OIKOS 80: 128–138. Copenhagen 1997

Covariation between life history and sexually selected traits: an example with cardueline finches

Alexander V. Badyaev

Badyaev, A. V. 1997. Covariation between life history and sexually selected traits: an example with cardueline finches. – Oikos 80: 128–138.

Traits associated with fecundity and survival are often subject to similar trade-offs because allocation of resources to one activity will limit the others. Such trade-offs have been proposed to account for sex-specific associations between life history and sexually selected traits. In this study I examined life history correlates of variation in sexual dimorphism in cardueline finches. These birds show strong variation in plumage sexual dichromatism. While this variation may reflect changes in intensity of sexual selection or cost of mate sampling, it could also be caused by differences in the costs of secondary sexual traits. I used path analysis to control for potential effects of breeding altitude, nest height, body size, migratory class, and phylogeny to show that variation in sexual dichromatism and plumage brightness in both sexes closely corresponded to variation in life history traits. Sexual dichromatism was negatively correlated with clutch size. Association between sexual ornamentation and fecundity was different for males and females. Male plumage brightness was negatively correlated with clutch size and numbers of broods, but female brightness was positively correlated with clutch size across extant cardueline finches. Nest height and altitude of breeding covaried with sexual dichromatism and with sexual ornamentation in both sexes. Association of sexual ornamentation with clutch size and numbers of broods was more similar between sexes in high-elevation species than in low-elevation species. In males, associations among plumage brightness and life history traits changed more with altitude compared to females. Similar selection pressures caused by equal sharing of parental care between sexes at higher altitudes may account for this pattern.

A. V. Badyaev, Div. of Biological Sciences, Univ. of Montana, Missoula, MT 59812, USA (abadyaev@selway.umt.edu).

The expression of secondary sexual traits may covary with such life history traits as fecundity and survival (McLain 1991, Promislow 1992, Winemiller 1992, Owens and Benett 1994, Promislow et al. 1994, McLain et al. 1995). Development of secondary sexual traits affects both current and future reproduction and could be subject to constraints similar to other aspects of general reproductive effort (Williams 1992). Concurrently, interspecific variation in secondary sexual traits may be affected by a balance between the intensity of sexual selection that favors expression of secondary sexual traits and viability costs associated with such traits (Darwin 1871, Kirkpatrick et al. 1990, Andersson 1994).

Association between sexually selected and life history traits could indicate common mechanisms causing variation in both kinds of traits (McLain 1991, 1993, Winemiller 1992). For example, variation in adult mortality may influence both sexual dimorphism and fecundity (Charlesworth 1980, Promislow et al. 1992); female mortality may constrain the upper limit of sexual dimorphism by limiting the maximum mortality rate of males (Promislow et al. 1994). Thus, negative correlation between species' fecundity and sexual dimorphism

Accepted 15 January 1997

ISSN 0030-1299

Table 1. Analysis of covariance of life history traits and sexual dichromatism among cardueline finches, while correcting for phylogeny and potential covariates.

	Dependent variables							
	Clutch size		No. of broods		Incubation length		Nestling stage length	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Altitude	8.33	0.008*	17.75	0.000*	16.53	0.000*	0.14	0.709
Nest height	5.07	0.024*	2.82	0.089	0.55	0.461	2.70	0.111
Migratory class	2.58	0.122	0.62	0.440	0.61	0.439	0.40	0.533
Body size	0.34	0.566	4.92	0.036	0.00	0.983	0.28	0.598
Sexual dichromatism	3.89	0.006*	1.03	0.320	3.09	0.089	0.46	0.505
Clutch size	···	···	···	···	0.96	0.336	0.68	0.416
No. of broods	2.50	0.139	···	···	···	···	···	···
Incubation length	0.34	0.564	0.02	0.879	···	···	9.77	0.004*
Nestling stage length	0.15	0.703	1.36	0.256	···	···	···	···
	$R^2 = 0.511$		$R^2 = 0.568$		$R^2 = 0.402$		$R^2 = 0.521$	
	$F_{8,32} = 2.88$		$F_{7,31} = 4.32$		$F_{6,38} = 3.47$		$F_{7,38} = 4.50$	

Note: * Indicates significance at $\alpha = 0.05$ level after correction using the table-wide sequential Bonferroni tests.

is expected if both correlations have a common cause (Andersson 1994).

Variation in paternal investment may also correlate with both sexual ornamentation and fecundity. Extensive paternal investment may limit male mating opportunities (Trivers 1972, Andersson 1994), thereby reducing the intensity of sexual selection (Kirkpatrick and Ryan 1991). Consequently, extent of paternal investment may decrease with development of male secondary sexual traits because variation in the intensity of sexual selection is widely assumed to exert strong selection on development of sexual ornamentation (Kirkpatrick and Ryan 1991, Williams 1992, Andersson 1994). Extent of parental care is also closely linked to the evolution of life history traits because investment in current reproduction affects current fecundity as well as survival and future fecundity (Williams 1966, Trivers 1972, Owens and Benett 1994, Martin 1995). In addition, species with reduced male help may exhibit lower fecundity (Lack 1968, Verner and Willson 1969). Thus, if male sexual ornamentation reflects paternal investment (Møller and Birkhead 1993, 1994), then, interspecifically, fecundity should negatively correlate with extent of male sexual ornamentation.

Females typically have higher investment in parental care and more mating opportunities (Trivers 1972). Thus, sexual ornamentation of females is often under strong natural selection (e.g., Breitwisch 1988, Promislow et al. 1992, 1994, Martin and Badyaev 1996). For example, in avian species where only females incubate, female sexual ornamentation negatively covaries with risk of nest predation (Martin and Badyaev 1996). Because nest predation is closely linked to fecundity (Slagsvold 1982, Martin 1995), species with more sexually ornamented females should exhibit higher fecundity compared to species with less ornamented females. Thus, males and females can differ in the direction of the relationship between sexual ornamentation and fecundity.

While life history and sexually selected traits may covary, environmental variation strongly constrains the evolution of both types of traits (Andersson 1994, Martin 1995). In particular, altitude is thought to be an important factor in the evolution of life history (e.g., Cody 1966, Berven 1982) and sexually selected traits (Badyaev unpubl.). Consequently, I controlled for effects of altitude while examining covariation between sexually selected and life history traits.

Variation in sexual dimorphism across 126 extant cardueline finch species provides a powerful system to examine interactions between life history and sexually selected traits. Cardueline finches are primarily arboreal or terrestrial seed-eating birds that occupy a wide variety of environmental conditions and exhibit extensive variation in plumage coloration and sexual dichromatism (Clement et al. 1993).

Here I examine associations among sexual dichromatism, male and female plumage brightness, and life history traits while controlling for potentially confounding effects of elevation, nest height, body size, migratory class, and phylogeny. I first examined whether variation in life history traits among finch species was associated with sexual ornamentation. I then compared associations among secondary sexual traits and life history traits for species breeding across an environmental gradient.

Methods

Plumage brightness was assessed by two persons, unaware of the questions being 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). The 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 (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 $r = 0.69$, $p < 0.001$), breast ($r = 0.89$, $p < 0.001$), head dichromatism ($r = 0.89$, $p < 0.001$), and overall brightness scores (males: $r = 0.79$, $p < 0.0001$, females: $r = 0.65$, $p < 0.001$). Log (female wing length) was used as a measure of body size. Mean scores for brightness and dimorphism in plumage are presented in Badyaev (unpubl.) and Martin and Badyaev (1996).

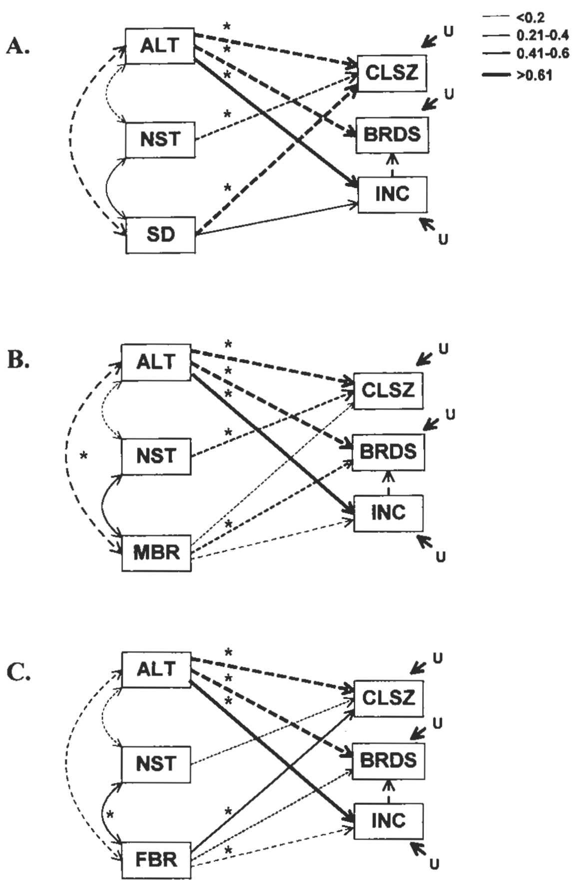

Fig. 1. Path model illustrating a causal model for the influences on clutch size (CLSZ), numbers of broods (BRDS), and incubation length (INC) by altitude of species' breeding (ALT), nest height (NST), and (A) sexual dichromatism (SD), (B) male plumage brightness (MBR), (C) female plumage brightness (FBR). Double-headed arrows indicate covariation between two variables. Single-headed arrows show that change in the variable at the base of the arrow will cause a change in the one at the arrow's head. The single-headed arrows with U indicate effects of unmeasured factors. Positive effects are indicated by solid lines and negative effects by dashed lines. Thickness of the arrows indicate the magnitude of effect (standardized partial regression coefficients). Model-wide significance of path coefficients based on the sequential Bonferroni test shown as * for $\alpha < 0.06$.

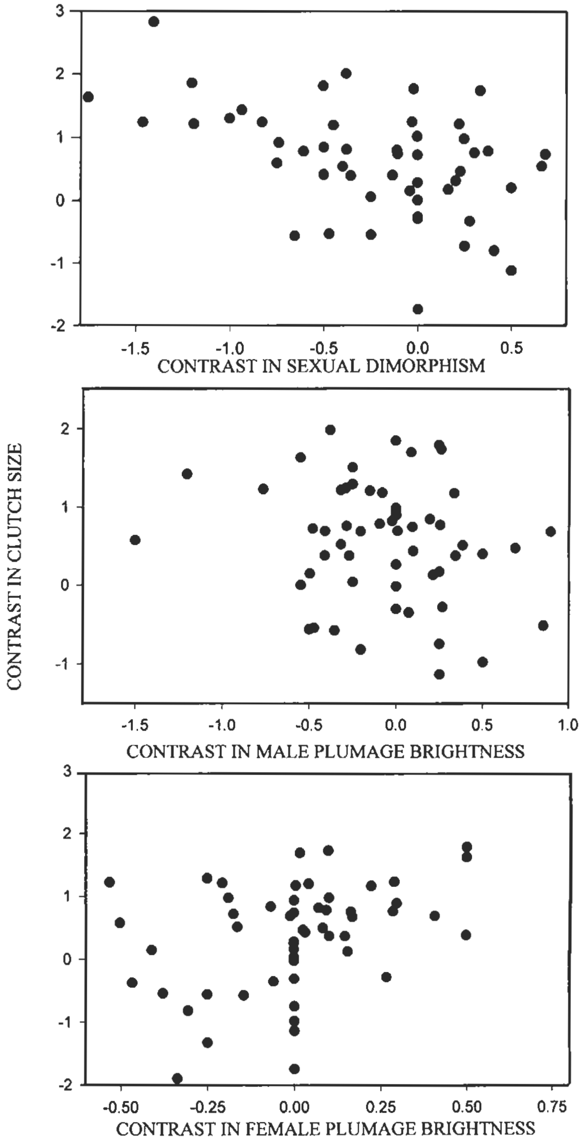

Fig. 2. Scatterplots of independent linear contrasts on the standardized residuals of clutch size (corrected for elevation and nest height) relative to sexual dichromatism ($b_{ST} = -0.37$, $p = 0.02$), male plumage brightness ($b_{ST} = -0.15$, $p = 0.06$), and female plumage brightness ($b_{ST} = 0.20$, $p = 0.04$).

I gathered published data for 126 extant carduelinae species [Appendix; Martin and Badyaev (1996) and Badyaev (unpubl.)] on breeding elevation, body size, nest height, and migratory class, because these factors have been found to account for interspecific variation in such life history traits as clutch size, numbers of broods, incubation and nestling stage lengths (Martin 1995).

Table 2. Effect coefficients of ecological factors and sexual dichromatism on life history traits among cardueline finches based on the model in Fig. 1A.

Variable	Effect on			
	Clutch size	No. of broods		Incubation length
	Direct	Direct	Indirect	Direct
Altitude	-0.518	-0.856	0.261	0.593
Nest height	-0.256	···	···	···
Sexual dichromatism	-0.367	···	0.067	0.165
Incubation length	···	-0.441	···	···
	$R^2 = 0.452$	$R^2 = 0.415$		$R^2 = 0.336$
	$F_{3,32} = 7.812$	$F_{2,32} = 9.013$		$F_{2,41} = 9.617$

To control for possible phylogenetic effects, all data were analyzed 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 slopes significantly different from zero, thus validating the assumption (Purvis and Rambaut 1995). To examine the influence of categorical factors during initial examination of 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). See Martin and Badyaev (1996) and Martin and Clobert (1996) for further details of phylogenetic analyses. All data were square-root- and log-transformed before statistical analyses.

The phylogeny of cardueline finches represents a consensus tree constructed by summarizing all recent systematic data available for each clade and is described in detail elsewhere (Badyaev unpubl.). I did not have consistent estimates of branch lengths because data came from studies using different methods. However, because all extant cardueline species were included in the phylogenetic tree and plots of standardized contrasts against the variances of the untransformed contrasts showed no significant correlation, the use of equal branch lengths was justified (Garland et al. 1993, Purvis and Rambaut 1995).

I used path coefficients to quantify the strength of each proposed effect, when all other effects and correlations among them were held constant (see Mitchell 1993). I used multiple regressions to test the a priori predictions about the direction of relationships between life history and sexually selected traits. I employed path analysis to demonstrate the relative importance of paths between life history and sexually selected traits with other ecological factors present in the model and to access the overall fit of models (see below). Thus, my justification for the use of path analysis was not to explore correlations among proposed factors, but to test specific predictions of relationships among proposed factors (e.g., Petraitis et al. 1996). Models were constructed based on background information on covariation among ecological factors and life history traits (Mitchell 1993, Martin 1995). To maintain statistical power, I used significant factors (Table 1) to construct direct (causal) path coefficients (Fig. 1). Path coefficients, overall fit of the model, and Akaikes's Information Criterion (AIC) coefficients were estimated using the Covariance Analysis of Linear Structural Equations (CALIS) of SAS software (SAS Institute 1989). Overall fit of the models (distributed as χ^2) were likelihood ratio tests for the concordance between the elements in the covariance matrix computed from data and the matrix predicted by the path coefficients. Non-significant χ^2 values indicate that the model predicts a pattern of correlation among the variables that does not differ from the observed correlation and, therefore, constitutes a "good fit" of data (SAS Institute 1989). I used AIC to choose the best model because it emphasizes the simplest model with the greatest predictive power; the model that yields the smallest value of AIC is considered best (SAS Institute 1989). I examined residual plots and residual statistics to ensure validity of normality and variance homogeneity assumptions in regression analyses; in regression models variance inflation factor (<30) and condition index (<10) indicated that multicollinearity did not significantly bias coefficient estimates (Montgomery and Peck 1992). The sequential Bonferroni tests were used to evaluate an individual coefficient's significance in ANCOVA and multiple regressions (Rice 1989).

Clutch size, numbers of broods, and length of incubation and nestling stage were the life history traits

Table 3. Summary of results for several sexual dichromatism models of effects on life history traits among cardueline finches.

Model	χ^2	df	p	AIC
1. Original model with SD (Fig. 1A)	0.825	5	0.975	−9.175
2. No path from SD to CLSZ	7.046	6	0.317	−4.954
3. No path from SD to INC	2.011	6	0.919	−9.989
4. No path from ALT to CLSZ	13.056	6	0.042	1.056
5. No path from ALT to BRDS	21.761	6	0.001	9.761
6. No path from ALT to INC	15.044	6	0.020	3.045
7. No path from NST to CLSZ	4.900	6	0.666	−7.919
8. No direct paths from SD	8.232	7	0.313	−5.768
9. No direct paths from ALT	48.210	8	0.000	32.210

used in this study. I used these traits instead of data on mortality because such direct data were few. Use of basic life history traits allowed increased statistical power to discriminate among influences of potentially confounding ecological factors.

Results

Sexual dimorphism in plumage and life history traits

Sexual dichromatism negatively correlated with clutch size, weakly positively correlated with duration of incubation, and did not vary with numbers of broods (Figs 1, 2, Tables 1–3, models 8 vs 1, $\chi^2 = 7.429$, df = 2, $p = 0.02$). Direct influence of sexual dichromatism on clutch size was much stronger than its influence on incubation length (AIC coefficient of −4.954 vs −9.989; Tables 2, 3). The model with the direct effect of sexual dichromatism on clutch size performed significantly better than the model without the path (Table 3, models 2 vs 1, $\chi^2 = 6.215$, df = 1, $p = 0.01$), as opposed to a lack of significant difference in performance of models with a direct effect of sexual dimorphism on incubation length vs without one (Table 3, models 3 vs 1, $\chi^2 = 1.186$, df = 1, $p = 0.28$). Breeding altitude and nest height were significantly correlated with cardueline life history traits (Tables 1–6). The effects of these variables were controlled in these analyses. Migratory class did not covary with measured life history traits (Table 1). Body size was significantly positively correlated with numbers of broods (Table 1), but models did not fit data significantly better when migratory class and body size were included (Fig. 1).

Male plumage brightness and life history traits

Male plumage brightness negatively covaried most strongly with numbers of broods, followed by a weak negative correlation with incubation length and clutch size (Fig. 3A, Table 4). The model without a direct effect of male brightness on numbers of broods performed significantly worse than the one with this effect (AIC coefficients −0.665 vs −6.335; Table 6; models 3 vs 1, $\chi^2 = 7.69$, df = 1, $p = 0.006$). Model performance did not differ when direct paths from male brightness to either incubation length or clutch size were excluded (Table 6, models 2 vs 1, $\chi^2 = 1.064$, df = 1, $p = 0.302$; models 4 vs 1, $\chi^2 = 2.702$, df = 1, $p = 0.1$). Overall, clutch size was more influenced by elevation of breeding and nest height than by male plumage brightness (Table 6). However, male plumage brightness explained a significant amount of variation in life history parameters and the model that included the direct effect of male brightness on life history traits performed much better that the one without direct paths (Table 6, models 6 vs 1, $\chi^2 = 11.456$, df = 3, $p = 0.009$).

Female plumage brightness and life history traits

Female plumage brightness most strongly negatively covaried with duration of incubation, followed by al-

Table 4. Effect coefficients of ecological factors and male plumage brightness on life history traits among cardueline finches (Fig. 1B).

Variable	Effect on			
	Clutch size	No. of broods		Incubation length
	Direct	Direct	Indirect	Direct
Altitude	−0.531	−0.800	0.185	0.579
Nest height	−0.323	…	…	…
Male plumage brightness	−0.150	−0.348	−0.073	−0.230
Incubation length	…	−0.319	…	…
	$R^2 = 0.439$	$R^2 = 0.532$		$R^2 = 0.290$
	$F_{3,58} = 14.349$	$F_{3,32} = 10.971$		$F_{2,41} = 7.964$

Table 5. Effect coefficients of ecological factors and female plumage brightness on life history traits among cardueline finches (Fig. 1C).

Variable	Effect on			
	Clutch size	No. of broods		Incubation length
	Direct	Direct	Indirect	Direct
Altitude	−0.596	−0.834	0.171	0.514
Nest height	−0.397	...	...	...
Female plumage brightness	0.204	−0.204	−0.122	−0.368
Incubation length	...	0.333	...	...
	$R^2 = 0.425$	$R^2 = 0.505$		$R^2 = 0.367$
	$F_{3,58} = 13.573$	$F_{3,32} = 9.535$		$F_{2,41} = 9.456$

most identical correlations with clutch size and numbers of broods (Fig. 3B, Table 5). The model, without direct effects of female brightness on incubation length, performed significantly worse than when it was included (Table 6, models 10 vs 7, $\chi^2 = 7.101$, df = 1, $p = 0.01$). Model performance did not differ when direct effects of female brightness on either clutch size or numbers of broods were excluded (Table 6, models 8 vs 7, $\chi^2 = 1.833$, df = 1, $p = 0.18$; models 9 vs 7, $\chi^2 = 1.985$, df = 1, $p = 0.16$). Nest height was more important in the model with female brightness compared to the model with male brightness (AIC coefficients of models 11 vs 5: −2.027 vs −3.857 correspondingly). Overall, female plumage brightness explained a highly significant amount of variation in life history parameters and the model with direct effects of female brightness on life history traits performed much better that the one without direct effects (Table 6, models 12 vs 7, $\chi^2 = 10.918$, df = 3, $p = 0.012$).

Covariation between sexual and life history traits along an environmental gradient

To assess whether sex-specific covariations of life history and sexually selected traits change with altitude, I conducted multiple regression and path analyses separately for high- and low-elevation species (Table 7). For males, partial regression coefficients (direct effects) of plumage brightness on life history traits significantly changed between high and low elevations for clutch size, numbers of broods, and incubation length (all p's < 0.05). For females, partial regression coefficients differed between elevations for clutch size, numbers of broods ($p < 0.05$), but not incubation length ($p = 0.41$).

Differences between sexes in direct effects of plumage brightness on life history traits were greater at low elevation than at high elevations with the exception of incubation length (Table 7). Between-elevation changes in direct effects of plumage brightness on life history traits were much greater in males than in females (Table 7).

Discussion

I found a strong association between sexually selected and life history traits in cardueline finches. I controlled for confounding factors to show that the direction of the interspecific relationship between sexual trait development and fecundity predictably differs between males and females (Figs 1–3). These findings are consistent with the prediction that close correspondence between life history and sexually selected traits indicates common mechanisms causing variation in both kinds of traits.

Table 6. Summary of results for several male plumage brightness models and female plumage brightness models of effects on life history traits among cardueline finches.

Model	χ^2	df	p	AIC
1. Original model with MBR (Fig. 1B)	1.645	4	0.801	−6.355
2. No path from MBR to CLSZ	2.709	5	0.745	−7.291
3. No path from MBR to BRDS	9.335	5	0.096	−0.665
4. No path from MBR to INC	4.347	5	0.501	−5.654
5. No path from NST to CLSZ (Fig. 1B)	6.143	5	0.293	−3.857
6. No direct paths from MBR	13.100	7	0.069	−0.900
7. Original model with FBR (Fig. 1C)	1.479	4	0.830	−6.521
8. No path from FBR to CLSZ	3.312	5	0.652	−6.689
9. No path from FBR to BRDS	3.464	5	0.629	−6.536
10. No path from FBR to INC	8.580	5	0.127	−1.420
11. No path from NST to CLSZ (Fig. 1C)	7.973	5	0.158	−2.027
12. No direct paths from FBR	12.397	7	0.088	−1.602

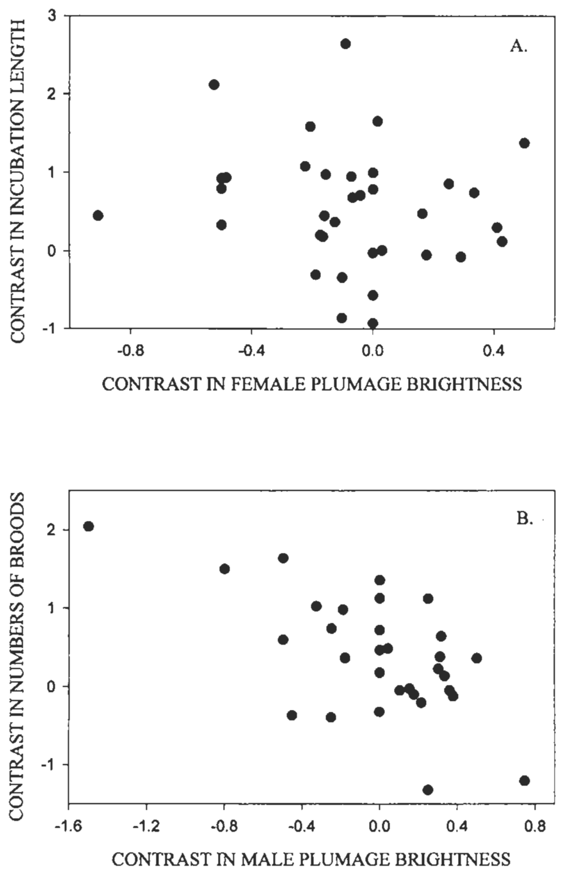

Fig. 3. Scatterplots of independent linear contrasts on the standardized residuals of (A) incubation length (corrected for elevation) relative to female plumage brightness ($b_{ST} = -0.37$, $p = 0.05$) and (B) numbers of broods (corrected by elevation and incubation length effects) relative to male plumage brightness ($b_{ST} = -0.35$, $p = 0.001$).

Sexual dichromatism

Finch species with greater sexual dichromatism had lower fecundity (Fig. 1, Table 2). This finding is consistent with the prediction that changes in adult mortality may cause variation in both sexual dimorphism and fecundity. For example, female mortality may constrain the upper limit of sexual dimorphism in species by limiting the maximum mortality rate of males (Promislow et al. 1992, 1994). Because adult mortality is closely linked to fecundity (Martin 1995), extent of sexual dimorphism is expected to negatively covary with fecundity, i.e., more dimorphic species are expected to produce smaller clutches. Fish show a similar association between life history and sexual traits; species with the largest clutches show the least sexual dichromatism (Winemiller 1992). Overall, sexual dimorphism is more common in species with small clutches, early maturation, and low juvenile survivorship, which may be related to sex-specific differences in reproductive rates and survival (Clutton-Brock and Vincent 1991).

Alternatively, a negative correlation between sexual dichromatism and fecundity can be explained by variation in nest predation. In cardueline finches, nest predation was negatively correlated with female brightness, but did not covary with male brightness (Martin and Badyaev 1996). Thus, species that experience a greater risk of nest predation also showed greater sexual dimorphism in plumage. I found that sexual dichromatism negatively varied with clutch size, a pattern that is expected under the assumption that nest predation mediates this relationship. Similarly, sexual differences in behaviors that associate with exposure to predation account for sexual dichromatism in snakes (Forsman 1995).

Both plumage brightness and participation in parental care are more similar between sexes in high-elevation finches than in low-elevation finches (Kovshar 1979, Badyaev 1993, 1994, unpubl.). As a result, sexes in high-elevation species could be subject to similar risks associated with parental care. Thus, I predicted smaller differences between the sexes in direct effects of variation in plumage brightness on life history traits at high elevations compared to low elevations. I found that sexes differed much less at high elevations than at low elevations with respect to the effects of plumage brightness on clutch size and number of broods, but not in effects on incubation length (Table 7).

Male plumage brightness

Finch species where males had more elaborate sexual traits exhibited lower fecundity compared to species with duller males (Figs 1 and 2, Table 4). This finding supports prediction that greater ornamentation of males would correspond to reduced parental investment and thus, to lower fecundity (Verner and Willson 1969). Sexual selection favors development of extravagant traits, such as bright plumage, through mate competition or mate choice (Andersson 1994). In turn, extent of paternal care often negatively correlates with mating opportunities and consequently influences the intensity of sexual selection (Trivers 1972, Westneat et al. 1990, Møller and Birkhead 1993, 1994). Thus, if greater ornamentation of males reflects greater intensity of sexual selection and corresponds to reduced parental investment, male ornamentation and fecundity should negatively correlate.

Breeding elevation positively covaries with male participation in parental care, and subsequently may correlate with development of male sexual traits; I found a negative correlation between elevation and male plumage brightness (Fig. 1; Badyaev unpubl). Thus,

Table 7. Standardized partial regression coefficients (b_{ST}) of plumage brightness effects on life history traits in cardueline finches. Analyses examine magnitude of coefficient change between elevations and sexes.

Effect on		Effect by		ΔMale-Female[b]	ΔMales[c]	ΔFemales
		Male brightness	Female brightness			
Clutch size	High elevation[a]	−0.001	0.050	0.051	0.495	0.445
	Low elevation	−0.496	−0.395	0.101		
Numbers of broods	High elevation	−0.014	0.096	0.110	0.845	0.269
	Low elevation	−0.859	−0.480	0.379		
Incubation length	High elevation	0.048	−0.349	0.397	0.522	0.021
	Low elevation	−0.474	−0.328	0.146		

[a] High elevation-maximum elevation of breeding ≥3000 m a.s.l. (weighted mean of the data set); low elevation-maximum elevation of breeding <3000 m a.s.l.; [b] differences between sexes; [c] differences between elevations.

males of low-elevation species may be exposed to additional mortality associated with their bright plumage and more intensive sexual competition (Promislow et al. 1992, 1994). Adult mortality closely associates with fecundity in birds (Martin 1995). Thus, if species with brighter males suffer higher mortality than species with duller males, then positive correlation between fecundity and male brightness is expected. On the contrary, I found negative correlation between these two traits – the pattern consistent with male brightness – paternal care hypothesis (see above). However, effects of male brightness on clutch size, number of broods, and incubation length significantly changed between high and low elevations, becoming much stronger at lower elevations (Table 7). This finding is consistent with predictions of both hypotheses because both paternal care and male sexual ornamentation change with breeding elevation (Badyaev unpubl.).

Female plumage brightness

In cardueline species with bright females, clutch sizes were larger and there were fewer breeding attempts per season than in species with dull females (Fig. 3B, Table 5). These results are consistent with patterns expected from variation in nest predation. In species where only females incubate, such as in cardueline finches, the effect of nest predation on female brightness may be especially prominent because bright colors are widely assumed to attract nest predators (Baker and Parker 1979, Shutler and Weatherhead 1990, Johnson 1991, Martin and Badyaev 1996). In carduelines, female brightness changes with nest height consistently with variation in nest predation; female brightness negatively correlates with nest predation (Martin and Badyaev 1996). Increased nest predation favors greater number of broods per season (bet-hedging) and consequently causes reduction in current clutch sizes (Slagsvold 1982, Martin 1995). Thus, nest predation may affect both female plumage brightness and fecundity; female brightness is expected to correlate positively with clutch size and negatively with numbers of broods. Also, correlation between nest height and plumage brightness was much stronger for females than for males; plumage brightness in males varied among nest sites differently than in females, and variation in male plumage brightness did not correspond to variation in nest predation (Martin and Badyaev 1996).

In contrast to males, female plumage brightness did not vary with changes in breeding elevation (Badyaev unpubl.). Thus, if plumage brightness is important to evolution of life history traits, there should be smaller changes in magnitude of direct effects of plumage brightness on life history traits in females than in males. I found that elevational changes in direct effects were smaller for females than for males (Table 7). Nevertheless, with exception of effect of brightness on incubation length, there was a significant change in direct effects of plumage on clutch size and numbers of broods between low and high elevations (Table 7).

In sum, sexually selected traits and sexual dichromatism were closely linked to variation in life history traits. Close association between life history and sexually selected traits may indicate common mechanisms causing variation in both life history and sexually selected traits. Males and females showed predictably opposite relationships between sexual ornamentation and fecundity. My results also suggest that intensity of sexual selection along altitudinal gradients may affect similarities between sexes in associations between life history and sexual traits.

Acknowledgements I am indebted to Tom Martin for the suggestion that I examine whether relation between dimorphism and life history traits is opposite between sexes. I thank Tom Mitchell-Olds and Dolph Schluter for statistical advice. I am grateful to Alison Banks, Bill Etges, Shannon Garner, Cameron Ghalambor, Paul Martin, Tom Martin, Wendy Parson, Andy Sheldon and Dolph Schluter for comments on the manuscript and many helpful suggestions. Toni Rapone and Bill Davison scored plumage brightness.

References

Andersson, M. 1994. Sexual selection. – Princeton Univ. Press. Princeton, NJ.

Badyaev, A. V. 1993. Breeding biology of the gold-fronted serin (*Serinus pusillus*) in conditions of subalpine bush zone

of the Phansky Mountains. – Biol. Sci. (Biol. Nauk.) 348: 89–99.
– 1994. Breeding biology of white-winged grosbeak (*Mycerobas carnipes*) in the Phansky Mountains. – Bull. MOIP (Biol. Div.) 99: 20–28.
Baker, R. R. and Parker, G. A. 1979. The evolution of bird coloration. – Phillos. Trans. R. Soc. Lond. B. 287: 63–130.
Berven, K. A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. I. An experimental analysis of life history traits. – Evolution 36: 962–983.
Breitwisch, R. 1988. Mortality patterns, sex ratios, and parental investment in monogamous birds. – Curr. Ornithol. 6: 1–50.
Charlesworth, B. 1980. Evolution in age-structured populations. – Cambridge Univ. Press, Cambridge.
Clement, P., Harris, A. and Davis, J. 1993. Finches and sparrows: an identification guide. – Princeton Univ. Press, Princeton, NJ.
Clutton-Brock, T. H. and Vincent, A. C. J. 1991. Sexual selection and the potential reproductive rates of males and females. – Nature 31: 58–60.
Cody, M. L. 1966. A general theory of clutch size. – Evolution 20: 174–184.
Darwin, C. 1871. The descent of man, and selection in relation to sex. – John Murray. London.
Felsenstein, J. 1985. Phylogenies and the comparative method. - Am. Nat. 125: 1–15.
Forsman, A. 1995. Opposing fitness consequences of color pattern in male and female snakes. – J. Evol. Biol. 8: 53–70.
Garland, T., Jr., Harvey, P. H. and Ives, A. R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. – Syst. Biol. 41: 18–32.
– , Dickerman, A. W., Janis, C. M. and Jones, J. A. 1993. Phylogenetic analysis of covariance by computer simulation. – Syst. Biol. 42: 265–292.
Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? – Science 218: 384–387.
Irwin, R. E. 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness? – Am. Nat. 144: 890–907.
Johnson, S. G. 1991. Effects of predation, parasites, and phylogeny on the evolution of bright coloration in North American male passerines. – Evol. Ecol. 5: 52–62.
Kirkpatrick, M. and Ryan M. J. 1991. The evolution of mating preferences and the paradox of lek. – Nature 350:33–38.
– , Price, T. and Arnold, S. J. 1990. The Darwin-Fisher theory of sexual selection in monogamous birds. – Evolution 44: 180–193.
Kovshar, A. F. 1979. Songbirds in the subalpine of Tien–Shan. – Nauka of Kazakh SSR, Alma-Ata.
Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. – Ecol. Monogr. 65: 101–127.
– and Badyaev, A. V. 1996. Sexual dichromatism relative to nest height and nest predation: contributions of females versus males. – Evolution 50: 2454–2460.
– and Clobert, J. 1996. Nest predation and avian life history evolution in Europe versus North America: a possible role of humans. – Am. Nat. 147: 1028–1046.
McLain, D. K. 1991. The r-K continuum and the relative effectiveness of sexual selection. – Oikos 60: 263–265.
– 1993. Cope's rules, sexual selection, and the loss of ecological plasticity. – Oikos 68: 490–500.
– , Moulton, M. P. and Redfearn, T. P. 1995. Sexual selection and the risk of extinction of introduced birds on oceanic islands. – Oikos 74: 27–34.
Mitchell, R. J. 1993. Path analysis: pollination. – In: Scheiner, S. M. and Gurevitch, J. (eds), Design and analysis of ecological experiments. Chapman and Hall, New York, pp. 211–213.
Møller, A. P. and Birkhead, T. R. 1993. Certainty of paternity covaries with parental care in birds. – Behav. Ecol. Sociobiol. 33: 261–268.
– and Birkhead, T. R. 1994. The evolution of plumage brightness in birds is related to extra-pair paternity. – Evolution 48: 1089–1100.
Owens, I. P. F. and Bennett, P. M. 1994. Mortality costs of parental care and sexual dimorphism in birds. – Proc. R. Soc. Lond B 257: 1–8.
Petraitis, P. S., Dunham, A. E. and Niewiarowski, P. H. 1996. Inferring multiple causality: the limitation of path analysis. – Funct. Ecol. 10: 421–431.
Promislow, D. E. L. 1992. Costs of sexual selection in natural populations of mammals. – Proc. R. Soc. Lond. B 247: 203–210.
– , Montgomerie, R. D. and Martin, T. E. 1992. Mortality costs of sexual dimorphism in birds. – Proc. R. Soc. Lond. B 250: 143–150.
– , Montgomerie, R. D. and Martin, T. E. 1994. Sexual selection and survival in North American waterfowl. – Evolution 48: 2045–2050.
Purvis, A. and Garland, T., Jr. 1993. Polytomies in comparative analyses of continuous characters. – Syst. Biol. 42: 569–575.
– and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analyzing comparative data. – Comp. Appl. Biosci. 11: 247–251.
Rice, W. R. 1989. Analyzing tables of statistical tests. – Evolution 43: 223–225.
SAS Institute. 1989. SAS/STAT user's guide, version 6. – Cary, NC.
Shutler, D. and Weatherhead, P. J. 1990. Targets of sexual selection: song and plumage of wood warblers. – Evolution 44: 1967–1977.
Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. – Oecologia 54: 159–169.
Trivers, R. L. 1972. Parental investment and sexual selection. – In Cambell, B. (ed.), Sexual selection and the descent of man, 1871–1971. Heinemann, London, pp. 136–179.
Verner, J. and Willson, M. F. 1969. Mating systems, sexual dimorphism and the role of male North American passerine birds in the nesting cycle. – Ornithol. Monogr. 9: 1–76.
Westneat, D. F., Sherman, P. W. and Morton, M. L. 1990. The ecology and evolution of extra-pair copulations in birds. – Curr. Ornithol. 7: 331–369.
Williams, G. C. 1966. Adaptation and natural selection: a critique of some current evolutionary thought. – Princeton Univ. Press, Princeton, NJ.
– 1992. Natural selection: domains, levels, and challenges. – Oxford Univ. Press, Oxford.
Winemiller, K. O. 1992. Life-history strategies and the effectiveness of sexual selection. – Oikos 63: 318–327.

Appendix. Data on clutch size (eggs per nest), numbers of broods (no. per year), incubation and nestling stage duration (d) for species used in analyses. For data on sexual dichromatism, male and female brightness, elevation of breeding, nest site, migratory classification, body size and for references, see Badyaev (unpubl.) and Martin and Badyaev (1996).

Species	Clutch size	No. of broods	Incubation length	Nestling stage length
Serinus pusillus[a]	4.2	2	12.0	14.0
Serinus pusillus[b]	3.7	1	12.0	14.0
Serinus serinus	3.8	2	12.7	14.6
Serinus syriacus	4.0	2	13.0	15.0

Appendix. (continued)

Species	Clutch size	No. of broods	Incubation length	Nestling stage length
Serinus canaria	3.8	2	13.5	16.0
Serinus canicollis	3.5	–	13.0	17.0
Serinus citrinella	4.5	2	13.5	16.5
Serinus mozambicus	3.0	–	13.5	20.5
Serinus dorsostriatus	3.0	–	–	19.5
Serinus scotops	3.5	–	–	18.0
Serinus flaviventris	4.0	–	–	15.0
Serinus sulphuratus	3.0	–	–	15.0
Serinus donaldsoni	–	–	–	15.0
Serinus nigriceps	2.5	–	–	16.5
Serinus citrinelloides	2.5	–	–	–
Serinus capistratus	3.0	–	–	–
Serinus leucopygius	3.5	–	–	19.5
Serinus atrogularis	3.0	–	12.5	16.5
Serinus menachensis	–	–	–	14.0
Serinus totta	4.5	–	16.0	17.0
Serinus symonsi	3.5	–	–	–
Serinus albogularis	3.5	–	–	15.0
Serinus gularis	3.0	–	13.5	15.5
Serinus mennelli	3.0	–	13.0	17.0
Serinus tristriatus	3.5	–	–	14.0
Serinus striolatus	3.5	–	–	15.0
Serinus rothschildi	–	–	–	15.5
Serinus citrinipectus	3.0	–	13.0	16.8
Serinus ankoberensis	3.0	–	–	14.0
Serinus xantholaema	–	–	–	19.5
Serinus alario	3.0	–	13.5	21.0
Carduelis cannabina	4.7	2	12.6	13.4
Carduelis spinus	4.3	2	12.5	14.0
Carduelis chloris	4.8	2	12.9	15.1
Carduelis sinica	5.0	2	12.5	14.5
Carduelis spinoides	4.0	1	13.0	–
Carduelis ambigua	4.0	–	12.5	18.5
Carduelis carduelis	4.9	2	12.0	14.7
Carduelis tristis	5.2	2	13.0	14.0
Carduelis psaltria	4.5	2	12.0	15.0
Carduelis pinus	3.5	2	13.0	14.5
Carduelis cucullata	4.0	1	12.0	15.0
Carduelis lawrencei	4.5	–	12.5	12.0
Carduelis flammea	4.8	2	10.7	11.5
Carduelis hornemanni	4.8	2	11.5	11.0
Carduelis flavirostris pipilans	5.7	2	12.5	11.5
Carduelis f. montanella	5.2	1	13.5	15.5
Leucosticte nemoricola	4.8	1	14.0	17.5
Leucosticte branti	3.5	–	–	–
Leucosticte a. atrata	4.5	2	13.0	18.0
Leucosticte a. arctoa	4.0	1	–	15.0
Callacanthis burtoni	2.0	–	–	–
Rhodopechys sanquinea	4.5	1.5	14.0	14.0
Rhodopechys githaginea	5.0	2	13.5	13.5
Rhodopechys mongolica	5.0	2	–	18.0
Rhodopechys obsoleta	4.8	2	13.8	13.5
Uragus sibiricus	4.5	1	–	–
Carpodacus e. erythrinus	4.9	1	12.1	11.6
Carpodacus e. ferghanensis	4.5	1	13.5	15.5
Carpodacus purpureus	4.5	2	13.0	14.0
Carpodacus cassinii	4.5	2	13.0	14.0
Carpodacus mexicanus	4.2	–	13.5	15.0
Carpodacus rhodochrous	4.5	–	–	–
Carpodacus synoicus	4.5	2	13.5	15.0
Carpodacus roseus	4.0	–	–	–
Carpodacus thura	3.7	–	–	–
Carpodacus rhodochlamys	4.0	1	15.0	16.5
Carpodacus rubicilloides	5.0	–	–	–
Carpodacus rubicilla	4.8	1	16.0	17.0
Carpodacus puniceus	4.0	–	–	–
Carpodacus pulcherrimus	3.0	–	–	–
Pinicolae nucleator	3.8	1	13.5	14.0
Loxia pytyopsittacus	3.8	2	15.0	22.0
Loxia curvirostra	3.7	2	15.0	23.0

Appendix. (continued)

Species	Clutch size	No. of broods	Incubation length	Nestling stage length
Loxia scotica	3.7	2	13.2	21.0
Loxia leucoptera	4.0	3	14.5	23.0
Pyrrhula aurantiaca	3.5	–	–	–
Pyrrhula erythrocephala	3.5	–	–	–
Pyrrhula erythaca	3.0	–	–	–
Pyrrhula pyrrhula	4.7	2	13.0	16.0
Coccothraustes coccothraustes	4.4	1	12.0	12.5
Eophona migratoria	4.5	–	–	–
Mycerobas icterioides	2.5	–	–	–
Mycerobas melanozanthos	2.5	–	–	–
Mycerobas carnipes	3.2	2	16.0	21.0
Coccothraustes vespertinus	3.0	1	13.4	14.1
Linurgus olivaceus	2.0	–	–	–

[a] mountain forest population; [b] subalpine population.