THE TAXONOMY OF REDPOLLS

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CONTENTS

1. INTRODUCTION

Among the holarctic passerines few species-level taxonomic problems have generated as much controversy as the case of the redpolls *Carduelis flammea/hornemanni*. For over a hundred years the various populations have been repeatedly grouped into different specific and subspecific assemblages (Table 1). It is not surprising that the birds were recently referred to as a 'taxonomic enigma' (Brit. Birds 78: 258).

1.1. THE SPECIES

The morphological characteristics of many forms appear to intergrade. This has been interpreted as evidence of hybridization, and constitutes the basis of an argument for treating all the redpolls as conspecific under the name *flammea* (Table 1, d). The conventional view is to ignore this problem and treat the birds as two separate species, the Common (*flammea, islandica, rostrata* and *cabaret*) and Arctic Redpolls (*hornemanni* and *exilipes*) (Table 1, h). This polarization of opinion forms the central issue in redpoll systematics.

Since the last review of redpoll taxonomy focused attention on this argument (Salomonsen 1928) it has moved no nearer to a consensus (Molau 1985, cf. Troy 1985). Part of the problem arises from different interpretations of the variation seen in some redpoll populations, which have often been studied in isolation from each other. In an attempt to clarify the characters of the races and

Table 1. Some of the proposed taxonomic arrangements of the various forms of redpolls. The two most frequently adopted in the recent literature are marked*.

a. Coues (1862b) gave specific status to *rostrata, fuscescens, cabaret, flammea, holboellii, exilipes* and *hornemanni*.

b. Brewster (1883) gave specific status to *rostrata* (although he called it *holboellii* by mistake).

c. Brooks (1917) grouped *exilipes* as a subspecies of *C. flammea*, but placed *C. hornemanni* separately.

*d. Salomonsen (1928, 1951) placed all the redpolls together under the name *flammea*. This view is followed by Dement'ev & Gladkov (1954), Williamson (1956, 1961), Voous (1960) and Troy (1985).

e. Hortling & Stuart-Baker (1932) gave *holboellii* specific status.

f. Todd (1963) believed *C. exilipes, C. hornemanni* and *C. rostrata* to be separate species in addition to *C. flammea*.

g. Molau (1985) suggested that *exilipes, hornemanni* and *islandica* each be treated as full species, separate from *flammea* (including the subspecies *rostrata* and *cabaret*).

*h. Most recent authors separate *flammea* (with *cabaret, islandica* and *rostrata*) from *hornemanni* (with *exilipes*), for example, Vaurie (1956, 1959), Howell *et al.* (1968), Mayr & Short (1970) and Voous (1977).

the pattern of variation in redpolls, I have examined museum specimens from throughout the range of the birds.

As the literature on redpolls is now sizeable and often conflicting, the discussion below brings much of it together. In addition to placing the findings of the present study in context, a different interpretation will be given to some earlier results. It will be shown that the redpolls comprise two sibling species, and that much of the past disagreement arose from over-narrow definitions of the variability of each. The results of other studies are not in conflict with this view. Details of recent field-work in Iceland and Finland will be presented elsewhere.

Throughout, unqualified reference to *flammea* or *hornemanni* should be taken to mean the nominate subspecies only. Binominal terminology is used where the species are being discussed.

1.2. THE SUBSPECIES

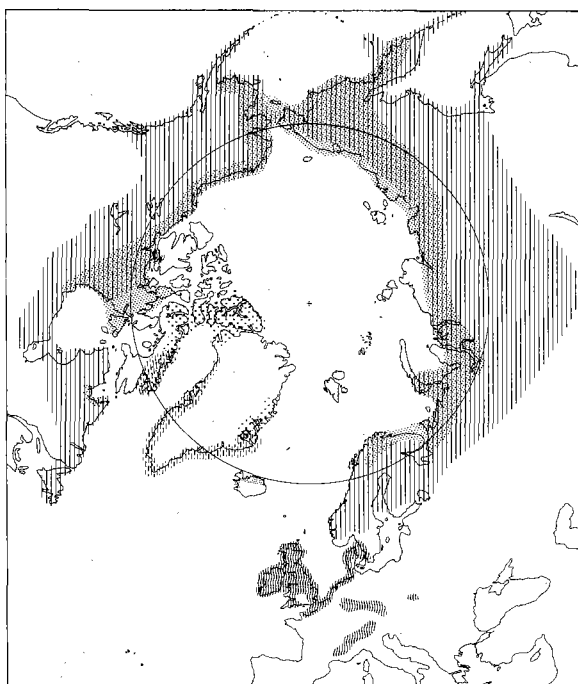Most recent authors (*e.g.* Vaurie 1959, Howell

Fig. 1. Breeding ranges of the subspecies of *Carduelis flammea* and *C. hornemanni.*

et al. 1968) accept the following subspecies of redpolls (Fig. 1):

1. *cabaret* Müller 1776, Lesser Redpoll, breeding range – British Isles, expanding since 1960/-1961 into the low countries (Blok & Spaans 1962), northern France, West Germany and, more recently, into Denmark (Hald-Mortensen 1970) and southwestern Sweden (Götmark 1978, 1981, Lindström *et al.* 1984); a second population is found in the mountains of Czechoslovakia and the Alps, recently expanding in West Germany (Fellenberg 1984), westwards in southern France (Duquet 1984) and northwards in East Germany (Schmidt 1984); introduced into New Zealand and Lord Howe Island;

2. *flammea* Linnaeus 1758, Mealy Redpoll, breeding range – northern Eurasia and North America (except Baffin Island, Greenland and Iceland) from the treeline (or further north) south to about latitude 52N. Occasionally breeds to the south of its normal range. Previously known as *linaria* Linnaeus 1758 but later it was shown by Lönnberg (1931) that Linnaeus had described the redpoll twice and the earlier name, *flammea*, had priority (B.O.U. 1932);

3. *rostrata* Coues 1862, Greater Redpoll, breeding range – Baffin Island and southern Greenland; at least irregularly in Labrador (Todd 1963) and Scotland (Murton & Porter 1961, Williamson 1961);

4. *islandica* Hantzsch 1904, Iceland Redpoll, breeding range – Iceland; often regarded as a hybrid swarm between *rostrata* and *hornemanni*;

5. *exilipes* Coues 1862, Hoary Redpoll, breeding range – tundras and forest edges of northern Eurasia and North America, broadly sympatric with *flammea*;

6. *hornemanni* Hölboell 1843, Greenland Redpoll, breeding range – Ellesmere Island, Baffin Island and northern Greenland.

From among the extensive synonymy, five other names are frequently encountered in the redpoll literature:

7. *britannica* Schmiedeknecht 1906 and

8. *disruptis* Clancey 1953, both now generally synonymised with *cabaret*, but proposed as names for a British subspecies; *disruptis* is a

replacement name for *britannica*, which became a junior secondary homonym of *Carduelis carduelis britannica* (Hatert 1903) when *Acanthis* was merged with *Carduelis*;

9. *fuscescens* Coues 1862, for a proposed species in Labrador (Coues 1862a); reduced by Coues himself, first to subspecific status (Coues 1872), and then recognised as the summer plumage of *C. f. flammea* (Coues 1874); now treated as a synonym of *C. f. flammea* (although recognised by, for example, Salomonsen 1928, Hellmayr 1938, Dement'ev & Gladkov 1954);

10. *holboellii* Brehm 1831, a name given to long-billed birds otherwise like *flammea*. They may be found mainly at the northern limit of the distribution of *flammea* in both America and Eurasia, but appear to be commonest in north-east Siberia (Vaurie 1956);

11. *pallescens* Homeyer 1880, often applied to birds with plumage said to be intermediate between *flammea* and *exilipes*, from northern Scandinavia (for example, Stejneger 1884, Payn 1947, Harris *et al.* 1965).

1.3. THE GENUS

The redpolls are part of a species-group which also includes the Twite *C. flavirostris* (Mayr & Short 1970). The redpolls and the Twite, along with their closest relatives (*C. cannabina*, *C. yemenensis* and *C. johannis*), are often placed together in the genus *Acanthis* Borkhausen 1797 (Morony *et al.* 1975, following Howell *et al.* 1968: 250, footnote). Recent opinion tends to include *Acanthis* within an extended genus *Carduelis* Brisson 1760 (Voous 1977). The redpolls in particular appear close to the Siskin *C. spinus* and Pine Siskin *C. pinus*. Considering the similarities in plumage pattern, anatomy, behaviour and vocalizations (*e.g.*, Mundinger 1979, although see also Zablotskaya 1984), there seem to be no pressing reasons for the separation of *Acanthis* from *Carduelis*. Evidence from a recent study of cardueline proteins confirms this view (Marten & Johnson 1986). *Aegiothus* Cabanis 1851 and *Linaria* Vieillot 1816 are synonyms of *Acanthis* commonly seen in the older literature.

2. METHODS

A total of 540 skins from the British Museum (Natural History), the Royal Museum of Scotland, Icelandic Museum of Natural History, the Museum of the Department of Zoology at the University of Aberdeen and several smaller collections were examined. No birds in juvenile plumage were used due to the small sample size for some populations.

It is difficult to determine the age and sex of redpolls from plumage characters, although some accounts suggest otherwise (*e.g.* Wood 1969). Recent discussion has helped to clarify matters (Evans 1966, Brooks 1973, Mead 1973, Davis 1975, Langslow 1975, Jones *et al.* 1975, Da Prato & Da Prato 1978, Boddy 1979, 1981, Svensson 1984). The recommended technique varies from race to race, and no method gives complete accuracy. Boddy (1981) has presented a useful discussion for *cabaret*.

The following measurements were taken from each specimen: culmen-length from the base of the feathering; bill-depth at the base; lower mandible width at the base (all these to the nearest 0.5 mm); poll-length; tail-length; wing-length, by the maximum length method (Svensson 1984: 16; these last three to the nearest mm). Several different methods for taking wing lengths have been used in previous studies and the results are therefore not strictly comparable (see for example Evans *et al.* 1967). Coues (1862a & b) showed toe-length to be a useful character for separating redpolls, but this proved impracticable to measure in most skins. Poll colour was scored on a scale from 1 (yellow) to 5 (red); cheeks, breast and rump were each graded from 1 (no pink) to 6 (red) after Brooks (1973). A colour-index was obtained by summing the scores for the cheeks, breast and rump, giving an index of $3 =$ no pink and $18 =$ maximum score. Age was determined from the shape of the tail feathers in birds in fresh plumage only (Svensson 1984: 253); otherwise the birds were not aged unless the breast was red, when it was taken to be an adult (Brooks 1973, Da Prato & Da Prato 1978 and others). Care was taken to try to identify any young birds that might have replaced some first-year tail feathers prematurely. (With live birds, tail feather shape can be used for ageing through to the spring and sometimes early summer, but the differences are less apparent in most museum specimens.) Throughout, the ageing term 'first-year' refers to birds between their post-juvenile moult and their first complete moult nearly a year later, *i.e.* in the latter part of their first calendar year through to late summer in their second calendar year. 'Adult' birds are older than this. A note was taken as to whether or not the bird had been sexed (if at all) by dissection. In the absence of gonadal evidence, birds with extensive red on the breast were assumed to be males (Da Prato & Da Prato 1978). Individuals were allocated to subspecies primarily by critical comparison of their plumages with large numbers of other birds collected at the same time of year, and only exceptionally by measurements. Detailed notes on plumage variability were recorded.

3. RESULTS

3.1. PLUMAGES

All the redpolls are very similar in appearance. When fully grown they have coloured polls which are usually a shade of red but sometimes are orange or, rarely, yellow. They have black bibs, small in autumn because of the wide pale edges to the feathers, but as the edges wear off the dark area extends down the throat and often onto the breast. The underparts are white, whitish or buffy, any

colour being most noticeable on the breast and flanks. The flaks particularly may be streaked. The feathers of the upperparts have dark centres and broad, paler brown, buff, grey or white edges. The rump is often paler and may be white. The wing and tail feathers are dark brown with paler edges. With wear, the paler edges of all the feathers abrade, often leaving only the dark centres to many feathers on the upperparts.

Adult males, to a lesser extent first-year males and even some females, have pink or red on the cheeks, breast, flanks and rump. The presence of any pink or red in the plumage of females, other than on the poll, was long disputed, despite the clear observations of Coues (1862b) over 120 years ago. In all birds in fresh plumage, any pink or red on the breast and other parts of the body are frequently masked by the light feather edges. As winter and spring progress these also wear, making the colour more obvious. Because of these extensive changes between the autumn moult and the following summer, it is essential when comparing the plumages of the different races only to examine birds from the same times of year. A difference of as little as a few weeks can have a significant effect on the appearance of the bird.

When segregated by the time of the year when they had been collected, almost all the redpolls were readily assigned to subspecies. Detailed plumage descriptions will be found in Witherby *et al.* (1938) and are not repeated here. This account summarises the differences between the fresh plumages of the races, based on the present series of skins. Comments on the identification of some forms are given in the Appendix.

cabaret: The smallest race with the most warmly coloured plumage. After the moult the edges of the feathers on the upperparts are rufous-brown, the same rufous colouring extending onto the sides of the head, breast, flanks and, although less intense, onto the edges of some of the wing and tail feathers. The back of the neck is particularly dark. The rump is often the same colour as the back, but in many cases it is noticeable paler, with grey feather-edgings.

flammea: This race has brown-buff feather edges on the upperparts. The rump colour varies considerably, but is usually paler than the back, often

comprising narrowly dark-centred feathers with broad white, whitish or grey edges, which may merge to give a clear white patch. Some adult males have an unstreaked, pink lower rump, up to 1 cm deep. The back of the neck is conspicuously paler than the back or mantle. The edges of the wing and tail feathers have less buff and are whiter than *cabaret*. Adult males have paler feather edges than other ages and females. The underparts of all the birds are less rufous than *cabaret* and the streaking is more intense. No evidence was found to support the recognition of *fuscescens* as a valid subspecies, although few breeding specimens from northern Quebec or Labrador were examined.

rostrata: Very like *flammea*, but larger and with darker feather edges. There is less variability in the colour of the back of the neck and the rump; both are quite dark. The flank streaks are coarser and the edges of the upper breast and flank feathers are buffer. The bib in *rostrata* tends to be slightly larger than in *flammea*.

exilipes (about the same size as *flammea*) and *hornemanni* (slightly larger than *rostrata*): Both *exilipes* and *hornemanni* are very pale, with greyish or whitish feather edges on the upperparts, wing and tail feathers and sides of head. The rump tends to be white, sometimes streaked in *hornemanni*, more frequently so in *exilipes*. The underparts are white with only a few, usually narrow, dark streaks on the flanks. The longest undertail coverts are occasionally unstreaked (especially in *hornemanni*), or have streaks that are, on average, narrower than those found in *flammea* or *rostrata*. The wing bars (pale tips to the median and greater coverts) are broad and white or whitish. In all features, *hornemanni* tends to be paler and brighter than *exilipes*. In both races, adult males tend to be paler than females or first year birds. First year birds are often buffer about the sides of the head, back of the neck, back, wing coverts, breast and flanks, particularly in *hornemanni* (Fig. 2). In *exilipes*, the ground colour of the upperparts is frequently a rich, warm buff-brown, most noticeable in fresh plumage, but sometimes recognizable through to the start of the breeding season. In fresh plumage especially, the contour feathers of both races feel soft and fluffy. Neither *hornemanni* nor *exilipes* achieves the in-
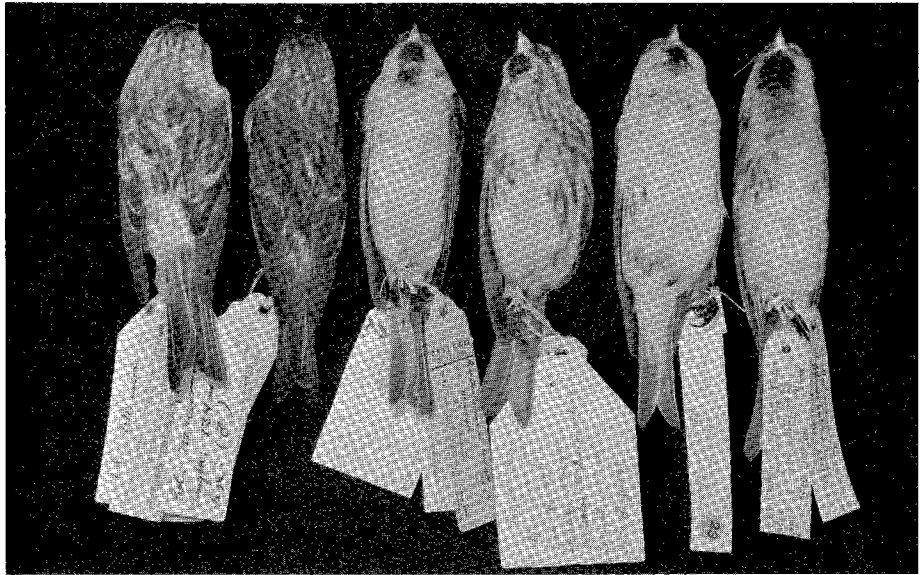
Fig. 2. Redpoll skins. From left to right: upperparts of typical examples of pale and dark *islandica*; underparts of pale and dark *islandica*, all four birds collected in Iceland in January; underparts of adult and first-year *hornemanni*, both collected in November.

tensity of redness on the breast that is seen in adult males of the *flammea*-group. Although some *exilipes* have uniquely small polls, there were only slight differences in the average measurements of poll sizes of all the subspecies, and the ranges of measurements overlapped broadly. Poll colour was found to be taxonomically uninformative.

3.2. INTERMEDIATE PLUMAGES

Flammea-exilipes: While many of the skins examined appeared to be (or were even labelled as) intermediate to these two types, only one, a recently-collected specimen from Alaska, proved to any extent difficult to assign to a race. All the others fell into two distinct types, although some were superficially intermediate. Most were indistinguishable from *flammea* other than by their slightly paler rumps. However, this feature is very variable in *flammea*, and these birds represented only part of that variation. The remaining birds were dark individuals of *exilipes*, including some with streaked rumps. The Alaskan skin was identified as *flammea* because of the lack of *exilipes* characters other than a narrow white rump. The colour of the back, sides of head, feather edges in wings and tail, and underparts all fell within the normal range of *flammea* variation. While it is possible that some of the birds examined were hybrids, apart from their rump colour (which is known to be variable), most were clearly either *flammea* or *exilipes*.

islandica: Skins collected in Iceland show a wide range of plumage variability, from dark birds with streaked rumps through to pale ones with pure white rumps (Fig. 2). This led Salomonsen (1951) to suggest that the population represented a hybrid swarm between *rostrata* and *hornemanni*, a view that has often been repeated. The need to examine birds from different seasons, or even months, separately was nowhere more important than with these Icelandic birds. Nor was the fact that the plumage differences between races of redpolls decreased as feather wear progressed more obvious or more critical than here. The Icelandic specimens examined included the Bird collection (Bird 1935, 1936; specimens now in BM (NH)). As with the last group of intermediates, when the skins from different times of the year were separated, most fell into two distinct categories, *rostrata*-like and *hornemanni*- (or *exilipes*-) like. The sides of the head particularly were clearly either buffy or greyish. On plumage alone the dark birds were almost indistinguishable from *rostrata* when compared month by month, although some individuals did have paler upperparts (particularly rumps) and there was a tendency to cleaner-looking underparts, both features seen best in fresh feathers. The pale birds were more frequently streaked on the rump than *hornemanni*, and had slightly more streaking on the underparts than many *hornemanni* or *exilipes*, but were otherwise similar to them in plumage.

Table 2. Wing-lengths (mm) of the races of redpolls, and the two forms of *islandica*. (n, sample size; SD standard deviation; imms, first-year birds; ads, adults.) Many birds were unaged and/or unsexed, hence not all sample sizes within a race or form are in agreement.).

	Females			Males			Both sexes		All birds
	imms	ads	all	imms	ads	all	imms	ads	
cabaret									
n	7	5	28	13	12	48	22	17	79
mean	67.1	68.6	68.5	70.2	70.8	70.1	69.3	70.2	69.5
SD	2.6	2.6	2.6	2.1	2.1	1.9	2.6	2.4	2.3
range	62–70	66–73	62–77	67–75	68–75	66–75	62–75	66–75	62–77
flammea									
n	26	17	77	26	45	122	57	65	213
mean	73.0	73.9	73.1	74.5	75.5	75.2	73.8	75.0	74.4
SD	1.7	2.0	2.0	2.3	2.2	2.0	2.1	2.3	2.2
range	70–77	70–78	70–78	71–80	72–81	71–81	70–80	70–81	70–81
rostrata									
n	11	6	20	21	12	44	37	18	71
mean	78.4	77.3	78.0	79.5	78.9	79.4	79.1	78.4	79.0
SD	2.0	2.5	2.0	2.4	2.6	2.3	2.2	2.6	2.4
range	75–82	74–80	74–82	75–84	73–81	73–84	75–84	73–81	73–84
dark *islandica*									
n	2	1	9	5	3	21	7	5	31
mean	74.0	77.0	76.0	78.6	79.0	78.5	77.3	78.4	77.7
SD	4.2	–	2.1	1.7	4.3	3.1	3.1	3.2	3.0
range	71–77	77	71–78	76–80	76–84	71–85	71–80	76–84	71–85
pale *islandica*									
n	3	4	11	4	8	18	7	12	29
mean	77.7	78.2	77.1	78.7	79.5	79.3	78.3	79.1	78.5
SD	2.9	1.3	2.2	3.1	2.1	2.5	2.8	1.9	2.6
range	76–81	77–80	73–81	76–83	77–83	76–85	76–83	77–83	73–85
all *islandica*									
n	5	5	20	9	11	39	14	17	60
mean	76.2	78.0	76.6	78.7	79.3	78.9	77.8	78.9	78.1
SD	3.4	1.2	2.2	2.2	2.6	2.8	2.9	2.3	2.8
range	71–81	77–80	71–81	76–83	76–84	71–85	71–83	76–84	71–85
exilipes									
n	16	5	31	5	18	34	26	23	73
mean	73.4	73.0	73.5	76.4	75.1	75.5	74.1	74.6	74.5
SD	1.5	2.0	1.7	2.3	1.6	1.7	2.0	1.9	1.9
range	71–76	71–76	71–77	74–79	71–78	71–79	71–79	71–78	71–79
hornemanni									
n	7	3	15	9	7	22	18	11	40
mean	82.0	84.3	82.4	85.7	85.3	85.1	84.2	85.1	84.1
SD	1.3	1.5	1.8	1.7	3.5	2.4	2.3	2.9	2.5
range	80–84	83–86	80–86	83–88	80–91	80–91	80–88	80–91	80–91

3.3. MEASUREMENTS AND COLOUR SCORES

Only a small proportion of each race were explicitly noted as having been sexed internally, the best sample being 26 out of 79 for *cabaret*. Generally, the sex noted on the specimen labels was found to be compatible with recent sexing criteria (see references above) in all but a few cases.

3.3.1. Intra-subspecific variation

The subspecies with the largest sample of birds of each age and sex was *flammea*. For this race there is a bimodal scatter in the distribution of colour-index against wing-length (Fig. 3). The upper cluster primarily consists of adult males and the lower of first-year males and females of all
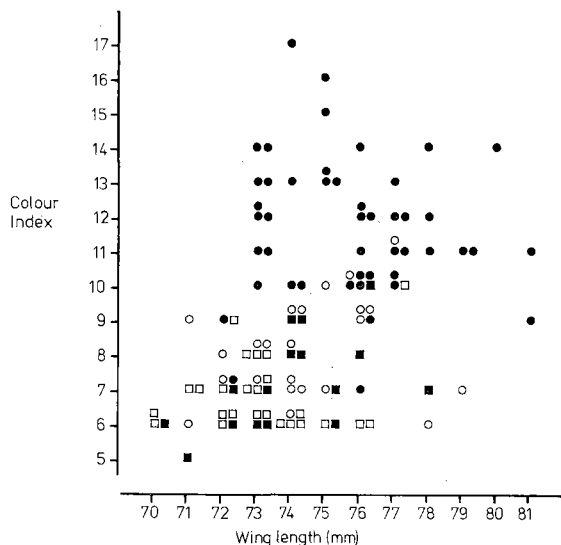
Fig. 3. Colour-index and wing-length for different ages and sexes in *flammea*. For calculation of colour-index, see text. Squares, females; circles, males; open symbols, first-year birds; filled symbols, adults.

ages. Males had, on average, longer wings than females (z-test; $z = 2.86, 7.21, P < 0.01$ for *cabaret* and *flammea*, the two largest samples) but there was much overlap (Table 2). Adult wing-lengths were longer on average than those for first-years of both sexes in *flammea* and *cabaret*, but the differences were not statistically significant. Of the three *rostrata* males aged as adults, one had no pink at all in the plumage, and the other two had colour-indices of 9 and 12. Salomonsen (1951) claimed that there was a dimorphism in the redness of adults in that race. My data confirm that some adult male *rostrata* have no pink on the cheeks, breast or rump. I cannot refute or substantiate the possibility of dimorphism, because the sample size was small and these results could also be obtained from inadequate sampling of a continuous variation. The breast colour of *flammea* males is variable but the almost complete absence of poorly-coloured adults suggests that this character is either not dimorphic in male *flammea*, or is very rare. Of the 26 internally sexed *cabaret*, only males had colour-indices greater than 7.

There was very little difference between the ages and sexes in average sizes of tails or bills, although the measurements of males, particularly adults, tended to be slightly larger. For this reason the age classes have been grouped in Tables 3–6.

Table 3. Tail-lengths (mm) of the races of redpolls, and the two forms of *islandica*. (See caption to Table 2 for details.).

	Females	Males	All birds
cabaret			
n	28	48	79
mean	49.6	50.1	50.4
SD	2.2	1.9	2.1
range	46–54	46–55	46–55
flammea			
n	77	120	211
mean	53.7	54.7	54.2
SD	2.2	2.0	2.1
range	49–59	50–62	49–62
rostrata			
n	19	43	69
mean	57.8	58.0	57.8
SD	3.2	2.4	2.5
range	52–63	53–62	52–63
dark *islandica*			
n	9	21	31
mean	56.0	58.2	57.5
SD	2.2	3.2	3.1
range	52–58	53–66	52–66
pale *islandica*			
n	11	18	29
mean	59.1	61.2	60.4
SD	3.0	2.5	2.9
range	52–63	56–66	52–66
all *islandica*			
n	20	39	60
mean	57.7	59.6	58.9
SD	3.1	3.3	3.3
range	52–63	53–66	52–66
exilipes			
n	31	33	72
mean	55.8	56.5	56.1
SD	2.0	2.2	2.1
range	52–61	52–62	52–62
hornemanni			
n	15	22	40
mean	62.1	62.8	62.4
SD	4.2	2.4	3.3
range	55–70	59–67	55–70

holboellii: Twelve *flammea* were found to have bill-lengths of 11 mm or more. The birds concerned were all large (wing-length 75–81 mm, average 77.4), but their plumage was that of typical *flammea*. Ten of the twelve birds were males (Table 7). They had been collected either in Britain (five birds, the only four fully dated had been collected in 1910; see Evans 1911) or north-western Europe (Fennoscandia and Archangel). Five

(out of 34 birds examined; 14.7%) had been collected between June and August, compared to seven (out of 177; 4.0%) in the other nine months of the year. The summer birds all had blackish bills (*c.f.* Coues 1869, Hortling & Stuart-Baker 1932).

3.3.2. Inter-subspecific variation

Fig. 4 shows the main patterns of variation between races. On wing-length, the smallest form is

Table 4. Bill-lengths (mm) of the races of redpolls, and the two forms of *islandica*. (See caption to Table 2 for details.).

	Females	Males	All birds
cabaret			
n	27	47	77
mean	8.3	8.6	8.5
SD	0.5	0.7	0.7
range	7.0–9.0	7.5–11.0	7.0–11.0
flammea			
n	75	122	210
mean	8.7	9.1	9.0
SD	0.8	0.9	0.9
range	7.5–11.5	7.0–13.0	7.0–13.0
rostrata			
n	19	42	67
mean	9.2	9.3	9.2
SD	0.5	0.6	0.6
range	8.0–10.5	8.4–11.0	8.0–11.0
dark *islandica*			
n	9	21	31
mean	8.7	8.8	8.8
SD	0.4	0.5	0.5
range	8.0–9.0	7.8–10.0	7.8–10.0
pale *islandica*			
n	8	18	26
mean	8.6	8.6	8.6
SD	0.4	0.4	0.4
range	8.0–9.3	7.8–9.0	7.8–9.3
all *islandica*			
n	17	39	57
mean	8.6	8.7	8.7
SD	0.4	0.5	0.4
range	8.0–9.3	7.8–10.0	7.8–10.0
exilipes			
n	30	34	72
mean	7.7	8.0	7.8
SD	0.5	0.5	0.5
range	7.0–9.0	7.0–9.1	7.0–9.1
hornemanni			
n	15	22	40
mean	8.9	9.2	9.1
SD	0.2	0.4	0.4
range	8.6–9.1	8.6–10.0	8.6–10.0

Table 5. Bill-depths (mm) of the race of redpolls, and the two forms of *islandica*. (See caption to Table 2 for details.).

	Females	Males	All birds
cabaret			
n	18	36	57
mean	5.3	5.6	5.5
SD	0.3	0.4	0.4
range	5.0–6.0	5.0–7.0	5.0–7.0
flammea			
n	40	69	115
mean	5.8	6.0	5.9
SD	0.3	0.4	0.4
range	5.0–6.0	5.0–7.0	5.0–7.0
rostrata			
n	14	32	50
mean	6.5	6.6	6.5
SD	0.4	0.4	0.4
range	6.0–7.0	6.0–7.3	6.0–7.3
dark *islandica*			
n	9	17	26
mean	6.4	6.4	6.4
SD	0.4	0.4	0.4
range	6.0–7.0	5.9–7.0	5.9–7.0
pale *islandica*			
n	9	16	25
mean	6.2	6.2	6.2
SD	0.3	0.5	0.5
range	5.9–6.6	5.0–7.0	5.0–7.0
all *islandica*			
n	18	33	51
mean	6.3	6.3	6.3
SD	0.4	0.5	0.4
range	5.9–7.0	5.0–7.0	5.0–7.0
exilipes			
n	22	17	44
mean	5.7	5.9	5.8
SD	0.,3	0.2	0.3
range	5.0–6.5	5.5–6.5	5.0–6.5
hornemanni			
n	9	18	29
mean	6.7	6.9	6.9
SD	0.3	0.4	0.4
range	6.0–7.0	5.9–7.8	5.9–7.8

cabaret ($z = 16.33$, $P < 0.01$); *flammea* has nearly the same wing-length as *exilipes* (no significant difference) but the latter has a longer tail ($z = 6.63$, $P < 0.01$) and a shorter bill ($z = 14.02$, $P < 0.01$). The bill difference may occur largely in the length of the horny sheath, as Troy (1985, his Table 3) found only slight differences in the size of the premaxilla of the two forms. *Rostrata* is larger than *flammea* in wing- and tail-length ($z = 15.33$,

Table 6. Bill-widths (mm) of the races of redpolls, and the two forms of *islandica*. (See caption to Table 2 for details.).

	Females	Males	All birds
cabaret			
n	25	43	71
mean	5.4	5.8	5.6
SD	0.3	0.4	0.4
range	5.0–6.0	5.0–7.0	5.0–7.0
flammea			
n	74	118	204
mean	5.8	5.9	5.8
SD	0.3	0.3	0.3
range	5.0–6.5	5.0–7.0	5.0–7.0
rostrata			
n	20	43	70
mean	6.3	6.3	6.3
SD	0.4	0.3	0.4
range	5.9–7.0	5.8–7.0	5.8–7.0
dark *islandica*			
n	9	21	31
mean	6.0	6.1	6.1
SD	0.0	0.3	0.2
range	5.9–6.5	5.9–7.0	5.9–7.0
pale *islandica*			
n	10	18	28
mean	6.0	6.1	6.0
SD	0.2	0.5	0.4
range	5.7–6.5	5.0–6.8	5.0–6.8
all *islandica*			
n	19	39	59
mean	6.0	6.1	6.1
SD	0.2	0.4	0.3
range	5.7–6.5	5.0–7.0	5.0–7.0
exilipes			
n	31	32	69
mean	5.8	5.8	5.8
SD	0.4	0.3	0.3
range	5.0–6.5	5.1–6.5	5.0–6.5
hornemanni			
n	15	22	40
mean	6.7	7.0	6.9
SD	0.3	0.4	0.4
range	6.3–7.0	6.0–7.9	6.0–7.9

Table 7. Age and sex of *flammea* specimens with bill-length of 11 mm or greater ('*holboellii*').

	Males	Unsexed	Females	Total
Adults	5	1	–	6
Unaged	4	–	1	5
First-years	1	–	–	1
Total	10	1	1	12

10.78, $P < 0.01$) but while the bill is only a little longer in *rostrata*, it is much deeper; *hornemanni* is the largest race (wing-length: $z = 10.41$, $P < 0.01$). The bill of *hornemanni* is almost the same length as that of *rostrata*, but it is deeper and wider ($z = 4.28$, 7.57, $P < 0.01$). *Islandica* is slightly shorter in the wing ($z = 1.96$, $P = 0.05$), though longer in the tail ($z = 2.11$, $P < 0.05$) than *rostrata*, and the bill is noticeably shorter ($z = 5.53$, $P < 0.01$), being almost the size of *cabaret*. There were no significant differences in the wing-length, or bill-length, -depth or -width of the *rostrata*-like and *hornemanni*-like Icelandic birds, although the tails of the latter were significantly longer ($z = 3.73$, $P < 0.01$).

Bill shape: in *flammea* the bill tends to be very slender, particularly at the tip; the culmen is straight but the sides of the beak are concave when viewed from above or below. *Cabaret* is somewhat like this, but in *exilipes* it is less acute; in *hornemanni* the bill is stronger still. The heaviest-looking bills (although not the deepest or widest at the base) are found in *rostrata* where the culmen and gonys are usually convex and the bill has a bulging appearance. Icelandic birds resemble some *hornemanni* and *rostrata* in bill shape, although it is less heavy in most birds.

4. DISCUSSION

A number of features of redpoll biology have contributed to the difficulties in understanding their relationships. Among these is the dynamic distribution of some forms. Redpolls have a mixed diet largely composed of seeds, those from birches *Betula* and spruces *Picea* being particularly important (Salomonsen 1951, Dement'ev & Gladkov 1954, Newton 1972). However, the seed-crops of these trees often fail, either locally or over a wide area. To cope with the varying food supply, the birds have become to some extent irruptive breeders, with the number of nesting pairs in any particular region changing from year to year (Taverner & Sutton 1934, Grinnel 1943), in correlation with local food abundance and spring weather (Rosenberg quoted by Hald-Mortensen 1970, Peiponen 1957, Enemar 1969, Hildén 1969, Enemar & Nyström 1981, Götmark 1982, Enemar *et al.* 1984). Occasionally redpolls nest far outside their 'normal' range. They are also partial migrants. The proportion of the population taking
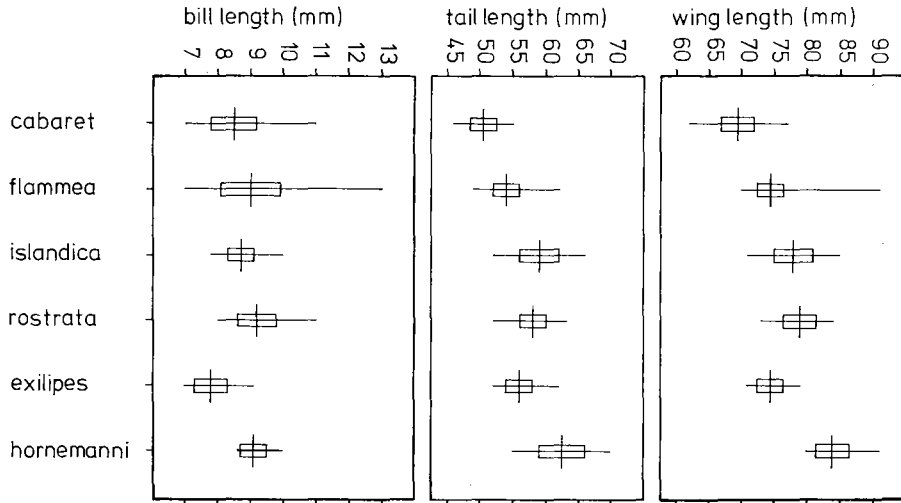
Fig. 4. Comparative measurements of the subspecies of *C. flammea* and *C. hornemanni*. Mean, ± one standard deviation, range.

part in the migration and the distance covered are highly variable, both within and between the different redpoll populations (Evans 1969, Newton 1972, Kennard 1976). Many of the specimens available for study in museums were collected while the birds were on passage or in their wintering areas, thus hindering interpretation of geographic variation.

The persistent confusion over redpoll taxonomy has been fuelled by three main factors.

1. With only one moult each year, normal wear together with the loss of whole feathers changes the appearance of redpolls from season to season. Indeed, the weight of the feathers of Alaskan redpolls is 31% greater in November than in July (Brooks 1968). Among the males especially, loss of pale feather edges reveals or enhances any pink or red on the cheeks, breast or rump. Although they were not working with retrapped individuals, and the movement or death of birds could have contributed to their results, Fennel *et al.* (1985) reported similar observations from a field study of introduced *cabaret* in New Zealand. They found that only 16% of the birds they sexed as males had red breasts in March, but by August 78% were red or very red. At the same time, the frequency of birds with slightly pink breasts decreased from 56% to 0%.

Wear also causes redpoll plumages to darken, often considerably, as abrasion re-

moves pale feather edges to leave the darker centres, particularly on the wings, tail, upperparts and streaked flank feathers. In some cases, clear white rumps on fresh plumaged birds can become noticeably streaked by the following summer as wear exposes previously concealed dark feather centres. The overall effect is to make fresh plumaged *flammea*, for example, superficially like worn *exilipes*. Although not eliminating the differences between subspecies, it tends to alter them as wear progresses, since birds which are pale (with broad, pale feather edges) in fresh plumage darken faster and to a greater extent than birds which are already dark (with narrow, less pale feather edges) in fresh plumage. Thus some birds which might be quite easily separated into subspecies in autumn can become more difficult to differentiate by summer. Only birds with plumage in the same state of wear should be compared for taxonomic purposes.

2. The plumage variation found in some forms is very wide. In particular, many *flammea* have quite pale rumps whereas in some *exilipes* they can be moderately streaked (most noticeably in worn plumage). In some respects many individuals of *flammea* appear as pale as the darker examples of *exilipes*. Narrow definition of the supposed characters of each race has frequently led to large proportions of birds being assigned to hybrid or intermediate categories. Wether-

bee (1937) even classed trapped birds into pure types, intermediates and intergrades between intermediates and pure types.

3. Within a subspecies, size and paleness also vary between age and sex classes. Adult males especially tend to be longer winged and paler than the smaller, darker females and first-year birds, but there are differences within the latter group too. This variation can be summarised:
Size: 1st-year birds tend to be smaller than adults   (1)
females tend to be smaller than males   (2)
Colour: 1st-year birds tend to be darker than adults   (3)
females tend to be darker than males   (4)
(References: Coues 1862b: 386–387 (3, 4); Evans 1966: 207 (1, 2); Fennell *et al.* 1985 (4); Molau 1982, 1985; Troy 1985 (2, 4); Watson 1957 (4); this study.)

These factors can be incorporated into a model of plumage, and to a lesser extent size, variation in redpolls (Fig. 5), although it is more applicable to some subspecies than others. In the model there is a spread of variation in size and paleness, ranging from, on average, the smaller, darker first-year and female birds at one end to the larger, paler adult males at the other, within each subspecies. In the case of *flammea* and *exilipes* the two spreads of variation overlap (the actual extent of the overlap in the figure is not meant to be significant). In a considerably simplified, diagrammatic form this represents the pattern of variation in redpolls. Fig. 5 can also be read from right to left to represent schematically the effect of wear on the plumage of individual birds, since redpolls become darker (and their wings slightly shorter) with abrasion such that some worn *exilipes* are as dark as fresh plumaged *flammea* (see above).

Although this is the first time that a description of redpoll variation has been assembled in this manner, the various components may be found in the literature of the last 120 years. Coues (1862b), for example, commenting on his newly described *exilipes* wrote 'The dimensions of the whole bird... the color and number of the streaks above and on the sides; the extent and purity of the white rump, &c., are all liable to great variations' and that 'the rump in adult birds is pure white... without spots
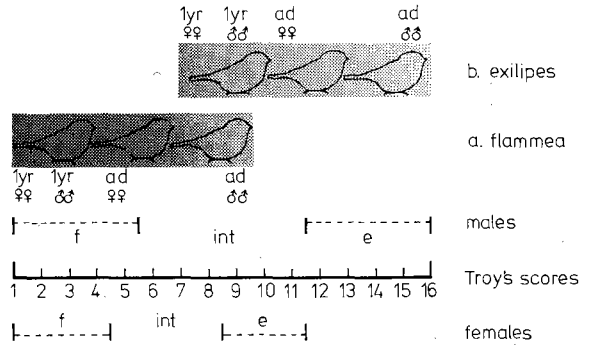

Fig. 5. A model of plumage variation in redpolls. Within any subspecies, plumage varies from dark to pale (a, or b). Males tend to be larger and paler than females, and adults tend to be larger and paler than first-year birds. *C. f. flammea* (a) is darker than *C. h. exilipes* (b), though some light *flammea* are as pale as some dark *exilipes*. An approximate average position for each age and sex group is indicated on the diagram, but within each group there is much variation. The precise extent of the overlap between (a) and (b) is not significant. A similar situation applies to *C. f. rostrata* and *C. h. hornemanni*. In addition, wear darkens plumage as the paler tips to the feathers abrade. This tends to shift the shade of individual birds to the left as wear proceeds.
Troy (1985) scored *flammea-exilipes* variation and assigned a 16-point scale, from the darkest birds (1) to the palest (16); lower scale on diagram. For each sex, he then divided this range of variation into three: *flammea*, unknown (intermediate) and *exilipes*, indicated above by f, int and e, respectively.
See text for further explanation.

or streaks; but in immature specimens it is frequently marked with dusky, though never so thickly as in (*flammea*)'. In 1883, Brewster reported that supposed intermediates between *rostrata* (although calling them *holboellii*) and *flammea* were only apparent when comparing large adult males of *flammea* with small females of *rostrata*, and that when the same ages and sexes were compared there were no real intermediates. A year later, Stejneger (1884), while thinking that hybridization between *flammea* and *exilipes* was a possibility, said that 'intergradation has been *supposed* to occur' but that it was also 'only apparent, because it is sometimes difficult to distinguish *young birds* of the two species' (his italics). More recently, as part of a phenetic study of redpolls in which he argues for the one-species theory (Table 1d), Troy (1985) scored the degree of rump, under tail-covert and flank streaking on *flammea* and *exilipes*. This ranged from 1 (dark; extreme *flammea*) to 16 (pale; extreme *exilipes*). He then divided the spectrum of *flammea-exilipes* varia-

tion into thirds representing '*flammea*, unknown (intermediate), and *exilipes* classes'. Troy found that females showed a much narrower range than males, and that 'no females were white enough to be considered *exilipes* on the scale used for males'. This is clearly explained by the model, in which adult and first-year males are found along the full length of Troy's scale, but no females are pale enough to have a score greater than 11 (Fig. 5).

It had previously been shown that first-year birds were smaller than adults (Evans 1966) and that females were smaller than males (Evans 1966, Troy 1985). Molau (1985) and the present study have confirmed and extended these observations on size, as well as the earlier descriptions of paler adults and darker first-years. In particular, Molau quantified the differences between the ages and sexes in extent and purity of the white rump and the width of the dark streak on the longest under tail-covert. In a detailed investigation of over 1100 breeding *flammea* and *exilipes* in Torne Lappmark, northern Sweden, he showed that only 4% of adult male *exilipes* had streaked rumps, compared to 49% of first-year females. The figures for adult females and first-year males were 35% and 37% respectively. The range of widths for the streak on the longest under tail-covert overlapped considerably in the two races, but in *exilipes* it averaged progressively broader in adult males, adult females, first-year males and first-year females. Less variation was seen in *flammea*, but the streak was narrowest on average in adult males. In a limited experiment during which he examined a small number of birds (6 *flammea* and 10 *exilipes*) before and after they moulted in captivity, Molau was able to corroborate these findings. With some birds it might have been misleading to compare worn, streaked rump feathers before the moult with freshly grown ones, in which small streaks could be concealed beneath broad, pale fringes. A similar reservation would not apply to the conclusions regarding the central streaks on the under tail-coverts, as wear rarely affects the pigmented area near the shaft.

A probable family of redpolls from the wild were moulted in captivity by Nyström & Nyström (1987). The presumed breeding birds had been classed as intermediate between *flammea* and *exilipes*. After the autumn moult, the juveniles acquired plumages similar to Arctic Redpolls, but

the adults still seemed intermediate. It seems likely that the adults were dark *exilipes*.

4.1. THE EVIDENCE FOR HYBRIDIZATION BETWEEN *EXILIPES* AND *FLAMMEA*

Although intergrades between several redpoll subspecies have been claimed, most of the taxonomic debate has concentrated on apparent hybridization between Common and Arctic Redpolls. Since it was these 'hybrids' that caused Salomonsen (1928) and others to consider all redpolls to be conspecific, it is appropriate to examine the evidence.

Birds intermediate between *exilipes* and *flammea* have been reported from Alaska (*e.g.* Kessel *et al.* 1964, Brooks 1968, Holmes & Black 1973), eastern Canada (*e.g.* Gabrielson & Wright 1951), northern Scandinavia (*e.g.* Meinertzhagen 1938, Harris *et al.* 1965, Hildén 1969) and across the U.S.S.R. (*e.g.* Grote 1943, Johansen 1944). The extent to which hybridization is said to occur in each of these areas is not always clear. Williamson (1961), for example, accepted intergradation in northern Fennoscandia, but considered that *flammea* and *exilipes* behaved as good species in Alaska.

The proportions of intermediates in mixed populations is reported to vary from 100% (Harris *et al.* 1965) to very few (Lobkov 1979) or almost none (Stejneger 1884, Svensson 1984). In sympatry the ratio of *flammea* to *exilipes* changes geographically and from year to year. At Churchill, Manitoba, Taverner & Sutton (1934) found *flammea* commoner than *exilipes* in 1930, but equal numbers of each in 1931; in 1940 Grinnell (1943) found only one *exilipes* to every twenty-five *flammea*. Jehl & Smith (1970) summarised further details of relative abundances at Churchill. These ranged from no Arctic Redpolls in 1953 to 50 : 50 in 1966. Since the number of birds in some pure populations also vary (*e.g.* in Newfoundland, Brooks 1936, Aldrich & Nutt 1939; in Scandinavia, Enemar & Nyström 1981, Enemar *et al.* 1984), this tells us little about the absolute numbers of either of the two forms, only that they change with respect to one another. Molau (1985) found the breeding population of *exilipes* to be relatively stable in northern Sweden, due to a reliable food supply (*Salix* buds and seeds). In the same area the numbers of *flammea* varied from season to season,

depending on the local birch seed crop on which they fed. West *et al.* (1968) found the ratio of *flammea* to *exilipes* to change considerably during spring migration at Fairbanks. In autumn, *flammea* is reported to leave the breeding grounds and migrate earlier than *exilipes* (Canada, Taverner & Sutton 1934; Finland, Tallgren & Ahola, quoted by Eriksson 1970). Rapidly changing ratios of one form to the other at any given breeding locality, together with the differences in migration, suggest that the factors responsible for determining population size and migration timing are acting largely independently in *flammea* and *exilipes*. Although different parts of the populations of some species sometimes migrate at different times (*e.g.* Irving *et al.* 1967), it usually happens with the different ages or sexes rather than as seen in the redpolls. The stong fluctuations in the ratios of one form to another from year to year is a less common intra-specific phenomenon.

4.1.1. Inference of hybridization

The case for hybridization originally rested on the presence of supposed hybrids or intermediates in mixed redpoll populations, particularly in museum collections. Confusion arose from the assumption that intermediate plumage birds were hybrids. It soon followed that interbreeding became widely reported, whereas what was actually meant was that 'intermediates' had been seen or collected. Futhermore, Stejneger (1884) wrote that Nelson had observed interbreeding between *flammea* and *exilipes* in Alaska, yet no mention of it was made by Nelson in either his 1883 or 1887 accounts of Alaskan redpolls. (Some of Nelson's other records have also been questioned; see Vaurie 1964). Because of the uncritical acceptance of intermediates as hybrids, the concept of interbreeding soon became established. Jehl & Smith (1970), in part quoting Gabrielson & Lincoln (1959), noted that redpolls were hybridizing freely in northern Alaska, whereas Gabrielson & Lincoln actually gave no direct evidence of this, apart from being unable to assign some intermediate plumage birds. They still regarded *flammea* and *exilipes* to be separate species with 'complimentary ranges that overlap at a few points'. (Jehl & Smith's other reference was to unpublished personal communications.) Eventually, Brooks (1968) asserted 'it is well known that [*flammea* and *exilipes*] commonly

interbreed...' despite finding that 'most of the birds... were close enough to one type or the other to be designated [*exilipes*] or *flammea*'.

The direct evidence for hybridization rests, not on observations of mixed matings, but on assumptions about the identity of presumed hybrid offspring. Yet there is no proof that these intermediates are hybrids. Despite the high proportion of intermediates/hybrids claimed to be present in some populations, there are no clearly documented occurrences of interbreeding. To the contrary, Oberholser (1918) claimed that *flammea* and *exilipes* bred sympatrically over a wide area from Ungava to Alaska, and that they still remained distinct 'although apparently sometimes hybridising'. Kessel *et al.* (1964) found *flammea, exilipes* and intermediates in western Alaska, but, although they saw apparent mixed pairs in the field they found no nests belonging to them. At Churchill, Manitoba, Taverner & Sutton (1934) found *flammea* and *exilipes* both breeding commonly, with nests as little as 50 yards apart, but no interbreeding. Harper (1953) wrote that 'The occurrence of both *exilipes* and [*flammea*] [at Nueltin Lake]... during the breeding season refutes Salomonsen's contention that all forms of redpoll should be regarded as conspecific'. In Scandinavia no interbreeding has been proved, despite sympatric breeding (Lundevall 1952, Nyström & Nyström 1987). Hildén (1969) questioned the specific distinctness of *exilipes* since he often saw apparent intermediates in northern Finland. Yet he discovered no mixed pairs at any of the large number of redpoll nests he found. Svensson (1984) summarized the issue by pointing out that while 'hybridisation is supposed on morphological grounds to occur between *C. f. flammea* and *C. hornemanni exilipes* in N. Norway... no actual interbreeding has been recorded'. Considering that interbreeding between *flammea* and the less distinctive '*holboellii*' has been reported several times (*e.g.* Svensson 1984, Witherby, quoted in Hortling & Stuart Baker 1932) it is perhaps significant that none has yet been found for *flammea* and *exilipes*, which should be much easier to separate in the field.

In the U.S.S.R., *flammea* and *exilipes* breed sympatrically over a huge area, yet birds with intermediate characters are quite scarce (Johansen 1944). Out of almost 50 pairs observed by nests or

on territories in Kamchatka, Lobkov (1979) found only one that was probably mixed (*exilipes* male, *flammea* female). The author did not report nesting, let alone successful breeding of this pair, even accepting their identification (no plumage details are given; some female *exilipes* closely resemble *flammea*). During 1977 there were unusually large numbers of *exilipes* present in Kamchatka. Lobkov quite often noticed interspecific displays that year, but located no nests belonging to mixed pairs. As redpolls usually display while in a loose flock, and breed semi-colonially, apparently without a proper territorial structure, care must be taken when assigning putative pairs. Alsop (1973) discovered three *exilipes* males feeding the same female at one nest in Canada.

4.1.2. Lack of differentiation

Brooks (1968) studied the adaptions of redpolls to the severe arctic environment in Alaska. His results showed that *flammea* and *exilipes* differed in feather texture, feather weight in winter, several aspects of behaviour as well as cold tolerance and other physiological responses. Although his experimental birds were only classed as *flammea* or *exilipes*, he nevertheless interpreted this as showing that the redpolls were all one species demonstrating morphological, behavioural and physiological gradients. Troy & Brush (1983) looked at the pigments and feather structure of 'extreme examples' of *flammea* and *exilipes*. They discovered 'morphological differences between [Mealy] and Hoary Redpolls' in their feather structure and concentration differences in the pigments. They, like Brooks (1968), then dismissed these findings as 'likely the ends of a gradient', concluding that 'the recognition of two species of redpolls is unwarranted'. In neither of these studies were intermediates examined, yet the authors felt able to postulate gradients between *flammea* and *exilipes*. This was clearly unjustified on the evidence presented, which could with greater strength be interpreted to support the validity of specific differences. Even if intermediate differences were demonstrated in intermediate plumage birds, this would not necessarily prove conspecificity.

When examining the chromosomes of Alaskan Mealy and Hoary Redpolls, Troy (1980) found that 'of the carduelines karyotyped to date, only *flammea* and *exilipes* have identical karyotypes'.

He argued that this supported the case for treating all redpolls as one species. However, the redpolls were the most closely related pair of species examined. No other carduelines from the same superspecies or species-group had then been karyotyped. In a wide review of avian chromosomal studies, Shields (1982) reported many species-pairs with identical karyotypes. The redpoll evidence thus confirms only that *flammea* and *exilipes* are indeed closely related.

More detailed information on the genetic relationship between Common and Arctic Redpolls was presented by Marten & Johnson (1986). Using starch gel electrophoresis, these authors surveyed 33 genetic loci in 19 species and subspecies of North American carduelines, including *flammea* and *exilipes*. Omitting the redpolls from their data, there was an average genetic distance (Nei's D) of 0.005 (range 0.002–0.010) between conspecific subspecies, and 0.178 (0.051–0.527) between congeneric species. The distance between *flammea* and *exilipes* was 0.028. Marten & Johnson concluded that the two redpolls were 'similar genetically', yet the distance between them is greater than they found for any subspecies, although it was less than for their congeneric species. The latter were all morphologically well-defined. On traditional criteria, the two redpolls are undoubtedly more closely related than any of the other species, and the genetic distance reported is entirely consistent with that expected for distinct members of a superspecies.

4.1.3. Analyses of intermediate phenotypes

Recently, Troy (1985) published a detailed phenetic analysis of redpolls from a number of Alaskan and Canadian locations. As described earlier, he divided the range of *flammea* (dark) – *exilipes* (pale) plumage variation into thirds. These he designated *flammea*, intermediate and *exilipes*. Analyzing the sexes separately Troy was able to distinguish his *flammea* from *exilipes* using skeletal measurements, but the differences were small and without a clear discontinuity. When he discovered that the birds which were intermediate in plumage characters were also intermediate in skeletal measurements, he concluded that 'the hypothesis that they included hybrids is supported' (p. 90). However, his 'pure' samples probably consisted of a high proportion of adult *exilipes* and first-year

flammea (see Fig. 5 here). Since his 'intermediates' were a combined sample of largely first-year *exilipes* and adult *flammea*, intermediate measurements were to be predicted.

Previously, Baldwin (1961) had found that composite samples of Alaskan redpolls 'showed trends for lighter colouring, larger wing and tail and shorter bill generally from southeast to northwest. However, when the subsamples were further broken down into darker and lighter individuals... the 'trends' showed simply as a reflection of the different proportions of occurrence of the two types,... *flammea*... and... *exilipes*'. He found that the northwestern *flammea* were only slightly different in measurements from the southwestern *flammea*, and there was even less difference within similar groups of *exilipes*. He also found intermediates, but nowhere did they outnumber the parental types. He wrote: 'Thus the two types have maintained their distinctness despite extensive geographical overlap and hybridisation in Alaska'.

Although he presented little data, Lobkov (1979) found the range of variation in widely allopatric populations of *flammea* and *exilipes* to be narrower than in areas of sympatric breeding within the U.S.S.R.. He identified some birds as hybrids, but he concluded that hybridization was less frequent than would be expected, considering the large areas of sympatry. He believed *flammea* and *exilipes* represented separate species.

4.2. THE EVIDENCE FOR HYBRIDIZATION BETWEEN *HORNEMANNI* AND *ROSTRATA*

Salomonsen (1928) described three birds with characters intermediate between *hornemanni* and *rostrata*. It has already been shown that most specimens previously considered to be hybrids can now be allocated to species without great difficulty, but even accepting Salomonsen's determination of these individuals, this limited evidence suggests that intermediates are rare. In 1936 Salomonsen (1951: 518) collected a mixed pair while they were copulating. The male was *rostrata* and the female *hornemanni*. This is the only time a mixed mating has been reported, and in this case a nest was not found. Wynne-Edwards (1952) found *hornemanni* and *rostrata* breeding sympatrically on Baffin Island, with no indication of any mixed pairs, possibly because *hornemanni* started to nest before

rostrata had returned in spring. Watson (1957) also found *rostrata* and *hornemanni* together on Baffin Island in 1953, and had no difficulty in separating the two types.

4.3. THE EVIDENCE FOR HYBRIDIZATION BETWEEN *FLAMMEA* AND *ROSTRATA*

Although not directly relevant to the main controversy, birds believed to be intermediate to these two subspecies have been reported from time to time (Salomonsen 1928, 1951, Wetherbee 1937). They are said to originate from Labrador or southern Baffin Island and it is possible that birds of this type may have been confused with '*fuscescens*', which is credited with characters intermediate between *flammea* and *rostrata*. On the other hand Salomonsen (1928), who accepted *fuscescens*, reported intermediates between both *flammea-fuscescens* and *fuscescens-rostrata*. On the evidence examined I am unable to recognize *fuscescens* or these intermediates.

4.4. THE ARGUMENT FOR SEPARATE SPECIES

Despite its long history, the suggestion that intermediate plumage birds are hybrids remains without substantive evidence. To the contrary, it has now been shown that intermediates represent part of the normal range of plumage variation in two separate taxa (Molau 1985, this study). Molau (1985), in particular, has demonstrated that many of the supposed intermediates are likely to be either (a) pale adult male *flammea* or (b) dark adult female or first-year birds of either sex belonging to *exilipes*. Even in the well-defined subspecies *cabaret*, the upperparts can be quite variable. Some birds are very pale, often with light rumps (Fennell *et al.* 1985, this study). In the New Zealand populations of *cabaret* it had been thought that this resulted from mixed-origin introductions (perhaps including some *flammea*), but Fennell *et al.* found similar variation in British *cabaret*. They attributed the increased frequency of pale birds in New Zealand to founder effects rather than hybridization. In *cabaret*, there are also occasional otherwise dark birds with pale rumps and light wings bars. Again, this illustrates the range of character variation within a relatively uncontroversial subspecies, yet similar variation in *flammea* or *exilipes* is regarded by some as proof of hybridization.

In the field, strong positive assortative mating among redpolls has been observed many times in both Old and New Worlds (*e.g.* Taverner & Sutton 1934, Lundevall 1952, Hildén 1969, Lobkov 1979, Nyström & Nyström 1987). Jehl & Smith (1970) reported positive assortative mating between *flammea* and *exilipes* at Churchill, Manitoba. Even though they had access to unpublished data inferring that hybrids made up a large proportion of the population, they still recognized two species.

Arctic and Common Redpolls are regarded by Troy (1985) and others as morphs of the same species (even though Troy claims variation is not discrete, but continuous, thereby making use of the term 'morph' inappropriate – Cooke 1985). Troy (1985) has argued that positive assortative mating should not be used as evidence of species distinctiveness, since it can be an intraspecies phenomenon. However, it is also the usual mechanism for the maintenance of specific integrity and is clearly demonstrated in the redpolls. Consistent, widespread, positive assortative mating between morphs would lead to speciation; in the two examples of wild birds cited by Troy (*Chen caerulescens* and *Stercorarius parasiticus*) it is not consistent (Cooke 1985). There is no evidence that this is the case in redpolls.

The argument against regarding Common and Arctic Redpolls as morphs is further strengthened by the complexity of their differences. Several characters in plumage colour are involved, as well as a number related to feather structure, behaviour, migration, physiology and morphology. Using multivariate analysis of external measurements, *flammea* and *exilipes* can be separated with an accuracy of greater than 99% (M. Herremans pers. comm.). Significantly, there are distinct, if sometimes subtle, differences in the calls and songs of *flammea* and *exilipes* (Zablotskaya 1981, 1984, Molau 1985, Veprintsev & Zablotskaya 1982, M. Herremans pers. comm., own obs.). These have been shown to exist in an area of sympatry (Knox), thereby ruling out the possibility that they are merely dialects.

As mentioned earlier, the numbers of *flammea* and *exilipes* also appear to vary semi-independently from year to year in any locality, suggesting different factors controlling their populations. In most dimorphisms the morph-ratio is usually either relatively stable or only slowly changing (*e.g.* Wunderle 1981, O'Donald 1983), rather than demonstrating the large amplitude shifts seen in the redpolls.

I am aware of no other case of polymorphism in birds where such a comprehensive array of differences exists between supposed 'morphs', except perhaps in the Western Grebes *Aechmophorus* spp. of the United States. In these grebes, two sympatric 'morphs' differ in several aspects of plumage and bare-part colouration, feeding behaviour and the timing of their nesting and plumage development. They share similar courtship behaviour and all but one of their calls. The only statistical difference in their measurements is in average culmen length in the females, and the 'morphs' show positive assortative mating (Ratti 1979, 1981, 1985, Nuechterlein 1981). In 1985 the A.O.U. accepted these 'morphs' as separate species *A. occidentalis* and *A. clarkii* (A.O.U. 1985; see also Storer & Neuchterlein 1985).

As a pair of sibling species, the degree of similarity between Common and Arctic Redpolls is not unique. Although largely allopatric, the Wood Pewees *Contopus virens* and *C. sordidulus* exist in areas of sympatry and are very alike in plumage characters. Their songs are quite distinctive, but discriminant function analysis on skeletal measurements gives only 87% accurate identification; DFA on external measurements is even less reliable with about 20% misidentified (Rising & Schueler 1980). Another species-pair, *Mionectes macconnelli* and *M. oleagineus*, are separable only on the presence or absence of buffy edges on the inner secondaries and wing coverts, or by multivariate analysis of several morphological characters. Even the latter is not completely accurate, yet protein electrophoresis has shown this species pair to differ genetically as much as other congeneric species (Capparella & Lanyon 1985).

The case reported by Grant & Grant (1983) is more intriguing: the population of *Geospiza conirostris* on Isla Genovesa, Galapagos, was divisible in one year into two types with alternating territories and different songs, average bill lengths, foraging techniques and frequency of a bill colour morph in the nestlings. These differences partly broke down in subsequent years. The integrity of the population as one species, and the incipient sympatric speciation both appear to have been

driven by inconsistent assortative mating. Although the complexity of this situation is probably exceptional among birds, it is clear that we must be cautious about the interpretation of evidence based on limited data, whether from the museum or the field.

4.5. ECOLOGICAL ISOLATION

Ecological or geographical factors may isolate *hornemanni/rostrata*, and *exilipes/flammea* during the breeding season. Certainly *hornemanni* and *rostrata* only come into contact in a few areas in Greenland, as the former is largely restricted to the high arctic and the latter to the low arctic zones (Salomonsen 1951). Waterston & Waterston (1970) reported *rostrata* was moving into the high arctic regions to breed. Detailed observations of its recent status would be desirable. On Baffin Island, *hornemanni* and *rostrata* show broader overlap without apparent hybridization (Wynne-Edwards 1952, Watson 1957).

Lundevall (1952) has suggested altitudinal zonation in redpolls, with *C. hornemanni* on the tundra and *C. flammea* lower down. Watson (1957) and others found this not to be the case in Baffin Island or in Scandinavia, where they found no clear distinction between the birds' habitats. However, redpolls range over wide areas in the breeding season – some are said to travel 20 km to feed (Molau 1985). Movements of much less than this magnitude could easily account for the broad overlap seen in the habitats of foraging birds, even if they were widely separated for nesting. Nevertheless, habitat differences between sympatric forms have been described. In northern Sweden, Molau (1985) reported *exilipes* dominated numerically when trapping redpolls above the tree line, whereas *flammea* was the commoner form at lower altitudes. The few Hoary Redpoll nests he found in his Lappmark study areas were all in open habitats. Mealy Redpolls did not normally breed above the tree line there, although they did so further south in Sweden. Dement'ev & Gladkov (1954, quoting Mikhel), report different habitats for *flammea* and *exilipes* on the lower Indigirka River. Many authors (*e.g.* Jehl & Smith 1970) generalise by attributing a tundra habitat to *C. hornemanni* compared with a forest biome for *C. flammea*. General differences in the diet of sympatric forms have been described by Molau (see

above), but further work is clearly called for. Nyström & Nyström (1987) found no significant differences in a small sample of *flammea* and *exilipes* in their behaviour or breeding biology. They also found *exilipes* nesting in dense birch forest, and *flammea* on montane heath.

Three studies have now found *C. hornemanni* to return to the breeding grounds earlier than *C. flammea*. On Baffin Island in 1950, the nesting of *hornemanni* was well under way when *rostrata* came in nearly two weeks later (Wynne-Edwards 1952). In northern Fennoscandia, Molau (1985) and Knox (in prep.) both noted *flammea* only arriving in numbers at least several days after *exilipes*. While differences in the mean date of arrival in spring by different age/sex classes and morphs have been reported in a number of migrant species, complete separation (Wynne-Edwards, Knox) is unusual. This represents a further substantive contrast between Common and Arctic Redpolls.

4.6. *ISLANDICA*

The presence of both pale and dark birds in the Icelandic population was not initially recognised. Early reports of redpolls in that country were attributed to *flammea*, but by the late nineteenth century many authors believed it was *hornemanni* that bred. Slater & Carter (1886) and Slater (1901) drew attention to this disagreement, and emphasised that *flammea* was the only breeding form, *hornemanni* merely occurring as a rare winter visitor. Coburn visited Iceland in 1899 and brought back adults, nests and eggs of birds he ascribed to *hornemanni*. This was said to be the first proof of that race breeding there, and he made no reference either to seeing or collecting any dark-plumaged birds (Coburn 1901). In the original description of *islandica* in 1904, Hantzsch compared his new race to *rostrata*, rejecting any association with *hornemanni*. His opinion was shared by Witherby *et al.* (1938) and Vaurie (1956) who synonymised the two forms. Timmermann (1949) and Williamson (1961) both recognised a similarity between *islandica* and *flammea*, although accepting a likeness to *rostrata* in some plumage states.

Bird (1935) examined specimens of wintering *rostrata* from Iceland, along with a number of dark *islandica*. He also received a series of pale *islandica* collected between March and May, but

he mistook them for *exilipes*, in the process dismissing all previous records of *hornemanni*. Similar pale birds were noticed by Timmermann, who recorded them particularly in spring (Timmermann 1938), or as winter visitors (Timmermann 1949). He was unsure of their true status or identification. Timmermann believed the dark, short-billed birds to be true *islandica*, which had a restricted breeding distribution in the country. He (1938) further noted occasional longer-billed, *rostrata*-like redpolls breeding all over the island, as in 1929, although in his 1949 book, *rostrata* is just listed as a passage visitor.

It was Salomonsen who suggested that the two redpolls from Greenland had interbred in Iceland to give a hybrid swarm with plumage characters ranging from some birds indistinguishable from *rostrata* to others like *hornemanni* (Salomonsen 1951). When Vaurie (1956) merged *islandica* with *rostrata* he had apparently only examined dark-plumaged birds. After seeing a larger series he somewhat reluctantly accepted the validity of *islandica*, but still only seems to have seen dark specimens (Vaurie 1957). He found the claimed shorter bill-length to be an inconsistent feature, and believed separation only to be possible on the slight differences in colour between *islandica* and *rostrata*. Nevertheless, the shorter bill-length of *islandica* has been affirmed many times (*e.g.* Salomonsen 1951, Svensson 1984) and is statistically significant (this study). *Islandica* also has a slightly shorter wing and longer tail than *rostrata*, although statistically these differences are not highly significant.

It is unfortunate that only Salomonsen (1951) and Williamson (1956) appear to have appreciated the full range of plumage variation in *islandica*, since it explains the otherwise contradictory statements in the literature. Far from being just winter visitors, the pale birds are part of the breeding population of redpolls in Iceland (Knox in prep.), often occurring only at low frequencies. Most of the breeding Icelandic redpolls can easily be assigned to either the light or the dark form.

The range of plumage colour found in Icelandic birds resembles that seen in sympatric populations of *flammea* and *exilipes*. However, unlike the latter situation, in Iceland the pale and dark birds differ significantly only in their tail-lengths. A different explanation may be required to account for

their coexistence. The presence of two separate species in Iceland is possible, but seems unlikely, unless reduced competition in arctic and subarctic ecosystems (see later) has allowed two forms to evolve convergently. Alternatively, an endemic, dark population (or *rostrata*) may have hybridised with *hornemanni* (or *exilipes*, or both) in Iceland, or may be highly variable for other, as yet unknown reasons. The complexity of the differences (colour and relative measurements) between the pale and dark birds suggests that they are not just morphs in the typical sense.

4.7. *HOLBOELLII*

Many early authors expressed doubts as to the validity of Brehm's *holboellii*. Although Coues (1864), among others, suggested that it was just a long-billed variant of *flammea*, Salomonsen (1928) and Hellmayr (1938) found the form to be acceptable. A review by Grote (1943) came to the same conclusion as Coues. The B.O.U. (1948), Dement'ev & Gladkov (1954) and Vaurie (1959) subsequently agreed, yet the name still appears regularly in the literature (*e.g.* Brooks 1973, James *et al.* 1976).

Holboellii is said to differ from *flammea* mainly by its long bill. It is also claimed to be darker-plumaged, be longer winged and to have a paler bill. Hortling & Stuart-Baker (1932) firmly believed they could separate *holboellii* from *flammea* in the field, and even distinguish their nests and eggs. They considered them to be separate species but, as they collected no specimens to substantiate their observations, their views should be treated with caution.

The geographic range of *holboellii* has never been clear, particularly as to whether it did, or did not (Hellmayr 1938) breed in North America. In northwest Alaska, Bailey (1948) found occasional birds with longer bills than *flammea*, but he thought these were not *holboellii*. He believed that claimed occurrences of *holboellii* from the United States and Canada were attributable to this unnamed Alaskan population. Nevertheless, in their 1957 Checklist, the A.O.U. included western and northern Alaska and the northern Yukon (as well as Siberia and Scandinavia) within the breeding range of *holboellii*. More recently, *holboellii* has been supposed to breed at low densities in scattered locations along the northern edge of the

range of *flammea*.

Troy (1984) examined the status of *holboellii* in North America. Based on the 1957 A.O.U. description of its range, he compared populations of birds collected in north and west Alaska ('*holboellii*') with those collected in central Alaska, the Northwest Territories and northern Quebec ('*flammea*'). While he found some differences in the skeletal measurements of the two groups, they were not very great and he concluded that the recognition of *holboellii* was unwarranted. However, north and west Alaska also fall within the range of *flammea*. Troy did not present any data to show that his supposed *holboellii* sample actually contained any specimens of that form, for he did not give any bill measurements of the birds prior to the preparation of their skeletons. Therefore, it could equally be concluded from his study that north and west Alaska does not lie within the range of *holboellii*, or that long-billed birds were rare there compared with *flammea*, as suggested by Bailey (1948).

Its large, ill-defined breeding range has always made *holboellii's* validity doubtful, particularly as it was said to be entirely sympatric with *flammea*, and interbreeding had been noted (Svensson 1984). Most authors have been unable to detect plumage differences between *holboellii* and *flammea*, and complete intergradation of bill measurements is reported (Salomonsen 1928, Vaurie 1956, Molau 1985, this study; Fig. 6). Birds with
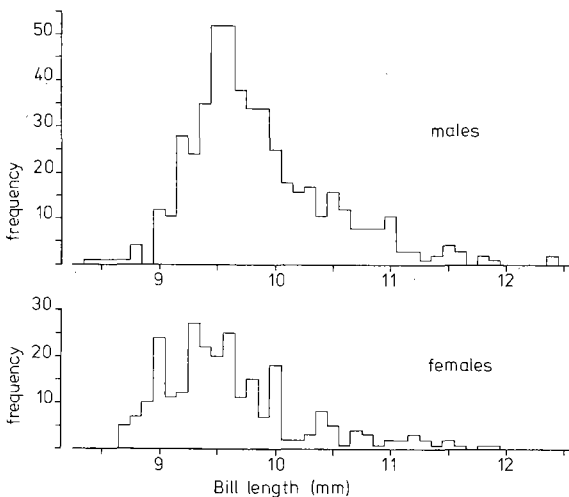
a bill length of 11 mm or more make up about 6% of the *flammea* samples examined during this study and that of Molau (1985; Table 8). If the same ratio (15 : 1) applied in Alaska, there would have been only two male and two female *holboellii* in Troy's combined samples. At that frequency they would have been undetectable with the methods exployed.

Table 8. Number of *flammea* specimens with bill-lengths of 11 mm or greater ('*holboellii*'). The data from Molau (1985) is extracted from his Figs. 2 & 3.

Studies		Sample size	With bills $\geqslant$ 11 mm	
			no.	%
This study		211	12	5.7
Molau (1985)	males	499	32	6.4
	females	258	15	5.8
	overall	968	59	6.1

It has been suggested that long-billed birds may be commoner in the summer than at other times of the year. Among the *flammea* examined here, significantly more were collected between June and August (5 out of 34; 15%) than in the other nine months of the year (7 out of 177; 4%; chi-squared test; P = < 0.05). However, Molau's birds were mainly examined in the breeding season, and they do not reflect a similar high proportion (Table 8). Four out of 46 (8.7%) *flammea* trapped in northern Finland in May/June 1984 were long-billed. Two different call notes from a single '*holboellii*' recorded at the same time are indistinguishable from calls of *flammea* (own obs.).

There is little substantial evidence to suggest that *holboellii* consists of anything other than long-billed individuals of *flammea*. Their measurements form the right-hand tail to the highly skewed bill-length distribution of that race (Fig. 6). This skew presumably occurs because, while the minimum bill-length for an individual is probably determined by structural constraints on the bill, particularly the length of the underlying premaxilla, the maximum length is more free to vary as a net product of rhamphothecal growth and wear. Bill-length changes seasonally in many other seed-eating birds. This is mainly due to dietary shifts, with shorter bills in winter when more ground feeding occurs and the birds are eating hard seeds. During the summer, many seed-eaters forage for soft-bodied insects among foliage and the bill becomes longer (Knox in press; for details

Fig. 6. Bill-length frequencies in *C. f. flammea*. Data extracted from Molau (1985), his Figs. 2 & 3.

of the process of bill growth in finches, see Lüdicke 1933). It seems likely, as was suggested over a hundred years ago by Wolley (in Yarrell 1882, see also Sundevall, quoted by Evans 1911) that some redpoll bills may be longer in summer than in winter due to differences in food and feeding habits. Since long-billed birds have been collected in winter as well as summer, and not all birds collected in the latter season are long-billed, the different foraging behaviour (and/or bill growth rates) of individuals may contribute further to the wide variation in bill-length in *flammea*. Food, foraging and/or growth rate probably also vary geographically, since long-billed birds seem to be more frequent in areas near the northern edge of the range of *flammea*.

5. CONCLUDING COMMENTS

The two redpoll species clearly differ in a number of respects. Arctic Redpolls arrive back on the breeding grounds earlier in the season than Common Redpolls. They sometimes nest in different habitats, although they may forage over widely overlapping areas. There may be differences in their diets, at least part of the time. They differ in their vocalizations, physiology, behaviour and morphology. Their population regulation is apparently influenced by different factors. In autumn, *C. flammea* migrates earlier than *C. hornemanni*.

There is no direct evidence for hybridization. The supposed intermediates have been shown to represent partially overlapping ranges in morphological variation in the two species. Even though I suspect occasional hybridization does occur between Arctic and Common Redpolls, successful interbreeding has never been reported from anywhere in the enormous area of sympatry, and few skins can unequivocally be determinded as hybrids.

The position of *islandica* remains obscure, although current research may help to clarify its characters and relationships. Even if Arctic and Common Redpolls are found to be hybridising in Iceland, this would represent only a localised breakdown of specific integrity. Overwhelming evidence from throughout the remainder of the redpolls' circumpolar distribution confirms that they otherwise behave as good species.

On plumage characters the redpolls (excluding *islandica*) fall into two groups – (1) *cabaret*, *flammea* and *rostrata* and (2) *exilipes* and *hornemanni*. On measurements, there is no such clear cut distinction, the birds forming a series from *cabaret* (small) through *flammea* and *exilipes*, then *rostrata* to *hornemanni* (large), although the ratios of one measurement to another vary from race to race. Similarities in size and bill shape led Molau (1985) to suggest that *exilipes* was most closely related to *flammea* and that *hornemanni* was closest to *rostrata*. He proposed treating *islandica* (for reasons not fully explained), *exilipes* and *hornemanni* as separate species. Following general ecogeographic rules, northern derivatives of *rostrata* and *flammea* stocks might both be expected to look paler and less streaked, with broader pale fringes to the feathers, longer tails and shorter bills than in the southern forms. However, there are many exceptions to these rules, and a number of other factors (*e.g.* food, migration) influence the size and proportions of birds. Thus, whereas northern forms are often larger than those further south (Bergmann's Rule), *exilipes* is much the same size as *flammea* (in the body), yet *hornemanni* is considerably larger than *rostrata*. The bill lengths of the two Greenland forms are not very different. Greater strength may be found in the argument that *hornemanni* and *rostrata* are the northern counterparts of *exilipes* and *flammea* respectively. In addition, the many close parallels in the plumage characters of the Arctic Redpolls suggest that they are sister taxa.

Of all the redpolls, *cabaret* is the most distinctive single race. Apart from *islandica* it is the only subspecies that is geographically separated from all others. Morphologically it is clearly defined, and it is the only race in which there are few, if any, identification problems. *Cabaret* probably developed from populations of *flammea* which became isolated in western Europe during the last glacial period (Johansen 1958). Unless significant gene flow exists, the disjunct range presently seen in *cabaret* is unlikely to date from the initial western isolation since little or no morphological differentiation exists between the populations in Britain and the Alps. Ringing has shown that some British redpolls migrate as far as Switzerland, Austria and Italy (Spencer & Hudson 1982). The southern

population of *cabaret* may have been started by some British birds remaining to breed in the wintering area instead of returning north in spring. Similar behaviour has frequently been noted in *flammea* (Götmark 1982), and even *rostrata* (Murton & Porter 1961, Williamson 1961), leading to many instances of nesting well to the south of the normal breeding range. Genetic continuity of the two *cabaret* populations may be maintained by one- or two-way exchanges of breeding birds between them. Clancey (1953) regarded the two populations as being taxonomically separable, implying reduced gene flow. Insufficient breeding birds from the Alps were available to me to allow re-evaluation. In Sweden, *cabaret* is presently breeding to the south of the normal range of nominate *flammea*, and in different habitats (Götmark 1981, 1982). Should the two eventually come together and fail to hybridise, *cabaret* will have to be treated as a separate species.

The relationships of the other isolated population, *islandica*, are less obvious. The dark birds show similarities to both *rostrata* and *flammea*. Although Salomonsen (1928) hypothesised a westerly origin for *islandica*, the broadly intermediate characters (of the dark birds) suggest otherwise. Most of the established Icelandic passerines have easterly relatives. The Icelandic Meadow Pipit *Anthus pratensis*, White Wagtail *Motacilla alba*, Wren *Troglodytes troglodytes*, Wheatear *Oenanthe oenanthe* and Redwing *Turdus iliacus* are all related to western European conspecifics. However, the Raven *Corvus corax* and Snow Bunting *Plectrophenax nivalis* affinities are uncertain and, among the non-passerines, the influence of the Nearctic fauna is indicated by the breeding of Great Northern Diver *Gavia immer*, Harlequin Duck *Histrionicus histrionicus*, Barrow's Goldeneye *Bucephala islandica* and Rock Ptarmigan *Lagopus mutus*. Thus, while most of the Icelandic passerines have easterly connections, those of the more arctic/subarctic elements of the avifauna (amongst which the redpoll might belong) are often either equivocal or Nearctic. There are no clear indications of the relationships or origin of *islandica*.

On the strength of the unproven '*fuscescens*', and geographical proximity, *rostrata* has been assumed to have had a westerly origin. If *islandica* is indeed intermediate to *rostrata* and *flammea*,

colonization from the east seems more likely. *Rostrata* is thought to have evolved its characters in a refuge off West Greenland during the last glaciation (Salomonsen 1972).

The Nearctic and Palearctic populations of *flammea* are treated here as uniform in characters, but this may not be so. There have been suggestions of weak clines and further subspecies (now synonymized); they were not investigated here. The redpoll group as a whole probably has a Palearctic origin, since this is where *Carduelis* (excluding the New World '*Spinus*' radiation) and in particular the *Acanthis* subgenus to which the redpolls belong have their centres of distribution. There is no reason to believe that this is a result of widespread extinctions elsewhere. The Nearctic population of *flammea* was a development of an eastward range extension, subsequent to the last glaciation (Salomonsen 1972). Harris *et al.* (1965) and Troy (1983) have suggested considerable continent-wide movement/gene flow in redpolls, although based on limited data. There is one record of a bird ringed in the Nearctic being recovered in the Palearctic (Troy 1983). This does not necessarily indicate intercontinental gene flow, although it must be a stong possibility considering the species' erratic breeding habits.

The centre of origin of *exilipes* is not known. As with *flammea*, the evidence suggesting a lack of differentiation along its circumpolar distribution has not been examined in detail here. The Arctic/Common Redpoll separation is the oldest within the redpolls and may date from the Tertiary (Johansen 1958), although biochemical evidence suggests that *flammea* and *exilipes* 'seem to have split' only 550,000 years ago (Marten & Johnson 1986). The Greenland Redpoll *hornemanni* is derived from *exilipes*, presumably from the west. It probably acquired its characters in the Peary Land refuge, near which its distribution is still centred in northern Greenland (Salomonsen 1972).

Many questions remain, apart from those indicated above concerning the history of the group. Contrary to widespread opinion, it seems that Common and Arctic Redpolls do not interbreed freely. Attention should be given to determining the amount and circumstances of any true interspecific hybridization. The parallel, circumpolar ranges of the two species must have developed over a period of time. The pattern of events that

gave rise to this distribution is largely unknown. Common and Arctic Redpolls are clearly near the boundary of species formation, and there may be areas or circumstances where reproductive isolation is incomplete, but this has yet to be demonstrated. The similarities between the species are considerable, so their ecological and behavioural differences are of interest. Why are the members of this species-pair so similar? How do they interact on the breeding grounds? Interspecific competition for food is said to be low in the arctic (Salomonsen 1972). This factor alone may permit the redpolls to co-exist (Wynne-Edwards 1952). Do the birds' anatomical differences reflect different foraging strategies? The considerable differences in bill size presumably reflect their seed, or other food, preferences, but we know little about the diet of sympatric forms during either the breeding season or winter. Similarly, we have scant knowledge of the reasons for *flammea's* intrasubspecific variation in bill length. How much of the other phenotypic variation in redpolls is non-genetic?

The special features seen in this species-group represent an outstanding opportunity to study in detail the interplay between systematics and ecology, and to examine the processes of evolution and speciation at a variety of levels.

6. ACKNOWLEDGEMENTS

7. SUMMARY

The subspecies of the circumpolar redpoll complex are usually either treated as conspecific under the name *Carduelis flammea*, or as two species, the Common Redpoll *C. flammea* (including *cabaret*, *islandica* and *rostrata*) and the Arctic Redpoll *C. hornemanni* (including *exilipes*). The two most widely distributed forms are broadly sympatric and intermediates are said to be common. It was generally assumed that they were the result of hybridization. This constituted the main argument for conspecificity. After examination of museum skins, it is shown that the plumages of most subspecies are very variable. The patterns of plumage variation are partly obscured by differences due to wear and because males tend to be paler than females, and adults tend to be paler than first-year birds. Several characters are taxonomically less informative than previously believed. The apparent intermediates are not hybrids; they are an artefact of over-narrow definition of specific characters. A review of the literature showed that, despite the high frequency of supposed hybrids in some populations, no confirmed record of interbreeding has ever been documented. The results of studies claiming to support redpoll conspecificity equally support their consideration as two species. Complex differences in the plumages, measurements, ecology and behaviour of Common and Arctic Redpoll are summarised. Differences of this nature are unlikely to be found within a freely interbreeding population. The *flammea* and *hornemanni* groups clearly behave as separate species, although they are very closely related and there may well be some localized hybridization (as yet unproven).

Pale and dark birds, which are both present in the Icelandic breeding population, show only slight differences in their biometrics. This requires further investigation.

The name *holboellii* is a synonym, representing long-billed individuals in the skewed bill-length distribution of nominate *flammea*. They may arise partly due to differences in food and feeding behaviour.

8. REFERENCES

Aldrich, J. W. & D. C. Nutt. 1939. Birds of eastern Newfoundland. Scient. Publs Cleveland Mus. nat. Hist. 4: 13–42.

Alsop, F. J. 1973. Notes on the Hoary Redpoll on its central Canadian arctic breeding grounds. Wilson Bull. 85: 484–485.

American Ornithologists' Union. 1957. Check-list of North American birds. 5th ed. A.O.U.

American Ornithologists' Union. 1985. Thirty-fifth supplement to the American Ornithologists' Union Checklist of North American birds. Auk 102: 680–686.

Bailey, A. M. 1948. Birds of Arctic Alaska. Colorado Mus. Nat. Hist. Popular Series No. 8.

Baldwin, P. H. 1961. Distribution, overlap, and hybridisation of two species of redpolls in Alaska. Bull. ecol. Soc. Am. 42: 152.

Bird, E. G. 1935. The status of Redpolls in Iceland. Ibis 13th ser. 5: 438–441.

Bird, E. G. 1936. Further note on Redpolls in Iceland. Ibis 13th ser. 6: 381.

Blok, A. A. & A. L. Spaans. 1962. Het voorkomen van de Barmsijs, *Carduelis flammea* (Linnaeus), als broedvogel in Nederland naar aanleiding van waarnemin-

gen op Vlieland in het voorjaar en de zomer van 1960 en 1961. Limosa 35: 4–16.

Boddy, M. 1979. Ageing and sexing Lesser Redpolls. Ringers' Bulletin 5: 87.

Boddy, M. 1981. Ageing and sexing British Lesser Redpolls. Ringing & Migration 3: 193–202.

Brewster, W. 1883. Holböll's Red-poll (*Aegiothus linaria holboelli*) in New England. Bull. Nuttall orn. Club 8: 95–99.

British Ornithologists' Union. 1932. Eighth report of the committee on the nomenclature and records of the occurrences of rare birds in the British Islands, and certain necessary changes in the nomenclature of the B.O.U. List of British Birds. Ibis 13th ser. 2: 94–100.

British Ornithologists' Union 1948. Eighteenth report of the committee on the nomenclature and records of the occurrences of rare birds in the British Islands, and on certain necessary changes in the nomenclature of the B.O.U. List of British Birds. Ibis 90: 319–322.

Brooks, A. 1917. Birds of the Chilliwack District, B. C. Auk 34: 28–50.

Brooks, E. A. 1936. Observations on some Newfoundland birds. Auk 53: 342–345.

Brooks, W. S. 1968. Comparative adaptations of the Alaskan Redpolls to the arctic environment. Wilson Bull. 80: 253–280.

Brooks, W. S. 1973. A tentative key for sex determination of Common Redpolls (*Acanthis flammea flammea*) in the northern United States during winter. Bird Banding 44: 13–21.

Capparella, A. P. & S. M. Lanyon. 1985. Biochemical and morphometric analysis of the sympatric, neotropical, sibling species, *Mionectes macconnelli* and *M. oleagineus*. In: P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely & F. G. Buckley (eds.). Neotropical ornithology. pp. 347–355. Orn. Monogr. No. 36.

Clancey, P. A. 1953. The British race of Lesser Redpoll. Bull. Br. Orn. Club 73: 72.

Coburn, F. 1901. Brief notes on an expedition to the north of Iceland in 1899. Zoologist 4th ser. 5: 401–419.

Cooke, F. 1985. Polymorphism. In: B. Campbell & E. Lack (eds.). A dictionary of birds. Poyser, Calton.

Coues, E. 1862a. Notes on the ornithology of Labrador. Proc. Acad. nat. Sci. Philad. 1861: 215–257.

Coues, E. 1862b. A monograph of the genus *Aegiothus*, with descriptions of new species. Proc. Acad. nat. Sci. Philad. 1861: 373–390.

Coues, E. 1864. Additional remarks on the North American *Aegiothi*. Proc. Acad. nat. Sci. Philad. 1863: 40–41.

Coues, E. 1869. On variation in the genus *Aegiothus*. Proc. Acad. nat. Sci. Philad. 1869: 180–189.

Coues, E. 1872. Key to North American Birds. Naturalists' Agency, Salem.

Coues, E. 1874. Birds of the Northwest. Government Printing Office, Washington.

Da Prato, E. S. & S. R. D. Da Prato. 1978. Criteria for sexing Lesser Redpolls. Ringing & Migration 2: 48–49.

Davis, P. G. 1975. Further thoughts on sexing Redpolls. Ringers' Bulletin 4: 86–87.

Dement'ev, G. P. & N. A. Gladkov (eds.). 1954. Birds of the Soviet Union. Vol. 5. Translated 1970; Israel Program for Scientific Translation, Jerusalem.

Duquet, M. 1984. Première preuve de reproduction du Sizerin flammé, *Carduelis flammea*, en Franche-Comté. Statut actuel de l'espèce dans le massif du Jura. Nos Oiseaux 37: 331–340.

Enemar, A. 1969. Gråsiskan *Carduelis flammea* i Ammarnäsområdet, Lycksele lappmark år 1968. Vår Fågelvärld 28: 230–235.

Enemar, A., L. Nilsson & B. Sjöstrand. 1984. The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. Ann. Zool. Fennici 21: 321–335.

Enemar, A. & B. Nyström. 1981. Om gråsiskans *Carduelis flammea* beståndsväxlingar, föda och häckning i fjällbjörkskog, södra Lappland. Vår Fågelvärld 40: 409–426.

Eriksson, K. 1970. Wintering and migration ecology of Siskin (*Carduelis spinus*) and Redpoll (*C. flammea*). Proc. XV Internat. Ornith. Congr. (Hague). P. 642.

Evans, P. R. 1966. Autumn movements, moult and measurements of the Lesser Redpoll *Carduelis flammea cabaret*. Ibis 108: 183–216.

Evans, P. R. 1969. Ecological aspects of migration, and premigratory fat deposition in the Lesser Redpoll, *Carduelis flammea cabaret*. Condor 71: 316–330.

Evans, P. R., R. A. Elton & G. R. Sinclair. 1967. Moult and weight changes of Redpolls, *Carduelis flammea*, in north Norway. Ornis Fenn. 44: 33–41.

Evans, W. 1911. Notes on the recent immigration of Mealy Redpolls (*Acanthis linaria*), including the form known as Holböll's Redpoll. Proc. R. phys. Soc. Edinb. 18: 196–203.

Fellenberg, W. 1984. Die Entwicklung der westfälischen Brutpopulation des Birkenzeisigs (*Carduelis flammea cabaret*) 1981–1983. Charadrius 20: 246–251.

Fennell, J. F. M., P. M. Sagar & J. S. Fennell. 1985. Variation within the Redpolls of Canterbury. Notornis 32: 245–253.

Gabrielson, I. N. & F. C. Lincoln. 1959. The birds of Alaska. Stackpole, Harrisburg, Pennsylvania.

Gabrielson, I. N. & B. S. Wright. 1951. Notes on the birds of the Fort Chimo, Ungava district. Can. Fld Nat. 65: 127–140.

Götmark, F. 1978. Gråsiskan *Carduelis flammea* – en expanderande häckfågel i sydvästra Sverige. Vår Fågelvärld 37: 133–135.

Götmark, F. 1981. Gråsiskans *Carduelis flammea cabaret* invandring till södra Sverige: resultat av en inventering 1978. Vår Fågelvärld 40: 47–56.

Götmark, F. 1982. Gråsiskans *Carduelis flammea* förekomst i södra Sverige under 'sydhäckningsåret' 1975. Vår Fågelvärld 41: 315–322.

Grant, B. R. & P. R. Grant. 1983. Fission and fusion in a population of Darwin's Finches: an example of the value of studying individuals in ecology. Oikos 41: 530–547.

Grinnel, L. I. 1943. Nesting habits of the Common Redpoll. Wilson Bull. 55: 155–163.

Grote, H. 1943. Beitrag zur Kenntnis des Birkenzeisigs (*Carduelis flammea*). J. Orn. 91: 136–143.

Hald-Mortensen, P. 1970. Lille Gråsisken (*Carduelis flammea cabaret* (Müller)) som ynglefugl i Danmark. Dansk. orn. Foren. Tidsskr. 64: 163–193.

Hantzsch, B. 1904. *Acanthis linaria islandica* subsp. nov.. Orn. Mber 12: 32–34.

Harper, F. 1953. Birds of the Nueltin Lake Expedition, Keewatin, 1947. Am. Midl. Nat. 49: 1–116.

Harris, M. P., F. I. Norman & R. H. S. McColl. 1965. A mixed population of Redpolls in northern Norway. Brit. Birds 58: 288–294.

Hellmayr, C. E. 1938. Catalogue of birds of the Americas. Publs Field Mus. nat. Hist., Zool. Ser., Vol 13, part 11.

Hildén, O. 1969. Über Vorkommen und Brutbiologie des Birkenzeisigs (Carduelis flammea) in Finnisch-Lappland im Sommer 1968. Ornis Fenn. 46: 93–112.

Holmes, R. T. & C. P. Black. 1973. Ecological distribution of birds in the Kolomak River-Askinuk Mountain region, Yukon-Kuskokwim Delta, Alaska. Condor 75: 150–163.

Hortling, I. & E. C. Stuart Baker. 1932. Bird-notes on a trip to Lapland. Ibis 13th ser. 2: 100–127.

Howell, T. R., R. A. Paynter & A. L. Rand. 1968. Subfamily Carduelinae in Check-list of birds of the world. Vol. 14. Mus. Comp. Zool., Cambridge, Mass.

Irving, L., G. C. West, L. J. Peyton & S. Paneak. 1967. Migration of Willow Ptarmigan in arctic Alaska. Arctic 20: 77–85.

James, R. D., P. L. McLaren & J. C. Barlow. 1976. Annotated checklist of the birds of Ontario. Life Sci. Misc. Publ., R. Ont. Mus.

Jehl, J. R. & B. A. Smith. 1970. Birds of the Churchill Region, Manitoba. Man. Mus. Man and Nature. Spec. Publ. No. 1.

Johansen, H. 1944. Die Vogelfauna Westsibiriens. II. J. Orn. 92: 1–105.

Johansen, H. 1958. Revision und Entstehung der Arktischen Vogelfauna. Acta Arctica 9: 1–132.

Jones, B., P. G. Davis & C. J. Mead. 1975. Sexing Redpolls: at last a consensus? Ringer's Bulletin 4: 99–100.

Kennard, J. H. 1976. A biennial rhythm in the winter distribution of the Common Redpoll. Bird Banding 47: 231–237.

Kessel, B., H. K. Springer & C. M. White. 1964. June birds of the Kolomak River, Yukon-Kuskokwim Delta, Alaska. Murrelet 45: 37–47.

Knox, A. G. In press. Seasonal variation in biometrics. In: G. Cracknell & R. J. O'Connor (eds.). Bird data. Poyser, Calton.

Langslow, H. 1975. Some problems in sexing Redpolls. Edinburgh Ringing Group 2(1974): 22–24.

Lindström, A., U. Ottosson & J. Pettersson. 1984. Sydlig gråsiska Carduelis flammea cabaret i Sverige samt förslag till kriterier för rasbestämning. Vår Fågelvärld 43: 525–530.

Lobkov, E. G. 1979. (On biology and interrelations of the Common (Acanthis flammea) and the Tundra (Acanthis hornemanni) Redpolls in Kamchatka.) Biol. Nauki 11: 64–68.

Lönnberg, E. 1931. Olof Rudbeck, Jr., the first Swedish ornithologist. Ibis 13th ser. 1: 302–307.

Lüdicke, M. 1933. Wachstum und Abnutzung des Vogelschnabels. Zool. Jb. (Anat.) 57: 465–534.

Lundevall, C. F. 1952. The bird fauna in the Abisko National Park and its surroundings. K. Svenska Vetensk Akad. Avh. Naturskydd. 7: 1–73.

Marten, J. A. & N. K. Johnson. 1986. Genetic relationships of North American Cardueline finches. Condor 88: 409–420.

Mayr, E. & L. L. Short. 1970. Species taxa of North American birds. Publ. Nuttall orn. Cl. No. 9.

Mead, C. 1973. Sex and the Redpoll ringer. Ringers' Bulletin 4: 46–47.

Meinertzhagen, R. 1938. Winter in arctic Lapland. Ibis 14th ser. 2: 754–759.

Molau, U. 1982. Gråsiskkomplexet i Sverige. Ringinform 5: 11–13.

Molau, U. 1985. Gråsiskkomplexet i Sverige. Vår Fågelvärld 44: 5–20.

Morony, J. J., W. J. Bock & J. Farrand. 1975. Reference list of the birds of the world. Am. Mus. Nat. Hist., New York.

Mundinger, P. C. 1979. Call learning in the Carduelinae: ethological and systematic considerations. Syst. Zool. 28: 270–283.

Murton, R. K. & S. C. Porter. 1961. Greenland-type Redpolls nesting in Inverness-shire. Brit. Birds 54: 251–253.

Nelson, E. W. 1883. Birds of Bering Sea and the Arctic Ocean. In: Cruise of the Revenue–steamer Corwin in Alaska and the N.W. Arctic Ocean. pp. 55–118. Government Printing Office, Washington.

Nelson, E. W. 1887. Report upon natural history collections made in Alaska between the years 1877 and 1881. Government Printing Office, Washington.

Newton, I. 1972. Finches. Collins, London.

Nuechterlein, G. L. 1981. Courtship behavior and reproductive isolation between Western Grebe color morphs. Auk 98: 335–349.

Nyström, B. & H. Nyström. 1987. Biotopval och häckning hos gråsiskor Carduelis flammea och snösiskor C. hornemanni i Ammarnäsområdet, södra Lappland. Vår Fågelvärld 46: 119–128.

Oberholser, H. C. 1918. Notes on North American birds. Auk 35: 463–467.

O'Donald, P. 1983. The Arctic Skua. C.U.P., Cambridge.

Payn, W. A. 1947. Redpolls from Norway. Bull. Br. Orn. Club 67: 41–42.

Peiponen, V. 1957. Wechselt der Birkenzeisig, Carduelis flammea (L.), sein Brutgebiet während des Sommers? Ornis Fenn. 34: 41–64.

Ratti, J. T. 1979. Reproductive separation and isolating mechanisms between sympatric dark- and light-phase Western Grebes. Auk 96: 573–586.

Ratti, J. T. 1981. Identification and distribution of Clark's Grebe. Western Birds 12: 41–46.

Ratti, J. T. 1985. A test of water depth niche partitioning by Western Grebe color morphs. Auk 102: 635–637.

Rising, J. D. & F. W. Schueler. 1980. Identification and status of Wood Pewees (Contopus) from the Great Plains: what are sibling species? Condor 82: 301–308.

Salomonsen, F. 1928. Bemerkungen über die Verbreitung der Carduelis linaria Gruppe und Ihre Variationen. Vidensk. Meddr. Dansk naturh. Foren. 86: 123–202.

Salomonsen, F. 1951. The birds of Greenland. Part III. Munksgaard, Copenhagen.

Salomonsen, F. 1972. Zoogeographical and ecological problems in arctic birds. Proc. XV Internat. Ornith. Congr. (Hague). Pp. 25–77.

Schmidt, K. 1984. Erster Nestfund des Birkenzeisigs in Thüringen. Falke 31: 131–133.

Shields, G. F. 1982. Comparative avian cytogenetics: a review. Condor 84: 45–58

Slater, H. H. 1901. Manual of the birds of Iceland. Douglas, Edinburgh.

Slater, H. H. & T. Carter. 1886. Notes from northern Iceland in the summer of 1885. Ibis 5th ser. 4: 45–52.

Spencer, R. & R. Hudson. 1982. Report on bird-ringing for 1981. Ringing & Migration 4: 65–128.

Stejneger, L. 1884. Notes on the genus *Acanthis*. Auk 1: 145–156.

Storer, R. W. & G. L. Nuechterlein. 1985. An analysis of plumage and morphological characters of the two color forms of the Western Grebe (*Aechmophorus*). Auk 102: 102–119.

Svensson, L. 1984. Identification guide to European passerines. 3rd edn. L. Svensson, Stockholm.

Taverner, P. A. & G. M. Sutton. 1934. The birds of Churchill, Manitoba. Ann. Carneg. Mus. 23: 1–83.

Timmermann, G. 1938. Zur Fortpflanzungsbiologie des Birkenzeisigs, (*Carduelis flammea* [L.]). Beitr. Fortpfl-Biol. Vögel 14: 201–206.

Timmermann, G. 1949. Die Vögel Islands. 3 Lieferung. Visindafelag Islendinga No. 28, Reykjavik.

Todd, W. E. C. 1963. Birds of the Labrador Peninsula and adjacent areas. Univ. Toronto Press, Toronto.

Troy, D. M. 1980. A phenetic and karyotypic investigation of the systematics of the Redpolls *Carduelis f. flammea* and *C. hornemanni exilipes*. M. Sc. Thesis, Univ. of Alaska, Fairbanks, Alaska.

Troy, D. M. 1983. Recaptures of Redpolls: movements of an irruptive species. J. Field Orn. 54: 146–151.

Troy, D. M. 1984. Holboell's Redpolls: do they exist? Can. J. Zool. 62: 2302–2306.

Troy, D. M. 1985. A phenetic analysis of the redpolls *Carduelis flammea flammea* and *C. hornemanni exilipes*. Auk 102: 82–96.

Troy, D. M. & A. H. Brush. 1983. Pigments and feather structure of the redpolls, *Carduelis flammea* and *C. hornemanni*. Condor 85: 443–446.

Vaurie, C. 1956. Systematic notes on palearctic birds. No. 19. Fringillidae: the genera *Fringilla, Serinus, Carduelis*, and *Acanthis*. Amer. Mus. Novit. No. 1775.

Vaurie, C. 1957. On the validity of *Acanthis flammea islandica* Hantzsch. Dansk. orn. Foren. Tidsskr. 51: 9–11.

Vaurie, C. 1959. The birds of the palearctic fauna. Passeriformes. Witherby, London.

Vaurie, C. 1964. Systematic notes on palearctic birds. No. 53. Charadriidae: the genera *Charadrius* and *Pluvialis*. Amer. Mus. Novit. No. 2177.

Veprintsev, B. N. & M. M. Zablotskaya. 1982. (Acoustic communication of the Hornemann's Redpoll *Acanthis hornemanni* (Holb.).) Sci. Centr. Biol. Res. Acad. Sci. USSR, Pushchino. 24pp.

Voous, K. H. 1960. Atlas of European birds. Nelson, London.

Voous, K. H. 1977. List of recent holarctic bird species. Ibis 119: 376–406.

Waterston, G. & I. Waterston. 1970. Greenland Redpoll (*Carduelis flammea rostrata* (Coues)) breeding in high arctic region. Dansk orn. Foren. Tidsskr. 64: 93–94.

Watson, A. 1957. Notes on birds in arctic Norway. Sterna 2: 65–99.

West, G. C., L. J. Peyton & S. Savage. 1968. Changing composition of a redpoll flock during spring migration. Bird Banding 39: 51–55.

Wetherbee, O. P. 1937. A study of wintering Hoary, Common, and Greater Redpolls, and various intermediates or hybrids. Bird Banding 8: 1–10.

Williamson, K. 1956. The autumn immigration of the Greenland Redpoll (*Carduelis flammea rostrata* (Coues)) into Scotland. Dansk orn. Foren. Tidsskr. 50: 125–133.

Williamson, K. 1961. The taxonomy of the redpolls. Brit. Birds 54: 238–241.

Witherby, H. F., F. C. R. Jourdain, N. F. Ticehurst & B. W. Tucker. 1938. The handbook of British birds. Vol. 1. Witherby, London.

Wood, M. 1969. A bird-bander's guide to determination of age and sex of selected species. College of Agriculture, Pennsylvania State Univ.

Wunderle, J. M. 1981. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, West Indes. Evolution 35: 333–344.

Wynne-Edwards, V. C. 1952. Zoology of the Baird Expedition (1950). 1. The birds observed in central and southeast Baffin Island. Auk 69: 353–391.

Yarrell, W. (& A. Newton.) 1882. A history of British birds. 4th edn. Vol. II. Van Voorst, London.

Zablotskaya, M. M. 1981. (Acoustical communication of the Common Redpoll *Acanthis flammea flammea* (L.).) Sci. Centre Biol. Res. Acad. Sci. USSR, Pushchino. 28pp.

Zablotskaya, M. M. 1984. Systematics and Carduelinae songs. Acoustic signalization of animals. Sci. Centre Biol. Res. Acad. Sci. USSR, Pushchino. 21pp.

9. SAMENVATTING

De taxa van het circumpolaire Barmsijs-soortscomplex worden meestal beschouwd als één soort (*Carduelis flammea*) of als twee soorten, de Barmsijs (*Carduelis flammea*) met als ondersoorten *flammea, cabaret, islandica* en *rostrata* en de Witstuitbarmsijs (*C. hornemanni* inclusief *exilipes*). De twee meest verspreide vormen (*flammea* en *exilipes*: Fig. 1) zijn over een groot deel van hun verspreidingsgebied sympatrisch en een aantal auteurs stelt dat er veelvuldig tussenvormen zouden voorkomen als het gevolg van hybridisatie. Daarin was het voornaamste argument gevonden om aan te nemen dat deze vormen tot één soort zouden behoren. Echter, museum onderzoek van balgen door de auteur wijst uit dat het verenkleed van de meeste ondersoorten heel variabel is, en ondersoortsgebonden variatie in dit verenkleed blijkt vaak door andere variatie te worden overschaduwd. Deze andere variatie komt voort uit een verschil in slijtage van het verenkleed of wordt veroorzaakt doordat mannetjes vaak lichter gekleurd blijken te zijn dan vrouwtjes, terwijl ook vaak volwassen vogels lichter van kleur zijn dan eerste-jaars vogels. Verscheidene kenmerken leveren dus minder informatie op voor de taxonomie van deze Barmsijzen dan wel geloofd werd. De schijnbare tussenvormen zijn volgens de auteur geen bastaarden, maar ze zijn als zodanig geïdentificeerd vanwege een te strikte definitie van de soortskenmerken. Literatuurstudie wees uit dat ondanks het hoge aandeel van zogenaamde bastaarden in sommige populaties er nooit goede aanwijzingen zijn gepubliceerd dat voortplanting werkelijk plaatsvindt tussen de twee taxa. De resultaten die gepubliceerd zijn in artikelen waarin gepleit werd voor één soort Barmsijs lijken ook gebruikt te kunnen worden om de idee te steunen dat er sprake is van twee soorten. In het artikel worden complexe verschillen wat betreft het verenkleed, biometrie, oecologie en gedrag van de Barmsijs en van de Witstuitbarmsijs samengevat. De verschillen tussen de twee vormen zijn van dien aard dat het onwaarschijnlijk moet worden geacht

dat die gevonden zouden kunnen worden in een panmictische populatie. De groep *flammea* en de groep *hornemanni* gedragen zich duidelijk als gescheiden, verschillende soorten, die echter nauw verwant zijn, alhoewel de auteur het niet onmogelijk acht dat er op beperkte schaal ergens in het sympatrische areaal hybridisatie zou kunnen optreden (maar daar is geen bewijs voor).

Lichtgekleurde en donkere individuen, beide aanwezig in de IJslandse broedpopulatie, vertonen slechts geringe biometrische verschillen en daar zou meer onderzoek naar gedaan moeten worden.

De naam *holboellii* is een synoniem gegeven aan langsnavelige individuen van de nominaatvorm *flammea*. Het vermoeden wordt uitgesproken dat deze individuen zulke lange snavels hebben vanwege bijvoorbeeld ander voedsel of ander voedselzoekgedrag.

In sectie 5 van zijn artikel bespreekt de auteur de mogelijke historische en evolutionaire ontwikkeling van het soortscomplex *Carduelis*.　　　　　　　　　　　　　H. H. T. Prins

10. APPENDIX

IDENTIFICATION OF REDPOLLS

It is not the intention to review here the identification features of Common and Arctic Redpolls, but some comments may be useful.

Distinguishing 'typical' *flammea* from typical *exilipes* on plumage characters presents few problems. However, separating pale *flammea* and dark *exilipes* can be very difficult. Some of these birds can only reliably be identified on plumage by reference to a correctly determined series of skins from the appropriate time of year. By that means, or with considerable experience, the range of colour in each species may be established. Failing this, persons otherwise familiar with 'typical' examples of the subspecies, but handling or seeing just a few

of the difficult birds may incorrectly judge the limits of specific variation. Other characters may be more useful. For example, measurements of birds in the hand (M. Herremans pers. comm., this paper) or, in the field, the relatively smaller, stubbier bill of *exilipes*, and vocalizations. Caution must be exercised and many individuals will seem unidentifiable, particularly in the field, pending further research. It would be very easy to misidentify a dark *exilipes* in a flock of *flammea*, even with typical *exilipes* available for comparison. Similarly, a very pale *flammea* among a flock of otherwise typical *flammea* might easily be mistaken for *exilipes*. The rump, especially, is less reliable than previously believed, being very pale, even white, in some *flammea*, and streaked in some *exilipes*. No single morphological character can be used to tell the forms apart. The colour of the forehead is unreliable (*contra* Molau 1985).

In Britain and continental Europe the problem is partly academic outside the breeding season, because of the possible presence of pale *islandica*. Some of these birds may be indistinguishable from dark *exilipes* (or pale *flammea*) in the field. Even in the hand many pale redpolls will be unidentifiable without reference to series of correctly determined reference specimens. The differences are not great, and comparisons should be made with birds collected at the correct time of year. *Islandica* usually has a larger bill than *exilipes*. In late winter the feather edgings on the mantle and back of *exilipes* are usually a richer, buffier brown than the greyer plumage of pale *islandica*. In early spring the same feathers on *exilipes* are whiter than on *islandica*. The underparts of *exilipes* are usually paler with less streaking than on *islandica*. There are many exceptions to these comments, and attempted separation of most *exilipes* from pale *islandica* is not recommended, again pending further research. In Europe, particularly Britain, the Faroes, or around the shores of the North Sea, where *islandica* might be expected sometimes to winter, any redpoll showing a pale rump and moderate streaking on the underparts could possibly be *islandica*.