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PLUMAGE VARIABILITY IN REDPOLLS FROM CHURCHILL, MANITOBA

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ABSTRACT.—Redpolls (*Carduelis flammea* and *C. hornemanni*) are well known for their extensive phenotypic variability. Various explanations have been proposed for the phenomenon, ranging from extreme variability within a single inclusive taxon, to more modest variation within frequently hybridizing or strictly isolated taxa. The predominant view favors the recognition of two largely sympatric and only slightly differentiated species: the Common Redpoll (*C. flammea*), comprised of the four subspecies *flammea, cabaret, islandica,* and *rostrata;* and the Hoary Redpoll (*C. hornemanni*) comprised of the two subspecies *hornemanni* and *exilipes.* We investigated the possible existence of sympatric redpoll forms in a large sample ($n = 209$) of breeding individuals from Churchill, Manitoba, where the putative forms *flammea* and *exilipes* were reported to co-occur. Groups of individuals of specific age and sex were analyzed independently. The sample was not divided *a priori* into *flammea* and *exilipes* subgroups. The pattern of variation within each age-and-sex group is described, and the differences between these groups are analyzed. We show that several pigmentation characters in specific age-and-sex groups are not distributed normally, and that pale and dark subgroups of second-year (SY) and after-second-year (ASY) males can be identified in a principal-components analysis (PCA) of seven characters reflecting the extent of melanin and carotenoid pigmentation. The pink- and red-breasted subgroups of ASY males match almost perfectly the pale and dark groups found in the PCA analysis. Further, when ASY males of different breast color (pink vs. red) are analyzed independently, all plumage characters are distributed normally. The analyses of SY and ASY females failed to provide good evidence for a plumage polymorphism. Our results support the idea that two relatively distinct redpoll forms breed at Churchill, which differ in several plumage characteristics involving both melanin and carotenoid pigmentations. These forms are more clearly differentiated in males than in females. They may be specifically distinct (*C. f. flammea* and *C. hornemanni exilipes*), as has frequently been suggested, but they also could be the product of different types of intraspecific genetic or ecophenotypic polymorphisms. Preliminary observations are presented that support the idea that plumage variants are largely genetically determined, but experimental work is needed to confirm this suggestion. *Received 28 May 1991, accepted 19 February 1992.*

ORNITHOLOGISTS HAVE long been intrigued by the extensive plumage variability seen in redpolls (*Carduelis* [*flammea*] spp.). Based roughly on the same type of data and analytical approach (i.e. colorimetric and morphometric studies), different investigators have described that variation as continuous (e.g. Harris et al. 1965, Troy 1985) or dimorphic (e.g. Todd 1963, Molau 1985, Knox 1988), and have divided the "complex" into one to four species (see Knox 1988:table 1). The taxonomic disagreement comes mainly from the different interpretations given to the origin of birds having intermediate attributes in sympatric populations. Some researchers hold that intermediate birds are common in many populations and represent either hybrids and backcross individuals (e.g. Williamson 1961, Harris et al. 1965), or merely central points in a homogeneous distribution of phenotypic variants within a single highly variable species (Troy 1985). Other investigators (e.g. Molau 1985, Knox 1988) have suggested that, when sexual and age dimorphisms are carefully taken into account, very few redpolls qualify as intermediate, and these probably are convergent variants of distinct sympatric species.

The most commonly encountered classification of redpolls is one in which two polytypic species are recognized, the Common Redpoll (*C. flammea*) comprised of the subspecies *cabaret, flammea,* and *rostrata,* and the Hoary Redpoll (*C. hornemanni*) comprised of the subspecies *exilipes* and *hornemanni* (Knox 1988). The taxonomic affinities of redpolls breeding in Iceland are un-

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certain, but they possibly form one or two more distinct taxa (Salomonsen 1951, Knox 1988, Herremans 1990). Recent systematic investigations have focused on the forms *flammea* and *exilipes*. These names apply, respectively, to the dark and pale birds that breed largely in sympatry on the mainland of North America and Eurasia (Knox 1988:fig. 1). Troy (1985) has studied these forms in a systematic and quantitative way in the Nearctic part of their range. He analyzed the extent of melanization of plumage from three body regions and, from those data, produced a character index that reflects the overall plumage darkness of an individual. He suggested that the characters he studied and his index were not useful at dividing his sample into subgroups that would correspond to the usually recognized forms *flammea* and *exilipes*; he then concluded that "any distinction between *flammea* and *exilipes* is an arbitrary one" (page 91) and that "the two taxa represent the ends of a continuum of plumage . . . variability" (page 94). Nyström and Nyström (1987) and Knox (1988) have suggested that Troy's analyses suffered from his failure to consider age dimorphism and, consequently, that his conclusions required reexamination. Another problem with Troy's work is that he expected that the putative species, if they actually exist, would have discrete distributions of scores for the specific measure of plumage variability he developed (i.e. his character index). However, complete separation of forms is only one of many possible outcomes in a character-index analysis and, in many cases, a continuous but bimodal distribution will be found even if the forms studied are reproductively isolated. Troy actually failed to mention that the distribution of both his male and female samples along his character-index axis are not normal, but rather appear bimodal (Kolmogorov-Smirnov-Lilliefors test of normality on data in Troy's fig. 6; for males, $D_{max} = 0.119$, $P < 0.001$; for females, $D_{max} = 0.127$, $P < 0.001$).

North American workers have commonly reported frequent hybridization between *flammea* and *exilipes* redpolls (e.g. Gabrielson and Lincoln 1959, Baldwin 1961, Jehl and Smith 1970). Troy (1985) went one step further in concluding that plumage variability in Nearctic redpolls is actually continuous and relatively homogeneous, and that distinct taxa should not be recognized. Considering how different this opinion is from those expressed recently by European researchers (Molau 1985, Knox 1988, Herremans 1990), it seemed necessary to analyze the relative importance of sexual and age dimorphisms in the plumage variability of Nearctic mainland redpolls, and to reexamine the potential for a phenotypic polymorphism independent of sex and age. We expected that such a polymorphism (i.e. related to the existence of two sympatric taxa) would result in the bimodal distribution of at least one plumage character in at least one age-and-sex group. However, bimodality per se is impossible to test statistically if *a priori* hypotheses for the distribution parameters of the variable for each mode within each age-and-sex group cannot be formulated. Therefore, we tested the simpler null hypothesis that the distribution of each character, within each age-and-sex series, did not deviate significantly from normality toward platykurtosis. A bimodal distribution with a complete separation of the modes is an extreme platykurtic distribution. Normal kurtosis is a reasonable expectation for the distribution of polygenic traits—which, we assume, plumage pigmentation characters in redpolls are—if no polymorphism exists. We have followed this analytical approach, which does not involve establishing groups *a priori* in a subjective manner, to avoid the possibility of circular reasoning (i.e. finding plumage differences between groups that are defined partly or totally on plumage characters). Alternatively, Herremans' (1990) formula for the morphometric identification of Palearctic redpolls could have been used, but its applicability with Nearctic birds has not been tested.

Our study focuses exclusively on birds from Churchill, Manitoba (58°45'N; 94°05'W). Analysis of a sample taken from a single site minimizes the possibility that patterns of variation are distorted by the pooling of geographic variants into a single sample. The skins and pictures of live specimens we examined comprise the large majority of redpoll summer material available from Churchill, and probably form the largest data set on plumage variability in breeding redpolls available for a single Nearctic location (Table 1). Knox (1988) has suggested that seasonal variability of plumage caused by feather wear is the source of much misunderstanding and controversy in the redpoll literature. We concur with that opinion and, therefore, restricted the analysis to specimens captured between 20 May and 31 July. The

plumage of all individuals studied was in approximately the same condition (i.e. moderately worn).

We use subspecific names (e.g. *flammea* and *exilipes*) to label samples of individuals belonging to different "phenotypic forms." This practice is adopted for simplicity and clarity but, as it will become clear in later discussions, we do not assume that these forms necessarily represent distinct evolutionary entities, whether these are subspecies or species. Also, for the sake of simplicity, we generally use unqualified subspecies names, so that the names *flammea* and *hornemanni* should be taken to refer to the nominate forms only.

Materials and Methods

Specimens collected in the summer of 1930 (Taverner and Sutton 1934) and preserved as study skins comprised the first series of birds analyzed. The second series was the result of field work conducted by the senior author in the summers of 1988 and 1989; a few specimens were collected and prepared as study skins, but the large majority were caught alive, measured, photographed, banded, and released. The age and sex distribution of individuals in these series is presented in Table 1. Live birds were sexed by the presence of a cloacal protuberance for males, or a brood patch for females (Pyle et al. 1987). All museum specimens were sexed by inspection of the gonads. Age was determined by looking at the shape of the central rectrices (Svensson 1984, Pyle et al. 1987), which allows one to discriminate second-year (SY) from after-second-year (ASY) birds. Age nomenclature follows Pyle et al. (1987): SY birds are individuals born in the previous calendar year. We found this aging technique to be useful for living birds until the end of July, as Molau (1985) did, but several museum specimens could not be aged. Using the above techniques, age and sex determinations were made without reference to the bird's pigmentation. All individuals that could not reliably be sexed or aged were excluded from all analyses.

Each bird was tentatively identified in the field, or when measurements were taken in the museum, as belonging to the *flammea* or *exilipes* form. These identifications were based on the criteria presented by Molau (1985), Knox (1988) and Lansdown et al. (1991), which require a subjective appreciation of an ensemble of characters, including overall darkness of the plumage, paleness of the rump and of the forehead band, width of the streak on the longest undertail covert, breast color, and the proportions of the bill. These criteria are more subtle than those presented in field guides and require that the sex and age of a bird are known.

During the 1988 and 1989 field seasons, two photographs were taken of each individual captured, one showing the back and one showing the side of the bird. A ring flash and an external light shield were used to ensure constant lighting conditions. The shield consisted of a 70-cm-long conical tube made of white opaque cardboard. The lens with flash was inserted in the small opening and the bird was held in the hand at the large opening. All pictures were taken at 60 cm with a 90-mm macro lens mounted on a 35-mm camera. Diaphragm aperture was held constant and all exposures were made using Kodachrome 64 ASA film. Similar photographs were taken from the back and the side of each museum specimen. Skins were laid on a neutral gray background (a Kodak Gray Card) and lighting was provided by a ring flash, but the external light shield was not used.

TABLE 1. Number of redpolls from Churchill, Manitoba, analyzed for plumage variability. Sample divided according to age, sex, and year of capture.

Age and sex	1930	1988	1989	Total
SY males	0	14	53	67
ASY males	13	23	42	78
SY females	3	11	21	35
ASY females	3	18	8	29
Total	19	66	124	209

Plumage characters.—Ten highly variably plumage characters were analyzed (Table 2). They reflect the color of specific carotenoid-pigmented areas (three "color" characters), and the extent of melanin (four "darkness" characters) or carotenoid (three "redness" characters) pigmentation on specific plumage regions.

Three nominal, nonordered, character states were recognized for breast color and rump color: red, pink, or no carotenoid pigmentation. Poll color varied approximately continuously from deep crimson red to orangish red; this range of variation was divided into three ordered character states. Slight variations in picture quality did not allow a finer analysis of color variation.

The width of the streak on the longest undertail covert and the length of the red poll were used as indexes of undertail-covert darkness and head redness, respectively. These characters were measured on live birds or specimens to the nearest 0.1 mm using dial calipers. Other characters were scored subjectively from the photographs. Rump darkness and side darkness are similar to Troy's (1985) "rump" and "lateral streaking" characters; one can appreciate the range of variation in these characters by examining figures 2 and 4 in Troy's paper. Eight ordered character states were recognized, representing gradually increasing intensity of melanin pigmentation. Forehead darkness, described by Molau (1985), characterizes the intensity of pigmentation on the band of non-red feathers between the base of the bill and the start of the red poll; it was scored as dark, mottled, or light. This

TABLE 2. Characters used in analysis of plumage variability in redpolls from Churchill, Manitoba, and agreement between scorers.

Character	No. categories	Agreement	
		Matching coefficient[a]	Kendall *W*
Rump darkness	8	0.92	0.90
Side darkness	8	0.84	0.88
Forehead darkness	3	0.65	0.74
Undertail-covert darkness[b]	Continuous	—	—
Rump redness	3	0.80	0.88
Breast redness	8	0.92	0.93
Head redness[b]	Continuous	—	—
Rump color			
Presence	2	0.80	—
Color	2	0.57	—
Breast color			
Presence	2	0.95	—
Color	2	0.92	—
Poll color	3	0.64	—

[a] Average over pairs of scorers.
[b] Single measurement obtained in field or on study skins.

character was not used by Troy (1985), but is discussed by Nyström and Nyström (1987), Knox (1988), and Lansdown et al. (1991). The characters breast redness and rump redness represent the extent of carotenoid pigmentation on these body regions, irrespective of the actual color (pink or red) and of the intensity of co-occurring melanin pigmentation; eight and three ordered character states were recognized, respectively.

Scoring procedure.—Using pictures taken in 1988, the senior author established a graded series of reference specimens for each character scored from the pictures. Using the series, the plumage of each individual was scored from the slides, using a transilluminator, by him and two naive persons. Scorers had no access to each others' results or to Seutin's field identifications. The agreement between scorers was estimated using the Kendall coefficient of concordance, and Sokal and Michener's (1958) simple-matching coefficient with the modification that for characters with more than three states, a mismatch by one state was considered as a match; for other characters, only perfect matches were accepted. For color characters, only the matching coefficient was used because of the qualitative nature of character states.

For darkness and redness characters, we calculated the mean score across scorers for each individual, except those included in the reference series for which only Seutin's scores existed. Scores for each character were transformed to range from 0 for the lightest birds to 1 for the darkest ones. For color characters, in cases of disagreement among scorers, the majority opinion was used; in no case did all three scorers disagree.

Data analysis.—A darkness index was produced by summing individuals' scores for the four darkness characters, and adjusting to vary from 0 to 1. It is similar to Troy's (1985) character index that, however, included only three variables (equivalent to the characters side darkness, rump darkness, and undertail-covert darkness used in the present study, but scored in a different way). Further studies should reveal that the two indexes are highly correlated.

Within each age-and-sex group, we tested the hypothesis that the distribution of scores for each plumage character was normally distributed with respect to kurtosis, using the procedure of D'Agostino and Pearson (1973). They provide critical test values for unilateral departure from normality toward platykurtosis in small samples ($n < 200$). Two variables, forehead darkness and rump redness, could not be tested because of the nature of the data (i.e. the fact that only three scoring categories were recognized and the close agreement between scorers meant that the distributions were necessarily bimodal or trimodal; see Fig. 1).

Principal-components analyses (PCAs) of darkness and redness characters were used to identify clusters of individuals with distinct phenotypes. PCA is usually used with continuous variables, but several researchers (e.g. Frontier and Ibanez 1974) have shown that results are not significantly distorted when ordered variables are employed. Distinct analyses were performed on SY and ASY males because univariate analyses revealed highly significant differences between the two groups (see Results). Such differences were not observed between females of different ages and, to increase sample size, all females were included in a single analysis. All individuals with missing data were excluded. PCAs were based on correlation—instead of covariance—matrices because the charac-

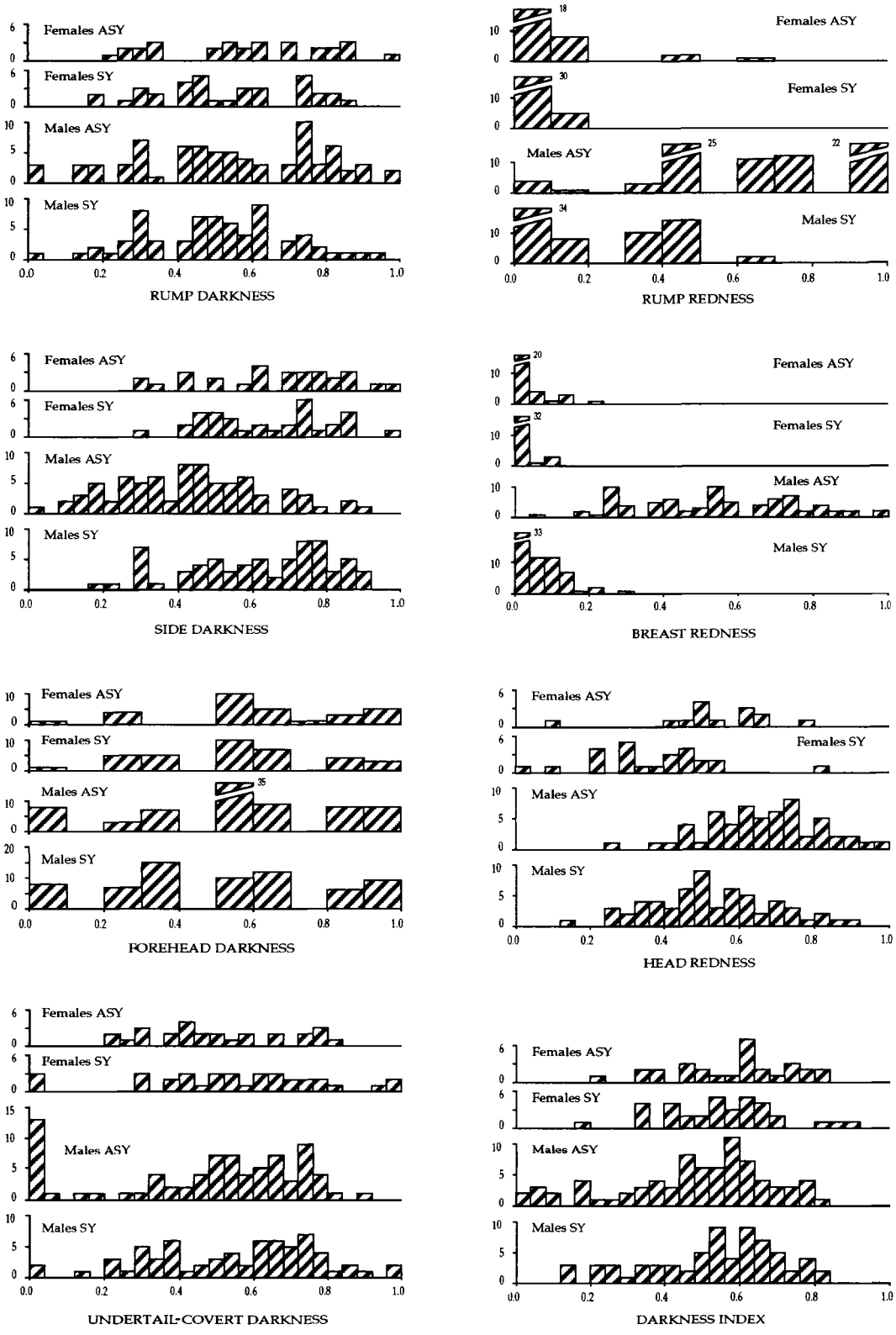

Fig. 1. Frequency distribution of character scores in four age-and-sex groups of redpolls from Churchill, Manitoba.

ters were not dimensionally homogeneous. The position of objects in the reduced space defined by a PCA based on the correlation matrix is different from that when the covariance matrix is studied. In each analysis, the lengths of eigenvectors were standardized to the square root of their eigenvalues, so that the correlations between the original characters are equal to the cosine of the angle their representative vectors form in the reduced space (Legendre and Legendre 1983). In an analysis based on the correlation matrix, this standardization has no effect on the dispersion of objects. For SY and ASY males, matrices of Euclidean distances between pairs of individuals in their PCA spaces were produced from individuals' coordinates on the seven PCA axes, weighted by the percentage of variance explained by each axis. This method of estimating interindividual distances was preferred over the more traditional way of calculating distances from the original data because it removes the effect of correlation between characters; further, it prevents darkness characters being weighted more in the analysis than redness characters because they simply are more numerous (four vs. three characters). UPGMA and WPGMA clustering algorithms (Sneath and Sokal 1973) were employed to evaluate relationships between individuals.

RESULTS

Scorer agreement.—Agreement among scorers was very good (Table 2), except for forehead darkness and two of the color characters (rump and poll color). Even in these cases, the agreement was sufficiently high to substantiate our scoring procedure and results (i.e. measurement error seems to be much smaller than sample variability).

Temporal variation.—Redpolls molt once a year, in the fall, and their breeding plumage is acquired by wear. Consequently, between-season variability is extensive for most plumage characters (e.g. Knox 1988). To determine whether within-season variation had to be considered as a potentially confounding factor in our study, we compared the distribution of darkness and redness scores of individuals taken during the first half (Julian days 150–181; before end of June) and the second half (Julian days 182–212) of the study period. We restricted the analysis to field-identified *flammea* birds because of the possibility that differences in the proportion of birds of each putative form at different times could alter the results. Two subsamples were large enough to permit statistical analysis, SY ($n = 43$) and ASY ($n = 55$ males). For most characters, birds from the late period tended to be darker than those from the early period, but none of the differences were statistically significant (Kolmogorov-Smirnov two-sample tests; all $P > 0.120$).

An assumption of these analyses is that the same population is sampled through the season; immigration or emigration of individuals of specific phenotypes could significantly bias the results. Nothing indicates that large-scale population movements occurred during the 1988 and 1989 seasons, and the data from 1930 contributed little to the analyses. Consequently, we believe that our results correctly indicate that seasonal variation is limited over the period considered, and should not affect further analyses.

Association between characters.—For characters reflecting the extent of pigmentation, two distinct groups of highly correlated variables were identified, corresponding respectively to the darkness and redness characters (Table 3). Within these groups, all but one correlation are highly significant, the exception being the marginally significant relationship between forehead and undertail-covert darkness. All correlations but the latter remain significant even if the Bonferroni correction for multiple tests is applied ($\alpha' = 0.05/21 = 0.0024$).

Most correlations between darkness and redness characters were weak. However, those between side darkness on one hand, and rump redness and breast redness on the other, were highly significant. These significant correlations result from concordant patterns of age and sexual dimorphism in these characters, and are absent when age-and-sex groups are analyzed independently (matrices not shown). Relationships between other pairs of character seemed to be relatively independent of patterns of age and sexual dimorphism.

Color characters.—Poll color in redpolls from Churchill varied from deep crimson red (darker than "Color 108A Poppy Red" in Smithe 1975) to reddish orange (similar to "Color 14 Scarlet" in Smithe 1975). We did not observe individuals with a yellow poll, as noted in birds from other locations (e.g. Knox 1988), but a few specimens had scattered light-orange or yellowish poll feathers. This phenomenon seems to be related to the dietary condition of the bird when molting (Weber 1961; Seutin pers. observ.). Poll color varied in a relatively continuous manner, as illustrated by a relatively low agreement between scorers (65%). The distribution of vari-

TABLE 3. Pearson product-moment correlations (above diagonal) and Spearman correlations (below diagonal) of plumage characters.

Character	Character						
	1	2	3	4	5	6	7
1 Rump darkness	—	0.496**	0.534**	0.404**	−0.006	0.161*	0.154
2 Side darkness	0.496**	—	0.438**	0.508**	−0.389**	−0.322**	−0.111
3 Forehead darkness	0.497**	0.416**	—	0.169*	0.022	0.108	0.147
4 Undertail-covert darkness	0.346**	0.435**	0.083	—	−0.066	−0.014	0.012
5 Rump redness	0.020	−0.354**	0.040	−0.011	—	0.760**	0.573**
6 Breast redness	0.148*	−0.312**	0.055	0.025	0.778**	—	0.499**
7 Head redness	0.152	−0.146	0.157*	−0.026	0.602**	0.549**	—

*, $P < 0.05$; **, $P < 0.001$.

ants differed significantly between sexes ($G = 28.10$, df = 2, $P < 0.001$), with females having an orange-tinged poll more frequently than males. The distributions for age groups also differed, with young birds tending to have an orange-tinged poll more frequently than older birds (for males, $G = 10.10$, df = 2, $P = 0.006$; for females, $G = 6.58$, df = 2, $P = 0.04$). Poll color seemed to vary independently from the color of other body regions (poll vs. breast color, $G = 2.15$, df = 2, $P = 0.35$; poll vs. rump color, $G = 0.53$, df = 2, $P = 0.75$).

Extensive carotenoid pigmentation on the breast and rump of Churchill redpolls was restricted to ASY males (Fig. 1; Table 4), as it is in birds from other locations (e.g. Troy 1985, Knox 1988). Under close examination, however, several females and SY males also showed some red in their plumage (apart from the poll that is always fully pigmented), especially on the cheeks and rump, but also on the breast (Fig. 1). In ASY males, breast and flanks color varied from light pink (similar to "Color 7 Pink" in Smithe 1975) to deep red (deeper than "Color 12 Geranium" in Smithe 1975). This variation was almost discrete, which is reflected by the close agreement between scorers (92%). Some birds had yellowish feathers intermixed with the red or pink breast feathers, and a few red-breasted birds had an orange tinge.

Extreme rump color variants in Churchill redpolls were similar to those seen on the breast, but the variation was less discrete, as reflected by relatively poor agreement between scorers (57%). There was a strong positive association between an individual's breast and rump color ($G = 29.31$, df = 1, $P < 0.001$).

Sexual and age dimorphisms.—Sexual and age dimorphism in redpolls is most noticeable in the extensive red or pink coloration on the breast, flanks, and rump of ASY males (described above). The influence of age and sex on the intensity of melanin pigmentation is not as striking (Fig. 1). For darkness characters, only the distribution of side darkness scores differed significantly among the four age-and-sex groups, due to a difference between age groups in males (Table 4). This could mean that age does not have a significant influence on most characters studied, contrary to suggestions by Molau (1985) and Knox (1988). However, because we did not subdivide *a priori* our sample between *flammea*

TABLE 4. Test of differentiation between age and sex groups of redpolls from Churchill, Manitoba. Kruskal-Wallis tests used to compare the four groups (df = 3); within-sex comparisons done using Kolmogorov-Smirnov two-sample tests (df = 2).

Character	All groups		Age within males		Age within females	
	H	*P*	*z*	*P*	*z*	*P*
Rump darkness	2.88	0.410	1.12	0.261	0.84	0.403
Side darkness	42.34	0.001	2.37	0.017	0.54	0.591
Forehead darkness	2.56	0.464	1.27	0.205	0.56	0.572
Undertail-covert darkness	3.02	0.389	0.96	0.336	0.86	0.388
Rump redness	122.67	0.001	3.99	0.001	0.94	0.346
Breast redness	159.48	0.001	5.63	0.001	0.89	0.371
Head redness	48.00	0.001	2.12	0.034	1.78	0.075
Darkness index	6.81	0.078	0.95	0.343	0.97	0.332

TABLE 5. Tests for normality of kurtosis in the distribution of plumage scores within age-and-sex groups of redpolls from Churchill, Manitoba.[a] Critical values for unilateral test from D'Agostino and Pearson (1973).

Character	Males		Females	
	SY	ASY	SY	ASY
Rump darkness	−0.272	−0.758*	−1.012*	−0.985
Side darkness	−0.785*	−0.399	−0.799	−0.786
Undertail-covert darkness	−0.384	−0.729*	0.119	−1.116*
Breast redness	2.396	−0.860*	12.813	3.010
Head redness	−0.432	−0.032	1.028	2.282
Darkness index	−0.512	−0.260	0.309	−0.603

*, $P < 0.05$.

[a] Kurtosis index values, g_2, presented.

and *exilipes* birds, as Molau and Knox did, our series were less homogeneous, and the finding of significant differences was less probable. Furthermore, if distinct phenotypic forms existed in the sample, a genuine pattern of age dimorphism might have been masked if the proportions of individuals belonging to each form differed between age classes. Thus, we preferred maintaining the division of the sample into four age-and-sex groups for the following analyses.

Character distribution within age-and-sex groups.—The distribution of scores for five characters within each sex-and-age group was analyzed for deviation from normality toward platykurtosis (Table 5). For 6 of the 24 tests (25%), the hypothesis of normality was rejected ($P < 0.05$). In ASY males, three of the five characters were not normally distributed. Head redness was the only variable distributed normally in all groups.

Because the nonnormality of patterns of phenotypic variability could have arisen from the pooling of phenotypically differentiated annual samples, we tested within each age-and-sex group and for each character, the hypothesis that the distributions of scores differed between annual series. For ASY males, samples from 1930, 1988, and 1989 were compared; for the other groups, we compared only the 1988 and 1989 series because specimens from 1930 were too few (see Table 1). The hypothesis that annual series were statistically the same was rejected only once (undertail-covert darkness in ASY males, Kruskal-Wallis test, $H = 9.79$, df = 2, $P = 0.008$), which could be expected even if the hypothesis was true since 32 tests were performed. Using the Bonferroni-corrected α probability for multiple tests (within age-and-sex groups, $\alpha' = 0.05/8 = 0.0063$), none of the differences were significant. These results indicate that differences between annual series were not responsible for the nonnormality of several character distributions.

Breast and flanks color in ASY male redpolls is considered by many to be a fairly reliable diagnostic criterion for the *flammea* (red-breasted) and *exilipes* (pink-breasted) forms in summer (e.g. Coues 1862, Gabrielson and Lincoln 1959, Lobkov 1979, Molau 1985). The possibility that nonnormalities were caused by the pooling of specimens belonging to distinct "color forms," therefore, was tested in these males by investigating red- and pink-breasted individuals separately. Differences in the distribution of character scores between the groups are striking (Fig. 2); Kolmogorov-Smirnov two-sample tests identified significant differences in the distribution of six of the eight characters (Table 6). Furthermore, the three characters that were not normally distributed when the whole series of ASY males was considered, were distributed normally within red males (test for normal kurtosis; all $P > 0.05$). The 14 individuals with a pink breast formed a sample too small to be analyzed for deviation from normal kurtosis.

Thus, there is a clear association in ASY males between breast color and the extent of melanin and carotenoid pigmentation on several body regions, and the pooling of the two "color forms" into a single sample seemingly explains the nonnormal distribution of several characters in the "composite" series. It is reasonable to suspect that nonnormal distributions in other age-and-sex groups can be explained in the same way, but because only ASY males showed a color dimorphism, the idea could not be tested. However, if phenotypically distinct subgroups exist within other age-and-sex series, they might be resolvable via multivariate analysis.

Multivariate analyses.—Distinct principal-

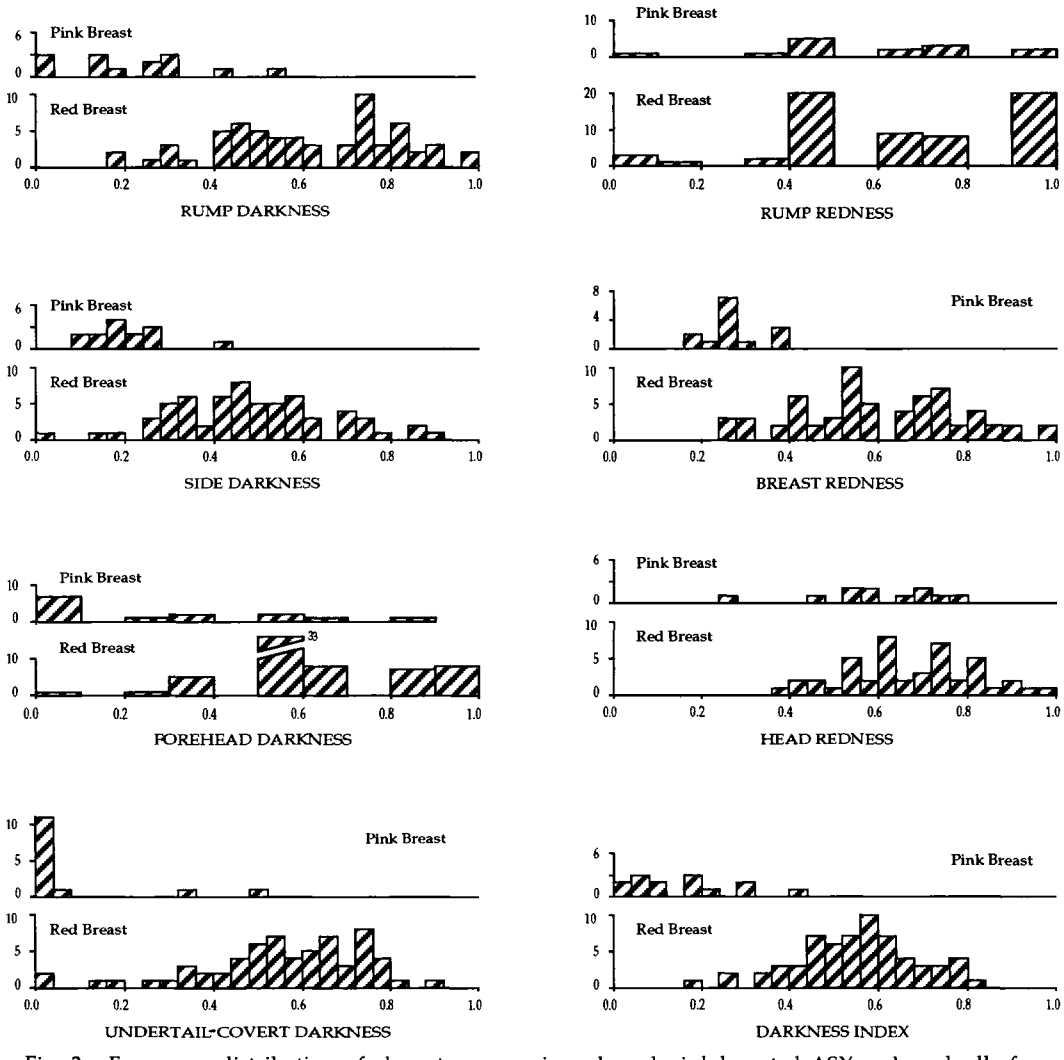

Fig. 2. Frequency distribution of character scores in red- and pink-breasted ASY male redpolls from Churchill, Manitoba.

components analyses were performed for SY males, ASY males, and females (see Materials and Methods). Typically, the first two eigenvalues were interpretable, their values being larger than the average value (Table 7). However, because in each analysis the second vector explained less variance than expected by chance (based on the broken-stick model; Frontier 1976), we focused our attention on the dispersion of individuals along the first axis. Both darkness and redness variables typically loaded heavily on that axis (Table 7).

The distributions of individuals along the first axis defined by each PCA are presented in Figure 3. For ASY males, the cluster of individuals

TABLE 6. Test of differentiation of plumage scores between pink- and red-breasted ASY male redpolls from Churchill, Manitoba. Differences tested using Kolmogorov-Smirnov test (df = 2); only males with colored breasts used.

Character	z^a	P
Rump darkness	2.58	0.010
Side darkness	2.82	0.005
Forehead darkness	2.04	0.041
Undertail-covert darkness	2.79	0.005
Rump redness	0.59	0.555
Breast redness	2.95	0.003
Head redness	0.79	0.431
Darkness index	2.98	0.003

[a] $n_{pink} = 14$, except for head redness ($n = 11$); $n_{red} = 63$, except for head redness ($n = 45$).

TABLE 7. Details of principal-components analyses of plumage variability in redpolls from Churchill, Manitoba. Values presented for first two components.

	SY males		ASY males		Females	
	I	II	I	II	I	II
Eigenvalue	2.85	1.43	2.95	1.42	2.48	1.46
Percent variance explained	42.71	20.49	42.09	20.34	35.38	20.82
Contribution to eigenvector						
Rump darkness	0.472	0.269	0.454	0.221	0.472	0.166
Side darkness	0.466	0.334	0.487	0.100	0.352	0.515
Forehead darkness	0.322	0.510	0.413	0.006	0.309	0.017
Undertail-covert darkness	0.360	−0.091	0.476	0.036	0.426	0.341
Rump redness	−0.361	0.535	0.048	0.661	−0.315	0.592
Breast redness	−0.327	0.442	−0.388	0.386	−0.382	0.138
Head redness	−0.299	0.257	−0.083	0.595	−0.363	0.470
Position in reduced space[a]						
Rump darkness	0.797	0.322	0.779	0.264	0.743	0.200
Side darkness	0.786	0.401	0.836	0.119	0.554	0.622
Forehead darkness	0.543	0.611	0.708	0.007	0.487	0.021
Undertail-covert darkness	0.608	−0.109	0.818	0.043	0.670	0.412
Rump redness	−0.609	0.640	0.080	0.789	−0.496	0.715
Breast redness	−0.552	0.529	−0.666	0.461	−0.600	0.167
Head redness	−0.505	0.308	0.142	0.710	−0.571	0.567

[a] Eigenvector length standardized to square root of the eigenvalue.

in the center and on the left represents dark birds with moderate to little red pigmentation on the breast (rump and head redness contributed little to the first axis in this analysis); individuals to the right represent paler birds. The distribution of individuals along this axis was linked to the breast-color dimorphism. Only one pink-breasted bird had a score below 1.5 (at position 0.73); beyond that point, all individuals but that one were red-breasted. Interestingly, the exceptional bird was subjectively assigned in the field to the form *flammea*, being the only exception in our sample to the rule that pink-breasted birds were identified as *exilipes* and red-breasted ones as *flammea*.

UPGMA and WPGMA analyses of the matrix of Euclidean distances between ASY males in the reduced space resolved two identical, well-differentiated clusters of birds; only the UPGMA dendrogram is presented (Fig. 4). Apart from the exceptional "pink-*flammea*" individual noted above, the clusters correspond to the dichotomy between pink- and red-breasted birds, and they correspond perfectly to the field classification of individuals.

The distribution of SY males along the first axis of their principal-components analysis is presented in Figure 3. Darkness characters loaded positively on the axis, and redness characters negatively (Table 7). All individuals classified as *exilipes* in the field are found on the right side and unidentified birds have a central position. UPGMA and WPGMA analyses both identified two distinct groups of individuals in the reduced space, separated at position 1.0 along the first axis (UPGMA results presented in Fig. 4). These groups correspond well to the field classification of individuals.

Although all females were analyzed jointly, the results for SY and ASY birds are presented on distinct histograms (Fig. 3). The distribution of both female age-series in their PCA space shows little pattern, although field-identified *exilipes* represented a nonrandom subset of the total sample, characterized by high scores on axis 1.

DISCUSSION

The existence of distinct, sympatric forms of redpoll is a controversial issue. Two of the three main factors identified by Knox (1988) as contributing to the confusion are relevant to our analysis of the presumptive forms *flammea* and *exilipes*. First, Knox (1988) pointed out that redpolls have only one molt a year and, therefore, experience substantial feather wear. Brooks (1968) showed that the total weight of redpoll feathers is 31% greater in November, just after the molt, than in July. Because of differential

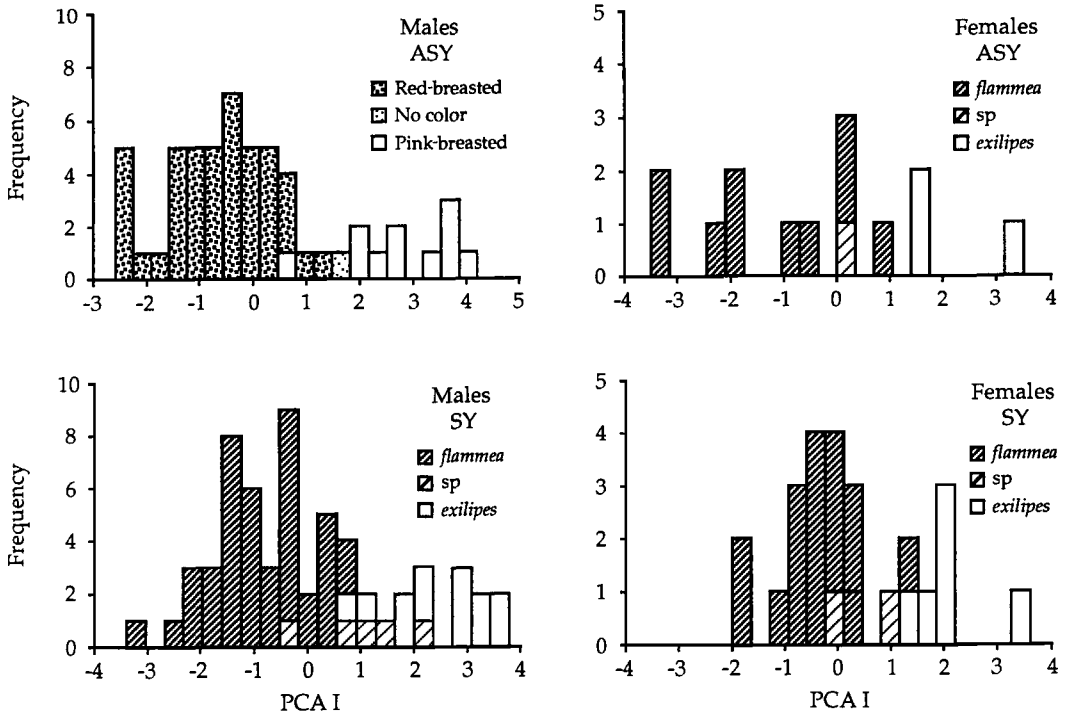

Fig. 3. Distribution of individual redpolls of specific age and sex along first axes of separate principal-components analyses. The designation "sp" indicates assignment to *flammea* or *exilipes* could not be made in the field.

distribution of melanistic pigments on body feathers, individuals get darker through the year, and specimens taken a few weeks apart may have fairly different plumage characteristics. Knox (1988) argued that the inclusion in one sample of birds taken over a period longer than a few weeks leads to an increase in the overall variance of the sample, and in the variance within each putative form. He suggested that this has masked the bimodality of plumage-character distributions in the composite samples studied by most researchers, and has led them to reject the idea of polytypy in redpolls.

In our sample, the trend was for birds to get darker and more extensively red through the sampling period, but never significantly so. This is probably because all specimens were taken over a relatively short period of time, and it indicates that temporal variability in late spring and early summer is not important enough to affect other analyses.

Second, Knox (1988) emphasized the importance of age and sex as determinants of plumage characteristics in redpolls. Our study confirms that males are usually redder and lighter than females (Fig. 1). The magnitude of age dimorphism is more difficult to describe, apart from the characteristic extensive redness of ASY males. Age-related variation in overall darkness was first mentioned by Coues (1862), but that factor has been basically ignored since, except in recent investigations by Swedish researchers (e.g. Molau 1985, Nyström and Nyström 1987). For melanin pigmentation, the trend reported from Sweden is that ASY birds are generally less densely pigmented than SY ones. Knox (1988) suggested that this pattern is true for all putative redpoll forms, and that the failure to recognize the phenomenon has prevented some researchers from detecting a polymorphism independent of age and sex in their samples.

In Churchill redpolls, we have found a significant difference beween SY and ASY individuals in only one darkness character (i.e. side darkness in males; Table 4). This result is surprising, as it does not correspond to the findings of Swedish researchers, and to the senior author's subjective assessment of the situation in the field. A number of reasons why age-related differences might have gone undetected in our

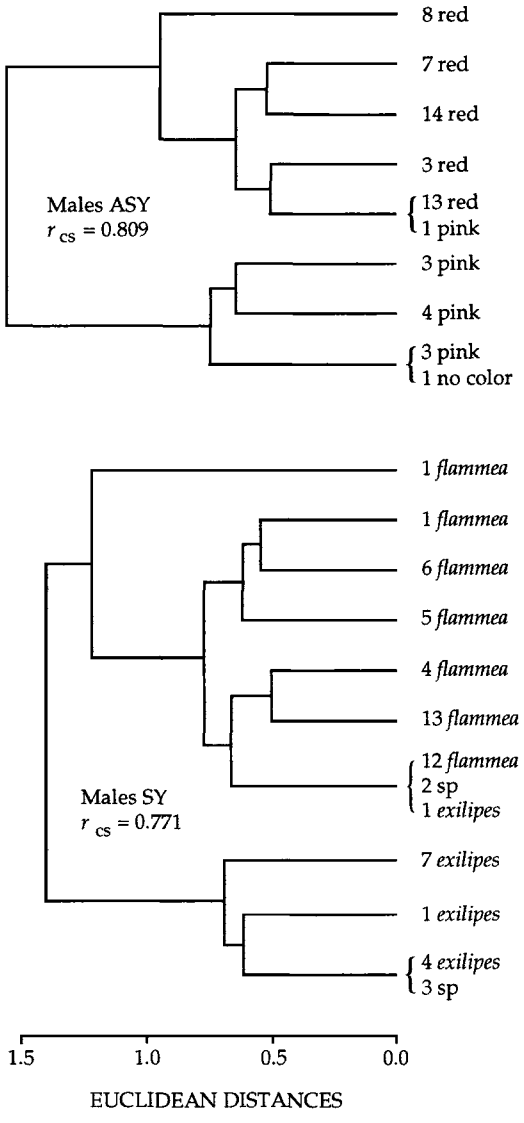

Fig. 4. Simplified UPGMA dendrograms showing relationships between ASY (above) and SY (below) male redpolls in phenotypic space defined by principal-components analyses (see text). Dendrograms produced from matrices of Euclidean distances (D_E) between individuals in PCA spaces. Branching networks below $D_E = 0.5$ are not shown, and values on left are numbers of individuals in each terminal branch, split according to breast color or field identifications. Cophenetic correlation coefficient (r_{cs}) indicates degree to which dendrogram reflects original distances. The designation "sp" indicates assignment to *flammea* or *exilipes* could not be made in the field.

sample, other than the absence of age dimorphism, were presented in the Results section. Hypotheses that acknowledge the existence of distinct sympatric forms cannot be tested for the moment since no objective diagnostic criterion, independent of plumage characters, exists for the putative redpoll forms. Consequently, we leave open the question of age dimorphism in Nearctic redpolls, but still recommend that future studies discriminate between SY and ASY birds.

Polymorphism within age-and-sex groups.—We did not expect, as did Troy (1985), that a phenotypic polymorphism in redpolls, independent of sexual and age dimorphisms, would necessarily result in the existence of disjunct clusters of individuals in the analytical space. Instead, we simply expected that some form of bimodality would be found in the distribution of one or more plumage characters in at least one age-and-sex group. However, because it was impossible to estimate *a priori* the expected distribution of individuals for each character studied, we could only test indirectly the hypothesis of a polymorphism. This was done by testing the distribution of each character within each age-and-sex series for deviation from normality toward platykurtosis (i.e. a bimodal distribution is platykurtic).

In our sample, several plumage characters were not normally distributed with respect to kurtosis (Table 5). In ASY males, these included breast redness and two of the characters most frequently cited as differentiating the presumed *flammea* and *exilipes* forms: rump darkness; and the width of the dark streak on the longest undertail covert (reflecting general undertail-covert darkness). In these birds, the color of the breast and flanks showed almost discrete variation, with most individuals being either clearly red or pink. This characteristic also has frequently been mentioned as a relatively reliable criterion for distinguishing *flammea* and *exilipes* redpolls in summer (e.g. Coues 1862, Gabrielson and Lincoln 1959, Lobkov 1979, Molau 1985). When ASY males were split according to breast color, the pink and red groups were found to differ significantly for six of the eight plumage characters analyzed (Table 6, Fig. 2), and the scores of red-breasted individuals for each character were normally distributed (pink-breasted individuals were too few to allow testing for normality). Further, cluster anal-

yses indicated that the two main groups of individuals resolved by the PCA analysis of darkness and redness characters corresponded (A) with one exception to the red–pink dichotomy, and (B) without exception to field identifications of the individuals. These results are significant because the PCA was not based on color characters; breast color, therefore, was a valid independent variable to interpret the results. Thus, the overall pattern of plumage variability in Churchill ASY male redpolls strongly suggests the co-occurrence of two types of individuals that differ in overall darkness and redness, and in the color of the carotenoid pigmentation of the breast and flanks.

In our series of SY males, only side darkness was not distributed normally (Table 5). Unfortunately, SY males typically do not have a colored breast, and the approach followed with ASY males could not be used. However, a visual inspection of the distribution of SY male scores for each character suggests that the distributions of undertail-covert darkness and rump darkness may also be bimodal with an unequal representation of the modes (Fig. 1). The PCA of SY males identified two clusters of individuals (Fig. 4), distinguishable primarily along the first axis on which darkness characters loaded heavily. The clusters correspond almost exactly to the groups identified in the field as *flammea* and *exilipes*. Thus, as for older males, these results support the idea that two plumage types co-occur in Churchill redpolls.

The analyses of SY and ASY females failed to provide good evidence for a plumage polymorphism. Because such a polymorphism was inferred in the analyses of the same characters in males, one has to conclude that, in females, a polymorphism is altogether absent, or that its manifestations are too subtle to be detected using our approach. Larger samples and additional analyses are required before a definitive conclusion can be reached. If redpoll plumage forms are distinct species, as several taxonomists have suggested (see Knox 1988:table 1), the fact that their differentiation is more pronounced in one sex than the other is not surprising; such a pattern is observed in the majority of avian species pairs. Thus, our failure to demonstrate the presence of a plumage polymorphism in female redpolls does not weaken the conclusion that a polymorphism is present in the group.

Our conclusion, which generally concurs with that of several recent European researchers (e.g. Lobkov 1979, Svensson 1984, Molau 1985, Knox 1988), is at variance with Troy's (1985) conclusion regarding Alaskan birds. Some problems with Troy's study were noted above, as well as by Knox (1988). In that several researchers have suggested that the situation in Alaska differs from that in Scandinavia or in northern Canada (Gabrielson and Lincoln 1959, Baldwin 1961, Jehl and Smith 1970, Troy 1985, B. Kessel pers. comm.), new analyses of Alaskan redpolls are clearly needed.

Origin of the polymorphism.—Redpoll plumage forms may be distinct species, as has frequently been suggested (e.g. Molau 1985, Knox 1988), but they also may be the product of an intraspecific genetic or ecophenotypic polymorphism. Several bird species are known to have plumage polymorphisms with a simple allelic basis that usually involve a single type of pigment (Cooke 1985, Cooke and Buckley 1987). A redpoll-like polymorphism, involving two types of pigment (i.e. melanin and carotenoid compounds), can arise if an allelic polymorphism exists at a major locus with either pleiotropic effects on numerous traits, or epistatic relationships with several structural loci. Similarly, redpoll plumage variants may be the different expression of a meristic character (i.e. a trait that varies in a discrete fashion even though it is affected by a continuous distribution of underlying genetic characters; Hartl and Clark 1989). Pigmentation in birds also can be significantly affected by environmental factors such as diet (Brush 1981, Slagsvold and Lifjeld 1985). Thus, ecophenotypic explanations for the redpoll polymorphism can be envisioned (Seutin 1990) in which the forms are the product of a threshold response mechanism or of developmental conversion (Smith-Gill 1983). Although ecophenotypic explanations like these are theoretically possible, they are unlikely, given that there is no known example of an avian polymorphism involving either of these mechanisms.

Even though redpolls have regularly been bred in captivity, no information is available regarding the heritability of their plumage characteristics. Recently, however, we have obtained preliminary data on the question. During the first part of the 1988 breeding season, the senior author captured immature birds in Churchill that were kept under identical con-

ditions until they developed adult plumage. Most birds actually were kept for more than one year. These individuals had been locally produced, being caught within their first week as fledglings. They developed typical *flammea* ($n = 2$) or *exilipes* ($n = 7$) plumage characteristics, an observation that virtually rules out the possibility that alternative redpoll forms are ecophenotypic variants produced in different years, at different times within a single breeding season, or in different locations. This also indicates that, if ecophenotypic interactions were responsible for the polymorphism, it is environmental conditions experienced by a bird before fledging that determine its phenotypic form. We further noticed that sibs kept in captivity—three pairs and one trio—developed similar phenotypes within sibships, indicating that phenotypic appearance is not related to hierarchy within broods or fledgling groups. Finally, all of the offspring developed the phenotype of their parents, which also were maintained in captivity (in two cases, only one parent was captured). These observations suggest that the plumage characters we analyzed are largely genetically determined, but larger samples and properly controlled experimental breeding (see Seutin 1990) will be necessary to obtain a clear understanding of the redpoll plumage polymorphism. In the meanwhile, the most parsimonious explanation for our observations on plumage variability in Churchill redpolls is the sympatric occurrence of two genetically determined phenotypic forms.

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