

The Breeding of the Knot *Calidris canutus* at Hazen Camp, Ellesmere Island, N. W. T.

By David N. Nettleship *

Abstract: Knots arrive on Ellesmere Island in late May or early June. At Hazen Camp small flocks were present on 3 June 1966, but the main influx occurred 5 June when many flocks were seen ranging in size from 6 to 60 individuals. The sexes appeared to arrive together, but the manner of pair-formation was not determined. By 7 June pairs were distributed over the tundra with large feeding flocks forming at snow-free wet marshy areas. Most nests were on *Dryas*-hummocked slopes and tundra, either dry or moist, with some on clay plains and summits in a mixed *Dryas* and *Salix* vegetation. A census area of 240 ha supported at least 3 breeding pairs, and possibly 5; the total number of pairs breeding in the Hazen Camp study area was estimated to be about 25 (1.09 pairs/km²). Egg-laying (4 nests) extended from 15 to 28 June, with 3 of the 4 sets completed between 20 and 23 June. Both sexes incubated, one of the pair more regularly than the other. The song-flight display of the male was performed most frequently during egg-laying and incubation. The incubation period of the last egg in one clutch was established as being between 21. 5 and 22. 4 days. Four nests hatched between 12 and 20 July, and the hatching period of the entire clutch was less than 24 hours. Four of 7 nests (57 %) survived and egg survival (53 %) was low. Families left the nesting area soon after hatching, concentrating at ponds where food was readily available for the young. Both adults attended the young during the pre-fledging period, but the females apparently departed before the young had fledged. Males left once the young could fly and the adult fall migration was complete by early August. Most of the young departed before mid-August. Fall migration is complete by late August or early September.

The breeding season appears to be timed to peak food supply for the young. Adult Chironomidae emergence was highest between 3 and 17 July, the period during which most successful nests hatched. The increasing scarcity of adult insects for the young after mid-July was offset by family movements over the tundra and the early departure of half the adult population.

Food also seemed to influence the distribution of breeding pairs over the tundra, restricting them to the general vicinity of marshes, streams, and ponds where food is most available when the young hatch. Territoriality in the Knot appears to be closely associated with the protection of the nest against predators and has at least a local effect in regulating the number of breeding pairs.

Plant material was important in the diet of adult Knots throughout the summer and the primary food from the time of arrival until mid-June. After mid-June the percentage of animal matter increased as dipterous insects became available (especially adult Chironomidae), but plant materials continued to constitute a large part of the diet, usually more than 50 %. The food of the young before fledging consisted principally of adult chironomids.

Zusammenfassung: Der Knot trifft Ende Mai oder Anfang Juni auf Ellesmere Island ein. Bei Hazen Camp wurden kleine Trupps bereits am 3. Juni 1966 beobachtet; der Haupteinflug fand jedoch erst am 5. Juni statt, als zahlreiche Trupps festgestellt werden konnten, deren Größe zwischen 6 und 60 Individuen schwankte. Die Geschlechter schienen gleichzeitig anzukommen, doch konnte die Art der Paarbildung nicht beobachtet werden. Am 7. Juni waren Paare über die Tundra verteilt, wobei sich große futtersuchende Trupps in schneefreien sumpfig-feuchten Bereichen bildeten. Die meisten Nester wurden auf von *Dryas*-Polstern übersäten Hängen und in der Tundra gefunden, sowohl an trockenen wie feuchten Standorten; einzelne fanden sich auch auf tonigen Flächen und Erhebungen in *Dryas* und *Salix*. Eine Erhebungsfläche von 240 ha trug wenigstens 3, möglicherweise sogar 5 brütende Paare; die Gesamtzahl der Brutpaare im Hazen-Camp-Untersuchungsgebiet wurde auf etwa 25 geschätzt (1.09 Paare pro km²). Die Eiablage (4 Nester) erstreckte sich vom 15. bis 28. Juni, wobei 3 der 4 Gelege zwischen dem 20. und 23. Juni vervollständigt wurden. Beide Geschlechter brüteten, ein Teil des Paares regelmäßiger als der andere. Der Gesangsflug des Männchens vollzog sich am häufigsten während der Eiablage und während des Brutgeschäftes. Die Bebrütung des letzten Eies in einem Gelege erstreckte sich über 21,5 bis 22,4 Tage. In vier Nestern schlüpfen die Jungen zwischen dem 12. und 20. Juli, wobei die Schlupfperiode des gesamten Geleges sich auf weniger als 24 Stunden belief. Nest-(43 %) wie Eiverluste (47 %) waren hoch. Die Familien verließen das Brutgebiet bald nach dem Schlupf und fanden sich an flachen Tümpeln zusammen, wo Futter für die Jungen leicht erreichbar war. Beide Elterntiere kümmerten sich um die Jungen vor dem Flüggewerden; die Weibchen verschwanden dann aber offensichtlich, bevor die Jungen fliegen konnten. Die Männchen zogen ab, sobald die Jungen flügge waren; der Herbstzug der Alttiere war Anfang August abgeschlossen. Die meisten Jungtiere verließen das Gebiet vor Mitte August. Ende August oder Anfang September war der Herbstzug beendet.

Die Brutperiode scheint mit der Zeit des optimalen Nahrungsangebots für die Fütterung der Jungtiere zusammenzufallen. Das Chironomidae-Vorkommen war am höchsten zwischen dem 3. und 17. Juli, d. h. während jener Periode, in der die besten Gelege schlüpfen. Die sich nach Mitte Juli abzeichnende Verknappung an Insekten für die Jungenaufzucht wurde durch Verteilung der Familienverbände über die Tundra und den frühen Abflug der Hälfte der adult. Population ausgeglichen.

Das Nahrungsangebot dürfte auch die Verteilung der Brutpaare über die Tundra beeinflussen, indem es sie auf die Nähe zu Sümpfen, Wasserläufen und Tümpeln beschränkt, wo Futter reichlich vorhanden ist, wenn die Jungen schlüpfen. Der Territorialanspruch des Knots scheint aufs engste verbunden zu sein mit dem Schutz des Nestes gegen Räuber und reguliert zumindest lokal die Siedlungsdichte.

Pflanzliches Material war ein wichtiger Bestandteil der Nahrung der Alttiere während des ganzen Sommers; von der Ankunft bis Mitte Juni bildete es die eigentliche Nahrungsgrundlage. Ab Mitte Juni nahm zwar mit dem Erscheinen zweiflügliger Insekten (vor allem Chironomidae) der Prozentsatz animalischer Nahrung zu, doch stellte pflanzliches Material auch weiterhin einen beträchtlichen Anteil, gewöhnlich mehr als 50 %. Die Nahrung der Jungtiere vor dem Ausfliegen bestand hauptsächlich aus fertigen Chironomidae.

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The Knot *Calidris canutus* is a highly disjunctive circumpolar shorebird species breeding in the high Arctic. Its breeding distribution is in general north of the 40°F July isotherm and extends to the extreme northern limits of land on Greenland and Ellesmere Island. Although its migratory movements and winter distributions are well known on both continents, knowledge of its breeding ecology and behaviour during summer months is scanty, mainly due to the remoteness of the breeding grounds.

Almost all the information on the Knot's breeding activities has been derived from observations recorded by members of early exploratory parties (e. g. Fielden 1877, 1878, 1879; Greely 1888; Peary in Feilden 1920) and faunal surveys (e. g. Manniche 1910; Ekblaw 1918; Gibson 1922; Sutton 1932; Bird and Bird 1941; Johnsen 1953; MacDonald 1953, 1959; Parmelee and MacDonald 1960). Several authors have compiled these observations, including Bent (1927), Pleske (1928), Witherby *et al* (1940), Salomonsen (1950), Bannerman (1961), Kozlova (1962), and Hobson (1972); but no detailed study of its breeding cycle has been performed.

This study of the breeding biology and feeding habits of Knots took place at Hazen Camp, situated at 81°49'N, 71°18'W, on the northwest shore of Lake Hazen, Ellesmere Island, in the Canadian Arctic Archipelago, between 3 June and 15 August 1966 and ran concurrently with a programme on the breeding ecology of Turnstones *Arenaria interpres* (Nettleship 1973).

METHODS

The methods used in this study were simple. Nests were searched for systematically over the census area which was surveyed at 3—5 day intervals through the summer. All nests were marked by placing two small rocks (diameter: 20—25 cm), marked with red spray paint, approximately 6 m apart, on opposite sides of the nest. Estimates on the timing of breeding and nesting success were largely determined by following the fate of all nests until hatching. Details of the methods used to study feeding habits and seasonal changes in distribution and abundance of the invertebrate food supply are given in Nettleship (1973). Data recorded in 1966 are supplemented by observations made in previous years by Colbo and Oliver (see Acknowledgements).

STUDY AREA

General description and habitats

Hazen Camp is bound by Lake Hazen to the south and the United States Range to the north. Lake Hazen is a large deep oligotrophic lake, 78 km long and approximately 11 km wide. It receives the spring run-off from surrounding ice-caps and snowfields and is drained primarily by the Ruggles River which flows southeastwards into Chandler Fiord. The United States Range consists of several mountain ranges and icefields, some of which reach an altitude over 2,700 m, including the Garfield Range which extends close to Hazen Camp. Savile (1964) and Oliver & Corbet (1966) have described the vegetation, habitats, and general ecology of a 23 km study area around Hazen Camp (Figure 1) and so only a brief description will be given here. A description of the avifauna has been made by Nettleship and Maher (1973).

The Hazen Camp study area extends from Lake Hazen (158 m above sea level) north to the crest of Mt. McGill (1,000 m), west to just beyond Blister Creek Delta, and east to Snow Goose Delta (Figure 1). This study was conducted mainly on the foothills and lowlands of the study area, with systematic coverage of events of the breeding cycle restricted to a census area outlined in Figure 1. In general, the area consists of clay hummocks and tundra plains, sparsely vegetated with *Dryas integrifolia*, either in almost

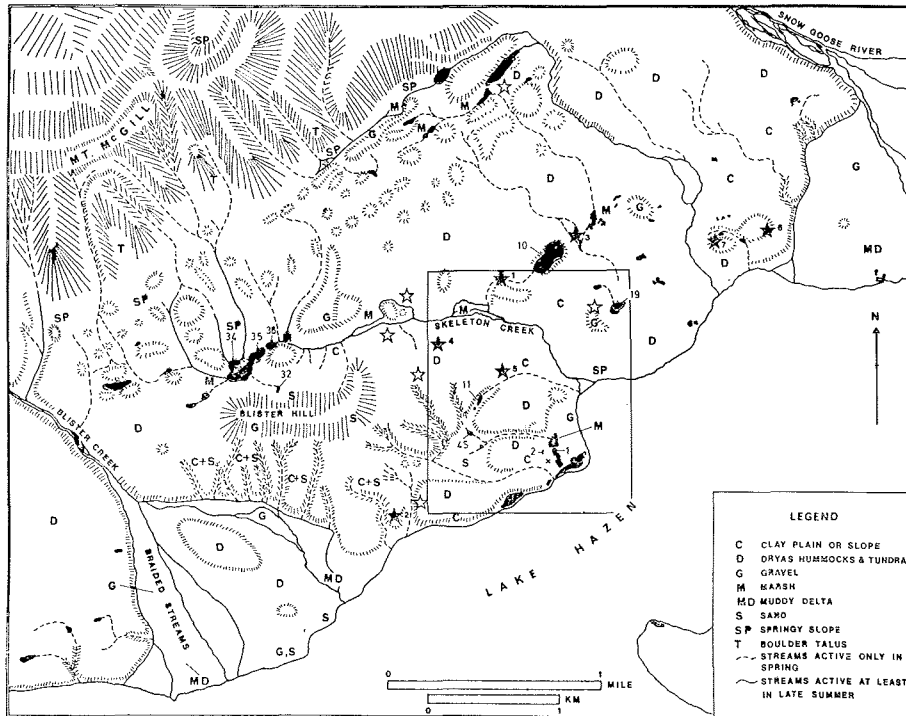


Fig. 1: Sketch map of the Hazen Camp study area, showing principal habitats (after Savile 1964) and locations of Knot nests found in 1966 (★) and 1963 (☆). The census area is outlined. Shaded areas are small lakes or ponds; ponds and nests discussed in the text are numbered.

Abb. 1: Lageskizze des Hazen Camp-Untersuchungsgebietes mit den wesentlichen Standorteinheiten (nach Savile 1964) sowie Lage der Knot-Nester 1966 (★) und 1963 (☆). Die Erhebungsfläche ist umrandet. Die geschwärzten Flächen stellen kleine Seen bzw. Tümpel dar; Tümpel und Nester, auf die im Text Bezug genommen wird, sind nummeriert.

pure stands or mixed with *Salix* and *Kobresia* sp., which gives the area a barren and desolate appearance. Although most of the area contains dry ground, it also includes several ponds, streams, and marshes, which are extremely important factors in the distribution and abundance of vegetation, insects, and birds. Rich vegetation is limited to regions of high moisture: pond borders, marshes, springy slopes (slopes kept wet for a substantial period each year by run-off from retreating permafrost), and permanent and semi-permanent streams. Sand and gravel regions support little vegetation. For the purpose of describing nest distribution, five major habitats have been recognized, all of which are based on physical characteristics of the terrain and vegetative cover:

(1) *Dryas*-hummocks or tundra. Hummocky tundra consisting of *Dryas*-capped hummocks separated by bare troughs of varying depths, usually not exceeding 15 cm. Vegetative cover is fairly high in well-hummocked areas where moisture from the spring thaw is trapped between hummocks for prolonged periods (Figure 2). A *Dryas-Cassiope* association often forms a closed cover on northward facing slopes which are snow-covered during the winter and remains moist through the summer.

(2) Clay-*Dryas*, and (3) Clay plain or slope. Level and exposed regions which dry rapidly after the spring thaw and support comparatively few plants (Figure 3). *Dryas*-capped hummocks in clay-*Dryas* habitat are fewer in number than *Dryas*-hummocked habitat,

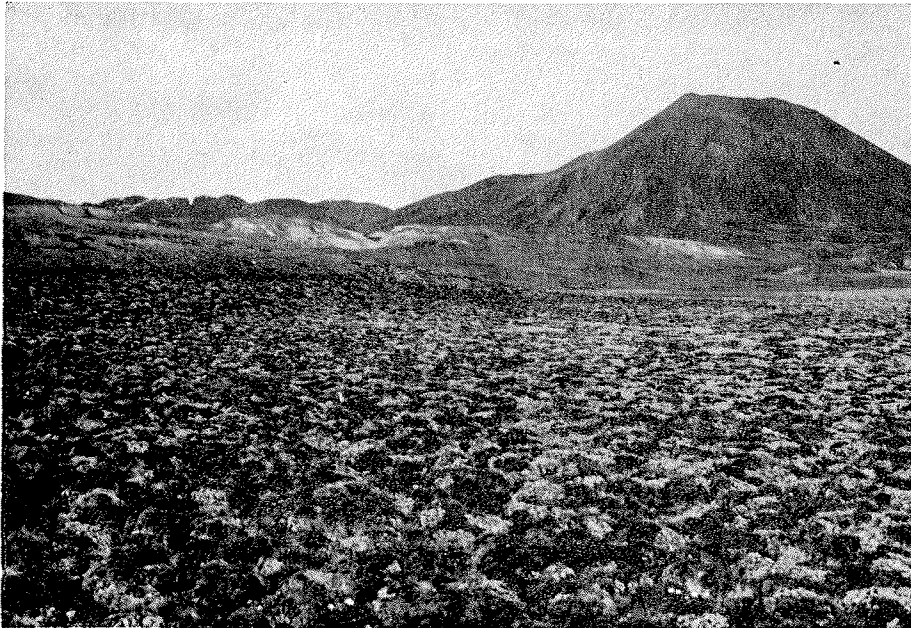


Fig. 2: Above, *Dryas*-hummocks or tundra habitat showing *Dryas*-capped hummocks.
Below, well-hummocked slope with a high percentage cover of *Dryas-Cassiope* association.
Abb. 2: Oben: *Dryas*-Hügel- bzw. Tundra-Standort mit von *Dryas* besetzten Hügeln.
Unten: Stark hügeliger Hang mit hoher Bedeckung durch eine *Dryas-Cassiope*-Gesellschaft.



Fig. 3: Above, clay-*Dryas* habitat showing a smaller number of hummocks than *Dryas*-hummocked habitat. Below, clay slope habitat supporting a sparse vegetation of *Salix*.

Abb. 3: Oben: Toniger *Dryas*-Standort, weniger hügelig als der in Abb. 2 beschriebene Standort. Unten: Standort auf tonigem Hang mit spärlicher *Salix*-Vegetation.



Fig. 4: Above, marsh habitat showing lush vegetation of a stream bed and skeletal material of a Musk-ox *Ovibos moschatus*. Below, marshy pond (c. 90 x 55 m) in mid-picture is typical of the tundra ponds scattered over the Hazen Camp study area.

Abb. 4: Oben: Stark vernäffter Standort mit üppiger Bachbett-Vegetation und Skelettresten eines Moschusochsen *Ovibos moschatus*. Unten: Der versumpfte Tümpel (ca. 90 x 55 m) in der Bildmitte ist typisch für die über das Untersuchungsgebiet verstreuten Wasserflächen.

while clay plain or slope habitat has a relatively smooth surface and supports only a sparse vegetation of xerophytic species, predominantly *Salix arctica*.

(4) Marsh. Marsh habitat is restricted to stream valleys and slopes which are flooded during the spring melt and receive abundant moisture for most of the summer from active streams and tundra ponds (Figure 4). Marshes support a rich vegetation of *Carex* spp. associated with *Eriophorum*, *Arctagrostis*, *Polygonum*, *Dryas*, and mosses. Marshy ponds are common and vegetation is luxuriant along pond-margins, primarily of *Carex*, *Eriophorum*, and mixed mosses.

(5) Gravel or sand. Sand, gravel and silt predominate in the southern portions of the study area, originating from the erosion of cliffs and transported by the spring run-off southward to the lake shore. Gravel is abundant along the lake margin east of Hazen Camp (Figure 5) and occurs, to a limited extent, along the entire lake shoreline. Plant cover in this habitat is very low, consisting of xerophytic species like *Saxifraga*, *Poa*, and *Erysimum*.



Fig. 5: Gravel or sand habitat showing gravel mounds bordering Lake Hazen.
Abb. 5: Kies- bzw. Sandstandort mit Kiesrücken entlang Lake Hazen.

Summer climate

Hazen Camp has a very favourable summer temperature regime, comparable to areas in far lower latitudes (Savile 1964, Oliver & Corbet 1966, Corbet 1967). July mean temperatures at Hazen Camp for 1962 (46.7°F), 1963 (43.8°F), 1965 (41.0°F), and 1966 (42.1°F) do not differ significantly from those recorded at southern Baffin Island (46°F), and Victoria Island (48°F). When the "frost-free season" and the total "growing-degree days" are compared with those of many southerly locations, Hazen Camp has a remarkably warm summer (Corbet 1967). Comparing the 1966 summer temperature pattern with those recorded in other years at Hazen Camp, the 1966 breeding season was slightly warmer than normal, but had a colder and more extended spring.

BREEDING HABITAT

There is no exact information on the breeding habitat of the Knot, probably because of the difficulty in finding nest sites and the remoteness of its breeding grounds. From the descriptions of the few nests which have been found it seems clear that the choice of nest site varies widely and would be difficult to express in any useful general form (see Manniche 1910, Feilden 1920, Bent 1927, Pleske 1928, Bird and Bird 1941, Salomonsen 1950, Godfrey 1953, Parmelee and MacDonald 1960). It was apparent, however, that Knots at Hazen Camp were numerous and nested on habitats ranging from marshy slopes and flats in the foothills and lowlands to well-drained clay and *Dryas*-hummocked slopes and tundra. Although a systematic attempt was made to locate all nests in the census area, which contained the complete range of nesting habitats, it is likely that some nests were missed because of the highly effective anti-predator behaviour of Knots in remaining on the nest even when in danger of being trodden upon.

Six of the seven nests found at Hazen Camp were on dry hummocked or frost-boiled terrain with poor vegetative cover. The nest sites were as follows (Figure 1): nests 2 and 7 were on the summit of dry clay slopes, nests 3 and 4 were in *Dryas*-hummocked tundra, nest 5 was towards the base of a hummocked slope in *Dryas*-hummocked tundra, nest 6 was at the base of a gravel mound in *Dryas*-hummocked tundra, and nest 1 was on a slightly raised *Dryas-Kobresia* area of a temporary stream bed. Four were scraped into a clump of *Dryas* (nests 2, 4, 5, 6), one (nest 1) into a *Dryas-Kobresia* patch, one (nest 3) into a *Dryas-Salix* patch, and one (nest 7) into bare clay beside a large *Salix* stem. All of the 22 old nest depressions found on the study area were scraped into patches of *Dryas*, or *Dryas-Kobresia* and *Dryas-Salix* association; some were on *Dryas*-hummocked tundra, but the majority were on *Dryas*-hummocked slopes. Nearly all these nests and depressions were close to relatively wet areas (marshes, ponds, or streams), the furthest distance away being about 165 m (nest 6). This distribution pattern is consistent for all nests recorded on the study area (Figure 1).

In summary, Knots at Hazen Camp seem to favour hummocked slopes and tundra, either dry or moist, for nesting. Nests are sometimes sited on clay plains and summits, which characteristically support a variable *Dryas* and *Salix* vegetation, but rarely on gravel slopes or hills. The nest depression is usually located in a *Dryas* clump, often situated in close proximity to a marsh, pond, or stream to which the young are directed after hatching, probably because most food is available for Knots in such areas (see p. 2).

BREEDING CYCLE

Arrival and dispersal

Populations of Knot breeding in Ellesmere Island migrate to winter in the Old World (Godfrey 1953, 1966). Large numbers stop over during the spring migration in Iceland, the majority of which depart during the last week of May for their northern breeding grounds (Morrison 1972, personal communication), where arrival occurs in late May and early June. In northeast Greenland, they have been sighted on 2 June 1907 and 28 May 1908 (Manniche 1910), and 28 May 1938 (Bird and Bird 1941).

Several arrival dates have been recorded for the north coast of Ellesmere Island. Near Alert, Feilden (1877) in 1875 and MacDonald (1953) in 1951 first sighted Knots on 5 June and 31 May respectively. At Fort Conger, Lady Franklin Bay, they arrived on 3 June in 1883 (Greely 1888) and on 30 May in 1915 (Ekblaw in Bent 1927). Arrival dates for the Fosheim Peninsula were 27 May 1951 (Tener in Godfrey 1953), 27 May 1953 and 1 June 1954 (Bruggeman in Parmelee and MacDonald 1960), and 30 May 1955 (Parmelee and MacDonald 1960). At Hazen Camp Knots have been seen in early June (Savile and

Oliver 1964); in 1965 they were first recorded on 4 June (Oliver, personal communication).

In 1966, small flocks of Knots were already present upon our arrival at Hazen Camp on 3 June, frequenting the lake shoreline and exposed wet tundra areas, though the main influx of birds did not occur until 5 June when many flocks were seen following the lake margin in a southwesterly direction. Seven flocks ranged in size from 6 to 60 birds, averaging 27 per flock; a roosting flock of about 150 individuals was flushed from a snowfree area east of camp. Knots were reported near Hare Fiord on 29 May.

At Hazen Camp, Knots appeared to be widely distributed over the tundra by 7 June with large flocks occurring only along the lake shoreline, and especially on wet marshy slopes. They disappeared from the shoreline by 10 June, by which time most birds were found in small groups feeding at inland marshes and ponds or in pairs elsewhere over the tundra.

Territoriality, song-flight display, and breeding density

Knots demonstrate territorial behaviour by area defence and advertisement. In June many long aerial pursuits were observed which became less frequent after the initial settling period. The chases involved one bird pursuing another at a height of 1.5 to 3 m uttering shrill cries, which terminates with the pursuer veering around in a glide with its wings held up in a V-shape and returning in the original direction giving the soft call of the song-flight display.

The most conspicuous activity advertising the territory is the song-flight display of the male which was heard from the time of our arrival until mid-July. The male (Bird and Bird 1941, Salomonsen 1950, personal observations) ascends from the ground in a steep rapid flight to a height of about 20 to 160 m where the song-flight display is performed in three phases: 1) the diagonal glide, 2) the horizontal glide, and 3) the quivering flight accompanied by almost continuous rapid calling (1 call per second) as shown in Figure 6. After the initial ascending flight the diagonal glide begins with outstretched wings held above the horizontal usually calling *whip-poo-mee*. This is followed by the horizontal glide with wings horizontal and a change to a two note flute-like call *poo-mee*. The quivering flight consists of rapid wing flapping in a very short arc, which serves to regain altitude lost during the glide, while sometimes uttering the *poo-mee*

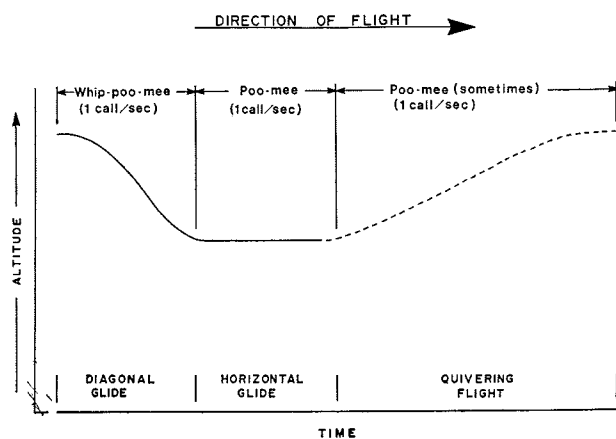


Fig. 6: Song-flight display of the Knot.

Abb. 6: Ablauf des Fluggesangs des Knuts.

call. The gliding and quivering flight both last 5 to 10 seconds each, with a series of this display often lasting 5 to 10 minutes. The flight to the ground is a swift glide on wings held high above the horizontal in a V-shape. It terminates in the wing-up display. In June the song-flight display of one bird often stimulated neighbouring birds to display, until at times three or four were displaying simultaneously.

Changes in territorial behaviour and area-attachment were measured by counting the number of series of the song-flight display (a series represents the period from ascent to descent) heard per 4-hour period in the census area. Aerial activity was highest between 13 and 19 June (average: 21 flight displays / 4-hours, range: 19—24) during egg-laying. It declined in early July (from 21 to 9 displays) and concluded at least by 20 July (from 9 displays to none), by which time most eggs had hatched and the family groups had abandoned their nest territories.

Nearly all the nests found in 1963 and 1966 were close to marshes, streams, or tundra ponds. Although it seems likely that one or two nests were missed in the census area, aerial activity suggested that the number of nests recorded was fairly typical of breeding densities in all the foothill and lowland regions. The census area (240 ha) supported at least 3 Knot pairs and possibly 5, based on observations of birds performing song-flight displays. The total number of pairs breeding in the Hazen Camp study area was estimated to be about 25 (1.09 pairs / km²).

Reproductive condition

Testes of male Knots reached maximum size before mid-June at Hazen Camp in both 1965 and 1966 (Figure 7). Testis size decreased from mid-June throughout the remainder of the summer season, though the exact manner of the decline cannot be estimated because of the small sample size.

The small number of adult females examined prevents a description of the gonad cycle in females. Sizes of the largest oöcyte of three birds in 1966 measured: 3.5 mm (12 June), 4.0 mm (20 June), and 6.0 mm (26 June).

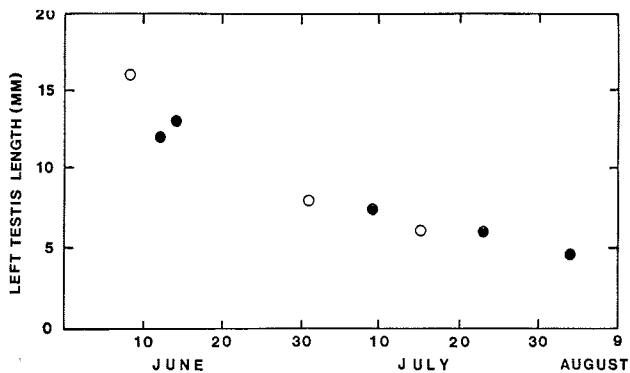


Fig. 7: Reproductive condition of male Knots. ○ 1965 specimens, ● 1966 specimens.
Abb. 7: Fortpflanzungsfähigkeit männlicher Knots (Exemplare ○ 1965, ● 1966).

Copulation

Coition was observed only once in 1966. It occurred in the egg-laying period shortly after the incubating adult had been flushed from nest 1. Below is a description of the copulation:

19 June (3:00 p. m.). The pair landed about 16 m from the nest on the opposite slope from where I was hiding. They made long wailing notes. The male then gave a courtship note and flew close to the female. As he landed in front of her he gave

a wing-up display, then moved behind and mounted her. Once on her back he flapped his wings rapidly. He remained on the female for 56 seconds, the last 15 to 20 of which wing-flapping ceased. The act was broken by the movement of the female causing the male to lose balance. At 3:15 p. m. the female (?) flew towards the nest, landing 0.5 m from it, and then walked over and settled on the eggs. The position of the tails of both birds was not observed.

An attempted copulation was observed near Hazen Camp on 12 June 1965 (M. H. Colbo, personal communication). The male approached the female with his tail raised high, stepped close to her, and then attempted to mount from the rear while pulling lightly at the feathers on her back and neck. Two attempts were made, but both were unsuccessful.

Egg-Laying

Only one of 7 nests in 1966 did not have a complete clutch when found. At this nest the interval between the laying of the third and fourth egg was slightly more than two days (checks made at roughly 12-hour intervals). In 1963, Oliver (personal communication) also recorded a two-day interval between a third and fourth egg at Hazen Camp.

By extrapolation from hatching dates using an incubation period of 22 days (Nettleship 1968) and an interval of six days for the laying of a four-egg clutch, the first eggs of the four successful nests were laid from 15 to 23 June (Table 1). Three of the four clutches were completed between 20 and 23 June. Of seven clutches recorded, five had 4 eggs, and two had 3 eggs.

Nest number	Date found	Estimated date of first egg	Estimated date of last egg	Number of eggs when found	Clutch size (eggs)	Number of young hatched	Date of hatching
1	19 June	15 June	20 June*	3	4	4	12 July
2	25 June	—	—	3	3	—	—
3	1 July	20 June	23 June	3	3	2	15 July
4	4 July	17 June	22 June	4	4	4	14 July
5	4 July	—	—	4	4	—	—
6	7 July	23 June	28 June	4	4	4	20 July
7	7 July	—	—	4	4	—	—

* known date

Tab. 1: Data on seven Knot nests found in 1966 at Hazen Camp. Hatch dates represent the day all viable eggs of a clutch had hatched.

Tab. 1: Angaben für sieben 1966 bei Hazen Camp gefundene Knot-Nester. Die Schlupfdaten beziehen sich auf den Tag, an dem das letzte Junge geschlüpft war.

Nests and eggs

Most of the nests of the Knot at Hazen Camp were cup-shaped depressions, often with well defined rims, scraped into the top or edge of a patch of *Dryas* (Figure 8); one nest was situated on bare clay bordered by *Salix*. All the nests were lined with dried leaves (*Dryas*, *Salix*, grasses) and pieces of a white lichen. Seven nest cups averaged 11.9 cm long (range: 11.0—12.5 cm), 11.1 cm wide (11.0—11.5 cm), and 4.4 cm deep (3.0—6.5 cm). In general, the overall greater size of the depression made Knot nests distinct from those of the Turnstone which nested in the same areas (see Nettleship 1973).

The eggs were typically subpyriform or ovate with a pale green ground colour streaked with spots and spirals of dark brown concentrated at the blunt end. Colour varied



Fig. 8: Nests and eggs of the Knot. Above, nest is a cup-like depression on *Dryas-Kobresia* tundra. Below, nest is a deep depression in a *Dryas*-capped hummock.

Abb. 8: Nest und Eier des Knuts.
Oben: Nest in einer tassen-ähnlichen Vertiefung in der *Dryas-Kobresia*-Tundra.
Unten: Nest in einer tiefen Mulde auf von *Dryas* besetztem Hügel.

considerably, some being more heavily marked with brown than others. Measurements of length and breadth of 23 fertile eggs at Hazen Camp in 1966 averaged 43.19 mm (range: 41.5—45.0 mm) and 29.63 mm (range: 28.9—30.7 mm), respectively.

Activities during incubation

Both sexes incubated the eggs, though one of the pair was typically on the nest more frequently than the other; which sex exhibited the greater attentiveness was not determined. Pairs were seldom seen during the periods of incubation and hatching. Usually only the incubating bird was present at a nest, and rarely did the bird's distress cries cause its mate to appear. On only three occasions were both birds of a pair seen close to the nest, twice during egg-laying (19 and 20 June) and once close to hatching (4 July). Probably after a bird is relieved at the nest it flies off the territory to feed in favoured locations. Flocks of Knots were seen regularly flying over the tundra and feeding at moist pond margins throughout the incubation period.

Hatching and young

The hatching period of 4 nests at Hazen Camp in 1966 extended from 12 to 20 July, with 3 hatches occurring between 12 and 15 July (Table 1). The incubation period of the last egg in nest 1 was between 21.5 and 22.4 days (see Nettleship 1968).

Three to four days before hatching slight cracks appeared on the blunt end of the egg. Eventually one or more small holes were formed which indicated the egg would hatch within 24 hours. Usually all the eggs of a clutch hatched out during a 24-hour interval. At the single nest where the time of laying of the individual eggs was partially known, the fourth egg hatched last. On 13 July (2015 hours) all 4 eggs at nest 4 were well-pipped; 14 hours later all the eggs had hatched and the young were 6 m from the nest.

Soon after the last egg hatched the chicks left the nest-site with the adults. Attempts to relocate family groups after they left the nest-site were largely unsuccessful. Before departure chicks were banded to assist in following family movements, but few banded chicks were seen again. The young from nest 1 were found about 225 m from the nest-site 16 hours after banding, near the entrance to pond 10; the following day they were relocated approximately 350 m from the nest-site feeding along the pond margin.

The first flying young were recorded on 2 August, but it is likely that some fledged in late July. Parmelee and MacDonald (1960) estimated the fledging period to be about 18 days.

Breeding success

Of the 7 nests under observation at Hazen Camp in 1966, three were destroyed before hatching (Table 1). Nest survival to hatching was 57%, while only 14 of the 26 eggs (53%) originally laid hatched. Both these values fall well below the ranges for nest survival and egg survival recorded for other *Calidris* species (Holmes 1966a, 1970; Soikkeli 1967; Jehl 1971) and Charadrii (Boyd 1942). In all three cases of failure the nest was simply found empty though intact. Fledging success was difficult to estimate, but observations of family size (the number of young accompanied by one or two adults) before fledging suggested that survival of young from hatching to fledging was low, usually less than 50%. Nearly all these chick losses may safely be attributed to predation by Long-tailed Skuas *Stercorarius longicaudus* (personal observations, Maher 1970) and to a lesser degree by Arctic Foxes *Alopex lagopus*.

Post-nesting movements

After hatching Knot families quickly moved away from the clay plains and tundra areas where they nested. Soon after hatching adults and broods were encountered only along the slopes or beds of marshy areas with concentrations located close to semi-permanent, permanent, and tarn ponds, especially ponds 10 and 34 (both tarns). On 20 July there were no birds on the study area, except for ponds 10 and 34 where there were large concentrations of Knot and Turnstone families.

By late July almost all adults and young had deserted inland areas, including tarn ponds, and could only be found near the gravel beaches and associated slopes bordering Lake Hazen. In early August most chicks had fledged and were seen flying along the lake shoreline unaccompanied by adults, often associated with juvenile Turnstones. At this time most adult Knots had departed, although two were seen as late as 12 August. Most juveniles left before 15 August. This suggests that the main exodus of young takes place after most adults have departed, and that almost the entire Knot population had deserted the breeding grounds by mid-August. Juveniles have been seen as late as 31 August at Eureka (Parmelee and MacDonald 1960) and 25 August on the north coast (MacDonald 1953).

FOOD

Source, importance, and availability

Insects are easily the principal food of most shorebirds during the summer breeding period in arctic regions (e. g. Manniche 1910; Bird and Bird 1940, 1941; Pitelka 1959; Parmelee and MacDonald 1960; Holmes 1966a, b; Holmes and Pitelka 1968; Holmes 1970, 1972). However, on western Ellesmere Island Parmelee and MacDonald (1960) found Knots feeding exclusively on plant matter (grass shoots, seeds, and other plant items) in the early summer, with a gradual switch to a predominantly insect diet (first Lepidoptera larvae, and then to adult insects, including chironomids and tipulids) as the season advanced. Other authors, including Feilden (1879) on the north coast of Ellesmere Island and Manniche (1910) in Greenland, have also noted the Knot's subsistence on vegetable foods at spring arrival on the breeding grounds before insects become available.

Since insect diversity is low at Hazen Camp, as in all arctic localities, with many of the orders and families which do occur represented by only one or two species (Downes 1962, 1964; Oliver 1963), the number of insect groups available as suitable prey is limited (Table 2). The most important group in the diet of breeding shorebirds at Hazen Camp was Chironomidae, the most numerous (in terms of absolute numbers and biomass) and exploitable insect group present. Other less important groups consisted of the larvae of Lepidoptera early in the season, and the larvae and adults of other Diptera. Such groups as Areneida, Coleoptera, Trichoptera, and Hymenoptera were either poorly represented in numbers or largely inaccessible. Details of availability and changes in numbers of potential prey organisms, both subterranean and surface species, in habitats frequented by Knots during breeding at Hazen Camp are given in another report (Nettleship 1973), but may be briefly summarized as follows: Chironomidae are available for most of the summer season, but show wide variation in local abundance. Chironomid emergence occurred in late June in the shoreward permanent and semi-permanent ponds and in early July in similar pond types that were located further inland and at higher elevations. The period of greatest emergence, and presumably availability, in the Hazen Camp area was between 3 and 17 July, with the peak at 8—12 July; one final important source of chironomids was Lake Hazen itself where emergence was highest in late July and August (Figure 9).

Araneida	Dictynidae: <i>Dictyna</i> Lycosidae: <i>Paradosa</i> , <i>Tarantula</i> Linyphiidae: <i>Erigone</i> , <i>Hilaria</i> Thomisidae: <i>Xysticus</i>
Coleoptera	several species
Trichoptera	Limnephilidae: <i>Apatania</i>
Lepidoptera (Larvae)	Lymantriidae: <i>Byrdia</i> Noctuidae: <i>Crymodes</i> Nymphalidae: <i>Boloria</i>
Diptera	Tipulidae: <i>Nephrotomia</i> , <i>Tipula</i> Chironomidae: many species Culicidae: <i>Aedes</i> Mycetophilidae: several species Sciariidae: several species Dolichopodidae: <i>Dolichopus</i> Empididae: <i>Rhamphomyia</i> Syrphidae: 4 species Calliphoridae: 3 species Tachinidae: <i>Petinartica</i> Muscidae: several species
Hymenoptera	Tenthredinidae: 4 species Ichneumonidae: several species

Tab. 2: Potential prey taxa for Knots at Hazen Camp in 1966.
Tab. 2: Potentielle Futtertiere des Knuts bei Hazen Camp 1966.

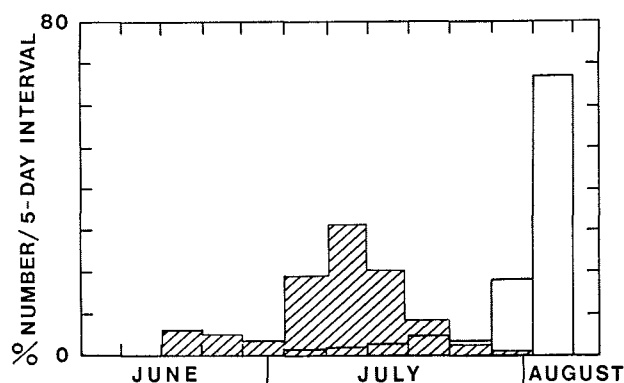


Fig. 9: Pattern of Chironomidae emergence from five inland ponds (ponds 1, 2, 11, 32, and 34) (diagonal shading) and Lake Hazen (open histogram).

Abb. 9: Schema des Chironomidae-Auftretens von fünf Inland-Tümpeln (1, 2, 11, 32 und 34, Schrägschraffur) und Lake Hazen (weiß).

Summer diet of Knots

The results of the analysis of the stomach contents of 13 adults, 5 chicks, and 1 flying young collected near Hazen Camp in the summers of 1965 and 1966 are summarized in Table 3.

From the time of arrival until mid-June the primary food was plant material, consisting chiefly of the perigynia and achenes of Cyperaceae (*Carex*) and the stems of Equisetaceae (*Equisetum*). Other potentially important food items included the bulbils of Polygonaceae (*Polygonum*) and moss sporophytes (*Polytrichum*). All of these plants are found in the wet snow-free marshes and springy slopes where Knots were most often seen in early June. The only animal material to appear before mid-June was Lepidoptera larvae, which occurred in the stomach of a single bird collected on 8 June 1965.

Food group	6 stomachs (adults) 4—14 June	3 stomachs (adults) 20 June— 1 July	3 stomachs (adults) 9—23 July	3 stomachs (chicks) 15—23 July	2 stomachs (chicks) 3 August	1 stomach (flying young) 3 August	1 stomach (adult) 3 August
Plant	<i>58.9</i>	<i>56.5</i>	<i>43.7</i>	<i>10.0</i>	<i>19.5</i>	<i>57.0</i>	<i>45.0</i>
Bryophyta	+			+	+		+
Equisetaceae	+	+	+				
Gramineae	+				+		
Cyperaceae	+	+	+	+	+	+	
Polygonaceae	+						
Caryophyllaceae					+		
Rosaceae	+				+		
indeterminable	+	+					+
Animal	<i>9.0</i>	<i>22.0</i>	<i>34.3</i>	<i>57.0</i>	<i>50.5</i>	<i>tr</i>	<i>35.0</i>
Trichoptera					+		
Lepidoptera	+	+					
Diptera							
Tipulidae			+				
Chironomidae							
adults		+	+	+	+		+
larvae & pupae			+				
Empidae			+	+			
Muscidae			+				
indeterminable				+			
Hymenoptera				+			
indeterminable	+					+	
Gravel and grit	<i>33.0</i>	<i>21.5</i>	<i>22.0</i>	<i>33.0</i>	<i>30.0</i>	<i>43.0</i>	<i>20.0</i>

¹) One adult (sample 9—23 July) and one chick (sample 15—23 July) were collected at Gilman Camp, Lake Hazen, in 1965.

²) Special thanks are given to M. H. Colbo for permission to examine stomachs of 5 adults and 1 chick collected at Hazen and Gilman Camps in 1965.

Tab. 3: Stomach contents of Knots of Hazen Camp ¹) in 1965 ²) and 1966. Numbers in italics represent the mean percentage of the total volume of the major divisions. Positive (+) sign indicates the occurrence of food items within the major groups. Unmeasurable food items are shown as trace (tr).

Tab. 3: Mageninhalt des Knuts von Hazen Camp 1965 und 1966. Die kursiven Zahlen stellen den mittleren Prozentanteil der drei Hauptgruppen an der Gesamtnahrung dar. Ein Pluszeichen (+) steht für die Beteiligung einzelner Arten am Nahrungsangebot. Kaum noch meßbare Nahrungsanteile sind mit (tr) gekennzeichnet.

After mid-June the percentage of animal matter increased as dipterous insects became available, but plant materials continued to constitute a large part of the diet, usually comprising more than 50% of all digestible food in the stomach contents. For most of the summer adult Chironomidae were the most important source of animal food of adult Knots, supplemented by various other dipterous insects, and by Lepidoptera larvae in early June. These birds foraged in most habitats on the Hazen Camp study area, but they concentrated at wet areas, especially along pond margins where they fed in the shoreline moss. The small sample size precludes a precise description of changes in the summer diet of adult Knots.

The food of the young before fledging consisted principally of dipterous insects, usually adult Chironomidae. Adults and young foraged together in marshes and along the slopes and shorelines of ponds where chironomids were plentiful. After the young had fledged, they appeared to feed almost exclusively on adult chironomids along the Lake Hazen shoreline in small flocks, often mixed with juvenile and adult Turnstones, although the single flying young examined contained only a trace of insect material.

Foraging behaviour

The foraging behaviour of Knots at Hazen Camp changed as the season advanced. In early June probing and jabbing techniques were most often seen at wet marshes and springy slopes where they took *Carex* seeds and *Equisetum*. They also probed into snow-free *Dryas* patches and hummocks, probably for Lepidoptera larvae and Araneida. By late June the occurrence of the probe-jab method declined and a pecking technique predominated, a change in foraging behaviour which coincides with the appearance of dipterous insects on the tundra. All young observed fed by pecking. In late July and August, Knots foraged along the lake shoreline and gravel beaches picking at adult chironomids.

DISCUSSION

Knot populations breed at high latitudes where suitable food is limited to a small part of the year, chiefly from June through August, the short arctic summer. It seems clear that the breeding season is timed to coincide with the short-lived peak in food availability and that the young hatch on average at the time when small-sized adult insects, principally chironomids, are most abundant on the tundra surface. But what determines the extremes of the breeding season is less clear. If food availability is important at both the beginning and the end, it seems possible that the energy-demanding process of egg formation limits the start of breeding whereas the increasing scarcity of adult insects over the tundra after mid-summer may cause the adults to leave the breeding area and move to coastal habitats where the food supply is more dependable or start their southward migration. Holmes (1966a, 1966b) has argued convincingly that the chief proximate factor influencing population movements, departure times, and other activities of Dunlin *Calidris alpina* during the summer period is weather, acting either directly or causing changes in prey availability. Further detailed work is required on the relationship between the variability in the abundance and availability of important prey species both within and between seasons and the annual physiological cycle if causal explanations are to be elucidated.

Food also appears to influence the distribution of breeding pairs over the tundra, restricting them to the general vicinity of marshes, streams, and ponds where food is most available when the young hatch. As the Knot avoids nest-predators by remaining on the eggs to escape detection (through cryptic colouration), which allows the non-incubating bird to move to a distant feeding area, it is reasonable to suppose that the distribution of nests within the potential nesting space depends on the maximum distance that newly hatched young can travel to a favourable food location. One possible consequence of this limited nesting range may be the occurrence of intra-specific competition for nest-sites, as a result of which the conspicuous song-flight display of the male during egg-laying and incubation has arisen. Thus territoriality in Knots seems to have two principal functions: first, to space out the breeding pairs so that nests are less easily detected by nest-predators; and second, to limit the number of pairs nesting to the upper limit which can be supported on the breeding grounds.

The relative importance of plant material in the diet of the Knot appears to be unique amongst shorebirds nesting in arctic regions. Other *Calidris* species studied by Holmes (1966b, 1970, 1972) and Holmes and Pitelka (1968) in Alaska did not utilize this food source to any great extent. Plant material was also important in the diet of the Turnstone at Lake Hazen in early June (Nettleship 1973), though the aggressive foraging behaviour of this species cited by MacDonald and Parmelee (1962) may enable it to

make better use of food resources not taken by the Knot. The ability to utilize plant material may probably then have an important survival value for the Knot.

In summary, Knots show synchronous hatching which appears to be timed to peak food supply for the young in the short arctic summer. Territoriality is believed to be closely associated with the protection of the nest against predators and has at least a local effect in regulating the number of breeding pairs.

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