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TAXONOMY AND EVOLUTION IN REDPOLLS

Carduelis flammea-hornemanni;

A MULTIVARIATE STUDY OF THEIR BIOMETRY

MARC HERREMANS

ABSTRACT Multivariate analyses were performed on four standard measurements (wing-chord, tail-length, bill-length and bill-depth) of over 1000 sexed Redpolls, including samples from all currently recognized taxa. Samples of *flammea* and *exilipes*, phenotypically defined by colour were separable biometrically, as were samples of *rostrata* and *hornemanni*. Dark Redpolls from Iceland were almost indistinguishable from *rostrata*, but their average biometry was different from the pale birds breeding on the same island. Furthermore, pale birds from Iceland are different from the allopatric pale taxa *exilipes* and *hornemanni*, though they are closer to *exilipes*. The pale phenotype from Iceland is the most distinct Redpoll on that island, and might deserve a new name; the name *islandica* should be restricted to the dark, *rostrata*-like birds. Current taxonomic arrangements of Redpolls in two polytypic species are rather poorly founded, because most similarities in morphological criteria may be the result of convergent evolution. Mainly based on zoogeographical argument, specific rank could be assigned to *hornemanni*, *exilipes*, *rostrata*, and *flammea*.

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INTRODUCTION

All Redpolls (*Carduelis*, subgenus *Acanthis*, species group *flammea-hornemanni*) are very alike and the radiation of these birds is either recent or very conservative. The taxonomy of Redpolls provokes much debate: some authors have argued to place all Redpolls under a single specific name, *flammea* (e.g. Salomonsen 1951, Troy 1985), but on the other hand, Todd (1963) proposed to split them in four separate species: *hornemanni*, *exilipes*, *rostrata*, and *flammea*. Currently two polytypic species, *flammea* and *hornemanni* are generally recognized (e.g. Voous 1977, Wolters 1979, Knox 1988). Molau (1985) found no signs of hybridization between *C.f.flammea* and *C.h.exilipes* during an extensive field study in Sweden, and Knox (1988) rejected all claims of hybridization between *C.f.flammea* and *C.h.exilipes*, and between *C.f.rostrata* and *C.h.hornemanni* in his excellent review, thus supporting the arrangement of Redpolls in two polytypic species. Although Knox cla-

rified many confusing situations (*exilipes-flammea*, *holboellii*, *rostrata-hornemanni*), he based his conclusions mainly on the study of plumages. Only univariate statistics were used to corroborate the findings also biometrically, which lead in some cases to somewhat weaker biometrical interpretations.

In this paper results of multivariate analyses on four external standard measurements of Redpolls are reported. The conclusions of Molau (1985) and Knox (1988) on the taxonomy of *exilipes* vs. *flammea*, *rostrata* vs. *hornemanni* and *holboellii* are corroborated and extended. The situation in Iceland and the radiation and relationships among Redpoll taxa are discussed.

MATERIALS AND METHODS

Sampling

Measurements of Lesser (*cabaret*) and Mealy Redpolls (*flammea*) were sampled during ringing

activities from birds on passage or wintering in Heverlee, central Belgium (50° 50' N; 4° 40' E) during the years 1976-1986; many Mealy Redpolls, including about 8.5% "*holboellii*"-forms were caught during a huge irruption to western Europe in late autumn 1986. Individuals of *cabaret* originated from Britain, Denmark and the low countries. Specimens representing all taxa were also studied from museum skins during visits to the British Museum (Natural History) (BMNH) at Tring, the Zoologisk Museum (ZMK) at København and the Koninklijk Belgisch Instituut voor Natuurwetenschappen (KBIN) at Brussels. Further specimens were obtained on loan from the American Museum of Natural History (AMNH), New York, the Royal Museum of Scotland (RMS), Edinburgh, the Stavanger Museum (SMN), Stavanger, the Zoologisches Museum der Humboldt Universität (ZMHU), Berlin, and the Icelandic Museum of Natural History (IMNH), Reykjavík. For accuracy, only measurements of specimens with well prepared, closed bills were used. No adjustment was made for the obvious increase in bill-length found during the breeding season in some specimens from the taxa *flammea*, *exilipes*, *cabaret*, *rostrata* and *islandica*. The effect of age, which is generally not significant on the biometry of Redpolls (Knox 1988) was not taken into account when analyzing biometrical data. Mixing of measurements from live birds and skins only causes minor influences on the statistical procedures generating population estimates from samples (see Herremans 1985);

it increases intra-group variation, resulting in smaller statistical discrimination between groups.

For the taxa *rostrata*, *islandica*, and *hornemanni*, only specimens from the breeding areas were used. According to recent views that immature and female *exilipes* generally are quite streaked on the rump and underside (Molau 1985, Knox 1988), birds apparently misidentified as to taxon were stored in a separate group ("unknowns"; 20 in total), and were not included in *flammea* or *exilipes*.

Specimens from Iceland were separated into three plumage classes: birds were considered "pale" when they showed pale overall plumage with whitish rump and underparts, at most moderately stre-

aked in adults; birds were considered "dark" when boldly streaked on partly buffish-brown underparts and boldly streaked on dark, brownish upperparts but lacking the white rump; birds showing combinations of features of both extremes were classified as "indeterminate". Measurements were not used to allocate taxa, though previous workers responsible for the identification on the labels might have done so.

Sexing of live birds was based on plumage characters (see Appendix). Sex of museum skins was taken from the labels. It is possible that up to 10% were erroneously sexed, but this is of little importance to the results reported below. The numbers of specimens used in the analyses are given in Table 1: males were predominant.

Measurements

Four measurements were taken: maximum wing-length, bill-length to feathering, and bill-depth at feathering were sampled according to procedures of Svensson (1984). Tail-length, however, was not measured with a ruler, but by inserting one end of a pair of pointed calipers between the central pair of rectrices, a procedure more easily applied to skins. Live birds were also weighed, but this parameter was only used in the investigation of "*holboellii*". The case of "*holboellii*" has been conclusively reviewed by Molau (1985) and Knox (1988), but this group is discussed in this paper as well, because of the implications it has on the treatment of *flammea* as a group.

Analyses

Principal component analysis (PCA) was performed on the correlation matrix, resulting in variation within the small variables (bill-length and bill-depth) having a similar level of importance as variation in the larger variables (wing and tail). PCA was used to draw a general view of all Redpoll taxa in the plane of most biometrical variation among all individuals. The eigenvalue of a principal component (axis) represents the amount of variation present in the direction of the corresponding eigenvector, itself a calculated linear function of the original variables.

Table 1. Number of Redpoll specimens used in the analyses.

Taxon	Males	Females	Sum
<i>hornemanni</i>	47	42	89
<i>pale islandica</i>	21	5	26
indeterminate <i>islandica</i>	40	23	63
<i>dark islandica</i> "breeding"	14	11	25
"not breeding"	22	20	42
<i>rostrata</i> "breeding"	58	25	83
"not breeding"	43	45	88
<i>exilipes</i>	47	37	84
<i>cabaret</i>	66	34	100
<i>flammea</i>	222	162	384
" <i>holboellii</i> "-form	31	23	54
"unknown" (<i>flammea</i> or <i>exilipes</i>)	7	13	20
Total	618	440	1058

Canonical variate (Canovar) analyses were used to investigate and visualize the maximum biometrical distance between some taxa or subsamples identified a priori on colour. It can also illustrate the position of individuals in the plottings representing the maximal separation of the taxa. When the total eigenvalue of an analysis is < 1 , the samples included in the analysis are accepted to be from only one statistical population. Critical statistics were evaluated by nonparametric tests on the scores of a discriminant function analysis. By this procedure DFA is only used to transform the original measurements into scores that maximize the differences between populations. The implications of required multinormality to perform multivariate statistics are avoided this way (Blackith & Reyment 1971).

PCA and canovar routines were written for PC by Dr. D. Meirte, following methods detailed in Greenstadt (1967), Sokal & Rohlf (1969) and Hebrant (1974).

The plot include sample means, centroids (95% probability predictions of the position of the population mean) and 95% equiprobable ellipses for the position of the whole population.

As a rule of thumb, nearly all individuals of each population can be identified when population ellipses fall apart (at most, 5% of the individuals

are at risk of mis-identification). When centroids fall apart, the means are distinct.

RESULTS

A general over-view of the taxa

Figure 1 illustrates the results of a PCA including all specimens from Table 1. Sexual dimorphism is well marked and significant in all populations, except *rostrata*. It is possible that the variation in the occurrence of red in males of *rostrata* has caused confusion in the past and introduced systematic errors in the sexing indicated on the labels. Several males of *rostrata* lack red on the underside, as mentioned by Knox (1988), but some females do show a considerable amount of red. As a consequence of the relatively more frequent missexing in this taxon, the variation within the sample of each sex may have increased and the differences among the sexes may have been obscured.

Two main isometrical chains can be recognized in Fig. 1, both roughly parallel to sexual dimorphism. In parallel to the general duality in plumage appearance among taxa (pale vs. dark; Knox 1988) there is, however, also a biometrical duality (contra Knox 1988): there is a chain of populations to the left, including *exilipes*, *pale islandica* and *horne-*

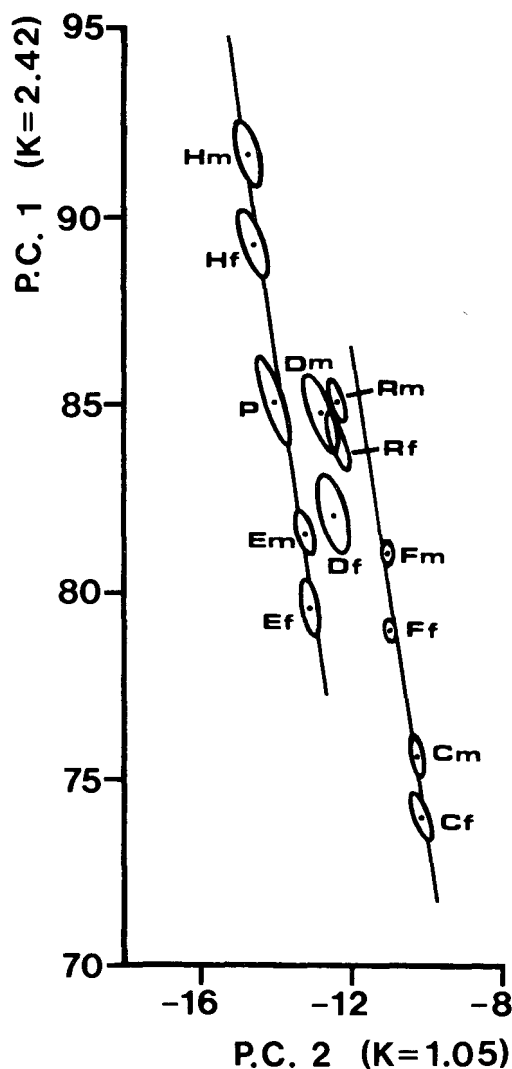


Fig. 1. Plot of principal component analysis on the correlation matrix of 4 measurements (wing, tail, bill-length and -depth) of all Redpoll specimens shown in Table 1. PC1 = 60.6 % and PC2 = 26.3 % of total variation. The right cline is defined by the mean of *cabaret* and *flammea* and the left by the mean of *exilipes* and *hornemanni*. Means (spots) and centroids indicated. Codes: f = females, m = males; C = *cabaret*, F = *flammea*, E = *exilipes*, R = *rostrata*, D = dark "islandica", P = pale "islandica", H = *hornemanni*.

Table 2. Correlations between the original measurements and the first two multivariate axes. A: Principal component analysis on all data (Fig. 1). B: Canonical variate analysis on males and females *exilipes* versus *flammea* (Fig. 2). C: Canonical variate analysis on males and females *rostrata* versus *hornemanni* (Fig. 4). D: Canonical variate analysis on males and females pale versus dark *islandica* (Fig. 6).

		Wing	Tail	Bill	
				length	depth
A.	PC 1	0.90	0.88	0.24	0.88
	PC 2	-0.02	-0.35	0.96	0.10
B.	CV 1	-0.47	0.90	-0.97	0.52
	CV 2	0.88	0.43	0.22	0.84
C.	CV 1	0.97	0.99	-0.83	0.98
	CV 2	0.23	-0.10	0.54	0.18
D.	CV 1	0.37	-0.42	0.95	0.99
	CV 2	0.93	0.90	-0.30	0.12

manni, and a right one, including *cabaret* and *flammea*; *rostrata* and dark *islandica* are in between (Fig. 1). Distinction between the chains of populations comes along the second principal axis, reflecting the allometry of tail-length (coefficient of determination 11.9%), and especially bill-length (coefficient of determination 92.1%). The left chain contains the relatively short-billed, but long-tailed birds, and the right chain consists of longer-billed, shorter-tailed birds, as can be inferred from the correlation between the original variables and the principal component axes (Table 2A). At first sight one could recognize in this figure a corroboration of current Redpoll taxonomy: *cabaret*, *flammea* and *rostrata* in the dark species (*flammea*), and *exilipes* and *hornemanni* in the pale species (*hornemanni*) (as e.g. in Voous 1977, Wolters 1979, Knox 1988). However, the finding of dark *islandica*, currently placed in *flammea*, near the right chain, and pale birds from the same population in the left chain is most intriguing and needs a more detailed analysis. The figure also shows that the

two pairs of sibling taxa (*sensu* Mayr 1963, see also Mayr & Short 1970) have a tendency to be separated by different mechanisms: *rostrata* and *hornemanni* mainly differ in the direction of PC1, representing size, but *flammea* and *exilipes* are segregated by PC2, indicating different proportions.

The “*holboellii*” taxon

In my sample of irruptive Mealy Redpolls from Belgium, several large-billed individuals were found. The frequency distribution of bill-lengths showed an important skewness (1.33 in 232 males and 1.43 in 171 females), resulting in large coefficients of variation (*SD*/*Mean* in males 8.1%, in females 9%). When “*holboellii*” males are defined by bill-length ≥ 10.5 mm and females by bill-length ≥ 10 mm (these limits mainly cut off the extra-symmetrical part from the frequency distribution of this measurement), 40 birds (8.6%) out of a total sample of 467 *flammea* were “*holboellii*”.

However, a canovar analysis on the remaining measurements (wing, tail, bill-depth and weight) did not reveal any distinction between these subsamples (eigenvalue $K = 0.39$; Herremans 1987). “*holboellii*” only represents an extreme skew of the *flammea* population; in the characters examined the effect is mainly restricted to bill-length. For the statistical analyses “*holboellii*” normally should be included in *flammea*. However, the skewness introduced by doing so greatly enhances the variation within *flammea*, resulting in less statistical discrimination and perhaps in weaker results because the multivariate normality conditions won't be met anymore.

The taxa *flammea* and *exilipes*

A canovar analysis (in casu DFA) of only four standard measurements shows samples of *exilipes* and *flammea*, phenotypically defined on colour, also to be biometrically distinct (eigenvalue $K = 2.46$; Fig. 2). Table 2B shows that the short bill and the long tail in particular characterize *exilipes*, as reported by Molau (1985). Sexual dimorphism is a matter of size, especially of wing length and bill depth. For methodological reasons explained

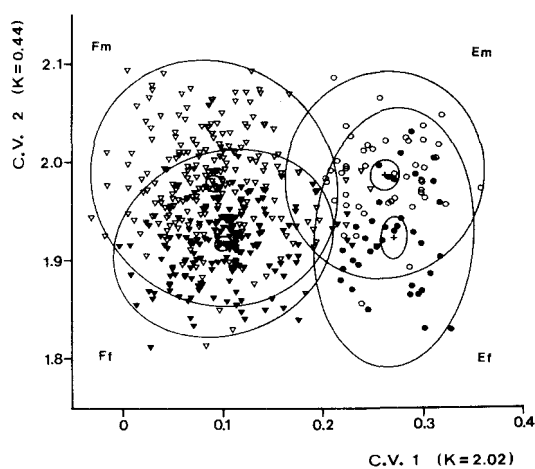


Fig. 2. Plot of canonical variate analysis on wing, tail, bill-length and -depth of *flammea* (excluding “*holboellii*” males (Fm, open triangles, $N = 222$) and females (Ff, dark triangles, $N = 162$) versus *exilipes* males (Em, open circles, $N = 47$) and females (Ef, dark spots, $N = 37$). Sample means (+), centroids and 95% equiprobable population ellipses shown. Total eigenvalue: $K = 2.46$.

above, “*holboellii*” is not included in *flammea* in this analysis. When “*holboellii*” individuals are plotted in Fig. 2, they are mainly situated at the upper left edge of *flammea* and are far separated from *exilipes*: their absence from the analysis does not bias the interpretation of overlap between the taxa (see also Fig. 7).

Biometrical differences agree with colour phenotypes, and I corroborate Molau's and Knox's view that *flammea* and *exilipes* are a pair of sibling species (see also Mayr & Short 1970), for which certain measurements are as useful for identification than most plumage characteristics. Some specimens, however, appear as yet impossible to identify, but multivariate biometrical overlap on these four measurements, as shown, is only about 5%. The samples used are composed of specimens from different seasons, different geographical origin, different preparation, which makes them subject to artificially increased intra-taxon variation, resulting in reduced statistical discrimination. Carefully sexed samples from one season and one area will probably be separable at about 1% level.

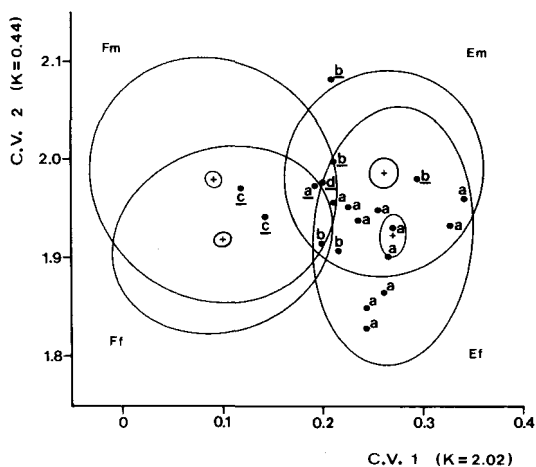


Fig. 3. Plot of the "unknown" *flammea* or *exilipes* specimens in the canovar figure of *flammea* and *exilipes*. a: *flammea* on the label, but re-identified as *exilipes*; b: labelled or suggested as (possible) hybrid, but re-identified as *exilipes*; c: labelled or suggested as (possible) hybrid, but re-identified as *flammea*; d: *exilipes* on the label, but re-identified as probable *flammea*; underlined are males, otherwise females.

In Fig. 2 four specimens of *flammea* are rather distant from their own taxon but are among *exilipes*. Although the plumage of these birds was as far as could be judged from the state of the skin within the range variation of *flammea* (the species indicated on the label), they were in fact more likely *exilipes*. When the specimens which I considered to have the wrong specific identity on the label (based on plumage appearances) are plotted in Fig. 2, they also turn out to be mainly *exilipes* females, although they were originally identified as *flammea* (Fig. 3). This is in agreement with recent views that variability in *exilipes* has been underestimated and that (juvenile) females of *exilipes* in particular can be quite streaked and very *flammea*-like (Molau 1985, Knox 1988).

The taxa *rostrata* and *hornemanni*

Although these two sibling taxa are generally considered less of a taxonomic problem, the overlap is considerable (ca. 35%) in a canovar of only four measurements (Fig. 4). The separation is

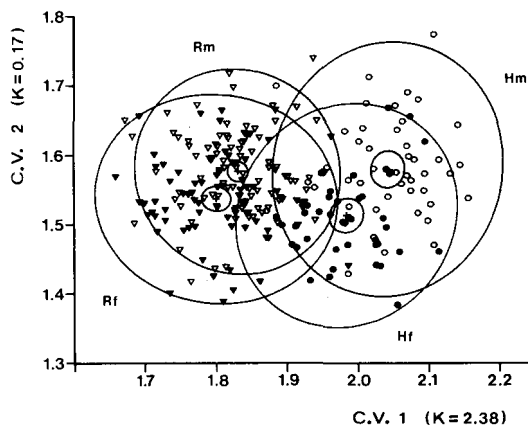


Fig. 4. Plot of canonical variate analysis on wing, tail, bill-length and -depth of *rostrata* males (Rm, open triangles, $N = 101$) and females (Rf, dark triangles, $N = 70$) versus *hornemanni* males (Hm, open circle, $N = 47$) and females (Hf, dark spots, $N = 42$). Sample means (+), centroids and 95% equiprobable population ellipses shown. Total eigenvalue: $K = 2.55$.

mainly based on overall size and on the short bill of *hornemanni*; the relative difference in tail-length is not important to separate these taxa (Table 2C).

The situation in Iceland

Up to now, only one taxon has been admitted as breeding in Iceland, *islandica*, although it has been known for a long time that this includes birds with plumages ranging from very dark to very pale. On plumage, dark birds breeding in Iceland appear almost indistinguishable from *rostrata* (Knox 1988). Some pale breeding birds are very white and almost indistinguishable from the palest *hornemanni* or *exilipes* (Knox 1988), but most are considerably more streaked, rather like darker individuals of *exilipes*. Many of my "indeterminate" specimens are more greyish on the back than dark birds or *rostrata* and they are also slightly less boldly streaked, looking more like *flammea*. It was generally easier to classify birds as dark than to decide between pale or indeterminate, even when the effect of age on plumages could be taken into consideration. The biometrical affinities of dark *islandica* to *rostrata* and *flammea* were investigated.

To avoid specimens of *rostrata* (possibly wintering on Iceland) being included in dark *islandica*, the canovar analysis was performed on samples which were also split by season: specimens collected from May to August were considered as “breeding birds” and those from September to April as “wintering birds”. Samples of “breeding” and “wintering” birds did not significantly differ for dark *islandica* or for *rostrata* (Fig. 5). Although some other sample means are distinct at 5% level (e.g. Dfb vs. Rfb and Df vs. Rf), canovar shows that all these 8 predicted populations of dark specimens could belong to one statistical population (Fig. 5, total eigenvalue $K = 0.77$). It can also be seen that differences between origins are smaller than between sexes. DFA on the males, the most critical groups because they contain mainly correctly sexed birds, shows no separation between

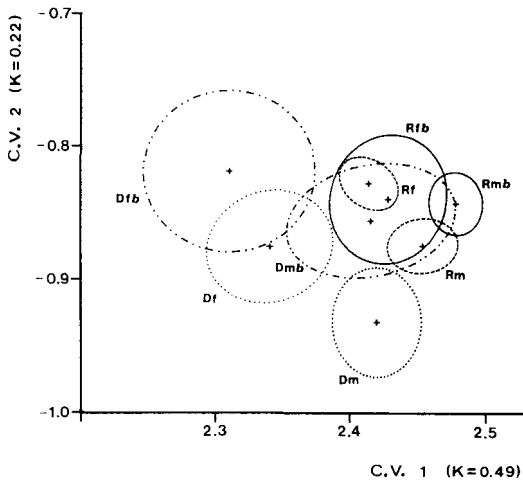


Fig. 5. Plot of canonical variate analysis on wing, tail, bill-length and -depth of dark *islandica* versus *rostrata*: Dfb = dark *islandica* females breeding season, $N = 11$; Dmb = dark *islandica* males breeding season, $N = 14$; Df = dark *islandica* females outside breeding season, $N = 20$; Dm = dark *islandica* males outside breeding season, $N = 22$; Rfb = *rostrata* females breeding season, $N = 25$; Rmb = *rostrata* males breeding season, $N = 58$; Rf = *rostrata* females outside breeding season, $N = 45$; Rm = *rostrata* males outside breeding season, $N = 43$; Only sample means (+) and centroids shown. Total eigenvalue: $K = 0.77$.

the populations predicted from the samples ($K = 0.21$), yet the sample medians of DFA scores are clearly distinct (Mann-Whitney-U test $Z = 4.8$, $P < 0.00001$). The population of dark *islandica* is as far as these 4 standard measurements are concerned not separable from *rostrata*, but it may be more distinct on criteria not included here. However, dark *islandica* can clearly be separated from *flammea* (eigenvalue $K = 2.23$, figure not shown).

Separation between populations predicted for pale and dark birds from Iceland is marginal (Fig. 6), but sample medians of DFA scores are highly significantly different between pale and dark males (Mann-Whitney-U test $Z = 5.9$, $P < 0.000001$). The separation is mainly based on the smaller bill and the somewhat longer tail of the pale birds (Table 2D). Sexual dimorphism is smaller than the difference between the pale and dark forms. When indeterminate birds are plotted in the canovar of pale and dark forms, they associate with the pale rather than with the dark birds (Fig. 6), from which their median scores of separate DFAS are also more dis-

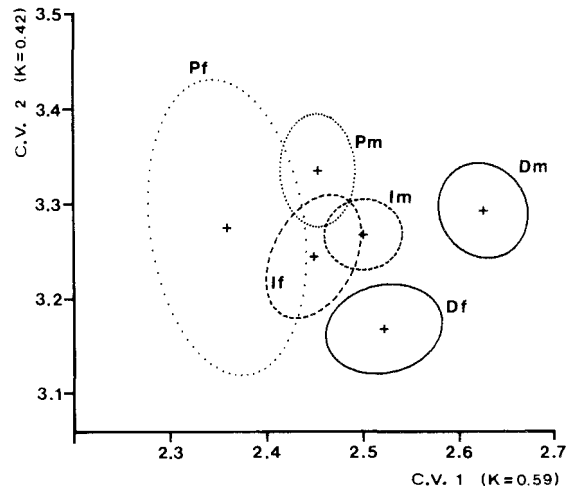


Fig. 6. Plot of canonical variate analysis on wing, tail, bill-length and -depth of dark males (Dm, $N = 36$) and females (Df, $N = 31$) (full line) versus pale males (Pm, $N = 21$) and females (Pf, $N = 5$) (dotted) from Iceland. Indeterminate males (Im, $N = 40$) and females (If, $N = 23$) afterwards plotted (dashed) following the canovar functions of pale versus dark. Only sample means (+) and centroids shown. Total eigenvalue: $K = 1.01$.

tinct. This agrees with the remark above that it was more difficult to assign a specimen as pale or indeterminate rather than as dark: the indeterminate group presumably contains many first year pale birds which are more streaked, and some old, paler, genetically dark birds. Although the sample size of pale females is very low for a multivariate analysis, it is obvious from the neat position of the population predicted from this sample (Fig. 6) that this group did not distort the analysis.

Furthermore, at population level, pale birds from Iceland are biometrically more distinct from *flammea* than *exilipes* is (Fig. 7).

On plumage, several pale birds from Iceland are similar to *exilipes*, some are even as bright as *hornemanni*, and the question arises if they do not merely belong in one of these taxa. A canovar analysis on all pale birds shows a chain of three populations with highly different means (Fig. 8, $K = 5.8$). Scores of separate DFAS are highly significantly different between pairs of samples with sufficient data (males): *exilipes* versus pale *islandica* (Mann-Whitney-U test $Z = 5.9$, $P < 0.000001$) and pale *islandica* versus *hornemanni* (Mann-Whitney-U test $Z = 6.4$, $P < 0.000001$). However, con-

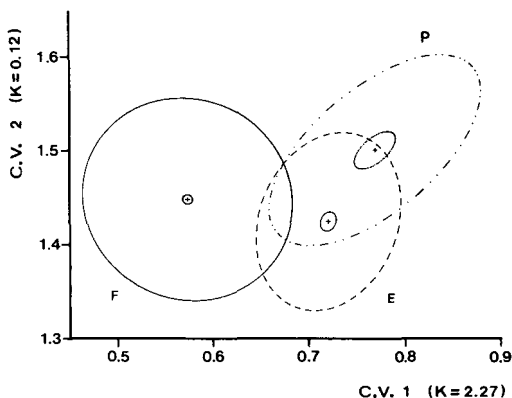


Fig. 7. Plot of canonical variate analysis on wing, tail, bill-length and -depth of *flammea* (including “*holboellii*”, F, full line, $N = 438$), *exilipes* (E, dashed, $N = 84$) and pale *islandica* (P, dotted & dashed, $N = 26$). Sample means (+), centroids and 95% equiprobable ellipses shown. Total eigenvalue: $K = 2.39$.

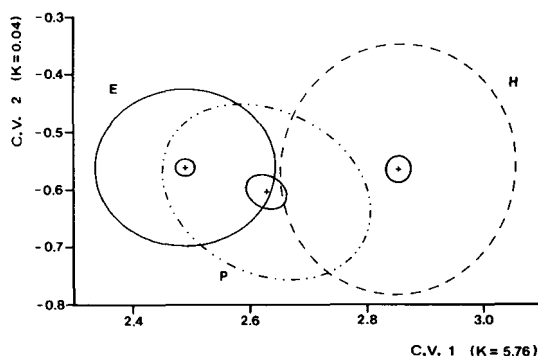


Fig. 8. Plot of canonical variate analysis on wing, tail, bill-length and -depth of the three pale taxa: *exilipes* (E, full line, $N = 84$), pale *islandica* (P, dotted & dashed, $N = 26$) and *hornemanni* (H, dashed, $N = 89$). Sample means (+), centroids and 95% equiprobable ellipses shown. Total eigenvalue: $K = 5.80$.

siderable overlap exists at population level and many individuals cannot be separated biometrically.

DISCUSSION

Taxonomic implications

The results concerning “*holboellii*” and the sibling pairs *flammea/exilipes* and *rostrata/hornemanni* are in agreement with Molau’s (1985) and Knox’s (1988) recent conclusions. Knox also showed these conclusions were not in conflict with earlier work on Redpolls, although some of the earlier data had to be reinterpreted. The overlap in biometry reported here between *flammea* and *exilipes* (ca.5%) is very similar to that reported by Troy (1985), based on skeletal measurements, between his samples of “pure” *flammea* and *exilipes*.

Vaurie (1956, 1957) questioned the distinction of *islandica*, after apparently only examining dark birds. He noted a small, yet inconsistent difference from *rostrata*. For the occurrence in so small a population as is only found in part of Iceland of a variety of plumage phenotypes the extremes of which are elsewhere only seen among species three possible conclusions may be suggested: (1) two spe-

cies occur in Iceland; (2) the Iceland population represents a hybrid swarm between dark *rostrata* and pale *hornemanni* (Salomonsen's (1951) suggestion, see also Wolters 1979); (3) the isolated population has been subject to considerable character release resulting in unusual variation.

Let us first examine the last possibility. Based on the significant difference in tail-length, Knox (1988) concluded that the dark and pale birds in Iceland did not simply represent colour-morphs, and this also rules out character release. The same conclusions follow from Fig. 6: average biometry is different between pale and dark birds. The linkage of plumage phenotypes (possibly under the control of major genes) and differences in average biometry (likely controlled by a number of additive effects) in Icelandic Redpolls makes the possibility of a hybrid swarm less likely, unless incomplete introgression and assortative mating occur. However, in the White-throated Sparrow *Zonotrichia albicollis*, a species which genetics are far better understood than those of Redpolls, the two plumage morphs are documented to differ also in several body measurements (Rising & Schields 1980), among other characters. Comprehensive genetic research of Icelandic Redpolls will help to clarify the genetic basis of this most confusing situation and it may reveal the rate of gene flow, if any. The presence of indeterminate birds in my classification mainly results from an oversimplification by defining dark and pale birds as rigid categories. If such rigid colour descriptions are to be applied to plumages in different seasons and to birds of different age categories, it is clear that many specimens do not match either dark or pale and will be classified as indeterminate. The situation resembles the traditional thinking about *flammea* and *exilipes*, which is now believed to be incorrect. Oversimplified definitions by typical plumages and underestimation of the real intraspecific variability, e.g. due to sex and age (Molau 1985), had lead to suggestions of hybridization. Fig. 5 of Knox applies also to the Iceland situation. That I only found 5 pale females in Iceland is reminiscent of the situation constructed by Troy (1985) for the Nearctic, where he only found two females of *exi-*

lipes in a sample selected on paleness of the plumage. Knox (1988) pointed out that the Troy-paradox forms a general model, explained by two separate populations with overlap of characters between some age and sex classes. It can be concluded that the Iceland population most likely consists of birds which genetically belong either to the pale or to the dark form. Knox's own observations that most birds could "easily be assigned to either the light or the dark form" during the breeding season is most significant (Knox 1988).

The population in Iceland seems to consist on the one hand of birds very similar to *rostrata* (dark *islandica*) and on the other hand of *exilipes*-like birds, ranging between rather heavily streaked phenotypes (very *flammea*-like; indeterminate here) and very pale phenotypes (pale *islandica*) much like "true" *exilipes* or *hornemanni*. Phenotypically, several museum specimens are impossible to allocate: the situation is especially complex due to the effect of age and of the seasonal changes in plumages which are greater than the inter-taxa differences. It can, however, not be excluded that some birds are true hybrids. My interpretation is that in Iceland an *exilipes*-like pale taxon has been subject to character release in its evolution towards an endemic form before it came more recently into contact with the second invader *rostrata*. If a hybrid swarm has then started to develop cannot be concluded at this stage of knowledge.

The question now arises to which bird the original name *islandica* was given. Unfortunately, in his original description of *islandica*, Hantzsch (1904) did not indicate a holotype, but used a sample of ten birds. I was able to relocate only 3 specimens of Hantzsch's original series (the n^os VII, VIII and X in his publication, now in ZMHU, Berlin). Although Hantzsch stated that all ten constituted a homogeneous series, in my classification VII and X are dark forms, but, as far as can be judged from its present state, VIII rather seems indeterminate. According to Hantzsch VII and VIII were breeding mates. However, Hantzsch most surprisingly mentions a pale rump ("bürzel weisslich"), which hardly fits dark forms, and he distinguishes between paler and darker birds ("hel-

leren" and "dunkleren Exemplaren"). It is possible and likely that his description applies to a heterogeneous series. Consequently, the name *islandica* could be considered as indeterminate. However, to conserve stability in nomenclature,

I advocate the use of *islandica* Hantzsch for the dark *rostrata*-like Iceland form and I restrict its use thereto. In doing so it is desirable to choose a lectotype and I designate his N° VII = n° 79.107 in ZMHU, Berlin. This specimen was collected by Hantzsch on 18 July 1903 north of Reykjalid, Myvatn (Hantzsch's spelling).

In Iceland there is therefore an apparently discontinuous population of dark forms very near to *rostrata* (true *islandica*) and paler forms most of which are like dark individuals of *exilipes*, although some are as bright as *hornemanni*. Biometrically, the paler birds on Iceland can hardly be the result of introgression following hybridization between any dark and pale taxon (Fig. 1). Unless strong assumptions are made concerning founder effects, the pale birds from Iceland constitute a separate entity in the chain of pale taxa, in between *exilipes* and *hornemanni* (Figs. 1 and 8). If there is a population of clearly distinct Redpolls in Iceland, it comprises the pale birds. Whatever the state of hybridization or introgression may be, there is evidence for the existence of an endemic pale taxon in Iceland. If gene flow between the two populations can be shown to be reduced, the pale birds should be given a new name.

On measurements and plumages the two populations in Iceland are very close to each other and are even closer than the dark and pale birds are in the other two species pairs. Further research may reveal criteria which could better separate them and suggest if etho-ecological or other mechanisms actually isolate them. It is possible that they are micro-geographically isolated by habitat as in *exilipes* vs. *flammea* (Molau 1985, though see also Nyström & Nyström 1987). In the few other cases in the world where two very similar taxa occur on a small island (or in restricted areas of larger islands), a (micro)-geographical segregation, enhanced by habitat and/or altitudinal preferences is apparent. On two of the Comoro Islands there is

a pair of parapatric bulbul species *Hypsipetes* segregated by altitude and habitat (Louette & Herremans 1985). The two endemic Jamaican hummingbird species *Trochilus* are allopatric, but also show differences in abundance according to altitude and habitat (Schuchmann 1978). Two species of brush warblers *Nesillas* on the small island of Moheli have slightly different altitudinal preferences, but mainly differ in niche (Louette et al. 1988). The situation of the Mascarene White-eyes *Zosterops borbonica* on Réunion Island seems more complex, but a segregation of phenotypes according to altitude and/or habitat is also apparent (Gill 1973).

Radiation and relationships among Redpolls

General The two roughly isometric groups in Fig. 1, which correspond with the dualism in general colour appearances seem to support the taxonomic view of two polytypic species. However, similarity in general paleness is a poor criterion to use for taxonomical conclusions in Redpolls. All Redpolls are so much alike in general colour pattern, that any isolated populations evolving pale plumage would become very similar. Paleness is a feature that is expressed in all populations in a parallel way: it always consists of more whitish parts in the plumage (especially rump, underside, nape and wing markings) and less heavy streaking, especially on the paler parts. Even within taxa, pale individuals cause confusion: pale specimens of *cabaret* very much resemble *flammea* (see e.g. the discussion about the origin of the pale New Zealand *cabaret* specimens: Stenhouse 1962 versus Fennell et al. 1985), and pale *flammea* is very difficult to distinguish from *exilipes* (see Troy 1985 versus Molau 1985 and Knox 1988). Furthermore, only the pale and less streaked specimens of *exilipes* resemble *hornemanni*, while others are more *flammea*-like.

The biometrical duality shown in Fig. 1 does not constitute a strong taxonomic basis either. It could merely represent ecological convergence: shorter-tailed, longer-billed birds that live in trees (*cabaret* and *flammea*) are in the right chain, and birds that adapted to more open, windy country show longer tails and shorter bills (possibly also

related to more ground feeding) and constitute the left chain. The darkest Redpoll, *rostrata*, living in the relatively open arctic, also tends towards the left chain. In fact, within the subgenus *Acanthis*, the Twite *Carduelis flavirostris*, which is also adapted to open, nearly treeless country, has a very short bill and a very long tail, representing a similar convergent evolution. The development of pale plumage in the open country taxa situated on the left chain is likely to be a co-adaptation to arctic conditions, simply following Gloger's rule, and not necessarily indicating close genetic relationship. The adaptation of pale plumaged taxa to more arctic conditions is also shown by their convergent fluffiness, resulting in better insulation and therefore broader temperature tolerance (Brooks 1968).

On bill morphology, *rostrata* and *hornemanni* from Greenland are distinct from all other Redpolls. Besides being the possible result of a split of the same old tribe in refugia in the extreme north-western Palearctic (e.g. Peary vs. coastal Greenland; Salomonsen 1970) this may also be the result of an obligate convergent adaptation to meet special feeding conditions on Greenland, and so would mask earlier morphological differences.

No morphological criteria yet investigated seem to be useful to build a strong taxonomy in the Redpolls.

Zoogeography Redpolls either radiated from a common ancestor during only one step of geographical isolation, or they are the result of a multiple step radiation. If all recent Redpoll taxa are the result of isolation during the last glacial period (Würm-Wisconsin) only, they must all be of about the same age. Consequently, they could all have acquired an equivalent taxonomic position: e.g. if the split between *cabaret*, *flammea* and *exilipes* dates from that period, *cabaret* may well be specifically distinct from those siblings. It also implies that the palest Redpoll (*hornemanni*) and the darkest one (*rostrata*) should have radiated from a common ancestor in only one step, both under arctic conditions. However, according to Marten & Johnson (1986) the Würm-Wisconsin glacial period would be much too recent an event to account for

the genetic distance found between *flammea* and *exilipes*. Redpolls more likely radiated in more than one step.

The actual distribution of *flammea* and *exilipes* appears to represent a rapid and successful spread through the contemporary interglacial boreal-arctic zone. Their long-distance migratory movements often show an east-west component (Troy 1983, Holgersen 1982, Runde 1984, 1985, 1987). This may represent a recapitulation of the colonization direction. Although I have not studied this aspect in detail, it seems as if over their huge range, both *flammea* and *exilipes* show no clear geographical differentiation, pointing to the rather recent history of this distribution and/or to extreme gene-flow. Because of similarities in colour and biometry and because these apparently show so little variation over the huge breeding ranges, *flammea* and *exilipes* could be regarded as the most recent sibling pair of Redpolls, separated only from the last glacial period onwards. However, some biochemical evidence indicates that separation of *flammea* and *exilipes* could be about 550 000 years old (Marten & Johnson 1986). Even if this date is only approximately correct, the two taxa must have been separated during an earlier glaciation. It is, however, very unlikely that *flammea* and *exilipes* have been as successful during previous interglacial periods as they are now, because if they have had huge ranges extending over the holarctic at such period, they should at least have radiated into polytypic species during the subsequent glaciation. The two taxa breeding on Greenland, *hornemanni* and *rostrata*, could indeed be considered as the result of such, and consequently they may have evolved from *exilipes* and *flammea*, respectively, during the last glaciation. The distinctiveness of the Greenland birds from their ancestors could be the result of enhanced evolution, not unlikely when very limited populations have been subjected to strong adaptive selection under peculiar insular conditions. The resemblance in bill morphology between *hornemanni* and *rostrata* could be the result of convergent adaptive selection to meet special feeding conditions in Greenland. The striking differences in colour and size could be interpreted as character

displacement, which in itself could be a proof of specific status for *rostrata* versus *hornemanni*. However, the colour resemblance of *rostrata* to *cabaret* is striking: both are very dark, heavily streaked, the dark brownish hue is especially distinctive. The occurrence of the much darker *rostrata* more to the north of *flammea* is strange, because it is in disagreement with the ecogeographical rule of Gloger, otherwise valid among Redpolls. It is possible that *flammea* was already differentiated before the last glacial period in a dark, westerly proto-*cabaret* and a paler, easterly proto-*flammea*. *rostrata* could have originated from the dark proto-*cabaret*, occurring in the western palearctic. The overall parallel in biometrical evolution is remarkable if one accepts that *hornemanni* evolved from a proto-*flammea*/*exilipes* ancestor, and *rostrata* from proto-*cabaret* (see Fig. 1). No character displacement would then be necessary to account for the present phenotypes. In view of the rapid and for Redpolls rather dramatic changes that *hornemanni* and *rostrata* went through, they can be argued to have reached specific status.

islandica is possibly merely a synonym of *rostrata* and the tendency for a smaller bill and paler plumage can be seen as the result of (present or ancient) partial introgression from pale birds. If no introgression was involved, *islandica* would be a poorly differentiated population of *rostrata* that became settled on Iceland only after the last glaciation. Pale birds from Iceland show affinities to *exilipes* and *hornemanni*, but seem closer to *exilipes*, from which taxon they may have evolved during the last glaciation. Their more striped plumage could be interpreted as an introgression from *rostrata*/*islandica*, but biometrically they are obviously in the chain of pale taxa. Intuitively one may expect pale birds from Iceland to be more closely related to geographically close *hornemanni* from Greenland. However, the zoogeographical picture in other landbirds in the northwestern Palearctic is not very consistent and helpful in clarifying the most likely affinities of the pale birds in Iceland. In the Lappland bunting *Calcarius lapponicus* European and Greenland birds are in the same subspecies, and the same holds for the Snow

bunting *Plectrophenax nivalis*, but here Iceland has an endemic subspecies. The resident Ptarmigan *Lagopus mutus* has been split in several more subspecies:

one each in Spitsbergen, Iceland, Scandinavia, eastern, western and northwestern Greenland, among other regions. A zoogeographical similarity is found between the Redpolls and the Bean/Pink-footed Goose complex: in the geese, there is a distinct species *Anser brachyrhynchus* in the extreme northwestern palearctic (Greenland, Iceland, Spitsbergen) and there are two paraspecies in Scandinavia and adjacent USSR (*fabalis/rossicus*), but further differentiation also occurred farther to the east. Differentiation within *exilipes* or *flammea* is possibly still to be discovered, and the affinities should be studied also in the other pale Redpolls apparently existing on islands in the extreme northwestern Palearctic (e.g. Spitsbergen, Jan Mayen). The existence there of *hornemanni*-like birds has been mentioned repeatedly (Fischer & von Pelzeln 1886, Ridgway 1901, Hartert 1903, Nathorst 1915, Van Franeker et al. 1986). It cannot be ruled out that some may constitute permanent populations and could be endemic offshoots close to *exilipes* or *hornemanni*.

The present distribution of *cabaret* in Europe is that of a postglacial alpine relict, which probably only recently colonized England and some of the nearby coastal areas. In my opinion its habit of returning to the continent on migration seems a recapitulation of the colonization route from the glacial refugium in Europe, rather than the opposite. Knox (1988) and Ernst (1988), on the contrary, argue that the Alps might have been colonized from Britain. If *cabaret* is older than the last glaciation, as suggested above to account for its apparent affinities to *rostrata*, a careful study of all isolated (alpine) populations of *cabaret* possibly may show differences among them. The relationship of *cabaret* to *flammea* is close, but unclear. The recent expansion of the former in southern Scandinavia may lead to contact with the latter. In view of differences in some of the vocalizations (Herremans 1989), the social interaction of these populations may be limited, and probably also the gene flow in

this future area of sympatry. Such could support the view that *cabaret* split off from *flammea* already before the last glaciation.

Although there is as yet no objective basis to measure Redpoll affinities, the following taxonomic arrangement of the Redpolls is proposed, mainly in the light of zoogeographical argument:

- Carduelis (h.) hornemanni*
Carduelis (h.) exilipes
Carduelis (h.) ssp. (pale Icelandic)
Carduelis (f.) rostrata (incl. *islandica*)
Carduelis flammea flammea
Carduelis flammea cabaret

Because most morphological criteria seem to constitute only poor evidence of the affinities in this complex group, field studies of etho-eco-phenological segregation may be of more interest in future. Detailed studies by biochemical techniques are also urgently needed: comprehensive knowledge of genetic distances seem of particular interest to quantify the affinities within this group, which apparently is phenotypically very conservative.

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SAMENVATTING

Barmsijzen werden taxonomisch onderzocht door de vleugellengte, staartlengte, snavellengte en snavelhoogte van meer dan 1000 gesexede individuen nauwkeurig te meten. Alle erkende taxa waren vertegenwoordigd. De meetresultaten werden met technieken uit de multivariate statistiek (Principale componenten analyse en Canonische analyse) verwerkt. Grote Barmsijzen (*flammea*) en Kleine Witstuitbarmsijzen (*exilipes*) die fenotypisch op kleur waren gedetermineerd konden ook biometrisch gescheiden worden; hetzelfde gold voor de 2 Groenlandse taxa (*rostrata* en *hornemanni*). Vogels die voldeden aan de criteria van Langsnavelbarmsijzen ("holboellii") waren zo goed als identiek met *flammea*: zij vertegenwoordigen blijkbaar slechts een extreme scheefheid van de snavellengte-frequentieverdeling bij *flammea*. Het donkere type barmsijzen van IJsland is nauwelijks te onderscheiden van de op Groenland voorkomende vorm *rostrata*, maar gemiddeld zijn ze zowel biometrisch als wat het verkleed betreft verschillend van het bleke type dat op IJsland broedt. Bovendien zijn de bleke barmsijzen van IJsland biometrisch verschillend van de twee andere, allopatrische taxa met bleke barmsijzen (*exilipes* en *hornemanni*), maar ze staan het dichtst bij *exilipes*. Bij de originele beschrijving van *islandica* werd er geen holotype aangeduid en de gebruikte serie vogels was mogelijk heterogeen. Omdat wellicht de donkere vorm bedoeld werd, wensen we voortaan de naam *islandica* tot deze vogels te beperken. Ze lijken sterk op *rostrata*; een lectotype voor *islandica* werd aangewezen. Van de beide vormen die op IJsland voorkomen zijn het de bleke vogels die het meest van alle andere barmsijzen verschillen: mogelijks verdienen ze een aparte, nieuwe naam.

De gebruikelijke taxonomische opsplitsing van de barmsijzen in twee polytypische soorten heeft een labiele onderbouw, omdat het verschil of de overeenkomst in morfologische criteria het gevolg kan zijn van convergente ontwikkelingen in de evolutie. Vooral op basis van zoögeografische argumenten kan de status soort worden toegekend aan *hornemanni*, *exilipes*, *rostrata* en *flammea*.

APPENDIX

Sexing

taxon cabaret: In this taxon adults showing no pink (except at poll) or at most some pinkish spottings in the cheeks and eventually also vaguely on the breast were considered females. In juveniles, females included birds without pink and with at most some brownish-pink spots in the cheeks. All birds with extensive pink on the cheeks and breast were considered males. Juveniles with pink cheeks and clearly pinkish spots on the breast were also ascertained as males.

taxon flammea: Females of this taxon have much more frequently and extensive pink in the plumage: only birds with extensive pink on cheeks and underside were considered males. Females include juveniles without pink on the underside, but also with at most some pinkish spots in the cheeks, and adults without pink or with at most some pink spots on cheeks, rump or underside. Several birds did not fit in these categories and were not sexed.

Descriptive statistics:

Taxon	Sex	N	Weight			
			Mean	SD	CV(%)	Range
<i>flammea</i>	M	181	13.3	0.96	7.2	11.0-16.0
	F	141	12.5	0.80	6.4	10.3-14.5
"holboellii"-form	M	18	14.9	1.05	7.1	13.0-16.8
	F	15	13.5	0.88	6.5	12.0-15.3

Taxon	Sex	N	Wing length			
			Mean	SD	CV(%)	Range
<i>hornemanni</i>	M	47	85.5	2.43	2.8	81.0-92.0
	F	42	82.7	2.13	2.6	79.5-88.5
<i>pale islandica</i>	M	21	79.2	1.90	2.4	76.5-84.5
	F	5	77.4	1.82	2.4	75.0-80.0
indeterminate <i>islandica</i>	M	40	78.2	1.93	2.5	72.5-82.5
	F	23	77.5	2.44	3.2	74.0-81.5
dark <i>islandica</i> "breeding"	M	14	78.6	2.54	3.2	75.0-83.0
	F	11	75.5	2.19	2.9	72.0-78.5
dark <i>islandica</i> "not breeding"	M	22	80.1	1.97	2.5	77.0-84.0
	F	20	77.1	2.08	2.7	73.5-81.0
<i>rostrata</i> "breeding"	M	58	80.3	1.96	2.4	74.0-86.0
	F	25	78.8	2.65	3.4	75.0-85.0
<i>rostrata</i> "not breeding"	M	43	80.3	2.00	2.5	75.5-86.0
	F	45	78.7	2.12	2.7	73.5-83.0
<i>exilipes</i>	M	47	76.3	1.72	2.3	72.0-81.0
	F	37	73.6	1.99	2.7	70.5-78.0
<i>cabaret</i>	M	66	71.1	1.92	3.1	67.0-75.0
	F	34	69.4	1.58	2.3	67.0-74.5
<i>flammea</i>	M	222	77.6	2.18	2.8	70.5-82.5
	F	162	75.2	1.75	2.3	70.5-80.0
"holboellii"-form	M	31	79.2	2.55	3.2	74.0-83.5
	F	23	76.5	1.03	1.4	75.0-78.5

Taxon	Sex	N	Tail length			
			Mean	SD	CV(%)	Range
<i>hornemanni</i>	M	47	65.5	2.44	3.7	59.5-70.0
	F	42	64.4	2.69	4.2	58.0-69.5
<i>pale islandica</i>	M	21	61.5	2.15	3.5	57.5-66.5
	F	5	61.0	2.70	4.4	58.5-65.0
indeterminate <i>islandica</i>	M	40	60.2	2.53	4.2	54.5-65.0
	F	23	60.8	2.72	4.5	54.0-65.5
dark <i>islandica</i> "breeding"	M	14	58.4	2.68	4.6	55.5-63.5
	F	11	57.6	1.98	3.4	54.5-60.5
dark <i>islandica</i> "not breeding"	M	22	60.4	2.19	3.6	57.5-65.5
	F	20	58.5	2.44	4.2	54.5-63.0
<i>rostrata</i> "breeding"	M	58	59.2	2.74	4.6	53.0-66.5
	F	25	59.0	2.75	4.7	54.5-66.0
<i>rostrata</i> "not breeding"	M	43	59.5	2.83	4.7	52.5-65.0
	F	45	59.2	2.71	4.6	52.0-64.5
<i>exilipes</i>	M	47	58.1	1.67	2.9	54.0-61.5
	F	37	57.4	1.60	2.8	53.5-60.5
<i>cabaret</i>	M	66	52.3	1.59	3.0	48.0-56.0
	F	34	51.5	1.56	3.0	47.5-54.5
<i>flammea</i>	M	222	55.2	2.04	3.7	49.0-60.5
	F	162	54.2	1.89	3.5	49.0-59.5
"holboellii"-form	M	31	55.4	1.86	3.4	53.5-61.0
	F	23	56.7	1.40	2.5	54.0-60.0

Taxon	Sex	N	Bill-length			
			Mean	SD	CV(%)	Range
<i>hornemanni</i>	M	47	8.94	0.58	6.5	7.8-10.6
	F	42	8.67	0.52	6.1	7.7-10.0
<i>pale islandica</i>	M	21	8.24	0.37	4.5	7.7- 9.3
	F	5	7.92	0.13	1.7	7.7- 8.0
indeterminate <i>islandica</i>	M	40	8.51	0.43	5.1	7.4- 9.3
	F	23	8.40	0.65	7.8	7.9- 9.1
dark <i>islandica</i> "breeding"	M	14	9.13	0.54	5.9	8.2- 9.9
	F	11	8.78	0.50	5.7	8.0- 9.4
dark <i>islandica</i> "not breeding"	M	22	8.73	0.48	5.6	8.0- 9.6
	F	20	8.66	0.67	7.7	6.6-10.0
<i>rostrata</i> "breeding"	M	58	9.47	0.55	5.8	8.3-11.0
	F	25	9.32	0.57	6.1	7.8-10.2
<i>rostrata</i> "not breeding"	M	43	9.11	0.49	5.4	8.0-10.0
	F	45	9.17	0.37	4.0	8.4- 9.9
<i>exilipes</i>	M	47	7.87	0.45	5.8	6.8- 8.8
	F	37	7.71	0.47	6.1	6.3- 8.5
<i>cabaret</i>	M	66	9.01	0.46	5.2	7.7-10.2
	F	34	8.81	0.36	4.1	8.1- 9.5
<i>flammea</i>	M	222	9.13	0.59	6.5	7.9-10.4
	F	162	8.83	0.56	6.3	7.5- 9.9
"holboellii"-form	M	31	10.67	0.45	4.2	10.5-11.6
	F	23	11.10	0.55	5.0	10.0-12.9

Taxon	Sex	N	Bill depth			
			Mean	SD	CV(%)	Range
<i>hornemanni</i>	M	47	7.11	0.24	3.4	6.3-7.5
	F	42	6.88	0.28	4.1	6.1-7.8
<i>pale islandica</i>	M	21	6.32	0.20	3.2	6.0-6.8
	F	5	6.18	0.08	1.4	6.1-6.3
indeterminate <i>islandica</i>	M	40	6.43	0.27	4.2	5.9-7.0
	F	23	6.33	0.06	4.2	5.7-6.8
dark <i>islandica</i> "breeding"	M	14	6.61	0.22	3.4	6.2-7.1
	F	11	6.33	0.19	2.9	6.0-6.6
dark <i>islandica</i> "not breeding"	M	22	6.65	0.28	4.2	5.9-7.1
	F	20	6.46	0.34	5.3	5.7-7.0
<i>rostrata</i> "breeding"	M	58	6.68	0.26	3.9	6.3-7.5
	F	25	6.64	0.25	3.7	6.3-7.3
<i>rostrata</i> "not breeding"	M	43	6.59	0.21	3.2	6.2-7.0
	F	45	6.46	0.23	3.6	5.9-7.2
<i>exilipes</i>	M	47	6.03	0.19	3.2	5.6-6.4
	F	37	5.92	0.22	3.8	5.3-6.3
<i>cabaret</i>	M	66	5.99	0.23	3.8	5.5-6.5
	F	34	5.82	0.26	4.5	5.2-6.5
<i>flammea</i>	M	222	5.91	0.25	4.3	5.3-6.8
	F	162	5.73	0.24	4.2	5.2-6.5
"holboellii"-form	M	31	6.28	0.19	3.0	5.8-6.8
	F	23	6.45	0.29	4.5	6.1-7.2

Canovar transformations for selected taxa

The correct use of these functions and the corresponding figures in the identification of individual birds is highly dependent on the measuring procedures. Please consult the method section and try to obtain beforehand similar average measurements for at least one taxon as detailed as in tables given here (alternatively, a correction factor should be applied to the data).

X = maximum wing-length, Y = tail-length, Z = bill-length from feathering, V = bill-depth at feathering.

The coefficient of determination (% in brackets) indicates how the distinctive power of each variable is divided between the canonical axes.

A. Canovar on *flammea* and *exilipes* (Fig. 2):

$$CV\ 1 = -0.006\ X\ (22\%) + 0.012\ Y\ (81.6\%) - 0.089\ Z\ (94.8\%) + 0.1196\ V\ (27.1\%)$$

$$CV\ 2 = 0.020\ X\ (78\%) - 0.001\ Y\ (18.2\%) - 0.018\ Z\ (4.8\%) + 0.106\ V\ (71.2\%)$$

B. Canovar on *rostrata* and *hornemanni* (Fig.4):

$$CV\ 1 = 0.010\ X\ (95\%) + 0.0099\ Y\ (99\%) - 0.0652\ Z\ (69.2\%) + 0.158\ V\ (96.8\%)$$

$$CV\ 2 = 0.026\ X\ (5\%) - 0.0156\ Y\ (1\%) + 0.0633\ Z\ (29.7\%) - 0.0287\ V\ (3.1\%)$$

C. Canovar on *flammea*, *exilipes* and *pale islandica* (Fig.7):

$$CV\ 1 = -0.00436\ X\ (5\%) + 0.0136\ Y\ (91.5\%) - 0.0632\ Z\ (92.4\%) + 0.126\ V\ (69.7\%)$$

$$CV\ 2 = 0.013\ X\ (95\%) + 0.0067\ Y\ (8.5\%) + 0.0146\ Z\ (7.6\%) - 0.010\ V\ (30.3\%)$$

D. Canovar on the pale taxa: *exilipes*, *pale islandica* and *hornemanni* (Fig. 8):

$$CV\ 1 = 0.0055\ X\ (99.9\%) + 0.0152\ Y\ (99.2\%) - 0.0013\ Z\ (100\%) + 0.2014\ V\ (99.7\%)$$

$$CV\ 2 = -0.0049\ X\ (0.1\%) - 0.0228\ Y\ (0.8\%) - 0.0505\ Z\ (0\%) + 0.253\ V\ (0.3\%)$$

E. Canovar on the dark taxa: *cabaret*, *flammea* and *rostrata* including dark *islandica* (additional Fig. 9):

$$CV\ 1 = 0.0022\ X\ (51.7\%) + 0.0068\ Y\ (93.3\%) - 0.039\ Z\ (33.4\%) + 0.1184\ V\ (98.3\%)$$

$$CV\ 2 = 0.0145\ X\ (48.3\%) + 0.0001\ Y\ (6.7\%) + 0.012\ Z\ (66.3\%) - 0.0834\ V\ (1.7\%)$$

Fig. 9. Plot of canonical variate analysis on wing, tail, bill- length and -depth of *cabaret* (C, full line, $N = 100$), *flammea* (F, dotted & dashed, $N = 438$) and *rostrata* + dark *islandica* (R, dashed, $N = 238$). Sample means (+), centroids and 95% equiprobable population ellipses shown. Total eigenvalue: $K = 3.75$.

