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MORPHOMETRIC VARIABILITY IN REDPOLLS FROM CHURCHILL, MANITOBA

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ABSTRACT.—Two plumage forms were observed in redpolls from Churchill, Manitoba, which correspond to the putative taxa *Carduelis flammea flammea* (dark-plumaged birds) and *C. hornemanni exilipes* (pale-plumaged birds). In a sample of breeding adults ($n = 277$), we examined whether morphometric differentiation parallels this plumage polymorphism. Males and females were analyzed independently, and age, date of capture, and status at measurement (study skin vs. live bird) were considered as covariates in univariate analyses. We used a separate phenetic analysis of plumage characters, rather than our subjective field identifications, to establish the groups to be compared statistically; this ensured that mensural characters (e.g. bill shape) were not utilized as classification criteria for the present investigation of metric traits. In both sexes, redpoll plumage forms differed significantly in three of seven external mensural characters. Discriminant-function analyses, based on the same characters, showed that the forms can be distinguished morphometrically with great confidence (jackknifed estimate of correctly classified individuals was 87% in both sexes). In males and females, the distribution of discriminant scores of typical individuals and of a set of unidentified birds is bimodal. In a bivariate-reduced space of plumage and morphometric variability, pale- and dark-plumaged ASY (after-second-year) males form distinct groups. In SY (second-year) males and in females, plumage forms are not strictly distinct, but in no case was there an abundance of intermediates as predicted under the hypothesis that the forms are distinct species that frequently interbreed. Redpoll types may be specifically distinct, as has frequently been suggested, but they also may be examples of intraspecific genetic or ecophenotypic polymorphism. Experimental breeding and an assessment of mating patterns in the field are required to test these possibilities. *Received 3 October 1991, accepted 5 September 1992.*

SEUTIN ET AL. (1992) have shown that male redpolls from Churchill, Manitoba, can be divided into two plumage types, which correspond to the putative taxa *Carduelis flammea flammea* and *C. hornemanni exilipes.* Strictly distinct forms could not be distinguished in females, but the general correspondence between the grouping of individuals in a principal-component space of plumage-pigmentation variability and independent field identifications tentatively supports the idea that females also are polymorphic. The finding that distinct plumage types exist in North American redpolls is opposite to Troy's (1985) conclusion based on a study of mainly Alaskan birds, but it parallels the views of several recent European ornithologists (e.g. Lobkov 1979, Molau 1985, Nyström and Nyström 1987, Knox 1988).

Researchers concluding that distinct redpoll plumage forms exist have usually assumed that they represent discrete biological species, not "color morphs" within a panmictic population (see Knox 1988). Considering that distinct species usually differ at a number of independent genetic loci, whereas color morphs differ only at loci involved in determining plumage appearance (and loci in close linkage with them), several authors have suggested that the finding of morphometric differences between redpoll plumage types would support the hypothesis of their taxonomic distinctness (e.g. Troy 1985, Knox 1988, Herremans 1990). This is not necessarily true, however, as several intraspecific genetic and ecophenotypic mechanisms can explain the existence of a complex polymorphism, involving both plumage and morphometric characters, within a single population. Seutin et al. (1992) have described possible mechanisms for the redpoll plumage polymorphism, all of which can be extended to a polymorphism of a wider scale. For instance, an allelic polymorphism at a major locus influencing genes for both pigmentation and morphometrics can induce a complex phenotypic polymorphism.

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TABLE 1. Summary statistics (mm) of seven external morphometric characters in male redpolls from Churchill, Manitoba. Reference series for dark and pale groups comprised typical individuals identified in plumage-pigmentation analyses of Seutin et al. (1992). Dark and pale birds correspond respectively to putative taxa *flammea* and *exilipes*. K_i is average difference between ASY and SY birds within a plumage type; L_i is analogous difference between individuals measured live and as study skins.

Variable	n	$\bar{x} \pm$ SD	Skewness	K_i	L_i
Dark birds					
Wing length	80	72.84 ± 1.44	−0.13	1.08**	0.05
Tail length	78	55.18 ± 2.04	−0.55	0.51	0.13
Tarsus length	80	14.73 ± 0.52	−0.85	−0.01	−0.16
Hallux length	80	4.65 ± 0.44	0.42	−0.09	0.40**
Bill length	80	7.67 ± 0.31	−0.01	0.13	0.09
Bill width	77	5.71 ± 0.23	0.20	−0.04	0.15
Bill depth	76	5.81 ± 0.20	0.27	−0.02	−0.24**
Pale birds					
Wing length	17	73.19 ± 2.44	−0.83	1.56	−0.33
Tail length	17	57.47 ± 2.06	−0.13	1.63	0.45
Tarsus length	17	14.59 ± 0.46	0.23	0.07	0.25
Hallux length	17	4.22 ± 0.55	0.31	−0.31	0.72*
Bill length	17	7.01 ± 0.27	−0.25	0.13	0.02
Bill width	17	5.66 ± 0.20	0.41	0.16	−0.11
Bill depth	17	5.77 ± 0.19	−0.43	0.18	−0.11

*, $P < 0.05$; **, $P < 0.01$; comparisons of groups with t-tests.

Such a situation is observed in the White-throated Sparrow (*Zonotrichia albicollis*) and the Dark-eyed Junco (*Junco hyemalis*), where chromosomal variants differ in plumage, morphology and behavior (Rising and Shields 1980). An ecophenotypic explanation also can be envisioned for a complex polymorphism if an environmental variable, or a set of correlated variables, influence the phenotypic expression of a number of genetic traits. It has been shown, for instance, that the morphometric characteristics of an adult bird can be significantly and permanently influenced by its diet as a nestling (Boag 1987; for empirical evidence, see Boag 1983, James 1983, Larsson and Forslund 1991). Since diet can also affect plumage pigmentation (e.g. Brush 1981, Slagsvold and Lifjeld 1985), a complex phenotypic polymorphism can result from a feeding-niche polymorphism within a panmictic population. However, the likelihood of a nongenetic explanation for a complex polymorphism in an avian taxon is slim, since strong developmental homeostasis seems to be the rule in birds as in most other higher vertebrates.

Here, we further examine the phenotypic polymorphism in redpolls from Churchill, Manitoba, by assessing whether morphometric differentiation parallels the plumage polymorphism described by Seutin et al. (1992). Our sample ($n = 277$; essentially those birds studied for plumage by Seutin et al. 1992) comprised only adults captured or collected between 20 May and 31 July during each field season. The restriction on the temporal origin of specimens was imposed to avoid seasonal variability introduced by plumage wear. We first assessed the nature of morphometric differences between redpoll plumage types through univariate analyses of seven conventional external characters (Table 1). We then used the same data in discriminant-function analyses to evaluate the overall level of morphometric differentiation between forms. Our expectation was that, if a clear morphometric polymorphism exists that parallels the plumage polymorphism, individuals should be distributed bimodally or disjunctly along a morphometric discriminant function axis.

A problem frequently encountered in morphometric investigations of taxa that are difficult to diagnose, like redpoll plumage forms, is the *a priori* assignment of individuals to groups. With the exception of Troy (1985), redpoll researchers have used their personal, subjective identifications for this purpose (e.g. Molau 1985, Knox 1988, Herremans 1990). A problem with this approach is that most people rely partly on bill shape to differentiate redpoll forms. In the context of a morphometric investigation in which bill measurements are considered, this implies that the classification criterion is not strictly independent of the variables analyzed,

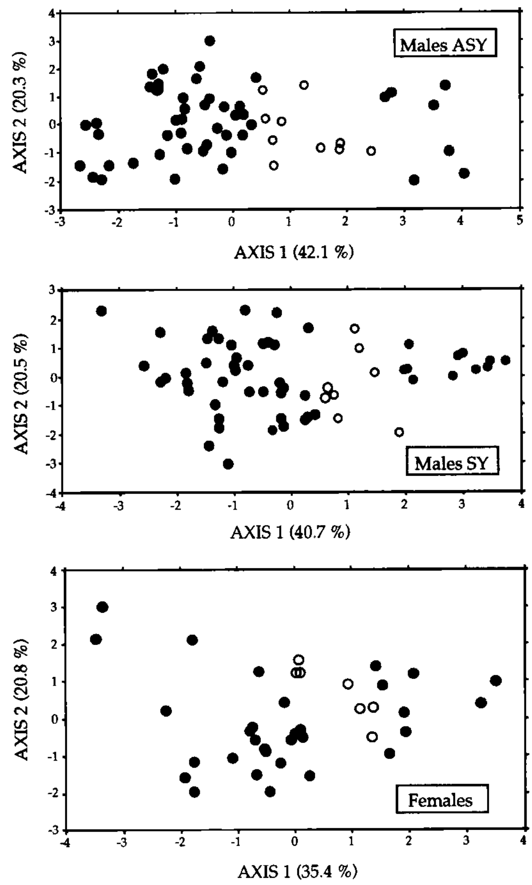

Fig. 1. Distribution of individual redpolls in reduced spaces of plumage pigmentation variability described in Seutin et al. (1992), showing birds considered typical of each plumage type for morphometric analyses. Percent of total phenotypic variation explained by each PCA axis indicated. ●, typical individuals; ○, other individuals.

which makes the logic somewhat circular. To avoid this problem, we established reference series for each plumage form, later referred to as the typical samples, from the results of the principal-component analyses of plumage characters presented by Seutin et al. (1992). Our procedure, presented in detail below, ensured that only plumage characters were used for *a priori* group assignment.

MATERIALS AND METHODS

Total sample and typical series.—Morphometric measurements were taken on all birds studied by Seutin et al. (1992), and on additional specimens ($n_{\mathrm{ASY\ males}} = 24$, $n_{\mathrm{SY\ males}} = 14$, $n_{\mathrm{ASY\ females}} = 13$, $n_{\mathrm{SY\ females}} = 7$; ASY = after second year; SY = second year) for which only incomplete plumage data were available. Individuals were sexed and aged as explained by Seutin et al. (1992); specimens that could not be reliably sexed or aged were excluded. We did not attempt to sample specific individuals on the basis of their phenotypic appearance; thus, our sample probably offers an unbiased representation of the redpolls that breed in Churchill.

For SY and ASY males, the typical series of pale- and dark-plumaged birds generally corresponded to the groups identified by Seutin et al. (1992) through UPGMA analysis of plumage principal-component scores. To ensure the homogeneity of typical series and because groups were not clearly separated in the plumage principal-component spaces, we excluded from the typical series the 20% most intermediate individuals between group centroids in the reduced spaces. We used G.S. field identifications of individuals to establish group centroids. This use of subjective identifications does not make the logic of our analyses circular (i.e. it does not mean that individuals get assigned to one or another typical form on the basis of morphological characteristics). Excluding more "intermediates" would probably have been better, but the limited number of *exilipes*-type birds available precluded leaving out more birds. In females, group limits were necessarily more subjective since forms were not clearly distinguishable in the plumage principal-component space, but again we excluded the most intermediate birds using the logic followed for males. Typical and nontypical specimens are shown based on principal-components analysis of plumage characteristics (Fig. 1). All other individuals available (e.g. intermediates in the plumage analyses and the specimens for which plumage data were partially or entirely missing) were pooled and formed the unknown series used in discriminant-function analyses.

Measurements.—G.S. measured all museum specimens and all live birds in 1988; in 1989, measurements were taken in approximately equal proportions by G.S. and an assistant (Anne Davies). Measurements were taken using dial calipers and recorded to the nearest 0.1 mm, except for wing length of live birds in 1989, which was measured to the nearest 0.5 mm with a stopped ruler. Wing length was measured as the chord of the unflattened folded wing; the right wing was used unless the primaries were in a markedly worse condition than those of the left wing. European researchers have frequently reported flattened and maximum measurements of redpoll wing length (e.g. Molau 1985, Knox 1988, Herremans 1990); our figures, therefore, are not strictly comparable to some previously published measurements. Tail length was measured following Baldwin et al. (1931) to the longest rectrix on either the right or left side. Hallux and tarsus lengths were measured following Baldwin et al. (1931). Bill length was measured from the anterior end of the nostril to the tip, bill width was taken at the gape, and bill height was taken at the vertical of the junction of the rami (where they form the gonys), which corresponds approximately to the posterior end of the exposed culmen.

Statistical analyses.—Analyses of covariance (ANCOVAs) were used to examine morphometric differences between typical series (Sokal and Rohlf 1981). Because sexual dimorphism is important in redpoll morphometrics (e.g. Troy 1985, Knox 1988), independent analyses were performed for each sex. Age seems to have a modest influence on redpoll measurements (e.g. Evans 1966, Molau 1985, Knox 1988) and, thus, was considered as a covariate in the analyses. Two other covariates were considered, date of capture and the status at measurement (i.e. live bird from 1988 and 1989 or study skin mostly from 1930 and 1931); these factors frequently have been reported to affect avian external morphometrics (e.g. Bjordal 1983, Herremans 1985). The BMDP P1V program was used for calculations (Dixon 1985).

Discriminant-function analyses (DFA) were performed using the BMDP P7M program. Independent analyses were conducted for each sex using log-transformed data. In view of our finding of age-related differences within sex and plumage type (see Results), separate analyses for each sex-and-age group were indicated; however, this was precluded by the small size of some typical series. Instead, for variables in which an age effect was detected through ANCOVAs, we corrected the measurements of SY individuals by adding an age correction factor, K, equal to the average difference of means between ASY and SY males (K_i) in the typical dark and pale series:

$$K = 0.5 \sum K_i = 0.5\,[(\bar{x}_{\text{ASY pale}} - \bar{x}_{\text{SY pale}}) + (\bar{x}_{\text{ASY dark}} - \bar{x}_{\text{SY dark}})]. \quad (1)$$

For variables in which ANCOVAs indicated a significant effect of status at measurement, a similar factor, L, was added to measurements taken on museum specimens:

$$L = 0.5 \sum L_i = 0.5\,[(\bar{x}_{\text{live pale}} - \bar{x}_{\text{skin pale}}) + (\bar{x}_{\text{live dark}} - \bar{x}_{\text{skin dark}})], \quad (2)$$

where L_i is the mean difference between birds of different status within a plumage type. Correction factors were estimated from males only because male samples were larger and, therefore, provided a better estimate of group differences. We have no reason to believe that sex-specific patterns of age or "shrinkage" variation existed.

Missing data were estimated only for individuals in the unknown group used in DFAs, and only for those birds with a single measurement missing. Estimates were obtained through multiple regression of each variable on the other six characters, using the BMDP PAM program. Because univariate analyses revealed significant morphometric differences between typical pale and dark samples (see Results), independent estimations of missing data for members of each plumage type were desirable. Group memberships for this were based on G.S. field identifications that Seutin et al. (1992) showed to generally match an objective classification of individuals based on principal-component analyses of the plumage characters. Wing and tail measurements were estimated for one male each, bill depth was estimated for four males and three females, and hallux length (which was measured differently on 1988 live birds than on all other specimens) had to be estimated in 28 males (15.3% of male sample) and 23 females (26.1% of female sample). Overall, only 3.1% of the measurements were estimated.

All DFAs were repeated using raw data, without applying corrections for variability due to age and status at measurement. The results were virtually identical to those presented below.

RESULTS

Univariate analyses.—Morphometric characteristics of typical male redpolls of the two plumage types are summarized in Table 1. Small values of the correction factor K indicate the limited effect of age on redpoll morphometrics; t-tests on log-transformed data revealed a significant difference between age groups in dark males only for wing length ($t = 3.63$, df = 78, $P < 0.001$), and none in pale individuals (all $P > 0.05$). A difference in average wing length (or tail length, see below) may be a consequence of different feather wear in the two age groups due to different molting schedules (Pyle et al. 1987). Hallux length of individuals measured alive and as study skins differed significantly in both dark ($t = 3.09$, df = 78, $P = 0.003$) and pale birds ($t = 2.79$; df = 15, $P = 0.014$). This probably does not reflect shrinkage of the hallux in study skins, but a difference in positioning the points of the calipers when measuring the two types of birds. Bjordal (1983) and Herremans (1985) gave the same explanation for differences in tarsus length between study skins and fresh specimens in other passerines. Bill depth was significantly greater in study skins than in live birds of the dark series ($t = 3.32$, df = 74, $P = 0.001$), but not of the pale one. This is probably due to the improper preparation of certain specimens (i.e. bills that were not maintained tightly closed during drying of skins). Postmortem changes in wing length, tail length, tarsus length, and bill dimensions have been reported in passerines (e.g. Knox 1980, Haftorn 1982, Bjordal 1983, Herremans 1985), but none of these variables was significantly affected in our samples.

TABLE 2. Summary statistics (mm) of seven external morphometric characters in female redpolls from Churchill, Manitoba. Reference series for dark (n = 23) and pale (n = 8) groups comprised typical individuals identified in plumage pigmentation analyses of Seutin et al. (1992). Dark and pale birds correspond, respectively, to putative taxa *flammea* and *exilipes*. Factors K_i and L_i were not estimated because some samples were very small.

Variable	$\bar{x}$ ± SD	Skewness
	Dark birds	
Wing length	70.00 ± 1.77	0.20
Tail length	54.27 ± 2.02	0.20
Tarsus length	14.67 ± 0.36	−0.38
Hallux length	4.75 ± 0.63	0.43
Bill length	7.35 ± 0.28	0.06
Bill width	5.60 ± 0.22	1.33
Bill depth	5.61 ± 0.17	0.28
	Pale birds	
Wing length	70.86 ± 1.96	−1.03
Tail length	55.50 ± 2.21	−0.17
Tarsus length	14.19 ± 0.52	0.65
Hallux length	3.94 ± 0.54	−0.01
Bill length	6.78 ± 0.21	0.04
Bill width	5.54 ± 0.43	−2.04
Bill depth	5.75 ± 0.05	0.00

Morphometric characteristics of typical females are summarized in Table 2. In dark individuals, no significant differences were found between SY and ASY birds (t-tests; all $P > 0.35$), or between individuals measured alive or as study skin (t-tests; $P > 0.15$). Pale individuals of different age or status at measurement could not be compared statistically due to very small sample sizes.

Results of the ANCOVAs conducted to test the morphometric differentiation of typical pale and dark individuals are presented for males and females (Table 3). In males, the analyses revealed that age has a significant effect on wing length, as noted above, but also on tail and bill lengths. No effect of age was noted in females. Status at measurement has a significant influence on hallux length and bill depth in males, but only on hallux length in females. Finally, the date of capture has a complex pattern of influence. In males, it significantly affects tail length and bill depth, and in females, tarsus length and bill width. In all cases, the effect was in the same direction in both sexes, but we have no explanation for the difference in intensity that produces a significant difference in one sex and not in the other; this may be due partly or entirely to chance.

When the influence of covariates is taken into account, pale and dark typical redpolls differ significantly in several morphometric characteristics. In males, the most important difference, as judged by F-values, was in bill length,

TABLE 3. F-statistics from ANCOVA of differences between typical male and female redpolls of two plumage types based on log-transformed data. Test of effect of covariates (age, status at measurement [study skin vs. live bird], and date of capture) is that slope of regression of dependent variable on covariates is equal to 0; a P-value smaller than 0.05 indicates covariate has significant effect on morphometric variable considered.

	Covariate			
Variable	Age	Status at measurement	Date	Main effect[a]
		Male		
Wing length	13.81***	0.33	0.09	0.83
Tail length	5.84*	0.02	5.62***	22.72***
Tarsus length	0.34	0.50	3.38	0.06
Hallux length	1.14	13.25***	1.42	15.68***
Bill length	4.58*	3.25	0.32	51.10***
Bill width	0.55	3.86	1.22	2.16
Bill depth	0.51	14.91***	8.54**	0.19
		Female		
Wing length	0.08	0.11	0.11	1.20
Tail length	0.09	0.44	0.33	2.02
Tarsus length	0.87	0.76	5.42*	3.92
Hallux length	0.50	6.46*	2.42	14.33***
Bill length	0.28	0.93	0.82	21.60***
Bill width	0.70	1.89	7.86**	2.49
Bill depth	0.71	0.02	0.00	4.47*

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; others ns, $P > 0.05$.

[a] Differences between forms.

followed by tail and hallux lengths; all of these differences are highly significant (Table 3). In females, bill length is the most highly differentiated variable, as it is in males, followed by hallux length and bill depth (Table 3). Virtually identical results were obtained in analyses (not shown) using raw data instead of log-transformed data.

Discriminant-function analyses.—The standardized coefficients of the original variables for the discriminant function maximally separating pale and dark typical redpolls are presented in Table 4. The magnitudes of the coefficients, regardless of sign, indicate the relative importance of each character for discriminating the groups. In males, bill, tail, and hallux lengths were the most useful variables, as expected from the ANCOVA results. The frequency distribution of males along the discriminant axis is shown in Figure 2. Mean discriminant scores of typical pale and dark individuals are highly significantly different, reflecting the separation of the groups (Fig. 2, Table 4). As for typical birds, the distribution of unknown individuals is bimodal (Fig. 2; Kolmogorov-Smirnov-Lilliefors test of normality, $D_{max} = 0.126$, $P < 0.01$). A very high percentage of correct identification of typical individuals was achieved with the function presented (Table 4), but also with a function based only on the three most useful characters noted above (average 91.3% correct).

In females, variables contributing the most to the discrimination between plumage types were, in decreasing order, bill length, wing length, bill depth, and hallux length (Table 4). The importance of wing length is somewhat surprising since univariate analyses indicated that groups did not differ for that variable; this probably results from the fact that wing length does not covary as strongly with the other characters as those do among themselves. Along the discriminant axis, group centroids were highly significantly differentiated, and typical individuals were clearly separated (Table 4, Fig. 2). The distribution of unknown females appears bimodal, with the modes corresponding well to those in typical birds, but it may statistically be interpreted as normal (Kolmogorov-Smirnov-Lilliefors test of normality, $D_{max} = 0.090$, $P > 0.05$). The four most important variables produced a function discriminating typical females with the same efficiency as the function presented in Table 4.

TABLE 4. Standardized coefficients of discriminant functions produced by discriminant-function analysis of typical pale and dark redpolls. Independent analyses performed for each sex on log-transformed data, and variation related to age and status at measurement handled as explained in text. *F*-statistics associated with Wilk's lambdas assess distinctness between group means along discriminant axis. Percentages of original cases correctly identified by function calculated using jackknifing technique of Lachenbruch and Mickey (1968).

Variable	Male	Female
Wing length	0.075	0.747
Tail length	0.430	−0.226
Tarsus length	0.044	−0.043
Hallux length	−0.394	−0.420
Bill length	−0.880	−0.949
Bill width	0.102	0.171
Bill depth	0.022	0.335
Wilk's lambda	0.460	0.318
Approximate *F*	14.085	7.042
P	<0.001	<0.001
Eigenvalue	1.174	2.143
Correct classification (%)		
Dark individuals	88.0	87.0
Pale individuals	82.4	87.5

Plumage and morphometric covariation.—In Figure 3, all birds for which complete plumage and morphometric data were available are plotted in the bivariate space defined by the first axis of a principal-component analysis of plumage variability (Seutin et al. 1992) and the morphometric discriminant-function axis presented above. The two axes are independent in the sense that strictly distinct sets of variables were used in each analysis. In Figure 3, nontypical birds necessarily showed up in an intermediate position between centroids along the plumage axis since they were selected on the basis of their intermediateness in plumage; it is their distribution along the morphometric axis that is instructive. In males, separate plots were produced for SY and ASY birds because of the importance of age dimorphism in plumage (Seutin et al. 1992). In females, all individuals were plotted simultaneously since age dimorphism is limited and birds of the two age classes were analyzed jointly for both plumage and morphometric variation.

The discrimination between pale- and dark-type ASY typical males is complete, and only one unknown individual can potentially be considered intermediate in both plumage and morphometry (Fig. 3). Results for SY males are less clear; the 95% equiprobable population el-

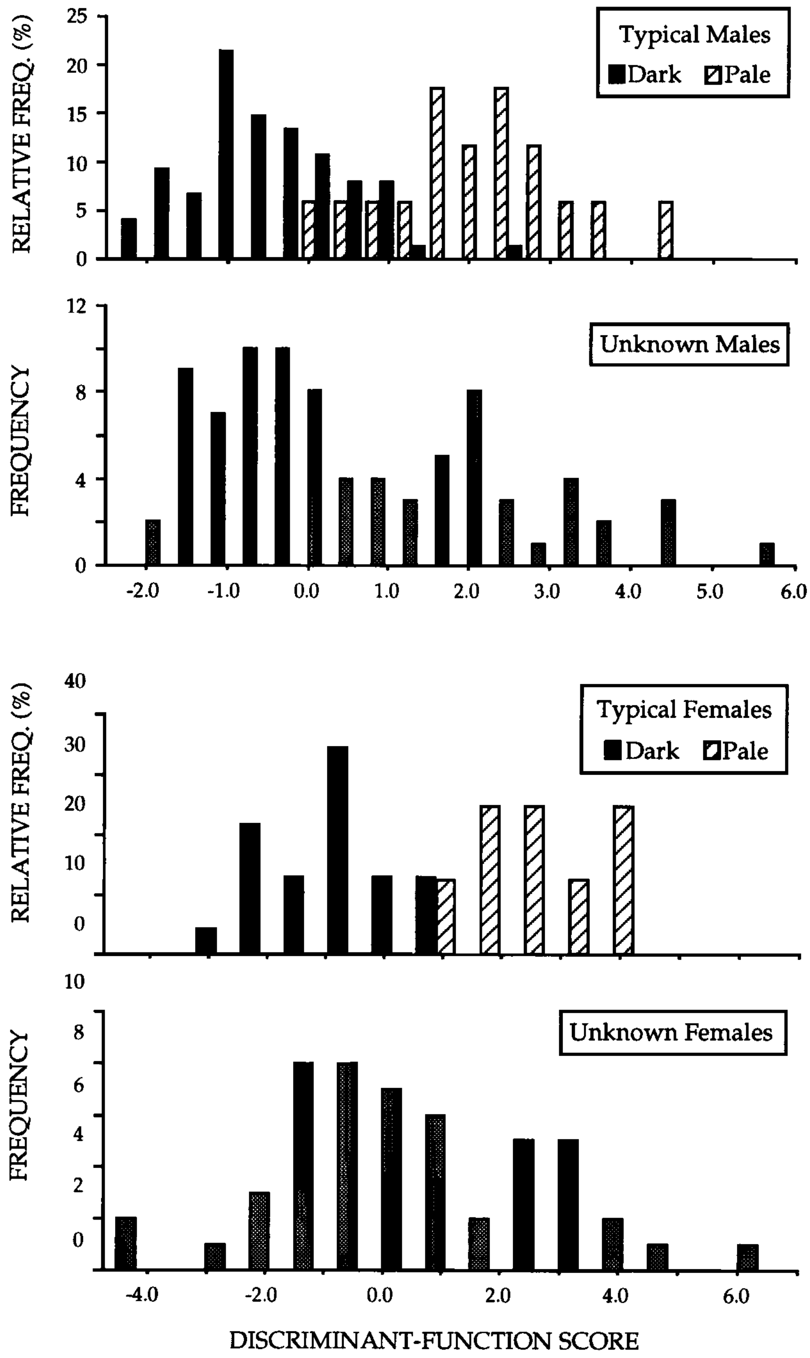

Fig. 2. Distribution of individuals of typical and unknown series along discriminant axes defined by functions presented in Table 4. Independent analysis performed for each sex, and variation related to age and status at measurement handled as explained in text.

lipses for the two plumage types (ellipses that probabilistically comprise 95% of individuals of population represented by sample; based, in present case, on parameters estimated from typical birds only) overlap slightly, but their separation is nevertheless excellent. Several unknown SY males were intermediate in both plumage and morphometry, and discriminant functions based specifically on SY male measurements did not provide a better separation of the forms (results not shown). In females also, the 95% equiprobable population ellipses overlap slightly. There is no obvious trend toward having an abundance of females in an intermediate position between centroids.

Discussion

Our goal was to establish whether the dimorphism in redpoll plumage described by Seutin et al. (1992) and others is paralleled by a dimorphism in morphometry. That question has been investigated previously by several researchers working on the *flammea-exilipes* "complex" (Harris et al. 1965, Molau 1985, Troy 1985, Knox 1988, Herremans 1990). Knox (1988) studied external measurements in specimens collected from very diverse geographic locations and times of the year. He found statistical differences in tail and exposed culmen lengths, but not in wing length. Molau (1985) presented data on wing and culmen lengths for a very large sample of breeding birds from northern Sweden, that support Knox's conclusions, but statistical analyses were not presented. Troy (1985) analyzed skeletal characteristics of Alaskan birds and found that for 19 characters his "typical" male and female samples of the two forms differed statistically in 13 and 15, respectively.

The results of our univariate analyses of external measurements of Churchill redpolls are in agreement with those of Molau (1985) and Knox (1988) for mainly Palearctic birds. In both our male and female samples, pale- and dark-plumaged birds differed significantly in three of the seven characters studied. However, un-

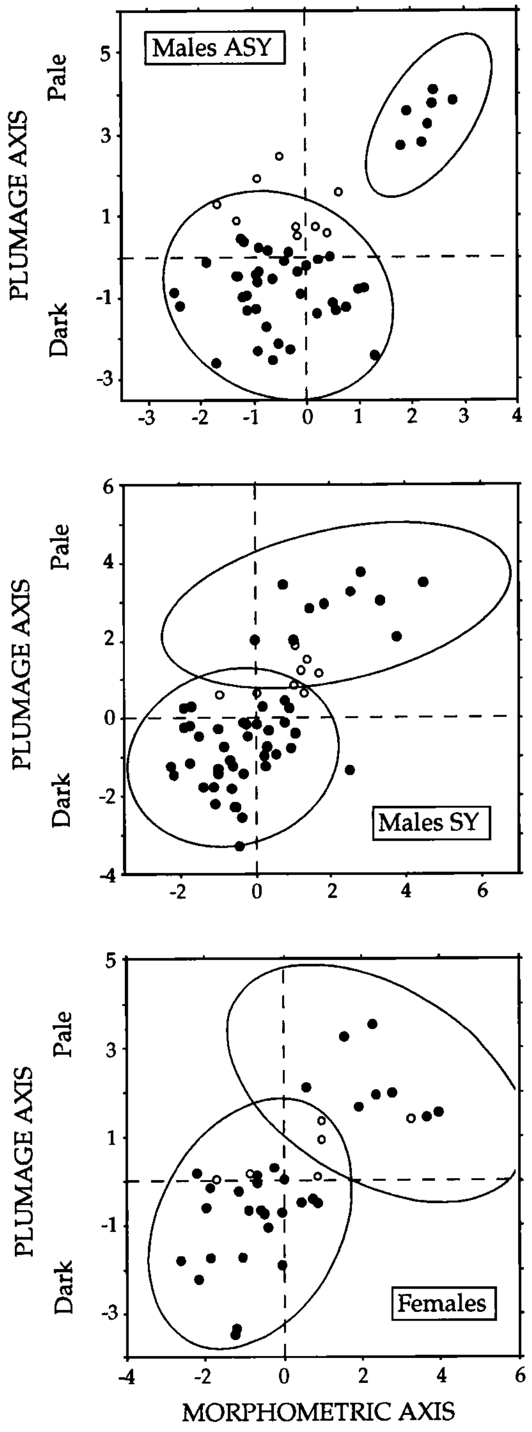

Fig. 3. Distribution of all individuals, for which complete plumage and morphometric data available, in bivariate space defined by discriminant axis in Table 4 (morphometric axis) and first axis of a principal-components analysis of plumage pigmentation characters (Seutin et al. 1992; plumage axis). Ellipses are 95% equiprobable population ellipses for each plumage type. ●, typical individuals; ○, other individuals.

←

like Molau and Knox, who relied on their subjective identification of individuals to be compared, typical samples in our investigation were defined from an analysis of plumage characters alone (Seutin et al. 1992). This lends increased credence to our morphometric conclusions, as the procedure insured the independence of the classification criterion from the variables being analyzed.

We further characterized the morphometric distinctness of redpoll plumage forms in Churchill through discriminant-function analyses, which also allowed us to determine morphometric characteristics of birds with intermediate plumage. Our expectations were that, if a clear morphometric dimorphism exists in Churchill birds that parallels the plumage dimorphism, (1) a mathematical function should be found that allows the proper morphometric identification of a majority of typical birds, and (2) the pattern of morphometric variation seen in typical individuals should be repeated in birds with intermediate and uncharacterized plumage (our unknown series).

Troy (1985) followed similar reasoning in his multivariate analysis of skeletal measurements of Alaskan birds, and suggested that hybridization between redpoll forms would be revealed by an abundance of birds intermediate in both plumage and morphometrics. Troy's (1985: fig. 10) results indicate that a pattern of morphometric bimodality observed for his "pure species" specimens is repeated in birds with intermediate plumage (his "unknown" sample). Troy (1985) recognized this, saying that the distribution of discriminant-function scores for birds with intermediate plumage "was somewhat bimodal" (p. 88), but then he argued that "[the 'unknown'] sample contained *many more* birds with intermediate . . . scores than did the reference samples" (p. 89, emphasis added), and that "the 'unknown' groups (intermediate plumage characteristics) were also intermediate . . . with respect to skeletal characters" (p. 90). A visual inspection of Troy's figure 10 suggests that these statements are not justified. Statistically, the joint distribution of Troy's "pure species" birds and that of his "unknowns" are not different in males ($X^2 = 27.22$, df = 21, $P = 0.164$) or in females ($X^2 = 15.84$, df = 11, $P = 0.147$; classes in Troy's figure 10 were grouped in pairs to provide sufficient numbers of observations in each cell). Further, differences in the frequency of birds with intermediate morphometry in Troy's "pure species" and "unknown" series are minimal, contributing less to the chi-square values than expected by chance (in males, observations in the range of -1.0 to -2.5 contribute to 5.8% of the chi-square value where they would have contributed 13.6% if all cells had equal contribution; in females, observations in the range of -1.0 to -3.0 contributed to 9.4% of the chi-square value instead of 16.7% if all cells had contributed equally). Thus, Troy's results do not indicate that redpolls with intermediate plumage characteristics are also intermediate in morphometrics. In contrast to Troy's (1985) interpretation, we suggest that his results indicate the existence of two relatively distinct redpoll morphotypes in Alaska with only a limited number of intermediates between them.

Herremans (1990), in a multivariate analysis of external morphometric characters in predominantly European redpolls, found that *flammea* and *exilipes* individuals of both sexes can be correctly identified with almost a 95% probability using only four external measurements (maximum wing length, tail length, bill length to feathering, and bill depth at feathering). Some reservations may be raised regarding his study because the criteria for the *a priori* identification of the individuals were not clearly specified, and because Herremans' assessment of the morphometric distinctness of the forms is based on the specimens from which the discriminant functions were produced and, therefore, is probably overestimated (e.g. see Seutin 1991). Notwithstanding these points, Herremans' investigation indicates, as we suggest Troy's (1985) study does, that redpoll plumage forms are morphometrically quite distinct.

Our findings on Churchill birds are similar to those of Herremans (1990). In males and females, we observed a bimodal distribution of individuals along the morphometric discriminant axes, present in the typical specimens from which the functions were established, and in birds with intermediate and uncharacterized plumages (the unknown series; Fig. 2). The pattern of phenotypic polymorphism in Churchill redpolls is most easily seen in a bivariate plot of variation in plumage (first PCA axes of plumage analysis of Seutin et al. 1992) and morphometrics (DFA axes in Table 4). For ASY males, ellipses delimiting the area that statistically comprises 95% of the typical populations of pale and dark birds were clearly distinct (Fig. 3). Under the hypothesis that redpoll plumage types are distinct taxonomic entities (*exilipes* and *flammea*) and that variability in both sets of characters is polygenic and additive, F_1 hybrids should have been easily identified as intermediates between the ellipses. Only one specimen qualified as such (Fig. 3), but it is equally probable that it is one of the few individuals expected normally to fall outside a 95% population ellipse. In any case, the distribution of ASY males in the plumage and morphometric space clearly is not that expected in a situation of massive introgression as has been proposed by several authors (e.g. Salomonsen 1951, Dement'ev and Gladkov 1954, Williamson 1961, Harris et al. 1965, Troy 1985).

In females and SY males, the substantial, although incomplete separation of population ellipses for the plumage types in the bivariate space of plumage and morphometric variability (Fig. 3) also supports the idea that two redpoll phenotypic forms exist in Churchill. However, the lack of a strict separation of the typical birds in the analytical space makes it impossible to qualify intermediates as putative hybrids (under assumptions presented above). Thus, it is possible, but remains to be shown, that some of the specimens falling between the form centroids are hybrids. Still, our data suggest that in females and SY males, as it was the case with older males, redpoll "hybrids" are not abundant, if they exist at all in Churchill.

This conclusion, and those drawn by previous redpoll researchers, are based on the assumption that hybrid redpolls are phenotypically intermediate between the parental forms. If dominance or epistatic interactions between characters were to cause hybrids to look like one parental form, hybridization would be more frequent than we suggested earlier. Such genetic phenomena are unlikely, but to refute their existence will require that the appearance of F_1 and other hybrids is securely established.

A better assessment of heritability and ecophenotypic variability in morphology and plumage in redpolls is needed. Unfortunately, little attention has been given to these questions by previous researchers. Seutin et al. (1992) presented limited data they have obtained from juveniles captured in Churchill during the 1988 breeding season, and kept in captivity under identical conditions until they developed adult plumage and reached adult size. The birds, certainly produced locally, developed typical *flammea* ($n = 2$) or *exilipes* ($n = 7$) characteristics, as judged from their position in the bivariate reduced space of morphological and plumage variability (data not shown). As discussed by Seutin et al. (1992), this and other observations rule out several ecophenotypic hypotheses for the redpoll polymorphism, and suggest that the phenotypic characters we analyzed are largely genetically determined. Our observations are still compatible with several ecophenotypic and genetic hypotheses presented by Seutin et al. (1992). Controlled experimental work (e.g. cross-fostering manipulations and experimental crossings), thus, will be necessary to obtain a better understanding of redpoll phenotypic variability.

Conclusion.—Our analysis of joint variation in plumage and morphometrics of redpolls from Churchill supports the idea that two distinct phenotypic forms exist in mainland North American birds. The forms, which correspond to the usually recognized taxa *flammea* and *exilipes,* differ in several plumage and mensural characters. The existence of some overlap of their phenotypic variability in females and SY males does not constitute a valid argument for considering that they are not distinct biological entities. They may be distinct species, as they are frequently considered (e.g. AOU 1983, Molau 1985, Knox 1988, Herremans 1990), but intraspecific genetic and ecophenotypic mechanisms also could explain the differences (Seutin et al. 1992). An intraspecific scenario is not a likely explanation for a large-scale polymorphism in a bird species, but a definitive conclusion on the taxonomy of redpolls will require that cross-fostering and interbreeding experiments be performed to assess the heritability and environmental variability of redpoll phenotypes. This should be complemented by a careful assessment of mating patterns in the wild.

At the taxonomic level, we suggest that recognition of *flammea* and *exilipes* redpolls as distinct species (e.g. AOU 1983) be maintained. The hypothesis that these phenotypic forms are specifically distinct is as plausible, or more so, than other hypotheses. Furthermore, having the two taxa split will more likely encourage further research on redpoll systematics than if they were lumped. Until evolutionary relationships in the complex are more fully understood, unsubstantiated statements on redpoll taxonomy (e.g. "the frequent hybridization . . . of *C. flammea* and *C. hornemanni*" [in Marten and Johnson 1986:418], and "*Carduelis hornemanni* . . . now regarded as a northern population of the 'Common' Redpoll" [in Peterson 1990:342]) should be avoided.

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