Ecology and energetics of breeding Puffins *(Fratercula arctica)* : variation in individual reproductive effort and success.

Thesis submitted for the degree of
Doctor of Philosophy

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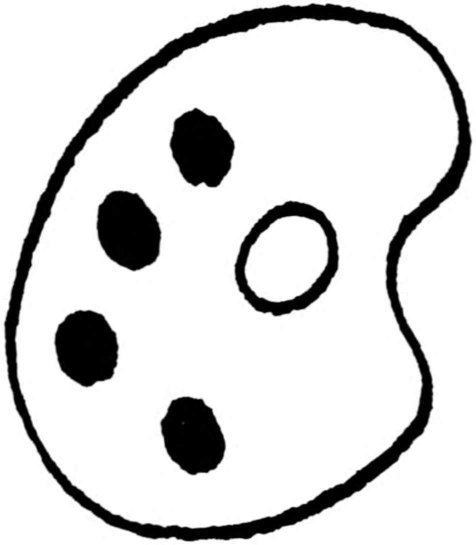

ABSTRACT.

This study investigated reproductive effort and success of individual Atlantic Puffins *(Fratercula arctica)* on the Isle of May, Firth of Forth, Scotland. It placed particular emphasis on the role of body condition in breeding. An energetics approach was taken, where individual 'quality' was considered in terms of foraging efficiency. The study also investigated whether breeding entailed costs for Puffins, in terms of individual survival and future reproductive potential, and whether such costs were mediated through body condition.

Colour-ringed pairs of Puffins were followed through 3 successive breeding seasons and their reproductive performance and condition were monitored. Energy reserves carried by individuals (body condition indices) were estimated from live mass and body dimensions, using a carcass-derived equation to predict lean wet mass. Attempts were made at increasing the effort of rearing young, by playing chick begging calls and exchanging chicks between burrows, and decreasing effort, by supplemetary feeding of young. Field energy expenditures were measured for a sample of parents during chick rearing using the doubly-labelled water technique, and these were compared with other potential measures of reproductive effort.

The breeding success of individual parents was not related to body condition when a correlative approach was taken. Field metabolic rates (FMR's) of 9 adults rearing young averaged 3.67 +/- 0.65 s.d cm^3 CO_2 $g^{-1}d^{-1}$ or 874 +/- 151 kJd^{-1} (c.3.5 times basal metabolic rate). Individual FMR's were not related to other measures of reproductive effort used in the study. The above results were evaluated using graphical models, to demonstrate mechanisms by which the confounding effects of inter-individual differences in foraging efficiency on body condition could mask relationships between body condition, FMR and reproductive performance.

The body condition of parents which experienced a decrease in rearing effort or an increase in effort did not differ significantly from that of controls at the end of the rearing period. This occurred even though parents whose young were fed substantially decreased the number of feeds they delivered to their young. Despite the apparent lack of an effect of the feeding treatment on condition, control pairs showed a lower return rate to the colony, lower breeding success, and produced young in 'poorer' condition at peak mass than experimental parents whose young were fed for them in the previous year. The higher reproductive success of the experimental group suggested that Puffins on the Isle of May (control group) incurred inter-year reproductive costs when rearing young under natural conditions. These results were obtained in years when breeding conditions appeared to be relatively unfavourable for Puffins on the Isle of May, consistent with the view that reproductive costs may only be detectable in 'bad' years. Mediation of such costs through body condition was not demonstrated, perhaps because the measure of condition used was unsuitable for Puffins; potential energy depots were discussed in relation to the life style of Puffins compared to other seabirds.

Quantifying disturbance was not an original aim of the study but during fieldwork it became apparent that Puffins were sensitive to handling. The effects that handling and general disturbance had on the results of the study were addressed but were unlikely to have influenced any of the conclusions presented.

ACKNOWLEDGEMENTS

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For Mum and Dad, and John ....

and the couple at number 10 ....

CONTENTS

CHAPTER 1 INTRODUCTION.

1.1 Introduction and aims of the thesis.

Many studies of seabirds have considered the factors influencing numbers and breeding success at the level of the population (Croxall,1987; Furness and Monaghan,1987 and references cited therein). By measuring variables from a sample of unknown individuals within a population in different years or different places, and comparing these with inter-annual or inter-site variation in breeding conditions (eg food supply, weather), some possible causes of fluctuations in breeding success, survival or population size, can be inferred (Potts *et al,* 1980; Birkhead and Furness,1985; Anker-Nilssen,1987). Only in relatively recent years have studies of marked birds begun to reveal differences in success amongst the individuals which comprise these breeding populations (Coulson and Porter,1985; Amundsen and Stokland,1990; Wooller *et al,* 1990; Bolton,1991;). These studies have focused on the variation between individuals in the number of offspring produced over the lifetime of individuals (often used as a measure of their lifetime reproductive success, Clutton-Brock,1988; Newton,1989) and, therefore, on the relative contributions of those individuals to the population gene pool. Few studies of seabirds, however, have sought to identify which characteristics of individuals, conveniently encompassed by the term 'quality', are responsible for differences in lifetime reproductive success.

In the present study, an energetics approach to the definition of adult quality was adopted. Measures of quality which were considered here included individual foraging efficiency; that is individuals were assumed to differ in their rate of income of energy (and other important nutritional requirements) and expenditure of energy per unit of foraging time. Foraging efficiency, and hence the ability to exploit a food supply, might vary with individual age or length of breeding experience *per se* (Curio,1983; Nol and Smith,1987), while for species which retain a mate from year to year, the length of time that the pair bond has been established might affect the quality of the pair in terms of their abilities to coordinate breeding activities (Coulson,1966; Brooke,1990), and so provision their brood more or less effectively. In the present study, the effects of such possible correlates of individual and pair quality on breeding success (presumed to be mediated by foraging efficiency), were partially addressed by following colour-ringed pairs of Puffins, of estimated or known age, through successive breeding seasons, and monitoring their breeding performance (Chapter 3).

The influence of avian body reserves (lipid and/or protein) or body mass on breeding success has been demonstrated in many studies (cited in Chapter 5), including those involving seabirds (Houston *et al*, 1983; De Korte,1985; Bolton *et al*, 1992). In this study, a measure of body condition was derived for adult Atlantic Puffins from their mass and body dimensions (Chapter 4) and relationships were examined between this measure and the breeding performance of individuals. The magnitude of body reserves carried by individuals probably reflects an optimal trade-off between the benefits of reserves as an 'insurance' against periods of reduced food availability and the costs associated with reserve maintenance and carriage (Martin,1987; Blem,1975; Lima,1986). The optimal solution to such a trade-off is likely to vary at the level of the individual as well as at the level of the population. The way in which body reserves vary with individual quality is poorly understood and, consistent with the energetics approach, a further aim was to examine relationships between individual body condition, reproductive effort and breeding success, and, hence, to evaluate whether effects of condition on performance could be detected at the level of the individual. Experimental manipulation of parental effort during chick rearing was attempted and its effects on body condition evaluated, to i) try to control for the potentially confounding effects of individual quality on body condition and ii) to reveal the effects of body condition *per se* on reproduction. This necessarily adopted a novel approach, since the conventional treatment of manipulating brood size, is not normally an option for a single chick species.

Differences in foraging efficiency, and hence success, might also be revealed if the energy expenditure of individuals is measured directly in the field and compared to measures of reproductive effort and success. The utility of the doubly-labelled water (DLW) technique (Lifson and McClintock,1966; Tatner and Bryant,1989) for measuring field metabolism has been demonstrated for seabirds (Birt-Friesen *et al*, 1989 for review) and ideally can be used concurrently with activity monitoring devices (Nagy *et al*, 1984; Trivelpiece *et al*, 1986; Gales *et al*, 1990) to measure the daily energy expenditure (DEE) of individuals along with the time spent in various activities. Specific aims using the DLW technique in the present study, were to evaluate the daily number of feeds delivered to young as a measure of parental effort and to investigate whether the body mass and/or condition of individuals influenced DEE (Chapter 6).

Extending the energetics theme, an additional aim of the present study was to show whether breeding entailed costs for seabirds in general, and Atlantic Puffins in particular, in terms of their future survival and reproductive potential (Williams,1966; Charnov and Krebs,1974), by

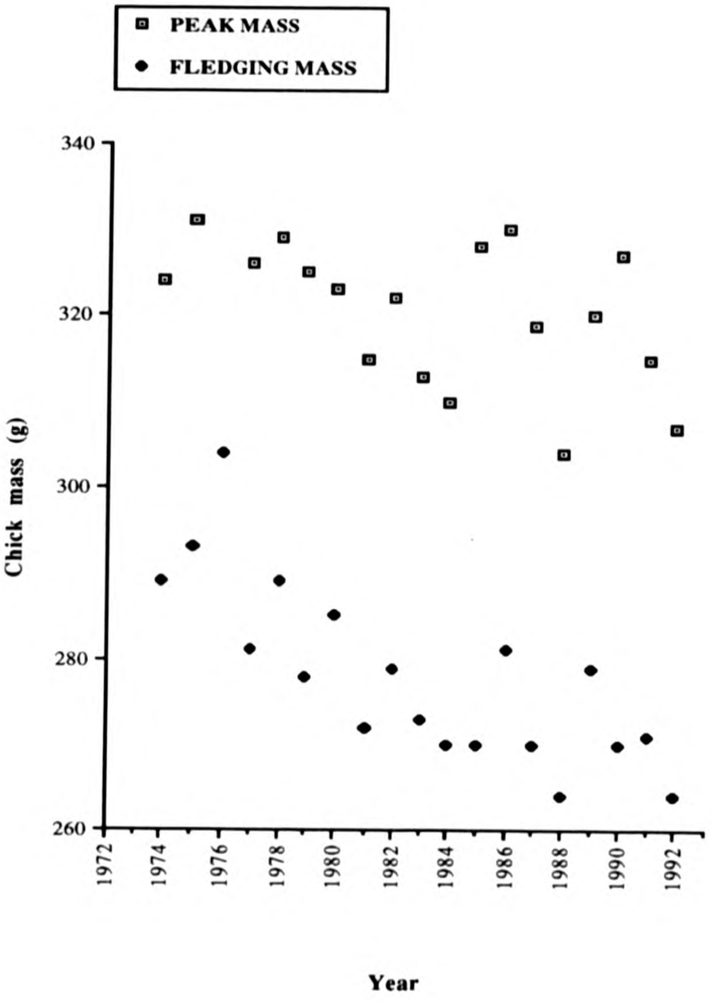


Figure 1.1 **Variation in the peak and fledging masses of Puffin young on the Isle of May, 1973 - 1992.**

(Data from M.P.Harris, pers.comm.)

experimentally decreasing the effort required by parents to rear their young. Body condition was monitored, assuming that the level at the end of breeding would reflect residual reproductive value (Martin,1987) and, hence future survival and reproductive potential, and that the link between effort and cost could be mediated by body condition. Short-term changes in body reserve levels, or their rate of depletion, could be detected and used to evaluate the survival chances of individuals (Drent and Daan,1980). Previous studies of the costs of reproduction have been carried out largely on species laying more than one egg per clutch and on small, passerine species, and most have experimentally increased rather than decreased parental effort in order to demonstrate such costs (such that the costs imposed on the experimental parents may have been artificially high). The experimental decrease in parental effort effected in the present study aimed to show that control adults experienced reproductive costs under natural conditions by improving the annual or lifetime reproductive success of the experimental birds relative to the controls.

1.2 The study species and study site.

The Atlantic Puffin *(Fratercula arctica)* {scientific names for all species referred to in the text may be found in Appendix 1}, subsequently referred to as the Puffin, is a medium-sized (c.400g body mass in Scotland) seabird belonging to the auk family (Alcidae). The biology of the species is discussed in full by Harris (1984) and Cramp and Simmons (1977), and only details relevant to the present study are given here. Puffins are long-lived (life expectancy 16-33 years, Harris (1984)) and produce a single-egg clutch from which a single youngster is raised each year. This was considered an advantage for the present study because the laying of a single egg suggested that breeding could be costly for Puffins (Lack,1968) and because the complications of differences in brood size were absent when measuring reproductive success.

The study was conducted on the Isle of May, in the Firth of Forth, on the east coast of Scotland (56°11'N, 2°84'W). The population of Puffins on the island increased rapidly from 5 pairs in 1959 to c.10,000 pairs in 1982, at an annual rate of increase on study plots of 19% from 1973 to 1981, after which the rate of increase slowed (Harris and Wanless,1991). The population was believed to be approximately stable at c.20,000 pairs during the present study (1990-1992). In the last 20 years, peak and fledging masses of Puffin young on the Isle of May have decreased (**Figure 1.1**), coinciding with a decline in the daily intake of energy by young (**Figure 1.2**) of 9kJd^{-1} year^{-1} (M.P.Harris,pers.comm.). In contrast, breeding success

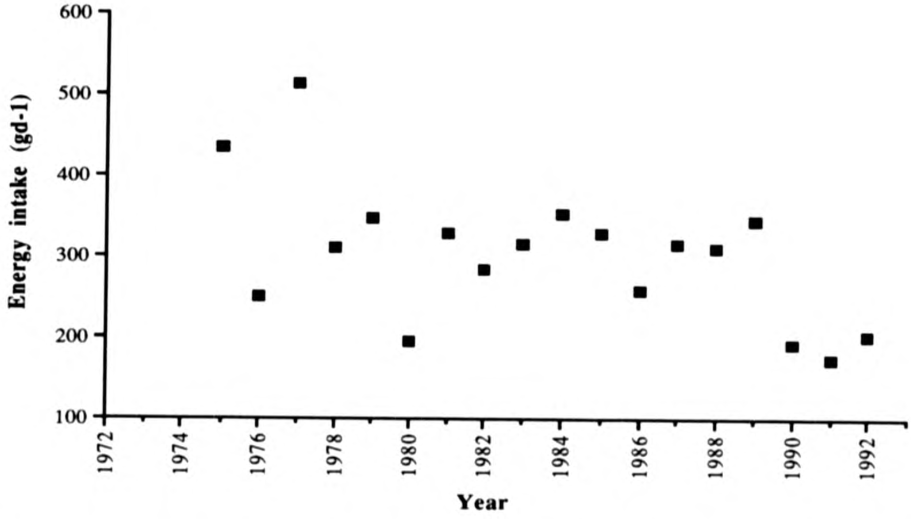


Figure 1.2 Variation in the daily energy intake of Puffin young on the Isle of May, 1975 - 1992.

(Data from M.P.Harris, pers.comm.)

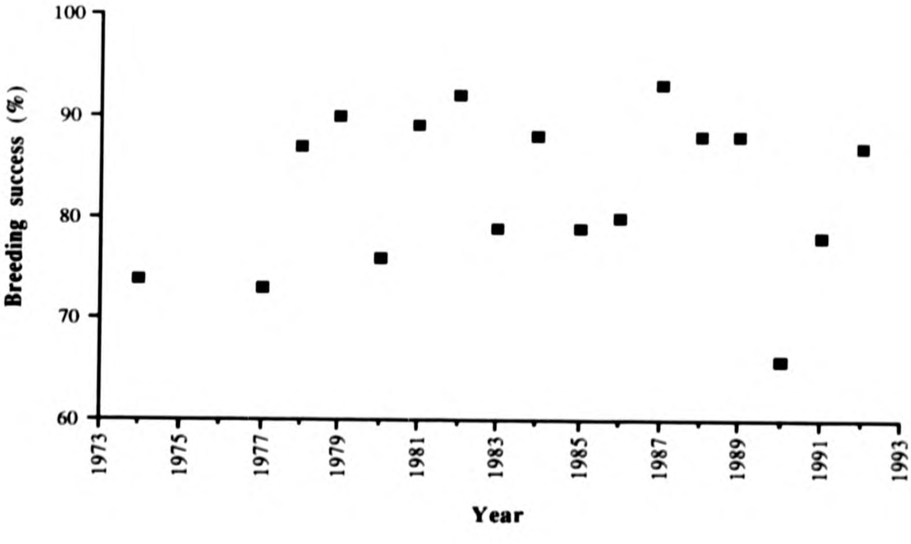


Figure 1.3 Variation in the breeding success (% pairs laying which fledged young) of Puffins on the Isle of May, 1973 - 1992.

(Data from M.P.Harris, pers.comm.)

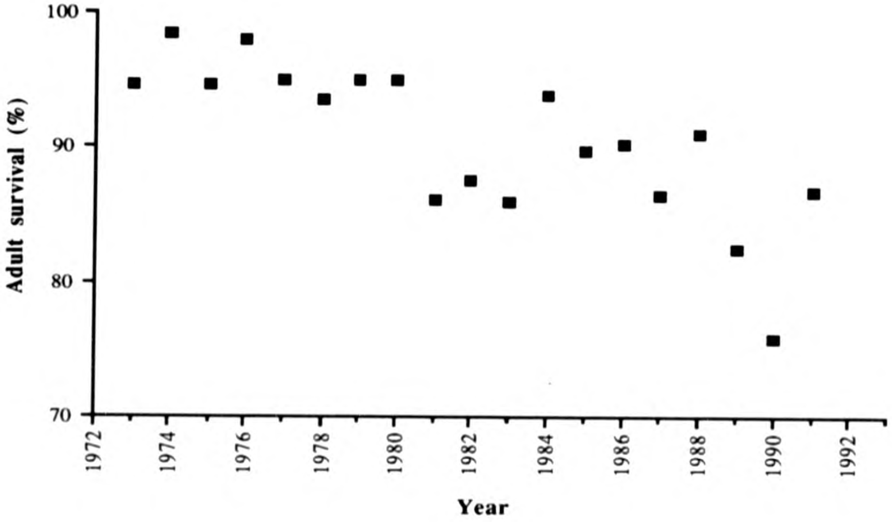


Figure 1.4 Variation in the return rates between years of adult Puffins on the Isle of May, 1973 - 1992. These are equivalent to survival rates except in the latest years (when a proportion of individuals may have been missed or may not have returned to the colony in that breeding season.

(Data from M.P.Harris, pers.comm.)

(young fledged per egg laid) has shown no significant trend, although 1990, the first year of the study, was a particularly poor year (**Figure 1.3**). Adult return rates from year to year were lower in the early 1990s than in the early 1970s (**Figure 1.4**). This suggested that breeding conditions for Puffins on the Isle of May could have been less favourable during the years of the present study than they were previously, either because of density dependent controls as the population increased (Ashmole,1963; Coulson,1983) or because of density independent factors influencing food supply, as has been suggested for Puffin populations elsewhere (Lid,1981; Barrett *et al,* 1985).

On the Isle of May, Puffins breed in burrows in the turf. This was seen as an advantage for a study in which adults and young needed to be handled regularly, as chicks could be removed from burrows during the day to be weighed without disturbing adults, which were themselves away at sea for most of the time, while adults were potentially easy to catch when they returned to the nest.

In spite of the anticipated advantages offered by the Puffin as a study species, the problems inherent in any study of a long-lived species, which include the majority of seabirds, remained (Newton,1989). In particular, the extent to which observations confined to a period of three years, shorter than the lifespan of most individuals under study, are representative of long-term patterns is debatable and can only be resolved by continuing with long-term studies. One solution to this quandary, however, is to adopt an experimental approach, involving matched treatments and controls, which is wholly feasible within the context of a short-term study. This reasoning underpinned the approach adopted here to the study of reproductive success in a long-lived seabird.

CHAPTER 2 GENERAL METHODS.

2.1 Study site preparation and maintenance.

Virtually all fieldwork for this study was carried out at the Little Hide site (**Plate 2.1**), at the northern end of the Burrian, on the eastern side of the island (**Figure 2.1**). The study site extended for 30m from east to west and 15m from north to south and had an observation hide midway along its northern boundary. The observation burrows were 3m to 15m from the hide. The ground sloped gently at c.10° eastwards towards the sea. The vegetation was mainly the grass Yorkshire Fog, with small patches of Common Sorrel and Small Nettle. In the dry summer of 1990, the vegetation remained low (less than 10cm in height) and some badly-eroded areas of bare soil had to be stabilised at the end of the breeding season with plastic mesh matting. In the wetter 1992 breeding season, the vegetation reached 40-50cm in height, while it was intermediate in height in 1991. In the latter two breeding seasons it was necessary to cut the vegetation regularly, to allow burrow markers and coloured rings on Puffin legs to be seen.

The total number of burrow entrances that could be observed from the hide was dictated by the local topography; the study site could not be extended downslope and eastwards towards the sea or upslope because of the unfavourable aspects of these areas for viewing, nor could it be extended southwards because of a gully in the rocks (**Plate 2.1**) or northwards because the hide was installed on the northern boundary before the study began.

In April 1990, 165 Puffin burrow entrances in the centre of the study area were marked with numbered posts. This number was increased to 240 in 1991, to cover every entrance within the study area. Of these burrows, 56 were used for some aspect of the study in 1990 and 96 in 1991 and 1992. The remainder were either burrows not used by Puffins or were too deep to allow chick monitoring, while some markers indicated multiple entrances to the same burrow, only one of which was generally used in any given breeding season.

2.2 Weighing, capture and processing of adults.

Methodological factors which might have caused artificial variation in the biological parameters requiring measurement were minimised by keeping bird handling to a minimum because of its potential adverse influence on behaviour and, therefore, on adult and chick

Plate 2.1 The Little Hide study site, the main site used in the present study (as seen from the observation hide).

Plate 2.2 Remote electronic balance (Ohaus CT1200) used to weigh adult Puffins without handling.

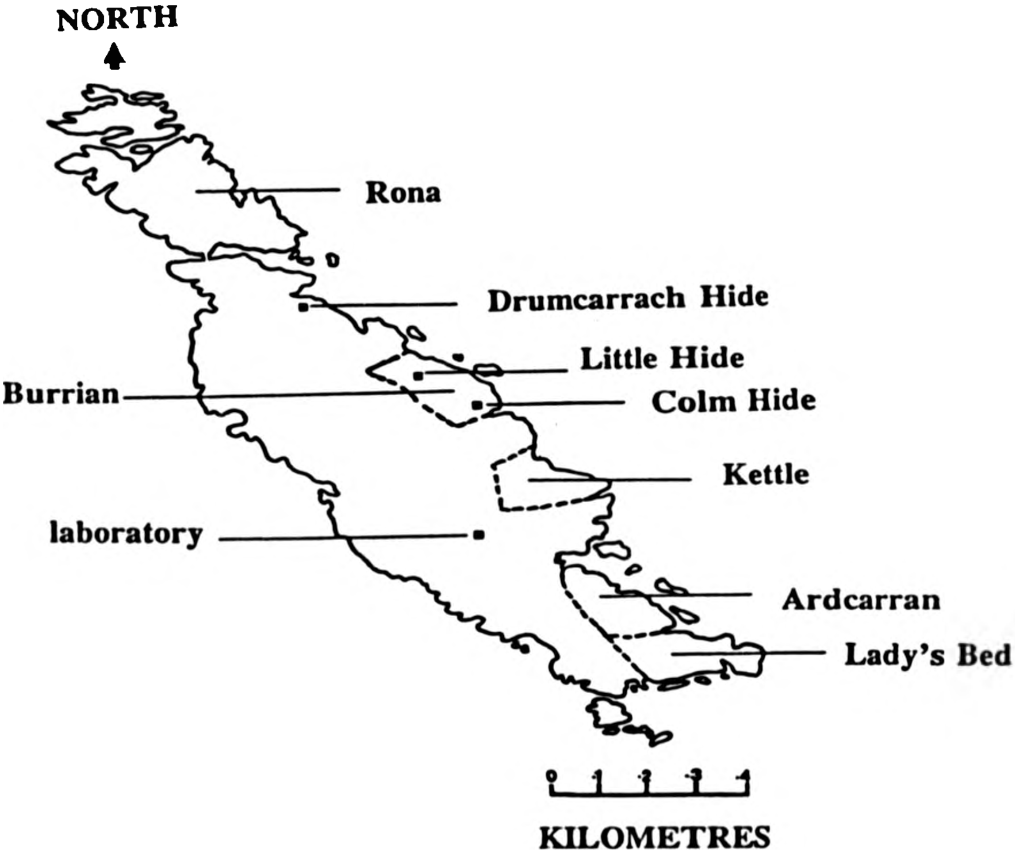


Figure 2.1 Map of the Isle of May showing areas referred to in the present study.

breeding parameters; the importance of this became obvious when it was shown that Puffins were particularly sensitive to handling (section 2.9 below). In 1990, body mass alone was measured as an indicator of adult condition (in terms of body reserves carried, Chapter 4), the aim being to refine the condition measure in subsequent years by independent measurement of protein and/or lipid reserves. A method of scoring the body lipid reserves of Puffins by visual or tactile means was, unfortunately, not found. Ultrasonic determination of breast muscle thickness (eg Sears,1988; Newton,1993) and external breast muscle 'profiling' (Bolton et al,1991) were tried as methods of determining the magnitude of protein reserves but both these techniques were found to be difficult to apply to Puffins because of the thickness of down feathers underlying the feathers of the breast. Both caused a substantial increase in bird handling time and were abandoned in view of the effect of the latter on the subsequent behaviour of individuals.

2.2.1 Automatic electronic balances.

It was hoped that most measurements of individual adult mass could be made without handling by using precision remote electronic balances. The balance system consisted of an Ohaus CT1200 balance (capacity 1.2kg, accuracy 0.1g), with a wooden block attached to the pan to form a weighing platform **(Plate 2.2)**, interfaced to a Psion XP personal organiser situated in the hide; both the balance and Psion were powered by a 12v car battery. The Psion program (Stirling Microsystems,1990) prompted the balance for a 'base reading' every 5 minutes, to provide a reference against which to compare the mass measurements of individual birds. This allowed correction for drift in the zeroing of the balance resulting from changes in humidity and wind. Part of the program allowed re-zeroing to be achieved from the hide. When a mass on the balance pan exceeded 300g, there was a 5s delay and then the mass was measured, displayed on the Psion screen and stored in its memory, together with the real time. A buzzer alerted the observer to the presence of a bird on the balance platform and the identity of the individual was recorded visually and later linked to its mass stored in the Psion's memory. The 5s delay before weighing ensured that the bird was, normally, standing still on the platform before it was weighed so that a stable mass was recorded. The Psion program incorporated a function to allow extra mass measurements to be requested in addition to the automatic one, so that the stability of the latter could be checked. In practice, mass measurements obtained from the balance were only used if two or more measurements of an individual agreed to within 1g because some repeat measurements of the same individual (within a short time period) indicated that some recorded masses were unreliable (especially if the bird moved on the balance platform).

Balances were waterproofed using silicon rubber gel and glass fibre cases and were sited to maximise the number of individually-identifiable birds which could be weighed. Three balances were available, although only one could be connected to the Psion at any given time. The six sets of power and interfacing cables were encased in heavy-duty hosepipe and firmly pegged down across the study site to protect them against pulling by Shags and young gulls, and from severing by Puffins and Rabbits. In April 1990, wooden blocks were used as dummy balances and were placed outside the entrances of 15 occupied burrows to assess whether the occupants would use them as vantage points. The blocks proved to be quite popular but it soon became apparent that it was not possible to keep moving the balances between individual burrows because of the time taken and hence the disturbance to the colony caused by moving the cabling. It was decided, therefore, to site the balances on the highest rocks around the site, where many individuals stood when they were above ground at the colony (**Plates 2.2 and 2.3**). Sets of cabling were laid to 6 of these rock 'look-out' sites and the balances could then be moved quickly between the sites as required. There was a continual turnover of individuals at these sites, and competition for use of the balance platforms as vantage points, so that many different individuals were weighed by this method during the 3 years of the study. In 1992, the 3 Psion-interfaced balances were supplemented by an Ohaus D1001-BA balance (capacity 1kg, accuracy 1g) with a large liquid-crystal display that could be read from the hide using a telescope.

Adult mass measurements made with the electronic balances were supplemented by capturing birds, for a number of reasons. First, it was impossible to control which birds were weighed or to target measurements to particular stages of breeding, so that some individuals were weighed regularly and others only once during the season or not at all. Second, the balances were unable to give stable mass measurements in strong easterly winds, which were, unfortunately, the prevailing weather conditions when large numbers of adults were standing on rocks at the colony, and, third, all 4 balances failed to work for periods during the 3 breeding seasons due to the effects of dampness/salt-spray and other unidentified problems.

2.2.2 Methods for capturing adults.

Each adult was caught at least once during the study in order to obtain body-size measurements and for the purposes of sexing and ageing (Sections 2.2.4 and 2.2.5 below).

Plate 2.3 Remote electronic balance (Ohaus CT1200) sited on a 'look-out rock' favoured by adult Puffins at the Little Hide study site.

Plate 2.4 'Box trap' sited on the edge of a favoured 'look-out rock' at the Little Hide study site. Such traps were used to catch adult Puffins away from their burrows.
(For mode of operation refer to Figure 2.2 and the text)

The most reliable methods of capturing particular individuals were to either remove them by hand from their burrows or to catch them when they were delivering food to their chicks by placing small 'purse nets' (designed for catching rabbits) in burrow entrances. Adults were only caught in burrows when their young had hatched because of the risk of desertion if they were removed earlier in the season (Harris,1984). Although this risk may not have been large (section 2.9), it was considered unacceptable due to the restricted number of burrows available for monitoring in the study area. Even so, it became apparent that the capture of adults from burrows during rearing could disrupt their behaviour for several hours to several days afterwards.

The desire to capture adults prior to chick rearing and to reduce the behavioural disturbance caused by capture from the burrow resulted in the testing of a number of methods for capturing adults away from their burrows. Mist-netting was attempted but was found to be too non-selective; few colour-ringed adults were caught, despite the large numbers present at the site, and the whole colony was seriously disrupted. Clap-netting of adults standing on 'look-out' rocks was attempted with some success. There were, however, some problems with 'inquisitive' immature Puffins and juvenile gulls, which disturbed the net so that it would not release; entering the study area to rectify such a problem resulted in all the birds leaving and a long wait was often required before the birds returned from the sea. Equally, the sample of Puffins caught by this method took up to 30 minutes to remove from the net, during which time all the others left the colony.

The most successful technique for capturing Puffins away from burrows was the manually-operated 'box-trap' (**Figure 2.2**). Each trap consisted of a wooden box of length and depth designed to match existing rock outcrops at the study site, and of width 20-40cm. Each had a lid which was hinged to drop inwards and roughened on the outside by mixing sand with the paint, to produce a non-slip surface on which Puffins would stand. The lid rested on the front panel of the box, the upper third of which was hinged to open outwards but was prevented from dropping by rubber bands attaching it to the box sides. The front section could be pulled open by a cord from the hide, allowing the lid to drop rapidly and catching any Puffins standing on the lid. The front then sprung back into place, each box being deep enough to contain any birds caught. The lid could also, however, be pulled back into the set position with a second cord from the hide, so that multiple captures were possible. Any birds caught remained calm inside the closed box and could be removed in seconds so that colony disruption was minimal; standing adults returned to the colony within a few minutes of the

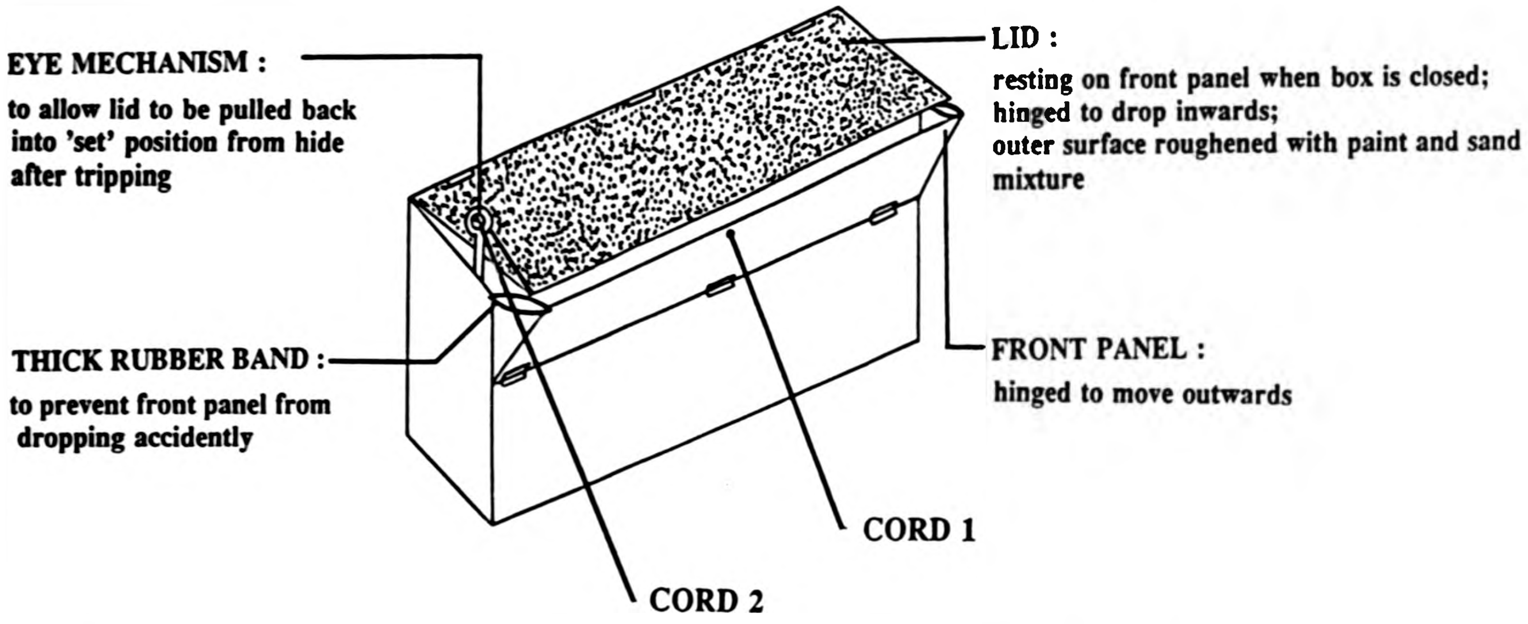


Figure 2.2 Design of 'box traps' used to catch adult Puffins away from their burrows at the Little Hide study site.

Cords 1 and 2 ran to the hide. The box was tripped by pulling cord 1 when Puffins stood on the lid. The hinged front panel moved forwards allowing the lid to drop inwards. The trap was reset by pulling the lid back into the 'set' position using cord 2.

(For dimensions and siting of box traps refer to the text and to Plate 2.4) observer returning to the hide. There were 7 of these traps placed along the edges of rocks used by Puffins as vantage points (**Plate 2.4**).

2.2.3 Processing of adults.

All adults which were caught were fitted with a metal British Trust for Ornithology numbered ring and a unique combination of 3 coloured rings. Some had been ringed in previous seasons and 16 were already colour-ringed. Each bird was weighed with a 500-g Pesola spring balance (to the nearest 1g). This balance was regularly checked by comparison with another Pesola spring balance and with the electronic balances and weights never differed by more than 1g.

The maximum straightened and flattened wing length, from the carpal joint to the tip of the longest primary feather (method 3 in Svensson,1992) was measured (to the nearest 1mm) with a stopped rule. All other measurements were made to the nearest 0.1mm using running slide calipers. Maximum head plus bill length was measured as the greatest distance from the centre-back of the head to the tip of the upper mandible, with the upper surface of the calipers resting on the top of the head and the uppermost part of the cere (bill sheath)(**Figure 2.3a**). Tarsometatarsal length (subsequently referred to as tarsal length) was measured from the notch on the back of the intertarsal joint to the point at which the toes diverge, where the toes were bent back at an angle of 90° to the tarsus (**Figure 2.3b**). This method is recommended (Svensson,1992) for species such as the Puffin where the scales at the lower end of the tarsus appear as a mixture of complete and divided. Three bill measurements were made and these were used in sexing (Section 2.2.4). The bill top length (subsequently referred to as bill top) was the chord from the anterior edge of the keratinous cere to the tip of the upper mandible. The length of the bill cutting edge (bill length) was measured from the anterior edge of the cere to the tip of the upper mandible, while bill depth was measured at the broadest point (the bill base) but excluding the cere (**Figure 2.3c**). All measurements used in the analyses were made by the author and were periodically checked for repeatability. Repeat measurements of wing length never differed by more than 1mm, head plus bill length by more than 0.5 mm, and other size measures by more than 0.2mm.

2.2.4 Sexing of adults.

Isle of May adult Puffins can be sexed using 3 bill measurements (described in Section 2.2.3

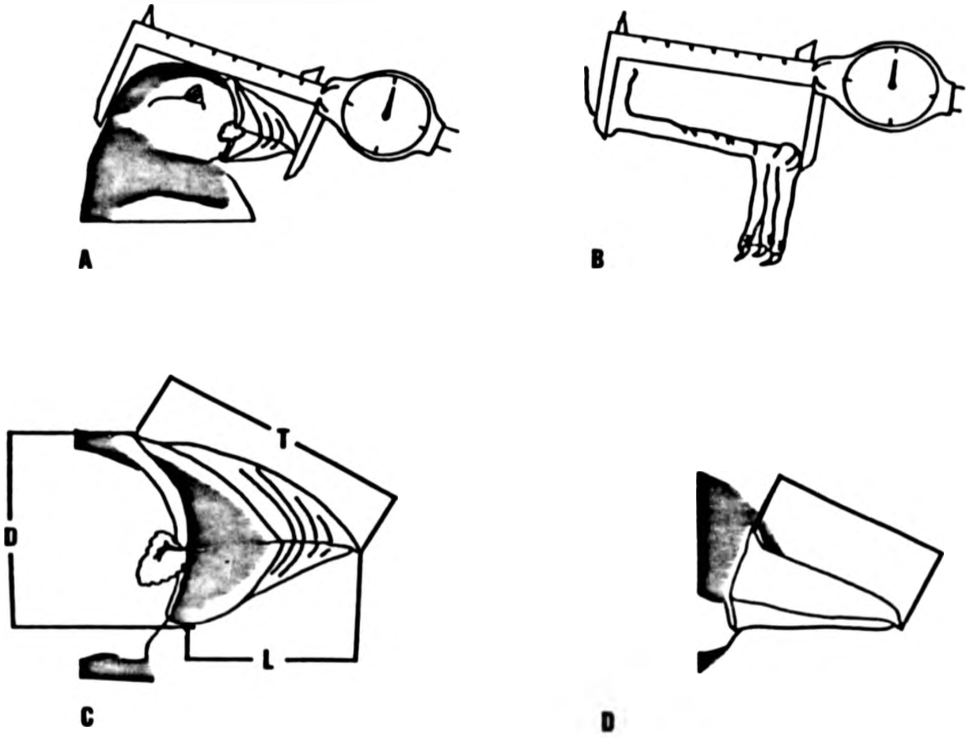


Figure 2.3 Methods used in the present study to measure Puffin adults and young.

A : Maximum head plus bill length
(callipers resting on top of head and top of cere)

B : Tarsometatarsal length
(from the notch on the back of the intertarsal joint to the point at which the toes diverge; toes at a 90° angle to tarsus)

C : Adult bill measurements
(T=bill top length; L=straight bill length (cutting edge); D=maximum bill depth)

D : Bill length of young

and illustrated in **Figure 2.3c**). The discriminant score (Harris,1981) was calculated as :-

$$\text{Bill score} = 0.601T + 0.748L + 1.99D \qquad \textbf{(Equation 2.1)}$$

where T was the bill top length (mm), L was the straight bill length (mm) and D was the maximum bill depth (mm). Individuals with a score of less than 120.6 were females and those with a score greater than 120.6 were males; the overall probability of misclassification was estimated to be 9% (n=52 birds). Members of pairs sometimes had very similar bill scores or scores where neither or both exceeded 120.6. For this reason, birds were only allocated a definite sex in this study if both were measured, in which case the one with the larger score was assumed to be the male. In cases where the scores were very close, birds were only sexed where one of the pair was seen either performing or receiving the pre-copulatory display. This display of head jerking and rapid wing fluttering, rarely seen on land, is performed only by males at females (Taylor,1984). Sex determinations made by both observation of display and bill score for the same individual were always in agreement (n=15).

2.2.5 Ageing of adults.

Features of the Puffin bill can be used as indicators of age (Petersen,1976; Harris,1979). The outer area of the upper mandible, anterior to the pale ridge separating the inner dark area from the reddish distal area, is dissected by a number of grooves, which have been shown to increase with age up to at least the fifth year of life (Harris,1979). Most breeding adults are at least 5 years old and have at least 2 of these grooves while very few (only 6 of 15,000 individuals examined in Harris' study) have as many as 4 grooves. The low variation in the number of grooves on breeding adults, and the individual variation in the number of grooves at any given age (Harris,1979), mean that it is impossible to confidently age individuals by this method after their fifth year of life. Although the use of these grooves as an indication of age is suitable for investigating how breeding parameters vary with age for a large sample of birds, the method was not considered appropriate for ageing when making detailed comparisons of the reproductive performance of individual pairs.

A total of 121 of the adults resident at Little Hide were fitted with metal numbered rings prior to the study. Of these, 14 had been ringed as chicks and were, therefore, of known age. A further 16 had less than 2 bill grooves when they were ringed and could, therefore, be aged to within 2 years (Harris,1979). In this study, birds ringed with one groove or less were assumed to be a maximum of 2 years old at ringing, those with more than one but less than 2 grooves were assumed to be a maximum of 3 years old at ringing, while birds ringed with 2 or more grooves were assumed to be of breeding age (a minimum of 4 years old). Puffin ages were expressed in calendar years regardless of the date in the season on which they were first ringed. Ages quoted for birds ringed with 2 or more grooves are minima because these birds may have been breeding for an unspecified number of years prior to ringing. The use of these ringing dates as indicators of relative age will be discussed further in Chapter 3.

2.3 Observations of adult behaviour.

Each observation session lasted 2-4 hours, with a 1-3 hour break between sessions; sessions were scheduled to cover the dawn to dusk period equally, with one complete daylight period observed every 2-3 days. In 1990, observations were made only during chick rearing (1st June-27th July; total of 175h), while in 1991 (18th March-30th July; total of 573h) and 1992 (22nd March-12th August; total of 572h) the whole breeding season was covered. Mass measurements of adults were made using the automatic balances during these observation sessions whenever the weather was suitable. The following types of behavioural data were collected during observation sessions :-

2.3.1 Fights : Instances involving colour-ringed birds were recorded.

2.3.2 Burrow maintenance activities (not 1990) : Instances of burrow digging and carriage of nest-lining material into the burrows by colour-ringed individuals were recorded.

2.3.3 Incubation behaviour (not 1990) : Two types of behaviour were recorded. First, a characteristic behaviour during incubation is the emergence of the incubating bird from its burrow, midway through an incubation shift, in order to defecate. The bird walks a short distance from the burrow, turns to face the entrance, defecates a powerful jet of excrement and rapidly disappears back down the burrow. When this behaviour was observed, the individual and time was recorded. The date on which this behaviour was first observed for each burrow within a season was recorded but the behaviour did not occur frequently enough to be used as an indicator of laying date. Second, incubation 'change-overs' were recorded, where one member of the pair returns to the burrow from the sea and the incubating bird leaves the burrow from a few seconds to up to an hour later. Incubating birds sometimes leave the egg for short periods, therefore a 'change-over' was only recorded when both the returning and leaving individuals were identified. Adult incubation behaviour will be discussed further in Chapter 3.

2.3.4 Provisioning visits to chicks : The date on which the first food delivery to each burrow was seen was recorded and was used in hatching date determination (section 2.5.2). The identities of individuals entering burrows with food loads were recorded wherever possible. This functioned both to confirm the identities of burrow occupants and provided a measure of the role of the sexes in the provisioning of young (Chapter 3). Attempts were made to determine the composition, size and number of fish within food loads but this proved difficult because of the speed with which the returning birds entered their burrows. Fish were therefore grouped into 4 species categories : sandeels (mainly Lesser Sandeels), clupeids (Herring or Sprat), gadoids (mainly Saithe) and Rockling and size was scored as either larval (very small, transparent fish), small (less than bill depth = up to c.40mm), medium (1-2 times bill depth = c. 40-80mm), large (2-3 times bill depth = c.80-120mm) and very large (more than 120mm long). The number of fish in each load was scored as the actual number when they could be counted (up to c.10 if the fish were at least of medium size) or as medium (for an unexceptional load) or large (for a load with an exceptional quantity of fish).

2.3.5 Kleptoparasitism and predation : Herring and Lesser Black-backed Gulls regularly stole food loads from Puffins arriving at the colony, while instances of losses to Arctic Terns (n=5), Razorbills (n=2), Kittiwake (n=1) and Arctic Skua (n=1) were also observed during the 3 breeding seasons of the study. The attacking species, target individual and/or burrow and the result (partial or total loss of the load) were recorded for all successful events of kleptoparasitism. Any predation of monitored Puffin chicks by gulls was recorded.

2.3.6 Appearance of young at burrow entrances : Instances of chicks emerging at burrow entrances, to stretch their wings prior to fledging, were recorded, and these were used to confirm fledging dates and fledging success (see section 2.6).

2.3.7 Attendance of adults at the Little Hide study site : This was the only form of time-budgeting that could be undertaken within the time limitations of the study. During each hide observation session in 1991 and 1992, the identities of all colour-ringed individuals present at the colony were recorded on a pocket tape recorder every 30 minutes. During each check, two sweeps were made across the study area and individuals were only recorded if both their legs were visible; this avoided biases towards well-known individuals which could be identified after seeing only one colour-ring because they favoured certain positions at the colony.

There was a greater probability of seeing both the legs of some individuals (eg those in burrows close to the hide) than those of others. To reduce this bias, the study site was divided into 4 areas, depending on the general visibility of the legs of standing birds, as follows :- area 1 - legs easily visible (burrows in the flat ground directly in front of the hide), area 2 - legs partially concealed due to aspect (burrows close to the hide but on a steep slope), area 3 - legs partially concealed due to distance from the hide (burrows in the eastern area of the study site, furthest from the hide), and area 4 - burrow entrances completely obscured due to very steep slopes or obstacles. On days when there were large numbers of adults at the study site, counts were made in the 4 areas to determine the proportion of birds with both legs visible. These counts were made on 16 days in 1991 and 10 days in 1992 and were evenly distributed over the range of dates on which attendance checks were made in the two seasons. The correction factors resulting from these counts (**Table 2.1**) were used to standardise raw attendance frequencies for inter-burrow comparisons. An equal chance of identifying all individuals when they were standing away from their burrows on rocks was assumed. This assumption probably did not hold precisely because undoubtedly certain individuals preferred certain rocks and certain positions on these rocks but too little was known about such preferences to allow further corrections to be made.

Observation sessions in which attendance checks were made were of 2-4 hours duration with a 1-3 hour break between sessions. Sessions were scheduled to cover the dawn to dusk period equally, with one complete daylight period covered every 2-3 days. A total of 633 checks was made in 1991, beginning on 25th March (pre-laying) and ending on 17th June (early chick rearing for most pairs) due to pressures of other work. In 1992, a total of 873 checks was made through the entire breeding season from 18th March to 9th August.

The percentage of checks during which each individual was present approximated to the percentage of the day spent above ground at the colony because checks were evenly distributed with time of day, and birds were rarely above ground at the colony at night (pers.obs.). The probability of missing an individual during a check (eg because it was lying breast-down) was quantified in 1991 by selecting 26 individuals which had burrow entrances clearly visible from the hide and whose lying positions next to their burrows were known. During each check the presence or absence of these individuals was recorded together with

Table 2.1 **Correction factors used to standardise percentage of the daylight hours that individual adult Puffins spent above ground at Little Hide for differences in the visibility of burrow entrances from the hide.**

(Counts of the 4 areas were made on 16 days in 1991 and 10 days in 1992.)

	1991		1992	
AREA[a]	Mean % birds with both legs visible	Correction factor	Mean % birds with both legs visible	Correction factor
1	73	1.0	66	1.0
2	47	1.6	33	2.0
3	22	3.3	11	6.0
4	64	1.1	54	1.2

<u>NOTES.</u> a Areas :
1-legs easily visible
2-legs partially concealed due to aspect
3-legs partially concealed due to distance from hide
4-burrow entrances completely obscured by steep slope

whether or not their legs were visible. It was not possible to perform a comparable test for birds lying on rocks away from their burrows. Birds were missed on approximately 10% of occasions (range 0-28% for the 26 individuals), so that the percentage of time spent above ground at the colony was underestimated by c.10%. Ideally all attendance checks should have been made when most birds were standing but this would have severly reduced the sample sizes obtained. It was, therefore, assumed that there was an equal chance of missing any individual and data from all checks were used in the analyses. Colony attendance figures presented in the analyses were not adjusted for the time individuals were missed.

The minimum number of checks required to calculate consistent measures of colony attendance for individual birds was determined in 1991 by plotting percentage attendance against the number of checks considered (in 50-check increments) for 22 individuals during the incubation period, when check sample sizes were largest (**Figure 2.4**). The number of checks after which a stable attendance figure was reached varied from 100 to 250, depending on the individual, and it was clear that attendance estimated from a very small number of checks could be highly biased. Such bias may have been caused by the cyclic nature of the attendance of adult Puffins at colonies and/or by weather conditions, which also seemed to influence numbers present at the study site. In 1991, a minimum sample of 100 checks for each individual in each breeding stage (pre-incubation, incubation and chick rearing) was used to calculate the proportion of time spent at the colony. The same minimum was retained in 1992, although in the latter year, check sample sizes during incubation and rearing normally exceeded 200 for each individual.

2.4 Daily provisioning rates (dawn-to-dusk watches).

Daily numbers of feeds delivered to individual burrows were determined by continuous dawn-to-dusk watching. Adults do not visit burrows with food during the hours of darkness (Harris,1984 and pers.obs.). In 1990 and 1991 only the area immediately in front of the hide was watched (area= 15m by 15m) and continuous watches were conducted on 4 days and 7 days throughout the chick rearing period in the two years respectively. In 1992, both the area watched in previous years (n=10 days) and a second area downslope to the east of the hide (area= 10m by 15m, n=6 days) were continuously watched.

On each continuous watch day a team of observers worked in 2-hour shifts to watch 20-50 burrow entrances. Burrow markers were placed behind the entrances in such a way that, when

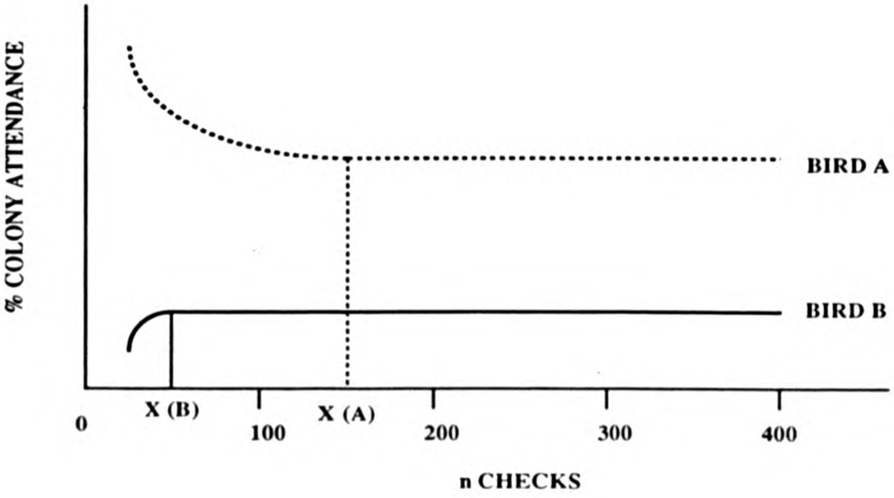


Figure 2.4 Method used to determine the minimum number of colony checks required to estimate the percentage of time spent by individual adult Puffins at the Little Hide site. Birds A and B show examples of the pattern obtained.

BIRD A :	Stable attendance value obtained at X (A) ie a minimum of 150 checks required.
BIRD B :	Stable attendance value obtained at X (B) ie a minimum of 50 checks required.

(Data were plotted for 22 individuals from the incubation period in 1991 and X varied from 100 to 250.)

viewed from the hide, the arriving adults had to pass in front of the markers before entering burrows; this clarified the identity of burrows being entered. On each day, all feeds delivered to burrows and all successful kleptoparasitism events within the defined watched area were recorded, together with the time of each event. Due to the observer concentration involved in watching a large number of burrows, other observations (Section 2.3) were not generally made on continuous watching days. In 1992 and on a single day in 1993, however, the identities of incoming and outgoing adults delivering feeds were recorded, where possible, in order to determine the duration of individual foraging trips (Chapter 6).

In watches of this type, burrows at the periphery of the study area may be underwatched. As an initial check for this potential source of error, the numbers of feeds delivered to individual burrows were plotted on maps of the watched area for 5 dawn-to-dusk watch days and the data were examined by eye for any pattern but none was apparent. As a further check, the distances of burrow entrances from the perceived centre of the watched area were measured and correlated with the number of feeds delivered to burrows on each watch day; the perceived centre of the watched area was identified independently by 3 observers and the results were in close agreement. No relationship was, however, found between burrow position relative to the centre of the area and the number of feeds delivered (Spearman rank correlation p always > 0.1).

2.5 Timing of breeding.

2.5.1 Laying date.

Laying dates were not determining directly by daily checking of burrows because of the risk of causing desertion, nor were they measurable by observation of incubation behaviours (Section 2.3.3) because these did not occur sufficiently frequently. In both 1991 and 1992, attempts were made to determine the laying dates of a small number of burrows by temperature monitoring (to detect the presence of a sitting bird). In the first week of April in 1991, before the main laying period, 4 apparently occupied burrows were selected in the 'Kettle' area on the east side of the island (**Figure 2.1**); burrows were assumed to be occupied if a characteristic finely-ground soil due to Puffin digging was present at the entrance. In each case, the most likely position of the nest chamber was established and a simple thermocouple was inserted into its roof (**Figure 2.5**), ensuring that the sensitive tip of the probe could not be damaged by the birds. One of the thermocouples was, however, damaged a few days after

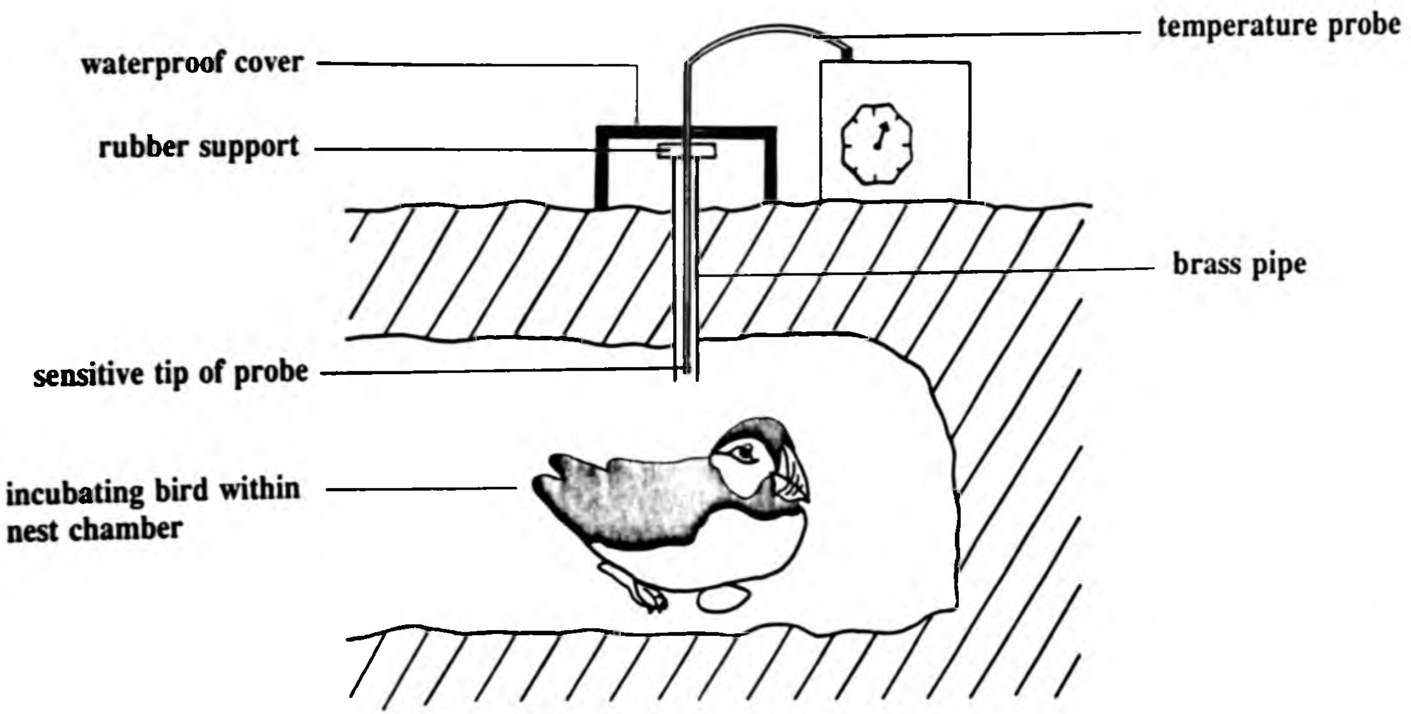


Figure 2.5 Apparatus used for temperature determination of Puffin laying date.

insertion and could not be replaced. A temperature reading (to the nearest 0.5°C) was recorded for each burrow every 2-3 hours each day for 18 days, after which time it was assumed (from observations at the Little Hide study site) that most pairs had laid. Each burrow was then checked for the presence and location of an egg and incubating bird. Burrow temperature was found to vary from 4-15°C, for the two shallower burrows, and from 9-15°C for the single deep burrow monitored, depending on ambient air temperature/time of day; no increase in burrow temperature due to the presence of an incubating bird was detected. When the burrows were checked, warm eggs were present in all three but in each case they were located some distance from the probe; it was, therefore, difficult to predict the location of the nest chamber. For this reason the procedure was repeated in 1992, when the 4 probes were placed into the roofs of 4 burrows (including 2 nestboxes) at the Little Hide site, in which the positions of the nest chambers were unambiguous. Temperatures were recorded before dawn each day, when ground temperatures were lowest and temperature increase due to the presence of a bird was, therefore, most likely to be detectable. Once again no temperature increase was detected and the method was abandoned.

In this study, hatching date rather than laying date was, therefore, used to indicate the timing of breeding of individual pairs. Laying dates were estimated by subtracting 41 days from hatching dates (Harris,1984) where it was necessary to define the approximate duration of the incubation period. It was not possible to consider the differences between individual pairs in the length of the incubation period in this study.

2.5.2 Hatching date.

Due to the risk of burrow desertion, hatching dates were not determined by direct burrow checking. In 1990, three indirect methods of hatching date determination were compared. Dates when adults were first seen entering burrows with food loads and dates when egg shells were ejected from burrows were recorded. Once a feeding visit was recorded, each burrow was checked and the bill length of the chick was measured. This measurement was used to age chicks, where :-

$$\text{Chick age (d)} = \frac{\text{Bill length (mm)} - 19.3}{0.29} \qquad \textbf{Equation 2.2}$$

(after Harris,1983) and their hatching dates were determined by back-calculation. First feed dates and chick bill lengths were available for 30 burrows, and the date of egg shell ejection was known for 16 of these burrows.

The date of egg shell ejection tended to underestimate chick age relative to the other two methods (**Table 2.2**) because the shell probably took a day or more to reach the burrow entrance. Large, fresh shells outside burrows probably gave a good indication of hatch date (accurate to 1-2 days) but problems of delayed ejection, shells rolling into side passages and not being ejected at all, and shells being carried away from their original burrow by wind or other birds before they were seen meant that egg shell ejection was an unreliable method for hatch date determination.

Observations of first food deliveries and chick bill length measurements produced similar hatch dates. In many cases, however, first feeds were observed later than the hatch date back-calculated from bill length; as the rate of provisioning of newly-hatched young is low (usually 0-4 feeds d^{-1} (Harris,1984 and this study)), feeds to a new chick could easily have been missed for several days when watching burrows for sample periods only.

In 1991, 45 burrows were observed frequently enough to obtain accurate dates of first food delivery. Taking these dates as hatching dates, a new relationship between bill length and age was established. Most chicks were measured within the first 12 days after hatching, and for these chicks, bill length increased linearly with age (**Figure 2.6a**) :-

$$\text{Chick age (d)} = \frac{\text{Bill length (mm)} - 18.00}{0.36} \qquad \textbf{Equation 2.3}$$

(r^2=0.829,F=213.688,p<0.0001,n=45). Consecutive measurements of the bill length of individual chicks during monitoring suggested that the rate of bill growth was greater in the first 10-12 days of rearing than later in the rearing period, and revealed that bills sometimes did not grow for several days or remained very short for the remainder of the nestling period. Such retardation of growth most often occurred between the ages of 20 and 30 days, which is probably the time of peak chick food demand (Harris,1984). **Equation 2.3** was, therefore, used to age all chicks which were first measured when less than 13 days old, in order to reduce ageing errors caused by slower or stunted bill growth later in the rearing period. In the case of frequently watched burrows, the date of first food delivery was taken as the hatch date if the chick was not measured until it was older than 12 days. Insufficient data were available to construct a separate bill growth equation for chicks aged 13-40 days (after the

Table 2.2 A comparison of 3 methods used to determine the hatching dates of Puffin young on the Isle of May in 1990.

BURROW	HATCH DATE FROM :-			Differences in hatch dates determined by the 3 methods		
	First feed[a]	Chick bill length[b]	Egg shell ejection[c]	a-b	a-c	b-c
1	1/6	29/5	--	-3	--	--
2	1/6	2/6	--	+1	--	--
3	3/6	6/6	3/6 (A)	+3	0	-3
4	7/6	9/6	9/6 (B)	+2	+2	0
5	7/6	7/6	--	0	--	--
6	7/6	9/6	--	+2	--	--
7	4/6	5/6	8/6 (B)	+1	+4	+3
8	8/6	10/6	10/6 (B)	+2	+2	0
9	1/6	28/5	--	-4	--	--
10	2/6	2/6	3/6 (C)	0	+1	+1
11	2/6	30/5	3/6 (C)	-3	+1	+4
12	2/6	1/6	--	-1	--	--
13	2/6	27/5	--	-6	--	--
14	3/6	4/6	--	+1	--	--
15	3/6	1/6	9/6 (A)	-2	+6	+8
16	5/6	1/6	9/6 (D)	-4	+4	+8
17	7/6	10/6	8/6 (A)	+3	+1	-2
18	6/6	8/6	9/6 (B)	+2	+3	+1
19	9/6	10/6	--	+1	--	--
20	2/6	31/5	3/6 (D)	-2	+1	+3
21	3/6	6/6	--	+3	--	--
22	4/6	7/6	4/6 (D)	+3	0	-3
23	3/6	2/6	--	-1	--	--
24	4/6	5/6	--	+1	--	--
25	4/6	3/6	5/6 (D)	-1	+1	+2
26	3/6	28/5	--	-6	--	--
27	1/6	28/5	31/5 (D)	-4	-1	+3
28	5/6	8/6	31/5 (D)	+3	-5	-8
29	7/6	6/6	--	-1	--	--
30	7/6	9/6	9/6 (B)	+2	+2	0
		MEAN		-0.3	+1.4	+1.1
		RANGE		-6-+3	-8-+8	-5-+6
		n		30	16	16

<u>NOTES.</u>

a The first day on which parents delivered food to the burrow.

b Hatching date back-calculated after aging the chick using the relationship between chick bill length and age (after Harris, 1983).

c The date on which an egg shell was found. State of the egg shell in parentheses : A-whole in nest chamber; B-whole outside burrow; C-most of shell outside burrow; D-small, fragmented and outside or slightly distant from burrow.

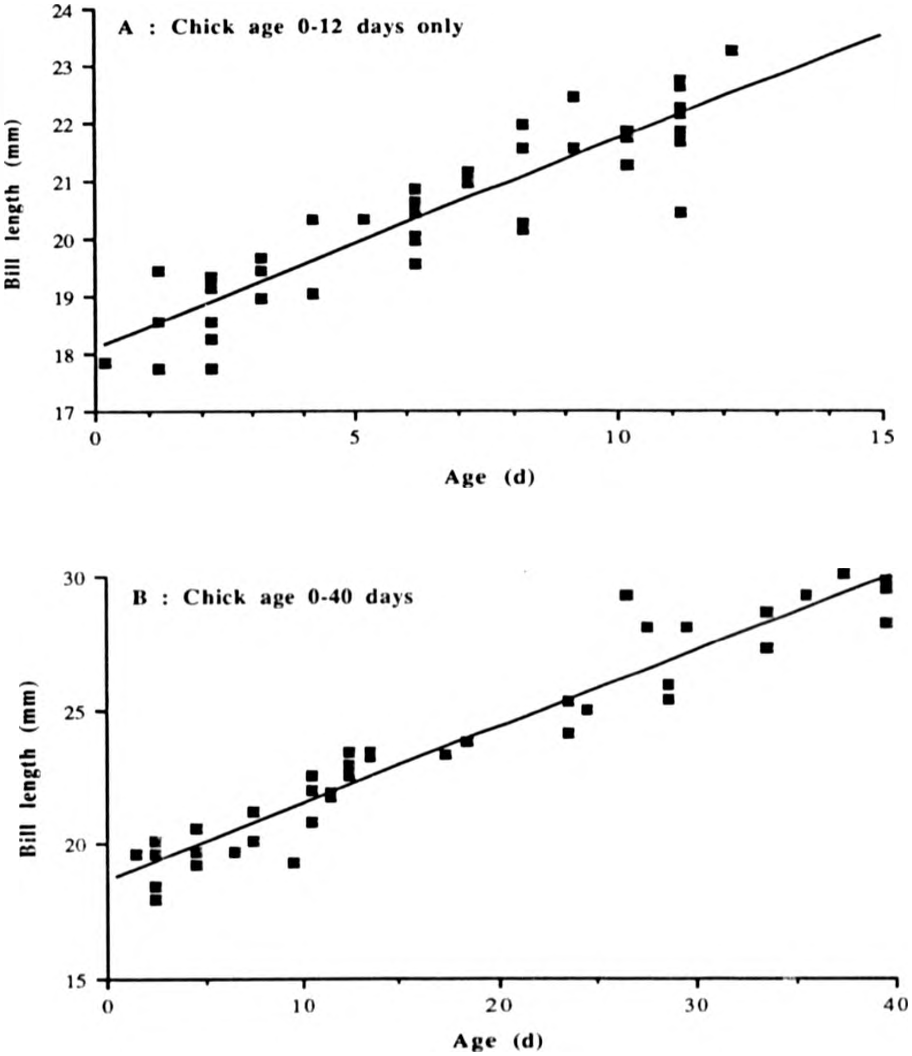


Figure 2.6 Growth of the bill of Puffin young on the Isle of May in 1991.

A : First 12 days of growth
Bill length (mm) = 18.00 + .36 Age (d)
r^2=.833 p<.0001 n=45

B : Days 0-40 of rearing
Bill length (mm) = 18.42 + .29 Age (d)
r^2=.926 p<.0001 n=39

age of 40 days no change in bill length occurred). For this reason, data for the whole chick rearing period (days 0-40) were used to produce a second linear relationship between bill length and chick age (**Figure 2.6b**) :-

$$\text{Chick age (d)} = \frac{\text{Bill length (mm)} - 18.42}{0.29} \qquad \textbf{Equation 2.4}$$

(r^2=0.926,F=461.844,p<0.0001,n=39) and this was used, out of necessity, to age chicks which were more than 12 days old when first measured and for which first feed dates were unavailable.

In this study, the stage of breeding of individual pairs was expressed in days relative to the hatching date (day 0); for example, day 10 indicated that the chick was 10 days old and day -10 indicated 10 days before hatching. Using this convention, incubation began on day -42 because it was assumed that it was 41 days in duration (Section 2.5.1 above).

2.6 Monitoring of the growth of young.

Individual burrows were, ideally, checked 5-10 days after the first food delivery was observed; some burrow entrances less easily watched were not noticed and checked for the first time until chicks were older, however. The nest chamber containing the chick was often not easily accessible from the burrow entrance so, in most cases, it was necessary to dig a shaft into the chamber from the ground surface to allow the chick to be repeatedly removed for weighing. Each such shaft was carefully covered with a slab of stone, ensuring that light did not penetrate the nest chamber; if this occurred the chick would often move to another part of the burrow, necessitating further digging, or, worse, there was a risk of adult desertion or of the chick wandering out of the burrow. Twenty-one nestboxes, made from wooden fishboxes or bricks buried in the soil with entrances made from sections of plastic drainpipe, were available at the Little Hide study site, 11 of which were used during this study. In the case of nestboxes, chicks were easily accessed via the nestbox lids.

The frequency of removal of chicks for monitoring purposes was necessarily a trade-off between the need to determine the pattern of growth accurately enough to allow inter-individual comparisons, time constraints imposed by other needs of the study, and the need to keep site disturbance to an acceptable level. Young were weighed in the middle part of the day, as close to noon as possible; this was the time of least provisioning activity and, therefore, less disturbance was caused by monitoring at this time. In 1990, each chick was visited every 5-10 days until it was approximately 30 days old, and then every 2 days until it fledged. At each visit the chick was weighed (to the nearest 1g) with a Pesola 500-g spring balance and maximum bill length (to the nearest 0.1mm), from the tip of the upper mandible to the anterior edge of the growing cere where this formed a 'v' shape **(Figure 2.3d)**, was measured with running slide calipers. Maximum straightened wing length (to the nearest 1mm) was measured with a stopped rule at every visit, once the primary feathers broke their sheaths. In 1991 and 1992, young were visited more frequently (for reasons given below) : every 4 days until fledging plumage was almost entire, and then every day until fledging. In 1991, bill length was measured on the first visit and intermittently until fledging, and wing length was measured each day when the young were of fledging appearance. In 1992, bill length was measured on the first visit and then intermittently during rearing. When young approached fledging, wing length, total head plus bill length (as for adult, **Figure 2.3a**) and tarsal length (as for adult, **Figure 2.3b**) were measured everyday. Repeat measurements of the same individual were always within 1mm for wing length, within 0.5mm for head plus bill length and within 0.2mm for tarsal length and bill length.

Young were judged to be close to fledging when most of the down feathers covering the fresh fledging plumage had disappeared, although some young fledged with down remaining on the head and neck and/or rump. Chicks were only assumed to have fledged successfully if they disappeared from burrows with plumage in this condition. Chicks which disappeared while still very downy were assumed to have left prematurely due to starvation or accident and their records were not used in analyses involving fledging masses or fledging ages. A burrow found to be empty on one visit was checked again the following day, in order to confirm that the chick had gone and was not hiding in an inaccessible part of the burrow. In the case of complex burrows with many interlinking passages, chick appearances at burrow entrances in the few days prior to fledging were used to confirm or reject fledging dates determined by burrow checking.

Young were ringed when aged c.10 days, to prevent confusion if burrows were interconnected or chicks wandered, and to allow identification of any carcasses dropped by gulls. Once adults had left the colony at the end of each breeding season, all burrows were thoroughly checked for interconnections (to confirm or disprove odd observations of chicks being fed by the incorrect parents) and for cold eggs/dead chicks, in the case of burrows in which young were not known to have been reared. Interconnections of burrows which could have lead to ambiguity in the following breeding season were blocked, if possible, and lids to nest chambers were made secure to prevent soil erosion during the winter months. In some cases of burrow collapse during the breeding season or the winter, complete burrow reconstruction with rocks and soil was required, all this being necessary to ensure that most of the limited sample of pairs in the study area could be monitored each year.

Growth of the chick bill has previously been discussed in relation to hatching date determination (section 2.5.2). The pattern of chick mass increase differed markedly between individual young **(Figure 2.7)**, although the overall pattern (determined using all non-manipulated chicks) was similar in the 3 years of the study **(Figure 2.8)**. This overall pattern consisted of a period of slow growth in the first few days after hatching, a period of rapid linear growth followed by a slowing of growth and attainment of peak mass, and, usually, a subsequent mass decline prior to fledging. Some chicks, however, showed slower growth in the linear phase, took longer to attain peak mass, and did not decline in mass before fledging **(Figure 2.7)**. The aim of chick monitoring in this study was to derive measurements, comparable between individual chicks, which could be used as indicators of parental effort and success. Due to the large variation in growth between individual young, it was necessary to extract from the monitoring data measures reflecting both chick mass and rate of growth as follows :-

Maximum growth rate (MGR in gd^{-1}) : measured between days 5 and 25 of rearing, when growth was linear for the majority of chicks.

Peak mass (PM in g) : the maximum mass measured during the regular weighings for the entire rearing period.

Age at which peak mass was attained (T_{PM} in d).

Fledging mass (FM in g) : mass on the day, on the evening of which, the chick fledged.

Age of fledging (T_F in d) : including the day on which the chick fledged.

In each year since 1974, the growth of 30-40 Puffin chicks in the Burrian area of the island has been monitored by M.P.Harris, using the visiting regime used in 1991 and 1992 in this study (every 4 days and everyday when close to fledging). There is, in general, a positive

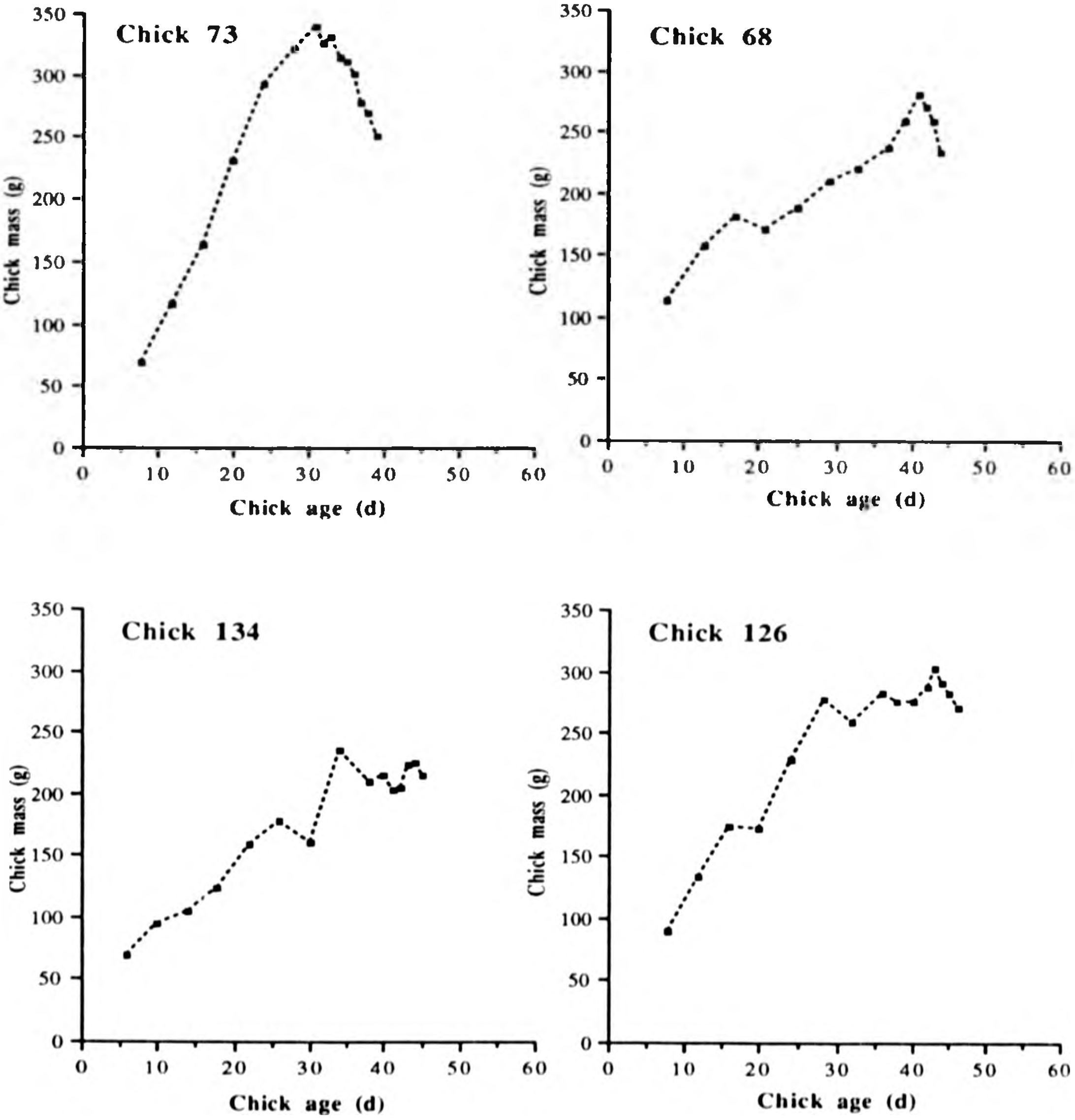


Figure 2.7 Variation in the pattern of growth (mass gain) of Puffin young on the Isle of May in 1992.

Chick 73 :	Linear increase followed by large recession.
Chick 68 :	Linear increase followed by small recession.
Chick 134 :	Linear increase with negligible recession.
Chick 126 :	Linear increase to asymptote with negligible recession.

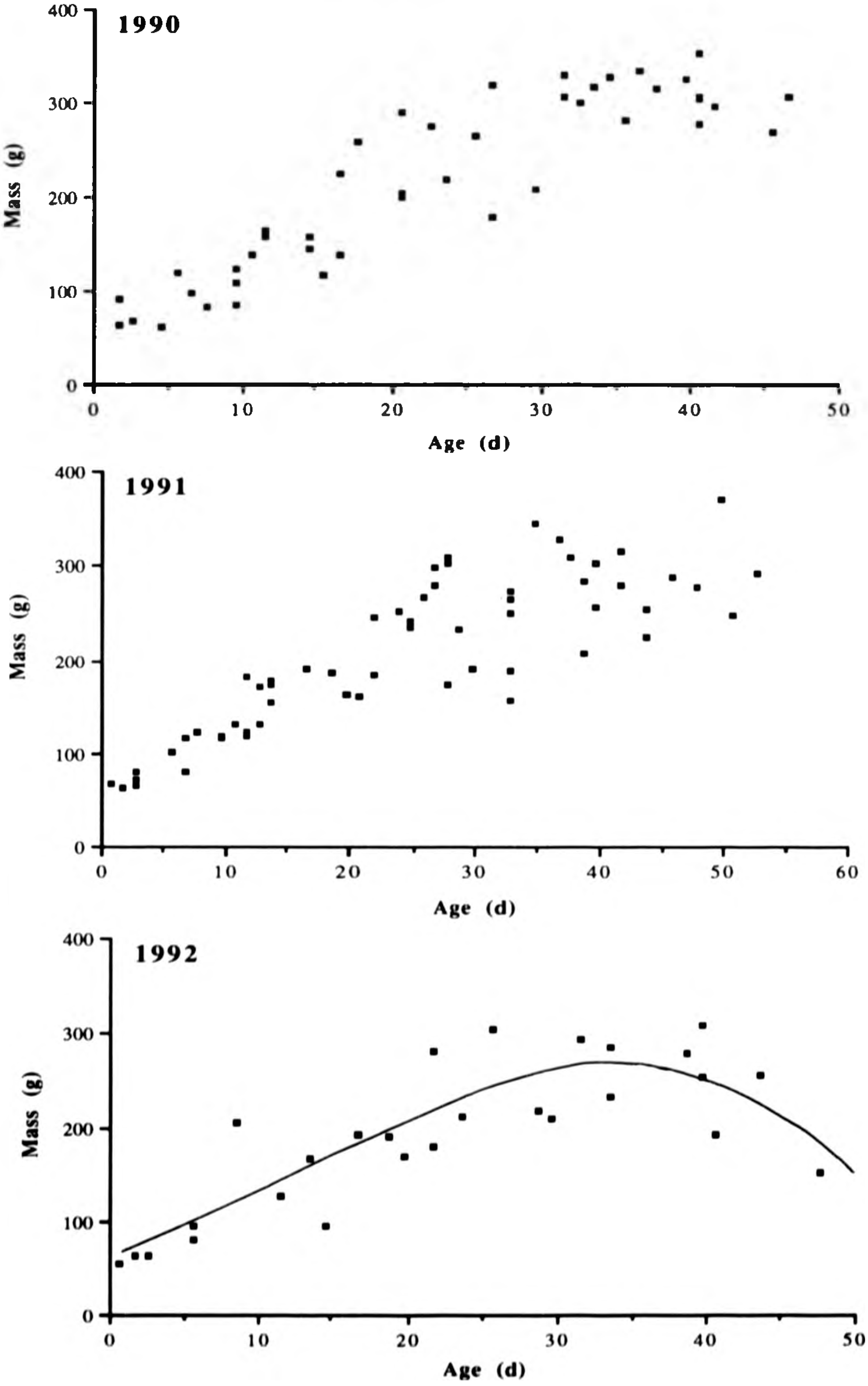


Figure 2.8 Growth (mass gain) of unmanipulated Puffin young on the Isle of May in 1990 (n=44), 1991 (n=62) and 1992 (n=27).
1992 : $y = 55.68 + 4.55x + .271x^2 - .0067x^3$ $r^2 = .759$, $p < .01$ (see Chapter 5).

relationship between the peak and fledging masses of individual chicks (M.P.Harris,pers.comm. and **Figure 2.9**). In 1990, the chicks in this study were visited less frequently than Harris' in order to reduce site disturbance. When their peak and fledging masses were compared with those of Harris' chicks (see section 2.9), peak masses were similar but the fledging masses of Harris' were lower, although not significantly so. There was no relationship between the peak and fledging masses of chicks from this study in 1990, which suggested that chicks were not weighed frequently enough to obtain true fledging mass. For this reason, chicks were weighed using Harris' visiting regime in 1991 and 1992. The 5 chick variables described above were estimated for the less-frequently weighed 1990 chicks by plotting the growth data for each individual and fitting curves, from which the variables could be derived, by eye. The variables were only derived when a reasonable curve could be fitted and, in interpreting analyses involving these measures, it is important to note that they were less accurate than those obtained in 1991 and 1992. The derivations of measures of chick condition are discussed in Chapter 4.

2.7 Diet of young.

In this study, it was not possible to obtain food loads from individual monitored burrows because of the unacceptable disturbance this would have caused. Repeated capture of food loads from the same burrow would, at best, have largely affected the breeding parameters that this study aimed to measure and, at worst, could have resulted in desertion of young. It was important, however, to attempt to quantify differences in the chick provisioning effort of individual pairs. The number of food loads received by each chick each day was quantifiable by continuous watching (section 2.4), while attempts were also made at quantifying differences in the size and composition of individual food loads by direct observation from the hide (section 2.3.4).

In addition, samples of food loads (10-20 per week) were obtained at approximately weekly intervals throughout the main chick rearing period in each of the 3 years of the study. This was achieved by setting three 15m mist-nets along the path at Holyman's Road (250m from Little Hide) before dawn and capturing adults arriving with food loads during the period of the day when feeding activity was most intense. Each load was weighed (to the nearest 0.1g) with a Tanita 100-g portable electronic balance and the numbers, species and lengths (to the nearest 1mm) of the component fish were recorded. The loads obtained gave some indication of chick diets in general and of whether or not these varied over the course of each breeding

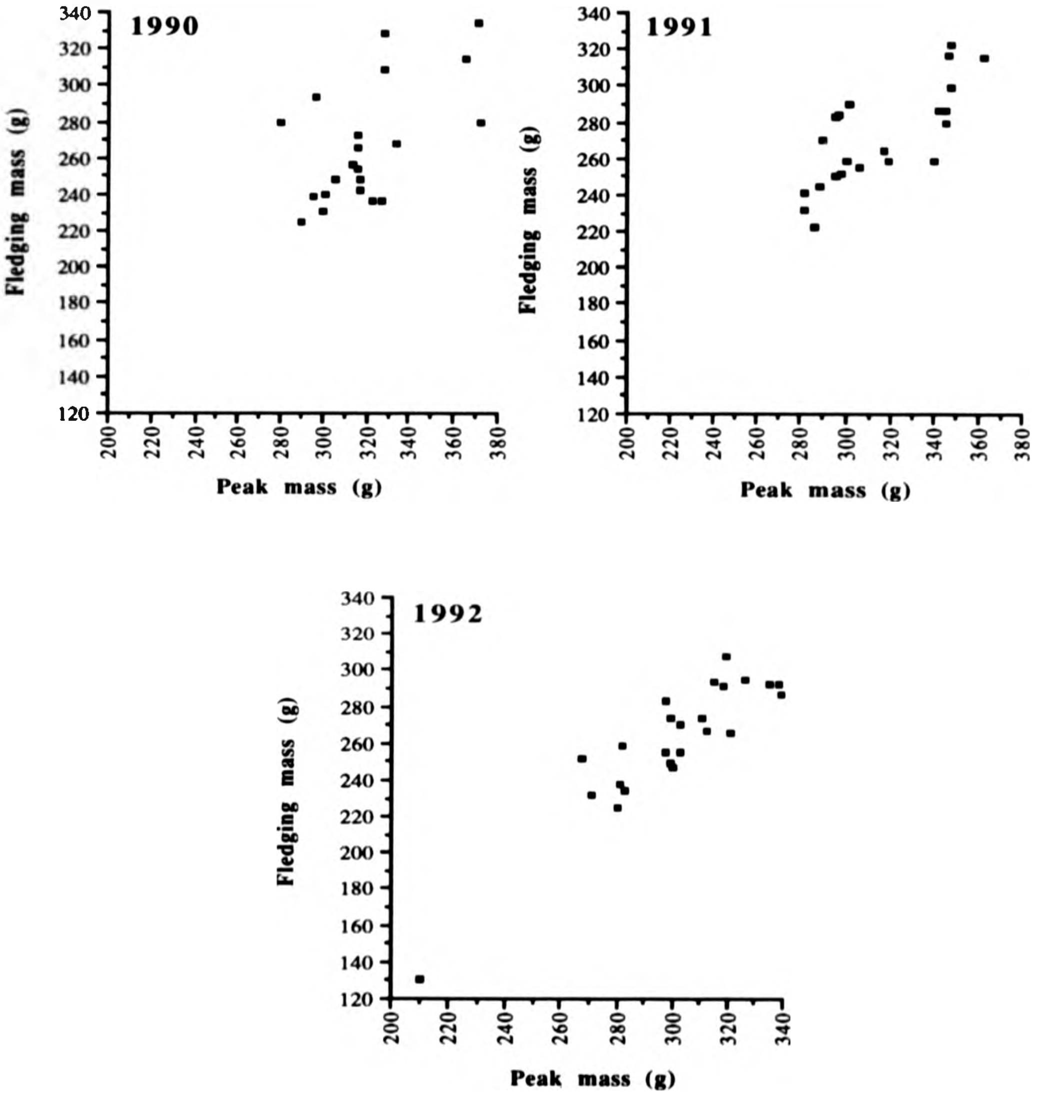


Figure 2.9 Relationship between peak mass and fledging mass of Puffin young on the Isle of May, 1990-1992.

1990 : Pearson r=.568 p<.01 n=21
1991 : Pearson r=.764 p<.001 n=22
1992 : Pearson r=.840 p<.0005 n=27

(Unpublished data of M.P.Harris for the Burrian).

season. The netting technique could not, however, be used to estimate prevalent feeding conditions (eg by the rate of capture of arriving adults), despite the standard net configuration, because the success of capture was largely dependent on wind speed and direction.

In 1991, the adults caught during mist-netting sessions were weighed and measured (section 2.2.3) and these data were used to investigate relationships between food load size/quality and adult body size/condition.

2.8 Weather data.

Weather data were obtained from Fifeness Coastguard Station, approximately 10km north of the Isle of May. Mean temperature (to the nearest 0.1°C), wind speed (to the nearest 1ms^{-1}), horizontal visibility (to the nearest 1km), cloud cover (in oktas) and wind direction (to the nearest 10°) were recorded every 3 hours, and rainfall (to the nearest 0.1mm) every 12 hours. Mean daily temperature, wind speed, visibility and cloud cover were calculated as the mean of the 8 records (taken from 0000h midnight to 2100h) available for each day. Total daily rainfall was the sum of the 2 records on each day (total from 0900h on that day to 0900h on the following day). Daily wind direction was expressed as the proportion of the 8 daily records for which the wind was onshore (0-90°, due north to due east) at the Little Hide study site.

2.9 Effects of disturbance on Puffins.

Quantifying the effects of disturbance was not an aim in the present study but during the fieldwork, it became apparent that Puffins were sensitive to handling. This section is included therefore, to present the evidence for disturbance effects from the study and to briefly evaluate any influence the disturbance may have had on results presented elsewhere in the thesis.

2.9.1 Capture and processing of individual colour-ringed adults.

An effect of capture and/or handling on the behaviour of adults was first noticed during the doubly-labelled water fieldwork in 1991. Most of the labelled birds (which were watched continuously) did not resume normal behaviour (provisioning visits to young) until 36-48 hours after their release and some appeared hesitant before entering burrows with food loads (discussed in Chapter 6). The disturbance to these individuals was not caused solely by the labelling protocol because other observations of colour-ringed adults at Little Hide revealed that some individuals did not return with food loads for several hours or even days after capture (for weighing and measuring, which took a maximum of 10 minutes). Many were hesitant before entering burrows, which seemed to result in higher losses of loads to gulls, and the effects were greater after the second capture of parents during the rearing period than after the first capture. For this reason in 1991 and 1992, parents were not caught for a second time until after their young had reached peak mass, and peak mass rather than fledging mass was used to derive a measure of chick condition for interburrow comparisons (Chapters 4 and 5).

Unfortunately, it was not possible to quantify the lengths of time for which the behaviour of captured birds were disrupted more accurately, or to quantify the effect of the disruption on parental effort. The extra losses of food loads to gulls may have resulted in an increased effort requirement by parents to replace lost loads or may have temporarily reduced the effort of disturbed birds, resulting in poorer chick growth (section 2.9.2 below). There was some evidence for compensatory increased effort by partners after one member of a pair was caught during rearing but assuming that both members of each pair were caught during rearing, such disturbance effects would cancel. The possibility that individuals varied in their response to capture could not be ruled out however, so that such disturbance may have increased the variation in the effort and success of individual pairs.

2.9.2 Effects on the growth of young.

Disturbance effects were sought by (i) comparing the growth of unmanipulated young at Little Hide with that of young in the monitored burrows of M.P.Harris on the Burrian, to the south of Little Hide and (ii) by comparing the growth at Little Hide in 1992 of young whose parents were unhandled in previous years and those where at least one parent was handled in 1991.

In order to make the first comparison, trends in chick growth variables across the Burrian were sought, to check that the growth of young at Little Hide did not differ from the other burrows due to position within the colony; position of burrows within the colony can influence the breeding performance of Puffins (eg Nettleship,1972; Harris,1978). It was possible to look for a trend across the Burrian because Harris' burrows followed a transect across the colony (with lowest burrow numbers furthest south from Little Hide and highest numbers closest to the burrows used in the present study) each year. In both 1990 and 1992, peak masses of young increased from south to north along the transect (**Table 2.3**) and the same was true of fledging mass, although the correlation was only marginally significant. Age at peak mass, fledging age and hatching date did not vary systematically along the transect, and none of the breeding variables was correlated with burrow number in 1991 because it was later found that burrow markers were not placed in the usual order in that year (J.Calladine,pers.comm.).

Table 2.4 summarizes comparisons made between breeding variables for Little Hide and Burrian burrows and between 'handled' and 'unhandled' Little Hide burrows. There were no differences between Little Hide and Burrian burrows in either 1990 or 1991, except for Little Hide young hatching significantly later than Burrian young in 1991. The latter difference also occurred in 1992, when Little Hide young had significantly lower fledging masses and reached peak mass significantly earlier than Burrian young. Peak masses of Little Hide young were also lower, and fledging ages higher, than those of Burrian young in 1992, although the differences were not significant. The breeding variables did not differ between 'handled' and 'unhandled' burrows in 1992, except for the fledging masses of 'unhandled' young being marginally significantly higher than those of 'handled' young. When the breeding variables were compared between Burrian burrows and 'unhandled' and 'handled' Little Hide burrows separately, there was little difference between Burrian and 'unhandled' burrows but peak masses and fledging masses were significantly higher for Burrian young than for 'handled' Little Hide young and the latter were significantly younger at peak mass than Burrian young.

Differences between Burrian and Little Hide young in 1992 were not caused by the positions of burrows within the colony because the differences were in the opposite direction to trends observed across the Burrian (**Table 2.3**). The 1992 comparisons suggested a continuum of breeding performance, this being highest in Burrian burrows and lowest in 'handled' Little Hide burrows. The continuum also reflected the variation in hatching dates of the three groups however, these being earliest for Burrian young and latest for 'handled' young. It was not possible, therefore, to decide whether disturbance caused the differences in chick growth directly or whether they were due to differences in hatching date, which may or may not have been the result of disturbance. The added possibility that the late hatching and reduced hatching success at Little Hide in 1992 were caused by a severe storm early in the laying period is discussed in Chapter 7. Disturbance at Little Hide early in the 1992 breeding season (due to capturing of adults in 'box traps') may have impaired incubation behaviour (eg by

Table 2.3 Evidence for trends in Puffin breeding variables along a transect across the Burrian, 1990-1992. (Data from M.P.Harris, unpubl.)

Coefficients shown are for Spearman correlations between burrow numbers and breeding variables, where burrow number 1 was furthest south from Little Hide and high burrow numbers were nearest Little Hide), significance levels highlighted where ** = $p<.05$ and * = $p<.1$

YEAR	PEAK MASS (g)	AGE AT PEAK MASS (d)	FLEDGING MASS (g)	FLEDGING AGE (d)	HATCHING DATE[b]
1990	$r= .494$ $p< .02$ ** ($n=22$)	$r= .021$ $p> .9$ ($n=22$)	$r= .395$ $p< .1$ * ($n=22$)	$r= .114$ $p> .6$ ($n=21$)	$r= .329$ $p> .1$ ($n=22$)
1991[a]	$r=1.014$ $p>.9$ ($n=22$)	$r= .300$ $p> .2$ ($n=20$)	$r= .059$ $p> .8$ ($n=22$)	$r= .160$ $p> .5$ ($n=20$)	$r= .335$ $p> .1$ ($n=20$)
1992	$r= .498$ $p< .005$ ** ($n=28$)	$r= .020$ $p> .9$ ($n=28$)	$r= .425$ $p< .05$ ** ($n=27$)	$r=-.268$ $p> .1$ ($n=27$)	$r=-.145$ $p> .4$ ($n=28$)

NOTES.

a No trends because burrow markers were not placed in the usual order.
b Hatching date where 1st May = 1.

Table 2.4 **Comparison of breeding variables between Little Hide burrows and those on the Burrian (M.P.Harris,unpublished data), 1990-1992.**

Variables expressed as mean +/- s.d (n) and significance levels highlighted where ** = p<.05 and * = P<.1

YEAR	AREA		PEAK MASS (g)	AGE AT PEAK MASS (d)	FLEDGING MASS (g)	FLEDGING AGE (d)	HATCHING DATE[d]
1990	LITTLE		328.4 +/- 4.5 (17)	33.0 +/- 1.1 (17)	283.1 +/- 4.4[a] (14)	41.7 +/- 0.9 (14)	36.9 +/- 1.9 (17)
	BURRIAN		321.8 +/- 5.6 (22)	33.7 +/- 1.0 (22)	268.6 +/- 7.1 (22)	40.4 +/- 1.0 (21)	34.4 +/- 1.4 (22)
	T-TEST		T = 0.89 p > .3	T = 0.46 p > .6	T = 1.51 p > .1	T = 0.93 p > .3	T = 1.09 p > .2
1991	LITTLE[b]		304.8 +/- 5.0 (22)	37.8 +/- 1.4 (30)	260.6 +/- 4.8 (30)	43.7 +/- 0.9 (31)	31.9 +/- 1.8 (32)
	BURRIAN		315.4 +/- 5.7 (22)	36.3 +/- 1.4 (20)	271.4 +/- 5.9 (22)	42.1 +/- 1.1 (20)	26.9 +/- 1.9 (20)
	T-TEST		T = 1.40 p > .1	T = 0.72 p > .4	T = 1.43 p > .1	T = 1.13 p > .2	T = 1.86 p < .1 *
1992	LITTLE[b,c]	1	302.1 +/- 18.5 (9)	35.1 +/- 1.7 (9)	255.9 +/- 10.3 (8)	41.5 +/- 1.5 (8)	38.9 +/- 5.0 (9)
		2	278.6 +/- 9.4 (19)	35.2 +/- 1.0 (19)	223.9 +/- 10.2 (18)	43.2 +/- 0.8 (18)	46.5 +/- 3.5 (19)
		3	286.1 +/- 8.8 (28)	35.2 +/- 0.9 (28)	233.7 +/- 8.2 (26)	42.7 +/- 0.7 (26)	44.1 +/- 2.9 (28)
	BURRIAN	B	304.3 +/- 6.6 (28)	38.0 +/- 0.9 (28)	263.6 +/- 6.8 (27)	44.4 +/- 0.7 (27)	25.6 +/- 1.3 (28)
	T-TEST	Bv1	T = 0.14 p > .8	T = 1.53 p > .1	T = 0.56 p > .5	T = 2.00 p < .1 *	T = 2.56 p < .05 **
		Bv2	T = 2.31 p < .05 **	T = 1.97 p < .05 **	T = 3.38 p < .005 **	T = 1.15 p > .2	T = 5.66 p < .001 **
		Bv3	T = 1.66 p > .1	T = 2.21 p < .05 **	T = 2.82 p < .01 **	T = 1.75 p < .1 *	T = 5.86 p < .001 **
		1v2	T = 1.27 p > .2	T = 0.05 p > .9	T = 1.90 p > .1	T = 1.04 p > .3	T = 1.27 p > .2

NOTES.

a Fledging mass higher at Little Hide because young were mostly weighed 2 days before fledging.
b Excludes pairs which were manipulated in the previous year.
c 1 = 'unhandled' 2 = 'handled' 3 = combined (see text for definitions).
d Hatching date where 1st May = 1.

delaying shift change-overs), resulting in more egg neglect and longer incubation periods or even egg desertions (eg Sealy,1984 for Ancient Murrelets, Crested and Least Auklets and Piatt *et al,* 1990 for the latter two species). This could explain the later hatching (**Table 2.4**) and reduced hatching success (Chapter 5) at Little Hide in 1992. Differences in the breeding performance of 'handled' and 'unhandled' pairs in 1992 initially suggested that individuals could 'remember' being handled in the previous year but a further possibility was that burrows monitored for the first time in 1992 were deeper the previously 'handled' burrows and contained higher 'quality' pairs; attempts were made to access even the deepest nest chambers to monitor young in 1992 but data on burrow characteristics were not collected to allow comparison between the two groups.

Repeated disturbance early in the breeding season, and the handling of birds outside burrows, were suspected of contributing to the decline of a Short-tailed Shearwater colony in Tasmania (Serventy and Curry,1984), while disturbance of adult Guillemots when regularly weighing young can reduce the mass of the 'disturbed' young at the time they leave their ledges (Birkhead,1976; Harris and Wanless,1984). It was not possible to conclude whether the observed differences in breeding performance between Little Hide and Burrian pairs were due to general site disturbance or to the capture of individual parents however.

2.9.3 Effects of adult capture before chick hatching on breeding success.

Burrows from all over the island, from which individuals were removed periodically for weighing during incubation and rearing, had an overall success (young fledged from eggs laid) of 83% (136/163), while those monitored by M.P.Harris (pers.comm.) in similar areas of the island (checked for the presence of an egg and incubating bird and later for a large chick) had an overall success of 86% (120/139). Removal of adults from burrows 1-3 times during the breeding season did not, therefore, significantly effect their breeding success in terms of the number of young fledged (χ^2=0.420, p>.4). Hatching and fledging success measured at Little Hide were not directly comparable with Harris' measure of success (differences in success between Little Hide pairs and those elsewhere on the island in 1991 and 1992 are discussed in Chapter 5).

At Little Hide in 1992, unmanipulated pairs from which at least one individual was caught prior to young hatching had a hatching success (young hatched by colour-ringed pairs present during pre-laying) of 30% (7/23), while the hatching success of pairs from which birds were not caught was 39% (7/18) and the difference was not significant (χ^2=0.060, p>.7). This suggested that the capture *per se* of individuals away from their burrows before their young hatched was not the cause of the reduced hatching success at Little Hide but this did not dispel the possibility that general disruption of the colony caused by the catching techniques caused an overall reduction in hatching success, regardless of whether individuals were caught.

2.10 Statistics.

Statistical procedures were performed with the aid of SPSS-X and MINITAB and followed Zar (1984). Data were examined for normality by graphical methods and using the Kolmogorov-Smirnov test. Non-parametric techniques were used on occasions when data were not normal (or could not be made to approximate a normal distribution by transformation), or when samples were too small to test satisfactorily for normality. A probability level <.05 was taken to indicate statistical significance throughout the thesis but results of 'marginal significance' (p <.1) were also highlighted in view of the small sample sizes in many of the analyses. Probability values are quoted as in classes of <.05, <.01, <.005 etc. for values <.05 and in 10% increments (>.2, >.3, >.4) for values >.1 . The following abbreviations are used in the text :-

ABBREVIATION	DEFINITION
p	probability level (see above)
n	sample size
s.d	standard deviation of mean
s.e	standard error of mean or regression estimate
T	Student's T statistic
U	Mann-Whitney U statistic
F	F statistic in analysis of variance
r	correlation coefficient (Pearson or Spearman specified when this is used)
r^2	coefficient of determination (for regression analyses)
I	intercept (for fitted regression lines)
b	slope (for fitted regression lines)

CHAPTER 3 THE PUFFIN PAIR : MATE AND BURROW FIDELITY, PAIR AGE AND THE ROLE OF THE SEXES IN BREEDING.

3.1 INTRODUCTION.

Lack (1968) believed that seabird species rearing only a single young each breeding season did so because, on average, this was the maximum production that could be maintained. This suggestion has been supported by evidence from twinning experiments carried out on seabirds with single-egg clutches, which showed that pairs cannot usually raise more than one chick (reviewed by Wittenberger and Tilson (1980) and for the alcids by Birkhead and Harris (1985)). In these seabirds, therefore, it is hardly surprising that both parents are required to invest in the care of the chick, and this need for biparental care may have been an important factor in the evolution of sexual monogomy in such species. Harris (1978) showed that Puffin chicks experienced stunted growth and higher mortality when they were reared by a single parent and both members of a Puffin pair are normally involved in care of the young (Harris,1988; Creelman and Storey,1991). It is clear that the quantity and quality of investment by both members of a pair and the quality of the relationship between the two birds might be important determinants of breeding success. The aim of this chapter is, therefore, to examine some characteristics of the pair relationship which might influence the success of individual Puffin pairs.

3.1.1 Mate and burrow fidelity.

Puffins are known to show high levels of fidelity both to their partner and to the breeding burrow (Ashcroft,1979; Harris,1984; Creelman and Storey,1991). A stable pair bond established over a number of years may result in improved reproductive success because the pair members learn how to coordinate their activities to the best advantage. Conversely, breeding failure may occur because of the inability of pair members to coordinate their activities (Coulson,1966). In such cases, divorce, here defined as a change of mate occurring when the previous mate is still alive and present at the colony, might be mutually advantageous, allowing selection of a new and perhaps more suitable partner. Divorce should, therefore, be expected to occur more frequently after breeding failure and this has been shown to be the case for a number of seabird species (Coulson,1966; Mills,1973; Imber,1987; Brooke,1990). Equally, the reproductive success of birds breeding with a new partner for the first time, as a result of divorce or disappearance of the previous partner, might be lower than that of established pairs. For example, in Manx Shearwaters, 71% of faithful birds but only 29% of newly divorced birds managed to raise chicks (Brooke,1990) and in Kittiwakes, breeding success was depressed for at least two years after divorce but then improved (Coulson,1966).

The acquisition of a new burrow must involve either the effort of digging (and, usually, the loss of one or more breeding opportunities while the digging takes place (Harris,1984)), or the eviction of occupants from an existing burrow (with the associated risks of injury through combat), or waiting for a burrow vacancy caused, for example, by the death of an occupant (with the risk of missing one or more years of breeding if no vacancy occurs). For these reasons alone, it should be advantageous for pairs to retain the same burrow from year to year. Additional, more subtle advantages may, however, accrue from an established occupation. In this study, individuals which moved from their original burrow to one closeby, or those which used a new entrance to their existing burrow when the original entrance became blocked, sometimes experienced difficulties in delivering food loads to young because they landed too far from the new entrance (by the original entrance), became 'confused', and often lost loads to gulls. It would seem that the flight approach to a burrow takes time to learn; mistakes will, at best, result in kleptoparasitic loss of food loads and, at worst, could result in mortality of parents at colonies where avian predators occur. Perhaps parents may also learn other intimate details about their burrows, which improve breeding success, after several years of occupation, for example, the driest or warmest place to lay the egg. It has also been suggested that fidelity to the burrow helps to reunite Puffin pairs at the start of each breeding season (Harris,1984).

As in the case of mate changing, a change of nest site might be more likely after breeding failure, as has been shown for Manx Shearwaters (Brooke,1990) and Fulmars (Ollason and Dunnet,1988). If failure was due to the original burrow being unsuitable, then a new burrow might offer more chance of success. Even if a pair are unable to assess the quality of a new burrow until they have bred in it, movements to new burrows after breeding failures will eventually result in most birds breeding in the most suitable available burrows because those in suitable burrows will be successful and will, therefore, remain there in future years (Thompson,1987). Breeding success might improve after a move to a new burrow, if the new burrow is more suitable than the original one, although the improvement may not be immediate if success depends on the occupants learning about the characteristics of, and approach to the new site.

In this study, mate and burrow fidelity were followed through two sets of successive breeding seasons (1990-91 and 1991-92). The aim here is to assess whether the observed mate and burrow changes had any detectable effect on breeding success.

3.1.2 Pair age and experience.

Several hypotheses have been proposed (Curio,1983; Nol and Smith,1987) to explain the frequently observed positive relationship between avian reproductive performance and age (reviewed by Saether,1990). In the 'Selection Hypothesis' (Nol and Smith,1987), samples of birds breeding for the first time are assumed to contain a higher proportion of poor quality individuals than samples of older birds because poor quality birds die at an earlier age than those of superior quality. In this case, the apparently higher performance of older birds would be a consequence of the positive correlation between survival and fecundity resulting from individual quality differences. In the 'Constraint Hypothesis' (Curio,1983), younger birds show inferior reproductive performance because they lack essential skills required for high performance. Nol and Smith (1987) suggested that the younger birds might lack skills which could only be learnt through attempting to breed (the 'Breeding Experience Hypothesis') and/or more general skills associated with day-to-day existence, such as those for foraging, competition and predator avoidance, which might improve with age alone (the 'Age Hypothesis'). Last, Nol and Smith's (1987) 'Residual Reproductive Value Hypothesis' proposed that the effort expended on reproduction increases with age because the chance of surviving to breed again declines as individuals approach the ends of their reproductive lives (Williams,1966; Pianka and Parker,1975). None of the hypotheses need be mutually exclusive.

In his review of age-specific variation in avian breeding performance, Saether (1990) showed that, for a range of seabird species, individuals breeding for the first time generally laid later (4/5 studies), laid smaller clutches (9/10 studies) and smaller eggs (5/5 studies), and achieved lower hatching success (6/7 studies), lower fledging success (6/6 studies) and lower overall fledgling production (10/10 studies) than older breeders. Fewer data were available to examine the pattern of variation in these reproductive traits with age but 27/44 comparisons between measures of breeding performance and age (for studies where values for 5 or more age classes were available) revealed significant linear or quadratic relationships (for a range of avian groups including a high proportion of seabird studies).

In studies of long-lived species with high levels of mate fidelity, such as the Puffin, it is often difficult to separate the effects of age *per se* from breeding experience and the duration of the pair bond on the performance of individual pairs; the above effects in Saether's (1990) review could be due to age, experience, pair bond duration or any combination of these factors. In studies of seabirds which have sought to find relationships between performance and experience within age classes (so controlling for age effects), experienced breeders were usually shown to be more successful (eg Nelson,1966; Davis,1976; Ainley *et al*, 1983; Thomas,1983; Furness,1984; Ollason and Dunnet, 1988). More recent studies which have sought to differentiate between age and experience effects have shown that changes in breeding performance can usually be explained satisfactorily by age rather than experience (eg Ainley *et al*, 1983; Boekelheide and Ainley,1989; Wooller *et al*, 1990; Croxall *et al*, 1992), although in some cases (eg Pyle *et al*, 1991) the converse may be true. It would seem, therefore, that that the relative contributions of age and experience to breeding success might vary with the measure of success considered as well as between species, and it is also difficult to differentiate between the influences of age, experience and duration of the pair bond in seabird species with high mate fidelity and survival because of the low frequency of pairs which break up and reform. Implications of mate change alone were considered in the previous section on mate fidelity. In a Short-tailed Shearwater colony studied for 40 years, both total breeding experience and pair bond duration were shown to have separate and additive effects on breeding performance (Wooller *et al*, 1989).

Age and experience may clearly influence the breeding performance of a long-lived seabird such as the Puffin, making it necessary to consider such factors, wherever possible, in any study addressing the reasons for inter-pair variation in breeding effort and success. In this study, the age and potential breeding experience was known for only very few individuals. The aim here is, therefore, to justify the use of the only available measure of pair age (and experience) for comparison with measures of breeding performance. Relationships between the chosen measure and breeding parameters are considered later in Chapter 5.

3.1.3 Role of the sexes in breeding.

Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chances of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Defined thus, parental investment included initial investment in the primary sex cells and any investment (such as feeding and guarding) benefitting the young. This definition ordinarily excludes effort expended in searching for mates or competing for mates, or territory defence where this was for the purpose of obtaining mates. In sexually monogamous species, such as the Puffin, both pair members invest in the raising of young. Trivers (1972) tentatively suggested that monogamous species showed somewhat greater female than male investment in offspring, beginning with a greater investment by the female in the primary sex cells. This assumption was supported by Emlen and Oring (1977), although they neglected aspects of parental investment which have since been shown to be important, such as offspring defence and care of the young after fledging. Extensive data exist for particular components of investment for many species but few studies have attempted to obtain complete data to examine all the components. Breitwisch (1989), in his review paper, concluded that too few data were available to support any general assumption about differences in investment between the sexes in monogamous birds.

Several studies (summarized in Harris,1988) have attempted to quantify the role of the sexes in two of the more obvious components of Puffin parental investment, incubation and chick feeding, while one further study (Creelman and Storey,1991) included further aspects of investment including involvement in burrow maintenance and aggression. Here, similar data collected during 3 breeding seasons on the Isle of May are presented with two objectives, important to the overall aims of the study. First, if the magnitude and/or timing of investment differs between the sexes, then by attempting to quantify such differences it might be possible to explain observed differences in the body condition of the sexes over time, or to target analyses involving body condition to the stage(s) of breeding when effort appears greatest. Second, there can be substantial differences amongst individuals within populations of monogamous, biparental birds in the level of individual parental investment relative to that of the mate (Grieg-Smith,1982; Burger,1987; Breitwisch,1988). These findings suggest that any overall attempt to quantify the relative investments of pair members at the population level should be based on large sample sizes and such differences in the relative rather than the absolute investment of the two pair members might directly influence reproductive success. For example, the breeding success of Herring Gulls was greater for pairs with equitable distribution of parental effort (Burger,1987).

The aims in this chapter are to present data collected during the study which suggest intersexual differences in the parental investment of Puffins in previous studies to seek differences between the sexes in the timing of parental investment and to quantify interpair differences in the relative roles of the sexes in breeding various activities. The effects of the interpair differences on breeding performance are considered later in Chapter 5.

3.2 METHODS.

3.2.1 Mate and burrow fidelity and breeding success.

In each of the 3 breeding seasons (1990-92), the identities of all burrow occupants at the Little Hide site were established and breeding success (defined in this chapter as whether or not a chick was fledged) was determined wherever possible. Burrow occupants were most confidently identified when they were seen delivering feeds to chicks. In the case of pairs which did not hatch young, individuals were associated with particular burrows using observations of burrow maintenance activities and incubation behaviour (Chapter 2, sections 2.3.2 and 2.3.3). Pairs were assumed to have fledged young successfully if regularly-weighed young disappeared from burrows in fledging plumage or if feeding visits were observed to span at least a 35-day period (the latter for chicks in inaccessible nest chambers which could not be weighed regularly).

Results were derived only from burrows where both members of the pair were colour-ringed and, therefore, individually identifiable. Thirty-seven pairs were followed from the 1990 to the 1991 breeding season and 69 pairs from 1991 to 1992; of the latter group, 36 pairs formed an independent sample as they comprised birds not followed from 1990 to 1991.

3.2.2 Pair age.

Estimated relative ages for individuals at Little Hide were obtained from dates on which metal rings had been fitted in the years prior to the study. Individuals could only be accurately aged where they had been ringed when less than 4 years old (with less than 2 bill grooves). Individuals ringed with 2 or more bill grooves were assumed to be of minimum breeding age (4 years) at ringing; ages derived for the latter were, therefore, minima because the birds may have been breeding for any number of years prior to ringing.

The age relationship between pair members was investigated in two ways. First, estimated male and female ages were correlated for all pairs where both birds had been ringed prior to this study. Second, age differences between members of a pair were estimated by comparing pair members whose ages were accurately known with the ages of their partners, where these were at least one year older. This was the only means by which some measure of age difference could be derived because most ages were minimal and accurate ages of both partners were only available for a single pair.

3.2.3 Role of the sexes in breeding.

The proportional contribution of pair members to burrow defence (fighting) and burrow maintenance (digging and nest building) were determined in 1991 and 1992 from observations at the study site. The role of the sexes in chick provisioning (measured as the proportion of food loads delivered by each sex) was also determined, from observations made in all 3 breeding seasons and the size of food loads obtained by mist-netting (Chapter 2, section 2.7) were compared between the sexes (where sex was determined using the bill descriminant score, Chapter 2, section 2.2.4). Observation sessions were scheduled to equally sample the hours of daylight, to avoid any bias if the proportional input of each sex varied with time of day. The total number of observation hours in each breeding stage differed between burrows, although the frequencies of behavioural events were comparable between members of the same pair. Frequencies of behavioural events were, therefore, converted to male and female proportions before analyses were performed using a non-parametric test for paired samples (Wilcoxon).

Insufficient manpower was available to allow the role of the sexes in incubation to be quantified by continuous observation. Instead, in 1991, the proportion of incubation defecation events (Chapter 2, section 2.3.3) attributable to each sex was quantified and incubation changeovers were observed to assess whether one sex incubated more at night. It was, however, first necessary to establish whether either of these two types of incubation behaviour occurred during the hours of darkness. This was achieved by placing thin slices of bamboo cane across burrow entrances after dark, so that burrow occupants could not enter or leave without dislodging the barriers. The procedure was carried out on two nights with clear skies and full moon, when it was thought most likely that nocturnal activity might occur. On each night, the cane slices were placed across 15 entrances to occupied burrows (where incubation behaviour had recently been observed) after dark and the barriers were rechecked before dawn on the following morning. In only one of these 30 burrows was the barrier dislodged the following morning. The same procedure was also used to verify previous evidence (Harris,1984) that young are not fed at night.

In 1992, monitoring of the role of the sexes in incubation was attempted using a metal-detecting device. In late March (pre-laying), one member of each of 8 pairs was caught and fitted with a steel ring instead of the alloy British Trust for Ornithology ring. Four steel-detecting antennae were available, each consisting of multiple wire coils encased in roofing felt to form a flat panel, which could be inserted into the burrow entrance so that occupants had to pass over it to reach the nest chamber. All 4 antennae were powered by 12v car batteries and were interfaced to a single Psion XP personal organiser located in the hide; they could all be used simultaneously so that 4 pairs could be monitored at one time. Each time the pair member with the steel ring passed over the antenna, the burrow number and real time was recorded in the Psion memory. This should have allowed the absolute roles of the pair members in incubation to be determined, assuming that both pair members were never in the burrow together for any length of time and that the egg was never deserted.

Concurrent use of the detector and observation of burrows showed that, in many cases, birds passed over the antennae too quickly or in such a way that the steel ring was not detected; the automatically-recorded movements did not, therefore, reflect the true pattern of burrow attendance. In an attempt to reduce this error, incubating individuals were removed from two burrows outside the main study area at the end of April and were fitted with steel rings. Antennae were placed directly under the eggs in these burrows so that the detecting system should have been activated all the time that a steel-ringed bird was incubating. It seemed, however, that in both cases the egg was deserted after insertion of the antenna. The detecting system was rarely activated and one of the pairs never hatched a chick, while the other pair hatched a chick 70 days later, presumably after laying a replacement egg in a different location in the burrow. Use of the metal-detecting system was, therefore, abandoned.

The proportion of the daylight hours for which each individual was present above ground at the colony was established during 3 breeding stages (pre-laying, incubation and rearing) in 1991 and 1992. Attendance values were determined by a sampling method from the proportion of colony checks during which a particular individual was present, where these checks were evenly distributed with time of day (Chapter 2, 2.3.7). This was the only form of time budgeting possible within the time constraints of the study. It was hoped that inferences about the differential roles of the sexes in the 3 breeding stages could be made from differences in above-ground colony attendance. Burrows differed both in the number of attendance checks made during each breeding stage and in the probability of identifying their occupants when they stood by their burrows due to the topography of the site. For this reason, individual sighting frequencies were comparable between pair members but not between pairs, and differences in attendance between the sexes were tested using a non-parametric paired test (Sign Test) on the raw attendance frequencies.

3.3 RESULTS.

3.3.1 Mate and burrow fidelity and breeding success.

Pairs were considered to have divorced if both pair members were alive and present at the colony in year II but bred with different partners than in year I. The divorce rate was similar from 1990 to 1991 and from 1991 to 1992 (independent samples, χ^2 test $p>.7$) at c.11% (**Table 3.1**). Twenty-four of the pairs remaining together from 1990 to 1991 could also be followed into 1992, and in this case, the divorce rate was lower at 4.5%, although it was not significantly different from that of the independent sample followed from 1991 to 1992 (Fisher Exact Test $p>.4$).

In the independent samples of pairs followed from 1990 to 1991 and from 1991 to 1992, successful pairs divorced more than unsuccessful pairs (**Table 3.2**), although the differences in divorce rates were not significant in either case and sample sizes of unsuccessful and divorced pairs were small. In the larger 1991-1992 sample (all pairs), unsuccessful pairs divorced slightly more than successful pairs (divorce rates of 12% and 9% respectively) but again the difference was not significant.

There was no significant difference in the breeding success of individuals which retained the same mate from year I to year II and those which, through mate disappearance or divorce, bred with a different mate in year II (**Table 3.3**). Nor did the breeding success of the latter in 1992 differ from that of pairs which had been faithful at least since the 1990 breeding season ($\chi^2=.01$, $p>.9$). Data were insufficient to allow comparison of other measures of breeding performance between 'established' and 'new' pairs.

Instances of burrow changes during the 3 year study are summarized in **Table 3.4**. Of the 8 instances where pairs moved together to new burrows, 3 pairs moved from accessible nestboxes to deep natural burrows, 3 moved to deeper burrows from shallow natural burrows, 1 instance involved a move at the end of a season in which the pair had bred unsuccessfully and the final case involved a pair which moved from a shallow to a deeper burrow from 1990

Table 3.1 **Mate fidelity of Puffin pairs on the Isle of May 1990-1992.**

	1990-91	1991-92[a]	1991-92[b]	1991-92[c]
n pairs year I	37	36	69	24
n same mate year II	25	31	60	21
n divorced year II	3	4	6	1
% divorced year II	10.7	11.4	9.1	4.5
	3/3+25	4/4+31	6/6+60	1/1+21
n at least one of pair disappeared year II	9	1	3	2

NOTES.
a independent sample (pairs not followed 1990-91).
b all pairs followed 1991-1992.
c pairs already faithful from 1990-91.

Table 3.2 **Mate fidelity of Puffins on the Isle of May 1990-1992 in relation to success (whether or not a chick was fledged) in the previous year.**

(Numbers divorcing compared using Fisher Exact Tests).

		1991 SAME MATE	DIVORCED	% DIVORCE	p
1990	SUCCESSFUL	22	3	12.0	>.7
	FAILED	3	0	0.0	

		1992[a] SAME MATE	DIVORCED	% DIVORCE	p
1991	SUCCESSFUL	25	4	13.8	>.5
	FAILED	5	0	0.0	

		1992[b] SAME MATE	DIVORCED	% DIVORCE	p
1991	SUCCESSFUL	43	4	8.5	>.8
	FAILED	17	2	10.5	

<u>NOTES.</u> a independent sample (pairs not followed 1990-91).
b all pairs followed 1991-92.

Table 3.3 **Comparison of the success (whether or not a chick was fledged) of Puffins which remained with the same mate and those which took a new mate on the Isle of May 1990-1992.**

(Birds changed mates as a result of divorce or the disappearance of their partner).

			1991			
MATE COMPARED TO 1990		SUCCESSFUL	FAILED	% SUCCESS	χ^2	p
1991	SAME	14	18	43.8	.08	>.25
	NEW	7	6	53.8		

			1992			
MATE COMPARED TO 1991		SUCCESSFUL	FAILED	% SUCCESS	χ^2	p
	SAME[a]	46	74	38.3	.01	>.9
1992	NEW	5	10	33.3	.01	>.9
	SAME[b]	14	26	35.0		

NOTES.

a all birds followed from 1991-92.
b birds with the same partners from 1990-92.

Table 3.4 **Burrow fidelity of Puffins on the Isle of May 1990-1992.**

(The 1991-92 sample includes some pairs followed from 1990-91).

		1990-91	1991-92
Pair in same burrow year II		21	56
Pair in new burrow year II		4	4
DIVORCE	Male same burrow, female moved	2	1
	Female same burrow, male moved	0	4
	Both pair members to new burrows	1	1
MALE DISAPPEARED	Female in same burrow	2	2
	Female to new burrow	1	0
FEMALE DISAPPEARED	Male in same burrow	5	1
	Male to new burrow	1	0
	TOTAL n burrows	37	69

to 1991 but returned to their original burrow in 1992, when their new burrow partially subsided and become shallow. In all cases, the new burrow was either unoccupied in the previous season or, in a single case, both the occupants had disappeared during the winter. The vacated burrow was only used in the season after vacation in 2 of the 8 cases. There was no suggestion that unsuccessful pairs were more likely to change burrows, as 7 of the 8 moves involved pairs which had successfully fledged a chick in year I. Insufficient data were available to consider whether burrow changes affected the breeding success of pairs.

In the 9 cases of divorce, the male retained the original burrow in 3 cases, the female retained it in 4 cases and in the other 2 cases both divorcees moved to new burrows. In the 12 cases where one of the pair did not return to the colony in year II, the remaining pair member usually retained its original burrow whether it was male (6/7 retained burrow) or female (4/5 retained burrow).

3.3.2 Pair age.

The ages of male and female pair members, estimated from ringing dates, were significantly correlated (Pearson r=0.372; p=.030; n=34) for pairs where both were ringed prior to the 1990 breeding season (**Figure 3.1**). When the ages of accurately aged birds were compared to those of their mates, where the mates were at least one year older, the male was older in 7 cases and the female in 5 cases. There was, therefore, no evidence that one sex tended to be older than the other (Sign Test p>.1). The differences between members of these pairs ranged from 1-11 years (median 5 years) where the male was older and from 1-9 years (median 5 years) where the female was older and the age differences were similar between these two groups (Mann-Whitney Test p>.1).

3.3.3 Role of the sexes in breeding.

There was no significant difference in the number of fights involving male and female colour-ringed birds; using data for the 1991 and 1992 breeding seasons combined, individual males were identified in 83 fights and females in 99 fights (χ^2=1.24, p>.05). Of 25 fights witnessed between birds of known sex, 15 (60%) were between a male and a female, 9 (36%) were between two females and only 1 (4%) was between two males. In the case of fights where both individuals were sexed, females therefore fought significantly more than males (χ^2=4.50, p<.05).

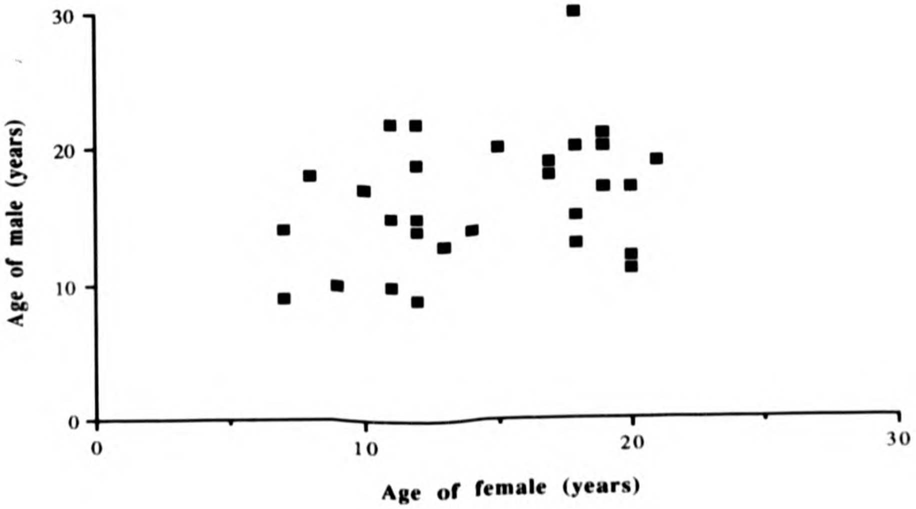


Figure 3.1 Relationship between the ages of male and female members of Puffin pairs.
(Pearson correlation r=.372, p<.05, n=34)

Males were involved in significantly more burrow maintenance events (median 77%, range 6-100%) than females in 1991 (Wilcoxon paired Test Z=-2.468, p=.014, n=21). In 1992, 55% (range 7-91%) of burrow maintenance events were carried out by males and 45% by females and the difference was not significant (Wilcoxon Test Z=-.415, p>.1, n=9) but the sample size was much reduced.

Of all the incubation defecation events observed in 1991, 149 (61%) were by males and 96 (39%) by females and the difference was significant (χ^2=11.04, p<.001). The defecation events did not, however, occur sufficiently frequently to allow male and female frequencies to be compared for individual burrows. Incubation changeovers showed two peaks during the day (**Figure 3.2**), the first during the middle of the morning (0600-1200) and the second in the evening (1800-2200). There was no evidence, however, that only one sex usually incubated at night, as there was no tendancy for one sex to begin incubating after the morning changeover and the other after the evening changeover (**Figure 3.3**). There was a suggestion, especially during the morning changeover peak, that females returned to resume incubation duties, after time at sea, earlier than males. It was not possible to quantify the role of the sexes in incubation more satisfactorily, or to measure the lengths of incubation stints, due to the failure of the automatic, metal-detecting monitoring system.

In all 3 breeding seasons, females delivered significantly more feeds to young than males (Wilcoxon Tests p<.05)(**Table 3.5**). The median percentage of feeds delivered by females ranged from 60-70% in the 3 years. In 1992, the provisioning data were sufficient to allow an analysis of the change in provisioning roles during the rearing period. The data were derived from 27 burrows where both pair members were individually-identifiable throughout rearing. Combining these data, there was a suggestion (**Figure 3.4**) that the male input to provisioning was lowest around days 10-15 of rearing and that it increased during late rearing (after day 40). It was not, however, possible to demonstrate changing provisioning roles during rearing for the occupants of individual burrows due to insufficient data. There were no significant differences in the size of food loads carried by males and females (**Table 3.6**).

Males spent a significantly larger proportion of the daylight hours above ground at the colony than females in all 3 breeding stages in both 1991 and 1992 (**Table 3.7**). The differences between pair members were, however, slight and only of marginal significance during the pre-laying period. Males spent c.2.5 times as much time at the surface of the colony as females during incubation and 2-3 times as much time at the colony as females during rearing.

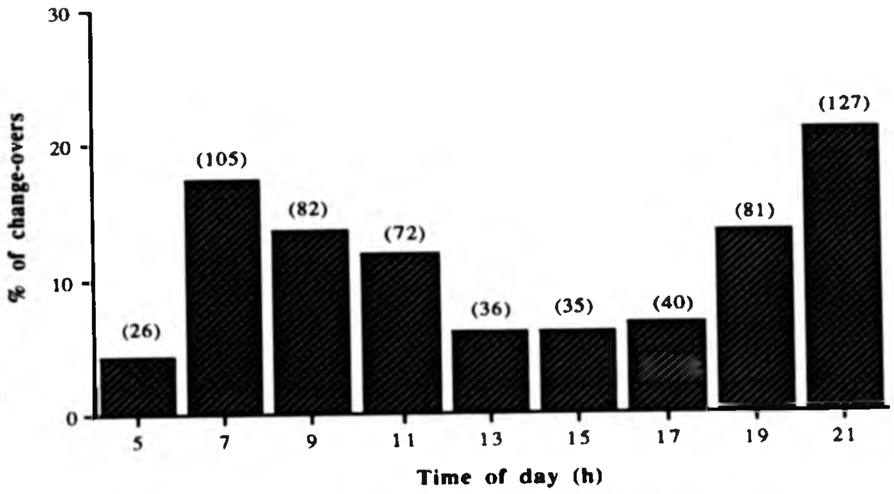


Figure 3.2 Pattern of Puffin incubation change-overs with time of day in 1991. (From a total of 604 observed change-overs, sample sizes in each time class in parentheses).

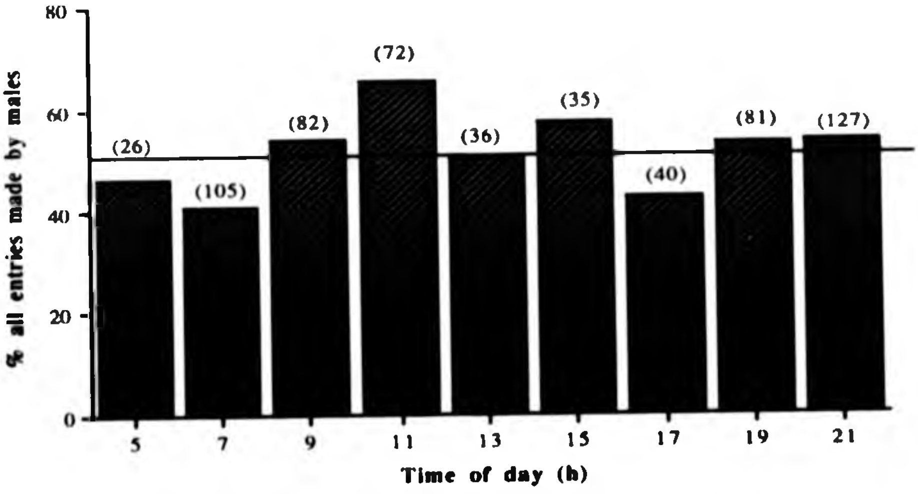


Figure 3.3 Variation with time of day in the proportions of change-overs in which the male Puffin began an incubation shift in 1991. (From a total of 604 observed entries, sample sizes in each time class in parentheses. The horizontal line shows equal male and female entries for comparison).

Table 3.5 **Role of the Puffin sexes in the provisioning of young : percentage of food loads delivered by males and females on the Isle of May 1990-1992.**

YEAR	% FEEDS BY MALE		% FEEDS BY FEMALE		WILCOXON PAIRED TEST		
	Median	Range	Median	Range	n	Z	p
1990	30	0-80	70	20-100	14	-2.291	.022
1991	38	18-70	62	30-82	36	-3.436	.001
1992	40	1-65	60	35-99	25	-3.011	.003

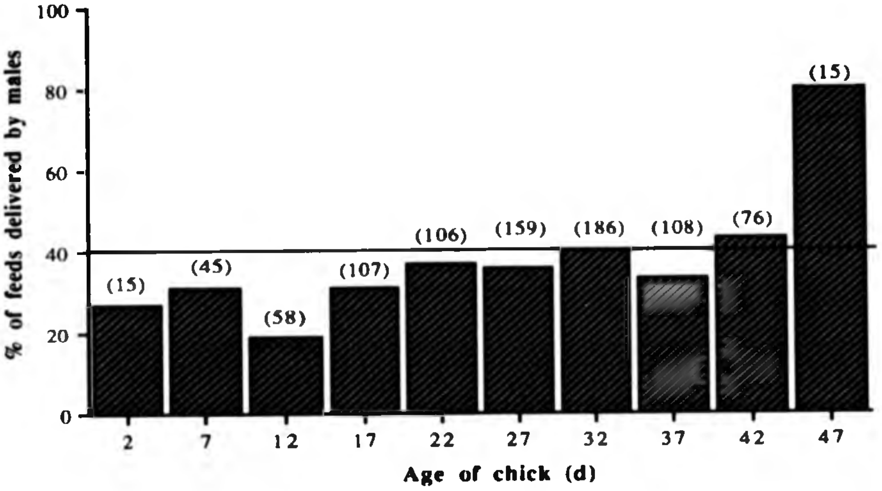


Figure 3.4 Variation with chick age in the proportion of feeds delivered by male Puffins in 1992.
(Number of feeds observed in each age class (derived from 27 burrows) shown in parentheses and the median role of the male in 1992 indicated by the horizontal line for comparison).

Table 3.6 **Comparison of the size of food loads delivered to young by male and female Puffins in 1992.**

Variables presented as mean +/- s.d (n)

	MEAN LOAD MASS (g)	MEAN FISH IN LOAD (n)	MEAN FISH LENGTH (mm)
♂♂	7.9 +/- 4.3 (54)	7.0 +/- 4.8 (54)	75.3 +/- 25.5 (54)
♀♀	8.0 +/- 4.6 (44)	6.1 +/- 4.7 (44)	78.6 +/- 31.1 (44)
T-TEST	T = 0.20 p > .8	T = 1.00 p > .3	T = 0.58 p > .5

Table 3.7 Comparison of the percentage of time spent above ground at the colony by male and female Puffins on the Isle of May during 3 phases of breeding in 1991 and 1992.

		% TIME SPENT AT COLONY BY MALE		% TIME SPENT AT COLONY BY FEMALE		SIGN TEST	
		Median	Range	Median	Range	n	p
PRE-LAYING	1991	17.7	7-34	15.1	8-32	10	.039
	1992	11.4	3-95	10.2	2-37	24	.093
INCUBATION	1991	6.3	2-19	2.6	0-9	24	.002
	1992	6.6	2-39	2.6	0-11	25	.001
REARING	1991	15.7	8-52	7.7	0-46	12	.039
	1992	5.8	1-51	2.1	0-42	24	.000

3.4 DISCUSSION.

3.4.1 Mate and burrow fidelity and breeding success.

The Puffin divorce rate of 11% per year, recorded for the two independent samples of pairs in this study, was similar to that of 8% on Skomer (Ashcroft,1979) and 9% on Gull Island, Newfoundland (Creelman and Storey,1991). The divorce rate was non-significantly lower (4.5% per year) for pairs which had already bred together for at least one year; this may have indicated that a random sample of pairs followed from year to year included a proportion of individuals (possibly young and/or inexperienced birds) which were 'experimenting' with mates, while divorce was less common amongst 'established' pairs which had already obtained suitable mates.

If divorce acts as a possible means of obtaining a more suitable mate, then it should tend to occur in pairs which have failed to breed successfully. In this study, sample sizes of divorcees were small and there was no suggestion that pairs which failed to raise a chick were more likely to divorce. Creelman and Storey (1991) suggested that two of their pairs divorced because of breeding failure, caused by poor quality burrows but their sample size was also small (total of 4 divorced pairs).

On the Isle of May, the breeding success of individuals which retained the same mate from year to year did not differ from that of those which changed mates, either due to mate disappearance or divorce. Similarly, Ashcroft (1979) was not able to detect any effect of mate change (total of 22 changed pairs) on breeding success. This is in contrast to a number of other studies of long-lived seabirds where mate change has been clearly demonstrated to result in depressed success for at least one year after the change (eg Coulson,1966; Wooller *et al*, 1989; Brooke,1990).

Both Ashcroft (1979) and Creelman and Storey (1991) suggested that unsuccessful pairs were more likely to move to new burrows than successful pairs. This was not supported by the results of this study, as only one of the eight pairs which moved to new burrows had failed to fledge a chick in the previous breeding season. There was, however, evidence to suggest that pairs improved their nest sites by moving from nestboxes and shallow burrows to deeper natural burrows, although data were insufficient to assess whether these burrow changes affected subsequent breeding success. On Skomer, pairs moving to new burrows (n=6) were equally as successful as those retaining their original burrows (Ashcroft,1979). This would perhaps be expected if the birds were unable to assess the quality of new burrows until they bred in them (as suggested by Thompson (1987) for Manx Shearwaters). In this case, the probability of obtaining a new burrow of better quality than the original might be 0.5, or less if most of the best burrows are already occupied, and the breeding success of the moving birds might not therefore improve relative to that of non-movers. On the Isle of May, individuals which changed burrows sometimes experienced difficulties when delivering feeds to young. Such behaviour may not have been sufficient to affect the fledging success of these pairs but may have operated in a more subtle manner by reducing chick condition at fledging, perhaps increasing the effort required to raise the chick or increasing the risk of aggressive encounters when adults landed in an incorrect area. Insufficient data were available to allow such potential effects to be addressed.

The causes of mate and burrow changing and their consequences may not have been revealed by considering only chick production as a measure of breeding success. As most pairs of Puffins usually fledge a chick each year on the Isle of May (Chapter 1 Figure 1.3), the resolution of the above analyses might be improved if success could be measured in terms of the survival and recruitment chances of the young (or as some predictor of the latter, such as chick fledging condition). Even if the majority of pairs may successfully fledge young whose survival and recruitment chances are similar, the effort involved in raising the young (and the subsequent costs to the parent in terms of future survival and reproductive potential) might differ substantially between pairs because of differences in the quality of individual pair members or in the quality of the pair relationship. This degree of effort, rather than the resultant fledged chick, might be used by individuals when deciding whether to change a mate or burrow.

Ashcroft (1979) believed that, on Skomer, at least one third of Puffins losing burrows were evicted, either by other Puffins or by Manx Shearwaters, because they had no burrow in the following breeding season. Eviction by Puffins usually involved only one member of a pair. On the Isle of May, none of the divorcees failed to find a new mate and burrow in the season after divorce and it was not possible to assess whether divorce occurred by choice or because of intervention by a third party. Where both members of a pair moved to a new burrow, this seemed to occur voluntarily, as in all cases the new burrow was previously unoccupied and in only 2 of 8 cases were the vacated burrows occupied by new pairs in the following breeding season. Males and females were equally likely to retain their original burrow if they divorced or if their mate disappeared from the colony, as was also the case on Skomer (Ashcroft,1979); in the latter situation, the remaining pair member usually retained the burrow and took a new mate.

There was no evidence from this study or from that on Skomer (Ashcroft,1979) that mate and/or burrow changes influenced breeding success in the year after the change, although sample sizes in both studies were small and success could only be compared in terms of whether or not young were fledged. As overall 80% of pairs consisted of the same individuals from year to year and 73% of pairs retained the same burrow in this study (in a total of 106 pair years), it was, however, assumed that any changes which occurred would not unduly affect analyses involving breeding performance; all pairs were, therefore, included in subsequent analyses (Chapter 5) regardless of observed mate and burrow changes.

3.4.2 Pair age.

In this study, the estimated ages of pair members were positively correlated and the median age difference between partners was 5 years, with no tendency for one sex to be older than the other. The correlation coefficient (r=.372) was lower than those normally demonstrated in other seabird populations (r ranged from .15 to .60 with a median of .44 for 9 long-lived bird species, 8 of which were seabirds; Reid,1988) but this was not surprising given that the ages of pair members were largely estimates.

Both members of a Puffin pair invest in reproductive duties, so that breeding performance may be influenced by the ages of both pair members. Mean pair age might, therefore, be the most appropriate summary measure of pair age. In many cases, however, an estimated age was only available for one member of a pair in this study. In analyses of the effect of age on reproductive performance (Chapter 5), where pair age was the independent variable, the age available for one pair member was used as an estimate of the average age of the pair. This choice of age measure was thought to be justified for several reasons. First, if the median age difference between pair members was 5 years, then the age of each pair member differed from this median by an average of 2.5 years, which was a small difference compared to the range of individual ages considered in the study (7-30 years). Second, there was no tendency for one sex to be older than the other and, therefore, the chosen age measure represented an unbiased sample of the population. Third, there is a general tendency for members of pairs of breeding seabirds to be of similar age (many studies cited in Reid,1988). This may be due to assortative mating (non-random mate selection with respect to age or experience), which occurs because experienced breeders have higher reproductive success making it advantageous to select an experienced mate or one of similar age (Coulson,1966; Mills,1973; Coulson and Horobin,1976; Shaw,1985). Alternatively, if individuals enter the breeding population at a similar age and tend to chose mates at the same time and/or location, if mortality is low and mate fidelity is high (as is the case in many seabird populations, including those of the Puffin), then an initial similarity in mate ages will be preserved for some considerable time; there will be a strong correlation between the ages of pair members even in the absence of active mate selection (Mills and Shaw,1980; Nisbet *et al*, 1984; Shaw,1985). Where estimated ages were available for both pair members in this study, the mean of the two ages was used as the measure of pair age.

It was impossible to separate the age and experience of Puffins in the Isle of May study because reproductive data for individual birds were not available for years prior to the start of the study. The measure of pair age used in analyses was based on age but, over the large age range of the individuals considered, would also reflect relative breeding experience to some extent. The separation of age and experience was not essential to the aims of this study because the main objective was to determine and, therefore, attempt to control for any effect of these two individual characteristics on reproductive performance, so that effects of body condition on performance might be more readily revealed. The effects of pair age on breeding performance are discussed in Chapter 5.

3.4.3 Role of the sexes in breeding.

The overall inputs of the sexes to a variety of breeding activities, from this and previous studies, are summarized in **Table 3.8**. The data indicated that males spend more time than females above ground at the colony during all 3 breeding stages (although the difference is slight during pre-laying) and that males undertake significantly more burrow maintenance (60-70%) than females. Conversely, female Puffins deliver significantly more feeds to young (60-70%) than males.

On the Isle of May, males were responsible for 61% of all observed incubation defecation events but this alone did not prove that the male role in incubation was larger than that of the female because there may have been a tendancy for one sex (females) to incubate more at night, when incubation defecations were not observed. Observations of incubation changeovers

Table 3.8 Role of the sexes in Puffin breeding : a summary of studies to date.

(Asterisks refer to the results of the present study on the Isle of May 1990-1992 and the numbers represent the number of studies in which the indicated relationship was found).

		MALE > FEMALE	FEMALE > MALE	MALE = FEMALE	References[b]
PRE-LAYING	Time in burrow	0	1	0	1
	Time at colony	1*	0	1	1
	Burrow maintenance[a]	2*	0	1	1,2
	Aggression[a]	1	1*	0	1
INCUBATION	Time in burrow	0	4	3	1-8
	Time at colony	2*	0	0	1
REARING	Time in burrow	0	0	2	1,2
	Time at colony	2*	0	0	1
	n food loads	0	3*	2	1,7,9,10
	Size of food loads	1	0	2*	1,2

NOTES.

[a] also includes events during incubation.

[b] References cited : 1-Creelman and Storey (1991); 2-Harris (1988); 3-Bent (1919) in Harris (1988); 4-Kaftanovskii (1951) in Harris (1988); 5-Lockley (1953) in Harris (1988); 6-Kozlova (1957) in Harris (1988); 7-Myrberget (1962); 8-Rosenius in Harris (1988); 9-Corkhill (1973); 10-Combined data from Corkhill (1973) and Harris in Harris (1988).

did not, however, indicate any tendency for females to incubate more than males at night, leaving the tentative conclusion that males incubated more than females. A comparison of this result with those from other studies suggested that conclusions could vary depending on the methods used to assess incubation roles, and overall the intersexual difference in incubation effort could be small. On the Isle of May, there was a suggestion that females returned from the sea to begin incubation shifts earlier in the morning (for the 'dayshift') and earlier in the evening (for the 'nightshift') than males, perhaps reflecting a greater female drive to incubate. There was no evidence from this or other studies of any difference in the role of the sexes in the brooding of young.

Only this and one previous study (Creelman and Storey,1991), have sought intersexual differences in Puffin aggressive behaviour, and the results at first appear conflicting. On the Isle of May, females seemed to fight more than males, while in Newfoundland, males were involved in more 'aggressive encounters' than females. These results were not, however, strictly comparable because of two methodological differences between the studies. First, Creelman and Storey recorded all aggressive encounters (including non-contact chases), while only contact fights were recorded in this study. It was, therefore, possible that, although males were involved in a greater number of aggressive encounters overall, more encounters involving females ended in contact combat. Second, Creelman and Storey compared the frequencies of aggression events between pair members, where the sex of the 'intruder' was not necessarily known (if it was unringed). A similar (but unpaired) comparison on the Isle of May produced no significant difference in the frequency with which the sexes were involved in fights. On the Isle of May, a significantly higher frequency of female fights was only apparent when data from the 25 fights in which both combatants were of known sex were analysed. The two types of analysis produced different results because most fights occurred between males and females or between two females, rarely between two males. Further analysis of the combatants in the 25 fights between birds of known sex on the Isle of May revealed that, in almost all cases, fights occurred either between a burrow occupant (male or female) and an intruding female, apparently without a burrow, or between a male and a female or two females which had previously bred unsuccessfully or were unsuccessful in the 1992 breeding season, when the fighting data were collected. In only one case was a fight observed between two successful burrow occupants (2 females in this case). The results of the two studies were, therefore, not necessarily conflicting; in the case of successful pairs occupying a burrow, the male seems to have a larger role in burrow defence than the female (Creelman and Storey,1991), while a larger proportion of 'intruders' may be females prospecting for mates and for burrows held by males (this study); these intruders were the birds which were not sexed in the Newfoundland study.

Trivers (1972) measured parental investment "by reference to its negative effect on the parent's ability to invest in other offspring." In practice, however, investment is often evaluated in terms of the frequency of, or time spent in various activities (as in this study). The summation of different types of investment is often difficult because of the problem of finding a common 'currency' (Walsberg,1983; Knapton,1984; Mock,1985). Most investments can be measured in terms of either energy expenditure or risk; these two currencies may be inter-related if a large energy expenditure increases the risk of mortality. Trivers (1972) exemplified one situation in which energy expenditure might be a poor approximation of investment; an individual defending its brood from a predator might expend very little energy but suffer a high chance of direct mortality. The few studies which have attempted to sum all aspects of investment for the two sexes have, however, used energy as the currency (eg Nol,1985) because of the extreme difficulties of assessing risk. In this study, the reasons for assessing the differential roles of the sexes in breeding were twofold : first, to determine whether the sexes differed in the timing of their investment in a way which might help to explain observed differences in body condition and, second, to assess whether the relative roles of pair members in various activities had any influence on breeding performance. The currency used to measure the roles was not, therefore, a problem because energy investment (rather than true parental investment incorporating risk) was a suitable measure with which to compare body condition changes. The relative roles of pair members were, in most cases, comparable in terms of the raw frequencies of activities and time spent in the various behaviours (Chapter 5).

In the Isle of May study, most adult body condition data were collected during the chick rearing period because of the difficulties of weighing adults prior to chick hatching. It was, therefore, most important to assess the differential energetic investment of the sexes during this stage of breeding. Time budgets could not be constructed with sufficient accuracy to allow construction of detailed energy budgets for the two sexes (see Chapter 6 for reasons). The aim here is, therefore, to assess in a qualitative manner, whether either sex was likely to invest more energy in reproduction during 3 breeding stages (pre-laying, incubation and chick rearing).

During the pre-laying period, the energetic investment of male Puffins is probably greater than that of females because males spend more time above ground at the colony, participating in more energetically-expensive acts of aggression and burrow preparation than females. Females spend more time in the burrow during this period, and may be involved in burrow preparation which is hidden from view, but it is unlikely that such activity would result in energy investments greater than those of males at this time. The energetic investment required to find and guard a mate is not known for Puffins; although this energy expenditure was not included in Trivers' (1972) definition of parental investment, it could nevertheless contribute to influencing the body condition of males during the pre-laying period. Astheimer and Grau (1990) suggested that the period in which the female forms the egg probably lasts for 10-18 days in alcids, comprising 8-13 days of yolk deposition and a further 2-5 days for albumen and shell synthesis. The same authors present an equation relating the energy expenditure required for yolk synthesis to female body mass, from which it is possible to calculate that yolk formation in the Puffin would require a daily energy expenditure of c.20% above standard metabolic rate. The costs of albumen and shell synthesis are not known but the energetic expense of producing the latter, and the yolk, could be higher than expected if protein (eg Astheimer and Grau,1985) or shell calcium were limiting rather than energy; in this case, more prey would need to be caught to provide the limiting nutrient(s) than to provide the energy requirement alone. Most aggressive encounters, in which the pair male has a larger input than the female, occur during the pre-laying period but it is not possible to decide whether the overall male and female energetic investments during pre-laying differ based on the available data.

During the incubation period, male investment probably surpasses that of the female. Males continue to spend more time above ground at the colony than females, participating in aggressive encounters and in burrow maintenance activities, while the two sexes probably take an approximately equal share in incubation itself. Even if the role of the female in incubation were somewhat larger than that of the male, it is unlikely that this would equalise male and female energy investment at this time because the energetic costs of incubation in seabirds appear to be lower than those for other everyday activities (Birt-Friesen *et al*, 1989) and this has also been suggested in some passerines (eg Biedenweg,1983; Roskaft,1983). The incubation of only a single egg, in a burrow in which heat loss may be dramatically reduced (eg White *et al*, 1978), is unlikely to be energetically demanding for Puffins. Restriction on time available for foraging may place an energetic constraint on individuals during incubation (Walsberg,1983) but this is unlikely to be the case for Puffins, where both sexes have a substantial input to the incubation effort and individual incubation shifts are not likely to be especially long (probably a maximum of 12-24 hours in length, pers.obs.).

In this study, females delivered 1.5-2 times as many feeds to young as males, while males spent a larger proportion of the day (2-3 times as long as females) above ground at the colony during the rearing period. When they were at the colony, males often stood in the vicinity of their burrow and were presumably guarding the entrance from prospecting non-breeders and young birds; the latter were numerous at this time and could drive a chick out of its burrow or attract it to the entrance, increasing the risk of predation by gulls. Such guarding had the potential to become costly for males if they became involved in fights but, in practice on the Isle of May, fights were rare and most prospectors were probably repelled by non-contact display behaviour. If all food loads were equal in terms of their content and the energetic expense of obtaining them, then females delivering more feeds than males might have a higher energetic input during rearing than males, which could be manifested in effects on body condition. There was no evidence in this study or that of Creelman and Storey (1991) of any differences in the sizes of food loads delivered by males and females but Harris (1988) found that males carried heavier loads, containing a larger number of fish, than females, although the differences were not significant. Looking at the problem from the opposite angle, males might deliver fewer feeds because the energetic cost of obtaining each feed is larger for males. For example, Nol (1985) suggested that male Oystercatchers, which are smaller than females with a lower wing loading, made more foraging trips to feed young than females because they incurred lower flight costs. The same could be true for Puffins, in which males have a higher body mass : wing length ratio (mean male ratio = 2.47, n=27 and mean female ratio = 2.28, n=28; T=5.55, p<.0001), resulting in 14% higher power requirements for flight (Pennycuick,1989) for males, all else being equal.

In summary, the results presented in this chapter suggested that the energetic investment of breeding male Puffins may have been greater than that of females during incubation but that the opposite could be true during chick rearing. The implications of these intersexual differences for adult body condition during breeding are considered in Chapter 5. There was considerable interpair variation in the roles played by the sexes, particularly in the provisioning of young, which suggested that the relative contributions of pair members to breeding activities might influence reproductive success (discussed in Chapter 5).

CHAPTER 4 BODY MASS AS A MEASURE OF PUFFIN BODY CONDITION.

4.1 INTRODUCTION.

4.1.1 Body condition of adult Puffins during breeding.

Body condition is a relative rather than an absolute measure, which may be used to describe the fitness of an individual to cope with its current and future needs (Owen and Cook,1977). Ideally, the condition of an individual should be assessed by comparing the magnitude of its body reserves with current and future expenditure of these reserves. It is, however, often difficult to determine reserve size in relation to requirements for a number of reasons. First, avian energy requirements can be adequately quantified but the extent to which these are met from lipid and protein reserves is still uncertain (eg Visser,1978; Brittas and Marcstrom,1982). Second, protein requirements for body maintenance and growth during the various stages of the avian annual cycle are still poorly understood. Third, information on other potentially-essential avian nutrient requirements is incomplete (Robbins,1983).

Condition is often assessed by comparing the body reserves of individual birds with the mean level of reserves found within the population at the appropriate time of the year, under the appropriate environmental conditions. Such reserve levels may have been selected during the course of evolution to confer maximum fitness for the stage of the annual cycle or under the environmental conditions in which they were measured (King,1972). An individual with body reserves above the mean level need not, therefore, be of superior condition (this is discussed later in Chapter 5). The term 'body condition' may, for practical purposes, be interpreted as the quantity of reserves present above a residual level, where the residual level is the quantity of reserves present at death through starvation (Wishart,1979; Piersma,1984). The residual level of body constituents should be determined by the skeletal dimensions of an individual, that is by its 'structural size' (Wishart,1979; Piersma and Davidson,1991).

In a study such as this, where the aim is to relate the body condition of individual adults to their reproductive effort and success, both within and between years, it is clearly impractical to measure body reserves by sacrifice of monitored individuals at various times during the breeding season. There are, in addition, strong ethical and conservational arguments against the sacrifice of large numbers of birds, outwith the substantial time and expense involved in the analysis of carcasses. The first aim in this chapter, therefore, is to assess the methods which were available for estimating the body reserves of live adult Puffins during breeding. It was not possible to measure protein and lipid reserves independently in this study. Visual fat scoring was not possible and determination of pectoral muscle protein reserves using ultrasound (Baldasarre *et al*, 1980; Sears,1988; Newton,1989 and 1993) and muscle-surface profiling (Bolton *et al*, 1991) was attempted but abandoned because of the extra handling time required and its potential effects on bird behaviour (Chapter 2, section 2.9.1).

Body mass comprises a structural component, with magnitude dependent on body size, and a labile component, loosely termed the body reserve. The reserve includes the contents of the digestive tract, water and protein reserves as well as stored lipid. The reserve component and structural size can vary independently, so that body mass is not necessarily correlated with reserve mass, although this may be the case in some species (reviewed by Blem,1990). Most methods used to estimate the (largely lipid) reserve mass from body mass and body dimensions of live birds involve the prediction of the structural component of body mass (lipid-free wet or dry mass) from body measurements and the subsequent estimation of reserve mass (lipid mass or total reserve mass) by subtraction of lean (structural) mass from fresh mass. If a small sample of (preferably starved) carcasses is available, then body lipids can be extracted and relationships between body dimensions and lean mass established. If the relationships are satisfactory, then the lean masses of live individuals can be estimated from their body dimensions and lipid reserve mass can be calculated by subtraction of lean mass from fresh mass. If predictive equations are obtained from the carcasses of birds which died of starvation (both lipid and protein reserves largely exhausted), then the reserve mass estimated for live birds will include both lipid and protein (all body reserves). Estimation of reserve mass using predicted lean mass has been termed the 'fat-free method' (Perdeck,1985) and is widely utilized in studies of avian body condition (eg Connell *et al*, 1960; Mascher and Marcstrom,1967; Bailey,1979; Davidson,1983). Alternatively, if carcasses of presumed healthy birds are collected at random, direct relationships between extracted lipid mass and fresh body mass and size can be sought (eg Mascher and Marcstrom,1967; Iverson and Vohs,1982; Piersma,1984; Piersma and Brederode,1990). Perdeck (1985) termed this the 'fat method' and, in this case, relationships between fresh body mass and body size are incorporated as independent variables in the regression model.

If carcasses are not available, relative body reserves of individuals can be estimated from the relationship between the body mass and body dimensions of live birds. This can be achieved using a multiple regression model with body mass as the dependent variable and size measures as independent variables (eg Ormerod and Tyler,1990) or by creating a body size parameter using principle components analysis (Reid,1987; Ankney and Afton,1988; Rising and Somers,1989; Freeman and Jackson,1990). If a satisfactory relationship between body mass and size exists, this can be used to estimate the relative reserve level for any individual from its fresh mass by subtraction of the predicted mass for an individual of appropriate body size. The estimated reserve level is expressed relative to the mean population level for a bird of any given size and may be positive (heavier than expected) or negative (lighter than expected). Alternatively, it is possible to control for size variation between individuals by standardizing all mass measurements to a mean bird size using the partial regression coefficients from the established relationship between body mass and biometrics. The approach taken to measuring avian body reserves will, therefore, depend both on the subsequent use of the data and on the availability of carcasses.

In this study, the suite of body dimensions available for adult Puffins varied between individuals (see methods). For this reason, it was felt necessary to kill a sample of adults to evaluate which of the various biometrics used to estimate the expected masses of live birds were the best indicator(s) of structural size and, hence, lean body mass. Some commonly measured external dimensions of birds may only be moderately correlated with structural size (eg Moser and Rusch,1988) and the most appropriate external measurements to represent structural size may differ widely, between even closely related species (eg Piersma,1988 for *Podiceps* grebes). The aim here was to demonstrate the relative merits of potential methods for predicting the reserve levels of live adult Puffins on the Isle of May, and to show how predicted reserve levels could be used to indicate the relative body condition of individual adults during breeding.

4.1.2 Body condition of young Puffins as a measure of reproductive success.

As a pair of Puffins can only raise a single chick each year, reproductive success can be measured in terms of whether or not a chick is fledged and in terms of the fitness of the fledged young. Fitness should be measured in terms of the probability of recruitment of the young to the breeding population and its subsequent lifetime reproductive success but these parameters cannot be measured in a short-term study of a species which does not breed until at least 4 to 5 years of age (Harris,1981). The overwinter survival of young after fledging could provide a short-term measure of fitness but even this is difficult to measure because very few Puffins return to the breeding colony in the year after fledging; these yearlings can form up to 15% of the individuals seen in rafts on the sea off the colony at the end of the breeding season and some fly over the colony but few land (Harris,1984). There is also evidence to suggest that many immatures do not return to their natal colonies (Kress,1982; Harris,1984). Monitoring the survival of young after fledging would, therefore, involve substantial time commitment to checking for immatures both at the natal colony and elsewhere, which was not feasible in this study.

The body reserve levels of young at the time of fledging might be a useful index of chick fitness and, hence adult reproductive success, if these body reserves influence the subsequent survival prospects of young. Positive relationships between body mass at fledging and subsequent survival of young have been demonstrated in several passerine species (eg Perrins,1965; von Haartman,1967) and in Manx Shearwaters (Perrins *et al,* 1973). The effects of fledging date and fledging mass on survival can be confounded however, in that early young tend to be heavier and have increased survival relative to later-fledged, lighter young. There is no evidence that peak or fledging mass (or date or age of fledging) influence the survival prospects of Puffin young (Harris,1980,1982; Harris and Rothery,1985). Most of the available data are from the Isle of May, when the population was increasing rapidly; conditions may, therefore, have been close to optimal for Puffins so that selection pressure was low allowing even the lightest young to survive. Equally, a relationship between fledging mass and survival might not be revealed if fledging Puffins were to show large variation in structural size, so that most mass variation was attributable to structural components.

In this study, the magnitude of the body reserves of young at peak mass rather than at fledging was considered because the capture of parents for weighing late in the rearing period may have had a large and unpredictable effect on the fledging mass of individual young (Chapter 2, section 2.9). Most adults were caught for the second time during rearing after young reached peak mass, so that peak mass was less influenced than fledging mass by the adult catching protocol. The body reserves of young at peak mass did, however, provide a reasonable measure of reserves at fledging because the peak and fledging masses of individual young are positively correlated within any year (Figure 2.9 in Chapter 2). Young were not killed for body composition analyses in this study. Relative body reserves were estimated only from relationships between the live peak masses of young and biometrics reflecting structural size, in the same way as for adults (described above).

The aim here is to demonstrate how estimated reserve levels of young at peak mass were used to indicate the relative condition of young at fledging and hence the relative success of individual Puffin pairs.

4.2 METHODS.

4.2.1 Analysis of adult carcasses.

Nine adult Puffins were killed under licence early in the morning on 21st and 22nd July, 1992 and immediately weighed (to the nearest 1g) using a Pesola 500-g spring balance before being frozen. All had fledged young in that breeding season. Five additional carcasses were obtained as casualties in the 1991 and 1992 breeding seasons. Of these, 3 were adults which flew into obstacles during the main chick rearing period (all with 2 or more bill grooves), one adult was found freshly dead and the last, an immature, was found paralysed in a patch of Small Nettles at the beginning of the rearing period. All 5 birds were weighed and frozen immediately.

After thawing, wing length, bill top, length and depth, total head plus bill length and tarsal length were measured (Chapter 2, section 2.2.3). Wing span was measured between the tips of the longest primary feathers on each wing with the wings fully extended, and keel length was measured (after removal of the skin) from the notch on the anterior ventral side of the sternum to the posterior end of the keel, including the area of flexible cartilage. Wing length and span were measured with a ruler to the nearest 1mm; all other measurements were made with running slide calipers to the nearest 0.1mm. Sex was established during dissection by inspection of the gonads.

The skin, with subcutaneous lipid layer intact, was removed from each carcass and half, divided along the mid-dorsal and mid-ventral lines, was used for lipid extraction; all feathers were left in place and the skin was removed to the joint between the humerus and the radius/ulna (wings) and to the joint between the femur and the tarsus (legs). Wings were removed from the carcass at the joint between the humerus and the radius/ulna and one was used for lipid extraction, with all feathers intact. The breast muscles *(pectoralis* and *supracoracoideus)* were removed from the body and those from the right side were used for lipid extraction. The gonads, liver, heart, kidneys and gut (with contents removed) were removed from the body shell and were analysed separately. In most cases the gut was empty and the fresh gut contents never totalled more than 1g. The remaining part of the carcass (the body shell) was weighed (to the nearest 0.1g) and finely minced in a commercial meat mincer; the resultant mince was reweighed and correction was made for the small quantity of material lost during the mincing process (1.2-8.4% of the fresh mince), assuming no bias in the type of material lost.

All body components were freeze-dried at -40°C for one week (to constant mass) and weighed on an Oertling R20 scientific balance (to the nearest 0.0001g) before lipid extraction. All components were extracted whole except for the body shell mince; this was ground to a fine homogenous powder in an electric kitchen grinder and one sample (approximately half) of this was extracted. Lipid extraction was performed in a standard Soxhlet apparatus using a mixture of 5 parts diethyl ether and one part chloroform. Skin samples were processed in the Soxhlet apparatus for 8 hours each day for 5 days (total 40 hours) and were left to soak in the solvent overnight (4 nights). Other body components were processed for 8 hours on each of 3 days (total 24 hours) and were soaked in the solvent for 2 nights. These extraction times were selected after several consecutive extractions and reweighings of test samples had been performed and constant mass had been achieved. At the end of each extraction, the solvent was allowed to evaporate from the sample and the remaining lean components were freeze-dried for a further week and stored in a desiccator overnight before final weighing.

Total body water was determined by subtraction of the sum of the dry masses of all the various body components from fresh (wet) mass. The lipid contents of the body components were calculated by subtraction of the appropriate lean (lipid-extracted) dry mass from dry mass.

4.2.2 Estimation of the body reserves of live breeding adults.

Methods of estimating the lipid reserves of live adults from external body measurements and fresh mass were investigated using multiple regression analysis. In such analyses, where a three-dimensional measure, such as mass, is related to linear size measures, all variables should, theoretically, be converted to the same dimension. In the analyses presented here, transformation of the linear measurements to three dimensions (by cubing in various combinations) did not increase the coefficients of determination in the regression analyses and, therefore, only analyses using untransformed data are presented here. In addition, principle components analysis (Rising and Somers,1989; Freeman and Jackson,1990) was tested as an alternative to multiple regression but the first principle component (representing size) did not explain any more variation in the dependent variable than the measures of body size which were significant in the regression models.

The standard error of the estimate in a multiple regression analysis is a measure of the absolute error in prediction of the dependent variable (where the standard error is the square root of the sum of the squares of the residuals, divided by the degrees of freedom of the sums of squares). In the analyses which follow, the various methods for predicting the lipid reserves of individuals were evaluated by comparison of their relative errors; these were calculated as the standard error of the appropriate estimate divided by the mean actual lipid content of the birds for which the estimate was being made (Perdeck,1985). Lipid reserves were predicted from the carcass data both directly, using total body lipid as the dependent variable, and indirectly, by predicting lipid-free mass and then estimating total body lipid by subtraction of the predicted lipid-free mass from fresh mass. All 14 carcasses were used in the prediction of lipid-free mass while only the 9 killed birds were used to predict total body lipid directly. It was, therefore, assumed that birds dying accidently were representative in terms of lean (structural) components but could be abnormal with respect to the lipid reserves they carried. These assumptions were supported in bivariate plots of lipid-free mass and total body lipid with measures of body size; birds which died accidently had residuals similar to those of the killed birds in plots of lipid-free mass but in plots of total body lipid were clearly outliers with high residuals.

Body dimensions which were found to be significant predictors of total lipid reserves from the carcass analyses were compared with those selected in analyses using data from live birds, where fresh mass was the independent variable and body dimensions were independent variables. In 1990 and 1991, 120 and 163 individual adult Puffins were weighed and measured (Chapter 2, section 2.2.3) throughout the breeding seasons respectively. The only body dimensions measured were wing length and the 3 bill dimensions and the stage of breeding was only known for those individuals which successfully hatched young and whose burrows were subsequently monitored. In these two years, measurements were derived from unmanipulated adults at the Little Hide study site throughout the breeding season. More comprehensive data sets were available in 1992, when 92 individuals were weighed and measured at Little Hide (first data set) and, in addition, 180 Puffin burrows all over the island were checked during incubation and again during chick rearing; adults from these burrows formed a second data set (117 individuals) composed of birds brooding chicks during rearing. A third 1992 data set was derived from adults caught by mist-netting as they delivered food loads to young (Chapter 2, section 2.7). It was hoped that the mass measurements in the three 1992 data sets would be more homogenous, varying less with respect to weather, season or breeding stage, than those in the 1990 and 1991 data sets. In 1992, total head plus bill length and tarsal length were measured in addition to the 3 bill dimensions and wing length. Head plus bill length and tarsal length were assumed to vary little between years once an adult was of breeding age, so that these measurements could be compared with the masses of the same individuals measured in the previous years (1990 and 1991).

In each of the data sets, a large proportion of the birds could not be sexed with certainty because only one member of a pair was measured. For the purpose of these analyses, individuals with a bill discriminant score of less than 120 were assumed to be females, those with a score greater than 121 were assumed to be males, while those with a score of 120-121 were omitted from the analyses (refer to Section 2.2.4 in Chapter 2 for use of the bill discriminant score for sexing).

4.2.3 Estimation of the body reserves of Puffin young.

Carcasses of young Puffins were not collected for lipid analysis and variation in the magnitude of reserves carried by individual chicks at peak body mass was estimated by expressing fresh mass (as a residual) relative to mass predicted for a given body size. In 1990 and 1991, only wing length at or near the time of fledging was recorded as a measure of chick structural size, while in 1992, total head plus bill length and tarsal length at fledging were also measured (for methods of measurement see Chapter 2, section 2.6). Peak body mass and size data were available for 23, 30 and 27 unmanipulated chicks from the Little Hide study site in 1990, 1991 and 1992 respectively.

4.3 RESULTS.

4.3.1 Body composition of adult Puffins.

The gross composition of adult Puffin carcasses subdivided with respect to sex, age (all but one were birds of breeding age) and manner of death is summarized in **Table 4.1**. Overall the birds comprised a mean of 63(+/-2)% water, 32(+/-1)% lean components and 6(+/-2)% lipid. Samples sizes were insufficient to assess whether gross body constituents differed significantly between sexes within death classes or between death methods within sex classes

Table 4.1 **Composition of Puffin carcasses collected on the Isle of May in 1991 and 1992, subdivided with respect to sex, age and cause of death.**

(Variables shown as mean +/- s.d)

CAUSE OF DEATH	Sex	Age	n	Fresh mass (g)	% of fresh mass			Lipid index (lipid/lean dry mass)
					% Water	% lean dry	% lipid	
KILLED	♂♂	Adult	6	394 +/- 18.3	63 +/- 1.8	32 +/- 0.7	6 +/- 2.0	.18 +/- .07
	♀♀	Adult	3	369 +/- 11.0	63 +/- 1.1	31 +/- 0.5	6 +/- 0.8	.20 +/- .03
	Total killed		**9**	**386 +/- 15.9**	**63 +/- 1.6**	**32 +/- 0.7**	**6 +/- 1.6**	**.19 +/- .06**
ACCIDENTAL	♂♂	Adult	1	402	65	31	4	.13
		Immature	1	435	58	30	12	.41
	♀♀	Adult	3	376 +/- 37.0	64 +/- 0.8	31 +/- 1.5	5 +/- 1.0	.17 +/- .04

but there was some suggestion that killed females carried more lipid for their size than males (comparison of dry indices) and that birds dying accidently (except the single immature) had lower lipid reserves.

Individuals differed little in the proportional contribution of body components to lean dry mass but were more variable with respect to the lipid content of body components (**Table 4.2**). Variation in the mass of subcutaneous lipid was responsible for a large part of the variation in total body lipid (as 28-56% of total lipid was located under the skin), while 31-47% of body lipid was located in the body shell. The liver, gut and pectoral muscles also varied in their lipid content but this was of less importance to total body lipid content because these body components contained only 1-8% of total body lipid in the case of the liver or gut, and 5-14% in the case of the pectoral muscles. The gonads, heart and kidneys each constituted less than 1% of lean dry body mass and were, therefore, of negligible importance as sites for lipid storage.

4.3.2 Estimation of adult body lipid content from carcass analyses.

Three multiple regression models were fitted for each dependent body composition variable using differing sets of body dimensions as independent variables. Estimate A used all 8 body dimensions derived from the carcasses, estimate B used the maximum of 6 dimensions measured on live birds (wing length, 3 bill measurements, head plus bill length and tarsal length), while estimate C used the minimum of 4 body dimensions (wing length and the 3 bill dimensions) available for live birds (**Table 4.3**).

Six of the body dimensions derived from the carcasses explained almost 100% of variation in carcass lean dry mass (**Table 4.3, Equation 4.1**). When the six body dimensions measured in the field were used (estimate B), only head plus bill length was selected as significant and the proportion of variation in lean dry mass explained decreased to 59% (**Table 4.3, Equation 4.2**). The coefficient of determination further decreased to 42% when only wing length and the 3 bill dimensions were used (estimate C) and bill length alone was selected as a significant predictor of lean dry mass (**Table 4.3, Equation 4.3**). When total lean wet mass was used as the dependent variable, head plus bill length and wing length together explained 85% of variation in lean wet mass (**Table 4.3, Equation 4.4**) but the coefficient of determination decreased to only 33% when only wing length and the 3 bill dimensions were used (**Table 4.3, Equation 4.5**), when bill length alone was selected as a significant predictor

Table 4.2 Variation in the proportional contribution of body components to lean dry mass and the proportion of the total lipid reserve found in body components of Puffins, subdivided by sex, age and cause of death.

(Variables shown as mean, s.d. and range).

CAUSE OF DEATH	Sex	Age	n	Lean dry mass (g)	% of lean dry mass in :-					Lipid mass (g)	% of total lipid in :-				
					Muscle[1]	Liver	Gut	Skin	Body shell		Muscle[1]	Liver	Gut	Skin	Body shell
KILLED	♂♂	Adult	6	125.7	15	5	4	23	52	22.2	10	3	2	46	37
				5.8	1	1	1	1	1	9.1	2	1	1	7	4
				119-135	14-16	4-5	3-4	22-24	50-53	13-34	7-13	2-5	1-3	38-54	31-42
	♀♀	Adult	3	116.0	16	5	3	22	52	22.6	10	4	2	47	35
				2.7	2	1	1	2	1	3.5	1	3	1	3	4
				113-118	14-17	4-5	3-4	21-24	52-53	19-26	9-11	2-8	2-3	44-50	31-39
ACCIDENTAL	♂♂	Adult	1	130.0	15	4	4	23	52	52.7	5	1	2	56	34
		Immature	1	123.4	16	4	3	23	52	15.9	14	5	8	39	31
	♀♀	Adult	3	116.7	15	4	4	23	51	19.1	9	6	4	38	40
				11.8	1	0	1	1	1	4.0	3	2	0	11	6
				107-130	15-16	4	3-4	23-24	50-52	17-24	6-11	4-7	4	28-49	35-47
	OVERALL RANGE (all birds)			**107-135**	**14-17**	**4-5**	**3-4**	**21-24**	**50-53**	**13-53**	**5-14**	**1-8**	**1-8**	**28-56**	**31-47**

NOTE.

[1] Muscle refers to the pectoral muscles only (see text).

Table 4.3 Multiple regression statistics for carcass-derived relationships between lean dry mass (LDM), lean wet mass (LWM) and total lipid mass (TLM) and measures of body size for Puffins.

N/A indicates that the variable was not included in the model and --- indicates that the variable was included in the model but was not selected as a significant influence on the dependent variable.

Equation number	DEPENDENT VARIABLE	Estimate (see text)	INDEPENDENT VARIABLES									MULTIPLE REGRESSION STATISTICS					
			wing length (mm)	wing span (mm)	bill top (mm)	bill length (mm)	bill depth (mm)	head & bill (mm)	tarsus (mm)	keel (mm)	fresh mass (g)	I	s.e	r.e^a	r^2	p	n
4.1	LDM	A	2.03	-0.89	2.47	---	-0.70	3.01	2.74	---	N/A	-108.0	0.38	.003	.998	<.0001	14
4.2	LDM	B	---	N/A	---	---	---	2.64	---	N/A	N/A	- 88.1	5.02	.041	.591	<.0005	14
4.3	LDM	C	---	N/A	---	5.08	---	N/A	N/A	N/A	N/A	22.5	6.00	.049	.416	<.005	14
4.4	LWM	A/B	3.26	---	---	---	---	7.72	---	---	N/A	-786.7	8.23	.366	.848	<.0001	9
4.5	LWM	C	---	N/A	---	12.21	---	N/A	N/A	N/A	N/A	17.8	16.99	.755	.330	<.05	9
4.6	TLM	A/B/C	---	---	---	---	---	---	---	---	0.26	- 77.2	5.37	.240	.414	<.05	9

NOTE.

a Relative error (for calculation refer to the text).

of lean wet mass. When total body lipid was related directly to fresh mass and body dimensions, only fresh mass was selected as a significant predictor of total body lipid, explaining 41% of the total variation (**Table 4.3, Equation 4.6**).

The analysis with total body lipid as the dependent variable demonstrated that only 41% of the variation in the lipid reserves of individuals would be considered if fresh body mass alone was used to indicate body condition. The relative error associated with the prediction of total body lipid reserve from fresh mass was 0.24 (standard error of 5.37g divided by the mean total body fat of the sample of 22g). Alternatively, the total lipid mass of a live bird could be estimated by predicting its total lean wet mass (from **Equations 4.4 or 4.5 in Table 4.3**) and subtracting this from fresh mass. If both head plus bill length and wing length were available, the latter resulted in a relative error of 0.37 in the estimation of total body lipid mass but the relative error was very high (0.76) when head plus bill lengths were not available (where it was necessary to use **Equation 4.5**).

The above methods of predicting lipid reserve mass were evaluated by comparing predicted reserve levels with the actual levels extracted from carcasses (**Figure 4.1**). When the extracted total lipid masses of killed birds were compared with those estimated using the equations for predicting lean wet mass (**Figure 4.1a and b**), the prediction was satisfactory when all the body dimensions available for live birds were used (Spearman $r=.819$, $p<.01$, $n=9$) but it was much poorer ($r=.502$, $p>.1$, $n=9$) when the more limited suite of size measurements was used. In the latter case, there was evidence to suggest that the sexes differed in their lipid reserves, females carrying more than males (**Figure 4.1b**). When extracted lipid masses were compared to those predicted directly from fresh mass (**Figure 4.1c**), the correlation was reasonable ($r=.693$, $p<.05$, $n=9$) but there was again evidence for a segregation of male and female values, with females carrying larger than predicted levels of lipid. The sample of killed birds was too small to allow analyses to be preformed for the sexes separately.

4.3.3 Estimation of body reserves from measurements of live adults.

Relationships between the body masses and body dimensions of live breeding adult Puffins in the 3 years of the study are summarized in **Table 4.4**. When the sexes were combined, the variation in body mass explained by the multiple regression models ranged from 39 to 54% when all the available body size measures were used, and from 32 to 42% when only wing length and the 3 bill measurements were available. There was little consistency in the body

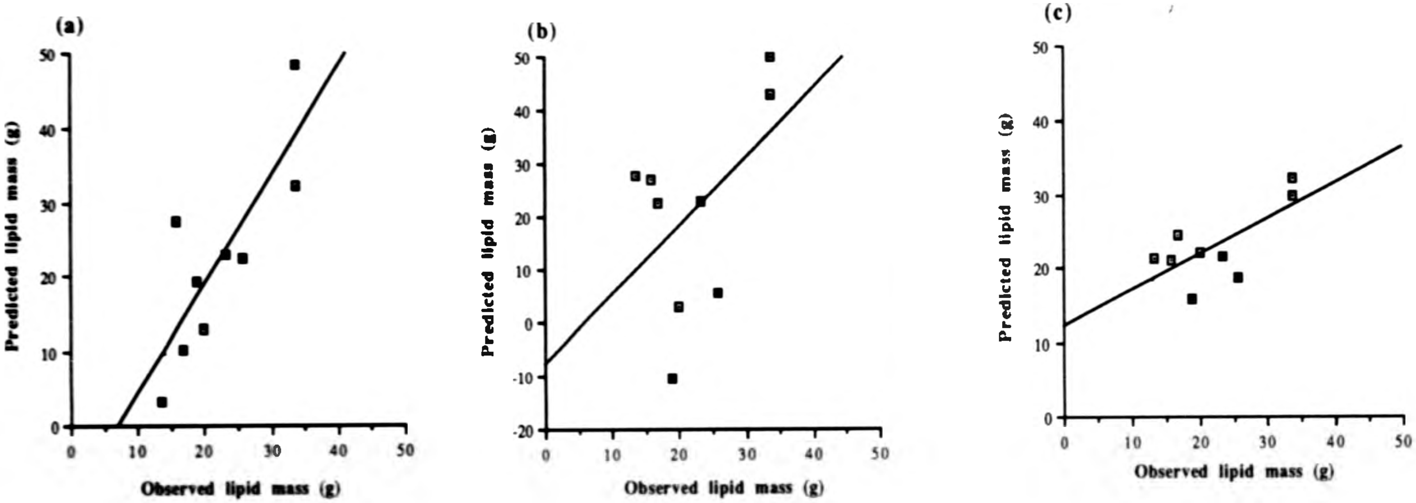


Figure 4.1 Evaluation of the carcass-derived equations used to predict the lipid reserve mass of live adult Puffins (open symbols are males and closed symbols females).

(a) Lean wet mass predicted from all body dimensions available for live birds (Equation 4.4 in Table 4.3).
(b) Lean wet mass predicted using the limited suite of body dimensions (Equation 4.5 in Table 4.3).
(c) Direct prediction of total lipid mass from fresh mass (Equation 4.6 in Table 4.3).

Table 4.4 **Multiple regression statistics for relationships between the live body mass during rearing of adult Puffins (dependent variable) and measures of body size (independent variables), 1990-1992.**

N/A indicates that the variable was not included in the model and --- indicates that the variable was included but was not selected as a significant influence on the dependent variable.

YEAR[a]	Sex	E[b]	INDEPENDENT VARIABLES						REGRESSION STATISTICS				
			bill top (mm)	bill length (mm)	bill depth (mm)	wing length (mm)	head & bill (mm)	tarsus (mm)	I	r^2	s.e	p	n
1990	All	B	10.01	---	---	---	---	---	- 69.6	.386	21.0	<.0001	38
	♂♂		---	---	---	1.78	---	---	115.3	.188	15.0	<.05	19
	♀♀		9.05	---	---	---	---	---	- 33.4	.330	19.2	<.005	20
	All	C	---	---	7.96	1.40	N/A	N/A	-126.7	.359	21.1	<.0001	81
	♂♂		---	---	---	1.48	N/A	N/A	164.0	.085	17.5	<.05	41
	♀♀		---	---	6.80	---	N/A	N/A	134.8	.181	19.7	<.005	38
1991	All	B	---	---	6.15	---	2.87	6.32	-230.5	.495	18.5	<.0001	80
	♂♂		---	---	---	---	---	---	------	----	----	NS	44
	♀♀		---	---	6.10	---	---	---	158.0	.138	17.3	<.05	36
	All	C	---	4.89	7.65	1.11	N/A	N/A	-205.5	.392	21.4	<.0001	141
	♂♂		---	---	5.05	---	N/A	N/A	222.4	.080	21.3	<.01	72
	♀♀		---	---	4.52	1.55	N/A	N/A	- 29.9	.125	20.6	<.01	63
1992 (A)	All	B	---	-8.10	4.69	---	8.71	4.90	-374.8	.544	18.4	<.0001	93
	♂♂		---	-9.37	---	---	9.06	---	- 47.9	.201	19.7	<.005	46
	♀♀		---	-7.65	---	---	7.79	6.51	-195.9	.359	15.9	<.005	45
	All	C	---	---	7.98	1.78	N/A	N/A	-197.3	.363	21.7	<.0001	93
	♂♂		---	---	---	1.98	N/A	N/A	79.5	.084	21.1	<.05	46
	♀♀		3.39	---	---	---	N/A	N/A	221.0	.068	18.3	<.05	45
1992 (B)	All	B	---	---	6.44	---	3.93	---	-155.7	.451	19.7	<.0001	118
	♂♂		---	7.26	11.42	---	---	---	-242.6	.356	19.7	<.0001	66
	♀♀		---	---	---	---	5.21	---	- 28.9	.166	20.6	<.005	41
	All	C	---	6.51	8.35	---	N/A	N/A	-104.2	.418	20.3	<.0001	118
	♂♂		---	7.26	11.42	---	N/A	N/A	-242.6	.356	19.7	<.0001	66
	♀♀		---	---	---	---	N/A	N/A	------	----	----	NS	41
1992 (C)	All	B	---	---	4.98	---	4.61	5.25	-307.3	.436	21.0	<.0001	113
	♂♂		---	---	---	---	4.21	12.44	-285.9	.348	21.0	<.0001	54
	♀♀		---	---	---	---	---	---	------	----	----	NS	46
	All	C	---	5.37	8.35	---	N/A	N/A	- 80.0	.323	23.0	<.0001	113
	♂♂		---	8.99	---	---	N/A	N/A	129.7	.092	24.7	<.05	54
	♀♀		---	---	---	---	N/A	N/A	------	----	----	NS	46

NOTES.

[a] For 1992, (A) refers to Little Hide adults, (B) to brooding adults and (C) to adults delivering chick feeds.

[b] Refers to the estimates described in the text.

dimensions selected in the regressions either between years or between sample groups in 1992, although head plus bill length and bill depth were usually selected when they were available in 1991 and 1992.

When the sexes were considered separately, less variation in body mass was explained by the regression models compared to that explained when the sexes were combined and, in several cases, the size variables selected differed between the sexes. There was no suggestion from the carcass analyses that relationships between body dimensions and lean body mass differed between the sexes and the results of the analyses using live birds therefore suggested that the body reserve mass carried by a bird of a given size differed between males and females (as was also suggested from the carcass analyses).

The 9 birds killed for the carcass work were all taken soon after their young had fledged and all the birds were removed from burrows at a similar time of day on two consecutive mornings with similar weather conditions. It was not, therefore, necessary to consider the influence of factors other than body size on reserve mass for these birds. The live individuals were weighed in a range of weather conditions and behavioural situations; some birds were caught while brooding young, some while delivering food to burrows and some were weighed while standing on rocks at the colony. The influence of short-term weather fluctuations on body reserve mass is considered in Chapter 5 but weather was not found to be an important cause of variation in body mass. Weather variables were excluded from the multiple regression models presented here because with no combination of weather and size variables did weather variables explain more than 5% of the variation in body mass.

The behavioural situation in which an individual was weighed may have influenced body mass because of its relationship to the amount of time that the individual had spent ashore before weighing or since its last feed. Multiple weighings of the same individuals using the automatic balances suggested that body mass could vary by as much as 30g during a single day (presumably due to changes in gut contents and/or body reserve levels), while mass could decrease by up to 10g after a single defecation event. It was not, however, possible to measure the time since the last feed or the time since the arrival of the bird at the colony prior to weighing and there was no evidence of any diurnal pattern of adult mass change when time of day was included as an independent variable in the regression models. The 3 sets of adult mass and size data from 1992 were presented in an attempt to test whether standardization of the behavioural situation in which individuals were weighed during rearing would decrease mass variation caused by the above factors and, therefore, improve the relationship between body mass and body size. In 1992, adults from the Little Hide site were weighed in a mixture of behavioural situations, those in the 'brooding' data set were all removed from burrows while brooding young at various times of the day, while those in the 'feeding' data set were all caught while delivering feeds to young in the first 3 hours after dawn; the latter data set was expected to contain the most homogenous mass measurements with respect to time since the last opportunity for self-feeding. There was some improvement in the fit of the multiple regression model when 'brooding' and 'feeding' birds were considered separately in the case of males but not for females (**Table 4.4**).

4.3.4 Estimation of the body reserves of young at peak mass.

The body dimensions of a young, growing bird reflect both its structural size and its age. When body dimensions are used to compare the structural sizes of individuals of differing age it is, therefore, first necessary to establish how body size increases with age and to control for this if necessary. In this study, the body reserves of young at peak mass were compared with body size measurements made on or just before the day of fledging. The ages at which chicks fledged differed from 34 to 56 days, however. The relationships between size measures and the ages at which they were measured were, therefore, established for each body dimension in each year before relationships between peak mass and body size were sought (**Table 4.5**).

In 1990, neither the relationship between chick wing length and age nor that between peak mass and wing length was significant (**Table 4.5**). Wing length increased significantly by 0.34mmd^{-1} when young were close to fledging in 1991; when all wing lengths were standardised to the mean fledging age of 43 days using this regression coefficient, there was a significant positive relationship between peak mass and wing length, the latter explaining 21% of variation in the peak mass of young. In 1992, none of the 3 body dimensions was influenced by the age of young at the time of their measurement and only head plus bill length was significant in the regression model, explaining 62% of variation in the peak body mass of young.

Table 4.5 **Derivation of a total residual reserve mass for Puffin young by controlling for structural size : relationships between body dimensions, age at the time of measurement and peak mass in 1990 - 1992.**

	Body dimensions measured	wing length (mm) near fledging	
1990	Correction for age of measurement	none (regression of size on age r^2=.107, p>.1, n=25)	
	Standardization of peak mass for body size	none (regression of peak mass on size r^2= .143, p>.05, n=23)	
	Body dimensions measured	wing length (mm) near fledging	
1991	Correction for age of measurement	wing length (mm) = 116.47 + 0.340 age (d)	(r^2=.163, p<.05, n=31)
	Standardization of peak mass for body size	peak mass (g) = -123.86 + 3.286 wing length (mm)	(r^2=.209, p<.01, n=30)
	Body dimensions measured	wing length (mm), head plus bill length (mm) and tarsal length (mm) near fledging	
1992	Correction for age of measurement	none (regression of size on age p>.1, n=27)	
	Standardization of peak mass for body size	peak mass (g) = -892.69 + 17.980 head plus bill (mm)	(r^2=.617, p<.0001, n=27)

4.4 DISCUSSION.

4.4.1 Problems associated with the analysis of carcasses.

If starved carcasses were used to determine a relationship between lean body mass and body dimensions, then body reserve mass predicted from such a relationship would include protein as well as lipid reserves. This would be the most satisfactory method for estimating body reserve mass, although even birds dying of starvation may carry some reserves (both of lipid and protein) because the nutritional state at death appears to be influenced by environmental conditions during starvation; absolute quantities of reserves remaining in such instances are, however, small (Davidson and Evans,1982; Davidson and Clark,1985; Blem,1990). In this study, carcasses were not derived from starved birds and reserve levels predicted for live birds from the carcass-derived relationships therefore represented all lipid reserves but only levels of protein differing markedly from the mean level in the carcasses. The types of solvent used to extract lipid reserves have been questioned (Dobush *et al,* 1985; Blem,1990) because the amount and type of lipid extracted depends on the nature of the tissue and the type of solvent used (Christie,1982; Dobush *et al,* 1985). Avian energy reserves consist of neutral lipids but some solvents (including some chloroform mixtures) also extract phospholipids, which are structural components of cell membranes and nervous tissue and are not important as energy stores (Blem,1990). Body reserve levels estimated for live birds in this study were not intended to represent absolute levels of energy reserves available but rather they provided a satisfactory means of comparing the relative reserve levels of individual birds.

The use of non-starved carcasses could bias predictions of body reserves for live birds if lean reserve levels were not linearly correlated with body dimensions, that is if protein stores were of relatively different size in individuals of different absolute size (Piersma and Brederode,1990). For the adult Puffins analysed in this study, 8 body dimensions measured on carcasses explained almost 100% of variation in lean dry body mass and 85% of variation in lean wet mass but none of the variation in total body lipid mass. This suggested that variation in lean reserves was negligible relative to variation in lipid reserve mass, at least at the end of the chick rearing period when most carcasses were obtained. In support of this, a comparison of the variation in the lipid and lean content of various body components between individuals showed that the components varied little in their lean dry mass but much more in their lipid content.

Carcass-derived equations for estimating body lipid reserves should, ideally, be tested by predicting the total lipid contents of a further independent sample of carcasses and comparing these to the lipid masses determined during extractions (Perdeck,1985; Blem,1990) but this was not possible in this study. The standard error involved in predicting the dependent variable for a new individual is always higher than that for an individual belonging to the sample from which the regression equation was derived (eg Draper and Smith,1966). The standard errors of estimates stated previously (Results section) would, therefore, be higher when body reserves of live birds were predicted from the carcass-derived relationships. The relative errors of such estimates depended on the absolute mean body reserve levels of the live birds for which estimates were made, however; the relative errors may not, therefore, have been higher than those stated for the carcass-derived equations if individuals were to carry higher levels of reserve during rearing than during the post-rearing period when the carcasses were collected, for example.

Prediction of total body lipid direct from body dimensions and fresh mass (by the 'fat method') is complicated if the sexes differ in the quantity of lipid they carry for a given structural size. For example, female Great-crested Grebes carried greater lipid reserves than males for a given body size (Piersma,1984) and a similar sexual difference was indicated for adult Puffins in this study. The sample size of killed birds (6 males and 3 females) was, however, insufficient to allow the sexes to be considered separately but the problem was solved by choice of the 'fat-free method' for predicting the reserve masses of live birds (see below).

4.4.2 Estimation of the relative body reserves of live adults: choice of method.

The proportion of variation in total body mass explained by lipid reserve mass varies widely between bird species (reviewed by Blem,1990), from 0% in Golden-crowned Kinglets (Blem and Pagels,1984) to 71% in Sandhill Cranes (Johnson *et al*, 1985). Body mass has been used alone to indicate relative levels of lipid reserve in some studies (eg Ankney,1979; Hobaugh,1985). For adult Puffins in this study, body mass explained only 41% of the variation in total body lipid mass and was, therefore, not a satisfactory indicator of relative body reserve levels. A direct prediction of total reserve mass from fresh mass and size measures was of no greater use than body mass alone because none of the body dimensions was selected as a significant correlate of total lipid mass. Use of the latter carcass-derived relationship to predict total body lipid mass was inappropriate because the equation estimated the mean lipid reserve mass of an individual of known live mass, regardless of structural size and only in the particular stage of the annual cycle and in the environmental conditions in which the carcasses were collected. The aim in this study was the converse of this (ie to control for the structural component of body mass), so that the true variation in the reserve mass of live birds could be revealed under any prevailing conditions.

The above aim was fulfilled by using the equation relating lean wet mass to body size, to determine total reserve mass by subtraction of estimated lean mass from fresh mass. The relationship was suitable for estimating the body reserve mass of a live adult Puffin at any stage of the annual cycle and under any environmental conditions as long as lean components of body mass varied only with body size. The problem of differences in the relative reserve levels of males and females disappeared when the latter equation was used (**Figure 4.1**) because the relationship between lean mass and size did not vary between the sexes sufficiently to impair estimation of total reserve mass.

For individuals for which measurements of both head plus bill length (HB) and wing length (WING) were available, total body reserve mass (TRM) was most satisfactorily estimated using the carcass-derived equation for predicting lean wet mass :

$$\text{LWM} = -786.71 + 7.72\ \text{HB} + 3.36\ \text{WING} \qquad \textbf{(Equation 4.4, Table 4.3)}$$

where LWM was the predicted lean wet mass (g) and body dimensions were in mm, and then by subtraction of predicted LWM from fresh mass :

$$\text{TRM (g)} = \text{fresh mass (g)} - \text{LWM (g)} \qquad \textbf{(Equation 4.7)}$$

The relative error of the prediction of total reserve mass for the carcasses used to derive the equation was rather high at 0.37 but was considered to be lower than the likely relative error if residual body mass was predicted from fresh mass using the equations derived from live birds. For the latter, the relative error depended on the mean residual body mass of the birds for which the prediction was being made but this mean residual body mass needed to be at least 40g (for the lowest standard error of 15g in **Table 4.4**) or at least 68g (for the highest standard error of 21g in **Table 4.4**) to produce a relative error as low as 0.37.

The relative error of the estimate of total body reserve mass increased to 0.76 when the carcass-derived equation (**Equation 4.5, Table 4.3**) was used to estimate reserves for individuals for which only wing length and the 3 bill measurements were available to indicate structural size. There was also evidence that this equation did not predict total reserve mass for males and females with equal success (**Figure 4.1b**). It was, therefore, preferable to estimate body reserve mass separately for each sex using the appropriate equation derived from live birds (**Table 4.4**) for individuals for which head plus bill measurements were not available (and **Equation 4.4** could, therefore, not be used). In this case, the mean residual body mass of the birds for which the estimate was made only needed to be 23g (for the lowest standard error of estimate of 17.5g in **Table 4.4**) or 33g (for the highest standard error of 24.7g in **Table 4.4**) for the relative error of the estimate to match the 0.76 error attached to the carcass-derived estimate (**Equation 4.5, Table 4.3**) and any problems of differences between the sexes in reserve levels relative to body size (**Figure 4.1b**) were overcome by using separate equations for males and females.

4.4.3 Total body reserve mass as a measure of body condition.

A bird in favourable condition should have large energy reserves relative to some measure of its energy expenditure (Ringelman and Szymczak,1985), which means that 1g of lipid is of more importance to the condition of a 10-g bird than to that of a 100-g bird because the heavier bird has a higher energy expenditure per unit time. Measurement of the total reserve mass of an individual may, therefore, be insufficient as a measure of body condition if individuals differ markedly in structural size; it may be necessary to express reserve mass relative to some measure of individual energy requirement. Variables chosen to represent energy demand are usually size-related measures, such as lean dry mass (eg Houston *et al*, 1983; Johnson *et al*, 1985), lean wet mass (eg Ringelman and Szymczak,1985), skeletal mass (Wishart,1979) or body dimensions reflecting structural size (eg Bennett and Bolen,1978; Bailey,1979). In most studies, body reserve (lipid) mass was divided by the variable chosen to represent energy demand so that the condition 'index' took the form of a ratio. Ratios might, however, be inappropriate for use in many common analyses involving body condition (Blem,1984; Packard and Boardman,1988) because data sets composed of ratios are generally not normally distributed and, therefore, violate the assumptions of many common statistical tests (Atchley,1978; Atchley and Anderson,1978).

In this study, it was assumed that the variation between individuals in body reserve levels was greater than the variation in individual energy expenditure attributable to differences in body size. In support of this assumption, there was no detectable relationship between daily energy expenditure and either body mass or any body size measure when the energy expenditures of 9 free-ranging adult Puffins were measured during chick rearing using the doubly-labelled water technique (Chapter 6). Adult body condition was, therefore, expressed as total reserve mass rather than a ratio of total reserve mass to structural size/energy requirements in this study; hence any problems associated with the use of ratios in statistical tests were avoided although a small proportion of individual variation in condition may have been lost by the use of such an approach.

4.4.4 Estimation of the total body reserves and condition of young.

For Puffin young, wing length at fledging and head plus bill length were selected as significant body size variables, explaining 21% and 62% of variation in chick peak mass in 1991 and 1992 respectively, while wing length when close to fledging was not significantly correlated with peak mass in 1990, perhaps because peak mass was derived from less frequent weighings of young in 1990 than in subsequent years (Chapter 2, section 2.6). It was not, therefore, possible to formulate a satisfactory condition index for young in 1990.

In 1991 and 1992, a predicted peak mass for each chick could be generated from the appropriate equation (**Table 4.5**) based on its body dimensions, and a total residual peak mass calculated by subtraction of the predicted mass from fresh mass. Head plus bill length was superior to fledging wing length as a measure of chick structural size and calculation of residual peak mass of young was, therefore, more satisfactorily achieved in 1992 than in 1991. It was not possible to exclude the component of body mass attributable to structural size in 1990, leaving body mass as the only available measure of chick condition at peak mass.

As head plus bill length and wing length were the body dimensions which most satifactorily predicted the lean mass of adult Puffins, they were considered to be suitable measures of structural size for young. The absence of carcass data for Puffin young was not thought to limit the derivation of relative condition indices for young in this study. A single size measure (head plus bill length) explained a large proportion (62%) of variation in chick peak mass in 1992, suggesting that body mass alone was a poor indicator of condition. This might explain previous failures to find relationships between body mass at fledging and subsequent survival for Puffin young (Harris,1980,1982; Harris and Rothery,1985).

Levels of body reserves carried by individual young were expressed as a total residual peak mass (TRPM, g) after subtraction of a predicted mass (based on body size) from fresh peak mass; no attempt was made to express residual mass as a ratio relative to chick size and hence energy demand (section 4.4.3 above). It is assumed hereafter that young with relatively high residual mass (high reserve levels) at peak mass also had high reserve levels at fledging and, therefore, had an increased probability of survival (ie the higher the residual peak mass of a chick, the more successful were its parents). No study has sought to assess how reserve mass rather than body mass at fledging affects the survival of Puffin young. In this study, it was assumed that some body reserves at fledging would be advantageous, providing an energy store during the period when the young must learn to feed itself. It was acknowledged, however, that too large a reserve mass could be disadvantageous if it results in increased costs of locomotion and foraging (flying and diving) or costs of the initial journey from the burrow to the sea (if extra mass impedes locomotion and/or increases predation risk). In subsequent analyses (Chapter 5), where condition (residual body mass) at peak mass is used as a measure of reproductive success for individual pairs, it is important to consider this latter limitation. It is possible that an optimal reserve mass exists, rather than young with the largest reserves being the most successful. In addition, the appropriateness of the chick condition measure increased from 1990, when peak body mass alone was a poor indicator of condition, to 1992, when a highly satifactory condition 'index' was determined after the prediction of the structural (lean) component of body mass from the body size (head plus bill length) of individual young.

CHAPTER 5 : INTRA-YEAR VARIATION IN THE REPRODUCTIVE EFFORT AND SUCCESS OF INDIVIDUAL PUFFIN PAIRS : THE ROLE OF BODY CONDITION.

5.1 INTRODUCTION.

5.1.1 Role of parental body condition for breeding.

The link between food supply and avian breeding success has often been discussed (reviewed by Drent and Daan,1980; Martin,1987; Arcese and Smith,1988). Provision of supplementary food prior to or during laying (reviewed by Boulin,1990) has resulted in advancement of laying dates (eg Yom-Tov,1974; Kallander,1974; Dijkstra *et al* ,1982) and/or increase in clutch size (Hogstedt,1981; Newton and Marquiss,1981; Dijkstra *et al*, 1982; Hiom *et al*, 1991) or egg size (Hiom *et al*, 1991). Such a link between food availability and success could be mediated by avian body condition if short-term changes in the balance or rate of depletion of body reserves can be detected by individuals and used to predict long-term food availability, or to evaluate future survival chances (Drent and Daan,1980).

The influence of avian body reserves (lipid and/or protein) or body mass on some measure of breeding success has been demonstrated in many studies. Pre-laying storage of reserves by birds was evident in 32 studies, with a mean of 64% of the lipid but only 13% of the protein required for egg formation deriving from energy reserves rather than from daily intake (review by Ward,1992). Female reserves can have a positive effect on the potential clutch size predicted from follicular growth (Jones and Ward,1976; Houston *et al*, 1983; Newton *et al*, 1983; Ankney and Afton,1988). Larger reserves may result in earlier laying (Ward,1969; Fogden,1972; Fogden and Fogden,1979; Masman,1986), larger realized clutch size (Ankney and MacInnes,1978; De Korte,1985; Masman,1986; Bolton *et al*, 1992) or eggs of superior quality in terms of their size or hatching success (Bolton *et al*, 1992). Lipid may be stored for direct use in egg formation or to act as an 'insurance reserve', allowing egg formation to be maintained during periods of temporary food shortage (eg Ward, 1992 for Swallows) or where breeding activities or the risk of shell damage (Fogden and Fogden,1979) limit the time available for foraging. If a particular nutrient required for egg formation is in limited supply, a lipid reserve could provide energy for foraging on a food rich in the deficient nutrient but low in energy content (Jones and Ward,1976). Pre-laying protein storage might be important for species whose diets are generally deficient in protein or in specific amino acids required for egg formation. The size of the labile protein store in avian skeletal muscles, including the pectoral flight muscles (Kendall *et al,* 1973), might act as the proximate regulator of clutch size as well as determining laying date (Jones and Ward,1976). Even when pre-laying reserves appear to have no gross effect on laying, higher reserves might allow females to replace eggs lost through predation, or enhance the survival of young through subtle effects on egg quality. For example, the pre-laying lipid reserve in Herring Gulls might allow the third (final) egg of a clutch to be laid with a higher albumen content at a time when the need to begin incubation decreases the time available for the female to forage (Houston *et al,* 1983); the third egg is commonly smaller than the first two because of its lower albumen content (Parsons,1976).

Species which fast during laying and/or incubation must store reserves to provide both the requirements for egg formation and the daily maintenance requirements of the parent; such species include Eider (Korschgen,1977; Parker and Holm,1990), Arctic-nesting geese (Ankney and MacInnes,1978; Raveling,1979; McLandress and Raveling,1981) and some penguins (Astheimer and Grau,1985). Species which feed between incubation shifts must store sufficient reserves during the period of foraging to sustain them through the next shift and subsequent journey to the feeding area. A parent with more body reserves could spend more time incubating, which can shorten the incubation period giving the advantages of earlier hatching (increasing success in many species), decreased risk of egg predation (Ricklefs,1969) and/or increased hatching success because the eggs are not exposed to low temperatures for too long. The body reserves required to continue a breeding attempt (ie for incubation and rearing) may be more limiting than those required for laying in some species (Martin,1987).

During the rearing period, parent birds may require body reserves to sustain themselves while they devote a much of each day to provisioning young. Adults often weigh less in the rearing period than during incubation (eg Bryant,1975,1979; Freed,1981; Westerterp *et al,* 1982; Nur,1984; Jones,1987; Croll *et al,* 1991; Barrett and Rikardsen,1992), and parents rearing artificially enlarged broods may show increased mass loss compared with those rearing their natural brood sizes (Hussell,1972; Askenmo,1977; Bryant,1979; Nur,1987; Reid,1987; Smith,1988; Martins and Wright,1993), although this may not always be the case (De Steven,1980; Korpimaki,1988; Dijkstra *et al,* 1990). Such mass loss during breeding has been interpreted as indication of adverse physiological 'stress' (Ricklefs,1974) and, therefore, a correlate of subsequent parental survival prospects (Hussell,1972; Askenmo,1977) or as a beneficial process, reducing the power requirements for flight and releasing energy to fuel work (Blem,1976; Freed,1981; Norberg,1981) and comparable to a process of 'adaptive anorexia' (Mrosovsky and Sherry,1980). These 'Breeding Stress' and 'Adaptive Mass Loss' hypotheses are unlikely to be mutually exclusive however, and mass (body reserves) carried during the breeding period probably reflects an optimal trade-off between the costs and benefits of reserve storage. Increases in physiological condition are likely to be advantageous only to some maximum level (Martin,1987), above which the disadvantages of the extra foraging time required to maintain the high reserve levels and the increased energetic and predation costs of the increased wing loading (Blem,1975; Lima,1986) should select against the over-accumulation of reserves. Such selective forces could operate in all stages of the avian annual cycle but the optimal level of reserves carried is likely to vary as more emphasis is placed on different activities at different times.

This study aimed to investigate the influence of parental body condition on the breeding performance of individual pairs of Puffins. Carcass-derived equations enabled the Total Body Reserve Mass (TRM in g, mainly lipids) to be estimated from the live mass and body dimensions of individuals (Chapter 4) and relationships between reserve mass and measures of parental effort, reproductive success and costs were sought for individual pairs under natural conditions and by experimental manipulation of effort.

5.1.2 Predicted relationships between body condition and reproductive performance.

The energetic costs of breeding and reproductive costs must be distinguished if the results of this study are to be clearly interpretable (Clutton-Brock,1984). Here, parental effort was defined as the proportion of total energy expenditure spent on breeding. Whilst expenditure of other nutrients and risk may also be included in parental effort (eg Low,1978; Martin,1987), it was not possible to measure these for Puffins in this study. The proportion of total energy expenditure devoted to reproduction is difficult to measure directly for any bird but is particularly difficult for seabirds; field metabolic rates can be quantified but time budgets are difficult to construct due to the problems of monitoring behaviour away from the breeding colony (see Chapter 6). Total energy expenditure might not reflect parental effort however, if individuals differ in their foraging efficiency. If energy expenditure relects energy income, a bird with high expenditure could be devoting a higher proportion of its income to its offspring but the converse could be true if the higher expenditure were a reflection of higher foraging costs (and lower income). Equally, high expenditure could be balanced by a high energy income but more of the income could be devoted to maintaining the energy balance of the parent rather than to breeding requirements. It was not practical to measure field energy expenditure for a large enough sample of parents in this study (Chapter 6) and, therefore, 3 possible correlates of energy expenditure (body mass change, feeding rates and growth rates of young) were measured as indices of parental effort. While body mass (reserve) change may not necessarily be a correlate of energy expenditure (see Bryant and Tatner,1988), it is a measure of the state of balance between income and expenditure during breeding. The number of feeds delivered to the young each day was a correlate of parental effort, assuming that the contents of loads and the energy required to obtain them did not vary between individuals (see section 5.1.3 below). Growth rates of young were assumed to directly reflect energy invested by parents (Klaassen *et al*, 1992) if environmental factors were constant.

Reproductive cost was defined in this study as a decrease in the residual reproductive value, where the latter represented the future survival and reproductive potential of the parent (Pianka,1976; Bell,1980). Parental effort is generally more easily measured than reproductive cost but it is through the latter that natural selection will operate (Pianka,1976). While energy spent on breeding might correlate with reproductive cost at a gross interspecific level (Stearns,1976; Ricklefs,1977; Bell,1980), the two measures need not be related for individuals within a species (Pianka and Parker,1975) because individuals may differ in 'quality' in terms of their foraging efficiency or access to resources. Reproductive costs may be measured directly by determining effects of breeding on parental survival and subsequent breeding performance (see Chapter 7). In the analyses of the intra-year effects of body condition on reproduction presented in this chapter, parental body reserves remaining at the end of the breeding attempt (ie at fledging) were used to indicate differences in reproductive cost between individuals, assuming these reserves were positively correlated with residual reproductive value (Martin,1987). A decrease in body condition might increase the risk of mortality due to starvation or the susceptibility of an individual to disease or parasitic infection. Survival has been positively correlated with condition or body mass both post-breeding (Bryant,1979; Nur,1984; Reyer,1984) and during the non-breeding season (Marcstrom and Kenward,1981; Haramis *et al*, 1986). Mortality linked to a reduction in condition might occur during stochastic deteriorations in environmental conditions (by depletion of 'insurance' lipid reserves, Lima,1986), or could be linked, by a more deterministic mechanism, to depletion of protein reserves (Newton,1993). The level of body reserves in young at the time of peak mass was used as an index of the reproductive success of individual pairs in this study (the reasons for this are discussed in Chapter 4).

Possible ways in which parental body condition might influence breeding performance in Puffins are now presented. Assume for simplicity that the calendar date of laying does not influence breeding performance and that reproductive success is positively and linearly correlated with parental effort; the validity of these assumptions will be examined later (sections 5.1.4 and 5.1.3 below). An individual with favourable body condition at the start of breeding will have more reserves available to 'spend' on reproduction. Such a bird may chose to devote more energy to reproduction than an individual in poorer condition, increasing its reproductive success for the same cost, or might chose to equal the effort of the bird in poorer condition while retaining more reserves for the end of breeding and hence a higher residual reproductive value. A combination of these two options would also be possible.

This simplistic approach might be justified for a species which relies solely on stored body reserves rather than energy income from foraging to fuel reproduction. Alternatively, reserves available during breeding might reflect the ability of individuals to obtain resources (energy and other nutrients) rather than the total energy reserves available for breeding. The relationship between the ability of an individual to acquire resources and the level of body reserves stored should be determined by the adaptive advantage accruing from reserve storage (section 5.1.1 above). If high reserve levels are advantageous during breeding, an individual with the greatest ability to acquire reserves should have the highest levels (**Figure 5.1a i**). If there are costs attached to reserve carriage, however, an individual with a high ability to obtain resources might maintain lower levels of reserves than an individual which finds resource acquisition difficult, the latter requiring larger insurance reserves to sustain it through periods when it cannot obtain resources (**Figure 5.1a ii**). The existence of an optimal level for body reserves, with deviations above or below proving disadvantageous, might result in optimal reserve levels in individuals with the highest ability to acquire reserves (**Figure 5.1a iii**), with deviations from the optimum reflecting either an inability to acquire enough resources to reach the optimum (individuals with reserve levels below optimal) or the need of some individuals to maintain larger insurance reserves (reserve levels above optimal), regardless of the associated risks. Such an optimal reserve level should be shaped by selection pressures so that it should match the mean reserves carried by individuals within the population at any given time.

For any species not relying solely on stored reserves to fuel reproduction, relationships between body condition and breeding performance will, therefore, depend on the shape of the function relating body reserves to reserve acquisition ability (as described above and in

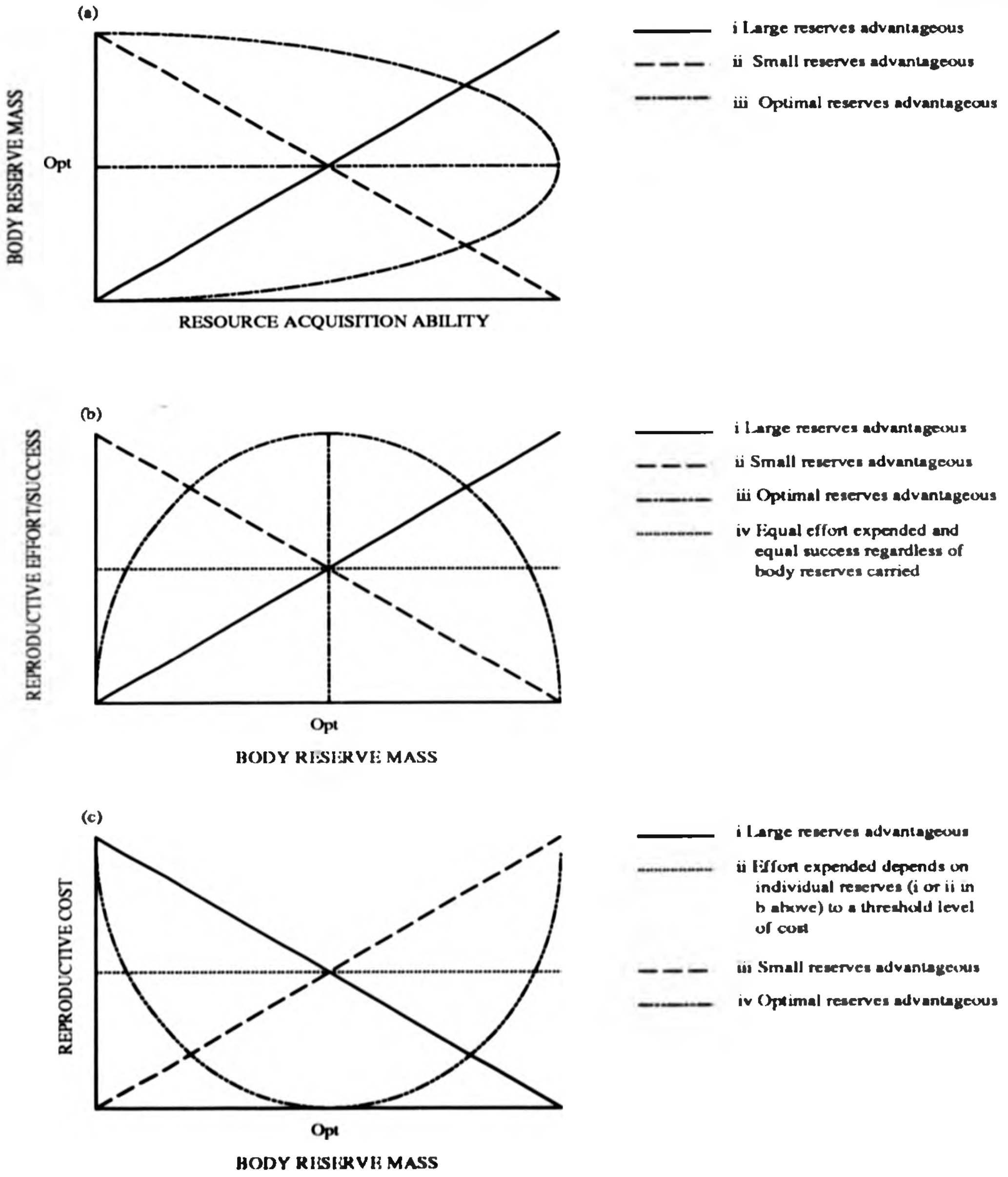


Figure 5.1 Suggested relationships between (a) the quality of individuals (in terms of their foraging efficiency, termed resource acquisition ability) and the mass of body reserves carried (body condition), and between body reserve mass and (b) breeding performance and (c) breeding costs.

Opt indicates the optimal level for body reserves and the options given in each graph are discussed in the text.

Figure 5.1a). If large reserves indicate high acquisition ability, a positive relationship between body condition and reproductive effort and success would be expected (**Figure 5.1b i**), while reproductive costs would either be negatively related to body condition (**Figure 5.1c i**) or equal for all individuals (**Figure 5.1c ii**); the latter would occur if energy was expended on parental effort until a lower limit on residual reproductive value (body condition) was reached. Conversely, a negative relationship between body reserves and breeding performance would be expected (**Figure 5.1b ii**) if a low level of body reserves indicated a high resource acquisition ability, and reproductive costs would either be positively related to reserve levels (**Figure 5.1c iii**) or equal (as described above). An optimal reserve level would be associated with a curvilinear relationship between body reserves and performance (**Figure 5.1b iii**) and the relationship with reproductive cost could be complex but in its simplest form might be the inverse of the function relating body reserves to effort and success (**Figure 5.1c iv**). Alternatively, all individuals might expend an equal amount of effort on reproduction, regardless of differences in their ability to acquire resources, resulting in equal reproductive success (**Figure 5.1b iv**) but differences in costs (**Figure 5.1c i or iii**). High investment by parents in current offspring would be unlikely to be favoured, however, in a long-lived species such as the Puffin because any small reduction in the probability of future survival could reduce the number of subsequent breeding attempts (Curio,1988; Pugsek and Diem,1990). A long-lived individual might allocate energy to current reproductive needs based on some critical threshold (of residual reproductive value) below which it would not allow its condition to fall (eg Monaghan *et al*, 1989,1992). If this were the case, all individuals might pay a similar reproductive cost regardless of their condition at the start of breeding (**Figure 5.1c ii**) but their differing reserve levels would be reflected in their effort and success (**Figure 5.1b i,ii or iii**).

It was not necessary to consider the complex reproductive decisions governing the number of eggs laid per clutch or the number of clutches per breeding season (Drent and Daan,1980; Martin,1987) for Puffins because only a single egg is ever incubated and a single young reared each breeding season (year). An individual in poor condition might, therefore, not breed at all in that breeding season, might abandon the breeding attempt midway through or might produce a young of inferior quality but it does not have the option of reducing clutch size or the number of clutches in a season. When breeding conditions have appeared unfavourable, Puffins have attempted to breed but eggs have failed to hatch (eg Lid,1981) and/or young have died during rearing (Lid,1981; Anker-Nilssen,1987), providing circumstantial evidence for a threshold of time and/or energy commitment to breeding by parents. It is not known what proportion of breeding Puffins return to the colony each year but fail to lay. In this study, it proved difficult to catch individual adults prior to their young hatching, except in 1992. For this reason, it was difficult to assess the influence of body condition on laying and incubation and most of the results presented in this chapter therefore concern parental body condition during the rearing period.

5.1.3 The need for manipulation of parental effort and choice of method.

A correlative approach might fail to reveal relationships between body condition and breeding performance for a number of reasons. First, variation in the quality of individual parents in terms of their foraging efficiency (energy content and/or nutritional quality of food acquired per unit of energy expended) could mask correlations between body condition and performance. For example, an efficient individual might be equally successful or more successful than a less efficient bird after utilizing the same quantity of energy, or undergoing an equal condition change, or making an equal number of feeding visits to its young (with larger or superior quality food loads). The relationship between perceived parental effort and success (assumed in section 5.1.2 above) may not, therefore, be linear or may not exist at all. Equally, the threshold of body condition below which reproductive costs begin to occur might vary considerably between individuals of differing efficiency if more efficient individuals require less insurance reserves. Second, a relationship between parental body condition and success in terms of chick condition could result from concurrent feeding conditions experienced by both parents and young rather than from an effect of parental body condition *per se*. Third, effects of parental body condition on performance might only be detectable when conditions for breeding are unfavourable, just as reproductive costs may only be detectable in 'bad' years (DeSteven,1980; Tuomi *et al*, 1983; Reznick,1985; Bell and Koufopanou,1986).

Experimental manipulation was required in order to overcome these potential problems associated with a correlative approach. For Puffins, parental body condition could not be altered directly by manipulation of food supply, as has been attempted for other species (reviewed by Boulin,1990), because adults would not consume fish left in or near the burrow (pers.obs.). In this study, the effort required by parents to raise their young was experimentally manipulated and the effects of this on adult body condition were assessed. The begging calls of starving young were played to parents when they visited burrows with food for their chicks (after Harris,1983) in an attempt to increase parental effort over the same duration as the normal rearing period. Replacement of young which were close to fledging with younger chicks (eg Hudson,1979; Harris,1983) attempted to increase the usual duration of parental effort. Two other potential methods for increasing effort, twinning (an additional young placed in the burrow with the parent's own young; Nettleship,1972; Corkhill,1973) and the removal of one parent from a pair (Nettleship,1972; Harris,1978), were not attempted because of the potential alterations to the normal family situation such manipulations would have caused. For example, twinned young could interact so as to interfere with normal parent-chick communication (Ricklefs,1987) because they act aggressively towards each other (Corkhill,1973; Harris,1984). In a further manipulation, young were given supplementary food (eg Harris,1978) in an attempt to prevent them actively soliciting food from parents, to reduce the effort required by parents during rearing.

Such manipulations of effort should have allowed body reserve change due to physiological stress to be separated from adaptive mass change according to a pre-determined schedule (eg under photoperiodic and/or hormonal control). Experimental increase or decrease in effort over the normal duration of the rearing period should alter levels of body reserves relative to controls if reserve change is caused by stress but should not do so if changes are pre-programmed. An increase in the length of the rearing period similarly should increase reserve loss if this occurs as a result of stress but not if mass loss is adaptive, occurring at a pre-determined time in the breeding cycle.

5.1.4 Factors other than body condition affecting parental effort and success.

Other factors influencing parental body condition, effort and success were assessed because these could mask relationships between body condition and performance. Weather conditions can influence the short-term energy expenditure of adult seabirds during rearing (Gabrielsen *et al*, 1987,1991; this study, Chapter 6), and the growth of seabird young, both directly by changing the costs of thermoregulation and energy available for growth and indirectly by altering the ability of parents to forage (Dunn,1973,1975; Birkhead,1976; Frank and Becker,1992).

Seasonal variation in weather and/or food supply could be responsible in part for observed effects of laying date or fledging date on seabird breeding success (eg Nisbet and Drury,1972; Nettleship,1972; Perrins *et al*, 1973; Jarvis,1974; Ashcroft,1979; Wanless and Harris,1988; Harris *et al*, 1992). Early-laid Puffin eggs have greater volume (Harris,1980) and produce heavier young at fledging (Nettleship,1972) but this may (Ashcroft,1979; Nettleship,1972) or may not (Harris,1980) result in higher fledging success for early pairs. Early laying would be advantageous if feeding conditions were to deteriorate during the breeding season or if early fledging were to leave more time for fledged young to grow and learn to forage successfully before the onset of winter (Ydenberg,1989). Early laying would also leave more of the season available for replacement laying if an egg was lost. Circumstantial evidence for a seasonal deterioration in feeding conditions comes from the abrupt and synchronized departure of Puffins (both breeders and young birds) from the colony at the end of the breeding season (Harris,1984 and pers.obs.) and from the desertion by parents of very late young up to a week before fledging (pers.obs.) but neither of these phenomena is necessarily caused by a decrease in food availability. If, however, the timing of laying is important for Puffins, the models in section 5.1.2 should be modified. Parents with poor body condition early in the breeding season might breed at the same time but less successfully than those in favourable condition or might delay laying until they have accumulated more reserves. It was important, therefore, to assess relationships between body condition, timing of breeding and reproductive success in this study.

An attempt was made to assess whether intrinsic qualities of parents influenced their body condition, parental effort, success and/or reproductive costs. These qualities included the age of individuals within each pair (Chapter 3) and the proportional contribution of pair members to the rearing effort (Chapter 3). The inability to measure individual quality in terms of foraging efficiency was admitted to be an important limitation in this study. Efficiency may be positively correlated with age and experience (Curio,1983; Nol and Smith,1987) or might be reflected in the relative contributions of pair members to chick feeding. An efficient forager might play a larger or smaller role in feeding the young depending on the relationship between foraging efficiency and the number of feeding trips made. An efficient forager might make more feeding visits than a less efficient bird for the same energy expenditure and deliver more energy to its young, or make fewer feeds than the less efficient bird, delivering the same energy to its young if both birds catch loads of similar quantity and quality. Alternatively, the more efficient forager might also carry back better quality loads. In this study, the proportions of the daylight hours for which individuals were present above ground at the colony were measured as a third possible correlate of foraging efficiency. Individuals which produced high quality young or whose young grew most rapidly might also have spent more time loafing at the colony. If these individuals also made fewer visits to young to deliver food, or a similar number to other less successful individuals, then they would be more efficient foragers (assuming that all individuals were foraging under similar environmental conditions).

5.2 METHODS.

5.2.1 Unmanipulated pairs.

The methods given here are intended as a brief overview and full details are to be found in Chapter 2. In 1990, adults were not colour-ringed until their young hatched and assessment of body condition was only possible during the rearing period, when 31 pairs were followed from hatching to fledging. In 1991 and 1992, some pairs were already colour-ringed at the start of the breeding season, so that it was possible to assess the body condition of some individuals prior to hatching but this was only successful in 1992 because of the problems of capturing adults before their young hatchedin the previous years; 50 and 30 pairs were followed from hatching to fledging in 1991 and 1992 respectively. Individuals involved in manipulations were not included as unmanipulated birds in the following year because of the potential inter-year effects of treatments (Chapter 7).

For each pair followed, an attempt was made to weigh each parent at least once during pre-laying and/or incubation (1991 and 1992 only), once during early chick rearing (preferably before day 10) and again during late rearing (preferably after the young had reached peak mass and had begun to lose mass). For a number of reasons (eg attendance of adults at the colony, effects of weather conditions on the success of captures and use of automatic balances, scheduling of other work), it was impossible to catch parents from different burrows at precisely the same stage of breeding. Each individual was caught at least once during each breeding season to measure body dimensions (Chapter 2, section 2.2.3). Adult condition was expressed as Total Reserve Mass (TRM, g) and was calculated by subtracting a predicted lean wet mass, based on body size, from fresh (live) mass (Chapter 4). Only adults for which both head plus bill and wing length measurements were available were used in TRM analyses because methods for predicting lean wet mass from other body dimensions did not accurately control for structural size (discussed in Chapter 4).

In each breeding season, burrows were first checked when young were 5-15 days old, except for burrows where it was difficult to observe the first delivery of food so that hatching was not detected until later in the rearing period. Young were aged by their bill length (Chapter

2, section 2.5.2) and were checked, weighed and measured regularly until they fledged (Chapter 2, section 2.6). The Maximum Growth Rate (MGR, g) and Peak Mass (PM, g) for each chick were derived from the regular weighings (Chapter 2, section 2.6). The condition of young at peak mass was expressed as Total Residual Peak Mass (TRPM, g) and was calculated by subtracting a predicted peak mass, based on structural size, from fresh peak mass (Chapter 4). The predicted peak mass was based on chick head plus bill length at fledging in 1992 and wing length at fledging in 1991, while it was not possible to control for chick size in 1990. Individual TRPMs could be more satisfactorily compared in 1992 than in 1991 (discussed in Chapter 4).

The numbers of feeds delivered per day to individual young were determined by dawn-to-dusk continuous watches (Chapter 2, section 2.4) on 4 days in 1990, 7 days in 1991 and 16 days (10 days for one sample of burrows and 6 days for a separate area of the colony) in 1992. The total number of feeds delivered to an individual young in a day was termed the Daily Feeding Frequency (DFF, feeds d^{-1}). The Mean Feeding Frequency (MFF, feeds d^{-1}) for each chick was calculated as the mean of the DFFs for all the days on which the burrow was watched during rearing (a minimum of 5 days per burrow, covering much of the rearing period was used in 1991 and 1992). The contribution of each pair member to the delivery of feeds was measured as the number of male versus female feeds observed for each burrow during rearing (Chapter 2, section 2.3.4) and was expressed as a proportion of the total number of feeds delivered by identified individuals to that burrow during rearing (referred to as MALE ROLE and FEMALE ROLE). The mean daily number of feeds delivered by the male and the female of each pair (referred to as MALE FEEDS and FEMALE FEEDS respectively) was calculated as the MFF multiplied by the MALE ROLE or FEMALE ROLE respectively. Quantification of the size, number and species of fish in food loads delivered to individual young was attempted (Chapter 2, section 2.3.4). The proportion of the daylight hours which individuals spent standing above ground at the colony was quantified during general observation sessions in 1991 and 1992 (Chapter 2, section 2.3.7) and is subsequently referred to as male or female Colony Attendance (MALE CA or FEMALE CA, as a proportion of the daylight hours). Abbreviations used in the text are summarized in **Table 5.1**.

The overall hatching success (at Little Hide) was calculated as the percentage of colour-ringed pairs present at the start of the season which subsequently hatched young (ie it included laying success). Overall fledging success was calculated as the percentage of young from colour-ringed pairs that fledged.

Table 5.1 **Reference table for abbreviations used in the text for measures of adult body condition and breeding performance.**

VARIABLE	ABBREVIATION	DEFINITION
ADULT BODY CONDITION		
Total reserve mass	TRM	Total adult body reserves[2] (g)
Initial total reserve mass	ITRM	TRM at the start of chick rearing
Initial residual reserve mass	IRRM	ITRM expressed as a residual[1]
Final total reserve mass	FTRM	TRM at the end of chick rearing
Final residual reserve mass	FRRM	FTRM expressed as a residual[1]
CHICK GROWTH		
Maximum growth rate	MGR	Growth rate days 10-25 of rearing (gd^{-1})
Peak mass	PM	Maximum mass during rearing (g)
Total residual peak mass	TRPM	PM standardized for size[2] (g)
CHICK FEEDING		
Daily feeding frequency	DFF	Number of feeds (feeds d^{-1})
Mean feeding frequency	MFF	Mean of DFF during rearing (feeds d^{-1})
Male feeding frequency	MALE FEEDS	MFF by male
Female feeding frequency	FEMALE FEEDS	MFF by female
Male role in feeding	MALE ROLE	Proportion of feeds delivered by male
Female role in feeding	FEMALE ROLE	Proportion of feeds delivered by female
ADULT COLONY ATTENDANCE		
Male colony attendance	MALE CA	Proportion of daylight hours spent above ground at the colony by males (rearing)
Female colony attendance	FEMALE CA	Proportion of daylight hours spent above ground at the colony by females (rearing)

NOTES.

1 Residuals from the 5-day moving mean of TRM with chick age (see text)
2 For derivation of condition variables see Chapter 4

Results from the 1991 and 1992 breeding seasons are presented here; adult body condition data were insufficient in 1990 and, in addition, chick growth was not satisfactorily monitored (Chapter 2, section 2.6). Data for 1991 and 1992 were analyzed separately because many of the pairs were followed in both years; lumping of the data would, therefore, have violated the assumption of independence in many of the intended statistical analyses. Sufficient data for the analysis of effects of body condition in the pre-hatching period were available only in 1992.

5.2.2 Influences of stage of breeding, calendar date and weather.

Any pattern of variation in parental body condition with stage of breeding within the population as a whole would have important implications for comparisons between the body condition of individuals, if the latter were not all measured at exactly the same stage of breeding (as in this study). It was necessary, therefore, to establish the overall pattern of variation in body condition with stage of breeding so that individual measurements could be standardized for stage of breeding when required. Establishing this overall pattern was not compatible with the main work in the study however, where the aim was to measure the body condition of all individuals as near to the same stage of breeding as possible. This latter aim produced data which were clumped with respect to breeding stage and contained many repeat measurements of the same individuals, and such data were unsuitable for establishing the overall trend in body condition during the breeding season. For this reason, in 1992 adults were removed (for weighing and measuring) from 180 burrows all over the island, during various stages of incubation. Each burrow was checked again soon after the young hatched and the hatching date was determined after measurement of chick bill length. The same burrows were re-checked and parents weighed periodically throughout rearing, to obtain body condition measurements equally covering the period from just after laying to fledging. When analyzing the data collected, each individual was included only once in each analysis. It was not possible to perform feeding watches away from the Little Hide site to provide more data from which to establish how feeding rates varied with chick age; a pattern was established based on the Little Hide data alone.

Seasonal effects on breeding performance were investigated by plotting the parental body condition, effort and success variables against hatching date. In addition, samples of food loads delivered to young were obtained throughout each breeding season by mist-netting (Chapter 2, section 2.7) and food load deliveries were observed (Chapter 2, section 2.3.4) to assess whether there was any seasonal change in chick diet.

Weather variables selected for the analyses are described in Chapter 2 (section 2.8). The 6 variables were not highly intercorrelated and could, therefore, be used in unison in a multiple regression model (Zar,1984). For this reason, an attempt to produce summary weather variables using principle components analysis (Norusis,1988) was found not to be useful (the Kaiser-Meyer-Olkin measure of sampling adequacy was only 0.56 = 'poor' and the first principle component explained only 37% of the total variation). For adult TRM during rearing and chick TRPM, the short-term influence of weather was investigated using multiple regression analysis with suites of weather variables covering (i) the day of condition measurement, (ii) the previous day, (iii) the mean over the previous 3 days and (iv) the mean over the previous 5 days as independent variables. It was not necessary to consider effects of weather on adult TRM in the pre-laying analyses because all individuals were caught around the same calendar date and in similar weather conditions. Longer-term effects of weather on chick growth were addressed, for MGR, by regression with mean weather variables over the same period as the growth rate was measured and, for chick TRPM, using mean weather variables for 25 days prior to the date on which PM was attained for each young.

5.2.3 Analysis techniques.

The relationships sought in the analyses were not necessarily linear (optimal solutions were possible). For this reason, the first step in any of the analyses was to produce a bivariate plot relating the two variables under consideration, which could initially be examined visually. Thus although the significance of results are expressed in terms of a linear correlation or regression coefficient, non-significant relationships were only so defined if the bivariate plot showed no pattern, linear or otherwise. Trends in adult TRM and DFF with breeding stage were not assumed to be linear; they were analysed both by linear regression and by smoothing to reveal non-linear trends by calculation of moving means. Individual adults or young were used only once in each type of analyses to maintain independence of the data. In the moving mean method, the number of days over which means were calculated was the minimum required to reveal a trend and data were plotted using the midpoint of the stages of breeding over which each mean was calculated.

5.2.4 Manipulation of parental effort.

5.2.4.1 Supplementary feeding of young.

Supplementary feeding was carried out at the Little Hide site in both 1990 and 1991. In each year burrows were paired in terms of hatch date and then randomly allocated to either the experimental or the control group, to control for any seasonal trend in breeding performance. The feeding treatment began when chicks were 10-15 days old, when they were capable of thermoregulation, rarely brooded by a parent (Harris,1984), and capable of picking up food dropped on the burrow floor (pers.obs.). The ration of frozen fish (the choice of which is discussed in Chapter 7, section 7.2.1), together with one drop of 'Abidec' multi-vitamin solution (Hudson,1979), was placed near the chick in the nest chamber at around noon each day. Adults do not feed older young but simply rush into burrows, drop the fish on the floor and leave (Harris,1984). Any remaining food was removed the following day before fresh food was added, to keep the burrow as clean as possible. Food was rarely left, however, except in the first few days of the treatment, when parents were still providing much food and the chick may not have located the new supply, and in the 2-3 days prior to fledging (the period of mass recession), when young appear to limit their food intake voluntarily (Harris,1976). The energy intakes of young via supplementary and control diets are compared in Chapter 7 (section 7.2.1).

Thirteen young were supplementary fed in 1990 and 27 in 1991 and these were matched by hatch date to the same number of controls in the two years. Experimental and control burrows were treated in exactly the same manner except for the addition of food. Young were weighed regularly and parental feeding behaviour was monitored by dawn-to-dusk watching, although sample sizes varied because not all burrows could be included in the watches. Capture of parents was attempted prior to the start of the treatment in 1990, and both prior to feeding and when young were close to fledging in 1991. Experimental parents were far harder to catch at the end of the treatment than controls because the former made so few feeding visits to their burrows.

5.2.4.2 Playing of begging calls to parents.

In 1990, small loudspeakers were inserted under the lids to the nest chambers of 10 randomly-selected burrows at Little Hide, when young were 11-25 days old. From 25th June until each chick fledged, the begging call of a hungry chick (on a continuous loop cassette) was played, as often as possible, when a parent entered one of the burrows. The call was played for c.3 minutes or until the adult left again, whichever was the shorter time. Unfortunately it was not possible to man the tape recorder continuously over each daylight period but times of intense feeding activity (notably the early mornings) were covered whenever possible. **Table 5.2** summarizes calls played in each burrow during the 1990 rearing period.

In 1992, the tape recorder equipment was altered so that begging calls could be played continuously to 4 burrows. On 3rd June, when young were 1-9 days old, speakers were inserted into the nest chambers of 4 burrows on Rona. Begging calls were played continuously to all 4 burrows simultaneously during the hours of daylight from dawn on 5th June to dusk on 27th June (when young were 26-34 days old).

In both 1990 and 1992, experimental burrows were matched by hatch date to an equal number of controls; the latter were disturbed to the same extent as the experimental burrows but did not have speakers inserted or calls played. Catching of parents prior to the start of the treatment and at the end of the treatment was attempted for all experimental and control burrows only in 1992. Young were regularly weighed and adult behaviour was monitored during dawn-to-dusk watches.

5.2.4.3 Chick replacements.

At the end of June in 1992, young aged 27-40 days were removed from 4 burrows on Lady's Bed and Ardcarran and were replaced with young 6-16 days younger. Parents were caught and weighed 1-3 days before the exchanges were made and their recapture was attempted just before the foster young fledged. The exchanges were, out of necessity, carried out using a few remaining relatively late-hatched young at a time in the season when time commitments to other areas of this study were reduced. For this reason, it was not possible to arrange ideal control burrows by replacing original young with foster young of the same age. Instead, the body conditions of manipulated parents and their young at fledging were compared to those of unmanipulated birds during the same stage of rearing (see results). Foster chicks were weighed regularly until they fledged but it was not possible to measure the number of feeds they received.

Table 5.2 Begging calls played to 10 experimental Puffin burrows in 1990.

Burrow number	Total n calls	Duration (chick age)	Temporal distribution Chick age (d)				Diurnal distribution (h)		
			10-20	21-30	31-40	41-50	0500-1100	1101-1700	1701-2300
87	27	12-35	12	10	5	0	22	2	3
149	28	24-47	0	12	12	4	20	4	4
144	32	17-40	8	17	7	-	20	3	9
104	[1]0	-----	--	--	--	-	--	-	-
102	[1]0	-----	--	--	--	-	--	-	-
10	16	23-36	0	5	11	0	12	2	2
14	14	25-45	0	2	9	3	12	1	1
54	22	19-40	3	9	10	0	20	2	0
56	[2]16	11-36	[2]9	3	4	0	[2]16	0	0
64	3	[3]15-17	3	0	0	0	3	0	0

NOTES.

1 Young deserted before call playing began.
2 Plus one extended playing session of 1.5h.
3 Young predated at age of 17 days.

5.3 RESULTS.

5.3.1 Change in adult body reserves with stage of breeding and time of day.

Adult total reserve mass (TRM) data covering the whole breeding season were only available in 1992 (**Table 5.3**) and these suggested that TRM was higher during incubation (means of 50-64g) than during rearing (means of 25-44g). In this sample of adults from all over the island, there was a significant effect of breeding stage on TRM but no differences in TRM between the sexes (2-way ANOVA : main effect stage $F_{4,173}$=9.136 p<.0001; main effect sex $F_{1,173}$=1.814 p>.1). For males, TRM during early and late incubation differed significantly from that during late rearing, while for females, TRM during only late incubation and late rearing differed significantly (Tukey multiple comparisons p<.05). There was a significant decrease in the TRM of both males and females during the whole breeding season (laying to fledging) in 1992 (**Table 5.4**) but not during incubation or rearing when the stages were analyzed separately. There was a significant decline, however, in the TRM of Little Hide males during rearing in 1991 and a marginally significant decline for females (**Table 5.4**). Individual females weighed in both early and late rearing had significantly less reserves in late rearing in both 1991 and 1992 (**Table 5.5**) but male reserves were only lower during late rearing in 1991.

Differences in adult TRM between the incubation and rearing periods were further revealed when data for the whole breeding season (from burrows all over the island in 1992) were smoothed using a 10-day moving mean (**Figure 5.2**). Both sexes carried high TRM during incubation. Male TRM decreased rapidly from hatching for the first 15 days of rearing and then increased, while the decrease in female TRM continued until day 30, with a temporary increase between days 15 and 24.

Five-day moving means for the rearing period only in 1992 showed a similar pattern of TRM change for both males and females (**Figure 5.3**) with two low points in TRM, the first between days 10 and 15 of rearing and the second between days 25 and 35. Both sexes began rearing with similar TRM levels (c.55g of reserve). Male TRM reached a minimum level for rearing (5g) during the first decline, while female TRM was minimal (11g) during the second decline (on day 30 of rearing).

There were fewer data for the rearing period in 1991 because they were only available for

Table 5.3 **Total reserve mass (TRM) of adult Puffins from the Isle of May (excluding Little Hide) in 1992.**

BREEDING STAGE	♂♂ TRM (g)					♀♀ TRM (g)				
	Mean	+/-	s.d	n		Mean	+/-	s.d	n	
PRE-LAYING (before day -41)	63.6	+/-	12.1	2					0	
EARLY INCUBATION (days -42 to -21)	51.7	+/-	20.4	21	a	49.8	+/-	24.5	9	
LATE INCUBATION (days -20 to -1)	50.7	+/-	26.5	27	b	56.8	+/-	25.8	20	a
EARLY REARING (days 0 to 25)	33.7	+/-	27.3	37		44.4	+/-	22.6	26	
LATE REARING (after day 26)	25.4	+/-	23.3	26	a,b	24.6	+/-	21.3	14	a

NOTE - For the sexes separately, stages coded with the same letter differed significantly (one-way ANOVA of TRM by stage, with Tukey multiple comparisons, $p<.05$)

Table 5.4 **Linear regression statistics showing the effect of breeding stage on the total reserve mass (TRM) of adult Puffins in 1991 and 1992.**

YEAR	BREEDING STAGE	SEX	I	b	s.e	r^2	p	n
1992	WHOLE SEASON	♂♂	42.18	-0.427	24.42	.179	<.0001	113
	(all island data)	♀♀	46.52	-0.343	24.33	.104	<.005	69
1992	INCUBATION	♂♂					>.2	75
	(all island data)	♀♀					>.3	45
1992	REARING	♂♂					>.1	66
	(all island data)	♀♀					>.4	41
1991	REARING	♂♂	71.10	-1.059	22.77	.320	<.0005	35
	(Little Hide data)	♀♀	46.90	-0.486	21.57	.110	<.1	27

Table 5.5 **Comparison of the total reserve mass (TRM) of individual adult Puffins weighed twice during rearing in 1991 and 1992.**

		1991 TRM (g)				1992 TRM (g)			
		Mean (s.d)	T	p	n	Mean (s.d)	T	p	n
♂♂	EARLY REARING	64.3 (23.4)	3.45	<.05	7	38.2 (23.2)	1.02	>.3	17
	LATE REARING	38.3 (12.9)				34.0 (17.1)			
♀♀	EARLY REARING	44.3 (16.3)	3.83	<.005	10	30.9 (12.9)	3.02	<.01	13
	LATE REARING	31.5 (18.3)				20.4 (13.5)			

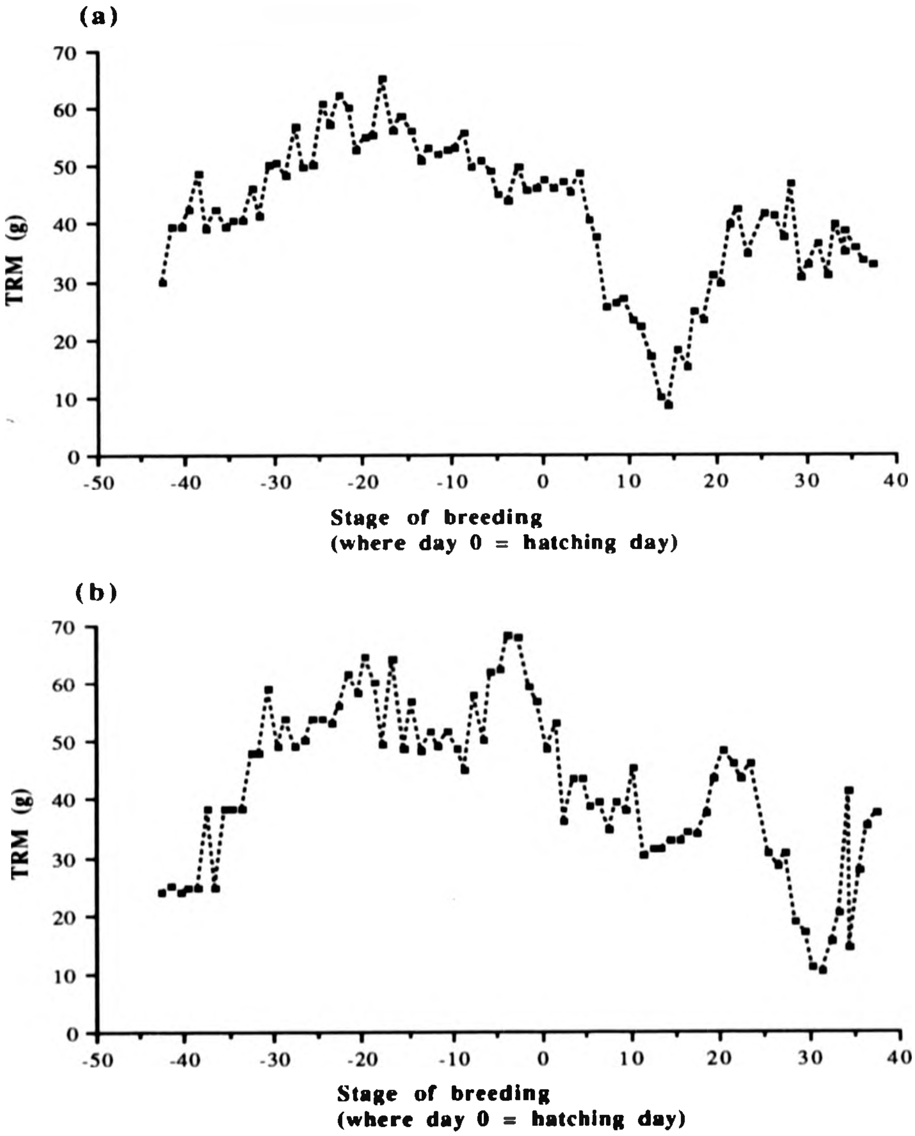


Figure 5.2 **Change in the total reserve mass (TRM) of adult (a) male and (b) female Puffins from laying to chick fledging in 1992 (all island data excluding Little Hide birds).**

Each point represents a 10-day moving mean plotted at the mid-point (see text).

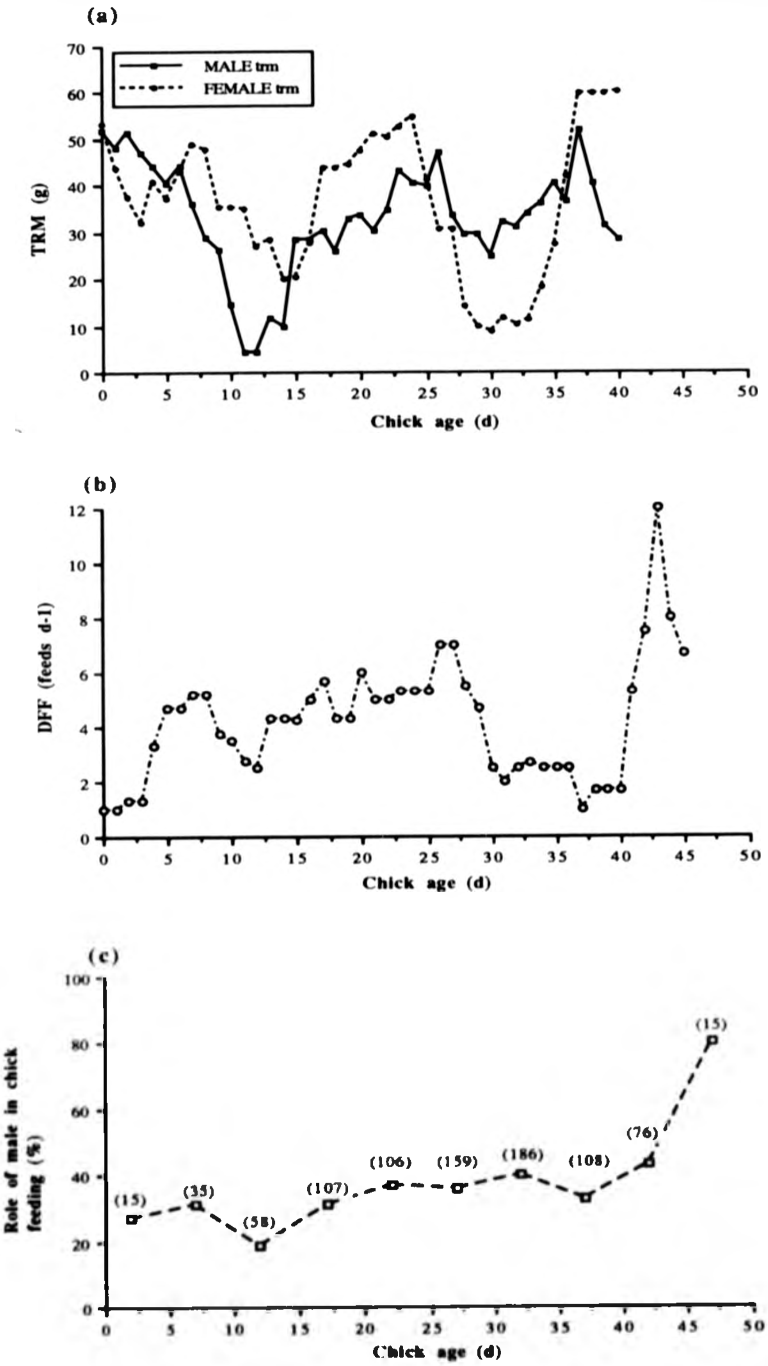


Figure 5.3 Variation with chick age in (a) the total reserve mass (TRM) of adult Puffins, (b) the daily number of feeds delivered to young (DFF) and (c) the proportion of feeds delivered by males in 1992.

(a) and (b) 5-day moving means plotted at mid-points (see text).
(c) total number of food deliveries shown in parentheses.

Little Hide birds (no data were available for females during days 17-23 of rearing). Females showed a more regular decline in TRM in 1991 than in 1992 (**Figure 5.4**), while males maintained higher TRM until c.day 40 of rearing in 1991 than in 1992, after which TRM levels were similar in the two years. In 1992, almost all Little Hide adults were weighed in the first 10 days of rearing and again when chicks were close to fledging; it was not possible to calculate moving means from these data to compare with those for adults caught all over the island and the latter birds were therefore assumed to be representative of all individuals (including those at Little Hide) in terms of their TRM during rearing.

Individual adults at the Little Hide site, whose TRM and breeding performance were to be compared, were not all weighed at exactly the same stages of rearing and it was necessary to control for this source of variation in TRM based on the above results. In 1991, TRM at the start of rearing (Initial Total Reserve Mass, ITRM, g) was calculated by standardizing any mass measurement in the first 25 days of rearing to day 0 (hatching day) using the appropriate regression coefficient for each sex (from **Table 5.4**). In 1992, when there was no significant trend in TRM with stage of rearing, any mass measured in the first 25 days of rearing was assumed to represent ITRM. For both years, all analyses using ITRM were also performed after expressing TRMs measured in the first 25 days of rearing as residuals, using the 5-day moving mean for each sex in each year as a prediction of TRM on any given day of rearing. This Initial Residual Reserve Mass (IRRM, g) was positive if an individual had more reserves than predicted for that stage of rearing at which it was measured and negative if the individual had less reserves than predicted. In 1992, adult TRM at the end of rearing (Final Total Reserve Mass, FTRM, g) was expressed both as any TRM measured after day 25 of rearing and as a final residual reserve mass (FRRM, g), using the appropriate 5-day moving mean as the predicted TRM for each chick age. There was no linear trend in TRM with stage of rearing for either sex in 1992. In 1991, FTRM was expressed as the residual of the linear relationship for the appropriate sex in **Table 5.4**, as the residual of the appropriate 5-day moving mean (FRRM, g) and, for males only, as a residual (FRRM2) from a significant linear relationship between late rearing TRM and chick age (**Figure 5.5**). The regression coefficient for the latter relationship indicated a greater rate of TRM loss for males during late rearing than that for TRM change over the entire rearing period (**Table 5.4**). TRMs of individuals weighed before laying in 1992 were not adjusted for breeding stage but only individuals weighed before day -43 of breeding (assumed to be the longest usual incubation period, Harris,1984) were used in pre-laying analyses.

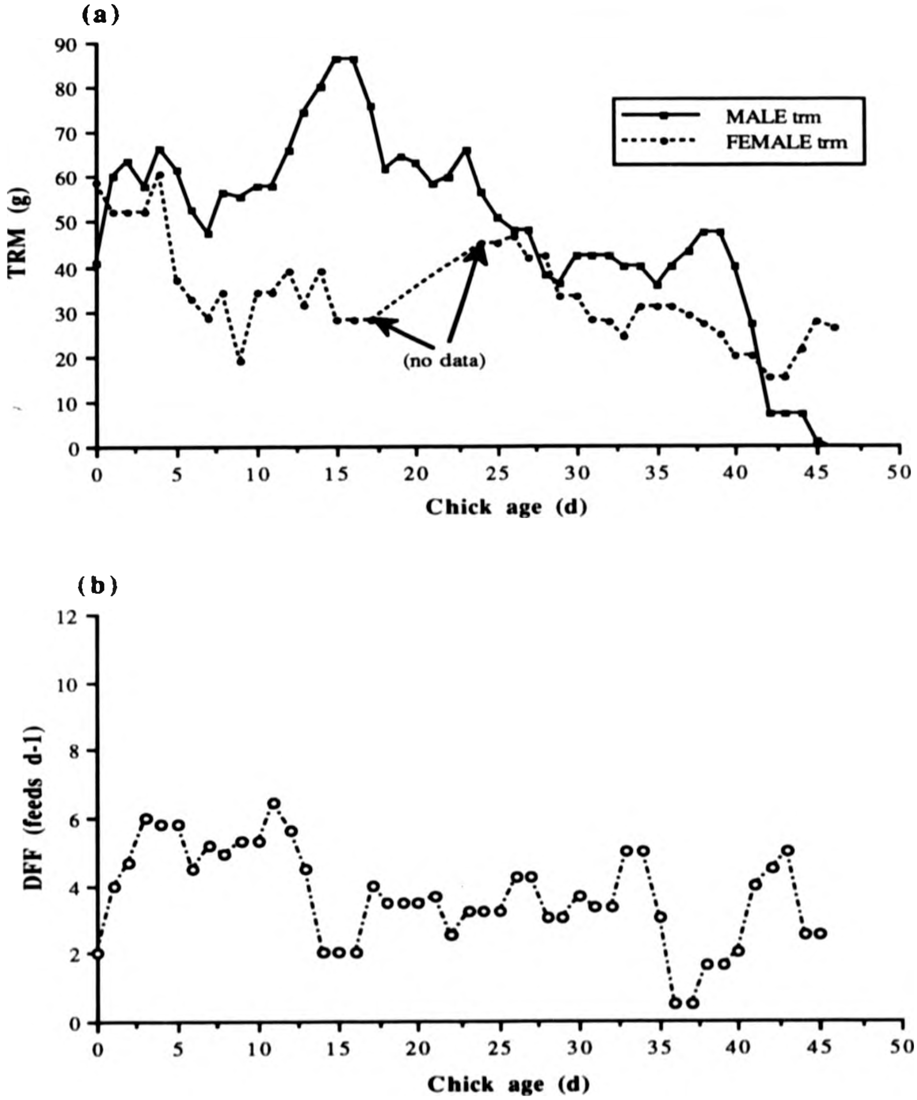


Figure 5.4 Variation with chick age in (a) the total reserve mass (TRM) of adult Puffins and (b) the daily number of feeds delivered to young (DFF) in 1991.

Each point represents a 5-day moving mean plotted at the mid-point (see text).

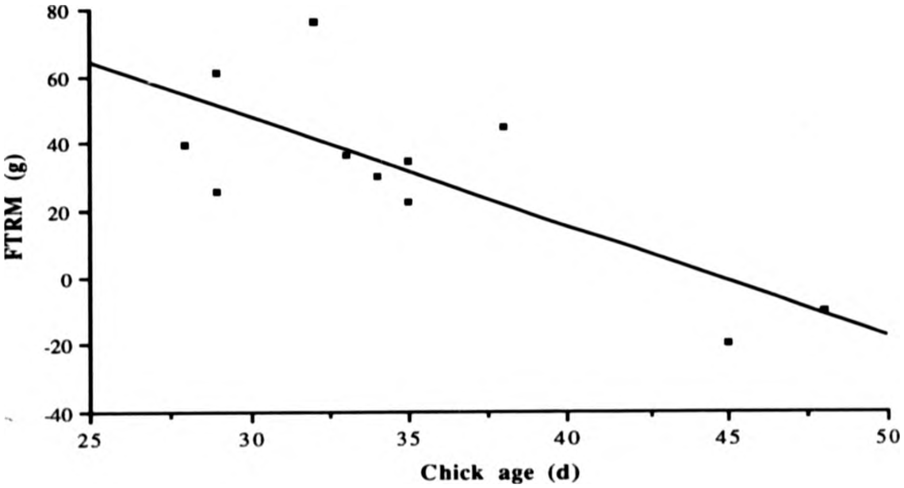


Figure 5.5 Relationship between the final total reserve mass (FTRM) of adult male Puffins in late rearing and stage of rearing in 1991. (Fitted regression line $y = 146.72 - 3.30x$ $r^2=.584$, $p<.01$, $n=11$).

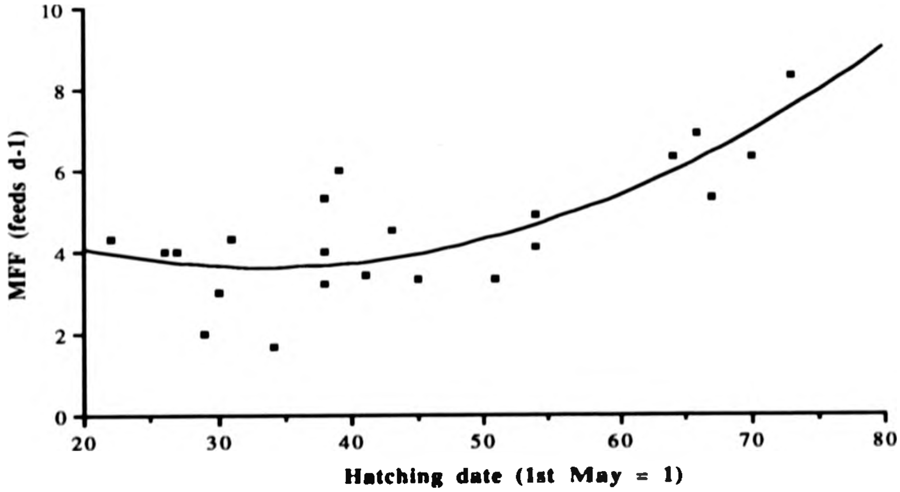


Figure 5.6 Variation in the mean daily number of feeds (MFF) delivered to Puffin young during the rearing period with hatching date in 1992. (Fitted polynomial $y = 6.45 - .170x + .003x^2$ $r^2=.603$, $p<.001$, $n=22$).

Adult TRM was not related to time of day during any breeding stage (in bivariate correlations or when time of day was included as an independent variable in the regression models in **Table 5.4**).

5.3.2 Adult pre-laying reserves, timing of breeding and success.

Data were only available in 1992. Pre-laying TRM was not correlated with hatch date for either sex or the sexes combined (Spearman correlation p>.2, n=12 males,10 females). There was no difference, for either sex, in the pre-laying TRM of individuals which subsequently hatched young and those which did not (**Table 5.6**). Similarly, their was no effect of pre-laying TRM on hatching success when the same data were subjected to logistic regression analysis (TRM logistic regression p>.4 for each sex and sexes combined, n as in **Table 5.6**).

5.3.3 Adult reserves during rearing and breeding performance : inter-year differences.

Table 5.7 shows a comparison of adult condition and breeding variables between 1991 and 1992. Both male and female TRM were significantly higher in early rearing in 1991 than in 1992. For females, TRM during late rearing was also higher in 1991 than in 1992 and the rate of reserve change during rearing did not differ between years. For males, TRM during late rearing was similar in the two years and the rate of reserve loss during rearing was significantly greater in 1991. Individual females which were weighed in both early and late rearing lost a significant mass of reserves in both years but males only lost reserves in 1991 (**Table 5.5**). Adult TRM fluctuated more with stage of rearing in 1992 than in 1991 (**Figures 5.3 and 5.4**) and the same was true for DFF with stage of rearing (section 5.3.4.5 below).

The median hatching date was significantly (c.1 week) earlier and hatching success significantly higher (over 2.5 times that in 1992) in 1991. MFF did not differ significantly between years but there was a suggestion that MFF increased (section 5.3.4.2 below) and chick diet quality decreased (section 5.3.4.2) late in the season in 1992. Chick MGR, peak mass and fledging mass were all higher in 1991 than in 1992 (although the difference was only significant for fledging mass), while fledging success was significantly higher (1.4 times that in 1991) in 1992. Combining the figures for hatching and fledging success, overall success (young fledged per pair at Little Hide) was 0.57 in 1991 and 0.30 in 1992.

Table 5.6 **Comparison of the total reserve mass (TRM) during pre-laying of adult Puffins which hatched eggs at Little Hide in 1992 and those which did not.**

	'HATCHERS'			'NON-HATCHERS'			T-TEST	
SEX	Mean	(s.d)	n	Mean	(s.d)	n	T	p
♂♂	50.3	(20.2)	5	58.6	(23.8)	16	0.69	>.5
♀♀	48.9	(22.9)	5	55.4	(55.4)	15	0.43	>.6
ALL	49.6	(20.4)	10	57.0	(27.3)	31	0.79	>.4

Table 5.7 Comparison of adult total reserve mass (TRM) during rearing and breeding variables of Little Hide Puffins in 1991 and 1992.

VARIABLE - mean +/- s.d unless otherwise stated (n)		1991	1992	TEST		COMPARISON
♂ TRM (g)	Early rearing (days 0-25)	51.2 +/- 28.1 (13)	32.7 +/- 25.2 (27)	T=2.10	p<.05	1991 > 1992
	Late rearing (after day 25)	31.1 +/- 27.2 (11)	33.7 +/- 16.6 (18)	T=0.32	p>.7	NS
	Rate of change (d^{-1})	-1.08 +/- 0.61 (8)	-0.16 +/- 0.73 (17)	T=3.05	p<.01	1991 > 1992
	Pattern of change with chick age	OPPOSING TRENDS IN 1991 AND 1992 (Figures 5.3 and 5.4)				
♀ TRM (g)	Early rearing (days 0-25)	39.2 +/- 26.7 (15)	22.0 +/- 20.8 (26)	T=2.30	p<.05	1991 > 1992
	Late rearing (after day 25)	29.8 +/- 17.8 (11)	11.8 +/- 19.7 (20)	T=2.52	p<.05	1991 > 1992
	Rate of change (d^{-1})	-0.63 +/- 1.15 (10)	-0.41 +/- 0.60 (18)	T=0.55	p>.5	NS
	Pattern of change with chick age	SIMILAR BUT LESS VARIABLE IN 1991 THAN IN 1992 (Figures 5.3 and 5.4)				
HATCHING	Median date	31 (32)	39 (29)	U=238.5	p<.005	1992 > 1991
	Range of dates	13/5 - 24/6	22/5 - 12/7			1992 > 1991
	Hatching success	89% (19)	34% (41)	χ^2=15.92	p<.001	1991 > 1992
FEEDING YOUNG	Mean feeding frequency (feeds d^{-1})	4.12 +/- 1.15 (17)	4.47 +/- 1.60 (22)	T=0.81	p>.4	NS
	Pattern with chick age	LESS VARIABLE IN 1991 THAN IN 1992 (Figures 5.3 and 5.4)				
	Chick diet	SPECIES OTHER THAN SANDEELS MORE IMPORTANT IN 1992 THAN IN 1991 (Tables 5.8 and 5.9)				
GROWTH OF YOUNG	MGR (gd^{-1})	9.90 +/- 2.70 (26)	8.38 +/- 4.08 (22)	T=1.50	p>.1	NS
	Peak mass (g)	302.3 +/- 39.4 (31)	286.7 +/- 45.7 (29)	T=1.42	p>.1	NS
	Age at peak mass (d)	36.6 +/- 8.7 (31)	35.5 +/- 4.8 (29)	T=0.63	p>.5	NS
	Fledging mass (g)	260.0 +/- 25.9 (30)	234.1 +/- 40.9 (27)	T=2.82	p<.01	1991 > 1992
	Fledging age (d)	43.4 +/- 5.4 (31)	42.9 +/- 3.8 (27)	T=0.43	p>.6	NS
	Fledging success	64% (45)	88% (32)	χ^2=4.04	p<.05	1992 > 1991
OVERALL SUCCESS (hatching and fledging success combined)		57%	30%			1991 > 1992

5.3.4 Factors affecting adult TRM and measures of effort and success.

5.3.4.1 Weather conditions.

In neither year did short-term variation in weather explain a significant proportion of variation in adult TRM during rearing (multiple regression p always >.05, n 1991 males=14 females=16 1992 males=66 females=41). DFF was not influenced by the weather on dawn-to-dusk watching days in either year (multiple regression p>.05, n 1991=7 days 1992=16 days).

In 1991, the proportion of time that the wind was onshore during the measurement period explained 20% of variation in chick MGR (MGR = 13.36 - .121 mean % onshore wind; F=7.24, p<.02, n=26) but there was no influence of weather on MGR in 1992 (multiple regression p>.05, n=22). In 1991, cloud cover and temperature on the day before weighing together explained 22% of variation in chick TRPM (TRPM = 184.10 - 14.901 cloud cover - 6.646 temperature; F=5.05, p<.02, n=30) but weather did not influence chick TRPM in 1992 (multiple regression p>.05, n=27). Neither adult TRM nor any measure of breeding effort or success are standardized for weather in the analyses which follow.

5.3.4.2 Timing of breeding (seasonal effects).

Neither bivariate plots nor multiple regression analyses (with adult TRM as the dependent variable and chick age and hatching date as independent variables) showed any influence of timing of breeding on adult TRM during rearing (p always >.05, n as for analyses for stage of rearing in **Table 5.4**).

There was no relationship between either MFF (n=18), chick MGR (n=26) or chick TRPM (n=30) and hatching date in 1991 (Spearman correlation p>.05). In 1992, there was a significant increase in MFF as the season progressed (**Figure 5.6**), especially for young hatched after the end of June and hatching date explained 60% of the variation in MFF. Chick MGR decreased with increase in hatching date for young hatched before the third week of June but increased again with hatching date for later hatched young (**Figure 5.7**). Chick TRPM showed no relationship with hatching date in 1992, however (**Figure 5.8**). In the analyses which follow, it was not necessary to correct the 1991 breeding variables for hatching date but for the 1992 data, analyses including MFF and chick MGR were also performed after the values for these variables were expressed as residuals (observed minus

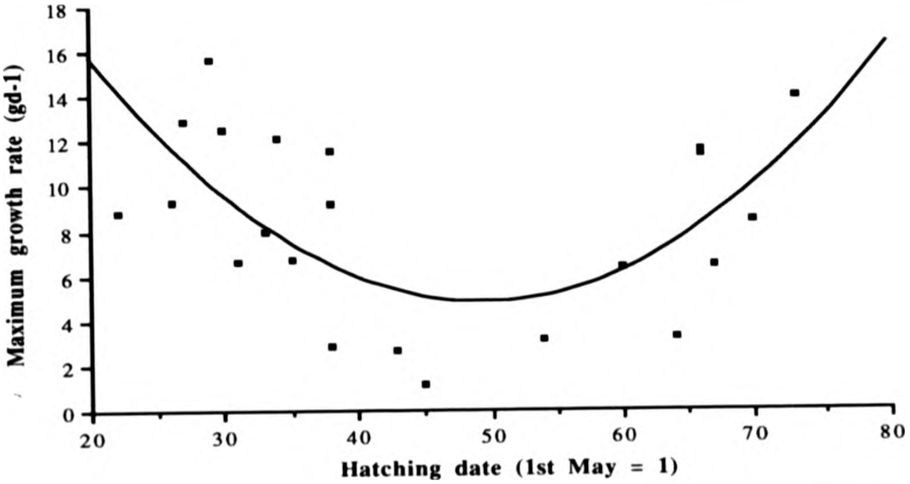


Figure 5.7 Variation in the growth rates of Puffin young with hatching date in 1992 (Maximum Growth Rate defined in text).
(Fitted polynomial $y = 35.47 - 1.238x + .012x^2$ $r^2 = .348$, $p < .001$, $n = 22$).

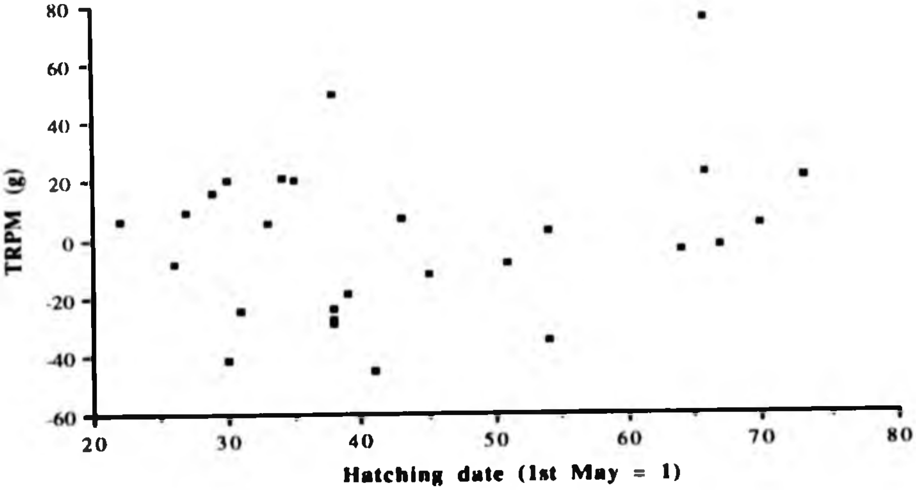


Figure 5.8 Variation in the total residual peak mass (TRPM) of Puffin young with hatching date in 1992.
(Both linear regression and 2° polynomial $p > .1$, $n = 27$).

predicted values) from the relationships in **Figures 5.6 and 5.7** respectively.

Data on the size and composition of food loads delivered to young on the Isle of May in 1991 and 1992 are summarized in **Tables 5.8 and 5.9** respectively. A detailed analysis of changes during the two breeding seasons was not intended but the data are presented to illustrate broad differences in diet between years and major changes during each year. There were no trends in mean load mass, number of fish per load or mean fish length within the two seasons and the means of these variables for each season did not differ significantly between the two years (t-tests p>.05). In 1991, sandeels dominated food loads, constituting 89% of individual food items and 74% of single-species food loads; there was little variation in the species composition of food loads during the season. In 1992, sandeels dominated in food loads obtained by mist-netting (constituting 82% of food items and 62% of single-species loads) but Saithe were also important early in the season and Rockling appeared in the diet at the end of the season, although few loads were collected after 15th July. Observational data for 1992 supported the importance of gadoids (presumably mainly Saithe) in chick diets early in the season, suggested a contribution of clupeids (probably Herring) in mid-season, and showed a large contribution of Rockling after 24th July (51% of observed food loads after that date were composed of Rockling). It was not known whether the size of food loads altered at the end of the 1992 season (ie after 24th July). It was not possible to record the content of food loads delivered to individual burrows on a large enough scale to allow interburrow comparisons of chick diet.

5.3.4.3 Age of parents.

There were no relationships between the age of pairs and either hatching date, MFF, chick MGR or chick TRPM in either 1991 or 1992 (Spearman correlations p>.05, n=13-21). There was no relationship between the age of an individual (of either sex) and ITRM or FTRM (Spearman correlations p>.05, n=4-14), or between age and the rate of adult reserve change during rearing (Spearman correlations p>.05, n=8/9), for which sufficient data were only available in 1992.

Table 5.8 Variation with date in season of food loads (obtained by mist-netting) delivered to Puffin young on the Isle of May in 1991 (no loads were obtained between 28th June and 4th July).

VARIABLE - mean +/- s.d (n)	6th June - 12th June	12th June - 20th June	21st June - 27th June	5th July - 18th July	WHOLE SEASON
LOAD MASS (g)	7.2 +/- 4.4 (18)	9.1 +/- 4.2 (32)	8.1 +/- 3.5 (58)	8.4 +/- 3.5 (17)	8.3 +/- 3.8 (125)
FISH PER LOAD (n)	7.8 +/- 5.3 (18)	5.7 +/- 4.0 (32)	8.9 +/- 5.0 (58)	6.8 +/- 4.1 (17)	7.6 +/- 4.7 (125)
LENGTH SANDEELS (mm)	65.1 +/- 15.1 (126)	77.4 +/- 23.2 (158)	67.8 +/- 14.6 (398)	71.7 +/- 21.2 (102)	69.8 +/- 17.3 (784)
LENGTH OTHER SPECIES (mm)	59.1 +/- 7.3 (17)	55.7 +/- 7.3 (24)	56.1 +/- 10.3 (52)	46.6 +/- 19.3 (7)	55.8 +/- 9.7 (100)
LOADS CONTAINING SPECIES OTHER THAN SANDEELS (%)	33 (18)	31 (32)	22 (58)	24 (17)	26 (125)
SANDEELS (% of n fish)	88 (143)	86 (182)	88 (450)	93 (109)	88 (884)
OTHER SPECIES (% of fish by number)	Saithe 12	Saithe 7 Herring 7	Herring 9 Saithe 2 Cod 1 Squid <1	Rockling 5 Cod 1 Pollock 1	Herring 6 Saithe 4 Rockling 1 Cod 1 Pollock <1 Squid <1

Table 5.9 Variation with date in season in food loads delivered to Puffin young on the Isle of May in 1992 (a) obtained by mist-netting (b) from observations at Little Hide.

(a)

VARIABLE - mean +/- s.d (n)	3rd June	10th June	15th June	23rd June	7th July	15th July	After 20th July	WHOLE SEASON
LOAD MASS (g)	6.0+/-4.0 (21)	8.4+/-4.7 (20)	9.0+/-5.3 (22)	8.5+/-3.5 (18)	6.6+/-3.1 (20)	10.9+/-4.5 (20)	6.0+/-4.1 (5)	8.1+/-4.2 (126)
FISH PER LOAD (n)	5.7+/-3.3 (21)	5.7+/-5.0 (20)	7.4+/-6.1 (22)	7.6+/-4.9 (18)	5.2+/-3.3 (20)	8.7+/-5.8 (20)	8.6+/-5.4 (5)	6.8+/-4.8 (126)
LENGTH SANDEELS (mm)	72.3+/-20.7 (67)	67.4+/-32.5 (73)	69.8+/-23.5 (145)	69.2+/-18.6 (135)	73.5+/-21.7 (87)	72.4+/-21.2 (157)	119 (1)	70.8+/-22.4 (665)
LENGTH OTHER SPECIES (mm)	52.7+/-5.2 (43)	59.9+/-11.5 (34)	53.7+/-4.0 (3)	55.5+/-6.4 (2)	36.4+/-5.8 (17)	36.5+/-3.9 (16)	48.7+/-5.5 (34)	49.9+/-6.6 (149)
LOADS CONTAINING SPECIES OTHER THAN SANDEELS (%)	57 (21)	70 (20)	14 (22)	11 (18)	35 (20)	25 (20)	100 (5)	38 (126)
SANDEELS (% of n fish)	61 (110)	68 (107)	98 (148)	99 (137)	84 (104)	91 (173)	3 (35)	82 (814)
OTHER SPECIES (% of fish by number)	Saithe 39	Saithe 25 Herring 7	Saithe 2	Saithe 1	Rockling 16	Rockling 9	Rockling 97	Saithe 9 Rockling 8 Herring 1

(b)

	Pre- 12th June	12th - 25th June	26th June-9th July	10th - 23rd July	After 23rd July	WHOLE SEASON
(n loads)	(41)	(50)	(50)	(164)	(210)	(506)
COMPOSITION (% of loads)	Gadoid 54 Sandeel 46	Sandeel 66 Gadoid 26 Clupeid 8	Sandeel 76 Clupeid 14 Gadoid 6 Rockling 4	Sandeel 72 Clupeid 23 Rockling 5	Rockling 51 Clupeid 27 Sandeel 22	Sandeel 50 Rockling 22 Clupeid 20 Gadoid 8

5.3.4.4 Role of the sexes in the provisioning of young.

The ITRM of individual parents (of either sex) did not influence the proportional role played by those individuals in delivering chick feeds in 1991 or 1992, nor were the roles of individuals related to the rate of change in their body reserves during rearing (Spearman correlations p>.05, n=8-24). In 1992, there was a significant negative correlation between MALE ROLE and MFF (**Figure 5.9b**) but no such relationship was apparent in 1991 (**Figure 5.9a**). There was a significant negative correlation between MALE ROLE and chick MGR in 1991 (**Figure 5.10a**) but not in 1992 (**Figure 5.10b**). Chick TRPM was not correlated with MALE ROLE in either year (Spearman correlation p>.05, 1991 n=20 1992 n=23). There was no relationship between MALE ROLE and the age of the pair in either year (Spearman correlation p>.05, 1991 n=18 1992 n=18).

There was no evidence that the reserve mass or rate of reserve change of one pair member influenced that of the other pair member, as there was no correlation in either year between the ITRM, FTRM or rate of reserve change of members within a pair (Spearman/Pearson correlations p>.05, 1991 n=4-11 1992 n=15-26). Equally, there was no relationship between the MALE CA and FEMALE CA of pair members during rearing in either year (Spearman correlation p>.05, 1991 n=6 1992 n=27).

5.3.4.5 Variation in daily feeding frequency (DFF) with stage of rearing.

There was no linear trend in DFF with chick age in either 1991 or 1992 (Pearson correlation p>.05, 1991 n=33 1992 n=33). When the same data were smoothed using a 5-day moving mean (**Figures 5.3 and 5.4**), the pattern of variation with stage of rearing in 1991 and 1992 was similar in that two periods of decreased DFF occurred, the first between days 10 and 15 of rearing and the second with the minimum level at c.day 35. DFF varied less in 1991 than in 1992, however, especially in the later stages of rearing; in 1991, DFF showed a temporary decrease between days 34 and 40 and then recovered, while in 1992, DFF decreased rapidly a week earlier than in 1991 (after day 27), recovered by day 43, and reached a peak for the season of 12 feeds d^{-1} on day 44 (the highest 5-day mean DFF in 1991 was 6.5 feeds d^{-1} on day 11 of rearing). Such variations in DFF with chick age were also evident when DFFs were plotted for individual 1992 young (examples in **Figure 5.11**).

In the analyses which follow, those involving MFF were also undertaken after calculating a

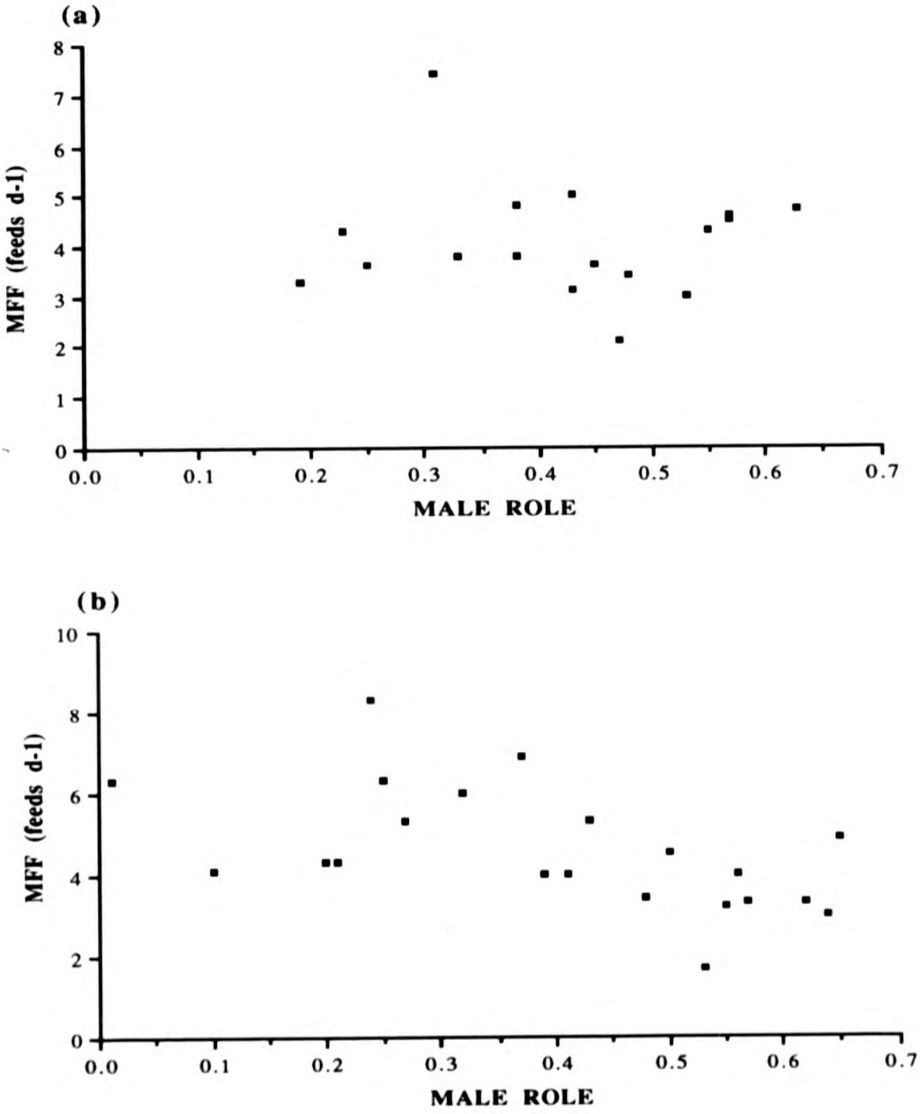
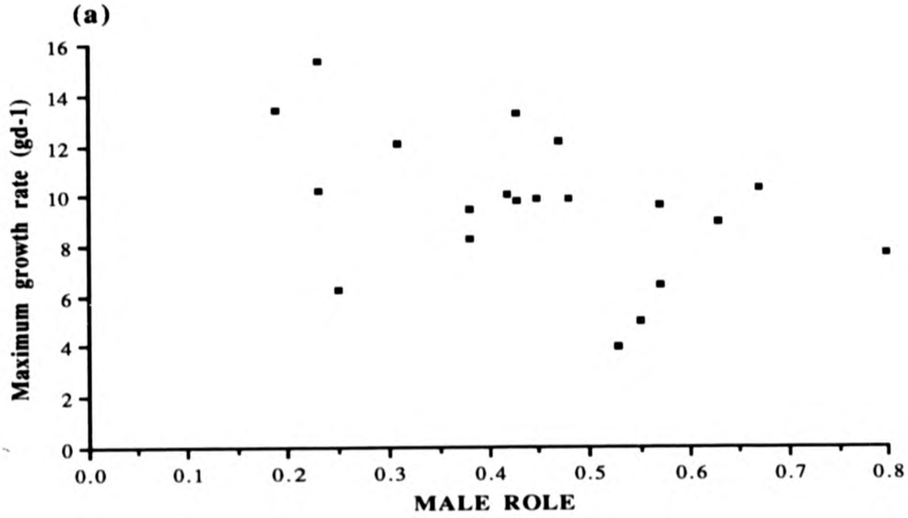


Figure 5.9 Relationship between the mean daily number of feeds (MFF) delivered to Puffin young during rearing and the proportion of feeds delivered by the male (MALE ROLE) in (a) 1991 and (b) 1992.

Spearman correlation	1991 r=.066	p>.4	n=17
	1992 r=-.609	p<.005	n=21



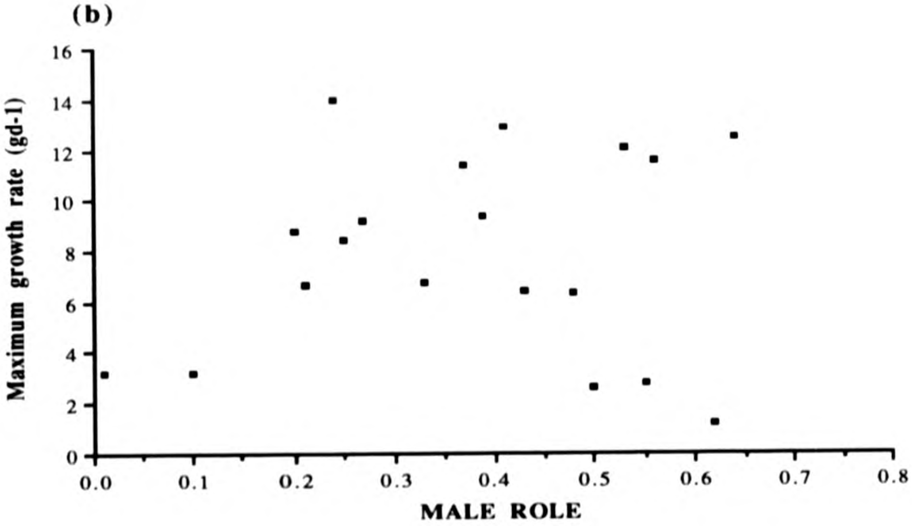


Figure 5.10 Relationship between the maximum growth rates (MGRs) of Puffin young and the proportion of feeds delivered by the male (MALE ROLE) in (a) 1991 and (b) 1992.

Spearman correlation	1991 r=-.451	p<.05	n=20
	1992 r=.030	p>.4	n=19

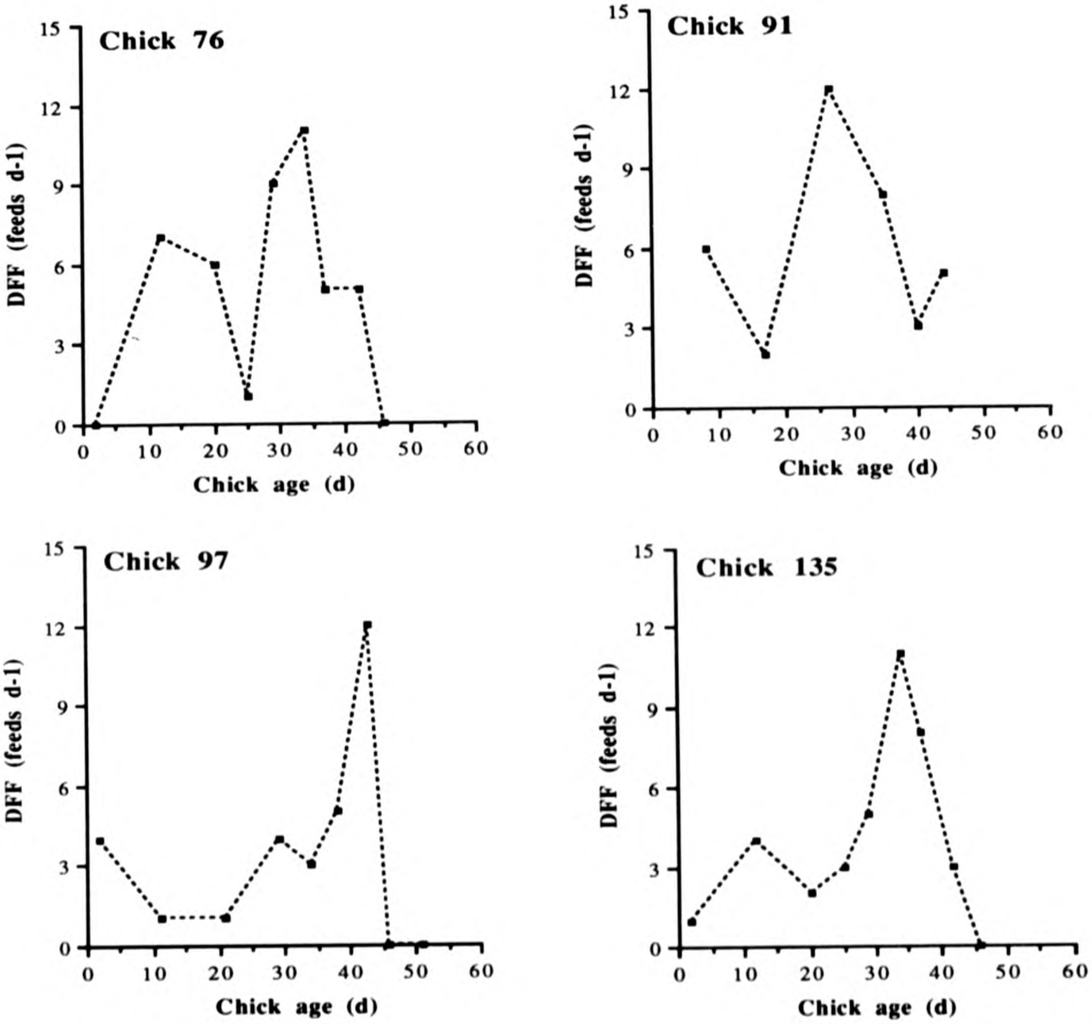


Figure 5.11 Examples of the change with age in the daily number of feeds (DFF) received by individual unmanipulated Puffin young at Little Hide in 1992 showing the variable nature of the feeding pattern.

residual feeding frequency for each pair. This was achieved by expressing each DFF for each pair as a residual of the 5-day moving mean for the appropriate year and age of young (observed minus predicted value) and using the mean of the residuals for each pair as an index of feeding effort. This method of controlling for interpair differences in the ages at which DFFs were measured was not found to improve the results of subsequent analyses, however, and only results using unstandardized MFFs are presented here.

5.3.4.6 Time spent by parents at the colony (CA) and breeding performance.

In 1992, there was no relationship between either MALE CA or FEMALE CA and ITRM, FTRM, rate of reserve change during rearing, MALE FEEDS/FEMALE FEEDS, chick MGR or TRPM for either sex or the sexes combined (Spearman correlations p>.05, n=16-26). In 1991, a maximum sample size of 8 was available for the above analyses and again no relationships with parental colony attendance were found.

5.3.5 Adult reserves during rearing and performance : individual unmanipulated pairs.

In 1992, there was a significant negative correlation between female ITRM and FEMALE FEEDS (**Figure 5.12b**); a similar pattern was apparent for males (**Figure 5.12a**) although the correlation was not significant. There was no relationship however between either chick MGR or TRPM and either male ITRM, female ITRM or the combined body reserves of pairs at the start of rearing (Pearson correlations p>.05, n=20-27). Sample sizes were smaller in 1991 (n=9-15) and there were no relationships between ITRM and MFF or chick MGR. There was a significant positive correlation between male ITRM and chick TRPM in 1991 (**Figure 5.13a**) although female ITRM was not related to TRPM (**Figure 5.13b**).

There were no relationships between the rate of parental reserve change during rearing and either MFF, chick MGR or TRPM in either year (Spearman correlations p>.05, 1991 n=9-18 1992 n=11-18). Nor was there any relationship between the total reserve change of individual males or females or pairs during rearing (the product of the daily rate of reserve change and the age at which young reached peak mass) and chick TRPM in either year (Spearman correlations p>.05, 1991 n=11-18 1992 n=15-18).

In 1991, male residual reserve mass at the end of rearing (male FRRM2) was positively correlated with MALE FEEDS (**Figure 5.14**) but no such relationship existed for females

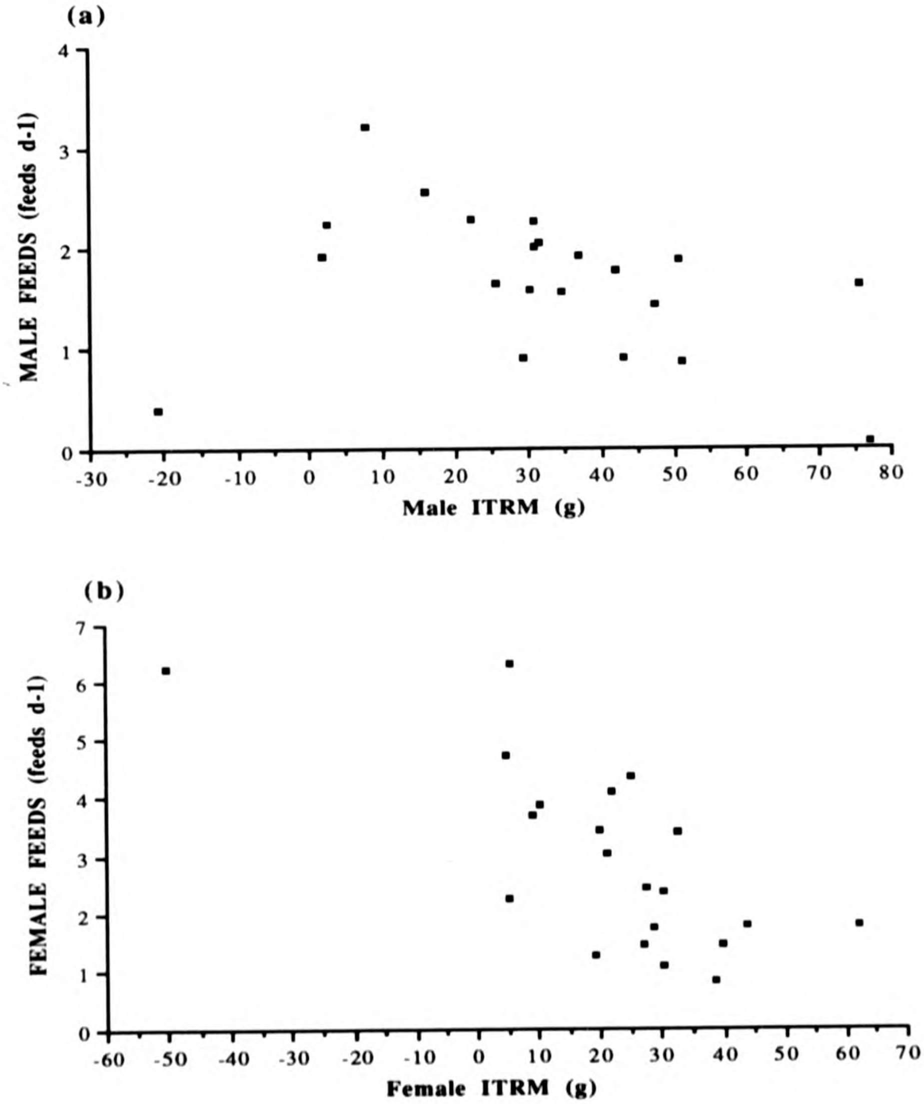


Figure 5.12 Relationships between the daily number of feeds delivered by individual Puffin parents to young (MALE FEEDS and FEMALE FEEDS) and their initial total reserve mass (ITRM) at the start of rearing for (a) males and (b) females in 1992.

Pearson correlation			
	1991 r=-.325	p=.150	n=21
	1992 r=-.712	p<.0005	n=21

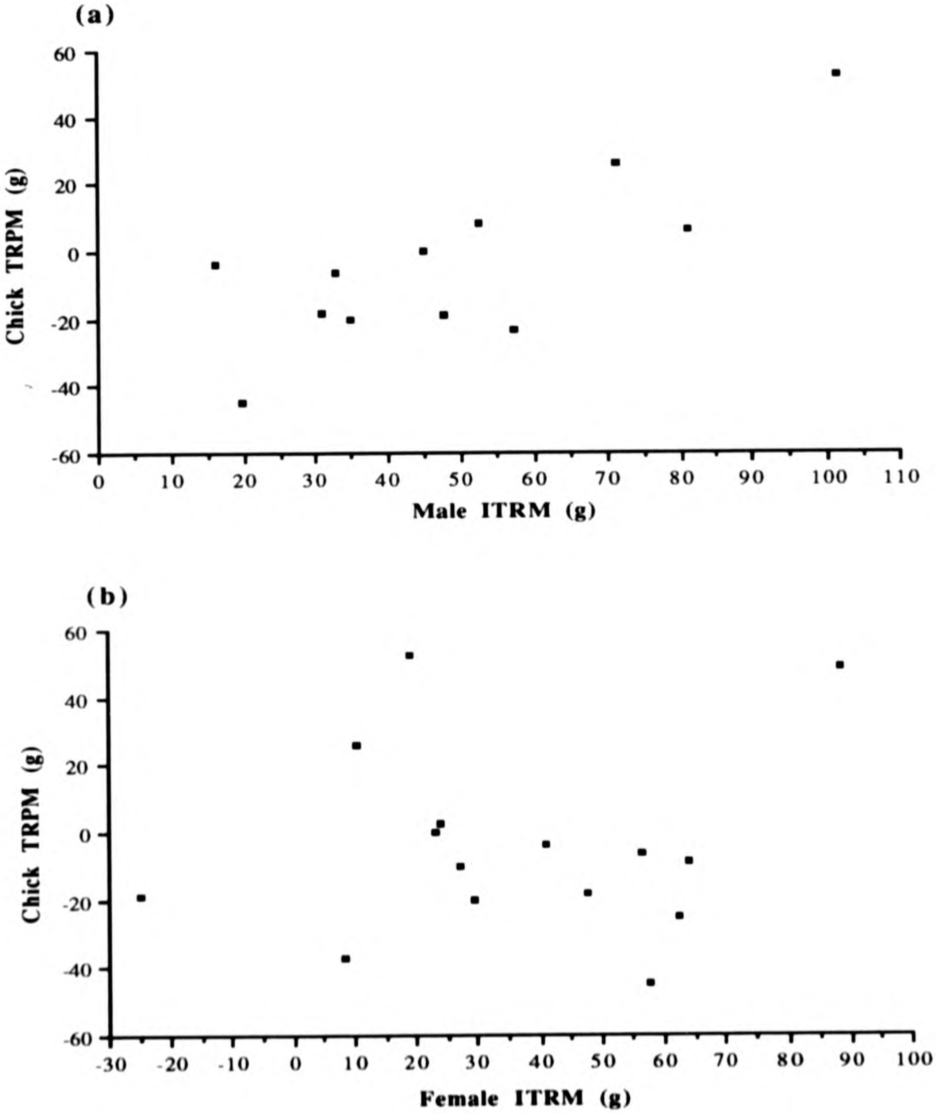


Figure 5.13 Relationships between the total residual peak mass (TRPM) of individual Puffin young and (a) male and (b) female parental initial total reserve mass (ITRM) at the start of rearing in 1991.

Pearson correlation	Males	r=.784	p<.005	n=12
	Females	r=.098	p>.7	n=15

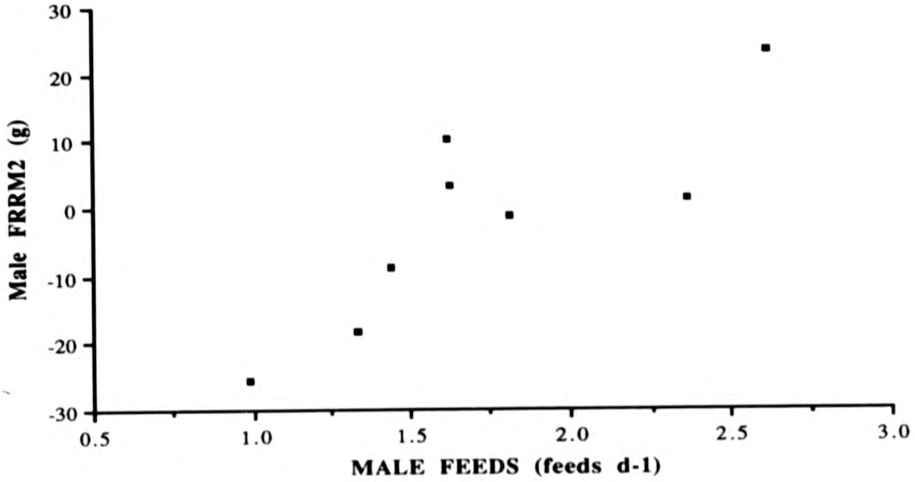


Figure 5.14 Relationship between the reserve masses of adult male Puffins at the end of rearing (FRRM2 - see text) and the mean daily numbers of feeds they delivered to young (MALE FEEDS) in 1991.
(Pearson correlation r=.835, p<.01, n=8).

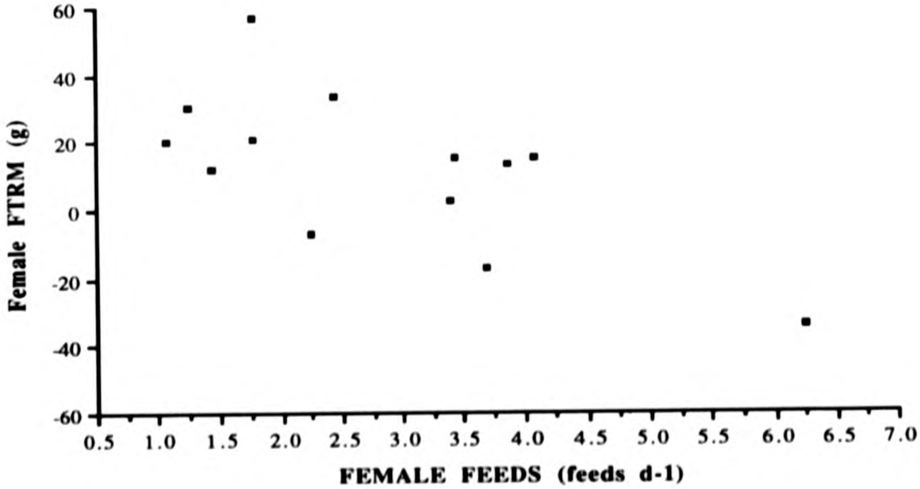


Figure 5.15 Relationship between the final total reserve masses (FTRMs) of adult female Puffins at the end of rearing and the mean daily number of feeds they delivered to young (FEMALE FEEDS) in 1992.
(Pearson correlation r=-.685, p<.01, n=13).

(Pearson correlation p>.05, n=8). In 1992, the converse occurred as there was no relationship between FTRM or FRRM/FRRM2 and MALE FEEDS (Pearson correlation p>.05, n=13) but a significant negative correlation between female FTRM and FEMALE FEEDS (**Figure 5.15**). There was no relationship between male, female or combined FTRM and chick MGR in either year (Pearson correlations p>.05, 1991 n=9 males, 9 females 1992=13 males, 15 females) or between male, female or combined FTRM and chick TRPM in 1992 (Pearson correlations p>.05, n=17 males, 18 females). In 1991, there was a positive correlation between male FTRM and chick TRPM however (**Figure 5.16**), although no such relationship existed for females (Pearson correlation p>.05, n=10).

5.3.6 Experimental manipulations of parental effort.

5.3.6.1 Supplementary feeding of young.

In both years, parents of supplementary fed chicks reduced their daily feeding frequencies within a week, and often within 2-3 days, of the start of the treatment. On any given watch day, fed young received fewer feeds than controls (**Tables 5.10 and 5.11**); the difference was only non-significant soon after the onset of the feeding treatment (27th June, 2 days after the start of the treatment, in 1990) or on days when the provisioning rates of controls were at the lower end of the normal range and/or sample sizes were very small (15th July in 1990 and 23rd June in 1991). Overall, feeding frequencies were reduced from a median of 4.4 feeds per day for controls to 1.7 per day for fed young in 1990 (Mann-Whitney Test U=0, p<.01) and from 3.8 to 0.2 feeds per day for control and fed young respectively in 1991 (U=0, p<.001). The effect of the treatment was relatively greater in 1991 than in 1990, with supplementary fed chicks receiving 5% and 39% of the daily feeds delivered to controls in the two years respectively. Effects of the feeding treatment on chick growth are considered in Chapter 7.

Experimental parents were more difficult to catch than controls during late rearing because of the reduced number of visits they made to burrows to feed young. For this reason, none of the experimental birds was caught at the end of rearing in 1990 and only 9 (8 females and 1 male) were recaught in 1991. Experimental females did not differ from controls in either the rate at which they depleted reserves during rearing or in FTRM (**Table 5.12a**). The single experimental male depleted reserves more slowly than its matched control and had higher TRM in mid-rearing (12 days after the start of the treatment) than the control male (**Table 5.12b**) but these differences could not be compared statistically.

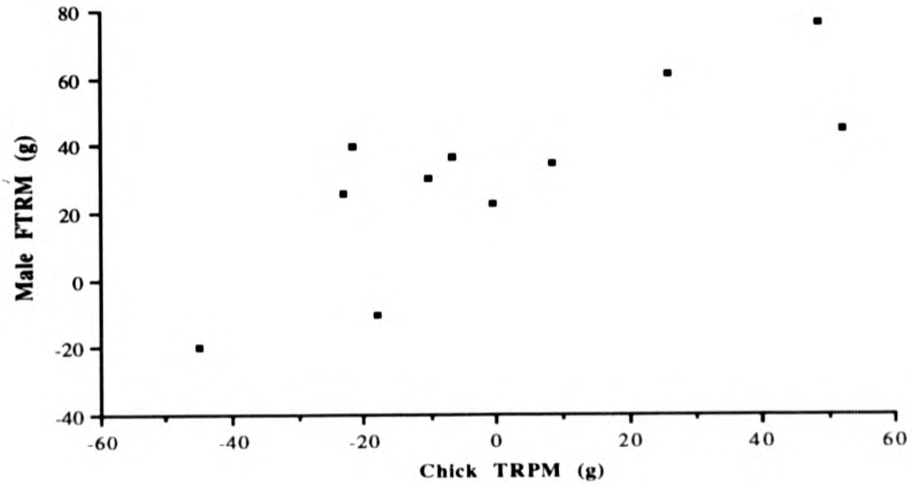


Figure 5.16 Relationship between the final total reserve masses (FTRMs) of adult male Puffins at the end of rearing and the total residual peak mass (TRPM) of their young in 1991.
(Pearson correlation r=.790, p<.005, n=11).

Table 5.10 Comparison of the daily number of feeds delivered by parents to supplementary fed and control Puffin young in 1990.

		27th June		3rd July		8th July		15th July		MEAN	
		FED	CONTROL	FED	CONTROL	FED	CONTROL	FED	CONTROL	FED	CONTROL
NUMBER OF FEEDS OBSERVED FOR EACH BURROW		4	2	1	7	0	3	0	1	1.67	3.25
		1	8	2	7	0	8	3	0	0.75	5.75
		6	6	1	7	2	7	1	1	3.00	5.25
		4	5	3	2	2	8	0	3	2.50	3.50
		1	8	1	5	0	6	0		0.50	7.00
		3	3	1	2	2				2.00	3.50
		1		1						1.00	
MEDIAN		3.0	5.5	1.0	6.0	1.0	7.0	0.0	1.0	1.67	4.38
n		7	6	7	6	6	5	5	4	7	6
MANN-WHITNEY TEST	U	9.0		3.0		0.0		7.0		0.0	
	p	<.1		<.005		<.005		>.4		<.005	

Table 5.11 Comparison of the daily number of feeds delivered by parents to supplementary fed and control Puffin young in 1991.

		16th June		23rd June		29th June		7th July		15th July		MEAN	
		FED	CONTROL	FED	CONTROL	FED	CONTROL	FED	CONTROL	FED	CONTROL	FED	CONTROL
NUMBER OF FEEDS OBSERVED FOR EACH BURROW		4	4	1	2	1	5	0	4	0	4	0.67	4.50
		0	6	1	0	3	3	0	0	0	0	1.00	3.29
		0	7	0	5	0	6	0	0	0	0	0.00	5.00
		6	1	0	1	1	3	0	0	1	4	2.00	3.00
		1	9	0	0	3	9	0	0	0	6	1.00	7.40
		0	5	0	1	0	0	0	0	0	4	0.25	2.33
			7	0	4	0	3	0	0	0	5	0.00	3.60
			4		0	0	8	0	1	0		0.00	3.75
			6		0	0	6	0	0	0		0.00	3.50
			6		4	0	6	0	2	0		1.20	4.83
			7		4	0	3	0	2			0.00	4.60
			7		0	0	5	0				0.00	3.14
			8		4	0						0.20	4.80
MEDIAN		0.5	6.0	0.0	1.0	0.0	5.0	0.0	0.0	0.0	4.0	0.20	3.75
n		6	13	7	13	13	12	12	11	10	7	13	13
MANN-WHITNEY TEST	U	8.0		24.5		12.5		42.0		11.0		0.0	
	p	<.005		<.1		<.001		<.05		<.005		<.001	

Table 5.12 Comparison of the rates of reserve change during rearing and reserve mass at the end of rearing (ftrm) in 1991 of adult (a) females and (b) males whose young were supplementary fed and control adults.

Experimental and control burrows were matched by hatching date and the stages of rearing at which adults were caught (referred to as stage in tables).

(a)

	RATE OF RESERVE CHANGE (gd^{-1})					Mann-Whitney Test		FTRM (g)				Mann-Whitney Test	
Medians	Hatch date[1]	Stage1	Stage2	Rate	n	U	p	Hatch date[1]	Stage	FTRM	n	U	p
FED	33	6.5	28.0	**-0.445**	6	15.0	>.6	28	31	**38.4**	5	10.0	>.6
CONTROL	37	6.0	28.5	**-0.489**	6			27	29	**47.4**	5		

(b)

	RATE OF RESERVE CHANGE (gd^{-1})						FTRM (g)				
Medians	Hatch date[1]	Stage1	Stage2	Rate	n		Hatch date[1]	Stage	FTRM	n	
FED	32	3.0	23.0	**-0.550**	1		32	23	**87.7**	1	
CONTROL	32	3.0	21.0	**-0.778**	1		32	21	**70.5**	1	

NOTE.

1 Hatch date where 1st May = day 1.

5.3.6.2 Playing of begging calls to parents.

In 1990, the sample of 10 experimental burrows was reduced to 7 because 2 young were abandoned before the start of the treatment and a further chick was predated when aged 17 days. There was no evidence that experimental burrows received more feeds than controls (**Table 5.13**) and no evidence for growth differences between experimental and control young (**Table 5.14**). None of the experimental parents was caught after the treatment in 1990.

There was no difference in the DFFs of experimental and control young after 5 days of the manipulation in 1992 (**Table 5.13**); a subsequent dawn-to-dusk feeding watch at the site, when the treatment had been carried out for longer, was not possible. In 1992, experimental and control young were not weighed sufficiently regularly to allow peak and fledging masses or dates to be obtained. Growth of young in the two groups was therefore compared by considering the masses of matched chicks on the same calendar dates, where masses were expressed as a percentage of predicted mass for their age (from Figure 2.8 in Chapter 2); this controlled for slight differences in the ages of matched chicks. There was no significant difference in mass (Mann-Whitney Test $p>.1$ $n=4$ experimental, 4 control) between experimental and control young compared by this method (**Table 5.15**). Although there was some suggestion that experimental young were heavier than controls, the difference was caused by one control of very low mass, which subsequently died, and there was little difference in mass within the other 3 pairs of young. As one of the experimental young disappeared when aged 21 days, only 3 pairs of experimental adults could be recaught near the end of rearing. The median hatching dates and stages of rearing at which parents were caught were matched to within 1 day for experimental and control burrows, making it unnecessary to control for these before adult reserves were compared. Although neither the rate of reserve change of parents during rearing or FTRM differed significantly between the experimental and control groups for either sex (**Table 5.16**), sample sizes were very small and experimental parents consistently depleted reserves at a greater rate than controls and had lower reserve levels than controls at the end of the rearing period.

5.3.6.3 Chick replacements.

Of the 4 fostered young, one disappeared 4 days after the exchange was made. The other 3 fledged successfully when slightly older than control young (fledging on the same dates) (**Table 5.17**), although the difference in fledging age was not significant (Mann-Whitney Test

Table 5.13 **Comparison of the daily number of feeds delivered by parents to burrows in which begging calls were played and to control burrows in 1990 and 1992.**

		1990										1992	
		27th June		3rd July		8th July		15th July		WHOLE SEASON		10th June	
		CALLS	CONTROL	CALLS	CONTROL	CALLS	CONTROL	CALLS	CONTROL	CALLS	CONTROL	CALLS	CONTROL
NUMBER OF FEEDS OBSERVED FOR EACH BURROW		6	4	2	3	5	5	1	1	3.50	3.25	5	5
		1	8	3	7	7	8	3	0	3.50	5.75	7	0
		6	10	3	4	6	2	0	0	4.75	5.33	5	7
		4	6	6	8	8	8	3	1	3.75	5.33	4	6
		6	3	3	7	6	7	7	4	4.00	5.25		
		6	3	6	3	4	5	3	3	5.75	3.75		
				8	2	5	6			5.50	3.50		
MEDIAN		6.0	5.0	3.0	4.0	6.0	6.0	3.0	1.0	4.00	5.25	5.0	5.5
n		6	6	7	7	7	7	6	6	7	7	4	4
MANN-WHITNEY TEST	U	16.5		21.0		22.5		12.5		24.0		7.5	
	p	>.8		>.6		>.7		>.3		>.9		>8	

Table 5.14 **Comparison of the growth of puffin young in burrows in which begging calls were played and in control burrows in 1990.**

Experimental and control burrows matched by hatching date.

VARIABLE	BEGGING CALLS Median	n	CONTROLS Median	n	MANN-WHITNEY TEST U	P
HATCHING DATE^{1}	39.0	7	38.0	7	19.0	>.4
PEAK MASS (g)	315.0	7	330.0	7	21.0	>.6
AGE AT PEAK MASS (g)	37.0	7	35.0	7	21.0	>.6
FLEDGING MASS (g)	285.5	6	273.5	6	16.0	>.7
FLEDGING AGE (g)	41.5	6	44.5	6	11.5	>.2
MGR^{2} (gd^{-1})	10.0	7	10.0	7	23.5	>.8

NOTES.

1 Hatching date where 1st May = day 1.
2 Maximum growth rate (in linear growth phase, days 10-25 of rearing).

Table 5.15 **Comparison of the growth of puffin young in burrows in which begging calls were played and in control burrows in 1992.**

CHICK NUMBER		DATE	AGE (d)	MASS (g)	PREDICTED MASS (g)	ACTUAL AS % OF PREDICTED MASS^{1,3}
BEGGING CALL	1	10/7	41	286	233	+22.7
CONTROL	1		40	243	239	+1.7
BEGGING CALL	2	11/6	17	209	178	+17.4
CONTROL^{2}	2		13	64	146	-56.2
BEGGING CALL	3	28/6	32	291	258	+12.8
CONTROL	3		29	273	251	+8.8
BEGGING CALL	4	24/6	20	232	201	+15.4
CONTROL	4		25	282	233	+21.0

NOTES. 1 From population growth curve for 1992 (see text).
2 Chick subsequently died
3 Median % of predicted mass +16.4 for begging calls, +5.3 for controls (Mann-Whitney Test U=3.0, p>.1).

Table 5.16 Comparison of the rates of reserve change during rearing and final total reserve mass in late rearing (FTRM) of adult puffins to whom begging calls were played and controls in 1992.

Experimental and control burrows were matched by hatching date and the stages of rearing at which adults were caught (referred to as stage in table).

	RATE OF RESERVE CHANGE (gd^{-1})					Mann-Whitney Test		FTRM (g)				Mann-Whitney Test	
Medians	Hatch date[1]	Stage1	Stage2	Rate	n	U	p	Hatch date[1]	Stage	FTRM	n	U	p
♂♂ CALLS	31	4	42	**-0.737**	3	2.0	>.2	31	42	**23.5**	3	3.0	>.5
♂♂ CONTROLS	31	5	40	**-0.833**	3			31	40	**37.8**	3		
♀♀ CALLS	31	4	40	**-0.528**	3	3.0	>.5	31	40	**11.2**	3	2.0	>.2
♀♀ CONTROLS	30	5	40	**-0.361**	3			30	40	**29.3**	3		
ALL CALLS	31	4	41	**-0.632**	6	11.0	>.2	31	41	**19.1**	6	8.0	>.1
ALL CONTROLS	31	5	40	**-0.134**	6			31	40	**31.3**	6		

NOTE.

1 Hatching date where 1st May = day 1.

Table 5.17 Comparison of the condition at fledging (total residual fledging mass, TRFM) of fostered puffin young (exchanged chicks extending the duration of rearing for parents) and control young in 1992.

Experimental and control young were matched by fledging date.

FOSTERED YOUNG						CONTROL YOUNG			
No.	Fledging date[1]	Fledging age (d)	TRFM[2]	ΔAge[3]	Duration[4]	No.	Fledging date[1]	Fledging age (d)	TRFM[3]
1	82	47	-23.31	16	63	1	81	43	+20.47
2	80	49	+26.69	9	58	2	79	44	+12.84
3	83	41	+56.61	12	54	3	85	47	-41.79
Medians	82	47	+26.69	12	58		81	44	+12.84

NOTES

[1] Fledging date where 1st May = day 1.

[2] Total residual fledging mass (TRFM, g) calculated as residuals from the linear regression equation relating chick fledging mass (g) to chick head plus bill length at fledging (mm) in 1992 - (Fledging mass = -933.86 + 17.72 head plus bill length, r^2=.647, p<.0001, n=26).

[3] Age difference (d) between foster and original young.

[4] The total duration (d) of the rearing period for foster parents.

p>.8, n=3 experimental and 3 control). There was no difference in the residual masses of foster and control young at fledging (Mann-Whitney Test p>.3, n=3), although there was a negative relationship between the total length of time that foster parents had to rear young and chick residual reserve mass at fledging (Spearman correlation r=-.866 but p>.05 with n=3).

Only 3 of the 6 foster parents (1 male and 2 females) were recaught when their foster young were near to fledging. The rates of reserve change and FTRM of these individuals were compared to those of control pairs which fledged young on similar calendar dates and whose reserves were initially measured approximately the same number of days prior to fledging as were those of foster parents (**Table 5.18**). The reserves of foster parents decreased at a lower rate than those of controls, although the difference was not significant (Mann-Whitney test p>.3, n=3 experimental and 3 control), and the FTRMs of foster parents were higher than those of controls at the same stage of rearing, the difference being marginally significant (Mann-Whitney test P=.081, n=3 in each group).

5.4 DISCUSSION.

5.4.1 Body reserves of adult Puffins and variation with stage of breeding.

The TRM of adult Puffins measured in this study ranged from zero (occasionally less than zero) to c.100g. The few negative TRM values may have occurred because individuals depleted reserves other than lipid or because of imperfection in the predictive power of the equation used to calculate lean wet mass (discussed in Chapter 4). Daily energy expenditures of adult Puffins during the rearing period ranged from 585-933 kJd^{-1} in 'good' weather and from 938-1153 kJd^{-1} in 'poor' weather (Chapter 6). At these rates of energy expenditure, the TRM of adults (assumed to be almost entirely lipid, Chapter 4) would be expected to sustain individuals for 0-6.5 days (**Figure 5.17**), if they relied solely on reserves rather than energy income from foraging (assuming the energy density of lipid = 40 kJg^{-1}, Kendeigh *et al*, 1977). Mean TRMs for all individuals (calculated from the 1992 data in **Table 5.3**) were 64g during pre-laying, 52g during incubation and 33g during rearing. Individuals could rely solely on these reserve levels for 2.3-4.3 days during pre-laying, 1.8-3.3 days during incubation and 1.2-2.2 days during rearing (**Figure 5.17**), assuming that daily energy expenditures were similar during the pre-hatching period and during rearing. It was not possible to measure field metabolic rates during incubation in this study, nor was it possible to model daily energy expenditure during incubation from a time-activity budget because of the difficulties of

Table 5.18 **Comparison of the rates of reserve change and final total reserve mass at the end of rearing (FTRM) of adult puffins for which the length of the rearing period was extended by exchanging chicks and for control adults in 1992.**

Experimental and control adults were matched by dates on which their young (or foster young) fledged and by the number of days prior to fledging over which their reserve change was measured (referred to as duration in table).

FOSTER PARENTS						CONTROL PARENTS					
No.	Sex	Fledging date[1]	Duration	Rate (gd^{-1})	FTRM (g)	No.	Sex	Fledging date[1]	Duration	Rate (gd^{-1})	FTRM (g)
1	♂	80	24	-0.417	46.7	1	♂	81	27	-0.778	+6.1
2	♀	80	22	-0.273	43.1	2	♀	79	30	-0.833	+14.3
3	♀	82	23	+0.348	24.2	3	♀	81	28	+0.179	-1.7
Medians		80	23	-0.273	43.1			81	28	-0.778	+6.1

NOTE 1 Fledging date where 1st May = day 1.

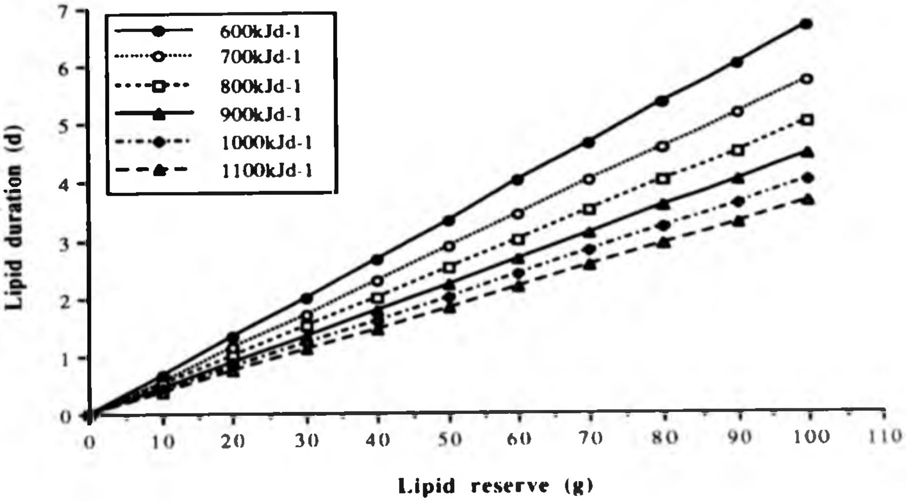


Figure 5.17 Predicted variation in the duration of energy supplied from lipid reserves with changes in the daily energy expenditure (kJd^{-1}) of breeding Puffins.

quantifying behaviour during that breeding stage. If, however, the energy expenditure of an average Puffin was to fall close to basal metabolism during an incubation shift, then 52g of lipid would last an absolute maximum of 8-9 days (assuming Puffin BMR = 10-11 kJh^{-1} or 240-260 kJd^{-1}, Chapter 6, **Table 6.5**). Puffins could not therefore rely solely on stored reserves for breeding but must have replenished reserves on a regular basis. The reserves carried by particular individuals therefore probably reflected the ability of those individuals to acquire resources (section 5.1.2 above) as well as reserves available to fuel a breeding attempt.

In the single year in which TRMs were measured throughout breeding (1992), the reserve levels of both sexes were higher during incubation than during rearing, as has been previously demonstrated for the Alcidae (Birkhead and Nettleship,1987; Harris and Wanless,1988; Croll *et al*, 1991; Gaston and Perin,1993 for guillemots; Harris,1979; Barrett and Rikardsen,1992 for Puffins; Gaston and Jones,1989 for Ancient Murrelets). Under the 'Stress Hypothesis', reserves are depleted involuntarily because of the inability of individuals to forage sufficiently to balance energy expenditure, while under the 'Adaptive Hypothesis', deliberate manipulation of reserve levels through adjustments in foraging duration or intensity is suggested. Reserve depletion due to physiological stress would be expected to be positively correlated with prevailing energy demands and should be higher when feeding conditions are poor. Conversely, adaptive depletion should occur abruptly or in a stepwise manner prior to the time of peak energy demand, that is at a constant stage of breeding each year regardless of environmental conditions (Gaston and Jones,1989; Croll *et al*, 1991). Recent studies of Brünnich's Guillemots (Croll *et al*, 1991; Gaston and Perin,1993) suggested that, at least in the years considered, the abrupt loss of adult mass around the time of hatching, and the lack of a decrease in mass thereafter, was an adaptation to reduce the costs of increased flying during rearing rather than a result of stress. Hatching dates were manipulated by exchanging eggs and mass loss occurred at the time of hatching *per se*, rather than being under hormonal control and programmed to occur at a pre-determined stage of the breeding cycle.

Changes in the reserve levels of Puffins in the present study (1992 data) were not consistent with the Adaptive Hypothesis, assuming that daily feeding frequencies were a true reflection of changes in parental effort during rearing. There was no linear trend in either DFF or adult TRM with stage of rearing but instead TRM was consistently low when DFF was low and *vice versa* (**Figure 5.3**). Periods of decrease in TRM were interpreted as a result of stress because they occurred immediately after periods of increased foraging for young. When TRM declined, adults decreased the DFF, presumably while they foraged for themselves to replace their depleted reserves. In 1992, two periods of decrease in TRM occurred, at a similar stage of rearing for each sex; male TRM decreased more than that of females in the first period, while the converse was the case in the second period (**Figure 5.3a**). The role that males played in chick feeding was lowest when male TRM was lowest and highest after female TRM declined abruptly (**Figure 5.3c**), supporting the previous evidence that low TRM occurred due to stress. Differences in the pattern of adult TRM change between years are discussed in section 5.4.3.1 below.

Recent studies of guillemots (Croll *et al*, 1991; Gaston and Perin,1993) suggested the lack of a linear decrease in mass during the rearing period was evidence for adaptive mass loss at the time of hatching. In contrast, the results of the present study suggested that stress during rearing might not operate in a linear fashion for long-lived seabirds, which might not compromise their own body reserves (and hence residual reproductive value) beyond a certain condition threshold (eg Monaghan *et al*, 1989,1992) and whose young are capable of surviving temporary spells of reduced provisioning (pers.obs.).

5.4.2 Pre-laying adult reserves, timing of breeding and success.

No relationships between pre-laying adult TRM and either timing of breeding (hatching date) or hatching success were found in the present study. Similarly, there was no effect of body mass in the pre-laying period on either timing of laying or breeding success for Guillemots (Harris and Wanless,1988). This result was not unexpected however, given the potential confounding effects of differences in individual 'quality' on TRM. These latter effects are discussed in Chapter 8 (section 8.1).

Alternatively, pre-laying adult TRM may have no influence on hatching success. The hatching failure of Puffins in the present study may have resulted from the inability of pair members to coordinate their incubation activities, for example in young and/or inexperienced pairs. Insufficient data were available to consider the effects of pair age on success in this study but poor hatching success amongst younger/less experienced individuals has been demonstrated in other long-lived seabirds (Saether,1990 for review and see Chapter3, section 3.1.2). If one pair member were to fail to return for its incubation shift, depletion of the body reserves of the incubating bird could be the proximate cause of egg desertion but this would only be detectable if individuals were weighed at the times their breeding attempts were abandoned (as in Monaghan *et al*, 1992). It was not possible to determine the stage at which breeding was abandoned for individual pairs in this study because of the risk of causing desertion if burrows were checked prior to hatching.

It was unlikely that an effect of adult body condition on hatching success was undetectable because of particularly favourable breeding conditions, given the low hatching success at Little Hide in 1992 (**Table 5.7**). It was equally unlikely that such a high degree of hatching failure was due to the age or inexperience of pairs.

5.4.3 Adult reserves during rearing and breeding performance.

5.4.3.1 Comparison between 1991 and 1992.

In 1992, unmanipulated pairs at Little Hide had significantly lower hatching success than in 1991. Chick growth rates, peak masses and fledging masses were all lower in 1992 (although only significantly so for fledging mass) and daily feeding rates were (non-significantly) lower in 1991, and fluctuated less with chick age, than in 1992 (summary in **Table 5.7**). Adults carried higher reserves at the start of rearing in 1991 than in 1992 but this alone was not sufficient evidence for an influence of body condition on breeding performance because of the differences in hatching dates between the two years. The lower reserve masses in 1992 may have been the result of later hatching, such that feeding conditions were more favourable at the start of rearing in 1992 and individuals could carry lower 'insurance reserves'. This suggestion was not consistent, however, with the very low hatching success in 1992; it seemed more likely that feeding conditions were less favourable in 1992, so that the lower reserve masses of adults in early rearing resulted from an increased stress of breeding. This would explain why fewer pairs hatched young and hatching was delayed in 1992. There was no evidence, however, for the 1992 breeding season being later than that of 1991 for the Isle of May as a whole (from the monitored burrows of M.P.Harris on the Burrian), peak masses and fledging masses did not differ significantly between 1991 and 1992 and overall success was higher in 1992 than in 1991 for the island as a whole. This suggested that unfavourable local feeding conditions were not responsible for the lower success at Little Hide in 1992 but that some other factor(s) were the cause of the later hatching and reduced hatching success at the study site. Two possibilities were a severe storm early in the laying period (discussed in Chapter 7, section 7.4.2) or disturbance during the pre-laying and incubation periods caused by attempts to capture individual adults for weighing (Chapter 2, section 2.9).

Whatever the cause of the late hatching in 1992, the patterns of adult reserve change and variation in daily feeding rates during rearing for the two years, showing greater fluctuations with chick age in 1992 than in 1991, suggested greater stress of rearing for adults in 1992. Differences between the sexes in the patterns of reserve change in the two years were in accordance with their differing roles during the rearing period. Female reserve change was similar in the two years (although reserves fluctuated more in 1992 than in 1991) but male patterns were markedly different in that during periods of reduced food delivery to young, male reserves increased in 1991 but not in 1992. Female reserves were low during the periods of reduced provisioning in both years. This suggested that breeding stress was experienced more by females, with their greater role in provisioning (Chapter 3), than by males, an effect on males only being obvious in the less favourable year (1992).

5.4.3.2 Individual reserves during rearing and performance.

Relationships found between the body reserve levels of individual Puffin parents and measures of breeding performance were few and are summarized in **Table 5.19**. The negative relationship (in 1992) between reserve mass in early rearing and the numbers of feeds delivered to young by individual parents suggested that either low reserves indicated individuals for which foraging was costly, so that they made fewer visits to young, or that low reserve levels belonged to efficient foragers, which reared young by delivering fewer food loads of superior quality (size or composition) than less efficient birds. Female reserves at the end of rearing were also negatively related to FEMALE FEEDS in 1992, which suggested that either high feeding rates resulted in an increased physiological stress of rearing and reduced reserve levels in females (reduced their residual reproductive value and increasing costs), or that females with low reserves in late rearing were efficient foragers, carrying lower insurance reserves and delivering a larger number of feeds to young than less efficient females. There was no evidence, however, for direct relationships between the rate of reserve change of individuals, of either sex, and their rate of effort expenditure, when effort was measured in terms of MFF or chick MGR; these relationships were expected if reserve levels were dictated by the level of stress experienced by parents. Nor was there a demonstrable relationship between the total reserve change (from hatching to chick peak mass) of parents and the final condition of their young, this analysis taking into account the often large differences in the length of the rearing period for Puffin young. The lack of consistent relationships between parental reserves and chick MGR or condition at peak mass (TRPM) suggested that the influence of parental body condition on performance manifested itself largely through

Table 5.19 **A summary of the direction of significant correlative relationships between the body condition of individual adult puffins and their breeding performance in 1991 and 1992.**

		FEEDING RATE (MFF, MALE and FEMALE FEEDS)	CHICK GROWTH RATE (MGR)	CHICK CONDITION AT PEAK MASS (TRPM)
RESERVE MASS IN EARLY REARING (ITRM)	♂♂	NEGATIVE (1992)	NONE	POSITIVE (1991)
	♀♀	NEGATIVE (1992)	NONE	NONE
RATE OF RESERVE CHANGE DURING REARING	♂♂	NONE	NONE	NONE
	♀♀	NONE	NONE	NONE
RESERVE MASS IN LATE REARING (FTRM)	♂♂	POSITIVE (1991)	NONE	POSITIVE (1991)
	♀♀	NEGATIVE (1992)	NONE	NONE
ROLE OF THE MALE IN PROVISIONING (MALE ROLE)		NEGATIVE (1992) SIMILAR PATTERN (1991)	NEGATIVE (1991) SIMILAR PATTERN (1992)	NONE

adjustments to the number of feeding trips required to rear young, rather than through direct effects on the condition of young at fledging.

The relationships above were apparent in the 1992 but not the 1991 breeding season. In 1991, the only significant relationships involved males (**Table 5.19**) and these suggested that carriage of reserves was advantageous for males; individuals with high reserves at the start (and end) of rearing produced young with higher TRPM, and those with high reserves in late rearing delivered the largest number of feeds to young.

The results in **Table 5.19** were not consistent with any single model of the relationship between parental body condition and breeding performance suggested in **Figure 5.1**, most importantly because adult body condition was related to provisioning rates but not to chick growth rates or condition at peak mass. These results were not unexpected given the limitations of the correlative approach taken in this part of the study (section 5.1.3 above). Possible ways in which variation in individual 'quality' could mask relationships between parental body condition and the measures of breeding performance used in the present study are discussed in Chapter 8 (section 8.1).

Factors other than parental body condition may have contributed to the condition of Puffin young in this study. There was some suggestion that weather influenced chick MGR and TRPM in 1991 (although less than 25% of the variation was explained in each case) but no suggestion of weather influences in 1992. The lack of carcass composition data for young was seen as a weakness in analyses involving the chosen measure of chick condition. In 1992, when extra size measurements of young were made prior to fledging, structural size explained more than 60% of the observed variation in chick peak mass. This suggested that when wing length at fledging was used to control for chick size in 1991, the resultant TRPM still contained a large size component and was not an accurate reflection of reserves carried by young. Without carcass data for young, it was impossible to discount the possibility that TRPM in 1992 was still incompletely corrected for body size and, therefore, relationships sought were those between parental body condition and chick size rather than condition. In 1991 and 1992, when overall peak and fledging masses at Little Hide were low compared to other areas of the island, all young may have carried minimal lipid reserves, so that differences between individuals were not detectable. This could only be confirmed by carcass analyses and the latter would be important in any future study involving the condition of young.

If all pairs produced young of similar condition at peak mass in 1991 and 1992, differences in parental foraging ability should have been reflected in the residual reproductive value of individuals (as indicated by body condition during late rearing in this study), with less efficient individuals incurring greater costs than efficient birds when producing young of equal quality. This was not expected for a long-lived species, however, the expected relationship being similar reproductive costs for all individuals and differences in individual ability reflected in the quality of the young produced (option ii in **Figure 5.1c**). The unexpected suggestion that all pairs produced young of similar quality may have been the outcome of the very low hatching success at Little Hide in 1992 (and to a lesser extent in 1991). Whatever the causal agent of this low success, its effect may have been to allow only higher quality parents to hatch young, reducing the variation in the quality of the young they produced. Such an effect would also explain why, contrary to all other results, fledging success at Little Hide was significantly higher in 1992 than in 1991.

The inability to measure the 'quality' of individuals independent of their body reserves was the major weakness in the correlative part of this study (see Chapter 8, section 8.1). There was no evidence for relationships between the estimated age of pairs (a possible correlate of foraging ability, Chapter 3) and their reproductive performance but this was to be expected given the method by which age was measured and the potential errors involved (Chapter 3). There were also no demonstrable relationships between breeding performance and the proportion of the daylight hours adults spent 'loafing' above ground at the colony (another possible correlate of foraging efficiency, section 5.1.3 above) but once again, errors involved in the measurement of CA may have been large because of the difficulties of correcting for biases in the ease of observation of different individuals (Chapter 2, section 2.3.7). In addition, adults spent only a small proportion of the daylight hours above ground at the colony, so that loafing time would have been better quantified by time-budgetting individuals at sea and in burrows; yet neither of these were possible for Puffins in the present study.

There was some evidence in both years that MFF and chick MGR were highest when the proportional contribution of the male to provisioning ranged from 0.2-0.4 (ie close to the median for the population, Chapter 3). This provided some evidence for differences in the quality of individuals within pairs. For example, the results could be interpreted as a lower involvement of males in provisioning if their foraging ability was poor and a higher involvement if those of their partners were poor. In Chapter 3, a higher power requirement for flight for male Puffins was suggested compared to females because of the significantly greater wing loading of the former sex. The mean proportional contribution to the provisioning effort of males within the population (c. 0.3-0.4) would be expected to be shaped by natural selection to represent the optimal solution for provisioning young, and there was some indication that this was the case for Puffins in the present study.

5.4.3.3 Manipulation of the effort of individual parents : effects on body condition.

The correlative results discussed in section 5.4.3.2 were originally intended as a minor part of this study, with emphasis placed on experimental manipulations (for the reasons given in section 5.1.3 and discussed above). Fewer data were obtained from the manipulations than intended however, due to the unforeseen difficulties encountered in capturing particular individuals after treatments. Conclusions drawn from the results of the experiments must be tentative therefore, because they are based on small samples.

The effects of the supplementary feeding (1992) and chick replacement experiments on adult body reserves and rates of reserve change were not consistent with the 'Stress Hypothesis' for explaining reserve loss during rearing. Females whose young were supplementary fed depleted reserves at a similar rate to controls and had similar reserves at the end of rearing despite making far fewer provisioning trips. This suggested that the reserve loss of control females was not a result of the limitation on the time available for self-feeding imposed by the need to provision young. Similarly, the 3 foster parents, which reared young for c.2 weeks longer than control adults, depleted reserves at a slower rate than controls, during the same stage of breeding, and carried more reserves when their young fledged than controls, suggesting that the reserve levels of foster parents returned to a pre-programmed post-breeding level despite the fact that they were still rearing young. Unfortunately, it was not possible to compare the reserve levels of foster parents, at the time the foster young fledged, with those of adults at the same stage after their young had fledged because of the difficulties involved in capturing adults away from their burrows after fledging.

There was no evidence in the present study for an increase in the frequency of food deliveries to young when begging calls were played to adults, in contrast to the results of Harris (1983). In 1990, the calls may not have been played sufficiently often to elicit a response. In 1992, it was impossible to ignore the possibility that a parental response took the form of a change in the size or nutritional quality of food loads delivered, rather than an increase in feeding frequency, or that, after only 5 days of call playing, sufficient time had not elapsed to elicit a response. There was no difference, however, in the growth of experimental and control young after the treatment in 1992 but some suggestion (especially for females) of a negative effect of the call playing on body condition. The experimental parents (females) may have increased their foraging effort but in a year when feeding conditions may have been less favourable for Puffins, this extra foraging may not have produced a demonstrable effect on chick growth.

In summary, neither the correlative results presented in this chapter nor the results of the experimental manipulations of effort were conclusive in terms of relationships between Puffin body condition and breeding performance. There were some suggestions both of physiological stress associated with chick rearing and of adaptive, pre-programmed changes in adult reserve levels during the rearing period.

5.4.4 Responses of parents to experimental manipulations of effort.

Parents responded to the supplementary feeding by significantly reducing the daily number of feeds they delivered to young, within a week (and often within several days) of the start of the experiment. Almost all the additional food was consumed each day, so the stimulus to reduce feeding may have come from the chick itself, not from the presence of surplus food in the burrow.

Two previous studies on Puffins differed in their conclusions about whether the feeding schedule was dictated by the parents (a pre-programmed pattern based on time since hatching) or by the chick (chick-parent communication or the use by parents of other cues to assess the age/nutritional state of the chick). Hudson (1979) concluded, from two experiments, that adults used a pre-programmed feeding schedule. The first experiment addressed the observation that daily feeding rates decreased between a chick age of 26 days and fledging (Ashcroft,1976). Hudson reared groups of chicks by hand in natural burrows. A comparison of one group receiving 80g Sprats per day (the maximum quantity of food normally delivered to control chicks) and another group fed 'ad lib' (c.120g per day) revealed that the 80g group did not reduce their food intake after day 26 while the 'ad lib' group did, although the latter still ate more than the 80g group. This occurred until the day before fledging, when the 80g group also decreased their intake slightly. He concluded that the reduction in the number of feeds delivered to wild chicks older than 26 days meant that adults were providing less than their chicks were capable of eating but the possibility that chicks could 'discourage' parents from bringing food was not eliminated. In a second experiment, where chicks of c.20 days old were exchanged with younger chicks (c.12 days old), with presumed lower food requirements, both sets of foster parents continued to deliver the same quantity of food that would have been required by their own chicks during the following 3 days when observations were made.

Harris (1983) concluded the opposite, when the playing of the begging call of a hungry chick to parents visiting burrows resulted in a significant and immediate increase in the number of feeds brought to young. It seemed that parents could respond to the needs of their chick and that sound was the stimulus controlling provisioning activity. Harris also exchanged chicks between burrows and showed that adults would feed young for much longer than normal (as was also demonstrated in the present study). Harris' pairs fed the chicks according to their needs, not simply for a set time period. Parents feeding foster chicks in Hudson's (1979) study also fledged them at their correct age rather than on the expected fledging date of their own chick. It seems likely that Hudson did not record a difference in the number of feeds delivered to foster chicks because the parents required more than the 3 days for which he observed them to adjust to their chick's needs.

The results of the present study demonstrated that adult Puffins could change their feeding rates to meet chick demands but that the adjustment (in this case a decrease) can take up to a week for some pairs to achieve. As parent and chick usually meet in near darkness, any feedback from the chick is likely to be auditory (Harris,1983). A rigid feeding programme with no chick feedback would appear not to be adaptive in seabirds which often experience conditions of fluctuating food supply. Such a schedule could result in death of the young if feeding conditions were poor or if one of the parents failed to feed the young for some reason (eg. death).

Wild Puffin chicks can survive for several days with little or no food if poor weather limits parental foraging (pers.obs.). The begging call played by Harris (1983) was broadcast at the same intensity and volume as that produced by young when they are extremely hungry. If obtaining food under poor conditions is more costly for parents, and chicks can withstand short periods without food, then it might be costly for young to beg in such a manner as soon as food delivery ceases. Begging itself may be energetically expensive for the young. Rather, young may begin to beg only when their body reserves reach some critical level, to fall below which would be fatal. Such a delay might be responsible for the lack of an effect after 3 days in Hudson's (1979) exchange experiments. However, if young only produce the begging call when they are starving, then some other behavioural change must have effected the reduction in provisioning after the start of supplementary feeding in this study. The method used by adult Puffins to feed their chicks has rarely been described because of the difficulties of observing events underground. Corkhill (1973) replaced the side of a nest chamber with glass and watched an adult feed a chick of less than 4 days old on three occasions. The adult stood in the centre of the chamber, "uttering a soft clicking call". The chick took some fish from the parent's bill, the rest were dropped and the chick retrieved them from the floor. "The chick squeaked excitedly throughout" but did not flap its wings or peck at the adult's bill. Adults spend far less time underground with older chicks, sometimes only a few seconds (Myrberget,1962; Corkhill,1973; Harris,1984; Pers.obs.), so presumably the fish are simply dropped on the floor in this case. Whether or not the "squeaking" described by Corkhill was the begging call is not known but it would seem probable that a chick capable of consuming food will make some sound and/or approach the adult when it arrives whereas a very well fed (supplementary fed) chick will not. Either a chick call or the sound/feel of the chick approaching could stimulate the adult to continue collecting feeds. Clearly further work on parent-offspring communication in such burrow-nesting species would be worthwhile.

Plasticity in the growth rate of young and thus in the length of the rearing period would be a useful adaptation in seabird species which experience marked inter-year variation in food availability. The ability of parents to rear chicks for longer than usual has been demonstrated in Audubon's Shearwater, where chick exchanges resulted in an increase in the length of the rearing period from 75 to 120 days (Harris,1969), as well as in Puffins (cited above). A feedback mechanism, determining parental provisioning duration and rate and based on stimuli from the chick, such as that demonstrated for Puffins in this study, would seem an appropriate means of reconciling chick growth rate with available food and parental effort, especially if a time delay were built into the chick response to hunger to allow for short-term reductions in food supply (described above).

In contrast, Ricklefs (1987) rotated chicks of Leach's Storm-petrels daily through differing numbers of nests (i chicks through n nests daily to produce i/n chick equivalents of food demand from 1 (i=6,n=6) to 2(i=2,n=1) per nest). The mean quantity of food delivered daily was found to be independent of the experimentally-created food demand, most variation in load weight being due to between-pair differences. Ricklefs concluded that the lack of a parental response to the increased food demand might be appropriate to the particular conditions experienced by the species. Underfed 'rotation' chicks restored mass to previous levels without any increase in provisioning rates when replaced in their natal burrows; thus the normal feeding schedule was sufficient to allow such a recovery after, for example, a spell of poor weather. Additionally, pairs at the colony in which Ricklefs worked rarely experienced periods of reduced feeding, thus chick undernourishment may have been a novel condition for parents. Lastly, as each member of a pair only fed its chick independently once every 2-3 days, the nutrition of the chick could vary greatly and unpredictably between visits depending on whether or not the partner had made a visit in the intervening period; thus it might be more reasonable for parents to provision at a more or less fixed rate to match mean food demands. This would not apply in the case of Puffins where feeding visits are made more regularly. However, Ricklefs was unable to discount the idea that parents might have been prevented from responding to increased chick demands because of limited food availability or the limited ability of parents to transport it to the colony (eg. Lack,1968).

CHAPTER 6 ENERGETICS OF CHICK REARING BY PUFFINS.

6.1 INTRODUCTION.

6.1.1 The energetic expense of breeding.

The period of chick rearing has been traditionally viewed as an energetic 'bottleneck' in the avian annual cycle (Drent and Daan,1980). Only in recent years, however, has the collection of empirical evidence to test this assumption begun, with direct measurement of field energy expenditure throughout the annual cycle (Bryant and Tatner,1988, for Dippers; Davis et al,1989, for Gentoo and Macaroni Penguins; Gales and Green,1990, for Little Penguins) and these few published sudies suggest that adult daily energy expenditure (DEE) is indeed highest during chick rearing. Other energetics studies (eg. Obst et al,1987, for Wilson's Storm-petrel; Montevecchi et al,1992, for Leach's Storm-petrel) have inferred that DEE should be higher during late chick rearing than during incubation or brooding. Drent and Daan (1980) suggested that parental energy expenditure during rearing might have an upper limit at around 4 times the basal metabolic rate (BMR), which they termed the 'maximum sustained work load'. They argued that to exceed this limit over a long period would impose physiological fitness costs (leading to an increased probability of mortality). Bryant and Tatner (1991) presented data on the field energy expenditure during rearing of 323 individuals of 21 species of small bird (body masses 10-150g) and showed that, although the modal metabolic intensity (MI = FMR divided by BMR) was c.3 times BMR, 48% of species and 30% of individuals exceeded the suggested 4 times BMR threshold; this was particularly marked among species with relatively costly foraging habits (aerial feeders). They concluded that no single metabolic intensity is likely to impose an upper limit on avian work rates and that any fitness cost related to energy expenditure during breeding is likely to be probabilistic and "will be sustained progressively and not precipitously as the 4 times BMR threshold implies".

Puffin breeding parameters have been monitored on the Isle of May since the early 1970's by M.P.Harris and breeding conditions appear to have deteriorated over this 20-year period. The peak and fledging masses of young have declined, coinciding with a decline in the mean daily energy intake of chicks. Adult survival has also decreased, although there has been no systematic trend in breeding success (young fledged per egg laid) (**Figures 1.1 to 1.4** in

Chapter 1). This energetics study aimed to determine whether Puffins on the Isle of May were currently exceeding the suggested MI threshold of around 4 times BMR during chick rearing and to compare Isle of May Puffin MI with that of other seabirds.

6.1.2 The use of chick feeding frequency as a measure of parental effort.

An overall aim of this study was to demonstrate whether differences in reproductive effort between individual pairs of Puffins affected their reproductive success. To fulfil such an aim, it was necessary to select satisfactory measures of both reproductive effort and success, and chick feeding frequency was, out of necessity, chosen as a component in the measurement of effort (Chapter 5). An examination of the relationship between chick feeding frequency and adult DEE was a further aim of the DLW work.

Bryant and Tatner (1991) found positive relationships between parental energy expenditure and brood provisioning rate in 7/10 studies of small birds in their review but such relationships have yet to be fully addressed in seabirds. Gabrielsen et al (1987) showed that FMR was higher for Kittiwakes raising 2 young compared with a single young, while the converse was true for Little Penguins (Gales and Green,1990) but in neither case was the difference significant. Assuming that avian parents maintain a stable mass (ie. they do not deplete stored body reserves), then a positive correlation between DEE and daily chick feeding frequency would suggest that the latter was an appropriate measure of parental effort. Similarly, if there was a negative relationship between body mass change or body condition change and daily feeding frequency (and/or DEE), this would also imply that feeding frequency was an appropriate measure of parental effort. If mass change or condition change was positively related to DEE and/or feeding frequency, however, then a positive relationship between DEE and feeding frequency would imply that feeding frequency was not necessarily a useful measure of effort. A positive relationship between mass change or condition change and DEE would suggest that low levels of energy expenditure were associated with reliance on stored body reserves. Individuals with high DEE's delivering larger numbers of feeds but maintaining or increasing their body reserves might be in superior condition to those making fewer feeding trips and here it would be debatable whether or not daily feeding frequency represented parental effort.

Differences in parental quality in terms of their foraging efficiency (defined as prey energy capture rate per unit of energy expenditure) could mask a relationship between DEE and feeding frequency. More efficient foragers would make more feeding trips than less efficient foragers for the same energy expenditure, producing no relationship between DEE and feeding frequency or even a negative relationship. The lack of a relationship between DEE and feeding frequency would be consistent with the suggestion of a maximum working level, with foragers of differing efficiency making the number of feeds possible for them within the daily energy limit. Equally, differences in the size and composition of food loads delivered to chicks could mask a relationship, or result in a negative relationship, between DEE and feeding frequency. Individuals with lower feeding frequencies might deliver feeds of higher mass or nutritional quality, each of which requires more energy to catch, than those birds delivering larger numbers of feeds each day. Evidence exists for a negative relationship between food load mass and daily feeding frequency in comparisons between different Puffin colonies (Harris and Hislop,1978) but it is not known whether such a trade-off occurs at the level of individual parents. In Blue-throated Bee-eaters, House Martins and Pied Kingfishers the brood provisioning rate (mass of food delivered per day) explained more of the variance in energy expenditure than the number of nest visits (Bryant,1988) but it was not possible to quantify differences in the size or composition of food loads delivered by individual adult Puffins in this study because of the disturbance this would have caused.

DEE, daily feeding frequencies and mass change of adult Puffins were measured concurrently in the present study to assess whether feeding frequencies could be used as a measure of DEE and/or parental effort during rearing.

6.1.3 The relationship between body mass and energy expenditure.

Knowledge of the consequences of body mass for avian energy expenditure is based largely on interspecific comparisons. The larger the bird, the higher its total metabolic energy requirements, although its metabolic requirements per unit are reduced (Calder,1974). Inter-individual differences in body mass also have implications for locomotory costs. The energetic cost of flight is highly dependent on mass (Pennycuick,1975) and carriage of lipid, 700 times the density of air (Campbell,1986), is disadvantageous, especially for species, such as auks, in which flight costs are ordinarily relatively high (Pennycuick,1987). At the level of the individual where structural size (eg. wing span) is fixed, carriage of extra mass will increase the power requirements for flight by increasing wing loading and/or body drag, the latter depending on the site of extra mass accumulation on the body. In species which forage underwater, however, thermoregulatory costs are potentially high because water conducts heat 25 times more efficiently than air (Wilson et al,1992). A layer of subcutaneous fat is a more efficient insulator than a layer of air trapped in plumage in this context because the air layer is compressed underwater and becomes a less efficient insulator, and the low density of air in feathers results in a substantial upthrust (increased buoyancy), which necessitates a high energy expenditure to overcome (Wilson et al,1992). The similar densities of lipid and water mean that if lipid is used as an insulator there is little resultant increase in upthrust and its insulatory properties are little affected at depth because it is largely incompressible. In diving and volant seabirds optimal mass (in terms of reserves carried) might, therefore, vary with the relative amounts of time spent flying and diving as well as on ambient air and water temperatures. Mass change will also influence the cost of less vigorous activities (eg. walking, surface swimming), although such effects are less fully documented in the literature. Increased body density might increase thermoregulatory costs in species which spend much time sitting on water because birds would tend to float lower with more of their surface area in contact with the water (Stahel and Nicol,1982; Wilson et al,1992).

Clearly, inter-individual differences in the body size, body mass or body condition (reserves carried for a given size) of Puffins will have complex implications for energy expenditure. Bryant and Tatner (1991) found relationships between body mass and energy expenditure in 5/11 studies of small bird and between body size and energy expenditure in 4/8 studies. These relationships with energy expenditure were not consistently positive or negative. Amongst the published studies of seabird field energy expenditure, positive relationships between FMR and body mass have been recorded in the Little Auk (Gabrielsen et al,1991) and Leach's Storm-petrel (Montevecchi et al,1992). Relationships between adult Puffin body mass, body size and condition and DEE during chick rearing were sought in the present study. The existence of such relationships might suggest reasons for parental mass loss during rearing (Chapter 5).

In the present study, the energy expenditure of Puffins during rearing was measured in the field using the doubly-labelled water (DLW) technique. In this technique, the body water of the bird is labelled by injection of heavy water containing deuterium (D=^{2}H) and oxygen-18 (^{18}O). The rationale for its use is based on the observation that the oxygen of respiratory carbon dioxide exchanges freely with the oxygen of body water (Lifson *et al*, 1949). The ^{18}O isotope is lost from the body either as carbon dioxide or as water, while loss of water can be determined independently from the loss of the deuterium isotope. Calculation of carbon dioxide production, and hence energy expenditure, is based on the difference in the turnover rates of the oxygen and hydrogen labels. The theoretical basis of the technique and the assumptions involved are discussed in Lifson and McClintock (1966), Nagy (1980) and Tatner and Bryant (1989). The field metabolic rate (FMR) measured using this technique is the total energy cost of the bird during the measurement period; it includes the costs of BMR, thermoregulation, posture, digestion and assimilation and all locomotory costs.

6.2 MATERIALS AND METHODS.

6.2.1 Effects of handling and captivity on behaviour.

On 15th June,1991, 3 adults were caught from separate burrows (not used for other parts of the study) at the Little Hide site. Captures were made with purse nets when the birds were making feeding visits to chicks between 0500 and 0630 hours. Each bird was weighed and measured (Chapter 2, section 2.2.3) and marked with a unique dye colour on the white upper breast feathers. Individuals were held in separate cardboard boxes (for 2 hours from the time of initial capture) and then released behind the hide, from where they flew out to sea. The site was observed from 1830 to 2130 hours on the evening of the 15th and a dawn-to-dusk feeding watch was conducted on 16th June (Chapter 2, section 2.4). None of the marked birds was seen on the evening after the capture but 2 brought food to young on the following day at the same rate as other birds at the site. One marked bird delivered all 4 feeds its young received on 16th June, another delivered 2/5 feeds made to its burrow and the third (the only male) made no feeding visits, although its mate delivered 5 feeds. Other non-manipulated young at the site received a mean of 5 feeds on 16th June. It was, therefore, assumed that the behaviour of all 3 trial birds lay within the range of patterns considered normal and that the field protocol was appropriate for a DLW study.

6.2.2 Protocol for each labelled bird.

Adults were captured either by hand from the burrow (while brooding) or with purse nets (when visiting chicks with food). Each was weighed and injected intraperitoneally with $10\mu l g^{-1}$ of heavy water (0.524g of 99% D_2O in 10ml 14APE $H_2{}^{18}O$). The bird was measured (Chapter 2, section 2.2.3) and held in a cloth bag in a quiet, dark, cool place for 1.5 hours from the time of injection, to allow equilibration of the isotope dose with the body water pool. Following this equilibration period, 6-10 heparinized glass capillary tubes (each 10 µl) of blood were collected from a leg or wing vein (= initial blood sample) and the capillaries were flame-sealed immediately by an assistant. Blood flow from the wound was restricted, the wound was cleaned and 'Germolene' was applied. Before being released (either from the breeding site or from the laboratory, less than 500m away) each bird was uniquely marked on the breast with yellow picric dye. In 1992, birds were also marked on the back of the head with a small, numbered tape tag attached to a few feathers with superglue. In 1992, 9 injected birds were released immediately after dosing, without taking an initial blood sample, to minimise holding time and the effects on subsequent behaviour this may have caused in 1991.

The behaviour of the labelled birds at the breeding site was observed during daylight hours (see below). Recaptures were effected with purse nets or trapdoors (when birds made feeding visits) or with box traps 35-96 hours after the time of the initial blood sample; each bird was re-weighed and a final blood sample was collected immediately from a vein in the opposite wing or leg to that used for the initial sample. Blood samples were obtained from 3 unlabelled adult Puffins in 1991 and 4 in 1992 in order to determine natural concentrations of oxygen-18 and deuterium.

6.2.3 Individuals, sites and observation periods.

In 1991 13 birds were labelled, 7 at the Little Hide site and 6 at Colm Hide c250m to the south. At Colm Hide, birds were extracted from burrows while brooding chicks, while at Little Hide they were caught in purse nets when delivering chick feeds. Burrows used at Little Hide were very deep (chicks unobtainable) and were, therefore, not used for other work at the site. In 1992 16 birds were labelled in 2 sessions at Drumcarrach, c.0.5km north of Little Hide; all birds were caught in purse nets. Only one bird from each pair was labelled except for 2 cases in 1991.

All labelled birds were observed for at least one full dawn-to-dusk period before recapture. At Little Hide the daily feeding frequency to burrows with labelled birds was compared to that for other monitored control burrows at the site (used in other parts of the study). At Colm and Drumcarrach, control feeding rates were obtained by marking a number of burrows in addition to those containing labelled birds. Control burrows were assumed to contain chicks if they received at least one feed on any dawn-to-dusk watch-day and only these burrows were used to calculate control feeding rates; the feeding frequencies of controls would have been overestimated slightly if any marked burrow contained a chick which did not receive a feed on that day.

The young of labelled birds were aged, where possible, by bill measurement (Chapter 2, section 2.5.2) or from the date of observed first feeding (for regularly observed burrows at Little Hide). At Drummcarrach, chick age limits were determined, for chicks which could not be measured directly, from 2 watches (on 31st May and 6th June) carried out prior to the labelling sessions. The purpose of these 2 watches was to assess which marked burrows contained chicks at this time so that parents with chicks more than 10 days old could be selected for labelling. It was assumed that adults with older chicks would be less likely to desert, and that chicks more than than 10 days old would also be able to withstand any short period of reduced feeding caused by the disturbance (as they required less brooding). The use of adults with young older than 10 days also avoided measuring the energy expenditure of adults indulging in extended periods of brooding. Details of individuals labelled, their breeding sites and observations undertaken are summarised in **Table 6.1**. Labelled birds were only sexed if both members of the pair were caught and measured during the season (Chapter 2, section 2.2.4).

6.2.4 Isotopic analyses.

The concentrations of oxygen-18 and deuterium in blood samples were measured using isotope ratio mass spectroscopy at the Scottish Universities Reactor Research Centre at East Kilbride by J.Weir (D) and the author (^{18}O).

The glass capilliaries containing blood samples were stored at room temperature prior to analysis. Concentrations of ^{18}O in blood samples were measured after conversion of sample water to carbon dioxide, via reactions with guanadine chloride and phosphoric acid (Boyer et al,1961; Degen et al,1985). The ratio of ^{18}O to ^{16}O in the carbon dioxide was measured using a VG SIRA 10 isotope ratio mass spectrometer. Concentrations of D were measured after conversion of sample water to hydrogen gas by passing the water through a uranium furnace at 800C (Wong and Klein,1986). The gas produced was collected in activated carbon and analysed using an OPTIMA (VG) isotope mass spectrometer. Full details of sample preparation techniques are given in Tatner and Bryant (1989).

Analyses were carried out in duplicate for each isotope label and each blood sample. A third replicate was analysed if the initial duplicates did not produce concentrations within 3% of one another for ^{18}O and within 5% for D. The mean concentration of the closest pair of replicates was used in subsequent calculations.

Table 6.1

Table 6.1 Details of all Puffins loaded with doubly-labelled water on the Isle of May in 1991 and 1992.

YEAR	BIRD[1]	SEX	SITE[2]	CAPTURE TYPE[3]	RELEASED (date,time)	RELEASE TYPE[4]	WATCHES[5]	FEEDS[6]	FIRST FEED (date,time)	CHICK[7] AGE (d)	RECAPTURE (date,time)
1991	1	?	C	B	17/6 2052 h	B	CON	2	19/6 1300 h	?	NO
1991	2	M	C	B	17/6 2120 h	B	CON	0	-----	21	NO
1991	3	F	C	B	18/6 0733 h	B	CON	5	19/6 1442 h	18	20/6 0632 h
1991	4	?	C	B	18/6 0805 h	B	CON	0	-----	15	NO
1991	5	M	C	B	18/6 1858 h	L	CON	1	20/6 0535 h	18	20/6 0602 h
1991	6	?	C	B	18/6 2000 h	L	CON	?	-----	?	NO
1991	7	M	L	F	28/6 0747 h	L	DDW	0	-----	29	NO
1991	8	?	L	F	28/6 0818 h	L	DDW	0	-----	?	NO
1991	9[a]	F	L	F	28/6 0840 h	L	DDW	1	-----	29	NO
1991	10[b]	M	L	F	28/6 1008 h	L	DDW	2	-----	6	1/7 1454 h
1991	11[a]	M	L	F	30/6 0843 h	C	DDW	0	-----	31	3/7 1054 h
1991	12	?	L	F	30/6 1006 h	C	DDW	0	-----	32	NO
1991	13[b]	F	L	F	30/6 1037 h	C	DDW	0	-----	8	NO
1992	17	?	D	F	16/6 0635 h	B	CON	2	18/6 0623 h	>10<17	19/6 0545 h
1992	18	F	D	F	16/6 0702 h	B	CON	9	17/6 0853 h	>17	19/6 0640 h
1992	19	?	D	F	16/6 0716 h	B	CON	5	18/6 0617 h	>10<17	20/6 0614 h
1992	20	?	D	F	16/6 0729 h	B	CON	3	18/6 0515 h	>17	NO
1992	21	?	D	F	16/6 0756 h	B	CON	3	18/6 0623 h	>10<17	NO
1992	22	?	D	F	16/6 0814 h	B	CON	3	18/6 0737 h	14	19/6 0523 h
1992	23	?	D	F	16/6 0940 h	B	CON	6	18/6 0747 h	>17	NO

1992	25	F	D	F	29/6 0542 h	B	CON	2	30/6 1722 h	>23	NO
1992	26	?	D	F	29/6 0610 h	B	CON	0	-----	<23	NO
1992	27	?	D	F	29/6 0625 h	B	CON	0	-----	<23	NO
1992	28	?	D	F	29/6 0821 h	B	CON	4	30/6 1623 h	26	1/7 1051 h
1992	29	F	D	F	29/6 0840 h	B	CON	3	29/6 2127 h	>23<29	1/7 1230 h
1992	30	?	D	F	29/6 0805 h	B	CON	1	30/6 1759 h	<23	NO
1992	31	?	D	F	29/6 0900 h	B	CON	3	30/6 1650 h	<23	NO
1992	32	?	D	F	29/6 1000 h	B	CON	1	30/6 1112 h	>29	NO
1992	33	?	D	F	29/6 1203 h	B	CON	0	-----	>23<29	1/7 0927 h

NOTES.

1 Birds with the same letters from the same burrow
2 Sites : C=Colm's Hide, L=Little Hide, D=Drumcarrach
3 Capture type : F=feeding chicks, B=brooding chicks
4 Release type : B=burrow, C=aerial at the colony, L=aerial at the laboratory
5 Watches : CON=continuous watching from time of release, DDW=single dawn-to-dusk watch only
6 Feeds : total number made by the labelled bird during the period for which it was watched
7 Age of the chick on the day of labelling

6.2.5 Calculation of energy expenditure.

Rates of carbon dioxide production were calculated from differences in the turnover rates of the oxygen and hydrogen labels using **equation 6.1** (equation 35 in Lifson and McClintock (1966)) :

$$rCO_2 = \frac{N}{2.08}(k_O - k_D) - 0.015k_DN$$ **Equation 6.1**

where
rCO_2 = carbon dioxide production rate (mMh^{-1})
2.08 = product of a fractionation factor ($H_2{}^{18}O_{(lq)}$ to $C^{16}O^{18}O_{(g)}$ = 1.04) and a stoichiometric factor (CO_2 has the oxygen equivalent of 2 molecules of H_2O)
N = volume of the body water pool (mM)
$0.015k_DN$ = correction for the fractionation effects due to evaporative water loss, assuming this accounts for 50% total water loss.
k_O and k_D = fractional turnover rates of oxygen and hydrogen labels respectively (calculated from **equation 6.2**)

$$k_O = \ln(^{18}O_i - ^{18}O_{bk}) - \ln(^{18}O_f - ^{18}O_{bk}) / t$$ **Equation 6.2**

where
$^{18}O_i$ = initial concentration of ^{18}O (ppm)
$^{18}O_f$ = final concentration of ^{18}O (ppm)
$^{18}O_{bk}$ = background concentration of ^{18}O in unlabelled birds (ppm)
t = time between initial and final blood samples (h)

For k_D replace ^{18}O with D in **equation 6.2**

The volume of the body water pool for each labelled individual was calculated from the mean water content of 13 breeding Puffins, killed immediately after weighing and freeze-dried to constant mass (Chapter 4), using **equation 6.3** :

$$N = (M*0.63) * (1000/18)$$ **Equation 6.3**

where
N = volume of body water (mM)
M = mean of initial and final mass measurements (g)
0.63 = mean proportional body water content
1000/18 = conversion of g H_2O to mM

In the case of the 3 individuals for which initial blood samples were not obtained, initial blood concentrations of ^{18}O and D were estimated from the mean mass-specific values for initial blood samples for the other 7 individuals which were recaught (assuming a mean equilibration period of 98 minutes).

The natural abundance level for ^{18}O was 2017ppm (range 2014-2019ppm) in 1991 and 2019ppm (range 2015-2024) in 1992. For deuterium the background was 151ppm (range 149-155ppm) in both years. Tatner and Bryant (1989) suggested that the lowest acceptable final excess ^{18}O concentration should be 40ppm above background and this was the criterion used in the present study. Two birds (numbers 11 and 19) were excluded from the analyses because final ^{18}O concentrations were below this threshold level.

Rates of carbon dioxide production were used to derive the average daily metabolic rate (ADMR in $cm^3CO_2g^{-1}h^{-1}$) using **equation 6.4** :

$$ADMR = rCO_2 * 22.4/M \qquad \textbf{Equation 6.4}$$

where 22.4 = conversion of mM CO_2 to cm^3
M = mean of initial and final body mass (g)

Daily energy expenditure (DEE in kJd^{-1}) was calculated, assuming a respiratory quotient (RQ) of 0.80 (Bryant and Furness,unpubl.), using **equation 6.5** :

$$DEE = ADMR * M * 24 * 25.13 \qquad \textbf{Equation 6.5}$$

where 24 = conversion from h to d
25.13 = conversion cm^3 CO_2 to kJ, assuming an RQ of 0.80 (Brody,1945)

The basal metabolic rate (BMR) of breeding adult Puffins from the Isle of May (n=4) was measured by Bryant and Furness (unpubl.). Based on their results, the BMR of a 395g Puffin (the mean mass of the 9 labelled birds which were recaught) is $10.55kJh^{-1}$ or 253 kJd^{-1}, assuming that BMR scales to body mass with an exponent of 0.796 (Bryant and Furness,unpubl., based on 11 species of Scottish seabird). This value for BMR was used in calculations of estimated DEE (see below), while the BMR's of labelled individuals were calculated as the product of mass-specific BMR and body mass. The metabolic intensity of each individual was calculated by dividing FMR by BMR.

6.2.6 Statistical analyses.

All relationships were initially examined by plotting and correlation, before inclusion of any variables in multiple regression models. To avoid some of the statistical problems associated with the analysis of ratios (Blem,1984), such as mass-specific FMR (ADMR), the dependence of FMR on a range of variables was examined by using DEE (kJd^{-1}) as the dependent variable in multiple regression, while always including body mass (mean of mass at the first and second blood sampling) as an independent variable. Adult body condition was expressed as total reserve mass (TRM, g), the derivation of which is discussed in Chapter 4. Only 4 body size measures (wing length and the 3 bill measurements) were used in the analyses, as these were the ones available for all 9 loaded birds (Chapter 2, section 2.2.3). The influence of the mean over the DLW measurement period of 6 weather variables (defined in Chapter 2, section 2.8) on FMR was analyzed by producing separate correlations for each variable with FMR and by multiple regression.

6.2.7 Comparison of field metabolic rates with estimated DEE.

The mean FMR (kJd^{-1}) measured in this study was compared to DEE estimated from (a) the allometric equations of Birt-Friesen (1989), relating seabird body mass to field metabolism, and (b) from a TAL (time-activity-laboratory) calculation (Mugaas and King,1981), using time budget data collected in the field and published measurements of activity-specific metabolic intensity (multiples of BMR). All calculations were made for a 395g Puffin (the mean mass of the 9 recaptured birds) unless otherwise stated and were the same regardless of sex.

6.2.7.1 Estimation of DEE from body mass.

FMR (kJd^{-1}) was estimated from body mass (kg) using **equation 6.6** (Birt-Friesen et al,1989, derived from 8 species of cold-water seabird using predominantly flapping flight) :

$$\text{FMR} = 3.24\ \text{Mass}^{0.727}$$ **Equation 6.6**

A second calculation was made using separate allometric equations (**equations 6.7 and 6.8** respectively) for metabolism at the nest (MET_N in kJh^{-1}, for 10 seabird species) and metabolism at sea (MET_S in kJh^{-1}, for 10 non-gliding seabird species)(Birt-Friesen et al,1989)

$$MET_N = 1.45\ \text{Mass}^{0.737}$$ **Equation 6.7**

$$MET_S = 1.89\ \text{Mass}^{0.662}$$ **Equation 6.8**

Puffins on the Isle of May spent the hours of darkness (c.5h in June/July) at sea (pers.obs.)

and 16.3% of the daylight hours at the colony during chick rearing (mean for the two sexes, Chapter 3). Although Puffins attending the colony participated in a range of activities (see below), **equation 6.7** was used for the 3.1h of the day that Puffins were ashore, while **equation 6.8** was used to calculate energy expenditure for the 20.9h spent away from the colony each day.

6.2.7.2 Estimation of DEE from a TAL budget.

Seabirds are less amenable to the development of time-activity-laboratory (TAL) budgets than many terrestrial species because of the practical difficulties of monitoring their activities at sea. Only recently have attempts been made to quantify seabird time budgets and activity-specific metabolic costs, with the application of the DLW technique to measure FMR and the advent of various devices for recording activities at sea (eg. Nagy et al,1984; Trivelpiece et al,1986; Wanless et al,1988a; Cairns et al,1987,1990; Gales et al,1990). Puffins seem particularly sensitive to the attachment of activity recording devices (S.Wanless and M.P.Harris,pers.comm.) and the use of such devices was not attempted in this study. Radio-tracking data are, however, available for a single Puffin from the Isle of May (Wanless et al,1988a and b) but construction of the TAL budget still necessitated several unverified assumptions about Puffin time allocation to various activities. In the present study, the TAL budget is mainly used as an exploratory tool to investigate how variation in parental time allocation to various activities might affect DEE, with special reference to chick feeding frequency.

Activity-specific metabolic costs.

Puffin activities were divided into 5 categories and each was allocated an appropriate metabolic intensity (BMR multiple) based on published activity-specific metabolic costs **(Table 6.2)**. Puffins attending the colony during chick rearing spend most of their time standing on rocks, preening and walking around the colony; they sometimes become involved in interactive behaviour, such as billing with conspecifics (Taylor,1984). Colony attendance time may also involve periods of rest, where birds lie on their breasts, and periods of more vigorous activity, such as 'wheeling' flight over the colony or aggressive encounters. No attempt was made to quantify the exact proportion of time spent in these onshore activities because the time allocation was highly variable, depending both on weather conditions and the number of individuals present at the colony (pers.obs.). Instead a value of 4 times BMR,

Table 6.2 **Activity-specific metabolic costs used in the TAL budget to predict the daily energy expenditure of Puffins on the Isle of May during chick rearing.**

ACTIVITY CATEGORY	MULTIPLE OF BMR	METABOLIC COST[1] (kJh^{-1})
Sitting on sea (night)	1.5	15.83
Sitting on sea (day)	2.0	21.10
Above ground at colony	4.0	42.20
Flying	7.7	81.24
Diving	6.0	63.30

NOTE.

1 For a 395g Puffin for which BMR = 10.55 kJh^{-1} or 253 kJd^{-1}

equivalent to the cost of 'walking' in penguins (Pinshow et al,1977; Dewasmes et al,1980), was used to represent the overall cost of attending the colony; lower cost activities (eg. rest and preening) and higher cost activities (eg. flying and infrequent fights) were assumed to balance each other (for the costs of these activities see below).

Most Puffins spent the night at sea during rearing and were assumed to rest rather than fly or dive during this time; Puffins do not deliver feeds to their young during the hours of darkness (Harris,1984; pers.obs.). The value of 1.5 times BMR used for the cost of resting on the sea at night was within the range of published empirical values (Schartz and Zimmerman,1971; Utter and LeFebvre,1973; Holmes et al,1979; Bryant et al,1985) and is the multiple of BMR commonly used in TAL budgets (eg. Burger,1981). Puffins floating on the sea surface during the day sometimes swim slowly about, sometimes preen and occasionally use their wings to 'fly' across the surface of the water if they are disturbed (pers.obs.). The value of 2 times BMR used to represent the cost of being on the surface of the sea was within the range of metabolic intensities for the cost of slow surface swimming in ducks of 3.5 times BMR (Prange and Schmidt-Nielsen,1970) and 3.1 times BMR in penguins (Hui,1983) and the cost of resting of c1.5 times BMR (see above); once again lower cost activities (sitting,preening) and higher cost activities (escape 'flights') were assumed to balance each other.

Few empirical measurements of flight or diving costs are available for seabirds. Measurements and derivations made in the laboratory have resulted in flight costs ranging from 3.1 times BMR for gliding in Herring Gulls (Baudinette and Schmidt-Nielsen,1984) to 11.1 times BMR for flapping flight in Laughing Gulls (Tucker,1972). Recent measurements of flight costs measured in free-ranging seabirds using DLW have produced BMR multiples of 2.4 in the Wandering Albatross (Adams et al,1986), 3.2 in the Grey-headed Albatross (Costa and Prince,1987), 4.2 in Wilson's Storm-petrel (Obst et al,1987), 4.8 in the Sooty Tern (Flint and Nagy,1984) and 11.3 in the Gannet (Birt-Friesen et al,1989). Clearly, species-specific aerodynamic and hydrodynamic adaptations might cause flight costs to vary substantially, making it difficult to select a flight cost for Puffins from the limited range of empirical measurements available. Seabirds display a continuum of foraging modes and associated locomotive adaptations ranging from those flying almost continuously while foraging (which include the albatrosses, Sooty Tern and Wilson's Storm-petrel) to those non-volant species which swim and dive to forage (penguins). Puffins and other auks practice both aerial and underwater locomotion, using their wings for propulsion in both media; thus they seem to represent a compromise between avian adaptations for locomotion in air and in water (Storer,1960). In support of this, auks have reduced wing span and wing area compared to other flying seabirds of similar mass (Pennycuick,1987). Of the seabird species for which field flight costs have been measured, only the Gannet uses its wings for propulsion underwater in a similar way to the auks, although to a more limited extent than the latter. There is, however, some evidence to suggest that Gannets have a low mass-specific BMR relative to other seabirds breeding in cold waters (Birt-Friesen et al,1989), which will elevate flying costs when they are expressed as a multiple of BMR. Power requirements for flapping flight (estimated from the computer programs of Pennycuick,1989) ranged from 4 to 5 times BMR for the range of observed Puffin flight speeds (discussed below). The value of 7.7 times BMR chosen to represent Puffin flight costs in the TAL budget came not from a seabird but from a value of 7.7 times BMR derived for the Dipper (Bryant et al,1985). This species uses its wings for both aerial and underwater propulsion, thus its flight costs should be more similar to those of Puffins than flight costs for seabirds which forage almost exclusively by aerial means. The flight cost of 7.7 times BMR fell within the central part of the range of measured flight costs.

Even fewer studies have measured avian diving costs and these have produced values of 6 times BMR for Dippers (Bryant et al,1985; Bryant and Tatner,1988), 6.1 times BMR for Adelie Penguins (Culik and Wilson,1991), 9.8 times BMR for Jackass Penguins (Nagy et al,1984) and 3.5 times the resting metabolic rate for Tufted Ducks, which use feet for propulsion under the water,(Woakes and Butler,1983). The value of 6 times BMR was chosen for the TAL budget because of the similarity between Dippers and auks in the use of wings for both underwater propulsion and flight. The cost of diving for Adelie Penguins was very similar, while that for Jackass Penguins may have been elevated because BMR was estimated from the allometric equation of Lasiewski and Dawson (1967) rather than being empirically measured; this equation has been shown to underestimate penguin BMR by a mean of 10% and a maximum of 26% (Ellis,1984), so use of a measured BMR value could reduce Jackass Penguin diving costs to 9 times BMR (10% underestimate of BMR) or even 7.8 times BMR (with 26% underestimate of BMR).

The TAL budget did not include thermoregulatory costs as a separate component. Ambient air temperatures during the DLW study ranged from 10.1-13.8°C and the sea temperature was 12°C at a depth of 20m in June (A.Russell,pers.comm.). Bryant and Furness (unpubl.) found no thermostatic effect on BMR's of 11 species of Scottish seabird, including the Puffin, in the temperature range 9-15°C; thus free-ranging Puffins were assumed to be operating within the thermoneutral zone in this study, at least when they were on land. This thermoneutrality may have been compromised in water, especially during diving (Wilson et al,1992), because of the reduction in the insulatory properties of air in the plumage. Empirical data are not, however, available to allow correction for such thermoregulatory expenses and these costs were, therefore, assumed to be contained within the costs of diving and surface swimming used in the TAL budget. Any thermoregulatory cost incurred because of loss of the insulatory capacity of the plumage during flight was assumed to be met by heat generated during flying (Tucker,1968).

Time budget.

In June/July each full day on the Isle of May consists of approximately 19h of daylight and 5h of darkness. Puffins spent all the hours of darkness at sea (pers.obs.) and 16.3% of the daylight period (ie. 3.1h) attending the colony (Chapter 3). This colony attendance time did not include brief provisioning visits to chicks, which at this stage of rearing (most chicks more than 10d old and rarely brooded) lasted only a matter of seconds (pers.obs.) and were thus considered negligible. The remaining 15.9h of daylight were spent flying to and from the colony with chick meals, foraging (diving) and swimming on the surface of the sea.

In the absence of empirical time budget data for Puffins at sea, the duration of a single foraging trip formed the basis of a time budget estimate. As both parents feed the young, the mean time of 2.4h between the delivery of alternate feeds to a burrow has been used to represent the duration of a feeding trip for Puffins on the Isle of May (Harris and Hislop,1978); the two shortest previously recorded trips lasted only 6 and 14 minutes, however, and birds often brought fish back to the colony alive, indicating that food could be obtained close to the colony. The duration of foraging trips is most useful when measured early in the morning, when adults are provisioning chicks most intensely (Harris,1984 and **Figure 6.1**). Trip durations recorded later in the day were much longer (pers.obs.) and were assumed to include time spent self-feeding and 'loafing' on the sea surface. In this study, the durations of 132 foraging trips (by 47 individuals) were recorded for birds which arrived back at the colony before 0800h. The period from dawn to 0800h was the period of peak chick provisioning at the colony, when 40% of all feeds were delivered (**Figure 6.1**). The mean trip duration was 0.81h but the distribution of trip durations was highly negatively skewed (**Figure**

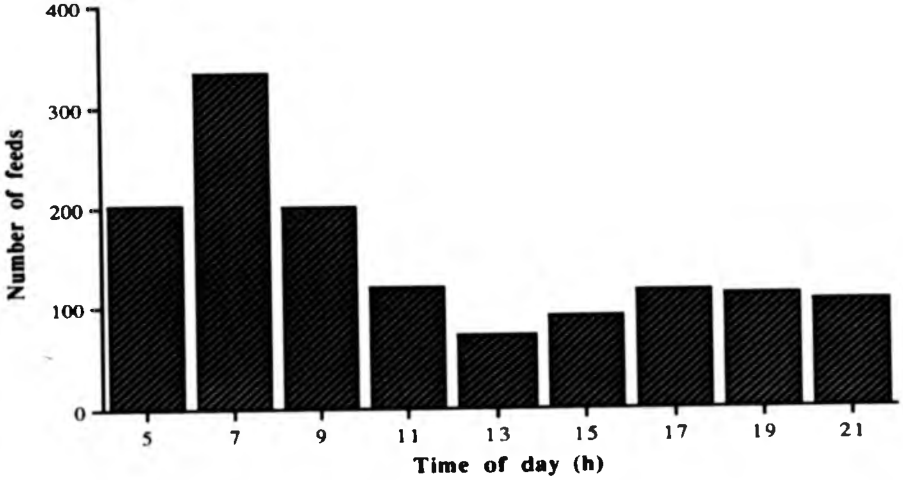


Figure 6.1 Distribution with time of day of feeds delivered to Puffin young on the Isle of May in 1992.
(From a total of 1348 observed food deliveries to burrows at Little Hide)

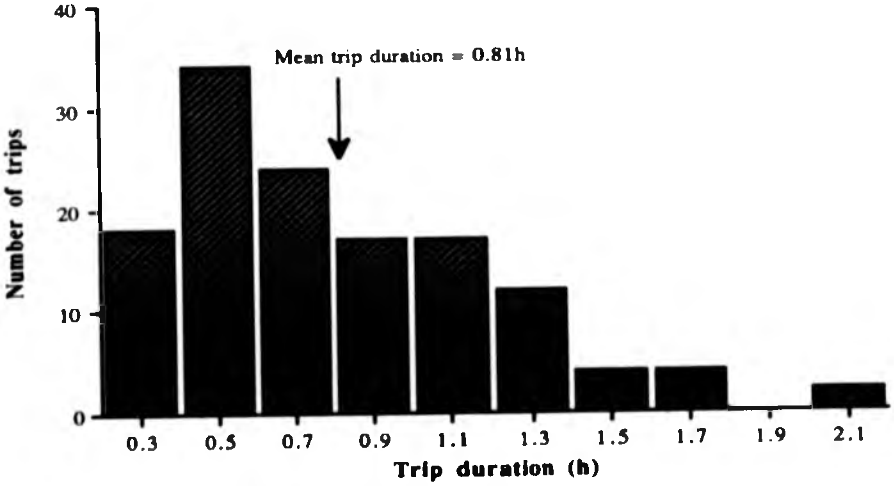


Figure 6.2 Duration of foraging trips, started and finished before 0800h, made by Puffins on the Isle of May in 1992.
(From a total of 132 trips made by 47 individuals)

6.2); the modal duration of 0.5h was, therefore, chosen to represent trip duration in the TAL budget.

The time spent making a single foraging trip (0.5h) was partitioned into time spent flying, diving and on the surface of the water. The single Isle of May Puffin tracked in 1987 always fed out of view from the shore (ie. more than 1km away) but 9/14 foraging trips were within 2km of the colony (Wanless et al,1988b). Similarly, on Skomer, most Puffins fed between 3km and 7km from the colony and none further than 13km (Corkhill,1973; Ashcroft,1976; Birkhead,1976). For the TAL budget Puffins were assumed to forage 1.5km from the colony. Puffin flight speed has been timed as 82kmh^{-1} (Meinertzhagen,1955) and 48kmh^{-1} (Corkhill,1973) but the value used to calculate flight time here was 63 kmh^{-1} (Pennycuick,1987); this speed was midway between the two other empirical measurements and was similar to the maximum range speed of 58kmh^{-1} estimated for a 395g Puffin (Pennycuick,1989). Puffins were assumed to fly in a straight line from the colony to the foraging site and back (verified by Wanless et al,1988b); the return flight time per trip (of 1.5km *2 at a speed of 63kmh^{-1}) was, therefore, 0.1h. The remaining 0.4h of each trip was assumed to represent a single foraging bout; the longest bout recorded by Wanless et al (1988a) was 1.4h so a bout of 0.4h was well within the reported range for a Puffin. The single tracked Puffin spent 78% of each foraging bout underwater and 22% in pauses on the surface (Wanless et al,1988a), which represented 0.3h diving and 0.1h on the surface per foraging trip in this study.

In the TAL calculation it was assumed that adults foraged for their own needs outwith the time spent foraging to provision chicks; time spent diving was, therefore, maximised in the calculation, rather than being a conservative estimate. It was assumed that adults fed themselves before they began feeding their young in the early morning, between trips or in the evening when they returned to sea after delivering the last feed of the day. It was assumed that they did not make extra flights to feed themselves or to attend the colony and this was supported by observations; Puffins rarely arrived at the colony without a food load during rearing except in 'poor' weather (pers.obs.). The diving time required for adult self-feeding was estimated by predicting both average chick DEE during rearing and adult DEE, for a 395g adult, from allometric equations. Chick DEE was estimated as 196kJd^{-1} (equation 6 in Walsberg,1983) and adult FMR as 885kJd^{-1} (from Equation 6.6 above, Birt-Friesen *et al*, 1989). It was assumed that each adult supplied 50% of the daily chick intake, so that the diving time required for self-feeding was 855kJd^{-1}/(196kJd^{-1}/2) = 9 times that required to provision an average chick (receiving c.2 feeds d^{-1} from each parent in this study, **Table 6.3**). Each parent therefore spent (0.3h $trip^{-1}$ * 2 feeds d^{-1} * 9) = 5.4h diving for self-feeding each day.

The DEE of a 395g Puffin was estimated, using the TAL method, for the range of daily feeding rates (0-3 feeds d^{-1}) made by labelled birds. It was also estimated for a feeding rate of 8 feeds d^{-1}, which was the maximum number of feeds seen delivered to a chick by a single adult in the 3 years of this study (derived from 16 feeds d^{-1} assuming each parent delivered 50%). It was assumed that the diving time required by the adult for self-feeding remained constant (at 5.4h d^{-1}) over the range of feeding rates considered, and that the extra time spent flying and diving with increasing feeding rate was traded off against time spent on water, rather than time spent at the colony (as there was no relationship between time spent above ground at the colony and chick feeding rate in this study (Chapter 5).

DEE was also estimated for Puffins of mass 374g and 411g, which was the observed mass range of the 9 recaptured labelled birds; in these calculations mass was assumed only to influence BMR, not the costs of locomotion.

6.3 RESULTS.

6.3.1 Puffin field metabolic rates during rearing.

Measured FMR for the 9 Puffins averaged 3.67 (+/-0.65 s.d) $cm^3CO_2g^{-1}d^{-1}$ or 874 (+/-151 s.d) kJd^{-1} (**Table 6.4**). Mean MI was 3.45 (+/-0.64 s.d). There was no obvious difference in energy expenditure between years or between sexes (although sample sizes were too small to make statistical comparisons) and so the results from all birds were pooled in subsequent analyses.

Measured FMR (874 kJd^{-1}) was 99% of the value predicted from Birt-Friesen et al's (1989) equation for a bird of 395g using predominantly flapping flight in a cold-water environment (885 kJd^{-1}). When the separate equations for metabolism at sea and at the nest were used, in conjunction with estimated time-budget data, measured FMR was 95% of the predicted value (921 kJd^{-1}).

The 9 labelled birds which were recaught each delivered a mean of 2 feeds d^{-1} to their young (**Table 6.3**). Their measured FMR was 108% of DEE predicted using the TAL budget (811

Table 6.3

Table 6.3 **Comparison of the numbers of feeds delivered to Puffin chicks with DLW loaded and control parents on dawn-to-dusk watch days in 1991 and 1992.**

DATE	LABELLED BIRD[1]	FEEDS TO LABELLED BURROWS (d^{-1}) LABELLED	PARTNER	UI[2]	TOTAL	COMPARISON WITH[3] CONTROL FEEDS (d^{-1})	MANN-WHITNEY TEST
19.6.91	1	3	0	0	0	LABELLED mean=3.3 SE=1.0 median=2.5 n=6 CONTROL mean=4.9 SE=0.7 median=5.0 n=14	U = 27.5 p > .2 NS
	2	0	3	1	4		
	•3	4	3	1	8		
	4	0	1	1	2		
	•5	0	1	0	1		
	6	?	?	2	2		
29.6.91	7	0	5	0	5	LABELLED mean=3.5 SE=1.8 median=3.0 n=4 CONTROL mean=4.4 SE=0.5 median=4.0 n=32	U = 53.0 p > .5 NS
	8	0	0	0	0		
	9	0	1	0	1		
	•10	1	6	1	8		
2.7.91	11	0	0	0	0	NO CONTROLS WATCHED	
	12	0	?	?	?		
	13	0	?	?	?		
17.6.92	•17	0	1	1	2	LABELLED mean=2.1 SE=1.2 median=1.0 n=7 CONTROL mean=5.7 SE=0.6 median=6.0 n=28	U = 32.5 p < .01
	•18	3	5	1	9		
	19	0	1	0	1		
	20	0	1	0	1		
	21	0	2	0	2		
	•22	0	0	0	0		
	23	0	0	0	0		

18.6.92	*17	1	5	0	6	LABELLED mean=5.3 SE=0.8 median=5.0 n=7 CONTROL mean=4.1 SE=0.4 median=4.0 n=31	U = 76.0 p > .2 NS
	*18	5	2	0	7		
	19	5	4	0	9		
	20	2	0	1	3		
	21	2	1	0	3		
	*22	2	1	1	4		
	23	4	0	1	5		
30.6.92	25	2	6	0	8	LABELLED mean=6.8 SE=1.5 median=6.0 n=9 CONTROL mean=7.9 SE=0.6 median=8.0 n=21	U = 75.0 p > .3 NS
	26	0	3	1	4		
	27	0	5	1	6		
	*28	4	6	1	11		
	*29	2	2	1	5		
	30	1	14	0	15		
	31	4	0	0	4		
	32	1	7	0	8		
	*33	0	0	0	0		

NOTES.

1 Where * indicates that the labelled bird was recaught and an FMR measurement was obtained

2 Unidentified bird delivering a feed

3 Overall feeding rates :

ALL LABELLED BURROWS	mean=4.5 SE=0.6 median=4.0 n=33 chick days
ALL CONTROL BURROWS	mean=5.2 SE=0.3 median=5.0 n=126 chick days
ALL LABELLED BIRDS	mean=1.3 SE=0.3 median=0.0 n=35 bird days
LABELLED BIRDS (RECAUGHT)	mean=1.8 SE=0.5 median=1.0 n=12 bird days

Table 6.4 Field metabolic rates of 9 adult Puffins measured during chick rearing on the Isle of May in 1991 and 1992.

BIRD	YEAR	SEX	MASS[1]	MASS CHANGE (%d^{-1})	ADMR (cm^{3}CO$_2$g^{-1}h^{-1})	DEE (kJd^{-1})	BMR (kJd^{-1})	MI[2]	DURATION[3] (h)	DARK[4] (%)	NORMAL[5] (%)	FEEDS[6] (d^{-1})	WEATHER[7]
3	1991	F	374	-0.28	3.83	865	242	3.57	47.0	21	44	2.56	'GOOD'
5	1991	M	404	-0.51	2.91	707	258	2.74	35.1	28	30	0.75	'GOOD'
10	1991	M	406	-2.32	3.50	855	259	3.30	76.8	20	?	?	'GOOD'
17	1992	?	411	-0.82	3.50	868	262	3.31	71.8	21	48	0.67	'GOOD'
18	1992	F	379	-1.17	2.56	585	244	2.40	71.4	21	71	3.03	'GOOD'
22	1992	?	411	0.42	3.77	933	261	3.58	69.2	22	46	1.06	'GOOD'
28	1992	?	387	-0.12	4.95	1153	249	4.63	50.5	20	46	1.88	'POOR'
29	1992	F	393	-2.30	3.96	938	252	3.72	51.8	19	75	1.36	'POOR'
33	1992	?	394	4.01	4.07	965	252	3.83	45.4	22	22	0.00	'POOR'
Mean			395	-0.34	3.67	874	253	3.45	57.7	22	48	1.41	
SD			14	1.88	0.65	151	7	0.64	14.8	2.6	18	1.02	
n			9	9	9	9	9	9	9	9	8	8	

NOTES.

1 Mean of weighings at the time of the first and second captures
2 Metabolic intensity (FMR divided by BMR)
3 Duration of the DLW measurement period
4 Proportion of the measurement period for which it was dark
5 Proportion of the measurement period spent in normal behaviour (see text for calculation)
6 Calculated as the total number of chick feeds delivered by the labelled bird during the measurement period divided by the total number of daylight hours in the measurement period and multiplied by the 19 daylight hours in a day
7 'GOOD' = total rainfall 2mm, mean visibility 31km, mean wind speed 4ms^{-1}, mean 34% onshore winds
'POOR' = total rainfall 24mm, mean visibility 10km, mean wind speed 11ms^{-1}, mean 100% onshore winds

kJd^{-1}) for an individual delivering 2 chick feeds each day (**Table 6.5**). The TAL budget predicted that variation in the daily feeding rate from 0 to 3 feeds would cause DEE to vary from 779 kJd^{-1} (3.08 times BMR) to 829 kJd^{-1} (3.27 times BMR), a difference in energy expenditure of only 6%. If the number of feeds delivered in a day was increased to 8, predicted DEE increased to 923 kJd^{-1} (3.65 times BMR), when adult food intake was held at 18 times that of the average chick (**Table 6.5**).

The mass variation of the 9 labelled individuals (374g to 411g) caused predicted DEE from the TAL budget to range from 776 kJd^{-1} to 837 kJd^{-1}, a difference of 8% (**Table 6.5**).

6.3.2 Factors influencing adult FMR during chick rearing.

DEE was not related to mean body mass during the measurement period (**Figure 6.3a**), mass change between the first and second blood sampling (**Figure 6.3b**) or any of the 4 body dimensions (p>.1, n=9). There was suggestion of a positive correlation between body condition and DEE (**Figure 6.3c**) but this was caused by a single individual with low reserve mass and low DEE, and the correlation was not significant. DEE was not related to the daily chick feeding rate (**Figure 6.4**) nor to chick age, where the latter was used as a further predictor of feeding effort (Chapter 5). There was, however, suggestion of a negative relationship between body mass at the start of the measurement period and and the subsequent daily feeding rate (**Figure 6.5**), although the correlation was not significant. The small numbers of loaded individuals which were recaught limited the resolution of analyses of factors contributing to variation in FMR however.

Of the 6 weather variables, only total rainfall was significantly correlated with DEE (**Figure 6.6**). Total rainfall during the measurement period was itself highly positively correlated with mean windspeed (Pearson correlation r=.920,p<.0001,n=9) and with the proportion of onshore winds at Little Hide (r=.928,p<.0001,n=9) and was highly negatively correlated with mean visibility (r=-.976,p<.0001,n=9) however. This suggested that the total rainfall variable was indicative of 'poor' weather conditions in general.

6.3.3 Effect of the labelling protocol on behaviour.

In any study using doubly-labelled water, it is important to assess whether the behaviour of labelled birds is altered by the field protocol and, if so, whether the behavioural alterations

Table 6.5 **Calculation of DEE for adult Puffins on the Isle of May during chick rearing using the TAL budget : predicted variation in DEE caused by variation in the daily number of feeds delivered to chicks and in adult body mass.**

	VARIATION IN CHICK FEEDING RATE FOR EACH ADULT					VARIATION IN MASS	
Bird mass (g)	395	395	395	395	395	374	411
BMR[1] (kJh^{-1})	10.55	10.55	10.55	10.55	10.55	10.09	10.90
Chick feeds (d^{-1})	0	1	2	3	8	2	2
DAILY COSTS ON SEA (NIGHT)							
Time on sea (hd^{-1})	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Cost on sea[2] (kJh^{-1})	15.83	15.83	15.83	15.83	15.83	15.14	15.14
Total cost on sea (kJd^{-1})	79	79	79	79	79	76	82
DAILY COSTS AT THE COLONY							
Time at colony (hd^{-1})	3.1	3.1	3.1	3.1	3.1	3.1	3.1
Cost at colony[2] (kJh^{-1})	42.20	42.20	42.20	42.20	42.20	40.36	43.60
Total cost at colony (kJd^{-1})	131	131	131	131	131	125	135
DAILY FLIGHT COSTS							
Time spent flying[3] (hd^{-1})	0.1	0.1	0.2	0.3	0.8	0.2	0.2
Cost of flying[2] (kJh^{-1})	81.24	81.24	81.24	81.24	81.24	77.69	83.93
Total flight cost (kJd^{-1})	8	8	16	24	65	16	17
DAILY DIVING COSTS (CHICK FEEDING)							
Time spent diving[4] (hd^{-1})	0	0.3	0.6	0.9	2.4	0.6	0.6
Cost of diving[2] (kJh^{-1})	63.30	63.30	63.30	63.30	63.30	60.54	65.40
Total cost of diving (kJd^{-1})	0	19	38	57	152	36	39
DAILY DIVING COSTS (SELF-FEEDING)							
Time spent diving[5] (hd^{-1})	5.4	5.4	5.4	5.4	5.4	5.4	5.4
Cost of diving[2] (kJh^{-1})	63.30	63.30	63.30	63.30	63.30	60.54	65.40
Total cost of diving (kJd^{-1})	342	342	342	342	342	327	353
DAILY COSTS ON THE SEA (DAY)							
Time spent on the sea[6] (hd^{-1})	10.4	10.1	9.7	9.3	7.3	9.7	9.7
Cost on sea[2] (kJh^{-1})	21.10	21.10	21.10	21.10	21.10	20.18	21.80
Total cost on sea (kJd^{-1})	219	213	205	196	154	196	211
TOTAL DEE[7] (kJd^{-1})	779	792	811	829	923	776	837

NOTES.

1 BMR from Bryant and Furness (unpubl.)

2 Calculated using metabolic intensities for on sea at night (1.5*BMR), at colony (4*BMR), flying (7.7*BMR), diving (6*BMR), on sea during the day (2*BMR)

3 Time spent flying = (n trips * h trip^{-1}) where h trip^{-1} = 0.1h

4 Time spent diving = (n trips * h trip^{-1}) where h trip^{-1} = 0.3h

5 Time spent diving for self-feeding assumed to be 9 times that required to feed half an average control chick receiving 4-5 feeds d^{-1} ie. (9 times the 0.6h spent diving for a chick receiving 2 feeds d^{-1} in the table)

6 Time on sea (day) = (24h-time on sea(night)-time at colony-time flying-time diving for chicks and self)

7 Total DEE = (total cost on sea(night)+total cost at colony+total flight costs+total diving costs(chick and self-feeding)+total cost on sea (day))

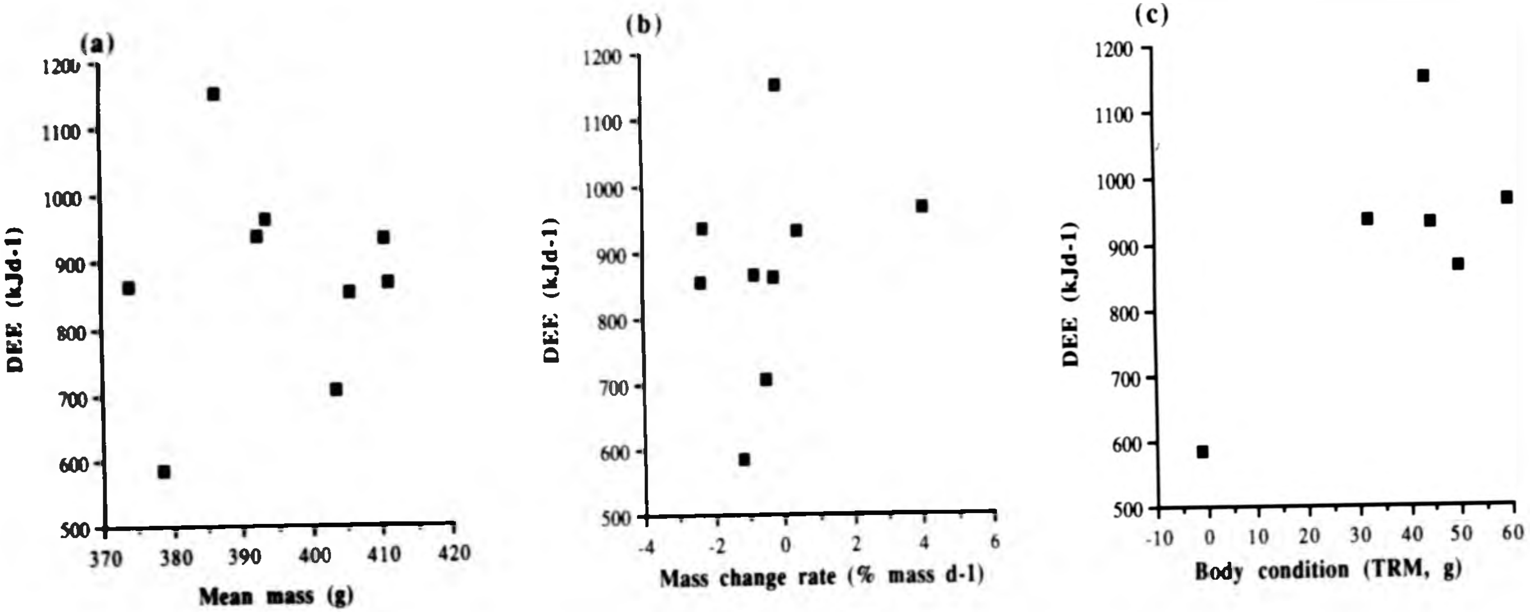


Figure 6.3 Relationships between the field metabolic rate (DEE) of adult Puffins and

(a) mean body mass during the measurement period (Spearman r=.033,p>.4,n=9)
(b) percentage body mass change rate (Spearman r=.533,P>.05,n=9), and
(c) mean body condition during the measurement period (Spearman r=.314,p>.2,n=6).

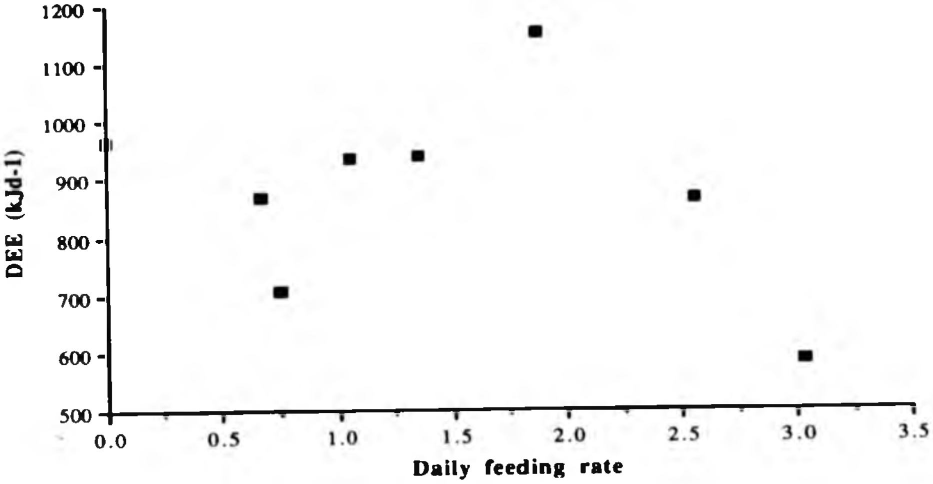


Figure 6.4 Relationship between the field metabolic rate (DEE) of adult Puffins and the daily number of feeds they deliver to young. (Spearman r=-.333, p>.2, n=8).

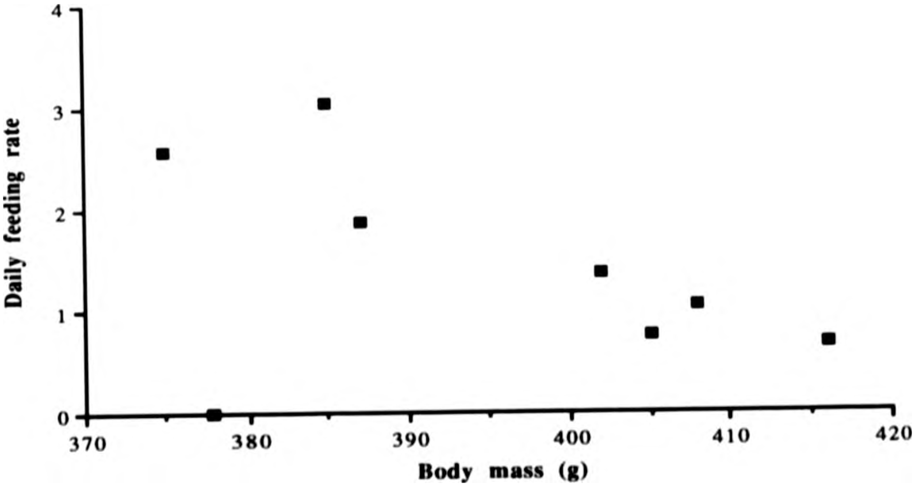


Figure 6.5 Relationship between the daily number of feeds delivered by adult Puffins to young during the DLW measurement period and the body mass of the adults at the start of that period. (Spearman r=-.429, p>.1, n=8).

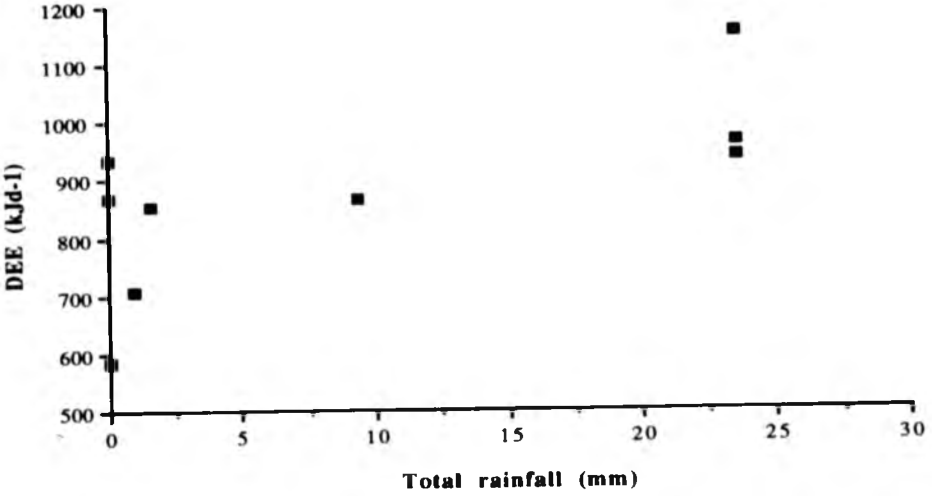


Figure 6.6 Relationship between the field metabolic rates (DEE) of adult Puffins and total rainfall during the DLW measurement period. (Spearman r=.656, p<.05, n=9).

Figure 6.7 Time of the first chick feed delivered after release by 17 DLW loaded adult Puffins after (where the loading day = day x).

Time classes :
1 = Evening of day x
2 = Morning of day x+1
3 = Evening of day x+1
4 = Morning of day x+2
5 = Evening of day x+2

have any measurable effect on FMR.

In this study only 11/29 labelled birds were recaught, partly because some birds were wary of entering their burrows with chick feeds, which suggested that the labelling may have had an effect on behaviour. The recapture rate was not improved by omission of the initial blood sampling and did not vary with the release point after injection. Labelled birds showed a small decrease in mass during the measurement period (a mean loss of $0.34\%d^{-1}$ +/- 1.88% s.d), which was no different from that normally shown by parents during chick rearing (Chapter 5). Labelled birds, therefore, seemed to feed themselves quite normally during the measurement period.

Of the 29 birds injected, 10 were never recorded bringing fish to young during the 2-4 days of observation after labelling (**Table 6.1**). Of the 17 birds which did make feeds and were watched continuously, most did not resume chick feeding until the evening of the day after the labelling day or the morning of the day after that (ie 36-48 hours after their release, **Figure 6.7**). On only one of four dawn-to-dusk watch days did chicks with a labelled parent receive significantly fewer feeds than controls (**Table 6.3**); this occurred on 17th June,1992, the day after labelling, when chicks with labelled parents received less than half the number delivered to controls. On 3 of the 4 other days, chicks with labelled parents received fewer feeds than controls although the differences were not significant. The possibility that partners compensated to some extent for the lower feeding rates of labelled birds could not be dismissed, especially because there were too few labelled birds of known sex to correct for potential differences in feeding rates between the sexes (demonstrated in Chapter 3).

Assuming that labelled birds behaved the same as non-labelled birds during the hours of darkness (there was no evidence to suggest that they stayed in burrows or above ground at the colony), then the proportion of the daylight hours during the measurement period after the delivery of the first feed could be used as a measure of the proportion of the measurement period spent in normal behaviour. This suggested that, on average, the labelled birds which were recaught spent 48% (+/-18% s.d) of the daylight hours behaving normally (range 22% to 75%) (**Table 6.4**). Multiple regression analyses with FMR (kJd^{-1}) as the dependent variable and including body mass as an independent variable did not show any dependency of FMR on either the proportion of the measurement period spent in normal behaviour ($p>.05$, $n=9$) or on the total length (h) of the measurement period ($p>.05$, $n=9$) however. Any behavioural alterations caused by the labelling did not, therefore, have any systematic effect on FMR. The effects of behavioural changes on measured FMR were clearly minimised because only the labelled individuals which behaved relatively normally and delivered chick feeds could be recaught.

Of the chicks whose parents were labelled, 27/29 were thought to have fledged successfully. The two which were believed not to have fledged (chicks of birds 8 and 10/13) were less than 10 days old when the labelling took place and may, therefore, have been unable to withstand disruption of feeding and/or brooding.

6.4 DISCUSSION.

6.4.1 Energy expenditure of Isle of May Puffins during chick rearing.

Puffin FMR was 95% of the value predicted using separate allometric equations for metabolism at sea and at the nest (Birt-Friesen et al,1989). It was probable, however, that the metabolism of Puffins attending the colony was higher than for species used to derive the original equation because Puffins were engaged in a variety of costly activities while at the colony (see methods). FMR was, however, still lower than the predicted value, indicating that Puffin metabolism at sea was probably lower than predicted; this may have been because they foraged close to the colony and, therefore, had reduced daily flight costs compared to other species with similar foraging modes (see Chapter 8, section 8.3).

The TAL budget was constructed quite independently of direct estimates of FMR. Measured FMR corresponded closely with the TAL estimate (for individuals delivering 2 chick feeds each day), however, indicating that either (a) the assumptions made during construction of the budget were reasonable or (b) that errors in the time and energy estimates balance out. Several of these assumptions warrant further comment however.

First, foraging trip durations measured in the present study were those made in the early morning, and it was assumed that trips increased in length later in the day because these later trips included time spent self-feeding and resting on the sea. The possibility that trip duration increased because prey became less accessible later in the day could not be discounted however. Unfortunately, the data used to derive the foraging trip duration were the only available but it was acknowledged that trip duration could have been underestimated and that the TAL budget was particularly sensitive to error in trip length; a doubling of trip length to

1h resulted in a 42% increase in predicted DEE for an average Puffin delivering 2 feeds d^{-1} to its chick (when all other budget parameters were held constant). This error may have been somewhat balanced however, by the assumption that all diving involved in adult self-feeding was undertaken outside the duration of foraging trips to provision young; an unknown proportion of the time spent on longer trips may have been spent self-feeding.

With trip duration held constant at 0.5h, DEE predicted from the TAL budget was little affected by foraging distances of the range (1-13km) suggested for British Puffins (Corkhill,1973; Ashcroft,1976; Birkhead,1976; Wanless *et al*, 1988b). A doubling of foraging distance to 3km resulted in a <1% increase in predicted DEE for the average Puffin, while an increase to a foraging distance of 13km resulted in only a 2% increase in DEE. This was because flying time was traded off against diving, an activity of similar, high cost, in the budget. Norwegian Puffins reportedly foraging up to 105km from the island of Røst (Anker-Nilssen and Lorentsen,1990) would have taken 1.7h to fly between their breeding colony and feeding site. It was not possible to predict their DEE within the TAL budget presented here without alteration of the trip duration and daily chick feeding rates. The authors did not present data on the latter variables but given the sensitivity of the current budget to trip duration, the distant foraging of Røst Puffins and probable high DEE would suggest a reason for the poor chick growth of their young in that year.

The assumption that the daily time spent self-feeding did not increase with chick feeding rate may not have been valid but any error could have been balanced if a trade-off existed between foraging distance and/or trip duration and the daily chick feeding rate, or if differences in feeding rates were the product of variation in the foraging efficiency of individuals. For example, an efficient forager could deliver more feeds to its young while requiring proportionally less time for self-feeding. In addition, the diving time required for self-feeding would have been overestimated if adults fed on larger prey, with higher energy gain per unit of foraging time, than they transported to young. The energy value of fish increases exponentially with length (Harris,1984), so that larger fish could give a larger return per unit foraging effort than smaller fish (if the former are equally available to the foraging bird). The carriage of very large fish back to the colony to feed young can, however, impair flight and make the parent more obvious to kleptoparasitic gulls (Harris,1984; pers.obs.). It is quite possible, therefore, that adults self-feed on larger fish than those that they deliver to young.

Time-activity energy budgets have the disadvantage that any biases in estimation of budget parameters may be "propagated through the calculations and errors of staggering magnitude can result" (Travis,1982). They nonetheless provide a useful means by which to explore the often complex relationships between the various components of DEE. Despite the many assumptions in the TAL budget presented here, estimated DEE corresponded sufficiently closely with FMR to make the budget a useful tool with which to demonstrate the potential impact of changes in parental time allocation on FMR.

6.4.2 The effect of chick feeding frequency on parental DEE.

FMR was not related to the number of feeds delivered to young each day. This suggested either that individual feeding frequencies were dictated by the foraging efficiencies of parents (more efficient foragers made more trips for a given energy expenditure) or that the food loads differed in size and/or composition between parents (birds delivering fewer loads carried larger and/or more nutritional loads requiring more energy per load to catch). Alternatively, the energetic costs of extra feeds may have been masked by other sources of individual variability in FMR.

Use of the TAL budget allowed calculation of the potential effect on DEE of changes in daily feeding rates. Within the range of feeding frequencies observed for loaded birds (0 to 3 feeds d^{-1}), predicted DEE varied by only 6%, assuming that the energy expenditure per load caught was constant. Such a difference would not be detectable given the precision of the DLW method because validation studies for birds (comparing DEE measured with DLW with predicted metabolism from gas analysis and/or food balance) have demonstrated errors in the DLW estimate of up to 10% (Hails and Bryant,1979; Westerterp and Bryant,1984; Williams,1985; Masman and Klaasan,1987). Puffins on the Isle of May seemed to forage close to the colony and so the time spent in activities with high metabolic costs while provisioning young (flight and diving) constituted a relatively small proportion of each day, so that chick feeding frequency was not a major influence on DEE. This does not mean that individual variation in DEE caused by differences in feeding frequency is not biologically important, rather such variation might not be large enough to be detected by the DLW technique given the small sample size and range of feeding frequencies, and the cost (per trip) differences between individuals.

The above calculations using the TAL budget showed that any slight change in the behaviour of the labelled birds (reduced chick visiting during part of the measurement period) was unlikely to make measured FMR unrepresentative of Isle of May Puffins in general. Few other seabird energetics studies utilising isotope turnover techniques have documented the effects of the labelling protocol on the behaviour of labelled birds. Birt-Friesen et al (1989) also concluded, however, that the slight behavioural changes caused by labelling had no important effect on measured FMR in Gannets; labelled birds spent slightly less time at the nest and more on the surface of the sea than unlabelled birds but FMR did not differ between apparently more- or less-disturbed individuals because the metabolic costs at the nest and at sea were similar.

Relationships between parental energy expenditure and chick provisioning effort were clearly not detectable by measuring feeding frequency alone. Further studies are required to clarify relationships between the number, size and nutritional content of food loads and how these variables, operating together, might influence parental DEE. Variation in parental foraging efficiency will be quantifiable if DLW and some method of measuring time budgets at sea are used concurrently to detect the effects on FMR of individual differences in foraging range and time spent flying and diving on each load delivered to the young. Only from this type of study could a firm relationship between chick feeding rates and parental effort be established. Such a study on Puffins is not yet feasible because of the disturbance to normal behaviour caused by activity monitoring devices. In conclusion, chick feeding rates alone did not provide a measure of parental effort in terms of daily energy expenditure.

6.4.3 The effect of body mass on DEE.

FMR was not related to parental body mass, body size or body condition (total reserve mass). This suggested that the anticipated increase in metabolic costs associated with increased mass was offset by energy savings, such as reduced costs of thermoregulation (due to improved insulation) or behavioural changes associated with mass differences.

The body mass of labelled birds varied between 374g and 411g; these birds would have BMR's of 10.1 kJh^{-1} and 10.9 kJh^{-1} respectively and estimated DEE's from the TAL budget of 776 kJd^{-1} and 837 kJd^{-1} **(Table 6.5)**, a difference of only 8% if the mass difference was assumed only to influence BMR (for individuals delivering 2 feeds each day). The observed mass differences were, additionally, calculated to produce a 7% difference in the power requirement for flapping flight (Pennycuick,1989) but this would have a negligible effect on predicted DEE because of the very small proportion of the day spent in flight. The effect of the observed mass variation on diving costs could not be realistically modelled because diving costs depend on body density (mass divided by body volume) and body shape, rather than on mass *per se* (Wilson et al,1992); diving costs would, therefore, depend on which body components were responsible for inter-individual mass differences.

It was possible, therefore, that variation in FMR caused by the effects of body mass on BMR and flight costs was not detectable within the resolution of the DLW analysis because mass variation may have produced only a 7-8% variation in DEE. Changes in diving costs associated with mass variation had a greater potential effect on DEE (because of the larger daily time allocation to diving), yet no relationship between FMR and body mass was apparent. In a volant, diving species such as the Puffin, the effects of inter-individual mass variation on existence metabolism, flight costs and diving costs could operate in opposing directions, so that no overall effect on FMR results.

There was some evidence that mass-related behavioural differences may have modified predicted relationships between mass and FMR. There was a suggestion that adult body mass at the start of the measurement period and subsequent daily chick feeding rates were negatively related. If both higher body mass and higher feeding rates were predicted to increase FMR, then such a relationship between body mass and feeding rate could mask relationships with FMR. Possible reasons for the negative relationship between parental body mass and chick feeding rate are discussed in Chapter 5, the most parsimonious being that males are heavier than females and generally deliver fewer feeds to their young (Chapter 3). Too few loaded birds could be sexed to test this hypothesis.

It was difficult to draw conclusions about relationships between FMR, chick feeding rates and body mass from this study because of the small number of individuals for which FMR was measured. A larger sample was prevented because of difficulties in recapturing labelled individuals within c.72 hours of dosing. The recapture rate might be improved if the FMR measurement could run over a longer period but the sample would then contain individuals whose behaviour had been progressively more disrupted by the labelling procedure. The analyses comparing FMR with mass and feeding rates also suffered from an inherent problem in correlative studies, that of differences in the 'quality' of individuals masking the relationships sought. In this study, individuals which were able to forage more efficiently could have made more feeding trips per unit effort than less efficient foragers so that no relationship between DEE and feeding frequency was apparent. Equally, the mass of individuals may have already been optimised to suit their foraging efficiency (Chapter 5), so that individuals could carry varying levels of body reserves for the same level of energy expenditure and so that no relationship was apparent between DEE and body mass. Further studies should, therefore, seek to manipulate parental effort (examples in Chapter 5) and body mass experimentally while concurrently measuring energy expenditure and time budgets. The Puffin would not be a suitable species for such studies however, because of the detrimental effects of handling and device attachment on behaviour.

6.4.4 Effect of weather conditions on FMR.

'Poor' weather conditions, characterised by heavy rainfall, strong onshore (easterly) winds and poor visibility, resulted in an increase in Puffin FMR from 3.35 $cm^3CO_2g^{-1}h^{-1}$ or 802 kJd^{-1} (n=6) to 4.33 $cm^3CO_2g^{-1}h^{-1}$ or 1019 kJd^{-1} (n=3). The FMR of Kittiwakes was shown to increase by 50% with an increase in wind speed from 8 ms^{-1} to 13 ms^{-1} because of the need for more costly flapping flight at higher wind speeds (Gabrielsen et al,1987). This was not the cause of the increased FMR of Puffins in 'poor' weather because Puffins ordinarily use predominantly flapping flight. Increased wind speed has, however, also been shown to increase FMR in Little Auks over the range of speeds 0 to 18 ms^{-1} (Gabrielsen et al,1991). On the Isle of May an increase in wind speed from 4ms^{-1} to 11 ms^{-1} was associated with a 29% increase in FMR; the same increase in wind speed would result in a 17% increase in Little Auk FMR (calculated from the equation relating FMR to body mass and wind speed in Gabrielsen et al,1991) and Little Auks also utilise predominantly flapping flight.

Gabrielsen et al (1991) did not suggest why the FMR of Little Auks should increase with wind speed. On the Isle of May, 'poor' weather associated with strong easterly winds sometimes resulted in reduced chick feeding rates and increased attendance of breeding adult Puffins at colonies on the eastern side of the island (pers.obs.). A decreased feeding frequency was not, however, observed for labelled birds during the spell of 'poor' weather compared to other days in this study. Increased time spent at the colony by labelled birds may, therefore, have resulted in less time sitting on the sea, rather than less time foraging. In this case the increased energy expenditure on 'poor' days must have been the result of either the increased metabolic cost of being ashore (4 times BMR) compared to sitting on the sea (2 times BMR), or of an increased activity-specific cost of onshore activities on 'poor' days, or of increased costs of flying or diving or locating prey on 'poor' days. Time spent ashore rather than sitting on the sea would result in an increase in metabolic costs of 21.1 kJh^{-1}, all else being equal. An individual would have to spend an extra 10 hours ashore to account for the difference between observed FMR's on 'good' and 'bad' days (a difference of 217 kJd^{-1}) and this could only be achieved by sacrificing time spent self-feeding **(Table 6.5)**. If a bird spent all the daylight hours, other than foraging time, at the colony, the estimated increase in FMR (for an individual delivering 2 chick feeds) would be only 18% compared to the observed increase of 29%. There was, however, evidence to suggest that the metabolic costs of being ashore might also be higher in 'poor' weather. In 'poor' weather greater numbers of Puffins attended the colony, resulting in increased opportunities for social interaction and aggression; 'wheeling' flights over the colony were frequent and individuals spent time 'hovering' in the wind (pers.obs.). Time budgets of individuals at the colony would, however, need to be quantified under varying weather conditions before effects of behavioural changes on metabolic intensity at the colony could be quantified. Alternatively, or additionally, 'poor' weather may have resulted in increased thermoregulatory costs (not considered in isolation in the TAL budget), increased costs of flying, diving or locating prey, or in increased costs of maintaining stability on a rough sea. Energy expenditures and time budgets of individuals of a single species under differing weather conditions would need to be measured concurrently to confirm or dismiss some of these possible effects on FMR.

Relationships between FMR and weather have been found in all of the three seabird studies where they have been addressed using the DLW technique (Gabrielsen et al,1987,1991; present study). This indicates the importance of reporting the weather conditions under which measurements of the field energy expenditure of seabirds are made.

CHAPTER 7 INTER-YEAR COSTS OF REPRODUCTION FOR PUFFINS.

7.1 INTRODUCTION.

Possible reasons for differences in the reproductive effort and success of individual Puffins within a single breeding season have been considered in previous chapters. The aim here is to examine whether effort and success in one year affects performance in the following breeding season, that is whether reproduction entails inter-year costs.

Studies of avian reproductive costs have focused on the evolution of clutch size. It is a basic assumption of much of life-history theory that organisms should allocate resources to reproduction so as to maximize their biological fitness, most simply expressed as their lifetime reproductive success (Stearns,1976, for review). Lack (1954) suggested that the most frequent clutch size for any given species should be that which yields the highest number of viable offspring. However, many tests of this hypothesis have shown that the most frequent clutch size is smaller than the most productive (Klomp,1970; Lessells,1986 and Murphy and Haukioja,1986 for reviews). The Trade-off Hypothesis (Williams,1966; Charnov and Krebs,1974) was proposed to account for this discrepancy, suggesting that high offspring production at any one breeding attempt incurs costs in terms of future reproductive potential.

Evidence that larger broods are more costly is not conclusive in correlative studies based on natural brood sizes. Some studies showed no evidence of costs attached to larger broods (Nur,1990, for review) while in others suggestions of costs were inconclusive. For example, in House Martins (Bryant,1979) and Great Tits (Kluyver,1971) the return rate of females in year n+1 was greater for single-brooded than for double-brooded individuals but no effect of clutch size on parental survival was demonstrated.

Brood sizes can be manipulated experimentally so as to assess the costs of rearing large versus small broods. These costs of rearing enlarged broods can take the form of reduced parental survival (Askenmo,1979; Nur,1984; Reid,1987; Dijkstra *et al,* 1990; Orell and Koivula,1990), later laying in the next year (Røskaft,1985; Lessells,1986), smaller clutch size (Gustafsson and Sutherland,1988) and decreased fledging success (Røskaft,1985) in the following year, and even reduced fecundity of the offspring produced (Gustafsson and Sutherland,1988).

Correlations between observed life-history parameters and natural brood sizes may fail to reveal trade-offs because individual phenotypes may adjust clutch sizes to compensate for differences in their ability to raise young. The Individual Optimization Hypothesis (Perrins and Moss,1975) proposes that parents lay the clutch size from which they can maximize recruitment, the differences between individuals reflecting differences in their 'quality' in terms of their body condition, age, experience and/or territory quality, for example (Hogstedt,1980; Coulson and Porter,1985; Korpimaki,1988). This could explain the positive relationships between brood size and parental survival observed in some studies (Hogstedt,1981; Nur,1990, for review). Non-manipulative studies are unlikely to reveal inter-year fecundity costs because individuals rearing large broods in one year are likely also to rear large broods in subsequent years so that clutch size is, at least in part, genetically controlled (van Noordwijk *et al*, 1981; Hailman,1986). Some form of experimental manipulation is therefore desirable in any study of inter-year reproductive trade-offs.

In manipulative studies of the costs of reproduction in birds, some results have been consistent only with the Individual Optimization Hypothesis in that females laid a clutch size which maximized recruitment potential (Pettifor *et al*, 1988; Pettifor,1993 and in his re-analysis of Nur,1981 *et seq*) and there was no effect of experimental brood size variation on future reproductive potential (eg. DeSteven,1980; Korpimaki,1988; Alatalo and Lundberg,1989). Others have demonstrated inter-year costs in terms of parental survival and/or future fecundity (cited above and in Nur,1990) and intra-year costs, varying the timing and/or success of second broods where first broods were manipulated (Slagsvold,1984; Finke *et al*, 1987; Hegner and Wingfield,1987; Smith *et al*, 1987; Tinbergen,1987; Linden,1988). Most published experimental studies have demonstrated some cost of reproduction (Nur,1990), although the form(s) of the cost varies among them.

Various methods for manipulating Puffin parental effort were attempted in the present study and the reasons for their choice were discussed in Chapter 5 (section 5.1.3). Only the treatment involving the supplementary feeding of young produced samples large enough to allow the reproductive performance of parents in the following year to be followed however, and it is the results of that experiment that are presented in this chapter. The supplementary feeding manipulation had two important advantages over the other treatments that were attempted. First, the experimental decrease in the requirements of the young elicited a rapid response from parents (in terms of a reduction in the daily number of feeds they delivered to young), while responses to the other forms of manipulation were less clear (see Chapter 5, section 5.4.4). Second, an artificial increase in reproductive effort by manipulation might impose costs on parents which do not exist in the natural situation. Only by artificially decreasing, rather than increasing, the effort required to raise young, therefore, can natural costs resulting from breeding be demonstrated.

To date, studies of reproductive costs have been carried out largely on species laying more than one egg per clutch, and on small, short-lived passerine species. The cause of this was, at least in part, due to the relative ease of manipulating effort in such species. The aim in this study was to assess whether reproduction entailed costs for Puffins by experimental manipulation of parental breeding effort and, if this was the case, to investigate what form these costs might take. Puffins have a single-egg clutch and only rear a single young each year.

7.2 METHODS.

7.2.1 Methods in the year of the treatment.

Thirteen young were supplementary fed in 1990 and 27 in 1991. These 'experimental' burrows were matched by hatching date to the same number of 'controls' in each year, to control for any seasonal variation in breeding performance. The feeding treatment began when young were 10-15 days old and continued until fledging. The ration of fish and vitamin supplement was placed in each burrow at noon and any remaining food was removed the following day, so that burrow did not become fouled.

The food ration per chick per day was 100g of 10cm-length, March-caught sandeels in 1990 and 80g of 10cm March-caught Sprats in 1991. Sandeels were selected as the supplementary food in 1990 because these form a large proportion of the diet of Puffin young on the Isle of May (Harris and Hislop,1978; Hislop and Harris,1985; Harris and Wanless,1986). In 1991, Sprats were the only fish of appropriate size available locally; these were considered suitable because they had earlier been important in the diet of Isle of May Puffins (Harris and Hislop,1978) and were used in previous supplementary feeding studies (Harris,1978; Hudson,1979). The daily ration of supplementary food was selected so as to be slightly more than the maximum normally delivered by parents in a day, so promoting a maximal reduction in parental effort while not leaving a surplus which might foul the burrow.

Energy values and composition of the supplementary foods were not determined directly. Comparison of the dietary energy content of control and fed young was possible using published energy densities however (Harris and Hislop,1978; Hislop et al,1991). Wet mass energy densities of fish are particularly sensitive to changes in hydration, which may occur during transport of prey to the colony (Montevecchi and Piatt,1987). For this reason, it is important to select published energy values appropriate to the state of hydration of the fish when they were received by the chick. For feeds delivered by parents, the sandeel energy density used was therefore that determined for fish obtained from Puffins arriving at Scottish colonies. Energy densities for the supplementary feeds were calculated using values for fish fresh from the sea. For the former, it was necessary to assume that the transport times/distances of Isle of May Puffins were similar to those from which fish samples were obtained (Harris and Hislop,1978). For the latter, a negligible effect of sorting and freezing of the fish on its water content were assumed (but see discussion section 7.4.1). Fish energy density also varies with fish length and time of year (Hislop et al,1991); energy equivalents used were therefore those for fish of similar length and capture date to the fish received by chicks in this study. In 1990, the energy intake via control and supplementary diets was 249 kJd^{-1} and 538 kJd^{-1} respectively **(Table 7.1)**, although the value for the supplementary food was believed to be rather elevated (see discussion). In 1991, supplementary fed chicks received more than twice the daily energy intake of controls, 499 kJd^{-1} compared to 210 kJd^{-1} for the controls **(Table 7.1)**.

Experimental and control burrows were treated in exactly the same manner except for the addition of food (for the importance of this see Chapter 2, section 2.9). All young were weighed regularly (Chapter 2, section 2.6) and parental feeding behaviour was monitored during dawn-to-dusk watches (Chapter 2, section 2.4) in the year of the treatment (referred to as year n). The capture of parents was attempted prior to the start of the treatment in 1990, and both prior to feeding and when the young were close to fledging in 1991.

7.2.2 Methods in the year following the treatment.

In the following year (referred to as year n+1), both experimental and control pairs were monitored as for unmanipulated pairs at Little Hide (Chapter 5, section 5.2.1). The derivation of measures used to compare adult and chick body condition between the two groups is discussed in Chapter 4. Initial sample sizes are reduced in subsequent analyses because not all the parent birds were caught and ringed in the year of the treatment; only adults colour-

Table 7.1 Comparison of the daily energy intake of supplementary fed and control Puffin young in 1990 and 1991.

			MEAN NUMBER OF FEEDS PER DAY [1]	MEAN LOAD WEIGHT [2] (g)	SANDEEL CONTENT OF DIET [2,4] (% by n)	MEAN FISH LENGTH [2,3] (cm)	WET ENERGY DENSITY [3,5] (kJg^{-1})	DAILY ENERGY INTAKE [3,6] (kJd^{-1})
1990	CONTROL		4.5	8.5	94	8	6.5 [a]	249
	FED -	NATURAL	1.6	8.5	94	8	6.5 [a]	88
		ADDITIONAL	1.0	100.0	100	10	4.5 [b]	450

								538
1991	CONTROL		3.9	8.3	89	7	6.5 [a]	210
	FED -	NATURAL	0.5	8.3	89	7	6.5 [a]	27
		ADDITIONAL	1.0	80.0	0 all sprats	10	5.9 [c]	472

								499

NOTES.

1 For natural feeds these are means from dawn-to-dusk watches.

2 For natural feeds these data were obtained from netted food loads.

3 Assumes natural feeds are 100% sandeels, compared to actual proportion in 4.

5 Data from Harris and Hislop (1978) and Hislop et al (1991) : a = sandeels 60-207mm, June-caught from Puffin food loads; b = sandeels 95mm class, March-caught from fishery samples; c = Sprats 95mm class, March-caught from fishery samples.

6 Calculated as [load mass (g) * daily number feeds (n) * wet energy density (kJg^{-1})].

ringed, and so recognizable, in the year after the treatment were monitored in that year. In the results which follow, some analyses were only possible for pairs followed from 1991 to 1992 due to the smaller number of experimental burrows in 1990. In 1992, the provisioning rates of parents were compared both in terms of the the mean numbers of feeds they delivered to young each day throughout rearing (referred to as the mean feeding frequency, MFF, in feeds d^{-1}) and using a residual feeding rate (corrected feeding frequency, CFF, in residual feeds d^{-1}), after controlling for an observed seasonal trend in MFF (see Chapter 5 **Figure 5.6** and 5.3.4.2). Measurement of the proportion of the daylight hours that parents spent standing above ground at the colony in 1992 is detailed in Chapter 2 (section 2.3.7).

7.3 RESULTS.

7.3.1 Effects of supplementary feeding in the year of the treatment (year n).

7.3.1.1 Parental effort.

The results of the feeding treatment on feeding rates by experimental and control parents are presented in Chapter 5 (**Tables 5.9** and **5.10**). In summary, experimental parents significantly reduced the daily number of feeds that they delivered to young in both years, from a median of 4.4 feeds d^{-1} for controls to 1.7 feeds d^{-1} for experimental young in 1990 (Mann-Whitney test U=0, p<.01) and from 3.8 to 0.2 feeds d^{-1} for control and experimental young respectively in 1991 (U=0, P<.001). Experimental young therefore received 39% and 5% of the daily number of feeds delivered by parents to control young in 1990 and 1991 respectively.

7.3.1.2 Chick growth.

In 1990, none of the chick growth variables differed significantly between the experimental and control groups (**Table 7.2**). Sample sizes were small however, and the growth variables were less accurately determined than in subsequent years because chicks were weighed less frequently (Chapter 2, section 2.6). In 1991, experimental young were, on average, 37g heavier at peak mass and 46g heavier at fledging than controls and the differences were significant (**Figure 7.1** and **Table 7.3**). The two groups did not differ in their wing length at fledging, so the experimental young also had significantly higher body condition (total residual peak mass, TRPM) than controls. Chick growth rates (maximum growth rate in the linear phase, MGR, in gd^{-1}) did not differ between the two groups. Experimental young

Table 7.2 Comparison of the growth of supplementary fed and control Puffin young in 1990.

Medians	FED (n=7)	CONTROL (n=7)	MANN-WHITNEY TEST U	 p
HATCHING DATE [1]	37	36	21.5	> .7
PEAK MASS (g)	311	326	12.0	> .1
AGE AT PEAK MASS (d)	35	36	20.0	> .5
FLEDGING MASS (g)	267	280	22.5	> .7
FLEDGING AGE (d)	42	42	20.5	> .6
MAXIMUM GROWTH RATE [2] (gd^{-1})	7.8	9.7	14.0	> .1

NOTES.

1 Where 1st May = day 1.
2 Rate of growth in the linear phase (days 10-25 of age).

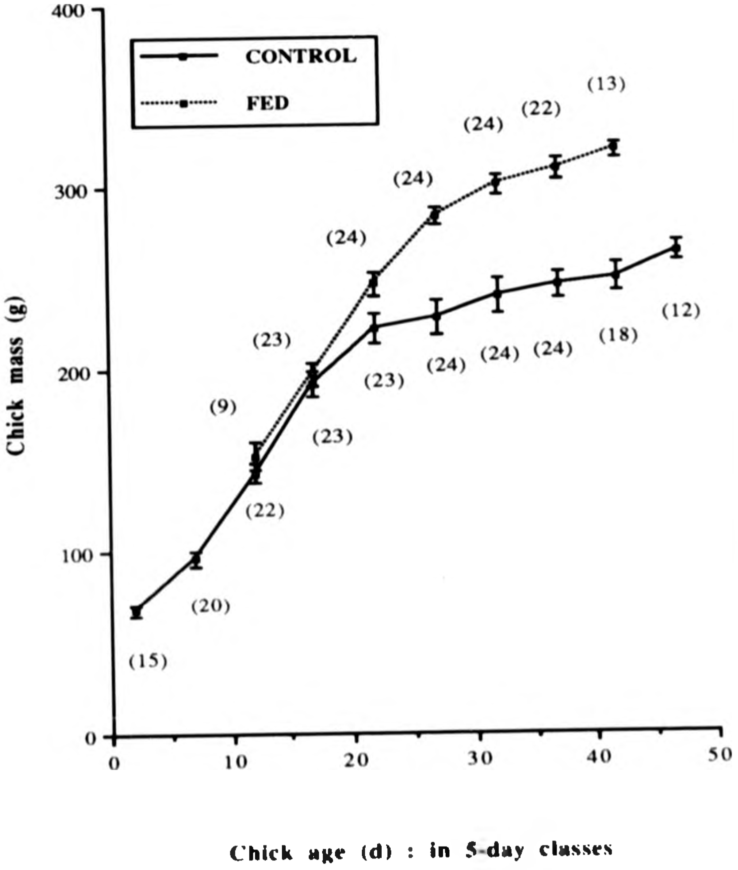


Figure 7.1 Comparison of the growth (mass gain) of supplementary fed and control Puffin young in 1991.

Each point represents the mean mass (+/- one standard error) of young in 5-day age classes (in which each chick was included only once), with sample sizes for each mean in parentheses. Data are plotted only until 50% of young in each group had fledged.

Table 7.3 **Comparison of the growth of supplementary fed and control Puffin young in 1991.**

Medians	FED (n=24)	CONTROL (n=24)	MANN-WHITNEY TEST U	 p
HATCHING DATE [1]	34	33	282.0	> .9
PEAK MASS (g)	328.5	295.0	111.5	< .001
AGE AT PEAK MASS (d)	37	39	228.5	> .2
FLEDGING MASS (g)	308.5	262.5	78.0	< .001
FLEDGING AGE (d)	40	44	167.5	< .05
MAXIMUM GROWTH RATE [2] (gd^{-1})	9.38 (n=23)	9.62 (n=23)	262.5	> .9
TOTAL RESIDUAL PEAK MASS (TRPM, g)	19.95	-9.67	146.0	< .005
WING LENGTH AT FLEDGING (mm)	131.5	130.5	265.0	> .6

NOTES.

1 Where 1st May = day 1.
2 Rate of growth in the linear phase (days 10-25 of age).

fledged significantly (on average 4 days) earlier than controls but with the same wing length at fledging, which suggested that the experimental young increased in structural size faster than controls (although this was not reflected in their mass increase rate during the linear growth phase).

7.3.1.3 Parental body condition.

Of the experimental parents, only 9 (8 females and 1 male) were caught when their young were close to fledging (in 1991). There was no evidence that these individuals differed from controls in either the rate at which they depleted their body reserves or their body condition (final total reserve mass, FTRM) at the end of rearing (**Table 5.11** in Chapter 5).

7.3.2 Effects of supplementary feeding in the following year (year n+1).

7.3.2.1 Return rates of parents.

The return rates of control adults to the colony differed markedly between the two years considered. 82.7% (62/75) of control adults monitored in 1990 returned in 1991 whereas the return between 1991 and 1992 was much higher at 98.4% (121/125). Return rates for the experimental adults were 94.7% (18/19) and 95.6% (43/45) from 1990-1991 and 1991-1992 respectively. The differences in return rates of the two groups were not significant in either set of years (1990-1991 χ^2=.92, p>.1; 1991-1992 χ^2=.007, p>.1) but more than three times more control than experimental adults failed to return between 1990 and 1991.

7.3.2.2 Success rates (% pairs returning to the colony which fledged a chick).

Only pairs which remained together from year n to year n+1 were compared to remove possible 'dilution' of the effects of the treatment caused by partner changes (ie when an experimental bird took a new mate which was not manipulated in the previous year). The success rates for experimental pairs in year n+1 were compared both with rates for controls which successfully raised chicks in year n and to those for all controls, whether successful or unsuccessful in year n (**Table 7.4**). The choice of comparison did not affect the significance of the result but the comparison of experimental pairs with all controls was considered the more appropriate because the experimental group may have included pairs which would not have successfully raised chicks were it not for the supplementary feeding.

Table 7.4 **Comparison of the success (% of pairs returning to the colony and remaining together, which fledged a chick) of experimental and control pairs in the year after the supplementary feeding.**

		1991			
		SUCCESSFUL	FAILED	%SUCCESS	p^1
	ALL CONTROLS	5	10	33.3	
1990	SUCCESSFUL CONTROLS	5	8	38.5	> .1
	SUPPLEMENTARY FED	3	1	75.0	

		1992			
		SUCCESSFUL	FAILED	%SUCCESS	p^2
	ALL CONTROLS	12	37	24.5	
1991	SUCCESSFUL CONTROLS	7	24	22.6	< .01
	SUPPLEMENTARY FED	11	5	68.8	

NOTES.

1 **Fisher Exact Test (significance level the same for comparison of supplementary fed versus all controls or successful controls only).**

2 **Chi-squared Test (significance level the same for comparison of supplementary fed versus all controls or successful controls only).**

In 1992, experimental pairs were significantly more successful than controls; 11/16 (68.8%) experimental pairs but only 12/49 (24.5%) control pairs reared young to fledging (χ^2=8.489, p<.005). The result was similar in 1991, when 3/4 (75%) experimental pairs and only 5/15 (33.3%) control pairs fledged young, although the difference was not significant (Fisher Exact Test, p>.1).

7.3.2.3 Timing of breeding.

In 1992, there was no significant difference in the calendar hatching dates of experimental pairs (median=14th June) and controls (median=7th June)(**Table 7.5**). When the 1992 hatch date for each burrow was expressed in relation to the 1991 date, experimental pairs hatched eggs, on average, 2 weeks later in 1992 than in 1991, while control pairs were only 2 days later, although this difference was not significant (**Table 7.5**).

7.3.2.4 Chick growth.

In 1992, experimental pairs raised young of significantly higher total residual peak mass (TRPM) than controls and the maximum growth rate (MGR) of experimental young was (marginally significantly) higher than that of controls (**Table 7.5**). The two groups of young did not differ in structural size, as indicated by head plus bill length at fledging and reached peak mass at similar ages.

7.3.2.5 Parental body condition.

The body condition of experimental and control parents was compared both during the pre-hatching period and during chick rearing in 1992 (**Table 7.6**). There was no significant difference in total reserve mass (TRM, g) between the two groups in any of the 3 comparisons made but experimental adults consistently carried larger reserves than controls. The rate of reserve depletion during rearing was greater for experimental females than for controls, and the rate of reserve gain of experimental males less than that of controls (although the differences were not significant).

Table 7.5 **Comparison of the growth in 1992 of young whose parents were experimental (whose young were fed for them) and those whose parents were controls in 1991.**

		FED	CONTROL	MANN-WHITNEY TEST U	MANN-WHITNEY TEST p
HATCHING DATE [1]	Median	45	38	49.0	> .4
	n	(12)	(10)		
RELATIVE HATCHING DATE [2]	Median	17	2	37.0	> .1
	n	(12)	(10)		
PEAK MASS (g)	Median	301.0	263.0	37.0	< .1
	n	(11)	(12)		
TOTAL RESIDUAL PEAK MASS [3] (TRPM, g)	Median	10.21	-8.44	23.0	< .05
	n	(9)	(12)		
AGE AT PEAK MASS (d)	Median	37.5	35.5	59.0	> .6
	n	(11)	(12)		
MAXIMUM GROWTH RATE (gd^{-1})	Median	8.31	6.42	17.0	< .1
	n	(9)	(12)		
HEAD + BILL LENGTH AT FLEDGING (mm)	Median	66.1	65.1	44.5	> .4
	n	(9)	(12)		

NOTES.

1 Where 1st may = day 1.
2 Calculated as [hatch date in 1992 - hatch date in 1991].
3 Mass standardized for chick size using head plus bill length (see text).

Table 7.6 **Body condition (total reserve mass, TRM) of adult Puffins in 1992, the year after the supplementary feeding experiment : comparison between parents whose young were fed in 1991 and controls.**

CONDITION VARIABLE	SEX	EXPERIMENTAL		CONTROL		MANN-WHITNEY	
		Median	n	Median	n	U	p
Pre-hatch TRM (g)	♂♂	59.9	9	52.9	15	61.0	> .6
	♀♀	66.3	5	59.2	13	27.0	> .5
Early rearing TRM (g) (days 0-25)	♂♂	33.8	12	28.8	10	47.0	> .3
	♀♀	24.2	11	19.3	11	49.0	> .4
Late rearing TRM (g) (after day 25)	♂♂	26.3	8	35.6	5	19.0	> .8
	♀♀	21.8	7	6.3	8	22.0	> .4
Mass change during rearing (gd^{-1})	♂♂	+0.01	8	+0.11	5	12.0	> .2
	♀♀	-5.17	7	-0.36	8	22.0	> .4

7.3.2.6 Parental behaviour.

Experimental and control adults did not differ significantly in the daily number of feeds they delivered to young in 1992 (**Table 7.7**), either when the feeding rate was expressed as a mean for the rearing period (MFF) or as a residual frequency (CFF) after controlling for the observed seasonal increase in the MFF of unmanipulated pairs. Experimental pairs had the higher feeding frequency in each case however.

There were no significant differences in the proportions of time that parents spent standing above ground at the colony between the two groups (**Table 7.8**) but there was a suggestion (for males at least) that experimental birds spent more time at the colony during rearing than controls.

7.4 DISCUSSION.

7.4.1 Effects of supplementary feeding on parental behaviour and chick growth.

The marked decrease in the daily feeding rates of experimental birds, within a week of the start of the treatment, demonstrated a clear ability of parents to respond to the nutritional state of their chick. This suggested that the effort of rearing young was considerably reduced for experimental adults in the year of the feeding treatment. The implications of the response of experimental parents for parent-young communication in Puffins are discussed in Chapter 5 (section 5.4.4).

In both 1990 and 1991, calculated daily energy equivalents suggested that supplementary fed chicks were receiving over twice the intake of controls (**Table 7.1**). In 1991, experimental chicks grew faster and attained significantly higher peak and fledging masses than controls, while there was no such difference in 1990. In both years, control young received less energy than wild chicks on the Isle of May had received in previous years (Chapter 1 **Figure 1.2**) and less than chicks previously fed supplementary food experimentally (Harris,1978; Hudson,1979). In these experimental studies, young fed *ad libitum* consumed fish with an energy equivalent of c.870 kJd^{-1}, during the main growth period. Therefore in neither 1990 nor 1991 were young receiving food at anywhere near their maximum physiological intake rate. It was possible that the supplementary sandeels and Sprats differed in some nutritional requirement other than energy content and that this was responsible for the improved growth

Table 7.7 **Daily numbers of feeds delivered to Puffin young in 1992, the year after the supplementary feeding experiment : comparison between controls and pairs which were experimental in 1991.**

		CONTROL	EXPERIMENTAL	MANN-WHITNEY TEST	
				U	p
[1]MFF (feeds d^{-1})	Median	4.3	5.1	42.0	> .6
	n	(8)	(12)		
[2]CFF (feeds d^{-1})	Median	-0.57	+0.71	32.0	> .2
	n	(8)	(12)		

NOTES.

1 Mean feeding frequency = the mean number of feeds delivered each day during the rearing period.

2 Corrected feeding frequency = MFF expressed as the residual of the relationship between MFF and hatching date (to control for seasonal trend in MFF) - see text for calculation.

Table 7.8 Proportion of the daylight hours spent standing above ground at the colony by adult Puffins in 1992, the year after the supplementary feeding experiment : comparison between parents which were controls in 1991 and those which were experimental (which had their young fed for them).

STAGE OF BREEDING	SEX	CONTROL		EXPERIMENTAL		MANN-WHITNEY TEST [1]	
		Median	(n)	Median	(n)	U	p
PRE-INCUBATION	♂♂	.29	(15)	.32	(11)	77.0	> .7
	♀♀	.28	(16)	.26	(11)	85.5	> .9
INCUBATION	♂♂	.21	(15)	.22	(11)	78.5	> .8
	♀♀	.16	(16)	.14	(11)	75.0	> .5
REARING	♂♂	.20	(15)	.25	(13)	64.0	> .1
	♀♀	.14	(16)	.17	(11)	71.0	> .4

of the experimental young fed on Sprats in 1991. Sandeels are believed (Murray and Burt,1969) to have a slightly higher overall protein content (17.8%) than Sprats (14.1-15.3%), although in gross terms both should supply enough protein for growing Puffins (Harris and Hislop,1978).

The most likely explanation for the lack of a growth improvement in chicks given supplementary food in 1990 was that energy inputs from the additional sandeels were much lower than calculated due to the poor state of the fish after freezing. Once thawed, the sandeels became pulpy and much of the mass of each 100g load thus consisted of liquid, an unknown proportion of which would simply have soaked into the burrow floor. Orphaned young reared in the laboratory on these sandeels found them difficult to manipulate and swallow (pers.obs.). In addition, some of the fish were probably trodden into the floor of the burrow before they could be consumed. The actual mass of sandeels ingested by each experimental chick each day may, therefore, have been overestimated. Thawed Sprats did not differ in texture from fresh ones and thus quantities consumed by the supplementary fed young in 1991 were determined accurately. The reduction in daily feeding rates caused by the provision of the supplementary food was less in 1990 than in 1991, supporting the suggestion that the energy supplied from the food supplement was lower in 1990 than in 1991, contrary to the calculations in **Table 7.1**.

The two previous studies involving supplementary feeding of young Puffins (Harris,1978; Hudson,1979) also showed that fed chicks attained higher masses than controls. Where the chicks given the food supplement were allowed to fledge normally (Hudson,1979), the difference in mass between fed young and controls was large and significant at peak mass but smaller and non-significant at fledging. The mass difference decreased just prior to fledging because the fed chicks voluntarily reduced their intake at this time and their mass decreased rapidly. Carrying extra mass in the form of fat during rearing may be advantageous for young Puffins as a buffer against periods of temporary food shortage. At fledging, optimal mass might be more of a compromise between, on the one hand, having enough reserves to sustain the chick while it learns to self-feed and, on the other hand, not having too much, as this could impair diving ability for foraging and escape from predatory gulls. In 1991, the large and significant difference in fledging masses of fed and control young may have been retained because the fledging masses of controls were unusually low due to disturbance effects (see Chapter 2, section 2.9.2) or because feeding conditions were poor (Chapter 1, section 1.2).

7.4.2 Mechanisms for inter-year transmission of reproductive costs in Puffins.

In the present study, experimental adult Puffins whose young were fed for them showed higher return rates (though not significantly so, see Chapter 8, section 8.2.2) and higher breeding success, and their young had higher body condition at peak mass than controls in the following year. This suggested that, under natural conditions, Puffins on the Isle of May incurred inter-year costs as a result of breeding.

Reproductive costs may have an ethological and/or a physiological component (Calow,1979). Ethological costs refer to the increased risk of death by accident or predation to which parents expose themselves during the behavioural processes associated with reproduction (courtship, territorial defence, copulation, pregnancy, parturition, parental care and so on). On the Isle of May adult Puffins suffered very low predation at the colony (by a few pairs of Great Black-backed Gulls only) and very few adults disappeared during breeding as a result of predation or accident during the present study (pers.obs.). Ethological costs were, therefore, unlikely to be responsible for the trade-offs demonstrated in this study. Reid (1987) reached the same conclusion in his study of reproductive costs in Glaucous-winged Gulls.

If reproduction takes precedence over other organismic processes for a limited supply of any resource, then both the future survival and reproductive performance of parents could be compromised (Calow,1979). For this reason, the physiological condition of individuals (defined in Chapter 4) might form the 'currency' of reproductive trade-offs. Reid (1987) concluded that the trade-off demonstrated in Glaucous-winged Gulls involved physiological costs; adults with enlarged broods lost more mass during rearing and their survival was lower than that of controls. Similarly in Herring Gulls, mortality rates are highest during the late summer, coinciding with the period of lowest mean body mass within the population (Coulson et al,1983).

Possible mechanisms by which the reproductive trade-offs demonstrated in this study could be transmitted from one breeding season to the next are illustrated in **Figure 7.2**. In these models, 'parental condition' could refer to one or a combination of condition components (eg lipid, protein), the importance of which may or may not vary between the sexes. The relative condition levels required for moult and breeding are unknown and are assumed, for simplicity, to be equal. Similarly, different components of body condition could be important for moult and breeding. The condition threshold for moult and/or breeding and the timing of the two

Figure 7.2

Figure 7.2 **Possible mechanisms for the transmission of Puffin reproductive costs via body condition : a comparison of controls and adults whose young were fed for them (where year n = the year of the feeding treatment).**

F_c and F_f **= fledging dates of control and fed chicks in year n respectively**
M_c/B_c and M_f/B_f **= dates of the start of moulting (M) and breeding (B) for control and experimental parents respectively**
C_c and C_f **= levels of body condition attained when moulting and breeding for control and experimental parents respectively**
r^1 and r^2 **= alternative rates of condition gain**

<u>(a) to (c)</u> : Experimental parents were in more favourable condition than controls at the time of chick fledging in year n ($F_c = F_f$).

(a) : Timing of moult and breeding controlled by date. Experimental parents begin moult and breeding in more favourable condition than controls in year n+1 but at the same time ($M_f = M_c$, $B_f = B_c$, $C_f > C_c$)

(b) : Timing of moult and breeding controlled by condition. Experimental parents moult and breed earlier than controls but at the same condition level in year n+1 ($M_f < M_c$, $B_f < B_c$, $C_f = C_c$)

(c) : A combination of (a) and (b), where the timing of moult and breeding shows limited plasticity. Experimental birds parents reach the condition level required for breeding earlier than controls (as in b) but cannot moult/breed that early; they continue to gain condition, still breed earlier than controls (though not as early as in b) and breed at a slightly higher condition level than controls (though not as high as in a) in year n+1.

<u>(d) to (f)</u> : Experimental parents are not in more favourable condition than controls at the end of rearing in year n but their young fledge earlier than those of controls ($F_f < F_c$).

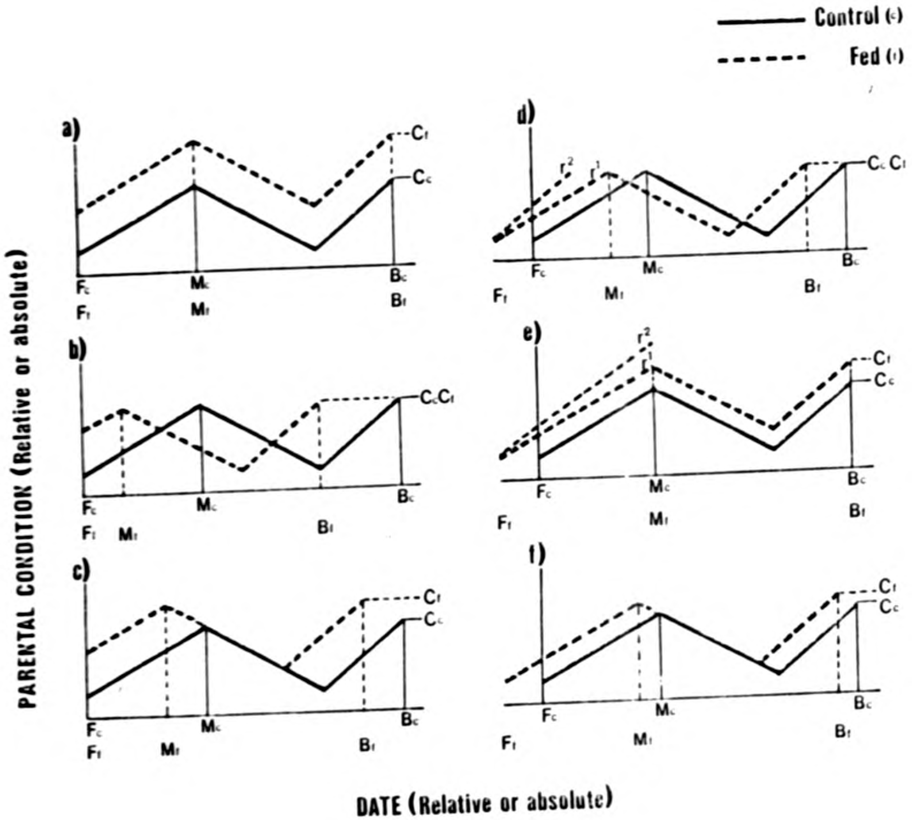
(d) : Timing of breeding and moult controlled by condition. Experimental parents are able to moult and breed earlier in year n+1 but at the same condition level as controls ($M_f < M_c$, $B_f < B_c$, $C_f = C_c$)

(e) : Timing of moult and breeding controlled by date. Experimental parents have more time to gain condition before they moult and breed at the same time as controls in year n+1 but at a higher condition level.
($M_f = M_c$, $B_f = B_c$, $C_f > C_c$)

Differences between experimental and control parents in year n+1 in (d) and (e) will be magnified if feeding conditions deteriorate later in the breeding season (see text), so that condition can be gained faster by parents whose young fledge earlier ($r^2 > r^1$).

(f) : A combination of (d) and (e) where the timing of moult and breeding shows limited plasticity (as in c above).

(f) : A combination of (d) and (e) where the timing of moult and breeding shows limited plasticity (as in e above).



processes could vary with bird 'quality', for example if some individuals are more efficient at acquiring and/or utilizing resources, hence the use of 'relative or absolute' condition or date on the model axes. The models assume that the reproductive success of Puffins is increased by improved body condition at the start of breeding and by early laying, assumptions which have already been examined in Chapter 5 (sections 5.1.1 and 5.1.4 respectively).

Parents whose young were provided with additional food in year n of the study may have been in better condition than controls at the end of rearing due to their decreased reproductive effort. In this case the increased breeding success of the former may have been a direct effect of the condition advantage maintained until the onset of breeding in year n+1 (**Figure 7.2a**). Alternatively, the condition advantage attained by the experimental birds may have allowed them to moult earlier and hence breed earlier in year n+1 (**Figure 7.2b**). Which of these two mechanisms was possible would depend on whether the onset of moult and/or breeding was controlled by condition (as in **Figure 7.2b**) or by date (as in **Figure 7.2a**). A combination of the two effects (**Figure 7.2c**) might occur, for example, if there were limited plasticity in the timing of breeding because birds would not begin until food availability was adequate for laying or to sustain them during incubation. In this case, the experimental pairs could have reached a threshold condition required for breeding well before the controls but unable to breed that early; these birds would have waited to lay, continuing to gain condition, and still bred slightly earlier than controls but also at a slightly higher body condition.

Female Canada Geese with artificially enlarged broods were lighter, moulted later and bred later in the following year than controls; however, the total removal of the broods of some pairs did not produce the opposite effect (Lessells,1986). The results of the present study provided little evidence for improved body condition in experimental parents either at the end of rearing in year n or in the following year. In the latter year, experimental adults carried consistently higher reserves during both the pre-hatching period and during rearing but the differences between their reserve levels and those of controls were not significant. The large variation in body condition between individual adults and the relatively small sample sizes for the body condition analyses may have masked differences between the two groups however (see Chapter 8, sections 8.1 and 8.2.2).

Variation in the total reserve mass (TRM) of adult Puffins was largely due to changes in the quantity of stored lipids (Chapter 4). Carriage of such reserves is likely to represent a compromise between maintaining enough of a store to act as 'insurance' during periods when demands cannot be met by daily intake, while avoiding the aerodynamic, hydrodynamic and energetic disadvantages of carrying excess mass (Chapter 5, section 5.1.1). Most birds only store small amounts of energy relative to their body size and rate of energy consumption (Walsberg,1983). It might, therefore, be unlikely that Puffins would maintain a condition advantage, resulting from the experimental decrease in rearing effort, until year n+1, if it existed at the end of rearing in year n. Coulson et al (1983) similarly concluded that Herring Gulls regulate reserves in response to winter weather conditions rather than relying on energy stored during the post-breeding period. In this respect birds are likely to differ from most mammals, for which the energetic disadvantage of carrying extra mass may not be as great (eg Clutton-Brock *et al,* 1983).

There was no difference in the calendar hatching dates of experimental and control pairs in year n+1 in the present study, so the increased performance of the former was not simply due to a seasonal change in weather or food supply. A comparison of hatch dates in year n+1 relative to those in year n between the two groups of pairs also showed no significant difference; all pairs hatched chicks later in 1992 than in 1991 and experimental pairs were, rather unexpectedly, 2 weeks later in hatching than controls.

On the Isle of May, the earliest Puffin eggs are usually laid in the first week of April, or exceptionally in the last week of March, with peak laying around 20th-25th April (Harris,1984 and pers.obs.). There were severe easterly gales from 29th to 31st March, 1992 when waves broke over the Little Hide study site and most burrows were probably flooded (J.Calladine,pers.comm.). This may have contributed to the late laying and reduced success of control pairs at the site. If the experimental pairs from the previous year had the ability to lay earlier than controls, it is possible that their laying was disrupted by these gales or even that early eggs were lost. The period of egg formation in alcids probably lasts for 10-18 days (Astheimer and Grau,1990), this being composed of 8-13 days for yolk deposition and a further 2-5 days for albumen and shell synthesis. Replacement laying in Puffins occurs 2-3 weeks after egg loss (Harris,1984), which further supports a period of at least 14 days for egg formation. Disruption of the process of egg formation, for example by poor feeding conditions caused by gales, may be less serious or may not occur in the early stages of yolk formation compared to the later stages of albumen and shell addition. Early laying Puffins on the Isle of May could have been in the final stages of egg formation or even just have laid eggs when the storm occurred. If the experimental pairs were ready to lay earlier than controls, then they may have suffered disruption from the gales or had to replace lost eggs, while most of the controls (preparing to lay later in April) may only have been in the early stages of egg formation at that time. Alternatively, all birds may have been at a similar stage of egg formation and have been affected by the storms but the experimental birds may have had a condition advantage allowing them to form replacement eggs or prevent laying disruption or egg loss while most controls could not. In this case, controls which suceeded in laying and rearing may have been lower 'quality' birds, which would normally have been later layers, hence the lower mass of chicks produced by controls relative to those produced by experimental pairs in 1992. It was impossible to determine the actual result of the gales in retrospect but if any of the above suggested events took place, experimental pairs might have been even more successful than controls in 1992 were it not for the need for replacement laying or the endurance of unfavourable conditions during the early part of the breeding season.

In contrast to the above, the supplementary feeding of young may have had no effect on parental condition in the year of the treatment. In 1991 (but not in 1990), the length of the rearing period was 4 days shorter for fed than control chicks and the difference was significant. The importance of such a shortening in the length of rearing might depend on how closely this variable is optimized to match the rearing ability of a particular pair. It may also depend upon whether feeding conditions deteriorate at the end of the breeding season and how rapidly this occurs. Circumstantial evidence for a deterioration in conditions comes from the abrupt departure of all Puffins (both breeders and younger birds) from the colony at the end of the season and is supported by desertion of late chicks by parents up to a week before they fledge whereas young fledging during the main part of the breeding season are fed until the day of fledging (pers.obs.). However, there is no direct evidence that the rapid, synchronized departure of birds at the end of the season is caused by a decrease in available food.

Experimental pairs may have attained the condition threshold required for moult and breeding earlier than controls if chicks of the former fledged in a shorter time; the timing advantage would be increased if a rapid decline in feeding conditions was to occur at the end of the season because pairs fledging their chicks earlier might suffer from the deterioration in feeding conditions proportionally less and acquire condition more rapidly than controls fledging chicks slightly later (**Figure 7.2d**). Alternatively, if the timing of moult/breeding was pre-programmed (under endocrine/photoperiodic control) rather than controlled by body condition, then experimental pairs finishing rearing earlier would have had more time to acquire condition prior to moult and might therefore have moulted and started breeding with a condition advantage the following year (**Figure 7.2e**). Again, a combination of these two effects would be possible (and might be more realistic) if plasticity in the timing of moult and/or breeding were limited (**Figure 7.2f**). In 1990, experimental chicks did not fledge earlier than controls however, yet an effect of the supplementary feeding on adult return rate was suggested in 1991; it was, therefore, unlikely that earlier fledging alone was responsible for the observed differences in success between the two groups in 1992. Earlier fledging may have acted in combination with undetected effects on adult condition (**Figure 7.2a to c**) to cause the increased success of the experimental birds in 1992.

7.4.3 Translation of physiological costs into effects on future survival and reproduction.

Parents of supplementary fed chicks were at an advantage compared to controls in year n+1 with respect to return rates, breeding success and the body condition of young produced. The way in which body condition might influence the survival chances of any organism is necessarily intuitive. It is also straightforward to envisage the method by which increased body reserves might increase the resources available for allocation to reproduction. The greater success of the experimental pairs (in terms of chicks fledged per pair returning to breed) was largely due to their increased laying/hatching success rather than differences in rearing success because very few pairs in either group failed during rearing. Experimental pairs therefore had either a greater ability to lay than controls, or perhaps a greater ability to relay or to sustain egg formation after the March gale, or a greater ability to sustain incubation after initial laying or replacement of lost eggs. Differences in success between the experimental and control pairs were likely due to fewer eggs being laid by controls than to eggs being lost after laying because no deserted eggs were found in burrows at the end of the season nor were any seen to be predated by gulls after ejection from burrows.

The lower laying success of controls in year n+1 could be explained if a condition 'threshold' for breeding exists. Monaghan *et al* (1989) suggested such a 'breeding threshold', below which adult Arctic Terns would not allow their body mass to fall during chick rearing; lighter individuals lost less mass during breeding than heavier birds and were considerably less successful. Equally, young Wandering Albatross females do not breed for the first time until they exceed a threshold mass of c.8kg irrespective of their age (Weimerskirch,1992). In albatrosses the ability of a female to lay in any given year depends on whether her ovary responds to the seasonal increase in gonadotrophin levels by producing progesterone or oestradiol. If the former is produced, no vitellogenesis occurs, the ovary does not mature and laying is impossible. If oestradiol is produced, normal ovary development and laying occur (Hector *et al*, 1986a,1990). High progesterone and low oestradiol levels occur in females before they begin their breeding lives (Hector *et al*, 1990) and in female Grey-headed Albatrosses, a typically biennially breeding species, in the non-breeding year, ie. the year after successfully raising a chick (Hector *et al*, 1986b). Female Grey-headed Albatrosses which failed during the previous year had oestradiol levels as high as successful females returning to breed after a year off however, and both these classes are able to lay (Hector *et al*, 1986b). Hector *et al* suggested that some environmental factor 'switches' the ovary between secreting either progesterone or oestradiol. The developmental potential of ovarian follicles might be influenced months before they mature. It is conceivable therefore, that early follicle development depends on female body condition; if condition is 'poor', properties of the follicle could be altered so that when the pituitary glands begins to secrete gonadotrophin the follicle responds with production of progesterone rather than oestradiol, so preventing breeding in that year.

The extent to which parallel hormonal changes occur in other marine birds is unknown. In seabirds, a continuum between annual breeding and biennial, or even less frequent, breeding of very long-lived species, such as some albatrosses, does seem to exist. It is increasingly being realised that absences from the colony or non-breeding years spent at the colony are a feature of the life-histories of a number of seabird species (eg. Wooller and Coulson,1977 : Kittiwakes absent on 8% of potential breeding occasions; Wooller et al,1989 : 12% of breeding Short-tailed Shearwaters absent in any given year). The same is true for Puffins; for example, 14% of breeding individuals were present at the Isle of May colony in 1990 and 1992 but were not seen in 1991 (M.P.Harris,pers.comm.). Body condition deterioration could be responsible, through hormonally-mediated changes in oocytes similar to those in albatrosses, for years of non-breeding in these other seabird species. It is possible that more experimental female Puffins than controls had the ability to lay in year n+1 (1992) in the present study for this reason, especially as there was evidence to suggest that controls experienced difficult breeding conditions in the previous year.

The higher masses of young produced by experimental pairs relative to controls may have been a direct effect of a body condition advantage, which allowed the experimental pairs to increase their reproductive effort in year n+1. In addition, it was possible that the controls which managed to rear young in year n+1 (1992) were poorer 'quality' birds (later layers) because of the distorting effects the gale early in the breeding season may have had on relative laying dates (discussed above), so that their rearing ability was inferior to that of the experimental pairs. There was no significant evidence that experimental pairs fed their chicks at a greater rate than controls in 1992, although the quality of food loads (size and/or composition) could have differed between the two groups. Experimental pairs spent slightly more time standing around at the colony during rearing than controls in 1992, which could indicate that the former were able to forage more efficiently (as rates of provisioning were the same) for some unknown reason.

CHAPTER 8 GENERAL DISCUSSION.

8.1 The role of body condition in Puffin breeding.

This study investigated variation in the reproductive effort and success of individual pairs of Puffins, with special emphasis upon the role of body condition in breeding. An energetics approach was taken, which involved bird 'quality' being considered in terms of the foraging efficiency of individuals. It was acknowledged that this efficiency may have been related to age and breeding experience (Curio,1983; Nol and Smith,1987) but too few individuals were of known age or experience to allow these factors to be examined fully.

The advantages of increases in body condition are likely to disappear above some maximum level (Martin,1987), so that individuals with optimal body condition may not carry the maximum reserve levels. A balance is thought to exist between the advantages accruing from reserve carriage, as 'insurance' against 'lean times', and the disadvantages of the increased foraging time required to maintain the reserves and increased energetic and predation costs of increased wing loading (Blem,1975; Lima,1986). The optimal level of reserves carried by individuals within a population should be selected during the course of evolution to confer maximum fitness for any given stage of the annual cycle and under the prevailing environmental conditions (King,1972). Relationships between the levels of body reserves and environmental conditions are poorly understood (Blem,1976; Dawson and Marsh,1989; Blem,1990). During favourable feeding conditions, individuals may carry lower reserves because there is less need for 'insurance' (Blem and Shelor,1986), or they may carry greater reserves than in poor conditions if no adjustment is made to foraging duration or intensity with changes in food availability. These relationships are likely to exist both at the population level and at the level of the individual, such that differences in foraging efficiency should produce differences in reserve levels, the latter being optimized for each individual.

In the present study, no relationship between adult body condition during the pre-laying period and either the timing of breeding or hatching success was found. Similarly, there was no effect of body mass during the pre-laying period on either timing of laying or breeding success for Guillemots (Harris and Wanless,1988). These results could reasonably be expected, however, given the potential confounding effects of differences in individual 'quality' on body reserve mass.

A possible mechanism by which such effects could operate is illustrated in **Figure 8.1**. If individual reserve levels are a reflection of foraging ability and there are disadvantages attached to excess carriage of reserves, efficient foragers might carry less reserves than less efficient birds; with their greater ability to acquire reserves, efficient foragers need less insurance reserves to sustain them through periods of decreased food availability. If Puffins time their breeding to coincide with the seasonal peak in food availability, feeding conditions should be improving with calendar date during the season and, in addition, the length of the daylight period is increasing, which might allow extra daily foraging time (it is not known whether Puffins can forage for themselves at night). Insurance body reserves, required to allow laying and to sustain incubation, might be expected to decrease with calendar date therefore. The above assumptions could result in efficient and inefficient foragers (and those intermediate between the two extremes) having similar body reserves at the same time in their breeding cycles because efficient foragers might lay earlier when food is scarcer (**Figure 8.1**). In this case, it would not be possible to detect a relationship between timing of breeding and individual TRM unless reserves could be experimentally manipulated (eg by providing food during the pre-laying period); this was not possible in the present study. The above assumes that it is advantageous to lay early but this advantage has not been clearly established for Puffins.

By the same arguments suggested in **Figure 8.1**, the mean body reserves of individuals not subsequently succeeding in laying or hatching young, weighed on any given calendar date prior to laying, could fall into either of several positions on the graphical model. If unsuccessful breeders were extremely inefficient foragers and spent all their time self-feeding to maintain high insurance reserves, their mean body reserve mass would lie above that of successful breeders (mean A in **Figure 8.1**). Lack of success could have been caused by individuals with a range of foraging efficiencies not acquiring the appropriate reserve levels for breeding, however. Their mean reserves would be lower than those of successful birds (mean B in **Figure 8.1**) only if efficient foragers were equally likely to fail to reach the appropriate reserve level as inefficient foragers. If less efficient foragers were less likely to reach the required reserve level than efficient birds, the mean body reserve mass of unsuccessful birds would lie within the range for successful birds (mean C in **Figure 8.1**); in this case, a very large sample size would be required to detect a difference in mean reserve mass between the two groups. There was an indication that unsuccessful hatchers had higher body reserves than successful individuals in the present study but the difference was far from significant and sample sizes were small.

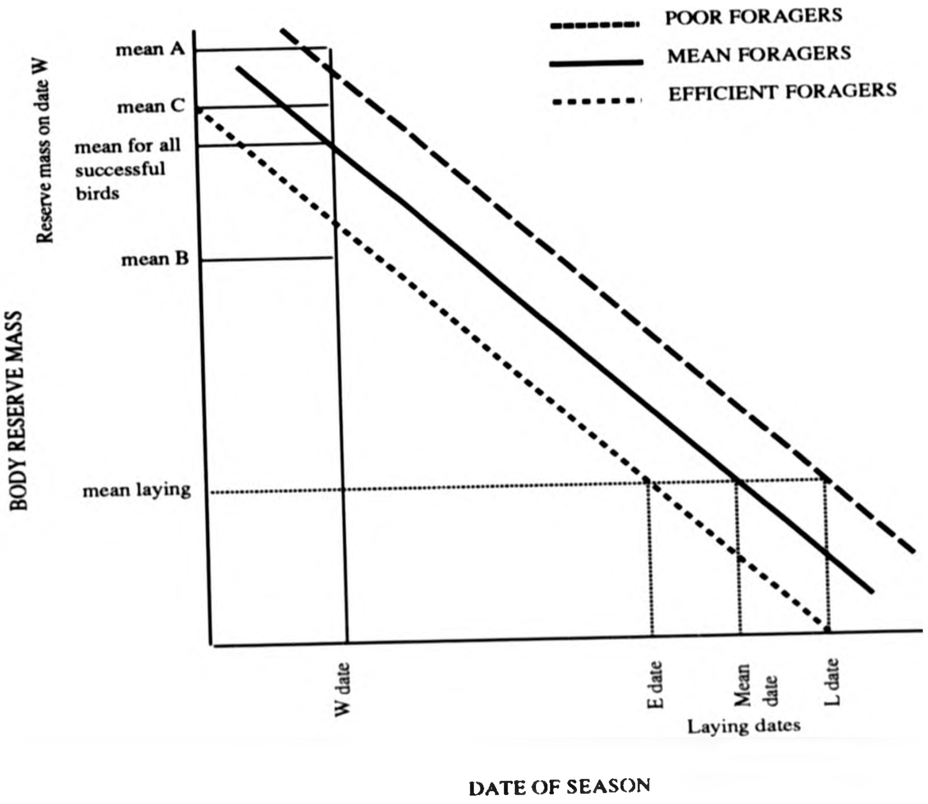


Figure 8.1 **Model of seasonal changes in body reserves for birds which differ in foraging efficiency, which demonstrates reasons for the lack of relationships between the pre-laying body reserves of adult Puffins and (i) timing of breeding and (ii) hatching success.**

The body reserves of individuals decrease with date of season as food availability and time available for foraging increase, and efficient foragers carry lower 'insurance reserves' than poor foragers (these assumptions are discussed in the text).

(i) If early laying is advantageous and efficient foragers lay earlier (E date) than poor foragers (L date), reserve levels at laying (mean laying) could be similar regardless of foraging ability and laying date.

(ii) On any date in the pre-laying period (eg W date) when birds were weighed, mean reserve levels of individuals not subsequently hatching young could be at mean A, B or C compared to successful birds :-

Mean A - unsuccessful because of very poor foraging ability necessitating all time spent self-feeding

Mean B - fail to reach reserve level appropriate to foraging ability (equally likely for all individuals regardless of foraging ability)

Mean C - as for B but poor foragers more likely to fail to reach required reserve levels than efficient foragers.

Mean C would be within the range of reserve levels for successful breeders and would be difficult to separate from the latter without a very large sample size.

Similar confounding effects of factors influencing body condition may have masked relationships between the chick rearing performance of individual pairs of Puffins and body condition in the present study. If individual Puffins carried reserves appropriate both to their own foraging abilities and to prevailing feeding conditions (assumptions as for **Figure 8.1**), a poor forager experiencing good feeding conditions could carry the same reserve levels as an efficient forager during poor feeding conditions, and this could occur regardless of the directions of relationships between body reserves, feeding conditions and foraging ability (**Figure 8.2**). Such cancelling effects of individual efficiency and feeding conditions on adult body condition would be most likely to mask correlative relationships between body condition and breeding performance if individuals of a particular foraging ability are likely to experience a particular level of feeding conditions (for example, if efficient foragers hatch young earlier in less favourable feeding conditions than poor foragers, as in **Figure 8.1**). Even without such a systematic bias, the relationships suggested in **Figure 8.2** be sufficient to distort relationships sought between adult condition and breeding performance, especially when sample sizes are small (as in the present study).

Similar effects of individual quality may have prevented the detection of relationships between adult body condition and inter-year reproductive costs in the present study. The body condition (residual reproductive value) threshold (Monaghan *et al*, 1989,1992), below which costs are experienced, might vary between individuals, in a similar manner as optimal reserve mass.

8.2 Costs of reproduction for long-lived seabirds.

In the present study, pairs of Puffins, under natural conditions, showed a lower return rate to the colony between years, lower breeding success (young fledged per pair) and produced young in 'poorer' condition than pairs whose young were fed for them to reduce their reproductive effort in the previous breeding season. This suggested that Puffins on the Isle of May incurred inter-year costs as a result of breeding.

8.2.1 Body condition and reproductive costs.

In Chapter 7, the physiological condition of parents was examined as a possible 'currency' for reproductive trade-offs, and mechanisms by which body condition could mediate inter-year costs were discussed. The results presented provided little evidence that the components of

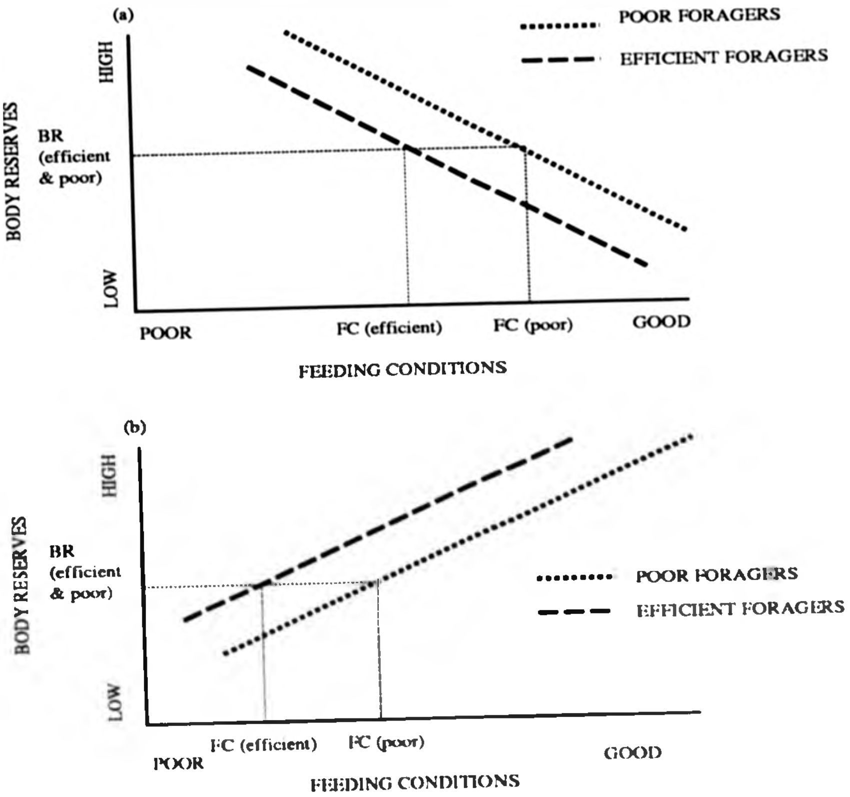


Figure 8.2

Model of body reserves in relation to feeding conditions for 'poor' and 'efficient' foragers. This demonstrates a mechanism by which the effects of food availability (feeding conditions) and individual foraging ability on adult body reserves could cancel, resulting in similar body reserves (BR efficient & poor) for poor foragers in good conditions, FC(poor), and efficient foragers in poor conditions, FC(efficient).

Such a mechanism would operate regardless of the direction of relationships between individual foraging ability and feeding conditions, and body reserve levels (discussed in the text) :-

(a) **Negative relationship between body reserves and feeding conditions, and between body reserves and individual foraging ability.**

(b) **Positive relationship between body reserves and feeding conditions, and between body reserves and foraging ability.**

body condition measured had influenced the observed inter-year costs, however. In contrast, Glaucous-winged Gulls rearing enlarged broods showed reduced survival compared to controls and also experienced greater mass loss during in the year of the enlargement (Reid,1987), which suggested that reduced body condition could have influenced their survival.

The greater success of pairs which underwent the supplementary feeding treatment in the present study could have been due to an unmeasured condition advantage being carried over to the following year. Newton (1989,1993) found a positive relationship between the size of the pectoralis muscle protein store in autumn and over-winter survival in male but not female Dippers, although there was no relationship between mass and survival. There was a suggestion that pectoralis protein was acquired at the expense of other body components; during the period of pectoralis protein accumulation there was no net change in lean dry mass or live mass of the birds but some evidence of a decrease in lipid stores. Measurement of body mass or lipid mass alone would not, therefore, have revealed any change in body components in this case. Newton concluded that increased breast muscle protein might enhance long-term prospects for Dippers more than lipid stores because the latter might incur higher aerodynamic/hydrodynamic costs than the former. Such protein stores could be mobilised if periods of negative energy balance were to arise, although less efficiently than lipid stores. The daily energy expenditure and apparent foraging rate of Dippers are highest in the spring (Bryant and Tatner,1988), at the time when pectoralis protein stores were found to be highest. Newton concluded that the extra "exercise" might account for part of the muscle increase (Marsh,1984) and that such a potential reserve might not be primarily intended for improvement of fecundity "but might instead generate the power to facilitate high levels of activity (including territorial contests) in spring". If such muscle protein levels were important for Puffins in spring they would have gone undetected in this study. Puffins must dive to forage and have high flight costs due to high wing loading (Chapter 6). It might be beneficial, therefore, for them to carry reserves as pectoralis protein rather than lipid because the latter could result in increased buoyancy and consequent diving costs (Wilson *et al*, 1992) while the former could provide greater power for flight. In this respect Puffins differ from gulls, which do not normally dive to feed and are, therefore, likely to be more specifically adapted for efficient flight; for the latter, carriage of lipid reserves might be more appropriate and condition variation among individuals might be more likely to be reflected in body mass differences (as in Reid,1987).

8.2.2 Influence of factors other than body condition on reproductive costs.

Site disturbance (see Chapter 2, section 2.9) could have been responsible for the differences in success of experimental and control pairs if a larger proportion of control individuals compared to experimental birds was handled during breeding. This was only true in 1991, when few experimental adults but most of the control parents were caught at the end of chick rearing. This second capture of control birds during rearing may have made them more hesitant when returning to the colony with food loads so that more loads were lost to gulls and more effort had to be expended in obtaining replacement loads. There was no available evidence for this interpretation. There was a suggestion, however, that parents were reluctant to provision young for several hours to several days after they were caught (pers.obs.). In this case, the second capture of controls would have slightly reduced the effort each individual put into rearing, if it had any effect. At all other times experimental and control pairs were subjected to equal quantities of disturbance, both in terms of captures and general disturbance to the site as a whole (experimental and control burrows were randomly distributed within the study site). General disturbance at the site may have reduced the success of all pairs, however, so highlighting the differences in success between the experimental and control groups.

It was impossible to discount the idea that differences in the success of the experimental and control groups in the present study were due to differing levels of parasitism (M.Petrie,pers.comm.). A reasonable quantity of literature exists on the effects of (mainly) ectoparasites on passerine birds (Moller *et al*, 1990). Parasites generally have limited mobility and are thus spread more effectively where nest sites are reused and hosts are in close proximity. Colonial, hole-nesting species are considered to be particularly prone to parasite infestation, and parasitism and disease are often assumed to represent the highest costs of colonial living (Wittenberger,1981; Wittenberger and Hunt,1985). Many seabirds, Puffins included, therefore appear to be at high risk of parasitism. However, few studies have considered the effects of parasites on seabird populations (eg. Feare,1976, Sooty Terns; King et al,1977a and b, Brown Pelicans; Duffy,1983, Peruvian Guano Cormorants; Brooke,1990, Manx Shearwaters; Danchin,1992, Kittiwakes) and the effects of such parasites on seabird breeding performance have yet to be tested experimentally.

In seabirds many ectoparasite infestations associated with haematophagous ticks of the genus Ixodes, which spend most of their life-cycle in close proximity to the nest and climb onto birds for only a few days every year to feed (Eveleigh and Threlfall, 1974). Therefore, the ticks occur mostly on birds which spend long periods at the nest ie. on young but not on adults except during incubation (Danchin,1992). Ticks affect hosts directly by blood extraction but are also vectors of disease-causing viruses (Nuttall,1984,1990). Ixodes ticks occurred on Puffins at the Little Hide site but the numbers found on both adult and young Puffins were small compared to those found on other seabird species on the Isle of May (T.Barton,pers.comm.).

Supplementary feeding resulted in improved chick growth and slightly earlier fledging in the year of the treatment (1991) and a decrease in parental provisioning effort and burrow visiting during rearing. The reduced provisioning effort (ie. assumed body condition increase) and decreased burrow visiting may have rendered the assisted adults less susceptible to the pathological effects of ectoparasites. Data on tick numbers were not collected in the present study but there were no obvious differences in tick loads between fed and control young, despite their growth differences. It was unlikely, therefore, that the differences in chick growth in 1992 were due to differences in the numbers of parasites overwintering in burrows and subsequently infecting chicks. Further detailed studies addressing the effects of parasites on seabirds are clearly required.

Reproductive trade-offs may only be detectable in 'bad years' (DeSteven,1980; Tuomi et al,1983; Reznick,1985; Bell and Koufopanou,1986). In the present study, inter-year reproductive costs for Puffins were only examined between two sets of successive breeding seasons, whereas more years of data would be useful before drawing firm conclusions. Puffin life-history parameters have been monitored on the Isle of May by Dr M.P.Harris since the early 1970's. It was therefore possible to evaluate the return rates, breeding success and chick masses observed in the present study in the context of previous years. During the last 20 years peak and fledging masses of Puffin young have declined, coinciding with a decline in mean daily chick energy intake. Breeding success, in terms of the number of young fledged per egg laid, has shown no significant trend, although 1990 was a particularly poor year. Adult return rates from one season to the next are much lower now than they were in the early 1970's (Chapter 1, **Figures 1.1** to **1.4**). The return rate between 1990 and 1991 of 75% was particularly low for the Isle of May as a whole, this being the year in which there was a large difference in return rates between the control and experimental individuals in this study. The return rates of controls from 1991 to 1992 was so high (98.4%) that an improvement due to the manipulation would have been most unlikely. Where survival rates are very high stochastic events rather than any systematic mortality factor might be responsible for the few losses and these would be equally likely to effect control and experimental adults.

The measure of breeding success used by Harris was not directly comparable to that used in this study so it was difficult to quantitatively assess the breeding success of control pairs in the context of long-term trends. The success rate of controls, of 0.25 chicks per pair returning, in 1992 must, however, have been lower than that for the island as a whole (0.87). Peak and fledging masses of control young in the present study were also significantly lower than those for the island as a whole in 1992 but whether this was due to disturbance effects or weather conditions early in the season remains debatable.

In conclusion, there was evidence to suggest that the years in which reproductive trade-offs were demonstrated in the present study were 'poorer' years for Puffins, both on the Isle of May as a whole compared to previous years and for control birds at the Little Hide site compared to those in other monitored areas of the island.

Most published experimental studies addressing reproductive costs have demonstrated inter-year trade-offs (Nur,1990), while some may have failed to show significant costs due to small sample sizes (giving insufficient statistical power in analyses). In the present study, return rates of experimental and control adults were similar between 1991 and 1992 (96% and 98% respectively) but between 1990 and 1991 the return rate of experimental individuals whose young were fed for them in 1990 was substantially higher (95%) than that of controls (83%). This difference was not statistically significant but if real, was highly biologically significant because of the difference in fitness, in terms of lifetime reproductive success, it could represent (Chapter 26 in Newton,1989).

The lack of a statistically significant difference between the return rates of experimental and control birds from 1990 to 1991 was to be expected given the sample sizes involved. Inadequate statistical power, due to small sample sizes, greatly affects the interpretation of most published brood enlargement studies , in which no effect of manipulations on parental survival has been claimed; type-2 errors have been committed in many cases (Graves,1991). With a difference in return rate of 95% versus 83% (12%) for the experimental and control adults in this study, and sample sizes of 19 and 75 individuals for the two groups respectively, there was less than a 50% chance of detecting a difference at $p<.05$. To have an 80% chance of detecting the difference as true at $p<.05$ a sample size of >175 birds in each group would have been required (from tables in Fleiss,1973). Fleiss (1973) and Cohen

(1988) suggest that statistical power should be set at 0.80 (80% chance of detecting a true difference) where the significance level is set (as it is now by convention) at p<.05; that is type-1 errors are considered four times as serious as type-2 errors so that the type-2 criterion should be four times that of the type-1 (Cohen,1988).

Only one other study has attempted to demonstrate inter-year reproductive trade-offs in a seabird laying a single-egg clutch. Harris (1970) added one extra chick to nests of the Swallow-tailed Gull and showed no difference in return rates between control and experimental parents. However, Harris concluded that conditions for breeding on the Galapagos were rarely as uniformly favourable as they were during his study period; twinned chicks grew as well as controls and the return rate of control adults was >97% . Reid (1987) showed a significant decrease in the survival of adult Glaucous-winged Gulls rearing enlarged broods, using a very large sample compared to most other studies (>300 nests in each group). For Black Guillemots, the survival rate of birds laying two eggs and rearing at least one chick was only 83% compared to a rate of 92% for birds laying two eggs but rearing no young, although the difference was non-significant (Asbirk,1979). This implied that survival costs may also be associated with the rearing of a normal number of offspring under natural conditions, as was suggested experimentally for Puffins in this study.

8.2.3 Consequences of inter-year costs for seabird life-history strategies.

The rearing of a single chick was shown to induce costs for Puffins, although such costs may only be detectable in 'bad years'. In a seabird species laying a single egg clutch, where integer reductions in clutch size are not possible if breeding conditions are poor, the 'safest' option (in terms of retaining residual reproductive value) in a poor year may be to give up at some stage during breeding or to not breed at all. The 'decision' to take a year off could be determined by low body condition at the end of a previous breeding attempt resulting in hormonal 'blocking' of breeding (Chapter 7).

The occurrence of reproductive costs implies an adaptive significance of the single-egg clutch and suggests a reason for the Puffins (and single-egg clutch seabirds in general) not attempting to raise twins and for single parents not being able to raise chicks in many cases (Rice and Kenyon,1962; Stonehouse, 1962; Huntington,1963; Harris,1966,1969,1970; Ydenberg and Bertram,1989, for review and Birkhead and Harris, 1985, for review of studies on alcids). Chicks may only be raised successfully in such situations if feeding conditions are particularly favourable (accounts for inter-year and inter-site differences in results) or if the particular pair is of above average 'quality' (accounts for inter-pair differences in results).

If there is a trade-off between current and future reproductive potential, then life-history theory predicts that a long-lived seabird should abandon a breeding attempt or not breed at all if the perceived risk to its survival is too high (eg. Drent and Daan,1980; Pugsek,1987). The relative importance of life-span and number of surviving offspring (recruits) in determining the lifetime reproductive success of individuals is still unclear (Chapter 26 in Newton,1989). In most species studied to date, it has only been possible to express lifetime reproductive success in terms of the number of fledged young, and then life-span usually emerged as the major determinant of lifetime reproductive success. In the few studies where the number of recruits was measured, life-span contributed less, however, especially in species where offspring survival varied greatly between years due to fluctuating food supply, which could be the case for seabirds, including Puffins. Few authors have discussed the impact of demonstrated reproductive trade-offs on fitness. Gustafsson (1990) stressed that although the negative effects of clutch size on future female fecundity, and survival (for birds aged >5 years), were very strong in the Collared Flycatcher, only the effect on fledgling survival (recruitment) was important in fitness terms because few adults survived for more than one or two breeding seasons. The relative importance of the costs demonstrated in the present study in influencing the lifetime reproductive success of Puffins can only be determined once the future survival and recruitment of Puffin offspring can be measured or when the effect of fledging body condition on these life-history parameters can be established. It could be that longer-lived individuals produce 'poorer quality' young, which have a lower chance of recruitment, than those produced by shorter-lived individuals that expend more effort on chick rearing in any given year ?

8.3 Energy expenditure of Puffins on the Isle of May during the chick rearing period.

Seabird studies in which field metabolic rate (FMR) was measured during the breeding season by isotope turnover, in species for which empirical determinations of basal metabolic rate (BMR) were also available, were reviewed (**Table 8.1**). FMRs measured in the present study showed that Isle of May Puffins were working at a level of 3.45 times BMR during chick rearing in 1991 and 1992. This metabolic intensity lay in the central part of the range for all seabird species (range 1.83 to 6.56 times BMR) but was lower than the mean of 3.81 times BMR for the 7 species which, in common with Puffins, are volant pursuit divers using

Table 8.1

Table 8.1 **The metabolic intensity of seabirds during breeding -**
A review of the literature with special reference to the chick rearing period.
(Species in italics are volant, cold-water pursuit divers using predominantly flapping flight).

SPECIES	MASS (kg)	BMR (kJd^{-1})	FMR (kJd^{-1})	MI[1]	BREEDING STAGE[2]	FORAGING MODE[3]	REFERENCES[4]
Adelie Penguin	3.868	1039	4002	3.85	BREEDING[a]	P	a,b
Little Penguin	1.092	465	920	1.98	BREEDING[a]	P	c,d
Little Penguin	1.050	426/268[5]	1860	4.37/6.94	CHICK REARING	P	c,e,f
Grey-headed Albatross	3.665	718	1729	2.41	INCUBATION	A,G	g,h
Wandering Albatross	8.417	1833	3354	1.83	CHICK REARING	A,G	i,j
Laysan Albatross	3.067	607	1802	2.97	BREEDING[a]	A,G	b,k
Southern Giant Petrel	4.044	976	4443	4.55	BREEDING[a]	A,G	b,g
Wedge-tailed Shearwater	0.384	146	614	4.21	INCUBATION/BROODING[c]	A,G	g,l
Wilson's Storm-petrel	0.042	37	157	4.24	(CHICK REARING)[d]	A,G	m
Leach's Storm-petrel	0.045	42	123	2.85	(CHICK REARING)[d]	A,G	n
Leach's Storm-petrel	0.046	45	142	3.16	CHICK REARING	A,G	o
South Georgia Diving Petrel	*0.109*	*112*	*464*	*4.15*	*CHICK REARING*	*P,F*	*p*
Common Diving Petrel	*0.137*	*130*	*557*	*4.27*	*CHICK REARING*	*P,F*	*p*
Gannet	3.210	742	4865	6.56	CHICK REARING	Pl,F	q

Kittiwake	0.386	314	794	2.53	CHICK REARING	A,F	r
Sooty Tern	0.184	86	340-410	3.96-4.77	(CHICK REARING)^{e}	A,F	s,t
Brown Noddy	0.195	95	352	3.71	INCUBATION	A,F	l,u
Guillemot	*0.940*	*348*	*1789*	*5.14*	*CHICK REARING*	*P,F*	*v*
Brunnich's Guillemot	*1.119*	*660*	*2080*	*3.15*	*CHICK REARING*	*P,F*	*w,x*
Black Guillemot	*0.381*	*284*	*863*	*3.04*	*CHICK REARING*	*P,F*	*y,z*
Least Auklet	*0.084*	*116*	*358*	*3.09*	*CHICK REARING*	*P,F*	*p*
Little Auk	*0.164*	*178*	*696*	*3.91*	*CHICK REARING*	*P,F*	*A*
Puffin	*0.395*	*253*	*874*	*3.45*	*CHICK REARING*	*P,F*	*B*

NOTES.

1 Metabolic intensity (FMR divided by BMR)

2 Breeding stage : a=stage not specified; b=foraging but trips are longer during chick rearing; c=includes time spent foraging; d=FMR integrated for 100% foraging (equivalent to that during rearing according to the authors); e=stated FMR's are for 100% off-nest during incubation and for 100% flight (equivalent to rearing ?)

3 Foraging mode : P=pursuit diver; A=aerial forager; Pl=plunge diver; G=predominantly gliding flight; F=predominantly flapping flight

4 References : a=Kooyman *et al* (1976); b=Nagy (1987); c=Stahel and Nicol (1982); d=Costa *et al* (1986); e=Gales and Green (1990); f= Baudinette *et al* (1986); g=Adams and Brown (1984); h=Costa and Prince (1987); i=Brown and Adams (1984); j=Adams *et al* (1986); k=Grant and Whittow (1983); l=Ellis (1984); m=Obst *et al* (1987); n=Ricklefs *et al* (1986); o=Montevecchi *et al* (1992); p=Roby and Ricklefs (1986); q=Birt-Friesen *et al* (1989); r=Gabrielsen *et al* (1987); s=MacMillan *et al* (1977); t=Flint and Nagy (1984); u=Ellis *et al* (1982); v=Cairns *et al* (1990); w=Johnson and West (1975); x=Flint *et al* (unpubl.) in Gabrielsen *et al* (1991); y=Gabrielsen *et al* (1989); z=Mehlum *et al* (unpubl.) in Gabrielsen *et al* (1991); A=Gabrielsen *et al* (1991); B=present study

5 Five measurements of BMR available (highest and lowest used)

predominantly flapping flight.

Puffin energy expenditure was not, therefore, exceptionally high and was, on average, well below the suggested sustained working threshold of 4 times BMR (Drent and Daan,1980). Most of the reviewed studies showed that seabirds work at 3 to 5 times BMR during chick rearing although a few, notably Gannets (6.6 times BMR) and Little Penguins (up to 6.9 times BMR), greatly exceeded the suggested working level. Isle of May Puffins worked at a level of 3.45 times BMR despite indications (Chapter 1) that they were experiencing some difficulty in raising their young, consistent with the concept of a maximum sustainable work load which they would not exceed, despite the evidence to suggest that their chicks would have benefitted from increased food delivery. If the chick feeding frequency was increased to the maximum observed level of 8 feeds by a single parent in a day, daily energy expenditure (DEE) predicted from a time-activity energy budget rose to 3.65 times BMR, still below the suggested 4 times BMR limit on metabolic intensity. It was noticeable that such high feeding rates were only sustained over short periods (usually 1-4 days, pers.obs.). In only one labelled individual did measured FMR exceed 4 times BMR and this was during 'poor' weather conditions.

In most studies where FMR has been compared to BMR to derive metabolic intensity, BMR measured in the laboratory was corrected to the mean body mass of the birds for which FMR was measured, using an appropriate allometric exponent. Such a derived BMR value was used in the current study (see section 6.2.5 p108 for method of calculation) to enable comparison to be made with literature values of metabolic intensity. The laboratory value of BMR was measured for 4 adult Isle of May Puffins during the breeding season; it should, therefore, have been representative of the BMR of birds for which FMR was measured in the field. The mass difference between the laboratory group (mean 329g) and the field group (mean 395g) was probably due to the loss of gut contents, body water and/or lipid reserves of negligible metabolic cost, in the former group, as a result of the laboratory protocol (R.W.Furness, pers.comm.). Hence the laboratory value for BMR of 218.5 kJd^{-1} (Bryant and Furness,1992) was representative of that for a typical Isle of May Puffin during breeding, without correction for mass differences between the laboratory and field groups. Using the latter value for BMR, Puffins in the current study (with a mean FMR of 874 kJd^{-1}) were working at a mean of 4.0 times BMR (range 2.7-5.3 times BMR). They were, therefore, working at the proposed metabolic intensity threshold of 4 times BMR (Drent and Daan,1980). Such a result was more consistent with other evidence that Puffins on the Isle of May were experiencing difficulty in rearing young during the years of the study. The present study highlighted the need for caution when selecting BMR values with which to compare FMR.

Puffin FMR obtained using the doubly-labelled water (DLW) method was almost identical to the value predicted from an allometric equation relating FMR to body mass (Birt-Friesen *et al*, 1989). The FMRs of 7 species of cold-water seabirds using wings for propulsion underwater and flapping flight, also estimated using DLW, were a mean of 124% of the values predicted from this equation (Gabrielsen *et al*, 1991). Deviations of measured FMR from the equation's predictions were smallest for Puffins (the present study) and Black Guillemots, intermediate in Guillemots, Brunnich's Guillemots and Least Auklets, and highest in South Georgia and Common Diving Petrels and Little Auks (**Table 8.2**). The extent of the deviation could depend on the distances the birds must fly in order to forage each day (ie. the product of the distances of foraging sites from the breeding colony and the number of trips made each day) and/or on the type of prey sought. The larger auks all feed their young on fish and generally forage close to the colony during rearing; the FMRs of these species were close to those predicted by Birt-Friesen *et al* (1989). Least Auklets, diving petrels and Little Auks all feed their young on zooplankton and their FMRs were substantially greater than those predicted from their body masses. Planktonic prey may be more expensive to catch than larger fish, requiring a larger time allocation to diving each day or incurring a higher diving cost per unit time. Little Auks at least are known to seize individual copepods underwater (Keats,1981), rather than ingesting a bill-full of water containing many prey items. Plankton may be a less spatially predictable prey source than fish and the planktivorous species considered here, Least Auklets excepted, probably forage further away from their breeding colonies than the piscivorous species. The lower FMR of the larger auks was, however, also consistent with the view that mass-specific energy costs are lower in larger individuals (Calder,1974). Further information on the time budgets of seabirds at sea will be required, however, before such interspecific differences in mass-specific FMR can be fully explained. Metabolic intensity differed between the 8 species in a similar pattern to deviations of FMR from predicted values (**Table 8.2**), except in the case of Least Auklets (where MI was lower than 'expected') and Guillemots (where MI was higher than 'expected'). Such apparent anomalies could result from differences in the protocol used for measuring BMR or from variation in the degree of adaptation of BMR to the prevailing environment of the species (operative temperatures, for example).

Table 8.2 **Comparison of the energy expenditures (FMR) during chick rearing of pursuit-diving, cold-water seabirds using predominantly flapping flight.**

SPECIES	% OF PREDICTED[1]	MI[2]	DISTANCE[3] (km)	FOOD TYPE (n load^{-1})	n FEEDS (d^{-1} adult^{-1})	DISTANCE[4] (km d^{-1})	REFERENCES[5]
Puffin	99	3.45	1-2	fish (several)	2.5	5-10	a,b
Black Guillemot	100	3.04	0.25-0.50	fish (single)	4.4	2.2-4.4	c
Guillemot	108	5.14	5-10	fish (single)	1.5	15-30	d,e,f
Brunnich's Guillemot	110	3.15	20-30	fish (single)	1-4	40-240	e
Least Auklet	125	3.09	5-10	plankton (many)	2.7	27-54	g,h,i
South Georgia Diving Petrel	134	4.15	50 ?	plankton (many)	1	100 ?	i
Common Diving Petrel	137	4.27	50 ?	plankton (many)	1	100 ?	i
Little Auk	149	3.91	<150	plankton (many)	4.3	potentially very large	j,k,l

NOTES.

1 Equation 6.6 in the text p109 (from Birt-Friesen *et al*, 1989)
2 Metabolic intensity (FMR/BMR); references as for Table 8.1
3 Distance between breeding colony and foraging site (most likely range or distance given where range is large and data for the specific site are not available)
4 Total distance travelled each day (twice the foraging distance multiplied by the number of feeding trips each day)
5 References : a=Wanless *et al* (1988b); b=the present study; c=Cairns (1987); d=Cairns *et al* (1987); e=Bradstreet and Brown (1985); f=Mahoney (1979); g=Hunt *et al* (1978); h=Roby and Brink (1986); i=Roby and Ricklefs (1986); j=Brown (1976); k=Gabrielsen *et al* (1991); l=Norderhaug (1980)

In conclusion, chick rearing did not appear to be notably demanding energetically for Puffins on the Isle of May, either when their metabolic intensities were compared to those of seabirds in general or to those of species living in cold waters with similar foraging mode. The possibility that the maximum sustainable working level suggested as 4 times BMR (Drent and Daan,1980) is lower for long-lived seabirds cannot be discounted, however, because the optimal trade-off associated with devotion of limited resources to either current and or future reproduction is likely to vary between short-lived (from which evidence for the sustained working threshold was derived)and long-lived species.

8.4 Benefits of an experimental approach to the study of individuals.

A correlative approach to the investigation of relationships between parental body condition, breeding performance and reproductive costs at the level of the individual might not succeed because of confounding effects of individual 'quality' on body condition (**section 8.1**). Equally, the importance of body condition for breeding may only be detectable in years which are less favourable for breeding (**section 8.2.2**). An experimental approach was intended at the outset of the present study but in practice was limited by the unforeseen sensitivity of Puffins to handling/colony disturbance.

Any manipulation of parental effort must be carefully chosen if the results of the experiment are to be clearly interpretable. Some previous studies in which experiments sought to increase effort failed to elicit a response. This may have been because parents were already working maximally (Drent and Daan,1980) and were unable to increase their effort further (Royama,1966; Tinbergen,1980; Bryant and Westerterp,1980; see also Smith,1988), or because parents failed to recognise the needs of additional young (Snyder and Snyder,1973; Geer,1981; Simmons,1986). Short-lived species should be more likely to increase provisioning effort to an enlarged brood than long-lived species because the latter gain more (in terms of lifetime reproductive output) from living longer than by breeding at full capacity each year (Simmons,1986; Korpimaki,1988; Saether *et al*, 1993). Evidence from twinning and adult removal experiments (references cited in **section 8.2.2**) suggests that seabird parents did not always increase food delivery as a result of manipulations sufficiently to raise young. In the few studies which measured the parental response to increased food demand directly, results differed between species. Puffins showed an ability to increase their feeding frequency,at least over a short period, when chick begging calls were played to parents during burrow visits and were also able to rear young for longer than normal in chick exchange experiments

(Harris,1983). Gray-backed Terns whose single chicks were substituted with those of the larger Sooty Tern were shown to increase the size and frequency of meals delivered, and to sustain the increase over long periods (Shea and Ricklefs,1985). In contrast, Leach's Storm-petrels did not respond to increased food demand achieved by exchanging chicks between burrows on a daily basis (Ricklefs,1987). The playing of begging calls failed to elicit a response in the present study, perhaps because breeding conditions were unfavourable and parents would not compromise their residual reproductive value by increasing their effort. The costs of reproduction demonstrated for Isle of May Puffins under natural conditions may only have been detectable during the present study, using an experimental decrease in parental effort, because control pairs were experiencing breeding difficulties.

In conclusion, much variation in 'quality' between individuals was suggested in the present study. Further studies with an energetics approach should focus on these presumed differences in foraging efficiency between individuals by attempting to manipulate effort and measuring energy expenditure while concurrently monitoring time budgets. Such studies are now possible with the advent of the doubly-labelled water technique for measuring field metabolic rates and various activity recording devices to measure time allocation. The Puffin is unlikely to be a suitable species for such work, however, given its apparent sensitivity to handling and disturbance during breeding.

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APPENDIX Scientific names used in text.

(Birds listed in systematic order)

Plants

Common sorrel	*Rumex acetosa*
Small nettle	*Urtica urens*
Yorkshire fog	*Holcus lanatus*

Non-bird vertebrates

Rabbit	*Oryctolagus cuniculus*
Cod	*Gadus morhua*
Herring	*Clupea harengus*
Pollock	*Pollachius pollachius*
Rockling	*Ciliata sp.*
Saithe	*Pollachius virens*
sandeel	*Ammodytes sp.*
Lesser Sandeel	*Ammodytes marinus*
Sprat	*Sprattus sprattus*

Birds

Gentoo Penguin	*Pygoscelis papua*
Adélie Penguin	*Pygoscelis adeliae*
Macaroni Penguin	*Eudyptes chrysolophus*
Little Penguin	*Eudyptula minor*
Jackass Penguin	*Spheniscus demersus*
Great-crested Grebe	*Podiceps cristatus*
Wandering Albatross	*Diomedea exulans*
Laysan Albatross	*Diomedea immutabilis*
Grey-headed Albatross	*Diomedea chrysostoma*
Southern Giant Petrel	*Macronectes giganteus*
Fulmar	*Fulmarus glacialis*
Wedge-tailed Shearwater	*Puffinus pacificus*
Short-tailed Shearwater	*Puffinus tenuirostris*
Manx Shearwater	*Puffinus puffinus*
Audubon's Shearwater	*Puffinus lherminieri*
Wilson's Storm-petrel	*Oceanites oceanicus*
Leach's Storm-petrel	*Oceanodroma leucorhoa*
South Georgia Diving-petrel	*Pelecanoides georgicus*
Common Diving-petrel	*Pelecanoides urinatrix*
Brown Pelican	*Pelecanus occidentalis*
Gannet	*Sula bassana*
Shag	*Phalacrocorax aristotelis*

Guano Cormorant	*Phalacrocorax bougainvillei*
Canada Goose	*Branta canadensis*
Tufted Duck	*Aythya fuligula*
Eider	*Somateria mollissima*
Sandhill Crane	*Grus canadensis*
Oystercatcher	*Haematopus ostralegus*
Arctic Skua	*Stercorarius parasiticus*
Herring Gull	*Larus argentatus*
Lesser Black-backed Gull	*Larus fuscus*
Great Black-backed Gull	*Larus marinus*
Glaucous-winged Gull	*Larus glaucescens*
Laughing Gull	*Larus atricilla*
Kittiwake	*Rissa tridactyla*
Swallow-tailed Gull	*Larus furcatus*
Common Tern	*Sterna hirundo*
Arctic Tern	*Sterna paradisaea*
Sooty Tern	*Sterna fuscata*
Brown Noddy	*Anous stolidus*
Little Auk	*Alle alle*
Razorbill	*Alca torda*
Brünnich's Guillemot	*Uria lomvia*
Guillemot	*Uria aalge*
Black Guillemot	*Cepphus grylle*
Ancient Murrelet	*Synthliboramphus antiquum*
Crested Auklet	*Aethia cristatella*
Least Auklet	*Aethia pusilla*
Puffin	*Fratercula arctica*
Pied Kingfisher	*Ceryle rudis*
Blue-throated Bee-eater	*Merops viridis*
Swallow	*Hirundo rustica*
House Martin	*Delichon urbica*
Dipper	*Cinclus cinclus*
Golden-crested Kinglet	*Regulus satrapa*
Great Tit	*Parus major*