that the proportion of emaciated birds in the population is very low, or that such birds are difficult to find. Despite the relatively high fat energy content of some grouse, the differences between the fat and protein levels for average birds and starved ones (Table 6) suggest that protein and fat may be of about equal importance during food shortage.

According to West (1968) and Moss (1973), the daily energy requirement of free-living Willow Grouse in winter is about 150 kcal. Although starving birds may require about half as much if they remain inactive (Grammeltvedt 1978), comparison of the daily requirement with the average (309 kcal) and maximum (626 kcal) available calorific contents shows that the sampled Willow Grouse were not storing large energy reserves. This may indicate that Willow Grouse seldom undergo periods of malnutrition (Myrberget & Skar 1976), but they will face difficulties in extreme situations when icing of vegetation suddenly occurs over large areas. The low energy storage of Willow Grouse is an interesting ecological problem, which requires further investigation.

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## Selostus: **Riekon ravitsemustilan määritystavoista**

Tutkimukset lintujen ravitsemustilasta ovat monesti ekologisesti tärkeitä. Ruumiinpaino on eniten käytetty ravitsemustilan mitta, mutta tarkemmissa tutkimuksissa analysoidaan usein myös valkuaisaine- ja rasvavarastot. Tällainen vararavinnon kokonaisselvitys on kuitenkin hyvin työlästä.

Tutkimuksen päätavoite oli kehittää linnun kuntoa mittaavat indeksit, jotka ottavat huomioon ruumiinkoon yksilölliset erot sekä ilmaisevat linnun sisältämän valkuaisaineen ja rasvan kokonaismäärän. Tätä varten tutkittiin 256 Ruotsin eteläiseltä tunturialueelta pyydetyn riekon ruumiinkoko, paino, rintalihasten paino ja rasvasisältö. Valkuaisainesisältö määritettiin 51 linnusta.

Sekä eri ikäryhmissä että eri aikaan vuodesta pyydetyissä linnuissa rintalihaksen rasvaton kuivapaino oli vahvasti riippuvainen valkuaisaineen kokonaismäärästä (kuva 1). Rintalihaksen rasvamäärä sen sijaan oli selvästi sidoksissa rasvan kokonaismäärään ainoastaan nuorilla, ei-täysikasvuisilla riekoilla. Linnun kuivapainon ja rasvattoman kuivapainon (vrt. kuva 2 ja taul. 4) välistä eroa voidaan kuitenkin käyttää tyydyttävänä rasvavaraston mittana muidenkin ryhmien riekoilla.

Rintalastan pituus osoittautui paremmaksi ruumiinkoon mitaksi kuin siivenpituus. Se korreloi merkitsevästi rintalihaksen rasvattomaan kuivapainoon, ja tätä suhdetta voitiin käyttää yksilöllisten kokoerojen korjaamiseen vararavinnon määrää tutkittaessa (kaavat IV—VIII). Vaikka lintujen rasvapitoisuus oli niinkinkin alhainen kuin 7 % tai pienempi (taul. 5), oli rasvan osuus energiavarojen vaihtelussa suurempi kuin valkuaisaineiden. Koska lintujen sisältämät valkuaisaineet ja rasva eivät ole selvässä riippuvuussuhteessa, on tarkassa tutkimuksessa riekkojen ravitsemustilasta määritettävä molempien osuus.

Tutkitun riekkoaineiston ja kahden nälkään kuolleen yksilön vertailu viittaa siihen, että käytettävissä oleva energiareservi on täysikasvuisella riekkokukolla runsaat 300 kcal (taul. 6). Nälkätilanteessa tämä riittää riekon energiantarpeeseen vain muutamaksi päiväksi.

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