A PHENETIC ANALYSIS OF THE REDPOLLS
CARDUELIS FLAMMEA FLAMMEA AND
C. HORNEMANNI EXILIPES

DECLAN M. TROY[1]

Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99701 USA

ABSTRACT.—A review of the historical treatment of Common and Hoary redpolls (*Carduelis flammea flammea* and *C. hornemanni exilipes*) revealed no diagnostic means of distinguishing the two taxa. Interpretations of species limits have varied, resulting in conflicting treatment of intermediate forms. Variability in plumage and skeletal characters of redpolls from 9 breeding locations in Alaska and Canada were examined to determine if a means of discriminating between the two taxa could be found, and to determine if individuals with intermediate plumage characteristics (potential hybrids) were also morphologically intermediate. Because sexes differed in most skeletal dimensions, all analyses were duplicated for the two sexes. A character index was developed based on three plumage characteristics: rump streaking, undertail covert streaking, and lateral (side) streaking. This index characterized redpolls on a darkness gradient from extreme *flammea* (dark, heavy streaking) to extreme *exilipes* (light, no streaking). The observed range of scores was divided into thirds to designate *flammea*, unknown (intermediate), and *exilipes* classes. Females showed a much narrower range of plumage variability than males. No females were white enough to be considered *exilipes* on the scale used for males. Most birds from the *flammea* and *exilipes* extremes of plumage variability could be distinguished by skeletal criteria (using discriminant function analysis); however, no discontinuity existed, as other birds were intermediate for both plumage and skeletal characteristics. Intermediates were found at all sampled localities where both plumage morphs occurred. Results of analyses based on plumage (character index) and skeletal measurements were very similar and showed that samples containing intermediate plumage birds were also intermediate skeletally. Considering the continuous variability of both plumage and skeletal characters and the lack of any diagnostic criterion for identifying the taxa, the two redpolls should be merged into a single taxon, *Carduelis flammea. Received 22 November 1983, accepted 23 May 1984.*

COMMON and Hoary redpolls (*Carduelis flammea* and *C. hornemanni*) are small finches of the subgenus *Acanthis* (A.O.U. 1983). The taxonomy of redpolls has long been perplexing. Jehl and Smith (1970) considered it to be "one of the most perplexing problems in North American ornithology." Similar concerns were expressed by Bannerman (1953), Todd (1963), and others. Coues (1862) recognized 6 species of redpolls in North America, plus another in Europe; Salomonsen (1950) listed only one worldwide, while the American Ornithologists' Union (1983) recognized two. Of the many problems in our understanding of the relations of the various redpoll taxa, the specific distinction of *C. flammea* and *C. hornemanni* is of pri-

mary importance. The relationship of the most widespread subspecies of each of these species, *C. f. flammea* and *C. hornemanni exilipes*, is central to this problem.

This study was an attempt to clarify the relationship between these two redpoll taxa using plumage and skeletal characters. Alaska redpolls were considered in detail because published accounts indicate that the greatest taxonomic difficulty in North America occurs in this region (Gabrielson and Lincoln 1959, Baldwin 1961). Smaller samples from across Canada also were analyzed.

Characteristics previously used to distinguish *exilipes* from *flammea* are listed in Table 1. No single character distinguishes these taxa from each other unequivocally. The generalizations that exist are useful for identification of extreme examples only. Unfortunately, no description of the range of variability in either *exilipes* or *flammea* has been made, resulting in

TABLE 1. Differences in bill and plumage characteristics used to distinguish between *Carduelis hornemanni exilipes* and *C. flammea flammea*.

Character	*exilipes*	*flammea*	Source
Bill length	Small	Moderate	Coues 1903
Bill shape	More conic, less compressed, darker colored with dense nasal plumuli	Opposite	Coues 1862
Superciliary stripe	More distinct	Less distinct	Coues 1862
Breast color	Rosy, many shades lighter than *flammea*	Darker	Coues 1862
Sides	Paucity of streaks	Strongly streaked flanks	Coues 1862 Bannerman 1953
Feet	Smaller, weaker Toes much shorter Tarsus > middle toe plus claw	Opposite Tarsus = middle toe plus claw	Coues 1862
General	Lighter	Much darker	Godfrey 1966

confusion as to how to identify specimens that are apparently intermediate in some characters.

Because they were originally described using morphological criteria, any attempt to determine whether *flammea* and *exilipes* are indeed separate species logically should look for at least one morphological feature to discriminate between them. If a character can be found with a range of states such that the distribution of scores of samples of the pure species is discontinuous (the discontinuity indicating species limits), suspected hybrids should have intermediate scores along this character.

Under the strictest definition of the biological species (Mayr 1970), the presence of any hybrids would make the specific distinction of the parental taxa suspect. However, it has been common practice to accept species distinctiveness if hybridization is limited. Hence, if few intermediates exist, whether they be hybrids or extreme variants of parental species, the separation of *exilipes* and *flammea* would be justified. For the purpose of this paper, both hybrid and intermediate are used to describe birds that possess characteristics intermediate between "typical" *flammea* and *exilipes*. If these two forms are morphologically distinct, then intermediates are probably true hybrids or their offspring. If *flammea* and *exilipes* are not distinct, the intermediate birds probably represent a segment of continuous variation rather than hybrids, and it is necessary to conclude that the recognition of two species is unfounded.

Two methods often used to detect the presence of hybrid individuals and/or populations are hybrid indices (examples using avian subjects include Sibley and Short 1959a, b; Sibley and West 1959; Short 1963; Szijj 1963; Rising 1970; and Scott et al. 1976) and multivariate analyses of skeletal dimensions (Rohwer 1972). Although frequently used to identify hybrids (or populations containing hybrids), hybrid indices do not directly reflect the hybrid nature of the individual to be scored. I have used the term "character index" because the scale is derived from several characters. Plumage characters used in character indices are often the same variables that give rise to the hypothesis of hybridization in the first place, and their use can lead to a circular argument (Scheuler and Rising 1976). I used the analysis of skeletal characters as an independent test of the findings of the character index analysis.

METHODS AND MATERIALS

Specimens.—Only adults collected during the breeding season were used in the plumage and skeletal studies. Alaska redpolls were collected in three regions: the Akulik-Inglutalik River delta, Norton Bay; Interior Alaska (no large collections were made, so this sample comprises three smaller samples: Talkeetna Mountains near Hatcher Pass, Denali Highway at the Brushkana River, and Fairbanks); and the Kongakut River, Arctic National Wildlife Refuge. Four redpolls collected at Kaktovik, Barter Island, were added to the Kongakut River sample. These speci-

TABLE 2. Number and location of specimens from which skeletal measurements were taken.

Location	Males	Females
Akulik-Inglutalik River delta, Alaska	100	51
Interior Alaska	21	11
Kongakut River, Alaska	67	31
Inuvik, N.W.T.	38	18
Krekovick Landing, N.W.T.	17	10
Coppermine, N.W.T.	16	11
Churchill, Manitoba	8	—
Winisk, Ontario	8	—
Fort Chimo, Quebec	37	8
Total	312	140

mens have been deposited in the collections of the American Museum of Natural History and Royal Ontario Museum. Samples from localities across Canada were measured at the Royal Ontario Museum. Canadian collection sites were Inuvik, Northwest Territories (N.W.T.); Krekovick Landing, Anderson River, N.W.T.; Coppermine, N.W.T.; Churchill, Manitoba; Winisk, Ontario; and Fort Chimo, Ungava Bay, Quebec. Numbers of specimens from each collection site are listed in Table 2. The location of each collection site is shown in Fig. 1.

Redpolls used in the following analyses were prepared as partial skins and skeletons, providing plumage and skeletal data from each specimen.

CHARACTER SELECTION

Skeletal characters.—A list of skeletal characters that have been used in avian morphological studies was compiled from the literature (Johnston 1969; Schnell 1970; Power 1971a, b; Robins and Schnell 1971; Johnston and Selander 1972; Rohwer 1972; Rising 1973). I selected 38 variables from the list as being of possible value in this study. The 38 variables were measured with dial calipers to the nearest 0.1 mm on a sample of 70 birds constituting the most extreme examples (based on rump color) of female *flammea* ($n = 25$), male *flammea* ($n = 20$), and male *exilipes* ($n = 23$) in my Alaska collections. Only 2 female redpolls with white rumps were found; hence female *exilipes* were not treated as a group in the preliminary analyses.

I tested the three groups using discriminant function analysis (DFA) to determine the value of skeletal characters in discriminating species. I also examined differences in the means of each variable between pairs of the three samples using *t*-tests, and omitted variables that were not significantly different between at least one pair of my reference groups. By these methods I reduced the character set to 19 variables that could be measured with good repeatability and would be useful in discriminating between morphs of redpolls (see Table 3).

An attempt was made to measure the length of the middle toe, as this was an important character in the description of *exilipes* by Coues (1862). Unfortunately, this character proved to be difficult to measure due to the problem of uniformly straightening the toe of dried specimens. Since Coues (1862) stated that all toes are short in *exilipes*, the hallux measurement should have provided an index of this characteristic. The hallux is a single bone and as such is more easily (and precisely) measured than the middle toe, which comprises three elements. Because I measured the hallux on skeletons, its length does not include the claw.

Plumage characters.—Several plumage characters may differ between *flammea* and *exilipes* (Table 1). Some differences are subtle, particularly during the breeding season when the feathers have become worn. In order to place birds on a gradient between the two species, it was desirable to have characters that showed a broad range of variability so that several classes could be established. Three characters were selected as having sufficient variability to be useful: 1) rump streaking, 2) undertail covert streaking, and 3) streaking on the sides and flanks.

For each of the three plumage characters scored, reference series were established showing the gradation from Common to Hoary plumage states. Six classes were used for each character, giving each variable equal weighting in the character index. The range of variability of these characters is shown in Figs. 2–4.

ANALYSES

Missing data estimation.—The use of multivariate statistical techniques such as DFA requires that no missing values exist in the case (individual) × variable data matrix. Unfortunately, skeletal characters occasionally were impossible to measure due to breakage (particularly if specimens were collected by shooting) or loss. Since a given specimen had few (if any) missing characters, I felt it was more desirable to include the specimen in the analysis than to omit it altogether. Missing values were estimated using regression equations of the character with the missing value and the character most correlated with it. Regressions were calculated for each sex and location, provided a sufficient number of individuals (15–20) were available. Approximately 1–2% of the measurements were estimated.

Sexual dimorphism.—The samples used in this study were tested for sexual dimorphism using the skeletal data set. These data were subjected to DFA (BMDP7M, Dixon 1975) for all locations pooled. Most studies using morphological data have included separate analyses for the sexes, but rarely have the differences between the sexes been specifically analyzed (see Johnston 1969). In evaluating the success of this and other discriminant functions (see *Skeletal analysis*) the
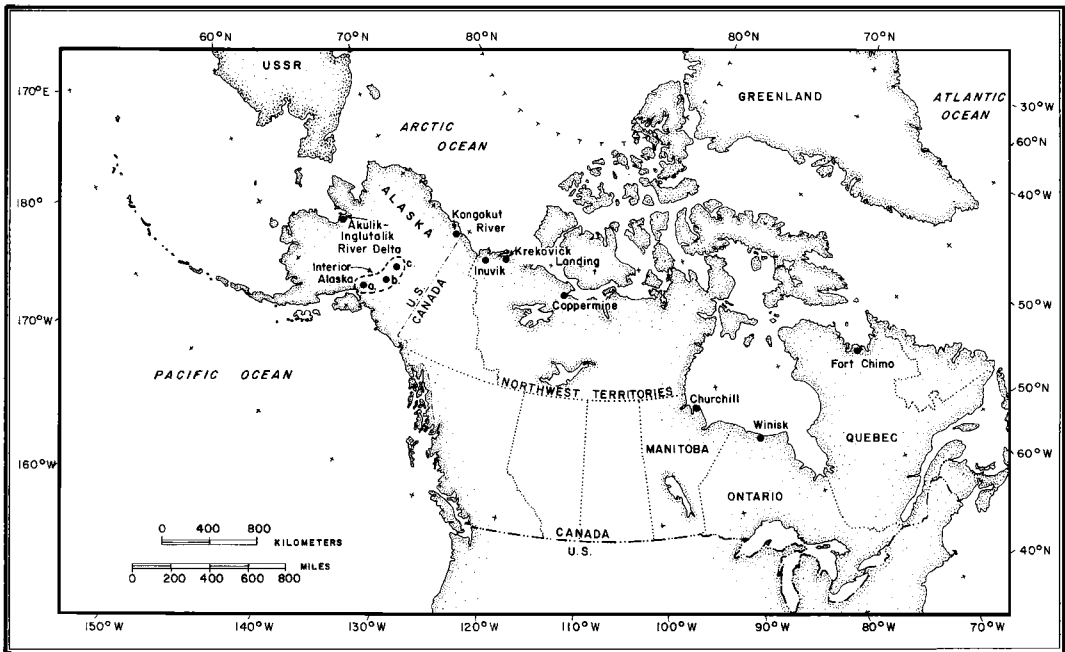
Fig. 1. Locations of collection sites of redpolls. Subsamples from Interior Alaska are: a) Hatcher Pass, b) Brushkana River, and c) Fairbanks.

jackknife method was used to determine the percentage of specimens that could be correctly classified.

Hybridization.—The ideal analysis of hybridization involves the collection of samples of each parental species (from areas of allopatry) and then of the putative hybrid population at an intermediate location. The difficulty in using this method with redpolls was in finding a region where only *exilipes* occurred. Several maps, such as those published in Dement'ev et al. (1954) and Ogilvie (1976), show a northern band where only this form occurs. This band is particularly broad in the Keewatin District, N.W.T. However, regional works such as Snyder (1957) and my own observations in western and northern Alaska and Keewatin District, N.W.T., indicate that both forms are sympatric in these areas as well. Wynne-Edwards (1952) wrote that the northern limit of *flammea* is roughly coincident with the northern limit of *hornemanni*. Thus, pure populations of *exilipes* may not exist, and it was necessary to select the reference series of the parental forms from the same samples as those containing the presumed hybrids. This method reduced the compounding effects of geographic variation since the entire analysis was done by location; however, a more precise means of delimiting the parental species had to be used.

Character index analysis.—One method of measuring the extent of hybridization in natural popula-

tions is the formulation of character (=hybrid) indices. To use this method, several characteristics that differ between the species are selected and a graded series is developed over the range of variability. A character index was computed for redpolls using the formula:

$$\text{character score} = \text{rump score} + \text{undertail} \\ \text{covert score} + \text{lateral} \\ \text{streaking score} - 2.$$

This scoring system resulted in each bird being placed along a gradient between 1 (extreme *flammea*) and 16 (extreme *exilipes*). The distribution of scores reveals the presence of intermediate (hybrid) birds. When examined by location, the scores indicate 1) where intermediates occur, 2) if both parental types are present, and 3) if variation is within or between populations.

Skeletal analysis.—For the purpose of this analysis, individuals were classed as *flammea*, unknown, or *exilipes* by dividing the range of character index scores into thirds. Females exhibited a narrower range of plumage variability than males; hence, a different classification scheme had to be used for each sex. For males, individuals with scores 1–5 were considered *flammea*, 6–11 were unknown, and 12–16 were *exilipes*. For females, individuals with scores 1–4 were considered *flammea*, 5–8 were unknowns, and 9–11

TABLE 3. Mean values (mm) of skeletal measurements of *exilipes* and *flammea*. Taxa are defined as for the discriminant function analyses. Pairs of values marked with an asterisk (*) are significantly different (*P* < 0.05). Significant differences between the sexes are not shown.

	Males			Females		
	exilipes		*flammea*	*exilipes*		*flammea*
Premaxilla length	7.73		8.09	7.49	*	8.03
Premaxilla width	4.59	*	4.51	4.49		4.49
Dentary symphysis length	4.52	*	4.88	4.32	*	4.90
Mandible width	11.79	*	11.47	11.58	*	11.36
Coracoid length	14.48	*	14.62	14.06	*	14.29
Scapula width	2.55		2.58	2.43	*	2.55
Furcula length	13.62		13.66	13.30	*	13.55
Tibiotarsus length	22.28		22.28	21.98		22.00
Tibiotarsus width	1.97	*	2.22	1.94	*	1.98
Tarsometatarsus length	14.18	*	14.35	13.96		14.00
Femur width	2.36		2.37	2.37	*	2.35
Hallux length	4.27	*	4.80	4.21	*	4.75
Humerus length	13.54		13.57	13.13		13.24
Ulna length	16.72	*	16.97	16.03	*	16.35
Radius length	14.91	*	15.14	14.24	*	14.51
Sternum length	17.07	*	17.30	16.32	*	16.71
Keel length	14.39	*	14.92	13.39	*	14.14
Keel depth	6.43	*	6.65	6.13	*	6.38
Synsacrum width	10.60	*	10.34	10.49	*	10.14

were *exilipes*. The *exilipes* and *flammea* classes included only extreme-plumaged birds; therefore if there are indeed two distinct taxa of redpolls, their classes almost assuredly would be "pure." Because I have no evidence that, for example, 5 is a better demarcation for *flammea* than is 6, the unknown samples may have included some *exilipes* and *flammea* as well as intermediates. These groups were then subjected to a DFA. The unknown group was not used in the calculation of the discriminant function, but individuals in this group were scored along it. If the intermediately plumaged birds included hybrids, it was predicted that some would have skeletal dimensions intermediate between those described for *flammea* and those for *exilipes*.

RESULTS

Sexual dimorphism.—Male and female redpolls had different dimensions for several skeletal elements. Using DFA, 89.0% of the pooled (all locations) sample could be sexed correctly using dimensions of skeletal characters (Fig. 5). The between-group difference was highly significant ($F_{7,447} = 77.18$, $P < 0.001$).

The important variables used for discriminating between sexes were radius length, tibiotarsus length, hallux length, keel length, ulna length, keel depth, and mandible width. The magnitude of the differences between sexes for

these and other skeletal measurements can be seen in Table 3.

CHARACTER INDEX SCORE ANALYSES

Figure 6 shows the distribution of character index scores for all individuals. Females were much less variable than males. Because the character states were defined independently of sex, the lower variability of females was a property of the birds rather than of the scale used. The three plumage variables used were those that had the greatest range of variability in females as well as in males, although the range was slightly less for females. (In my samples the maximum score for rump and lateral streaking in females was 5; all classes of undertail coverts were found.) Both sexes had continuous distributions of scores.

Males.—The distributions of scores were analyzed by locality (Fig. 7). The three Alaska locations had very different proportions of the redpoll phenotypes. Interior Alaska redpolls were only of the *flammea* type. Both of the remaining locations had a broad range of plumage variants; however, the redpolls of the Akulik-Inglutalik River delta were distributed rather evenly across all classes, whereas the distribution of scores from the Kongakut River
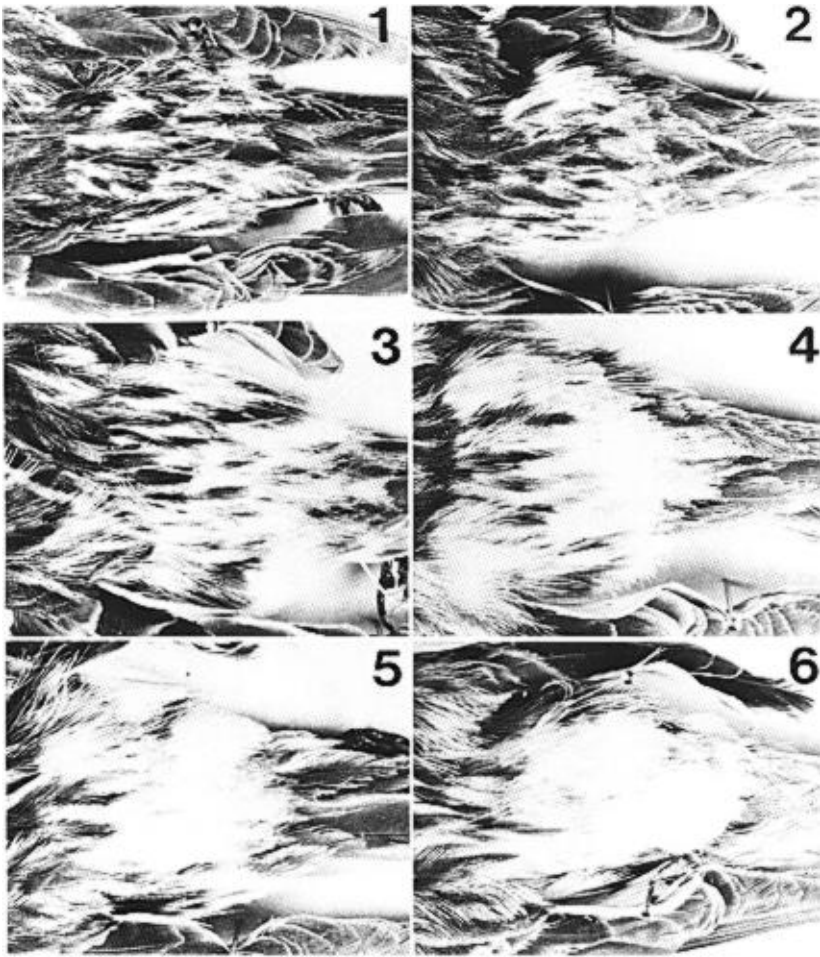
Fig. 2. Character states for the plumage character "rump."

site was skewed toward the *exilipes* type. Since both the Akulik-Inglutalik River delta and the Kongakut River locations had both phenotypic extremes but no evidence of bimodality in the distributions, it appears that interbreeding occurs freely where both alleged species occur together. Both Krekovick Landing and Coppermine had predominantly *exilipes*-like birds but with several intermediates. The remaining locations (Inuvik, Churchill, Winisk, and Fort Chimo) had distributions weighted to the *flammea* end of variability but with intermediates (and occasionally *exilipes*, as at Inuvik) also present.

For males, southern locations tended to have only redpolls of the *flammea* type; *exilipes* predominated in the north but not in pure popu-

lations. If only one extreme was present, the distribution was usually skewed, indicating that intermediates were present. Nowhere were both forms present without intermediates.

Females.—The results of the analysis of females were similar to those for males. The distributions of scores are shown in Fig. 8. The Interior Alaska sample contained only birds from the *flammea* range of variability. The Akulik-Inglutalik River delta and Kongakut River samples both included a broad range of morphs. Of the remaining samples, Krekovick Landing and Coppermine both had mostly *exilipes*-like birds but also some intermediates. Inuvik was the reverse, with primarily *flammea* tendencies.

As with males, the female samples provided little evidence for the recognition of two dis-
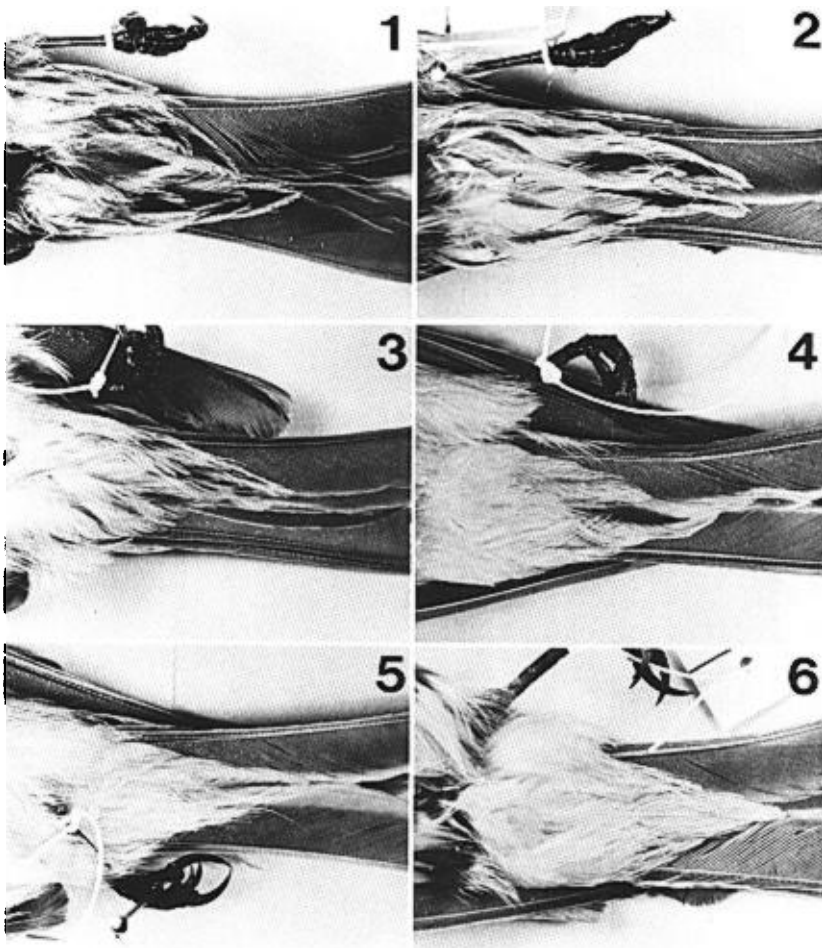
Fig. 3.   Character states for the plumage character "undertail coverts."

tinct species of redpolls. Either a continuum of plumage types or only one extreme was present at each locality.

DISCRIMINANT ANALYSES

Both males and females had continuous score distributions (Fig. 9). The absence of a gap between the distributions of the reference samples makes the detection of morphologically intermediate specimens impossible. References to intermediates in the remainder of this analysis indicate that, for the sample under consideration, a greater proportion of birds had scores in the intermediate zone (close to −1) than occurred in the analysis using only "pure" *flammea* and *exilipes*.

Males.—Figure 10 shows the distribution of scores for the *exilipes, flammea,* and unknown samples as defined by character index scores. The two reference samples (extremes) could be separated with a high degree of confidence (96.1% correctly classified) based on skeletal measurements. The difference between these two groups was highly significant ($F_{5,147} = 72.40$, $P < 0.001$). The variables used to maximize the differences between the two reference samples were hallux length, mandible width, premaxillary length, tarsometatarsus length, and keel length.

The sample of unknowns was different from either reference sample in that it had a broad distribution of DFA scores and was somewhat bimodal. However, this sample contained many
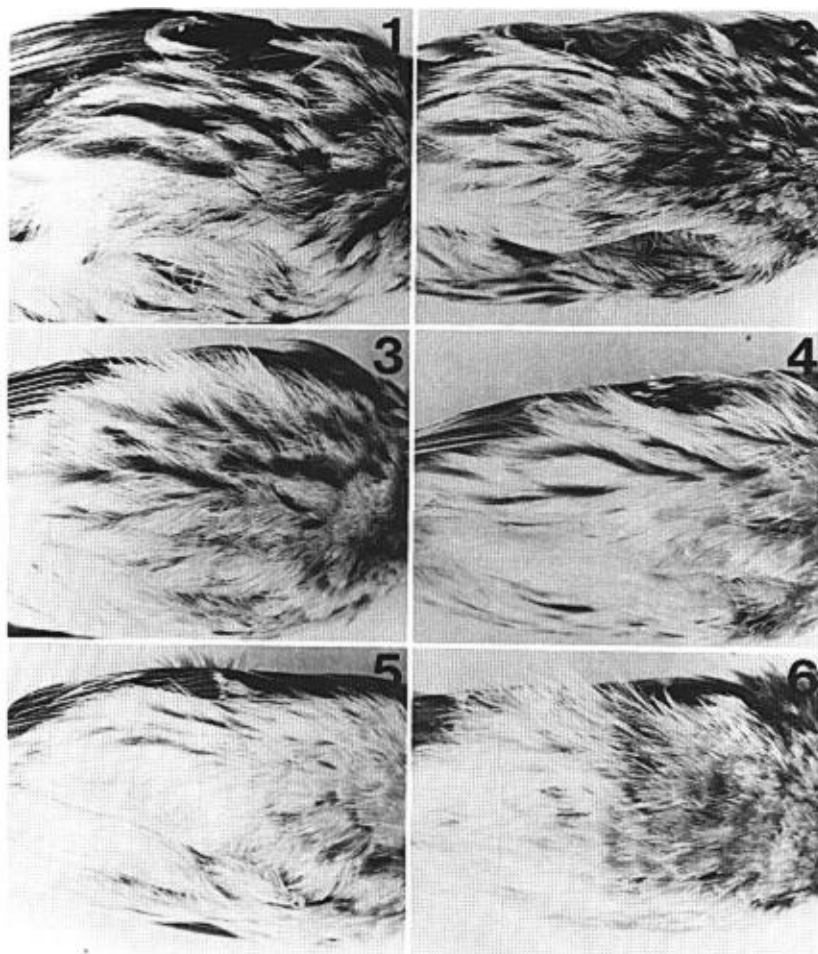
Fig. 4. Character states for the plumage character "lateral streaking."

more birds with intermediate (close to −1) scores than did the reference samples, as was predicted for a sample that contained hybrid birds.

When examined by location (Fig. 7), the results were similar to those from character index scores. The Interior Alaska sample was restricted (with one exception) to the *flammea* range of the distribution. The Akulik-Inglutalik River delta sample was variable, with all types fairly evenly represented. Great variability also occurred in the Kongakut River sample; however, this sample had a skewed distribution with *exilipes*-type predominating. Both the Krekovick Landing and Coppermine samples were predominantly *exilipes* but included some intermediate and *flammea*-like specimens. Inuvik redpolls were predominantly *flammea*-like, but

a few birds were skeletally intermediate or like *exilipes*. The remaining samples from Churchill, Winisk, and Fort Chimo were almost exclusively in the *flammea* range.

Females.—The results of the DFA of female redpolls are illustrated in Fig. 10. Although the distributions of scores of the *exilipes* and *flammea* classes showed no overlap, the more conservative jackknifed classification analysis resulted in 94.3% correct identification, thus indicating some potential overlap. The two groups were significantly different in skeletal characteristics ($F_{3,661} = 69.36$, $P < 0.001$). The variables used in the discrimination were hallux length, premaxillary length, and synsacrum width.

When females of intermediate plumages were classified using the same function, the scores
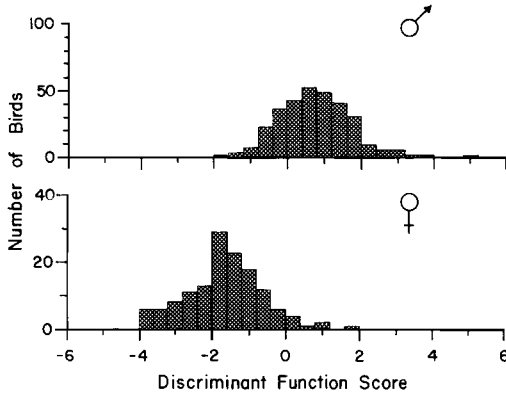
Fig. 5. Distribution of scores of male and female redpolls along the discriminant axis maximizing the differences between sexes (all locations pooled).
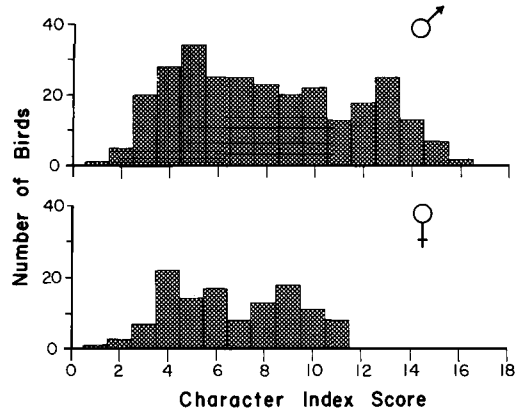

Fig. 6. Frequency distributions of character index scores (all locations pooled) for male and female redpolls.

encompassed the same entire range of variability (2 birds had even higher scores than birds considered to be *exilipes* by plumage). As with males, many more birds were skeletally intermediate in the unknown sample than in either the *exilipes* or *flammea* samples.

When each location was considered individually (Fig. 8) the results were similar to those found for males. All individuals from Interior Alaska had scores in the *flammea* range of variability. Both the Akulik-Inglutalik River delta and the Kongakut River samples exhibited almost continuous variation. The Kongakut River sample distribution was skewed with many *exilipes*, fewer intermediates, and still fewer *flammea*-type redpolls. All of the Krekovick Landing individuals had scores in the *exilipes* range. The Coppermine sample was predominantly *exilipes*, but the extreme of variability extended into the *flammea* range. The Inuvik sample was predominantly *flammea*-type, but there were a few birds in the *exilipes* range of scores.

Overall, skeletal variability in female redpolls appeared similar to that of males. At some locations birds were predominantly of one form (e.g. *flammea* in Interior Alaska, *exilipes* at Krekovick Landing), but wherever both extremes were present, there was no evidence of bimodality in the distributions. It thus appears that wherever the two redpolls are sympatric, they behave as a single species.

DISCUSSION

The analyses show that at some Alaska locations the entire range of plumage and skeletal

variability exists. Although the groups that I defined as *flammea* and *exilipes* by plumage characters could be separated using skeletal measurements with a high level of accuracy, the difference was small and there was no discontinuity in variation between the groups. Since the "unknown" groups (intermediate plumage characteristics) were also intermediate between the two "pure species" with respect to skeletal characters, the hypothesis that they included hybrids is supported. This conclusion is strengthened by the fact that similar results were obtained for interlocality and intralocality comparisons, regardless of sex or character set examined.

Canadian samples provided supportive results. Although none of the samples examined contained the entire range of variability, most had skewed distributions, including phenotypically intermediate birds. Samples that contained both *flammea* and *exilipes* always contained intermediates as well.

The absence of a discontinuity between the distributions of the *flammea* and *exilipes* reference samples in the DFA results hindered the detection of hybrids, thus making statements about individual birds impossible. The lack of a discontinuity in itself indicates that there is little morphological difference between these taxa. Rohwer (1972) found much larger differences between the two similar-appearing meadowlarks, *Sturnella magna* and *S. neglecta*. The meadowlarks could be separated using principal component analysis, thus demonstrating that the major trends in variation reflected species differences.
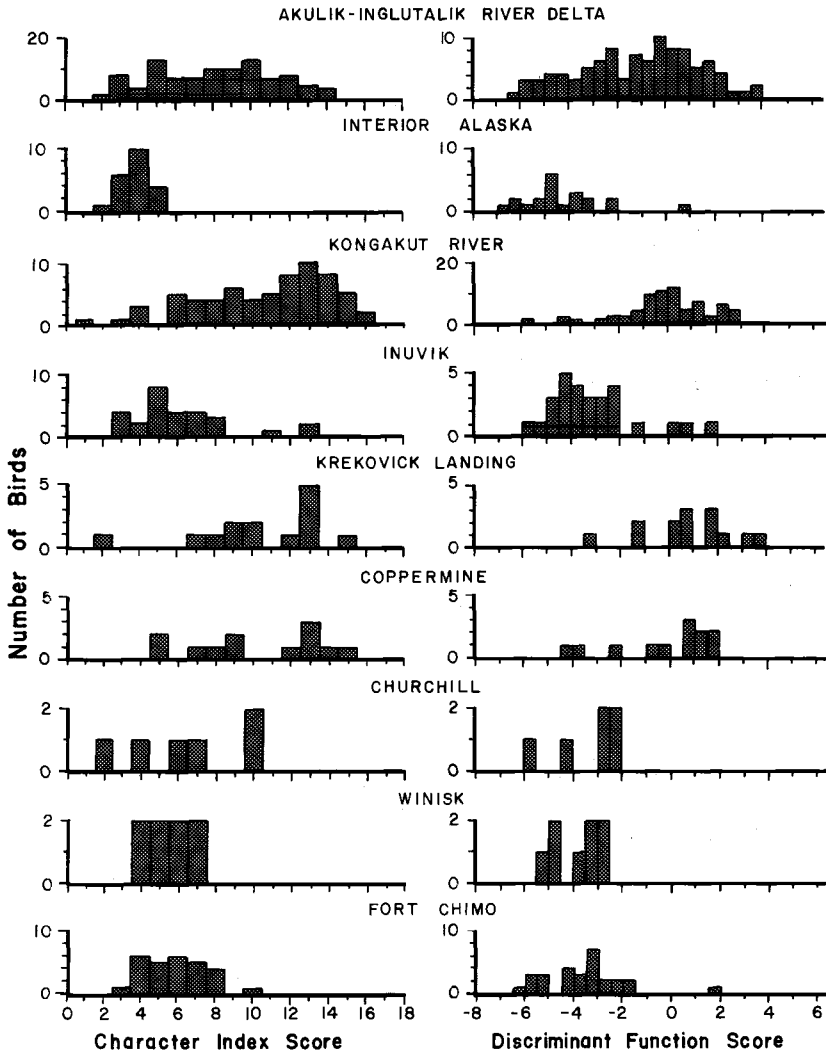
Fig. 7. Frequency distributions of character index and discriminant function scores of male redpolls.

Although there were both plumage and skeletal differences between extreme *flammea* and *exilipes*, the morphological differentiation was slight. Both skeletal and plumage characters show continuous variation. It is necessary to conclude that any distinction between *flammea* and *exilipes* is an arbitrary one. This conclusion is in agreement with the views of authors from other portions of the redpoll's range, in particular those of Salomonsen (1950) in Greenland, Williamson (1961) and Harris et al. (1965) in northern Europe, and Dement'ev et al. (1954) in the Soviet Union.

There are some published opinions in disagreement with my findings that need to be addressed. These opinions relate to the subject of assortative mating and of the morphs found at some of my sample locations.

Positive assortative mating of redpolls was reported by Jehl and Smith (1970) at Churchill and by Wynne-Edwards (1952) on Baffin Island. The possibility of assortative mating poses two questions: How can it be measured, and does it matter? The distribution of character index scores (Fig. 6) showed that females never become as "hoary" as males. In fact, under the system I used to define male *exilipes* there would be no female *exilipes*. An *exilipes* male would have to be paired with a darker female. I have observed such mixed pairs of redpolls, but be-
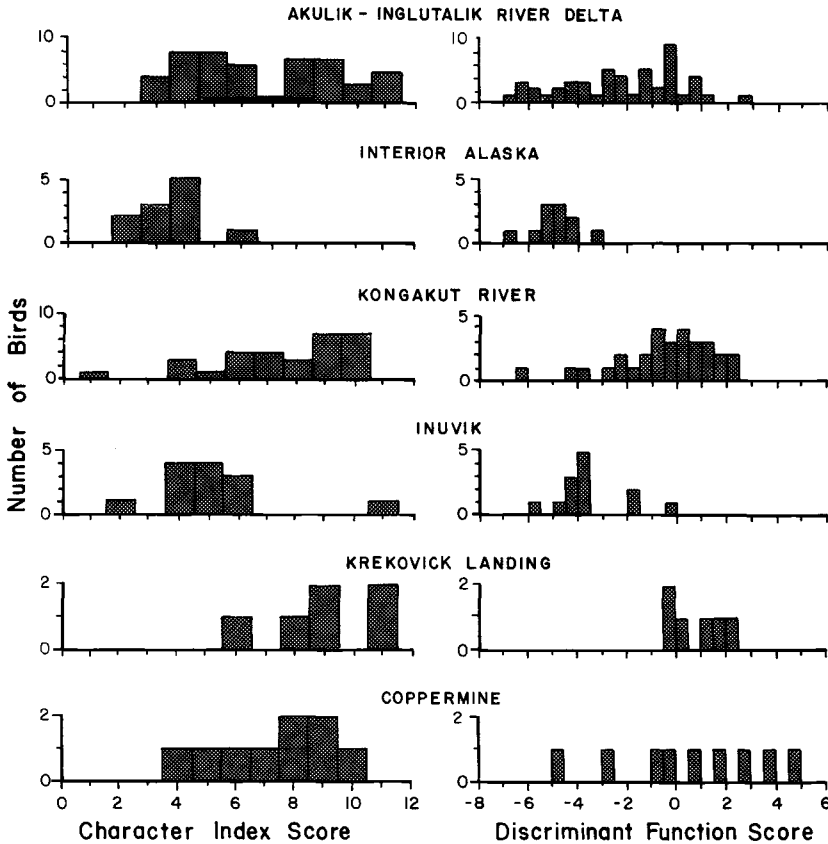
Fig. 8. Frequency distributions of character index and discriminant function scores of female redpolls.

cause of the absence of light-colored females, I have refrained from citing this as evidence of interbreeding. Any report of assortative mating is open to question unless a description of population variability at a location is presented and an objective means of defining the two taxa is used.

Even if assortative mating occurs, should it be used as evidence of species distinctiveness? I think not. Cooch and Beardmore (1959) demonstrated that positive assortative mating (association of similar plumaged individuals) occurred in a mixed population of the blue and white color morphs of Snow Geese (*Chen caerulescens*). Indeed, Cooke and Cooch (1968) hypothesized that assortative mating might be responsible for maintaining the polymorphism. Cooke (1978) found that Snow Geese selected mates similar in color to that of the family in which they were raised. O'Donald (1959) reported positive assortative mating among color

morphs in Parasitic Jaegers (*Stercorarius parasiticus*). Klint (1978) found that coloration of the mother and siblings affected mate selection (again positive assortative mating) in normal and in white mutant Mallards (*Anas platyrhynchos*). Negative assortative mating has been demonstrated for the White-throated Sparrow (*Zonotrichia albicollis*; Lowther 1961, Thorneycroft 1976). Thus, I would suggest that, without supportive evidence, the argument of assortative mating is not necessarily useful in a discussion of the taxonomy of any pair of taxa since it is also an intraspecies phenomenon.

There is also a potential controversy over the type of redpoll occurring at some of the locations included in this study. In particular, there are published accounts that disagree with my finding of predominantly *flammea*-like birds at Churchill and Fort Chimo. Gabrielson and Wright (1951) found both taxa at Fort Chimo and listed *exilipes* as the more abundant form.

Similarly, Jehl and Smith (1970) listed both forms at Churchill; however, Jehl and Smith cited several studies that showed among-year variation in the proportion of *exilipes* at Churchill from 0 to 50%. My findings (unpubl.) of changes in abundance of the two forms between years are consistent with those of Jehl and Smith. That both extremes may occur sympatrically and interbreed in some years may account for the skewed distributions of predominantly *flammea*-type redpolls in some of my samples.

I conclude that *exilipes* and *flammea* represent the extremes of a single, highly variable species. This conclusion leads to questions regarding the reason for so much variability and for comparative adaptations of the extremes. These questions cannot be adequately answered at this time; some introductory information is available, however.

Wynne-Edwards (1952) could find no differences in habitat selection where the two forms were sympatric. Similarly, my samples from the Akulik-Inglutalik River delta and the Kongakut River were collected in relatively homogeneous habitats, yet both extremes were present. However, Jehl and Smith (1970) noted that at Churchill *flammea* was most common at tree line and *exilipes* in open areas (tundra). The large shift in frequencies of phenotypes from Inuvik (spruce forest) to Krekovick Landing (tundra) is in agreement with Jehl and Smith's observation. In general, *flammea* occurs throughout the range of *exilipes*; however, the converse is not true. At tree line and in more southerly areas, *exilipes* is rare or absent (e.g. in Interior Alaska, at Inuvik, and at Winisk).

The absence of *exilipes* from forested areas may indicate that it is poorly adapted in these regions, at least during the summer. Perhaps foraging adaptations are involved since one of the major morphological differences between *exilipes* and *flammea* is of bill size. Newton (1967) found a close association between bill dimensions (length and shape) and diet of *Carduelis* finches.

Other differences may be related to winter survival. Brooks (1968) found that *exilipes* possessed several minor physiological differences, when compared with *flammea*, that made it more tolerant of low temperatures. He suspected that there was a gradient in adaptation between the two extremes, i.e. that his findings did not indicate species differences. These physiological
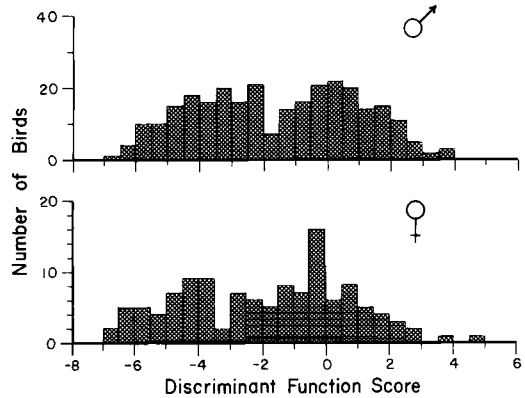

Fig. 9. Frequency distributions of scores along the discriminant axis maximizing the differences between *Carduelis f. flammea* (low scores) and *C. hornemanni exilipes* (high scores). All locations and plumage variants were pooled.

differences permit *exilipes* to winter farther north than *flammea* and, although not accounting for the plumage and morphological differences between *exilipes* and *flammea*, provide a mechanism for partially segregating the phenotypes during the winter. If this segregation extends into the early breeding season (for example until mate selection), this could contribute to the persistence of *exilipes*-type birds even in the absence of behavioral isolating mechanisms.

None of the factors discussed here provides an adequate explanation for the plumage differences found among redpolls, particularly when we take into account the present geographic distribution of the phenotypes. This problem is not unique to redpolls, as several other arctic and subarctic vertebrates, including Northern Fulmars (*Fulmarus glacialis*), Snow Geese, Rough-legged Hawks (*Buteo lagopus*), Gyrfalcons (*Falco rusticolus*), Pomarine Jaegers (*Stercorarius pomarinus*), Parasitic Jaegers, harbor seals (*Phoca vitulina*), and arctic foxes (*Alopex lagopus*) also have light and dark morphs that occur sympatrically yet vary in their relative proportions over the species' ranges. In none of these examples is a morphological difference known to be correlated with color phases.

This study has shown that all plumage types of redpolls are present at some breeding locations. This fact implies that the selection pressures that produced the present plumage characteristics are perhaps not operative in the
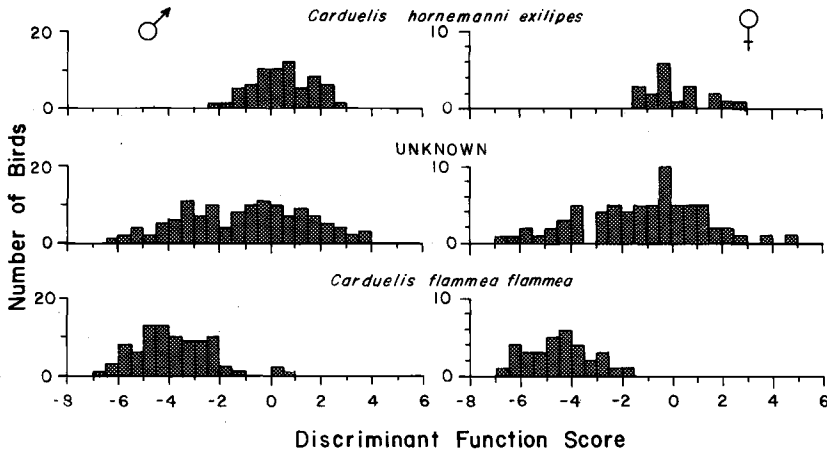
Fig. 10. Frequency distributions of scores along the discriminant axis maximizing the differences between *Carduelis f. flammea* and *C. hornemanni exilipes* for *flammea* and *exilipes* reference samples and for birds with intermediate plumage characters (unknown). All sample locations were pooled.

summer or may no longer exist. Salomonsen (1928) postulated that *flammea* and *exilipes* originated during the Pleistocene glaciation in separate areas in Asia—*flammea* in the interior region of southern Russia and *exilipes* in a refugium in central Siberia (*cabaret* probably was isolated in western Europe). If Salomonsen's hypothesis is true, the isolated redpoll populations may have acquired their differences during that period. As the climate moderated and the redpoll isolates expanded their ranges (including the colonization of North America) and became sympatric, their differences were insufficient to make them specifically distinct and interbreeding occurred, resulting in the continuum of characteristics we see now.

CONCLUSIONS

I have found no evidence to support the specific distinction of *flammea* and *exilipes*. These two taxa represent the ends of a continuum of plumage and skeletal variability. If they were once distinct species, hybridization has resulted in introgression to the extent that any species delimitation now is arbitrary. These findings are in agreement with those of Salomonsen (1928), Williamson (1961), and others who have studied redpolls in Greenland and Eurasia. I differ from some of these authors in that I would not recognize *exilipes* at the subspecific level. Subspecific recognition of *flammea* and *exilipes*

would result in the awkward situation of sympatric subspecies, a condition generally not accepted by zoological taxonomists.

I recommend that *C. f. flammea* and *C. hornemanni exilipes* be merged into a single taxon for which the former is the correct name. Since similar conclusions regarding species distinctiveness have been reached in the study of other redpoll taxa [e.g. Salomonsen (1950) with *rostratus* and nominate *hornemanni*], it is appropriate to extend this merger beyond the limits of *flammea* and *exilipes* and to consider all redpolls one species, *Carduelis flammea*. Clarification of the taxonomic relationships of the subspecies *flammea, hornemanni, rostratus, cabaret,* and other named forms awaits further study.

Peter J. Bente kindly took the time to acquire a small sample from Kaktovik, Alaska.

Skeletonization of specimens collected in Alaska was made possible by the advice and facilities provided by Francis H. Fay of the Institute of Marine Science. Heinrich K. Springer generously provided me with a copy of plumage character states used in his unpublished research; this information provided the basis for the selection of variables and character states used in my study. I received help and advice in analysis from Edward C. Murphy, Frederick C. Dean, Curvin B. Metzler, and Robert M. Burgess.

Drafts of the manuscript (or the thesis from which it was extracted) were improved by the comments of Daniel D. Gibson, Dale R. Herter, Brina Kessel, Stephen F. MacLean, Edward C. Murphy, James D. Rising, Gerald F. Shields, and George C. West. I also appreciate the comments of the *Auk* reviewers: Richard F. Johnston, Kenneth C. Parkes, Dennis M. Power, and D. Scott Wood.
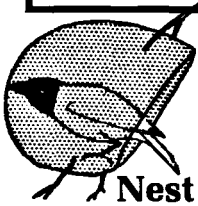
Field work at the Akulik-Inglutalik River delta was supported by a contract from NOAA (through the Outer Continental Shelf Environmental Assessment Program) to Gerald F. Shields and Leonard J. Peyton. The Chapman Fund generously supported field work in the Talkeetna Mountains and contributed to the museum work in Ontario.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. Sixth ed. Baltimore, Amer. Ornithol. Union.

BALDWIN, P. H. 1961. Distribution, overlap, and hybridization of two species of redpolls in Alaska. Bull. Ecol. Soc. Am. 42: 152 (Abstract).

BANNERMAN, D. A. 1953. The birds of the British Isles, vol. 1. Edinburgh, Oliver and Boyd.

BROOKS, W. S. 1968. Comparative adaptations of the Alaskan redpolls to the artic environment. Wilson Bull. 80: 253–280.

COOCH, F. G., & J. A. BEARDMORE. 1959. Assortive mating and reciprocal difference in the Blue-Snow Goose complex. Nature 183: 1833–1834.

COOKE, F. 1978. Early learning and its effect on population structure. Studies of a wild population of Snow Geese. Z. Tierpsychol. 46: 344–358.

———, & F. G. COOCH. 1968. The genetics of polymorphism in the goose *Anser caerulescens*. Evolution 22: 289–300.

COUES, E. 1862. A monograph of the genus *Aegiothus* with descriptions of new species. Proc. Acad. Nat. Sci. Philadelphia 13: 373–390.

———. 1903. Key to North American birds. Fifth Ed., vol. 1. Boston, Page.

DEMENT'EV, G. P., N. A. GLADKOV, A. M. SUDILOVSKAYA, E. P. SPANGENBERG, L. V. BOEHME, I. D. VOLCHANETSKII, M. A. VOINSTVENSKII, N. N. GOECHAKOVSKAYA, M. N. KORELOV, & A. K.

RUSTAMOV. 1954. Birds of the Soviet Union. Jerusalem, Israel Program for Sci. Trans.

DIXON, W. J. (Ed.). 1975. BMDP biomedical computer programs. Berkeley, California, Univ. California Press.

GABRIELSON, I. N., & F. C. LINCOLN. 1959. Birds of Alaska. Washington, D.C., Wildl. Mgmt. Inst.

———, & B. S. WRIGHT. 1951. Notes on the birds of the Fort Chimo, Ungava Bay. Can. Field-Naturalist 65: 127–140.

GODFREY, W. E. 1966. The birds of Canada. Natl. Mus. Canada Bull. No. 203.

HARRIS, M. P., F. I. NORMAN, & R. H. S. McCOLL. 1965. A mixed population of redpolls in northern Norway. Brit. Birds 58: 288–294.

JEHL, J. R., JR., & B. A. SMITH. 1970. Birds of the Churchill region, Manitoba. Man. Mus. Man Nature, Spec. Publ. No. 1. Winnipeg.

JOHNSTON, R. F. 1969. Character variation and adaptation in European sparrows. Syst. Zool. 18: 206–231.

———, & R. K. SELANDER. 1972. Variation, adaptation, and evolution in the North American House Sparrows. *In* Productivity, population dynamics and systematics of granivorous birds (S. E. Kendeigh and J. Pinowski, Eds.). Proc. gen. meeting of the working group on granivorous birds, IBP, PT section.

KLINT, T. 1978. Significance of mother and sibling experience for mating preference in the Mallard (*Anas platyrhynchos*). Z. Tierpsychol. 47: 50–60.

LOWTHER, J. K. 1961. Polymorphism in the white-throated sparrow, *Zonotrichia albicollis* (Gmelin). Can. J. Zool. 39: 281–292.

MAYR, E. 1970. Populations, species, and evolution. Cambridge, Massachusetts, Belknap.

NEWTON, K. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109: 33–98.

O'DONALD, P. 1959. Possibility of assortive mating in the Arctic Skua. Nature 183: 1210–1211.

OGILVIE, N. A. 1976. The winter birds. New York, Praeger.

POWER, D. M. 1971a. Statistical analysis of character correlation in Brewer's Blackbirds. Syst. Zool. 20: 186–203.

———. 1971b. Evolution of the House Finch on Santa Cruz Island, California. Canadian J. Zool. 49: 675–684.

RISING, J. D. 1970. Morphological variation and evolution in some North American orioles. Syst. Zool. 19: 315–351.

———. 1973. Morphological variation and status of the orioles, *Icterus galbula*, *I. bullockii*, and *I. abeillei*, in the northern Great Plains and in Durango, Mexico. Canadian J. Zool. 51: 1267–1273.

ROBINS, J. D., & G. D. SCHNELL. 1971. Skeletal analysis of the *Ammodramus–Ammospiza* grassland

sparrow complex: a numerical taxonomic study. Auk 88: 567–590.

ROHWER, S. A. 1972. A multivariate assessment of interbreeding between the meadowlarks, *Sturnella*. Syst. Zool. 21: 313–338.

SALOMONSEN, F. 1928. Bemerkungen über die Verbreitung *Carduelis linaria* Gruppe und ihre Variationen. Videnskab. Medd. fra Dansk Naturhist. Forening. 16: 123–202 (from partial translation in Grinnell 1947).

———. 1950. Grønlands fugle. København, Einair, Munksgaard.

SCHEULER, F. W., & J. D. RISING. 1976. Phenetic evidence of natural hybridization. Syst. Zool. 25: 283–289.

SCHNELL, G. D. 1970. A phenetic study of the suborder Lari (Aves) I. Methods and results of principal components analysis. Syst. Zool. 19: 35–57.

SCOTT, D. M., C. D. ANKNEY, & C. H. JAROSCH. 1976. Sapsucker hybridization in British Columbia: changes in 25 years. Condor 78: 253–257.

SHORT, L. L., JR. 1963. Hybridization in the wood warblers *Vermivora pinus* and *V. chrysoptera*. Proc. Intern. Ornithol. Congr. 8: 147–160.

SIBLEY, C. G., & L. L. SHORT, JR. 1959a. Hybridization

in some Indian bulbuls *Pycnonotus cafer* × *P. leucogenys*. Ibis 101: 177–182.

———, & ———. 1959b. Hybridization in the buntings (*Passerina*) of the Great Plains. Auk 76: 443–463.

———, & D. A. WEST. 1959. Hybridization in the Rufous-sided Towhees of the Great Plains. Auk 76: 326–338.

SNYDER, L. L. 1957. Arctic birds of Canada. Toronto, Univ. Toronto Press.

SZIJJ, L. J. 1963. Morphological analysis of the sympatric populations of meadowlarks in Ontario. Proc. Intern. Ornithol. Congr. 8: 176–188.

THORNEYCROFT, H. B. 1976. A cytogenetic study of the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). Evolution 29: 611–621.

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

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

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