

# Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses

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The colder climate and disjunct distribution of nesting and foraging habitats at high elevations increases the necessity of biparental care for successful breeding in birds. If differences in parental investment between the sexes correlate with intensity of sexual selection, the intensity of sexual selection should covary with ecological factors associated with elevation. I used sexual dimorphism as an indirect measure of intensity of sexual selection and examined variation in sexual dimorphism in 126 extant species of cardueline finches. I controlled for phylogeny and potential confounding factors and tested the prediction that the extent of sexual dimorphism negatively covaries with elevation of breeding. As predicted, interspecific variation in sexual dimorphism was more strongly associated with changes in elevation than with habitat, nest dispersion and placement, and migratory status. Species occupying lower elevations were more sexually dimorphic in plumage than species at higher elevations. This variation was largely due to increased brightness of male plumage at lower elevations. I address possible explanations of this trend, which may include increased opportunities for extrapair fertilizations at lower elevations, an increase in the cost of secondary sexual trait production (i.e., molt) and maintenance at high elevations, and elevational variation in predation pressure. *Key words:* cardueline finches, elevation, plumage brightness, sexual dimorphism, sexual selection. [*Behav Ecol* 8:675–690 (1997)]

Variation in sexual selection arising from variable mating opportunities and mating competition can exert strong selection on sexual dimorphism (Andersson, 1994; Kirkpatrick and Ryan, 1991; Williams, 1992). As a result, interspecific variation in the extent to which each sex contributes to parental care may influence sexual dimorphism because of the possible effects of parental investment on sexual selection; the sex with greater parental investment (typically female) is generally sought by a greater number of potential mates and has greater mating opportunities, while the sex with less investment (often male) usually suffers more mating competition (Trivers, 1972). Thus, variation in ecological determinants of parental investment should cause variation in sexual dimorphism (reviewed in Andersson, 1994).

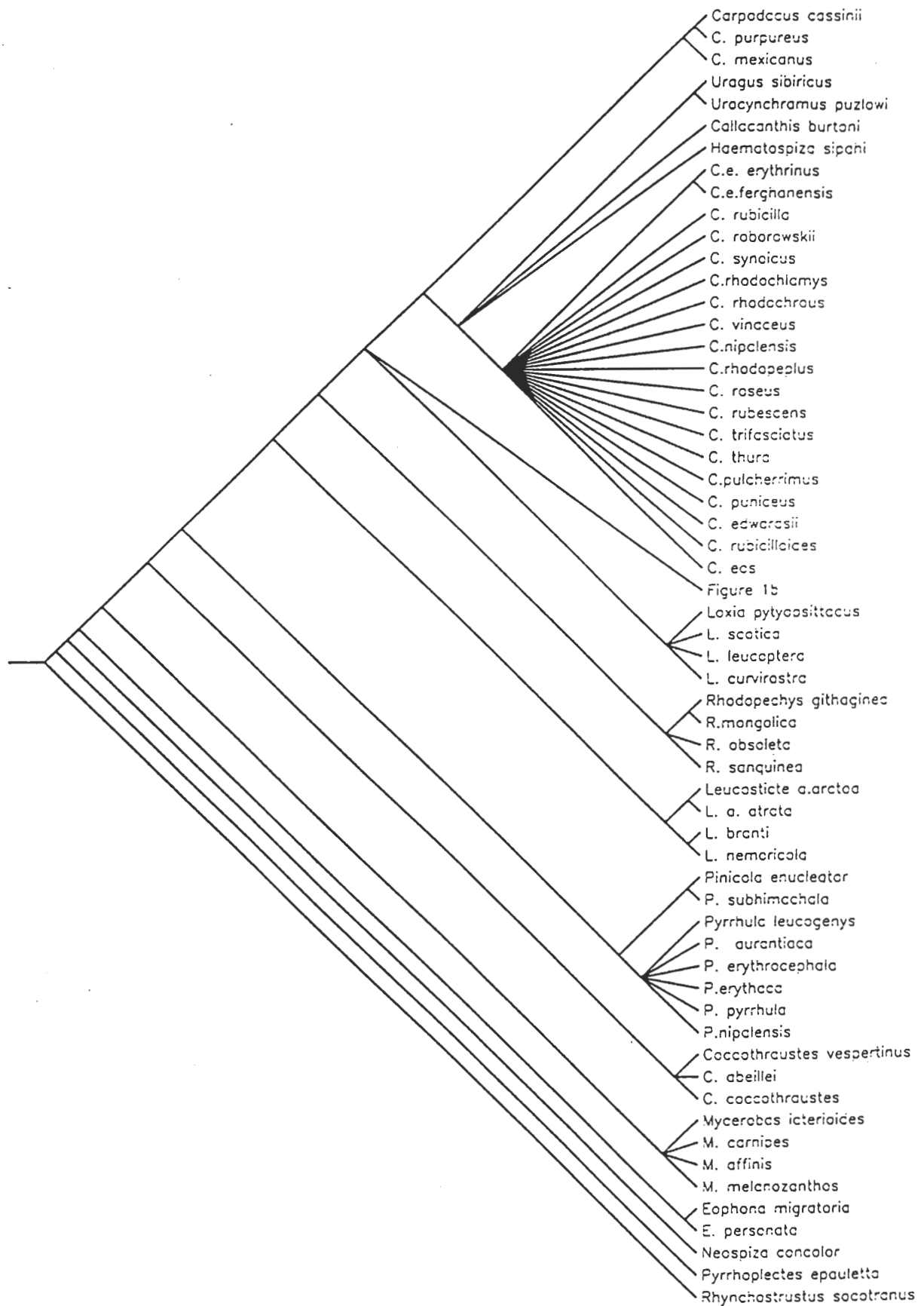
Male parental investment can differ among species with variation in ecological factors such as climate or resource (e.g., foraging or nesting sites) distribution (Andersson, 1994). For example, a colder nest microclimate is thought to favor increased male investment and, thus, greater biparental care in birds (Lyon and Montgomerie, 1987). Spatial separation of nesting and feeding resources is also thought to favor greater male care because incubating and brooding females cannot obtain adequate food resources on their own (Badyaev, 1993, 1994; Frey, 1989b; Kovshar, 1979). Consequently, areas with cold climates and disjunct feeding and nesting resources should favor greater male care. Such conditions are characteristic of high-elevation sites (e.g., Kovshar, 1979). Although there is some evidence that males provide most of the food for incubating and brooding females in a number of highland and arctic species and populations (e.g., Badyaev, 1993, 1994; Frey, 1989a; Kovshar, 1979; Lyon et al., 1987; Pullianen, 1979), no comparative studies have addressed elevational variation in male parental care. Here I examine whether male parental care varies with elevation.

High male parental investment demands high paternity assurance (i.e., reduced solicitation by females of extrapair

males and high solicitation of social mates), which along with greater synchronization of nesting among neighboring pairs, could reduce opportunities for extrapair fertilizations (Møller and Birkhead, 1993; Westneat et al., 1990; Westneat and Sherman, 1993). Increased male parental care is thought to be one of the major benefits of female breeding synchrony (Knowlton, 1979). Greater synchronization of breeding and shorter nesting season at higher elevation (Kovshar, 1979) also could affect the extent and cost of mate search and thus influence the intensity of sexual selection (Andersson, 1994). Thus, in monogamous species, the intensity of sexual selection should covary with ecological factors associated with the elevation of a species' distribution. Sexual dimorphism often has been used as a measure of the intensity of sexual selection in both interspecific (Barraclough et al., 1995; Fitzpatrick, 1994; Hamilton and Zuk, 1982; Møller and Birkhead, 1994) and population-level studies (Hill, 1991; Price, 1984). Using variation in sexual dimorphism as an indirect measure of the intensity of sexual selection, I examined the resulting prediction that the extent of sexual dimorphism decreases with elevation.

A number of factors besides colder climate and male care could covary with elevation. For example, altitudinal variation in predation pressure, parasite loads, diet, molt duration, and physiological constraints could affect the expression of secondary sexual traits potentially independently of changes in intensity of sexual selection (Badyaev, 1997b). I also examined these alternative hypotheses.

In this study I used a phylogenetic approach to determine the relative roles of various ecological factors on the degree and form of sexual dimorphism in the cardueline finches. These birds exhibit extensive variation in sexual dimorphism among closely related taxa and even within species (Table 1). Cardueline finches occupy a wide variety of habitats and geographic areas, and selection pressures imposed by variable habitats affect the social structure of breeding populations (Boehme, 1954; Frey, 1989b; Newton, 1973). Because the current phenotype of a species is the result of both current selection and historical factors, interspecific studies are especially useful when they incorporate information on the direction of phylogenetic change (Baum and Larson, 1991; Björklund, 1991; Felsenstein, 1985; Harvey and Pagel, 1991). Orogenic



**Figure 1**

Phylogenetic hypothesis for the taxa used in analyses. The phylogeny represents a consensus tree based on molecular, karyotypic, paleontological, morphological, and behavioral data (see Methods for references).

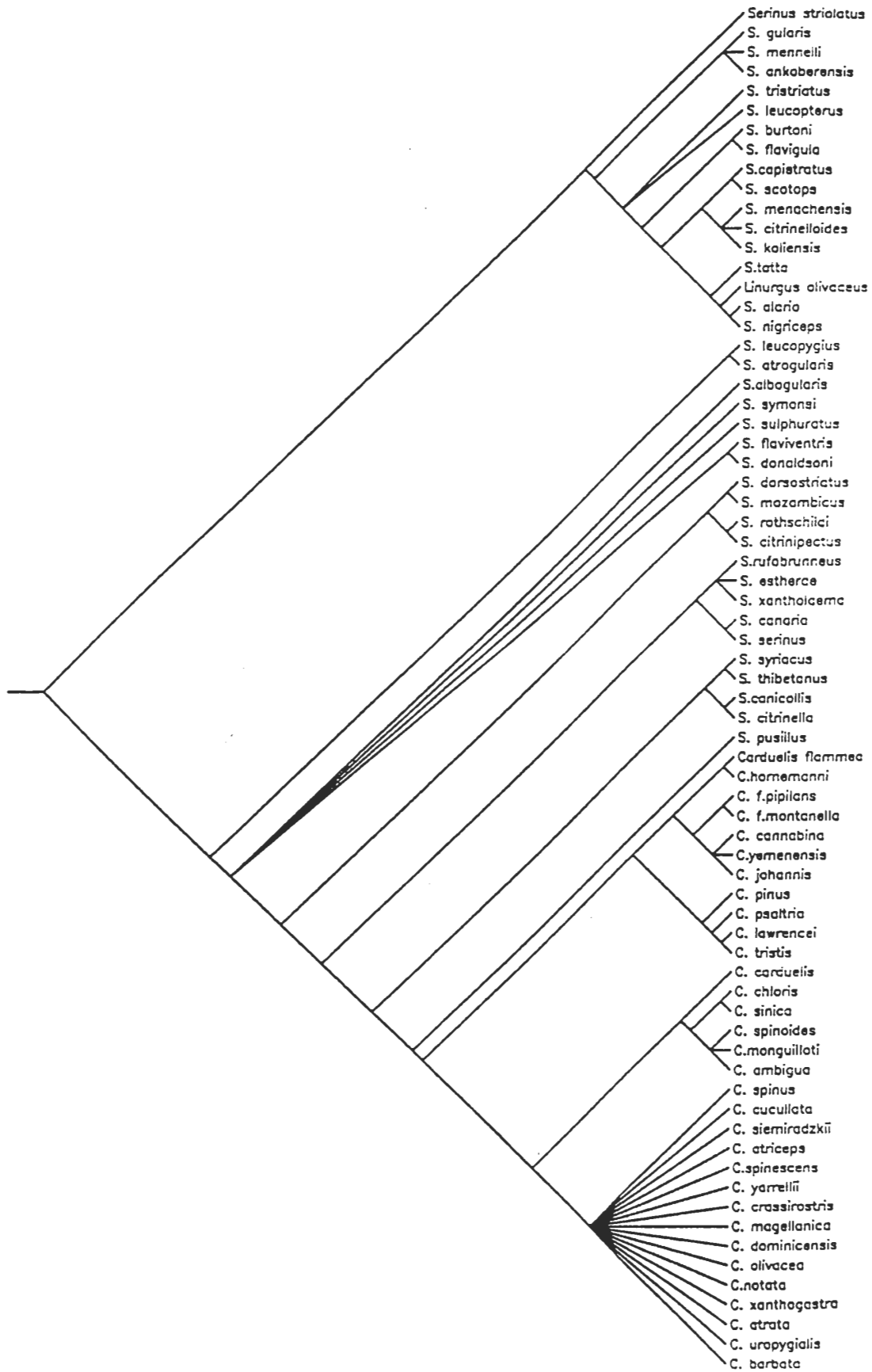


Figure 1  
Continued.

processes and corresponding changes in elevation are closely associated with speciation and the distribution of present cardueline taxa (Banin, 1987, 1988; Boehme, 1975; Clement et al., 1993; Kozlova, 1975; Vaurie, 1972), which allow the historical direction of evolutionary change to be traced. Thus, cardueline finches offer an unusually good opportunity to examine factors that might influence the evolution of dimorphism in secondary sexual traits. Although in this paper I deal only with interspecific data on elevation, I believe that the patterns and arguments pertain to latitude and populations as well.

## METHODS

Plumage brightness and dimorphism were assessed by two persons, unaware of the questions to be investigated, from illustrations of males and females in Clement et al. (1993). The overall brightness of each sex was scored on a scale from 1 to 6 (after Hamilton and Zuk, 1982). Sexual dimorphism in plumage brightness was computed by subtracting the mean female score from the mean male score (e.g., Møller and Birkhead, 1994). Two independent observers also scored dichromatism for three body regions: rump, breast, and head. Dichromatism was recorded for each body region as 0 if there was little or no dichromatism, 1 for moderate dichromatism, and 2 for high dichromatism (e.g., Irwin, 1994). The plumage dichromatism index was then the mean sum of scores for the three regions between the two observers. Mean interscorer values were used in analyses. There was a strong positive correlation between scorers for rump (Spearman  $r = .69$ ,  $p < .001$ ), breast ( $r = .89$ ,  $p < .001$ ), and head dichromatism ( $r = .89$ ,  $p < .001$ ) and overall brightness scores (males:  $r = .79$ ,  $p < .0001$ , females:  $r = .65$ ,  $p < .001$ ). To examine biases in observers' scoring, scores provided by human observers in this study were compared to scores for brightness, saturation and hue obtained for the same data set by using the Colortron scoring device (Badyaev AV and Hill GE, unpublished manuscript). There was close agreement between the observers' and Colortron scoring for all body regions and dimorphism measures (all  $r$ 's  $> 0.65$ ,  $p < .0001$ ; Badyaev AV and Hill GE, unpublished data). Sexual size dimorphism was calculated as  $[\log(\text{male trait}) - \log(\text{female trait})]$ . I used  $\log(\text{female wing})$  as a measure of body size.

I gathered published data for 126 extant cardueline species (Appendices A and B) on body size, nest dispersion, nest placement, migratory status, social system, and habitat type because these factors have been proposed to account for interspecific variation in plumage and size dimorphism (Baker and Parker, 1979; Björklund, 1990b; Fitzpatrick, 1994; Irwin, 1994; Webster, 1992; see Appendix B for definitions). In carduelines, nest dispersion and social system may vary with altitude and habitat type; finches tend to form nest aggregations and are more gregarious at high elevations, often independently of habitat type (Badyaev, 1993, 1994, unpublished data). Sexual dimorphism in size and coloration can also vary with body size (e.g., Webster, 1992); thus, I controlled for body size in ANCOVA on independent contrasts (see below) for plumage and size dimorphism (see Björklund, 1990b). In carduelines, data on parasite infestation were available for 19 species (Greiner et al., 1975; Peirce, 1981), extent of hybridization for 24 species (Panov, 1989), and nest predation data for 12 species (data summarized in Martin and Badyaev, 1996).

I constructed the working phylogenetic hypothesis of cardueline finch subfamily (Figure 1) by summarizing all recent systematics data available for each clade (Bartherl et al., 1992; Christidis, 1980; Clement et al., 1993; Deshayes, 1971; Groth, 1994; Herremans, 1990; Irwin, 1961; Marten and Johnson, 1986; Nemeschkal et al., 1992; Newton, 1973; Panov, 1989;

Ruelle, 1986a; Sibley and Ahlquist, 1990; Stempel, 1987; van den Elzen and Classen, 1992; van den Elzen and Nemeschkal, 1991; Vaurie, 1956). Most of the disagreements among published phylogenetic hypotheses were in relation to the status of the *Serinus* group: species *Carpodacus synoicus*, *Pinicola subhimachala*, and *Rhodopechys githaginea*. All suggested substitutions with these species were tried and trends reported here were essentially the same independent of specific phylogeny used. I set branch lengths as equal because such data were available only for a few species. All extant cardueline species were included in the phylogenetic tree, and plots of standardized contrasts against the variances of the untransformed contrasts (see below) showed no significant correlation, thus justifying the use of equal branch lengths (Purvis and Rambaut, 1995).

To control for species relatedness within the subfamily, I analyzed data using pairwise comparisons, independent linear contrasts, and genus-nested ANCOVA (in plumage brightness analyses; genera were divided into monophyletic groups based on the phylogeny in Figure 1) (Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Garland, 1991; Pagel, 1994; Purvis and Garland, 1993). In pairwise comparisons, pairs of closely related species (Badyaev 1997a: Appendix 2) (Figure 1) were ranked by potential effect and then compared with respect to dimorphism (e.g., Møller and Birkhead, 1994). I then tested any concordance with prediction using a sign test. This method provides the most direct test of concordance between altitude and dimorphism because it makes fewer assumptions about phylogenetic relations among clades in the subfamily.

I also analyzed data using the independent contrast method of Felsenstein (1985) and incorporating the methods of Purvis and Garland (1993) for incompletely resolved phylogenies, based on the software described by Purvis and Rambaut (1995). By using this method I assumed that different clades are equally likely to develop similar proportional changes in each variable included in independent contrast computations. None of the regressions of absolute values of contrasts versus their estimated nodal values showed significant slopes, thus validating the assumption (Purvis and Rambaut, 1995). To examine the influence of categorical factors, dummy variables were created for potential covariates and then phylogenetically transformed as described in Purvis and Rambaut (1995). Regression models were then used on the independent contrasts to test the influence of factors after potential covariates were entered into the model (Garland et al., 1992; Martin and Badyaev, 1996). Statistical significance of categories was tested by the cumulative change in sums of squares when these dummy variables were entered as a group (see Martin and Clobert, 1996). All regressions were forced through the origin (Garland et al., 1992). All morphological measures were log-transformed and standardized with mean zero and unit variance.

Pairwise comparisons potentially reduce the importance of confounding factors because related taxa usually are similar in ecology and morphology (e.g., Møller and Birkhead, 1994). However, because a number of potentially confounding variables such as habitat and nest dispersion varied even between closely related taxa, I report results from all methods.

## RESULTS

### Sexual dimorphism

#### Plumage dimorphism

Twenty-five pairs of closely related species and subspecies had data on both plumage dichromatism index and elevation. In 18 (72%) of these pairs, species with higher altitudinal distribution exhibited lower sexual dichromatism (sign test,  $p = .02$ ). Twenty-three pairs showed variation in elevation and di-

**Table 1**  
Sexual dimorphism in cardueline finches

| Genus (no. of species)     | Dimorphism |        |        |        |        |        | Brightness  |           |
|----------------------------|------------|--------|--------|--------|--------|--------|-------------|-----------|
|                            | Plumage    | Weight | Wing   | Tarsus | Tail   | Bill   | Male        | Female    |
| <i>Callacanthis</i> (1)    | 5.0        | NA     | 1.04   | 1.00   | 1.05   | 1.00   | 3.0         | 2.0       |
| <i>Carduelis</i> (32)      | 1.9 (5.5)  | 1.01   | 1.00   | 1.01*  | 1.02   | 1.01** | 3.0 (4.5)** | 2.5 (3.0) |
| <i>Carpodacus</i> (22)     | 5.3 (2.0)  | 0.99   | 1.03** | 1.01*  | 1.03** | 1.01** | 3.2 (2.5)** | 1.5 (1.0) |
| <i>Eophona</i> (2)         | 1.0 (2.0)  | NA     | 1.07*  | NA     | 1.00   | 1.04   | 2.7 (0.5)   | 2.7 (0.5) |
| <i>Haematospiza</i> (1)    | 6.0        | 1.02   | 1.04   | 1.00   | 1.07   | 1.00   | 6.0         | 2.0       |
| <i>Coccothraustes</i> (3)  | 3.0 (3.5)  | 1.04   | 1.02** | 0.99   | 1.03** | 1.02   | 3.3 (0.5)   | 2.7 (1.5) |
| <i>Leucosticte</i> (3)     | 0.5 (2.0)  | 1.09   | 1.04** | 1.00   | 1.04*  | 0.99   | 1.3 (1.0)   | 1.4 (1.0) |
| <i>Linurgus</i> (1)        | 3.0        | 1.00   | 1.05   | 1.00   | 1.00   | 1.00   | 4.0         | 2.0       |
| <i>Loxia</i> (4)           | 5.7 (1.0)  | 1.05   | 1.03** | 1.00   | 1.04** | 1.03** | 3.6 (1.0)** | 1.8 (0.5) |
| <i>Mycerobas</i> (4)       | 4.4 (2.5)  | 1.13   | 1.20   | 1.01** | 1.02   | 1.01   | 4.0 (3.5)   | 2.1 (2.0) |
| <i>Neospiza</i> (1)        | 0.0        | NA     | 1.00   | 1.00   | NA     | 1.00   | 2.0         | 2.0       |
| <i>Pinicola</i> (2)        | 6.0 (0.0)  | 1.01   | 1.04   | 0.99   | 1.01   | 1.01** | 3.5 (0.0)   | 2.2 (0.5) |
| <i>Pyrrhoptes</i> (1)      | 6.0        | 1.00   | 1.03   | 1.00   | 1.06   | 1.00   | 2.5         | 2.0       |
| <i>Pyrrhula</i> (6)        | 2.2 (4.0)  | 1.01   | 1.01   | 1.01*  | 1.01   | 1.01** | 3.1 (1.0)** | 2.2 (1.0) |
| <i>Rhodopechys</i> (4)     | 2.2 (3.5)  | 1.01   | 1.03   | 1.03   | 1.04** | 1.00   | 2.4 (1.0)   | 1.5 (1.0) |
| <i>Rhynchostruthus</i> (1) | 0.0        | 1.00   | 1.00   | 1.00   | NA     | 1.00   | 3.0         | 3.0       |
| <i>Serinus</i> (38)        | 1.0 (4.0)  | 0.99   | 1.02** | 1.01   | 1.01   | 1.00   | 2.2 (3.5)** | 2.0 (2.5) |
| <i>Uragus</i> (1)          | 5.0        | 1.31   | 1.03   | 1.00   | 1.06   | 1.00   | 3.5         | 1.5       |
| <i>Urocynchramus</i> (1)   | 5.0        | NA     | 1.00   | NA     | NA     | 1.00   | 2.5         | 1.5       |

NA, data not available. Sexual dimorphism is expressed as a ratio of male trait to female trait using untransformed values. Plumage dimorphism is a mean score of plumage dimorphism among species in a genus. Ratios = 1.0 represent no dimorphism and ratios increasingly different from 1.0 represent increasingly greater dimorphism). Differences of means were used for statistical tests. Probability levels are for one-way ANOVA.

\*  $p < .1$ ; \*\*  $p < .05$ .

morphism in brightness, and 17 (74%) of these pairs showed lower dimorphism in brightness with higher altitudinal distribution (sign test,  $p = .03$ ). Species dwelling in closed habitats were more sexually dimorphic in plumage dichromatism index than related species in open habitats (sign test: 15 of 19,  $p = .009$ ). However, species occupying closed habitats were no more sexually dimorphic in plumage brightness than their open-habitat relatives (sign test: 6 of 16,  $p > .2$ ). Only four pairs of species had variation in nest dispersion, but all four showed that species that nested solitarily were more dimorphic than species that nest in aggregations or colonies (sign test: 0 of 4,  $p = .06$ ). Sexual dichromatism was not associated with migratory status, although resident species tended to be less sexually dimorphic than their migrant relatives (sign test: 5 of 15,  $p = .1$ ). When phylogenetic history was incorporated into the model using independent contrasts and body size was controlled, the plumage dichromatism index varied negatively only with elevation and migratory status (Tables 2 and 3, Figure 2A). Similarly, dimorphism in brightness negatively covaried only with elevation (Table 2, Figure 2B).

Because only two variables can be compared at one time using the pairwise comparison method, the comparisons of dichromatism with habitat and migratory status were not controlled for elevation effects. When potential factors were examined together in multiple regression analyses, the effect of habitat on sexual dimorphism in plumage was not significant (Table 2). Thus, changes in sexual dichromatism were most persistently associated with elevation. Species occupying lower elevations were more sexually dimorphic in plumage than higher-elevation species.

#### Body size and ornament dimorphism

In pairwise comparisons, elevation was not associated with wing, tail, tarsus, or bill dimorphism (sign tests, all  $p > .2$ ). Dimorphism tended to be greater in species that dwell in open habitats than in closed habitats, but the association was not significant for wing (8 of 21,  $p > .2$ ), tail (4 of 11,  $p >$

.2), tarsus (4 of 11,  $p > .2$ ), or bill (3 of 12,  $p > .07$ ) dimorphism. Variations in nest dispersion and nest placement were not related to body size dimorphism in pairs of closely related species (both  $p > .2$ ). Resident species were less dimorphic than their more migratory relatives in wing dimorphism (sign test: 3 of 16,  $p = .01$ ), but migratory status was not associated with tail, tarsus, or bill sexual dimorphism (all  $p > .4$ ). When phylogenetic history was incorporated into the analysis via independent contrasts and body size effects were controlled, only wing dimorphism showed significant negative variation with altitude (Table 2, Figure 2C). Species that occupied lower elevations were more dimorphic in wing length than highland species.

Overall, dimorphism in plumage was the most variable and prevalent form of sexual dimorphism in the subfamily (Tables 1 and 2). Variation in elevation of breeding was the strongest negative predictor of plumage dimorphism.

#### Plumage brightness

##### Males

In pairwise comparisons, males in 19 of 25 (76%) pairs of species had brighter plumage at lower elevations than their highland relatives ( $p = .007$ ). Similarly, male plumage brightness was negatively correlated with elevation when the independent contrast method was used ( $n = 64$ , Pearson  $r = -.28$ ,  $p = .002$ ). In the multiple regression model, only altitude ( $\beta_{ST} = -.50$ ,  $t = -2.55$ ,  $p = .01$ ), nest placement ( $\beta_{ST} = -.49$ ,  $t = -2.65$ ,  $p = .02$ ), and nest dispersion ( $\beta_{ST} = -.39$ ,  $t = -1.89$ ,  $p = .07$ ) accounted for variation in male brightness. However, nest placement did not account for any portion of the variation in male brightness (percentage of variance = 0.0,  $F = .97$ ,  $p = .5$ ) in the genus-nested ANCOVA. Thus, variation in male plumage brightness was most consistently associated with elevation.

Table 2

Standardized coefficients from multiple regression of sexual dimorphism traits of cardueline finches on potential effects while correcting for phylogeny using the method of linear contrasts

| Predictors       | Dependent variables |            |       |         |         |         |
|------------------|---------------------|------------|-------|---------|---------|---------|
|                  | Plumage             | Brightness | Tail  | Tarsus  | Wing    | Bill    |
| <b>Covariate</b> |                     |            |       |         |         |         |
| Body size        | -0.33**             | -0.50**    | 0.24  | -0.73** | -0.26   | -0.59** |
| Nest placement   | 0.06                | 0.19       | -0.03 | 0.06    | -0.08   | -0.19   |
| <b>Factors</b>   |                     |            |       |         |         |         |
| Maximum altitude | -0.56**             | -0.49**    | 0.00  | 0.22    | -0.54** | -0.29   |
| Habitat type     | -0.27               | 0.00       | 0.36  | -0.02   | -0.18   | -0.26   |
| Nest dispersion  | -0.24               | 0.18       | 0.05  | -0.23   | 0.46    | 0.25    |
| Migratory status | -0.38               | -0.23      | -0.34 | -0.01   | -0.25   | 0.40    |
| Model $R^2$      | 0.59**              | 0.52**     | 0.31  | 0.41    | 0.46**  | 0.55**  |

$p$  value is for  $H_0$ : parameter = 0; \*\* indicates significance at  $\alpha = 0.05$  level after correction using the model-wide sequential Bonferroni tests; all others nonsignificant.

### Females

Female plumage brightness was not significantly associated with elevation (sign test: 10 of 24,  $p > .2$ ) when pairwise comparisons were used, but varied with nest placement ( $\beta_{ST} = -0.47$ ,  $t = -2.20$ ,  $p = .04$ ) and altitude ( $\beta_{ST} = -0.40$ ,  $t = -2.22$ ,  $p = .04$ ) when independent contrasts were used. In the genus-nested ANCOVA, nest placement was a highly significant predictor of female brightness ( $R^2 = .43$ ,  $F = 2.15$ ,  $p = .02$ ).

Thus, females show no consistent pattern of brightness variation with altitude and a significant association with nest placement. Given that plumage and brightness dimorphism showed strong elevational patterns, I conclude that variation in brightness dimorphism between males and females is largely due to variation in male brightness; females of high- and low-altitude species were equally dull (or bright), while male brightness varied the most along elevation. Variation in male plumage brightness also contributed the most ( $r_p = .64$ ,  $p < .001$ ) to the variation in overall brightness dimorphism.

### Plumage index dichromatism

Variation in rump dichromatism was most closely related to nest placement (Table 3). When body size was controlled, variation in sexual dimorphism in breast and head plumage was most closely associated with changes in breeding elevation

(Table 3). Head plumage dimorphism contributed the most to the overall dimorphism index ( $\beta_{ST} = .49$ ), followed by breast and rump dimorphism (Table 3).

### Altitude and male parental care

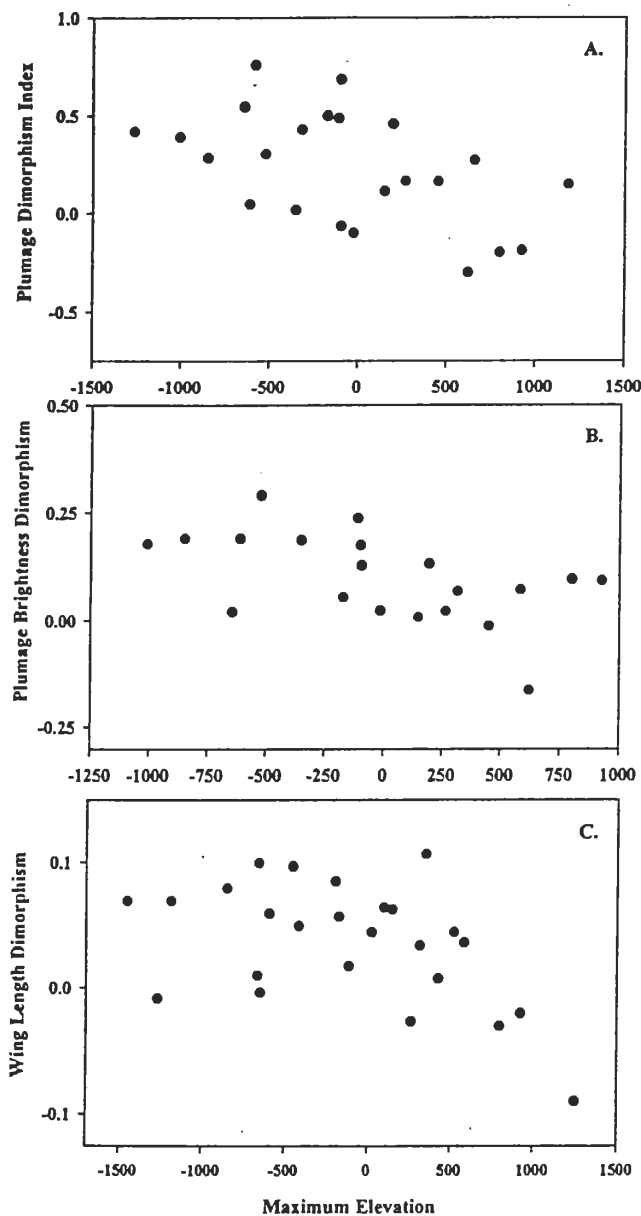
To test the assumption that male parental investment increases with altitude, I used independent contrasts to examine the relationship between altitude and the number of days when males provide >65% of the food for the brooding females and nestlings during the nestling period (65% was the closest to the 50% estimate obtainable from studies). Because the number of days the female has to brood nestlings varies significantly with weather conditions during observation, the mean values of at least three field seasons per species were used (Badyaev, 1993, 1994; Cramp and Perrins, 1994; Coutlee, 1968; Kovshar, 1979; Linsdale, 1957) (Figure 3). I included clutch size in the regression model to control for brood size variation between elevations (Badyaev, 1997a). Elevation was a highly significant positive predictor of the number of days the male provides >65% of food for the nestlings and brooding female (Figure 3).

Table 3

Standardized coefficients from multiple regression of plumage dimorphism traits of cardueline finches on potential effects while correcting for phylogeny using method of linear contrasts

| Predictor                 | Dichromatism index |          |          |
|---------------------------|--------------------|----------|----------|
|                           | Rump               | Head     | Breast   |
| <b>Covariates</b>         |                    |          |          |
| Body size                 | 0.20               | -0.37**  | -0.44**  |
| Nest placement            | 0.72***            | -0.10    | -0.08    |
| <b>Factors</b>            |                    |          |          |
| Maximum altitude          | 0.24               | -0.58*** | -0.47*** |
| Habitat type              | 0.00               | 0.20     | 0.08     |
| Nest dispersion           | -0.35              | 0.26     | 0.18     |
| Migratory status          | 0.08               | -0.16    | -0.29*   |
| Model $R^2$               | 0.67***            | 0.56***  | 0.59***  |
| % of total index variance | 13.71              | 79.00    | 0.07     |

$p$  value is for  $H_0$ : parameter = 0; \*  $p < .1$ ; \*\*  $p < .05$ ; \*\*\*  $p < .01$ ; all others nonsignificant.

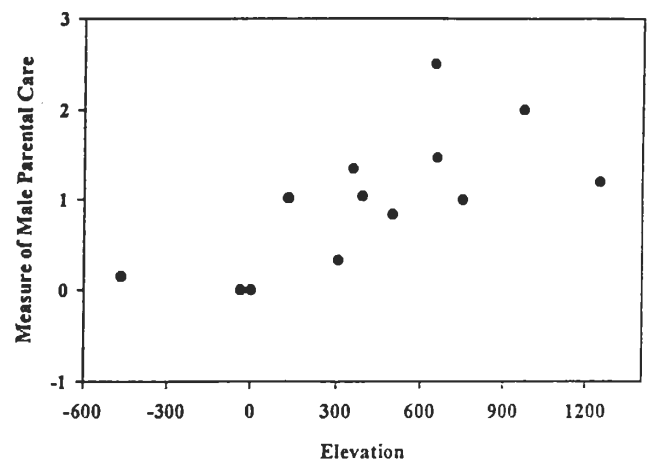


**Figure 2**  
Partial regression residual plots of data transformed by the method of standardized independent contrasts (which controls for possible phylogenetic effects) illustrating the relationship between elevation and sexual dimorphism in (A) plumage dimorphism index, (B) plumage brightness, and (C) wing length.

#### Altitude and parasite infestation, nest predation, and extent of hybridization

Blood parasite level did not correlate with maximum elevation (independent contrasts, Spearman  $r = .01$ ,  $p = .72$ ), but weakly positively correlated with minimum elevation ( $r = .32$ ,  $p = .02$ ). However, in the 19 species investigated, blood parasite level was not related to variation in either male or female plumage brightness or plumage dichromatism (both  $r < .005$ ,  $p > .7$ ).

Nest predation rate was weakly negatively correlated with minimum elevation (independent contrasts, Spearman  $r = .27$ ,  $p = .08$ ), but not with maximum elevation ( $r = .002$ ,  $p = .65$ ). In nested ANCOVA, nest predation significantly decreased with elevation only in *Carpodacus* and *Leucosticte* finches. In the 12 species investigated, nest predation was



**Figure 3**  
The relationship between linear contrasts of the number of days a male provides >65% of food to brooding female (male parental care; see text for details) and linear contrasts for elevation of observation site ( $R^2 = 0.73$ ,  $F_{1,14} = 34.59$ ,  $p = .0001$ ;  $\beta_{\text{CT}} = .85$ ,  $t = 5.89$ ,  $p < .0001$ ). The data are for the following species: *Serinus pusillus* (Tien-Shan), *S. pusillus* (Pamir-Alai), *C. carduelis carduelis*, *C. carduelis caniceps*, *C. tristis*, *C. psaltria*, *C. lawrencei*, *Leucosticte nemoricola*, *Carpodacus e. erythrinus*, *Carpodacus e. ferghanensis*, *Loxia curvirostra*, *Eophona migratoria*, *Mycerobas carnipes* (Tien-Shan), and *M. carnipes* (Pamir-Alai).

weakly positively correlated with sexual dimorphism in plumage (Spearman  $r = .28$ ,  $p = .09$ ) and tended to correlate positively with plumage brightness in males ( $r = .25$ ,  $p = .11$ ) but not in females ( $r = .01$ ,  $p = .77$ ).

The number of hybrids each species is known to form with other species correlated positively with extent of plumage dimorphism (independent contrasts; brightness dimorphism:  $n = 21$ ,  $r = .44$ ,  $p = .005$ ; weakly with dichromatism index:  $r = .33$ ,  $p = .10$ ) and plumage brightness in males ( $r = .26$ ,  $p = .11$ ) but not in females ( $r = -.003$ ,  $p = .98$ ). In the 24 species examined, extent of hybridization did not significantly correlate with elevation (all probabilities  $> .30$ ).

#### DISCUSSION

Sexual dimorphism was highly negatively correlated with elevational distribution in cardueline finches from throughout the world. This robust, but previously unrecognized, pattern is consistent with the a priori prediction that the intensity of sexual selection varies with elevation of breeding. Here I examine the evidence for possible mechanisms causing the sexual dimorphism–elevation relationship.

#### Uneven sex-specific selection along elevation gradient

Reduced sexual selection and dimorphism may occur at high elevations because of constraints placed on males by parental care; successful breeding is strongly dependent on male parental investment at high elevations and latitudes because colder climatic conditions and patchy resource distribution impede the ability of incubating and brooding females to obtain sufficient food on their own (Badyaev, 1993, 1994; Frey, 1989a,b; Lyon et al., 1987). For example, in the white-winged grosbeak (*Mycerobas carnipes*), even a short absence of the female from the nest during egg-laying causes lethal cooling of eggs, especially early in the season (Badyaev, 1994; Kovshar, 1979). In a color-marked population of gold-fronted serins (*Serinus pusillus*), two females abandoned their clutches after their mates disappeared, presumably because these females

were unable to maintain incubation while foraging at a remote feeding habitat (Badyaev, 1993). Furthermore, the period of female dependency on male care is longer in highland than in lowland cardueline taxa because females at higher elevations often begin incubation with the first egg and have longer incubation periods (Badyaev, 1997a; Frey 1989a; Kovshar, 1979). These patterns are supported more generally by the analyses that show male parental care increases with elevation (Figure 3).

The disjunct distribution of foraging and nesting habitats at high elevations facilitates foraging in flocks by male finches and potentially contributes to synchronization of breeding attempts by different pairs (Frey, 1989a; Newton, 1973). Greater breeding synchrony is thought to reduce opportunities for extrapair matings (e.g., Westneat et al., 1990). Moreover, intensive mate guarding by males and frequent intrapair copulations are typical for highland finches (Badyaev, 1993, 1994; French, 1954; Johnson, 1972; Kovshar, 1979; Shreeve, 1977) and may contribute to high paternity assurance, reinforcing high male parental investment. Incubation beginning with the first egg and infrequent foraging by females during incubation further decrease the potential for extrapair copulations by restricting female movements to the immediate nest vicinity.

Climatic conditions and resource distribution allow females of lowland species to forage during incubation, and the periods when females need to brood nestlings are shorter and less frequent (Badyaev, 1993, 1994; Boehme, 1954; Björklund, 1990a; Cramp and Perrins, 1994; Hill, 1993b; Mal'chevski and Pukinski, 1983; Stjernberg, 1979). Females are often able to raise a brood after the disappearance of their mate, while longer breeding seasons provide additional breeding opportunities and may decrease synchronization in breeding among pairs (e.g., Hill et al., 1994). Consequently, parental care places fewer constraints on males in many lowland species (Figure 3). Thus, the potential for sexual selection could be greater in lowlands because reduced demands for male parental investment can increase male opportunities to solicit females and provide greater mating opportunities for females. Alternatively, sexes might be subject to more similar selection pressure at higher elevations as a result of more similar contributions to parental care (Badyaev, 1997b).

Plumage brightness of males and the magnitude of sexual dichromatism has been shown to covary with extrapair paternity in a number of bird species (Møller and Birkhead, 1994). In cardueline finches, variation in sexual dichromatism is largely driven by increased brightness of male plumage at lower elevations. It is possible that the potential for extrapair copulations is greater for both sexes at lower elevations (see above). Indeed, in lowland cardueline finches, males often have been observed to intrude into neighboring territories, and both males and females are known to solicit extrapair copulations (e.g., Björklund, 1990a; Cramp and Perrins, 1994; Hill, 1993b; Middleton, 1993; Nakamura, 1982; Shreeve, 1977; Stjernberg, 1979). Thus, altitudinal changes in sexual dimorphism and male brightness in finches could relate to the pursuit of mixed reproductive strategies, and extrapair paternity could play an important role in the expression of sexually dimorphic traits.

The expression of a male's secondary sexual characters may vary with his resistance to parasites (Hamilton and Zuk, 1982; Møller, 1990). If altitudinal variation in sexual dimorphism in finches was due to parasitism levels, then parasite loads should be lower in highlands than in lowlands. Indeed, Bennett et al. (1992) suggested that the absence of suitable parasite vectors in high arctic regions, which are similar to high elevations, leads to a scarcity of blood parasites in bird species there (Greiner et al., 1975; Peirce, 1981; Seutin, 1994). However,

variation in parasite infestation generally did not correlate with either elevation or plumage brightness in finches and thus cannot account for the negative correlation between dichromatism and elevation, although more analyses are needed on other types of parasites and a wider variety of finch species.

The expression of secondary sexual traits could also be related to mating discrimination between closely related species (Andersson, 1994); sexual dimorphism within a taxonomic clade or within a community is expected to increase with species diversity (Barraclough et al., 1995). To account for the observed correlation between dimorphism and elevation, this hypothesis has to assume more finch species in the lowlands. Extent of hybridization did not covary with elevation in carduelines; however, finches with a higher degree of hybridization show brighter and more sexually dimorphic plumages. In house finches (*Carpodacus mexicanus*), females preferentially paired with brighter males, despite their mate plumage pattern being dissimilar to males in their own subspecies (Hill, 1993a). This finding and my results suggest that mating discrimination cannot account for the relationship between dichromatism and elevation, although it may contribute to plumage brightness variation in the subfamily.

#### Variation in cost of trait maintenance along elevation gradient

Female brightness and rump dichromatism covary with nest placement (Table 3), suggesting the importance of nest predation for the evolution of female plumage (Martin and Badyaev, 1996). However, nest placement did not covary with male brightness and did not by itself explain the altitudinal change in overall sexual dichromatism. Increased predation on adults could limit expression of secondary sexual traits and select for more cryptic males, especially in environments where males provide substantial parental care (e.g., Badyaev, 1997b; Johnson, 1991; Promislow et al., 1992). Alternatively, if bright coloration serves as a signal of unprofitable prey, high predation should select for bright plumage in males (Baker and Parker, 1979; Götmark, 1995). In carduelines, male plumage is brighter in lower elevation species. Brighter plumage in males of low elevation may not lead to increased nest detection by predators because in these species males contribute less to parental care as compared to high elevation species. Nest predation rate weakly negatively correlated with altitude in most carduelines and positively correlated with male but not with female plumage brightness (this study; Badyaev, 1997b). More data on altitudinal variation in predation on adults are needed to investigate the interaction among predation pressure, plumage brightness, and parental care.

In many carduelines, carotenoid-based plumage coloration varies with availability of carotenoids in the diet during post-breeding molt (e.g., Brush and Power, 1976; French, 1954; Hill, 1992; Hill and Montgomerie, 1994). Thus, observed variation in plumage coloration could in part be due to the differential availability or quality of carotenoid-rich foods at different elevations. For example, geographical variation in intensity of red coloration among subspecies of the house finch is influenced by local access to carotenoids (Hill, 1993a). Thus, access to carotenoids and ability to produce carotenoid-based coloration could affect interspecific variation in sexual dichromatism in the subfamily. Energy and time expenditures of considerable male parental investment at high elevations and short nesting season may decrease the time and energy available for molt and thus for development of sexual traits (Hill and Montgomerie, 1994; Møller et al., 1995). This prediction is corroborated by observations of overlap between breeding and molting, which is typical of many high elevation birds (Kovshar, 1979).



Intensity of pigmentation and coloration could influence the energy exchange between the organism and its environment. Therefore, observed differences in plumage brightness along an elevation gradient could be due to variation in physiological constraints imposed by high elevations. However, in wood warblers, plumage coloration and brightness were shown to be less important for thermoregulation than behavior and ptiloerection (Burt, 1986). Thus, differences in access to carotenoids during molt would appear to be a more plausible explanation for altitudinal variations in dichromatism than would physiological constraints on coloration imposed by climate.

In sum, interspecific variation in sexual dichromatism in cardueline finches is most closely associated with changes in elevation. The variation in plumage brightness dimorphism is largely due to increased brightness of male plumage at lower elevations. The altitudinal variation in sexual dichromatism may reflect increased potential for sexual selection at lower elevations (e.g., greater extrapair fertilization opportunities or longer period of mate selection). Alternatively, higher paren-

tal investment by males at higher elevations may (1) decrease time and energy available for molt, affecting development and thus extent of secondary sexual traits and (2) place an upper limit on plumage brightness because bright males might attract predators to the nest. In addition, altitudinal variation in diet could contribute to the relationship between elevation and dichromatism. Further reviews and experimental tests of potential mechanisms are needed to better address the ecological and phylogenetic factors causing the elevational variation in sexual dichromatism.

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#### APPENDIX A

Data on rump (RD), head (HD), and breast (BD) dichromatism; plumage brightness, and mean morphological measurements (mm) of carduelines (references are given in Appendix B)

| Genus species         | Dichromatism |     |     | Brightness |     | Males |      |        |       | Females |      |        |      |
|-----------------------|--------------|-----|-----|------------|-----|-------|------|--------|-------|---------|------|--------|------|
|                       | RD           | HD  | BD  | M          | F   | Wing  | Tail | Tarsus | Bill* | Wing    | Tail | Tarsus | Bill |
| <i>Serinus</i>        |              |     |     |            |     |       |      |        |       |         |      |        |      |
| <i>pusillus</i>       | 0.0          | 0.0 | 0.0 | 3.0        | 3.0 | 75.9  | 55.7 | 14.3   | 10.5  | 73.4    | 53.2 | 14.2   | 10.5 |
| <i>serinus</i>        | 0.0          | 1.0 | 1.0 | 3.5        | 3.0 | 72.7  | 50.6 | 13.6   | 10.4  | 69.4    | 48.1 | 13.4   | 10.6 |
| <i>syriacus</i>       | 0.0          | 0.0 | 0.5 | 2.5        | 2.5 | 77.8  | 55.2 | 14.8   | 10.6  | 74.6    | 53.4 | 14.4   | 10.7 |
| <i>thibetanus</i>     | 0.0          | 1.0 | 0.0 | 2.5        | 2.5 | 70.0  | 41.5 | 14.5   | 12.0  | 67.0    | 43.5 | 14.5   | 13.0 |
| <i>canaria</i>        | 1.0          | 1.0 | 1.0 | 2.5        | 2.0 | 72.7  | 58.8 | 17.2   | 10.9  | 70.2    | 56.9 | 17.2   | 10.8 |
| <i>canicollis</i>     | 0.0          | 1.0 | 1.0 | 2.5        | 2.0 | 78.5  | 56.0 | 15.0   | 9.3   | 75.5    | 53.0 | 15.0   | 9.3  |
| <i>citrinella</i>     | 0.0          | 0.5 | 0.5 | 3.0        | 3.0 | 76.6  | 53.8 | 14.6   | 11.7  | 74.6    | 52.3 | 14.5   | 11.6 |
| <i>mozambicus</i>     | 0.0          | 1.5 | 0.0 | 3.5        | 3.0 | 68.0  | 44.0 | 13.0   | 9.0   | —       | —    | —      | —    |
| <i>dorsostratus</i>   | 0.0          | 0.0 | 1.0 | 3.0        | 3.0 | 83.0  | 61.0 | 18.0   | 14.0  | 81.5    | —    | 18.0   | 14.0 |
| <i>scotops</i>        | 0.0          | 0.5 | 0.0 | 2.5        | 2.5 | 66.0  | 51.0 | 15.0   | 11.0  | 66.0    | 51.0 | 15.0   | 11.0 |
| <i>flaviventris</i>   | 0.5          | 1.5 | 1.5 | 4.0        | 2.0 | 72.0  | 52.0 | 18.0   | 11.0  | 71.0    | —    | —      | —    |
| <i>sulphuratus</i>    | 0.0          | 1.0 | 0.0 | 3.0        | 2.5 | 83.0  | 61.0 | 18.0   | 14.0  | 81.5    | 61.0 | 18.0   | 14.0 |
| <i>donaldsoni</i>     | 0.0          | 1.5 | 1.5 | 3.5        | 2.0 | 81.0  | —    | —      | —     | 81.0    | —    | —      | —    |
| <i>nigriceps</i>      | 0.0          | 2.0 | 1.0 | 3.0        | 3.0 | 77.0  | —    | —      | —     | 77.0    | —    | —      | —    |
| <i>citrinelloides</i> | 0.0          | 1.5 | 1.0 | 3.0        | 2.5 | 67.0  | 49.0 | 14.8   | 11.3  | 66.0    | 49.0 | 14.8   | 11.3 |
| <i>capistratus</i>    | 0.0          | 1.5 | 1.0 | 3.0        | 3.0 | 62.0  | 40.5 | —      | —     | 62.0    | 40.5 | —      | —    |
| <i>koliensis</i>      | 0.0          | 0.0 | 0.0 | 2.5        | 2.5 | 64.0  | —    | —      | —     | 64.0    | —    | —      | —    |
| <i>leucopygius</i>    | 0.0          | 0.0 | 0.0 | 1.5        | 1.5 | 66.0  | 41.0 | 13.0   | 7.5   | 66.0    | 41.0 | 13.0   | 7.5  |
| <i>atrogularis</i>    | 0.0          | 0.0 | 0.0 | 1.5        | 1.5 | 68.5  | 44.0 | 12.0   | 8.5   | 66.0    | 44.0 | 12.0   | 8.5  |
| <i>menachensis</i>    | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 72.5  | —    | —      | —     | 72.5    | —    | —      | —    |
| <i>totta</i>          | 0.0          | 0.5 | 0.5 | 2.5        | 2.0 | 70.0  | 51.0 | 14.5   | 9.8   | 70.0    | 51.0 | 14.5   | 9.8  |
| <i>symonsi</i>        | 0.0          | 1.0 | 1.0 | 2.0        | 1.5 | 75.5  | 56.5 | 16.5   | 10.8  | 75.5    | 56.5 | 16.5   | 10.8 |
| <i>albogularis</i>    | 0.0          | 0.0 | 0.0 | 0.5        | 0.5 | 77.5  | 57.0 | 21.0   | 13.5  | 77.5    | 57.0 | 21.0   | 13.5 |
| <i>gularis</i>        | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 82.5  | 63.0 | 15.5   | 12.8  | 79.0    | —    | —      | —    |
| <i>menelli</i>        | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 82.5  | 52.0 | 13.5   | 11.3  | 82.5    | 52.0 | 13.5   | 11.3 |
| <i>tristriatus</i>    | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 67.0  | 54.0 | 16.5   | 10.0  | 67.5    | —    | —      | —    |
| <i>leucopterus</i>    | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 73.0  | 57.5 | 18.0   | 12.5  | 73.0    | 57.5 | 18.0   | 12.5 |
| <i>striolatus</i>     | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 69.5  | 62.0 | 20.0   | 12.8  | 69.5    | 60.8 | 20.0   | 12.8 |
| <i>rothschildi</i>    | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 69.0  | —    | —      | —     | 63.0    | —    | —      | —    |
| <i>citrinipectus</i>  | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 66.5  | 39.2 | 13.5   | 12.0  | —       | —    | —      | —    |
| <i>ankoberensis</i>   | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 74.5  | 52.0 | 16.0   | 13.0  | 74.5    | 52.0 | 16.0   | 13.0 |
| <i>burtoni</i>        | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 91.0  | 68.0 | 19.0   | 16.3  | —       | —    | —      | —    |
| <i>flavigula</i>      | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 67.0  | 50.0 | —      | —     | —       | —    | —      | —    |
| <i>xantholaema</i>    | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 66.8  | 47.0 | 15.0   | 9.5   | —       | —    | —      | —    |
| <i>alaris</i>         | 0.0          | 2.0 | 2.0 | 3.5        | 2.0 | 66.5  | 45.5 | 14.0   | 8.5   | 65.0    | 45.5 | 14.0   | 8.5  |
| <i>rufobrunneus</i>   | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 79.5  | 45.0 | 18.5   | 12.5  | 79.5    | 45.0 | 18.5   | 12.5 |
| <i>estherae</i>       | 0.0          | 1.0 | 0.5 | 2.5        | 2.0 | 68.0  | 45.5 | 13.5   | 9.0   | 67.5    | 42.5 | 12.0   | 9.0  |

## APPENDIX A, continued

| Genus<br>species      | Dichromatism |     |     | Brightness |     | Males |      |        |                   | Females |      |        |      |
|-----------------------|--------------|-----|-----|------------|-----|-------|------|--------|-------------------|---------|------|--------|------|
|                       | RD           | HD  | BD  | M          | F   | Wing  | Tail | Tarsus | Bill <sup>a</sup> | Wing    | Tail | Tarsus | Bill |
| <i>Carduelis</i>      |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>cannabina</i>      | 0.0          | 1.0 | 1.5 | 2.5        | 2.0 | 79.6  | 50.6 | 15.6   | 12.9              | 77.6    | 49.9 | 15.3   | 12.6 |
| <i>spinus</i>         | 0.5          | 1.5 | 1.0 | 3.0        | 2.5 | 73.3  | 46.1 | 13.7   | 13.2              | 71.4    | 45.0 | 13.8   | 13.1 |
| <i>chloris</i>        | 0.0          | 0.0 | 0.0 | 2.5        | 2.5 | 87.5  | 55.7 | 17.3   | 16.6              | 85.2    | 53.5 | 17.4   | 16.6 |
| <i>sinica</i>         | 0.0          | 0.5 | 0.0 | 2.5        | 2.5 | 80.0  | 57.5 | 16.0   | 11.5              | 80.7    | 57.5 | 16.0   | 11.5 |
| <i>spinooides</i>     | 0.0          | 0.0 | 0.5 | 3.0        | 2.5 | 79.5  | 47.0 | 15.0   | 15.0              | 76.0    | 48.0 | 15.0   | 15.0 |
| <i>monguilloti</i>    | 0.0          | 0.0 | 1.0 | 2.5        | 2.0 | 70.5  | —    | 11.0   | 10.5              | 70.5    | —    | 11.0   | 10.5 |
| <i>ambigua</i>        | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 81.0  | —    | 11.0   | 11.0              | —       | —    | —      | —    |
| <i>carduelis</i>      | 0.0          | 0.0 | 0.0 | 4.5        | 4.5 | 80.4  | 48.4 | 14.7   | 16.2              | 77.6    | 47.1 | 14.4   | 15.4 |
| <i>tristis</i>        | 0.5          | 2.0 | 0.5 | 4.0        | 2.5 | 71.1  | 48.1 | 14.4   | 10.3              | 68.2    | 46.3 | 14.4   | 10.3 |
| <i>psaltria</i>       | 0.0          | 2.0 | 1.0 | 3.5        | 2.5 | 63.0  | 43.0 | 11.5   | 9.8               | 62.0    | 43.0 | 11.5   | 9.8  |
| <i>pinus</i>          | 0.0          | 0.0 | 0.0 | 1.5        | 1.5 | 73.5  | 46.3 | 14.3   | 10.3              | 71.0    | 46.3 | 14.3   | 10.3 |
| <i>cucullata</i>      | 0.5          | 2.0 | 2.0 | 6.0        | 3.5 | —     | —    | —      | —                 | —       | —    | —      | —    |
| <i>siemiradzkii</i>   | 0.5          | 2.0 | 1.0 | 4.0        | 2.5 | —     | —    | —      | —                 | —       | —    | —      | —    |
| <i>atriceps</i>       | 0.0          | 0.0 | 0.5 | 2.5        | 2.5 | 71.5  | —    | —      | —                 | —       | —    | —      | —    |
| <i>spinescens</i>     | 0.0          | 2.0 | 1.0 | 3.0        | 2.0 | 64.0  | —    | —      | 11.0              | 64.0    | —    | —      | 11.0 |
| <i>yarellii</i>       | 0.0          | 2.0 | 1.0 | 4.0        | 2.5 | 68.0  | —    | 9.0    | 9.0               | 68.0    | —    | 9.0    | 9.0  |
| <i>crassirostris</i>  | 0.0          | 1.0 | 1.0 | 3.5        | 2.5 | 78.0  | 50.0 | —      | —                 | 79.0    | 48.5 | —      | —    |
| <i>magellanica</i>    | 0.5          | 2.0 | 1.0 | 3.5        | 2.5 | 72.0  | —    | 9.0    | 9.0               | 70.0    | —    | —      | 9.0  |
| <i>dominicensis</i>   | 0.5          | 2.0 | 1.5 | 3.0        | 2.0 | 65.2  | 41.0 | 15.0   | 9.0               | 63.5    | 41.0 | 15.0   | 9.0  |
| <i>olivacea</i>       | 0.0          | 2.0 | 1.0 | 3.5        | 2.5 | —     | —    | —      | —                 | —       | —    | —      | —    |
| <i>notata</i>         | 0.0          | 0.0 | 0.5 | 3.5        | 3.5 | 64.5  | —    | —      | —                 | 63.0    | —    | —      | —    |
| <i>xathogastra</i>    | 2.0          | 2.0 | 1.5 | 2.5        | 2.5 | 32.8  | 39.5 | 13.5   | 10.0              | 63.5    | 37.0 | 13.5   | 10.0 |
| <i>atrata</i>         | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 78.5  | 49.7 | —      | 9.2               | 77.4    | 49.0 | —      | 9.0  |
| <i>uropygialis</i>    | 0.0          | 0.0 | 0.5 | 3.0        | 3.0 | 82.0  | 49.0 | 12.0   | 9.5               | 82.0    | 49.0 | 12.0   | 9.5  |
| <i>barbata</i>        | 0.0          | 1.5 | 0.5 | 3.0        | 2.5 | 73.0  | 48.0 | 13.0   | 10.5              | 73.0    | 48.0 | 13.0   | 10.5 |
| <i>lawrencei</i>      | 0.0          | 2.5 | 1.0 | 3.0        | 2.5 | 67.5  | —    | —      | —                 | 64.5    | —    | —      | —    |
| <i>flammea</i>        | 0.5          | 1.5 | 1.5 | 3.0        | 2.0 | 74.1  | 55.9 | 14.5   | 12.9              | 72.2    | 54.8 | 14.4   | 12.4 |
| <i>hornemanni</i>     | 0.0          | 0.0 | 0.5 | 2.5        | 2.5 | 77.9  | 60.6 | 15.0   | 11.6              | 75.2    | 59.7 | 14.4   | 11.4 |
| <i>flavirostris</i>   | 1.5          | 0.0 | 0.0 | 1.5        | 1.5 | 77.7  | 58.5 | 15.8   | 11.5              | 75.6    | 56.9 | 15.8   | 11.5 |
| <i>yemenensis</i>     | 0.0          | 0.0 | 0.0 | 2.5        | 2.5 | 79.0  | —    | 14.4   | 11.4              | 70.5    | —    | 14.4   | 11.4 |
| <i>johannis</i>       | 0.0          | 0.5 | 0.0 | 3.0        | 3.0 | 75.0  | —    | 13.0   | 9.0               | 75.0    | —    | 13.0   | 9.0  |
| <i>Leucosticte</i>    |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>nemorica</i>       | 0.0          | 0.0 | 0.0 | 2.0        | 1.5 | 99.5  | 68.5 | 20.5   | 13.5              | 99.0    | 66.5 | 20.5   | 13.5 |
| <i>branti</i>         | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 117.5 | 77.7 | 21.0   | 13.8              | 111.0   | 72.0 | 21.0   | 14.5 |
| <i>a. atrata</i>      | 0.0          | 1.0 | 1.0 | 2.0        | 1.0 | 112.0 | 67.5 | 20.0   | 11.5              | 105.5   | 67.5 | 20.0   | 11.5 |
| <i>a. arctoa</i>      | 0.0          | 0.0 | 0.0 | 1.0        | 1.0 | 116.4 | 76.0 | —      | 11.7              | 112.4   | 72.6 | —      | 11.6 |
| <i>Callacanthis</i>   |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>burtoni</i>        | 1.0          | 2.0 | 2.0 | 3.0        | 2.0 | 100.0 | 64.0 | 19.0   | 18.0              | 98.5    | 61.0 | 19.0   | 18.0 |
| <i>Rhodopechys</i>    |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>sanquinea</i>      | 0.5          | 0.5 | 0.0 | 3.0        | 2.0 | 107.1 | 57.7 | 20.5   | 16.4              | 102.6   | 55.5 | 19.7   | 16.3 |
| <i>githaginea</i>     | 1.0          | 1.5 | 1.5 | 2.5        | 1.0 | 87.8  | 50.9 | 18.1   | 12.3              | 85.6    | 48.9 | 17.4   | 12.6 |
| <i>mongolica</i>      | 1.0          | 1.0 | 1.5 | 2.0        | 1.0 | 91.1  | 54.1 | 17.4   | 12.5              | 87.9    | 51.8 | 17.2   | 12.3 |
| <i>obsoleta</i>       | 0.0          | 0.5 | 0.0 | 2.0        | 2.0 | 88.1  | 59.9 | 17.3   | 14.7              | 85.8    | 58.1 | 17.1   | 14.6 |
| <i>Uragus</i>         |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>sibiricus</i>      | 1.0          | 2.0 | 2.0 | 3.5        | 1.5 | 74.5  | 80.0 | 15.8   | 8.5               | 72.0    | 75.5 | 15.8   | 8.5  |
| <i>Urocynchramus</i>  |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>pylzowi</i>        | 1.0          | 2.0 | 2.0 | 2.5        | 1.5 | 71.2  | —    | —      | 10.0              | 71.0    | —    | —      | 10.0 |
| <i>Carpodacus</i>     |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>rubescens</i>      | 2.0          | 2.0 | 2.0 | 4.0        | 1.0 | 82.5  | 52.0 | 18.0   | 14.0              | 78.5    | 50.5 | 18.0   | 14.0 |
| <i>nipalensis</i>     | 1.0          | 2.0 | 2.0 | 3.0        | 1.5 | 88.5  | 59.5 | 21.5   | 14.5              | 82.0    | 57.0 | 21.5   | 14.5 |
| <i>e. erythrinus</i>  | 1.5          | 2.0 | 2.0 | 3.5        | 1.5 | 84.8  | 56.3 | 19.0   | 14.2              | 82.7    | 55.4 | 19.1   | 14.3 |
| <i>e. ferganensis</i> | 1.5          | 2.0 | 2.0 | 3.5        | 1.5 | 86.7  | 58.2 | 19.2   | 14.7              | 82.2    | —    | 19.3   | 14.4 |
| <i>purpureus</i>      | 1.5          | 2.0 | 2.0 | 3.5        | 2.0 | 80.5  | 56.5 | 17.8   | 11.0              | 79.0    | 56.5 | 17.8   | 11.0 |
| <i>cassinii</i>       | 0.5          | 2.0 | 2.0 | 3.0        | 2.0 | 93.0  | 63.7 | 18.3   | 12.5              | 89.2    | 63.7 | 18.3   | 12.5 |
| <i>mexicanus</i>      | 2.0          | 2.0 | 2.0 | 2.5        | 1.5 | 80.2  | 59.6 | 17.2   | 10.0              | 77.3    | 57.7 | 17.2   | 10.0 |
| <i>eos</i>            | 1.5          | 2.0 | 2.0 | 3.0        | 1.5 | 72.5  | —    | —      | —                 | 72.5    | —    | —      | —    |
| <i>rhodochrous</i>    | 1.0          | 2.0 | 2.0 | 3.0        | 1.5 | 73.0  | 60.0 | 19.5   | 15.0              | 69.0    | 60.0 | 19.5   | 15.0 |
| <i>vinaceus</i>       | 2.0          | 2.0 | 2.0 | 3.5        | 1.5 | 70.0  | 58.0 | 20.0   | 14.0              | 70.0    | 58.0 | 20.0   | 14.0 |
| <i>edwardsii</i>      | 2.0          | 2.0 | 2.0 | 2.5        | 1.5 | 82.0  | 64.0 | 23.5   | 15.0              | 79.5    | 62.5 | 23.5   | 15.0 |
| <i>synoicus</i>       | 0.5          | 2.0 | 1.5 | 2.0        | 1.0 | 92.4  | 62.1 | 19.9   | 13.7              | 87.4    | 59.2 | 19.7   | 13.6 |
| <i>roseus</i>         | 1.0          | 2.0 | 2.0 | 3.5        | 2.0 | 90.3  | 64.3 | 20.5   | 15.2              | 86.6    | 60.8 | 20.6   | 14.6 |
| <i>trifasciatus</i>   | 1.5          | 2.0 | 2.0 | 4.0        | 2.0 | 85.0  | 72.5 | 21.5   | 15.5              | 85.0    | 72.5 | 21.5   | 15.5 |
| <i>rhodopeplus</i>    | 2.0          | 2.0 | 2.0 | 3.5        | 1.5 | 86.0  | 70.5 | 23.0   | 14.5              | 86.0    | 70.5 | 23.0   | 14.5 |

## APPENDIX A, continued

| Genus species          | Dichromatism |     |     | Brightness |     | Males |      |        |                   | Females |      |        |      |
|------------------------|--------------|-----|-----|------------|-----|-------|------|--------|-------------------|---------|------|--------|------|
|                        | RD           | HD  | BD  | M          | F   | Wing  | Tail | Tarsus | Bill <sup>a</sup> | Wing    | Tail | Tarsus | Bill |
| <i>thura</i>           | 1.0          | 2.0 | 1.5 | 2.5        | 1.0 | 84.0  | 75.0 | 25.0   | 14.0              | 81.5    | 65.0 | 25.0   | 14.0 |
| <i>rhodochlamys</i>    | 2.0          | 2.0 | 2.0 | 3.5        | 1.0 | 88.5  | 71.5 | 21.0   | 14.8              | 90.0    | 67.5 | 21.0   | 14.8 |
| <i>rubicilloides</i>   | 1.0          | 2.0 | 2.0 | 3.5        | 1.5 | 105.0 | 88.0 | 24.5   | 18.0              | 102.0   | 88.0 | 24.5   | 18.0 |
| <i>rubicilla</i>       | 2.0          | 2.0 | 2.0 | 4.5        | 1.5 | 117.5 | 88.1 | 23.7   | 20.0              | 113.7   | 84.2 | 24.0   | 19.9 |
| <i>puniceus</i>        | 1.0          | 2.0 | 2.0 | 2.0        | 1.0 | 113.0 | 78.5 | 23.5   | 18.0              | 111.0   | 76.0 | 23.5   | 18.0 |
| <i>roborowskii</i>     | 1.0          | 2.0 | 2.0 | 3.5        | 1.5 | 122.0 | 90.0 | 21.0   | —                 | 122.0   | 90.0 | 21.0   | —    |
| <i>pulcherrimus</i>    | 1.5          | 2.0 | 1.5 | 2.5        | 1.0 | 77.5  | 63.0 | 20.0   | 13.0              | 76.0    | 63.0 | 20.0   | 13.0 |
| <i>Pinicola</i>        |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>enucleator</i>      | 2.0          | 2.0 | 2.0 | 3.5        | 2.5 | 109.4 | 84.8 | 22.2   | 21.0              | 109.2   | 84.9 | 22.5   | 21.0 |
| <i>subhimachala</i>    | 2.0          | 2.0 | 2.0 | 3.5        | 2.0 | 101.0 | 78.5 | 23.0   | 15.5              | 94.0    | 76.5 | 23.0   | 15.5 |
| <i>Haematospiza</i>    |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>sipahi</i>          | 2.0          | 2.0 | 2.0 | 6.0        | 2.0 | 103.0 | 64.5 | 20.5   | 18.0              | 99.0    | 60.5 | 20.5   | 18.0 |
| <i>Loxia</i>           |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>pytyopsittacus</i>  | 1.0          | 2.0 | 2.0 | 3.0        | 1.5 | 104.4 | 64.7 | 19.2   | 24.2              | 101.5   | 60.7 | 19.6   | 23.7 |
| <i>curvirostra</i>     | 2.0          | 2.0 | 2.0 | 4.0        | 1.5 | 97.4  | 58.3 | 18.3   | 22.9              | 95.3    | 55.9 | 18.3   | 22.5 |
| <i>scotica</i>         | 2.0          | 2.0 | 2.0 | 4.0        | 2.0 | 99.8  | 58.6 | 18.3   | 22.8              | 97.4    | 57.0 | 18.2   | 22.3 |
| <i>leucoptera</i>      | 2.0          | 2.0 | 2.0 | 3.5        | 2.0 | 92.1  | 60.9 | 16.1   | 20.3              | 88.4    | 58.9 | 16.1   | 19.6 |
| <i>Pyrrhula</i>        |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>nipalensis</i>      | 0.0          | 0.0 | 0.0 | 3.0        | 3.0 | 86.5  | 75.0 | 17.0   | 12.5              | 83.5    | 70.0 | 17.0   | 12.5 |
| <i>leucogenys</i>      | 0.0          | 0.0 | 0.0 | 2.5        | 2.5 | 79.0  | 66.0 | 19.0   | 12.0              | 79.0    | 66.0 | 19.0   | 12.0 |
| <i>aurantiaca</i>      | 0.0          | 2.0 | 1.0 | 3.0        | 2.0 | 81.5  | 57.5 | 18.0   | 13.0              | 81.5    | 57.5 | 18.0   | 13.0 |
| <i>erythrocephala</i>  | 0.0          | 2.0 | 2.0 | 3.5        | 2.0 | 76.5  | 65.0 | 18.5   | 11.5              | 78.0    | 65.0 | 18.5   | 11.5 |
| <i>erythaca</i>        | 0.0          | 0.0 | 2.0 | 3.0        | 2.0 | 83.0  | 70.0 | 17.0   | 12.0              | 82.0    | 70.0 | 17.0   | 12.0 |
| <i>pyrrhula</i>        | 0.0          | 2.0 | 2.0 | 3.5        | 2.0 | 93.8  | 70.5 | 18.0   | 15.5              | 91.8    | 69.6 | 17.7   | 15.2 |
| <i>Coccothraustes</i>  |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>coccothraustes</i>  | 0.5          | 0.5 | 0.0 | 3.5        | 3.5 | 103.6 | 57.2 | 21.4   | 25.3              | 101.4   | 55.5 | 20.9   | 24.4 |
| <i>vespertinus</i>     | 1.5          | 2.0 | 1.0 | 4.0        | 2.5 | 115.0 | 64.4 | 21.2   | 23.2              | 112.2   | 62.3 | 22.2   | 23.2 |
| <i>abellii</i>         | 0.5          | 2.0 | 1.0 | 4.0        | 2.0 | 103.0 | —    | —      | —                 | 103.0   | —    | —      | —    |
| <i>Eophona</i>         |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>migratoria</i>      | 0.0          | 2.0 | 0.0 | 2.5        | 2.5 | 102.5 | 78.5 | —      | 22.5              | 96.0    | 78.5 | —      | 22.5 |
| <i>personata</i>       | 0.0          | 0.0 | 0.0 | 3.0        | 3.0 | 115.0 | 89.0 | —      | 25.0              | 106.5   | 89.0 | —      | 23.0 |
| <i>Mycerobas</i>       |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>icterioides</i>     | 2.0          | 2.0 | 2.0 | 5.5        | 2.0 | 131.0 | 92.5 | 24.0   | 26.3              | 127.5   | 92.5 | 24.0   | 26.3 |
| <i>affinis</i>         | 1.0          | 1.5 | 1.0 | 5.5        | 3.0 | 129.5 | 92.5 | 27.5   | 27.0              | 126.5   | 87.0 | 27.5   | 27.0 |
| <i>melanozanthos</i>   | 1.0          | 2.0 | 1.5 | 3.0        | 2.5 | 128.5 | 77.0 | 23.5   | 28.0              | 127.0   | 75.0 | 23.0   | 29.5 |
| <i>carnipes</i>        | 0.0          | 1.5 | 2.0 | 2.0        | 1.0 | 116.5 | 94.0 | 27.5   | 30.0              | 67.0    | 94.0 | 27.5   | 28.0 |
| <i>Linurgus</i>        |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>olivaceus</i>       | 0.0          | 2.0 | 1.0 | 4.0        | 2.0 | 76.5  | 50.5 | 20.0   | 13.5              | 73.0    | 50.5 | 20.0   | 13.5 |
| <i>Rhynchostruthus</i> |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>socotranus</i>      | 0.0          | 0.0 | 0.0 | 3.0        | 3.0 | 89.0  | —    | 16.0   | 9.9               | 89.0    | —    | 16.0   | 9.9  |
| <i>Pyrrhoptes</i>      |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>epauletta</i>       | 2.0          | 2.0 | 2.0 | 2.5        | 2.0 | 77.5  | 58.0 | 19.5   | 13.5              | 75.5    | 54.5 | 19.5   | 13.5 |
| <i>Neospiza</i>        |              |     |     |            |     |       |      |        |                   |         |      |        |      |
| <i>concolor</i>        | 0.0          | 0.0 | 0.0 | 2.0        | 2.0 | 104.0 | —    | 20.0   | 21.0              | 104.0   | —    | 20.0   | 21.0 |

Data were not available for missing values in the table.

<sup>a</sup> To skull.

## APPENDIX B

Data on continent and altitude of species distribution, nest dispersion, nest placement, and migratory classification of cardueline finches

| Species                              | Continent <sup>a</sup> | Habitat <sup>b</sup> | Elevation <sup>c</sup> |      | Nest dispersion <sup>d</sup> | Nest placement <sup>e</sup> | Migratory status <sup>f</sup> | References <sup>g</sup> |
|--------------------------------------|------------------------|----------------------|------------------------|------|------------------------------|-----------------------------|-------------------------------|-------------------------|
|                                      |                        |                      | Min                    | Max  |                              |                             |                               |                         |
| <i>Serinus pusillus</i> <sup>h</sup> | PALEAR                 | C                    | 2000                   | 3000 | 1                            | 1                           | 0                             | 1, 2, 3, 28             |
| <i>Serinus pusillus</i>              | PALEAR                 | SC                   | 2000                   | 4600 | 2                            | 1                           | 1                             | 4                       |
| <i>Serinus serinus</i>               | PALEAR                 | SC                   | 0                      | 1200 | 2                            | 2                           | 2                             | 5, 6, 28                |
| <i>Serinus syriacus</i>              | PALEAR                 | SC                   | 900                    | 1800 | 2                            | 1                           | 2                             | 1, 17, 28               |

## APPENDIX B, continued

| Species                        | Continent <sup>a</sup> | Habitat <sup>b</sup> | Elevation <sup>c</sup> |      | Nest disper-<br>sion <sup>d</sup> | Nest place-<br>ment <sup>e</sup> | Migra-<br>tory<br>status <sup>f</sup> | References <sup>g</sup> |
|--------------------------------|------------------------|----------------------|------------------------|------|-----------------------------------|----------------------------------|---------------------------------------|-------------------------|
|                                |                        |                      | Min                    | Max  |                                   |                                  |                                       |                         |
| <i>Serinus thibetanus</i>      | PALEAR                 | C                    | 2800                   | 4000 | —                                 | —                                | 1                                     | 1                       |
| <i>Serinus canaria</i>         | PALEAR                 | C                    | 0                      | 1700 | 2                                 | 3                                | 0                                     | 6, 7, 28                |
| <i>Serinus canicollis</i>      | AFRICA                 | SC                   | 2000                   | 4300 | 3                                 | 2                                | 0                                     | 1, 8, 9, 10             |
| <i>Serinus citrinella</i>      | PALEAR                 | C                    | 1000                   | 3000 | 3                                 | 2                                | 1                                     | 11, 28                  |
| <i>Serinus mozambicus</i>      | AFRICA                 | SC                   | 0                      | 1800 | —                                 | 3                                | 2                                     | 1, 9, 12, 13            |
| <i>Serinus dorsostriatus</i>   | AFRICA                 | SC                   | 1000                   | 2000 | —                                 | 3                                | 0                                     | 1, 9, 14, 17            |
| <i>Serinus scotops</i>         | AFRICA                 | C                    | 0                      | 1800 | —                                 | 3                                | 0                                     | 1, 9, 15, 17            |
| <i>Serinus flaviventris</i>    | AFRICA                 | O                    | 0                      | —    | —                                 | 3                                | 0                                     | 1, 9, 15                |
| <i>Serinus sulphuratus</i>     | AFRICA                 | O                    | 1000                   | 2400 | —                                 | 3                                | —                                     | 1, 9, 15                |
| <i>Serinus donaldsoni</i>      | AFRICA                 | O                    | 0                      | 1300 | —                                 | —                                | 0                                     | 1, 9                    |
| <i>Serinus nigriceps</i>       | AFRICA                 | SC                   | 1800                   | 4100 | —                                 | 1                                | 0                                     | 1, 9, 14                |
| <i>Serinus citrinelloides</i>  | AFRICA                 | O                    | 1000                   | 3000 | 3                                 | 1                                | 0                                     | 1, 15, 17               |
| <i>Serinus capistratus</i>     | AFRICA                 | C                    | 0                      | 1500 | —                                 | 3                                | —                                     | 1, 15                   |
| <i>Serinus koliensis</i>       | AFRICA                 | SC                   | 900                    | 1600 | —                                 | —                                | 0                                     | 1, 6                    |
| <i>Serinus leucopygius</i>     | AFRICA                 | O                    | 0                      | 1000 | —                                 | 3                                | 0                                     | 1, 9, 15                |
| <i>Serinus atrogularis</i>     | AFRICA                 | O                    | 900                    | —    | 3                                 | 3                                | 2                                     | 1, 12, 13               |
| <i>Serinus menachensis</i>     | ARABIA                 | O                    | 2000                   | 3666 | —                                 | 4                                | —                                     | 1, 9, 16                |
| <i>Serinus totta</i>           | AFRICA                 | O                    | —                      | —    | —                                 | 4                                | 1                                     | 1, 15, 17               |
| <i>Serinus symonsi</i>         | AFRICA                 | O                    | 2400                   | —    | —                                 | 1                                | 1                                     | 1, 15                   |
| <i>Serinus albogularis</i>     | AFRICA                 | O                    | 0                      | —    | —                                 | 1                                | 2                                     | 1, 9, 15                |
| <i>Serinus gularis</i>         | AFRICA                 | C                    | 1200                   | 2000 | 2                                 | 3                                | 2                                     | 8, 9, 14, 15, 18        |
| <i>Serinus mennelli</i>        | AFRICA                 | SC                   | 600                    | 1950 | 1                                 | 2                                | 2                                     | 6, 8, 9, 17, 19         |
| <i>Serinus tristriatus</i>     | AFRICA                 | SC                   | 1060                   | 3330 | —                                 | 3                                | —                                     | 1, 9, 14                |
| <i>Serinus leucopterus</i>     | AFRICA                 | SC                   | —                      | —    | —                                 | 1                                | 0                                     | 1, 6, 15                |
| <i>Serinus striolatus</i>      | AFRICA                 | SC                   | 1300                   | 4300 | —                                 | 3                                | 0                                     | 1, 9, 15, 17            |
| <i>Serinus rothschildi</i>     | ARABIA                 | SC                   | 1000                   | 2800 | —                                 | —                                | 0                                     | 1, 9, 16                |
| <i>Serinus citrinipectus</i>   | AFRICA                 | O                    | 0                      | 750  | —                                 | 1                                | 2                                     | 9, 12, 20               |
| <i>Serinus ankoberensis</i>    | AFRICA                 | O                    | 2980                   | 3200 | 1                                 | 4                                | —                                     | 9, 21, 22               |
| <i>Serinus burtoni</i>         | AFRICA                 | SC                   | 1500                   | 3000 | —                                 | —                                | —                                     | 1                       |
| <i>Serinus flavigula</i>       | AFRICA                 | O                    | 1400                   | 1500 | —                                 | —                                | 0                                     | 1, 22                   |
| <i>Serinus xantholaema</i>     | AFRICA                 | O                    | 0                      | —    | —                                 | —                                | 2                                     | 1, 9                    |
| <i>Serinus alario</i>          | AFRICA                 | O                    | —                      | —    | 3                                 | 1                                | 2                                     | 9, 13, 15               |
| <i>Serinus rufobrunneus</i>    | AFRICA                 | SC                   | 0                      | 900  | —                                 | —                                | —                                     | 1, 9                    |
| <i>Serinus estherae</i>        | PALEAR                 | O                    | 1400                   | 3400 | —                                 | —                                | —                                     | 1, 23                   |
| <i>Carduelis cannabina</i>     | PALEAR                 | SC                   | 0                      | 2200 | 3                                 | 1                                | 4                                     | 5, 7, 24, 25, 26        |
| <i>Carduelis spinus</i>        | PALEAR                 | C                    | 0                      | 1800 | 2                                 | 2                                | 2                                     | 7, 24, 27, 28           |
| <i>Carduelis chloris</i>       | PALEAR                 | SC                   | 0                      | 1400 | 2                                 | 3                                | 4                                     | 5, 7, 24, 28            |
| <i>Carduelis sinica</i>        | PALEAR                 | SC                   | 0                      | 2400 | 1                                 | 2                                | 4                                     | 29, 30, 31              |
| <i>Carduelis spinoides</i>     | PALEAR                 | C                    | 1600                   | 4400 | 3                                 | 2                                | 1                                     | 32, 33                  |
| <i>Carduelis monguilloti</i>   | PALEAR                 | C                    | 1000                   | —    | —                                 | —                                | —                                     | 1                       |
| <i>Carduelis ambigua</i>       | PALEAR                 | SC                   | 1800                   | 4000 | —                                 | 1                                | 2                                     | 32, 34                  |
| <i>Carduelis carduelis</i>     | PALEAR                 | SC                   | 0                      | 4250 | 2                                 | 2                                | 2                                     | 2, 7, 24, 35, 36        |
| <i>Carduelis tristis</i>       | NAMERI                 | SC                   | —                      | —    | —                                 | 2                                | 2                                     | 37, 38, 39              |
| <i>Carduelis psaltria</i>      | NAMERI                 | O                    | 0                      | 3100 | 3                                 | 3                                | 2                                     | 37, 40                  |
| <i>Carduelis pinus</i>         | NAMERI                 | C                    | —                      | —    | 3                                 | 2                                | 2                                     | 37                      |
| <i>Carduelis cucullata</i>     | SAMERI                 | SC                   | 280                    | 1300 | —                                 | 2                                | 2                                     | 41, 42                  |
| <i>Carduelis siemiradzkii</i>  | SAMERI                 | SC                   | 0                      | 800  | —                                 | —                                | —                                     | 1                       |
| <i>Carduelis atriceps</i>      | MAMERI                 | SC                   | 2350                   | 3050 | —                                 | —                                | —                                     | 1                       |
| <i>Carduelis spinescens</i>    | SAMERI                 | SC                   | 1800                   | 4100 | —                                 | —                                | 2                                     | 1, 41                   |
| <i>Carduelis jarrellii</i>     | SAMERI                 | SC                   | 0                      | 500  | —                                 | —                                | —                                     | 1, 41                   |
| <i>Carduelis crassirostris</i> | SAMERI                 | O                    | 3000                   | 4800 | —                                 | —                                | 2                                     | 1                       |
| <i>Carduelis magellanicus</i>  | SAMERI                 | O                    | 0                      | 5000 | —                                 | —                                | 2                                     | 1                       |
| <i>Carduelis dominicensis</i>  | MAMERI                 | SC                   | 1500                   | —    | 3                                 | —                                | 1                                     | 1                       |
| <i>Carduelis olivacea</i>      | SAMERI                 | C                    | 1200                   | 3000 | —                                 | —                                | —                                     | 1                       |
| <i>Carduelis notata</i>        | MAMERI                 | C                    | 1000                   | 2750 | —                                 | —                                | 2                                     | 1                       |
| <i>Carduelis xanthogastra</i>  | SAMERI                 | C                    | 1400                   | 3700 | —                                 | 2                                | 0                                     | 1, 43                   |
| <i>Carduelis atrata</i>        | SAMERI                 | O                    | 1800                   | 4800 | —                                 | —                                | 0                                     | 1, 44                   |
| <i>Carduelis uropygialis</i>   | SAMERI                 | SC                   | 2500                   | 4000 | —                                 | —                                | 2                                     | 1                       |
| <i>Carduelis barbata</i>       | SAMERI                 | SC                   | 0                      | 1500 | —                                 | —                                | 2                                     | 1                       |
| <i>Carduelis lawrencei</i>     | NAMERI                 | O                    | 0                      | —    | 3                                 | 2                                | 2                                     | 37, 45                  |
| <i>Carduelis flammea</i>       | HOLARC                 | SC                   | 0                      | —    | 2                                 | 5                                | 4                                     | 7, 46, 47, 48           |
| <i>Carduelis hornemanni</i>    | HOLARC                 | O                    | 0                      | —    | 3                                 | 5                                | 4                                     | 7, 28, 49               |
| <i>Carduelis flavirostris</i>  | PALEAR                 | O                    | 0                      | 1000 | 1                                 | 0                                | 4                                     | 50                      |
| <i>Carduelis f. montanella</i> | PALEAR                 | O                    | 3000                   | 4850 | 3                                 | 5                                | 4                                     | 7, 28                   |
| <i>Carduelis yemenensis</i>    | ARABIA                 | O                    | 1800                   | 3660 | 3                                 | —                                | 1                                     | 1, 51                   |
| <i>Carduelis johannis</i>      | AFRICA                 | SC                   | 1200                   | 2400 | —                                 | —                                | —                                     | 1, 52                   |
| <i>Leucosticte nemoricola</i>  | PALEAR                 | O                    | 2300                   | 5300 | 3                                 | 4                                | 2                                     | 2, 32                   |
| <i>Leucosticte branti</i>      | PALEAR                 | O                    | 3950                   | 6000 | 3                                 | 4                                | 0                                     | 7, 32                   |
| <i>Leucosticte a. atrata</i>   | HOLARC                 | O                    | 0                      | 100  | 1                                 | 4                                | 0                                     | 53, 54, 55              |
| <i>Leucosticte a. arctoa</i>   | HOLARC                 | O                    | 3000                   | 5000 | 3                                 | 4                                | 1                                     | 7, 56                   |
| <i>Callacanthus burtoni</i>    | PALEAR                 | SC                   | 2270                   | 3330 | —                                 | 2                                | 1                                     | 1, 35                   |
| <i>Rhodopechys sanquinea</i>   | PALEAR                 | O                    | 2000                   | 3200 | 2                                 | 0                                | 1                                     | 1, 32, 66               |
| <i>Rhodopechys githaginea</i>  | PALEAR                 | O                    | 350                    | 2000 | 1                                 | 4                                | 4                                     | 7, 32, 57, 58           |
| <i>Rhodopechys mongolica</i>   | PALEAR                 | O                    | 400                    | 4750 | 3                                 | 4                                | 2                                     | 57, 58                  |
| <i>Rhodopechys obsoleta</i>    | PALEAR                 | O                    | 0                      | 1500 | 3                                 | 2                                | 2                                     | 7, 59, 60               |
| <i>Uragus sibiricus</i>        | PALEAR                 | SC                   | —                      | 3400 | —                                 | 1                                | 2                                     | 1, 7                    |

## APPENDIX B, continued

| Species                              | Continent <sup>a</sup> | Habitat <sup>b</sup> | Elevation <sup>c</sup> |      | Nest disper-<br>sion <sup>d</sup> | Nest place-<br>ment <sup>e</sup> | Migra-<br>tory<br>status <sup>f</sup> | References <sup>g</sup> |
|--------------------------------------|------------------------|----------------------|------------------------|------|-----------------------------------|----------------------------------|---------------------------------------|-------------------------|
|                                      |                        |                      | Min                    | Max  |                                   |                                  |                                       |                         |
| <i>Urocynchramus pylzowi</i>         | PALEAR                 | O                    | 3050                   | 5000 | —                                 | —                                | 0                                     | 1                       |
| <i>Carpodacus nipalensis</i>         | PALEAR                 | SC                   | 3030                   | 4800 | —                                 | —                                | 1                                     | 1                       |
| <i>Carpodacus mexicanus</i>          | NAMERI                 | SC                   | 0                      | 1500 | 1                                 | 2                                | 0                                     | 65                      |
| <i>Carpodacus rhodopeplus</i>        | PALEAR                 | O                    | 3000                   | 5000 | —                                 | —                                | 1                                     | 1                       |
| <i>Carpodacus purpureus</i>          | NAMERI                 | C                    | 0                      | —    | 1                                 | 2                                | 2                                     | 1, 62                   |
| <i>Carpodacus cassinii</i>           | NAMERI                 | C                    | 1500                   | 3000 | 1                                 | 2                                | 2                                     | 1, 63, 64               |
| <i>Carpodacus rhodochlamys</i>       | PALEAR                 | SC                   | 2720                   | 4900 | 1                                 | 3                                | 1                                     | 2, 4, 7, 32             |
| <i>Carpodacus rubicilloides</i>      | PALEAR                 | O                    | 3700                   | 5800 | —                                 | —                                | 1                                     | 32                      |
| <i>Carpodacus eos</i>                | PALEAR                 | O                    | 3950                   | 5300 | —                                 | —                                | 1                                     | 32                      |
| <i>Carpodacus e. erythrinus</i>      | PALEAR                 | SC                   | 0                      | 1999 | 1                                 | 1                                | 3                                     | 7, 24, 28, 61           |
| <i>Carpodacus e. ferghanensis</i>    | PALEAR                 | O                    | 2000                   | 4550 | 1                                 | 1                                | 3                                     | 2, 7, 28, 76            |
| <i>Carpodacus rubicilla</i>          | PALEAR                 | O                    | 3000                   | 5100 | 2                                 | 4                                | 1                                     | 7, 28, 32               |
| <i>Carpodacus roborowskii</i>        | PALEAR                 | O                    | 4500                   | 5400 | —                                 | —                                | 0                                     | 1                       |
| <i>Carpodacus rhodochrous</i>        | PALEAR                 | SC                   | 2250                   | 4540 | —                                 | 2                                | 1                                     | 32                      |
| <i>Carpodacus synoicus</i>           | PALEAR                 | O                    | 2000                   | 3350 | 2                                 | 4                                | 0                                     | 28, 32                  |
| <i>Carpodacus roseus</i>             | PALEAR                 | SC                   | 0                      | 3030 | —                                 | 2                                | 3                                     | 28, 32                  |
| <i>Carpodacus vinaceus</i>           | PALEAR                 | SC                   | 1970                   | 3500 | —                                 | —                                | 0                                     | 1                       |
| <i>Carpodacus trifasciatus</i>       | PALEAR                 | SC                   | 2130                   | 3050 | —                                 | —                                | 1                                     | 1, 32                   |
| <i>Carpodacus rubescens</i>          | PALEAR                 | C                    | 3000                   | 5000 | —                                 | —                                | 1                                     | 32                      |
| <i>Carpodacus thura</i>              | PALEAR                 | O                    | 3200                   | 5000 | —                                 | 1                                | 0                                     | 32                      |
| <i>Carpodacus pulcherrimus</i>       | PALEAR                 | O                    | 3600                   | 5000 | —                                 | 1                                | 0                                     | 32                      |
| <i>Carpodacus puniceus</i>           | PALEAR                 | O                    | 3000                   | 5700 | —                                 | 4                                | 0                                     | 32                      |
| <i>Carpodacus edwardsii</i>          | PALEAR                 | SC                   | 3050                   | 4240 | —                                 | —                                | 1                                     | 1                       |
| <i>Pinicola enucleator</i>           | HOLARC                 | C                    | 1250                   | 2000 | 1                                 | 2                                | 2                                     | 7, 28                   |
| <i>Pinicola subhimachala</i>         | PALEAR                 | O                    | 3500                   | 4200 | —                                 | —                                | 1                                     | 1                       |
| <i>Haematospiza sipahi</i>           | PALEAR                 | C                    | 1600                   | 3355 | —                                 | 3                                | 1                                     | 1                       |
| <i>Loxia curvirostra</i>             | HOLARC                 | C                    | 0                      | 4500 | 1                                 | 2                                | 2                                     | 2, 7, 24, 28            |
| <i>Loxia leucoptera</i>              | HOLARC                 | C                    | 0                      | —    | 3                                 | 2                                | 2                                     | 7, 67, 68, 69           |
| <i>Loxia scotica</i>                 | PALEAR                 | C                    | 0                      | —    | 1                                 | 2                                | 2                                     | 1                       |
| <i>Loxia pytyopsittacus</i>          | PALEAR                 | C                    | 0                      | —    | 3                                 | 2                                | 4                                     | 1                       |
| <i>Pyrrhula leucogenys</i>           | PALEAR                 | C                    | 1250                   | 1750 | —                                 | —                                | 1                                     | 1                       |
| <i>Pyrrhula erythrocephala</i>       | PALEAR                 | C                    | 2700                   | 4200 | —                                 | —                                | 1                                     | 32                      |
| <i>Pyrrhula erythaca</i>             | PALEAR                 | C                    | 2500                   | 4500 | 0                                 | —                                | 1                                     | 32                      |
| <i>Pyrrhula auranitiaca</i>          | PALEAR                 | C                    | 3000                   | 4300 | —                                 | 2                                | 1                                     | 32                      |
| <i>Pyrrhula pyrrhula</i>             | PALEAR                 | C                    | 0                      | 2900 | 0                                 | 3                                | 4                                     | 5, 70                   |
| <i>Pyrrhula nipalensis</i>           | PALEAR                 | SC                   | 2200                   | 4000 | —                                 | —                                | 0                                     | 32                      |
| <i>Eophona migratoria</i>            | PALEAR                 | C                    | 0                      | 2000 | —                                 | 3                                | 4                                     | 1, 7                    |
| <i>Eophona personata</i>             | PALEAR                 | SC                   | 0                      | —    | —                                 | 2                                | 4                                     | 1, 7                    |
| <i>Mycerobas icteroides</i>          | PALEAR                 | SC                   | 1800                   | 3500 | —                                 | 2                                | 1                                     | 1, 32                   |
| <i>Mycerobas affinis</i>             | PALEAR                 | SC                   | 2700                   | 4800 | —                                 | —                                | 1                                     | 1, 32                   |
| <i>Mycerobas melanozanthos</i>       | PALEAR                 | C                    | 2400                   | 3600 | —                                 | 2                                | 1                                     | 32                      |
| <i>Mycerobas carnipes</i>            | PALEAR                 | SC                   | 2800                   | 4600 | 2                                 | 3                                | 1                                     | 2, 71                   |
| <i>Coccothraustes coccothraustes</i> | PALEAR                 | C                    | 0                      | 3000 | 2                                 | 2                                | 4                                     | 5, 7                    |
| <i>Coccothraustes vespertinus</i>    | NAMERI                 | C                    | 2000                   | —    | 1                                 | 2                                | 2                                     | 72, 73                  |
| <i>Coccothraustes abeillei</i>       | MAMERI                 | C                    | 1000                   | 3350 | —                                 | —                                | 0                                     | 1                       |
| <i>Linurgus olivaceus</i>            | AFRICA                 | C                    | 1524                   | 3048 | —                                 | 1                                | 0                                     | 15, 74                  |
| <i>Rhynchostruthus socotranus</i>    | ARABIA                 | SC                   | 1060                   | 3100 | —                                 | —                                | 0                                     | 75                      |
| <i>Pyrrhoplectes epauletta</i>       | PALEAR                 | O                    | 2800                   | 4800 | —                                 | —                                | 1                                     | 32                      |
| <i>Neospiza concolor</i>             | SAOTOM                 | C                    | —                      | —    | —                                 | —                                | —                                     | 1                       |

Data were not available for missing values in the table.

- <sup>a</sup> Continent: PALEAR, Palearctic; NAMERI, MAMERI, SAMERI, North, Middle, and South Americas; HOLARC, Holarctic; SAOTOM, São Tomé; <sup>b</sup> Habitat type: C, closed (i.e., montane and lowland forests, parks); SC, semiclosed (i.e., subalpine and lowland shrubs, ecotones); O, open (i.e., alpine and lowland meadows, mountain and lowland steppe, agricultural fields). <sup>c</sup> Breeding range elevation; <sup>d</sup> Nest dispersion: 1, solitary (i.e., dispersed); 2, dispersed/aggregated (mixed); 3, aggregated, and 4, colonial. <sup>e</sup> Nest placement: 0, ground; 1, shrubs; 2, trees; 3, shrubs/trees; 4, crevices; 5, ground/shrubs. <sup>f</sup> Migratory status: 0, resident; 1, altitudinal migrant; 2, local/short distance migrant; 3, migrant; 4, 2+3. <sup>g</sup> References: 1) Clement et al., 1993; 2) Kovshar, 1979; 3) Badyaev, 1993; 4) Badyaev AV, unpublished data; 5) Newton, 1973; 6) van den Elzen and Nemeschkal, 1991; 7) Boehme, 1954; 8) Brickel, 1987; 9) van den Elzen, 1985; 10) Wolff and Jacobsen, 1980; 11) Brandl and Bezzel, 1988; 12) Irwin, 1979; 13) Brickel, 1989; 14) Mackworth-Praed and Grant, 1953; 15) Macworth-Praed and Grant, 1963; 16) Everett, 1987; 17) van den Elzen, 1983; 18) Irwin, 1977; 19) Vernon, 1979; 20) Clenslow, 1993; 21) Ash, 1979; 22) Ash and Gullick, 1990; 23) Bishop and King, 1986; 24) Mal'chevski and Pukinski, 1983; 25) Tast, 1970; 26) Ruelle, 1986a; 27) Senar, 1984; 28) Cramp and Perrins, 1994; 29) Haredo and Nakamura, 1970; 30) Nakamura, 1982; 31) Nakamura, 1991; 32) Boehme, 1975; 33) Ruelle, 1986b; 34) van den Elzen and Classen, 1992; 35) Desfayes, 1969; 36) Conder, 1948; 37) Bent, 1968; 38) Middleton, 1988; 39) Middleton, 1993; 40) Lindsdale, 1957; 41) Meyer de Schauensee and Phelps, 1978; 42) Coats and Phelps, 1985; 43) Miller, 1963; 44) Navas and Bo, 1991; 45) Coutlee, 1968; 46) Pulliainen, 1979; 47) Troy and Shields, 1979; 48) Seutin et al., 1991; 49) Herremans, 1990; 50) Marler and Mudinger, 1975; 51) Bowden and Brooks, 1987; 52) Ash and Miskel, 1981; 53) Johnson, 1983; 54) French, 1954; 55) Shreeve, 1977; 56) Potapov, 1963; 57) Panov, 1989; 58) Bartherl et al., 1992; 59) Ponomareva, 1981; 60) Yosef, 1991; 61) Björklund, 1990b; 62) Wootton, 1996; 63) Samson, 1976; 64) Medwaldt and King, 1985; 65) Hill, 1993a; 66) Gubin, 1979; 67) Benkman, 1989; 68) Benkman, 1992; 69) Pulliainen and Tuomainen, 1978; 70) Bijlsma, 1982; 71) Badyaev, 1994; 72) Fee and Bekoff, 1986; 73) Scott and Bekoff, 1991; 74) Ellis, 1981; 75) Martins, 1987; 76) Iovchenko, 1986.
- <sup>b</sup> Mountain forest population. <sup>c</sup> Subalpine population. <sup>d</sup> *C. f. pipilans*.

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