4.2.8. Supplementary Documents

b) Short title of thesis of less than 56 characters.

ECOLOGY AND FEEDING BEHAVIOUR OF ARCTIC SKUAS IN ICELAND

ECOLOGY AND FEEDING BEHAVIOUR OF THE ARCTIC SKUA (STERCORARIUS PARASITICUS LINNAEUS) IN ICELAND

by

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ABSTRACT

Breeding and feeding ecology of Arctic Skuas was studied at Vik i Myrdal, Iceland, in the summer of 1973. In the early part of the breeding season skuas fed on arthropods and pirated kittiwakes. At the time of hatching of skua eggs, which coincided with the hatching of puffin eggs, skuas switched their feeding activity to puffins, and fish stolen from puffins was the principle item of their diet thereafter. Skua chicks experienced a heavy mortality, apparently due to inadequate feeding from their parents.

Skuas successfully induced puffins to drop their fish in 69 percent of all chases. Multiple regression analysis was used to investigate the determinants of skua success. The overall conclusion of the study is that the skua population responds to changes in the available food supply (fish carried by puffins) in a numerical and functional way.

RESUME

Au cours de l'été 1973, nous avons étudié la reproduction et la nutrition du Labbe parasite, à Vik i Myrdal, Islande. Au tout début de la periode de nidification, les Labbes se nourrissait principalement d'arthropodes et de praies qu'ils volent aux Mouettes tridactyles. A partir de l'éclosion des oeufs de Labbes, laquelle coincide avec celles des oeufs des Macareux arctiques, les Labbes modifient leur régime pour se nourrir principalement de poissons volés aux Macareux. Les poussius de Labbes connaissent une forte mortalité, qui semble attribuable à une alimentation déficiente.

Les Labbes ont forcé les Macareux à laisser tomber leurs poissons dans 69% des cas. Nous avons utilisé une analyse de régression multiple afin de déterminer l'importance relative des différents facteurs du succès des Labbes. La principale conclusion de cette étude est que la population de Labbes réagit de facon numérique et fonctionnelle (situ Hollings 1959a,b) aux changements d'abondance de nourriture (poissons transportés par les Macareux).

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STATEMENT OF CONTRIBUTION OF CANDIDATE

The thesis has been prepared as a manuscript to be submitted to the Ibis in co-authorship with P.R. Grant (Einar Árnason & P.R. Grant. Ecology and feeding behavior of the Arctic Skua (Stercorarius parasiticus Linnaeus) in Iceland). The candidate is responsible for all parts therein, except the last two paragraphs of the introduction and the last paragraph of the discussion which were written by P.R. Grant, who also made several suggestions for improving other parts of the manuscript.

In accordance with the regulations of the Faculty of Graduate Studies and Research (section 4.2.7(h)) a full introduction is provided by the candidate.

INTRODUCTION FOR M.SC. THESIS

with supplementary references (Section 4.2.7(h)).

The skuas, Stercorariidae, although gull-like in appearance are generally more oceanic birds, staying at sea throughout the winter and returning to land only to breed in the summer. The Arctic Skua, *Stercorarius parasiticus*, has the widest breeding distribution of the skuas, extending from the High Arctic to Scotland and Northern Europe, Asia and America (Fisher & Lockley 1954, Godfrey 1966). The Pomarine, *S. pomarinus*, and Long-tailed Skuas, *S. longicaudus*, are more restricted in their breeding distribution than the Arctic Skua. The Great Skua, *S. skua*, is unique among the skuas in having a bipolar distribution. On migrations the Arctic Skua rarely crosses land, but stays over sea, travelling low, singly or in pairs (Brooks 1939). It largely follows the migration routes of terns and crosses the equator in both the Atlantic and the Pacific oceans on its way to its wintering waters in the southern hemisphere (Fisher & Lockley 1954). The other skuas behave similarly on migrations. Large concentrations of the Pomarine Skua are found off the west coast of Africa in winter. The winter-distribution of the Long-tailed Skua is least known but it is likely to be more oceanic and more scattered than the others.

The nesting habitat of the Arctic Skua is quite variable, often mossy or grassy areas but frequently also marshes and even dry sand (Gudmundsson 1954a). The Great Skua of the North Atlantic which has its main breeding areas on the great glacio-fluvial sands in Iceland (Gudmundsson 1954b) possibly competes with the Arctic Skua for breeding places.

The Arctic Skua is of genetic interest due to a colour polymorphism which it shows (Southern 1943). Individual skuas have either a dark or pale belly. A similar polymorphism is also found in the Pomarine Skua (Southern 1944). In the Long-tailed Skua melanistic individuals are hardly found. The Arctic Skua shows a cline in the polymorphism, with the dark individuals being predominant in the south and the pale becoming progressively more frequent as one moves north (Southern 1943, Bengtson & Owen 1973), although some departure from this pattern has been noted (Hildén 1971). Williamson (e.g. 1951) has made an extensive study of the breeding biology of the Arctic Skua in Fair Isles, England. From the data from Fair Isles, O'Donald & Davis (1959) concluded that two alleles are responsible for the colour phases of the Arctic Skua. Berry & Davis (1970) found that light males tended to breed later than dark males. Following this O'Donald (1972a,b) computed the selection coefficients of intermediate and light males and found that dark males are at a considerable selective advantage, thus suggesting that sexual selection may be important in maintaining the polymorphism in the Arctic Skua. In any event, O'Donald's analysis suggests that mating behavior and polymorphism in the Arctic Skua may provide a suitable arena for a quantitative study of the Darwinian theory of sexual selection.

One hypothesis for the maintenance of polymorphism that has received attention recently is that of apostatic selection (Clarke 1962a,b, 1969) (apostates are phenotypes that depart widely from the norm). The hypothesis stems from the work of Tinbergen (1960) that in order to maximize their feeding effort some predators, which are intelligent enough, form a "search image" of the most common food; they actively search for this and leave out other food which thereby gains an advantage. Payne (1967) has extended this hypothesis to include selection for polymorphism in parasitic cuckoos. It is reasonable to expect anti-predator behavior to be of selective advantage to prey (Kruuk 1964). A prey therefore gets a protective advantage by forming an "evil image" of its most common predator, and constantly responds to it by avoidance. In this way a prey species can act as an apostatic selective agent on its polymorphic predator (Paulson 1973), responding differentially to the morphs. There is some evidence (Arnason unpublished data) that puffins may in this way select for polymorphism in the Arctic Skua which pirate them. This is likely to be so in piratic situations because of the frequent contact between pirate and host which will allow the host (prey) to readily form an "evil image" of the pirate (predator) which it has to avoid.

In contrast to the genetics and general life history characteristics of the Arctic Skua, relatively little is known of its feeding ecology in relation to breeding. Lack (1954, 1966, 1968) has argued convincingly that in general "each species of bird has evolved those ecological adaptations for breeding which enables it to reproduce as rapidly as it can in its natural environment." Reproductive success will have evolved through natural selection to give rise to the greatest number of surviving young, the limiting factor being the amount of food the parents can bring to their young. It is therefore of obvious evolutionary advantage to a bird to adjust its breeding to the time when the highest quality food is available in large quantities, and continues to be so for considerable time. However the energy requirements of the female may be important and the timing of breeding may be related to the time when the highest quality food is available to form an egg (Perrins 1970). In any event food is likely to be an important determinant of breeding success.

In feeding habits the skuas are very characteristic. In winter they rely on other seabirds which they pirate for food (cleptoparasitism). During breeding the Pomarine and Long-tailed Skuas are effectively terrestrial feeders and prey mainly on rodents and their numbers and breeding success seem to vary with the cyclic fluctuations of the lemming population in the Arctic (Pitelka et al. 1955a,b, Maher 1970a,b, Andersson 1971, 1973). The Arctic Skua is less well known. Although also known to prey on lemmings (Pitelka et al. 1955a) it is more maritime during the breeding season and it appears to rely heavily on other seabirds which it pirates for food. In addition it preys upon small birds such as passerines and waders (Congreve & Feme 1930, Gudmundsson 1954a, Schmidt 1954, Arnason unpublished data), upon insects and plant food (mainly berries of Empedrum sp. and Vaccinium) (Witherby et al. 1938-1941, Gudmundsson 1954a) and in Iceland it is an important predator of eggs and goslings of the Pink-footed Goose, Anser brachyrhyncus, (Gardarsson & Sigurdsson 1972).

The habit of food piracy mentioned above appears to be a widespread phenomenon among seabirds, but only recently has it been studied quantitatively. It is manifested mostly by members of the Stercoraridae (Schmidt 1954, Nørrevang 1960, Grant 1971), Fregatidae (Nelson 1967, Ashmole 1971) and to a lesser extent Laridae (Nørrevang 1960, Ingolfsson 1969, Hatch 1970, Hays 1970, Hopkins & Wiley 1972, Nettleship 1972, Corkhill 1973, and Dunn 1973).

Most of the recent studies have concentrated on the factors affecting success of the piratic species and it has been revealed that in important ways the pirate-host dynamics have points in common with predator-prey dynamics (Dunn 1973, Grant 1971, Hatch 1970). Grant (1971) studied the interactions between the Arctic Skua (pirate) and the Common Puffin, Fratercula arctica (host) in Iceland. However, the study was restricted to the final three weeks of the breeding season, so the importance of the interactions to the breeding success of the interactants is not known. To place the interactions in better perspective, a further field study was undertaken at the original site in Iceland throughout one full breeding season; with the emphasis placed upon the Arctic Skua. It was designed specifically to fill the gap in our knowledge of the feeding ecology and behavior of this species in relation to breeding.

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ECOLOGY AND FEEDING BEHAVIOUR OF THE ARCTIC SKUA (STERCORARIUS PARASITICUS LINNAEUS) IN ICELAND

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INTRODUCTION

Food piracy appears to be a widespread phenomenon among seabirds, but only recently has it been studied quantitatively. It is manifested mostly by members of the Stercorariidae (Schmidt 1954, Nørrevang 1960, Grant 1971), Fregatidae (Nelson 1967, Ashmole 1971) and to a lesser extent Laridae (Nørrevang 1960, Ingolfsson 1969, Hatch 1970, Hays 1970, Hopkins & Wiley 1972, Nettleship 1972, Corkhill 1973 and Dunn 1973).

Most of the recent studies have concentrated on the factors affecting success of the piratic species and it has been revealed that in important ways the pirate-host dynamics have points in common with predator-prey dynamics (Dunn 1973, Grant 1971, Hatch 1970). Nettleship's study differed in that it focused on the vulnerability of the exploited species and the consequences of being exploited, whereas equal attention was given by Grant (1971) to the behavioral stratagems of the pirate and host species.

The last mentioned study was conducted in the final three weeks of the breeding season, so the importance of the interactions to the breeding success of the interactants is not known. The species are the Arctic Skua, *Stercorarius parasiticus*, (pirate), and the Common Puffin, *Fratercula arctica*, (host). To place the interactions in better perspective, a further field study was undertaken at the original site in Iceland throughout one full breeding season. It has revealed that the Skua-puffin interaction occurs throughout a large part of the skua breeding season, and that the fish robbed from puffins is an important food source of the skua. This extensive study allows a detailed investigation of such aspects as the grouping of skuas and fish size selection by the skua. The focus in this paper is on the skua; in particular on breeding in relation to the breeding of the puffin, and the interactions between the two species throughout the breeding season.

METHODS

Field work was done by the first author at Vik i Myrdal (63^{o} 25'N, 19^{o} 30"W), close to the southernmost point of Iceland (Fig. 1) between 24th April and 8th September 1973. The area is particularly suitable for this study as most of the skua-puffin interactions occur over land.

The skuas nest above the cliffs, where the puffins breed (Grant & Nettleship 1971), but feed both above and below the cliffs as well as out at sea. The areas above and below the cliffs were visited, weather permitting, twice a week throughout the summer, for the purpose of assessing the state of breeding and the nature of feeding. The state of breeding of skuas and puffins was noted and comparisons were made of the timing of breeding of pirate and host. Hatching dates for the hole-nesting puffins were determined by subtracting 53.4 days (fledging period, Nettleship 1972) from the time of fledging, and for skuas they were determined by observation.

Quantitative information on the skua-puffin interactions was gathered in the following manner. A day at the cliff was divided into 2 hour periods from 0500 to 0700, 0700 to 0900 up to 1900 hours. Information from each time interval constitutes one data point. In the first hour of each period the following were recorded: number of skuas, gulls and puffins on census areas and the number of puffins arriving in a given time interval, usually 15-30 minutes. Skuas were censused as they were patrolling at the cliff by scanning a volume of air (approximately 1.8×10^{7} m^{3}). Gulls were censused on a permanent area (2.4×10^{4} m^{2} approximately) in the talus below the cliffs, and puffin attendance at the colony was assessed by counting their number at the cliff (an area of 5×10^{3} m^{2} approximately).

In the latter hour, characteristics were noted of all chases that occurred in a constant volume of air (approximately 1.8 x 10^7 m^3). These characteristics were the number of skuas and gulls that participated in a chase; which individual skuas (as determined by colour morphs, where possible); whether fish were dropped or not; the number and size of fish dropped (fish size was recorded as small, medium and large); whether the dropped fish were secured by skua, gull or neither; which skua in the line of pursuit secured the fish; whether fish were secured in the air or on the ground; number and approximate size of fish secured; duration of the chase measured in seconds with a stopwatch; direction in relation to cliff; and height and distance from the cliff when the chase began and ended. Height was measured in relation to conspicuous features of the cliff and what had been determined as being 50, 100, 150 and 200 m was later found by simple trigonometric methods (Grant 1971) to be 56, 96, 119 and 145 m respectively. To give approximately even spacing the last two recording intervals were grouped into a single category 100-150 m. Distances from the cliff were determined as being on the cliff side of the road, telephone line and an electrical power line, as shown on the map. Later measurements showed these distances to be 150, 300 and 450 m respectively.

On other days the number and length of fish the puffins were carrying were recorded. Length of fish was estimated at the colony south of Vik where puffins nest among boulders. The observer positioned himself at a conspicuous place at the colony and watched within a distance of less than 50 m the fish-carrying puffins that landed and hesitated for a moment before going to their burrow. In this way it was possible to count the number of fish each puffin was carrying and to estimate the length of the fish as reaching from the puffin's beak to some feature of the puffin's body. The features used were the boundary of the grey and black colours on the neck; the boundary of black and white lower on the neck; midway between the black-white boundary and the tip of the wing; the tip of the wing; midway between the tip of the wing and the uppermost portion of the leg; and the uppermost portion of the leg itself. Later by projecting a photograph of a puffin on a screen, it was possible to estimate the length of the fish in relation to these body features by using the depth of the puffin bill as a standard unit (bill depth = 35.2 mm, Corkhill 1972).

The feeding of skuas on arthropods at the breeding grounds was noted. Estimations of size and kind of arthropods were rarely possible. No quantitative information was collected on skua-tern or skua-Kittiwake interactions as the former occurred only sporadically close to the shore, and the latter over sea far offshore (10 km approximately) as was verified during a boat-trip on 20th June.

Statistical methods are taken from Siegel (1956), Steel & Torrie (1960) and Sokal & Rohlf (1969).

RESULTS

The results are presented in three sections; details of skua breeding (Section A), skua-puffin interactions (Section B) and skua energetics in these interactions (Section C).

Section A. The breeding phenology of the Skua

The first skuas arrived at Vik on May 3 (Figure 2). In May they established territories and built nests. The first eggs were laid on May 26. Most eggs in the 15 nests studied were laid at the end of May and beginning of June (between May 29 and June 1). The incubation period is 27-28 days. The majority of the eggs hatched on June 25 and 26 (Hatching success: 88.89 percent, N = 27 eggs). The young left the nest shortly after hatching but stayed within the boundaries of the territories. The young were fledged by July 24 about 30 days after hatching, but were cared for and fed by the adults until the skuas left the breeding grounds in the latter part of August and beginning of September. Fledging success was quite low (0.267 fledglings/pair, N = 15 pairs). Most (79.16 percent) of the young died and/or disappeared in the first week after hatching.

Timing of breeding of Skuas and Puffins

The timing of breeding events of skuas and puffins is shown in Figure 3. Hatching dates for the puffin were determined by subtracting 53.4 days (fledging period, Nettleship 1972) from the fledging dates. Thus the peak hatching periods for both species coincided between June 22 and June 28. The skua young hatched from eggs at a time when puffins started to bring fish for their young; and fish secured from puffins by adult skuas were delivered to young skuas.

Feeding of the Skua in relation to breeding

The feeding of the skua in relation to breeding activities is shown in Figure 2. In the nestbuilding and incubation periods skuas fed by robbing kittiwakes out at sea. In addition skuas fed on arthropods (Arachnida, Coleoptera and larval Lepidoptera mainly) on the breeding grounds. Sporadically skuas were seen to pirate terns when these were around. Skuas were also seen to search for eggs at the ternery, but terns were of little importance to skuas as a food source since the terns did not breed at Vik this summer. At the time that skua eggs hatched, there was a sharp decline in feeding on arthropods and robbing kittiwakes when individual skuas switched from these food sources to robbing puffins of their fish. Some skuas with distinctive plumages were known to do this, and for others not individually recognizable this switch was inferred. The frequency of robbing increased gradually in the first week of hatching, at the end of which the robbing of puffins by skuas had reached maximum intensity and remained at this level until the end of August. Fish robbed from puffins was the main food source of the skua in July and August. By the beginning of September both species had left their breeding grounds.

Food of young skuas was determined from regurgitations and observations on food deliveries by adults. In the first few days after hatching the food mainly consisted of arthropods, but fish soon became the sole food of the young. The young were wholely dependent on the adults for food until the skuas left the breeding grounds.

In the middle of July there was an influx of nonbreeding skuas (2 and 3 years old as judged from plumage) to the breeding grounds. These youngsters went from pair to pair and begged food from the adults. The adults were never observed feeding these intruders although their presence on the territories was tolerated by the adults. These nonbreeders also took part in communal bathing, a characteristic habit of the skua. They were furthermore seen at the cliff chasing puffins. The nonbreeding skuas left at the end of July and beginning of August, a month earlier than the breeding population.

In summary, the breeding seasons of skuas and puffins are largely coincidental. Skuas are relatively opportunistic in their feeding habits until the time that puffin eggs and their own eggs hatch. Thereafter the skuas gradually become more specialized in their feeding, and fish seeured from puffins forms the principle item of their diet for the remainder of the breeding season.

Section B. The Skua-Puffin Interactions

General description

The skua-puffin interactions occurred mostly in the close vicinity of the cliff of the East colony where puffins bred. As described by Grant (1971) skuas circle in the air, patrolling among the arriving puffins. At the sight of an incoming puffin the skua approaches it rapidly in order to see if it has fish, and upon locating a fish carrier it starts a chase. During the chase, which most of the time is initiated from behind and above, the skuas show two strategies. The most common one is to fly below the puffin and attempt to grasp the fish dangling from the puffin's beak. The other is to fly on top of the puffin and kick at its back with the feet. The chase ends with the puffin escaping or dropping some or all of its fish. When the fish has been dropped the skua tries to catch it in the air as the skua crosses the descent path of the fish or else the skua brakes and dives after it. If the puffin drops more than one fish at the same time, the skua sometimes succeeds in securing more than one. This is achieved by actually chasing the falling fish.

Up to six skuas take part in a chase and sometimes more than one skua succeeds in securing fish. The skuas fly more or less in a straight line behind the puffin and although shifts in position in this sequence occur the skuas can easily be recognized as being the first, second, etc., in line of pursuit.

The puffin tries to escape by reaching its burrow or else it turns back and tries to return to the sea where it can reach safety by diving. When chases occur close to the cliff and approximately parallel to it the skuas invariably stay at the cliff side of the puffin, thereby preventing it from landing. There is obviously a great pressure on the puffin to avoid the skua's attack. Once a puffin is being chased, it has two options: drop the fish or try to escape and retain the fish. The latter option runs a small risk of death. Three times in the summer puffins were seen to break their necks when flying into a telephone line that runs beside the cliff. Although this can be considered an unusual situation the possibility exists that they might risk their lives by hitting the cliff, although this was never observed.

Six species of gleaners compete with the skua at the east colony for fish dropped by puffins. The most common ones are Lesser Black-backed Gulls, Larus fuscus, and Herring Gulls, L. argentatus, (actually a L. argentatus x L. hyperboreus hybrid, Ingolfsson 1970). These two species fly low over the ground at the foot of the cliff searching for dropped fish in the marram grass, (Elymus maritimus). They also attend chases when these occur close to the ground and often succeed in securing the fish, mostly after it has fallen to the ground. These species can and occasionally do chase puffins by themselves and succeed in inducing puffins to drop their fish. Ravens, Corvus corax, in attendance at some chases, often follow the puffin to the burrow and sometimes partially enter searching for fish. This behaviour was also observed in the Herring Gull. Both of these species were seen to secure fish occasionally, but their success as ground pirates was not assessed quantitatively.

Great Black-backed Gulls, L. marinus, were mostly concentrated close to the refuse dumps. They gleaned whatever food was dropped to the ground in their area. Great skuas, Stercorarius skua, and kittiwakes, Rissa tridactyla, only sporadically seen among the gleaners at the east colony, were important pirates and gleaners at the south colony.

Alternative Hosts of the Arctic Skua

The skua-kittiwake interactions occur over sea approximately 10 km offshore. Kittiwakes hunt by dipping at the sea surface and swallow the fish in the air. The skuas attack before the kittiwake has swallowed the fish. This behaviour was not studied quantitatively. Arctic Terns, Sterna paradisea, attempted but failed to breed at Vik this summer. The terns occasionally succumbed to piracy from the skua.

Fulmars, Fulmarus glacialis, nested at the same cliffs as the puffins, but these were never chased by skuas at Vik. However, in Burfell, an area further inland 9 km west of Vik and 6 km from shore, fulmars flying towards their breeding grounds were attacked by skuas and forced to regurgitate food (see also Gudmundsson 1954).

Characteristics of the Skua-Puffin interactions

Except where specified these did not vary systematically within the breeding season, so data for the whole breeding period, June to August, are pooled.

Spatial variation. Puffins are chased both towards and away from the colony. On the inward chases puffins that drop their fish do so relatively more frequently when they are more than 150 m away from the cliff (Table 1, a:b). Sometimes puffins fly back to the sea in an attempt to escape from skua attack. On these outward chases puffins which drop their fish most often do so when they are close to the cliff, but drop fish proportionately more frequently further away (Table 1, c:d), ~~i.e. at the start of their outward journey~~. Altogether puffins more often drop their fish when chased away from the colony than towards it (Table 1, $\Sigma a:\Sigma b:\Sigma c:\Sigma d$). Thus skua attacks are most successful well away from the cliff on inward flights, and close to the cliff on outward flights.

Skuas most often started a chase at a height of 100 m or more, whereas the majority of chases ended below 100 m (Table 2, a + b : c + d), often within a few meters of the ground. Similarly there was a significant difference between the heights of the chases that ended with a puffin dropping its fish and those that ended with the puffin escaping (Table 2, c·d), indicating that most puffins which drop their fish do so at a height of 50 m or less. Thus puffins which drop their fish most often descended before doing so, while puffins that were chased but did not drop their fish tended to fly at the same height throughout the chase. On the other hand, the height at which skuas started a chase did not determine whether puffins dropped their fish or not (Table 2, a:b).

Once the fish has been dropped the skua tries to catch it in the air. The catching success of the skua is directly related to the height from which the fish was released by the puffin (Table 2, e: f + g).

Interactions with competitor species. Gulls frequently interact with skuas in securing the dropped fish. The relative success of skuas and gulls is highly dependent on the height from which the fish was dropped. The greater the height, the greater the relative success of the skua (Table 2, e:f), but correspondingly the poorer is the relative success of gulls (f:g). Skuas most often secure the fish in air, whereas gulls most often get the fish after it has fallen to the ground. The different exploitation patterns of the interactants are highly significant statistically. (Table 3, a:b: Σc:Σd).

On the other hand, gulls are not the only determinants of skua ground success. The chances of a skua securing the fish that falls to the ground are directly related to the structure and density of the vegetation; with a single exception skuas secured fish only in a sparsely vegetated area (Table 3, c: d + e). In the same way the vegetation determines the relative success of skuas and gulls on the ground. Whereas skuas secure fish almost only in a low and sparse vegetation (Table 3, c:d), gulls have no difficulty in securing fish in either vegetation type (Table 3, d:e). The differential success of skuas according to ground vegetation is explained by the way the birds pick up fish from the ground. Having located a fish, the skua hovers over the ground and then following a sudden dive it grasps the fish with its bill, hardly touching the ground. Skuas must have free space to perform this dive and thus a high and dense vegetation is a serious obstacle for them. Gulls on the other hand, pick up the fish as they walk on the ground and the vegetation is a small obstacle for them. Skuas may also have difficulty in seeing the fish from the air when the fish is lying in vegetated rather than exposed places.

Grouping and its effect on success. Frequently more than one skua participated in a chase. Groups of 2 to 6 skuas were observed. A group of skuas was relatively more successful in inducing puffins to drop their fish than was a single skua (Table 4, a:b). Sometimes puffins change their flight direction in an attempt to escape skua attack. When more than one skua participates in a chase one of the group members may cut across a corner resulting in a failure of the puffin to escape. The skuas are more persistent when chasing in groups and the puffin thus becomes more tired when chased by a group than by a single skua, and apparently as a consequence, it drops fish more frequently. The length of the successful chases also indicates this. The average length of group chases (15.59 secs.) is significantly longer than the average length of chases of single skuas (12.41 sec., $F_{1,143} = 3.99$, $0.05 > p > 0.025$). Thus after a tiring chase the puffin resorts to dropping as a last effort to escape from skua attack:

A group of skuas was relatively more successful in securing the dropped fish than was a single skua (Table 4, c: d + e). On the other hand the relative success of skuas and gulls in securing the dropped fish is the same irrespective of the number of skuas participating in a chase (Table 4, (c·d)).

Data were also collected to find out if any particular individual of a group was more successful than others by virtue of its position in line of pursuit. When skuas chase in groups they fly in a line behind the puffin, and although changes in positions occur, the skuas can easily be recognized as being the first, second, etc., in line of pursuit. The immediate pursuer of the puffin does not always get the fish and the data in Table 5 show that position in the chase is an important determinant of success. Position here refers to the arrangement of skuas when the chase ends, i.e. when the fish is dropped. The data for groups of 2 and 3 were tested with chi square and the null hypothesis that every bird has an equal success is rejected. The indication is that the skua in the penultimate position has the highest chance of securing a fish.

The net success of the skua is presented in Figure 4. It is evident from the figure that the mean success per individual skua is inversely related to the number of skuas participating in a chase. On the other hand the chances of some skua being successful increases in a group of 2, 3 and 4. In a group of 5 and 6 the chances of some skua securing fish is equal to singles, but the data are ~~small~~ few. This suggests that the best strategy for the average skua is to hunt alone.

The success of the best and worst positions shown in the figure was deduced from the values presented in Table 5. The skua in the best position is as successful as a skua chasing alone.

Using subtle colour differences among the skuas as cues, it was sometimes possible to follow an individual throughout a chase and thus determine success of initiators and joiners of a group chase. Although the data are few they do not show any significant differences between success of initiators and joiners ($N = 7$; $X^2 = 0.143$, d.f. 1. $0.9 > p > 0.5$).

The size and number of fish in relation to success. Puffins usually carry one to six fish transversely in their bill. The fish are mostly sandeels (Ammodytes sp., 98 percent). As the number of fish the puffin is carrying increases from one to four, the average length of each fish decreases (Figure 5). From measurements of Ammodytes the relationship between weight and length was found. This relationship is given by the equation $\log y = 3.33 + 0.25 x$, where y is the dry weight of fish measured in grams and x is the length in cm ($N = 203$; $r = 0.967$; $p < 0.001$). Combining these two relationships it is found that the total weights of fish carried by puffins with 1 to 6 fish are 1.29, 1.08, 0.84, 1.04, 1.10 and 1.25 g of dry weight respectively. Thus it appears that each puffin is carrying an approximately equal weight of fish.

Single fish carried by a puffin were considered to be large, 2 or 3 to be medium and 4, 5 and 6 to be small. Puffins carrying large fish were chased preferentially by skuas (Table 6, a:b). Similarly once the fish has been dropped the chance of the skua catching it is directly related to fish size. Larger fish tend to be lost proportionately less frequently than the smaller ones (Table 6, c:d). If the puffin drops more than one fish, the chances are that the skuas will only secure some of the fish. No significant association was found between the number of fish dropped by the puffin and the number of fish secured by the skua ($\tau = 0.016$, $0.9 > p > 0.5$, $N = 125$). This is probably related to what was found earlier with success in relation to heights of chases, in that some of the dropped fish fall to vegetated ground before the skuas have time to secure the fish. Another possible explanation is that when several fish are carried by a puffin these are usually small fish which are less readily seen by the skua after they have been dropped, and therefore are more often lost. Whatever the reason, such apparent constraints upon discovery make it advantageous for the skua to chase the puffins with only one large fish rather than those with many small ones.

Chasing frequency. In order to isolate the components which give the best prediction of the variation in skua feeding success, step-wise multiple regression analyses were carried out with skua success (Y) as the dependent variable and other components as independent variables. The independent variables are selected and entered into the multiple regression analysis in their order of importance in reducing the variation in Y. The explanation of the variables is as follows:

The numbers represent the different variables, and X and Y refer to independent and dependent variables respectively.

X1 = number of skuas on census area

X2 = log number of puffins arriving per hour

X3 = mean number of skuas per chase

X4 = number of chases per hour

X5 = number of times fish dropped per hour

X6 = number of times fish secured per hour

Skua feeding success was considered as number of successful chases per hour. The results of the multiple regression analyses are shown in a path diagram in Figure 6. Number of securings per hour (Y6) is explained by number of drops per hour (X5), the mean number of skuas participating in a chase (X3) and unknown factors. The multiple regression equation is Y6 = 16.01 + 0.74 (X5)*** + 2.99 (X3)*** (81.5%).[1] In turn the number of times puffins drop fish in an hour (Y5) is accounted for by the chase frequency of the skuas (X4) and unknown factors. The simple regression equation is

$Y5 = 0.63 + 0.65\ (X4)^{***}$ (84.4%). The chasing frequency of the skuas is determined by the number of skuas present at the cliff (X1) and the logarithm of the number of puffins arriving in an hour (X2), which are themselves positively correlated. This relationship indicates a numerical and functional response of the pirate to host density. The multiple regression equation is $Y4 = 6.41 + 0.74\ (X1)^{**} + 3.90 \cdot \log (X2)^{*}$ (22.8%). A large amount (77.2%) of the variation in chase frequency (Y4) is unknown, possibly due to inaccurate sampling.

In summary the skua population responds to variation in the number of arriving puffins in a numerical and functional way which is manifested as a varying number of chases per hour. This largely determines the number of fish drops per hour, which in turn largely determines the number of times in an hour that fish are secured by skuas. In this way the available food supply is monitored and adjusted to by the skua population.

1) The asterisks represent significance levels.

*	$P<0.05$
**	$P<0.01$
***	$P<0.001$

Section C. Energetics of the Skua robbing Puffins

With information on skua feeding frequency and efficiency (Section B), it is now possible to estimate the profitability of chasing puffins, and to relate this to breeding success (Section A).

The average number of chases per hour that skuas secured fish was found for every week of the skua-puffin interaction period. The mean number of fish secured per chase is 1.08 weighing on the average 0.655 g dry weight. With a conversion factor of 4.924 kcal/g dry weight (Thayer et al. 1973), it is found that on the average 3.49 kcal are secured per chase by an average skua. Assuming that an average skua spends 14 hours a day hunting, and knowing the number of successful chases per hour as well as the number of skuas present, one can calculate the average energy yield in kcal per skua per day, for every week of the summer.

The average weight of skuas is 0.4094 kg (SE = 0.0029, N = 74). From the equation $\log M \quad \log 78.3 + 0.723 \times \log W$ (M is the basal metabolic rate in kcal/day and W is the weight in kg of a nonpasserine bird, Lasiewski & Dawson 1967), one finds that an average skua needs 41.11 kcal/day for basal metabolic functions. Assuming that an average skua rests 10 hours a day and that for the remaining 14 hours of the day its basal metabolic rate is increased on the average 50 percent, one finds that an average skua needs 53.01 kcal/day.

With the information on energy yield and requirements, an energy balance (yield/requirements) for an average skua is found for every week. The assumptions behind the calculations of energy balance are such that energy yield is maximized while energy requirements are minimized. Thus the assumptions are safe and do not bias the results. Specifically whatever the bias, if any, it is likely to be systematic and therefore does not alter the relative proportions between weeks. The results are presented in Figure 7. In the first week the energy balance is negative but rises sharply in the next two weeks reaching a peak in the third week. At a negative energy balance in the first week an adult skua does not meet its own energy requirements, let alone the requirements of the newly hatched chicks which are not taken into account in the calculations. Thus the heavy mortality of the young in their first week becomes understandable. Since the energy balance is positive in the second and third weeks it is concluded that it would have been better for the skuas to breed a week later than they did.

After the third week the energy balance decreases and becomes negative again. This is the time when nonbreeding skuas enter the area and start to take part in chases. This implies that some skuas are less efficient than others and therefore the energy balance of an average skua is lowered. The nonbreeders are younger and less experienced hunters than the older ones, and it is probably these which experience low success and thus bring down the average.

DISCUSSION AND CONCLUSIONS

This study has shown that the breeding of skuas and puffins is largely concurrent, and that the puffins provide the major food item (fish) for breeding skuas at Vik. Despite this the breeding success of the skua in 1973 was very low (0.27 fledglings /pair), much lower than that of the same species on Fair Isles, England (1.24 fledglings/pair, O'Donald 1972), but comparable with what has been found for other hunting species such as the Tawny Owl, Strix aluco, in Wytham Woods, England, in years of low food abundance (Lack 1966; Southern 1970). Skua chicks experienced a heavy mortality, (disappearance), in the first few days after hatching. Perhaps the skuas bred a little too early to take full advantage of the fish which puffins brought to their newly hatched young. In the first week of chasing puffins, individual skuas were at a negative energy balance with regard to feeding on puffin-transported fish and thus, apparently, were not able to provide enough food for their young in addition to their own needs.

Since the energy balance of the skuas improved in the following weeks it is reasonable to expect higher survival rates among those chicks hatching late. Too few chicks survived to permit detection of a trend. On the other hand it would be a disadvantage to have a dependent young at the end of the breeding season when the food supply had diminished with the departure of most of the puffins. These opposing tendencies to breed early and late are presumably balanced.

To enhance the survival of their chicks, another possibility open to the skuas is to exploit an alternative food at the time when their eggs hatch. They do feed upon arthropods at this time but not to any great extent. Potential prey are small birds such as passerines and waders (Congreve & Freme 1930, Gudmundsson 1954, Schmidt 1954, Arnason unpubl. data) and larvae of the antler moth, Charaeas graminis, which has periodic outbreaks in this part of Iceland (Gigja 1961). Skuas could also prey on and pirate terns as an alternative. Some skuas were seen to search for food (eggs and/or chicks) at the ternery in mid and late June and skuas are also known to pirate terns in Vik (Grant 1971). It is therefore possible that usually the terns are an important food source until the skua can take full advantage of the puffin; if so, the skua lost this important food source with the failure of the terns to breed at Vik in 1973 and consequently experienced a heavy mortality of young. A similar situation is found on Coquet Island, England, where Roseate Terns, Sterna dougallii, rob a number of other tern species of their fish. The timing of breeding varies for different host species and the piratic Roseate Terns switch from one host to another as the season progresses, thereby gaining a relatively constant food supply through their own breeding season (Dunn 1973).

Skuas breeding farther inland at Burfell west of Vik also pirate fulmars. If there is a food shortage for the skua in Vik, the question arises why the skuas do not harrass the fulmars that breed in the same cliffs as the puffins at Vik. When skuas chase fulmars at Burfell the chases are long (2-3 minutes). The fulmar, in an attempt to escape from the skua, often flies a distance of 3 to 4 km, in the direction of the sea, before giving up and regurgitating for the skua. In Vik the distance to safety at sea is shorter and it is therefore concluded that it is not profitable for the skua to chase the fulmar at Vik since the latter has a means of escaping most of the time.

Natural selection is considered to maximize the yield of usable energy in relation to the energy invested to locate, capture and digest the food (Emlen, 1966, MacArthur & Pianka 1966, Schoener 1971), and in this way feeding strategies evolve. These strategies are often compromises between conflicting demands. Since fish carried by puffins was the major food item of skuas after their eggs had hatched, much attention was devoted to the skua-puffin interactions in order to learn more about feeding strategies exhibited by the skuas. Grant (1971) had likewise studied the feeding behavior of the skuas, but only in the last ~~two~~ three weeks of the breeding season. Nevertheless the present, much more extensive, results complement and extend his. The picture which emerges can be summarized as follows. Depriving puffins of their food is difficult, an energetically feasible way of life for only the most skilled skuas. Individual skuas can maximize their share of the energy flow by using certain behaviors (principally those that maximize the likelihood of a puffin dropping its fish and/or minimizing the likelihood that a gull will secure the fish) that give the highest energy yield/effort ratio.

For the Arctic Skua pirating puffins, a correct stratagem is to be in the right place at the right time to maximize the likelihood that a chase once initiated will lead to successful capture of the fish. The farther away from the colony a skua starts a chase the greater the chances of the skua being able to force the puffin to drop the fish. If the puffin gets close to the cliff the skua will fly on the cliffside of the puffin to prevent it from landing. By chasing the puffin away from the cliff the skua enhances its success as puffins drop fish more frequently when chased back to sea.

Skuas usually start a chase at a greater height than the target puffin. With a fast downward flight the skua can rapidly get close to the puffin and attempt to grasp the fish dangling from the puffin beak. If the puffin does not drop the fish immediately it is advantageous for the skua to drive the puffin to low altitude since the puffin drops fish more frequently after having descended. However, there is a disadvantage which tends to ~~neutralise~~ counteract this benefit. As the skua most often secures the fish in the air, the probability of the skua successfully securing the fish is directly related to the height from which the fish is released. If the fish falls to the ground, gulls, being good scavengers, have a better chance of getting it, particularly if it falls into vegetation. Here then is an example of a conflict and compromise, referred to earlier, between the need to induce a puffin to drop its fish and the need to secure the fish when dropped.

Skuas chasing in groups are more successful in inducing puffins to drop their fish than are skuas chasing alone. Groups are also more successful in securing the dropped fish. Thus the net success per group increases, but the mean success per individual decreases as the number of skuas taking part in a chase increases. These observations on success for the skua are in accordance with those of Grant (1971) and Hatch (1970). They suggest that the best strategy for the individual skua is to hunt alone, but an equally good strategy is to join a chase if one is nearby and get into the optimal position.

It is not clear ~~how~~ whether and ~~if~~ how skuas can appreciate what an optimal position is. Based upon his study of Laughing Gulls, Larus atricilla, pirating terns in Maine, U.S.A., Hatch (1970) suggested that joiners have a higher success than the initiators of a chase which may indicate a position effect. However in the present study skuas joining a chase had the same success as initiators. Similarly the leading skua does not have the best chance of securing a fish. The best chance goes to the skua in the penultimate position.

When the puffin drops the fish, it is no longer carried onwards and starts falling to the ground. The skuas following the puffin brake but often overshoot the fish which now has become their target. Diving after the fish a reversal of positions occurs with the skua in the former ultimate position often now being the leader of the group. When it comes to securing the fish, the skua immediately following the leader can often drive the first skua away from the fish and secure the fish for itself. In this way the skua in the penultimate position is favored. But no obvious competition for this position during chases was observed. It is therefore concluded that the position effect is one attribute of success that is not under the skua's control.

The gulls at the East colony occasionally behave as pirates and chase puffins in the air. The gulls are less successful in inducing puffins to drop their fish than Arctic Skuas (Table 7). Great Skuas chasing puffins over sea at the South colony also are less successful than Arctic Skuas in forcing puffins to drop their fish. Kittiwakes similarly are less successful than Arctic Skuas in inducing puffins to drop their fish, although the results are not significant, possibly due to small sample size. The Arctic Skua also has the highest securing success, although the differences between Arctic Skua on the one hand and gulls or Kittiwakes on the other are not significant. The lack of significance in the latter case is again possibly due to small (Kittiwake) sample size. Gulls, being good scavengers (Ingolfsson 1967), invariably secure the dropped fish. Their ultimate success as pirates is thus determined solely by their ability to force puffins to drop their fish. Comparison of Arctic Skuas with pirates from other studies reveals the same thing (Table 7). Arctic Skuas for example are almost as successful as Laughing Gulls (Hatch 1970) in inducing their victim to drop it's fish, but the skuas are much inferior to the gulls in securing the fish.

The skuas lost a greater proportion of the dropped fish to gleaner species in 1973 than in 1969 (Grant 1971) (Table 7). The difference is most likely due to greater competition from an increased number of gleaners in the area close to the cliff where the skua-puffin interactions occurred. In 1969 the refuse dumps of the village were located approximately 10 km east of Vik, but were moved close to the cliff in 1972. Gulls follow the refuse dumps and consequently their numbers increased at the cliff where they were also able to take advantage of the fish that were dropped by puffins.

Aerial and ground piracy by large gulls appear to be equally successful ways of hunting (Nettleship 1972, Corkhill 1973). The success of these pirates appears to depend solely on their ability to induce their hosts to give up the food. The necessary skills for doing so may only be possessed by a few members of the gull population, so that the population is ecologically polymorphic (Levins 1962, 1963, 1964, Van Valen 1965). The Laughing Gulls on Petit Manan Island, Maine very efficiently pirate terns and perhaps their high success is best explained in terms of extreme specialization of a few individuals of the population (Hatch 1970). In the skua there also appears to be some specialization. Within the local population of skuas in Vik one individually recognizable skua never chased puffins, although other known individuals did so. Thus the results provide some evidence for the niche-variation model of Van Valen (1965) in which some individuals of a population may gain an advantage by exploiting a subniche not utilizable (or utilized inefficiently)by other members of the population.

Puffins with a single large fish were chased preferentially by the skua, and the probability of the fish being secured by a skua once dropped by the puffin was highest for the large single ones. Thus, a skua maximizes its energy yield/effort by chasing a puffin with a single large fish. Skuas most often secure only one fish in every chase irrespective of the number released by the puffin. Therefore, it is advantageous for the skua to chase a puffin with a single large fish, since the whole weight load the puffin is carrying is then secured without losing a part of it to the gleaner species. The skua is helped by the fact that a puffin with a large fish is more readily detected as a fish carrier from the nonbreeding puffins with no fish, than is a puffin with many small fish. These observations on fish size selection by skuas are similar to those of interactions between terns in Maine, U.S.A., where the most frequent targets of piratic chases were those terns carrying the largest fish, thus giving the highest yield/cost ratio (Hopkins & Wiley 1972). However Dunn (1973) found that piratic Roseate Terns preferentially chased hosts carrying intermediate sized fish although these did not yield the highest weight return/effort. As Dunn points out this was probably due to the low availability of terns with large fish, an active selection of which would require too long a search time and thus not be beneficial in the long run. Furthermore the terns and their chicks had some difficulties in handling large fish. This is similar to what was observed in the present study in that skuas have some difficulty in swallowing large fish immediately upon capture and sometimes succumb to attacks from other skuas and/or gulls and ravens before the skua can swallow. Although a skua was once seen to lose a fish in this way, it is unlikely to exert a strong pressure on the skua not to chase puffins with a large fish, as this secondary piracy is a rare event.

Increases in food availability permit enhanced individual skua hunting success (functional response) and more individuals to be successful (numerical response) (Holling 1959a,b). The results provide evidence that the skua population is capable of both types of response to changes in available food, although the monitoring of the food supply is far from perfect. As the density of arriving puffins increases, the frequency of chases increases; and correlated with the latter the number of skuas present increases, although the actual number of skuas per chase is constant. The success of the skua in securing fish increases as the host density increases.

The process can thus be visualized as a flow of energy (fish) from sea to young puffins in their terrestrial burrows. As the rate of flow increases, an increasing amount is diverted to the skua population and to the population of gleaner species, although never more than 4 percent in the main part of the breeding season (Figure 8). We calculate that on the average approximately one in 25 puffins is forced to drop its fish;

or, in other words, a puffin bringing fish to its young is forced to drop the food once in every 25 visits to the colony. A puffin chick is fed on the average 3.6 times a day maximally by both parents (Nettleship 1972) so the average parent loses its weight load approximately once every two weeks. This is a very small proportion, a small "piracy load" the breeding puffin has to bear. However certain individual puffins (young?), may be particularly susceptible to skua attacks, lose their food much more frequently than the population average and breed with less success. Nettleship (1972) found this to be so among puffins exploited by gulls in Newfoundland.

In conclusion four sources of information indicate that exploiting puffins for food in 1973 was difficult for skuas; (1) the proportion of puffins arriving with fish which were induced to drop their fish was small (Figure 8), (2) individual hunting success was low (Table 7), (3) breeding success was low and (4) the estimated weekly energy balance of the average skua was often negative (Figure 4). Selection for attributes which increase skua success is therefore likely to be strong at times. For example O'Donald (1972) studying selection for breeding time in the Arctic Skua on Fair Isles, England, has calculated selection coefficients as high as $s = 0.41$. A prescription for skua success has emerged from our studies which, but for small points of detail, probably applies to other pirate species as well, such as terns and gulls. Timing of breeding in relation to the breeding of host species would appear to be one important determinant. Use of alternative hosts is another. A third is the ability to monitor food supply and adjust hunting behavior appropriately. Hunting success is dependent upon early identification of a target, and correct choice of a potential victim with high energy reward. It is also dependent upon launching an attack from the right position at the right time, or upon joining an attack already started, and finally upon full deployment of individual skills such as manoeuvrability and speed in flight.

SUMMARY

Breeding and feeding ecology of Arctic Skuas was studied at Vik i Myrdal, Iceland, in the summer of 1973. In the early part of the breeding season skuas fed by robbing kittiwakes of their food at sea and by eating arthropods at the breeding grounds. At the time of hatching of the skua eggs, which coincided with the hatching of puffin eggs, skuas switched their feeding activities to puffins, and fish stolen from puffins was the principal item of the skua's diet thereafter. Breeding success of skuas was low (0.3 fledglings/pair) mostly due to death (disappearance)of newly hatched chicks. At the time of hatching of skua eggs, the energy balance of an average skua pirating puffins was estimated to be negative but changed to positive in the following weeks. Therefore the initial heavy chick loss is attributed to lack of adequate feeding by the parents.

Skuas successfully induced puffins to drop their fish in 69 percent of all chases, but they secured the fish in only 44 percent of the chases. The balance (25 percent) was lost to gleaner species (gulls and ravens). By utilizing certain behaviors, principally related to the choice of time and position to launch an attack on a target puffin, skuas can maximize the likelihood that a puffin drops its fish and/or minimize the likelihood that a gull will secure it. Skuas can enhance their success by joining a chase already started and by getting into the "best" position. The skua in the penultimate position has the highest probability of securing fish. By selecting a target puffin with a large fish the skua maximizes its energy yield/effort ratio.

Increases in food availability permit enhanced individual skua hunting success(functional response) and more individuals to be successful (numerical response). The results provide evidence that the skua population is capable of both types of response to changes in available food, although the monitoring of the food supply is far from perfect.

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Figure 1. Sketch map of the study area around Vik, Iceland. Puffins nest in the cliffs. O is the observation post at the east colony.

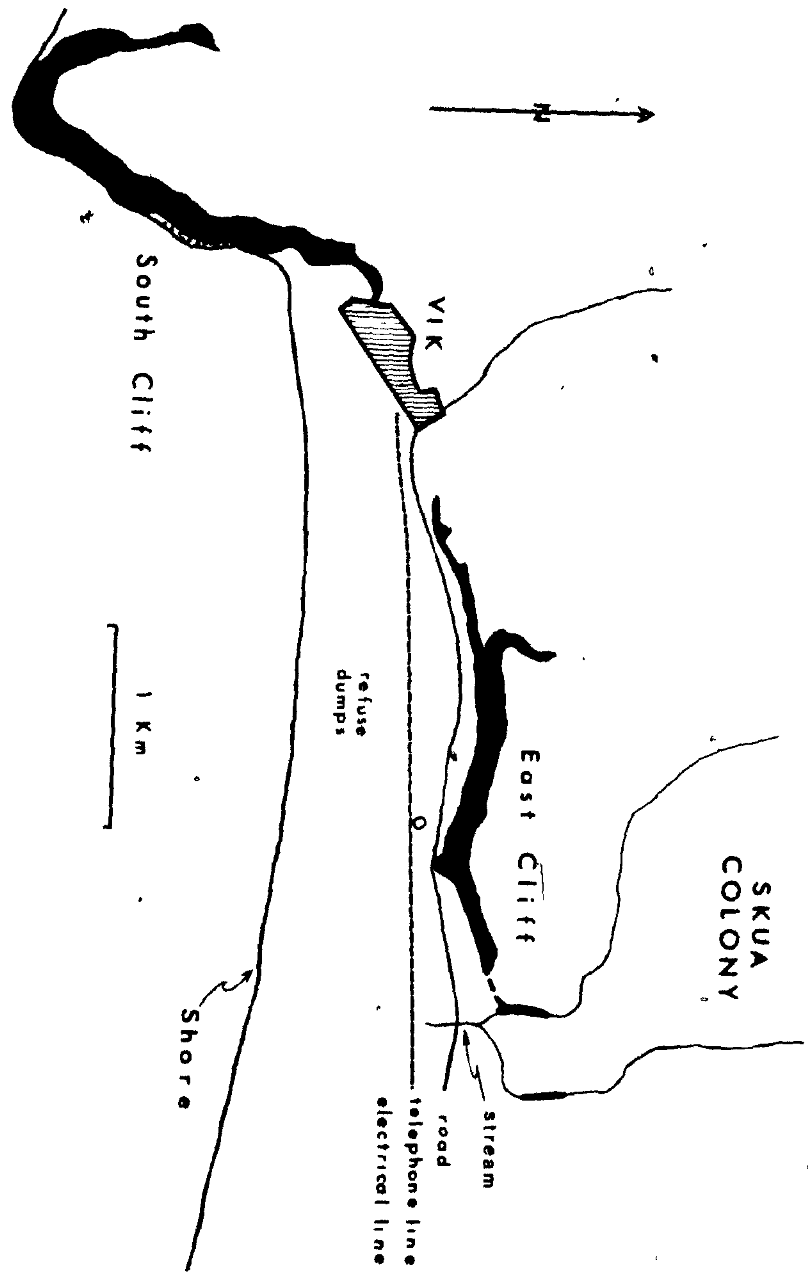
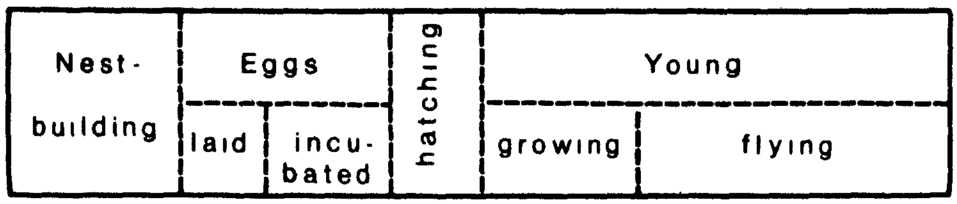

N
VIK
South Cliff
East Cliff
SKUA
COLONY
refuse
dumps
1 Km
Shore
stream
road
telephone line
electrical line

Figure 2. A simplified diagram of the relationship between breeding and feeding activities of the Arctic Skua. The thickness of the bars in the feeding activity is a rough indication of the relative importance of the different items in the diet of the skua.

BREEDING



FEEDING

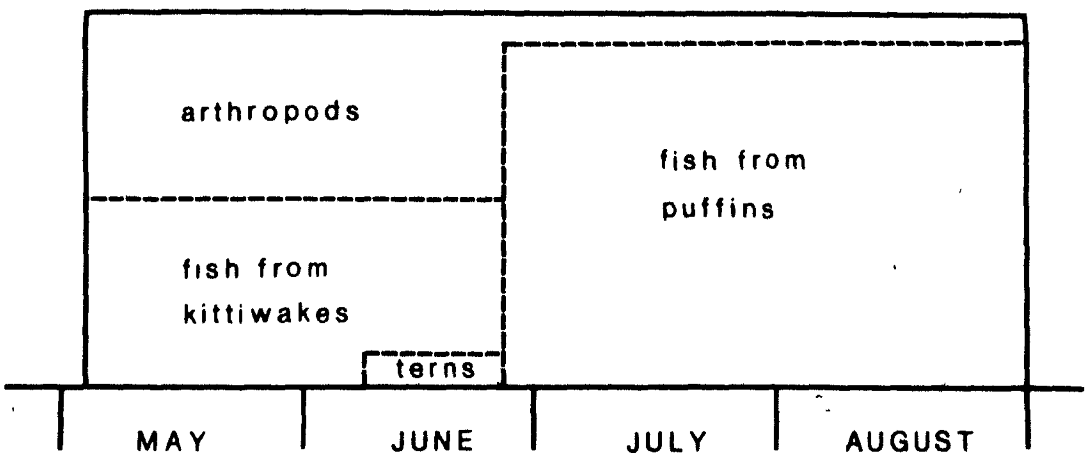
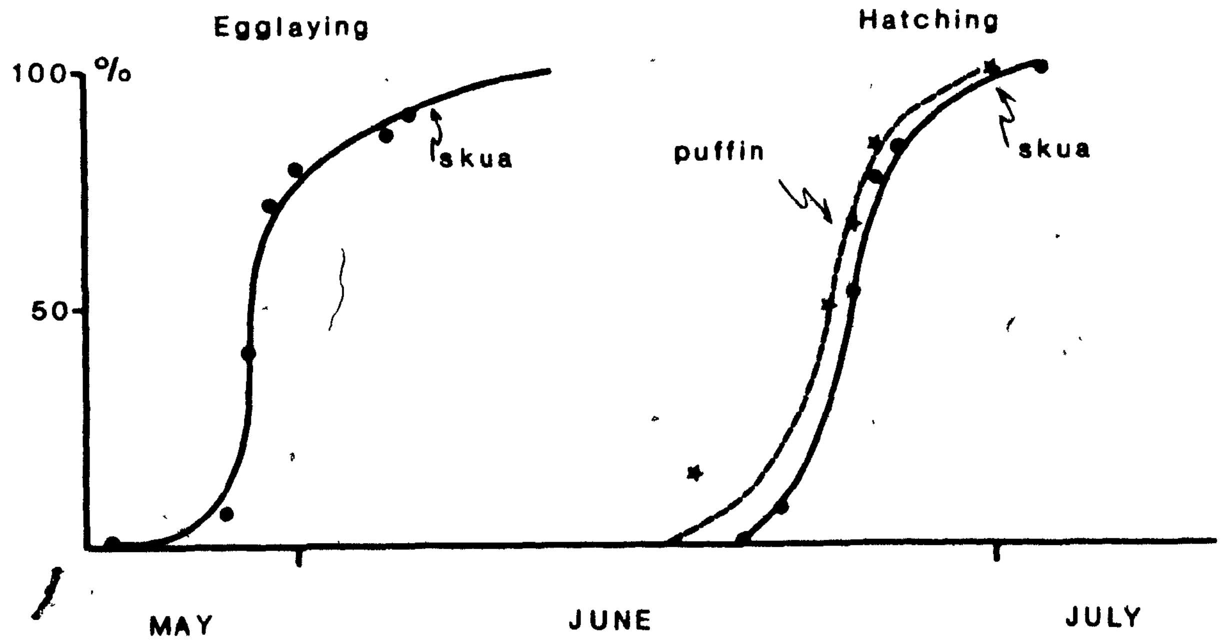


Figure 3. The timing of breeding of skuas and puffins. The points represent cumulative percentages on different days. The circles are for skuas and stars for puffins. The lines were fitted by eye.

The difference in hatching dates of skuas and puffins was tested for significance by Kolmogorov-Smirnov two-sample test. No significant difference was found ($X^2 = 1.058$, d.f.2., $0.5 > p > 0.3$).



Egglaying
Hatching
100
%
50
skua
puffin
skua
MAY
JUNE
JULY

Figure 4. Net success of piracy of puffins by skuas chasing in groups of different sizes. Group success and mean success per individual are shown with solid lines. The success of the "best" and "worst" (dashed lines) refers to position in line of pursuit. These were derived from values in Table 5 and are presented here as percentages of total group success that falls to the "best" and "worst" positions respectively. Dotted lines connect points based on small sample size. N is the total number of chases by groups of different sizes.

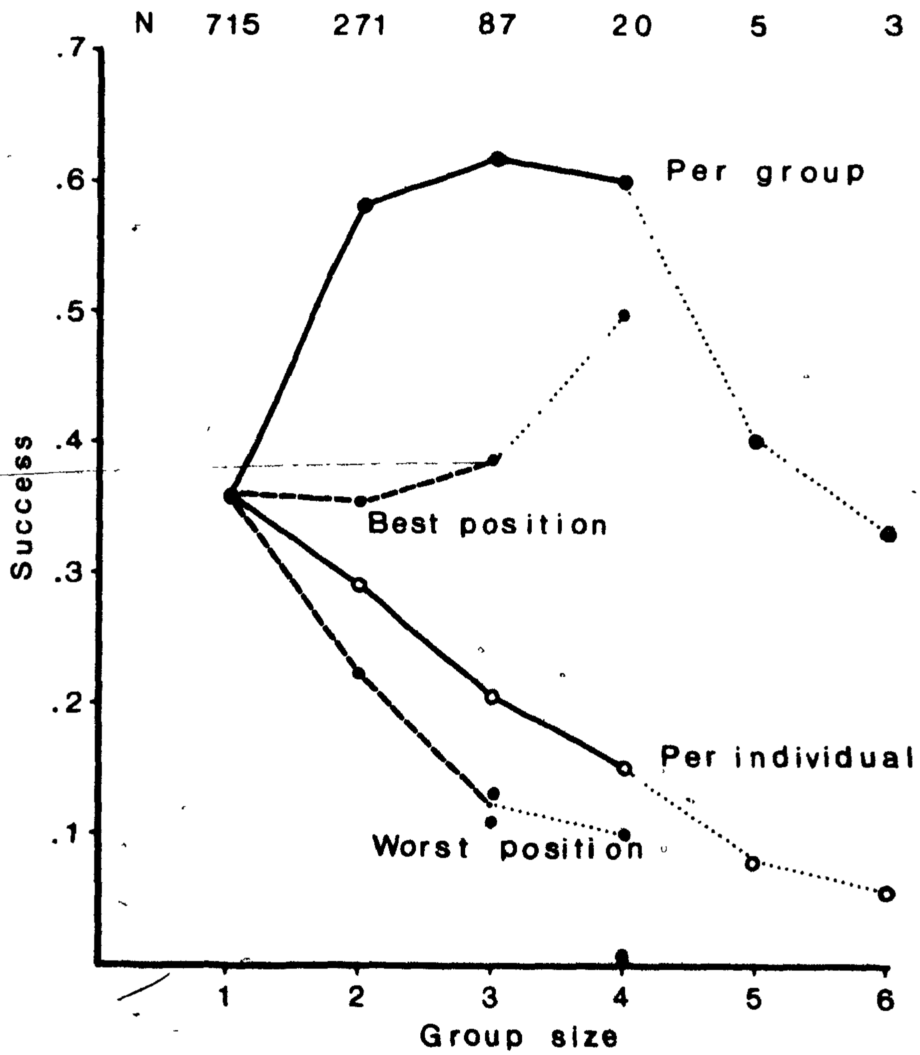

N
715
271
87
20
5
3
Success
.7
.6
.5
.4
.3
.2
.1
Per group
Best position
Per individual
Worst position
1
2
3
4
5
6
Group size

Figure 5. The lengths of fish in the beaks of puffins carrying 1 to 6 fish. The sample means are shown by the horizontal lines. The total range of variation is shown by the heavy vertical lines. The black portion of the bar represents two estimated standard errors to each side of the mean ($2s_x$) and the white bar at either end indicates one sample standard deviation (s) on either side of the mean.

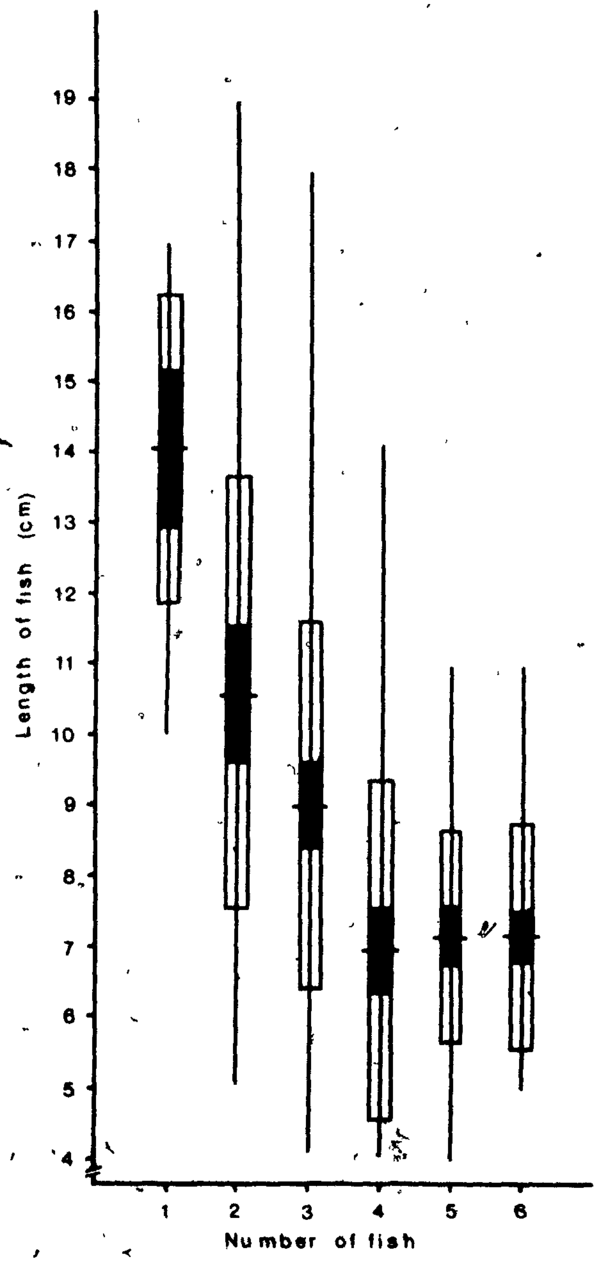

Length of fish (cm)
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
1
2
3
4
5
6
Number of fish

Figure 6. Path diagram showing relationships among variables as indicated by step-wise multiple regression analysis. Coefficients associated with each path show the proportion of the variation in the variable at the end of the path (dependent variable) that is explained by the variable at the beginning of the path.

Note: The coefficients of each path are b'r elements of the equation $R^2_{y,1..k} = b'_1 r_{y1} + b'_2 r_{y2} + \ldots + b'_k r_{yk}$. R is the multiple correlation coefficient and its square equals the proportion of variation in the dependent variable that is explained by the simultaneous effect of the independent variables. r_{yi} is the correlation coefficient between the dependent variable and the ith independent variable and b'_i is the standard partial regression coefficient. The unknown (or error) term is found simply from the equation $r^2_{yu} = 1-R^2_{y,1...k}$.

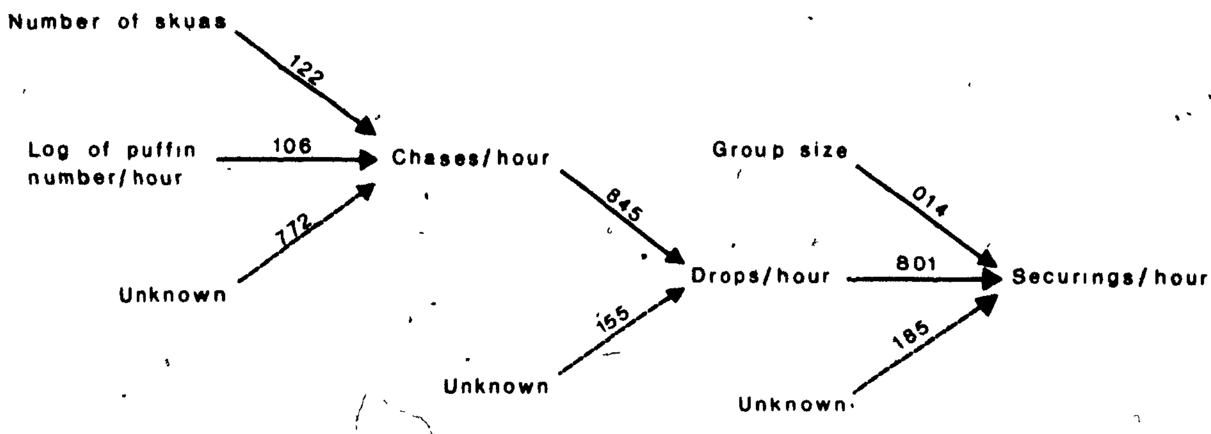

Number of skuas
122
Log of puffin number/hour
106
Chases/hour
Unknown
.772
.645
Unknown
.155
Drops/hour
Group size
.014
.801
Securings/hour
.185
Unknown

Figure 7. The energy balance of individual skuas, in relation to the number of skuas present. Balance is given by yield/expenditure in Kcal/skua/day. The points are given by numbers which indicate the different weeks of the summer. The first week is from 28 June to 4 July inclusive.

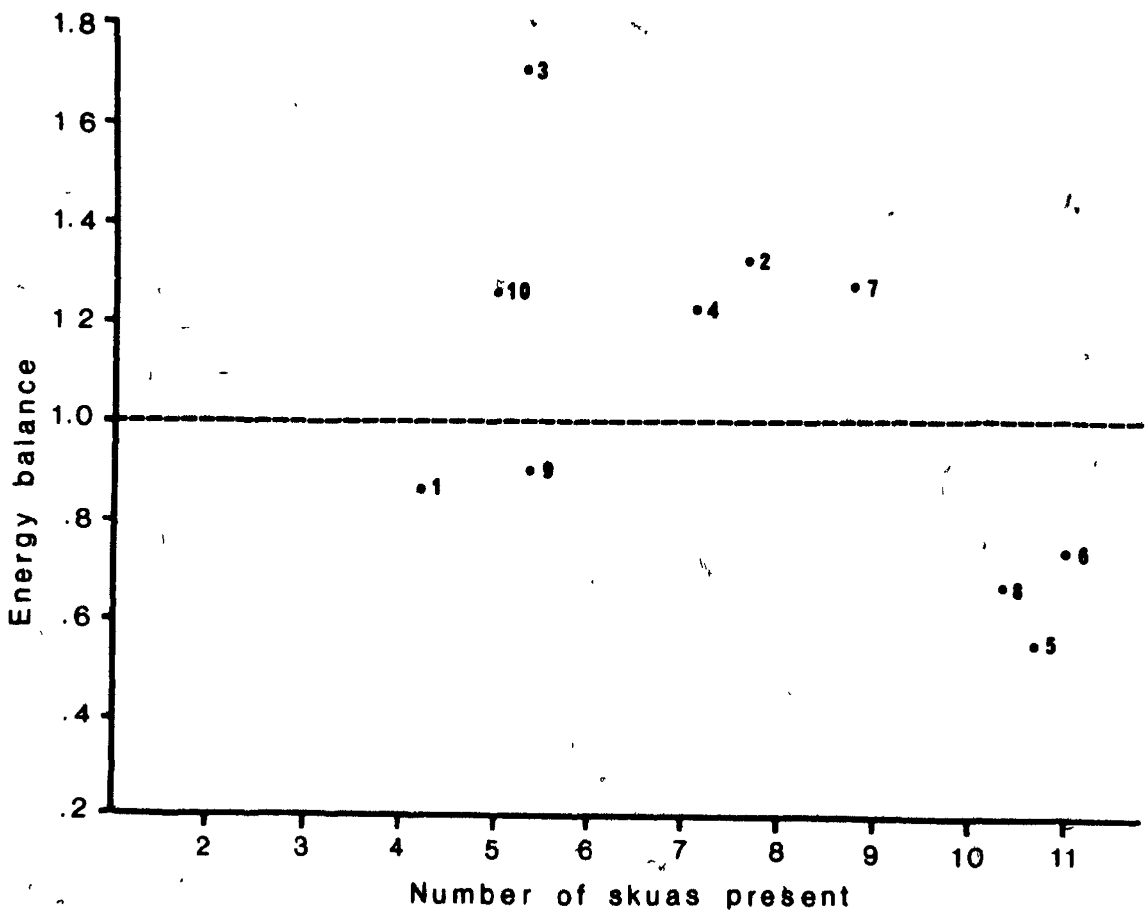

Energy balance
1.8
1 6
1.4
1 2
1.0
.8
.6
.4
.2
2
3
4
5
6
7
8
9
10
11
Number of skuas present
3
10
4
2
7
1
9
8
6
5

Figure 8. Energy flow diagram for the skua-puffin interactions. All figures are in Kcal/hour. Note that fish lost immediately after a chase may nevertheless be discovered by gleaning species sometime later.

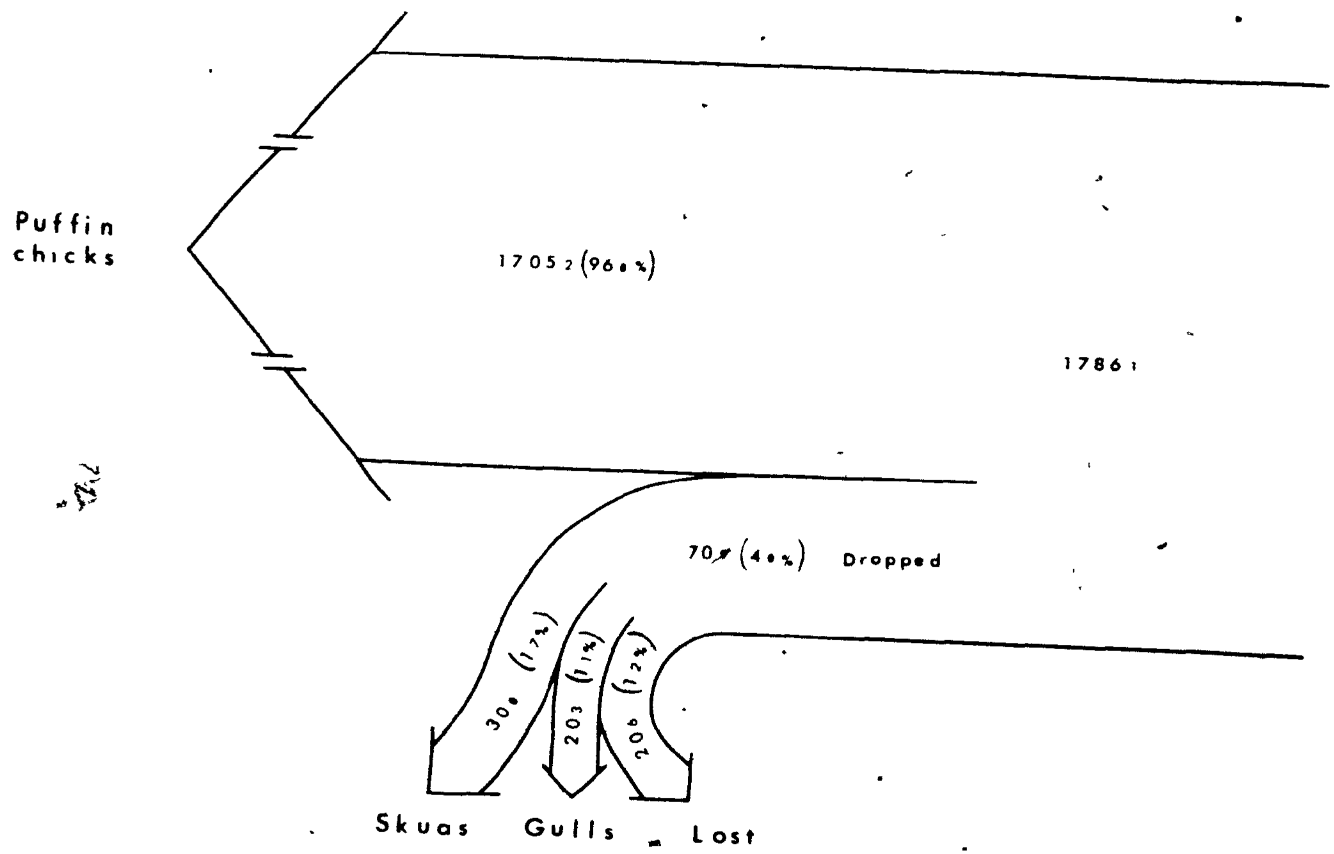

Puffin chicks
17052 (96.0%)
17861
709 (4.0%) Dropped
300 (1.7%)
203 (1.1%)
206 (1.2%)
Skuas
Gulls
Lost

TABLE 1

Success of skuas in relation to distance from the cliff

Distance from cliff at the end of the chase (m)	Number of times puffins were chased towards the cliff: fish dropped	Number of times puffins were chased towards the cliff: fish not dropped	Number of times puffins were chased away from the cliff: fish dropped	Number of times puffins were chased away from the cliff: fish not dropped
	a	b	c	d
0 - 150	140	161	216	179
150 - 300	41	16	109	32
300 - 450	12	2	148	80
Total (Σ)	193	179	473	291

a:b	$X^2 = 19.073$	d.f.2	$p<0.001$
c:d	$X^2 = 18.516$	d.f.2	$p<0.001$
Σa:Σb: Σc: Σd	$X^2 = 54.123$	d.f.1	$p<0.001$

TABLE 2.

Success of skuas in relation to height of chases

Heights of the interactants	number of chases with				
at the beginning of the chase (m)	fish dropped	fish not dropped	fish secured by skua	fish secured by gull	fish secured by none
	a	b			
0 - 50	15	9	-	-	-
50 - 100	44	36	-	-	-
100 - 150	82	61	-	-	-
at the end of the chase (m)	c	d	e	f	g
0 - 50	407	117	192	121	94
50 - 100	222	141	175	13	34
100 - 150	76	90	64	0	12

a:b	$X^2 = 0.433$	d.f.2.	$0.9 > p > 0.5$
c:d	$X^2 = 67.343$	d.f.2.	$p < 0.001$
e:f	$X^2 = 87.855$	d.f.2.	$p < 0.001$
e: (f + g)	$X^2 = 79.669$	d.f.2.	$p < 0.001$
(a + b): (c + d)	$X^2 = 225.770$	d.f.2.	$p < 0.001$
f:g	$X^2 = 24.784$	d.f.2.	$p < 0.001$

TABLE 3.

The relative success of skuas and gulls in securing the dropped fish

Fish secured	vegetation	Number of chases with fish secured by skua	gull	none
		a	b	
in air	–	410	6	–
		c	d	e
on ground	tall, dense	1	75	97
	short, sparse	28	69	65
	Total (Σ)	29	144	162

(a:b): (Σc: Σd)	$\chi^2 = 430.677$	d.f.1	$p<0.001$
c:d	$\chi^2 = 23.180$	d.f.1	$p<0.001$
d:e	$\chi^2 = 1.266$	d.f.1	$0.30>p>0.20$
c: (d+e)	$\chi^2 = 29.528$	d.f.1	$p<0.001$

TABLE 4

The effect of grouping on the success of skuas

	Dropping success		Securing success		
			fish secured by		
Group size	fish dropped	fish not dropped	skua	gull	none
	a	b	c	d	e
1	453	262	258	84	111
2	216	55	157	39	20
3	68	19	54	9	5
4,5,6	20	8	15	3	2

a:b	$X^2 = 28.501$	d.f.3.	$p<0.001$
c:d	$X^2 = 4.301$	d.f.3.	$0.5 > p > 0.1$
c:(d+e)	$X^2 = 24.874$	d.f.3.	$p<0.001$

TABLE 5

The skua which secured the fish when two or more skuas participated in a chase and fish were only secured by one member of the group

	Number in line of pursuit					
Group size	1st	2nd	3rd	4th	5th	6th
2	74	46	-	-	-	-
3	7	21	6	-	-	-
4	0	0	5	1	-	-
5	1	0	0	0	0	-
6	0	0	0	0	1	0

Group size 2: $X^2 = 6.533$ d.f.1. $0.025>p>0.01$

Group size 3: $X^2 = 12.412$ d.f.2. $0.005>p>0.001$

Note: Expected values are based on equal success.

TABLE 6

The relationship between size of fish and success.[1]

	Number of puffins		Number of dropped fish	
Size of fish	with fish	chased by skua	secured by skua	secured by gulls or none
	a	b	c	d
Small	39	49	45	82
Medium	44	48	39	14
Large	17	65	47	19

a:b	$X^2 = 15.610$	d.f.2	$p<0.001$
c:d	$X^2 = 33.537$	d.f.2	$p<0.001$

1. The data in the first column (a) were gathered at the south colony on different days from the rest of the data which were gathered at the east colony.

TABLE 7

The relative success of different species of pirates in robbing fish from their hosts.[1]

Pirate species	reference	total chases	percent of chases with fish dropped	t[2]	p	percent of chases with fish secured	t	p
Stercorarius parasiticus	present study	1101	68.76			43.96		
Stercorarius skua	present study	32	34.38	3.512	p<0.001	25.00	2.248	0.02>p>0.01
Larus fuscus L. argentatus	present study	29	34.48	2.993	p<0.001	34.48	1.035	0.4 >p>0.2
Rissa tridactyla	present study	7	42.86	1.397	0.2>p>0.1	14.29	1.780	0.1 >p>0.05
Stercorarius[3] parasiticus	Grant 1971	117	50.43	3.902	p<0.001	39.32	1.000	0.4 >p>0.2
Larus argentatus	Corkhill 1973	15	26.75	3.338	p<0.001	26.75	1.392	0.2 >p>0.1
Larus argentatus	Nettleship 1972	416	31.73	13.204	p<0.001	31.73	4.415	p<0.001
Larus atricilla	Hatch 1970	87	78.16	1.921	0.1>p>0.05	78.16	6.463	p<0.001
Sterna dougallii	Dunn 1973	2358	7.13	38.814	p<0.001	7.13	24.958	p<0.001
Corvus monedula	Corkhill 1973	89	6.74	12.999	p<0.001	6.74	8.409	p<0.001

nt'd ....

TABLE 7

1. Most of the species listed are aerial pirates with the exception of Nettleship's (1972) gulls and Corkhill's (1973) Jackdaws which pirate puffins on the ground.

   The host species is puffin except in Hatch's (1970) and Dunn's (1973) studies, in which the hosts are tern species.

2. Test of equality of percentages (Sokal and Rohlf 1969:608). All comparisons were made with the Arctic Skua in the present study.

3. Comparison of data from Grant (1971) (15-30 August) with data from an equivalent time period in the present study gives the same statistical results as above. The percent dropped (63.21, N = 337) and the percent secured (42.43) are almost the same as those for the whole study period.