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Aspects of the life-cycle energetics of two subspecies of Dunlin *Calidris alpina*

by

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Abstract

Aspects of the life-cycle energetics of two subspecies of Dunlin Calidris alpina

BY Mansour AL-Mansour **Ph.D. 2000**

Dunlin from two breeding populations, *C.a.schinzii* from Iceland and *C.a.alpina* from northern Scandinavia, were studied during and after migration through Teesmouth, north-east England, and in captivity. *C.a.schinzii* winters in north-west Africa and has a much longer migration pathway than *C.a.alpina* which winters in Britain and around the North Sea.

Measurements of Resting metabolic Rate (RMR) were made for the two subspecies of Dunlin in March and November in order to establish the relationship between resting metabolic rate and temperature and hence energy costs of living at different temperatures (20 °C – 0 °C). Energy costs of living in *C.a.alpina* were 21% higher than *C.a.schinzii.*

Measurements of Basal Metabolic Rate (BMR) were made for the two subspecies (before, during and after moult) in conjunction with measurements of body compositions using Total Body Electrical Conductivity (TOBEC) in order to estimate the costs of moult. Energy costs of moult were 1692 KJ for *alpina* and 1016 KJ for *schinzii.*

Energy costs of migration were estimated by measuring the amount of fat laid down before departure by wild Dunlin of the two populations, with the aid of Total Body Electrical Conductivity (TOBEC). Energy costs of migration were estimated as 3489 KJ for *alpina*, and 5156 KJ for *schinzii.*

Energy costs of egg production and incubation were estimated from other workers' studies of other (similar) species. Energy costs of egg production were only 220 KJ for the two subspecies whereas the costs of incubation were 1232 KJ and 1143 KJ in *alpina* and *schinzii*, respectively.

In contrast to the suggestion by Drent and Piersma (1990), I have found that the costs of migration are considerably less than the costs of living. Also the total annual energy cost for those Dunlin wintering in colder areas i.e. *C.a.alpina* is much higher than for those wintering in tropical regions i.e. *C.a.schinzii.* Energy costs are not the only factors that affect a bird's lifetime output of young. *C.a.alpina* uses a different migration strategy to *C.a.schinzii* but may breed on better breeding grounds, and hence achieve more successful reproduction.

No part of this thesis has previously been submitted for a degree in this or any other University. The work described is my own except where duly acknowledged

CONTENTS

3.0 Energy costs of living

4.0 Energy costs of moult

5.0 Energy costs of migration

6.0 Energy costs of egg production and incubation

7.0 General discussion

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Chapter 1
General introduction

1.1 Background

Geographic segregation between different migratory populations of a single species of bird has been recognised for almost a century. The reasons for racial differences in wintering grounds remain a subject for conjecture however. In several species, populations perform what has been called 'leap-frog' migration, where the more northerly breeders migrate further and pass over the other populations to winter beyond the more southerly breeders. Salomonsen (1955a,b) was the first to discuss this phenomenon in shorebirds, namely ringed plover *Charadrius hiaticula* and redshank *Tringa totanus*. Some of the characteristics of leapfrog migration also are shown by pairs of shorebird species e.g. dunlin *Calidris alpina* / curlew sandpiper *C. ferruginea*, common snipe *Gallinago gallinago* / great snipe *G. media*, curlew *Numenius arquata*/ whimbrel *Numenius phaeopus* (Alerstam & Hogstedt, 1980).

Salomonsen (1955b) proposed a body size hypothesis to explain this phenomenon: northern populations of small-sized individuals were meant to migrate further south than large-sized conspecifics because, large bodies have lower surface-to-mass (volume) ratios than small ones and are therefore energetically more efficient than small ones in keeping warm in cold environments. This hypothesis has received little support because: (i) many exceptions to its predictions have been reported e.g. least sandpiper *C. minutilla* and western sandpiper *C. mauri* in which the smaller-sized males winter on average further north than females (Myers, 1981), (ii) it is difficult to establish cause and effect in a relationship between wintering latitude and body size, since body size might not have evolved in response to the winter climate (Salomonsen, 1955b) but to the climate on arrival in the breeding grounds (Hale, 1980). Greenberg (1980) and Bell (1996, 1997) have suggested hypotheses to explain leapfrog migration based on optimal time allocation. Greenberg (1980) proposed a trade-off between migration costs and increasing survival rates. He supposed that northerly breeders, which have to spend the longest time in each year away from their breeding sites, may minimise their total mortality by migrating to more southerly wintering areas where survival is higher than in mid-latitudes. Bell (1996, 1997) applied his model of optimal winter latitude, based on a trade-off between latitude-dependent winter survival, and migration survival incorporating the critical effects of differences in timing of spring fattening, to the leap-frog migration systems of the Yellow Wagtail *Motacilla flava* (Bell, 1996) and the Fox Sparrow *Passerella iliaca* (Bell, 1997). He supposed that northerly breeders with a late spring migration from their winter quarters can afford to wait for, and take advantage of, the surge of spring food at southerly latitudes. In contrast, for southerly breeders, this surge of spring food occurs too late in relation to the optimal arrival time at the breeding sites. For these populations, a short migration, requiring only small amounts of fat as fuel, is the more favourable option.

Some authors have proposed hypotheses for the evolution of leap-frog migration based on competition rather than optimal time allocation (Pienkowski & Evans, 1985). They suggested that it is more favourable for birds to winter as close as possible to their breeding grounds: (i) to be in a better position than longer-distance migrants to win limited resources, such as territories (Myers, 1981a) or holes for nests (von Haartman, 1968) on the breeding grounds. Competition on wintering grounds can occur amongst juveniles and between juveniles and adults, which forces some juveniles to leave the wintering areas nearest to the breeding grounds and may lead to lower survival (Pienkowski & Evans, 1985; see Pienkowski & Evans, 1984; Greenberg, 1980). (ii) By remaining during winter within the same climatic regime, they should be able to respond to variations in weather and return to breeding grounds as soon as these become favourable (Alerstam & Hogstedt, 1980). Drent and Piersma (1990) proposed an energetic-based hypothesis to explain the very different migration strategies of two Bar-tailed Godwit *Limosa lapponica* populations. The first of these, the "European" population, winters around the North and Irish sea coasts and breeds in Northern Europe, around the basin of White Sea. The second population, the "Afro-Siberian", winters on the north-west coast of Africa and breeds further east and at higher latitudes than the "European" population, with a breeding area stretching from the Pechora river to the eastern Taymyr peninsula in Siberia. The "Afro-Siberian" birds reach their breeding grounds following two or more long-distance flights, during which they stop-over at some of the same North sea estuaries in which the European birds are wintering. This over-lapping of two migration routes can also be described as a "leap-frog" migration system though it involves East/West as well as North/South movements. Drent & Piersma accept that displacement of populations in winter must be attributed to the avoidance of competition. They hypothesise that, assuming that it is more favourable for birds to winter as close as possible to their breeding ground, the European Godwits are in the optimal wintering area where space is limited, and the Siberian birds are forced to move on (i.e. resources cannot sustain all of them during winter). The Siberian birds compensate for the large costs of long flights and the need to put on more fat by wintering on the coast of north-west Africa where the energetic costs of keeping warm are very low since the average daily winter temperature is 18 °C, (Meteorological Office, 1983). Drent & Piersma (1990) suggest that, in total, the annual energy expenditure of both populations is the same, so that both migration patterns persist.

1.2 Aims of study

My study aimed to test whether Drent & Piersma`s model (1990) can explain the migration strategies of two geographically discrete breeding populations of Dunlin *Calidris alpina*, by creating annual energy budgets for the two populations.

1.3 Approach

In order to calculate the annual energy budget of a migratory bird, it is necessary to measure or estimate the following quantities:

1) Daily energy costs on the breeding grounds.
2) Daily energy costs on the stopover sites during migration.
3) The energy costs of moult.
4) The energy costs of migration.
5) Daily energy costs on the wintering grounds.
6) The energy costs of egg production and incubation.

Quantities 1, 2 and 5 in particular will be affected by ambient temperature. As detailed later, I estimated the energy costs of daily activity (DEE) by measuring the metabolic rate of captives of each race throughout each individual's annual cycle, using open-flow respirometry to determine the relationship between Resting Metabolic Rate (RMR) and temperature, and then assuming that the DEE is a fixed multiple of RMR, following the analysis by Drent and Daan (1980). This may not be strictly true for *interspecific* relationships (Ricklefs *et al,* 1996), but should allow valid *intraspecific* comparisons. I estimated the extra energy needed for migration by measuring the amount of fat laid down before departure, with the aid of Total Body Electrical Conductivity (TOBEC) measurements, for both wild and captive Dunlin of the two races. I estimated the extra energy needed for producing new plumage (i) by looking for changes in BMR during moult and (ii) by measuring the mass of plumage that is produced and obtaining values of the energy requirements for producing feathers from other workers' studies of other species. The extra energy needed for egg production and incubation was also estimated from other worker's studies of other (similar) species.

1.4 Study area

Dunlin were studied on the Tees Estuary (54°37' N 1°12'W) in north-east England which supports internationally important populations of waterfowl, i.e. over 20000 (Waters *et al*, 1998). My studies concentrated particularly on Seal Sands, an area of 140 hectares of sand and mud which form the largest inter-tidal area on the estuary. Teesmouth lies about 35th in importance amongst British estuaries for its numbers of waterfowl (Cranswick *et al,* 1999); but in terms of wildfowl densities it ranks amongst the very highest. When numbers of wildfowl are added to those of shorebirds, it meets the criteria to be designated as a Ramsar site (wetland of international importance). The mudflats of Seal Sands contain an invertebrate fauna restricted in species but some present in high densities, namely *Hydrobia ulvae, Nereis diversicolor*, *Corophium volutator,* small oligochaetae and polychaetes, and nematodes. This area is particularly important as a feeding area for shorebirds, as there is restricted access to the public so that, apart from birds of prey, disturbance is very limited. Seal Sands and the Tees in general provide significant habitats for large numbers of wildfowl and shorebirds such as Dunlin, Grey Plover *Pluvialis squatarola*, Curlew, Bar-tailed Godwit, Redshank *Tringa totanus* and Knot *Calidris canutus*, both in winter and during spring and autumn migration (Evans, 1997). The estuary and surrounding habitats are illustrated in Figure 1.1.

Seal Sands (Figure. 1.2) is bordered by slag walls 6-7m high on the three sides, the largest wall built during extensive reclamation in the 1970's. The intertidal area consists of a range of sediment types. In the east is Peninsula Sands, an important area for high water roosting for Dunlin and other shorebirds and seabirds and appropriate for catching birds using cannon netting. However, this area is not important as a feeding site. Central Bank, separated from Scalloped Mud by Central Channel, is an area of firm sandy mud. In summer it is covered mainly by algae *Enteromorpha* spp. but in winter it forms the main feeding site for shorebirds. In the west is Greenabella Bank, which forms the other main feeding area. This site is exposed for only for three to four hours in each tidal cycle and consists of soft mud with a corner of muddy sand. To the south of this is Scalloped Mud, which consists of medium to soft muds. At present Seal Sands is exposed and available for shorebird foraging for about eight hours out of each tidal cycle. As a result of this, some birds cannot obtain enough food to satisfy their daily requirements during the period of exposure, so they move to higher tidal flats on North Gare or nearby coastal beaches to feed when Seal Sands is covered by the incoming tide.

1.5 The history of the Tees in brief;

The history of the Tees Estuary shows that huge destruction took place of the intertidal area, to build port facilities and as industrial land-claim, throughout the last two centuries (Davidson *et al*, 1991).

In 18th century, the discovery of iron ore in the region led to the development of an iron and steel industry in the upper parts of the estuary; however, the main basin of the estuary was left mainly untouched. At the beginning of the 19th century, the Tees estuary comprised about 2400 hectares of intertidal sand and mudflats. In late 18th and early 19th centuries large agricultural land-claims of saltmarshes took place on both sides of the estuary. However, the single largest land claim (900 hectares) took place between 1850 and 1881, and land was claimed at over 33 hectares per year, until the mid 1970s.

The last major land claim on Seal Sands occurred between 1971 and 1974 so that the total intertidal area of the estuary had been reduced by this succession of land claims to 470 hectares by mid the 1970s, an overall reduction of 86% of the total intertidal area of the estuary (Davidson *et al*, 1991). The loss of intertidal area at the Tees estuary since the mid-eighteenth century is summarised in Appendix IX.

In 1995 the remaining 140 hectares of Seal Sands was designated as a National Nature Reserve by English Nature under the Wildlife and Countryside Act (1981).

1.6 The study species

The Dunlin has a holarctic breeding distribution with several distinct subspecies (Cramp & Simmons, 1983), of which two form the subject of this thesis. This species has been described as a leapfrog migrant by Alerstam and Hogstedt 1980. The first of these two subspecies used in this study, the "Northern European" *Calidris a. alpina* which breeds in northern Scandinavia and north-west Russia (east to the Kolyma river) is a common migrant wader in Europe. This subspecies winters mainly on the coasts of western Europe, as far north as Britain, Netherlands and Germany and passes through the Baltic in July and August (Leslie & Lessels, 1978). Some *alpina* stop over at Ottenby in southeastern Sweden during autumn migration; these include some actively moulting birds (Holmgren *et al*, 1993).

The Wadden Sea area (Denmark, Germany, Netherlands) and the Wash (England) are the most important moulting grounds in western Europe for nominate *alpina* (Holmgren *et al*, 1993), though smaller numbers use many other North Sea estuaries. Adults arrive from mid-July, juveniles from mid-August, and adults begin moult from mid-July to early August, with the outermost primary feathers full-grown by early September to early October, and replacement of flight feathers lasting from eighty to ninety days. After moulting, many *alpina* move westwards to wintering sites around the North and Irish Sea coasts, or southwards to France (Pienkowski & Evans, 1984). In spring, they migrate from these sites back to the Arctic, probably in a single flight to eastern Fenno-Scandinavia, where they may refuel (Evans & Davidson, 1990).

The second subspecies, the "Afro- Icelandic" *C.a.schinzii* breeds in Iceland and southern Greenland (Davidson *et al*, 1986). It is present on Icelandic breeding grounds from May to August, passing through Britain in July-August (adults) and August-September (juveniles) and through France and Portugal in August - September (Hardy & Minton, 1980). The majority of this subspecies winters and moults further south, in southern Europe and N.W Africa, especially in Morocco and Mauritania (Pienkowski & Dick, 1975). Birds arrive in Morocco from late July, stopping-over in Britain en route. Return migrations of this population pass chiefly along the West coasts of Britain, from mid-April to early May (Ferns, 1981; Hardy & Minton, 1980) to re-occupy Iceland in May.

The nominate *alpina* tend to be larger and have, on average, longer bills than *schinzii*. *Alpina* have rich chestnut mantle fringes with a large belly patch while *schinzii* tend to have yellowish-red mantle fringes with a small belly patch (Prater *et al*, 1977).

1.7 The timing of migration through Teesmouth of adults and juveniles of *Calidris a. alpina* and *C.a.schinzii*

Counts of Dunlin at Teesmouth between July 1996 and July 1997 are summarized in Figure 1.3. This figure shows that numbers of birds were highest in winter, peaking in mid-January. Juvenile Dunlin started to appear at Teesmouth from late July. Numbers of juveniles increased through August and early September to reach a peak in mid-September. From late September until late June it is difficult to age Dunlin in the field by observation, so birds are recorded as full-grown. Numbers of full-grown Dunlin decreased through September and October before remaining stable through November and December. Numbers reached a peak in mid-January before they decreased dramatically through February and March.

Ringing and recovery data from Northumbria (Evans, 1966) and the Tees Estuary (Norman, 1988 and Appendix VIII) show that the race *C.a.alpina* spends the winter at Teesmouth, whilst *C.a.schinzii* is present only during spring and autumn migrations. Adult *alpina* begin to arrive at Teesmouth in mid-September and most of them leave in late February or early March but some remain until May when they may be joined briefly by passage birds that have wintered further west. Adult *schinzii* start arriving at the Tees from early July to pass through the Tees by the end of August en route for wintering areas in NW Africa. Juvenile *schinzii* pass through the Tees in the second half of August and early September, later than adults. Juvenile *alpina* occur in the Tees by early November coming from north-west Russia via the northern and then western Norwegian coasts (Leslie, 1978).

Figure 1.1: The position of Seal Sands and other inter-tidal areas around the Tees estuary (Teesmouth). Shaded areas indicate intertidal land claimed since 1750

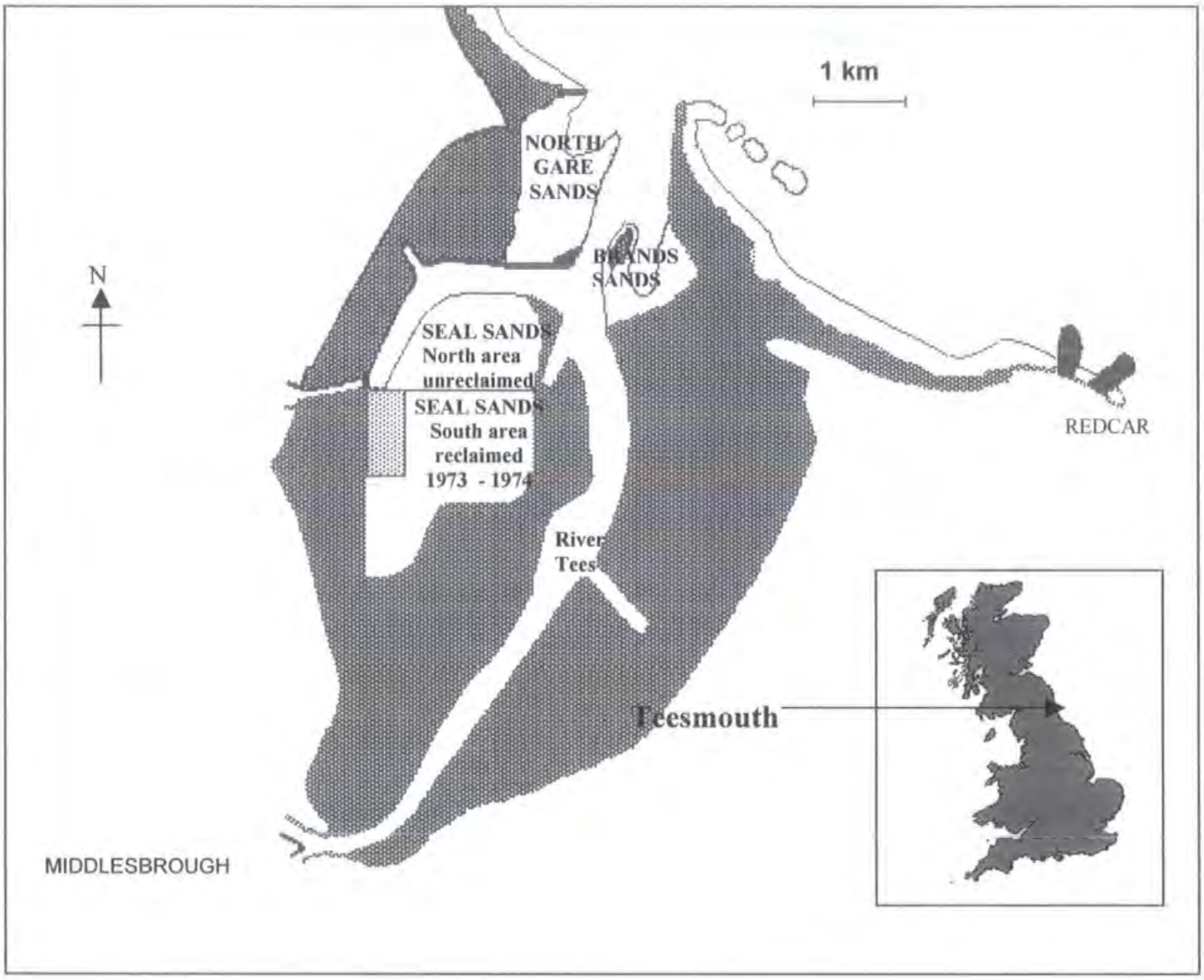


Figure1.2: Seal Sands and its constituent shorebird feeding areas. Key to numbered areas: **1** Peninsula Sands; **2** Eastern Channel; **3**, **8** and **10** Central Bank; **4** and **5** Scalloped Mud; **6** Greenabella Bank; **9** Enclosure; **12** Central Channel.

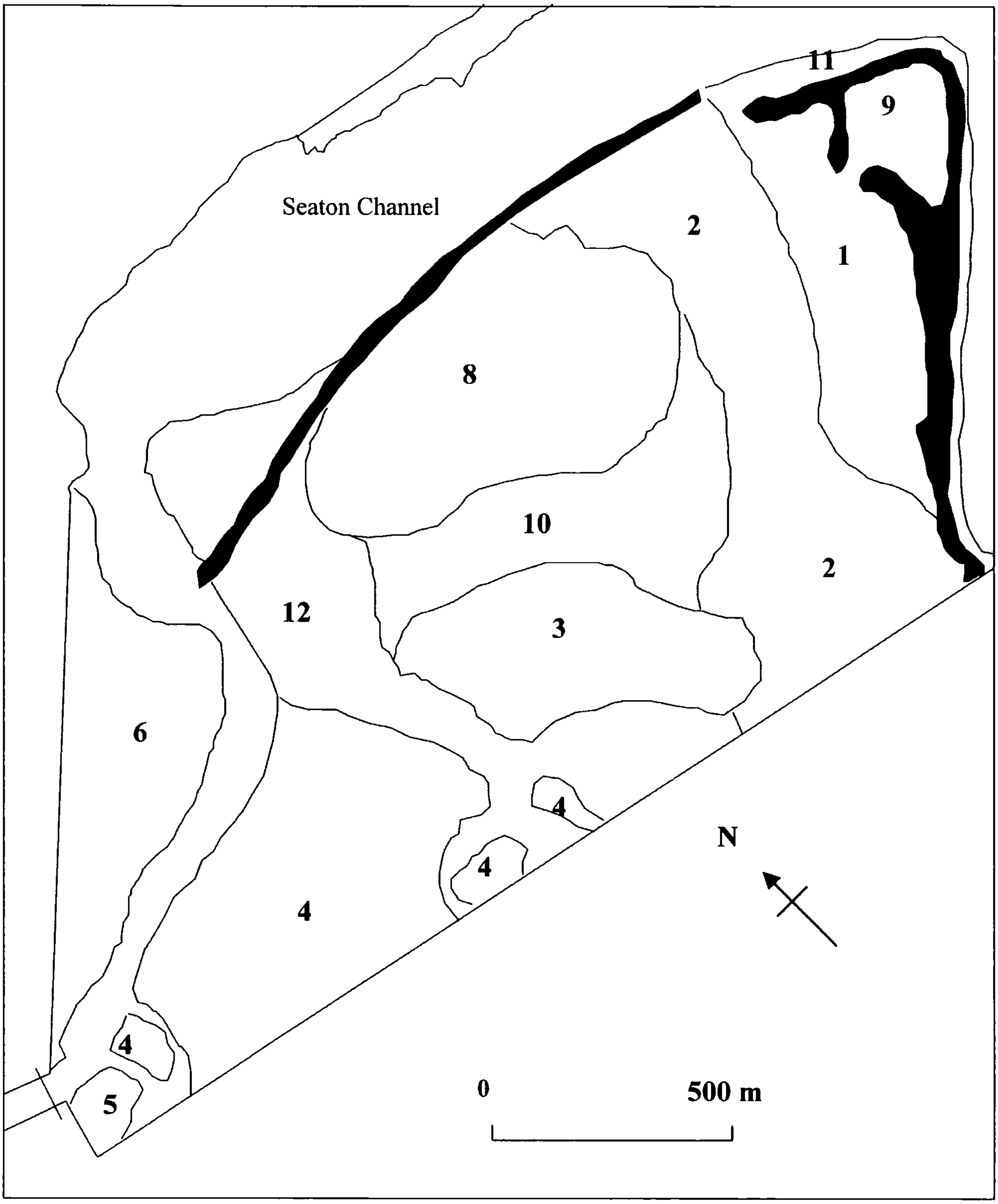
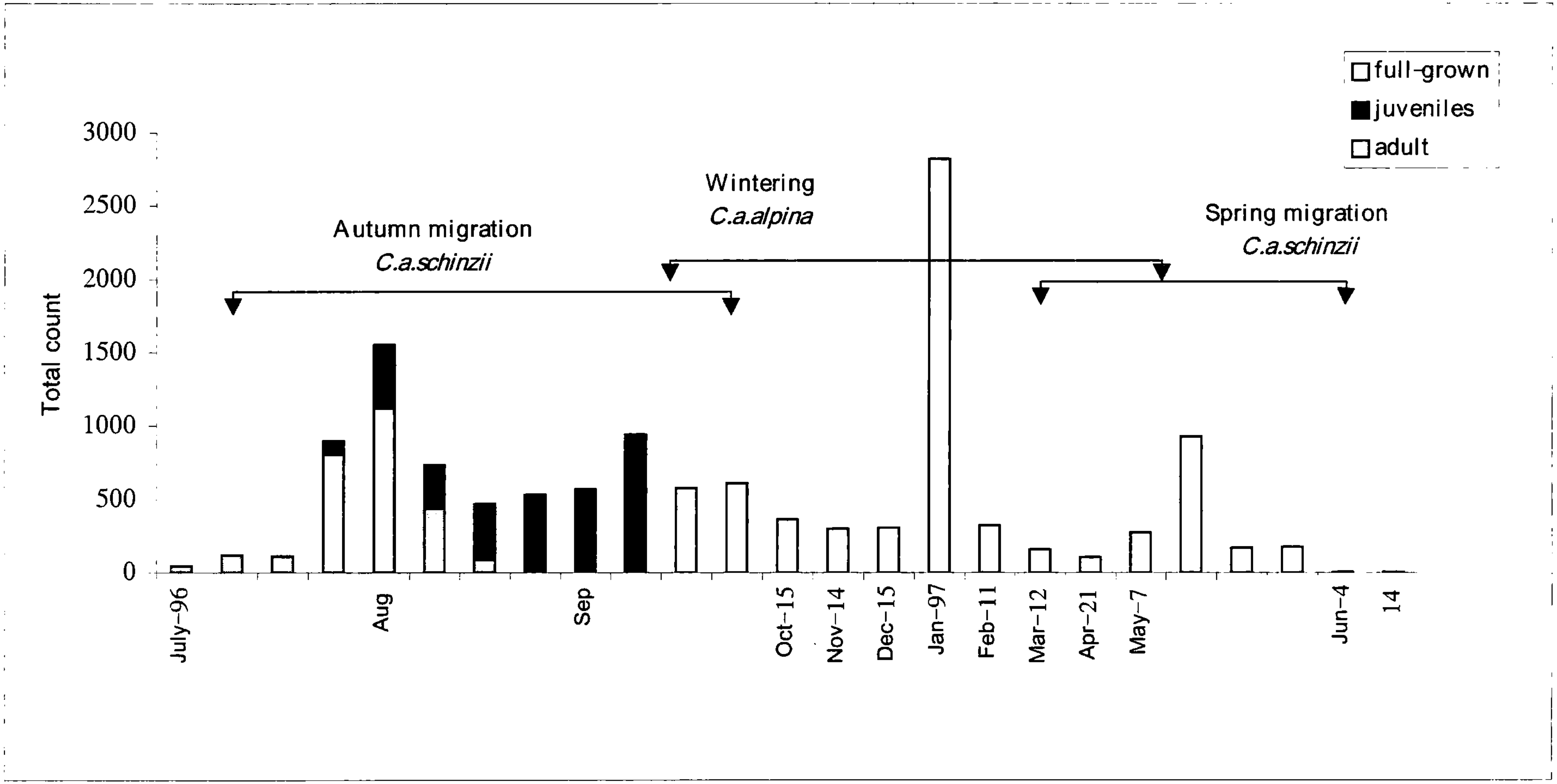
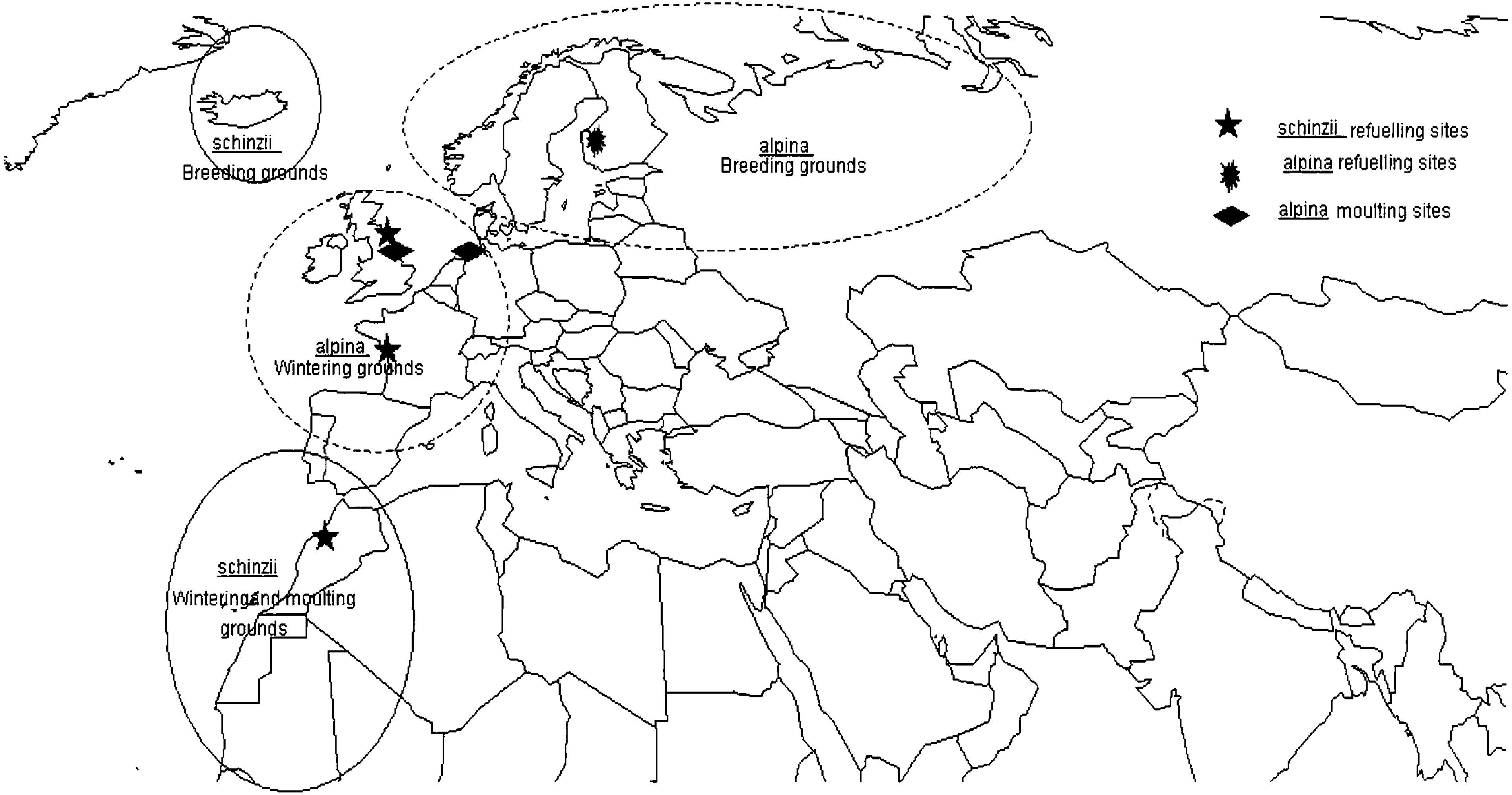


Figure1.3: Counts of Dunlin adults and juveniles at Seal Sands (Teesmouth)



Map 1: The main breeding areas, wintering areas, moulting areas and refuelling areas for the two subspecies of Dunlin



Chapter 2,
Materials and Methods

2.1 Measurement of Total Body Electrical Conductivity (TOBEC)

Measurement of Total Body Electrical Conductivity (TOBEC) is a relatively new non-destructive method for estimating body composition in live animals (Walsberg, 1988) and is now a popular technique among ornithologists for estimating fat reserves in birds (Asch & Roby, 1995). This method was developed in the early 1970's and has recently been used widely in the agricultural and medical fields (Herenroede, 1989).

TOBEC is based on the principle that when an electrical conductor (the bird in this case) is positioned inside a solenoidal coil producing an alternating electromagnetic field, the change in the electromagnetic field is proportional to the total electrical conductivity of the conductor (the bird's body in this case) (Harker, 1973). It is known that the electrical conductivity of lipids is around 4-5% of those of an equivalent mass of body fluids, lean tissues and bone (Pethig, 1979). Therefore, total lean mass is the basic contributor to the TOBEC measured value.

In order to obtain an index of total body electrical conductivity, birds can be restrained using a soft plastic cylindrical jacket with Velcro fastenings before inserting into the measurement chamber, head first and legs close to body, until a maximum value (**B**) is obtained. TOBEC readings are taken with the chamber empty (**E**) and then full (**B**), repeated four times alternately to counteract any drift in the baseline reading. Half-way along the measurement chamber is the most uniform and strongest part of the magnetic field produced by the solenoid (Scott *et al,* 1991); this produces the maximum value of **B**. Reference numbers (**R**) are obtained from the apparatus before and after each set of readings. The index of total body electrical conductivity (**I**) is calculated from the Equation 1 below;

$$\mathbf{I = [(E-B)/R] * a} \quad \text{.......... Equation 1}$$

Where **a** is a normalisation constant provided by the manufacturer, **E** is the average of four readings with chamber empty, **B** is the average of four readings with the bird inside the chamber and **R** is the average of the two reference numbers. The machine must be calibrated for each species to be studied (for details, see Appendix I).

Predicted Total Lean Mass (PTLM) for Dunlin can be obtained using the two equations below

(i) PTLM = (0.53 * I) + 21.4 grams (calibrated by Scott *et al,* (1991)) for wild Dunlin.

(ii) PTLM = (0.42 * I) +21.7 grams (calibrated by this study) for captive Dunlin.

Predicted Mass of Fat (PFM) is calculated by subtracting PTLM from Body Mass (BM);

$$\mathbf{PFM = BM - PTLM} \quad \text{........... Equation 2}$$

2.1.1 Advantages of TOBEC;

The TOBEC method has many advantages, the most important are **(i)** avoidance of the need to kill the subject, so that changes in body composition of an individual can be followed through time. **(ii)** portable and small enough for use in the field. **(iii)** suitable for use in fluctuating temperature conditions (Walsberg,1988). **(iv)** the measurements can be obtained rapidly without complicated procedures. However, there are many factors that affect the TOBEC index so they must be taken into account when using the apparatus (see section 2.1.2). Moreover, the SA-1 must be connected to the power at least half an hour before starting measurements and the battery charge must not be low when used in the field.

2.1.2 Factors that affect the TOBEC index:

The main factors are summarised below.

a) Body geometry, has an effect in TOBEC index in complex way (Fiorotto *et al*, 1987), so that birds of the same mass but different shape may have different indices.

b) Body temperature; the relationship between the average TOBEC index and body temperature is linear but the slope of the relationship differs significantly between species, as determined by warming whole dead specimens,

For Dunlin, $I = 0.80\ T°C + 20.21$ ($r = 0.99, n = 6$)

For Knot, $I = 3.50 T°C + 102.7$ ($r = 0.94 , n = 6$)

Where T°C = Temperature between 15 and 40 °C

For each 1°C change, the TOBEC index changed at 40 °C (close to the normal body temperature of most birds) by 1.53% (which would produce 0.7g change in estimated total lean mass) for Dunlin and 1.44% (1.6g) for Knot. See Scott, *et al* (1991) for more details.

c) Presence of metal leg rings;

TOBEC indices increased by a mean of 13% for Dunlin and 40% for Redshank when 7 Dunlin and 8 Redshank were measured before and after ringing (Scott *et al* 1991). The ring size for Redshank was larger than that used for Dunlin so may explain larger effect on TOBEC index. The composition of the metal alloy needs to be taken in account (Scott *et al,* 1991). Roby (1991) found that there was no significant difference in TOBEC measurement in birds with aluminium rings compared to birds without, but aluminium is not ferromagnetic, whereas most British rings are.

d) Contamination by sea water;

Contamination by salt water increased TOBEC indices by a mean of 30% in five dead Dunlin immersed briefly in sea-water. Even after 12 hours drying the TOBEC indices were still 10% higher than before immersion (Scott *et al*, 1991). Hence in the field, birds, which get salt-water contamination, should be left to dry, and very wet individuals should not be used for TOBEC measurements.

e) Position of the bird within the measurement chamber;

The horizontal position of the bird affects the TOBEC index measured by the SA-1 apparatus a great deal whereas vertical position is not important (Scott *et al*, 1991). The optimum position along the measurement chamber (i.e. that gives the maximum reading) varies slightly with the shape and size of the specimen

(Scott *et al*, 1991). However, some studies (Meijer *et al*, 1994; Skagen *et al*, 1993; Morton *et al*, 1991) held each bird at the same position in the centre of the chamber, irrespective of size of the reading in relation to maximum value.

f) Hydration state of the specimen;

The TOBEC index of lean body mass increased significantly by an average of 15% when Walsberg (1988) dehydrated Gambels Quail (*Callipepla gambelii*) over three days. Davidson (1984) showed that Dunlins and Knots lose up to19% and 23%, respectively, of their total body mass (chiefly body water) during the first 8 hours of captivity. Therefore birds should be measured within a few hours of capture.

2.1.3 The accuracy of SA-1 equipment:

The SA-1 has satisfactory precision for use in larger passerine birds and shorebirds. Walsberg (1988) and Castro *et al.* (1990) considered SA-1 to be useful for estimating body composition of subjects as small as10g live mass but James *et al.* (1995) said that this technique provides greater accuracy for species weighing about 20g. Asch & Roby (1995) showed that body *fat* estimates for birds weighing 10-125g could be imprecise because in this range of masses there is less interaction between body water volume and the electromagnetic field. Small subjects produce small TOBEC values, which mean lower measurement precision and lower accuracy of estimation of PTLM and hence fat. Asch and Roby (1995) indicated that the accuracy of fat estimates in smaller subjects could be improved by using a smaller chamber equipped with a smaller coil. SA-1 and SA-2 machines are most accurate for species of about 175- 275 g, which is near to the maximum size that can be inserted in the measurement chamber (Roby, 1991). In my study there was very little variation between the four readings used to calculate the TOBEC index for each bird and because each bird was positioned to give a maximum reading there was no between-observer bias.

2.2 Measurement of metabolic rate: general principles

Metabolic rate refers to the energy metabolism per unit time. Schmidt-Nielsen (1997) listed three different ways for measuring metabolic rate;

1) By determination of the difference between the energy value of all food eaten and the energy value of all excreta (primarily faeces and urine). This method needs to ensure that the organism has not experienced changes in body composition and in body mass. Hence it must be carried out over a sufficiently long period of observation. This method is awkward and cannot be used to measure Basal Metabolic Rate (see Section 2.2.1) by definition.

2) By determination of the total heat production of the organism;

This method ought to give complete information about energy used. Although it is the most accurate method, it is technically a complex procedure where every item such as heating of ingested food, vaporisation of water, etc. must be entered into the total heat budget and in addition, all external work performed by the organism that does not appear as heat, must be added to the account.

3) By determination of oxygen consumption (and/or carbon dioxide production);

This is a relatively simple technique, and customary it is used for estimation metabolic rates. Oxygen can be used as an indirect measure of metabolic rate because the amount of heat produced for each litre of oxygen used in aerobic metabolism changes by no more than 5%, irrespective of what substrate has been oxidised (see Table 1). The respiratory quotient RQ (CO_2 formed /O_2 used) gives information about the fuel used in metabolism. RQ is usually found to lie between 0.7 and 1.0. An RQ of near 1.0 indicates primarily carbohydrate metabolism, and of near 0.7 suggests primarily fat metabolism. An intermediate RQ could indicate metabolism of protein, or a mixture of fat and carbohydrate, or a mixture of all three.

Measurement of carbon dioxide production is less suitable than that of oxygen consumption for estimating metabolic rate for two reasons (i) the body contains a large pool of carbon dioxide which, although always present in the body, changes easily (e.g. in hyperventilation of the lungs). In heavy exercise, the lactic acid that forms in muscles will enter the blood, carbon dioxide will be expelled from the blood and released in the lung in large amounts. (ii) different foodstuffs give very different energy equivalents for each litre of carbon dioxide produced (up to 20% variation, see Southwood, 1978).

2.2.1 Conditions required for measurement of BMR

BMR (Basal Metabolic Rate) is defined as the minimum rate of energy expenditure (heat production) that an individual animal requires to maintain normal body temperature, during the non-active phase of the day, when the animal is unstimulated by the digestion and assimilation of food or by low/high temperatures outside the thermoneutral zone, and is not involved in growth, moult or reproduction (Aschoff & Pohl, 1970; Speakman *et al,* 1994; McNab, 1997).

Table1: The energy equivalents of oxygen consumption for various values of RQ, due to utilisation of different proportions of foodstuff (modified from Southwood 1978).

19.6kJ per litre O_2 consumed appropriate for a RQ of 0.70
19.8kJ per litre O_2 consumed appropriate for a RQ of 0.75
20.1kJ per litre O_2 consumed appropriate for a RQ of 0.80
20.3kJ per litre O_2 consumed appropriate for a RQ of 0.85
20.6kJ per litre O_2 consumed appropriate for a RQ of 0.90
20.8kJ per litre O_2 consumed appropriate for a RQ of 0.95
21.1kJ per litre O_2 consumed appropriate for a RQ of .1.00

2.3 Materials and Methods

2.3.1 Captive Dunlin:

A total of 14 Dunlin *C.a. alpina* (n = 6 juveniles) and *C.a.schinzii* (n= 4 juveniles & 4 adults) were caught under licence from English Nature by cannon-netting at high tide roosts at Teesmouth, north-east England and held in captivity for periods ranging from 23-34 months, between September 1996 and June 1999. Dunlins were held in two groups according to their race in indoor aviaries of 2.4m(l) x 1.2m(h) x1.2 (w), under temperature and simulated photoperiod regimes close to external conditions (Durham City). Commercial trout pellets (Trout Excel 23,Trouw Aquaculture, Nutreco, UK) and blow-fly larvae *Calliphora sp.* were provided as food. A mineral supplement SA-37 (Intervet, UK Ltd, Cambridge) was added to the food monthly. Fresh water was constantly running through the aviaries and hence was available for bathing and drinking purposes. The aviaries were cleaned three times every week and disinfected before any new birds entered the aviary.

2.3.2 Measurement of Total Body Electrical Conductivity (TOBEC) indices

TOBEC was measured using the EM-Scan (3420 Constitution Drive, Springfield, Illinois 62707, USA) SA-1 Small Animal Body Composition Analyser. The SA-1 was used in the laboratory and also in the field when it was powered by a 12V battery via an Oertling PC-01 converter to provide 240V, 50 cycles AC. Each of the captive birds was weighed using a Pesola spring-balance to the nearest g and its TOBEC index calculated at least once every 2 weeks. Birds caught using cannon nets and mist nets at Teesmouth were sometimes slightly splashed with sea-water and were allowed to dry in hessian sacks or in hessian-lined keeping cages for at least 1 hour before measuring TOBEC. Even captive birds were isolated from the cage for 1 h before measuring TOBEC values. Birds which were very wet, both wild and captive, were exempted from TOBEC measurement. All TOBEC measurements in the field were made within three hours to avoid the effect of any dehydration on the TOBEC index (Walsberg, 1988). All factors affecting the TOBEC index (see section 2.1.2) were taken in to account when measuring TOBEC.

2.3.3 Measurement of Basal Metabolic Rate: Open-flow Respirometry

The 14 juveniles and adult Dunlin, caught at Teesmouth in September 1996 and August 1997 and held in captivity thereafter, were used for studies of seasonal variation in BMR.

The metabolic heat production of each bird was estimated by determination of rates of oxygen consumption using a paramagnetic oxygen analyser (Servomex plc, Crowborough, East Sussex, Model1111D/000) and carbon dioxide production using an infrared analyser (Lira 3000, Mine Safety Appliances Company, Pennsylvania, USA) in an open-circuit system described by Scott *et al* (1996), (see Figure 2.2). For measuring BMR, each bird was removed from the aviary at 09:00 GMT and kept isolated in a box for a minimum of one hour without food or water. Around 1100 GMT the bird was weighed using a Pesola spring-balance to the nearest g and then its TOBEC measurement taken. The bird was placed in one of the two identical metabolic chambers measuring 24.5cm (height) x 21cm (diameter).

BMR measurement started at or after 13:00h, after a period of at least 2 hours of acclimation by birds to the metabolic chamber and 4 hours of fasting to ensure that the individual was post-absorptive. The chamber was in complete darkness and was placed in a controlled temperature cabinet (LMS, Sevenoaks, Kent) at a constant temperature of 25°C (within the thermoneutoral zone of Dunlin). Dry air was drawn through the chamber at a rate of 60 litre/hour^{-1}. Gas analyses were performed on samples taken from both the inlet and outlet gases via gas mass-flow controllers (Brooks Instruments, Netherlands, 5878 & 5850 TR series) at rates of 3.6L/h^{-1} for O_2 and 4.8 L/h^{-1} for CO_2. Both inlet and outlet gases were dried prior to measurement by passing them over columns of dried coarse mesh silica gel. A measurement of BMR on a single individual was taken over a period of time ranging from between 90-120 minutes to ensure that a stable measurement of BMR was obtained for each run. If any periods of raised metabolic rate (MR) occurred during a measurement these were assumed to be periods of activity and the measurements were not used, although this was rare (Al-Mansour, pers. Obs.). Under normal circumstances, birds remained at rest throughout the measurements, as proven by the lack of traces on activity-recording paper used to line the floor of the chamber. A period of 15-20 minutes was necessary between the first and second individual's BMR measurements when measurements were carried out on two birds on the same day, to enable the levels of O_2 and CO_2 to return to the pre-measurement baseline levels. To avoid CO_2 building up in the metabolic chamber not undergoing a BMR measurement, a constant flow of dry air was provided through this metabolic chamber using a simple diaphragm pump. Calibration was performed before each day's measurements, using dry, oil-free 100%N_2 and then a certified mixture of 21% O_2, 0.03% CO_2 in N_2 (SIP Analytical Ltd.). During each analysis, measurements were taken every minute over a ten-minute period in which O_2 consumption and CO_2 production were appeared to be stabilised at a basal level. The means of O_2 and CO_2 levels over these ten-minute periods were used to calculate RQ (CO_2 production / O_2 consumption) and BMR expressed in W (using an energy value per litre O_2 consumed appropriate for the RQ), Table1. The levels of O_2 and CO_2 were recorded onto a flatbed recorder (Kipp and Zonen, Delft, Netherlands, Model BD 112).

2.3.4 Measurement of Resting Metabolic Rate: Open-flow Respirometry

Resting metabolism can be defined as the minimum rate of energy utilisation that an individual animal requires to maintain body temperature, when the animal is resting, post-absorptive and undisturbed at particular temperature, whether inside or outside the thermoneutral zone (TZ). Measurements of resting metabolic rate RMR were made to establish the MR/temperature relationship below the TZ.

In order to obtain RMR, procedures in section 2.3.3 were repeated. However, when estimating RMR, measurements were taken at three different temperatures in a single day, starting at the highest temperature and then decreasing by 5°C each time. A period of 45-60 min was taken between each measurement to allow the controlled temperature cabinet to stabilise at the new temperature (10-20min) and to allow the bird to acclimate to the new temperature 30 min.

2.3.4.1 Technical factors that affect the accuracy of the estimates of basal/resting metabolic rate:

To obtain the best results, the following points are considered to be very important when using open-flow respirometry.

(i) The O_2/CO_2 analysers must be allowed to warm up for at least one hour before calibration or starting the measurements.

(ii) The O_2/CO_2 analysers should be used at a temperature similar to that at which it was calibrated.

(iii) The O_2/CO_2 analysers should be used with a sample flow rate the same as used for calibration.

(iv) The metabolic chamber must be sealed firmly.

2.3.5 Day and Night variation in BMR:

To determine whether diurnal variation in BMR occurred in captive Dunlin, the value obtained during the day was compared with a subsequent value recorded at night, 30 hours after the day-time determination, for the same individual Dunlin. This was repeated for six birds. In daytime determinations, as before, birds were isolated at 9.00 GMT and weighed and the TOBEC measured. An individual was put in the chamber at 13.00 GMT after 4 hours fasting, and the measurements ended at 15.00 GMT. At night, individuals were isolated at 21.00 GMT and at 22.30 GMT were weighed to the nearest g and TOBEC measurements taken. They were then placed in the chamber (in the cabinet) at 25 °C. Metabolic measurements started at 01.00 GMT, after fasting the birds for a period of 4 hours; measurement stopped at 3.00 GMT.

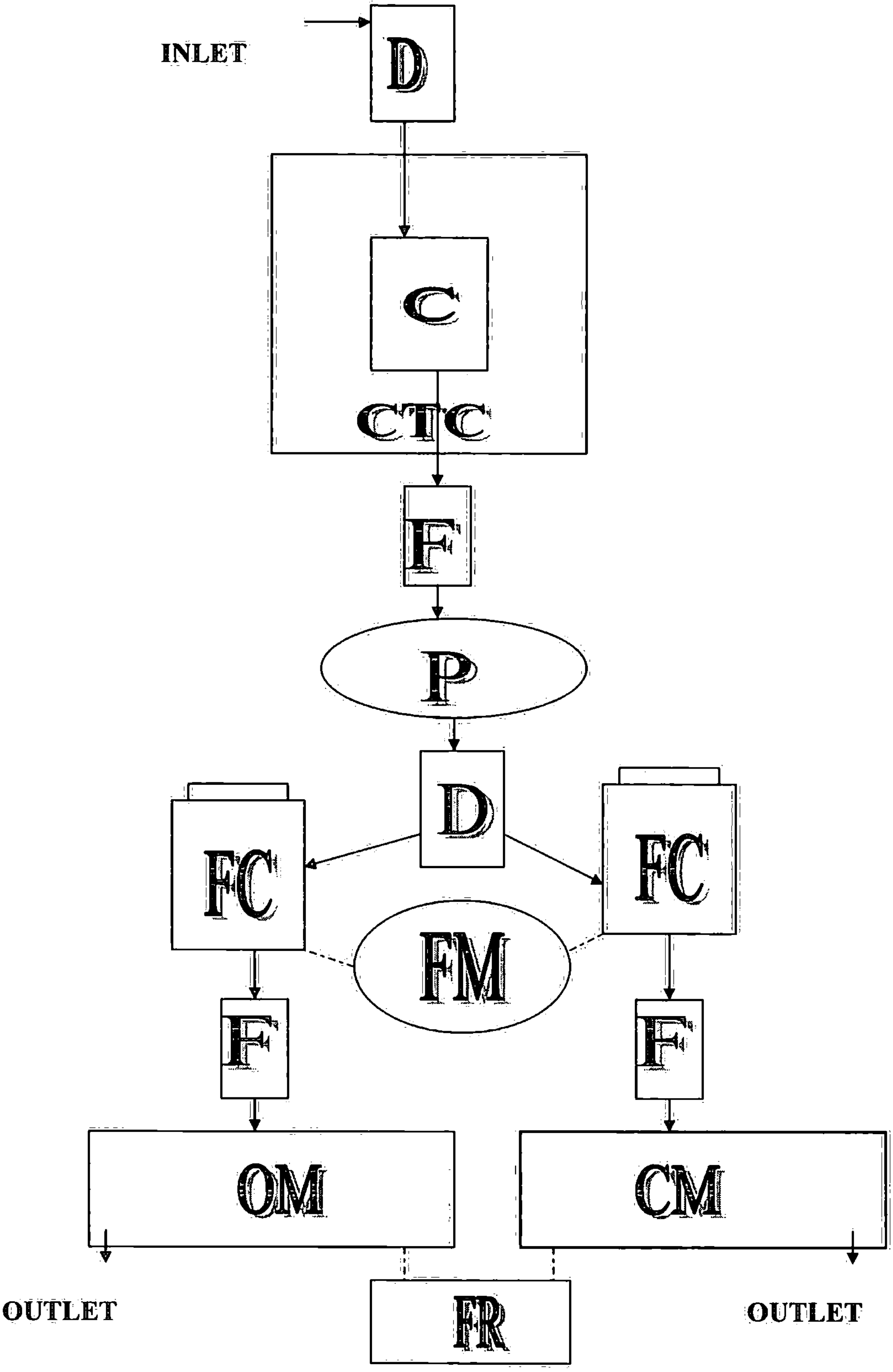


Figure 2.2: Schematic diagram of the apparatus used to measure the metabolic rate of birds during the course of this study. **D**= air drier, **C**= measurement chamber, **P**= pump, **CTC** = controlled temperature cabinet, **CM** = carbon dioxide meter, **OM** = oxygen meter, **F** = gas flow meter, **FC**= mass flow controller, **FM** = flow meter machine, **FR** = flatbed recorder, → direction of air.

Chapter 3,
Energy costs of living

3.1. Introduction

The aim of the work presented in this chapter was to estimate the energy costs of daily activities for the two subspecies of Dunlin on their breeding, moulting and wintering grounds by measuring metabolic rate and its relationship with ambient temperature using open-flow respirometry.

3.1.1 Metabolic rate:

Animals need a supply of food to obtain chemical energy to carry out various functions. All the biochemical reactions and inter-conversions involved can be referred to as metabolism. Energy output can be estimated in animals by measuring the oxygen that they use to oxidise foodstuffs. However, metabolism can also occur without the use of oxygen. This kind of metabolism is called anaerobic.

The amount of heat produced for each litre of oxygen used in aerobic metabolism varies by less than 5% according to the type of substrate oxidised, whereas the caloric equivalent of CO_2 production is much more variable. This is why using oxygen is a practical measure for estimating metabolic rate (see chapter 2, section 2.2 for more detail).

The total daily oxygen consumption of large animals obviously must be higher than of small ones. However, the rate of oxygen consumption per unit body mass decreases progressively with increasing body mass (Schmidt-Nielsen, 1997).

In general, passerine birds (finches, crows, etc.) have higher metabolic rates than non-passerines of the same mass by about 65% (the difference between k=1.11 and k=0.679 from the two equations below of the form MR= K x BM^X). The regression line for metabolic rate on body mass BM for 58 species of non-passerine birds, ranging in size from a 0.003 kg hummingbird to the 100 kg ostrich is: MR =0.679 x $BM^{0.723}$; whereas for 36 species of passerine birds, ranging in size from 0.006 kg to 0.866 kg, it is: MR= 1.11 x $BM^{0.724}$. The slopes of the regression lines of BMR against body mass are, however, the same for passerine and non-passerine birds (Lasiewski & Dawson, 1967).

Shorebirds are claimed to have higher BMRs than expected allometrically, when compared with other bird groups (Kersten & Piersma, 1987). This conclusion, however, was based on measurements of birds which spend the winter in north-western Europe and they thought that the main reason for this apparent elevation in BMR was to cover the high costs of thermoregulation as consequence of their energy demanding way of life. Klaassen *et al* (1990) hypothesised that the BMR of the same species of waders in the tropics was reduced since the maintenance energy requirements of captive birds in Mauritania and Guinea-Bissau were low, even when the high ambient temperature in the tropics was taken into account. Kersten *et al* (1998) also reported that BMR of waders wintering in coastal Africa is well below that of waders wintering in temperate areas but that breeding latitude does not correlate with BMR on the wintering grounds. As migrant waders have a higher BMR during autumn migration, further north, Kersten *et al* (1998) hypothesised that birds reduce BMR upon arrival in the tropics under hormonal control, by reducing organ sizes and probably suppressing thyroid activity in response to the high ambient temperatures in the tropics.

3.1.2 Temperature regulation:

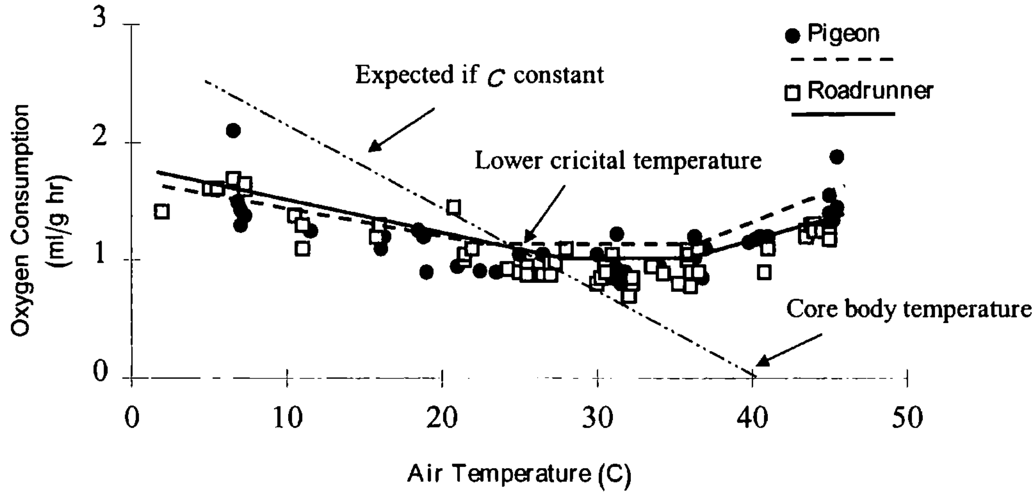
The body temperature of most animals follows ambient temperature. Higher vertebrates, however, raise their body temperature above ambient temperature and may regulate it by either behavioural or physiological means. For the body temperature to remain constant, the rate of heat gain plus metabolic heat production must equal the rate of heat loss. Heat exchange between the body and the environment takes place by conduction (including convection), radiation and evaporation.

Animals with high surface conductance (low insulation) tend to lose heat rapidly, whereas animals with low conductance (high insulation) tend to lose heat relatively slowly. We can express:

Rate of heat loss Q = C (Tb - Ta), where C is the conductance value, Ta is the ambient temperature and Tb is body temperature.

Some birds follow the mammalian pattern of rate of heat production with regression lines that extrapolate to core body temperature (Figure1). Other birds, however, vary from this pattern (Figure1) as they may not adhere to the simple equation H (heat production) = C (Tb-Ta), in which C remains constant at low temperatures, because (i) in these birds the conductance value, C, gradually decreases with falling ambient temperature, Ta and (ii) some species allow body temperature to decrease at low temperatures.

Figure 1: Oxygen consumption of two bird species at different temperatures. The regression lines do not extrapolate to the body temperature (40°C) of the pigeon and of the roadrunner as they commonly do in mammals, but to a much higher temperature, above 50°C. Modified from Calder and Schmidt-Nielsen (1967).



There are three possible ways for birds to increase insulation (decrease conductance):

(i) By raising the feathers and drawing the feet up into the feathers.

(ii) By allowing the peripheral tissues to undergo an appreciable temperature drop whilst keeping the core temperature constant

(iii) By changing posture to alter the amount of body surface area directly exposed to ambient conditions (at low temperatures some birds tuck their heads under their wings).

Figure 2 shows that metabolism rises as ambient temperature falls below the lower critical temperature or rises above the upper critical temperature because, outside the thermoneutral zone (TZ), the animal must carry out physiological work to maintain its stable internal body temperature. The lower critical temperature (LCT) is the point at which insulatory adjustments become inadequate to compensate for further falls in ambient temperature. Thus, below the LCT the rate of heat loss from the animal increases and must be countered by an increase in the rate of heat production to maintain a constant body temperature. This requires a rise in metabolic rate.

The upper critical temperature (UCT) is the point above which insulation is minimised. Further increase in ambient temperature leads to an increase in metabolic rate because, as the thermal difference between animal and environment falls, so the metabolic heat cannot be dissipated fast enough, even with minimal insulation. Many birds and mammals respond by sweating, panting or allowing their body temperature to rise to some extent. These mechanisms demand an increase in metabolism.

The thermoneutral zone is the range of temperature in which the metabolic heat production is unaffected by ambient temperature change. The width of the thermoneutral zone depends on the conductance value and whether the animal is Arctic or tropical, as the metabolic response in Arctic animals is less pronounced than in tropical mammals (Schmidt-Nielsen, 1997).

Figure 2: General type of relation between resting metabolic rate and ambient temperature for a typical bird (Calder and King 1974).

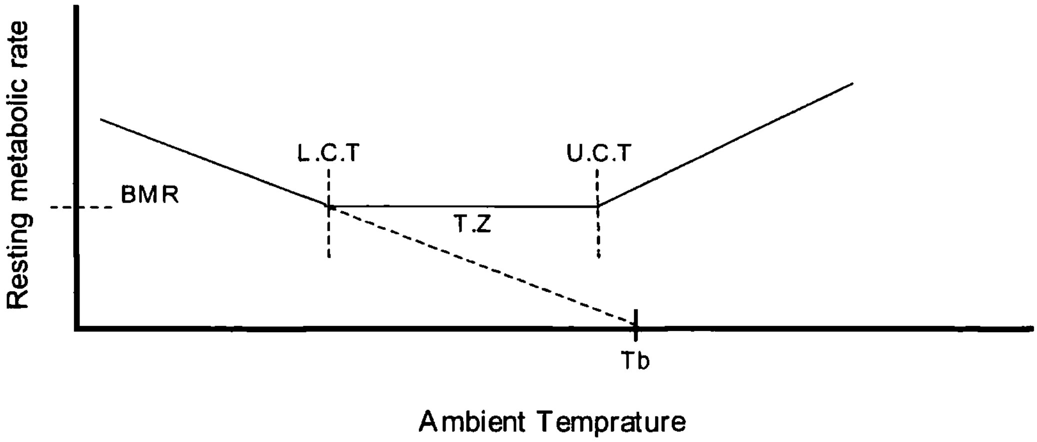
UCT means upper critical temperature

LCT means lower critical temperature

TZ means thermoneutral zone

Tb means body temperature

BMR means basal metabolic rate



3.1.3 The relationship between the slope of the metabolic rate / temperature line and body size:

Body size affects insulation because small birds have higher surface-to-mass (volume) ratios than large ones. Thus they lose heat at a greater rate per unit of mass for a given difference between body and ambient temperature.

Small birds tend to increase their metabolic rate (expressed in mass-specific terms) more steeply below the lower critical temperature than do larger ones. This occurs not only because small birds have higher size-related conductance (per unit area) but also because larger birds tend to have thicker coats of feathers than smaller ones, which leads to relatively higher insulation in larger birds.

The relationship between insulation and body mass is not perfect because animals of similar size have significant interspecific differences in insulatory capabilities. But well-insulated (large) animals tend to have relatively larger ranges of thermoneutral zones than poorly-insulated (small) animals.

3.1.4 The relationship between Basal Metabolic Rate and Daily Energy Expenditure

Basal metabolic rate (BMR) was defined (section 2.2.1) as the minimum level of energy expenditure that an individual animal requires to maintain normal core body temperature, during the non-active phases of the day, when the animal is unstimulated by the digestion and assimilation of food or by low/high temperatures outside the thermoneutral zone, and is not involved in growth, moult or reproduction (Aschoff & Pohl, 1970; Speakman *et al,* 1994; McNab, 1997). Daily energy expenditure (DEE) generally refers to the rate of energy metabolism per 24 hours of an active animal. The relationship between BMR and DEE has been the subject of several hypotheses. King (1974) was the first to state that DEE of free-living adult birds parallels BMR, whereas the first attempt to quantify this relationship was carried out by Drent *et al* (1978). They found in Charadriiform birds (mostly gulls and auks) and waterfowl species with body weights between 100 and 1000g, that DEE averages about 2.6 BMR, whereas cage existence metabolism at 10°C amounts to approximately 2 BMR. Drent and Daan (1980) later suggested the existence of a 'maximum sustained working level' (DEE) of parent birds feeding their young of approximately four times BMR. Bryant and Tatner (1991), however, reported that 4 times BMR is not a universal upper limit to the sustained work rate of small birds as the upper limits tend to be higher in species with energy-expensive foraging habits. Kersten and Piersma (1987) measured BMR, existence metabolism (EM) and costs of thermoregulation in three captive shorebirds species and also hypothesised that there is constant proportionality between BMR and DEE. Moreover, Daan *et al* (1990) using data for 26 species of bird and Daan *et al* (1991) using data for two more species of birds and 15 species of mammal, found significant correlations between the residuals for each species of the deviations from the overall DEE/body size regression and the overall BMR/body size regression. Koteja (1991) applied a similar analysis but found only a weak correlation between BMR and DEE among birds engaged in reproduction (r = 0.23, n=23). There was however, a strong correlation among mammals (r = 0.83, n= 18). Ricklefs *et al* (1996) confirmed Koteja's results and found no significant relationship between DEE and BMR in birds but a strong relationship (r = 0.86) in mammals. Contrary to these findings, however, Dutenhoffer and Swanson (1996) reported a significant positive correlation between BMR and summit (maximum) metabolism (r= 0.861) in 10 species of passerine. Metabolic rates in Dutenhoffer and Swanson's (1996) studies were measured using open-circuit respirometery throughout, to avoid any complications that may arise from combining data using different experimental techniques (see Daan *et al*, 1990). The data analysed by Ricklefs *et al* (1996), were collected from a wide range of studies, using a wide range of experimental techniques.

3.1.5 The effects of captivity on Basal Metabolic Rate

A few reports in the literature compare the values of BMR obtained from freshly caught birds and those of birds held in captivity for extended periods. These reports disagree on the effects of captivity on BMR. Weathers *et al* (1983) compared the BMR's of four Apapanes *Himatione sanguinea* held in captivity for one year with those of four freshly caught ones. They found no significant difference (see also Dawson & Carey, 1976; Wasser, 1986). However, Warkentin and West (1990) reported that Merlins *Falco columbarius*, held in captivity for periods ranging from 7 months to 3 years had significantly higher BMRs and body temperatures than freshly caught birds. In their study, none of the captive birds were able to fly, due to wing fractures, and data from only 4 captive birds out of six (and different ages) were compared with those from 9 wild conspecifics. Piersma (1994) and Piersma *et al* (1996) found that long-term captive Knot had lower BMRs than those of wild birds. This was claimed to be due primarily to a decrease in mass of the digestive organs i.e. intestines and stomach.

In my study, I was concerned with the comparison of the DEE's of the two subspecies of Dunlin, so that even if the general level of BMR decreases or increases in captive birds, the validity of the comparison will not be affected as long as the decreases or increases occur to an equal extent in both subspecies, which seems highly probable.

3.2 Methods

3.2.1 Day and night variation in BMR

To determine whether diurnal variation in Basal Metabolic Rate (BMR) occurred in captive Dunlin, the value obtained during the day was compared with a subsequent value recorded at night (see chapter 2 section 2.3.6 for more details)

3.2.2 Resting metabolic Rate in the two subspecies of Dunlin

6 juvenile *C.a.alpina* and 4 juvenile and 4 adult *C.a.schinzii* were caught on 24/9/96 and 6/8/97 respectively under licence from English Nature, using cannon-netting on Teesmouth. They were held in captivity for 23-34 months under the conditions described in Chapter 2 section 2.3.1. In order to estimate the energy costs of living, measurements of basal metabolic rate (BMR) every month and resting metabolic rate (RMR) in March and November were made using the protocols described in Chapter 2 sections2 .3.3 and 2.3.4. I assumed that DEE was a fixed multiple of BMR or RMR, following the analysis by Drent *et al,* (1978). This may not be strictly true for the *interspecific* relationship (Ricklefs *et. al* 1996), but should allow valid comparisons between two races of a single species. Using average temperatures on their breeding, wintering, moulting and refuelling sites (Meteorological Office, 1982). Drent *et al,* (1978) assumed that DEE is 2.6 BMR. However, I assumed that DEE is 2RMR to allow for thermoregulation. I estimated the RMR and energy costs of living from the RMR/temperature graphs (Figures 5 and 6).

3.3 Results and discussion

3.3.1 Day and night variation in BMR

The mean level of BMR of the six birds was slightly lower during the night. However, paired t-tests indicated that this reduction was not statistically significant (t. = 1.116, $P > 0.05$) and did not occur in all individuals (Table 1). Scott (1991) and Selman (1998) have also found no significant change in BMR of individual shorebirds measured during a day and the next night. There is no reason that increases BMR in waders at night as their feeding in the wild likely to be governed by the tide and not by the light intensity (see Kersten & Visser, 1996).

Table 1: Day and night BMR and Mass-Specific BMR in six Dunlin

Individual Dunlin	MR(Watts) during day	BMR(Watts) during night	Mass-specific BMR (Watts/kg) during day	Mass-specific BMR (Watts/kg) during night
DG	0.736	0.733	14.7	14.9
OR	0.74	0.74	15.4	15.4
LG	0.87	0.82	15.9	15.5
BL	0.75	0.71	17.9	17.28
YEL	0.73	0.76	13.5	14.00
RE	0.55	0.53	12.78	12.27
Mean	0.729	0.716		

SE= 0.01238, For the differences between pairs: t. = 1.116, $P > 0.05$

3.3.2 The relationship between Resting Metabolic Rate and temperature in the two subspecies of Dunlin

Measurements of resting metabolic rate were made for the two subspecies of Dunlin in March and November in order to establish the relationship between resting metabolic rate and temperature and hence energy costs of living at different temperatures. Measurements were taken twice, in different seasons, in order to check the stability of this relationship. Figures 3a, 3b, 4a and 4b summarise the results for *C.a.alpina* (Figure 3) and *C.a.schinzii* (Figure 4) in the two months. No significant differences in the slope or in the intercept were found between measurements taken in March and in November for each of the two subspecies of Dunlin (slopes: paired t-test=1.7, intercept paired t-test = 1.64 in *alpina* and slopes: paired t-test =1.5, intercept: paired t-test = 0.92 for *schinzii*). Therefore, I combined the two sets of measurements (March and November) in order to establish the relationship between RMR and temperature for each subspecies (see Appendix V). The difference between the two slopes of the two subspecies is 0.00052, which is less than the S.E. of either of the two slopes. That means that the two regression line of the two subspecies do not differ significantly at the P = 0.05 level (Figure 4c).

Figure 3a: The relationship between Resting Metabolic rate (RMR) and temperature measured in March for six *C.a.alpina*. Bars indicate SE.

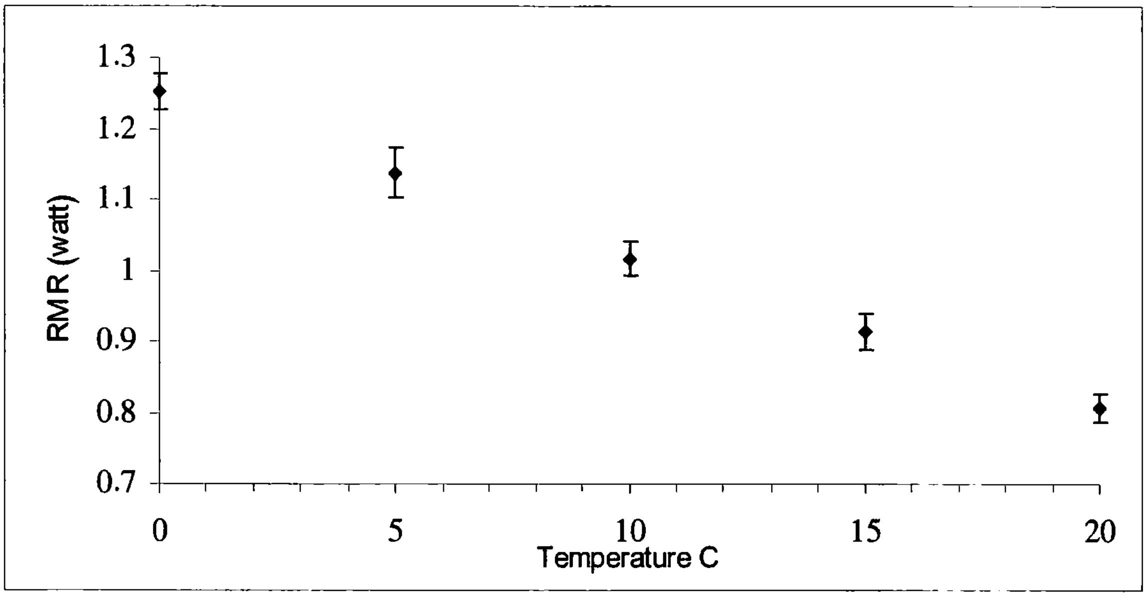


Figure 3b: The relationship between Resting Metabolic rate (RMR) and temperature measured in November for six *C. a. alpina*. Bars indicate SE.

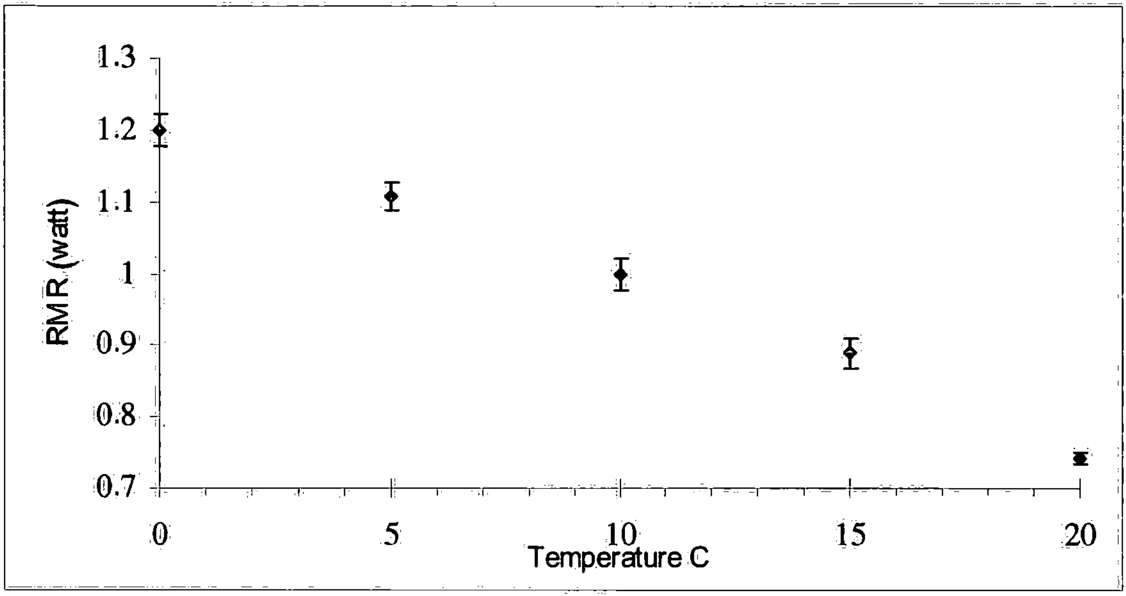


Figure 4a: The relationship between Resting Metabolic rate (RMR) and temperature measured in March for eight *C. a. schinzii*. Bars indicate SE.

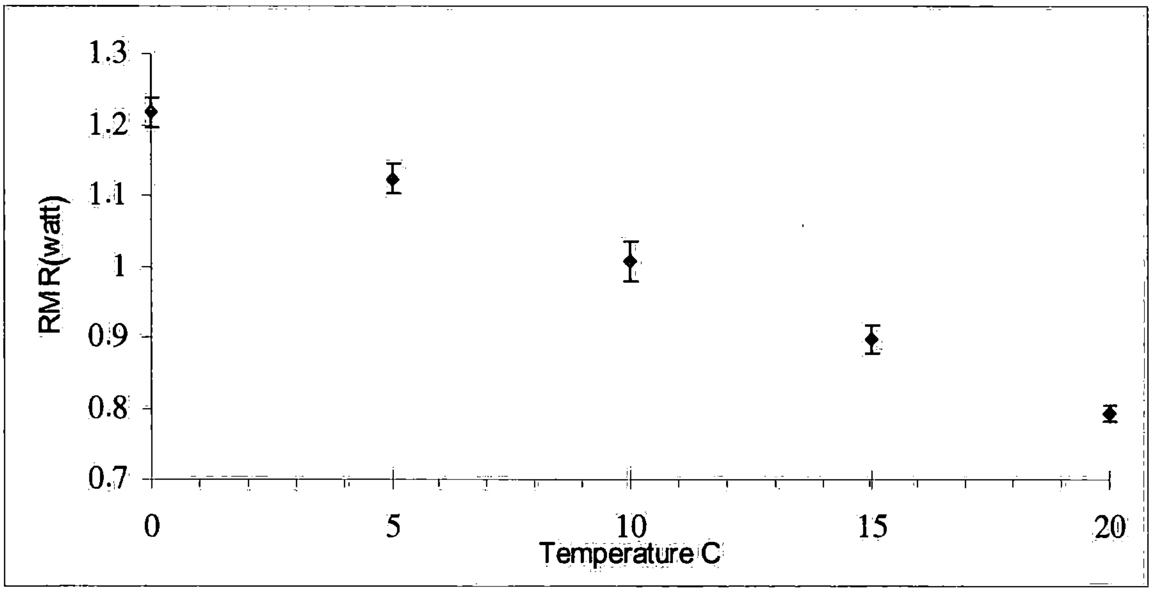


Figure 4b: The relationship between Resting Metabolic rate (RMR) and temperature measured in November for five *C.a.schinzii*. Bars indicate SE.

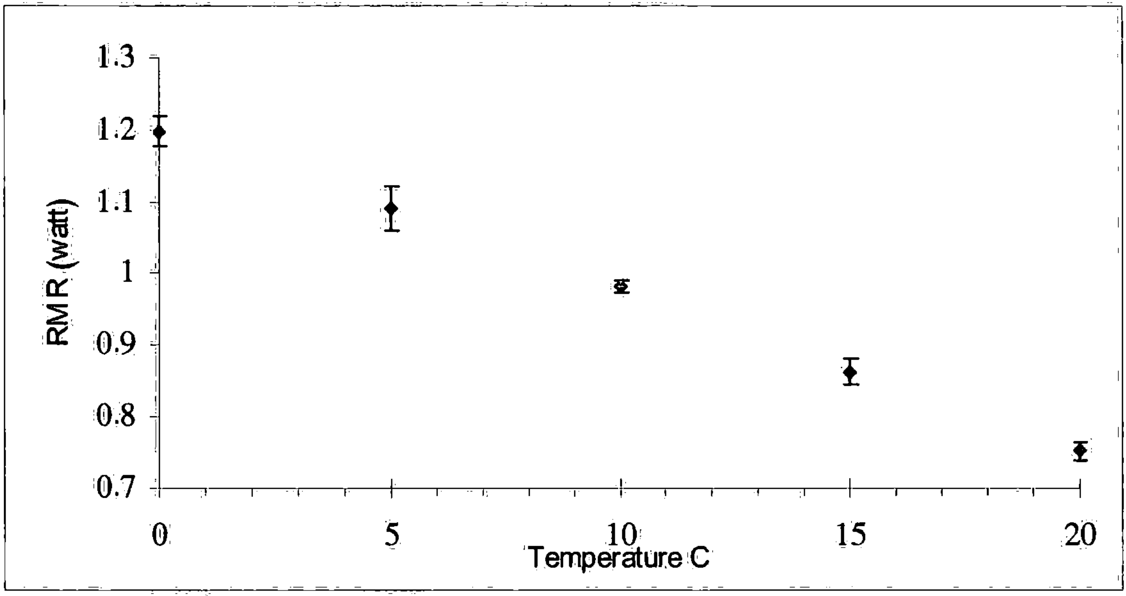
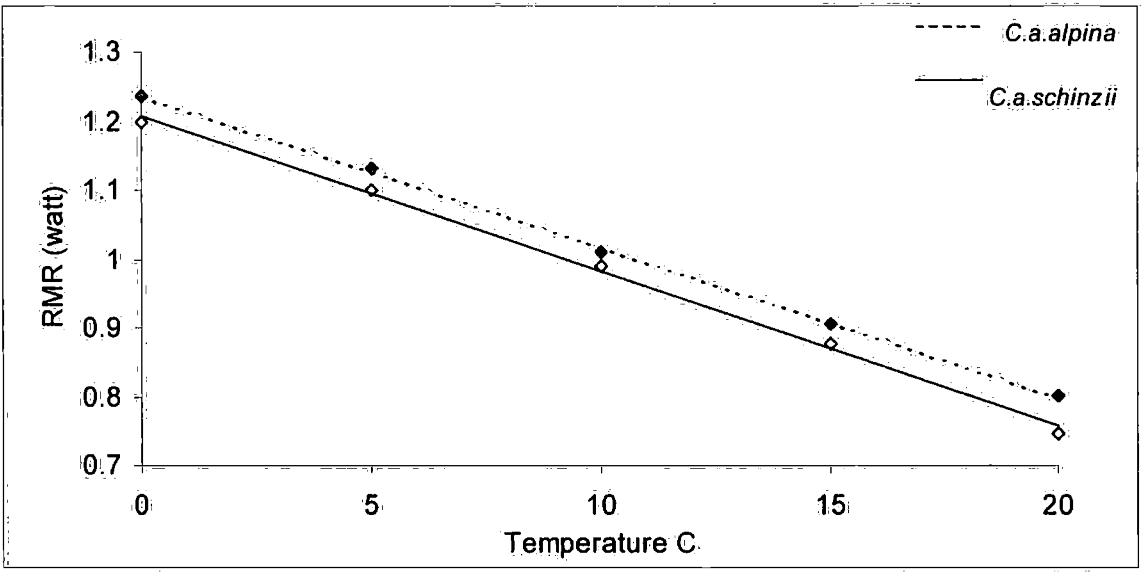


Figure 4c: Regression lines of RMR against temperature for the two subspecies



3.3.3 Energy costs of living in *C.a.alpina* and *C.a.schinzii*

The nominate subspecies of Dunlin *C.a.alpina* breeds in north Scandinavia and Russia east to the Taimyr Peninsula (Hale, 1980; Gromadzka, 1989), but the majority are found only as far east as the Yamal peninsula (Wennerberg *et al*, 1999; Wenink *et al,* 1996). This subspecies breeds mainly from early May until late July. Energy costs of living while on breeding grounds are summarised in Table 1.1. This subspecies moults mainly on the Wadden Sea and the Wash in East England (Holmgren *et al*, 1993) and winters in western Europe, mainly in Britain, Ireland and France (Pienkowski & Pienkowski, 1983; Gromadzka, 1989). The energy costs of living on their moulting and wintering grounds are summarised in Table 1.2 and 1.3 respectively. Energy costs of living while fattening in Schleswig-Holstein (Germany) and in the (Turku-Pori) region of Finland are summarised in table 1.4 and 1.5 (see ringing and recoveries maps in appendix VIII for evidence of use of these sites as fattening areas).

The other subspecies of Dunlin I studied, *C.a.schinzii*, breeds mainly in Iceland and moults and winters in Morocco and Mauritania. The energy costs of living in these areas are summarised in table 2.1, 2.2 and 2.3. This subspecies probably uses three staging posts during their spring and autumn migrations (see ringing and recoveries maps appendix VIII). The energy costs of living while fattening at the probable staging posts are summarised in table 2.4 and 2.5.

Table 3.1 shows the total energy costs of living, throughout their annual cycle, for the two subspecies of dunlin. It can be seen that the total energy costs of living are highest in 'winter' because this season is the longest and temperatures are the lowest. Also it can be seen that the energy costs of living in 'winter' in *C.a.alpina* are much higher than in *C.a.schinzii* as they former winter further north where the temperatures are lower. This difference constitutes almost half of the (21%) higher total costs of living increased by the race *C.a.alpina.* Although energy costs of living on the breeding grounds are nearly the same for the two subspecies of Dunlin, energy costs of living on the moulting grounds are interestingly much higher in *alpina* than in *schinzii*, that might be attributed to the fact that *alpina* moult in areas with lower temperatures (on the Wadden Sea and the Wash) than do *schinzii* (Morocco and Mauritania); also moult itself in *alpina* takes longer than in *schinzii* (three months as opposed to two). However, energy costs of living on the fattening grounds in *schinzii* are higher than in *alpina* because *schinzii* spend longer on migration. It can also be seen from table 3.1 that the energy costs of living on moulting and wintering grounds constitute almost all of the (21%) higher total costs of living increased by the race *C.a.alpina.*

Table 1.1: Estimation of energy costs of living on breeding grounds in north Scandinavia and Russia east to Vaigach Island for *C.a.alpina.*

	May (31 days)	June (30 days)	July (20 days)
Average maximum temperature °C	8.5	14	18
Average minimum temperature °C	0.5	6	9.5
Average daily temperature °C	4.5	10	14
RMR (Watt)	1.135	1.020	0.935
Daily EE (KJ)	196	176	162
Monthly EE (KJ)	6076	5280	3240

Total Energy costs of living on breeding grounds for *C.a.alpina* is approximately =14596 KJ

Notes: Daily Energy Expenditure estimated as 2 x RMR
RMR / temperature relationship shown in Figure 5.
EE: means Energy Expenditure

Table 1.2: Estimation of energy costs of living on moulting grounds in the Wadden Sea and the Wash in England for *C.a.alpina*.

	August (20 days)	September (30 days)	October (31 days)
Average maximum temperature °C	20	18	13
Average minimum temperature °C	13	11	7.5
Average daily temperature °C	16.5	14.5	10
RMR (Watt)	0.875	0.920	1.020
Daily EE (KJ)	151	159	176
Monthly EE (KJ)	3020	4770	5456

Total Energy costs of living on moulting grounds for *C.a.alpina* is approximately =13246 KJ

Note: See Table 1.1.

Table 1.3: Estimation of energy costs of living for *C.a.alpina* on their wintering grounds in W Europe mainly in Britain, France and Ireland.

	November (30 days)	December (31 days)	January (31 days)	February (28 days)	March (31 days)
Average maximum temperature °C	10	7.5	6.5	7	9.5
Average minimum temperature °C	5	3	1.5	1.5	3
Average daily temperature °C	7.5	5	4	4	6
RMR (Watt)	1.07	1.12	1.15	1.15	1.1
Daily EE (KJ)	185	194	199	199	190
Monthly EE (KJ)	5550	6014	6169	5572	5890

Total Energy costs of living on wintering grounds for *C.a.alpina* is approximately =29195 KJ

Note: See Table 1.1

Table 1.4: Estimation of energy costs of living on stopover grounds during autumn migration for *C.a.alpina.*

	Schleswig-Holstein Germany	Turku-Pori Finland
	August (10 days)	July (10 days)
Average maximum temperature °C	19	21
Average minimum temperature °C	15	11
Average daily temperature °C	17	16
RMR (Watt)	0.865	0.885
Daily EE (KJ)	149	153
(10 days) EE (KJ)	1490	1530

Total Energy costs of living on stopover grounds in autumn migration for *C.a.alpina* is approximately = 3020 KJ

Notes: See Table 1.1

Table 1.5: Estimation of energy costs of living on stopover grounds during spring migration for *C.a.alpina*

	Schleswig-Holstein Germany	Turku-Pori Finland
	April (20 days)	April (10 days)
Average maximum temperature °C	8	6
Average minimum temperature °C	4	-3
Average daily temperature °C	6	1.5
RMR (Watt)	1.100	1.205
Daily EE (KJ)	190	208
Total EE (KJ)	3800	2080

Total Energy costs of living on stopover grounds in spring migration for *C.a.alpina* is approximately = 5880 KJ

Notes: See Table 1.1

Figure 5: The relationship between Resting Metabolic Rate (RMR) and ambient temperatures. RMRs presented here are the average of those measured in March and November for six *C.a.alpina*

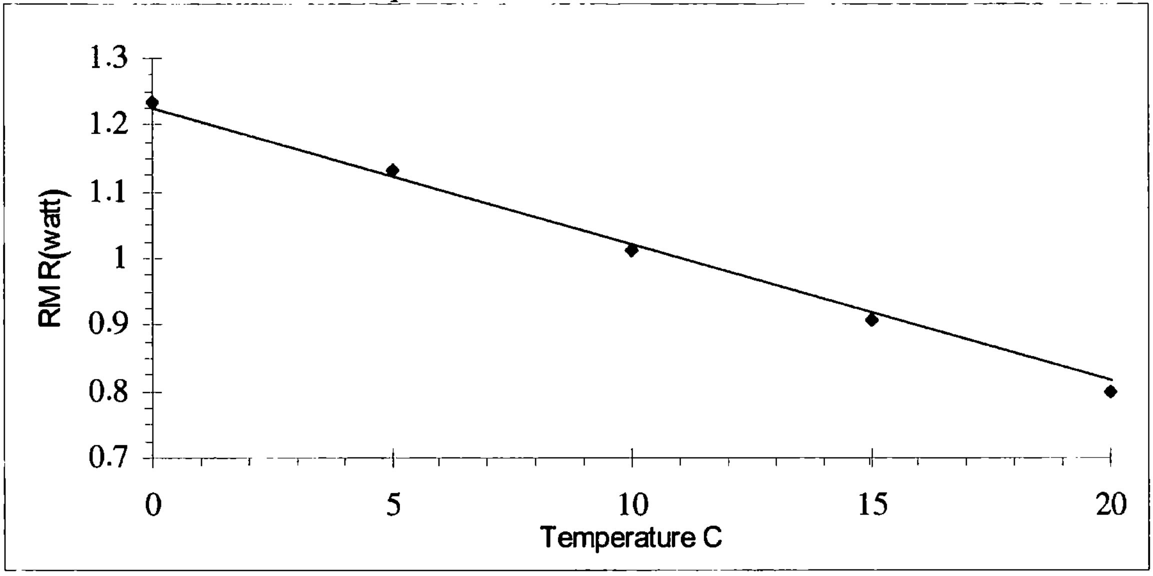


Table 2.1: Estimation of energy costs of living on breeding grounds in Iceland for *C.a.schinzii.*

	May (15 days)	June (30 days)	July (30 days)
Average maximum temperature °C	8.2	11.2	12.7
Average minimum temperature °C	3	5.8	7.7
Average daily temperature °C	5.5	8.5	10
RMR (Watt)	1.08	1.02	0.98
Daily EE (KJ)	187	176	169
Total EE (KJ)	2805	5280	5070

Total Energy costs of living on breeding grounds for *C.a.alpina* is approximately =13155 KJ

Notes: Daily Energy Expenditure estimated as 2 x RMR
RMR / temperature relationship shown in Figure 6.

Table 2.2: Estimation of energy costs of living on moulting grounds in Morocco and Mauritania for *C.a.schinzii.*

	September (30 days)	October (31 days)
Average maximum temperature °C	27	26
Average minimum temperature °C	18.5	16
Average daily temperature °C	23	21
RMR (Watt)	0.7	0.75
Daily EE (KJ)	121	130
Monthly EE (KJ)	3630	4030

Total Energy costs of living on moulting grounds for *C.a.alpina* is approximately =7660 KJ

Notes: See Table 2.1.

Table 2.3: Estimation of energy costs of living on wintering grounds in Morocco and Mauritania for *C.a.schinzii.*

	November (30 days)	December (31 days)	January (31 days)	February (28 days)	March (31 days)
Average maximum temperature °C	23	20	19	20.5	22
Average minimum temperature °C	14	11	10	10.5	12
Average daily temperature °C	18.5	15.5	14.5	15.5	17
RMR (Watt)	0.80	0.87	0.89	0.87	0.83
Daily EE (KJ)	138	150	154	150	143
Monthly EE (KJ)	4140	4650	4774	4200	4433

Total Energy costs of living on wintering grounds for *C.a.schinzii* is approximately =22197 KJ

Notes: See Table 2.1.

Table 2.4: Estimation of energy costs of living on stopover grounds during autumn migration for *C.a.schinzii.*

	Teesmouth NE England	SW France	Morocco
	August (10 days)	August (10 days)	August (10 days)
Average maximum temperature °C	19	22.5	27.6
Average minimum temperature °C	11	14.5	18.5
Average daily temperature °C	15	18.5	23
RMR (Watt)	0.875	0.80	0.70
Daily EE (KJ)	151	138	121
(10 days) EE (KJ)	1510	1380	1210

Total Energy costs of living on moulting grounds for *C.a.alpina* is approximately = 4100 KJ

Notes: See Table 2.1.

Table 2.5: Estimation of energy costs of living on stopover grounds during spring migration for *C.a.schinzii.*

	Morocco	SW France	Teesmouth NE England
	April (15 days)	April (15 days)	May (15 days)
Average maximum temperature °C	21.7	14.5	14
Average minimum temperature °C	12	8	6
Average daily temperature °C	17	11	10
RMR (Watt)	0.830	0.965	0.985
Daily EE (KJ)	143	167	170
(15 days) EE (KJ)	2145	2505	2550

Total Energy costs of living on moulting grounds for *C.a.alpina* is approximately = 7200 KJ

Notes: See Table 2.1.

Figure 6: The relationship between average Resting Metabolic Rate (RMR) and temperatures. RMRs presented here are the average of those measured for *C.a.schinzii* in March (n=8) and November (n=5)

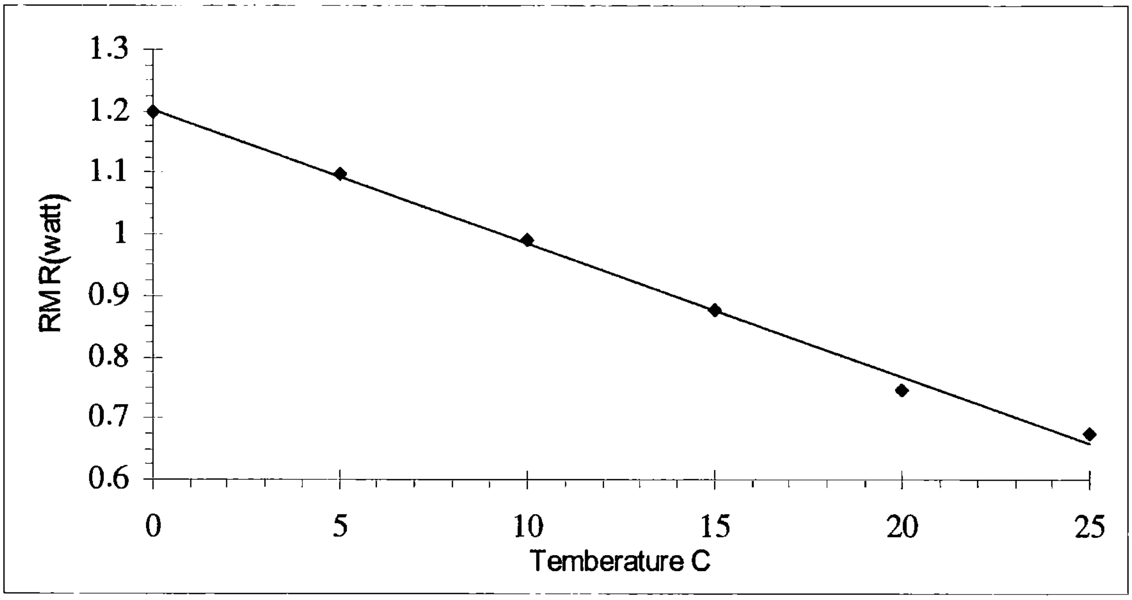


Table 3.1: Total energy costs of living at different sites for the two subspecies of dunlin

		Total energy costs of living on each site (KJ)	Annual costs of living (KJ)
C.a.alpina	On breeding grounds	14596	**65937**
	On moulting grounds	13246	
	On wintering grounds	29195	
	On fattening grounds	8900	
C.a.schinzii	On breeding grounds	13155	**54312**
	On moulting grounds	7660	
	On wintering grounds	22197	
	On fattening grounds	11300	

Chapter 4,
Energy costs of moult

4.1 General introduction

The most obvious feature of birds, which distinguishes them from all other living animals, is their plumage, the collective name for the outer covering of feathers. Feathers are probably the most complex derivatives of the integument to be found in any vertebrate. Five main structural categories of feathers can be recognised in a bird: contour (body and flight) feathers, semiplumes, down feathers, bristles and filoplumes (Stettenheim, 1972).

The functions of body and flight feathers are as follows. The former are distributed over the general body surface of the bird providing protection against the environment and also streamlining the body and wing surface during flight, as the feathers point backwards towards the tail and each feather is overlaid by the one in front to form a barrier to wind and rain. They are also very important in helping to regulate the bird's body temperature by insulating it from the environment by a layer of air trapped around the body. In addition body feathers play vital roles in the incubation of eggs, protection of the young, camouflage and sexual communication (Stettenheim, 1976 in Murphy, 1996). In waterbirds, body feathers have an additional important function by forming a water-repellent layer, and their body plumage is more compact and more oily than in other birds (Ginn & Melville, 1983).

Feathers of the wings and tail are adapted for their crucial roles in flight, stability and manoeuvrability as they are relatively large, rigid and mostly pennaceous (Amadon, 1966).

Although feathers are strong and regularly cared for by preening, they are subjected to progressive wear and tear, which reduce their structural integrity, and hence they have to be replaced by new ones.

The repeated replacement of all or parts of the plumage by new feathers is known as moult and is an important event in the annual cycle of a bird. This replacement of feathers is needed to (i) aid in regulating body temperature, (ii) maintain a high level of flight performance (iii) maintain feathers waterproofed (iv) allow seasonal changes in appearance for courtship and mating (Campbell & Lack, 1985). Most species undergo at least one full moult in the year and many do so twice. In a few species moult can occur three times a year. Most birds moult the wing feathers symmetrically in pairs from either side. Moult requires an increased rate of energy expenditure (e.g. Dietz *et al,* 1992; Murphy & King, 1992; Lindstrom *et al,* 1993) see section 4.3.2 in this chapter. Flight performance may be reduced during the moult of the wing feathers (Pennycuick, 1975; Swaddle & Witter, 1997) and therefore birds are exposed to increased risk from predators. These factors may explain why moult in most bird species, especially in temperate regions, is separated from migration and reproduction. Some species do however overlap breeding and moult to some extent, in species in which feather replacement extends over a long period of the year so that the extra energetic demands are well spread, and in those living in hot tropical areas where thermoregulatory energy demands should not be increased by moult (Campbell & Lack, 1985). In some species moult continues even when nutrients are very limited (Murphy, 1996). Timing and duration of moult differ between species and even between populations of the same species. In migrant species some start to moult near their breeding grounds but suspend moult during migration, others complete moult in their wintering quarters or at special moult sites part of the way along their migration route.

4.1.1 Moult in Dunlin *C.a.alpina* and *C.a.schinzii*

The timing and duration of moult in Dunlin differs between populations and even between sexes. Nominate *C.a.alpina* leave breeding grounds in Russia and Scandinavia (Lessels, 1974; Leslie & Lessels, 1978) to moult at a few large estuaries or intertidal areas, for example in the Wadden Sea areas of Denmark, Germany and Netherlands (Boere, 1976). Along the east coast of Great Britain (e.g. at the Wash, Hale, 1980) they start moulting between early July and early August and finish between early September and early October, a period of 80-90 days. Late starting birds moult more quickly than early starters and females moult more quickly than males (Ginn and Melville, 1983). Nominate *schinzii* also moult after migrating from their breeding grounds (in Iceland and south-east Greenland) to Morocco and Mauritania where they renew their primaries in 60-70 days between early September and late November (Pienkowski & Dick 1975; Pienkowski *et al*, 1976; Boere, 1976; Nieboer, 1972).

4.2 The Energetic Costs of the whole moult process

4.2.1 Methods of measuring the energy costs of moult

The costs of feather production differ a great deal between bird species. The energy costs of feather synthesis can be measured or estimated by four methods (i) as metabolised energy during moult, (ii) by summing caloric equivalents of overnight changes in body mass during moult, (iii) by estimation of the energy intake required to supply the sulfur-containing amino acids (SAA) needed for plumage synthesis, (iv) by measuring oxygen consumption during moult.

The first method, involving measuring the metabolised energy (ME) of birds throughout their moults, provides a summation of their daily energy expenditures (DEE). This method has potential errors associated with diurnal variation in rates of feather production and associated processes (Murphy, 1996). This attribute of the ME method, however, limits its usefulness for estimating the costs of individual components of an animal's energy budget, such as plumage production, because adjustments in components of the energy budget can mask one another (Murphy, 1996). Moulting birds usually reduce, for example, their level of activity (e.g. Newton, 1966; Morton & Morton, 1990; but see also Dow, 1973) and the saving in energy needed for activity can be almost equivalent to the energetic costs of moult (Lindstrom, 1993). This method provide estimates of energy costs of moult that are in agreement with estimates derived from measures of oxygen consumption when measures of ME are made before, during and after moult (Murphy & King 1984b; Dietz *et al*, 1992), but some estimates may be significantly higher (e.g. in Chaffinch *Fringilla coelebs*, Dolink & Gavrilov, 1979).

The second method of measuring energy costs of moult is to obtain the caloric equivalents of overnight changes in body mass. This method assumes that energy costs for moult are constant through each hour of the 24-hour cycle and it also include the unlikely assumption that the proportions of fat, carbohydrate, protein, and water lost overnight remain unchanged through the course of moult (Murphy, 1996). This method was used extensively by Dolnik (1965,1967) and assumes a caloric equivalent of mass loss equal to 13.8KJ g^{-1}, based on the total energy costs for moult in 15 species of Palaearctic passerines. Dolnik's method based on mass loss appears to produce higher estimates for the total energy costs of moult than measures of oxygen consumption or metabolised energy (Murphy, 1996).

The third method for estimating the energy costs of moult was suggested by Gavrilov and Dolnik (1974) and later termed the 'aminostatic hypothesis 'by Murphy and King (1984b). The main assumption of this method is that the energy costs of moult (KJ ME) can be estimated by comparing the cystine content of the bird's diet and the cystine needed for plumage synthesis. They assumed that the apparent difference between the energy cost of the whole moult process and the energy deposited in new plumage can be accounted for by the energy demanding conversion (oxidation) of large amounts of food to extract the essential amino acid cystine necessary for feather synthesis. This method involves five questionable assumptions and is fundamentally flawed (for more details see Murphy & King, 1984b; Murphy & King, 1987).

The fourth method relies on measurement of oxygen consumption, usually made during the bird's normal resting period in each 24 hour. This method assumes that the rate of plumage production and accompanying metabolic processes are constant through the 24-hour cycle. The increase in resting metabolism in moulting birds is assumed to result from processes associated with feather regeneration. Feather production may proceed at the same rate both by day and night (Wood, 1950; Newton, 1966; Murphy & King, 1986b) but also may not (e.g. Lillie & Wang, 1940).

The most useful of these methods are those that can provide an energy expenditure per mass of plumage produced, assuming that the intensities of the processes occurring within moult are proportional to the intensity of plumage production. Patterns of energy expenditure during moult more or less support this hypothesis (e.g. Murphy &

King1984b; Lindstrom *et al*, 1993; Murphy, 1996), perhaps with the exception of changes in thermoregulation costs (Blackmore, 1969).

4.2.2 The effect of moult on the metabolic rate and thermoregulation

A general rise in resting energy metabolism during moult has been reported for several species. This increase above non-moulting levels ranged widely from 9-111% in different species (King, 1981; Lindstrom *et al.* 1993). Some of the causes of this variation between species will be discussed later in this section. In moulting birds both body temperature and metabolic rate suggest that moult involves increased energy requirements. This increase in energy metabolism in moulting birds occurs when wild birds are often unusually inactive, indicating that moult itself is responsible for the increase in metabolism (Payne, 1972). When birds moult, their insulation also decreases. Therefore, they require more energy to maintain the same core body temperature. But in many species core body temperature rises because the heat produced by the intensified metabolism of moulting birds more than offsets the decrease in insulation (Gavrilov, 1974 in Murphy, 1996), and heat dissipation may provide a thermoregulatory challenge for moulting birds causing elevated body temperatures (e.g. Newton, 1968b; but see also Chilgren, 1977). Also moulting birds must produce new feathers which require increased (i) protein (amino acids especially the essential amino acids such as cystine, lysine, arginine and tyrosine) to supply substrates, (ii) energy, (iii) iron for erythrocyte production for an increased blood volume (Murphy & King, 1992). Many birds moult at times of year with relatively warm ambient temperatures, which minimise the thermostatic costs during moult.

4.2.3 The possible causes of interspecific variation in costs of moult

The cost of moult differs substantially between species. It has been argued whether differences in body mass, basal metabolic rate, diet, or the latitude of moult could explain these interspecific variations. The increase in metabolic rate during moult not only reflects the cost of formation of keratin alone, but may also include energy spent on production and maintenance of tissues needed for feather synthesis (King, 1981; Murphy & King, 1984,1991a; Dietz *et al*, 1992) as the energetic efficiency of feather production (5%-20%) is much lower than the 40%-50% efficiency found in the synthesis of other protein (Reeds 1991). Murphy and King (1990,1991a) suggested that the differences in cost of feather replacement between species might be related to day length during the moult period. They argued that much energy is lost when birds store protein during the day for use in feather synthesis during non-feeding periods in the 24-hour cycle, for example at night. The more protein that has to be stored and transformed, the greater this loss would be. Thus, feather production costs would be proportional to night length and therefore to the latitude at which the birds normally moult. Murphy and King (1984b) also suggested that the differences in costs of feather production between small seed-eaters and raptors might be related to their diets. Lindstrom *et al* (1993) studied the cost of moult in bluethroat, *Luscinia s. svecica* (an insectivorous songbird) and in common redpoll, *Carduelis f. flammea* (a seed-eater). They found that both bluethroats and redpolls had higher moult costs than most values reported earlier (Murphy & King, 1991; Dietz *et al*, 1992), even though they moulted in almost continuous daylight. They also found that feather production costs in the seed-eating redpoll were not significantly higher than in the insectivorous bluethroat, whereas a difference would have been expected (redpolls higher) if the diet hypothesis were correct. They concluded that the cost of feather production was significantly correlated with both body mass and mass-specific BMR, and that neither diet nor latitude alone could explain the differences between species. During peak moult intensity, the average metabolic rate was 111% higher than the premoult value for bluethroats and 106% higher for redpolls. The postmoult metabolic rate was 15% higher than the premoult values for bluethroats whereas it was 18% lower than the premoult values in redpolls. Body mass and fat score increased during the first half and after the completion of moult. During the second half of the moult period, total body mass decreased whereas fat scores stayed stable (Lindstrom *et al,* 1993). The changes in total mass during moult are mainly due to changes in water mass, which is correlated with feather growth (e.g. Newton, 1968b; Evans, 1969; Chilgren, 1977).

The energy costs of production of a given amount of feather mass have only rarely been measured. Lindstrom *et al,* (1993) produced relationships between the energy cost of moult, body mass and mass-specific BMR, from the few published studies which have been made of the energy costs of feather production, and from their own study. They found that the cost per gram of feather growth (Cf), in the seven species which have been studied by indirect calorimetry, correlated significantly with mass (m kg) according to the equation

$$\log Cf = 1.984 - 0.382 \ \log m \ \ldots\ldots\ldots\ldots\ldots \ \textbf{(1)} \quad (r^2 = 0.67)$$

Since the costs of moult involve several metabolic processes in addition to keratin synthesis (King, 1981) and since these require energy in proportion to mass, moult costs should be related to the mass-specific BMR (MSBMR) according to equation (2) (Dietz *et al*, 1992). This explains more of the observed variance in energy costs of feather synthesis ($r^2 = 0.82$) than equation 1.

$\log Cf = 2.459 + 0.843 \log MSBMR$ ....**(2)**

Costs of feather production per gram for a species with known mass-specific BMR can be estimated roughly from the equation $Cf = 270\ MSBMR$ ....**(3)** (Lindstrom *et al*, 1993).

According to equations (2) and (3), the energy costs of moult per gram feather mass (but not the total costs) increase with decreasing body mass because MSBMR increases also.

4.3 Energy costs of moult in Dunlin

Two methods were used to estimate the energy costs of moult in my study:

1) Measurement of the mass of plumage produced by Dunlin of the two races and their body mass and hence calculation of values for the energy requirements from equation (1) of Lindstrom *et al,* (1993).
2) Measurement of changes in BMR during moult. Any significant variation in basal metabolic rate with stage of moult would allow estimation of the cost of feather production (KJ. [g dry feathers]$^{-1}$,since costs of activity are eliminated.

4.4 Methods

(1) In order to measure the mass of Dunlin plumage, 26 adults Dunlin that had died on the Severn (south-west England) and Tees (north-east England) estuaries were used. All feathers were plucked and flight feathers (primaries, secondaries, greater coverts and tail) and body feathers (the rest of the feathers) dried (using vacuum oven at 40 °C) and weighed on a torsion balance to the nearest 10 mg, separately.

(2) Metabolic Measurements: were made by Open-flow Respirometry (see section 2.3.3)

Metabolic heat production was estimated by determination of rates of oxygen consumption using protocols described in Chapter 2 (section 2.3.3). BMR was taken before birds started to moult and then every two weeks during moult and for a period of 14 days after moult completion.

(3) Body composition was monitored during moult at least once every two weeks using the TOBEC technique. The protocols of this technique were described in Chapter 2 (see section 2.3.2).

(4) Moult scoring

Moult score was taken every week, according to the methods described by Ginn & Melville (1983). Old feathers scored 0, growing feathers scored 1-4 depending on their length, a new feather fully developed with no trace of waxy sheath remaining at base was scored as 5. Wing feather scores refer to the left wing. In order to assess the general progress of moult, a primary score was calculated for each moult-scoring date by adding the score for the ten large primaries. Therefore, the score will be 0 when moult has not started and 50 when all primaries are new. Duration of moult was calculated as the time between the dropping of the first primary and the day when waxy sheaths were no longer present on any of the primary feathers.

4.5 Calculation

4.5.1 Calculation of the energy costs of moult in *C.a.alpina*

The average body mass of *C.a.alpina* was 52.9g (SE = ±1.28, n=43) and the average mass of feathers of an adult *alpina* Dunlin is approximately 3.16 g (Table 1.1). Therefore, the energy cost per gram of feathers produced (Cf), derived from:

log Cf = 1.984-0.382 log m (body mass kg) is:

logCf = 1.984-0.382 * log 0.0529

logCf = 2.47

That means the energy cost of moult is approximately 296 kJ/g dry feathers.

Since the average mass of feathers of an adult Dunlin is 3.16g, the total energy costs of producing new feathers in last summer is approximately 3.16*296 = 935.4 kJ. The average mass of *body* feathers of an adult *alpina* is 2.44g, so the energy costs of body moult alone in spring are approximately 2.44*296 = 722.2 kJ. The total energy cost of moult therefore is approximately 1657 kJ for the whole annual cycle, therefore since birds moult only body feathers before breeding but undergo complete moult after breeding.

Table 1.1: Masses of body, flight and total feathers (g) of 16 adult *C.a.alpina* which died in winter on Severn (south-west England)

Body Feathers (g)	**Flight Feathers (g)**	**Total Feathers (g)**
2.224	0.652	2.876
2.468	0.617	3.085
2.271	0.645	2.916
2.542	0.542	3.084
2.769	0.624	3.393
2.690	0.860	3.550
2.560	0.645	3.205
2.896	0.889	3.785
2.430	0.941	3.371
2.722	0.608	3.330
2.429	0.895	3.324
2.324	0.813	3.137
2.101	0.724	2.825
2.357	0.674	3.031
2.100	0.676	2.776
2.172	0.675	2.847
Mean 2.441	**0.718**	**3.156**
SE = 0.61	**SE = 0.03**	**SE = 0.07**

4.5.2 Calculation of the energy costs of moult in *C.a.schinzii*

The average body mass of *C.a.schinzii* is 47.6 g (SE = ± 0.39, n=232) and the average mass of feathers of an adult is approximately 2.70 g (Table 1.2). Therefore, the energy cost per gram of feathers produced (Cf), derived from log Cf = 1.984-0.382 log m (body mass kg), is

LogCf = 1.984-0.382 * log 0.0476

LogCf = 2.489

That means the energy cost of moult is approximately 308 kJ/g dry feathers.

Since the average mass of body and flight feathers of an adult *schinzii* is 2.70 g, the total energy costs of producing new feathers in last summer is approximately 2.70*308 = 831.6kJ. The average mass of *body* feathers of an adult *schinzii* is 2.02 g, so the energy costs of body moult alone in spring, are approximately 2.02*308 = 622 kJ. The total energy cost of moult is therefore 1454 kJ the sum of the costs of late summer and spring moults.

Table 1.2: Masses of body, flight and total feathers (g) of 10 adult *C.a.schinzii* which died in spring and autumn at Teesmouth

Body Feathers (g)	**Flight Feathers (g)**	**Total Feathers (g)**
2.100	0.799	2.899
1.930	0.596	2.526
1.990	0.798	2.788
1.944	0.683	2.627
2.180	0.683	2.863
1.970	0.653	2.623
2.110	0.750	2.860
1.980	0.629	2.609
2.130	0.653	2.783
1.870	0.560	2.430
Mean 2.020	**0.680**	**2.700**
SE=0.03	**SE=0.02**	**SE=0.05**

4.6 Results of studies on captive birds

4.6.1 Timing and duration of moult

Captive *alpina* started to moult on average on July 16 (Range late June to mid August) and completed primary moult on average on October 16. Replacement of flight feathers required on average 91days (SE= ± 2.0) (see Table 1.2). This is similar to their moult in the wild, as they start moult between early July and early August and complete primary moult in September or early October, replacement of flight feathers lasting 80-90 days (Cramp & Simmons, 1983).

In *schinzii*, only three of the seven captives exhibited complete (flight and body feather) moult. Two adults exhibited only flight feather moult. These five individuals started to moult on average on August 27 (range mid August to mid September) and completed primary moult on average on October 26, around 61 days later (SE = ±1.69) (see Table 1.3). Again this is similar to wild *schinzii*, which moult between early September and late November, for 60-70 days (e.g. Boere, 1976; Pienkowski *et al*, 1976).

Table 1.2 Timing and duration of primary moult of six captive *C.a.alpina*

Individual	Start	Finish	Duration (days)
DG	26/06/98	21/09/98	87
LG	12/08/98	10/11/98	90
OR	04/07/98	06/10/98	94
YEL	29/07/98	04/11/98	98
RE	12/08/98	04/11/98	84
BLU	21/06/98	21/09/98	92

Average duration = 90.8, SE= 2.04

Table 1.3. Timing and duration of primary moult of five captive *C.a.schinzii*

Individual	**Start**	**Finish**	**Duration (days)**
LLG*	14/09/98	09/11/98	56
WOR	28/08/98	01/11/98	65
WDG	17/08/98	12/10/98	61
LYEL*	17/08/98	16/10/98	60
WBLU	28/08/98	01/11/98	65

Average duration = 61.4, SE= 1.69

* did not moult body feathers

4.6.2 Body composition during moult

In captive *alpina*, total body mass decreased slightly just before birds started to moult (Figure 1.1), with a concomitant decrease in lean mass. The lowest body and lean masses occurred at the beginning of primary moult, but then recovered towards the end of moult, though fat levels declined until a marked short-lived increase just prior to wing-feather growth completion. After completion of moult, body and fat masses started to decrease again (Figure 1.1 and 1.2).

These changes in body and lean mass during moult may result partly from (i) protein turnover, which is defined as the overall rate at which protein is synthesised and degraded in the body (ii) increases in body water content associated with expansion of the circulation needed for sustaining the growing feather and pulp (Murphy, 1996). Decreases in body mass occur in most birds species just before and at the beginning of moult which often coincides with the late stages of breeding, or shortly afterwards. As this time body masses are at, or near, their lowest for the year (e.g., Barnett, 1970; Carey *et al*, 1978; Coulson *et al*, 1983). Maintaining low body mass during the period of moult may minimise maintenance costs (Ankney, 1979). The peak of fat seen at the end of moult coincides with a time when many *alpina* Dunlin move a few hundred kilometres from moulting grounds to wintering areas (Pienkowski & Evans, 1984).

In captive *schinzii,* (Figure 1.3a) body masses were at their lowest just before moult, and increased slightly afterwards. As in *alpina*, they reached their peak just before completion of moult, decreasing again in three birds after the completion of moult. Two individuals (WOR and LYEL) put on much larger amounts of fat (Figure1.3 b), which they retained even after the completion of primary moult. Some *schinzii* migrate whilst in the last stages of active wing moult (Ginn & Melville, 1983) and the levels of fat deposited by WOR and LYEL are similar to those seen in wild *schinzii* before long distance migration.

Figure 1.1: Mean predicted lean mass (PTLM) and predicted fat mass (PFM) before, during and after moult for six captive *alpina* (predicted using TOBEC).

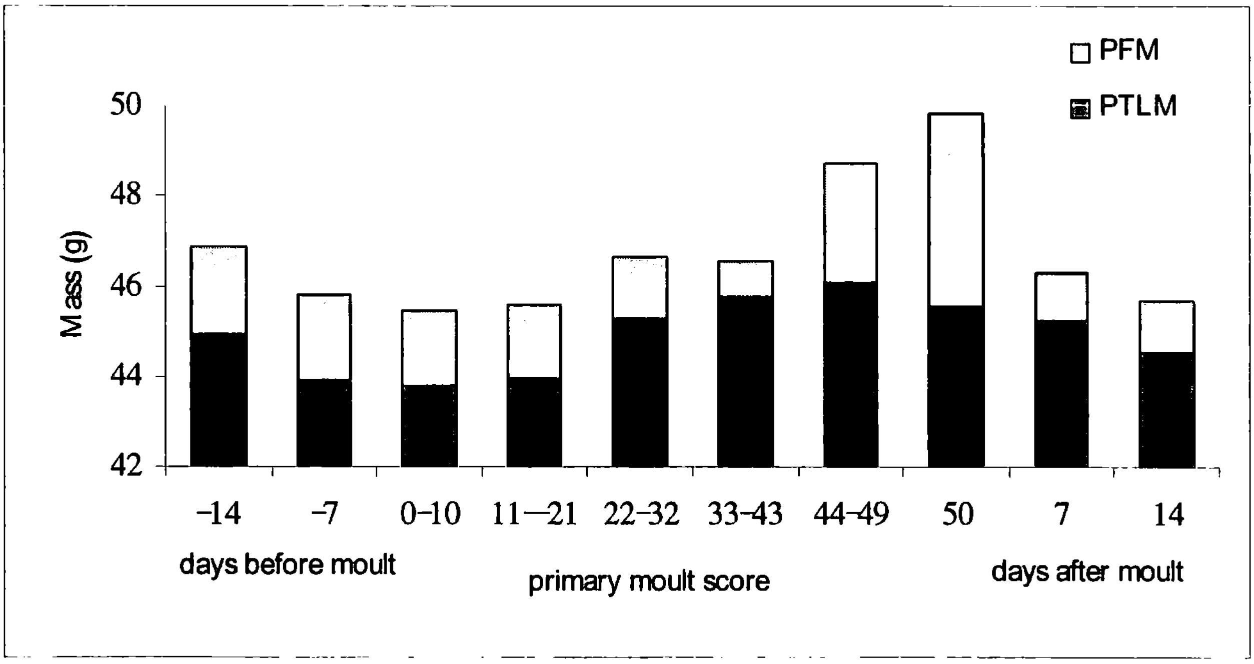


Figure 1.2: Average body masses (bars indicate SE) of six *alpina*, before, during, and after moult

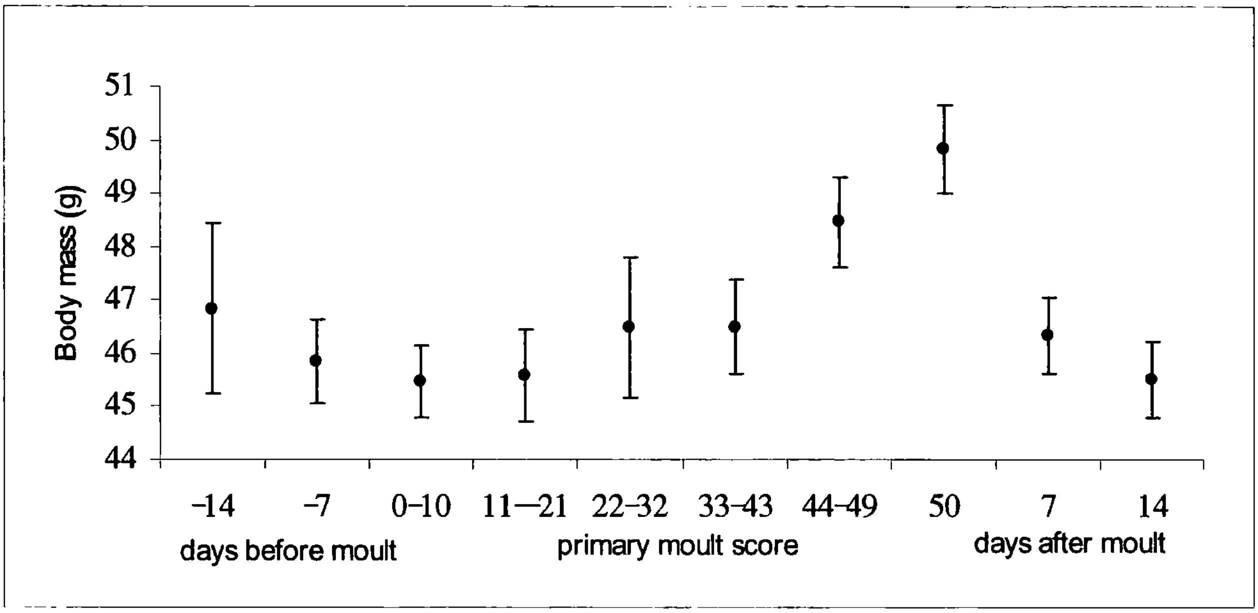


Figure 1.3a: Mean predicted lean mass (PTLM) and predicted fat mass (PFM) before, during and after moult for three captive *schinzii*

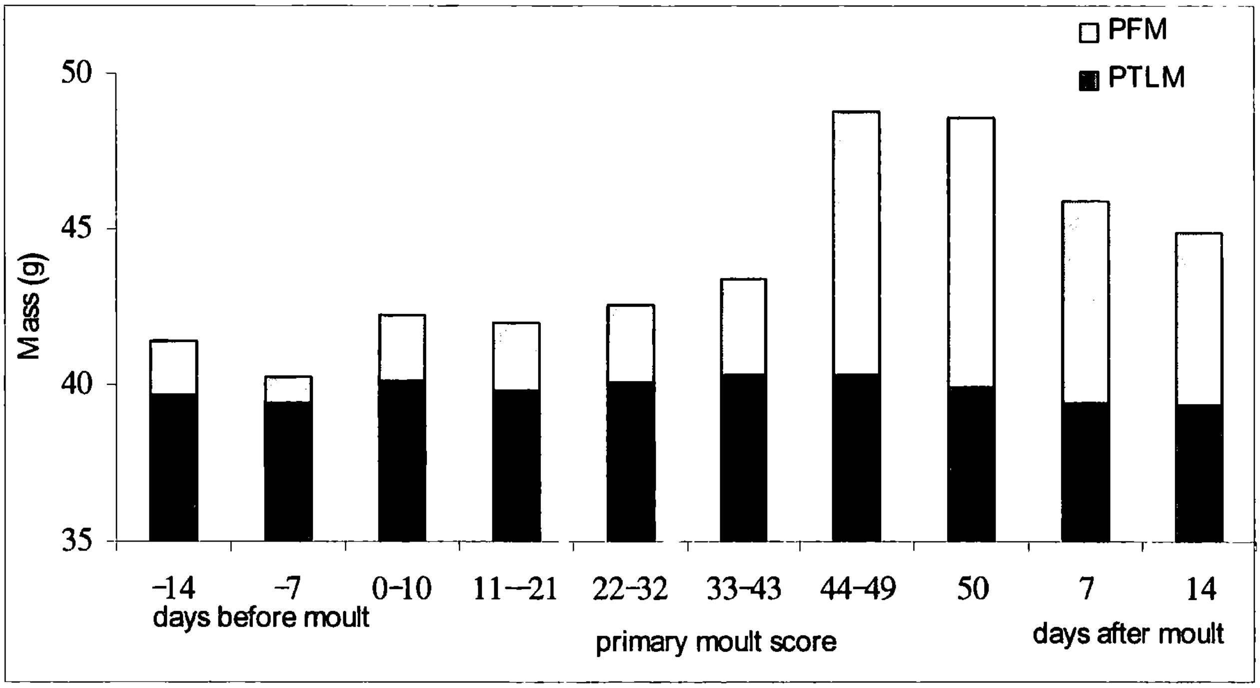
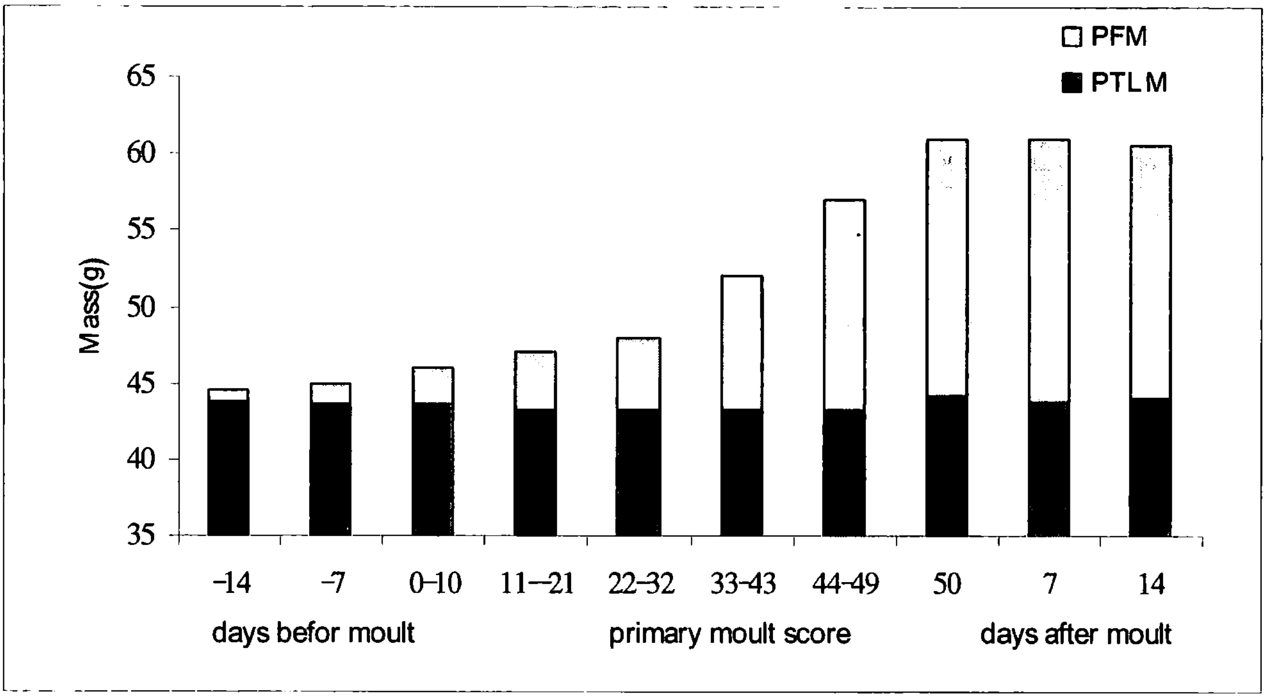


Figure 1.3b: Mean predicted lean mass (PTLM) and predicted fat mass (PFM) before, during and after moult for two captive schinzii (WOR, LYEL)



4.6.3 Metabolic rate

In the following discussion I have used the average of the non-moulting BMRs (premoult and postmoult) as a baseline value. In six *C.a.alpina*, nonmoulting BMR was on average 0.69 watt. During the middle of moult, the average BMR increased to 0.93 watt, 36% higher than non-moulting values (Figure 1.4). In five *schinzii*, however, nonmoulting BMR was on average 0.66 watt, whereas during the middle of moult, the average BMR increased to 0.87 watt, 32% higher than nonmoulting values (Figure 1.5). The increase in average BMR during the middle of moult in the six *alpina* was slightly higher than in the five *schinzii*. This might be expected as *alpina* is slightly larger than *schinzii* which means that *alpina* is producing more feathers and more energy may be required to maintain the same core body temperature.

The increase in BMR during the middle of moult in the two subspecies of Dunlin may due both to poorer insulation in this stage of moult and to the increased rate of producing new feather material which requires both an intensification of amino acid metabolism (Murphy, 1996) and an acceleration of whole body protein turnover (Murphy & Taruscio, 1995; Taruscio & Murphy, 1995). Even though BMR increases during moult in captive birds of many species (summarised by Lindstrom *et al*, 1993 and Murphy, 1996), many species of wild birds become less active during this period (e.g. Newton 1966; Owen and Ogilvie 1979; Bailey 1985; Morton and Morton 1990; but see also Dow 1973), so that total daily expenditure may remain unchanged if savings in activity completely offset the energy costs of moult (e.g. Davis 1955; Lindstrom *et al*, 1993).

Although there is a small difference in the percentage increase in BMR during moult between *alpina* and *schinzii*, this difference is not of major importance in relation to differences in total energy costs of the annual cycle in the two subspecies of Dunlin.

Figure 1.4: Average BMR, before, during and after moult for six *C.a.alpina.* Bars indicate 2x SE

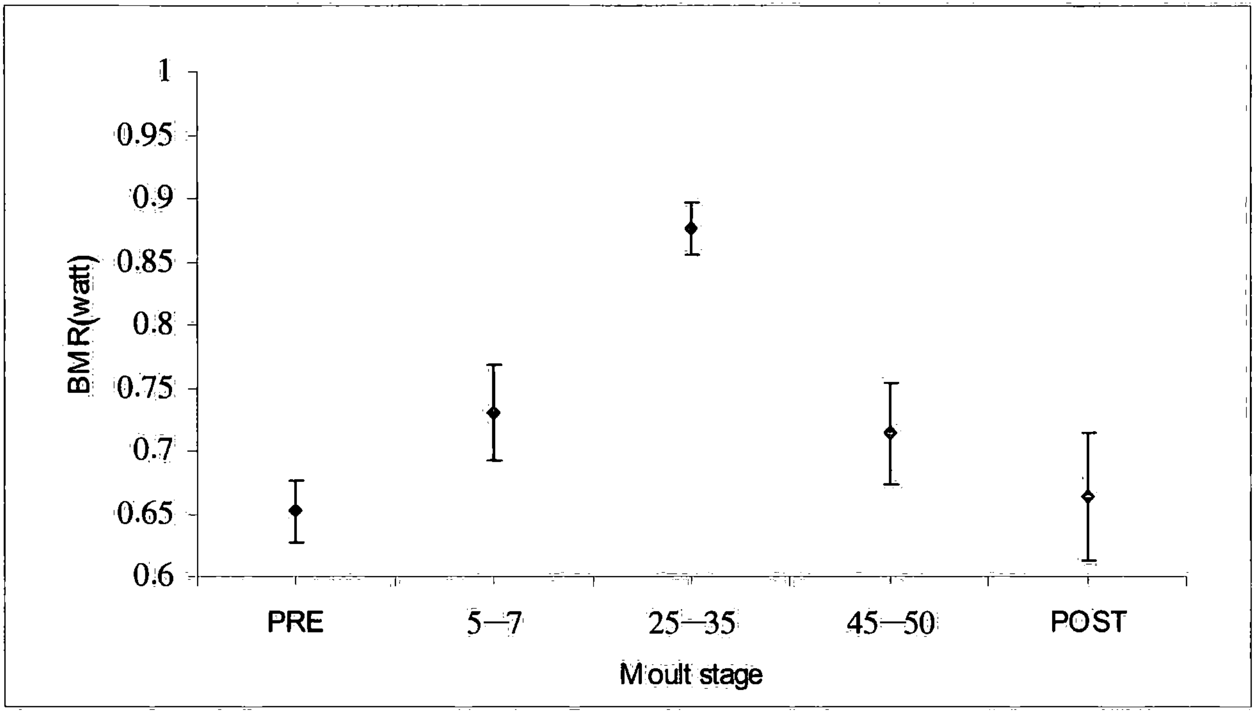
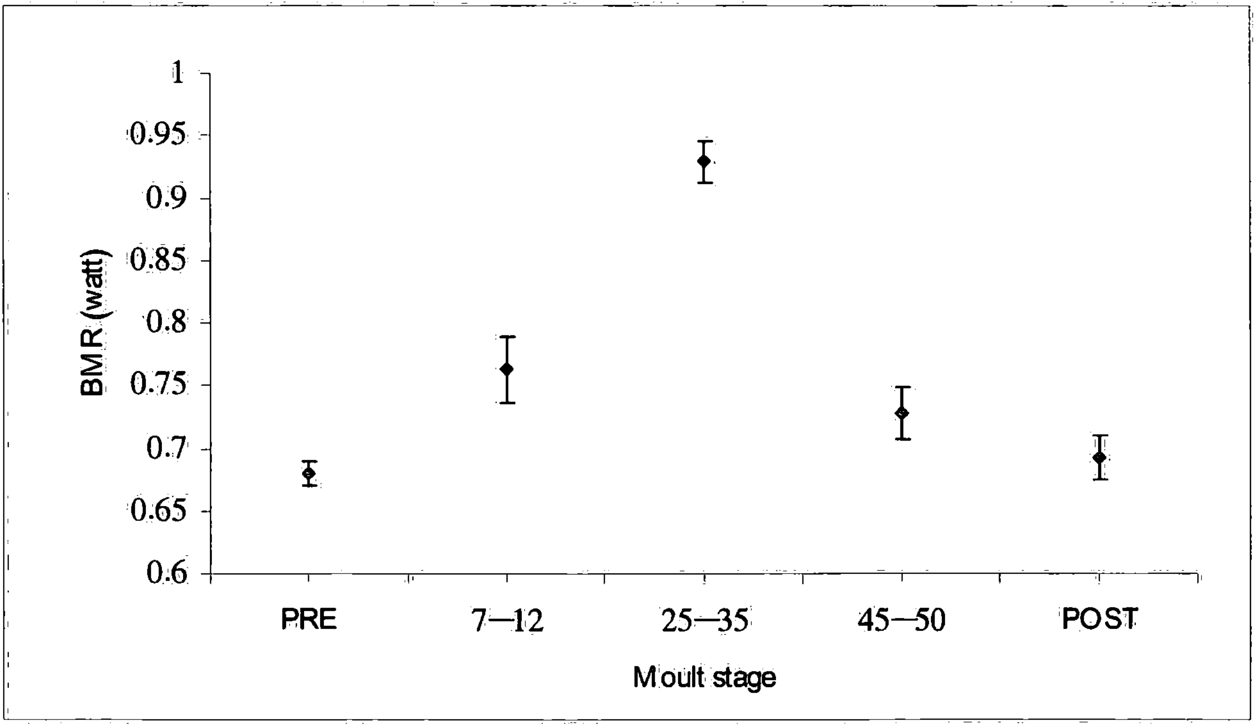


Figure 1.5: Average BMR, before, during and after moult for five *C.a.schinzii*. Bars indicate 2x SE



4.7 Final conclusion

Energy costs of moult, above the daily costs of living, were calculated from Figures 1.4 and 1.5 as follow:

If daily energy costs during moult increased *steadily* over a period of x days to a maximum near the middle of the period of wing moult, then total increase in energy required to maintain constant body temperature between start and the time of most intense moult = ½ X days * change in MR (KJ/day) ....**(1)**

And the total increase in energy required between the time of most intense moult and end of moult (a period of y days):

= ½ y days * change in MR (KJ/day) .... **(2)**

∴ Total 'cost' of moult (additional to normal living costs):

= Equation **(1)** + Equation **(2)**

For *C.a.alpina*:

Total increase in energy required between start and middle of moult:

= ½ 41.8 * 21.6 = 451.4 KJ (see Table 1.3).

Total increase in energy required between middle and end of moult:

= ½ 49 * 20.56 = 503.7 KJ (see Table 1.3).

∴ Total 'cost' of moult = 451.4 + 503.7 = 955 KJ

This means that the total energy costs of moult (late summer moult), which include body and flight feathers is 955 KJ. Since body temperature and the insulation of moulting bird in the spring moult (body feathers) in late summer moult is nearly the same, since the energy costs of producing 3.16g (body and flight feathers) = 955 KJ (in late summer moult).

The energy costs of producing body feathers of 2.44 g:

= 955 * 0.772

= 737 KJ

∴ The total energy costs of moult = 955 + 737

= 1692 KJ

This estimation of energy costs of moult (1692 KJ) is very close to the calculation made in section 4.6.1 (1657 KJ) using the formula made by Lindstrom *et al* 1993.

For *C.a.schinzii*:

The same approach was made for this subspecies:

Total increase in energy required between start and the time of most intense moult is

= ½ 31.2 * 19.44 = 303.3 KJ (see Table 1.4).

Total increase in energy required between middle and end of moult:

= ½ 30.2* 18.4= 277.8 KJ (see Table 1.4).

∴ Total 'cost' of moult = 303.3 + 277.8 = 581 KJ

This means that the total energy costs of moult (late summer moult), which include body and flight feathers is 581 KJ. Since body temperature and the insulation of moulting bird in the spring moult (body feathers) and in late summer moult is nearly the same, since the energy costs of producing 2.70g (body and flight feathers) = 581 KJ (in late summer moult).

∴ The energy costs of producing body feathers of 2.02 g:

= 581 * 0.748 = 435 KJ

The total energy costs of moult = 581 + 435 = 1016 KJ

This estimation of energy costs of moult (1016 KJ) is about two third of the calculation made in section 4.6.2 to estimate the energy costs of moult (1454 KJ) using the formula made by Lindstrom *et al*, 1993.

Table 1.3

Individual	**Days between start and middle of moult**	**Days between middle and end of moult**
DG	33	54
LG	55	35
OR	39	55
YEL	39	59
RE	55	29
BLU	30	62
Average duration	**41.8**	**49**

Table 1.4

Individual	**Days between start and middle of moult**	**Days between middle and end of moult**
LLG	22	34
WOR	39	26
WDG	28	33
LYEL	28	32
WBLU	39	26
Average duration	**31.2**	**30.2**

Chapter, 5

Energy costs of migration

5.1 General Introduction

Many birds perform migrations twice each year between their breeding and non-breeding areas, thereby optimizing the use of seasonal environments (Alerstam & Hogstedt, 1982). Discoveries during recent decades, using ringing, systematic field observations and radar, have created more opportunities to appreciate the magnitude and complexity of bird migration. Bird species vary in the extent of their migrations, some moving only short distances but others many thousands of kilometers. Several species e.g. Ringed plover *Charadrius hiaticula*, Redshank *Tringa totanus* (Salomonson 1955a,b) and Dunlin *Calidris alpina* (Alerstam & Hogstedt 1980, 1985; Pienkowski *et al*,1985), perform what has been termed as leap-frog migration where the more northerly breeding populations migrate over the other populations to winter beyond even the most southerly breeding races. The reasons for this leapfrog pattern remain a subject of speculation (see Chapter 1). Long distance flights over inhospitable environments require the storage of sufficient nutrient reserves to supply the birds with energy throughout their travel periods without the need to refuel. Energy reserves for these movements (if performed by flapping flight) are stored mainly as lipid in the form of triglycerides (Blem, 1976). Flapping flight, the predominant mode of avian locomotion in smaller birds, is thought to be the most expensive mode of locomotion per unit time in animals using this sort of flight (Saunders & Klemm, 1994).

Because of the high energy-costs of flight, birds choose light and high-energy content materials for energy storage, namely fat. The energetic yield by oxidation of one gram of fat is up to 40KJ, which is about eight times higher than the yield from wet protein (5 kJ) (Piersma, 1990). For long-distance migrants, energy reserves (mainly fat but to a much lesser extent protein) are stored prior to migration and also at intermediate staging sites along the migration route. These reserves are stored primarily in discrete depots subcutaneously and associated with the mesenteries, and also intercellularly in skeletal muscle and the liver (for more immediate use). The deposition of fat is achieved by an increase in adipocyte volume without an increase in adipocyte cell number (Odum, 1960; Blem, 1976). Several strategies may be adopted by migrant birds to aid fat deposition which is achieved mainly by hyperphagia (increased food intake) (e.g. Odum, 1960; Blem, 1976, 1980). On the Banc d'Arguin in West Africa, waders (e.g. Dunlin *Calidris alpina*) increase total feeding time in each 24 hours by continuing to feed at night and during neap tides, to achieve extra daily food intake during the spring fattening period (Ens *et al*, 1990). Some birds such as Turnstone *Arenaria interpres*, however, prepare for migration by increasing feeding rates, by reducing time spent on vigilance (Metcalfe & Furness, 1984). Other strategies include a reduction in locomotor activity with a concomitant reduction in daily energy expenditure (Stokkan *et al*, 1986; Cherel *et al*, 1987; Lindgard *et al*, 1992).

The amount of fat that birds store before and during migration depends upon the species, migratory distance and the general circumstances of the migratory path (Biebach, 1996). Birds have to decide their optimal fuel load prior to migration taking into account the advantages and disadvantages of carrying extra fuel (see later in this section). Long-distance migrants consume their fat reserves during flight throughout the night as well as by day and then stop for several days on the refueling sites. Rates of fat deposition during these stopovers can be relatively high. The median rate can reach 1.3% of lean body mass per day in waders (n = 27 species) and 2.4% in passerines (n = 31) the range for both groups lying between 1% and 7% (Alerstam & Lindstrom, 1990). Data on maximal deposition rates indicate that shorebirds with a body mass of 20-100 g deposit fat equivalent to 2.6-4.3% of lean body mass per day and passerines with a body mass of 10-20 g deposit 4.3-5.4% (Lindstrom, 1991). Waders and passerines accumulate fat before migration to between 50% and 90% (n= 17 species) and 40% to 70% (n=17) of total lean body mass, respectively (Alerstam & Lindstrom, 1990). Autumn pre-migratory fat reserves can be larger than spring pre-migratory fattening in some waders but not in all. McNeil (1969) suggests that this may be due to the greater non-stop flight distances of the autumn migration. A similar pattern is seen in some European passerines (e.g. Merkel, 1966). However, pre-migratory fattening can be larger and more rapid in spring than in autumn as in the North American passerine, *Zonotrichia leucophrys gambelli*. This was suggested to be related to the slower pace of the autumn migration rather than to distance differences (King & Farner, 1965). And finally, pre-migratory fattening rate is about the same in spring and autumn in *Fringilla montifringilla* (Dolnik & Blymental, 1964), and in *Locustella fasciolata* (Nakamura, 1969).

Historically it was assumed that only fat was stored prior to migration in passerines (Odum *et al*, 1964), but it is now known that protein (lean mass) also increases during periods of fat deposition in some passerines (Evans, 1969; Fry *et al*, 1970; March, 1984), geese (Newton, 1977; McLandress & Ravelling, 1981, Dubowy, 1985) and shorebirds (Davidson *et al*, 1986; Klassen *et al*, 1997; Selman, 1998). At least four possible functions of protein reserves have been reviewed by Evans *et al*. (1992a). The pectoral muscles are known to increase in mass some species of wader before migration (Davidson, 1981a; Davidson & Evans, 1988; Evans, 1992). This hypertrophy of the flight muscles will increase their maximum power output, which will enable a migrating bird to carry additional mass of fat reserves (Evans, 1969; March, 1983, 1984; Davidson & Evans, 1988). However, the increase in protein reserves is not due solely to flight muscle hypertrophy (McLandress & Raveling, 1981; Evans, 1992). Red Knots at a Norwegian stop-over site during spring migration increased in body mass by an average of 64 grams in two weeks, of which 49g was fat and 15g was wet lean tissue. The pectoral muscles contributed only 3g (Evans, 1992; see also Lindstrom & Piersma, 1993). Furthermore, the decrease in pectoral muscle mass with the decrease in fat load during flight in the Knot is far less than expected from theoretical flight mechanics (Pennycuick, 1978; Davidson & Evans, 1988). Other possible reasons for increases in lean mass before migration may be that protein stores are needed for maintaining protein turnover and muscle repair, during flight (Piersma, 1990) or during periods of low protein intake in the wintering area (McLandress & Raveling, 1981), or to provide glucogenic precursors to maintain glucose homoeostasis during flight (Jenni & Jenni-Eiermann, 1991). These last two hypotheses are supported by the finding that during long-distance flight, birds have not only high fat metabolism but also high breakdown of protein (Piersma & Jukema, 1990; Jenni & Jenni-Eiermann, 1992). Protein stores might also aid rapid egg formation at the breeding grounds.

However, Evans *et al*, (1992) found no differences in the mass of the protein stores between sexes of the waders they studied. About 90% of the energy needed for migration comes in the form of fat, even when just 50% of the deposited mass is fat (Piersma, 1990).

Although energetic constraints play a vital part in bird migration, water-balance may be important too, and these two factors could interact with each other to determine several aspects of migration behavior, such as stop-over duration, mode of flight and particularly altitude of flight (Klaassen, 1996). Some dead migrants were found to have reached critical values of dehydration even though they still had large amounts of fat reserves. However, exhausted or dying small passerines collected during migration through the Sahara had consumed all their fat reserves, whereas their water content was still normal (Haas & Beck, 1979 in Klassen, 1996; Biebach, 1991). Eurasian Reed-Warblers accumulated fat to migrate across the Sahara, whereas their water content before departure was at a level usually interpreted as dehydrated (Fogden, 1972). Time constraints can be an important factor as favorable seasons are of limited duration (Klaassen, 1996) and early arrivals might be rewarded with a higher competitiveness for limiting resources (von Haartman, 1968).

The benefits of fat storage in birds have been widely studied, in relation to quantity, morphological distribution, composition etc. (see e.g. Blem, 1976, 1990). However, the costs of depositing the fat reserves have received far less attention. Increases in fuel stores will lead, for instance, to a rapid increase in energy costs of flight per unit distance (Pennycuick, 1975, 1989). Witter and Cuthill (1993) reviewed the costs of carrying fat, such as:

(1) Increases in the risks of predation due to reduced take-off ability and decreases in manoeuvrability.

(2) Injury, due to collision during flight and landing as the accuracy of pre-landing manoeuvres will be more difficult.

(3) Pathological costs, as increases in body mass may place extra stress on the muscular and skeletal system especially during flight, which may lead to failure of the flight skeleton or damage to the flight musculature, (but this risk can be minimised by adaptation such as remodelling the bone during periods of enhanced loading (see Lanyon *et al.* 1982)).

(4) A decrease in foraging efficiency, especially arboreal foraging and feeding on the wing.

Therefore, the total amount of fuel stores is probably a trade-off between the effects of fuel stores on the energetics, duration and risk of migration.

Many authors (e.g. Gwinner 1981, 1986) suggest that migratory fattening in certain passerines is controlled by an endogenous, circannual clock. The annual photocycle is the most significant external (environmental) variable for synchronising these clocks to the environment and for temporal control of migratory fattening (Gwinner 1977, 1986). Among waders, Redshank have the ability to regulate their total body mass, independently of food supply. Scott *et al* (1994) found that Redshank in captivity maintained body masses comparable to those of the same species in the wild throughout winter and spring.

Although for a given body mass flying is a far less expensive way to move than is running, it is more expensive than swimming (Schmidt-Nielsen, 1984) and requires a high rate of energy expenditure per unit time. The energy costs of flight in birds have been estimated by different techniques. Norberg (1996) listed three. First, the doubly labelled water technique (DLW), which depends on oxygen in respired carbon dioxide being in isotopic equilibrium with the oxygen in body water via the action of carbonic anhydrase in the blood (Lifson *et al*, 1949). The carbon dioxide produced during activity is proportional to the difference between the oxygen turnover in body water and the hydrogen turnover, and provides an estimate of metabolic rate. The CO_2 production is obtained from the equation $CO_2 = (N/2.08)(K_O-K_D)-0.015K_DN$ Where K_O and K_D are the fractional turnover rates of ^{18}O and D, respectively, and N is the mean body water content. For more details see Lifson and McClintock (1966) and Nagy (1980, 1989). The second technique is wind tunnel respirometry (WTR), which is based on direct measurements of O_2 consumption and CO_2 production (see Norberg (1996) for more details). The third method is measurements of mass loss (ML) over a long flight, which can be calculated from the equation;

$$\text{Mass loss} = m_{co2} - m_{o2} + m_f + m_d + m_{wl}$$

where

m_{co2} = mass loss by CO_2 produced
m_{o2} = mass gain by O_2 consumption
m_f = mass loss by fuel consumption
m_d = mass loss due to defecation
m_{wl} = mass loss of water

Norberg (1996) produced a list of metabolic costs of flight in birds from different studies based on the doubly labeled water technique (DLW), wind tunnel respirometry (WTR), and mass loss over long flights (ML). When the metabolic costs (watt) of flight for 12 bird species based on **WTR** are plotted against body mass, the least squares regression for is

$$P = 60.5M^{0.735}, r^2=0.93 \ ....(1)$$

Using the **DLW** technique on 8 species, the regression of power required against body mass based on time- energy budget data is

$$P= 49.4M^{0.851}, r^2= 0.84 \ ....(2)$$

and using mass loss **(ML)** technique on 17 species, the regression is

$$P= 55.9M^{0.819}, r^2=0.83 \ ....(3)$$

Overall, the metabolic power required for flight derived from the combination of the three data sets of 33 species becomes

$$P= 57.3M^{0.813}, r^2= 0.86 \ ....(4)$$

5.1.1 Migration route of the two subspecies of Dunlin *C.a.alpina* and *C.a.schinzii*

The nominate subspecies of Dunlin *C.a.alpina*, is a common migrant wader in Europe (e.g. Cramp & Simmons, 1983). This subspecies breeds in north Scandinavia and Russia east to the Taimyr Peninsula (Hale, 1980; Gromadzka, 1989; also see Wennerberg *et al*, 1999), and winters in western Europe, mainly in Britain, Ireland and France (Pienkowski & Pienkowski, 1983; Gromadzka, 1989). Ringing and recoveries suggest that some juveniles pass through Varangerfjord, NE Norway, during August and then migrate south-westerly along the west coast of Norway, whilst adults migrate during July, taking a more southerly route using the Gulf of Bothnia and the Baltic coast (Leslie & Lessells, 1978). This subspecies moults mainly on the Wadden Sea (Denmark, Germany, Netherlands) and the Wash in England (Holmgren *et al*, 1993). The subspecies *C.a.schinzii* breeds chiefly in Iceland and moults and winters further south, in southern Europe and N.W Africa, especially in Morocco and Mauritania (Pienkowski & Dick, 1975).

5.2 Estimation of costs of migration for the two populations of Dunlin

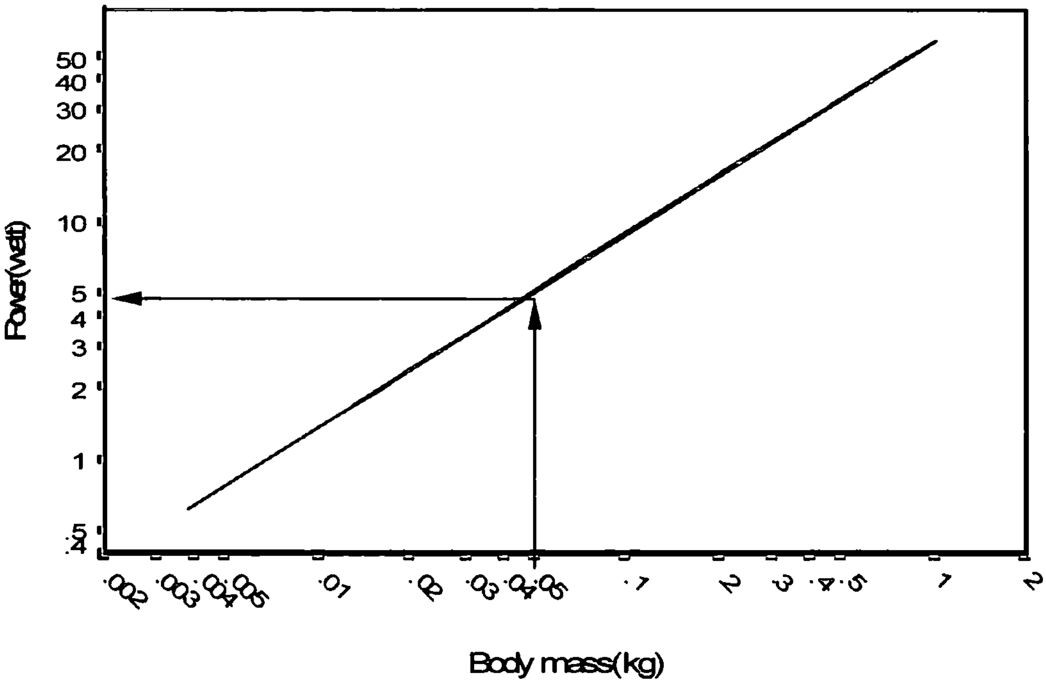
Energy costs of migration have been estimated in two ways: by estimating the energy stored as fat for the flights (see sections 5.3) and by calculation (see below).

Flight energy costs have been calculated for *C.a.alpina* and *C.a.schinzii* by multiplying the estimated power requirements for flight obtained from equation 4 (Figure 1) by the relevant times needed to complete the migration. These times were calculated by dividing the total migration distances by Dunlin flight speed, an average of about 47 km/h, obtained from radar measurements in light winds or still air (Rayner, in Brooke & Birkhead, 1991). Table 1 shows these calculation which have been made for the two subspecies of Dunlin and for the two sexes because these differ in body mass.

Table1: Total energy costs of the migratory flights for the two sexes of the two subspecies of Dunlin derived from the equation P = 57.3 * $M^{0.813}$

	Body mass (kg)	**Energy cost of flight KJ/h**	**Flight distance (km)**	**Flight time (h)**	**Total energy costs of flight (KJ)**	**Total energy costs of return flight (KJ)**
Male *C.a.alpina*	0.0506	18.2	4000	85	1547	3094
Female *C.a.alpina*	0.055	19.5			1658	3316
Male *C.a.schinzii*	0.0442	16.3	6000	127.6	2080	4160
Female *C.a.schinzii*	0.0496	17.9			2284	4568

Figure 1: The relationship between energy cost of flight and body mass for Dunlin derived from P = 57.3 * $M^{0.813}$, the best relationship established so far for 33 species of birds by Norberg (1996)



5.3 Methods of estimation of fat stored for migration

A total of 1,119 juveniles and adults Dunlin were caught by cannon-net and mist-net at Teesmouth between autumn 1996 and spring 1999. Measurements of biometrics (bill length and wing length (maximum chord)), body mass and TOBEC of 477 were taken (see chapter 2 section 2.3.2) just before migratory departures and just after arrival in order to estimate the extent of fat deposition and hence the maximum energy costs of the final stage of their migration. Then, by knowing their migratory routes and stop-over sites from ringing recoveries, we can estimate the maximum energy costs of migration by assuming that every gram fat reserves could yield 40 KJ and that all fat is used during each flight stage of the migration. Age was determined from plumage characteristics (Prater *et al*, 1977) with birds being identified as less than 1 year old (i.e. first years, Euring codes 3 and 5) and greater than 1 year old (i.e. adults, Euring codes 4 and 6). In spring, birds were assigned to race from their plumage (Prater *et al*, 1977): yellowish-red mantle fringes as *schinzii*, and rich chestnut mantle fringes as *alpina*.

5.4 Results and discussion

5.4.1 Fat stores during spring migration in adult and juveniles *C.a. schinzii* at Teesmouth

A total of 135 adult *schinzii* were caught during spring migration at Teesmouth in order to measure TOBEC and hence estimate fat reserves. These birds leave NW Africa and pass through southern Europe, using Teesmouth as a refuelling site on their route to breed in Iceland. Figure 2 summarises lipid indexes ((fat mass/total body mass)*100) of adult *schinzii* caught in May, some just after arrival and some just before migratory departure. The average departure LI is taken as 25% (Figure 2).

$\because$ Fat mass / (predicted lean mass + fat mass) = 0.25

$\therefore$ Absolute fat mass = 0.33 predicted absolute lean mass

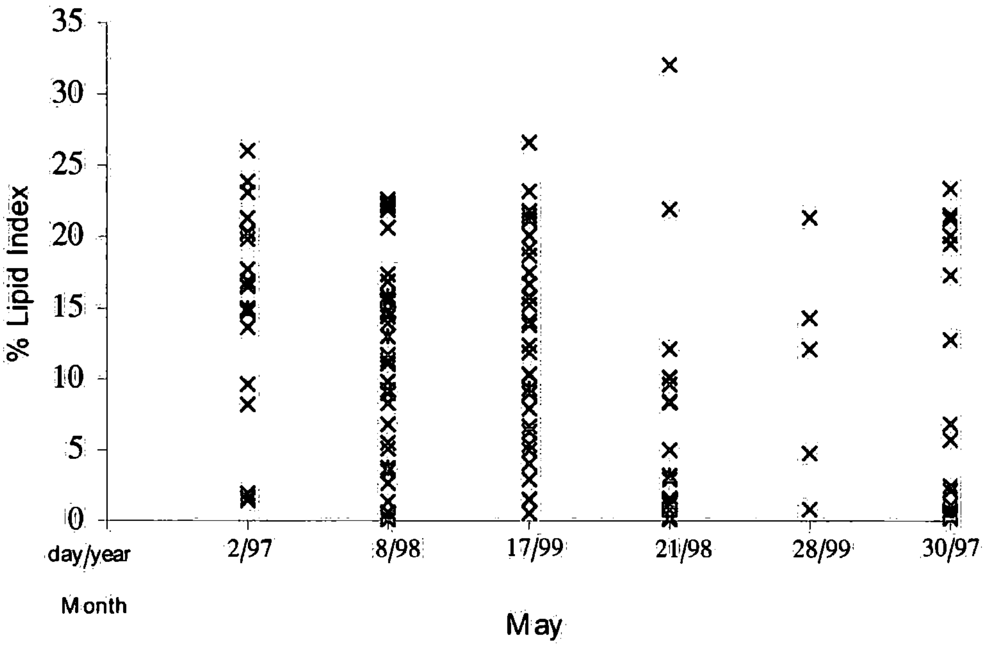
Table 1 shows the average estimated energy store at departure for Iceland adult male and female *schinzii* at Teesmouth during spring migration.

I assumed that birds with very little fat reserved, that they had just arrived. Those with large fat reserves suggested that they were more or less ready to resume their migration.

Table1: Average PTLM, hence energy stores of adult *schinzii* at Teesmouth before migrating to Iceland in spring, assuming 1 gram fat yields 40 KJ, and maximum fat mass = 0.33 predicted lean mass

Average PTLM Male (g)	Average maximum fat load Male	Average energy store Male (KJ)	Average PTLM Female (g)	Average maximum fat load Female (g)	Average energy store Female (KJ)
42.4 (n=29)	14	560	45.6 (n=43)	15	600

Figure 2: Lipid indexes ((fat mass/total body mass)*100) for 135 adult *schinzii* caught in spring at Teesmouth



Only 5 one-year old *schinzii* were caught, with LI: between 1-15%, but these are insufficient for reliable calculations.

5.4.2 Fat stores during spring migration in adult and juveniles *C.a. alpina* at Teesmouth

A total of 14 adult and 6 juvenile *alpina* were caught in order to take TOBEC measurements and hence estimate fat stores of birds before leaving their wintering grounds at Teesmouth to breed in northern Scandinavia and Russia east to the Taimyr Peninsula (Hale, 1980; Gromadzka, 1989). The average maximum LI is taken as 27% and 25% for adult and juveniles respectively (Figure 3).

For adults;

$\because$ Fat mass / (predicted lean mass + fat mass) = 0.27

$\therefore$ Absolute fat mass = 0.37 predicted absolute lean mass

For juveniles:

$\because$ Fat mass / (predicted lean mass + fat mass) = 0.25

$\therefore$ Fat mass = 0.33 predicted lean mass

The average estimated energy stores at Teesmouth for adult and juveniles of this subspecies of Dunlin are shown in Tables 2 and 3.

Table 2: Average PTLM, hence energy stores of adult *alpina* at Teesmouth before migrating to northern Scandinavia and Russia in spring, assuming 1gram fat yields 40 KJ, and maximum fat mass = 0.37 predicted lean mass

Average PTLM Male(g)	Average fat load Male(g)	Average energy store Male (KJ)	Average PTLM Female (g)	Average fat load Female (g)	Average energy store Female (KJ)
42.9 (n=6)	15.9	635	48.3 (n=5)	17.9	716

Figure 3: Lipid indexes ((fat mass/total body mass)*100) for 14 adult and 6 juveniles (circles) *alpina* caught in spring at Teesmouth

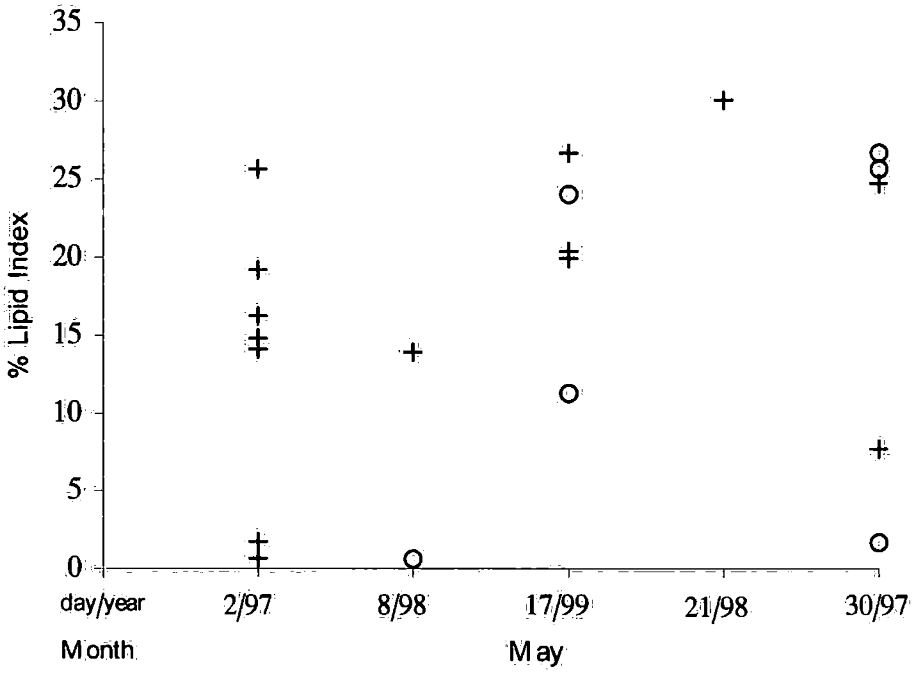


Table3: Average PTLM, hence energy stores of juveniles *alpina* at Teesmouth before migrating to northern Scandinavia and Russia in spring, assuming 1gram fat yields 40 KJ, and maximum fat mass = 0.33 predicted lean mass

Average PTLM (g)	Average fat load (g)	Average energy store (KJ)
46.7 (n=6)	15.4	616

From Tables 2 and 3 it can be seen that the average energy store for the two sexes of *alpina* was 635KJ (males), 716 KJ (females) and 616 KJ (juveniles). This amount of energy is presumably sufficient to enable them to reach northern Scandinavia or a refuelling site in southern Finland, suggested by ringing recoveries (Appendix VIII), on the way to their breeding ground in northern Russia.

5.4.3 Fat stores during autumn migration in adult and juvenile *C.a. schinzii* at Teesmouth

In order to estimate energy stores during autumn migration, a total of 109 adult *schinzii* were caught at Teesmouth in July and August and TOBEC measurements taken. The average maximum LI for adult *schinzii* in autumn was taken to be 24% (Figure 4).

$\because$ Fat mass / (predicted lean mass + fat mass) = 0.24

$\therefore$ Absolute fat mass = 0.32 predicted absolute lean mass

For juveniles the average maximum LI was taken as 20% (Figure 5).

$\because$ Fat mass / (predicted lean mass + fat mass) = 0.20

$\therefore$ Absolute fat mass = 0.25 predicted absolute lean mass

It can be seen from Figure 4 that the majority of adult *schinzii* leave the Tees during the middle of August on their way to winter in NW Africa. This subspecies of Dunlin uses southwestern of France as the next refuelling site (ringing recoveries in appendix VIII). Therefore the amount of energy stored (see Table 4) is presumably the maximum needed to reach southwestern France to refuel again before migrating to their final destination in NW Africa to winter there.

Table4: Average PTLM, hence energy stores of adult and juvenile *schinzii* at Teesmouth before migrating to western Europe and NW Africa in autumn assuming 1 gram fat yields 40 KJ. Plumage usually abrade in autumn which make it difficult to sex the birds

Average PTLM adult (g)	Average fat load adult (g)	Average energy store adult (KJ)	Average PTLM juvenile (g)	Average fat load juvenile (g)	Average energy store juvenile (KJ)
42.2 (n=109)	13.5	540	40.7 (n=84)	10.2	408

Figure 4: Lipid indexes ((fat mass/total body mass)*100) for 109 adult *schinzii* caught in autumn at Teesmouth

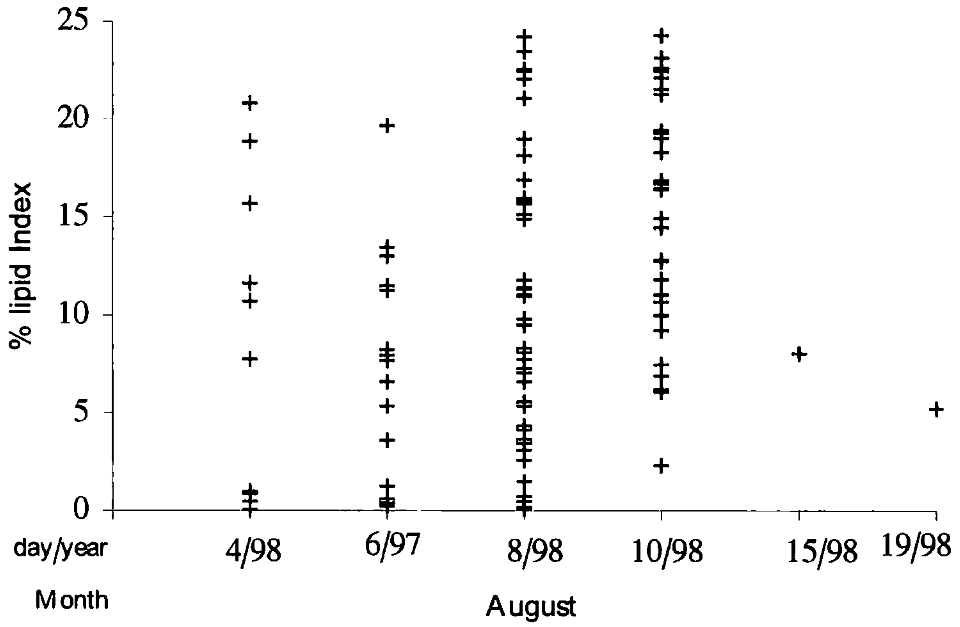
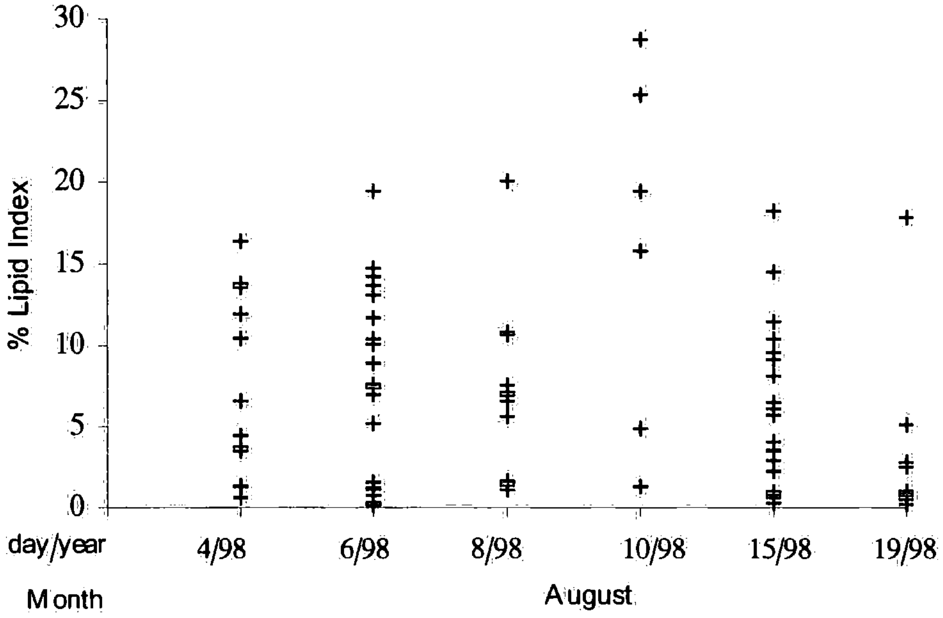


Figure 5: Lipid indexes ((fat mass/total body mass)*100) for 84 juvenile *schinzii* caught in autumn at Teesmouth



5.4.4 Total energy costs of migration in *C.a.schinzii*

To estimate the total energy costs of migration for *C.a.schinzii* I have used the estimated mean fat load in spring at departure from Teesmouth (14g for males and 15g for females) to estimate the total energy costs of migration in still air for this subspecies in the following way:

Distance between Teesmouth and Iceland = 1350 km

Fat loads carried by males before departure in spring from Teesmouth to Iceland = 14g which would yield 560KJ at maximum. This amount of fat must be enough to reach Iceland since no refuelling site is known in the north-west Scotland (see also flight ranges formula by Summers & Waltner 1979; Greenewalt 1975; Pennycuick, 1975).

Mean fat loads before departure in autumn from Teesmouth are close to those in spring (13.5g for birds of unknown sex because breeding plumage is abraded by this time).

This suggests a flight of similar distance to the Teesmouth / Iceland journey and points to a staging post in south-west France (also used in spring). The final destination is the Banc d'Arguin in Mauritania, about 5800 km from Iceland. It is likely that a further staging post is located in Morocco, about 1500 km from Southwest France.

If a flight of about 1350 km requires 560 KJ and the whole migration is covered in four almost equal steps, the total energy costs of migration for male (one way) = 6000 / 1350 x 560 = 2489 KJ at maximum.

The same calculation was made for female *schinzii* (see table 5)

Table 5: Total energy costs of migration for male and female *C.a.schinzii*

	Distance from Teesmouth to Iceland (km)	Costs of migration from Teesmouth to Iceland (KJ)	Total distance migration (km)	Total costs of migration (KJ)	Total costs of both return migrations KJ
Female	1350	600	6000	2667	5334
Male		560		2489	4978

These estimations of energy costs of migration (on average 5156 KJ) are a little higher than the estimates of the energy costs of flight (on average 4364KJ) which were derived from $P = 57.3 * M^{0.813}$ (see Table 1). The figures in Table 5 are based on the assumption that birds arriving in Iceland have used all the fat carried at departure from Teesmouth. This is unlikely to be true, but no figures are available for fat loads of incoming migrants in Iceland.

5.4.5 Total energy costs of migration in *C.a.alpina*

To estimate the total energy costs of migration for *C.a.alpina* I have also used their mean fat loads in spring at departure from Teesmouth (15.9g for male and 17.9g for female) to estimate the total energy costs of migration in still air for this subspecies.

The distance between Teesmouth and south-west Finland (the nearest staging site shown from ringing and recoveries) = 1550 km

Fat loads carried by males before departure in spring from Teesmouth to SW Finland = 15.9g which would yield 636 KJ at maximum. This amount of fat must be enough to reach SW Finland (see also flight ranges formula by Summers and Waltner 1979; Greenewalt 1975; Pennycuick 1975). The total migration distance to Russia breeding areas is probably a maximum of 4000 km (to Vaigach Island).

The total energy costs of migration for males = 4000 / 1550 x 636 = 1641 KJ

It is not known whether this subspecies uses another stopover site between SW Finland and the breeding areas. These calculations have been made to estimate the energy costs of migration in still-air. Again it should be borne in mind that it is not necessary for the bird to use all the fat it stores, as most waders arrive after migratory flights with some fat reserves remaining. However, the two subspecies of Dunlin arrived at Teesmouth with less than one gram of fat reserve as has been shown earlier.

The same calculation was made for female *alpina* (see table 6)

Table 6: Total energy costs of migration for male and female *C.a.alpina*

	Distance from Teesmouth to southern Finland (km)	Costs of migration from Teesmouth to southern Finland (KJ)	Total distance migration (km)	Total costs of migration (KJ)	Total costs of return migration (KJ)
Female	1550	716	4000	1848	3696
Male		636		1641	3282

These estimated energy costs of migration (on average 3489 KJ) are quite close to the estimates of the energy costs of flight (on average 3205KJ) which have been derived from $P = 57.3 * M^{0.813}$ (see Table 1).

Chapter, 6

Energy costs of egg production and incubation

6.1 General introduction

Just as body size varies widely between bird species, from a few grams to more than 100 kg, so also there is interspecific variation in egg size in birds. Rahn *et al*, (1975) produced a relationship between egg mass and female body mass derived from data for 809 species in 17 orders of birds;

$W=0.277B^{0.77}$ ....(1)

Where W= egg mass (g) and B = female body mass (g)

Egg size can also vary within a species in relation to factors such as geographical location, laying time within a season, clutch size and individual female (see Carey, 1996 for more details).

The egg of a bird contains a rich supply of food for the developing embryo. Birds assist their developing eggs by process by which they apply/dissipate heat to/from their eggs. This process is called incubation. Birds use various incubation strategies. In about 50 % of the species within birds families, both sexes incubate (Van Tyne & Berger, 1976) by alternating incubation duties, and sharing any energetic demands associated with keeping eggs warm (Drent *et al*, 1985). This pattern is found in all families of seabirds and in some passeriformes (Carey, 1996). In some birds, however, only one parent incubates.

The core body temperature of birds is relatively high, typically 39-42 °C. Heat production by the incubator increases proportionately with reduction in egg temperature during the absence of the parent from the nest. Most species incubate their eggs at average temperatures between 32 and 35 °C, irrespective of environment, incubation strategy or body size (Drent, 1975: Burger & Williams

1979; Haftorn, 1988). However, egg temperature averages between 33.7 and 39.5 °C for species nesting in hot environments. In such environments, however, birds protect their eggs from overheating by covering eggs continuously during the hottest time of the day. Some species of Charadriiformes soak their ventral feathers in water to keep eggs cool while incubating (Grant, 1979 in Williams 1996). Eggs that are exposed to relatively high or low temperatures may require longer incubation periods or even to fail to hatch. When ambient temperatures are low, birds protect their eggs by modulation of their metabolic rate while covering the eggs and by variation in the amount of time that body heat is applied to eggs. Birds have less time for foraging when incubating (Walsberg, 1983) and most incubate in spring when both ambient temperature and food resources are relatively low (Drent *et al*, 1985; Williams, 1987). Incubating birds increase their daily energy expenditure, which can cause an elevation in the lower critical temperatures (Weathers, 1985).

6.1.1 Energy costs of egg production in birds

Walsberg (1983) produced an equation to show the direct relationship between the energy content of the fully-grown ovary plus oviduct and the body mass of the female:

$\text{In} E_O = \text{In}\ 0.6555 + 0.938\ M_B$ ....(2)

Where E_O is energy content of the ovary and oviduct (KJ) and M_B is body mass (g). Costs of the growth of ovary and oviduct may increase to no more than 2-9% of the daily basal metabolic rate of the female if costs of growth are spread equally over the period of growth (Walsberg, 1983). Many methods have been used to estimate the energy cost of egg production. Measuring the caloric content of the egg (King, 1973) is the simplest method but it does not quantify many factors such as maintenance of the ovary during clutch formation, cost of transport of egg contents into the egg and cost of shell synthesis. The cost of egg production can be estimated fairly well if the average caloric content and egg mass of a certain bird family or genus are known. Rahn *et al* (1985) formulated an equation for calculation of the energy cost of egg production in passerines:

$E = 1.3 \times 4.23 \times W$ ....(3)

Where E is the energy cost of egg production (kJ), 1.3 is the inverse of 0.77, the net efficiency of egg production ($kJ \cdot kJ^{-1}$), 4.23 is the average energy content of passerine eggs ($kJ \cdot g^{-1}$ egg) and W is egg mass (g). If the theoretical cost of egg production is spread over the days needed to make the egg, daily costs will vary from 82-128% of the BMR in shorebirds, 13-41% in passerines and even to over 200% in waterfowl (see Robbins, 1993).

6.1.2 Energy costs of incubation in seabirds

Metabolic rate has been estimated during incubation for 32 species of seabirds in relation to body mass (ranging from 37g to 13.4 kg). Williams (1996) has produced an equation for the relationship between body mass and incubation metabolic rate (IMR) using data from 30 various studies:

Log IMR (KJ/d) = 0.521 + 0.712 log body mass (g) $r^2 = 0.95$........ (4)

Three methods were used to determined this relationship; (i) measurement of body mass loss to estimate IMR, (ii) respiratory gas analysis, where metabolic rate is measured while seabirds are incubating within a metabolic chamber or with a mask placed over their face, (iii) doubly labelled water (DLW) method to estimate CO_2 production from the decline of isotopes of hydrogen and oxygen in the body water pool (Nagy, 1980). Validation studies on a variety of species indicate that metabolic rates measured by DLW method are within ±8% of direct measures of energy expenditure (Williams & Nagy 1984). The amount of energy required from birds to maintain their eggs at appropriate temperatures for embryological development is significantly influenced by ambient temperature, body size of the incubator, clutch size and type of incubation pattern (Williams, 1996). Incubating passerines with a clutch size of four or more eggs have higher incubation metabolic rates than non-incubating individuals by 19-50% when temperatures are below their lower critical temperature (Weathers, 1985; Haftorn and Reinertsen, 1985).

6.1.3 Breeding and incubation in the two subspecies of Dunlin *C.alpina*

Incubation in the two subspecies of dunlin is shared by both sexes. Females tend to incubate the eggs during night and males during day. Incubation lasts about 22 days (n=23) (Soikkeli, 1967 in Cramp & Simmons, 1983). After hatching, chicks become independent at or just before fledging, after a period of 19-21 days (Heldt 1966 in Cramp & Simmons, 1983).

Most eggs of the two subspecies of Dunlin *C.a.alpina* and *C.a.schinzii* are laid in May. The clutch size of this bird on average is four eggs, as in most waders. There is no significant geographical or racial variation in the clutch size. Four eggs were found in 83% of 295 clutches in Germany (Heldt, 1966) and 88% of 203 clutches in southern Finland (Soikkeli 1970b in Cramp & Simmons, 1983). Replacements may be laid after egg loss but rarely after early loss of young. Replacement and late clutches tend to contain fewer eggs.

6.2 Energy costs of egg production and incubation for *C.a.alpina* and *C.a.schinzii*

I have estimated the energy cost of egg production for the two subspecies of Dunlin using equation (3), although this equation (i) was developed for passerines (ii) may underestimate the real cost of egg production as this equation ignores the costs associated previously listed (section 6.1.2). However, the energy cost of producing eggs is relatively small, and should not affect the annual energy costs of the two subspecies. Since the clutch size is four eggs on average and since there is no significant geographical or racial variation in the clutch size of the two subspecies, the energy costs of producing eggs for the two subspecies should be the same from equation (3):

Energy cost of producing eggs = 1.3 x 4.23 x 40 = 220 KJ

I have calculated the energy costs of incubation using equation (4) to produce results shown in Table 1.1. Since the average daily temperatures on the breeding grounds for the two subspecies of dunlin is nearly the same in May (see Tables 1.1 and 2.1 in Chapter 3), since they have the same clutch size and since the equation involves the body mass of the incubator, using equation (4) is more or less reliable for estimating the energy cost of incubation for the two subspecies.

Table1.1 Energy costs of incubation for the two subspecies of Dunlin using the equation: Log IMR (KJ/d) = 0.521 + 0.712 log body mass (g)

	Average body mass for both sexes (g)	Incubation period (days)	Total Incubation Metabolic Rate (KJ)
C.a.alpina	52.9	22	1232
C.a.schinzii	47.6		1143

Chapter 7

General discussion

7.1 Total annual energy costs for the two subspecies of Dunlin *C.a.alpina* and *C.a.schinzii*

It can be seen from Table 1 that the total annual energy costs of *C.a.alpina* are estimated to be about 17% higher than those of *C.a.schinzii*. This is obviously due to the large difference in the energy costs of living between the two subspecies (Table 1). If we look at these in more detail (Table 2) we notice that nearly all of the 21 % higher costs of living in *alpina* are due to the costs on wintering plus moulting grounds. Table 1 also shows that although the costs of migration are much less than the costs of living, they are higher than the sum of the costs of moult, egg production and incubation. As expected, the energy costs of migration in *schinzii* (5156 KJ) are higher than those in *alpina* (3489 KJ) as *schinzii* migrates longer distances; but these extra costs are small by comparison with the differences between the subspecies in the costs of living (energy costs of living in *alpina* are higher than those in *schinzii* by 11625 KJ).

7.2 Can Drent and Piersma's hypothesis explain the two distinct strategies of migration of the two subspecies of Dunlin?

Drent and Piersma (1990) hypothesised that there is a trade-off in energy costs between migration and wintering, with short-distance migrants requiring less energy for migration, but spending more energy in colder winter areas than the long-distance migrants which migrate to more tropical regions in winter. They suggested that, in total, the annual energy expenditure of both populations is the same. However, I have proved that the cost of migration is considerably less than the costs of living. Also I showed that the total annual energy cost for those wintering in colder areas i.e. *C.a.alpina* is much higher than those wintering in tropical regions i.e. *C.a.schinzii*. Since the total annual energy costs of *alpina* are higher than *schinzii*, that could mean that the annual mortality rate of *C.a.alpina* will be higher. If that is the case, why did these two subspecies evolve these two migratory strategies and why are they maintained?

(i) The answer to this question may lie in a comparison of survival rates on wintering plus moulting grounds on the one hand and migration on the other hand. *Alpina* appears to have lower energy costs during migration (costs of migration plus costs of living on fattening grounds) than *schinzii* because they migrate shorter distances, which also involves less time. This may lead to higher survival of *alpina* during migration even though their survival rate in autumn and winter may be lower, because the daily and total energy costs of living on wintering and moulting grounds are higher. Adult Dunlin breeding in western Scotland have higher mortality on their wintering grounds plus migration (13%) than on their breeding grounds (4%) (Jackson 1988 in Evans 1991), even though they winter (alongside *schinzii* Dunlin from Iceland) in north-west Africa.

(ii) The success of any animal's life depends (in evolutionary terms) on success in:

(i) Reproduction (number of young/year which survive to breed)

(ii) Length of reproductive life, related to survival rate

Energy costs, which could affect survival rate, are not the only factors that affect a bird's lifetime output of young. Although *alpina* uses a different migration strategy to *schinzii*, it may use better breeding grounds, and hence achieve more successful reproduction. Moreover, feeding condition in the wintering grounds may determine breeding success (Pienkowski and Evans, 1984). If we look to the condition of the main wintering grounds of *schinzii* in Morocco and Mauritania we will notice that these grounds are unexpectedly poor, as food resources potentially available to waders are very small compared to the resources in more northern temperate areas (Altenburg *et al*, 1982). Also because of the low prey biomass and high wader densities combined with high feeding percentages (e.g. foraging percentages of small waders is more than 95% during low tide), the competition between and within species is thought to be high (Altenburg *et al*, 1982; Moser, 1980). Therefore body condition at start of migration may not be so good and also on arrival in Iceland, so that may affect breeding success of *schinzii*. It is known that it is more favourable for birds to winter as close as possible to their breeding grounds to be in better position to win limited resources and to be able to respond to variations in weather and return to breeding grounds as soon as these become favourable (Alerstam & Hogstedt, 1980), so why *schinzii* do not do so?

The answer may be simply that in winter many invertebrates burrow deeper in the substrate, this changes in prey behaviour in winter lead to increased difficulties for shorebirds feeding upon them (see Evans, 1979a) and because *schinzii* have shorter bill length, that may force them to winter in more tropical regions even if the resources are poor.

To conclude, the two factors that determine life reproductive success in the two subspecies could be the same for the two subspecies, if *C.a.alpina* produces more young per year, even if its mortality is higher than that of *C.a.schinzii*.

Table 1: Annual energy costs for the two subspecies of Dunlin

		Energy costs KJ/Year	**Total annual energy cost (KJ)**
C.a.alpina	Costs of living	65937	**72550**
	Costs of migration	3489	
	Costs of moult	1692	
	Costs of egg production and incubation	1432	
C.a.schinzii	Costs of living	54312	**61827**
	Costs of migration	5156	
	Costs of moult	1016	
	Costs of egg production and incubation	1343	

Table 2: Energy costs of living at different sites for the two subspecies of dunlin

		Total energy costs of living on each site (KJ)	Annual costs of living (KJ)	
C.a.alpina	On breeding grounds	14596		**65937**
	On moulting grounds	13246	42441	
	On wintering grounds	29195		
	On fattening grounds	8900		
C.a.schinzii	On breeding grounds	13155		**54312**
	On moulting grounds	7660	29857	
	On wintering grounds	22197		
	On fattening grounds	11300		

7.3 The accuracy of the estimation

It can be seen from table 1 that energy costs of living consist of more than 87% of the total annual energy costs of the two subspecies. That means that costs of living is the most sensitive factor in estimating the annual energy costs. It can also be seen from table 1 that the energy costs of living of *alpina* is 21% higher than those of *schinzii* assuming that daily energy expenditure (DEE) equal 2RMR. Even when DEE equal 2.5RMR, energy costs of living of *alpina* still 21% higher than those of *schinzii* (Table3). Therefore my estimation will be valid for comparative porpoises which I am looking for rather than absolute estimation. Had time permitted it would have been instructive to calculate confidence intervals at each stage and use this range as input to subsequent stage of the model in addition to regression sensitivity analysis, by changing parameter estimate within reasonable biological limits, may have been instructive.

However, the very large change in DEE modeled here indicates that the main conclusion will remain unchanged.

Table 3: Energy costs of living when DEE = 2.5RMR

		Total energy costs of living on each site (kJ)	Annual costs of living (kJ)
C.a.alpina	On breeding grounds	18235	**82387**
	On moulting grounds	16570	
	On wintering grounds	36442	
	On fattening grounds	11140	
C.a.schinzii	On breeding grounds	16455	**67815**
	On moulting grounds	9552	
	On wintering grounds	27783	
	On fattening grounds	14025	

References

Aidley.D.J. and R.Wilkinson 1987. Moult of some Palaearctic Warblers in northern Nigeria. *Bird study* **34**:219-225.

Alerstam T. and Hogstedt G. 1980. Spring predictability and leapfrog migration. *Ornis Scand.* **11**: 196-200.

Alerstam T. and Hogstedt G. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scand.* **13**: 25-37.

Alerstam T. and Hogstedt G. 1985. Leapfrog arguments: reply to Pienkowski, Evans and Townshend. *Ornis Scand* **16**: 71-74.

Alerstam T. and Lindstrom A. 1990. Optimal bird migration: The relative importance of time, energy and safety. pp 331-351 *in* Bird migration: Physiology and ecophysiology. (E. Gwinner, Ed). Springer-Verlag, Berlin.

Altenburg W., Engelmoer M., Mes R. and Piersma T. 1982. Wintering waders on the Banc d'arguin (Mauritania). Report of the Netherlands ornithological Mauritania expedition 1980.

Amadon D. 1966. Avian plumages and moult. *Condor* **68**: 263-278.

Asch A. and Roby D. D. 1995. Some factors affecting precision of the total body electrical conductivity technique for measuring body composition in live birds. *Wilson Bull.* . **107(2)**: 306-316.

Aschoff J. and Pohl H. 1970. Rhythmic variations in energy metabolism. *Federation Proceedings.* **29**: 1541-1552

Bailey R.O. 1985. Protein reserve dynamics in post-breeding adult male Redheads. *Condor* **87**:23-32.

Barnett L.B. 1970. Seasonal changes in temperature acclimatisation of the Hose Sparrow, *Passer domesticus. Comp. Biochem. Physiol.* **33**: 559-578.

Bell C.P. 1996. Seasonality and time allocation as causes of leap-frog migration in the Yellow Wagtail. *J. Avian Biology.* **27**:334-342.

Bell C.P. 1997. Leap-frog migration in the fox sparrow: minimising the cost of spring migration. *Condor* **99:** 470-477.

Biebach H. 1991. Is water or energy crucial for trans-Sahara migrants? In Acta XX congressus Internationalis Ornithologici, ed.B. Bell et al. pp. 773-779. New Zealand Ornithological Congress Trust Board Wellington, N.Z.

Biebach H. 1996. Energetics of winter and migratory fattening. pp 280-323 *in* Avian energetics and nutritional ecology. Carey C. (Ed). Chapman and Hall, New York.

Blackmore F.H. 1969. The effect of temperature, photoperiod, and moult on the energy requirements of the House Sparrow, *Passer domesticus*. *Comp. Biochem. Physiol.* **30**: 433-444.

Blem C. R. 1976. Patterns of lipid storage and utilisation in birds. *Am. Zool.* **16**:671-684.

Blem C.R. 1980. The energetics of migration *in* Animal migration, orientation, and migration pp 175-224 Gauthreaux Jr. S.A. (Ed). Academic Press, New York.

Blem C.R. and Shelor M.H. 1990. Avian energy storage in Current Ornithology **(7)** pp 59-113 Johnston R.F. (Ed). Plenum Press, New York.

Boddy M.1983. Autumn moults of adult and juvenile Lesser Redpolls in Nottinghamshire, England. *Ornis Scand.***14**: 299-308.

Boere G. C. 1976. The significance of the Dutch Waddenzee in the annual life cycle of the arctic, subarctic and boreal waders. Part I. The function as a moulting area. *Ardea* **64**:210-291.

Brooke M. and Birkhead T. 1991. The Cambridge Encyclopaedia Ornithology. Cambridge University Press.

Burger A. and Williams A. J. 1979. Egg temperatures of the Rockhopper Penguin and some other penguins. *Auk* **96**: 100-105.

Calder W.A. and King J.R. 1974. Thermal and caloric relations of birds. In Franer D.S., King J.R. and Parkes K.C.(Eds.) *Avian Biology,* vol. **IV**: 259-413. Academic Press, New York.

Calder W.A. and Schmidt-Nielsen K. 1967. Temperature regulation and evaporation in the pigeon and the roadrunner. *Am. J. Physiol.* **213**: 883-889

Campbell B. and Lack E. 1985. A dictionary of birds. T. and D. Poyser, Calton.

Carey C. 1996. Female reproductive energetics. pp 324-374 *in* Avian energetics and nutritional ecology. Carey C. (Ed). Chapman and Hall, New York.

Carey C. and W.R. Dawson and L.C. Maxwell and J.A. Faulkner 1978. Seasonal acclimatisation to temperature in cardueline finches. II. Changes in body composition and mass in relation to season and acute cold stress. *J. Comp. Physiolo.* **125**: 101-113.

Castro G. and Myers J. P. 1989. Flight range estimates for shorebirds. *Auk* **106**:474- 476.

Castro G., Wunder B. A. and Knopf F. L. 1990. Total body electrical conductivity (TOBEC) to estimate total body fat of free-living birds. *Condor* **92**:496-499.

Cherel Y., Stahl J. C. and Le Maho Y. 1987. Ecology and physiology of fasting king penguin chicks. *Auk* **104**:254-262.

Chilgren J.D. 1977. Body composition of captive White-crowned Sparrows during postnuptial moult. *Auk* **94**: 677-688.

Conway C. J., Eddleman W. R. and Simpson K. L. 1994. Evaluation of lipid of the Wood Thrush. *Condor* **96**: 783-790.

Coulson J.C. and P. Monaghan and J. Butterfield and N. Duncan and C. Thomas, and C. Shedden 1983. Seasonal changes in the Herring Gull in Britain: Weight, moult and mortality. *Ardea* **71**: 235-244.

Cramp S. and Simmons K.E.L. 1983. The birds of the western Palearctic, Vol. III. Oxford University Press, Oxford.

Cranswick P., Pollitt M., Musgrove A. and Hughes B. 1999. The wetland bird survey 1997-1998. Wildfowl and wader counts. BTO, WWT, RSPB and JNCC.

Daan S., Masman D. and Groenewald A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure. *Amer. J. Physiol.* **259**: R333-340.

Daan S., Masman D., Strijkstra A. and Kenagy G. 1991. Daily energy turnover during reproduction in birds and mammals: its relationship to basal metabolic rate. Acta XX Congressus Internationalis Ornithologici, pp 1976-1988

Davidson N.C. 1981a. Seasonal changes in nutritional condition of shorebirds (*Charadrii*) during the non-breeding seasons. Ph.D. Thesis, University of Durham.

Davidson N.C. 1984a . Changes in the condition of dunlins and knots during short-term captivity. *Canadian Journal of Zoology* **62** **(9)**: 1724-1731.

Davidson N.C. and Evans P.R. 1988. Prebreeding accumulation of fat and muscle protein by arctic-breeding shorebirds.pp 342-352 *in Proc. 19th Int. Ornith. Congr., Ottowa.*

Davidson,N. C., Evans, P. R. and Pienkowski, M. W. 1986. The origins and destinations of waders using the coasts of Suffolk and Essex *.Ring. and Migr.*7: 37-49.

Davidson N.C., Evans P.R. and Uttley J.D. 1986. Geographical variation of protein reserves in birds: the pectoral muscles of Dunlin in winter. *J. Zool. Lond.* (A) **208**: 125-133.

Davidson N.C., d' A Laffoley D., Doody J. P., Way L. S., Gordon J., Key R., Drake C. M., Pienkowski M. W., Mitchell R. and Duff K.L. 1991. Nature conservation and estuaries in Great Britain. Peterborough, Nature Conservancy Council.

Davis E.A. Jr. 1955. Seasonal changes in the energy balance of the English Sparrow. *Auk* 72: 385-411.

Dawson W.R. & Carey C. 1976. Seasonal acclimatization to temperature in Cardueline finches-I. Insulative and metabolic adjustments. *J. Comp. Physiol.* **112:** 317-333.

Dietz M.W.,S. Dann and D. Masman 1992. Energy requirements for moult in the Kestrel, *Falco tinnunculus.Physiol.Zool.***65**: 1217-1235.

Dobush G. R., Ankney C.D. and Krementz D. G. 1985. The effect of apparatus, extraction time, and solvent type on lipid extraction of snow geese. *Can. J. Zool.* **63**:1917-1920.

Dolnik V.R. and Blyumenthal T. I. 1964. The bioenergetics of bird migration. *Succ. Mod. Biol.* **58**: 280-301.

Dolnik V.R. and Gavrilov V.M. 1975 . A comparison of the seasonal and daily variations in bioenergetics,locomotor activities and major body composition in the sedentary House Sparrow (Passer d. domesticus (L.)) and the migratory Hindian Sparrow (Passer d. bactrianus Dar .et Kudasch.) *Ekol.Pol.***23**: 211-226.

Dolnik V.R. and V.M. Gavrilov 1979. Bioenergetics of moult in the Chaffinch (*Fringilla coelebs*). *Auk* 96: 253-264.

Dow D.D. 1973. Flight moult of the Australian honey-eater *Myzantha melanocephala* (Latham). *Australian. J. Zool.* **21***:* 519-532

Drent R. H. 1975. Incubation. In Avian biology, ed. Farner D. S. and King J. R., pp. 333-420. Academic Press, New York.

Drent R. H. and Daan S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**:225-252.

Drent R.H., Ebbinge B. and Weijand B. 1978. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verth. Orn.Ges. *Bayern* **23**: 239-263.

Drent R.H., Tinbergen J. M. and Biebach H. 1985. Incubation in the Starling, Sturnus vulgaris: Resolution of conflict between egg care and foraging. *Netherlands J. Zool.* 35: 103-123.

Drent R. and Piersma T. 1990. An exploration of energetics of leap-frog migration in arctic breeding waders. pp 399-412 *in* Bird migration: Physiology and ecophysiology. (E. Gwinner, Ed). Springer-Verlag, Berlin.

DuBowy P.J. 1985 Seasonal organ dynamics in post-breeding male Blue-winged teal and Shovelers. *Comp. Biochem. Physiol.* **82A**: 899-906.

Dutenhoffer M.S. & Swanson D.L. 1996. Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. *Physiol. Zool.* **69(5)**: 1232-1254.

Ens B.J., Piersma T., Wolff W.J., and Zwarts L. 1990. Homeward bound: problems waders face when migrating from the Banc d'Arguin, Mauritania, to their northern breeding grounds in spring. *Ardea* **78**:1-16.

Evans P.R. 1966. Wader migration in north-east England. Trans. Nat. Hist. Soc. Northumberland, Durham and Newcastle-upon-Tyne. **16**: 126-151.

Evans P.R. 1969. Ecological aspects of migration, and pre-migratory fat deposition in the Lesser Redpoll, *Carduelis flammea cabaret. Condor* **71**: 316-330.

Evans P.R. 1991. Seasonal and annual patterns of mortality in migratory shorebirds: some conservation implications. *In* Bird population studies. Perrins C.m., Lebreton J.D. and Hirons G.J. (Eds.), pp. 346-359. Oxford University Press.

Evans P. R. 1992. The use of Balsfjord as a staging post by Knot during spring migration: Fat deposition, muscle hypertrophy and flight strategies. *Wader Study Group Bull.* **63:**126-128.

Evans P.R. 1997. Improving the accuracy of predicting the local effects of habitat loss on shorebirds: lessons from the Tees and Orwell estuary studies. *In* Predicting the Effects of Habitat loss and change on Waterfowl. Gross-Caustard J., Ruino R., Luis A. eds., HMSO, London, PP 35-44.

Evans P.R. and Davidson N.C. 1990. Migration Strategies and Tactics of Waders breeding in Arctica and North Temperate Latitudes. Bird Migration, E. Gwinner (Ed.). pp. 387-398 .

Evans P.R. and Smith P.C. 1975. Studies at Lindisfarne 2. Fat and pectoral muscles as indicators of body condition in bar-tailed godwits. *Wildfowl* **26**: 64-76.

Evans P. R., Davidson N. C., Uttley J. D. and Evans R. D. 1992. Premigratory hypertrophy of flight muscles: an ultrastructural study. *Ornis. Scand.* **23**: 238-243.

Ferns P. N. 1981. The spring of migration of Dunlins through Britain in 1979. *Wader Study Group Bulletin* **32**: 14-19.

Fiorotto M. L. ,Cochran W.J., Funk R. C.,Sheng H. P. and Klish W. J. 1987. Total body electrical conductivity measurements :effect of body composition and geometry . *Am J. of Physiol* . **252**: R794-R800.

Fogden M. P. L. 1972. Premigratory dehydration in the Reed Warbler *Acrocephalus scirpaceus* and water as a factor limiting migratory range. *Ibis* **114**: 548-552.

Fry C.H., Ash J.S., and Ferguson-Lees I.J. 1970. Spring weights of some palearctic migrants at Lake Chad. *Ibis* **112**: 58-82.

Ginn H. B. and Melville D. S. 1983. Moult in birds. BTO Guide 19.

Greenberg R. 1980. Demographic aspects of long-distance migration. *In* migration birds in the Neotropics. Smithson. Inst. Press, Washington DC. pp 493-504

Gromadzka J. 1989. Breeding and wintering areas of Dunlin migrating through southern Baltic. *Ornis. Scand.* **20**: 132-144.

Gwinner E. 1977. Circannual rhythms in bird migration. *Ann. Rev. Ecol. System.* **8**: 381-405.

Gwinner E. 1981. Circannual rhythms: their dependence on the circadian system. *In* Biological Clocks in Seasonal Reproductive Cycles, eds. B. K. Follett and D.E. Follett, pp. 135-169, Jhon Wright and Sons, Bristol, England.

Gwinner E. 1986. Circannual rhythms in the control of avian migrations. *Adv. Stud. Behav.* **16**:191-228.

Haftorn S. 1988. Incubating female passerines do not let the egg temperature fall below the 'physiological zero temperature' during their absences from the nest. *Ornis Scand.***19**: 97-110.

Haftorn S. and Reinertsen R. E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit (Parus caeruleus). *Auk* **102**: 470-478.

Hale W.G. 1980. Waders. The new naturalist **65**. *Collins*, London.

Hardy A.R. and Minton C.D.T. 1980. Dunlin migration in Britain and Ireland .*Bird Study*. **27**: 81-92.

Harker W. H. 1973. Method and a: aratus for measuring fat content in animal tissue either *in vivo* or in slaughtered and prepared form. US Patent 3,735,247.

Helms C. W. and Drury Jr. W. H. 1960. Winter and migratory weight and fat field studies on some North American Buntings. *Bird Banding*, **31(1),** pp1-31.

Herbert B. 1996. Energetics of winter and migratory fattening. pp 280-323 I*n* Avian energetics and nutritional ecology. Carey, C. (Ed). Chapman and Hall, New York.

Herenroede A. C., Wong W. W. Price-Jones B. A. Fiorotto M. L. andKlish W.J. 1989. Body composition in ballet dancers by TOBEC measurements. *Clin. Res.* 36:39A.

Holmgren N., Ellegren, H. and Pettersson J. 1993. The adaptation of moult pattern in migratory Dunlin *Calidris alpina.Ornis Scand.* **24**: 21-27.

Jackson D.B. 1988. Habitat selection and breeding ecology of three species of waders in the Western Isles of Scotland. Ph.D. thesis, University of Durham.

Jenni L. and Jenni-Eiermann S. 1992. Metabolic patterns of feeding, overnight fasted and flying night migrants during autumn migration. *Ornis. Scand.* **23(3)**: 251-259.

Jenni-Eiermann S. and Jenni L. 1991. Metabolic responses to flight and fasting in night migrating passerines. *J. Comp. Physiol.* **161B**: 465-474.

Kaiser A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. *J. Field Ornithology*, **64(2)**, pp. 246-255.

Kersten M. and Piersma T. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea* **75**: 175-187.

Kersten M. and Visser W. 1996. The rate of food processing in the Oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. *Funct. Ecol.* **10(4):** 440-448.

Kersten M., Bruinzeel L.W., Wtersma P. and Piersma T. 1998. Reduced basal metabolic rate of migratory waders wintering in coastal Africa. *Ardea* **86**: 71-80.

King J. R. 1973. Energetics of reproduction in birds. In breeding biology of birds, ed. Farner D. S, pp. 78-120. National academy of sciences, Washington, D. C.

King J. R. 1974. Seasonal allocation of time and energy resources in birds. pp 4-85 *In* Avian Energetics. Paytner R.A. (Ed). Nuttall Ornithological Club, Cambridge, Mass.

King J. R. 1981. Energetics of avian moult. *Acta Internatl. Ornithol. Congr.* **27**: 312-317.

King J. R. and Farner D. S. 1961. Energy metabolism, thermoregulation and body temperature. In biology and comparative physiology of birds, ed. Marshall A. J., pp. 215-288. Academic Press, New York.

King J. R. and Farner D. S. 1965. Studies of fat deposition in migratory birds. *Ann. New York Acad. Sci.* **131**: 422-440.

Klaassen M., Kersten M. and Ens B. 1990. Energetic requirements for maintenance and premigratory body mass gain of waders wintering in Africa. *Ardea* **78**: 209-220

Klaassen M. 1996. Metabolic constraints on long-distance migration in birds. *J. Exp. Biol.* **199**: 57-64.

Klaassen M., Lindstrom A. and Zijlstra R. 1997. Composition of fuel stores and digestive limitations to fuel deposition rate in the long-distance migratory thrush nightingale, *Luscinia luscinia. Physiol. Zool.* **70(1)**:125-133.

Koteja P. 1991. On the relationship between basal and field metabolic rates in birds and mammals. *Funct. Ecol.* **5**:56-64.

Krementz D.G. and Pendleton G.W. 1990. Fat scoring: sources of variability. *Condor* **92**: 500-507.

Lanyon L.E., Goodship A. E., Pye C.J. and MacFie J.H. 1982. Mechanically adaptive bone remodelling. *J. Biomech.* **15**: 142-154.

Lasiewski R. C. and Dawson W. R. 1967. A re-examination of the relation between metabolic rate and body weight in birds. *Condor* **69**: 13-23.

Leslie,R. and Lessells,C.M. 1978. The migration of Dunlin *Calidris alpina* through northern Scandinavia . *Ornis Scand.* **9**: 84-86.

Lessels C.M. 1974. Wader expedition to Norway. *Wader study group bull.* **13**: 8-9

Lifson M. G. and McClintock R. M. 1966. Theory and use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* **12**: 46-74.

Lifson M. G., Gordon N. B., Visscher and Nier A. O. 1949. The fate of utilized molecular oxygen of respiratory CO_2, studied with the aid of heavy oxygen. *J. Biol. Chemistry* **180**: 803-811.

Lillie F.R. and Wang H. 1940. Physiology of development of the feather. IV. The diurnal curve of growth in the Brown Leghorn Fowl. *Proc. Natl. Acad. Sci. U.S.A.* **26**: 67-85.

Lindgard K., Stokkan K.A., Le Mayo Y. and Groscolas R. 1992. Protein utilization during starvation in fat and lean Svalbard ptarmigan (Lagopus mutus hyperboreus). *J. Comp. Physiol.* **162A**: 607-613.

Lindstrom A. 1991. Maximum fat deposition rates in migrating birds. *Ornis Scand.* **22**: 117-129.

Lindstrom A. and Piersma T. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* **135**: 70-78.

Lindstrom A., G. H. Visser and S. Dann 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiol.Zool.***66**: 490-510.

Lyons J.E and Susan M. Haig 1995. Estimation of lean and lipid mass in shorebirds using Total Body Electrical Conductivity. *Auk* **112(3)**: 590-602.

Marsh R. L. 1983. Adaptations of the Gray Catbird *Dumetella carolinensis* to long-distance migration: Energy stores and substrate concentrations in plasma. *Auk* **100**: 170-179.

Marsh R. L. 1984. Adaptations of the Grey Catbird *Dumetella carolinensis* to log-distance migration: flight muscle hypertrophy associated with elevated body mass. *Physiol. Zool.,* **57(1)**: 105-17.

McLandress M.R. and Raveling D.G. 1981. Changes in diet and body composition in Canada geese before spring migration. *Auk* **98**: 65-79.

McNab B.K. 1997. On the utility of uniformity in the definition of basal rate of metabolism. *Physiol. Zool.***70(6)**: 718-720.

Meijer T., Mohring F.J.and Trittmich F. 1994. Annual and daily varition in body mass and fat of Starlings Sturnus vulgaris . *J. Avian Biology* **25**: 98-104.

Metcalfe N.B. and Furness R.W. 1984. Changing priorities- the effect of pre-migratory fattening on the trade-off between foraging and vigilance. *Behav. Ecol. Sociob.* **15(3)**: 203-206.

Meteorological Office 1982. Tables of temperature, relative humidity, precipitation sunshine for the world. Part III and IV.

Mitchell P.I. 1996. Energetics and nutrition of British and Icelandic Redshank (*Tringa totanus*) during the non-breeding season. Ph.D. Thesis, University of Durham.

Morton G.A. and Morton M.L. 1990. Dynamics of postnuptial moult in free-living mountain White-crowned Sparrow. *Condor* **92**: 813-828.

Morton J. M. and Kirkpatrick R. L. 1991. Comments on estimating total body lipids from measures of lean mass. *Condor* **93**: 463-465.

Moser M.E. 1980. Shorebird studies in north west Morocco. Durham University 1980 Sidi Moussa expedition.

Murphy M. E. 1996. Energetics and nutrition of moult. pp 158-198 *in* Avian energetics and nutritional ecology. Carey, C. (Ed). Chapman and Hall, New York.

Murphy M. E. and J. R. King 1982. Amino acid composition of the plumage of the White-crowned Sparrow. *Condor* **84**: 435-438.

Murphy M. E. and J. R. King 1984a. Dietary sulfur amino acid availability and moult dynamics in White-crowned Sparrows. *Auk* **101**: 164-167.

Murphy M. E. and J. R. King 1984b. Sulfur amino acid nutrition during moult in the White-crowned Sparrow .1.Does dietary sulfur amino acid concentration affect the energetics of moult as assayed by metabolised energy? *Condor* **86**: 314-323.

Murphy M. E. and J. R. King 1984c. Sulfur amino acid nutrition during moult in the White-crowned Sparrow .2.Nitrogen and sulfur balance in birds fed graded levels of the sulfur-containing amino acids. *Condor* **86**: 324-332.

Murphy M. E. and J. R. King 1986b. Diurnal constancy of feather growth rates in White-crowned Sparrows exposed to various photoperiods and feeding schedules during the postnuptial moult. *Can. J. Zool.* **64**: 1292-1294.

Murphy M. E. and King J. R. 1987. Dietary discrimination by moulting White-crowned Sparrows given diets differing only in sulfur amino acid concentration. *Physiol.Zool.* **60**: 279-289.

Murphy M. E. and J. R. King 1991a. Nutritional aspects of avian moult. In *Acta xx Congressus Internationalis. Ornithologici*, ed B.B. Bell et al. pp, 2186-2193. New Zealand ornithological Congress Trust Board, Wellington N.Z.

Murphy M. E. and J. R. King 1992. Energy and nutrient use during moult by the white-crowned sparrow Zonotrichia leucoghrys gambelii. *Ornis Scand.* **23**: 304-313.

Murphy M.E. and T.G. Taruscio. 1995. Sparrows increase their rates of tissue and whole body protein turnover during their annual moult. *Comp. Biochem. Physiol.* **IIIA**: 385-396.

Myers J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can. J. Zool.* **59:** 1527-1534.

Nagy K. A. 1980. CO_2 production in animals: an analysis of potential errors in the doubly-labeled water method. *Am. J. Physiolo.* **238**: R466-R473.

Nagy K. A. 1989. Doubly-labeled water studies of vertebrate physiological ecology. In Stable Isotopes in Ecological Research, eds. P. W. Rundel, J. R. Ehrlinger and K. A. Nagy, pp. 270-287. Springer-Verlag, New York.

Nagy K.A. and Costa D.P. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* **238**: R454-R465.

Nakamura T. 1969. Physiological and ecological studies on bird migration with special reference to body lipids. *Bull. Fac. Educ.* Yamanashi University no. **4** 131-163.

Newton I. 1966. The moult of the Bullfinch *Pyrrhula pyrrhula. Ibis* **108**: 41-67

Newton I. 1968b. The temperatures, weights, and body composition of moulting Bullfinches. *Condor* **70**: 323-332.

Newton I. 1977. Timing and success of breeding in tundra-nesting geese pp113-126 *in* Evolutionary ecology Stonehouse, B. and C.M. Perrins, C.M. (Eds). Macmillan, London.

Nieboer E. 1972. Preliminary notes on the primary moult in Dunlins *Calidris alpina. Ardea* **60**: 112-119.

Norberg U. M. 1996. Energetics of winter and migratory fattening. pp 280-323 *in* Avian energetics and nutritional ecology. Carey C. (Ed). Chapman and Hall, New York.

Norman W. 1988. Autumn and winter Dunlin populations at Teesmouth. *County of Cleveland bird report* pp. 52-57. Teesmouth bird club.

Odum E.P. 1960. Premigratory hyperphagia in birds. *Am. J. Clin. Nutr.* **8**: 621-629.

Odum E.P., Rogers D.T., and Hicks D.L. 1964. Homeostasis of the non-fat components of migrating birds. *Science* **143**:1037-1039.

Owen M. and M.A. Ogilvie 1979. Wing moult and weights of Barnacle Geese in Spitsbergen. *Condor* **81**: 42-52.

Payne R.B. 1972. Mechanisms and control of moult. *In* avian Biology, vol. II, ed. Franer and King J.R., pp. 103-155. Academic Press, New York.

Pennycuick C. J. 1975. Mechanics of flight. pp 1-75 in Farner D. S. and King J. R. (Eds.). *Avian biology*. Vol. V. Academic Press. London.

Pennycuick C.J. 1978. Fifteen testable predictions about bird flight. *Oikos* **30**: 165-176.

Pennycuick C. J. 1989. Birds flight performance: A Practical Calculation Manual. Oxford University Press, Oxford.

Pethig R. 1979. Dielectric and Electrical Properties of Biological Materials. John Wiley, Chichester.

Pienkowski M. W. and Dick, W. J. A. 1975. The migration and wintering of Dunlin *Calidris alpina* in north-west Africa. *Ornis Scand.* **6**: 151-167.

Pienkowski M .W. and Evans, P.R. 1984. Migration behaviour of shorebirds in the Western Palearctic . In *Shorebirds : Migration and Foraging Behaviour* ,eds.J. Burger and B.L. Olla. Plenum Press, New York .

Pienkowski M .W. and Pienkowski A. E. 1983. WSG project on the movements of wader populations in western Europe: eighth progress report. *Wader Study Group Bull.* **38**: 13-22.

Pienkowski M .W., Evans P. R. and Townshend D. J. 1985. Leapfrog and other migration patterns of waders: a critique of the Alerstam and Hogestedt hypothesis and some alternatives. *Ornis Scand.* **16**: 61-70.

Pienkowski M.W.,Knight P.J., Stanyard D.J. and Argyle F.B. 1976. The primary moult of waders on the atlantic coast of Morocco. *Ibis* **118**: 347-365.

Pienkowski M.W., LLoyd C.S. & Minton C.D.T. 1979. Seasonal and migrational weight changes in Dunlins. *Bird Study* **26**:134-148.

Piersma T., Davidson N.C. & Evans P.R. 1984. Estimation of the protein reserves of waders: The use and misuse of standard muscle volume. *Wader Study Group Bull.* **42**:19-22.

Piersma T. 1990. Pre-migratory 'fattening' usually involves more than the deposition of fat alone. *Ring. and Migr.* **11**:113-115.

Piersma T., Koolhaas A. & Dekinga A. 1993. Interactions between stomach structure and diet choice in shorebirds. *Auk* **110(3)**:552-564.

Piersma T. 1994. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. Ph.D. Thesis, University of Groningen.

Piersma T. and Jukema J. 1990. Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. *Ardea* **78(1-2)**: 315-337.

Piersma T., Cadee N. & Daan S. 1995. Seasonality in basal metabolic rate and thermal conductance in a long-distance migrant shorebird, the Knot (*Calidris canutus*). *J. Comp. Physiol. B* **165(1)**:37-45.

Piersma T., Bruinzeel L., Drent R., Kersten M., Van der Meer J. &Wiersma P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot *Calidris canutus*) reflects shifts in organ sizes. *Physiol. Zool.* **69 (1)**: 191-217.

Prater A. J., Marchant J. H. and Vourinen J. 1977. Guide to the identification and ageing the holarctic waders. BTO Guide 17, Tring, Herts.

Rahn H., Paganelli C. and Ar A. 1975. Relation of avian egg weight to body weight. *Auk* 92: 750-765.

Rahn H., Southerland P. R. and Paganelli C. V. 1985. Interrelationships between egg mass and adult body mass and metabolism among passerine birds. *J. ornithol.*. **126**: 263-271.

Reeds P.J. 1991. The energy cost of protein deposition. *In* C. Wenk and M. Boessinger, eds pp. 473-479. Energy metabolism of farm animals. European Association for Animal Production (EAAP) publication 58.

Ricklefs R.E., Konarzewski M & Daan S. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *Am. Nat.* **147**:1047-1071.

Robbins C. T. 1993. Wildlife feeding and nutrition, 2nd ed., Academic Press, New York.

Roby D.D.1991. A comparison of two non-invasive techniques to measure total body lipid in live birds. *Auk* **108**: 509-518.

Salomonsen F. 1955(a). Evolution and bird migration. *Acta XI Congr Int Ornithol.* pp 337-339.

Salomonsen F. 1955(b). The evolutionary significance of bird migration. *Dan. Biol. Medd.* **22, no. 6**: 1-61

Saunders D.K. and Klemm R.D. 1994. Seasonal changes in the metabolic properties of muscle in blue-winged teal, *Anas discors*. *Comp. Biochem. Physiol.* **107A**: 63-68.

Schmidt-Nielsen K. 1997. Animal Physiology: adaptation and environment. 5th edition. Cambridge University Press, Cambridge.

Scott I., Mitchell P. I. and Evans P. R. 1995. The reliability of fat scores as predictors of the mass of fat carried by individual birds. *Ardea* **83**:359-363.

Scott I.,Mitchell P.I. and Evans P.R. 1996. How does variation in body composition effect the basal metabolic rate of birds?. *Functional Ecology* **10**: 307-313?

Scott I.A, Mitchell P.I. and Evans P.R. 1994. Seasonal changes in body mass, body composition and food requirements in wild migratory birds. *Proc. Nutrition Soc.***53**: 521-531.

Scott I.A,Grant M. andEvans P.R. 1991 . Estimation of fat-free mass of live birds: Use of total body electrical conductivity (TOBEC)measurements in studies of single species in the field. *Functional Ecology* **5**: 314-320.

Scott I.A.1991. Studies on seasonal variation in metabolic rate related to changes in body composition with particular reference to shorebirds (Charadrii). Ph.D. Thesis , University of Durham.

Selman C. 1998. The causes of individual and seasonal variation in the metabolic rate of Knot *Calidris canutus*. Ph.D. Thesis, University of Durham.

Skagen S.K.,Knopf F. L. andCade B.S.1993. Estimation of lipids and lean mass of migration sandpipers . *Condor* **95**: 944-956.

Southwood T. R. E. 1978. The estimation of productivity and the construction of energy budgets.Ecological methods with particular reference to the study insect populations. Cambirdge University Press.

Speakman J.R., Racey P.A., Haim A., Webb P.I., Ellison G.T.H. and Skinner J.D. 1994. Inter- and intraindividual variation in daily energy expenditure of the pouched mouse (*Saccostomus campestris*). *Funct. Ecol.* **8**: 336-342.

Stettenheim P. 1972. The integument of birds. pp. 2-63 in Farner D. S. and King J. R. (Eds.). *Avian biology*. Vol. **II**. Academic Press. London.

Stokkan K.A., Mortensen A. and Blix A.S. 1986. Food intake, feeding rhythm and body mass regulation in Svalbard rock ptarmigan. *Amer. J. Physiol.* **251**: R264-271.

Swaddle J. P. Witter M. S. 1997. The effect of moult on flight performance, body mass, and behaviour of European starlings (*Sturnus vulgaris*): an experimental approach. *Can. J. Zool.* **75**:1135-1146.

Taruscio T.G. and M.E. Murphy 1995. 3-methylhistidine excretion by moulting and non-moulting sparrows. *Comp. Biochem. Physiol.* **IIIA**: 397-403.

Van Tyne J. and Berger A. J. 1976. Fundamentals of ornithology, 2nd ed. Jhon Wiley, newYork.

von Haartman L. 1968. The evolution of resident versus migratory habitat in birds. Some considerations. *Ornis. Fennica.* **45**: 1-7.

Walsberg G.E.1983. Avian ecological energetics. In avian biology, vol. 7, ed. Farner D. S., King J. R. and Parkes K. C., pp. 161-220. Academic Press, New York.

Walsberg G.E.1988. Evaluation of a non destructive method for determining fat stores in small birds and mammals. *Physiol. Zool.* **61(2)**: 153-159.

Warkentin I.A. & West N.H. 1990. Ecological energetics of wintering Merlins *Falco columbarius*. *Physiol. Zool.* **63**: 308-333.

Wasser J.S. 1986. The relationship of energetics of Falconiforme birds to body mass and climate. *Condor* **88**: 57-62.

Waters R., Cranswick P., Musgrove A. and Pollitt M. 1998. The wetland bird survey 1996-1997. Wildfowl and wader counts. BTO, WWT, RSPB and JNCC.

Weathers W. W. 1985. Energy cost of incubation in the canary. *Comp. Biochem. Physiolo.* **81A**: 411-413.

Weathers W.W., Weathers D. L. and van Riper III C. 1983. Basal metabolism of the apapane: comparison of freshly caught birds with long-term captives. *Auk* **100**: 977-978.

Wenink P. W., Baker A. J., Rosner H. U. and Tilanus M. G. 1996. Global mitochondrial DNA phylogeography of Holarctic breeding Dunlins (*Calidris alpina*). Evolution **50**: 318-330.

Wennerberg L., Holmgren N. M., Jonsson P-E and Von Schantz T. 1999. Genetic and morphological variation in Dunlin Calidris alpina breeding in the Palaearctic tundra. *Ibis* **141**: 391-398.

Williams J. B. 1996. Energetics of avian incubation. pp. 375-416 *in* Avian energetics and nutritional ecology. Carey C. (Ed). Chapman and Hall, New York.

Williams J. B. and Nagy K. A. 1984. Validation of the doubly-labeled water technique for measuring energy metabolism in Savannah Sparrows. *Physiol. Zool.* **57**: 325-328.

Williams J.B. 1987. Field metabolism and food consumption of Savannah sparrows during the breeding season. *Auk* **104**: 227-289.

Witter M. S. and Cuthill I. C. 1993. The ecological costs of avian fat storage. *Phil. Trans. R. Soc. Lond.* **B340**: 73-92.

Witter M.S. and Goldsmith A.R. 1997. Social stimulation and regulation of body mass in female starlings. *Anim. Behav.* **54**: 279-287.

Wood H.B. 1950. Growth bars in feathers. *Auk* **67**: 486-491.

Appendix I

Calibration the use of Total Body Electrical Conductivity (TOBEC) for estimating total lean mass in live Dunlin

Introduction

Many species of birds are known to vary in body composition seasonally, influenced by phases of the avian life cycle such as reproduction and migration (Blem and Shelor, 1990). The ability to measure and follow changes in body composition (lean mass, lipid mass) between and within individual birds is important for ecological and physiological understanding.

There are many ways in which fat mass and lean mass can be determined in shorebirds. The four most popular are (i) using solvents to extract stored lipids from dried carcasses (e.g. Evans and Smith 1975; Davidson, 1981a; Dobush *et al* 1985). This destructive method has many limitations: lipid extraction is expensive and time consuming and requires the killing of samples. Ethically, big samples are unacceptable but inconclusive results may come from small sample sizes. Moreover, the need to kill the samples does not allow changes in body compositions to be followed.

(ii) The most widely used technique for quantifying the amount of stored fat in live birds is "fat-scoring" of visible subcutaneous deposits (e.g. Helms & Drury, 1960; Kaiser, 1993;Conway *et al,* 1994). Fat levels have been divided into from four to nine classes (Fry *et al.* 1970), based on the amount of fat that can be seen either in the furcular region, the abdominal fat depots, or both. This method does not require the death of the bird, is quick and gives an estimate of average fat levels carried by groups or populations. However, its accuracy is not enough to monitor the change in fat-level in an individual (Scott *et al*, 1995) and it may also be highly inaccurate in some species (Krementz and Pendleton, 1990).

(iii) Formulae based on various morphological features (e.g. wing-length, tarsus-length) can be used to predict the total lean mass (TLM) and hence, by subtraction from total mass, lipid content (e.g. Davidson, 1981a). This method provides a single lean mass value for a given body size and does not take into account any seasonal changes in total lean mass within an individual (Mitchell, 1996). Castro & Myers (1989) found that the application of a formula they derived to predict fat mass in Sanderling *Calidris alba*, had to be restricted to the population from which the measurements were taken.

(iv) Total lean mass (TLM), and hence fat mass (FM), may be estimated from measurements of Total Body Electrical Conductivity (TOBEC) (e.g. Walsberg, 1988;Witter & Goldsmith, 1997). This method is based on the principle that a restrained bird within a solenoidal coil acts as a conductor of electricity and alters the electromagnetic field predictably. The electrical conductivity of lipids is only around 4-5% of the rest of the body on a unit mass basis (Pethig, 1979). Therefore, total lean mass is the main contributor to and highly correlated with the TOBEC index (Walsberg, 1988;Castro *et al*, 1990; Roby, 1991; Scott, *et al* 1991; Skagen *et al* 1993; Scott *et al* 1996). The predicted total fat mass (PFM) of an individual is obtained by subtracting the predicted total lean mass (PTLM), derived from the TOBEC index from the total body mass. There is a need to calibrate the TOBEC indices against the actual TLMs derived from sacrificing a small sample of individuals of a given species immediately after measurement of their TOBECs. Later their TLMs are obtained by destructive carcass analysis. Scott *et al* (1991) found that predictive models derived from single species give better estimates of TLM than those obtained from interspecific equations. The same error is attached to predicted fat mass (PFM) as to predicted total lean mass PTLM, but it usually represents a greater proportion of the actual lipid mass since TLM is generally greater than fat mass (Morton, *et al*, 1991) except at migration times. Many recent studies employing TOBEC to estimate lipid mass have predicted this directly from multiple regressions with TOBEC as an independent variable alongside body size measures, see section 2.1 for more details.

Table 1: Abbreviations and their definition used in this Appendix

Abbreviation	Definition
TOBEC	Total body electrical conductivity
BM	Total body mass
I	TOBEC index
TLM	Total lean mass, obtained from carcass analysis
FM	Fat mass, obtained from BM-TLM by carcass analysis
TDBM	Total dry body mass
TLDM	Total lean dry mass
PTLM	Predicted total lean mass, derived from the linear regression equation of TLM with I (Equation 1)
PFM	Predicted fat mass derived from BM - PTLM
ID	Bird identification number

Methods

In order to obtain a regression that allows prediction of TLM from TOBEC, the actual measurements of TLM obtained from carcass analysis must be regressed against TOBEC indices. Predictive equations were obtained using a sample of 11 adult Dunlin (see Table 2), held in captivity for a periods ranging between 23-34 months under conditions described in chapter 2, section 2.3.1. Individuals were weighed to the nearest gram on a pesola balance, then TOBEC measurements (model SA-1, EM-SCAN) taken and birds killed humanely. Birds were then sealed in polythene bags and frozen. On a later day, birds were defrosted, feathers plucked and the birds dissected. The left pectoral muscle block (pectoralis major and supracoracoideus), stomach, liver, intestine and heart were dissected out. The birds were then sexed by gonadal inspection, and the measurements of intestines and four skeletal measurements taken to the nearest 0.1mm using vernier callipers. The purpose of the dissection was to compare organ masses of captive birds with those of a sample of wild birds. The organs and dissected carcass were weighed to the nearest mg on a torsion balance. The carcass and organs were then dried to constant mass in a vacuum oven at 40°C and their masses summed to give a total dry body mass (TDBM). Once dry, the carcass and the organs underwent lipid extraction separately using a Soxhlet apparatus with petroleum ether as a solvent. Petroleum ether was chosen because it tends to remove fewer polar lipids than other solvents such as chloroform (Dobush *et al,* 1985; Conway *et al,* 1994). After all lipid had been extracted, the carcasses and the organs were dried once again to a constant mass in a vacuum oven at 40°C. Then the sum of all the organs and the carcass was calculated to obtain the total lean dry mass (TLDM). TLDM was subtracted from TDBM to obtain the actual fat mass (FM). Fat mass was subtracted from BM to give total lean mass (TLM). See Table 1 for a summary of abbreviations used.

Linear regression and second-order polynomial models were fitted to plots of TLM against the TOBEC index (I) in order to obtain a predicted total lean mass (PTLM) and an estimate of fat mass (PFM).

Results and discussion

The equation produced by regressing TLM on TOBEC Index for the 11 captive Dunlin (Figure 1) whose body compositions are detailed in Table 2 is shown below:

$\mathrm{PTLM} = (0.42{*}\mathrm{I}) + 21.7 \qquad (r^2 = 0.87)$

Whereas the equation produced by Scott *et al* (1991) for 11 *wild* Dunlin was

$\mathrm{PTLM} = (0.53{*}\mathrm{I} + 21.4)$

Which means that the formula produced by Scott *et al* (1991) would overestimate the PTLM if it was applied to captive birds.

Many studies support the idea that the body composition of wild and captive birds of the same skeletal (or biometric) size differs. Mitchell (1996), Selman (1998) and this study (Appendix II) show that there is a reduction in the mass of digestive organs in captive birds when compered to wild conspecifics. That may lead to differences in the body shape of wild and captive conspecifics. Since the bird's body in the chamber acts as a conductor that alters the electromagnetic inductance of the solenoid coil, differences in the TOBEC indices between wild and captive birds of the same size may have occurred because of the differences in their shape.

Figure 1: The relationship between Total Lean Mass (TLM) and TOBEC Index for 11 captive Dunlin

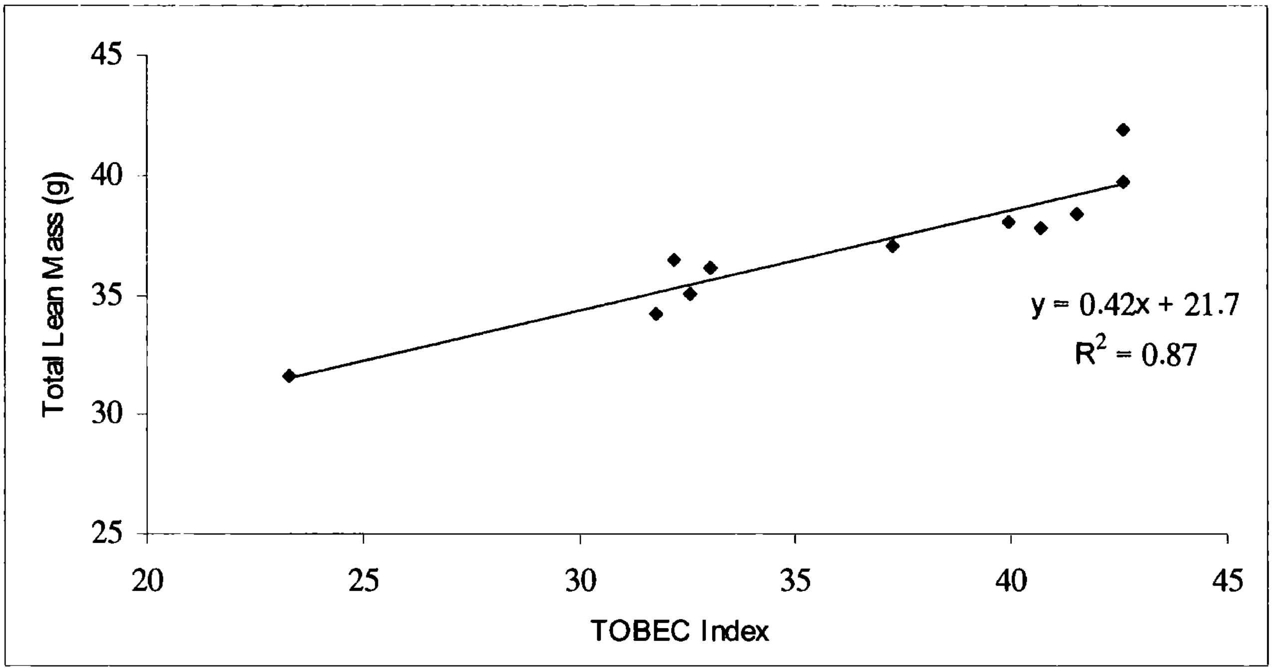


Table2: The actual values of total lean mass (TLM), total fat mass (FM), % of water and TOBEC index for 11 captive Dunlin

ID	BM (g)	% Water	TLM (g)	FM (g)	TOBEC index
LG(F)	57	65.7	41.9	15.1	42.6
DG(F)	45	64.6	37.1	7.9	37.2
YEL(F)	48	66.5	39.7	8.3	42.6
BL(M)	39	67	36.1	2.9	33.0
OR(M)	55	65.2	38.1	16.9	39.9
RE(M)	43	69.7	37.8	5.2	40.7
LRE(F)	39	67.3	36.5	2.5	32.2
LYEL(M)	39	66.6	35.1	3.9	32.6
WBL(M)	35	64.3	31.6	3.4	23.3
WOR(F)	47	65.6	38.4	8.6	41.5
WDG(M)	39	65.9	34.2	4.8	31.8
MEAN	*44.2*	*66.2*	*37.0*	*7.2*	
SD	*7.1*	*1.49*	*2.77*	*4.86*	
SE	*2.1*	*0.45*	*0.84*	*1.46*	

% Water = (Total water content / TLM)*100

Appendix II

Comparison of body composition of wild and captive Dunlin

Introduction

Many wild species of shorebirds such as Dunlin *Calidris alpina*, Redshank *Tringa totanus* and Knot *Calidris canutus* show seasonal fluctuations in body mass, caused by variation in both lean and fat mass components (see Pienkowski *et al,* 1979; Davidson, 1981; Scott *et al*, 1994; Mitchell, 1996).

Many studies have also shown these changes in body composition in captive shorebirds (e.g. Scott et al, 1994; Mitchell, 1996; Selman 1998; this study). Scott *et al* (1994) and Mitchell (1996), showed that there was no difference in the size of the seasonal body mass changes between wild Redshank wintering on Teesmouth and in captive Redshank taken from that estuary. However, there was a reduction in the digestive organ mass in captive Redshank when compared with wild conspecifics. The reduction in lean mass in captive shorebirds has been well documented in Knot (Piersma *et al* 1995; Selman 1998) and in Redshank (Mitchell 1996). These studies compared the masses of various organs (liver, kidney, gut, and stomach) in wild and captive conspecifics. These organs have been given the term the 'digestive organs' (Piersma 1994).

Methods

A total of 22 wild and captive Dunlin were killed humanely under licence and dissected in order to do carcass analysis. The captive birds were held for periods ranging from 23-34 months between September 1996 and June 1999 under conditions described in chapter 2 section 2.3.1 (*C. a. alpina* n=6 birds & *C.a.*

schinzii n=5). They were sacrificed, 20 hours after measurement of BMR to offset any dehydration experienced during a measurement of BMR. The 11 wild Dunlin were collected after they had been killed accidentally during cannon-netting at Teesmouth, north-east England on (26/7/95 (n=2), 11/11/97 (n=2), 8/5/98 (n=1) and on 8/8/98 (n=4) and on the Severn estuary (22/2/81 n=2). All were sealed in plastic bags and frozen at -20°C until carcass analysis was carried out at later date.

The heart, liver, stomachs, intestines and pectoral muscle blocks (left pectoralis major and left supra-coracoideus) were dissected out. All organs were dried to constant dry mass at 40°C in a vacuum oven and then weighed to the nearest mg on a torsion balance. The bird was sexed by gonadal inspection, the gut length measured and four skeletal measurements were taken to the nearest 0.1mm using vernier callipers, following the methods of Piersma *et al.* (1984), in order to calculate a standard muscle volume SMV (Evans & Smith, 1975). The mass of one lean dry pectoral muscle block was then expressed as a proportion of the SMV to produce an index of muscle size, independent of total body (skeletal) size, known as SMI or standard muscle index. Stored lipids (triglycerides) were extracted from the carcass and the dissected organs using a Soxhlet extractor with petroleum ether as a solvent. The carcass and organs were subsequently dried once again using constant mass at 40°C in a vacuum oven and the fat-free masses were then obtained.

Results and discussion

Table 1 summarise differences between wild and captive Dunlins of the same overall size, as judged by bill-length. The mean liver mass was 35% lower in captive birds, and the mean gut mass (stomach + intestine), had decreased by over 60%. The mean length of the intestine had also decreased by 40% in captive birds when compered to wild conspecifics. However, the mean values of pectoral muscle indices in captive birds were slightly higher than those wild conspecifics. Piersma (1994), Mitchell (1996) and Selman (1998) showed that captive shorebirds reduce the sizes of some of their organs, especially digestive organs. This reduction could be due to disuse atrophy (see Piersma *et al* 1993).

Table: Comparisons of dry lean organ mass, gut length and bill length between wild and captive Dunlin. Values are means with standard errors in parentheses.

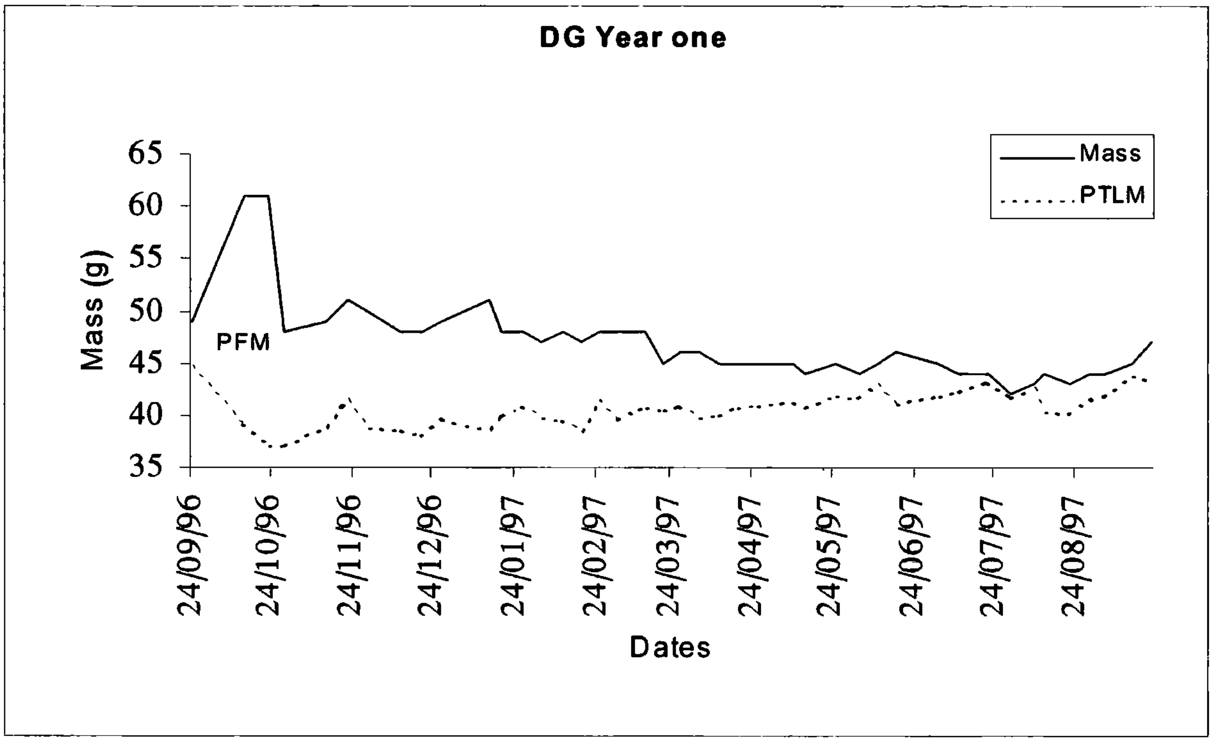
Organ	Wild	Captive	% Reduction
Bill length (mm)	30.2 (0.55) n=11	31.02 (1.14) n= 11	
Liver (g)	0.51 (0.04) n=11	0.33 (0.02) n= 11	35
Gut mass (g) = (Stomach + intestine mass)	0.74 (0.07) n=11	0.29 (0.014) n= 11	61
Heart (g)	0.24 (0.02) n= 11	0.17 (0.007) n=11	29
Intestine length (cm)	31.1 (1.2) n= 11	22.2 (0.76) n=11	29
Standard muscle index (SMI)*	0.00023 (6.7) n= 11	0.0003 (1.14) n=11	Captive increase by 30%

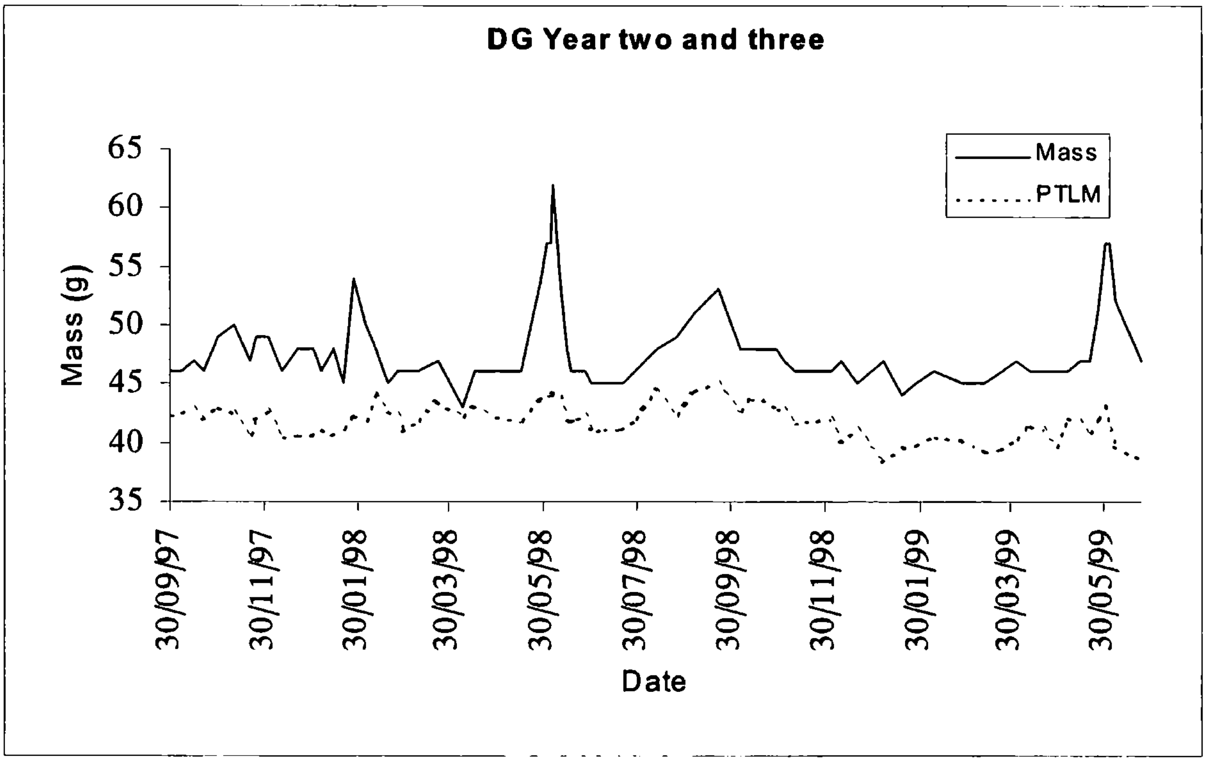
SMI: Mass of left lean dry pectoral muscle mass/ standard muscle volume (Evans and Smith, 1975)

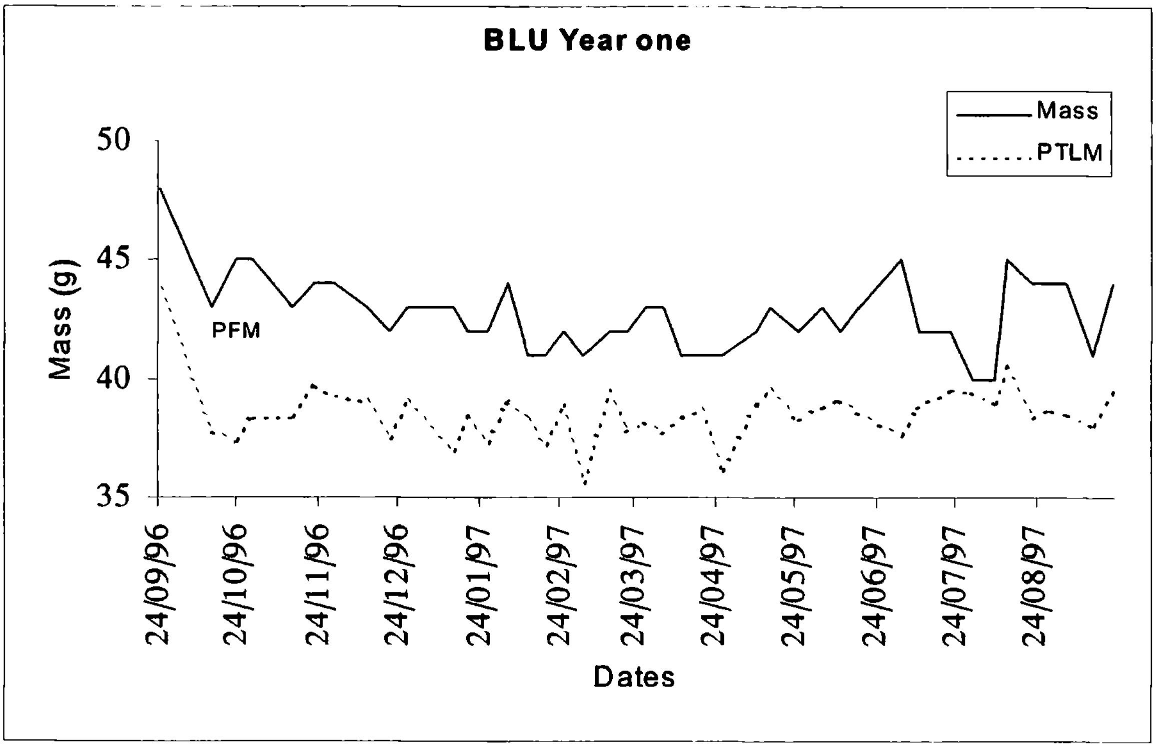
% Reduction: indicates the difference between mean organ mass of captive and wild Dunlin, as % of wild Dunlin mass

Appendix III

Body composition throughout captivity for *C.a.alpina* (individuals DG, BLU, LG, YEL, RE and OR) and for *C.a.schinzii* (individuals WBL, LYEL, WDG, LRE, WOR, LBL, WLG and WRE)



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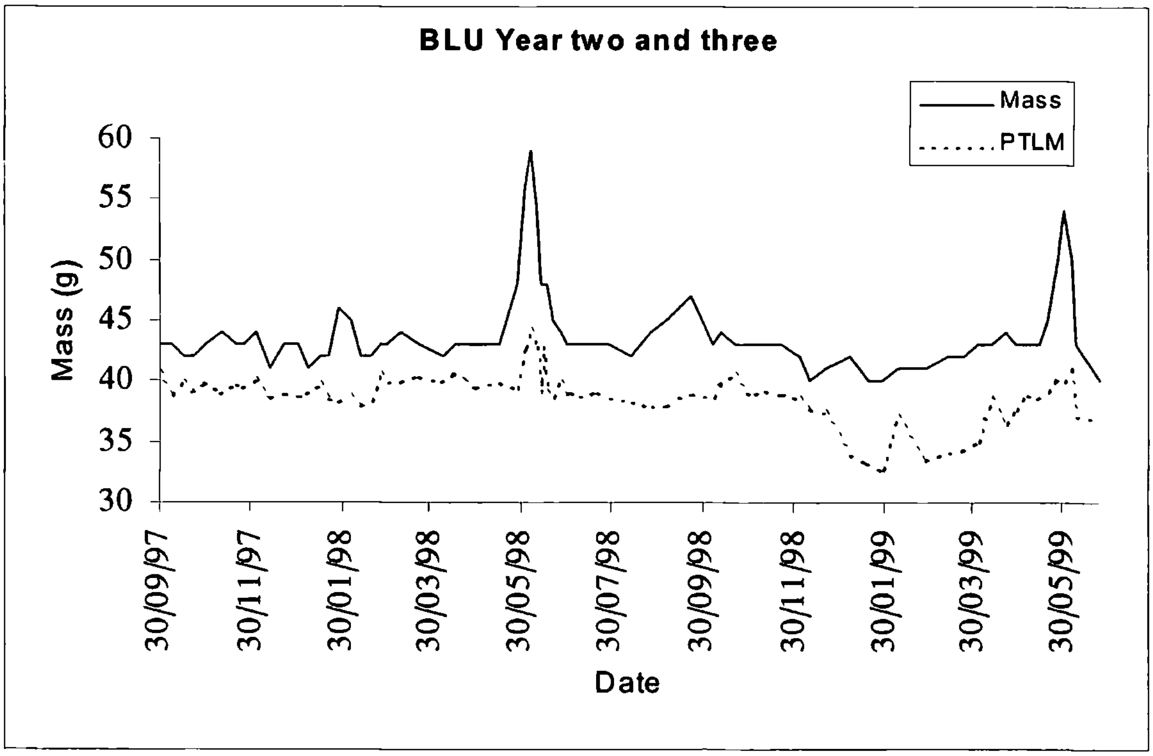
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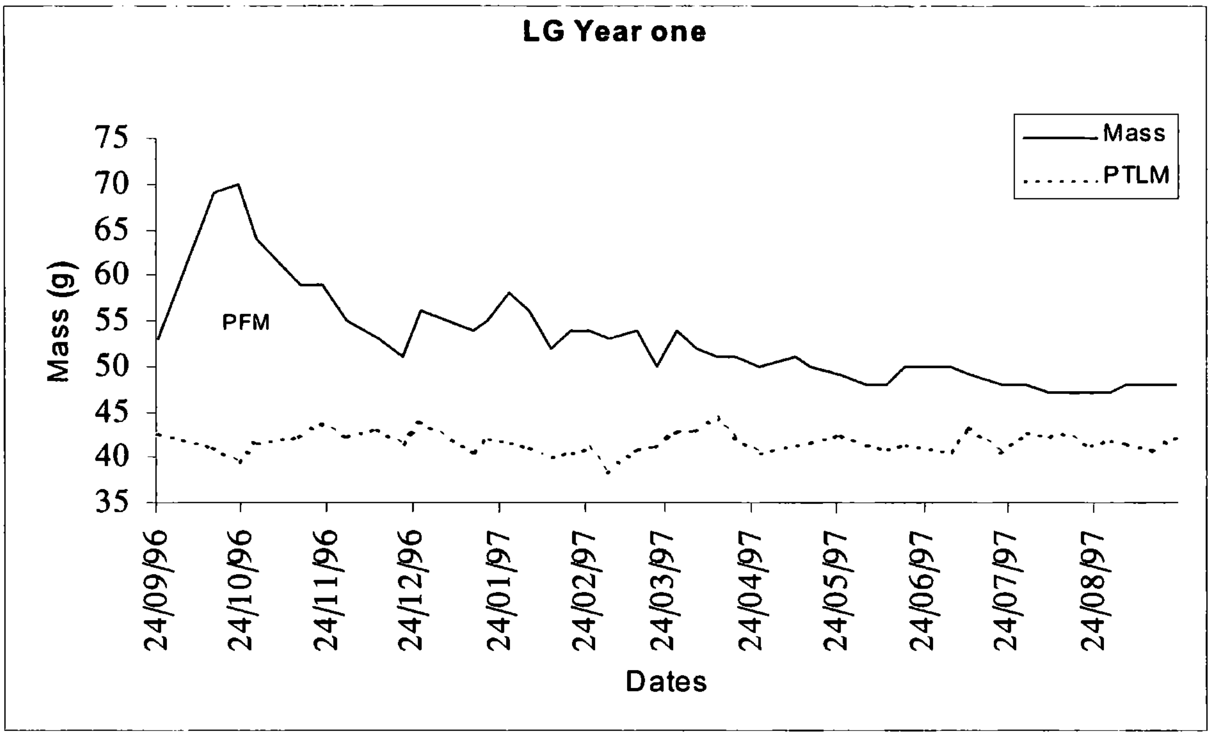
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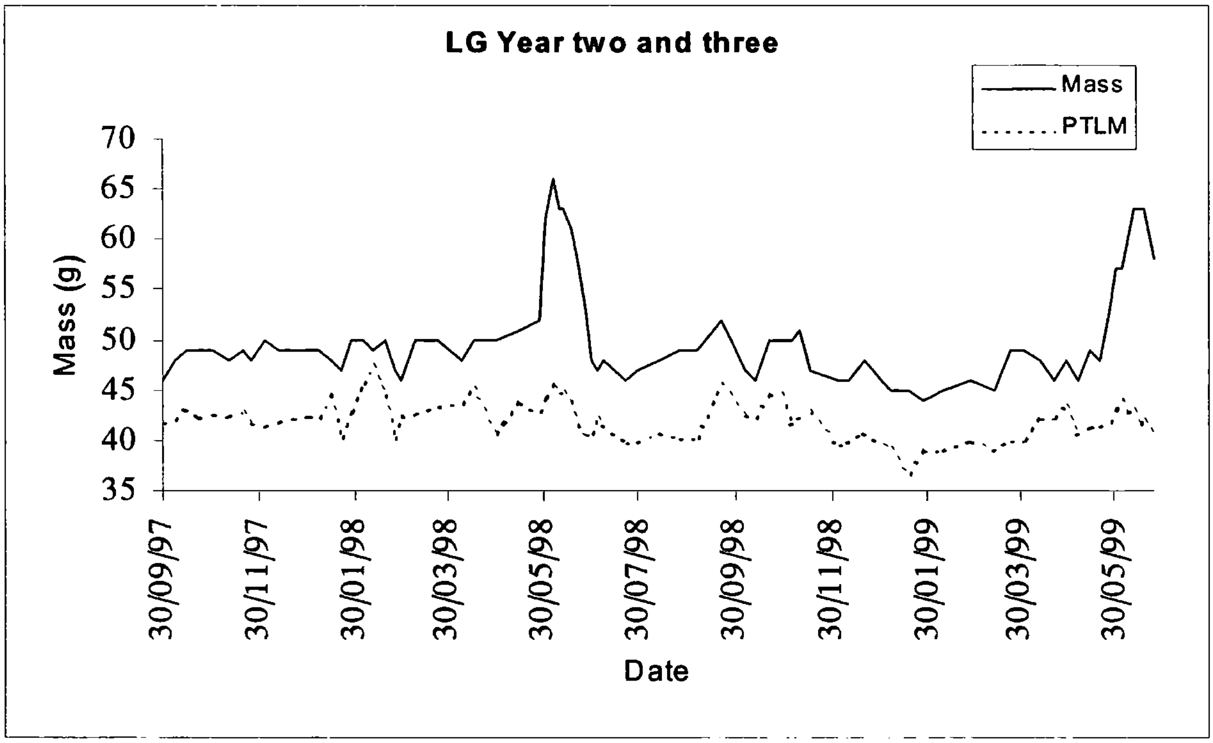
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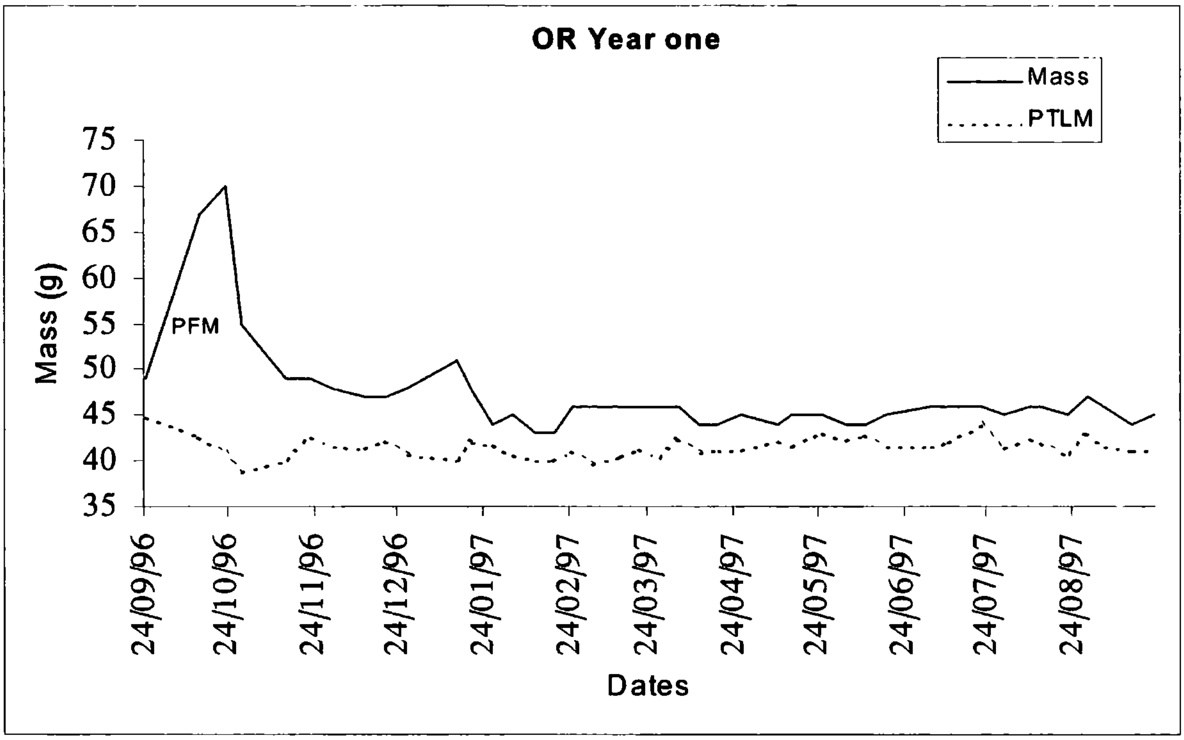
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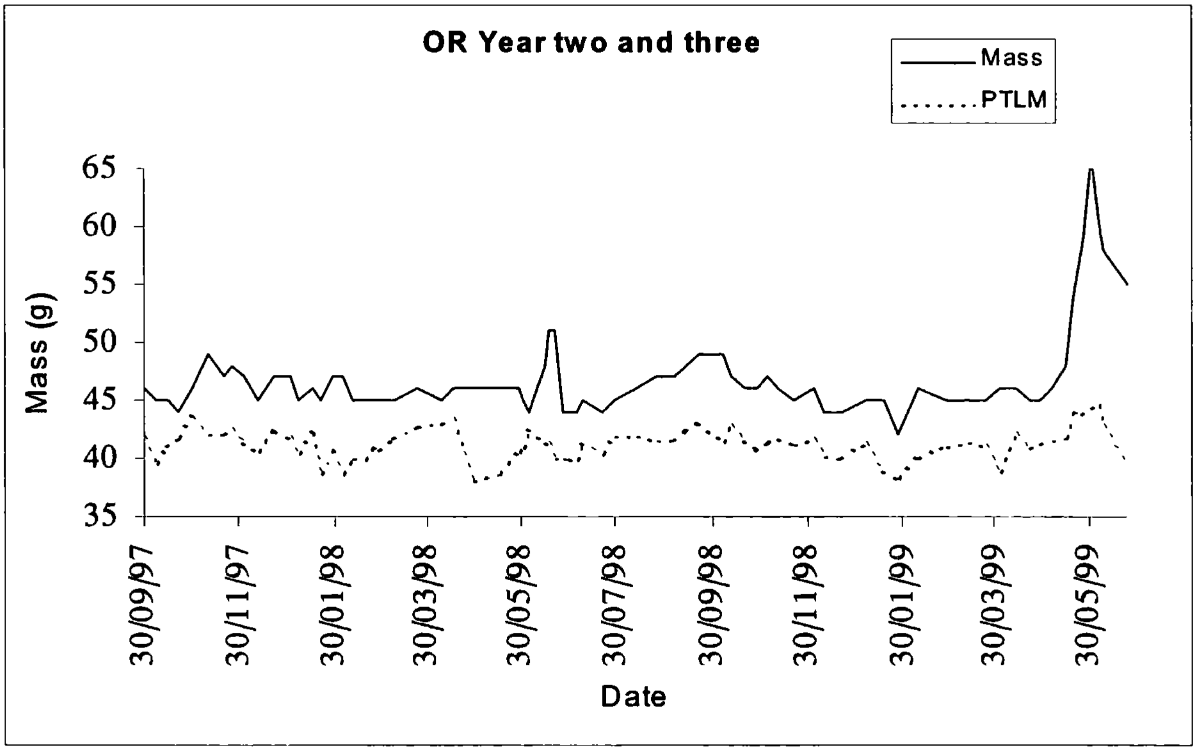
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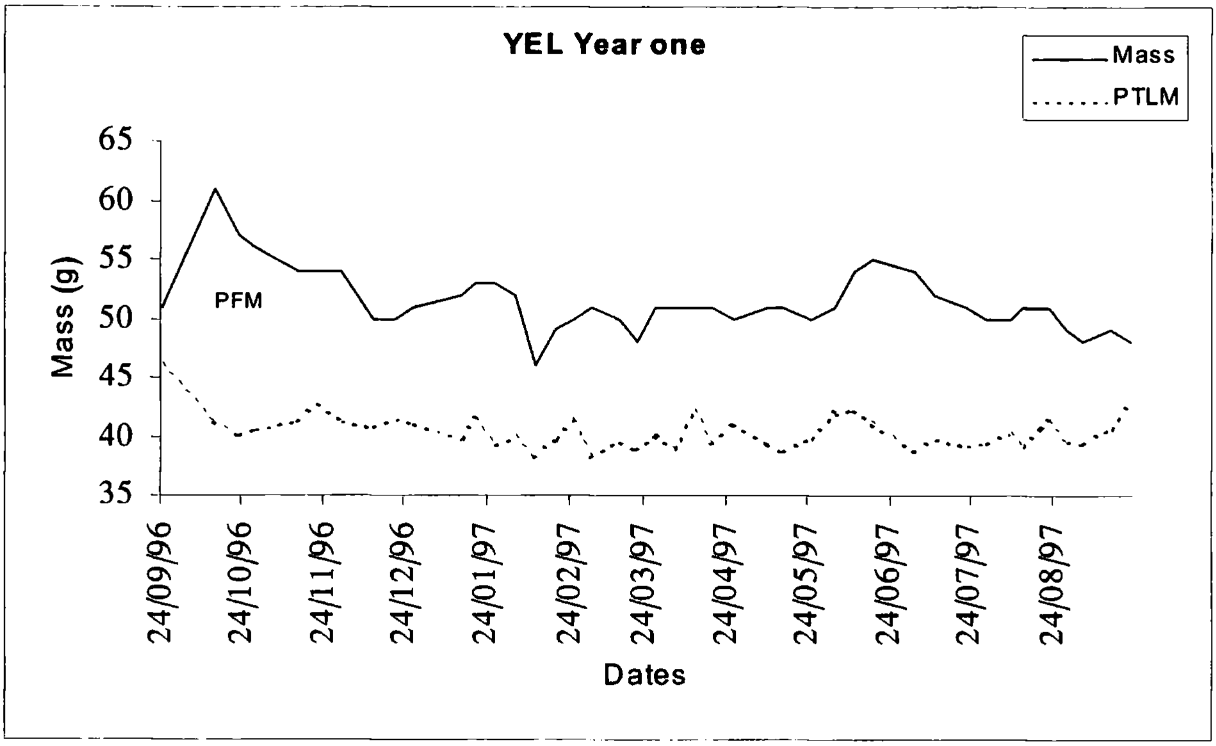
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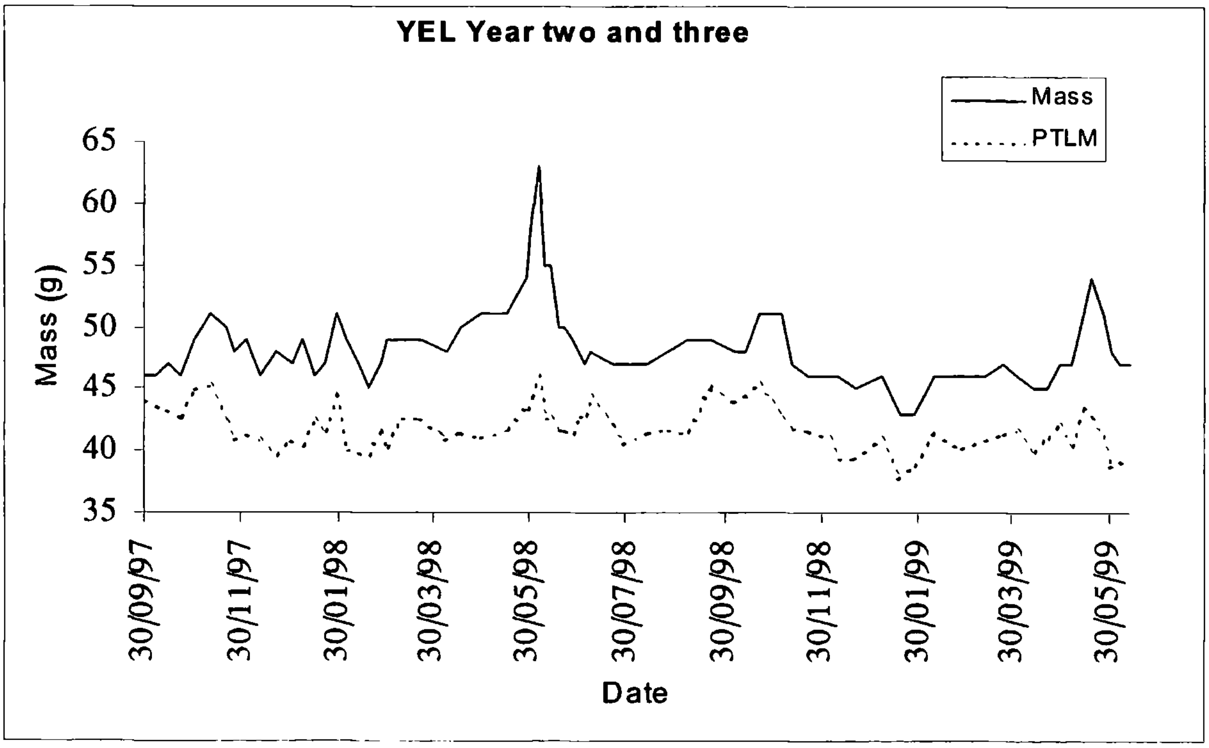
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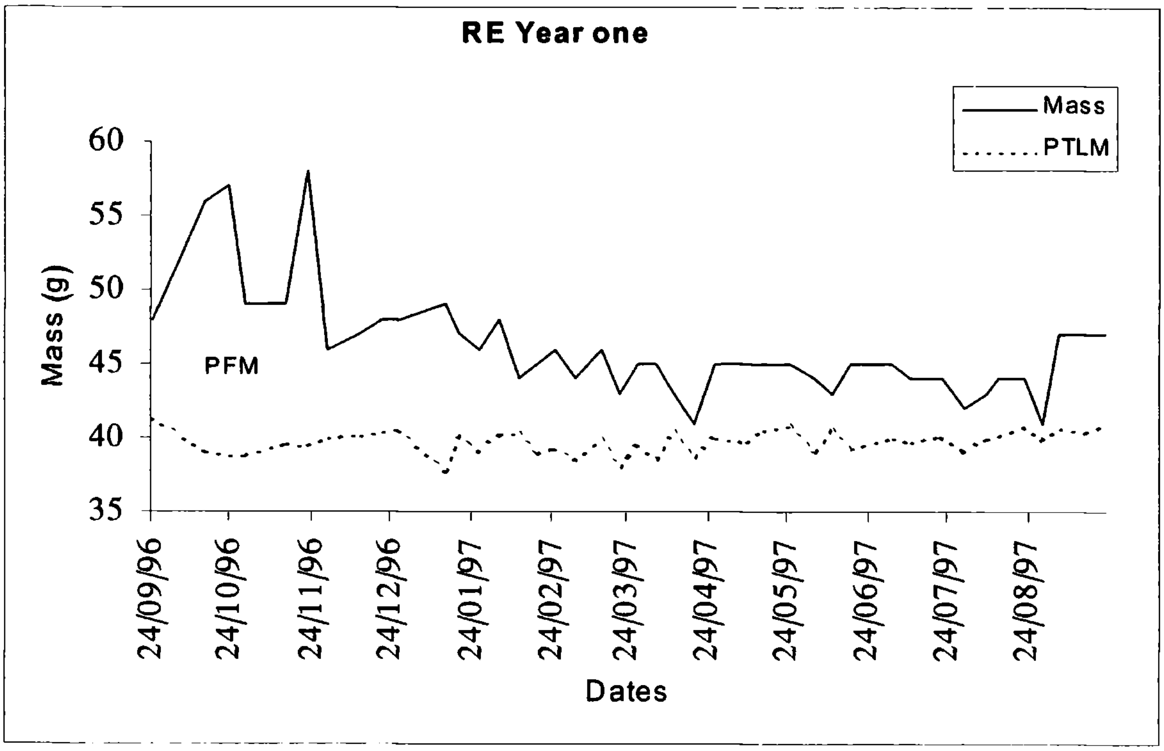
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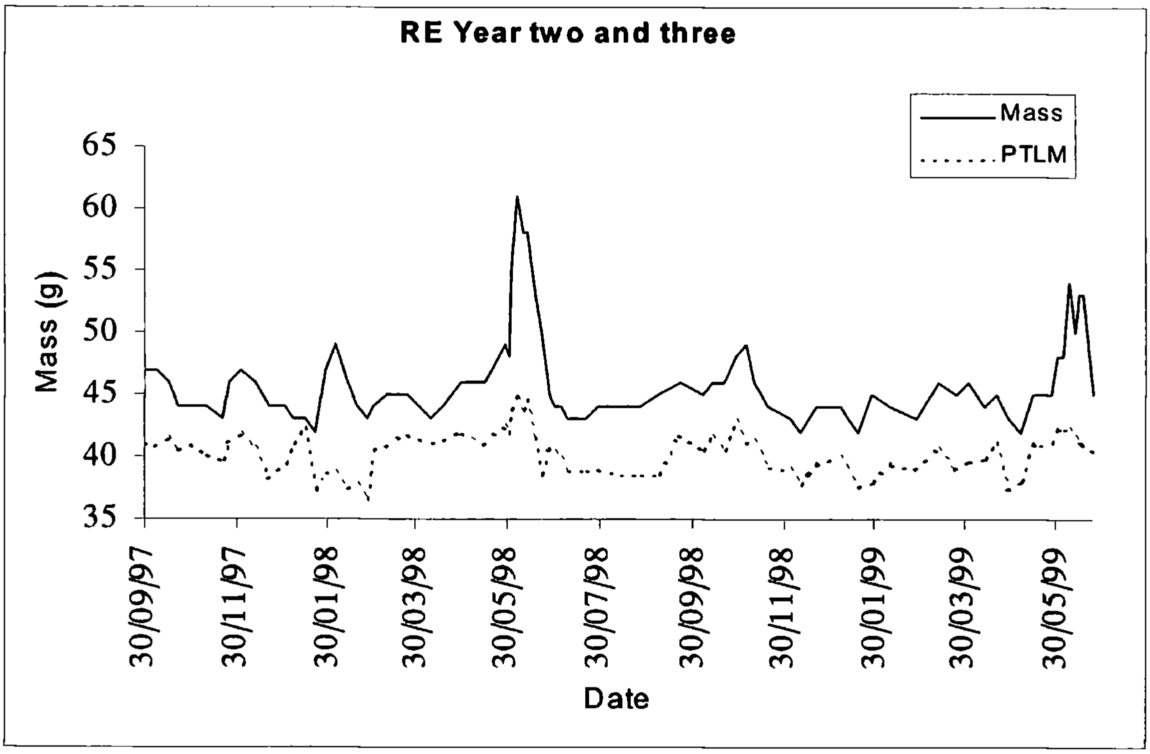
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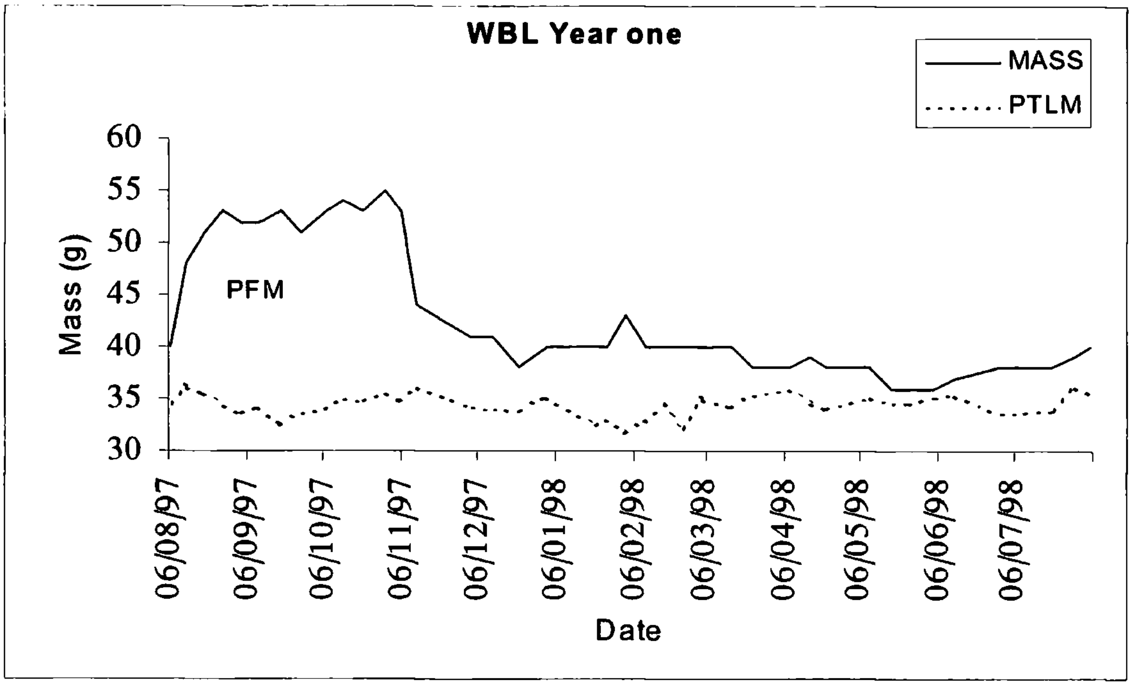
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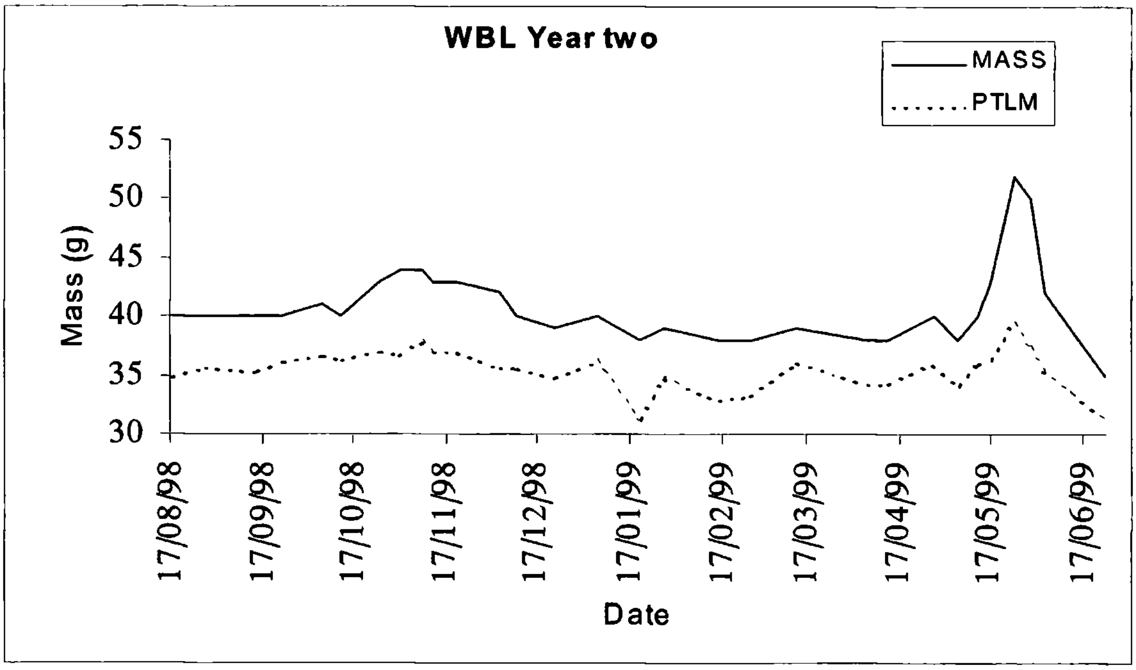
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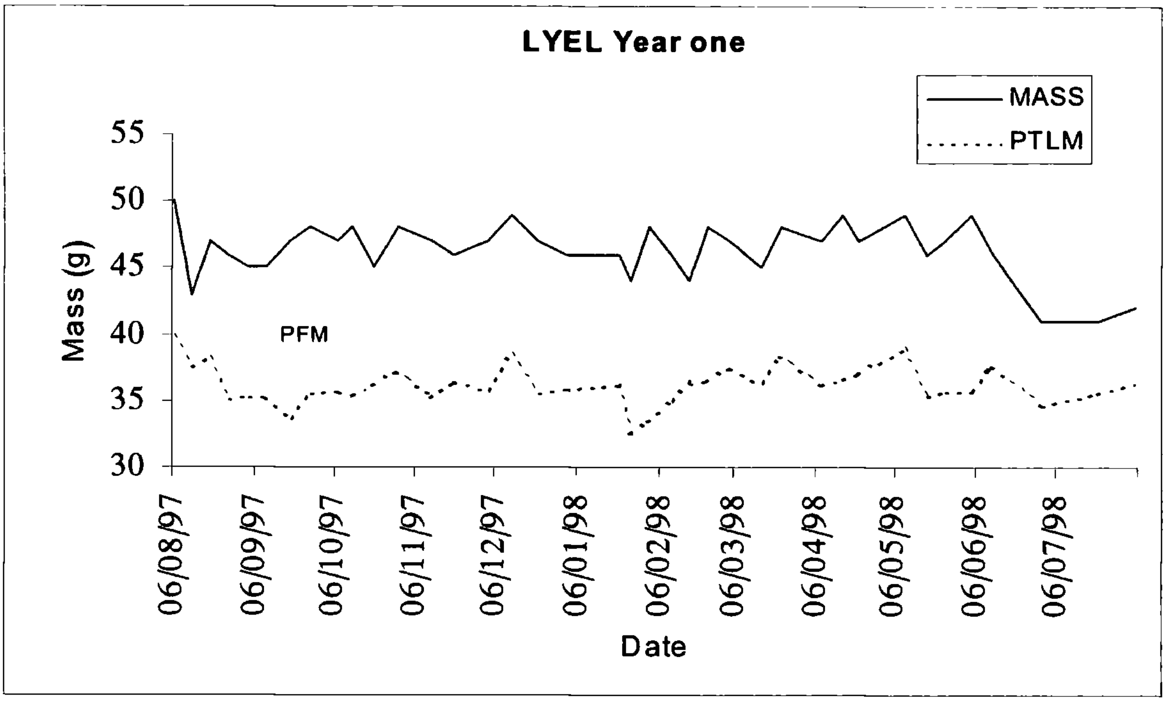
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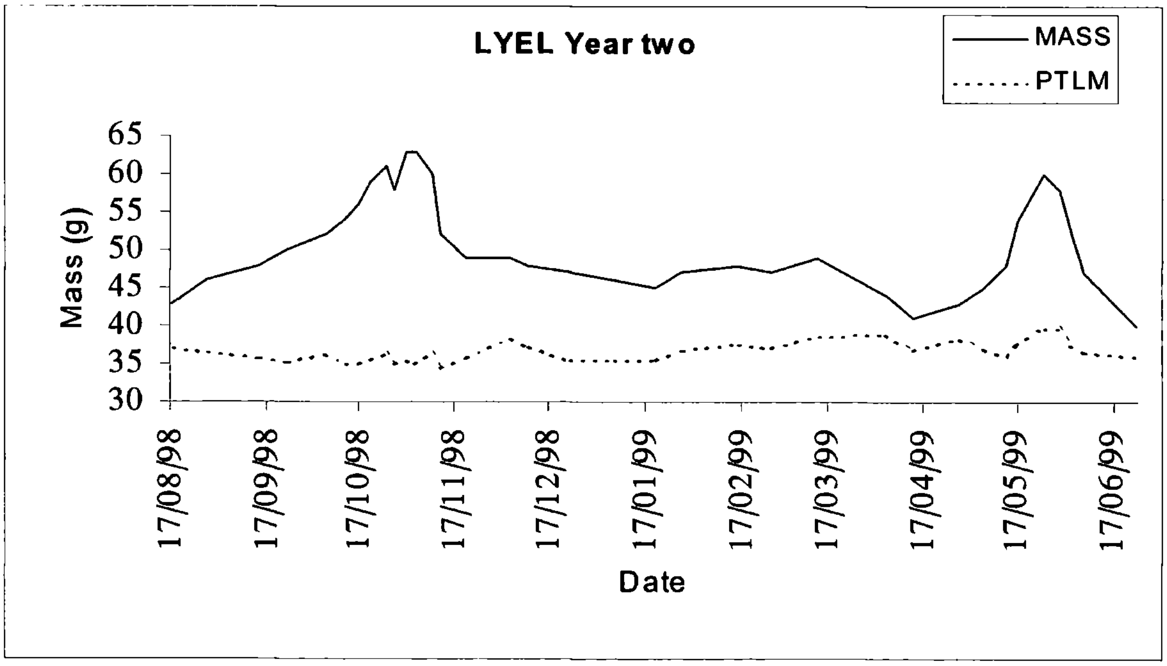
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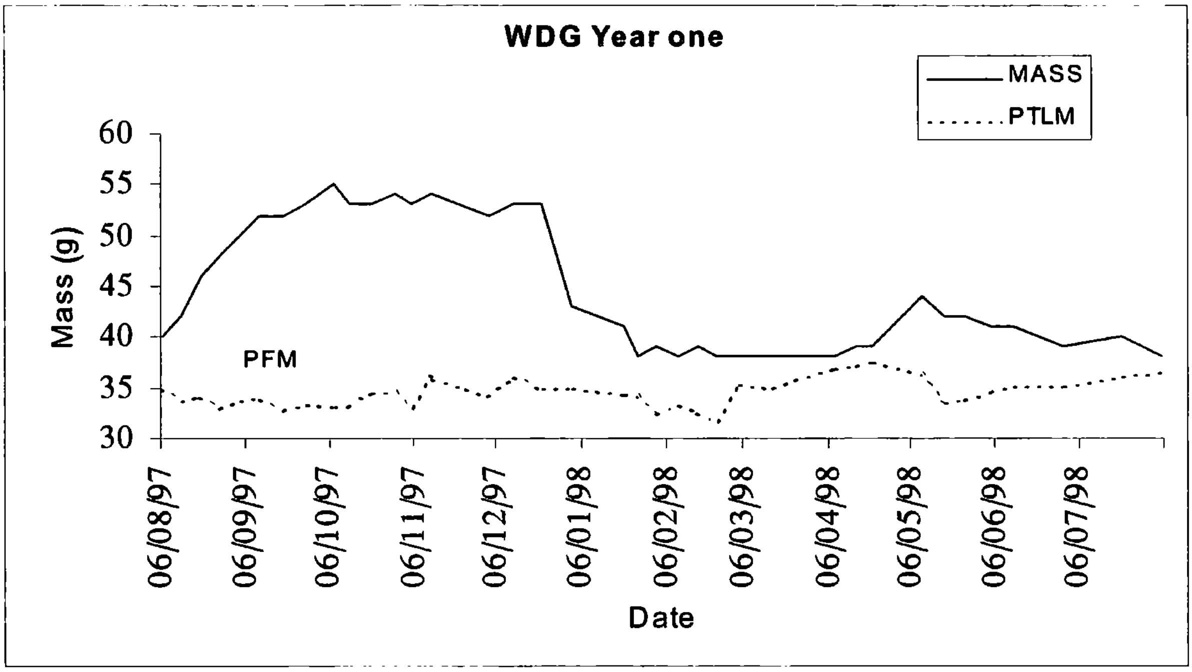
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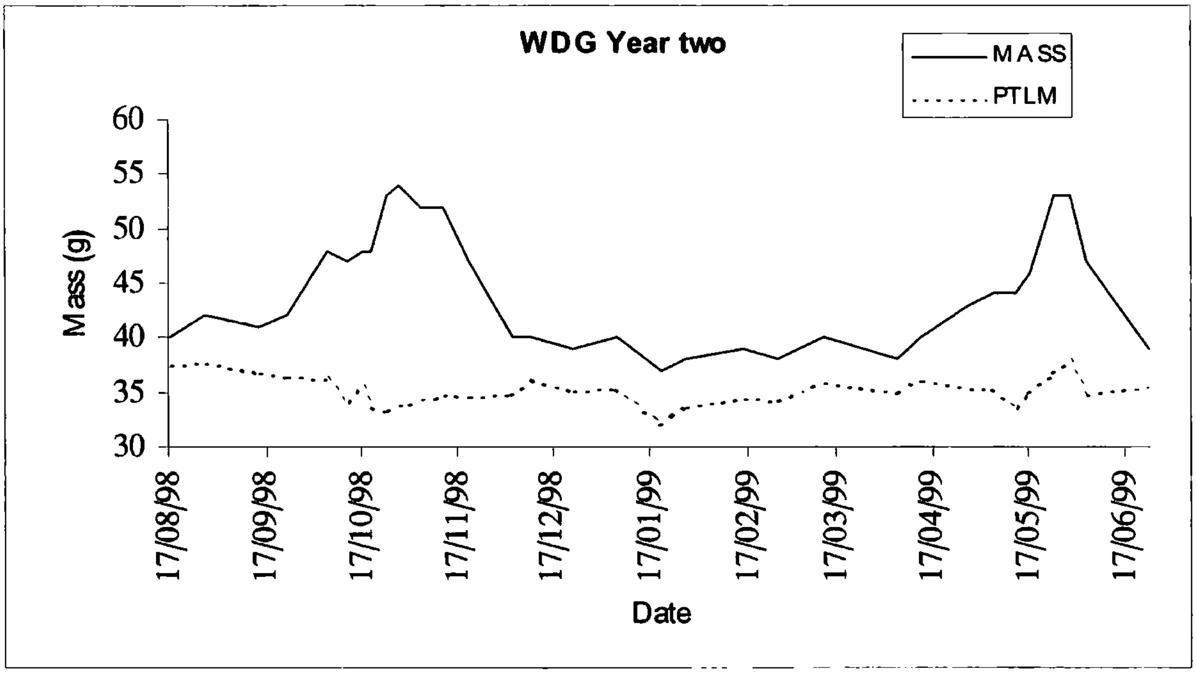
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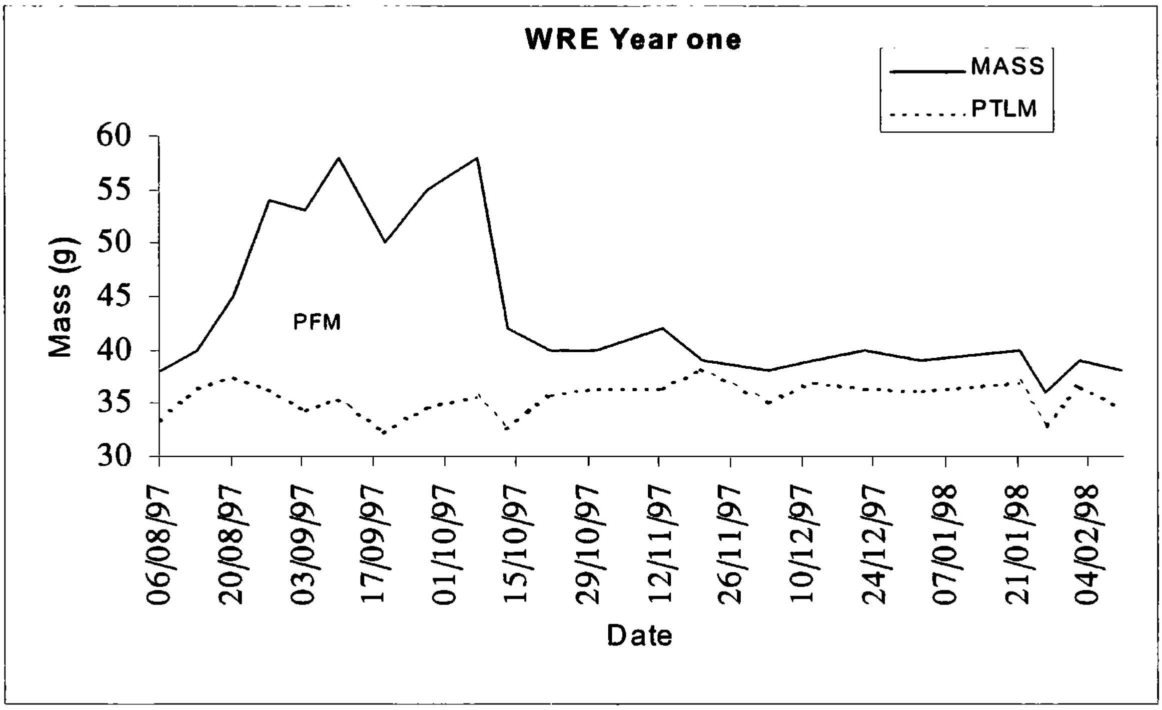
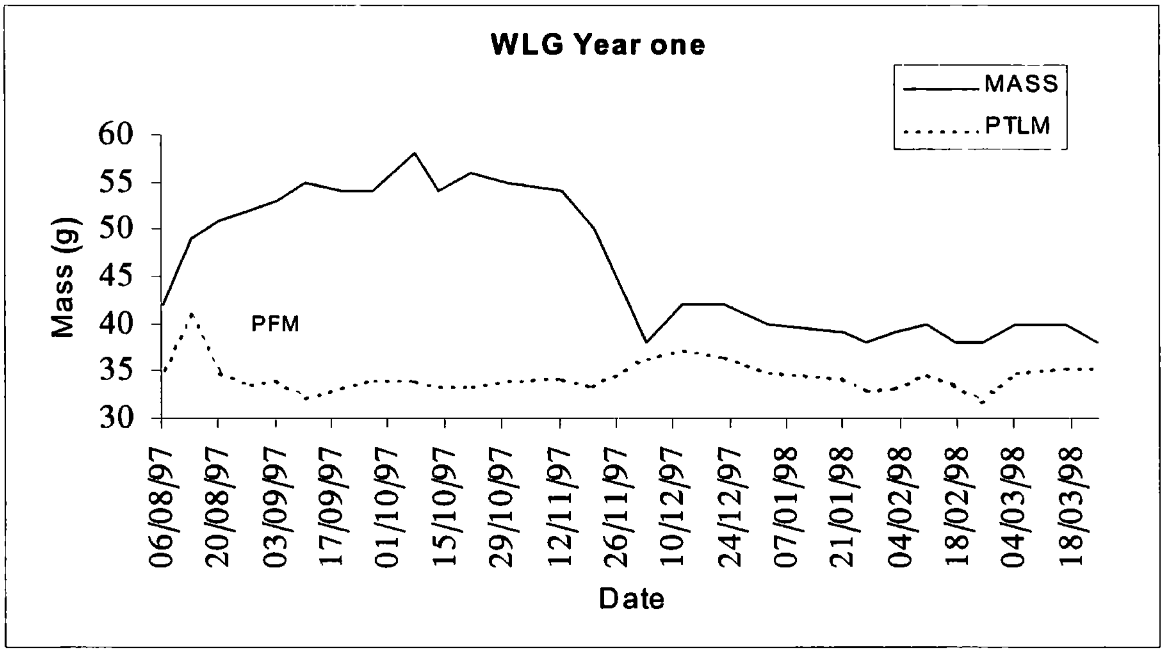
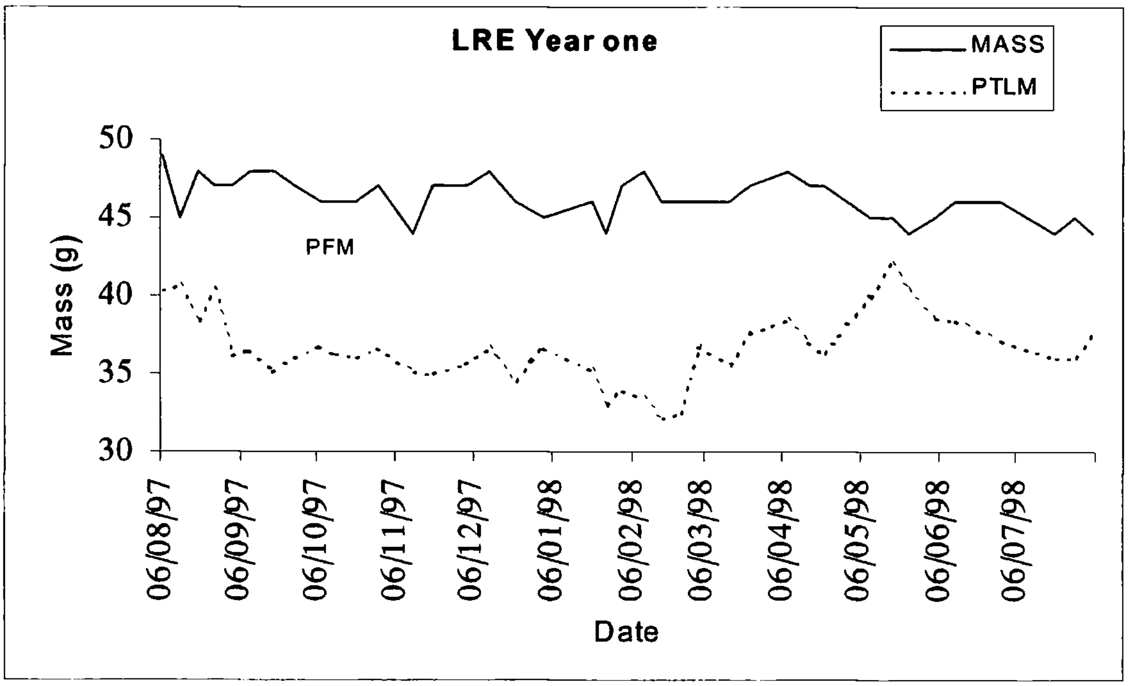
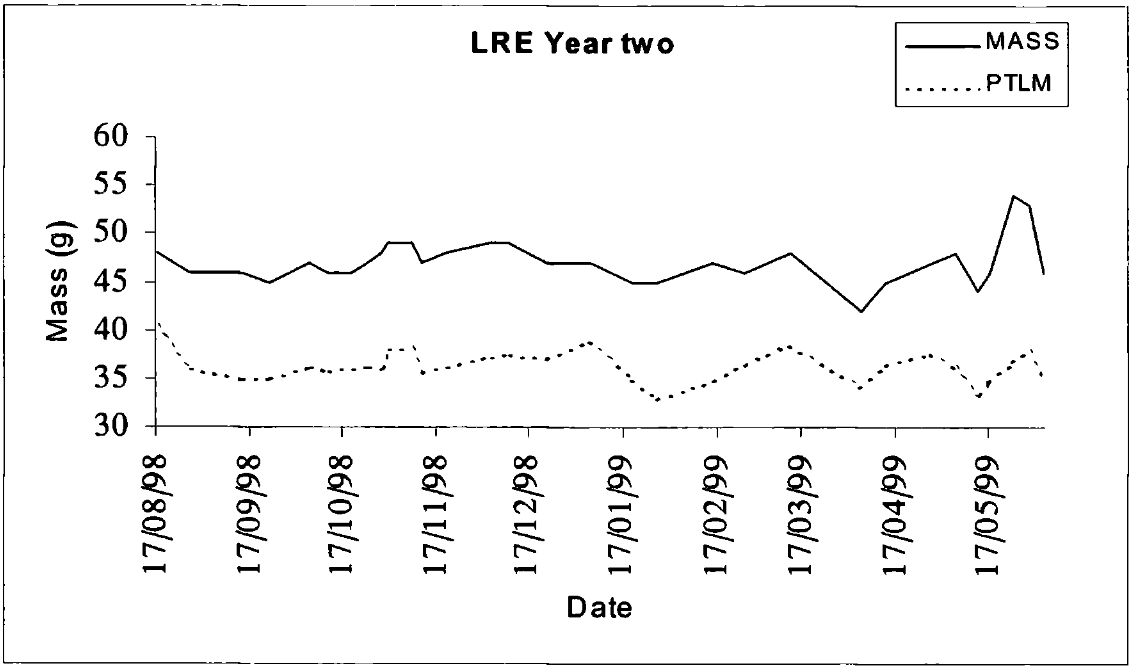
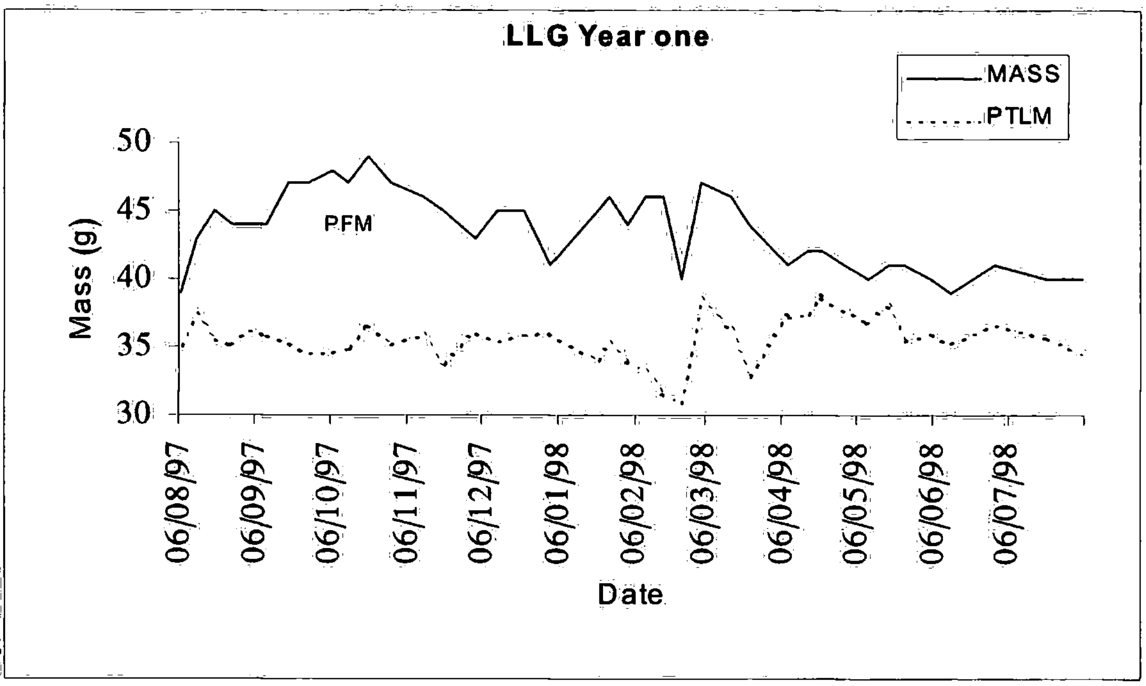
17/06/99
Date

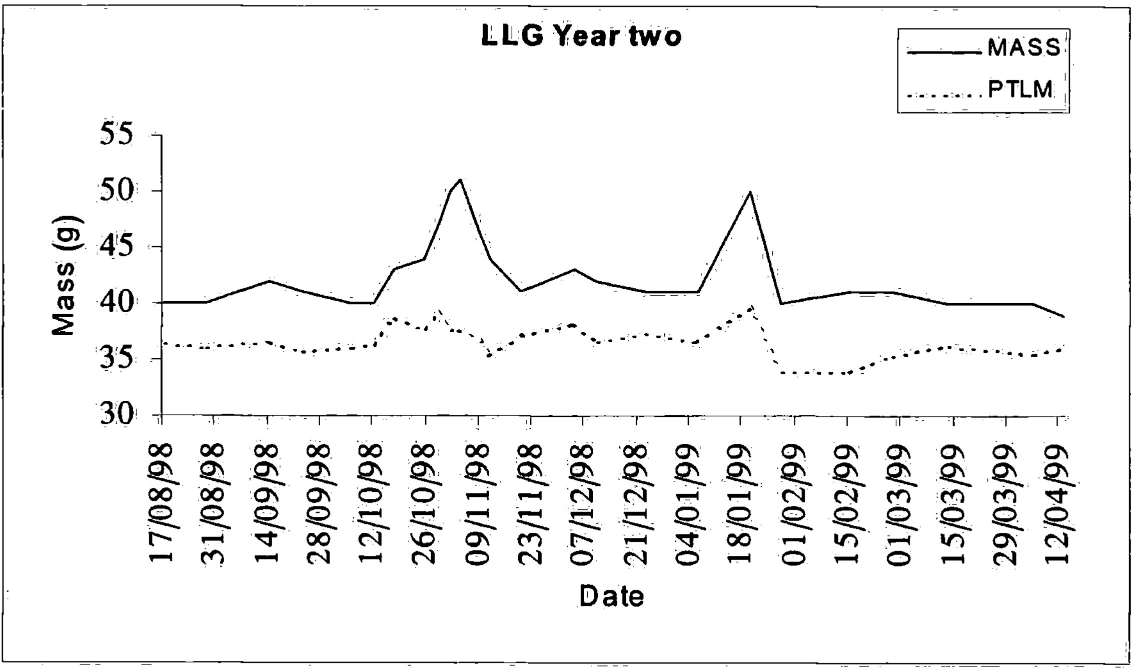

WRE Year one
MASS
PTLM
PFM
Mass (g)
60
55
50
45
40
35
30
06/08/97
20/08/97
03/09/97
17/09/97
01/10/97
15/10/97
29/10/97
12/11/97
26/11/97
10/12/97
24/12/97
07/01/98
21/01/98
04/02/98
Date

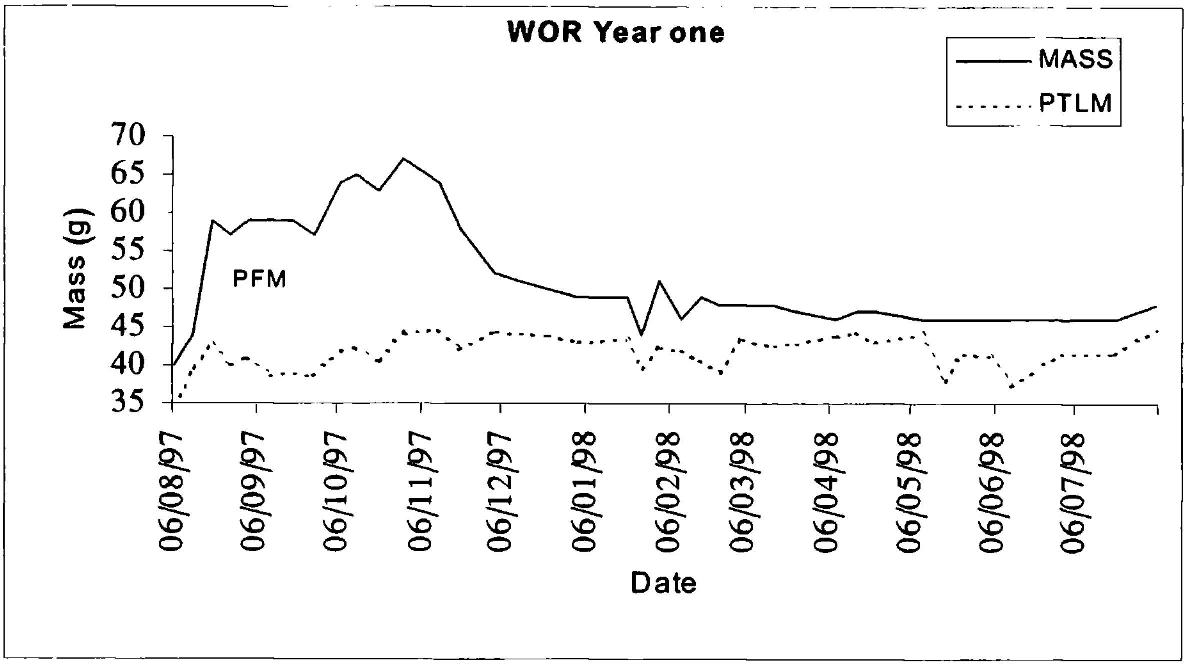

WLG Year one
MASS
PTLM
PFM
Mass (g)
60
55
50
45
40
35
30
06/08/97
20/08/97
03/09/97
17/09/97
01/10/97
15/10/97
29/10/97
12/11/97
26/11/97
10/12/97
24/12/97
07/01/98
21/01/98
04/02/98
18/02/98
04/03/98
18/03/98
Date

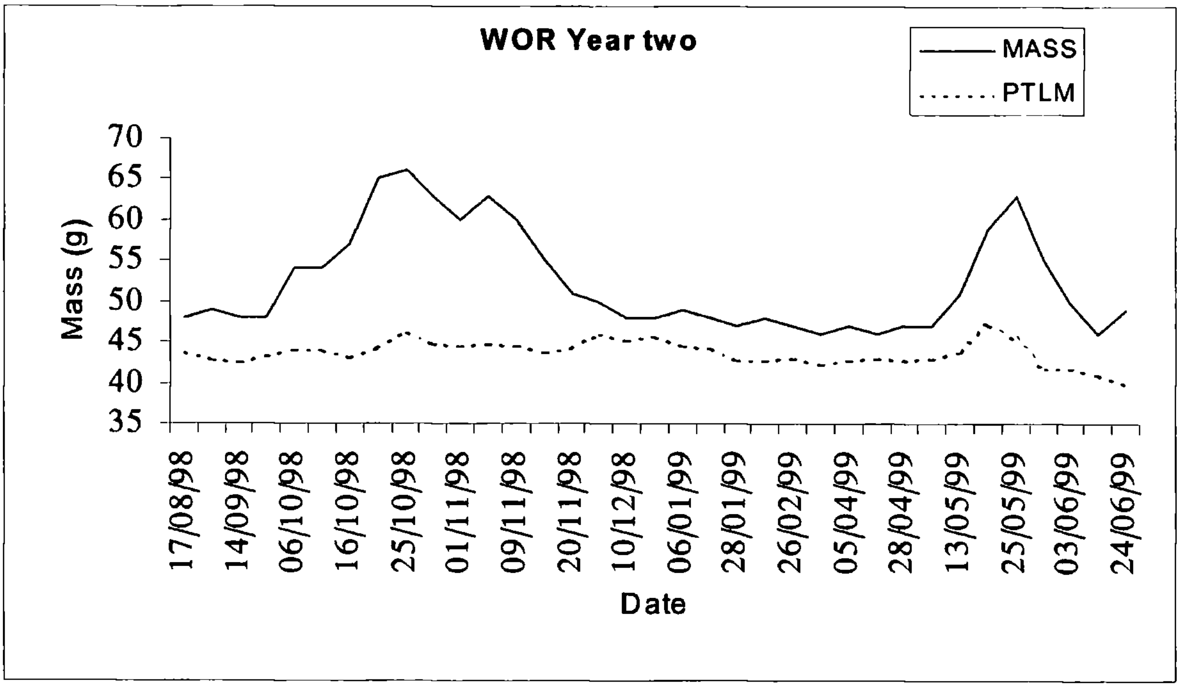

LRE Year one
MASS
PTLM
PFM
Mass (g)
50
45
40
35
30
06/08/97
06/09/97
06/10/97
06/11/97
06/12/97
06/01/98
06/02/98
06/03/98
06/04/98
06/05/98
06/06/98
06/07/98
Date

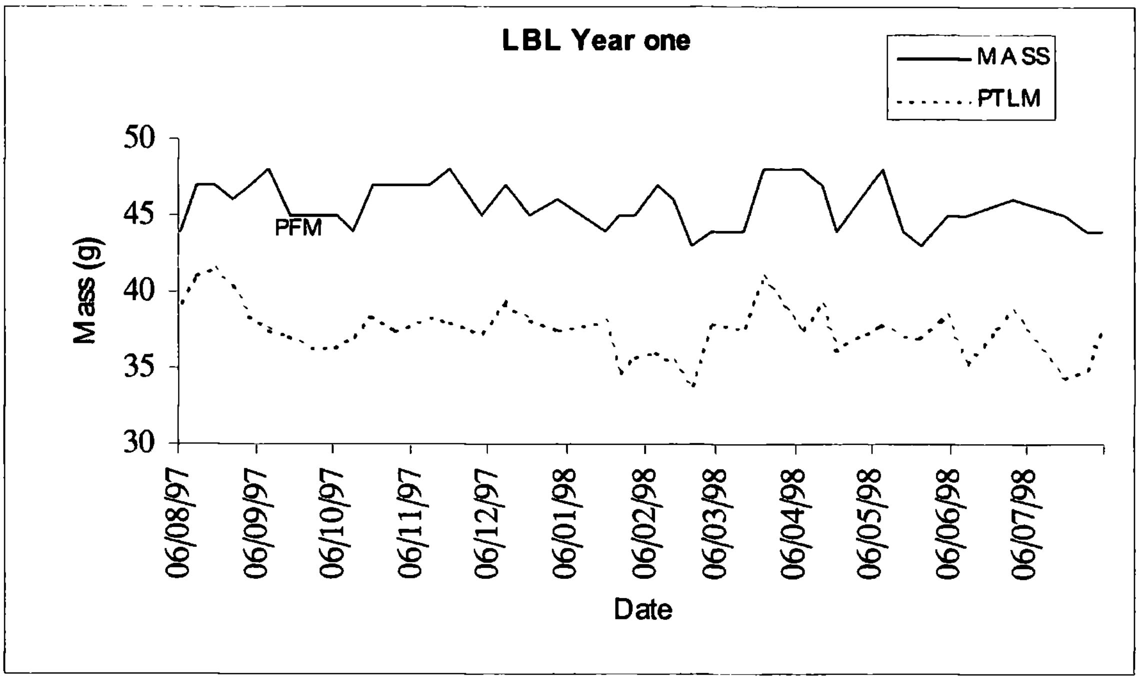

LRE Year two
MASS
PTLM
Mass (g)
60
55
50
45
40
35
30
17/08/98
17/09/98
17/10/98
17/11/98
17/12/98
17/01/99
17/02/99
17/03/99
17/04/99
17/05/99
Date


LLG Year one
MASS
PTLM
PFM
Mass (g)
50
45
40
35
30
06/08/97
06/09/97
06/10/97
06/11/97
06/12/97
06/01/98
06/02/98
06/03/98
06/04/98
06/05/98
06/06/98
06/07/98
Date


LLG Year two
MASS
PTLM
Mass (g)
55
50
45
40
35
30
17/08/98
31/08/98
14/09/98
28/09/98
12/10/98
26/10/98
09/11/98
23/11/98
07/12/98
21/12/98
04/01/99
18/01/99
01/02/99
15/02/99
01/03/99
15/03/99
29/03/99
12/04/99
Date


WOR Year one
MASS
PTLM
Mass (g)
70
65
60
55
50
45
40
35
PFM
06/08/97
06/09/97
06/10/97
06/11/97
06/12/97
06/01/98
06/02/98
06/03/98
06/04/98
06/05/98
06/06/98
06/07/98
Date


WOR Year two
MASS
PTLM
Mass (g)
70
65
60
55
50
45
40
35
17/08/98
14/09/98
06/10/98
16/10/98
25/10/98
01/11/98
09/11/98
20/11/98
10/12/98
06/01/99
28/01/99
26/02/99
05/04/99
28/04/99
13/05/99
25/05/99
03/06/99
24/06/99
Date


LBL Year one
MASS
PTLM
PFM
Mass (g)
50
45
40
35
30
06/08/97
06/09/97
06/10/97
06/11/97
06/12/97
06/01/98
06/02/98
06/03/98
06/04/98
06/05/98
06/06/98
06/07/98
Date

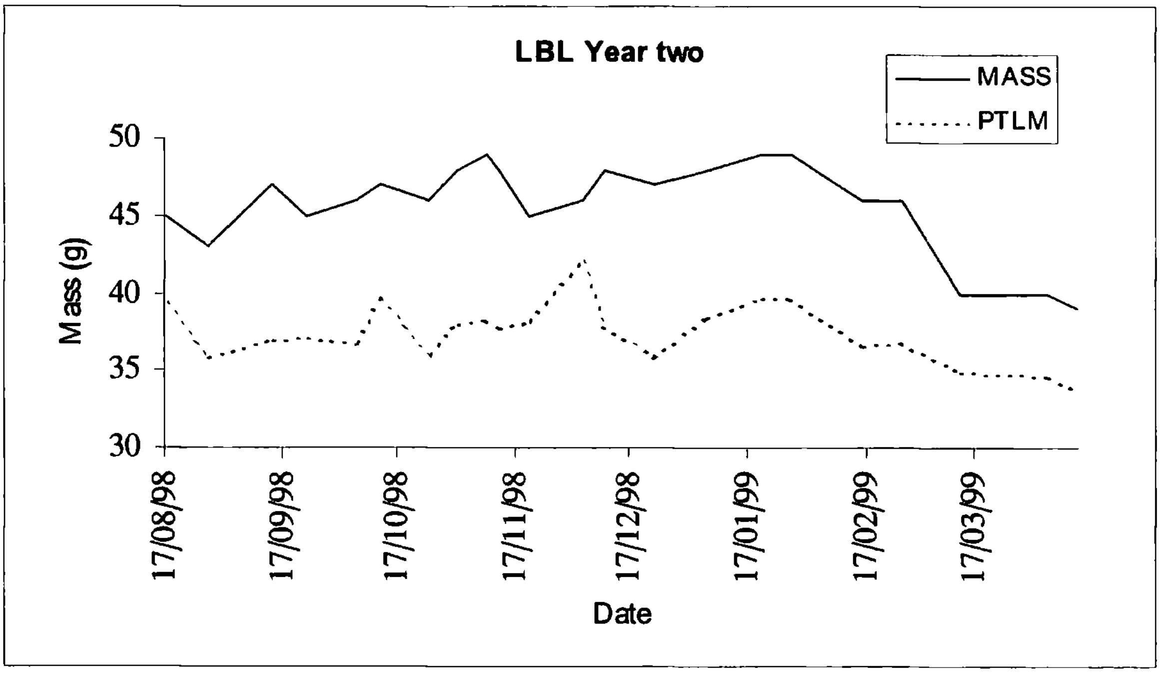

LBL Year two
MASS
PTLM
Mass (g)
50
45
40
35
30
17/08/98
17/09/98
17/10/98
17/11/98
17/12/98
17/01/99
17/02/99
17/03/99
Date

Table 1: ***C.a.alpina***

Colour marks	**Date of capture**	**Age at capture**	**Sex***
DG	24/9/1996	Juvenile	Male
LG	=	=	Female
OR	=	=	Male
BLU	=	=	Male
YEL	=	=	Female
RE	=	=	Male

* Determined by dissection at the end of experiment

Table2: ***C.a.schinzii***

Colour marks	**Date of capture**	**Age at capture**	**Sex***
WBL	30/9/97	Juvenile	Male
WOR	=	Juvenile	Female
LRE	=	Juvenile	Female
LLG	=	Adult	Female
WRE	=	Juvenile	Male
LBL	=	Adult	Male
LYEL	=	Adult	Male
WDG	=	Juvenile	Male
WLG	=	Adult	Female

* Determined by dissection at the end of experiment

Appendix IV

Measurements of Basal Metabolic Rate (BMR), Predicted Total Lean Mass (PTLM) and Predicted Fat Mass (PFM) for *C.a.alpina* (individuals DG, BLU, LG, YEL, RE and OR) and for *C.a.schinzii* (individuals WBL, LYEL, WDG, LRE, WOR, LBL, WLG and WRE) throughout their periods of captivity

OR **Juvenile**

	Mass (g)	PTLM (g)	PFM (g)	BMR (watts)
29/10/96	55	38.82	16.18	0.749
30/11/96	48	41.65	6.35	0.739
25/12/96	48	40.75	7.25	0.739
21/01/97	48	42.04	5.96	0.736
21/02/97	43	39.93	3.07	0.578
21/03/97	46	41.26	4.74	0.67
25/04/97	45	41.13	3.87	0.73
14/05/97	45	41.54	3.46	0.686
17/06/97	45	41.56	3.44	0.609
10/07/97	45	42.08	2.92	0.64
12/08/97	43	42.06	0.94	0.63
11/09/97	42	41.55	0.45	0.67
22/10/97	44	41.6	2.40	0.636
25/11/97	48	42.3	5.7	0.73
15/01/98	47	41.64	5.36	0.83
10/03/98	46	42.7	3.3	0.73
29/04/98	46	38.08	7.92	0.689
28/05/98	46	40.6	5.40	0.77
10/06/98	48	41.32	6.68	0.92
30/06/98	44	40.07	3.93	0.67
04/07/98	44	39.87	4.13	0.768
12/08/98	46	41.85	4.15	0.939
21/09/98	49	43.05	5.95	0.754
21/10/98	46	41.53	4.47	0.71
04/11/98	47	41.44	5.55	0.71
06/01/99	45	41.15	3.84	0.74
08/02/99	46	39.95	6.05	0.674
12/04/99	46	42.07	3.93	0.698
14/05/99	48	41.75	6.25	0.729
20/05/99	54	43.98	10.02	0.91
26/05/99	59	43.87	15.13	0.93
31/05/99	66	44.25	21.75	0.96
05/06/99	60	44.47	15.53	0.98
08/06/99	58	42.70	15.30	1.09
23/06/99	55	39.40	15.59	0.829

Note: PTLM was estimated from the TOBEC index (I) using the calibration graph for captive birds PTLM = (0.42 * I) + 21.7

DG Juvenile

	Mass (g)	PTLM (g)	PFM (g)	BMR (watts)
29/10/96	48	37.1	10.9	0.796
30/11/96	50	38.73	11.27	0.736
25/12/96	49	39.61	9.39	0.688
21/01/97	48	39.88	8.12	0.876
21/02/97	47	38.36	8.64	0.761
21/03/97	45	40.54	4.46	0.596
25/04/97	45	40.94	4.06	0.54
14/05/97	44	40.73	3.27	0.689
17/06/97	46	41.11	4.89	0.635
10/07/97	44	42.32	1.68	0.56
12/08/97	44	40.35	3.65	0.78
05/09/97	44	41.91	2.09	0.74
22/10/97	46	42	4	0.69
25/11/97	49	41.9	7.1	0.6
01/01/98	48	40.59	7.41	0.666
10/03/98	46	41.8	4.2	0.639
29/04/98	46	42.16	3.84	0.647
28/05/98	54	43.72	10.28	0.801
02/06/98	57	44.09	12.91	0.899
06/06/98	62	44.4	17.6	0.934
10/06/98	53	43.84	9.16	0.955
13/06/98	48	42.07	5.93	0.82
21/06/98	46	42.02	3.98	0.672
04/07/98	45	40.92	4.08	0.781
29/07/98	46	42.04	3.96	0.93
06/09/98	51	44.32	6.68	0.709
06/10/98	48	42.67	5.33	0.697
04/11/98	47	42.85	4.15	0.71
06/01/99	47	38.46	8.54	0.73
08/02/99	46	40.5	5.5	0.706
12/04/99	46	41.5	4.5	0.698
14/05/99	47	41.8	5.2	0.8
20/05/99	47	40.83	6.17	0.88
26/05/99	51	42.03	8.97	0.655
31/05/99	57	42.99	14.01	0.982
03/06/99	57	41.19	15.81	0.95
07/06/99	52	39.7	12.3	0.83
23/06/99	47	38.59	8.41	0.7

LG **Juvenile**

	Mass (g)	PTLM (g)	PFM (g)	BMR (watts)
29/10/96	64	41.6	22.4	0.732
30/11/96	55	42.2	12.8	0.874
25/12/96	56	44.09	11.91	0.724
21/01/97	55	42.04	12.96	0.759
21/02/97	54	40.52	13.48	0.564
21/03/97	50	41.05	8.95	0.61
25/04/97	50	40.44	9.56	0.55
14/05/97	50	41.5	8.5	0.655
17/06/97	50	41.31	8.69	0.653
10/07/97	49	43.29	5.71	0.67
12/08/97	47	42.68	4.32	0.74
05/09/97	48	41.7	6.3	0.83
22/10/97	49	42.2	6.8	0.737
25/10/97	48	41.7	6.3	0.72
01/01/98	49	42.36	6.64	0.82
10/03/98	50	42.5	7.5	0.68
29/04/98	50	40.6	9.4	0.754
28/05/98	54	42.71	11.29	0.687
01/06/98	62	44.22	17.78	0.812
04/06/98	66	45.33	20.67	0.87
08/06/98	63	44.79	18.21	0.924
29/07/98	47	39.77	7.23	0.69
12/08/98	48	40.82	7.18	0.808
21/09/98	52	45.51	6.49	0.93
29/10/98	50	44.45	5.55	0.76
06/11/98	47	42.76	4.24	0.72
06/01/99	45	38.63	6.37	0.68
08/02/99	45	39.04	5.96	0.704
12/04/99	48	42.1	5.9	0.74
14/05/99	49	41.45	7.55	0.77
20/05/99	48	41.37	6.63	0.83
26/05/99	53	41.78	11.22	1.008
30/05/99	57	42.99	14.01	0.98
03/06/99	57	44.02	12.98	0.95
07/06/99	60	42.72	17.28	1.02
11/06/99	63	43.03	19.97	1.03
14/06/99	63	41.51	21.49	0.96
17/06/99	63	42.01	20.99	0.93
23/06/99	58	40.42	17.58	1.122

BLU **Juvenile**

	Mass (g)	PTLM (g)	PFM (g)	BMR (watts)
29/10/96	45	38.3	6.7	0.699
30/11/96	44	39.3	4.7	0.967
25/12/96	43	39.01	3.99	0.876
21/01/97	42	38.35	3.65	0.75
21/02/97	41	37.22	3.78	0.579
21/03/97	42	37.7	4.3	0.765
25/04/97	41	36.07	4.93	0.68
14/05/97	43	39.54	3.46	0.67
17/06/97	43	38.63	4.37	0.66
10/07/97	42	38.76	3.24	0.69
12/08/97	42	40.49	1.51	0.77
11/09/97	40	38.51	1.49	0.75
22/10/97	42	39	3	0.652
05/12/97	44	39	5	0.81
01/01/98	43	38.86	4.14	0.66
10/03/98	44	40	4	0.719
29/04/98	43	39.34	3.66	0.662
28/05/98	48	39.46	8.54	0.756
02/06/98	56	42.68	13.32	0.867
06/06/98	59	44.19	14.81	0.884
10/06/98	54	42.64	11.36	0.914
13/06/98	48	39.03	8.97	0.687
30/06/98	43	38.86	4.14	0.725
21/07/98	43	39.04	3.96	0.89
06/09/98	45	37.89	7.11	0.701
12/10/98	44	39.8	4.2	0.66
10/11/98	43	39.24	3.76	0.658
06/01/99	42	33.98	8.02	0.687
08/02/99	41	37.08	3.92	0.674
12/04/99	43	38.63	4.37	0.66
14/05/99	43	38.62	4.38	0.648
19/05/99	45	39.04	5.96	0.82
26/05/99	50	40.16	9.84	0.91
30/05/99	54	39.94	14.06	0.968
04/06/99	50	40.92	9.08	1.08
08/06/99	43	37.1	5.9	0.66
23/06/99	40	36.78	3.22	0.63

RE **Juvenile**

	Mass (g)	PTLM (g)	PFM (g)	BMR (watts)
29/10/96	49	38.76	10.24	0.774
30/11/96	46	39.99	6.01	0.8
25/12/96	48	40.56	7.44	0.722
21/01/97	47	40.13	6.87	0.796
21/02/97	45	38.95	6.05	0.581
21/03/97	43	37.95	5.05	0.549
25/04/97	45	39.95	5.05	0.515
14/05/97	45	40.54	4.46	0.66
17/06/97	45	39.34	5.66	0.56
10/07/97	44	39.67	4.33	0.58
12/08/97	44	40.08	3.92	0.67
11/09/97	47	40.74	6.26	0.8
22/10/97	44	40.43	3.57	0.658
05/12/97	47	41.76	5.24	0.76
01/01/98	44	39.4	4.6	0.667
10/03/98	45	40.8	4.2	0.657
29/04/98	46	42	4	0.66
28/05/98	49	42.5	6.5	0.83
01/06/98	55	43.71	11.29	0.836
04/06/98	61	44.72	16.28	0.91
08/06/98	58	43.79	14.21	0.935
21/07/98	43	38.83	4.17	0.693
12/08/98	44	38.56	5.44	0.725
21/09/98	46	41.7	4.3	0.937
12/10/98	46	41.58	4.42	0.73
10/11/98	46	41.22	4.78	0.68
06/01/99	44	39.9646	4.0354	0.672
08/02/98	44	39.39	4.61	0.683
12/04/99	44	39.84	4.16	0.699
14/05/99	45	41.1	3.9	0.72
19/05/99	45	40.93	4.07	0.74
26/05/99	45	41.14	3.86	0.66
31/05/99	48	42.24	5.76	0.88
04/06/99	48	42.32	5.68	0.83
08/06/99	54	42.29	11.71	0.84
11/06/99	50	41.64	8.36	0.73
14/06/99	53	41.3	11.7	0.77
17/06/99	53	41.2	11.8	0.965
23/06/99	45	40.41	4.59	0.67

YEL Juvenile

	Mass (g)	PTLM (g)	PFM (g)	BMR (watts)
29/10/96	56	40.59	15.41	0.82
30/11/96	54	41.27	12.73	0.727
25/12/96	51	41.09	9.91	0.681
21/01/97	53	41.45	11.55	0.71
21/02/97	49	39.77	9.23	0.556
21/03/97	48	38.96	9.04	0.509
25/04/97	50	41.03	8.97	0.63
14/05/97	51	38.71	12.29	0.67
17/06/97	55	41.02	13.98	0.657
10/07/97	52	39.74	12.26	0.82
12/08/97	51	39.11	11.89	0.65
04/09/97	48	39.84	8.16	0.738
22/10/97	46	42.6	3.4	0.711
25/11/97	48	40.8	7.2	0.747
01/01/98	47	40.76	6.24	0.648
10/03/98	49	42.6	6.4	0.63
29/04/98	51	41	10	0.71
28/05/98	54	43.31	10.69	0.82
01/06/98	58	44.22	13.78	0.85
04/06/98	63	46.1	16.9	0.961
08/06/98	55	42.7	12.3	0.982
21/07/98	47	41.9	5.1	0.667
29/07/98	47	40.59	6.41	0.77
06/09/98	49	41.43	7.57	0.95
29/10/98	51	43.9	7.1	0.707
21/11/98	46	41.61	4.39	0.687
06/01/99	46	40.956	5.0443	0.695
08/02/98	46	41.45	4.55	0.709
12/04/99	45	39.83	5.17	0.69
14/05/99	51	43.39	7.61	0.91
19/05/99	54	42.55	11.45	0.866
26/05/99	51	41.14	9.86	0.81
31/05/99	48	38.76	9.24	0.726
05/06/99	47	39.23	7.77	0.8
11/06/99	47	38.85	8.15	0.78

WBL **Juvenile**

	MASS (g)	PFM (g)	FAT (g)	BMR (watts)
12/11/97	44	36.11	7.89	0.677
02/01/98	40	35.1	4.9	0.75
02/02/98	43	31.72	11.28	0.57
24/03/98	38	35.31	2.69	0.68
22/04/98	38	34.03	3.97	0.66
29/07/98	39	36.17	2.83	0.619
17/08/98	40	34.75	5.25	0.644
28/08/98	40	35.6	4.4	0.701
06/10/98	41	36.69	4.31	0.889
01/11/98	44	36.64	7.36	0.679
12/11/98	43	36.92	6.08	0.655
06/01/99	40	36.14	3.86	0.59
26/02/99	38	33.2	4.8	0.621
13/04/99	38	34.18	3.82	0.65
13/05/99	40	36.02	3.98	0.63
17/05/99	43	36.21	6.79	0.72
25/05/99	52	39.3	12.7	0.94
30/05/99	50	37.33	12.67	1.022
04/06/99	42	35.5	6.5	0.66
24/06/99	35	31.11	3.89	0.54

LYEL **Adult**

	MASS (g)	PTLM (g)	FAT (g)	BMR (watts)
12/11/97	47	35.32	11.68	0.69
02/01/98	46	35.89	10.11	0.83
02/02/98	48	33.48	14.52	0.74
24/03/98	48	38.5	9.5	0.697
22/04/98	47	37.06	9.94	0.82
12/06/98	46	37.72	8.28	0.77
21/07/98	41	35.5	5.5	0.668
17/08/98	43	37.2	5.8	0.757
14/09/98	48	35.81	12.19	0.875
06/10/98	52	36.29	15.71	0.774
20/10/98	59	35.54	23.46	0.723
28/10/98	58	35.03	22.97	0.831907
04/11/98	63	34.89	28.11	0.88423
09/11/98	60	36.27	23.73	0.914152
12/11/98	52	34.54	17.46	0.805
20/11/98	49	35.92	13.08	0.805
06/01/99	46	35.54	10.46	0.58
26/02/99	47	37	10	0.61
13/04/99	41	36.97	4.03	0.633
13/05/99	48	36.06	11.94	0.72
17/05/99	54	37.68	16.32	0.94
25/05/99	60	39.69	20.31	0.81
30/05/99	58	39.85	18.15	0.993
03/06/99	52	37.67	14.33	0.802
07/06/99	47	36.52	10.48	0.7
24/06/99	40	35.94	4.06	0.63

WDG JUV.

	MASS (g)	PTLM (g)	FAT (g)	BMR (watts)
12/11/97	54	35.91	18.09	0.64
02/01/98	43	34.9	8.1	0.78
02/02/98	39	32.31	6.69	0.547
22/04/98	39	37.51	1.49	0.71
12/06/98	41	35.1	5.9	0.69
05/08/98	38	36.6	1.4	0.632
17/08/98	40	37.41	2.59	0.738
14/09/98	41	36.81	4.19	0.876
06/10/98	48	36.28	11.72	0.685
17/10/98	48	35.44	12.56	0.608
20/10/98	48	33.62	14.38	0.65732
29/10/98	54	33.81	20.19	0.72806
01/11/98	53	33.85	19.15	0.6977
05/11/98	52	34.45	17.55	0.6977
09/11/98	52	34.48	17.52	0.6977
12/11/98	52	34.73	17.27	0.708
06/01/99	40	35.34	4.66	0.642
26/02/99	38	34.21	3.79	0.56
13/04/99	40	35.96	4.04	0.59
13/05/99	44	33.39	10.61	0.71
17/05/99	46	34.85	11.15	0.798
25/05/99	53	36.85	16.15	0.836
30/05/99	53	37.86	15.14	0.9
04/06/99	47	34.68	12.32	0.724
24/06/99	39	35.49	3.51	0.6

WRED **Juvenile**

	MASS (g)	PTLM (g)	FAT (g)	BMR (watts)
12/11/97	42	36.3	5.7	0.64
02/01/98	39	36.28	2.72	0.75
02/02/98	39	36.5	2.5	0.61

WLG **Adult**

	MASS (g)	PTLM (g)	FAT (g)	BMR (watts)
12/11/97	54	34.13	19.87	0.72
02/01/98	40	34.9	5.1	0.78
02/02/98	39	33.15	5.85	0.57
24/03/98	38	35.24	2.76	0.69

LRED **Juvenile**

	MASS (g)	PTLM (g)	FAT (g)	BMR (watts)
12/11/97	44	35.12	8.88	0.69
02/01/98	45	36.68	8.32	0.79
02/02/98	47	33.98	13.02	0.66
24/02/98	46	32.49	13.51	0.7
22/04/98	47	36.25	10.75	0.78
25/05/98	44	40.33	3.67	0.675
29/07/98	45	36.06	8.94	0.711
28/08/98	46	35.9	10.1	0.7
20/10/98	46	35.97	10.03	0.645
23/12/98	47	37.11	9.89	0.77
15/02/99	47	34.79	12.21	0.669
13/03/99	48	38.47	9.53	0.654
13/04/99	45	36.5	8.5	0.72

LLG **Adult**

	MASS (g)	PTLM (g)	PFAT (g)	BMR (watts)
12/11/97	46	35.9	10.1	0.75
02/01/98	41	36.09	4.91	0.75
02/02/98	44	33.97	10.03	0.668
24/03/98	44	32.86	11.14	0.72
22/04/98	42	38.7	3.3	0.71
12/06/98	39	35.3	3.7	0.64
17/08/98	40	36.39	3.61	0.625
14/09/98	42	36.61	5.39	0.674
06/10/98	40	36.09	3.91	0.84
29/10/98	47	39.02	7.98	0.752
10/12/98	42	36.62	5.38	0.61
06/01/99	41	36.63	4.37	0.678
26/02/99	41	35.41	5.59	0.642
13/04/99	39	36.1	2.9	0.67

LBL **Adult**

	MASS (g)	PTLM (g)	PFAT (g)	BMR (watts)
12/11/97	47	38.27	8.73	0.72
02/01/98	46	37.47	8.53	0.84
02/02/98	45	35.71	9.29	0.7
24/03/98	48	40.89	7.11	0.72
22/04/98	44	36.21	7.79	0.78
29/07/98	44	34.84	9.16	0.739
28/08/98	43	35.8	7.2	0.75
23/12/98	47	35.75	11.25	0.7
15/02/99	46	36.62	9.38	0.656
13/04/99	39	33.7	5.3	0.683

WOR **Juvenile**

	MASS (g)	PTLM (g)	PFAT (g)	BMR (watts)
12/11/97	64	44.75	19.25	0.73
02/01/98	49	43.1	5.9	0.735
02/02/98	51	42.31	8.69	0.61
24/03/98	47	42.77	4.23	0.69
22/04/98	47	43.09	3.91	0.77
12/06/98	46	37.32	8.68	0.73
05/08/98	48	44.77	3.23	0.69
28/08/98	49	42.79	6.21	0.779
12/10/98	54	43.97	10.03	0.9
20/10/98	65	44.24	20.76	0.68
28/10/98	63	44.87	18.13	0.723
01/11/98	60	44.51	15.49	0.89
05/11/98	63	44.87	18.13	0.868
09/11/98	60	44.51	15.49	0.824
12/11/98	55	43.89	11.11	0.806
20/11/98	51	44.3	6.7	0.806
06/01/99	49	44.5	4.5	0.694
26/02/99	47	43.01	3.99	0.678
13/04/99	46	43.15	2.85	0.69
13/05/99	51	43.9	7.1	0.74
17/05/99	59	47.21	11.79	1.08
25/05/99	63	45.43	17.57	0.96
30/05/99	55	41.9	13.1	0.941
03/06/99	50	41.94	8.06	0.72
07/06/99	46	41.15	4.85	0.67
24/06/99	49	39.96	9.04	0.78

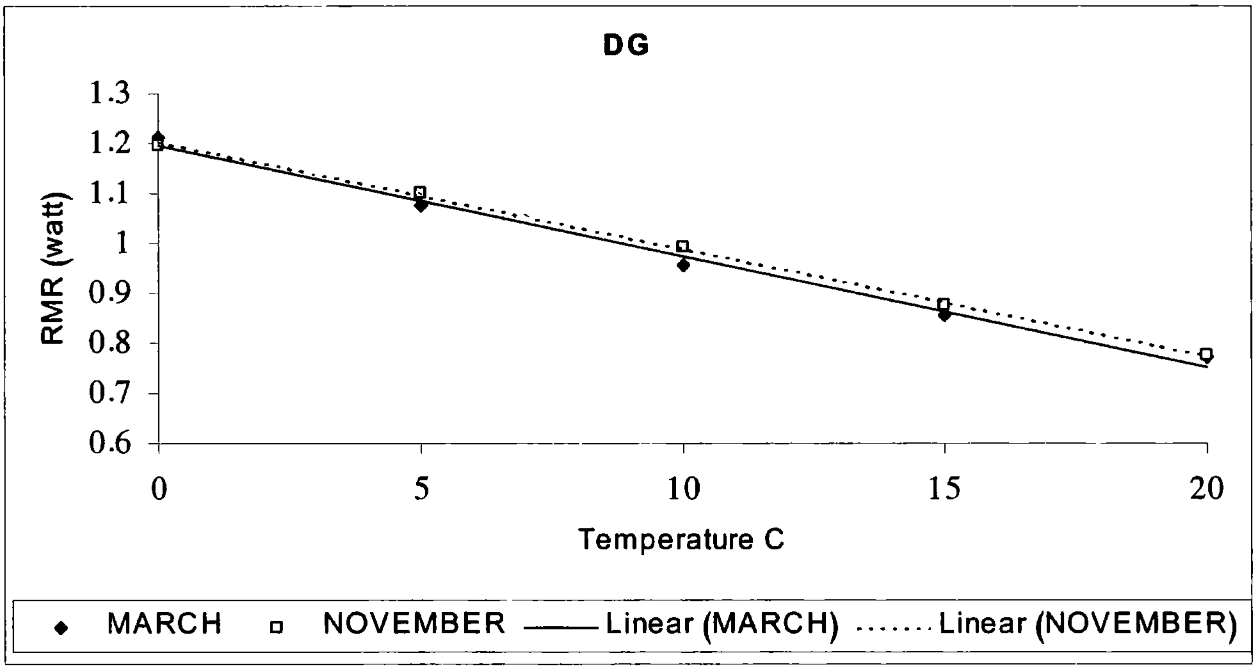
WOR **Juvenile**

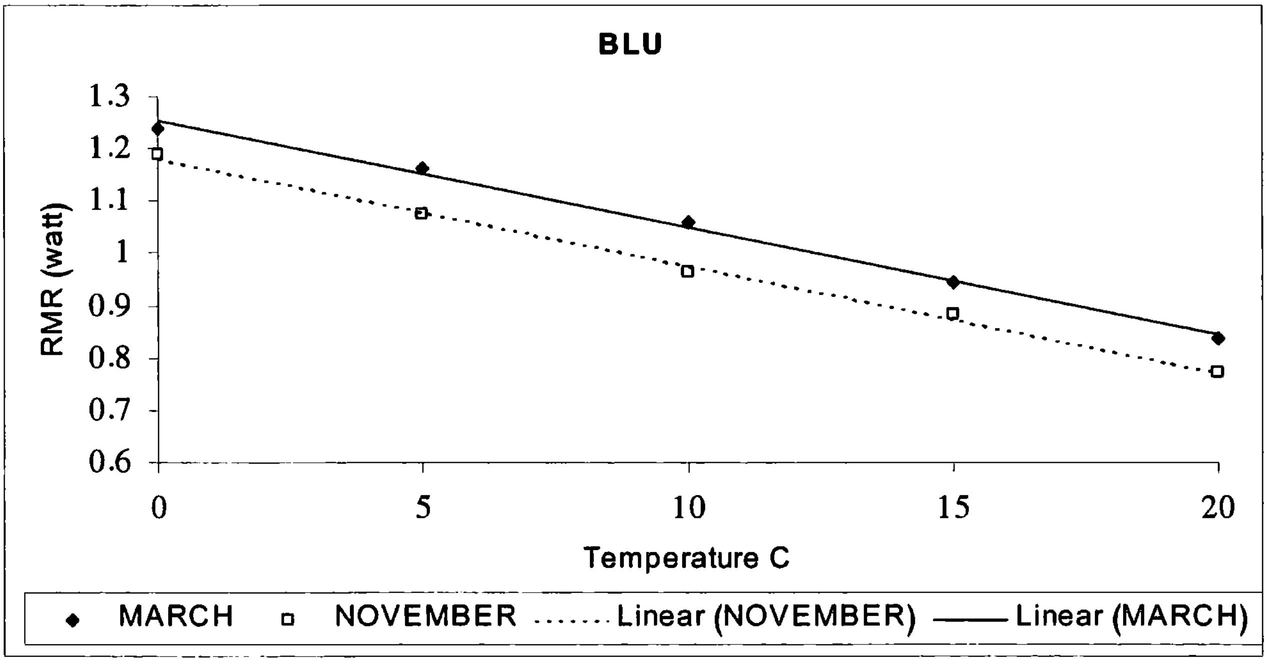
	MASS (g)	PTLM (g)	PFAT (g)	BMR (watts)
12/11/97	64	44.75	19.25	0.73
02/01/98	49	43.1	5.9	0.735
02/02/98	51	42.31	8.69	0.61
24/03/98	47	42.77	4.23	0.69
22/04/98	47	43.09	3.91	0.77
12/06/98	46	37.32	8.68	0.73
05/08/98	48	44.77	3.23	0.69
28/08/98	49	42.79	6.21	0.779
12/10/98	54	43.97	10.03	0.9
20/10/98	65	44.24	20.76	0.68
28/10/98	63	44.87	18.13	0.723
01/11/98	60	44.51	15.49	0.89
05/11/98	63	44.87	18.13	0.868
09/11/98	60	44.51	15.49	0.824
12/11/98	55	43.89	11.11	0.806
20/11/98	51	44.3	6.7	0.806
06/01/99	49	44.5	4.5	0.694
26/02/99	47	43.01	3.99	0.678
13/04/99	46	43.15	2.85	0.69
13/05/99	51	43.9	7.1	0.74
17/05/99	59	47.21	11.79	1.08
25/05/99	63	45.43	17.57	0.96
30/05/99	55	41.9	13.1	0.941
03/06/99	50	41.94	8.06	0.72
07/06/99	46	41.15	4.85	0.67
24/06/99	49	39.96	9.04	0.78

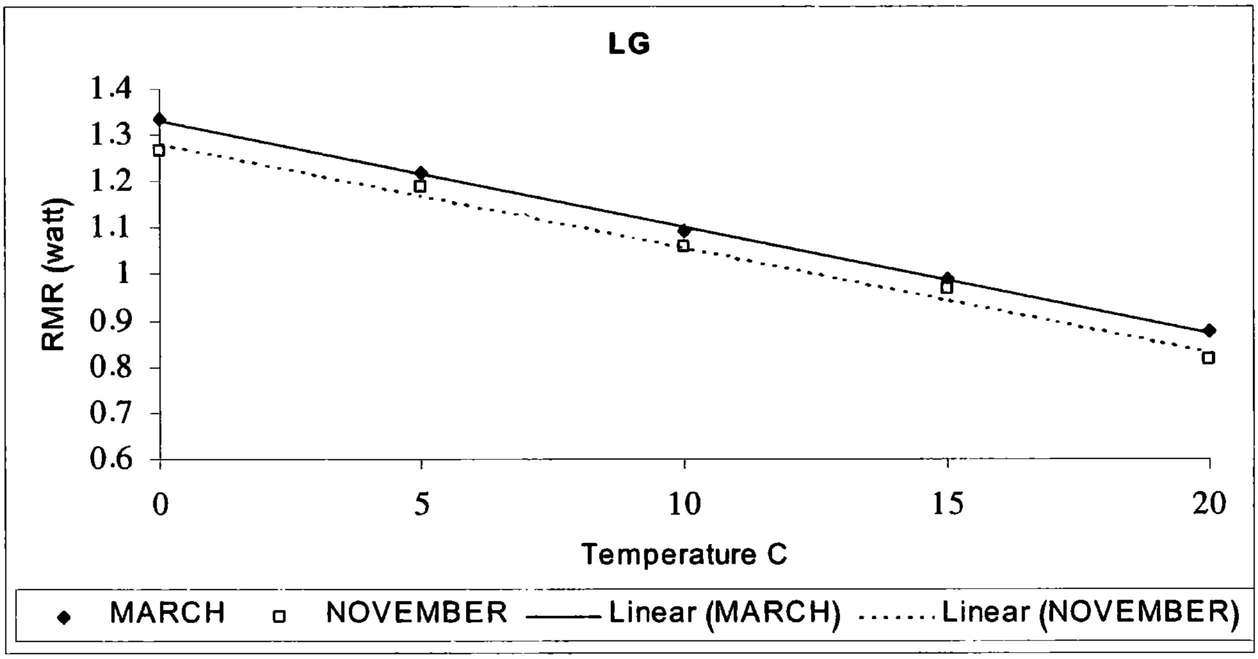
Appendix V

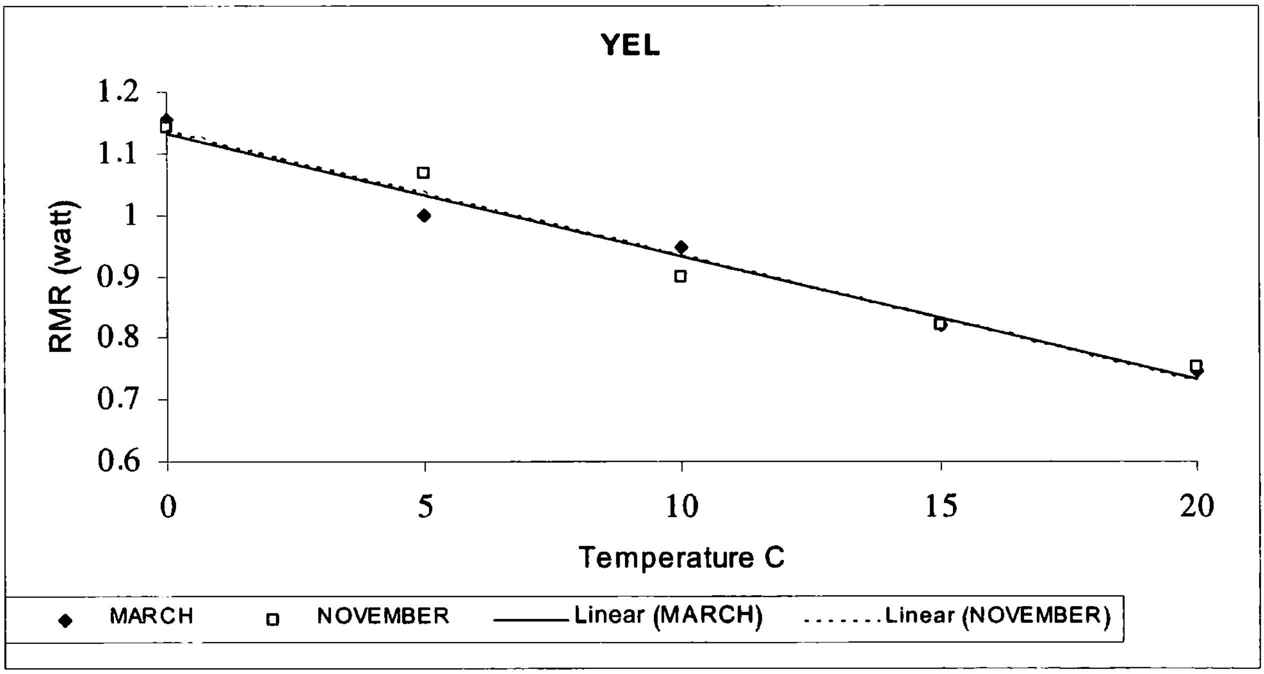
The relationship between Resting Metabolic Rate and Temperature in individual *C.a.alpina* and in *C.a.schinzii*

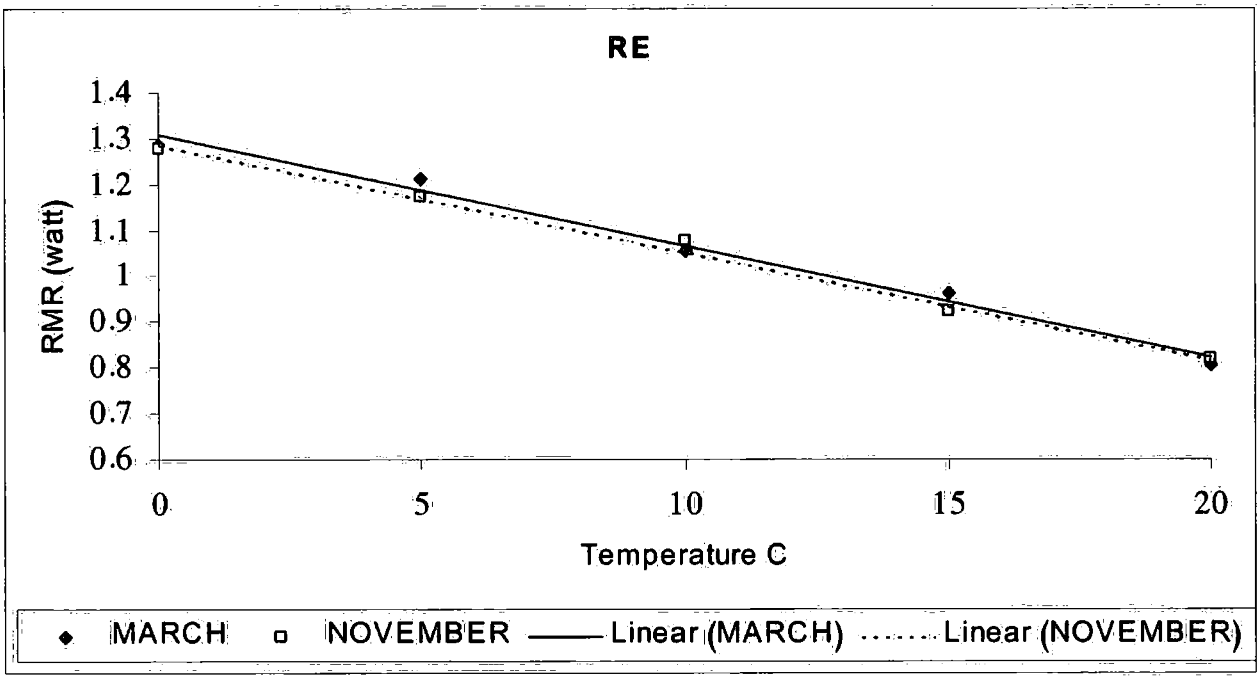
Individuals DG, BLU, LG, YEL, RE and OR are captive *C.a.alpina* and individuals WBL, LYEL, WDG, WOR and LLG are *C.a.schinzii*






LG
RMR (watt)
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0
5
10
15
20
Temperature C
MARCH
NOVEMBER
Linear (MARCH)
Linear (NOVEMBER)


YEL
RMR (watt)
1.2
1.1
1
0.9
0.8
0.7
0.6
0
5
10
15
20
Temperature C
MARCH
NOVEMBER
Linear (MARCH)
Linear (NOVEMBER)


RE
RMR (watt)
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0
5
10
15
20
Temperature C
MARCH
NOVEMBER
Linear (MARCH)
Linear (NOVEMBER)

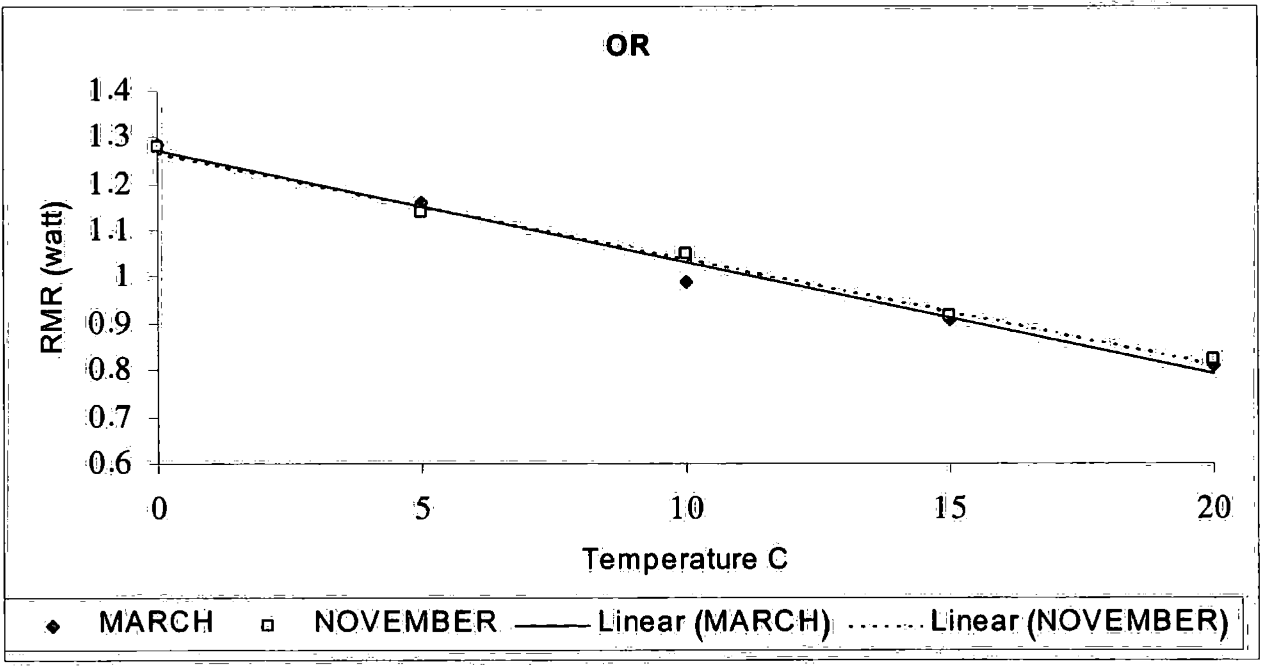
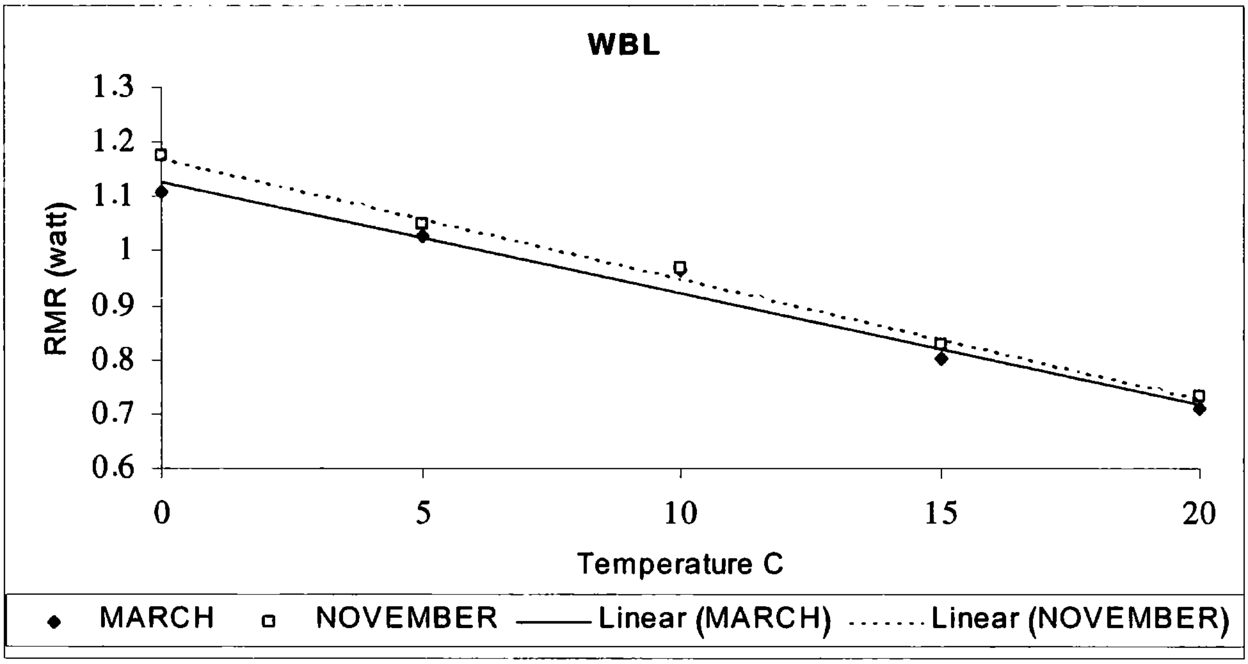
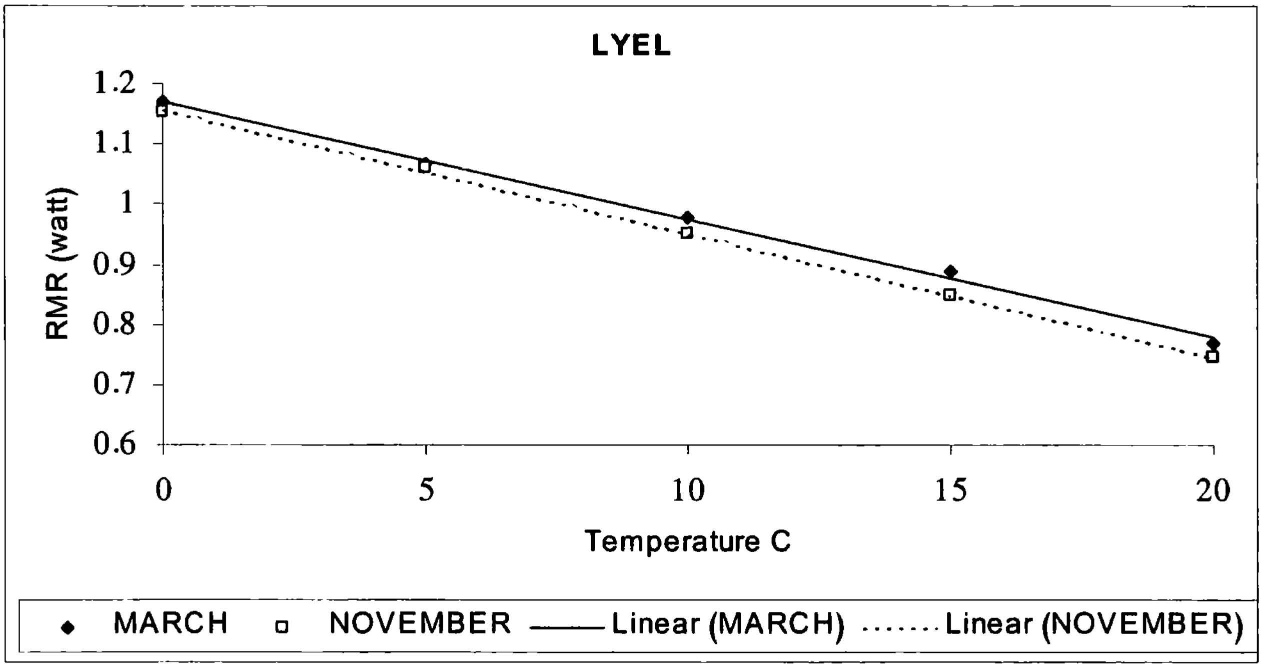
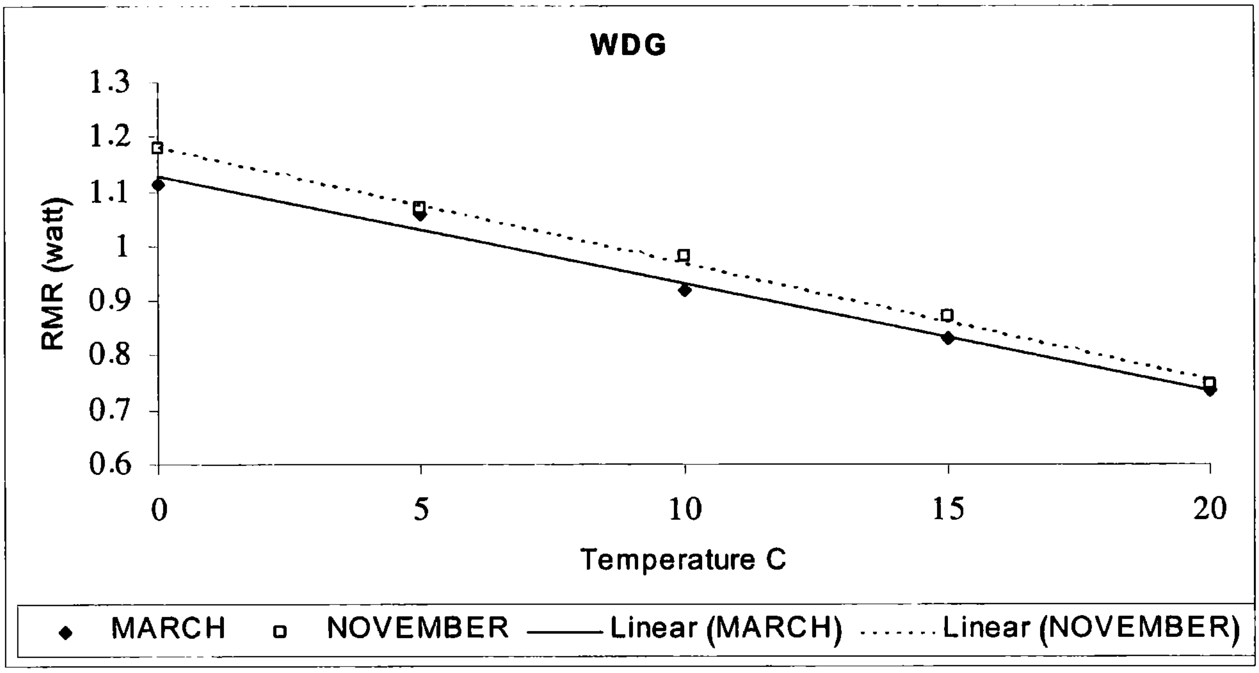

OR
RMR (watt)
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0
5
10
15
20
Temperature C
MARCH
NOVEMBER
Linear (MARCH)
Linear (NOVEMBER)

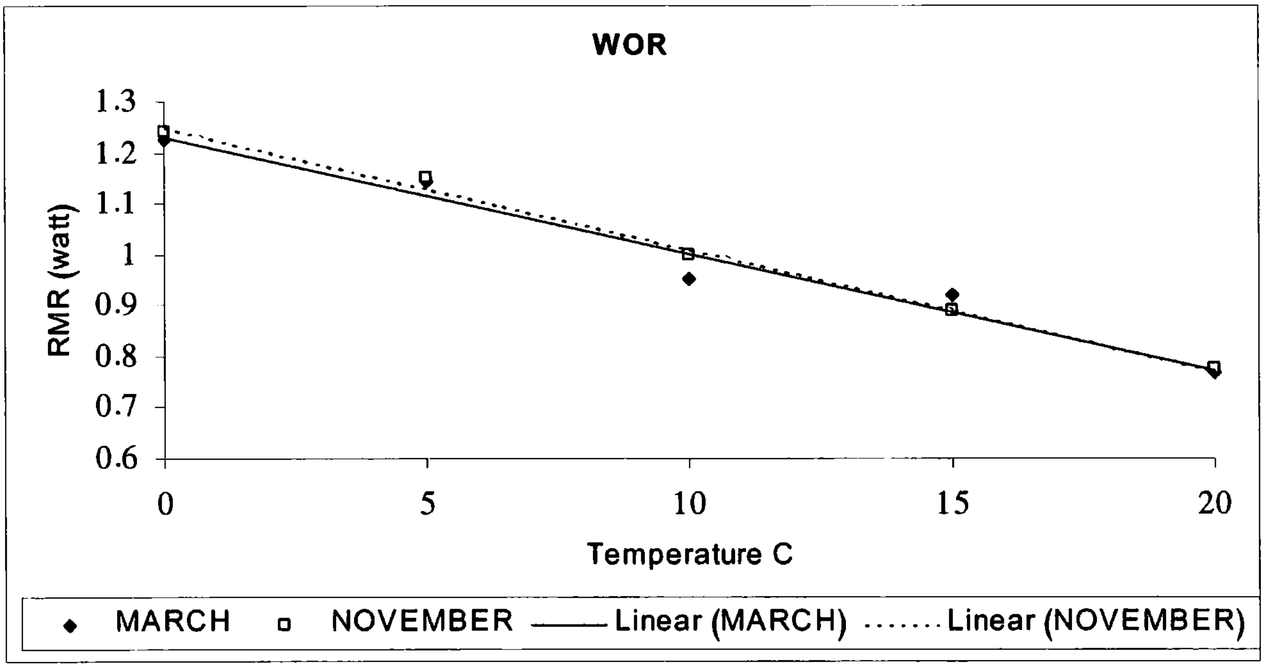
Table 1: Slopes (watts per °C) and intercept values at 0 °C (watts) of the relationship between RMR and temperature taken in March and November for six *C.a.alpina*

Individual	March		November	
	Slope	**Intercept**	**Slope**	**Intercept**
DG	0.0221	1.195	0.0213	1.2021
YEL	0.0200	1.1334	0.0203	1.1397
LG	0.0229	1.3306	0.0224	1.2824
BLU	0.0203	1.2524	0.0204	1.1807
OR	0.0241	1.272	0.0212	1.2694
RE	0.0243	1.3068	0.0233	1.2864


WBL
RMR (watt)
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0
5
10
15
20
Temperature C
◆ MARCH
□ NOVEMBER
—— Linear (MARCH)
······ Linear (NOVEMBER)


LYEL
RMR (watt)
1.2
1.1
1
0.9
0.8
0.7
0.6
0
5
10
15
20
Temperature C
◆ MARCH
□ NOVEMBER
—— Linear (MARCH)
······ Linear (NOVEMBER)


WDG
RMR (watt)
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0
5
10
15
20
Temperature C
◆ MARCH
□ NOVEMBER
—— Linear (MARCH)
······· Linear (NOVEMBER)


WOR
RMR (watt)
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0
5
10
15
20
Temperature C
◆ MARCH
□ NOVEMBER
—— Linear (MARCH)
······· Linear (NOVEMBER)

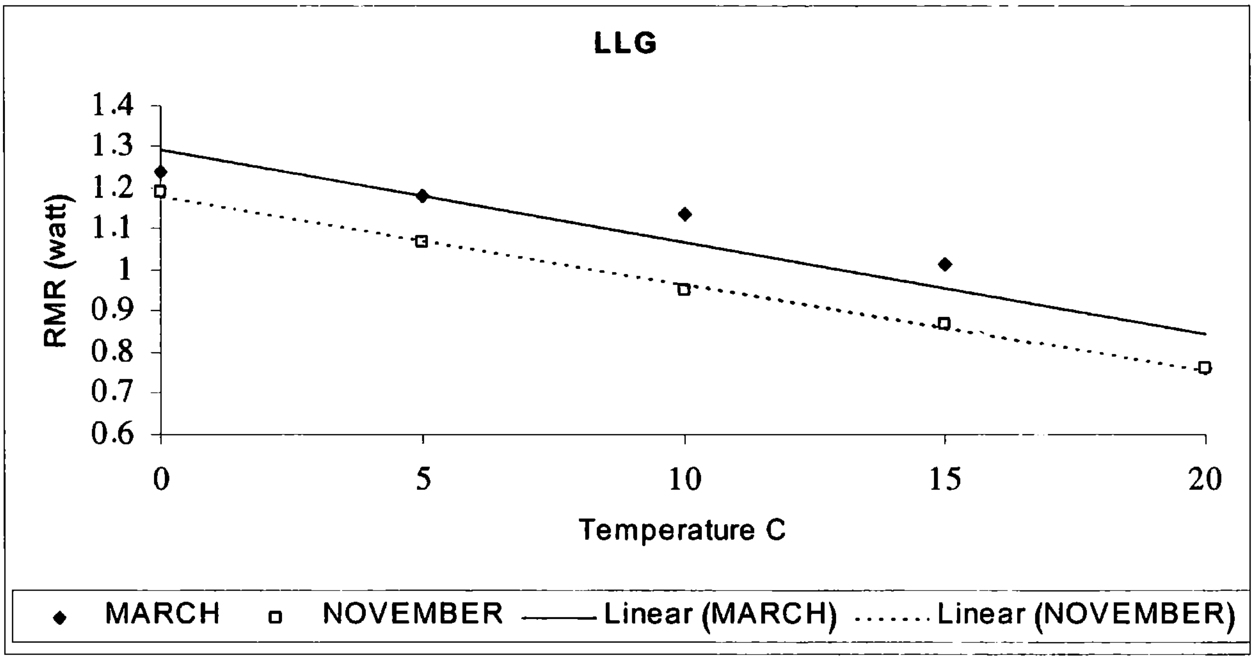


Table 2: Slopes (watts per °C) and intercept values at 0 °C (watts) of the relationship between RMR and temperature taken in March and November for five *C.a.schinzii*

	March		**November**	
Individual	**Slope**	**Intercept**	**Slope**	**Intercept**
WBL	0.0203	1.1258	0.0221	1.1716
LYEL	0.0195	1.1696	0.0205	1.157
WDG	0.0198	1.1292	0.0213	1.1822
WOR	0.0229	1.231	0.0237	1.248
LLG	0.0223	1.2908	0.0212	1.18

Appendix VI

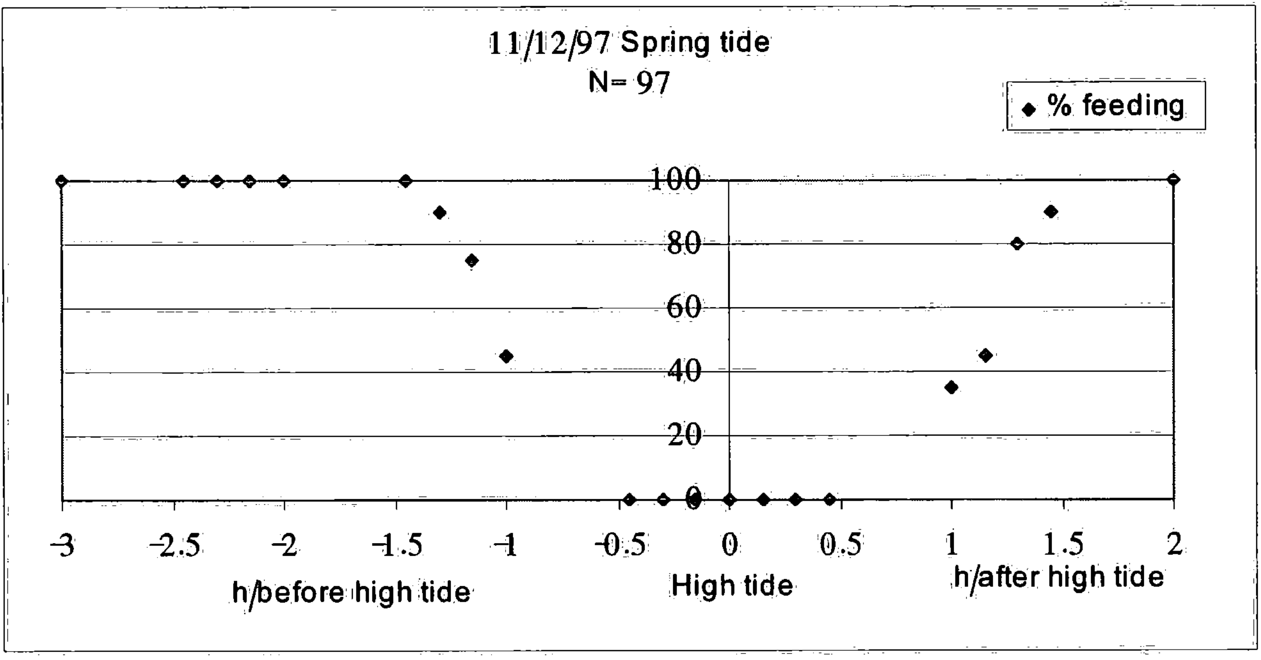
Feeding duration in wild Dunlin

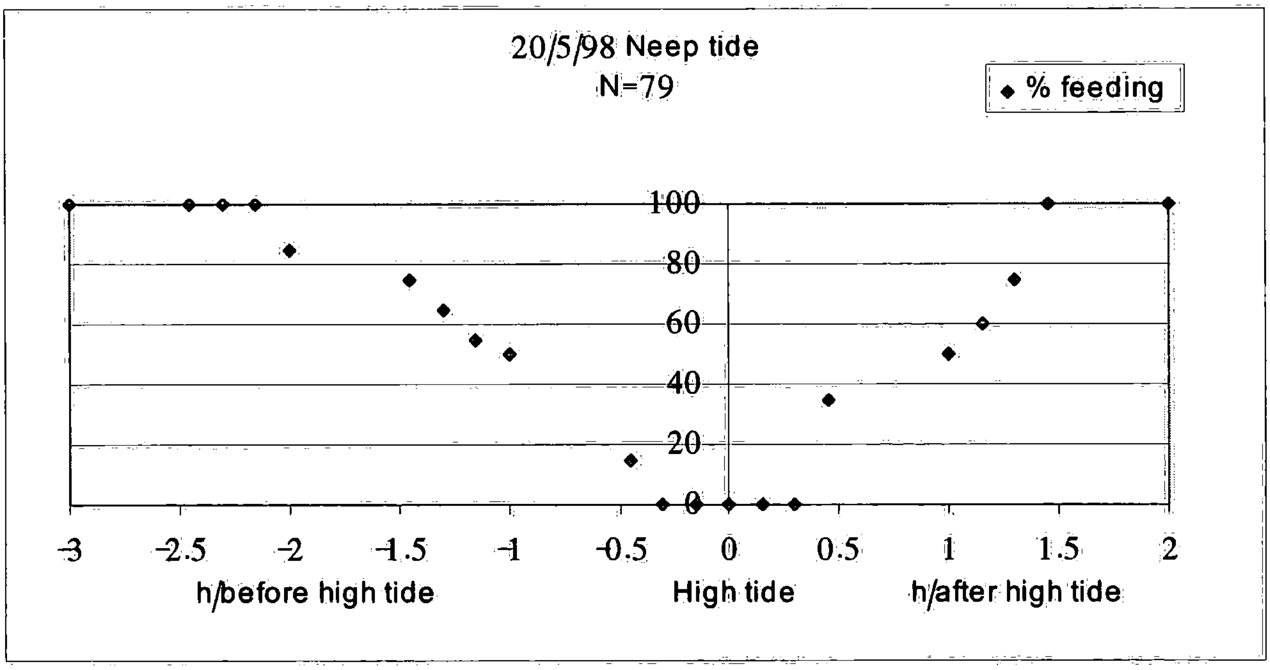
I attempted to estimate daily feeding durations for individual Dunlin in winter and during spring and autumn migration in order to extrapolate it to energy intake. However, it was very difficult to obtain enough reliable information. I should have made feeding observation many times every season, taking into account many factors that affect feeding duration such as temperatures, air speed and other weather conditions. Also some observations had to be cancelled because of disturbance (e.g. birds of prey), weather conditions or simply because Dunlin did not come to feed on that day for some reasons. I have presented the observations I was able to make in graphs in this Appendix.

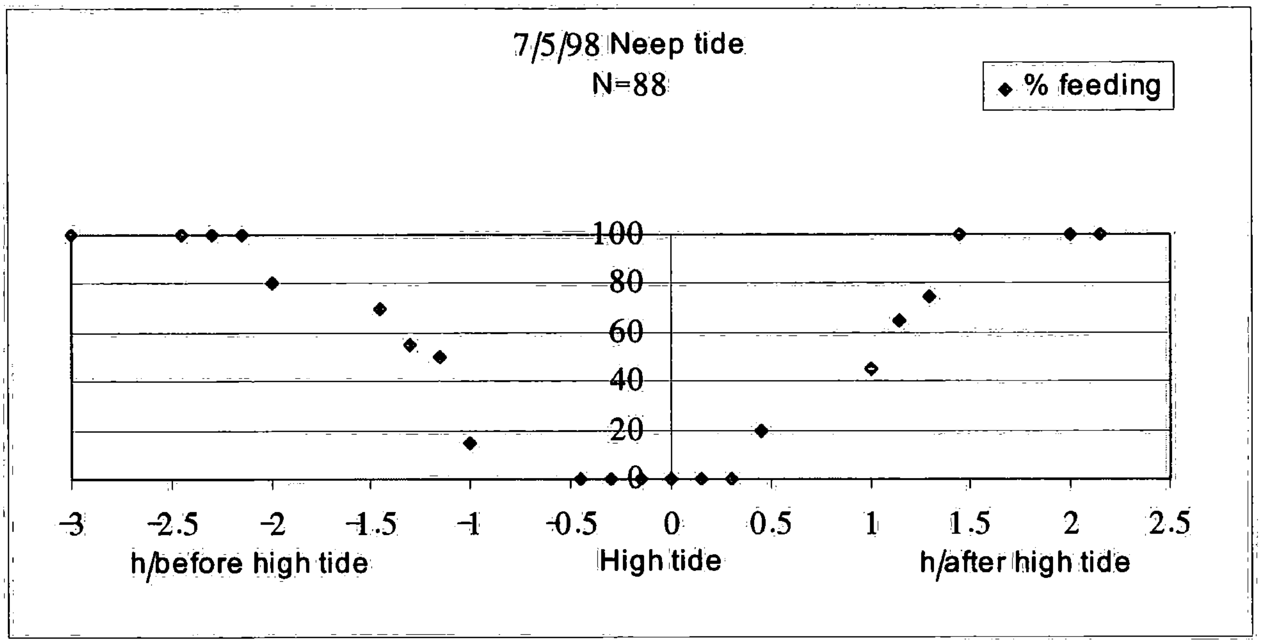
Methods

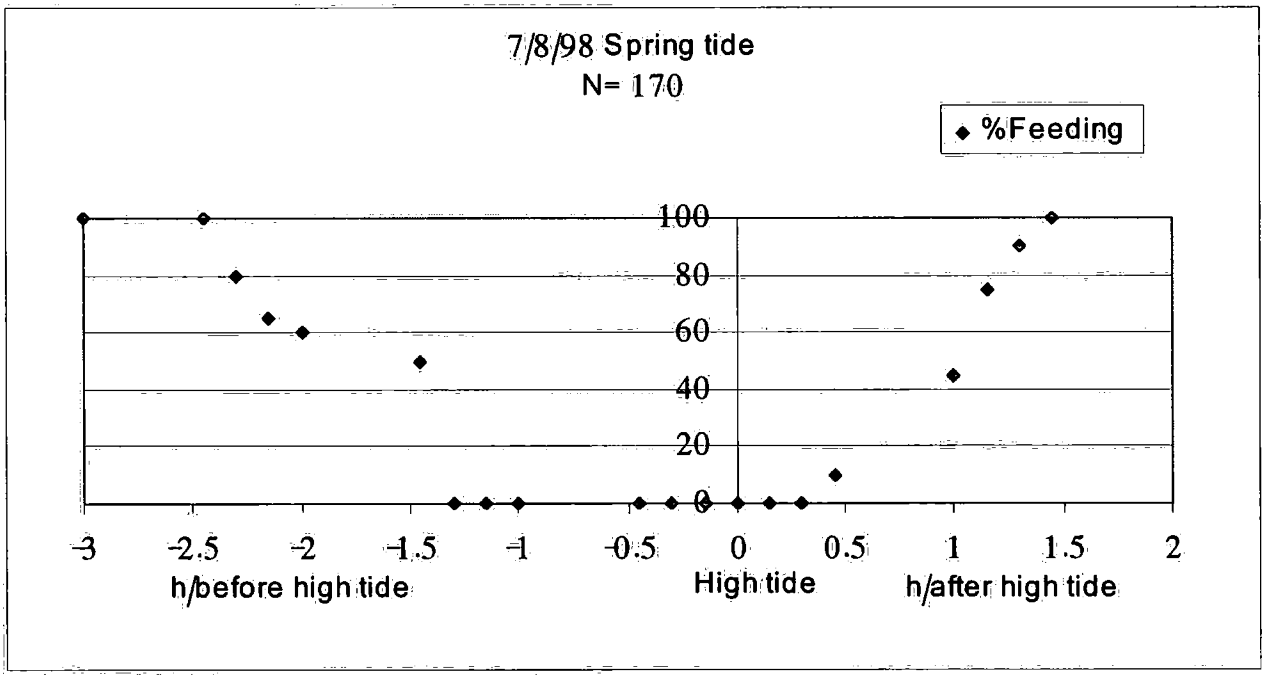
Daily feeding durations for Dunlin were estimated at Seal Sands, Teesmouth by observing birds with a 22-60x 80mm (Optolyth T.B.G. 80) telescope and a pair of binoculars 10x40B(ZEISS, Dialyt) from a vehicle which served as a mobile 'hide', or from a permanent hide. Feeding measurements were made during spring tides (i.e. those with low water levels less than 1.3m OD) and neap tides (i.e. those with low water levels greater than1.3 m OD) in winter, spring and autumn of 1997and 1998. Observations started 2-4 hours before high water (before Dunlin start roosting) and continued until they flew to roost, and again when they left the roost and began feeding again. Observations were made every 15 minutes. The duration of non-feeding (roosting) was subtracted from the time between successive high waters (12.5h) to give an estimate of the total time spent foraging.

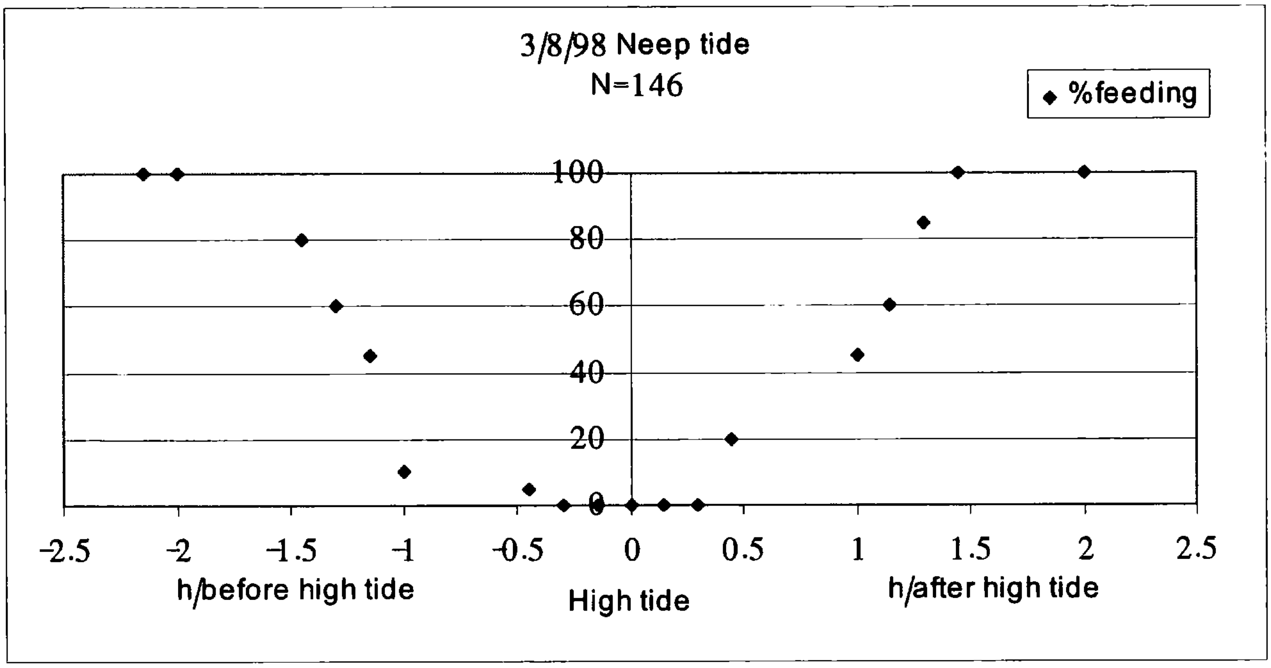
Feeding duration graphs

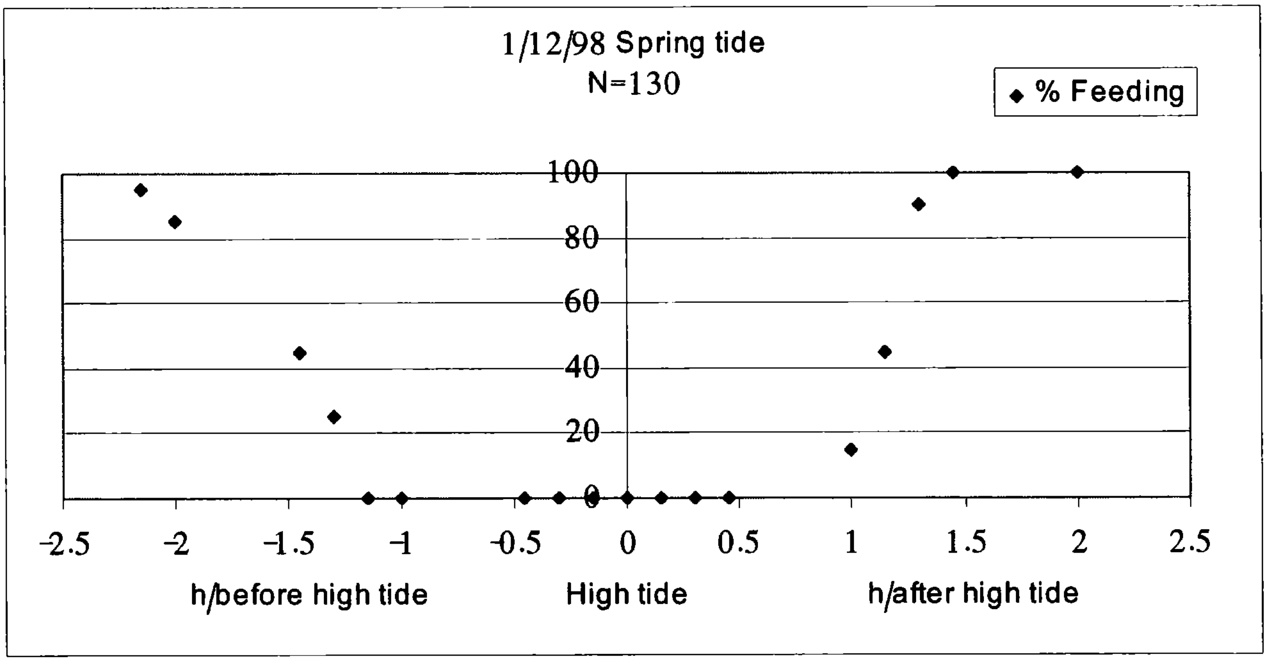


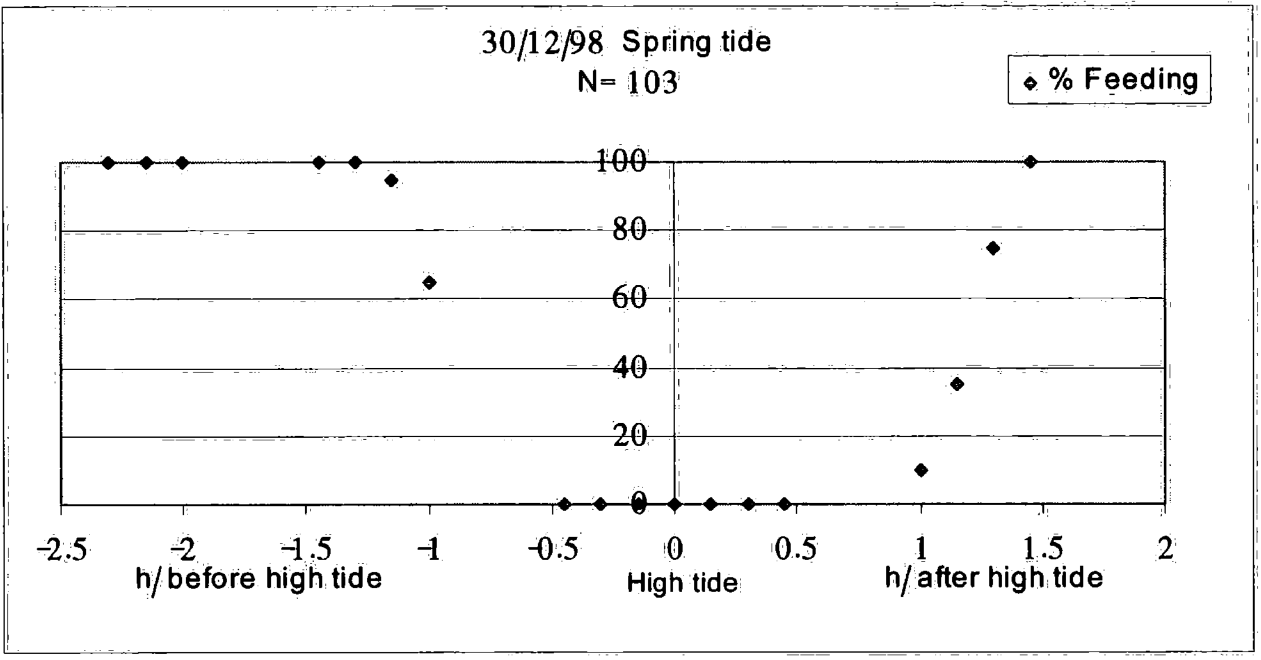



7/5/98 Neep tide
N=88
% feeding
100
80
60
40
20
0
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
h/before high tide
High tide
h/after high tide


7/8/98 Spring tide
N= 170
%Feeding
100
80
60
40
20
0
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
h/before high tide
High tide
h/after high tide


3/8/98 Neep tide
N=146
◆ %feeding
100
80
60
40
20
0
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
h/before high tide
High tide
h/after high tide


1/12/98 Spring tide
N=130
◆ % Feeding
100
80
60
40
20
0
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
h/before high tide
High tide
h/after high tide


30/12/98 Spring tide
N= 103
◆ % Feeding
100
80
60
40
20
0
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
h/ before high tide
High tide
h/ after high tide

Summary of results

Date	Hour before HW when 50% of birds stopped feeding	Hour after HW when 50% of birds started feeding	Roosting period (hour)	Potential feeding period in tidal cycle (hour)	Average of roosting period (hour)	Average of Potential feeding period in tidal cycle (hour)
20/5/98*	1	1	2	10.5	2.5	10
7/5/98*	1.25	1.25	2.5	10		
3/8/98*	1.25	1.25	2.5	10		
7/8/98*	1.75	1.25	3	9.5		
11/12/97**	1.25	1.5	2.75	9.75	2.75	9.75
1/12/98**	1.75	1.5	3.25	9.25		
30/12/98**	0.75	1.5	2.25	10.25		

***Spring and autumn migration period**

**** Winter period**

Comments

Potential feeding periods during migratory stopover are slightly longer than winter, but winter day-lengths are only about 8 hours, so daylight feeding could be reduced to about 5 hours in winter but would be the full 10 hours in spring and late summer.

Appendix VII

Figure 1: Sites where average daily temperatures were taken for *Calidris alpina schinzii*

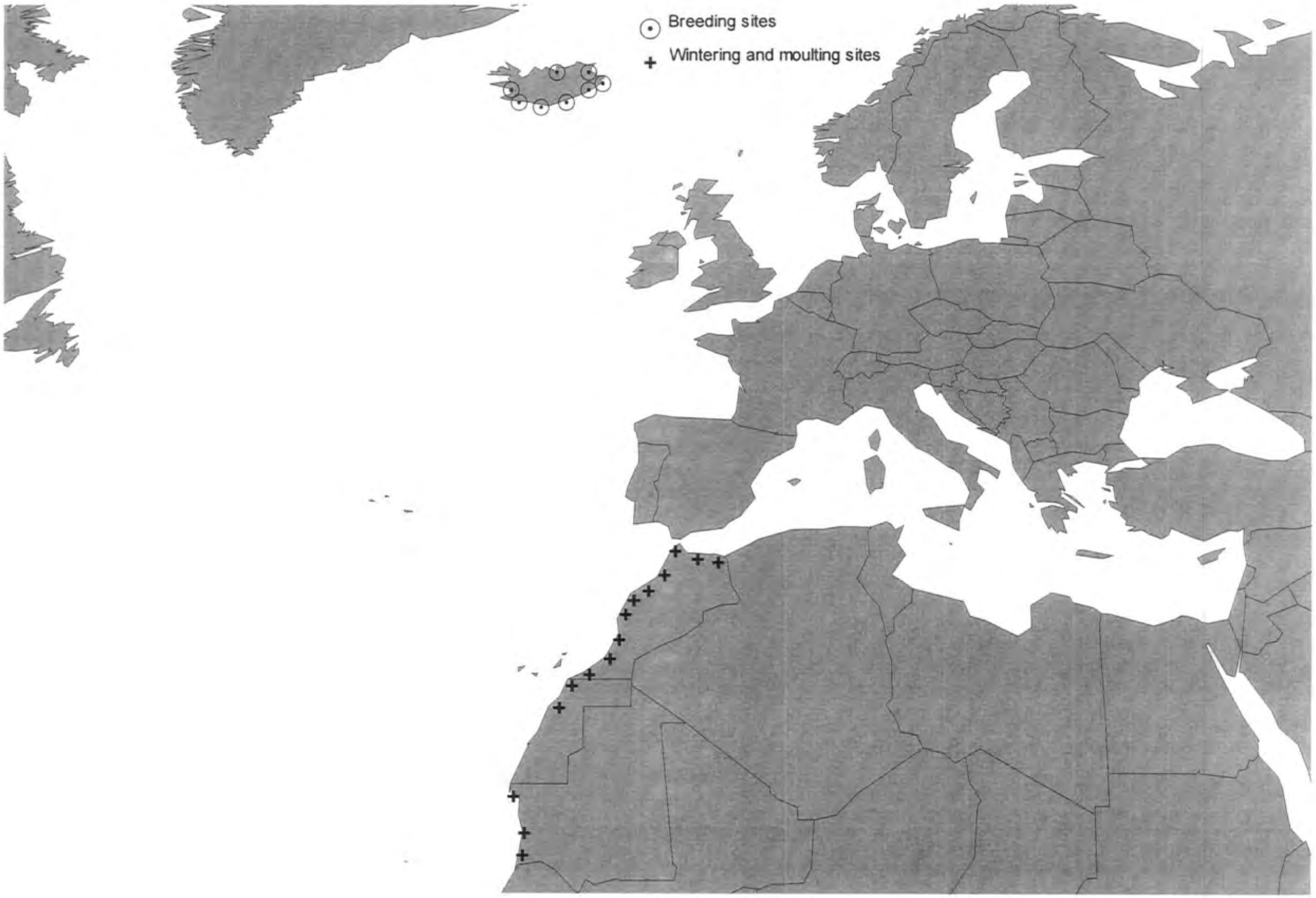


Figure2: Sites where average daily temperatures were taken for *Calidris alpina alpina*

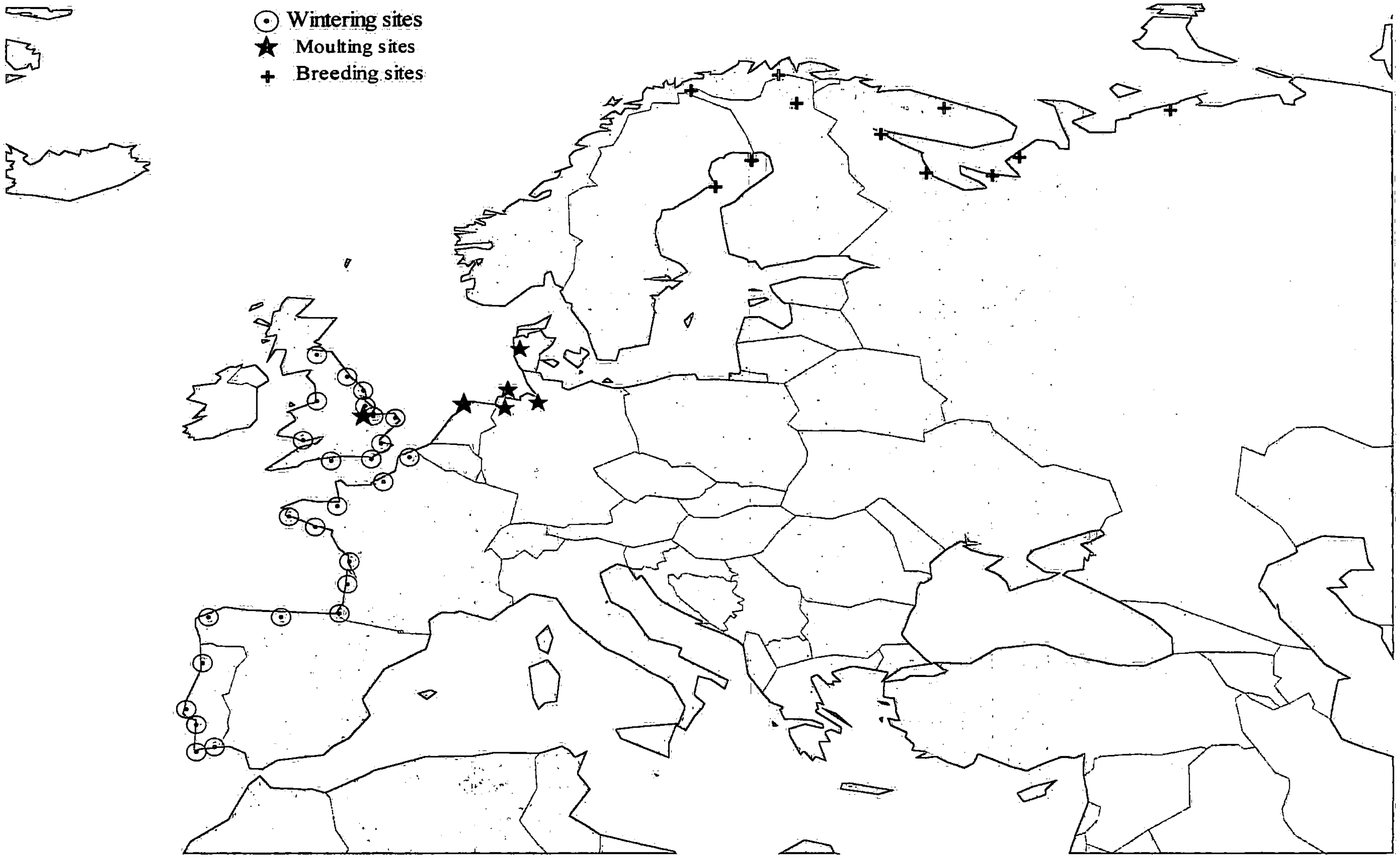
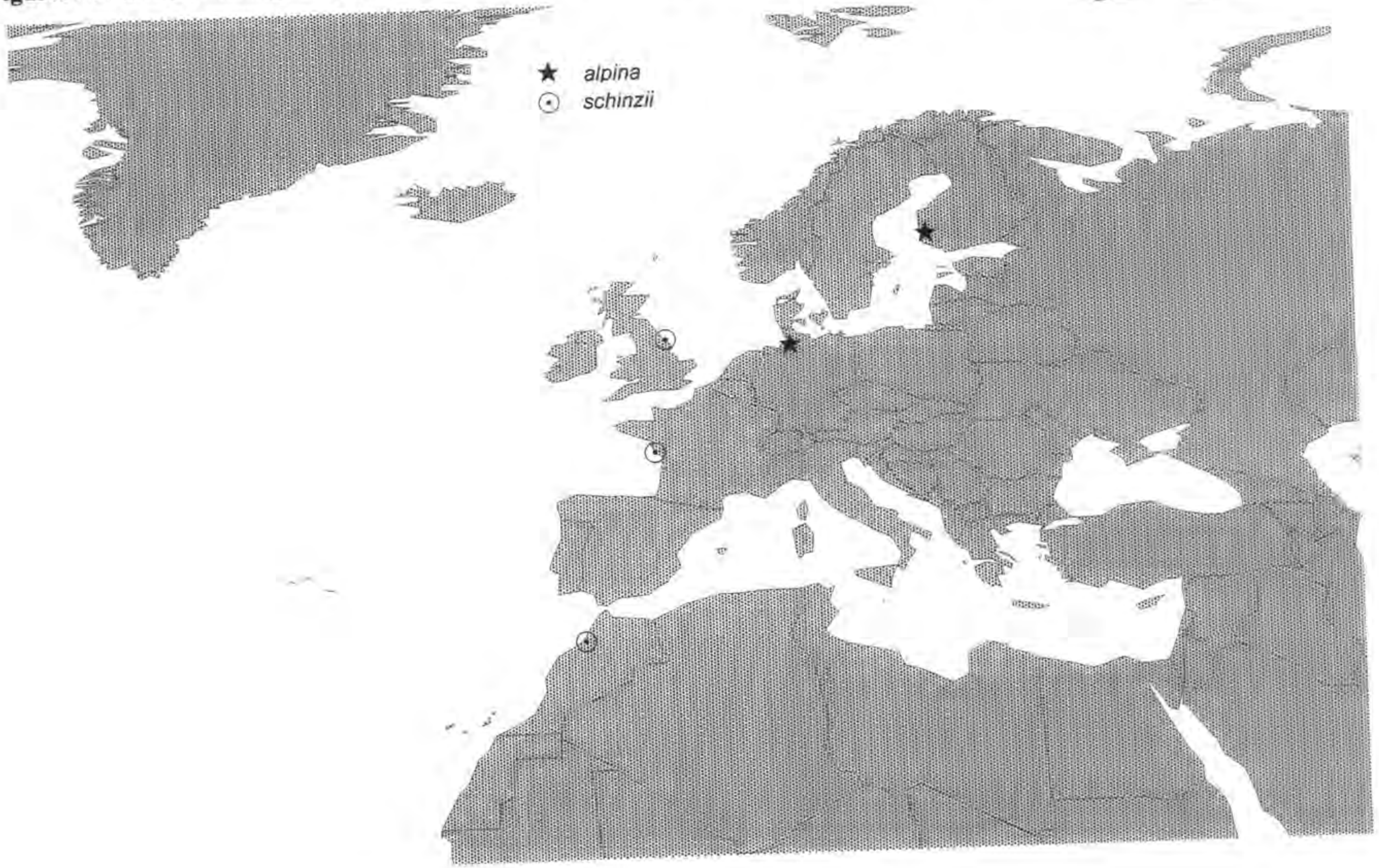


Figure3: Sites where average daily temperatures were taken for the two subspecies of Dunlin on their refuelling sites



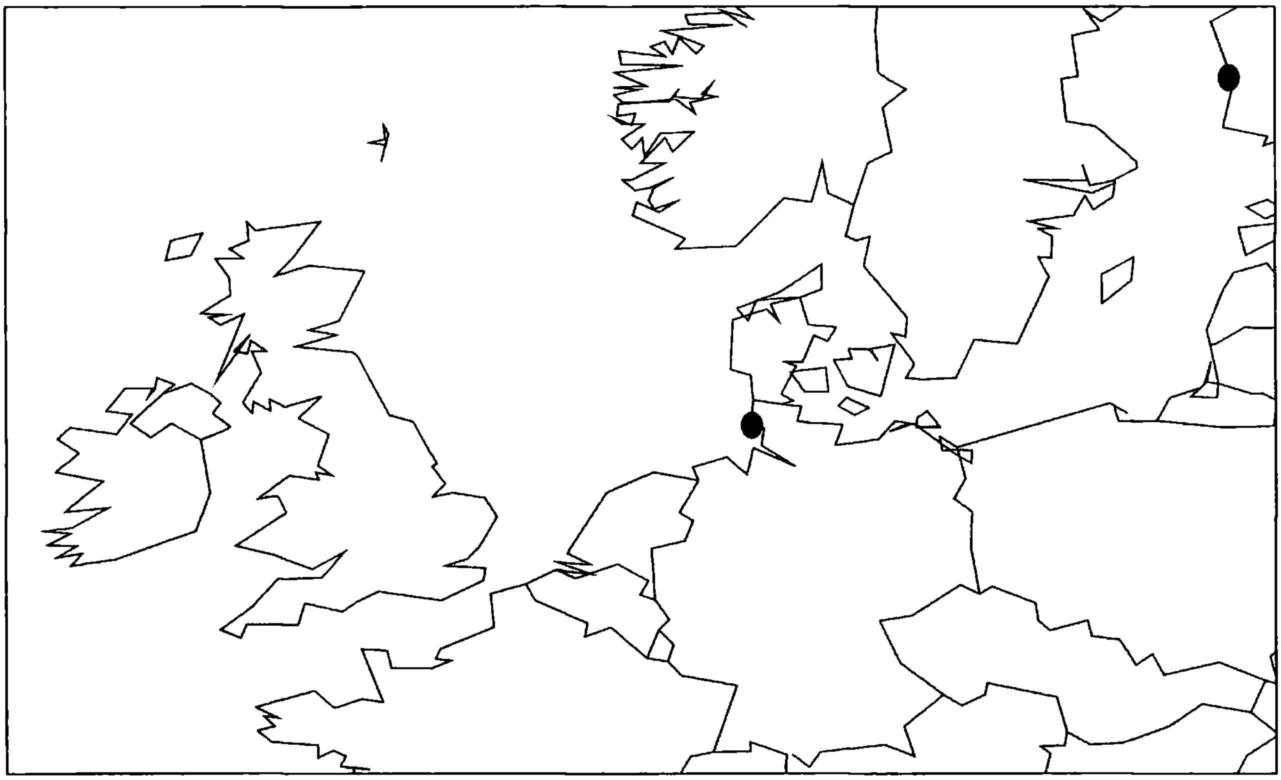
Appendix VIII

Ringing and Recoveries Maps

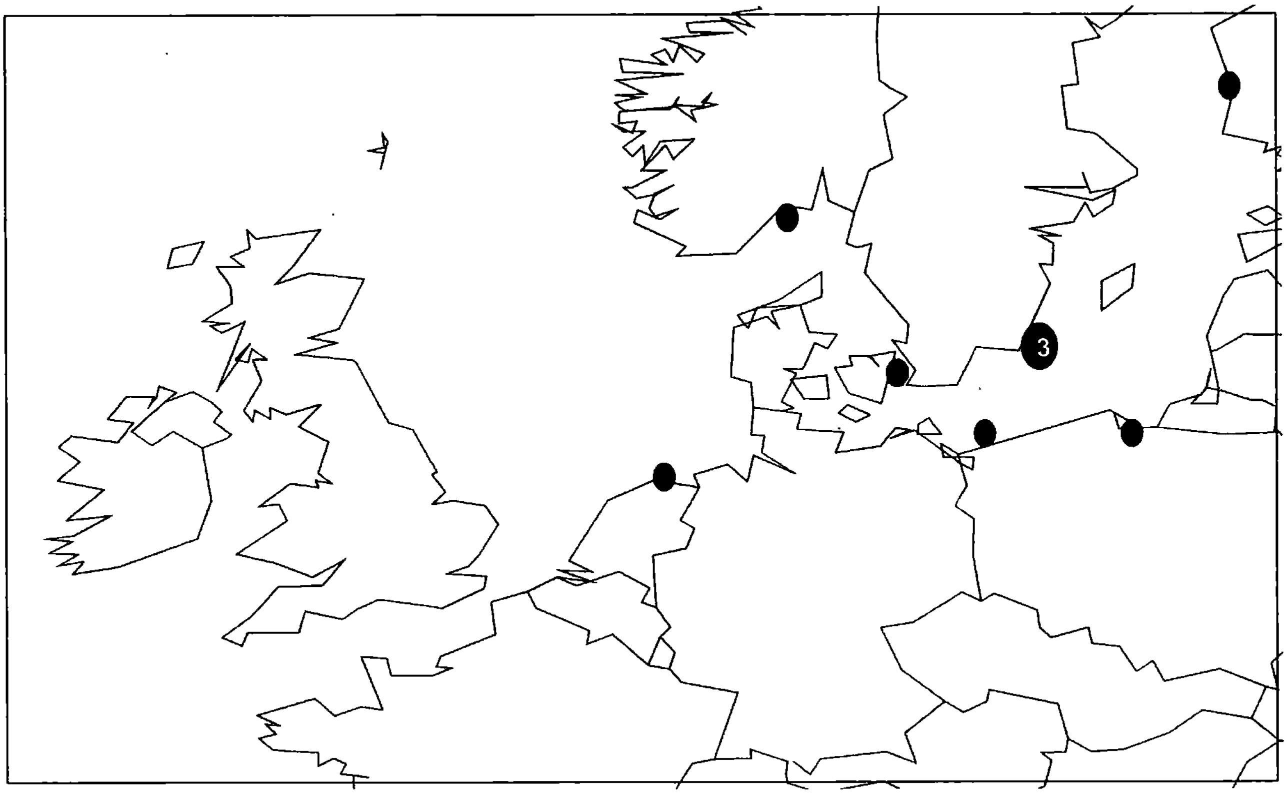
For Dunlin ringed in Cleveland

- **GBCV refers to the place code of Cleveland in Great Britain**
- **Numbers refer to months (1= January, 2= February, etc.)**
- **Number inside symbols indicates number of recoveries, symbols without number mean one recovery.**

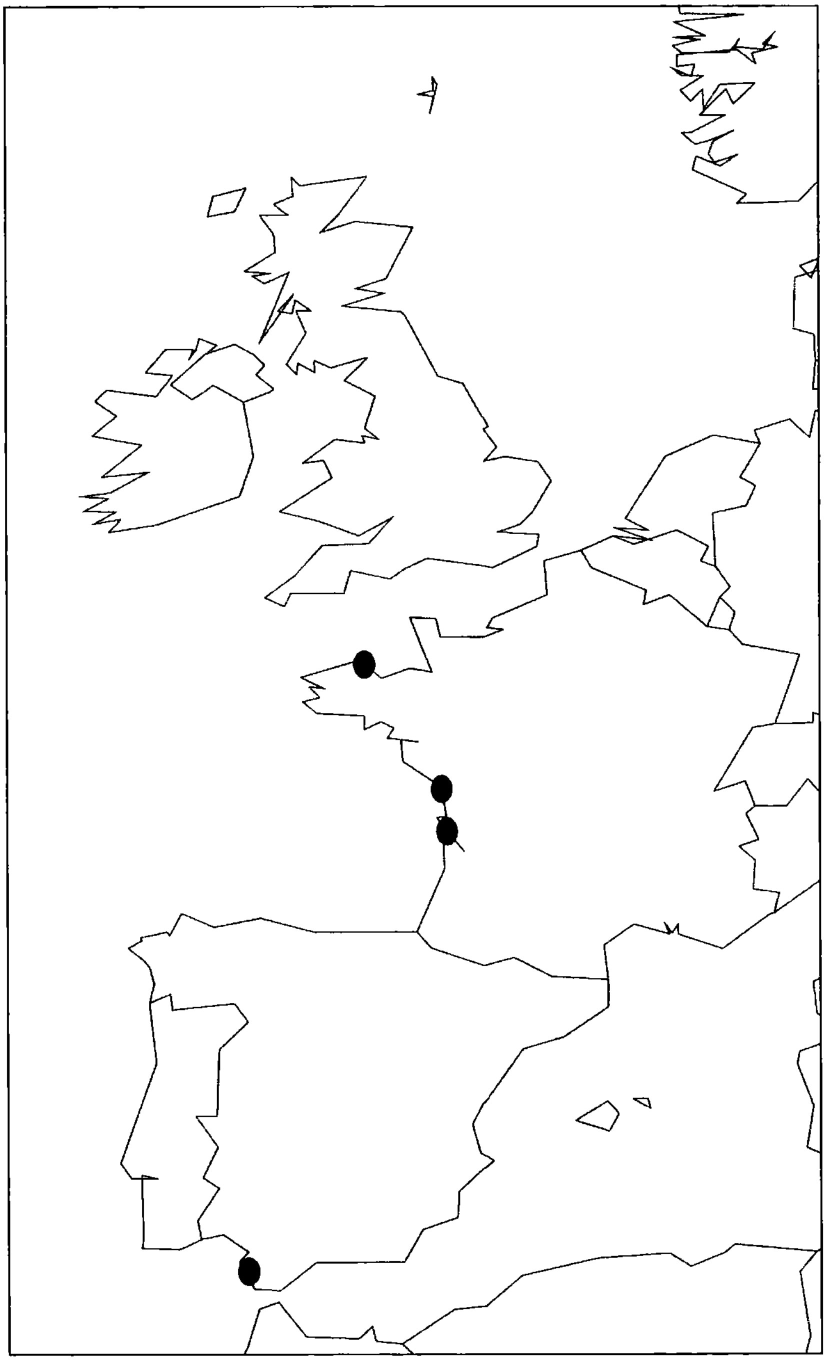
MAP 1: Adult Dunlin ringed in GBCV in 4, 5 and 6 and recovered outside Great Britain in 4, 5 and 6.



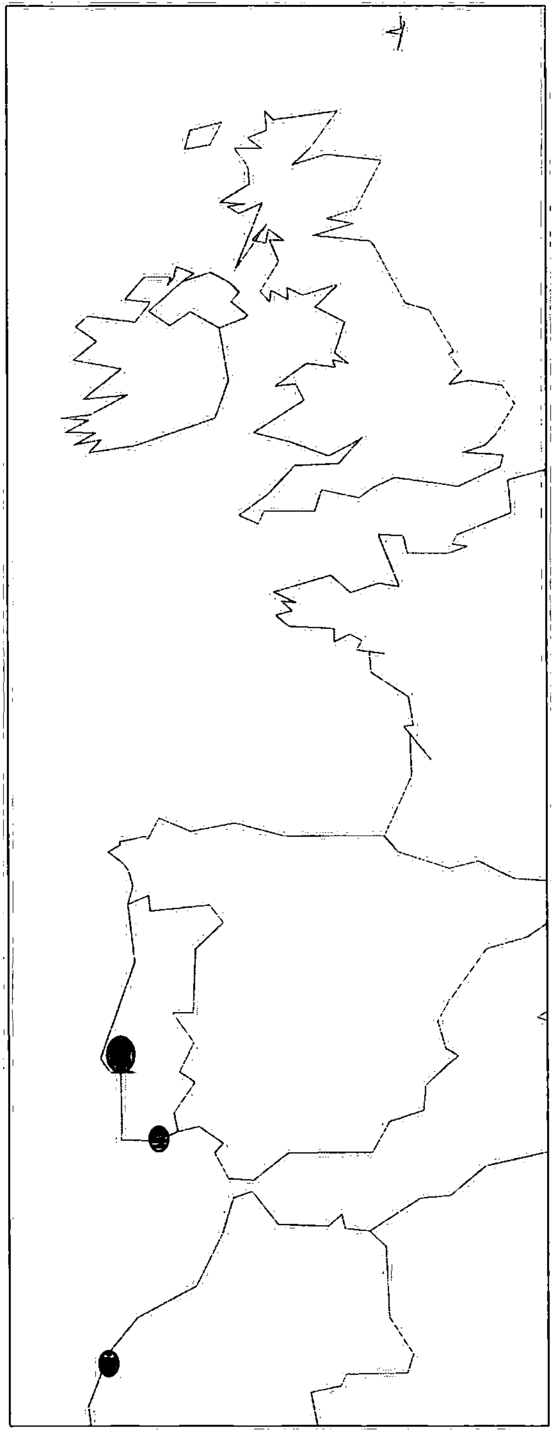
MAP 2: Adult Dunlin ringed in GBCV in 4, 5 and 6 and recovered outside Great Britain in 7 and 8.



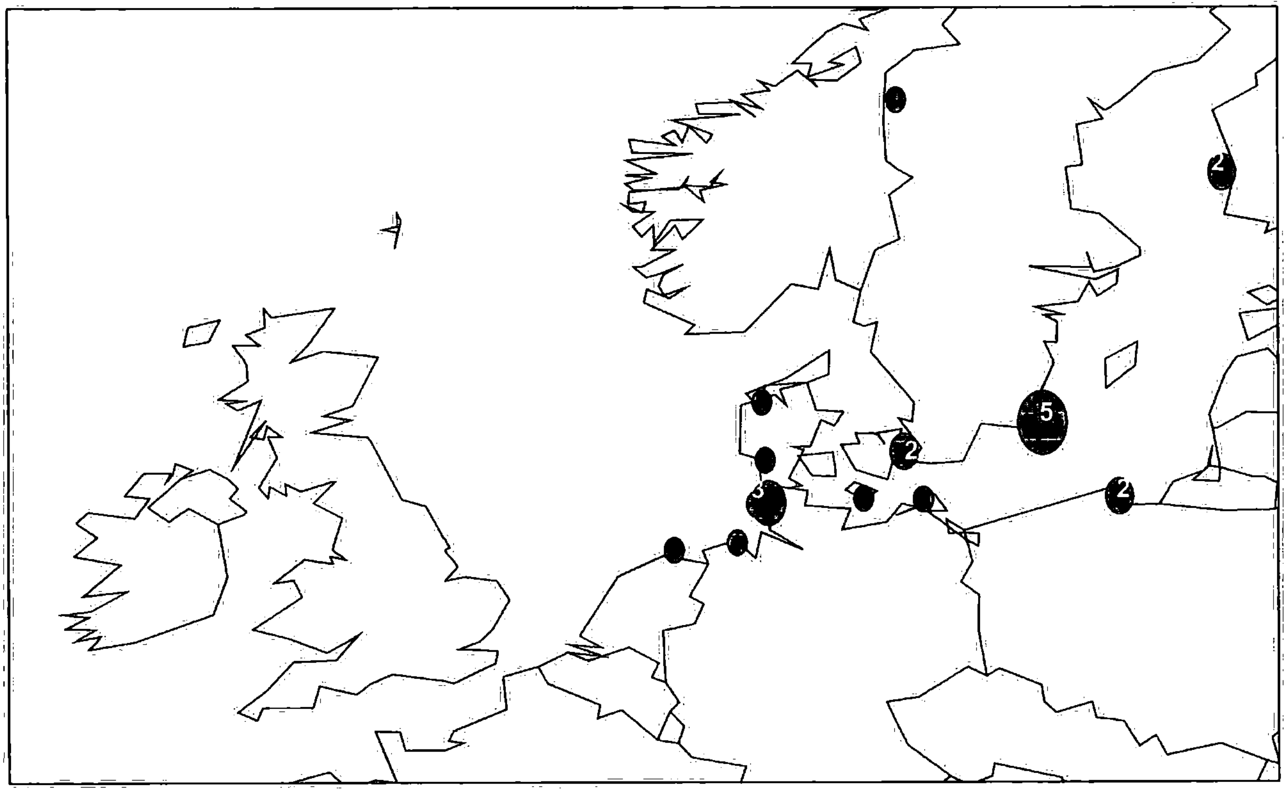
MAP 3: Adult Dunlin ringed in GBCV in 7 and 8 and recovered outside Great Britain in 8, 9, 10, 11, 12 and 1.



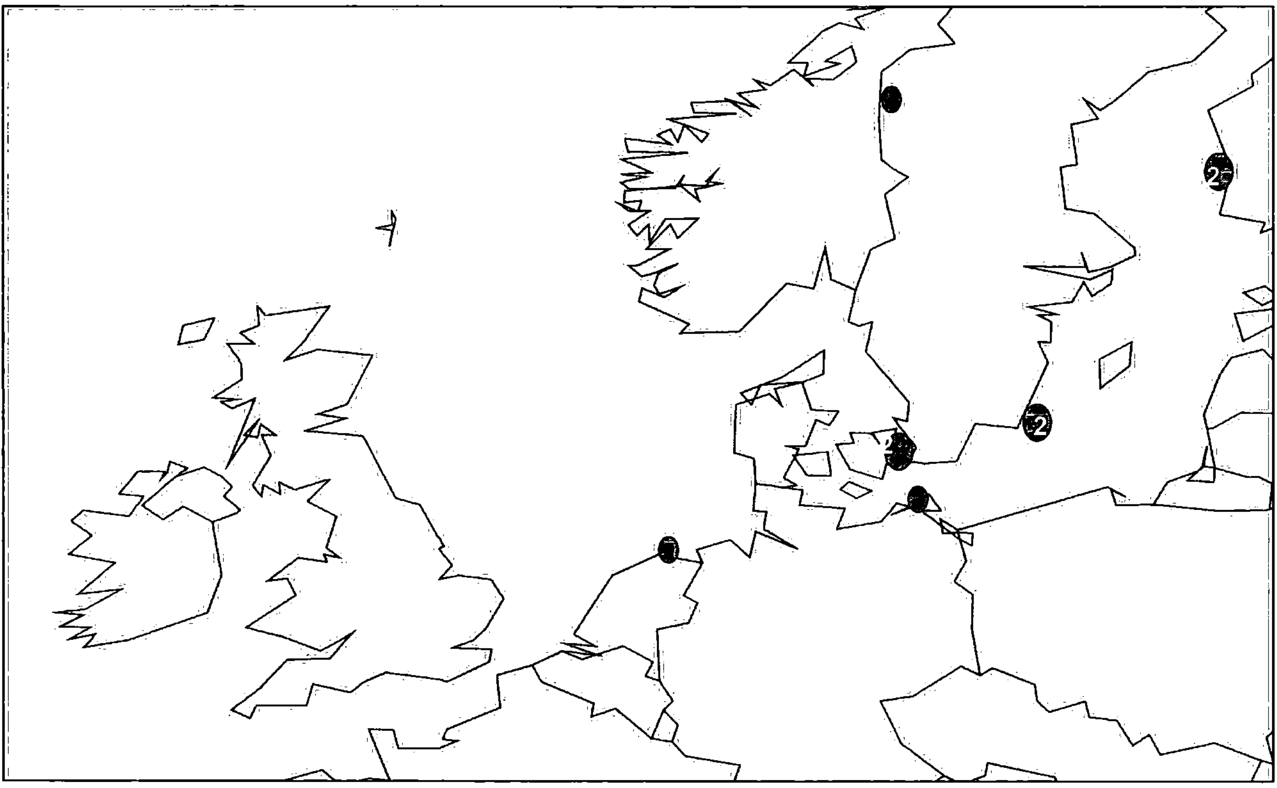
MAP 4: Adult Dunlin ringed in GBCV in 7 and 8 and recovered outside Great Britain in 2, 3, 4, 5 and 6.



MAP 5: Adult Dunlin ringed in GBCV in 9, 10,11, 12, 1, 2 and 3 and recovered outside Great Britain in 4, 5 and 6.

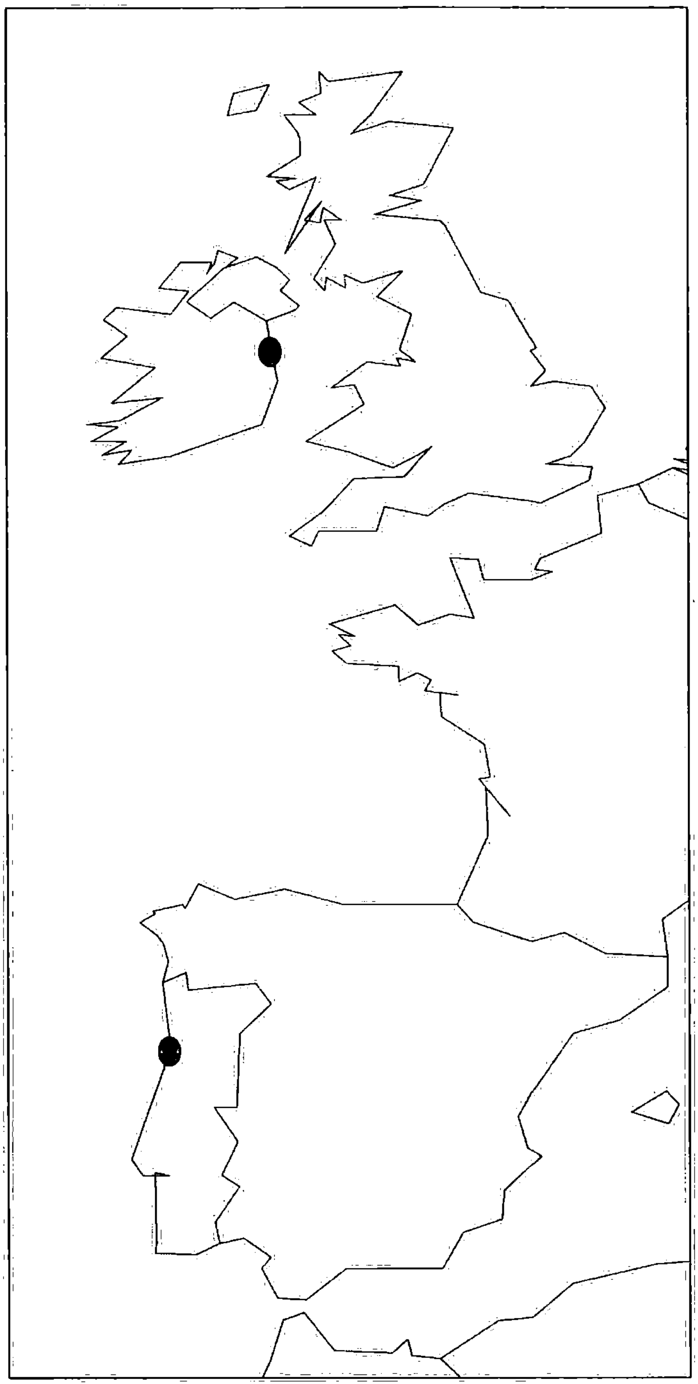


MAP 6: Adult Dunlin ringed in GBCV in 9, 10,11, 12, 1, 2 and 3 and recovered outside Great Britain in 7, 8 and 9.



MAP 7: Juveniles Dunlin ringed in GBCV in 7 and 8 and recovered outside Great Britain (in same year as ringed) in 9, 10, 11 and 12

MAP 8: Juveniles Dunlin ringed in GBCV in 9 and 10 and recovered outside Great Britain (in same year as ringed) in 9, 10, 11 and 12



Appendix IX

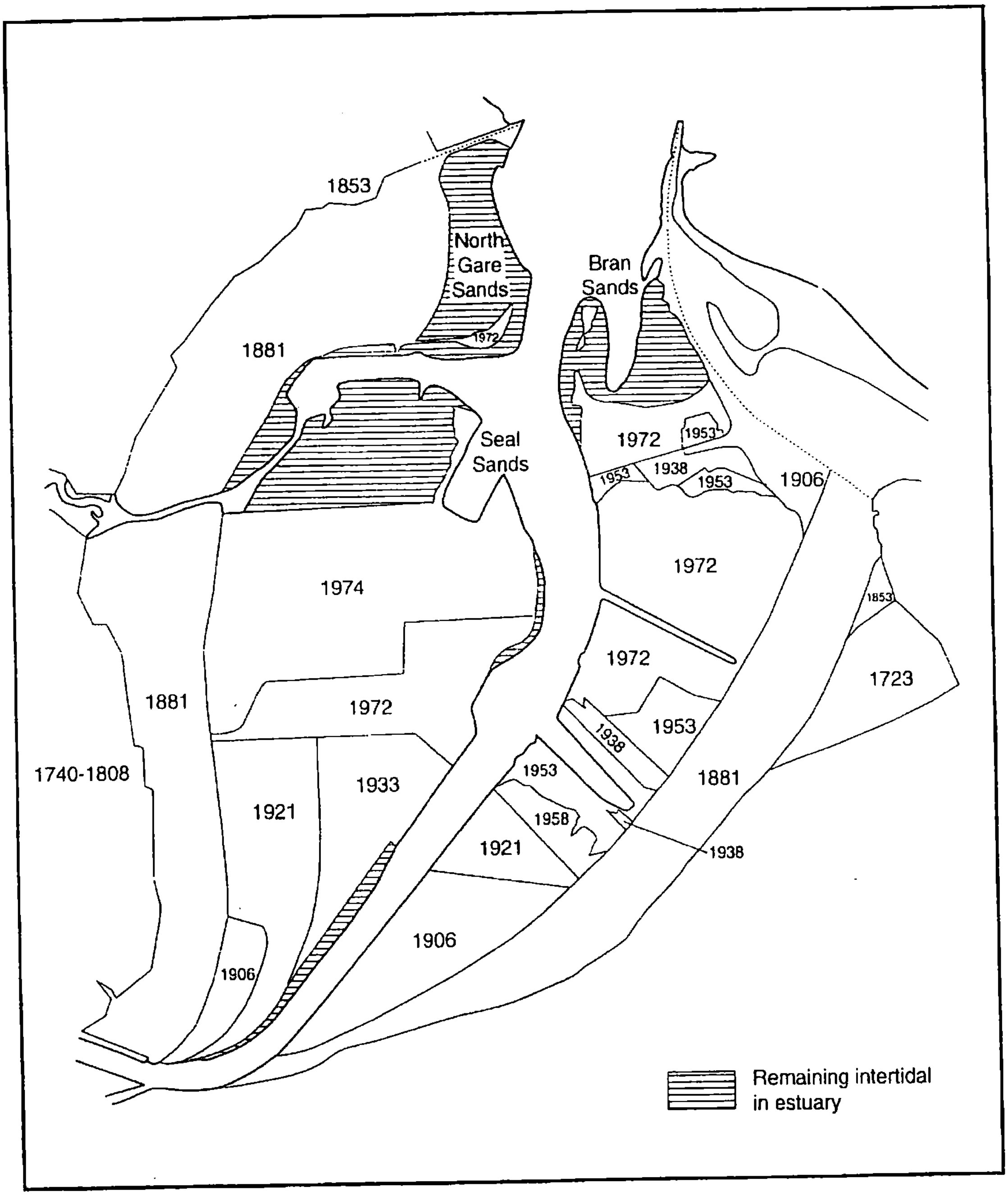


Figure: 1 The progressive land-claim in the Tees Estuary. Dates within each block are those when the land-claim is known to have been completed. Redrawn from Davidson *et al*, 1991.

Fat stores during autumn migration in adult *C.a.alpina* at Teesmouth

The subspecies *alpina* leaves the breeding grounds in northern Scandinavia and Russia (east to the Taimyr Peninsula) and winters in western Europe (Pienkowski & Pienkowski, 1983; Gromadzka, 1989).

Figure 2 shows LI for adults and juveniles *alpina*. It can be seen that juveniles have higher LI than adults, which suggests that adults may spend their winter at the Tees or nearby whereas juveniles with high LI may migrate further south to winter in the Wash (eastern England) or France, or west to winter in Ireland.

Figure 2: Lipid indices ((fat mass/total body mass)*100) for 9 adults (bold squares) and 40 juveniles (triangles) *alpina* caught in late autumn at Teesmouth