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## ECOLOGY OF THE LONG-TAILED SKUA, *STERCORARIUS LONGICAUDUS* VIEILLOT, 1819, AT SCORESBY SUND, EAST GREENLAND. PART THREE: CLUTCH SIZE, LAYING DATE AND INCUBATION IN RELATION TO ENERGY RESERVES

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### ABSTRACT

Energy reserves, gonad development and breeding of Long-tailed Skuas were investigated in East Greenland at Kap Stewart in 1973 and 1974, at Gåseelv and Ugleelv in 1975, and at Kaerelv in 1975. In spring adults arrived along the ice edge and on the tundra with maximal energy reserves, with testes of sub-maximal size and enlarged follicles close to the size at which rapid follicle growth may start. In paired birds the loss of energy reserves in the pre-breeding period decided how far rapid follicular growth proceeded and whether none, one or two eggs were laid. In 1973 and 1975 one-egg and two-egg pairs had similar energy reserve losses until hatching of the young, regardless of clutch size. Non-breeding birds in 1974 lost their energy reserves at a faster rate than did breeding birds in 1973 and 1975, weights of laid eggs included. Timing of egg laying was correlated with the disappearance of snow-cover and the experience of the pair and not with body energy reserves. One - egg and two - egg clutches in 1973 and 1975 had the same average completion date (13 June). First clutches were completed between 4 June (Gåseelv 1975) and 5 July (Kap Stewart 1973) and replacement clutches until 14 July (Kaerelv 1979). Testes and largest follicles started to regress at or soon after (failed) breeding. In non-breeders regression started later than in early breeders. All breeding and non-breeding territorial birds developed brood patches, which started to appear in the first days of pair formation. In females, only breeding birds had full-size patches, which were attained at clutch initiation. Males attained full-size patches some days before or after clutch initiation and some of them also without eggs being produced. In early breeders patches started to regress between two and three weeks after clutch initiation, in late breeders within a week. In 1975 about 61% of the incubation was done by the female.

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## 2. INTRODUCTION

In 1973, 1974 and 1975, I studied the Long-tailed Skua at Kap Stewart, Gåseelv and Ugleelv (southeast Jameson Land) and Kærelv (northeast Hurray Inlet). In 1979, Hansen (1981, 1982, 1984) continued the fieldwork at Kærelv and his data are integrated in the study. In part 1 of this series of papers, a description of the study areas and the weather in successive years was given, and distribution and densities were discussed (de Korte, 1977). Compared with 1973, 1975 and 1979, the weather in 1974 was very unstable. In that year, extensive and late - thawing snow cover prevented Long-tailed Skuas in June from utilizing large areas in June, which they had occupied in June of the previous year. Territorial pair density fluctuated from 0.2 pairs per km<sup>2</sup> at Kap Stewart in 1974 to 0.9 at Ugleelv in 1975. Breeding densities fluctuated from 0 (all areas visited in 1974) to 0.6 per square km at Ugleelv in 1975. In part 2, arrival, site tenacity and departure were treated (de Korte, 1984). The first Long-tailed Skuas arrived singly or in small groups on 21 May along the ice edge, and 27 May inland. In areas with snow-free patches, they established territories within a few days after arrival. Site tenacity from year to year was recorded in many cases. Territorial birds, regardless of breeding success, frequented their territories with or without their partner until mid-August. Immatures were first seen at sea on 13 June, and on land 21 June; they joined groups of roaming non-territorial adults, non-breeding territorial birds and failed breeders. Immatures had departed from the tundra by the end of July and were not seen at sea after mid-August.

In this paper, development of gonads, egg laying dates, clutch size and energy reserves in the course of the breeding season are discussed. Age is an important factor in gonad development and therefore criteria for age are discussed in order to assess the age of the birds studied. In addition, certain measurements correlated with sex and used for the energy reserve index are summarized in this paper.

Copies of the basis data files of specimens, living birds and eggs from Scoresby Sund will be deposited at the Zoological Museum in Amsterdam.

## 3. MATERIAL AND METHODS

### 3.1 *General*

Territorial pairs of Long-tailed Skuas, including breeders and non-breeders, were widely scattered and only a limited number could be examined each year, although about 30 km was covered daily from the last week of May until the last week of July. In May and the first half of June we travelled mainly on skis; in the second half of June and in July, we covered the area on foot. Thirty five breeding birds were captured with a walk-in cage trap placed over the nest and with a clap net or with a fowler's net (fleyg). Usually the two members of the pair were caught with some days interval in order to reduce the effects of disturbance. The birds were ringed with aluminum rings of the Zoological Museum in Copenhagen, and with plastic colour rings. In 1975 one member of each pair was dyed yellow on the breast with picric acid which remained clearly visible for more than a month. All birds caught were weighed with spring balances of 300 g and 1000 g, accurate to the nearest 1 g and 2 g, respectively. Measurements of wing (maximum chord), bill (chord from base of feathering to tip), tail feathers, tarsus and gonys were taken. Detailed observations on breeding behaviour were done from a hide, placed about 30 m from the nest.

For more extensive study than was possible on living birds with regard to gonad development, energy reserves, plumage and food a total of 82 (73 adults, 9 immatures) specimens was collected in the field work seasons. Thirty-three of these were obtained from Greenlandic hunters who had shot the birds along the ice edge, on open sea, or along the coast for the purpose of dog food. The others were collected in Jameson Land, Kjøveland and Liverpool Land, between 20 and 100 km away from the

study areas, whereas immatures have also been collected within the study areas. The dead birds were weighed and measured within a few hours after they had been killed in the same way as the captured birds. For body weight, I took total weight minus the weight of food in the oesophagus and stomach in excess of 5 g because it was my experience that injured birds regurgitated when they contained more than about 5 g food. Captured birds also often regurgitated and for these I assume that their weight also includes less than 5 g stomach content. Birds killed instantly could have much heavier stomach plus oesophagus content. Measurements of testis and largest follicle were taken from fresh specimens to the nearest 0.1 and 0.5 mm respectively, with a pair of calipers. In all instances, the left testis which usually is the largest in birds (Friedmann, 1927; Johnston, 1956) was undamaged and its measurements are used to calculate testis volume. Testes were found to be ellipsoid in shape and for calculating volume the formula for the volume of an ellipsoid was used:  $V = \pi 1/2 L (1/2 B)^2$ , where  $L$  = largest diameter and  $B$  = width (Blanchard, 1941; Johnston, 1956 a; Maher, 1974). Following convention, which will make it easy to compare my results directly with those of others (Johnston, 1956a b; Maher, 1974), I have chosen to present testis size in volume on a logarithmic scale (fig. 5) and follicle size in diameter on a linear scale (fig. 6). The status of oviduct and of brood patches were also studied on fresh specimens. Female gonads were preserved in alcohol for subsequent examination. The collected specimens were skinned and prepared in the field and brought to the Zoological Museum, Amsterdam (ZMA) for further examination and permanent storage. In addition to these specimens, I examined 21 specimens already in ZMA, 38 in the Zoological Museum, Copenhagen (ZMK), 42 in the United States National Museum, Washington D.C. (USNM), and 45 in the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH).

Statistical procedures included t-tests; the significance limit is chosen at  $P = 0.01$ .

### 3.2 Age criteria

The age of a given bird or specimen is defined as follows: juvenile = first calendar year bird = from fledging to December first winter; second calendar year bird = from January first winter to December second winter etc.; adult = bird without feathers typical of immature plumage (cf. Cramp & Simmons, 1977).

There are as yet no records of Long-tailed Skuas ringed as nestlings and recovered in subsequent years. Therefore the age of live birds and specimens studied had to be deduced from characteristics that are known to have a certain correlation with age. Glutz von Blotzheim & Bauer (1982) and Roselaar in Cramp & Simmons (1983) consider the Long-tailed Skua to moult from juvenile plumage through a succession of immature plumages into adult plumage in the course of about three years. The information about plumage and moult insofar as useful for age determination may be summarized as follows. In autumn adults replace their breeding plumage, which is rather uniform white, grey and brown (fig. 3), by a winter or non-breeding plumage, which has a mottled and barred appearance. During this post-breeding moult the long central tail feathers ( $T_1$ ) are replaced by short ones. In early spring the non-breeding plumage is replaced by the breeding plumage. During this pre-breeding moult the short winter  $T_1$  is replaced by the long summer  $T_1$ . The other tail feathers ( $T_{2-6}$ ) and the primaries ( $P_{1-10}$ ) are replaced once a year, during winter. Immatures start moulting for the first time in the beginning of their second calendar year. The rounded  $T_1$  of the juvenile is replaced by a short pointed  $T_1$ . This feather is replaced then again in summer, much later than in adults (see below). Moult of the other tail feathers and primaries is completed in summer and starts again in winter at the end of the second calendar year or the beginning of the third calendar year, when  $T_1$  is replaced again. From then on primary and tail feather moult follows the same pattern as in adults. Pre-breeding moult of body feathers in second and third calendar year birds starts later

and is less complete than in adults, and causes immatures to resemble closely adults in non-breeding plumage.

Moult of Long-tailed Skuas mostly takes place during their pelagic life far away from the breeding grounds and few specimens have been secured and studied from this period. I could not discern from the literature mentioned above a clear-cut plumage type for each year class. Therefore I re-examined plumage characteristics that have been used as age criteria: shape and length of rectrices, shape of primaries, colour patterns on underwing coverts and axillaries, and the extent of black pigmentation on feet and legs, which in other Stercorariidae is supposed to increase with age (de Korte, 1972). The bill/ bill nail ratio slightly decreases with age, but differences between year classes are too small to separate one year class from the next (Walter, 1962; Roselaar in Cramp & Simmons, 1983).

#### First calendar year birds.

Two juveniles some days before fledging (own observations Kærelv 1975) and two juveniles (ZMK 46.352, 46.971) still wearing traces of down from the breeding grounds in Northeast Greenland had  $T_1$  rounded, still growing and not exceeding  $T_{2-6}$ . Forty-three specimens (23 in RMNH, 17 in ZMA, 3 in USNM) collected between 24 August and 23 November had full-grown rounded  $T_1$  exceeding  $T_6$ , 16-34 mm. I classify these specimens as juveniles. All of them had lesser and medium under wing-coverts, intensely barred grey-white and dark brown. The barring on axillaries and greater under wing-coverts varied considerably however, with some having only traces of barring on the latter.

Walter (1962), who did not clearly distinguish between first and second calendar year birds, and Glutz von Blotzheim & Bauer (1982) state that first and second calendar year birds have  $T_{2-6}$  and outer primaries with smoothly rounded tips, while third calendar year and older birds have these tips slightly pointed. The above mentioned first calendar year birds indeed had the tips slightly less

pointed than the 73 adults brought to ZMA. However the variation of this phenomenon within the first calendar year birds and within the adults was considerable. Three first calendar year birds from November had them more pointed than seven from August; twelve adults from August had them more pointed than five from May. Probably as a result of wear, old feathers have a more pointed tip than new feathers. Because adults have older feathers in summer than first calendar year birds in autumn, the adults' feathers are more pointed. It is a useful criterion to determine the relative age of the feather, not the age of the bird.

#### Second calendar year birds.

Moult of primaries and tail feathers in summer may characterize second calendar year birds (Stresemann & Stresemann, 1966). Of 189 birds from the breeding grounds (including live birds and specimens) older than first calendar year only one (ZMA 27.853) had some moult of tail feathers, whereas of 20 specimens collected in late spring and summer at sea far away from the breeding areas nine were moulting. The latter specimens offered data about plumage succession after the first calendar year. Specimens of 11 May (USNM 495.274), 3 and 5 June (USNM 493.822 & 497.697) and 16 July (ZMK 46.355) had not yet completed their moult of primaries and tail feathers. Specimens from 13 July (ZMK 23.136) 16 July (ZMK 46.356), 1 August (ZMK 46.365) and 8 August (USNM 544.932) had a full-grown set of new primaries and  $T_{2-6}$  but were still replacing  $T_1$ . The barring on under wing-coverts and axillaries showed the same pattern and variation as in juveniles. I classified them as second calendar year birds. A specimen of 6 August (RMNH Cat. 5), with full-grown sets of new primaries and tail feathers and intense barring on under wing-coverts and one of 15 August (ZMA 27.853) in the dark morph (which in this species occurs regularly in the immature but is exceptionally rare in the adult, Roselaar in Cramp & Simmons, 1983) with growing  $T_1$  not extending beyond the rest of the tail, and a set of full-grown new primaries, are also classified as se-

cond calendar year birds. This classification is supported by their foot colour (see below).

The timing of moult of central tail feathers in second calendar year birds seems to be rather individual but probably can be summarized as follows. The rounded "summer"  $T_1$  of the first calendar year (still present in a 23 November specimen, USNM 49.179) are replaced by pointed "winter"  $T_1$  in the first winter (11 May and 3 June specimens had  $T_1$  full-grown and 38 and 28 mm extending). These are replaced by "summer"  $T_1$  earlier or later in summer (5 June, 13 and 16 July and 8 and 14 August specimens had  $T_1$  missing or not extending and still growing, while 16 July and 6 August specimens had them new, full-grown and extending 70 and 83 mm), which are worn until the next winter (an 8 October specimen had them rather old and extending 70 mm, a January specimen third calendar year had them extremely worn and extending 45 mm). From table I it can be deduced that primary moult in the second winter probably runs parallel with that of older birds (cf. Lambert, 1980), but that tail moult is still retarded.

### Third calendar year birds.

Eight specimens collected by me between 13 June and 24 July, 12 from 26 June to 13 August already in ZMA, and two from 4 and 7

November (Table I) all had barring on under wing-coverts and axillaries but from July to November the barred feathers were replaced by progressively less strongly barred ones. Some specimens had only traces of barring on lesser and median under wing-coverts. I classify these as third calendar year birds. This is supported by leg colour (see below).

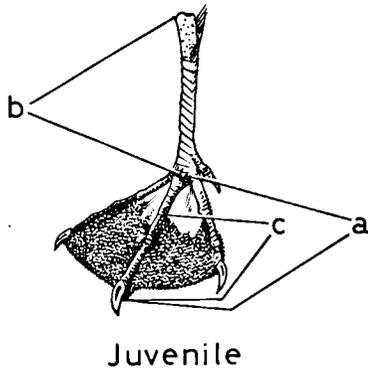
### Fourth calendar year and older birds.

Birds without barring on under wing-coverts and axillaries are classified as fourth calendar year birds or older. A specimen of 12 July (ZMA 27.172), still in winter plumage, falls also in this category. Some breeding birds, among which were old birds, had retained barred winter feathers among upper and under tail-coverts indicating that winter feathers are not a good age criterion but rather an indication of some retarded moult. After the third calendar year, plumage (including  $T_1$ , see below) no longer gives an indication for age. The extent of black pigmentation on feet and tarsus in skuas is variable but may give such an indication (de Korte, 1972).

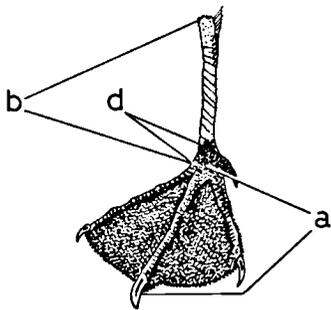
In juvenile skuas, the distal parts of toes and webs are black. The proximal part is blue and flesh colour. As the borderline between black and blue or flesh colour is rather capricious, I calculated the percentage of black on the foot by measuring the length of the middle toe from the

Table I. Moult of primaries and rectrices in winter. L = left, R = right, O = feather old, A = feather absent, G = feather growing,  $\frac{1}{2}$  = feather half grown, N = feather new.

Collection no.	Date	Area	Age in cal. year		Primaries										Rectrices						$T_1$ - $T_6$ mm	% foot surface black	Hindtoe black	
					1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6				
USNM 284731	4.11.1920	S. Atlantic	III	L	O	O	O	O	O	O	O	O	O	O	O	A	O	O	O	O	O	—	100	—
				R	O	O	O	O	O	O	O	O	O	O	G	O	O	O	O	O	O	O	—	—
USNM 284728	7.11.1920	S. Atlantic	>III	L	O	O	O	O	O	O	O	O	O	O	A	O	O	O	O	A	—	100	+	
				R	O	O	O	O	O	O	O	O	O	A	O	O	O	O	A	—	—	+		
USNM 284733	7.11.1920	S. Atlantic	III	L	A	A	O	O	O	O	O	O	O	N	A	N	N	N	O	36	100	+		
				R	A	A	O	O	O	O	O	O	N	A	N	N	N	O	—	—	+			
USNM 284734	7.11.1920	S. Atlantic	>III	L	N	$\frac{3}{4}$	A	A	O	O	O	O	O	N	O	N	N	N	O	30	100	+		
				R	N	$\frac{3}{4}$	$\frac{1}{2}$	A	O	O	O	O	N	A	N	N	N	O	—	—	+			
RMNH Cat. 14	?.01.1856	S. Atlantic	III	L	N	N	N	N	$\frac{9}{10}$	$\frac{1}{10}$	O	O	O	O	O	O	$\frac{1}{4}$	O	O	O	45	96	—	
				R	N	N	N	N	$\frac{9}{10}$	$\frac{1}{10}$	O	O	O	O	O	O	$\frac{1}{4}$	O	O	O	—	—	—	



Juvenile



Young adult

Fig. 1. Measuring black pigmentation on foot and leg in Stercorariidae. Percentage of black pigmentation on toe =  $100 c \times a^{-1}$ , on tarsus =  $100 d \times b^{-1}$  and on toe + tarsus =  $(c + d) \times (a + b)^{-1}$

distal tip of the skin on the underside of the claw up to the proximal end of the middle toe (*a* in fig. 1) and the distance from the distal tip (as above) to the proximal end of the black colouration on the dorsal side of the middle toe (*c* in fig. 1). The black on the tarsus at first appears on the lower part as a continuation of the black on the foot, later black also appears on the up-

per part as a continuation of the black on the tibia (I did not measure the extent of black on the tibia). In successive stages of increasing black colouration, black spots may appear at any place on the tarsus. In the early stages of colouration on the tarsus I assessed the percentage of black on the tarsus by measuring tarsus length (*b* in fig. 1) and distance from the distal end of the tarsus to the proximal end of colouration (*d* in fig. 1). To derive the percentage of black on the foot and tarsus combined, I used a combination of the measurements discussed above  $(c + d) \times (a + b)^{-1}$ . In later stages of blackening I estimated only the percentage on the tarsus. On average, middle toe length (33.2 mm, as defined above) is 44% and tarsus length (42.2 mm, table IV) is 56% of total length of middle toe plus tarsus.

At hatching, legs and toes of Long-tailed Skua chicks were completely blue and hindtoes had a flesh colour (11 pulli Kærelv 1975). At the end of the second week the distal parts of toes and webs started to turn black rapidly (two young Kærelv 1975). A specimen of 17 August (ZMK 46.293) just fledged had 31% of foot + tarsus (71% of foot) black. Percentages of black on foot and tarsus of birds in different age classes are presented in table II. Juveniles from August (*n* = 7), September (*n* = 23) and October (*n* = 10) did not show significant differences and they are grouped together (average collecting date 18 September, range 24 August - 31 October). Second calendar year birds (average collecting date 16 July, range 3 June - 14 August) had significantly more black than juveniles and significantly less than third calendar year birds (average collecting date 19

Table II. Extent of black pigmentation on foot and leg in percentage of surface, and percentage of black hindtoes in different year classes.

Age in cal. year	Collecting period	n	% foot surface black			% tarsus surface black			% foot + tarsus surface black			% hindtoe black
			Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	
I	August-October	40	70.3	4.32	62-78	0	0	0	30.9	1.85	27-35	0
II	June-August	9	87.2	9.81	75-100	0	0	0	38.2	3.32	34-44	6
III	June-August	22	99.1	2.26	93-100	4.0	3.99	0-15	45.9	3.42	41-51	21
IV & older	May-August	104	100			35.4	27.84	4-95	63.8	15.87	46-97	91

July, range 13 June - 22 August). Regression of percentage black on foot + tarsus against age in months until August third calendar year gave the best fit with  $Y_i = 30.5 + 0.6 t$  ( $n = 71$ ,  $r^2 = 0.81$ ,  $t_0 =$  July first calendar year). If blackening after the third calendar year continued at the same speed as in the first two years (7.2% per year), all birds would have completely black legs by their 12th calendar year. In all probability, several of the breeding birds caught or collected by me and included in the category of fourth calendar year and older birds in table II, were much older because Long-tailed Skuas are long-lived seabirds (Andersson, 1981; Taylor, 1974) and they may, just as in the closely related Arctic Skua, *Stercorarius parasiticus*, easily become older than 20 years (O'Donald, 1983; Venables & Venables, 1955). However none of the birds caught or collected by me nor any of the specimens in the museums had a completely black tarsus. Therefore I conclude that after the third calendar year the increase of black slows down. Birds with more than 90% of foot + tarsus black are probably over 20 years old. This would mean an average increase of black of 2.5% after the third calendar year. In young adults this will be between 7.2 and 2.5%, in old adults between 2.5 and 0%. In table II, the category fourth calendar year and older birds comprises the fourth calendar year birds. Because in third calendar year birds the extremes differ 10%, I assume that the range of black in fourth calendar year birds is 46 - 56%. Regression through the minimum of each range in first, second, third and fourth calendar year birds of table II gave the best fit with  $Y_i = 26.3 + 13.7 \log t$  ( $n = 4$ ,  $r^2 = 0.98$ ,  $t_1 =$  first calendar year). Minimum in fifth calendar year birds is predicted as 48%. Adults with less than 48% black on foot + tarsus (less than 7% of tarsus black) are considered to be fourth calendar year and those with more than 56% (more than 21% of tarsus black) are considered fifth calendar year or older birds.

Blackening of the hindtoes runs more or less parallel with that of the distal end of the tarsus but it may occur already at a time when black pigmentation has not yet reached the tarsus and

may also be postponed until 50% of the tarsus has turned black (ZMA 27.852).

Length of central tail feathers ( $T_1$ ) is variable but seems to increase with age (Roselaar in Cramp & Simmons, 1983); it has been used as an indicator of relative age (Andersson, 1976). In general, relatively large birds have longer  $T_1$  than small birds. To compensate for size in some way, I used the difference between  $T_1$  and  $T_6$ . Defined in this way the tail tip is up to 32 mm longer than the part of  $T_1$  extending beyond  $T_2$  (data of 71 specimens and 32 live birds). Winter tail tip (28-60 mm in all year classes, see above, table I, Lambert, 1981) is short compared with summer tail tip (table III) and is not useable as an age criterion in non-breeding plumage. In table III, summer tails that were broken or very worn are left out. Because there was no significant sexual difference in tail tip in the group of fifth calendar year and older birds, I have also com-

Table III. Length (in mm) of tail tip ( $T_1$ - $T_6$ ) of summer tails in different year classes. In juveniles (I)  $T_1$  is rounded; in other year classes it is pointed.

Age in cal. year	n	Mean	S.D.	Range
I	40	24.3	5.21	16 - 34
II	3	74.3	7.51	70 - 83
III	19	108.3	29.50	60 - 154
IV	14	169.9	16.85	138 - 199
V & older	48	171.0	21.81	125 - 231

bined the sexes in the other groups. Except for the juveniles the tail tip in each year class is very variable and there is quite an overlap between the year classes. Of the successive year classes, only the difference between third calendar year birds (still immatures) and fourth calendar year birds (adults) is significant. Two adults ringed in 1975 (rings ZMK 513.612 and 513.625) had in 1979  $T_1$ , 37 mm shorter and 1 mm longer, respectively (after Hansen, 1982). I conclude that after the fourth calendar year tail tip does not increase significantly and that it cannot be used to assess relative age in adults.

### 3.3 Sex criteria

Long-tailed Skuas show no marked sexual dimorphism. If relative position during copulation, or begging (which is only done by the female, Andersson, 1971; Taylor, 1974; own observations), is not observed, a general practise in the field is to consider the largest of the two partners to be the female. Manning (1964) found females to have significantly longer bill and wing, although the overlap was considerable. In the adults of table IV, sexual

Table IV. Sexual variation in measurements (mm) and weights (g) in adults from Scoresby Sund.

	Sex	n	Mean	S.D.	Range
Culmen	♂	40	28.0	1.31	25.8 - 30.2
	♀	49	27.8	1.46	24.4 - 31.5
Tarsus	♂	40	42.1	1.53	38.4 - 44.6
	♀	49	42.2	1.37	39.8 - 45.4
Wing	♂	38	306.8	6.9	293 - 318
	♀	49	311.4	7.9	300 - 334
Tail tip (T <sub>1</sub> -T <sub>6</sub> )	♂	21	172.6	27.0	125 - 231
	♀	27	169.9	17.2	127 - 208
Weight	♂	38	269.6	21.6	218 - 320
	♀	48	307.2	39.2	262 - 444
Starving weight (see text)	♂	38	191.7	12.3	167 - 223
	♀	49	195.3	12.6	174 - 222

variation in culmen and tarsus length was small and insignificant, but it was significant in wing length. For birds not sexed on the basis of copulation or begging, I considered birds with a wing shorter than 296 mm (lower 95% confidence limit females) to be males and those with a wing longer than 320 mm (upper 95% confidence limit males) to be females. The wing of females from dissected pairs and pairs seen copulating or begging was 9 mm (S.D. 8.52,  $n = 15$ ) longer than that of their mates, ranging from -3 to + 25 mm. The lower 95% confidence limit of the wing of females was 7.7 mm shorter than the wing of her mate. For unsexed pairs with difference in wing length of 8 mm, I consider the bird with the largest wing to be the female. Sexual variation in tail tip was not significant, but standard deviation in males was

much larger than in females. Unsexed birds with tail tips longer than 204 mm (upper 95% confidence limit females) are considered to be males. The difference in colour of males and females with darker underparts in the latter (Manning, 1964; Parmelee & McDonald, 1964) was not clear and is a rather unreliable sex criterion (cf. Kampp, 1982). I did not use as discriminators aspects of behaviour which in general are more often shown by the female, such as incubating, or more by the male, such as territorial defence (Andersson, 1971; Taylor, 1974; Kampp, 1982; own observations) because sexes may show reverse behaviour (Parmelee & MacDonald, 1960). Relying on the criteria discussed above I was able to sex 14 of the 18 breeding pairs caught in the study areas.

### 3.4 Egg laying date

For only one clutch could the date of laying of the last egg be ascertained exactly, as it was found before completion. Of three clutches for which the hatching dates were known, egg laying dates could be calculated assuming an incubation period of 24 days, plus or minus one day (Manniche, 1910; Maher, 1970, 1974; Andersson, 1976a; Hansen, 1982). In these clutches cracks appeared at the surface of the eggs three days before hatching. In three clutches in which such cracks appeared, but in which the young did not hatch, I assumed that the eggs had been incubated for a period of 21 days until the cracks appeared, giving a total of seven clutches (12 eggs) for which I was able to estimate the laying date with an accuracy of plus or minus one day.

It is a well established fact that eggs lose weight during incubation (Barth, 1953; Drent, 1975). The total percentage weight loss over the entire period may vary but is at least 16% (Rahn & Ahr, 1974; Drent, 1975). Before the egg is cracked the rate of loss per unit of time is constant (Barth, 1953). After the egg is cracked the rate increases by increasing metabolism of the working chick and by opening of the egg (fig. 2). By measuring the rate of weight loss and egg volume, the age of an incubated egg

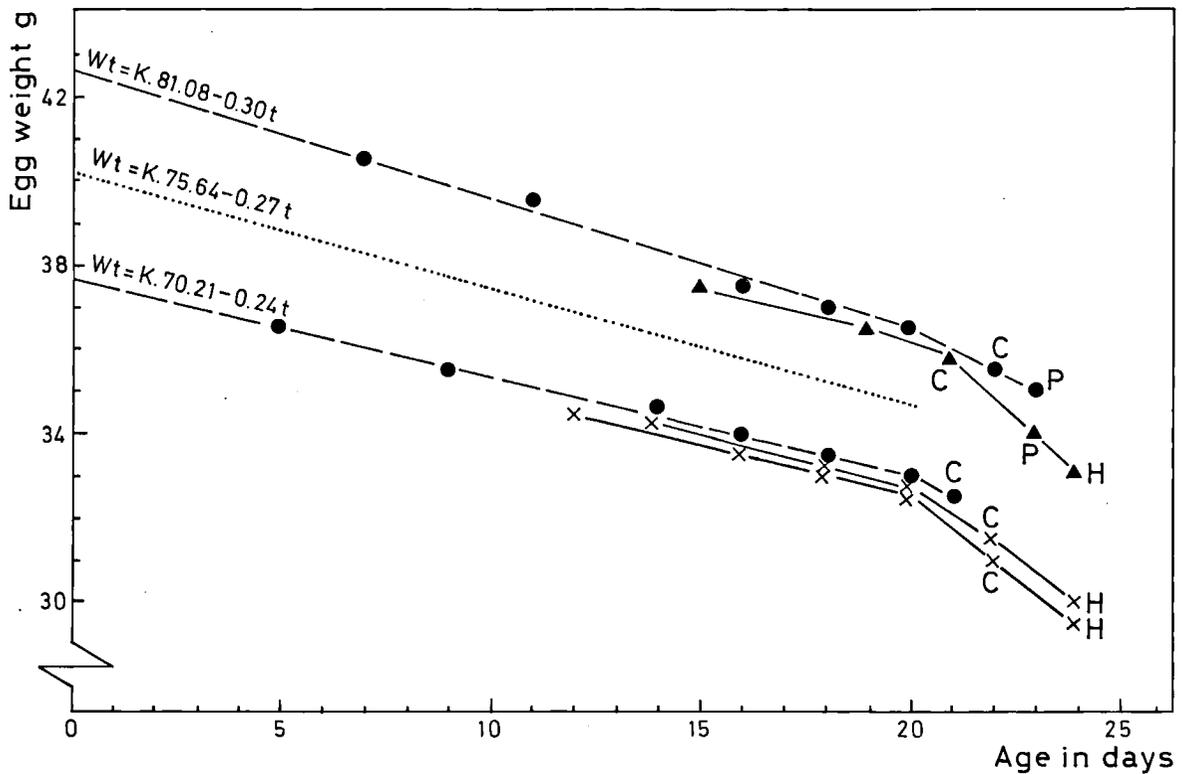


Fig. 2. Egg weight in relation to days after laying. Eggs of the same clutch have the same symbols (dot, triangle, cross). Solid lines join observations on the same egg. Broken lines indicate regressions in two eggs; the dotted line indicates regression in the "standard egg" ( $W_0 = K \cdot LB^2$ ). C indicates egg cracked, P egg pipped, H young hatched.

can be estimated. The weight of a freshly laid egg can be expressed by  $W_0 = K \times LB^2$ , in which  $K$  is the product of specific gravity of the egg when freshly laid, and a factor depending on the shape of the egg, varying little within a species (cf. Worth, 1940; Preston, 1974);  $L$  is length and  $B$  is width. Weight of an egg with age  $t$  days can be expressed by  $W_t = K \times LB^2 - a t$ , in which  $a$  is the rate of weight loss before cracking. As I could only weigh to the nearest 0.5 g, I have used for calculating  $a$  only the two eggs for which I had weighings over a period of more than eight days from first weighing date until cracking date (fig. 2). Linear regressions gave the best fit ( $r^2 = 0.98$ ) and gave  $W_t = K \times 81.08 - 0.30 t$  g for the largest and  $W_t = K \times 70.21 - 0.24 t$  g for the smallest of the two eggs. The average values in these equations give  $W_t = K \times 75.64 - 0.27 t$  g for the "standard egg", and  $W_t = K \times LB^2 - 0.27 \times LB^2$

$\times 75.64^{-1} t$  g for any Long-tailed Skua egg.  $K$  for 12 eggs of known age (see above) was calculated: mean 0.533, S.D. 0.006, range 0.525 - 0.541. Age of 20 other eggs in 15 clutches could be calculated now with an accuracy of plus or minus three days.

We did not obtain clutch data before hatching for five breeding pairs in 1975 but calculated hatching dates and consequently laying dates from the size of their small pulli (de Korte, in prep.).

The dates of replacement clutches in fig. 4 are an estimate inferred from data provided by Hansen (1982). Eight days are added to the date of loss of the former clutch because this is approximately the time needed for the production of an egg in this species (Ricklefs, 1974; Walsberg, 1983) corresponding with the minimum time found by Maher (1970) and Taylor (1974) in cases of replacements. The

dates fall well within the time span in which the eggs were known to have been laid.

In nine two-egg clutches, eggs had been laid with an estimated interval of two days, and in two such clutches within one day. In the following sections, I will presume an interval of two days (cf. Manniche, 1910; Andersson, 1976a; Hansen, 1982).

### 3.5 *Energy reserve index*

Weight in relation to weighing date gives an impression of fluctuations of energy reserves through the season. However when dealing with different individuals this method gives an inaccurate picture because weight alone is a poor indicator of energy reserves in a species which is quite variable in size (table IV). In dissected specimens subcutaneous and mesenteric fat give an indication of the relative amount of energy reserves, but it is difficult to establish an accurate fat scale which can be used universally. Moreover such a scale is of no use in living birds.

Energy reserves can be defined as the residual weight above the weight at death through starvation (Wishart, 1973). These energy reserves are made up of fat and protein (Jones & Ward, 1975; Blem, 1976; Evans & Smith, 1976; Ankney & Mc Innes, 1978). In the last phases of starvation, when fat reserves are exhausted, protein reserves become also depleted (Lø Maho *et al.*, 1981).

The starvation weight is determined by the basic dimensions or structural size. Many authors have discussed how to measure the structural size of a bird. Connell *et al.* (1960), Rand (1961), and Davidson (1983) chose wing length as an indicator. Evans & Smith (1975), Modafferi (1957), and Britts & Marcström (1982) considered sternum length a better measure of size. Coulson *et al.* (1984) used head and bill length. Iverson & Vohs Jr. (1982) and Piersma (1984) found that the product of total length, keel length and wing length was the best possible combination of measurements to

define structural size. Linear (see above) and two-dimensional (Connell *et al.*, 1960) measurements have been used, but three-dimensional use of measurements gives the best indication of structural size because weight is directly proportional to the cube of linear measurements (Davidson, 1983; Piersma, 1984).

I did not obtain starving Long-tailed Skuas from the study areas. Five first calendar year birds on migration (three in ZMA, one courtesy J. Fjeldså, one courtesy D. S. Melville) found dying of starvation or shortly after they had died (no oiled or traffic killed birds) were used to estimate structural size. First year birds often have relatively shorter wings than adults, but species in which efficient flight is indispensable for food capture and which carry out long migrations develop primaries of proportionally full length (Fjeldså, 1977). The immatures for which the measurements have been used are from autumn and winter and have primaries that on average are some months newer than those of adults from spring and summer and state of wear is therefore about the same.

Total length and keel length which in combination with wing length may give accurate indications of structural size (Piersma, 1984) were not available for all of the specimens and birds studied by me. I tried out different products of the available measurements (wing, outer tail feather, bill and tarsus) and found that the product of (wing length)<sup>2</sup> and tarsus length gave the smallest intercept and largest coefficient of determination:  $S = 41.2 + 0.38 W^2 T$  ( $r^2 = 0.92$ ,  $n = 5$ ). The equation still has an intercept of about 20% of the values of structural size. As this equation was derived from five specimens for which the range of structural size was relatively small, it seems that the structural size of small individuals will be over-estimated and those of large individuals under-estimated. When forced through the origin we get the equation  $S = 0.48 W^2 T$  ( $r^2 = 0.89$ ,  $n = 5$ ) of which the coefficient of determination is slightly smaller but which also is significant and does not have the disadvantage mentioned

above. I have used this equation to estimate structural size (table IV). Energy reserve index is defined as the weight of energy reserves as a percentage of structural size (figs. 8, 9, 10, 11).

Metabolic rate was estimated using standard relationships for existence metabolism (energy expended in standard metabolism and free movement, except for flight, when the bird maintains a constant weight at a given ambient temperature, Kendeigh, 1970). Existence metabolic rate for non-passerines at 0° C =  $4.14 W^{0.544}$ , where the metabolic rate is in kcal per day and  $W$  is body weight in g (Kendeigh *et al.*, 1977). The energy equivalents of fat and protein were taken as 9.5 kcal per g and 4.0 kcal per g, respectively (Petrušewich & Macfadyen, 1970).

## 4. RESULTS

### 4.1 *Habitat and nest site*

Territories were well spaced and nests were generally situated between one and two km apart. The nest was a shallow unlined scrape or depression. Twenty-two of the 24 nests found were placed on well-drained gentle slopes or slight elevations on plains (fig. 3). Eleven lay among *Dryas*, nine among *Cassiope*, and one among moss vegetation; three lay on predominantly barren clay spots. In the first half of June some lay in very moist sites a few meters from retreating snow, with melt water oozing through the nest bottom. However nests were never found in grassy areas beneath melting snow fans. All nest had dry surroun-



Fig. 3. Two-egg clutch in *Dryas* vegetation, about 200 m from the shore, with female. Kaerelv 19 June 1975  
Photograph: J. de Korte.

dings at the end of June. Direct observations and vegetation types revealed that the nests were never situated in places which had been snow-free during late winter and early spring (gravel), but on the contrary, were placed most frequently in places that had a snow-cover until early June (*Dryas* - *Cassiope* associations), and occasionally in places that were still snow-covered by mid-June (Clay - *Cassiope* associations). The lowest one was situated a couple of metres above sea level about hundred metres from the coast (Kærelv 1975), and the highest one more than 200 m above sea level (Kap Stewart 1973). Territorial pairs were found up to 350 m above sea level, about three km inland (Modiolaelv, 1974). The nests seen on our farthest trips inland were about 13 km from the coast (Gåseelv & Ugleelv, 1975).

#### 4.2 Egg laying dates and clutch size

Estimated completion dates of clutches in the study areas are presented in fig. 4 together with two dates derived from females which had an egg in the oviduct and which were collected in areas not far from the study areas (Kap Stewart and Ugleelv). Clutch completion dates at Kærelv inferred from Hansen (1982, 1984) are also presented.

In 1973 average date of clutch completion was 20 June (one-egg clutches 22 June, two-egg clutches 17 June); in 1975 at Gåseelv and Ugleelv 9 June (one-egg clutches 9 June, two-egg clutches 9 June) and at Kærelv 13 June (one-egg clutches 12 June, two-egg clutches 14 June). Average date of completion of all clutches combined was 13.4 June, 52% in the second week of June (one-egg clutches 13.4 June, 39% in the second week of June; two-egg clutches 13.3 June, 73% in the second week of June). In 1979 at Kærelv the average date of completion of first clutches was 10 June (two-egg clutches only). Two replacements of one egg each were laid in the fourth week of June and the second week of July. In 1973 and 1975 replacements were not recorded.

The female parents of the two latest clutches in 1975, the male parent of the latest clutch in 1973 and the male parent of the clutch completed on 10 June 1975 were, judging from leg colour, in all probability fourth calendar year birds. The pair of this last clutch bred again in the same territory in 1979 (1975 one egg; 1979 two eggs, initiated two days later than in 1975). The male parent of the clutch completed on 14 June 1975 bred again in the same territory in 1979 with another female (both years two eggs; in 1979 three days earlier than in 1975).

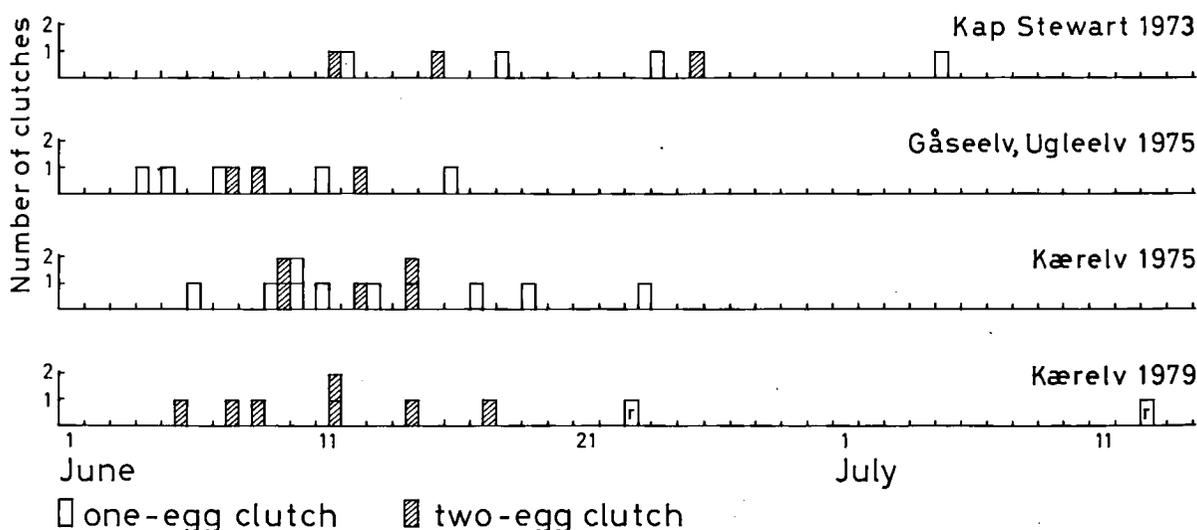


Fig. 4. Dates of clutch completion in different areas and years; r indicates one - egg replacement clutch. Data from Kærelv 1979, after Hansen (1982, 1984).

Table V. Number of eggs per pair, and egg biomass per pair in different years and areas at Scoresby Sund. Data 1979 after Hansen (1982, 1984).

Year	Area	Mean number of eggs		Average egg biomass g	
		per terr. pair	per breeding pair	per terr. pair	per breeding pair
1973	Kap Stewart	0.8 (n = 12)	1.5 (n = 6)	31	59
1974	Kap Stewart	0.0 (n = 6)	0.0 (n = 0)	0	0
1975	Kaerelv	1.2 (n = 16)	1.4 (n = 14)	49	56
1979	Kaerelv	1.7 (n = 10)	2.1 (n = 8)	75	93

Clutch size and egg biomass per territorial pair and per breeding pair at Kap Stewart and Kaerelv in different years is given in table V. In a few cases in 1975 and 1979 at Kærlev in which I did not obtain egg weights, but knew clutch size, I estimated the eggs to be of average weights in the respective years. Mean clutch size of breeding pairs in 1975 at Gåseelv and Ugleelv combined was 1.4. In 1979 at Kaerelv it was 2.0 in first clutches and 1.0 in replacements. In 1973 at Kap Stewart average clutch size of pairs with territories bordering the sea (0.7,  $n = 6$ ) did not differ significantly from that of inland territories (0.8,  $n = 6$ ). In 1975 at Kaerelv, territorial pairs along the coast had significantly larger clutches (1.6,  $n = 8$ ) than

pairs with territories not along the coast (0.9,  $n = 8$ ). At Ugleelv and Gåseelv both of the only two pairs with territories bordering the sea had two eggs; five pairs with nests inland had one egg each.

Weights of one-egg clutches in 1973 ( $n = 3$ ) and 1975 ( $n = 9$ ) did not differ significantly nor did weights of two-egg clutches in 1973 ( $n = 3$ ) and 1975 ( $n = 7$ ). Therefore egg weights of these two years are pooled in table VI, in which egg weights from Kaerelv 1979 and from other areas in Northeast Greenland are also included. In 1973, 1975 and 1979 weight differences between first and second eggs were insignificant. In 1973 and 1975 weight differences between eggs from one-egg clutches and two-egg clut-

Table VI. Fresh clutch and egg weights ( $W_0 = 0.533 LB^2$ ) in Northeast Greenland, arranged according to clutch size. I = one-egg clutch, II = two-egg clutch, a = first laid egg, b = last laid egg.

Area	Year	Mean clutch size	Clutch type	n	Mean weight g	S.D.	Range	Source
Scoresby Sund	1979	2.0	II	6	90.7	7.98	79.4-101.7	Hansen, 1982
			a + b	12	45.4	4.28	39.3-52.4	
			a	3	41.8	2.61	39.3-44.5	
			b	3	43.5	3.67	40.1-47.4	
			I (relay)	2	37.6		30.7-44.6	
Scoresby Sund	1928	2.0	II	1	88.4			Pedersen, 1930
			a + b	2	44.2		41.2-47.2	
Mackenzie Bugt	1931	$\leq 2.0$	II	5	84.5	6.03	77.8-93.0	Schaanning, 1933
			a + b	10	42.3	3.06	38.3-48.1	
Danmarkshavn	1908	$\pm 1.7$	II	5	81.6	10.78	70.4-95.5	Manniche, 1910
			a + b	10	40.8	5.25	35.2-47.8	
			I	2	43.5		42.3-44.6	
Scoresby Sund	1973 1975	1.4	II	10	77.7	4.14	73.0-84.4	This paper
			a + b	20	38.9	2.25	36.2-44.2	
			a	10	39.3	2.77	36.2-44.2	
			b	10	38.5	1.63	37.0-42.4	
			I	12	39.9	1.25	36.3-43.8	
Mestersvig	1974	$\geq 1.0$	I	1	28.9			Green & Greenwood, 1978

ches were also insignificant. Two-egg clutches in 1979 were significantly heavier (17%) than two-egg clutches in 1973 and 1975.

When all eggs of 1973 and 1975 are pooled, linear regression of egg weight on laying date gave a positive regression coefficient for one-egg clutches ( $W_t = 36.5 + 0.34 t \text{ g}$ ,  $n = 12$ ,  $r^2 = 0.41$ ,  $t_0 = 1 \text{ June}$ ) and a negative one for eggs in two-egg clutches ( $W_t = 40.7 - 0.13 t \text{ g}$ ,  $n = 12$ ,  $r^2 = 0.12$ ,  $t_0 = 1 \text{ June}$ ). However, neither of these was significantly different from zero.

#### 4.3. Gonads

Testis volume against collecting date is shown in fig. 5. The males of 1, 13 ( $n = 3$ ), 14 June 1974, 11, 12 August 1973, and 14 August 1974 were collected at sea, those of 6, 15 June 1975, 17 June 1974 ( $n = 3$ ) and the upper one of 24

June 1974 in their territories, the others from groups on the tundra. Testes volumes of adults from the Pacific (USNM 495.213) and from Alaska (USNM 422.942) are also presented for comparison. Mean testis volume of nine juveniles from September and October in ZMA was  $3 \text{ mm}^3$  (range  $1\text{-}8 \text{ mm}^3$ ). The group of males from which the testes of fig. 5 are measured is very heterogeneous as it comprises breeding, failed breeding, and non-breeding territorial birds (all territorial birds presumably show indications of brood patches, see below), but also pre-breeders and non-territorial birds of different age classes (without indications of brood patches). In many cases in July and August 1973 I could not ascertain whether a collected territorial male was a non-breeder or a failed breeder. In 1973 and 1975 regression for testis volume on date for territorial birds (breeders, failed breeders and territorial non-

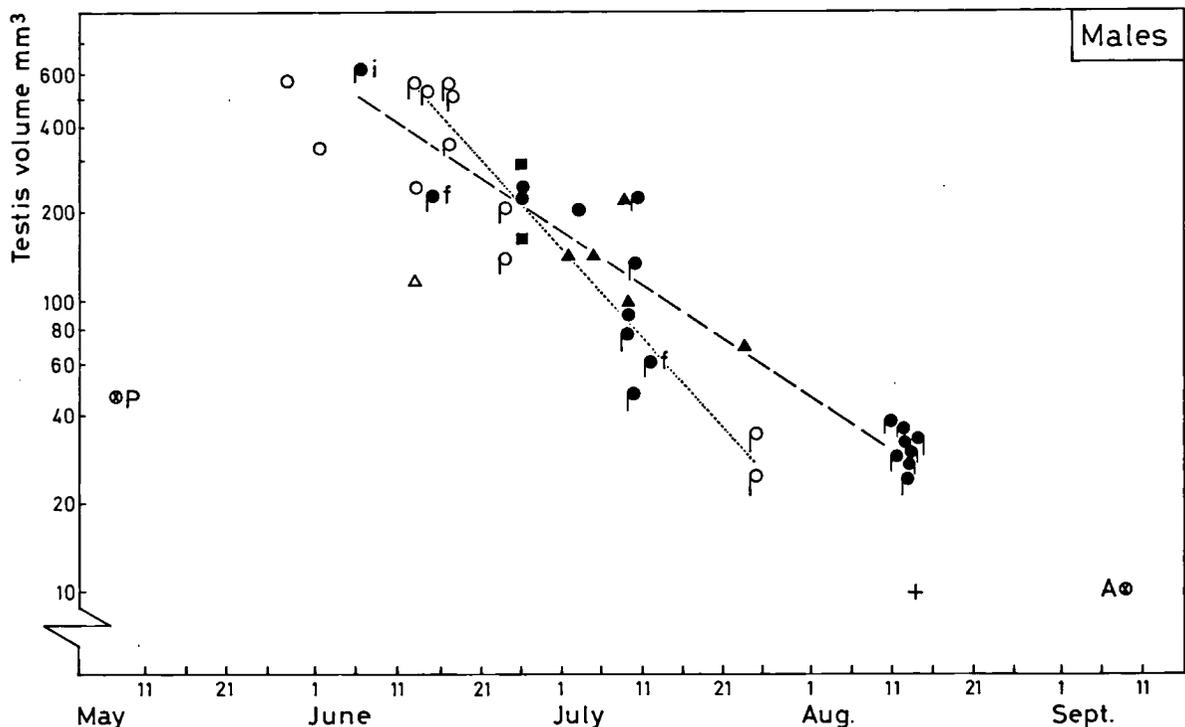


Fig. 5. Testis volume in relation to collecting date in pre-breeding, non-territorial, territorial non-breeding (brood patch), breeding (brood patch), and failed breeding (brood patch) males. *P* indicates bird from the Pacific ( $13^\circ \text{ N } 151^\circ \text{ W}$ ), *A* from Alaska, *i* at clutch initiation, *f* proved failed breeder, + second calendar year male. Other symbols are explained in fig. 6. The broken line (territorial birds 1973, 1975) is  $Y_t = 501 e^{0.04t}$ , the dotted line (territorial birds 1974) is  $Y_t = 548 e^{0.07t}$ .

breeders) gave the best fit with  $Y_t = 501 e^{-0.04t}$  ( $n = 14$ ,  $r^2 = 0.84$ ,  $t_0 = 6$  June). In 1974 regression for testis volume on date for territorial birds (non-breeders only) gave the best fit with  $Y_t = 548 e^{-0.07t}$  ( $n = 10$ ,  $r^2 = 0.96$ ,  $t_0 = 13$  June). The two regression coefficients differ significantly.

Diameter of largest follicles against collecting date is presented in fig. 6. The females of 23 May 1973 ( $n = 2$ ), 3 ( $n = 2$ ), 4, 8 ( $n = 2$ ), 13 June 1974, and 25 July 1973 ( $n = 4$ ) were collected at sea, those of 30 May 1974, 6, 15 June

1975, and 24 June 1974 in their territories, the others from groups on the tundra. The group of females from which the follicles are measured is as heterogeneous as the group of males presented above and comprises the same categories. In the case of ruptured follicles, the diameter of the largest non-ruptured follicle is given. Until the largest follicle reached a size of about 9 mm the next largest was a few millimeters smaller. From 9 mm onwards the difference became increasingly larger. A bird of 17 June 1974 with a largest follicle of 15 mm

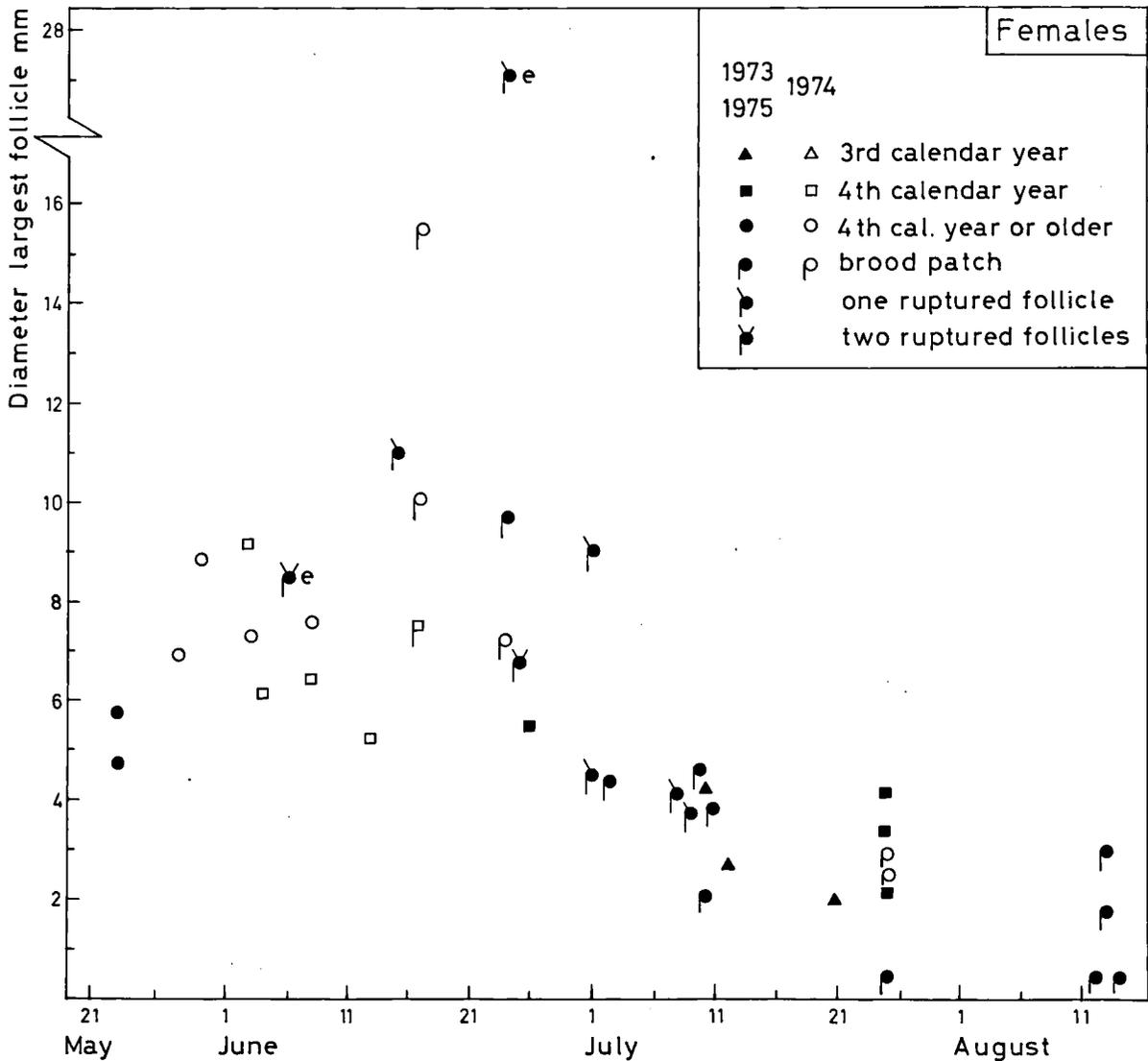


Fig. 6. Diameter of largest follicle in relation to collecting date in pre-breeding, non-territorial, territorial non-breeding (brood patch), breeding (brood patch) and failed breeding (ruptured follicle) females; e indicates egg in oviduct.

had a next largest of 10 mm. One bird of 24 June 1973 with a complete egg in the oviduct and a largest follicle of 27 mm had a next largest follicle of 13 mm. Another bird of 6 June 1975 with two ruptured follicles and an egg with an uncalcified shell in the oviduct had a largest follicle of 9 mm. In the second half of June and the first half of July the flaccid structure of several non-ruptured follicles indicated that they were smaller than they had been earlier that season and that their contents were being resorbed again. These atretic follicles were found in all females with one ruptured follicle ( $n = 6$ ) and in two without ruptured follicles, but not in the two with two ruptured follicles.

Shape and size of the oviduct is very variable and depends on age and time of the year. Assigning oviducts to different classes according to development is an arbitrary matter as they develop gradually from one stage into another but the following classification can be made: narrow and straight, swollen and straight, narrow and distally twisted (has laid egg at sometime), strongly swollen and twisted (Lofts & Murton, 1973; van Franeker, 1983; Voous *in lit.*, 1985). All birds which had an egg in the oviduct or had laid an egg recently (indicated by ruptured follicles) had strongly swollen and twisted oviducts. Several females of July 1973 also showed this stage of oviduct, but did not show ruptured follicles. These follicles probably had been already resorbed, because often within two weeks after rupture there are no further macroscopic signs of rupture (Paludan, 1951; Johnston, 1956 b). In 1974, a non-breeding year, only a single female (17 June) with a largest follicle of 15 mm, had a strongly swollen and twisted oviduct. Females collected in May, June and July with largest follicles 4.7 - 10 mm had a swollen and twisted oviduct, except for fourth calendar year females (fig. 6), which had the oviduct swollen and straight. In July fourth calendar year birds with follicles smaller than 4.5 mm and third calendar year birds, which all had follicles smaller than 4.5 mm, had a straight and narrow oviduct. Adults in July and August with largest follicles

under 4.5 mm could have any stage of development of the oviduct.

#### 4.4 Brood patches

Both sexes in the Long-tailed Skua may develop a pair of oval brood patches laterally placed in the apteria (figs 5 & 6). Outside the breeding period these apteria are covered with down. The first indication of a brood patch is the loss of down in the apteria. When the patch expands, several rows of contour feathers are shed. The final phase of development occurs when eggs are laid and the patches become vascularized. The length of a fully developed patch ranged between 50 and 60 mm (average 55 mm,  $n = 17$ ) in both males and females. Regression of the patches started with growth of body feathers in the pterygiae. Somewhat later down feathers started to grow in the apteria.

The occurrence of brood patches is shown in figs. 5 and 6; all birds presented in figs 8 and 9 had brood patches. All immatures were lacking brood patches. Indications of brood patches did not occur in birds collected along the ice edge (1973) and on the tundra (1974) in May. They were also not found in birds shot along the ice edge between 1 and 8 June 1974 nor in any of the four adults shot on 13 and 14 June 1974. After 14 June (all years combined), within the group of certain fourth calendar year birds ( $n = 11$ ), 54% (6) did not show any sign of brood patches. Within the group of collected fourth calendar year or older birds, 16% (5) of the males ( $n = 31$ ) did not show brood patches while all females in this group ( $n = 29$ ) did. Four of the five males without brood patches in this category were fourth or fifth calendar year birds. Except for a female of 30 May, collected in territory, none of the birds without brood patches offered indications that they were paired.

Two males shot along the ice edge on 13 and 14 June 1974 had bare spots of about 1.5 cm. On 17 June three non-breeding territorial females and one of their mates had incomplete patches (2-3 cm), while the other two mates had

complete patches. A non-breeding territorial female collected on 24 June 1973, the partners of a non-breeding territorial pair and a single male collected 24 June 1974 on the tundra all had incomplete patches (2-3 cm). All birds except for the two males shot along the ice edge, the stomach contents of which proved that they had been on land, and the single male from the tundra provided evidence that they were paired.

A female of 6 June 1975 between the laying of her first and second egg had full-size, but not vascularized brood patches. The patches of her mate were about 2 cm. A female of 24 June 1973 just prior to the lying of her single egg had full-size and slightly vascularized patches. In 1973 and 1975, all breeding males and females, regardless of clutch completion date, had after clutch completion full-size and vascularized patches until the last week of June. In the first days of July all of these had growing feathers medially on the patches. In early breeders (eggs laid before 11 June) the patches were full-size, without a trace of new feathers until 16 to 18 days after clutch completion, in late breeders (eggs laid after 23 June) new feathers did appear 4 to 6 days after clutch completion. The start of growing of these new feathers was synchronized within some days among the partners in the same breeding pair. Birds with young had, between 10 and 16 July, about one third of the surface covered with new feathers.

A pair of failed breeders (date of clutch loss unknown) had full-size patches on 15 June 1975. The patch of the female was a little vascularized, but that of the male was not.

Birds that had lost their eggs and paired birds that had not bred (inferred from status of follicles and indications of large brood patches), collected after 24 June (all years), had new feathers growing medially on the patches. Such birds collected between 7 and 13 July had one-third to two-thirds of the surface covered by new feathers again and on 25 July three-quarters or more was covered. Birds collected between 10 and 14 August in which blood-quills indicated that the feathers were new, had the patches completely covered by feathers and down.

#### 4.5. Incubation behaviour

Both sexes in the Long-tailed Skua incubate. Random observations ( $n = 156$ ) of marked and sexed pairs in different phases of the incubation period done between 10 and 21 hours local time, showed that in 63 percent of the cases when a bird was seen incubating it was the female. Some aspects of incubation behaviour, observed during a 26 hour watch on 22 and 23 June, are shown in fig. 7 for a pair of old birds (according to leg colour), eight days after clutch completion. The eggs were incubated 59% of the time by the female and 37% by the male. They were not incubated 4% of the time. Total non-incubating time (54 minutes) minus non-incubating caused by relief of observer (15 minutes) was 39 minutes. This time was spent chasing away an Arctic Fox (*Alopex lagopus*) (48%), chasing away other Long-tailed Skuas (8%), in retarded incubating reliefs (36%) and in abortive incubating reliefs (8%). Of the total

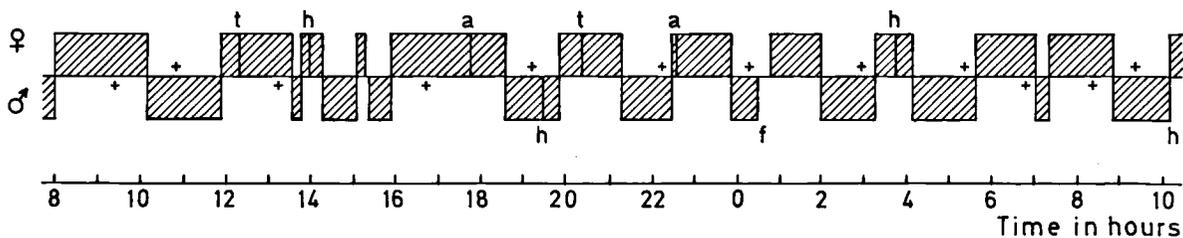


Fig. 7. Incubation behaviour of male and female of a two-egg clutch, eight days after clutch completion; + indicates eggs turned, *t* absence due to territorial fight, *h* to human interference, *a* to abortive incubating relief, *f* to chasing an Arctic Fox.

incubating time the female sat 61% (average shift 84, range 10-165 minutes) and the male 39% (average shift 54, range 6-102 minutes) on the eggs. These periods include breaks in the shifts. At incubating relief the female left only after the mate stood near the nest in 91% and the male in 40% of the cases. The female left the nest twice (two and one minute(s), *a* in fig. 7) when the male was circling over her, but she resumed incubating when he did not alight. Eggs were turned, by both birds, with average intervals of 121 minutes (range 60-191 minutes). The off-duty male was seen foraging on the tundra and in the leads among the ice at sea, the female only on the tundra. They were not seen feeding each other.

Detailed observations of another two-egg pair, an old male and a younger female (probably fifth calendar year, according to leg colour), 19 days after clutch completion were stopped when the female did not take over after a shift of 10 minutes by the male. When after

19 minutes he came back to the nest, the female joined him and begged repeatedly while the eggs remained uncovered. After two minutes they both flew away again. The next day they were seen foraging in the tundra at the same time. The eggs cracked but the embryos died. Both birds were seen incubating at times until 26 days after clutch completion.

#### 4.6. Energy reserves

Energy reserve indices of breeding males and females, in relation to number of days after clutch completion are shown in fig. 8 and fig. 9, respectively. Some of these birds have been weighed more than once, and their energy reserve indices on different days have been plotted accordingly. As I found no significant differences among clutch size, egg weight, and energy reserve indices in 1973 and 1975, data of birds from these years have been pooled for calculating regression of energy reserve indices

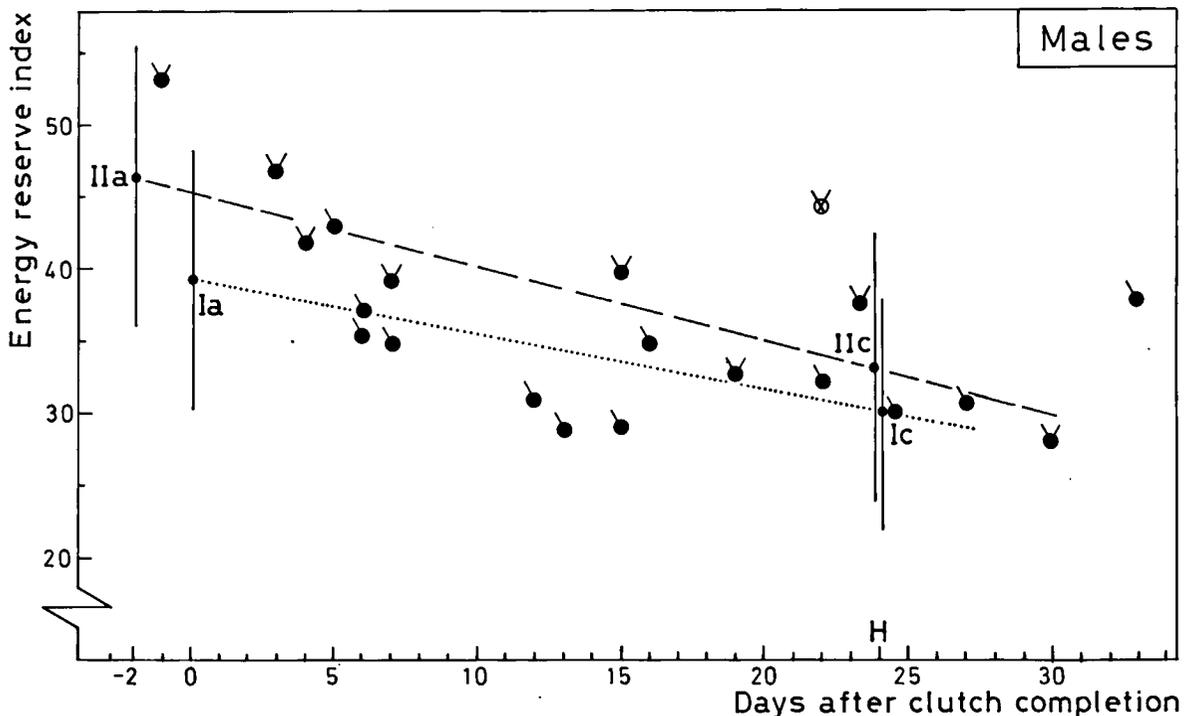


Fig. 8. Energy reserve index in relation to time after clutch completion in breeding males in 1973 and 1975. *Ia* indicates range of energy reserve index (95% confidence limits) of one-egg males at clutch initiation, *Ic* at hatching of young. *IIa* of two-egg males at clutch initiation, *IIc* at hatching of second young. Other symbols are explained in fig. 9. The dotted line is  $Y_t = 39.8 - 0.41 t$ ; the broken line is  $Y_t = 45.1 - 0.49 t$ .

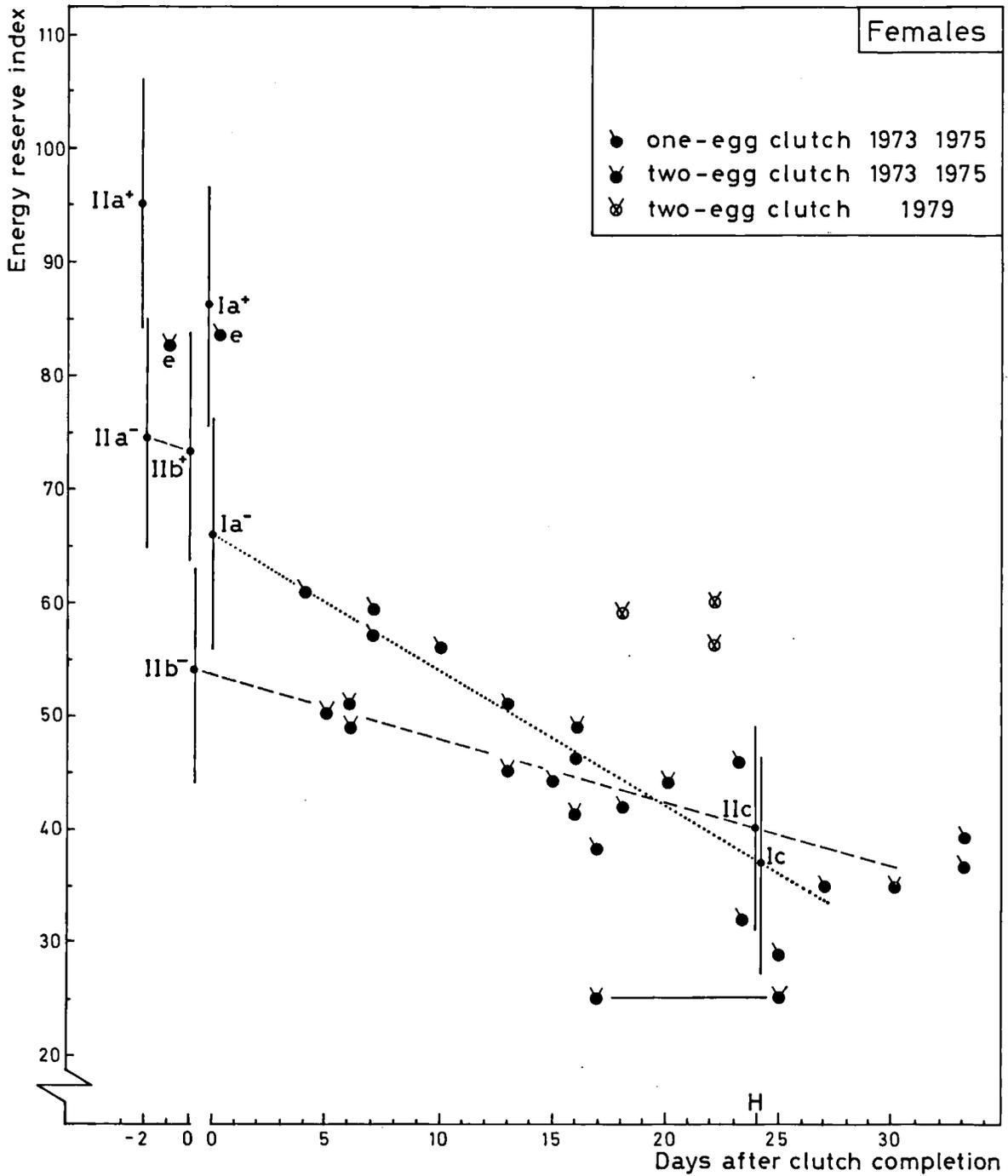


Fig. 9. Energy reserve index in relation to time after clutch completion in breeding females in 1973 and 1975. Data from Kærelv 1979 after Hansen (1982 1984).  $Ia^+$  indicates range of energy reserve index (95% confidence limits) of one-egg females prior to laying,  $Ia^-$  after laying,  $Ic$  at hatching of young;  $IIa^+$  indicates range of energy reserves of two-egg females prior to laying of first egg,  $IIa^-$  after laying of first egg,  $IIb^-$  after laying of second egg,  $IIc$  at hatching of second young. Solid line joins observations on the same bird,  $e$  egg in oviduct,  $H$  hatching day. The dotted line is  $Y_t = 65.8 - 1.24 t$ ; the broken line is  $Y_t = 53.5 - 0.56 t$ .

against days after clutch completion. Energy reserve indices of birds caught in 1979 at Kaerelv, inferred from Hansen (1982) are not pooled with those of 1973 and 1975 because mean clutch size, egg weight and energy reserve indices differed considerably.

Linear regression for males of one-egg clutches resulted in  $Y_t = 39.8 - 0.41 t$  ( $n = 10$ ,  $r^2 = 0.62$ ) from day 0 until day 27, and for two-egg males in  $Y_t = 45.1 - 0.49 t$  ( $n = 7$ ,  $r^2 = 0.75$ ) from day 0 until day 30. The slopes of the two equations do not differ significantly. The energy reserve index of two-egg males at clutch initiation (two days before clutch completion, average 46.1, *IIa* in fig. 8) was significantly higher than that of one-egg males at clutch initiation (average 39.8, *Ia* in fig. 8), but not at hatching of their last young and only young respectively (average 33.3 in two-egg males, *IIc* in

fig. 8; average 30.0 in one-egg males, *Ic* in fig. 8).

Linear regression in females of one-egg clutches resulted in the equation  $Y_t = 65.7 - 1.23 t$  ( $n = 12$ ,  $r^2 = 0.78$ ) from day 0 until day 27 and for females of two-egg clutches in  $Y_t = 53.6 - 0.56 t$  ( $n = 9$ ,  $r^2 = 0.79$ ) from day 0 until day 30. The slopes of the two equations differ significantly. At the day of hatching of the only chick of one-egg females and of the last chick of two-egg females the energy reserve index of one-egg females (average 36.2, *Ic* in fig. 9) is not significantly different from that of two-egg females (average 40.2, *IIc* in fig. 9). At the day of clutch completion the energy reserve index of one-egg females (average 65.7, *Ia* in fig. 9) is significantly higher than that of two-egg females (average 53.6, *IIb* in fig. 9).

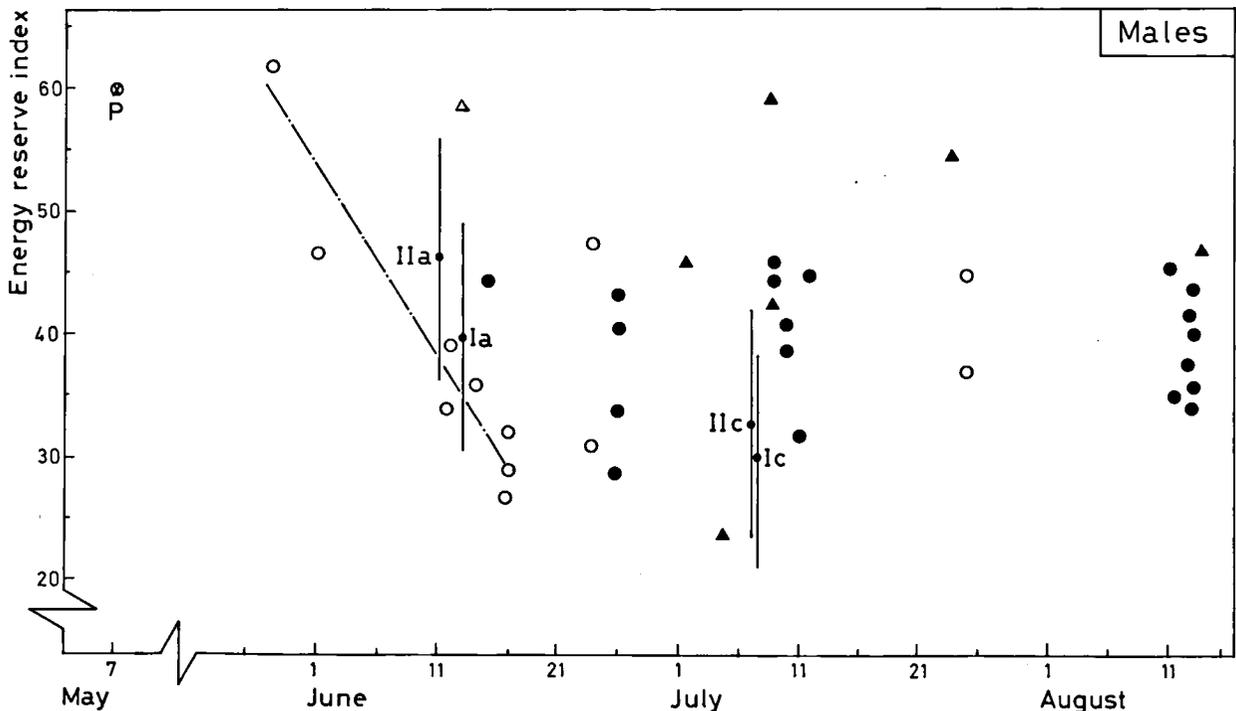


Fig. 10. Energy reserve index in relation to date in pre-breeding, non-breeding and failed breeding males in 1973, 1974 and 1975. Ranges of energy reserve indices for one-egg males (*Ia*) and two-egg males (*IIa*) at clutch initiation are plotted at the average clutch initiation dates of 1973 and 1975 combined. *Ic* and *IIc* indicate range of energy reserve index for one-egg and two-egg males at hatching of young. *P* indicates bird from the Pacific (13° N 151° W). Other symbols are explained in fig. 11. The broken line (non-breeders 1974) is  $Y_t = 60 - 1.55 t$  ( $t_0 = 28$  May).

Energy reserve index prior to laying may be calculated by adding the weight of the egg to the weight of the female just after laying. Fresh egg weight was 20.2% (S.D. 1.81, range 17.2 - 23.5,  $n = 14$ ) of structural size of breeding

females. This gives in one-egg females an average reserve index of 85.9 ( $Ia^+$  in fig. 9) just prior to laying of the only egg and in two-egg females 73.8 ( $IIb^+$  in fig. 9) just prior to laying of the second egg. Energy reserve index

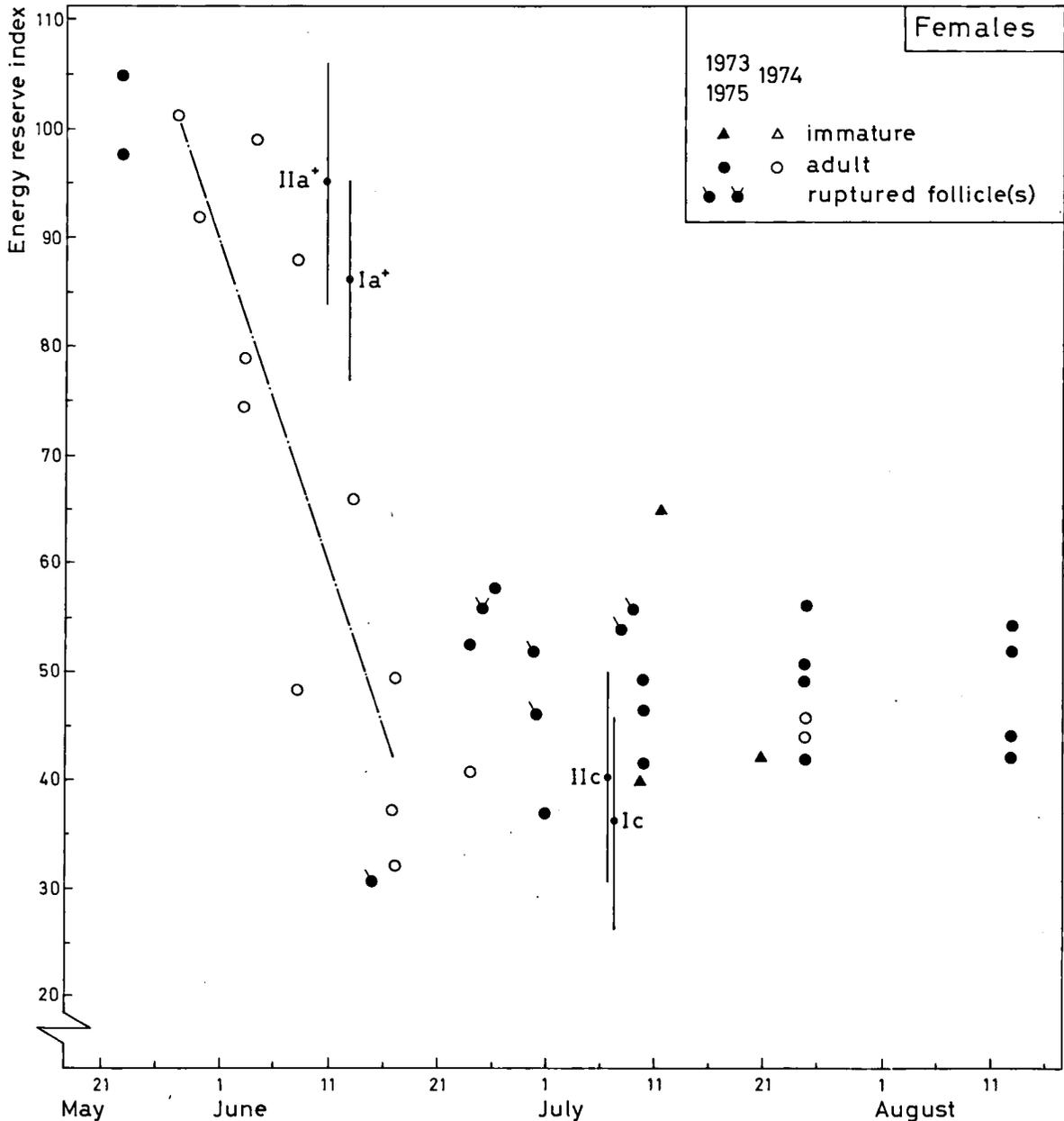


Fig. 11. Energy reserve index in relation to date in pre-breeding, non-breeding and failed breeding females in 1973, 1974 and 1975. Range of energy reserve indices for one-egg females ( $Ia^+$ ) and two-egg females ( $IIa^+$ ) prior to clutch initiation are plotted on average clutch initiation dates of 1973 and 1975 combined.  $Ic$  and  $IIc$  indicate ranges of energy reserve indices at hatching of the young for one-egg and two-egg females, respectively. The broken line (non-breeders 1974) is  $Y_t = 101 - 2.94 t$  ( $t_0 = 28$  May).

of two-egg females, just after laying of the second egg was estimated by assuming that during the two days between the laying of the eggs, rate of energy reserve loss was the same as during incubation which gave an average of 74.9 ((IIa<sup>-</sup> in fig. 9). Energy reserve index just before laying of the first egg was estimated by adding the weight of another egg which gave an average of 95.1 (IIa<sup>+</sup> in fig. 9). A female with one ruptured follicle and an egg with coloured shell in the oviduct is plotted as a one-egg female at day 0 as her index of energy reserve was entirely within the calculated range of one-egg females just before laying and her largest follicle showed signs of regression. Another female had two ruptured follicles and an uncalcified egg in the oviduct; she is plotted as a two-egg female at day -1.

Energy reserve indices of pre-breeding, non-breeding (non-territorial and territorial) and failed breeding males and females in 1973 and 1975 and of pre-breeding and non-breeding (non-territorial and territorial) males and females in 1974 in relation to date are presented in fig. 10 and fig. 11. These heterogeneous groups of males and females are made up of immatures and adults, some of which (judging from brood patches) had occupied a territory and some of which (judging from ruptured follicles in females) also had had eggs. Information about area (at sea or on land, in territory or in groups) for each of these birds is presented in the chapter about gonads.

In males linear regression of energy reserve index on collecting date in the non-breeding year 1974 (28 May-17 June) gave the best fit and yielded the equation  $Y_t = 60 - 1.21 t$  ( $n = 8$ ,  $r^2 = 0.75$ ,  $t_0 = 28$  May, fig. 10). If we assume that adult males on 28 May in 1973 and 1975, just like in 1974, arrived with an average energy reserve index of 60, then the average rate of energy reserve index loss in pre-breeding birds until clutch initiation was 1.25 in one-egg males and 0.98 in two-egg males. Weights and weight losses derived from energy reserve indices are presented in table VII.

Non-breeding and failed-breeding adult males from July and August did not show any

apparent trend in energy reserve index in the course of these months (mean 41, range 32-46).

In females linear regression of energy reserve index on collecting date in the non-breeding year 1974 (28 May-17 June) gave the best fit and resulted in the equation  $Y_t = 101 - 2.94 t$  ( $n = 11$ ,  $r^2 = 0.75$ ,  $t_0 = 28$  May, fig. 11). If we assume that adult females on 28 May in 1973 and 1975, just like in 1984, arrived with an average energy reserve index of 101, then the average rate of energy reserve index loss in pre-breeders until clutch initiation was 0.93 in one-egg females and 0.43 in two-egg females. Weights and weight losses derived from energy reserve indices are presented in table VII.

Non-breeding and failed-breeding adult females from July and August did not show any apparent trend in energy reserve index in the course of these months (mean 48, range 41-56).

## 5. DISCUSSION

The Long-tailed Skua is a seabird spending about three quarters of its life on the open sea and, like other seabirds, comes to land only for reproduction (Ashmole, 1971). It breeds on arctic tundra and there its feeding habits are more or less similar to those of birds of prey (Salomonsen, 1950; Maher 1970, 1974; Andersson, 1971, 1976 a b; Taylor, 1974; own observations). During the breeding time not all birds of this species come to land, and not all birds coming to land establish a territory. Once a territory has been established, and a pair has been formed, not all pairs succeed in laying eggs. Clutch size and timing of egg laying in different years and areas can be quite different. In 1974 not a single territorial pair bred, however in 1975 only 12% failed to do so. What are the proximate factors that stimulate the paired birds producing a maximal clutch of two eggs and what factors cause the asynchrony of egg laying in populations and the differences in egg laying time in different areas and years? Body energy reserves and food supplies in the foraging area are important factors (review in Drent & Daan, 1980; Walsberg, 1983), but age

(Johnston, 1956 a b; Coulson & White, 1958; Carrick & Ingham, 1967; Coulson, 1980) and timing of appearance of suitable nesting sites (Lack, 1933; Bertram *et al.*, 1934) also play a role.

### 5.1. *Gonad development in territorial birds*

In the first week of May, three weeks before the first Long-tailed Skuas arrive along the ice edge, the acceleration or progressive state in testis development in adults has started and testes are already larger than in August and September when they are in regression (fig. 5). Upon arrival at the tundra in the last days of May and the first days of June the testes have developed to sub-maximal size, a pattern also found in the Pomarine Skua (*Stercorarius pomarinus*) in Alaska (Maher, 1974). After a territory has been established, an activity in which the male usually plays a leading role (Andersson, 1971) and a mate has been acquired, testis size may become larger and may culminate during the days prior to egg laying, when actual insemination occurs (Lofts & Murton, 1973). Thereafter in the refractory period, testis size in the population of adults regresses quite rapidly during one to two months (fig. 5).

Testis size of territorial birds (non-breeders, breeders, failed breeders) in 1973 and 1975 varied more and decreased slower than in 1974 (non-breeders only). I found no indications that in non-breeding territorial males testes started to shrink earlier than in (failed) breeding males, as was concluded by Maher (1974). In territorial non-breeders a sub-maximum testis size was probably kept until the middle of June; thereafter regression started quite synchronously and continued with a constant rate until the last week of July. In (failed) breeders regression started probably soon after egg laying (cf. Lofts & Murton, 1973). A failed breeder from 15 June (fig. 5), judging from the status of the ruptured follicle of his mate, already has regressed testes about a week after clutch completion. Portenko (1973) reports regressed testes of 301 mm<sup>3</sup> and 118 mm<sup>3</sup> in males that were still incubating. Late breeders attain or

still have maximal testis size in the second half of June or even in the beginning of July (including replacements) when insemination occurs. A male of 6 June with maximal testis size (*i* in fig. 5) was collected between the laying of the first and second egg of its clutch. A failed breeder collected on 12 July (fig. 5), 27 days after clutch completion (clutch lost in the first week of July) had very regressed testes. If we assume that on the day before clutch completion this failed breeder had a similar testis size as the 6 June bird, and use an exponential curve fit, the equation for regression of testis volume on days since egg laying is  $Y_t = 638 e^{-0.08t}$ . The regression coefficient of this equation does not differ significantly from that in the population of territorial non-breeders (- 0.07) indicating that once regression has started, its rate is similar in breeding and non-breeding adults.

Follicle growth of adult females showed a pattern similar to testis growth in adult males. Follicles of adult females arriving along the ice edge in the fourth week of May were enlarged compared with those in the refractory and regeneration period in July and August and oviducts had developed to the twisted and rather swollen stage. The follicles continued to grow in the last week of May to reach a maximum size of about 10 mm in the first week of June in case rapid follicular growth was postponed or did not occur at all. The 10 mm diameter may be a threshold level from which rapid follicular growth starts for the laying of the first egg if proper stimuli are present. Only in paired females did I find larger follicles (fig. 6). As a rule the female will start rapid follicular growth only after having been together with a mate for a certain amount of time (review, see Immelman, 1971). In one case a female had an egg in the oviduct, a follicle of 27 mm and one of 12 mm, indicating that once rapid follicular growth has started in the first two follicles, others may become enlarged somewhat above the 10 mm level but without rapid follicular growth. Not all paired females in the second half of the breeding period had follicles that were, or had been, in the phase of rapid

growth, indicating that in some paired birds the "decision" for not-laying may be taken before rapid growth has started. However, as all birds with one ruptured follicle and some birds with non-ruptured follicles showed more or less strong atresia of their largest follicle and a bird in the non-breeding year 1974 had a follicle in the stage of rapid growth (fig. 6), although judging from her energy reserve index she should have been unable to produce an egg, it is also clear that the "decision" to lay or not to lay, may be taken when the follicles have already developed considerably, sometimes near maximal size. Gilbert in his review (1971) concluded that once rapid follicle growth had started, it was never arrested for some time, but either culminated in ovulation or turned into regression. Which proximate factor causes paired females to ovulate?

## 5.2. *Energy reserves and breeding*

Upon arrival along the ice edge and on the tundra Long-tailed Skuas had large energy reserves (figs. 10, 11). In Peary Land (Johnsen, 1953), Arctic Canada (Manning & Macpherson, 1961, specimens courtesy Ouellet, Nat. Mus. Canada), Alaska (specimens in USNM) and Siberia (Portenko, 1973), birds collected at or within a few days after first arrival were relatively very heavy as well. Maximal energy reserves of males and females were 62 and 105 percent, respectively, of their starving weight. The great energy reserves of an adult male of 7 May from the Central Pacific (fig. 11) which had completed its primary moult and nearly had completed its tail feather moult, suggest that a month before arrival on the breeding grounds the large reserves have been accumulated either in the winter quarters in the southern hemisphere or elsewhere on the southern part of the spring migration route to the north. Many if not all birds store energy reserves prior to breeding (Lack, 1966; Ashmole, 1971; Coulson *et al.*, 1983; Wijnandts, 1984) and lose weight during incubation (review, see Drent, 1975; Sibley & McCleery, 1983; Furness, 1984).

Though the data are scant I venture to assume that most adult males as well as adult females, when they arrive from the sea in spring, have about the same energy reserve index for each year. The assumption that males arrive with an average energy reserve index of about 60 and females arrive with one of about 101, provides the possibility to estimate average weight loss in different phases of the breeding cycle (see, figs 10 and 11). In 1973 and 1975, females which had lost no more than 6% (12 g) of their energy reserves from arrival until egg laying, laid two eggs; those that had lost between 6% and 17% (12-33 g) laid either two eggs or one egg; those that had lost between 17% and 25% (33-49 g) laid one egg, and those that had lost more than 25% (49 g) did not lay at all. The breeding females of 1979 (fig. 9) had larger energy reserves at the end of the incubation period than females in 1973 and 1975; they had also larger clutches (table VI) and probably they had started egg laying with larger energy reserves because they had better feeding opportunities (de Korte in prep.; Hansen, 1982). One of them produced two successive replacements of one egg (Hansen, 1982, 1984). If we take the period between first arrival and average date of clutch initiation in 1973 and 1975 combined as the standard pre-breeding period we can calculate the average rate of weight loss during different stages of the breeding cycle (table VII). In the first three weeks after arrival in 1974, energy reserves of non-breeding females were depleted faster than of one-egg females (1973, 1975) and a little slower than of two-egg females (1973, 1975) in the pre-breeding period, costs of egg production included. After three weeks the non-breeding females had used on average 59% (115 g) of their energy reserves (about 30% of their total body weight) while no eggs had been produced.

Though energy reserves may be sufficient for three eggs, Long-tailed Skuas very rarely produce three-egg clutches (Hart, 1880; Andersson, 1981). Andersson (1976 b) provided evidence that a Long-tailed Skua is unable to incubate successfully more than two eggs at a time. In years in which maximal energy

Table VII. Estimated average energy reserves (g) at arrival and energy reserve losses (g) after arrival. In brackets energy reserve loss per day. Pre-breeding period: 28 May until average clutch initiation date in 1973 and 1975 (two-egg birds 11 June, one-egg birds 13 June), 28 May until 17 June in 1974 (non-breeders).

		Arrival reserves	Pre - breeding loss		Breeding loss	Total loss
			excl. egg laying	incl. egg laying		
Females	0 egg	197	115 (5.7)	-	-	115
	1 egg	197	29 (1.8)	68 (4.3)	58 (2.4)	126 (3.2)
	2 eggs	197	12 (0.8)	91 (6.5)	28 (1.1)	119 (3.0)
Males	0 egg	111	60 (3.0)	-	-	60
	1 egg	111	39 (2.5)	-	19 (0.8)	58 (1.5)
	2 eggs	111	27 (1.9)	-	24 (0.9)	51 (1.3)
Pairs	0 egg	308	175 (8.7)	-	-	175
	1 egg	308	68 (4.3)	107 (6.7)	77 (3.2)	184 (4.6)
	2 eggs	308	39 (2.8)	118 (8.4)	52 (2.0)	170 (4.3)

reserves can be kept until egg laying, they lay two large eggs (table VI). If their energy reserves become somewhat less than maximum they respond with producing medium-sized eggs in two-egg clutches. With still lower energy reserves, clutch size is reduced to one medium-sized egg or one small egg. Replacements probably are produced when about a week after clutch loss, energy reserves are more than 75% of the level at arrival. Rapid follicle growth may start in paired females, also in minimum years, but if after a few days it turns out that body energy reserves are depleted much faster than follicles are growing, atresia will start.

In 1973 and 1975, females of one-egg clutches used their energy reserves before and after egg laying about twice as fast as females of two-egg clutches (table VII). One-egg males also lost their energy reserves faster than two-egg males, but only in the pre-breeding period; in the breeding period their rate of loss was about the same. If we include in one-egg and two-egg females also the weight of the produced eggs, the rate of energy loss in one-egg and two-egg females is about the same over the pre-breeding period and the breeding period combined. Therefore, notwithstanding the costs of producing and incubating an extra egg (King, 1973; 1974; Ricklefs, 1974; Drent, 1975), two-egg females (61% of their energy reserves, 31% of their body weight) did not lose more energy

reserves than one-egg females (65% of their energy reserves, 33% of their body weight). This phenomenon was also observed in Weaverbirds (*Quelea quelea*) (Jones & Ward, 1974) and Lesser Snow Geese (*Chen caerulescens caerulescens*) (Ankney & McInnes, 1978) where energy reserves of females having laid clutches of different size were not significantly different. Rate of energy loss before egg laying may act as a proximate regulator of clutch size (Drent & Daan, 1980). Two-egg pairs obviously are more efficient than one-egg pairs and possibly they have territories with better feeding opportunities. In 1975 pairs in territories bordering the sea had significantly larger clutches than pairs in territories not bordering the sea. However in 1973 and 1979 this correlation was not found and it is known that Long-tailed Skuas may breed very successfully completely independent from sea food (see review in Salomonsen, 1950; Dementiev et al., 1969; Cramp & Simmons, 1983). It is probable that, only in years with little food on the tundra do pairs in territories bordering the sea have relatively better feeding opportunities.

Females arrived with on average 86 g (70%) higher energy reserves than males. These extra reserves equal the weight of a heavy two-egg clutch (table VI). Energy costs of producing eggs are equal to the energy contents of the new tissues plus the costs of synthesizing them (King, 1974). In 1973 and 1975 pre-breeding

females lost less weight than pre-breeding males, although they had to use extra energy for synthesizing eggs and maintaining their extra weight (see below). This presumes that they eat more and fly less than males in this period (cf. Rijnsdorp *et al.*, 1981). In the pre-breeding period males spend much more time and energy in establishing and defending a territory than do females, while they also may feed the female to a certain extent (Andersson, 1971; Taylor, 1974).

During incubation females lost energy reserves faster than males; they incubated about 61% of the time and assisted in territorial defence (fig. 7). In years of food abundance the female may incubate about 70% of the time or more and may rarely assist in territorial defence (Andersson, 1971; Taylor, 1974; Kampp, 1982). However, Parmelee & MacDonald (1960) report a male spending more time on the nest than the female in a year of scarcity. The female may be fed lemmings by the male and the sitting bird may leave the nest for a while to join its mate, when the latter has caught this prey (Andersson, 1971; Taylor, 1974). Cooperation in tearing apart a lemming is more efficient than handling it singly (Andersson, 1971). We did not observe the male feeding the female during our observations in the incubation period, not even when she was begging repeatedly, probably because lemmings (in Greenland only the Collared Lemming, *Dicrostonyx groenlandicus*, occurs) were rather scarce and the birds had to resort to other food (de Korte, in prep.). In West-Greenland where lemmings do not occur, Kampp (1982) observed that the male provided the female sea food. The female with lowest energy reserves in fig. 9 was seen begging on several occasions toward the end of the incubation period but the male was never observed to feed her. Eggs of this pair were deserted at times and the embryos died before hatching (see 4.4 Incubation behaviour). This female had energy reserves of about 25% of her starving weight without further decreases in the last week of incubation. The lowest energy reserves of Long-tailed Skuas on the tundra declined to about 25% of

starving weights (figs. 8, 9, 10 and 11). When energy reserves have become depleted to this level (about 75% of arrival reserves consumed = 38% of arrival body weight) the birds probably can not afford to lose more energy and feeding obtains the highest priority of all activities. It is also known from Arctic Geese (Harvey, 1971; Ankney & Mc Innes, 1978) and tropical seabirds (Harris, 1969) that eggs are deserted in times of food shortage. In 1974 some territorial males were approaching the critical 25% level in the third week of June (fig. 11). Males that were not continuously guarding a territory had higher energy reserves.

Birds that had given up breeding and defending a territory and roamed over the tundra had in general larger energy reserves than birds in the last days of incubation and caring for small young in the first days after hatching when reserves seem to become depleted further. In minimum years the maintenance of a territory means a high energy cost compared with the way of living after having relinquished it, but the ultimate advantage is that it will be easier to claim the territory in the next year with the same mate. This is also the reason why birds, after having given up guarding their territory, constantly keep coming back to it until August (de Korte, 1984).

Though in 1974 no eggs were produced, females used their energy reserves faster than males in the first three weeks after arrival, losing on average 2.7 g more per day than males (table VII). In these three weeks females used, owing to their greater body weight (see methods), on average 9.2 kcal more per day for their existence metabolism than males. A substantial part of the energy reserves of females is made up of proteins stored for the production of eggs (Jones & Ward, 1975; Evans & Smith, 1976; Ankney & Mac Innes, 1978). After the initial use of fat, they will also start to burn their protein reserves for their metabolism energy (cf. Croxall, 1982). In general the birds which burn their energy reserves use progressively more of their protein reserves, which means a greater weight loss per kcal metabolized than with the burning of fat. This may ex-

plain that the best fits for regression of weight on date, were all linear (figs 8, 9, 10 and 11) and not exponential as one would expect from the formula for existence metabolism. Reckoning that the 9.2 k cal extra in females is provided partly by fat and partly by protein, females used between 1.0 g (by burning fat only) and 2.3 g (by burning protein only) more per day than males. Thus the actual difference in weight loss per day (2.7 g) can only partially be explained by difference in existence metabolic rate. In 1974 snow cover lasted much longer than usual and for a period of some weeks the birds had to fly from their potential snow-covered territories inland to the sea and back. After having established the territories they continued to fly to the sea and back, but at greater intervals. Females with their greater weight must have used more energy for flying than males. At sea they had ample feeding opportunity (de Korte, 1984) to compensate for this extra loss, but not on the tundra where food was scarce. As flight performance decreases with increasing weight (Andersson & Norberg, 1981) their manoeuvrability for getting the sparse agile prey on the tundra will also be less than that of males when they are heavier. After the birds have lost most of their energy reserves, females in general retain more energy reserves than males during summer (figs. 10, 11). This can be explained by the fact that males, after failed breeding and non-breeding in poor years, spend more time in territorial defence (own observations).

### 5.3. *Timing of laying*

Taking into account the short period in which reproduction for arctic tundra birds is possible (Salomonsen, 1950; de Korte, 1975; de Korte *et al.*, 1981; Meltofte, 1985), egg laying in the Scoresby Sund area showed little synchrony (fig. 4). Ignoring replacement clutches, ranges per year and area had a minimum of 12 days and a maximum of 24 days. Over all years and areas the range was 31 days (4 June - 5 July). When replacements are included the range was 39 days (4 June - 13 July). Asynchrony of lay-

ing dates without peak laying seems to be quite common in the Long-tailed Skua as it is also reported from Alaska and Canada (Maher, 1970, 1974; Taylor, 1974). Which factors are responsible for the asynchrony of laying dates? Long-tailed Skuas arrive unpaired in the breeding area (de Korte, 1984), thus rapid follicular growth can start only after arrival when the female is stimulated by a male (see, review Immelman, 1971). In a species of the size of the Long-tailed Skua the period between the start of rapid follicular growth and egg laying is seven to eight days (rapid follicular growth six to seven days, egg in oviduct about one day, King, 1973; Ricklefs, 1974; Walsberg, 1983; Wijnandts, 1984), so the earliest possible egg laying date is seven to eight days after arrival. A replacement can occur, also at the earliest, seven to eight days after clutch loss. Earliest arrival dates at Scoresby Sund (27 and 28 May) and earliest egg laying dates (3 and 4 June) indicate that in the Long-tailed Skua rapid follicular growth may start on the day of arrival. Andersson (1976 a) found in Lapland egg-laying before 1 June and Maher (1974) in Alaska on 1 June, which was eight days after earliest territory establishment. The high-arctic Barnacle Goose (*Branta leucopsis*) and Pink-footed Goose (*Anser brachyrhynchus*) may produce eggs within a few days after arrival (Pedersen, 1930; de Korte, 1974; de Korte & Bosman, 1975). However, geese are paired in the winter quarters and in these species rapid follicular growth has started already before they arrive on the breeding grounds (Raveling, 1978).

In our study areas almost the entire breeding population of Long-tailed Skuas had arrived in the first days of June. Egg laying dates after 10 June indicate that a large part of the population did not lay seven to eight days after arrival but postponed the start of rapid follicular growth for up to some weeks. High and low energy reserves give a sufficient explanation for early or late egg laying in many temperate bird species (Drent & Daan, 1980) but not in the Long-tailed Skuas we studied. In 1975 two-egg birds did not lay earlier than one-egg birds though their energy reserves were larger. In

1979 when energy reserves were higher than in 1975, eggs were not laid significantly earlier. Andersson (1976 a) found in Lapland, that among years with similar food richness, egg-laying dates in the same area could differ more than a week. Intra-annual and intra-areal asynchrony can be explained partly by asynchronic arrival of individual birds (about a week), and partly by the difference in pair composition. Experienced breeders usually return to their last year's territory and pair formation will generally take little time in these birds. Inexperienced birds and birds that mate with a new partner will need more time for successful territory establishment and pair formation. The latest breeding pair in 1973 and the two latest in 1975 all had one fourth calendar year bird. The latest breeding pair in 1975 had prolonged and violent territorial fights with a neighbouring pair, which was one of the few pairs in our study area which did not breed that year. In the Arctic Skua, pairs from previous years are always breeding earlier than new pairs (O' Donald, 1983); a phenomenon observed in many other seabirds as well (Coulson & White, 1956; Blues & Keaty, 1978). In the Long-tailed Skua this is probably the main reason for the difference in egg laying dates in a certain area and year.

The inter-annual and inter-areal difference was correlated with snow melt conditions in different areas and years as was also found for other tundra birds (Bird & Bird, 1940; Green *et al.*, 1977; Meltofte, 1979, 1985; de Korte *et al.*, 1981.). A potential territory has to be snow-free to a minor extent (cf. Meltofte *et al.*, 1981) before it is established and before partners start to stimulate each other (de Korte, 1984). In 1974, snow disappeared very late at Kap Stewart and the few territories that became established were established as late as the middle of June. When after the middle of June, more than 90% of an extensive area was snow-covered, the last year's territories were not established at all. In the second half of June, gonads in non-breeding birds start to regress, and once regression has set in, it probably continues (figs 5 and 6). As a result the drive to

establish a territory and to gain a partner fades, probably earlier in the female than in the male since female non-breeders in general fail to reach the gonad maturity achieved by the non-breeding males (Marshall, 1952). In 1973 snow disappeared earlier at Kap Stewart than in 1974, but later than at Kaerelv in 1975 and in 1979, which were years showing similar conditions. Considering all years and areas, Gaaseelv and Ugleelv in 1975 were snow-free earliest (de Korte, 1977, 1984; Hansen, 1984).

For areas in northeast Greenland, north of Scoresby Sund, exact data about time of egg laying are scant and pertain to many different areas and years. The following is a short outline of egg laying dates derived from finds of eggs and young and from chipping and fledging dates. Scoresby Sund: first week of June to first week of July, replacements in first and second week of July (this paper, Pedersen, 1930). Scoresby Land and Mestersvig area: second week of June to first week of July (Hall, 1966; Hall & Waddingham, 1966; Smart & O'Brien, 1971; Green *in litt.*, 1974; Green & Greenwood, 1978; Boertmann *in litt.*, 1982; Newton *in litt.*, 1984). Mackenzie Bugt: second to last week of June (Kolthoff, 1903; Schaanning, 1933; Hjort, 1976; Blomquist & Elander *in litt.*, 1982). Wollaston Forland: second to last week of June (Rosenberg *et al.*, 1971). Hochstetter Forland: second to last week of June, assumed replacements in first and second week of July (Løppenthin, 1932; Pedersen, 1934; Bird & Bird, 1941; Meltofte *et al.*, 1981). Germania Land: second week of June to first week of July (Manniche, 1910; Meltofte, 1975, 1977). From these data it appears that the range of egg laying dates in different areas in northeast Greenland for the Long-tailed Skua is about the same. This was also found for different wader species in that area, and can be explained by the fact that territories more to the north in general become snow-free at about the same time as those more to the south, where temperature are somewhat higher in spring but where the tundra has a thicker snow-cover than in the relatively dry High Arctic part in the north (Meltofte, 1985). Earliest arrival dates of Long-

tailed Skuas in northeast Greenland were also similar in different places (de Korte, 1984).

In years with extremely rich food abundance and moderate or late disappearance of snow-cover, egg-laying may be well synchronized when more than 90% of first clutches are laid within a week (Schaanning, 1916; Andersson, 1971, 1976a). Due to snow-cover the earliest arrivals will not be able to (re)establish their territories earlier than the birds that arrive later and they will congregate on the few bare spots (cf. Taylor, 1974). This will facilitate synchronic territory establishment and pair formation at a time when an excess of food becomes available (cf. Meltofte *et al.*, 1981), which favours synchronic start of rapid follicular growth. Lack of experience in young adults in such years plays a less important role than in poorer years.

#### 5.4. *Brood patches*

Only territorial birds develop brood patches. Shedding of feathers on these patches starts at pair formation in both females and males. Females develop full size patches only when they lay eggs, and full size is reached at clutch initiation. Males may develop full size patches also when no eggs are produced, and in case eggs are laid, they sometimes reach full size some days after clutch completion. Early breeders develop their patches early in the season and these patches remain completely bare for two to three weeks. Late breeders develop their patches late in the season which remain completely bare for less than a week. Regression of patches in breeding birds thus is not strictly correlated with the time elapsed since the onset of breeding but it is also correlated with time of the year. In late breeders the patches start to involute about two weeks before the end of incubation, a phenomenon not reported in tropical and temperate birds (see review Drent, 1975). One may expect that in late breeders heat exchange between skin and egg is reduced compared with early breeders and that consequently the incubation period of late breeders will be somewhat longer. The

question remains whether in birds with involuting patches which lose their clutch and lay a replacement clutch, involution continues, is arrested, or is reversed.

#### 5.5. *Non-territorial birds*

Non-territorial birds on land comprised a minor part of the fifth or older calendar year males, about half of the fourth calendar year birds and all of the third calendar year birds that came to the tundra. Obviously Long-tailed Skuas pair for the first time after their third calendar year and some males as late as in their sixth calendar year. At Scoresby Sund fourth calendar year birds arrived at the same time as older birds (fig. 6) and had similar energy reserves (compare figs 6 and 11). Upon arrival their gonads were greatly enlarged compared with the regeneration period, though they tended to be somewhat smaller than in adults. Females all had oviducts developed to the stage rather swollen and twisted. When they did not pair, gonads tended to start shrinking somewhat later than in older birds, but at about the same rate as in these.

The most important factor that inhibits fourth calendar year and older birds that come to land from establishing a territory is probably inexperience in gaining a partner and a territory. They have to compete with experienced birds that mostly return to last year's territories and mates (Andersson, 1976 a; de Korte, 1984; Maher, 1970, 1974; Taylor, 1974). Experienced birds only refrain from establishing a territory when they are unable to reclaim last year's territory because of snow cover (1974). The Arctic Skua has territorial and partner attachment like the Long-tailed Skua and its age of first breeding is also the fourth calendar year, with many breeding for the first time in their fifth and sixth calendar year (O'Donald, 1983). Unlike experienced birds in the two former species, experienced birds in the Pomarine Skua do not establish territories in years with rather poor feeding conditions while in years of food abundance, a small percentage of the breeding population may consist of immature

females (Pitelka *et al.*, 1955 a, b; Maher, 1974; Taylor, 1974); a phenomenon which never has been reported for the Long-tailed Skua and Arctic Skua. The habits of the Pomarine Skua enlarge mating chances for inexperienced birds compared with the chances these birds have in the other two skua species.

The earliest third calendar year immature Long-tailed Skuas normally arrive along the ice edge in the middle of June and on the tundra in the fourth week of June and only by exception earlier (Meltofte *in litt.*, 1985). Upon arrival gonads were much enlarged compared with gonads in the regeneration period but they were significantly smaller than in arriving adults (fig. 5). In the first weeks after arrival they may, just like in adults after arrival, continue to grow somewhat but their maximum size remains much smaller than in adults. As their gonad size starts to decrease later than in adults, which was also found in immature gulls (Johnston, 1956 a b), they may have gonads of similar size in July. However, in third calendar year females oviducts were always narrow and straight while in adults they could be in any stage. Energy reserves of third calendar year birds show a great variation. In immature males highest and lowest energy reserves were of similar magnitude as the extremes in adult males (fig. 10). Probably immatures with great reserves had come directly from the sea while those with small reserves had been foraging on the tundra for quite a long time when collected. For the first two years of their lives Long-tailed Skuas normally do not come to land and forage only at sea. In their third year, when they come to the tundra, their only experience on the tundra dates from the first months of their life when they were fed and guarded by their parents. Another factor which will reduce foraging success compared with experienced birds is the fact that they are not tolerated in suitable areas which are occupied by territorial birds. The strong territorial behaviour of established pairs in June may be an important factor that keeps immatures from coming to the tundra in that month. Foraging possibilities are still restricted in June as only in the last week of

that month do insects (an important energy source for the inexperienced birds, de Korte, *in prep.*) start to emerge. In July territories are guarded less zealously and by then the immatures appear in force and join the failed breeders which roam over the tundra in small flocks. Their energy reserves may become much depleted but in this way they get experience with land life which will be of advantage in later years.

The category of birds not coming to the tundra in the breeding time consists of some adults including fourth calendar year birds, a substantial part of the third calendar year birds and most of the second calendar year birds. The adults collected at sea in spring and summer far from the breeding grounds in general had retarded moult of primaries and rectrices and had moderate energy reserves (deduced from specimens in USNM). Third calendar year immatures that spend the summer in waters south of the breeding grounds had in general moderate energy reserves (deduced from specimens in USNM). Second calendar year immatures in summer had not yet finished moult of primaries and rectrices and energy reserves were generally small. In gulls, this year class shows hardly any increase in size of gonads during the summer (Johnston, 1956 a b) and this probably holds true for the Long-tailed Skua (fig. 5). Data of this category are scant but it is likely that when birds are unable to gain a moderately high level of energy reserves at sea they do not come to the tundra.

## 5.6. *Conclusions*

The main conclusions of this study can be summarized as follows. Adult birds arrive on the tundra in breeding condition with sub-maximally enlarged testes and largest follicles enlarged to the threshold level at which rapid follicular growth may start. No direct environmental releasers are required to start this rapid growth but partner stimulation. However, rapid growth starts and continues only when the female manages to keep her energy reserves above a certain level in the pre-

egg laying period. Her body energy reserves or rate of energy loss determine whether none, one, two, or more than two eggs (replacements included) will be laid. As the birds arrive with maximal energy reserves, partner stimulation determines when rapid follicular growth will start and eggs will be laid. This stimulation may occur as soon as territories have become established. Territories become established only after the breeding area has become snow free to a certain extent.

For Kaerelv in 1975 the June snow cover was average when compared with that for other years and for other areas in Scoresby Sund. At Gåseelv and Ugleelv in 1975, snow disappeared a week or more, earlier and average date of egg laying was about four days earlier than at Kaerelv in 1975, the earliest egg laying dates in the former areas being the earliest possible for this region when arrival dates and required period of rapid follicle growth are taken into account. At Kap Stewart in 1973, snow disappeared a week or more later, and average date of egg laying was about a week later than at Kaerelv in 1975. In those two years the birds had similar clutch size and similar energy reserves at clutch initiation. At Kap Stewart in 1974, snow disappeared three weeks or more, later than at Kaerelv in 1975, and eggs were not laid at all, while energy reserves became even further depleted than in breeding birds in 1973 and 1975.

### 5.7. *Robustness of conclusions and perspective*

The conclusions drawn in this study have been derived from relatively few data and one may wonder how valid they are and whether they are of use in other circumstances. Calculations of structural size of adults was based on structural size of only five starved juveniles (males + females). The extent to which each of these five had been emaciated could have been different, which mean that not all weights, exactly indicated starving weight. There is also possibly a difference between males and females, and juveniles and adults in the way body dimensions are related to structural size. The assump-

tion that adult males as well as adult females arrive in the breeding area each year with about the same energy reserve indices and the assumed values of these indices is, especially in males, based on few data (figs 10 and 11). In several cases egg laying dates and hence days after clutch completion (figs 2, 8 and 9) were accurate to plus or minus three days only. However, the trends found were significant.

In this study I have tried to develop methods with which it would be possible to formulate conclusions and theories about energy budgets in bird species, such as the Long-tailed Skua, which by their low breeding densities and way of living, can only be caught in small numbers during the breeding time. To assess a more reliable measure of absolute structural size or starving weight in adults (as defined in methods), with sacrificing as few live birds as possible, one could capture two or three adult males and two or three adult females with relatively large differences in body dimensions (for deriving valid equations over a long range), and starve them. This method, I admit, could spoil the pleasure of doing this kind of research. This consideration holds true also for collecting birds. However if we want to know more about energy reserves prior to arrival and at arrival, some collecting is necessary because only through this method it is possible to answer the question of when the high energy reserves of the arriving birds have been accumulated. Interference with the normal course of events in the study area should be ruled out as much as possible and collecting therefore preferably should occur far from the study area. Future field work should concentrate on methods to weigh birds more frequently without disturbing them which probably could be done by placing a balance under some nests (Sibly & McCleery, 1980).

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