Development of feeding and foraging behaviour in young Ringed Plovers *Charadrius hiaticula,* in Greenland and Britain

(Med dansk resumé: Udvikling af føde og fødesøgningsadfærd hos unger af Stor Præstekrave Charadrius hiaticula *i Grønland og England)*

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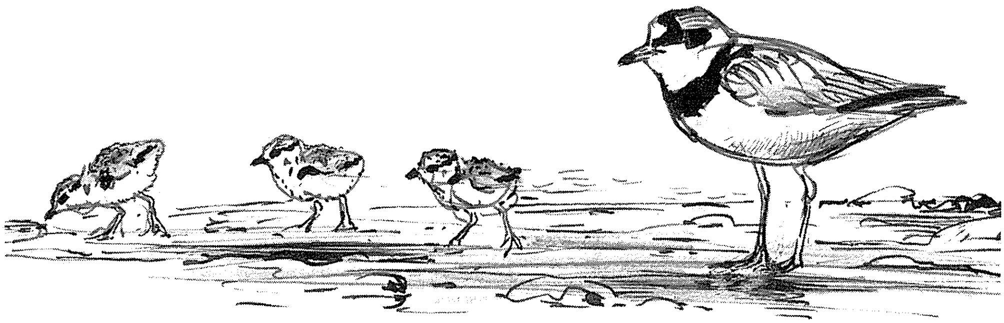

INTRODUCTION

Waders have become popular subjects for study in recent years, partly because of increasing threats to their wintering areas, and partly because of their convenience for observation while feeding on relatively simple prey communities. Unfortunately for such studies, most species become highly cryptic in the breeding season, particularly when near the nest and with young. Observations on the behaviour and feeding of the latter are generally difficult to obtain, and detailed studies are lacking, except for the Oystercatcher *Haematopus ostralegus,* which is atypical of waders in that adults feed the young (Buxton 1939, Tinbergen & Norton-Griffiths 1964, Lind 1965, Norton-Griffiths 1967, Heppleston 1972).

The aim of this study was to investigate feeding and foraging behaviour of chicks in relation to age, area, season and environmental conditions, and to see how changes in these affected growth rates and survival.

STUDY AREAS

Scoresby Land, Greenland

Observations were made from 25 June to 16 August 1974, near Statens Luftfartsvæsen, Mestersvig, (72° 14'N, 23°55'W), Scoresby Land, NE Greenland (Fig. 1.) during the Joint Biological Expedition to North East Greenland. The first young hatched on 24 July, and the first fledged just before our departure.

The detailed study area around Mestersvig station was mainly »river-bed« shingle and sparse tundra vegetation (i.e. 30-60% covered by vascular plants; organic crust of lichen covering ground between heath plants; some disturbance by frost heaving – see Green et al. 1978, Green 1978). During the study period, snow cover decreased progressively from more than 90% on 25 June to less than 10% by late July. Generally a damp zone was formed in the latest areas from which snow had melted, and also in small pools and streams. The shore of a small inlet of the sea, Noret, was ice covered

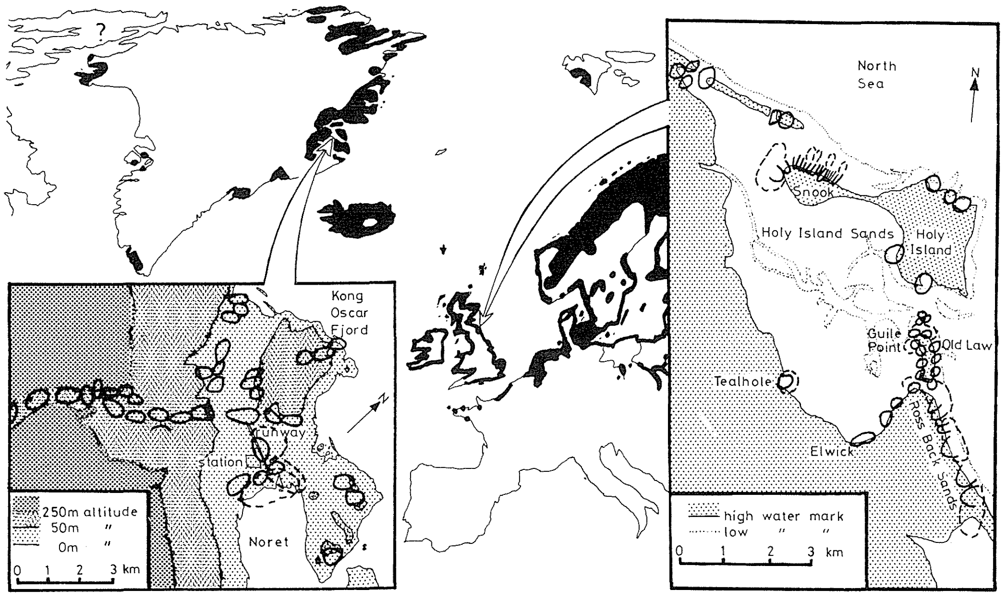

Figure 1.
Part of the breeding distribution of Ringed Plovers *Charadrius hiaticula* (based on J. Fjeldså *in litt.*) showing locations of the study areas, and inset maps of the main study areas at Mestersvig (Scoresby Land) and Lindisfarne (Northumberland). Solid lines show territories of Ringed Plovers, and dashed lines feeding ranges of some broods.
Dele af Stor Præstekraves yngleudbredelse (baseret på J. Fjeldså i litt.), der viser placeringen af de undersøgte områder. Detajlkort er indsat for undersøgelsesområderne i Mestersvig og Lindisfarne. Helt optrukne grænser viser territorier, stiplede grænser fødesøgningsområder for nogle kuld.

until mid-July, after which melt run-off and slight tidal movement gave rise to another damp zone there. The Mestersvig area has more snow and later clearance of sea-ice than many high arctic areas. Some of the other areas visited in NE Greenland had more vegetation cover, but Ringed Plovers tended to occupy the more barren areas (see Green 1978, Ferns 1978).

Northumberland, England

Studies at Lindisfarne National Nature Reserve (55°40'N, 1°50'W; Fig. 1.) and adjacent parts of the Northumberland coast took place from 1973 to 1976, but principally in 1975 and 1976.

At Lindisfarne, the Ringed Plovers breed on or near the shore. Detailed studies took place mainly around Holy Island Snook, a peninsula of sand-dunes where the breeding habitat includes sandy and pebbly beaches and lower intertidal areas. In other parts of the Reserve, some muddy areas were included, as well as exposed sandy beaches, with pronounced strand lines but little intertidal feeding area.

METHODS

Birds were watched using a tripod-mounted 15-60x telescope, at Lindisfarne usually from a hide on dunes adjacent to the shore or from a car. At Mestersvig, where the plover family parties tended to range more widely, an observer stood in the open and moved when necessary, but kept sufficiently distant so as not to cause disturbance. In the arctic continuous daylight, family parties were watched at all stages of the 24 h period. Although, at the latitude of Lindisfarne, the short summer nights are not very dark, it was not usually possible to watch family parties during the night. Some observations were made in 1976 using an image intensifier (Pienkowski 1983a).

Prey was identified from visual observations and examination of potential prey types in the areas the birds were feeding: usually the possible range was very limited. Pecking rates in Greenland were measured using a stopwatch, the numbers of identifiable items also being noted. In Northumberland, pecking rates were measured, both by this method and by using a

Figure 2.
Newly hatched Ringed Plover in a nest scrape at Mestersvig, NE Greenland, 1974.
Nyklækket unge af Stor Præstekrave ved Mestersvig i Nordøstgrønland 1974.

continuously running tape-recorder to record, additionally, times for each foraging behaviour and distances moved, as described by Pienkowski (1983a). Using frame-by-frame analysis of ciné-film, Pienkowski (1982, 1983a) found that prey indentifications, and estimates of rates of taking prey, by these methods were valid for adult birds. Furthermore, at least 88%, and probably 98%, of pecks resulted in a prey item being taken. Similar checks using ciné-film were carried out for chicks, the youngest for which suitable short-range ciné-film was available being about one week old. Here, at least 89% of pecks resulted in a prey item being taken. There are, however, indications that some younger chicks may be less successful (see below).

During observations, note was kept of weather conditions, including air temperature at ground level, wind force and direction, and rainfall. In Greenland, these were supplemented by records from the meteorological station, which was within the study area.

In both study areas, as many chicks and adults as possible were marked with individual combinations of colour rings.

TERMINOLOGY

Plovers feed mainly in a very characteristic manner. The bird stands still for a time, before running rapidly to peck at prey, or to a new waiting position. The durations and rates of occurrence of the various components of foraging behaviour vary in different circumstances, but the distinctive »stop-run-peck« pattern remains (see Burton 1974, Pienkowski 1981a, 1983a for more details). While waiting, an upright stance, with head higher than body (termed here »up«), is usually adopted. Occasionally, the body may be tilted downwards, with the head pointing towards the ground (»down«). »Waiting time« is the time spent in one of these waiting positions, before pecking at a prey item. »Giving-up time« is the time spent in such a position before moving to a new waiting position without making a peck. Once a pecking movement was started, it was generally completed (i.e. the bill made contact with the ground or prey). Occasionally, however, the pecking movement was stopped before reaching the prey; such movements are termed »aborted pecks«. The time to move to a prey, capture and swallow it, and resume a waiting position is the »handling time«.

Table 1. Summary of prey of chicks and newly-fledged young identified during field observations at the North Shore of Holy Island Snook, Northumberland.
Stor Præstekraves ungers byttedyr identificeret ved feltobservationer ved nordkysten af Holy Island Snook, Northumberland.

Age of chicks (days)	0	1	2	3	4	5	6	7	9	10	15	16	20	22	24	26	28	31	40
Total pecks	57	794	206	266	9	928	70	405	68	372	962	23	261	211	72	105	33	20	35
Thin red worms	0	0	2	0	0	6	16	0	4	8	9	0	4	6	3	19	3	0	0
Arenicola[1]	0	0	0	0	0	1	0	0	0	5	5	0	0	2	0	12	0	0	0
Sandhoppers	–	–	–	–	–	59	–	–	–	57	16	16	73	59	–	–	–	5	–
Small flies	–	–	–	–	–	23	–	–	–	24	167	4	–	71	–	–	–	–	–
Blowfly	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–
Hydrobia	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	2	–	–	–
Unidentified small prey	–	–	22	11	–	266	7	14	5	91	339	3	152	59	9	58	7	15	35
Pecks of unknown outcome	57	794	182	255	9	571	47	391	59	187	421	–	32	14	60	14	23	–	–
Unsuccessful pecks	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–

Note 1: *Arenicola* taken included worms of approximate length up to the height of the bill from the ground (about 5 cm at first, increasing to about 8 cm at fledging). One bill-height *Arenicola* taken at 15 days was not swallowed. Five *Arenicola* were seen to be taken from the substratum tail-first (and were therefore probably at the head of their tail shaft while defaecating – see Smith 1975), and one head-first.

RESULTS

Development

The growth rates of Ringed Plover chicks are reported by Pienkowski (1984a). Detailed studies of the development of body organs were not made, although a few dead chicks were examined. Those parts of the body associated with self-feeding, including legs, eyes, bill, gizzard, intestine and liver, were large and well developed at hatching. The downy plumage was cryptic (see Fjeldså 1977), and also apparently adapted to absorb radiant heat (Keskpaik et al. 1970). Flight feathers and pectoral muscles developed late, wing feathers (allowing fluttering escape flight) preceding tail feathers. This is as would be expected from the life style of the precocial, self-feeding young.

Prey composition

The prey taken by Ringed Plover chicks, and fledged young of known age, at Holy Island Snook are detailed in Table 1. Some of the variation displayed in the table is undoubtedly due to variations in viewing conditions, such that prey were less identifiable on some days. However, the high proportion of pecks with unknown outcome in very young chicks, particularly on the day of hatching and that following, suggests that a high proportion of pecks at this age were indeed unsuccessful, or that only very small prey were taken. Sandhoppers *Talitrus saltator* and small flies, mainly *Coelopa,* were the main prey identified from the fifth day after hatching onwards. These probably formed most of the unidentified prey taken even before this time (and fragments of flies were also found in some droppings examined). However, intertidal invertebrates were also taken, thin worms being noticed from two days after hatching, *Arenicola* from five days, and *Hydrobia* occasionally. Although all *Arenicola* and many thin worms would have been identifiable, many smaller items probably were not. Feeding locations and methods suggested that other prey included small Crustacea (amphipods and isopods).

Comparison with prey taken by parent birds in the same area (Table 2 and Pienkowski 1980) is difficult, since work was concentrated on the young. There was clearly great overlap in range of prey types taken, although adults appeared to take a wider range, and possibly a slightly higher proportion of intertidal prey.

Fewer data are available on prey of chicks from sites at Lindisfarne outside the main study area at the Snook. Items taken from thick algal beds between clumps of *Spartina,* at Tealhole, appeared to include large insect larvae and pupae. Many of the items taken on the sea-beaches at Ross Back Sands and Old Law were thought to be sandhoppers and small flies. The gizzard of one small chick found dead above the mud-flats at Elwick on 30 June contained fragments of at least 8 *Hydrobia,* 74 mandibles of *Nereis,* several fragements of vegetable matter and grains of sand and small stones. *Hydrobia* and *Nereis* are both abundant in this area. Fledged young, aged 28 to 72 days, on Holy Islands Sands or off Guile Point, took

Table 2. Summary of prey of fully grown Ringed Plovers identified during field observations at the North Shore of Holy Island Snook during the breeding season.
Stor Præstekrave, voksne individers byttedyr identificeret ved feltobservationer ved nordkysten af Holy Island Snook i ynglesæsonen.

Month	March	April	May	June	July	August
Aborted pecks	0	0	0	0	1	1
Total pecks	1201	1319	242	187	421	731
Prey of which all sizes should be visible:						
Arenicola (whole)	2	5	1	0	7	18
Arenicola (tails)	5	4	1	0	0	0
Crabs	0	0	0	0	1	0
Algae	5	6	1	0	1	2
Prey of which not all sizes visible:						
Thin worms (principally *Notomastus*)	240	111	19	9	41	55
Mollusca (*Macoma, Hydrobia, Littorina*)	0	1	0	0	2	0
Other Crustacea (non-crab)	0	21	1	0	0	0
Sandhoppers	0	0	0	0	1	1
Flies	0	3	0	0	2	4
Successful pecks: prey not identified	144	554	122	85	188	224
Unsuccessful pecks	0	1	0	0	0	0
Pecks of unknown outcome	805	613	97	93	178	427

thin red worms and small, unidentified prey, as did adults there (Pienkowski 1982).

The outcome of pecks made by chicks and adults at Mestersvig are detailed in Table 3. Again great variation is apparent, due to varying observation conditions on different days. On some days it was clear that most prey were very small adult Diptera (mainly Nematocera – midges, gnats, mosquitos, etc.), which were taken off the sand, soil or vegetation surface, or occasionally in flight. Examination of feeding sites suggested that these very abundant items were the main prey at other times also. Other fairly common prey identified were spiders (Aranea) and large items, probably large insect larvae, including Lepidoptera.

Prey of adults at this time appeared to be fairly similar. Earlier in the season, probably fewer adult insects were taken (fewer had emerged), and possibly more spiders. Examination of feeding sites indicated that some of the small items taken in late June and July were dipteran larvae (again mainly Nematocera). Examination of droppings of chicks and of gizzard contents of seven adult Ringed Plovers, collected in the same area by R.W. Summers and G.H. Green, supported this general assessment of diet.

Feeding rates

The chicks began pecking almost as soon as they left the nest but at a very low rate (see below). Feeding behaviour, which developed rapidly, was mainly the stop-run-peck type of movement, typical of plovers (p. 135), but during rapid feeding on abundant small prey, particularly in Greenland, the »run« element was almost eliminated.

At Mestersvig, the total pecking rate increased significantly with increasing age of chick (Fig. 2.) and air temperature (Fig. 3.), and decreasing rainfall (Table 4.). These relationships were paralleled by the variations in rates of taking identified insects, observed prey, and

Table 3. Summary of prey of chicks and adults identified during field observations at Mestersvig.
Byttedyr hos unger og voksne identificeret ved feltobservationer ved Mestersvig.

											Adults	
Age (days)	0	2	3	7	9	11	12	16	17	21	Jul.	Aug.
Total pecks	107	173	361	1447	1736	447	522	235	1935	3858	2010	891
Spiders	–	–	–	2	1	1	7	3	2	–	26	4
Large caterpillars	–	–	–	2	–	22	6	5	12	–	2	–
Small flies	–	–	–	–	–	25	–	–	646	2	158	335
Small unidentified	22	–	16	148	3	58	117	53	83	1923	128	285
Pecks of unknown outcome	85	173	345	1295	1732	341	392	174	1192	1933	1696	267

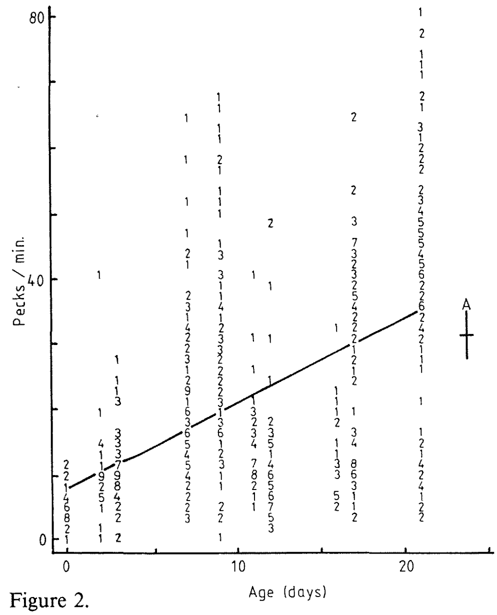

Figure 2.
Rate of pecking by chicks at Mestersvig (Greenland) in relation to age. Numerals indicate number of coincident points. Fitted regression line is y=1.30x + 8.00 (r=0.49; P ⟨ 0.00001). Mean value (± 1 standard error) for adults in the same area indicated at »A«.
Fødesøgningsbevægelser hos kyllinger ved Mestersvig i relation til alder. Tallene viser antal sammenfaldende punkter. Regressionslinien har ligningen y=1,30x + 8,00 (r=0,49. P ⟨ 0,00001). Gennemsnitsværdien ± 1 standardafvigelse fra middeltallet) for voksne i det samme område er vist med »A«.

pecks of unknown outcome (Table 4.). These parallels resulted from the predominance in the diet of small flies throughout the period.

At Lindisfarne, total pecking rate did not vary linearly with chick age (Tables 5, 6). However, this numerical measure appears to hide considerable variation, due to the more varied diet in terms of both species and size. Rates of taking observed prey (i.e. all pecks seen to be successful), of taking *Arenicola,* and of taking thin worms all increased with increasing chick age and decreasing wind force, whereas rates of pecking with unknown outcome (in the main, small prey or failed pecks) varied in the opposite direction (Tables 5, 6.). Rain also tended to depress feeding but, as birds tended also to stop feeding during rain, the sample was too small to give significant results with individual prey types. Air temperature seemed to have little effect on feeding rate. Diurnal temperature variation had a strong influence on pecking rate at Mestersvig but, at Lindisfarne, the fluctuations in temperatures occur around much higher levels and did not appear to influence pecking rate (Pienkowski 1980, 1984a).

Because of the overwhelming predominance of one type of prey (the very small flies) in the diet at Mestersvig, and the record of time spent feeding throughout 24 h periods (Pienkowski, 1984a), it is possible to make an estimation of the minimum energy intake of chicks at this site (Table 7.). All pecks were assumed to result in a prey item being taken (p. 135) and all prey items were assumed to bee small flies of an estimated calorific value of 0.8 cal each. Other items were seen to be taken (Table 3.), and the calorific contents of spiders and crane-flies are, respectively, more than 30x and more than 100x that of small flies (Greenwood 1974a, present study). Thus, the effect of the

Table 4. Correlation coefficients between feeding rates of Ringed Plover chicks and age and environmental conditions at Mestersvig, Scoresbyland. For significant relationships, the correlation coefficient is given and the level of significance (P ⟨ 0.05, ⟨ 0.01, ⟨ 0.001) indicated after it by 1 to 3 asterisks. For those relationships which remained significant in multiple regression analysis, significance levels in that analysis are indicated before the coefficient. – indicates those correlations which were not statistically significant (P ⟩ 0.05).
Correlationscoefficienter mellem fødesøgningsrate hos unger af Stor Præstekrave samt deres alder og forskellige vejrfaktorer ved Mestersvig, Scoresbyland. For signifikante correlationer er correlationscoefficienten opgivet, og signifikansniveauet (P ⟨ 0,05, ⟨ 0,01, ⟨0,001) er angivet med en til tre stjerner efter tallet. For de correlationer, som også var significante i en multibel regressionsanalyse, er signifikantsniveauet herfor angivet foran correlationscoefficienten. – betyder at correlationen ikke var statistisk signifikant (P ⟨ 0,05).

Rates of:	Total pecks	Taking observed prey	Pecks of unknown outcome	Taking small prey	Taking insects
Age	***0.49***	***0.41***	*0.13**	***0.37***	0.14***
Air temperature	0.36***	**0.19***	***0.21***	***0.12**	0.17***
Wind force	–	–	**–0.09**	–	–
Rain	*–0.08*	–0.09*	–	–	–
Cloud cover	–	–0.22***	*0.20***	–0.20***	–0.09*

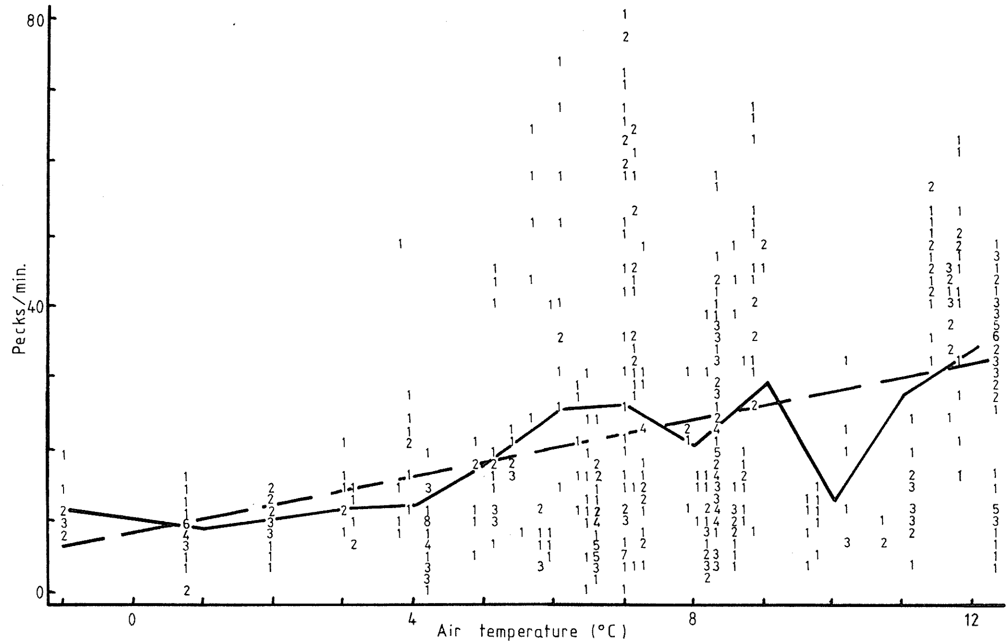

Figure 3.
Rate of pecking by chicks at Mestersvig in relation to air temperature. Solid line joins means for each C°. Dashed line is fitted regression, y=1.95x + 8.12 (r=0.36; P ⟨ 0.00001).
Fødesøgningshastighed ved Mestersvig i relation til lufttemperatur.

Table 5. Correlation coefficients between feeding rates of Ringed Plover chicks and age and environmental conditions on the North Shore of Holy Island Snook, Northumberland. Arrangement as for table 4.
Correlationscoefficienter mellem fødesøgningsrate hos unger af Stor Præstekrave samt deres alder og forskellige vejrfaktorer ved nordkysten af Holy Island Snook, Northumberland. Forklaring til tallene som i tabel 4.

Rates of:	Total pecks	Taking observed prey	Pecks of unknown outcome	Taking small prey	Taking thin worms	Taking Arenicola	Making aborted pecks[1]
Age	–	***0.46***	*–0.16**	***0.42***	***0.22***	0.36**	–
Air temperature	–	*0.16*	–	*0.16*	–	–	–
Windforce	–	–0.39***	***0.24***	–0.35***	–0.30***	**–0.31***	–
Rain	–0.15*	–	–	–	–	–	0.11*
Cloud cover	–	–0.16**	–	–0.16**	–	***0.14*	–

[1]Aborted pecks involve movements of the head and bill towards the ground, as for a peck, but stopped before the substrate is reached.

Table 6. Correlation coefficients between feeding rates of Ringed Plover chicks and age and environmental conditions at Lindisfarne away from the North Shore (Northumberland). Arrangement as for table 4.
Correlationscoefficienter mellem fødesøgningsrate hos unger af Stor Præstekrave ved Lindisfarne. Forklaring til tallene som i tabel 4.

Rates of:	Total pecks	Taking observed prey	Pecks of unknown outcome	Taking small prey	Taking thin worms	Taking Arenicola	Making aborted pecks[1]
Age	–	**0.37**	–	***0.37***	*0.21***	0.18**	–
Air temperature	–	–0.47**	0.49**	–	–	–	–
Windforce	–	***–0.34**	***0.41***	***–0.36***	–0.19***	–0.20***	–
Rain	–0.12*	–	–0.12*	–	–	–	0.10*
Cloud cover	–	–	–	–0.17**	–	–0.17*	–

Table 7. Estimated minimum energy intake per 24 hours of chicks at Mestersvig.
De anslåede minimumsværdier for indtagelse af føde pr. døgn hos unger af Stor Præstekrave ved Mestersvig.

Age (days)	Mean no. of pecks/min	% of 24h spent feeding	Mean no. pecks taken per 24h	Energy ingested/24h (kcal)	Mean weight of chick (g)	Basal Metabolic Rate (kcal/24h) (from Keskpaik et al. 1970)	Intake as multiple of BMR
0	8.0	23	2650	2.1	8	1.4	1.5
7	17.1	29	7140	5.7	19	4.8	1.2
9	19.7	55	15600	12.5	24	6.0	2.1
11	22.3	59	18950	15.1	29	6.6	2.3
16	28.8	68	28200	22.6	41	9.3	2.4
17	30.1	67	29040	23.2	44	10.0	2.3
21	35.3	74	37620	30.1	54	12.3	2.5

Note: See text for discussion of limitations of these estimates.

latter asumption considerably outweighs the former, so that the energy intake figure obtained is an underestimate. Using values of Basal Metabolic Rate (BMR) for chicks of various ages obtained experimentally by Keskpaik et al. (1970), Table 7. estimates the minimal total energy intakes as multiples of BMR. This gives a value of 1.2 – 1.5 in the first week after hatching, rising to 2.1 on day 9, and stabilizing at 2.3 – 2.5 from day 11. While bearing in mind that these digures are probably underestimates, it is noteworthy that the values reach a relatively high level, and stabilize, around the time that the young become largely thermally independent, and when brooding by parents is much reduced (Pienkowski 1984a).

Foraging behaviour

Both waiting and giving-up times of chicks at Lindisfarne increased with age of chick (Table 8.), as did the frequency of »successful« pauses (»up« followed by »peck«). The frequency of »unsuccessful« pauses (»up« followed by »run« to another »up«) fell with increasing age (Fig. 4.), as did the frequency of »downs«. »Handling time« did not vary with age, although size of prey taken did tend to increase with age (see above). Number of paces (both to move position and to take prey) showed no significant trends with age or weather conditions, possibly due in part to small sample size. However, there was an increase in pace-length, from about 6 cm shortly after hatching to about 10 cm when fully grown (measured from tracks of young of known age).

Increasing windforce was associated with decreasing waiting time in the »up« position but with increasing rate of »unsuccessful« pauses. Despite the small number of observations during rain, the rate of »successful« pauses decreased with increasing rainfall, and the rate of »abortive pecks« increased. With increasing cloud cover, both »waiting« and »givingup« times decreased, and rates of »unsuccessful« pauses and »downs« increased. There were no

Table 8. Foraging behaviour of Ringed Plover chicks at Lindisfarne (Northumberland) in relation to age and environmental conditions. Arrangements as for Table 4.
Fourageringsadfærd hos unger af Stor Præstekrave ved Lindisfarne (Northumberland) i relation til deres alder og forskellige vejrfaktorer. Forklaring til tallene som i tabel 4.

	Age of chick	Air temperature	Windforce	Rain	Cloud cover
Giving-up time	0.23***	–	–	–	–0.21**
Waiting time	**0.19**	–	–0.20**	–	–0.24***
Rate of »unsuccessful waits« ('up' followed by 'run' to another 'up')	***–0.57***	–	0.22***	–	*0.30***
Rate of »successful waits« ('up' followed by peck with or without intervening run)	0.16*	–	–	–0.13*	–
Rate of 'downs'	–0.26***				0.12*
Handling time	–	–	–	–	–
Number of paces run to new 'up' position	–	–	–	–	–
Number of paces run to take prey	–	–	–	–	–

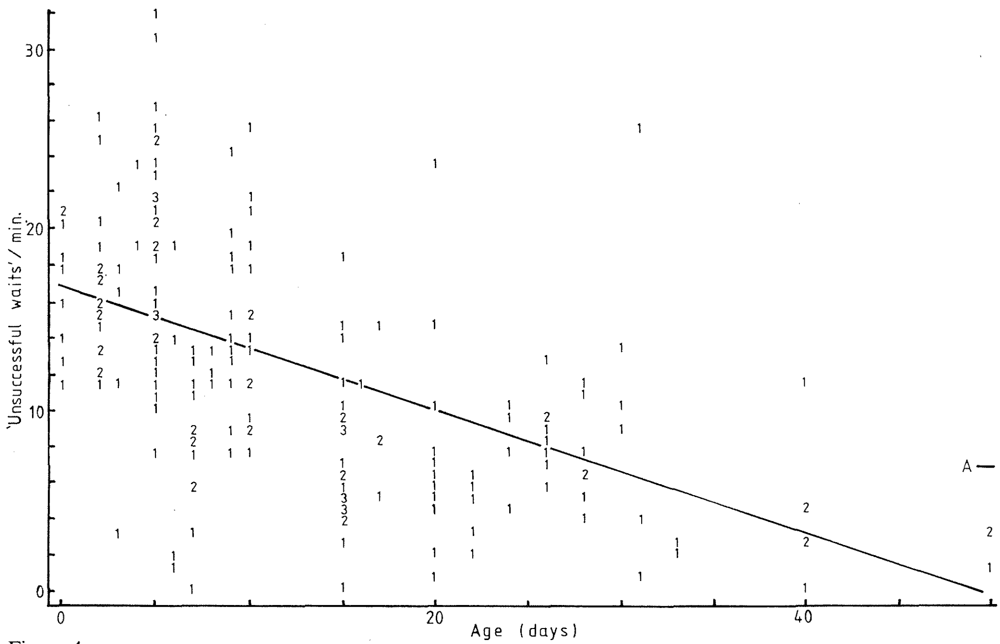

Figure 4.
Rate of »unsuccessful waits« (»up« followed by »run« to another »up«) by young at Lindisfarne, in relation to age. Fitted regression line is y=16.46 – 0.35x; (r=–0.57; $P < 0.00001$). Mean value for adult birds in the same area indicated at »A«.
Mængden af stop under fødesøgningen der ikke har før til byttefangst i forhold til ungernes alder ved Lindisfarne. Regressionslinien har ligningen y=16,46 - 0,35x. (r= - 0,57. P⟨ 0,00001). Gennemsnitsværdien for voksne fugle i det samme område er markeret med »A«.

significant relationships with temperature, but this was mainly above 12°C. Foraging behaviour of adults is considered by Pienkowski (1981b, 1983a).

The use of foot-vibration, apparently to stimulate the activity of some prey (particularly small Crustacea) and thereby increase their availability, is described by Pienkowski (1983b). In the breeding areas at Lindisfarne, foot-vibration was recorded in a 10-day old chick and in another around fledging time. These were the only recorded occurrences in chicks, compared with 164 observations of foraging without the use of foot-vibration. In contrast, foot-vibration was frequent in parent birds (35 cases with foot-vibration; 134 without) in the same areas over the same period. These differences were significant ($x^2_1 = 19.8$, $P < 0.001$). Foot-vibration was not recorded in adults or young at Mestersvig. The lack of foot-vibration in the foraging by chicks in both areas may be due to the predominance in the diet of Diptera, the detection and capture of which are unlikely to be aided by such behaviour.

Feeding by fledged young

The feeding behaviours of fledged young and older birds, at Lindisfarne from late summer onwards, are compared in Table 9. In August and September, the only significant difference detected was a higher incidence of »downs« in young birds (as tended to occur also in unfledged chicks). In October-November the rate of pecking (and rate of »ups«) was significantly higher in adults than young. In December-February, although pecking rates were similar, there was some indication that prey taken by juveniles tended to be smaller. No significant differences were apparent in March-May.

DISCUSSION

Diet, prey and precociality

Pienkowski (1984a) argued that food supply was not limiting growth rate or chick survival in the present study. This was based on the constancy of growth rates observed, the abundance of available prey, the »unused« potential feeding time at times of the day when feeding

Table 9. Comparison of foraging between Ringed Plovers in their first year and older birds at Lindisfarne, Northumberland. Comparisons between age groups were made, for each season, of the following rates: of making pecks, of taking small prey, of taking thin worms, of taking Arenicola, of assuming 'up' positions, of assuming 'down' positions. Only the following comparisons showed statistically significant differences (data for March to May gave none):
Sammenligning af fouragering hos Store Præstekraver i deres første leveår og hos ældre fugle ved Lindisfarne, Northumberland. Sammenligning mellem de to aldersgrupper blev i hver sæson gjort for følgende faktorer (opgivet som antal pr. minut): fourageringsforsøg, små byttedyr, små orme som byttedyr, Sandorme som byttedyr, pauser under fourageringen med næbbet henholdsvis opad eller nedad. Kun de følgende sammenligninger viste statistisk signifikante forskelle (data fra perioden marts til maj viste ingen forskelle):

Rate (min^{-1})	Juvenile[1]	Student's t (P)	Post-juvenile[1]
August			
'Downs'	1.30±0.19 (65)	5.17 (⟨0.001)	0.26±0.08 (87)
September			
'Downs'	0.67±0.18 (40)	2.10 (0.039)	0.23±0.11 (38)
October/November			
Total pecks	13.88±0.65 (57)	2.30 (0.023)	16.38±0.87 (62)
'ups'	16.93±1.16 (57)	2.16 (0.033)	20.46±1.16 (62)
December to February			
Small prey taken	5.93±1.24 (21)	2.47 (0.014)	3.11±0.36 (188)
(total pecks	13.84±1.92 (21)	(n.s.)	14.38±0.65 (188)

[1]Given as mean ± standard error (sample size)

was apparently profitable, and the fact that those chicks that did not survive were probably lost to predators and not by starvation.

Apart from some weather-induced reductions in availability (see below), food appeared to be superabundant in both of the present study areas. The young clearly did not require particular types of prey: whilst small flies were undoubtedly the most typical component, small spiders, sandhoppers, insect larvae, small intertidal worms and small intertidal snails were important prey in some situations. Although parent birds appeared to take a wider range of prey than chicks, there was undoubtedly great overlap between the diets of the two age-classes.

Most waders never receive food from their parents, and thus must be able to feed effectively by the time that the yolk reserve is used up (within the first few days). This may be possible only in areas of superabundance of obvious mobile prey, in most cases adult Diptera. In arctic areas, the locations of such superabundance may vary rapidly; they may coincide, for example, with the wet areas which accompany the receding snow melt in NE Greenland. This reinforces Holmes' (1966) suggestion that precociality may be particularly advantageous in the Arctic, in that the young are able to move, sometimes long distances, to locally favourable feeding sites. The extent of such movements at Mestersvig may be atypically small because of the proximity of good feeding areas on the shore. More generally, this movement may be even more marked in Ringed Plovers than in some other species, as they nest on the barren gravels which are the first to dry out. This adaptation to early movement away from the nesting site allows the wide breeding distribution in NE Greenland, where Ringed Plover is the commonest wader.

The »off-duty« adult tended to feed a little distance (rarely more than 100 m and usually much less) from the rest of the family. This was probably not to avoid prey depletion, since birds and most prey animals were mobile. It may, however, have reduced immediate interference in feeding, and provided a vantage point away from the brood, from which to detect potential predators and give alarm calls (cf Lenington 1980). Young tended to feed further apart from each other, and from the attendant parent, as they grew older. It is not known whether this was to avoid interference, or simply the result of greater mobility. At Mestersvig, migrant juveniles tended to approach persistently broods of chicks, and to attempt to feed near them, but were continually chased away by the parents, as were other waders.

Unlike many other species of arctic-breeding waders, both parent Ringed Plovers tended to stay with their young until after these had fledged (Pienkowski 1984a). This may be because, in the fairly open habitats used by this species, protection by both adults is very advantageous, as suggested above. Both this adult behaviour and the high degree of precociality in the chicks may also be important in temperate breeding areas, more disturbed by predators and humans (see also Pienkowski 1984b).

As in Spotted Flycatchers *Muscicapa striata* (Davies 1976) and Sandwich Terns *Sterna sandvicensis* (Dunn 1972), the improvement in foraging performance appeared to be the result of growth and experience, rather than of copying from adults, unlike the Oystercatcher *Haematopus ostralegus* (Norton-Griffiths 1969) and Ring Dove *Streptopelia risoria* (Wortis 1969).

Development of foraging behaviour and energetic independence, and the effects of weather

The rapid increase in foraging success during the first days after hatching may be related to an improving ability to recognise suitable cues or to greater selectivity, or both. The constancy of »handling time«, despite increasing prey size, indicates progressive improvement in handling ability with age. Similarly, the number of paces moved to take prey did not change, despite an increase in pace length, so that the range at which prey were taken must have increased. The decreasing frequency of »down« waiting positions with age may reflect an increasing ability to react to cues rapidly from a distance, without the need for a »second look«. The increased »waiting« and »giving-up« times suggest increasing selectivity (see Pienkowski 1983a).

Food intake appeared to be less than energy expenditure in the first day or two after hatching, as weight fell in this time and yolk reserves were used up (Pienkowski 1984a). However, weights recovered from about the third day (present study, and Keskpaik et al. 1970). The changes, with age, of the estimated daily intakes agree with this (Table 7.). The feeding rate, in Greenland, showed a relationship with temperature and rain (Table 4.); this matched variation, with temperature and rain, in the activity of the prey animals (Greenwood 1974b, 1978). At Lindisfarne, temperatures, which were generally higher than in Greenland, did not influence feeding rate, but this was depressed by rain and strong winds. This was probably due to the depression of activity of flies by rain and wind (personal observations), or reduction in the efficiency of foraging movements (Table 8 & Pienkowski 1981b). Therefore, feeding rate appeared to be limited in adverse weather conditions by prey availability. Presumably, exceptionally adverse weather could be particularly critical in the first few days after hatching (see Meltofte 1976). As discussed earlier, however, losses due to inadequate food supply throughout the rest of the pre-fledging period seem unlikely in the present study areas. This is because excess feeding time was generally available, prey abundant, and strongly adverse weather conditions rare.

Not surprisingly, feeding activity was concentrated at the times when feeding rates were highest, and so varied with weather conditions (Pienkowski 1984a). The effect of temperatures resulted in a strong diurnal pattern at Mestersvig. This could mean that the birds optimise their feeding by learning a diurnal pattern which matches variations in prey availability. However, in view of the large day-to-day variations in the pattern, a more direct response to temperature or prey availability seems more likely. At Lindisfarne, the nocturnal peaks of activity (Pienkowski 1980, 1983b) of sandhoppers and some intertidal invertebrates, included in the diet, probably compensated for the depression in insect activity then. This may account for the lack of a diurnal rhythm in foraging activity at Lindisfarne.

Post-fledging and winter feeding

By the time of fledging, feeding rates and foraging behaviour of young were very similar to those of adults, and this remained true throughout the early autumn (Table 9.), although young birds tended to feed for longer, presumably as growth continued (Pienkowski 1982).

On the wintering grounds, as adverse weather conditions develop in autumn and winter, food demands increase and prey becomes less available, often being detectable only by brief, subtle cues (Pienkowski 1981a,b, 1982, 1983b). At these times, differences, between adults and juveniles, in feeding ability were revealed again (Table 9). There is evidence that juvenile waders, of some species, occur on their first autumn migration mainly in different habitats to adults; or that they may roost on the fringes of main flocks, or in smaller roosts (Pienkowski 1975, Pienkowski & Dick 1976, W.J.A. Dick unpublished). It is not known if this is due to exclusion of the young birds by competition or aggression of the adults.

Table 10. Comparison of feeding observations made at Holy Island Sands in October between Ringed Plovers which left Lindisfarne for the winter and those which stayed. Given as mean ± s.e. (n).
Sammenligningen af observationer af fouragering mellem de Store Præstekraver, der forlod Lindisfarne om vinteren og de, der forblev på stedet. Observationerne er gjort ved Holy Island Sands i oktober og er angivet som gennemsnit ± standard error, antal i parentes.

	Leavers	Probability level of t test	Stayers
Total time of observations (min	34		44
Total pecking rate (min^{-1})	13.5 ±1.0 (20)	0.163	15.5±1.0 (22)
Estimated rate of taking thin worms (min^{-1})	8.3 ±0.6 (20)	0.084	9.7±0.6 (22)
Estimated rate of taking unidentified prey (min^{-1})	0.11±0.09(20)	0.040*	0.97±0.38(22)
Estimated rate of taking small items (min^{-1})	3.6 ±1.2 (20)	0.016*	0.3 ±0.1 (22)
Rate of making pecks of unknown outcome (min^{-1})	7.1 ±1.0 (20)	0.004**	11.5 ±1.0 (22)
Rate of successful waits (ups followed by pecks with or without intervening run) (min^{-1})	12.4 ±0.7 (15)	0.071	15.3 ±1.3 (16)
Rate of unsuccessful waits (up followed by run to new up) (min^{-1})	4.9 ±0.6 (15)	0.421	5.6 ±0.6 (16)
Mean 'giving up time' (sec)	2.3 ±0.2 (15)	0.513	2.2 ±0.2 (16)
Mean 'waiting time' (sec)	2.1 ±0.1 (15)	0.061	1.9 ±0.1 (16)
Mean 'giving up' or 'waiting' time (sec)	2.2 ±0.1 (15)	0.050*	1.95±0.1 (16)

Weights of juvenile Ringed Plovers tend to be lower than those of adults during the winter (Eades & Okill 1976, McGregor & Jones 1979). This may be because they are not yet fully grown, but could also be due to an inability to maintain condition (see Evans & Smith 1975, Pienkowski et al. 1979, Dick & Pienkowski 1979, Pienkowski 1981a, 1982, Davidson 1981).

Poorer feeding performance, in many cases limited to periods of food scarcity, by juveniles as compared to adults, as well as instances of subordinancy in aggressive encounters, have been recorded in, e.g., Turnstones *Arenaria interpres* (Groves 1978), Sandwich Terns *Sterna sandvicensis* (Dunn 1972), Cattle Egrets *Ardeola ibis* (Siegfried 1971, 1972), and Brown Pelicans *Pelecanus occidentalis* (Orians 1959). This may be the reason for higher mortality of juveniles during unfavourable seasons (e.g. Recher & Recher 1969, Murton et al. 1971). In Oystercatchers, young birds may take three years to become as efficient as adults at feeding on Mussels *Mytilus edulis* (Norton-Griffiths 1967, 1969). Annual survival of juvenile Ringed Plovers (59%) was lower than that of adults (80%) (Pienkowski 1984a), but it is not known if this varies in relation to harshness of conditions.

The period in late autumn and winter, when differences in foraging between age categories of birds could be detected (implying difficulty in feeding for at least some juveniles), coincided with the period when most of those birds which left Lindisfarne for part of the year were absent (Pienkowski 1984a). Why some individuals stay and others leave is, however, unknown. It is known that differences have occurred even within a brood: from one brood of three, two stayed for the winter (and at least one for the following winters also) and one was not seen between mid-October and early March.

The possible advantages to staying may be:

1. Young birds do not have to learn suddenly to feed in a new type of habitat or on a new type of prey. Young waders, newly arrived in early autumn in NW Africa, were frequently seen trying to feed in unsuitable situations (Pienkowski 1975, Dick 1976, Dick & Pienkowski 1979). Resident Ringed Plovers may even learn the cues given by potential winter foods before fledging, as at Lindisfarne.
2. Apart from habitat differences, the birds do not have to learn the characteristics and geography of particular new sites, e.g. the locations of good feeding areas.
3. Young and inexperienced individuals are not subject to the risks of migration, and the need to feed sufficiently to deposit fat reserves for this. (Also, this may allow the raising of extra broods in the partly sedentary populations in the south of the species' range).
4. The birds do not have to fit their moult into a migration schedule (cf Pienkowski et al. 1976).
5. Resident birds are present to take up territories as soon as conditions are suitable.

The main disadvantage appears to be that birds are subject to a harsher winter climate, and consequent lower prey availability, than those which move. Perhaps the average risks and benefits of the two behaviours are fairly similar at Lindisfarne, or vary in a frequency-dependent way, so that both co-exist. Feeding observations are available in October (the last month when many potential migrants were present) from three colour-ringed individuals known to have stayed at Lindisfarne (22 observation sessions totalling 44 min), and 13 believed to have departed later that autumn (20 totalling 23 min). These suggest some possible differences in feeding rates and behaviour (Table 10), but probabilities border on the 5% significance level. Individuals which were to stay possibly pecked more frequently than those which departed, and took more worms. More of the pecks by departers were of small prey (P = 0.016), whereas the stayers took more unidentified prey (which tended to be larger than »small items«) (P = 0.04), and made more pecks of unknown outcome (P = 0.004). Both the mean »waiting time« and mean »giving-up time« of stayers tended to be shorter than those of departers, and the stayers may have had more »successful waits«. If real, these differences could mean either that stayers were detecting more prey or that they were less selective. The suggested differences in rates of prey taken imply the former to be more likely. Thus, these data are compatible with the idea that those birds which stay at Lindisfarne are the better feeders; but the data are inadequate to test this critically, and further work is needed.

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Ringed Plover chick foraging on sandy shore amongst casts of *Arenicola,* Lindisfarne, July 1976.
Stor Præstekrave unge der fouragerer på en sandet kys imellem ekskrementhobe fra Sandorme. Lindisfarne juli 1976.

SUMMARY

The food and foraging behaviour of Ringed Plover chicks were studied in 1974 at Mestersvig, NE Greenland, and from 1973 to 1976 at Lindisfarne, NE England. Post-fledging feeding was also investigated for the Lindisfarne population.

Small Diptera were the main prey, both in the tundra study area in Greenland and on the sea-shore at Lindisfarne, where sandhoppers and a wide range of intertidal invertebrates were also taken. At Mestersvig, pecking rates increased with air temperature (and therefore decreased at night) and decreasing rainfall, probably due to similar variations in prey activity. At Lindisfarne, temperatures were higher and apparently did not influence feeding rates, but the latter were depressed by high winds and rain, via effects on prey availability and the efficiency of foraging behaviour. Foraging performance and calorific intake rate increased with age. The early development of effective self-feeding, and high mobility of the chicks in response to changes in areas of prey abundance, together with the guarding by both parents, may be important behaviours in allowing a widespread breeding distribution in open arctic habitats. They may also be beneficial in more disturbed temperate areas.

Despite the relationships between feeding rates and weather conditions, there appeared generally to be enough feeding time in both study areas for adequate food intake. However, food availability and foraging ability may influence feeding rate and survival of young in later autumn and winter. The alternative strategies of residency and migration are discussed in relation to Lindisfarne Ringed Plovers, and the needs for further work indicated.

DANSK RESUMÉ

Udvikling af føde og fødesøgningsadfærd hos unger af Stor Præstekrave *Charadrius hiaticula* i Grønland og England.

Føde og fourageringsadfærd hos unger af Stor Præstekrave blev undersøgt i 1974 ved Mestersvig i Nordøstgrønland og i perioden 1973 til 1976 ved Lindisfarne i Nordøstengland. Fødesøgning hos flyvefærdige unger blev tillige undersøgt i populationen ved Lindisfarne.

Små tovingede insekter (Diptera) var det vigtigste byttedyr såvel i tundraområdet i Grønland som ved kysten ved Lindisfarne, hvor der desuden blev taget tanglopper og forskellige tidevandsinvertebrater. Ved Mestersvig steg fødesøgningsraten med stigende lufttemperatur og med aftagende nedbør, hvilket sandsynligvis afspejlede variationer i byttedyrenes aktivitet. Ved Lindisfarne var temperaturen højere, og den påvirkede tilsyneladende ikke fødesøgningsraten, selv om denne blev lavere ved høje vindstyrker og i regnvejr. Dette skyldtes sandsynligvis en påvirkning af byttedyrenes tilgængelighed og effektiviteten af fourageringsadfærden. Effektiviteten af fourageringen og indtagelsen af kalorier blev højere med fuglenes alder. Den tidlige udvikling af effektiv fouragering på egen hånd og ungernes store bevægelighed i forhold til forekomsten af byttedyrene samt beskyttende adfærd fra begge forældrefuglene er altsammen faktorer, der er vigtige adfærdsmønstre hos en art, der har et udstrakt yngleområde i åben, arktiske habitater. Disse adfærdsmønstre kan også være fordelagtige i tempererede områder med mange forstyrrelser.

På trods af sammenhængen mellem fødesøgningsraten og vejrforholdene syntes der i begge undersøgelsesområder at være tid nok til en tilstrækkelig indtagelse af føde. Imidlertid kan fødens tilgængelighed og evnen til fødesøgning påvirke fourageringsraten og dermed overlevelsen af ungerne i det sene efterår og om vinteren. alternative strategier med hensyn til ynglested og trækforhold diskuteres i relation til de Store Præstekraver ved Lindisfarne, og behovet for yderligere undersøgelser påpeges.

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