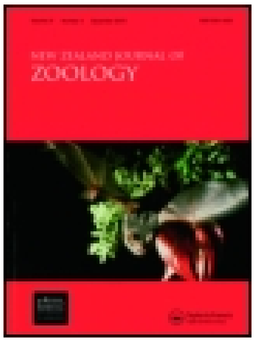

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Lipid levels in the South Island pied oystercatcher (*Haematopus ostralegus finschi*)

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(*Received 31 January 1975*)

Wing lengths and some major body components were compared among the sexes and age classes of a sample of 48 South Island pied oystercatchers (*Haematopus ostralegus finschi*). Immature males were significantly lighter in wet weight and fat-free weight than either immature females or adults, and were significantly lighter than adults in lean dry weight. No statistical differences were found in wing length, total lipids, or fat measure for birds in this sample. In a larger sample of 182 birds, fat measure varied similarly in the age classes, from a low in autumn to a peak in spring just before vernal migration. Massive pre-migratory fattening typical of many small passerines does not occur in this species, but even so the average fat reserves in spring adults are sufficient for an approximate flight range of 2140 km, well in excess of need. It is hypothesised that the amount of fat deposited before vernal migration is a compromise between the energy cost of acquiring and transporting extra fat and the advantages of arrival at the breeding grounds with sufficient fat reserves for early achievement of breeding condition.

INTRODUCTION

Body weights of birds vary seasonally in a rather regular manner, but fat-free weights (body weight minus fat) and lean dry weights (body weight minus fat and water) remain relatively constant throughout the year (Odum & Perkinson 1951; Odum & Connell 1956; Odum 1958, 1960a; Connell *et al.* 1960; Rogers & Odum 1964; Odum *et al.* 1964; Helms *et al.* 1967). The seasonal pattern of weight change may be paralleled by seasonal changes in liver weight and tissue water content, but by far the greatest component is attributable to the deposition or depletion of fat in specific depots (George & Berger 1966). Seasonal variation in lipid reserves is most marked in migratory birds, especially in long-distance migrants that have to cross barriers such as oceans or deserts by prolonged flight (Odum *et al.* 1961). Such species often develop hyperphagia, and feed voraciously to build up extensive lipid deposits shortly before departing on long migratory flights (Odum 1960b).

The conspicuous pre-migratory fattening in long-distance migrants is characterised by rapid deposition of fat in the peritoneal or visceral depot, and this reserve is usually exhausted at the end of migration (Odum & Perkinson 1951). According to George & Berger (1966) the peritoneal or 'migratory' fat can be distinguished from the subcutaneous or 'winter' fat, but this seems a rather artificial division since lipids from both depots are probably mobilised to meet the energy cost of migratory flight.

Despite the extensive literature on lipid deposition in birds, relatively little is known about lipid levels in non-passerine migrants. For shorebirds the major studies are those of Johnston & McFarlane (1967) on the golden plover (*Pluvialis dominica*), McNeil (1969)

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TABLE 1—Sample data for South Island pied oystercatchers (*Haematopus ostralegus finschi*) used in this study

			Sample Composition			
Season	Locality	Sample obtained	Adult ♂♂	Adult ♀♀	Immature ♂♂	Immature ♀♀
Winter	Heathcote-Avon Estuary	16 Jun. 1970	26	7	12	6
	,, ,, ,,	18 Jun. 1971	9	3	2	0
			35	**10**	**14**	**6**
Spring	Heathcote-Avon Estuary	29 Jul. 1970	12	10	16	5
Summer	Ashley River, Canterbury	11 Nov. 1970	2	2	0	0
	Heathcote-Avon Estuary	13 Jan. 1971	0	0	4	3
	,, ,, ,,	5 Feb. 1971	12	9	2	3
			14	**11**	**6**	**6**
Autumn	Parapara Inlet, NW Nelson	12 Apr. 1971	2	0	1	0
	Heathcote-Avon Estuary	23 Apr. 1971	13	8	5	8
			15	**8**	**6**	**8**

and McNeil & Cadieux (1972) on several charadriids and scolopacids, and Page & Middleton (1972) on the semipalmated sandpiper (*Ereunetes pusillus*). Nothing seems to be known about lipid deposition in oystercatchers (Haematopodidae).

As part of a broader study of morphological variation in the South Island pied oystercatcher (*Haematopus ostralegus finschi*), I trapped samples of birds at various times of the year to obtain critical information on seasonal variation in standard measurements and body weight (Baker 1975). These samples also provide material for an investigation of lipid levels in this species. The primary objectives of this study were to quantify some of the major body components, especially total lipids, to investigate seasonal variation in lipid levels, and to estimate the average flight range of this species.

MATERIALS AND METHODS

SAMPLING DETAILS

Eight samples of South Island pied oystercatchers were trapped over the period June 1970 to June 1971 (Table 1). After collection each bird was weighed, sexed by dissection, and its wing length measured to the nearest 1 mm. Visible fat in the discrete perivisceral and ventral subcutaneous fat depots was removed and weighed. The weight of this depot fat, hereafter called 'fat measure', was used as an index of total lipid content. Weighings were carried out on a Mettler balance, and were recorded to the nearest 0.1 g. In the South Island pied oystercatcher the perivisceral fat extends from the posterior end of the stomach along the intestinal mesentery to the base of the abdominal cavity, and can be neatly removed in two pieces, one either side of the intestinal tract. The ventral subcutaneous fat is more diffusely distributed, so only that portion between the furcula and the ventral aspect of the pelvis was removed, its lateral margins being arbitrarily defined by horizontal lines through the uncinate processes of the ribs.

For analysis of seasonal variation in lipid levels the samples had to be allocated to seasons. In this study biological rather than strictly seasonal criteria were used to achieve this partition, such that autumn, winter, spring, and summer correspond to post-migration and moult, over-wintering, pre-migration, and breeding periods respectively (Table 1). It should be noted, however, that the summer sample contains birds taken in early February, most of which are probably post-migratory.

Although 4 age classes can be distinguished in the South Island pied oystercatcher (*see* Baker 1974), in this study the data were too few to permit a thorough statistical analysis of variation in major body components at this level. Hence a limited analysis was carried

TABLE 2—Wing length and major body components of South Island pied oystercatchers (*Haematopus ostralegus finschi*) in extraction sample

	Variable (Mean ± S.E.)						
Age class and sex	Wing length (mm)	Wet weight (g)	Total lipids (g)	Fat measure (g)	Fat-free weight (g)	Lean dry weight (g)	*n*
Adult ♂	254±1.4	538.3± 7.29	46.6 ±3.53	4.0±0.59	491.7± 6.10	100.4±0.86	23
Adult ♀	257±1.6	558.8± 6.11	44.6 ±4.96	3.9±1.07	514.2± 6.68	104.9±1.79	11
Imm. ♂	252±1.8	488.6± 9.5	46.5 ±4.20	4.4±0.95	442.1± 7.45	91.6±1.12	7
Imm. ♀	256±2.2	525.7±11.98	39.1 ±8.27	3.2±1.15	486.6±10.68	98.8±3.45	7
							48

out in which first- and second-year birds were pooled as 'immatures', and sub-adults and adults were pooled as 'adults'.

Forty-eight birds from the April and June samples in 1971 were selected at random for extraction of total lipids. Undigested food was removed from the alimentary tract, and then each plucked carcass was minced separately in an apparatus described by Bamford (1970). The feathers were discarded because of practical difficulties of incorporating them in the homogenate, and hence do not contribute to the 'lean dry weight' values below. Unfortunately this procedure eliminated the estimation of the water content of each carcass, since it is deduced from the difference between wet and dry weights. After each bird was processed the mincer was flushed with 95% ethanol and the resulting mixture was further homogenised in a Waring blender. The homogenate from each bird was dried in an oven at 65°C until constant dry weight was achieved (approximately 7 days). Weighings were made with the sample in a dessicator. The dried samples were ground to a coarse powder with a mortar and pestle, and then placed in separate 180×60-mm fat-free extraction thimbles. Lipids were extracted from the samples in a 5-litre Soxhlet extractor, using a 5:1 mixture of petroleum ether and chloroform as solvent. The fat-free residues were dried in an oven to constant weight, and the 'total lipid' values were calculated by difference between the dried samples before and after extraction of lipids. Although petroleum ether extracts all lipids, including a fraction which is unavailable as fuel, the energy in this 'structural' or tissue fat is compensated for by the potential for catabolism of muscle protein (Rogers & Odum 1966). Hence, 'ether-extractable' lipids may be used to estimate the flight range of migratory birds.

RESULTS

WING LENGTH AND MAJOR BODY COMPONENTS OF EXTRACTION SAMPLE

Wing lengths and some major body components of the birds in the extraction sample are summarised in Table 2. Differences among means were tested by single classification analysis of variance followed by the sums of squares simultaneous test procedure, an *a posteriori* multiple comparisons test (Gabriel 1964). Although wing length differs considerably with sex and age in South Island pied oystercatchers (Baker 1975), in this sample there are no statistically significant differences between the sexes or age classes. Nonetheless, it is noteworthy that the means are larger for females than for males within respective age classes, and are larger for adults than for immatures within the sexes. The lack of a significant age difference in mean wing length may be partly due to the pooling of first- and second-year birds in the immature category, as it has been established that the wing reaches maximum length in the bird's second year of life (Baker 1975).

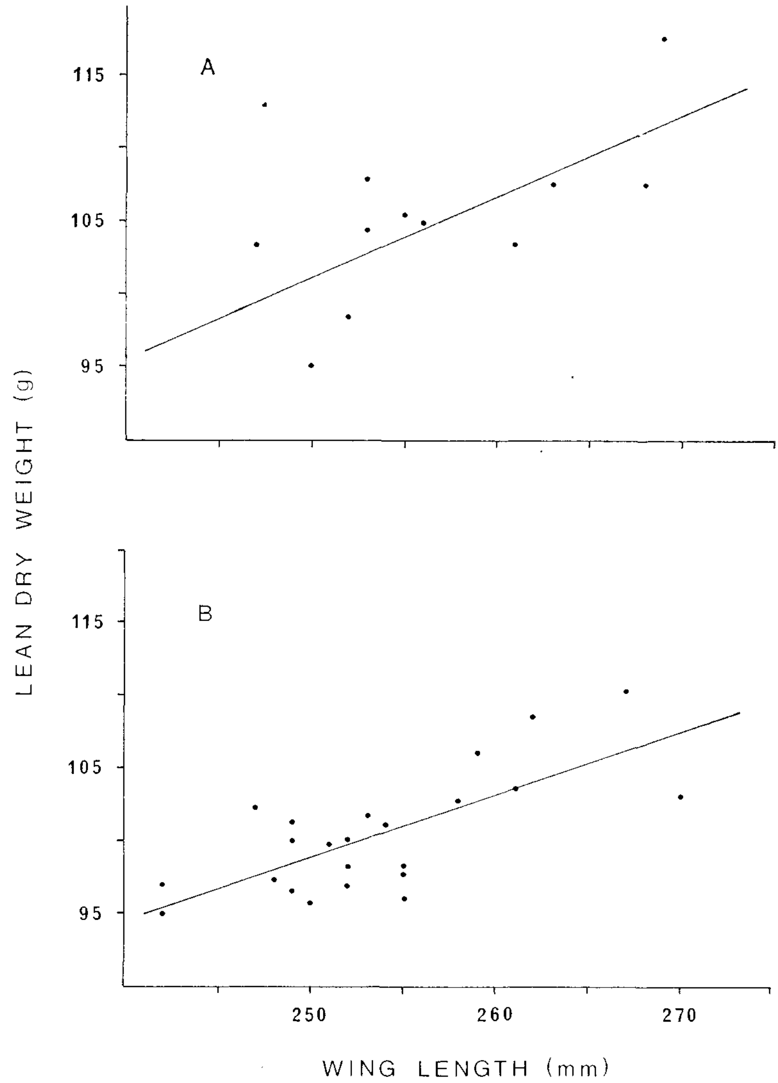

FIG. 1—Regression of lean dry weight on wing length for extraction sample of *Haematopus ostralegus finschi*: A, ♀♀; B, ♂♂.

Immature males are significantly lighter in mean wet weight than either immature females or adults (F = 6.710, $0.01 > P > 0.001$). Total lipids do not differ statistically among the sexes or age classes. This result is perhaps surprising in that adults might be expected to have larger lipid reserves than immatures, since many non-breeding birds do not undertake inland migratory movements to breeding localities. However, 21 of 34 adults in the extraction sample were taken in April not long after they had returned to the coastal winter feeding grounds after migrating northwards from their inland breeding sites in southern New Zealand. Lipid levels in adults were low after the breeding season, probably because of the heavy energy expenditure associated with breeding activities and post-breeding migration (*see* below). April adults have also recently completed their annual moult, and the lipid reserves of some birds are known to contribute to the energy demands of moulting (Koch & Debont 1944, Wallgren 1954, Ward 1964, Helms *et al.* 1967). Differences among mean fat measures of the sexes and age classes are also not significant.

The mean fat-free weight of immature males is significantly lower than that of either immature females or of adults ($F = 10.756$, $P < 0.001$), which is in accord with differences in their wet weights. Immature males and females do not differ statistically in lean dry weight, but immature males are significantly lighter than adults of either sex ($F = 8.831$, $P < 0.001$), again paralleling differences in their wet weights and indicating that the sexes and age classes have similar water contents.

REGRESSION ANALYSIS

It was of interest in this study to determine whether lean dry weight increases directly with body size as measured by wing length, as has been demonstrated for the semipalmated sandpiper and some small passerines (Connell *et al.* 1960, Rogers & Odum 1964, Farrar 1966, Page & Middleton 1972). Only data for adults are considered in the ensuing analysis because of the age differences in lean dry weight outlined above, and the sexes are treated separately because of sexual dimorphism in wing length. Using Bartlett's Model II technique, statistically significant regressions were obtained for either sex (for males, $t_o = 3.478$, $0.01 > P > 0.001$; for females, $t_o = 2.571$, $0.05 > P > 0.01$). The respective regressions are illustrated in Fig. 1. Wing length]of linear dimension) may often be used as an indicator of size (Hamilton 1961), and lean dry weight may be used as an indicator of mass (of cubic dimensions), so it was of further interest to test if their relationship contained any statistically significant curvilinear component. For males $t_L = 1.318$ ($P > 0.20$) and for females $t_L = 1.545$ ($P > 0.10$), indicating that there are no significant deviations from linearity (*see* Davies 1971 for details of this test statistic). Hence it seems that even in a relatively large bird such as the South Island pied oystercatcher, increasing mass is compensated for by a linear increase in wing length.

Regression analysis has also been applied to studies of lipid levels of birds in a predictive sense, usually where some index of visible fat is used to predict total lipids (*see* McNeil 1969). In the present study fat measure can be considered as an index of 'visible' fat, and therefore seems a likely variable for predicting the remaining or 'extractable' lipids in a carcass. Total lipids can then be obtained by summing fat measure and extractable lipids. For predictive purposes, extractable lipids were regressed on logarithmically transformed values of fat measure. All 48 birds were used in the following analysis, since the sexes and age classes do not differ statistically in either of these variables. The Model I least squares fit ($r = 0.952$) gave the following predictive equation:

$$\text{extractable fat} = 10.041 + 50.927 \log (\text{fat measure} + 1.0)$$

On the basis of the extraction sample data it seems possible to predict total lipids of a bird with reasonable accuracy given its fat measure.

SEASONAL VARIATION IN FAT MEASURE

Since the sexes have been shown not to differ in fat measure they have been pooled to increase sample sizes in the ensuing analysis, though for convenience adults and immatures are treated separately. Seasonal trends of variation in fat measure are shown in Fig. 2. The patterns of fat deposition and depletion are broadly similar in adults and immatures, none of the respective seasonal means differing significantly between the age classes. From a low in autumn the birds gradually increased their depot fat reserves through winter to a peak in spring, and then largely expended this energy store by late summer. The marked increase in stored fat from autumn to spring is in accord with winter fattening, though some migratory fat may be accumulating at this time (mid June). Adults show a statistically

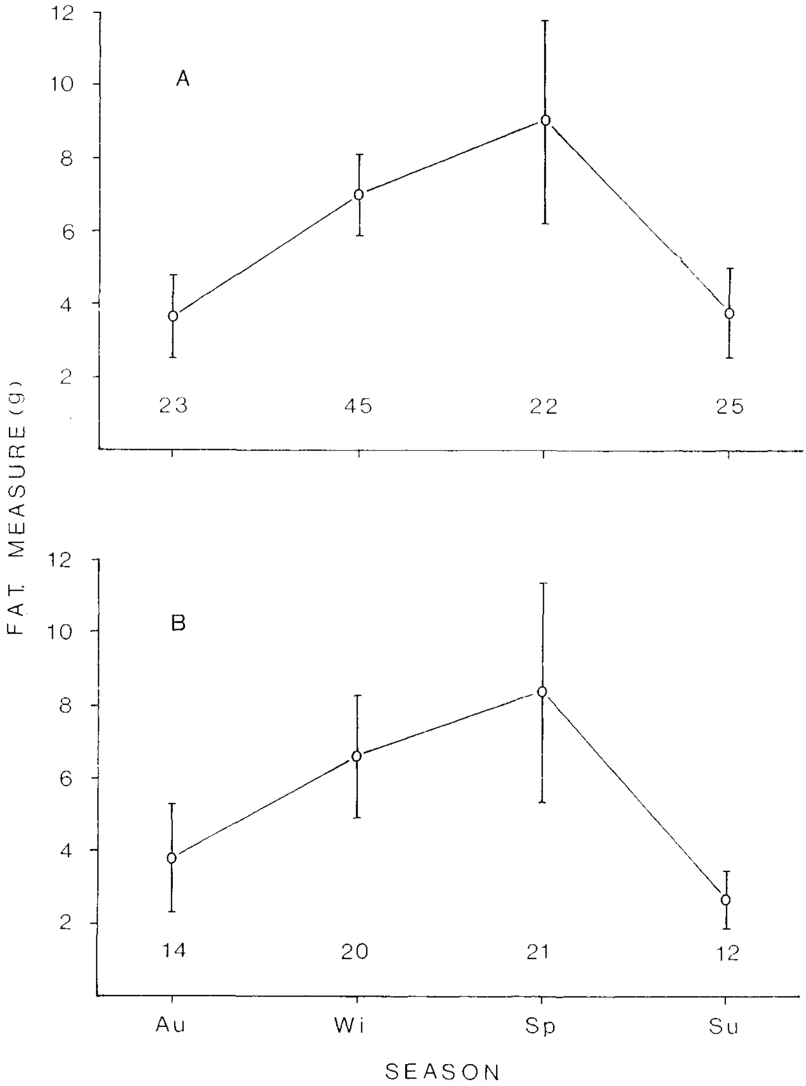

FIG. 2—Seasonal variation in fat measure of *Haematopus ostralegus finschi:* A, adults; B, immatures (O, means; vertical lines, 95% confidence limits of means).

significant increase in fat measure from winter to spring ($t = 2.216$, $0.05 > P > 0.01$), whereas immatures do not ($t = 1.130$, $P > 0.20$). However, if only second-year immatures are compared from winter ($n = 13$) and spring ($n = 5$), a statistically significant increase is detected ($t = 4.192$, $P > 0.001$). This is consistent with the observation that second-year birds undertake vernal migration whereas first-year birds do not (Baker, in press). Since the increase in fat reserves in spring is restricted to potentially migratory birds it may be ascribed to pre-migratory fattening. The consequent marked depletion of the reserves through spring to late summer is consonant with heavy energy expenditure during migration and/or breeding, though factors such as ambient temperature and daylength are also known to affect fat levels (Newton 1969). Unfortunately the summer sample comprises mainly post-migratory birds taken at the Heathcote-Avon estuary in early February, so it is not known whether they fatten extensively for the autumnal migration. However, the 20 post-migratory adults from this sample have a mean fat measure of 3.49 g, which corresponds to a total content of 43.3 g. Provided these birds had only recently arrived at the estuary (and thus had not had sufficient time to accumulate fat), then it is reasonable to assume that the observed fat measure represents the unexpended balance from autumnal pre-migratory fattening.

FLIGHT RANGE

The approximate flight range of a migratory non-passerine may be estimated from the following equation given by McNeil (1969):

$$\text{flight range (miles)} = (\text{G.V} \times 9.5\ \text{kcal/g})/\text{MV} \ldots\ldots\ldots\ldots\ldots (1)$$

where G is the weight of fat in grams, V is the speed of the bird in miles/h, and MV is the metabolism of the bird during flight in kcal/h. The value of MV (=FM) can be calculated from the equation of Raveling & LeFebvre (1967):

$$\log \text{FM} = \log 37.152 + 0.744 \log \text{W} \pm 0.074 \ldots\ldots\ldots\ldots\ldots (2)$$

where W is the wet weight of the bird in kg. Three other equations for estimating MV from body weight have been proposed (*see* King & Farner 1961, Lasiewski & Dawson 1967), but I prefer Raveling & LeFebvre's formulation because it estimates flight metabolism as maximally 12 times greater than basal metabolism, and therefore gives a conservative estimate of flight range. For the South Island pied oystercatcher, spring adults (sexes combined) have a mean wet weight of 586 g (n = 22), a mean fat measure of 9.0 g, and estimated mean total lipids of 70.0 g. Although no flight speeds are available for New Zealand *Haematopus ostralegus*, Meinertzhagen (1955) gives speeds in the range 45–49 miles/h for European *H. ostralegus*, so for flight range estimation a flight speed of 50 miles/h was chosen. Substituting these values in equation (2) gives an energy consumption during flight of 24.963 kcal/h, and substitution of this figure in equation (1) gives an approximate average flight range of 1330 miles (2140 km). Since the maximum distance that South Island pied oystercatchers have to traverse during migration is probably less than 1100 miles (1770 km; for extreme northern New Zealand wintering birds), and is often considerably less than this, it is apparent that on average they have large enough energy stores to complete this journey in one prolonged flight. However, it is doubtful whether they commonly do this. Judging from the large number of sight records of migrant birds at localities between major breeding grounds and wintering areas it appears that the more usual mode of migration is a series of shorter journeys punctuated by brief pauses for feeding and resting (Recording Scheme data, Ornithological Society of New Zealand). Since the pauses are usually very short, and often at localities unfavourable for voracious feeding, it seems unlikely that any conspicuous fattening occurs during migration in this species. However, it is possible that depleted reserves could be at least partially replaced, as has been demonstrated for the semipalmated sandpiper (Page & Middleton 1972). Hence, it seems probable that many adults arrive at the breeding grounds with adequate lipid reserves to allow breeding activity to begin immediately.

DISCUSSION

South Island pied oystercatchers taken at the Heathcote-Avon estuary in spring just before migration had average fat reserves of 70.0 g, representing 12% of their average wet weight. This contrasts with corresponding values of about 49% for some small passerines (Odum 1965) and 17.4% for the golden plover (Johnston & McFarlane 1967), though the latter figure is an underestimate caused by the accidental loss of some heavy birds from the extraction sample. Hence, the South Island pied oystercatcher can be categorised as having moderate initial fat reserves. These reserves are, however, more than adequate to meet the energy cost of spring migration for the Heathcote-Avon birds, as they would have a maximum flight range of only 300 miles (483 km) to reach breeding grounds in extreme southern New Zealand. Extensive vernal pre-migratory fattening therefore appears not to be necessary in this species, and may possibly be selected against, since the acquisition and transport of massive amounts of extra fuel may result in a relatively small net gain of energy. A similar argument has been advanced for some small passerines during periods of intracontinental movement (Helms & Smythe 1969). Alternatively, because of food intake requirements it is possible that large birds such as the South Island pied oystercatcher are not able to deposit the same relative weight of lipids as can smaller migrant birds, but instead can compensate for their lower energy stores by increased flight speed (Johnston & McFarlane 1967).

Although selection and/or food intake before migration may set upper physiological limits to the amount of fat which is deposited and transported in the South Island pied oystercatcher, it is apparent that most birds lay down fat reserves well in excess of that required to reach their breeding grounds. Hence a compromise is likely to be involved in which opposing advantage accrues from having relatively large fat reserves on arrival at the breeding grounds. Such selection could operate through the time of laying by the female, since this is strongly influenced by her physical condition and by the supply of available nutrients (Perrins 1970, Immelmann 1971). Fat reserves in breeding birds could advance laying dates by contributing directly to the formation of a clutch and/or by shortening the length of the pre-laying period. South Island pied oystercatchers do not have sufficient fat to account for the total biomass of a 4-egg clutch (*ca.* 120 g) on arrival at the breeding grounds, since they have an average of only 70 g before vernal migration commences. However, if the fat which is surplus to migratory needs is metabolised for normal maintenance and thermogenic requirements of a female, then it is possible that nutrients acquired from feeding may be used primarily in the formation of eggs. This could well shorten the time between arrival and egg-laying; Hogstedt (1974) has shown that the length of the pre-laying period in the lapwing (*Vanellus vanellus*) is negatively correlated with the supply of nutrients available to the female at this time.

Mercer (1968) has shown that female European oystercatchers (*H. ostralegus*) lose up to 16% of their peak pre-breeding weight (presumably metabolism of stored fat) in the month before laying, and Harris (1969) has suggested that this probably results from the energy demands of territory defence and egg formation. Oystercatchers lay large-yolked eggs typical of nidifugous species; a 4-egg clutch may represent as much as 30% of the body weight of the female at laying, and its formation imposes a high energy demand. In Europe, early breeding oystercatchers raise, on average, approximately 8 times as many young as do late breeders, because their young are being fed at a time when terrestrial food is largest and most abundant (Safriel 1967, cited by Harris 1969). These early breeders consequently make a larger genetic contribution to the next generation.

Selection for early attainment of breeding condition relates primarily to the female of a pair, but there is also considerable selective advantage in the male having relatively high fat reserves on arrival at the breeding grounds. Similar energy expenditure occurs in either sex: both birds vigorously defend their territory and young, they share incubation duties approximately equally, and they both spend considerable time feeding the young.

South Island pied oystercatchers most commonly breed on the beds of large, snow-fed rivers in the South Island which are subject to flash floods from heavy spring rains and sudden thaws in the snowfields of the Southern Alps. In some years these floods destroy most early clutches, and early re-nesting is imperative if young are to be raised while the terrestrial insect food is still abundant. Fat reserves may be important in this context too; in mountain breeding populations of the white-crowned sparrow (*Zonotrichia leucophrys oriantha*) females retain fat through incubation, permitting rapid re-nesting if the first clutch is lost (Morton *et al.* 1973).

A possible further advantage of early breeding relates to autumnal migration. Early breeders and their young would have considerable time after fledging to lay down fat reserves for the journey to coastal wintering localities, whereas late breeders and their young would have only a short time available to accomplish this, and might arrive at the winter grounds with very low fat reserves. This could be critical to late-fledged young, since they take several months to learn how to feed efficiently on littoral organisms (Baker 1969). A direct relationship between mortality of young and the time between fledging and autumnal migration has been established for the Manx shearwater (Harris 1966).

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