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Avian life history variation along altitudinal gradients: an example with cardueline finches

Abstract Elevation has long been considered a major influence on the evolution of life-history traits. Most elevation-induced variation in life history traits has been attributed to changes in climate, duration of breeding season, predation, and food limitation. I use a phylogenetic approach to show that life histories are closely associated with breeding elevation in extant cardueline finches. Finches at high elevations had smaller clutches, fewer broods, and longer incubation periods. Neither food limitation nor nest predation appear to readily account for this strong elevational variation in cardueline life histories. However, juvenile survival may be greater at higher elevations as a result of prolonged parental care and shorter natal dispersal and can potentially compensate for reduced fecundity in high-elevation finches.

Key words Cardueline finches · Breeding elevation · Life-history traits

Introduction

Populations and species that occupy different environments often show extensive variation in life histories. Such variation is thought to arise from genetic differentiation caused by variable selection regimes or from phenotypic variability exerted by different environments (Schmalhausen 1949; Endler 1977; Hoffmann and Watson 1993; Stearns 1986; Via et al. 1995). Interactions of these two mechanisms can lead to adaptive responses to changing environments (Williams 1966, 1992).

Intraspecific assessment of the mechanisms behind environmental variation in life histories is complicated because phenotypic plasticity may be non-genetic and thereby irrelevant for selection on life history strategies

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(Price and Liou 1989; Grant and Dunham 1990; Brooks and McLennan 1991). On the other hand, comparative studies of covariation among life histories and environmental gradients are likely to uncover adaptive patterns of phenotypic responses to specific environmental conditions; they cannot, however, reveal genetic correlations behind such covariation (Harvey and Pagel 1991).
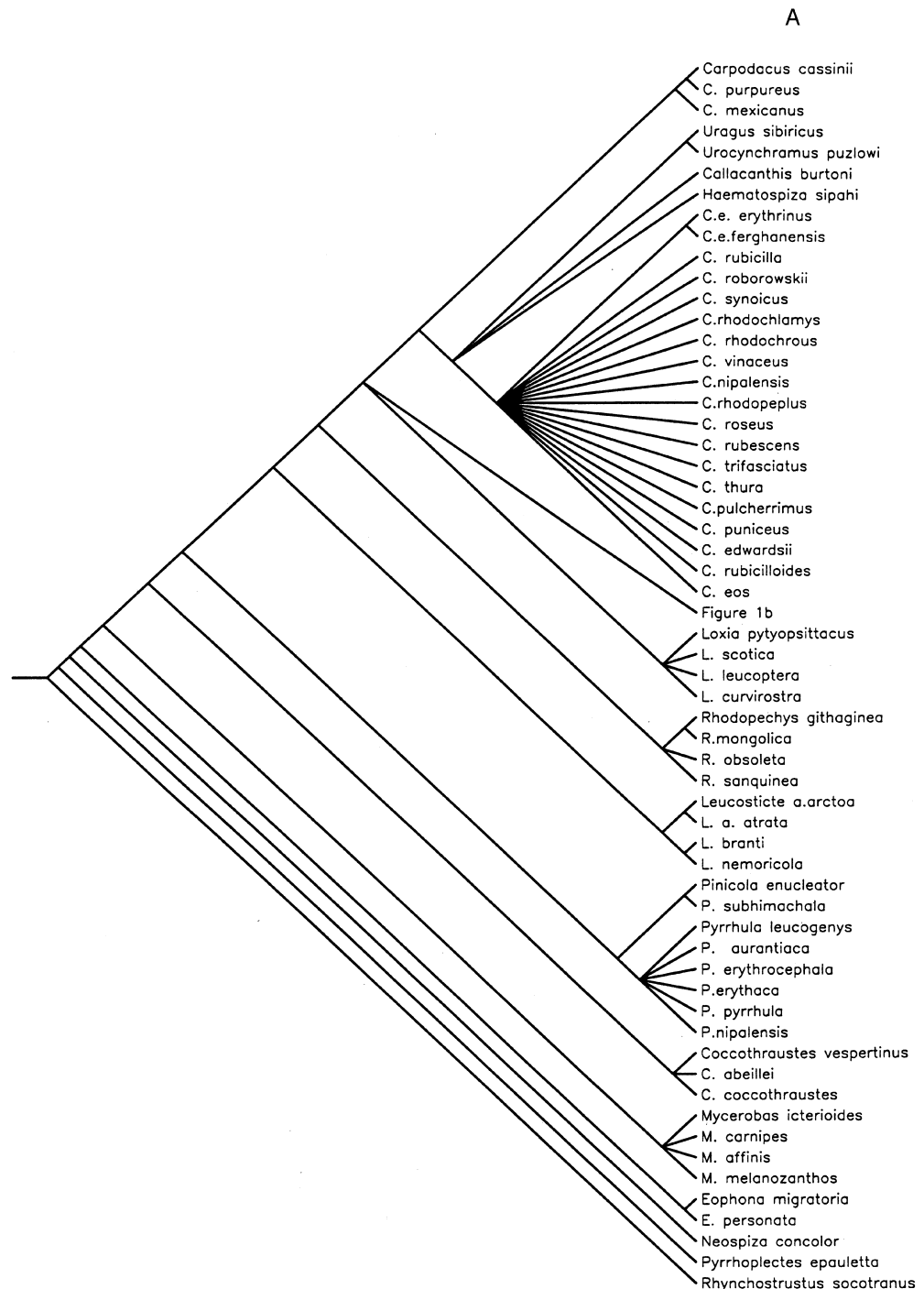
Most studies of the ecological basis for variation in avian life histories have focused on the relative importance of food availability (Lack 1948, 1968; Martin 1992) and nest predation (Skutch 1949, 1985; Lack 1948, 1968; Slagsvold 1982; Kulesza 1990; Martin 1993). Indeed, recent reviews have shown that mortality and food limitation may interact to influence life history traits (Martin 1992, 1995, 1996; Owens and Bennett 1995). Elevation is one environmental variable that has long been considered an important factor in the evolution of life history traits (e.g., Cody 1966; Berven 1982; Grant and Dunham 1990; Mathies and Andrews 1995; Badyaev 1997a). Most altitude-induced variation in life history traits has been attributed to variation in climate, duration of breeding season, predation, and food limitation (Cody 1966; Boyce 1979; Kovshar 1981; Krementz and Handford 1984 and references therein). For example, it has long been assumed that unpredictable environments, low population densities, and limited food availability at higher elevations select for higher productivity in high-elevation species (Cody 1966). However, more recent studies showed little support for this original argument and, at best, have produced mixed results (reviewed in Krementz and Handford 1984). As yet, there have been no tests using modern comparative methods for evidence of an interspecific elevational variation in avian life histories.

In this paper I use a phylogenetic approach to show how breeding elevation affects variation in life history traits in the subfamily of cardueline finches. Cardueline finches are primarily arboreal or terrestrial seed-eating birds that occupy a wide variety of environmental conditions, occurring across the largest range of elevations of any extant bird subfamily (Clement et al. 1993). Most

nest-building is done by females, and with exception of three or four species, only females incubate; in almost all of the species males provide food to females during incubation. Cardueline finches do not defend their foraging territories and collect food both near nests and at considerable distance. I first examine altitudinal variation in clutch size, numbers of broods, incubation and nestling periods of carduelines. I then discuss potential mechanisms that may account for such variation, including changes in nest predation, food limitation, phenology of breeding, and climate.

Methods

For all extant Cardueline species, I gathered published data on elevation of breeding, body size, and nest height [Table 1, appendices in Martin and Badyaev (1996) and Badyaev (1997a)], 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 1). Log (female wing length) was used as a measure of body size. Most of the extant cardueline finches occur within a very limited range of latitudes (Boehme 1975; Clement et al. 1993), thus variation in
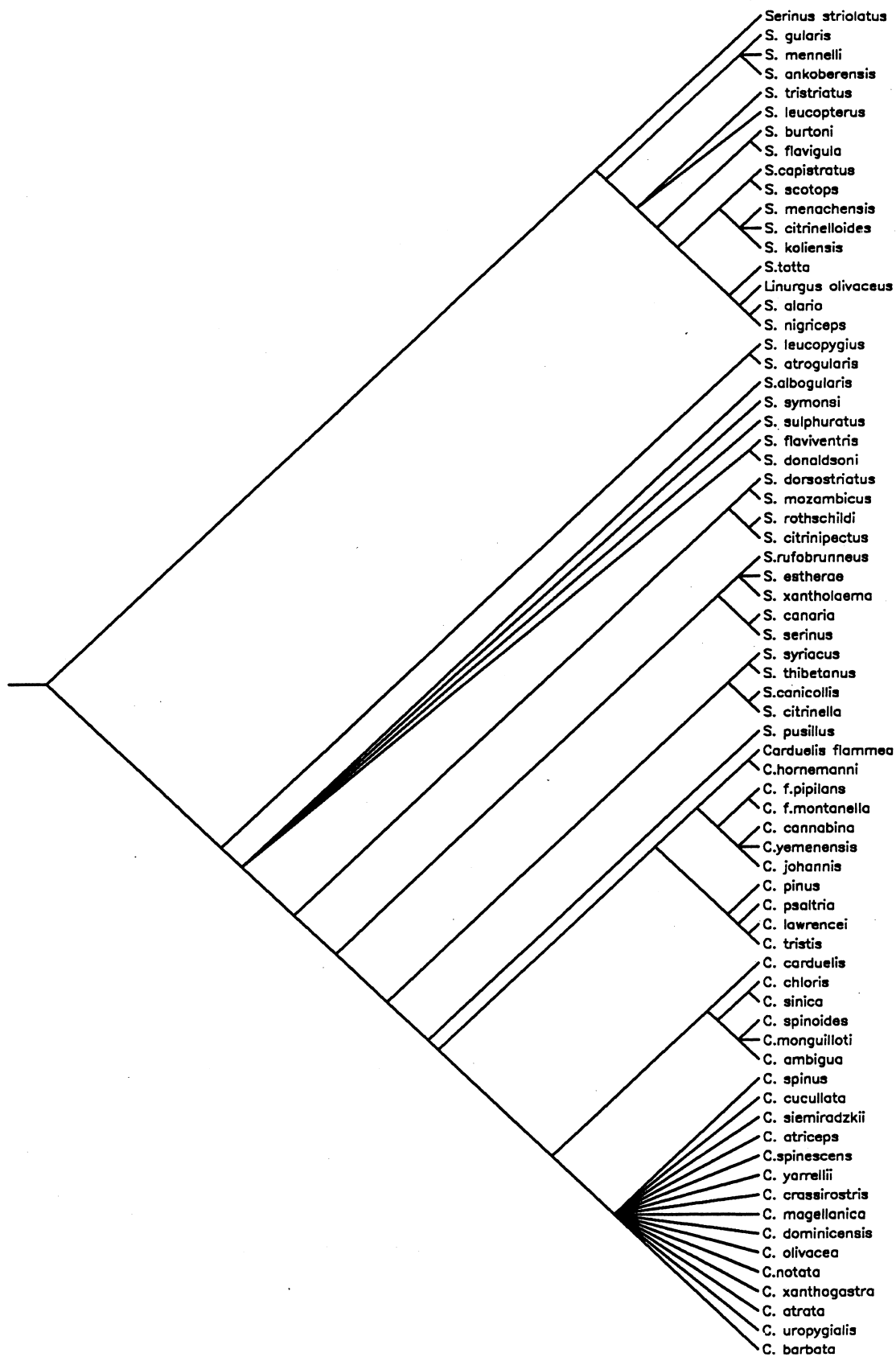
Fig. 1A, B Phylogenetic hypothesis for the taxa used in analyses. The phylogeny represents a consensus tree based on molecular, paleontological, morphological, and behavioral data

A

Carpodacus cassinii
C. purpureus
C. mexicanus
Uragus sibiricus
Urocynchramus puzlowi
Callacanthis burtoni
Haematospiza sipahi
C.e. erythrinus
C.e.ferghanensis
C. rubicilla
C. roborowskii
C. synoicus
C.rhodochlamys
C. rhodochrous
C. vinaceus
C.nipalensis
C.rhodopeplus
C. roseus
C. rubescens
C. trifasciatus
C. thura
C.pulcherrimus
C. puniceus
C. edwardsii
C. rubicilloides
C. eos
Figure 1b
Loxia pytyopsittacus
L. scotica
L. leucoptera
L. curvirostra
Rhodopechys githaginea
R.mongolica
R. obsoleta
R. sanguinea
Leucosticte a.arctoa
L. a. atrata
L. branti
L. nemoricola
Pinicola enucleator
P. subhimachala
Pyrrhula leucogenys
P. aurantiaca
P. erythrocephala
P.erythaca
P. pyrrhula
P.nipalensis
Coccothraustes vespertinus
C. abeillei
C. coccothraustes
Mycerobas icterioides
M. carnipes
M. affinis
M. melanozanthos
Eophona migratoria
E. personata
Neospiza concolor
Pyrrhoplectes epauletta
Rhynchostrustus socotranus

B

Serinus striolatus
S. gularis
S. mennelli
S. ankoberensis
S. tristriatus
S. leucopterus
S. burtoni
S. flavigula
S.capistratus
S. scotops
S. menachensis
S. citrinelloides
S. koliensis
S.totta
Linurgus olivaceus
S. alaria
S. nigriceps
S. leucopygius
S. atrogularis
S.albogularis
S. symonsi
S. sulphuratus
S. flaviventris
S. donaldsoni
S. dorsostriatus
S. mozambicus
S. rothschildi
S. citrinipectus
S.rufobrunneus
S. estherae
S. xantholaema
S. canaria
S. serinus
S. syriacus
S. thibetanus
S.canicollis
S. citrinella
S. pusillus
Carduelis flammea
C.hornemanni
C. f.pipilans
C. f.montanella
C. cannabina
C.yemenensis
C. johannis
C. pinus
C. psaltria
C. lawrencei
C. tristis
C. carduelis
C. chloris
C. sinica
C. spinoides
C.monguilloti
C. ambigua
C. spinus
C. cucullata
C. siemiradzkii
C. atriceps
C.spinescens
C. yarrellii
C. crassirostris
C. magellanica
C. dominicensis
C. olivacea
C.notata
C. xanthogastra
C. atrata
C. uropygialis
C. barbata

Table 1 Data on elevation of breeding, m (lowest and highest), clutch size (eggs per nest) (CLSZ), numbers of broods (no. per year) (BROODS), incubation (INCDS) and nestling stage (NSTDS) duration (days), and female wing length, mm (FWING) for species used in analyses. For data on nest site, nest predation and for references, see Badyaev 1997b and Martin and Badyaev (1996)

Species	Elevation		CLSZ	BROODS	INCDS	NSTDS	FWING
Serinus pusillus[a]	600	3000	4.2	2.0	12.0	14.0	73.4
S. pusillus[b]	2000	4600	3.7	1.0	12.0	14.0	73.4
S. serinus	0	1300	3.8	2.0	12.7	14.6	69.4
S. syriacus	900	1800	4.0	2.0	13.0	15.0	74.6
S. canaria	0	1700	3.8	2.0	13.5	16.0	70.2
S. canicollis	2000	4300	3.5	–	13.0	17.0	75.5
S. citrinella	1000	3000	4.5	2.0	13.5	16.5	74.6
S. mozambicus	0	1800	3.0	–	13.5	20.5	–
S. dorsostriatus	1000	2000	3.0	–	–	19.5	81.5
S. scotops	0	1800	3.5	–	–	18.0	66.0
S. flaviventris	0	–	4.0	–	–	15.0	71.0
S. sulphuratus	1000	2400	3.0	–	–	15.0	81.5
S. donaldsoni	0	1300	–	–	–	15.0	81.0
S. nigriceps	1800	4100	2.5	–	–	16.5	77.0
S. citrinelloides	1000	3000	2.5	–	–	–	66.0
S. capistratus	0	1500	3.0	–	–	–	62.0
S. leucopygius	0	1000	3.5	–	–	19.5	66.0
S. atrogularis	900	–	3.0	–	12.5	16.5	66.0
S. menachensis	2000	3666	–	–	–	14.0	72.5
S. symonsi	2400	–	3.5	–	–	–	75.5
S. albogularis	0	–	3.5	–	–	15.0	77.5
S. gularis	1200	2000	3.0	–	13.5	15.5	79.0
S. mennelli	600	1950	3.0	–	13.0	17.0	82.5
S. tristriatus	1060	3330	3.5	–	–	14.0	67.5
S. striolatus	1300	4300	3.5	–	–	15.0	69.5
S. rothschildi	1000	2800	–	–	–	15.5	63.0
S. citrinipectus	0	750	3.0	–	13.0	16.8	–
S. ankoberensis	2980	3200	3.0	–	–	14.0	74.5
Carduelis cannabina	0	2200	4.7	2.0	12.6	13.4	77.6
C. spinus	0	1800	4.3	2.0	12.5	14.0	71.4
C. chloris	0	1400	4.8	2.0	12.9	15.1	85.2
C. sinica	0	2400	5.0	2.0	12.5	14.5	80.7
C. spinoides	1600	4400	4.0	1.0	13.0	–	76.0
C. ambigua	1800	4000	4.0	–	12.5	18.5	–
C. carduelis	0	4250	4.9	2.0	12.0	14.7	77.5
C. tristis	–	–	5.2	2.0	13.0	14.0	68.2
C. psaltria	0	3100	4.5	2.0	12.0	15.0	62.0
C. pinus	–	–	3.5	2.0	13.0	14.5	71.0
C. cucullata	280	1300	4.0	1.0	12.0	15.0	–
C. lawrencei	0	–	4.5	–	12.5	12.0	64.5
C. flammea	0	350	4.8	2.0	10.7	11.5	72.2
C. hornemanni	0	400	4.8	2.0	11.5	11.0	75.2
C. flavirostris pipilans	0	1000	5.7	2.0	12.5	11.5	75.5
C. f. montanella	3000	4850	5.2	1.0	13.5	15.5	71.6
Leucosticte nemoricola	2300	5300	4.8	1.0	14.0	17.5	99.0
L. branti	3950	6000	3.5	–	–	–	111
L. a. atrata	0	100	4.5	2.0	13.0	18.0	106
L. a. arctoa	3000	5000	4.0	1.0	–	15.0	112
Callacanthis burtoni	2270	3330	2.0	–	–	–	98.5
Rhodopechys sanquinea	2000	–	4.5	1.5	14.0	14.0	103
R. githaginea	350	2000	5.0	2.0	13.5	13.5	85.6
R. mongolica	400	4750	5.0	2.0	–	18.0	88.0
R. obsoleta	0	1500	4.8	2.0	13.8	13.5	85.8
Uragus sibiricus	–	3400	4.5	1.0	–	–	72.0
Carpodacus e. erythrinus	0	1999	4.9	1.0	12.1	11.6	82.7
C. e. ferghanensis	2000	4550	4.5	1.0	13.5	15.5	82.2
C. purpureus	0	–	4.5	2.0	13.0	14.0	79.0
C. cassinii	1500	3000	4.5	2.0	13.0	14.0	89.2
C. mexicanus	0	1500	4.2	–	13.5	15.0	77.8
C. rhodochrous	2250	4540	4.5	–	–	–	69.0
C. synoicus	2000	3350	4.5	2.0	13.5	15.0	87.4
C. roseus	0	3030	4.0	–	–	–	86.6
C. thura	3200	5000	3.7	–	–	–	81.5
C. rhodochlamys	2720	4900	4.0	1.0	15.0	16.5	90.0
C. rubicilloides	3700	5800	5.0	–	–	–	102
C. rubicilla	3000	5100	4.8	1.0	16.0	17.0	114
C. puniceus	3000	5700	4.0	–	–	–	111
C. pulcherrimus	3600	5000	3.0	–	–	–	76.0

Species	Elevation		CLSZ	BROODS	INCDS	NSTDS	FWING
Pinicola enucleator	0	2000	3.8	1.0	13.5	14.0	109
Loxia pytyopsittacus	0	–	3.8	2.0	15.0	22.0	102
L. curvirostra	0	4500	3.7	2.0	15.0	23.0	95.3
L. scotica	0	–	3.7	2.0	13.2	21.0	97.3
L. leucoptera	0	–	4.0	3.0	14.5	23.0	88.4
Pyrrhula aurantiaca	3000	4300	3.5	–	–	–	81.5
P. erythrocephala	2700	4200	3.5	–	–	–	78.0
P. erythaca	2500	4500	3.0	–	–	–	82.0
P. pyrrhula	0	2900	4.7	2.0	13.0	16.0	91.8
C. coccothraustes	0	3000	4.4	1.0	12.0	12.5	101
Eophona migratoria	0	–	4.5	–	–	–	96.0
Mycerobas icterioides	1800	3500	2.5	–	–	–	128
M. melanozanthos	2400	3600	2.5	–	–	–	127
M. carnipes	2800	4600	3.2	2.0	16.0	21.0	67.0
C.vespertinus	2000	–	3.0	1.0	13.4	14.1	112
Linurgus olivaceus	1524	3048	2.0	–	–	–	73.0

[a] Mountain forest population;
[b] Subalpine population

latitudes of species distribution is negligibly small compared to variation in elevational range.

The phylogeny of the cardueline finch subfamily (Fig. 1) represents a consensus tree constructed by summarizing the most recent molecular, paleontological, morphological, and behavioral data available for each clade and is described in detail elsewhere (Badyaev 1997b). 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. 1992; Purvis and Rambaut 1995).

To control for species relatedness within the subfamily, I analyzed data using pairwise comparisons and independent linear contrasts. In pairwise comparisons, pairs of closely related species (Table 2) were ranked by breeding elevation and then compared with respect to a life history trait (e.g., Møller and Birkhead 1992). Any concordance with prediction was then tested with a sign test. This method provides the most direct test of concordance between elevation and life history traits, because it makes fewer assumptions about phylogenetic relations among clades in the subfamily, and is statistically more powerful than ANCOVA on independent contrasts when phylogeny has unresolved nodes with multiple species (see Martin and Badyaev 1996). I also analyzed data using the independent contrast method of Felsenstein (1985) and incorpo-

Table 2 Pairs of closely related species used in the pairwise comparisons

|		
Serinus pusillus (forest population)	*S. citrinelloides*	*C. pinus*
S. pusillus (subalpine population)	*S. menachensis*	*C. psaltria*
S. leucopterus	*S. citrinella*	*C. johannis*
S. tristriatus	*S. canicollis*	*C. yemenensis*
S. capistratus	*S. flavigula*	*C. chloris*
S. scotops	*S. burtoni*	*C. sinica*
S. atrogularis	*S. rufobrunneus*	*C. ambigua*
S. leucopygius	*S. estherae*	*C. spinoides*
S. flaviventris	*Carduelis flammea*	*Pinicola enucleator*
S. donaldsoni	*C. hornemanni*	*P. subhimachala*
S. mozambicus	*C. flavirostris pipilans*	*Uragus sibiricus*
S. dorsostriatus	*C. f. montanella*	*Urocynchramus pylzowi*
S. serinus	*Leucosticte arctoa arctoa*	*Rhodopechys githaginea*
S. canaria	*L. a. atrata*	*R. mongolica*
S. alario	*L. nemoricola*	*R. sanguinea*
S. nigriceps	*L. branti*	*R. obsoleta*
S. citrinipectus	*Carpodacus purpureus*	*Eophona migratoria*
S. rothschildi	*C. cassinii*	*E. personata*
S. symonsi	*C. e. erythrinus*	
S. albogularis	*C. e. ferganensis*	
S. mennelli	*Carduelis cannabina*	
S. gularis	*C. yemenensis*	
S. ankoberensis	*C. tristis*	
S. tristriatus	*C. lawrencei*	
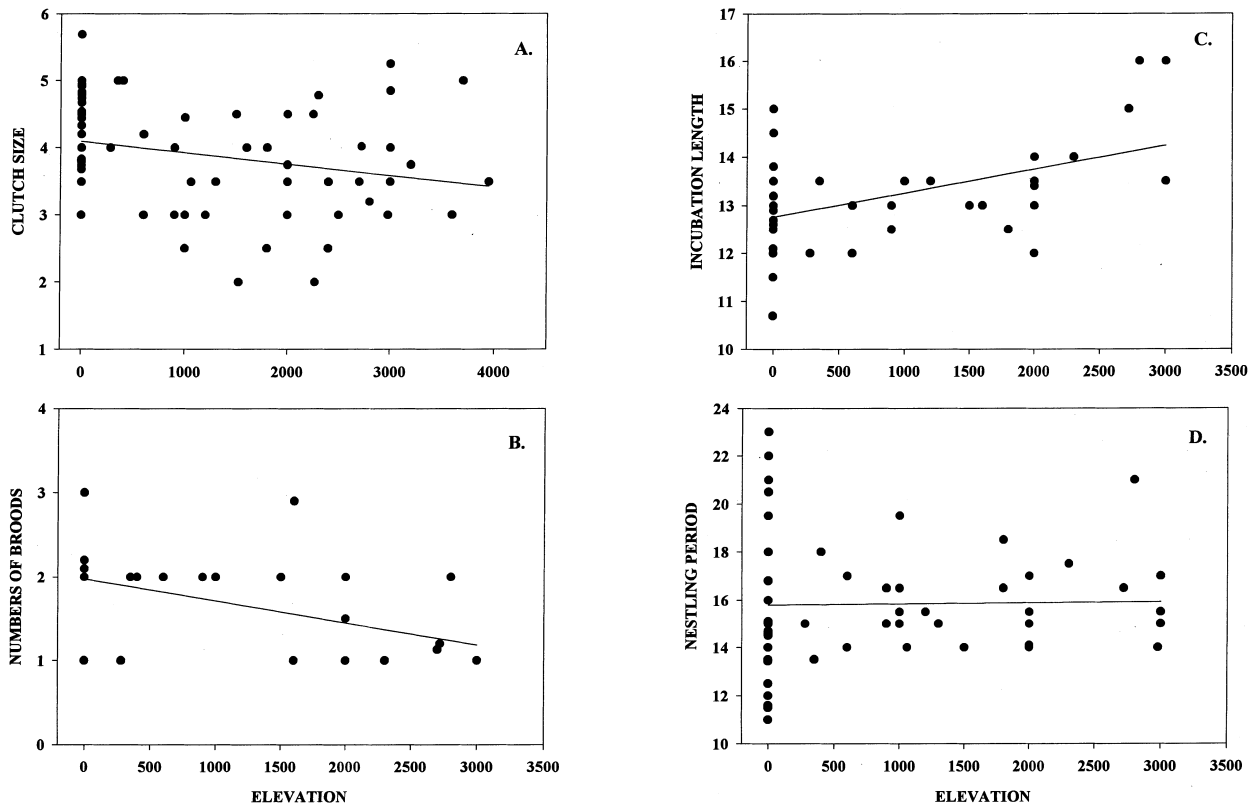
Fig. 2A–D Regression plots of raw data illustrating the relationship between breeding elevation and **A** clutch size ($b_{ST} = -0.25$, $P = 0.03$), **B** numbers of broods ($b_{ST} = -0.62$, $P = 0.001$), **C** incubation length ($b_{ST} = 0.47$, $P = 0.001$), and **D** nestling period ($b_{ST} = 0.02$, $P = 0.90$)

rating 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 significantly different from zero slopes, thus validating the assumption (Purvis and Rambaut 1995). All regressions were forced through the origin (Garland et al. 1992). See Martin and Badyaev (1996) and Badyaev (1997a) for further details of phylogenetic analyses. All data were square root- or log-transformed before statistical analyses.

Results

Clutch size

Twenty-three pairs of closely related species and subspecies showed variation in both breeding elevation and clutch size. In 20 (87%) of these pairs, species with higher elevational distribution had smaller clutch sizes (sign test, $P = 0.0001$). Clutch size strongly decreased with increase in breeding elevation across all cardueline species (phylogenetically untransformed data: $b_{ST} = -0.25$, $n = 77$ species, $t = -2.24$, $P = 0.03$; Fig. 2A; phylogenetically transformed data: $b_{ST} = -0.56$, $n = 61$ independent contrasts, $t = -5.06$, $P < 0.0001$; Fig. 3A); even

when effects of body size and nest height were controlled in analyses of independent contrasts ($b_{ST} = -0.52$, $P < 0.001$).

Numbers of broods

Seven pairs of closely related taxa showed variation in both breeding elevation and number of broods. In six (86%) of these pairs, species with higher altitudinal distribution had fewer broods per reproductive season (sign test, $P = 0.054$). Number of broods strongly decreased with increase in breeding elevation (phylogenetically untransformed data: $b_{ST} = -0.62$, $n = 39$ species, $t = -4.81$, $P = 0.001$, Fig. 2B; phylogenetically transformed data: $b_{ST} = -0.82$, $n = 20$ independent contrasts, $t = -5.63$, $P < 0.0001$; Fig. 3B). The relationship remained significant when effects of body size and nest height were controlled in analyses of independent contrasts ($b_{ST} = -0.86$, $P < 0.001$).

Duration of incubation and nestling periods

Twelve pairs of closely related species showed variation in both breeding elevation and incubation length. In 11 (92%) of these pairs, species with higher altitudinal distribution had longer incubation periods (sign test, $P = 0.003$). There was no association between altitude of breeding and duration of nestling period (sign test, 8 out of 18, $P = 0.70$). Incubation duration increased with increase in breeding elevation (phylogenetically un-
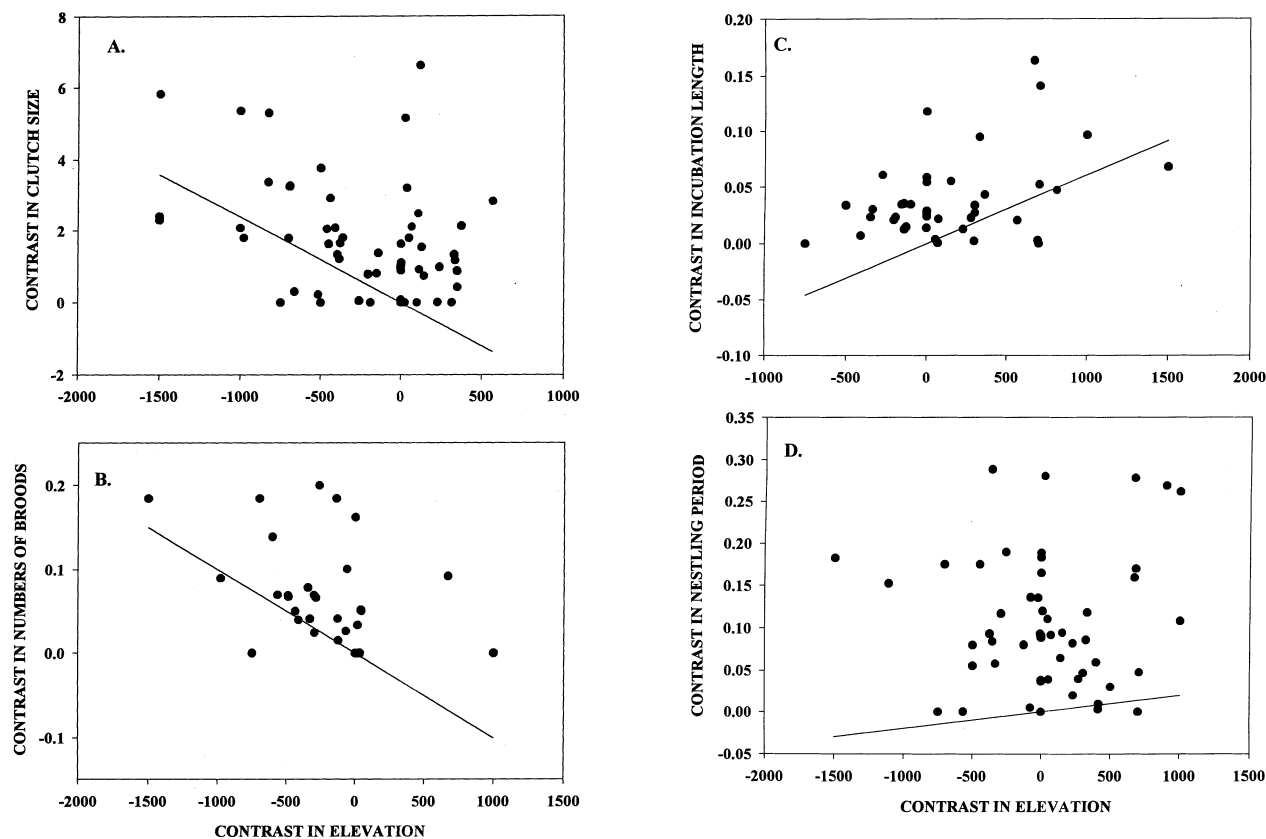
Fig. 3A–D Regression plots of data transformed by the method of standardized independent contrasts (which controls for possible phylogenetic effects) illustrating the relationship between breeding elevation and **A** clutch size ($b_{ST} = -0.52$, $P < 0.001$), **B** numbers of broods ($b_{ST} = -0.86$, $P < 0.001$), **C** incubation length ($b_{ST} = 0.59$, $P < 0.001$), and **D** nestling period ($b_{ST} = 0.11$, $P = 0.41$)

transformed data: $b_{ST} = 0.47$, $n = 49$ species, $t = 3.52$, $P = 0.001$, Fig. 2C; phylogenetically transformed data: $b_{ST} = 0.54$, $n = 42$ independent contrasts, $t = 4.04$, $P = 0.0002$; Fig. 3C, including when effects of body size and nest height were controlled: $b_{ST} = 0.59$, $P < 0.001$). Neither raw nor phylogenetically transformed nestling stage duration varied with changes in elevation (phylogenetically untransformed data: $b_{ST} = 0.02$, $n = 61$ species, $t = 0.12$, $P = 0.90$, Fig. 2D; phylogenetically transformed data: $b_{ST} = 0.11$, $n = 55$ independent contrasts, $t = 0.83$, $P = 0.41$; Fig. 3D).

Discussion

Life histories of cardueline finches closely covary with breeding elevation. At higher elevations, species had smaller clutches, produced fewer broods, and had longer incubation periods (Figs. 2 and 3; Badyaev 1997a). Speciation in cardueline finches closely followed mountain-formation events and corresponding changes in elevation (e.g., Boehme 1975; Banin 1987) and predictable changes in ecological conditions along elevation gradient could favor population divergence. Indeed,

there were greater differences in life histories between subspecies occupying different elevations than among populations (Kovshar 1981).

Elevational correlates of life history variation

Altitudinal variation in life history traits have long been attributed to four major mechanisms: variation in nest predation, food limitation, breeding phenology, and climate (Cody 1966; Boyce 1979; Kovshar 1981; Krementz and Handford 1984). Here I examine the evidence for possible influences of these factors.

For temperate species, nest predation is closely associated with variation in fecundity (Slagsvold 1982; Lima 1987; Martin 1992, 1995), thus the small clutches of high-elevation species may be a result of high nest predation. However, in carduelines, nest predation decreases with elevation (Fig. 4; Badyaev 1997b). In addition, high nest predation usually associates with repeated nesting attempts and shorter nestling periods (Martin 1995). On the contrary, high-elevation species have fewer nesting attempts (Figs. 2 and 3), which is consistent with conditions of low nest predation (Badyaev 1997a). In addition, there was no altitudinal variation in duration of nestling period in finches despite the suggestion of Kovshar (1981) that the nesting period of high-elevation species tends to be longer than in low-elevation species. Thus, variation in nest predation appears unable to fully account for altitudinal variation in life history traits in finches.
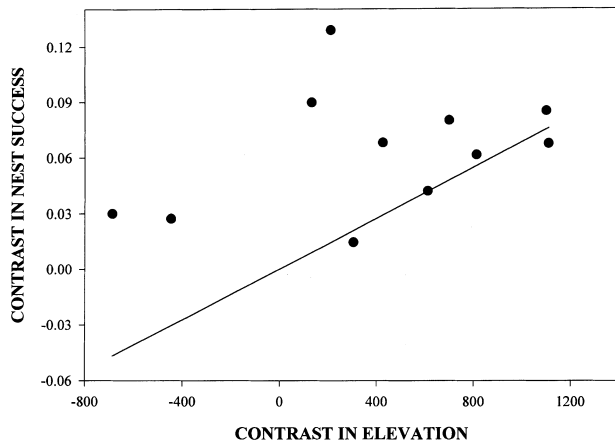
Fig. 4 Regression plots of data transformed by the method of standardized independent contrasts (which controls for possible phylogenetic effects) illustrating the relationship between breeding elevation and nesting success (data summarized in Martin and Badyaev 1996). Nest predation rate is weakly negatively correlated with breeding elevation (Spearman $r = 0.27$, $P = 0.08$)

Limited food availability or low food quality can limit productivity and slow developmental rates of young (Lack 1948, 1968; Ricklefs 1976; Martin 1992, 1995). Wide spatial separation of nesting and feeding resources, which is common at high elevations (Kovshar 1981; Badyaev 1987, 1993, 1994), could reduce nestling provisioning rates thereby favoring small clutch sizes. In addition, wide spatial habitat segregation and colder climate prevents females from foraging on their own during incubation and from collecting food for nestlings during a considerable part of nestlings' development. During these times most food is provided by males only (Kovshar 1981; Badyaev 1993, 1994). Restriction of food provisioning to the males could further reduce nestling provisioning rates. The number of seed-eating species increases with elevation (Boehme 1975), thereby potentially increasing food competition. However, low food availability often favors slow development rates and, thus longer nestling period at high elevations, which is not observed in finches (Figs. 2 and 3; Badyaev 1997a). Indeed, while food delivery rates per nestling were slightly lower at high elevations, the number of actual food portions transferred to nestlings was not different between high- and low-elevation populations of gold-fronted serin (*Serinus pusillus*) and white-winged grosbeak (*Mycerobas carnipes*) (Badyaev 1993, 1994). Similarly, Kovshar (1981) documents analogous food provisioning rates for subalpine and forest-dwelling birds.

Shorter breeding seasons and colder climate are thought to account for fewer renesting attempts and longer incubation periods in high-elevation birds (e.g., Kovshar 1981). Direct tests of such influences are lacking, but several observation indicate strong climatic effects on phenology of breeding in high-elevation species. High-elevation species show much stronger preference for nesting on sun-exposed slopes than do low-elevation

species (Kovshar 1981; Badyaev 1987). Nesting starts earlier on such slopes and pairs in such locations use fewer thermoisolating materials than pairs nesting elsewhere, reducing nest-building time and shortening the nesting cycle (Kovshar 1981; Badyaev 1987). Kovshar (1981) examined a number of ethological adaptations that make it possible for some subalpine species to produce two clutches per season. These include overlap between nesting attempts where only males continue to provision first brood while females incubate a second clutch, extensive incubation feeding of females by males, reuse of old nests, and overlap between molting and nesting (Kovshar 1981; Badyaev 1987). Development of such behaviors by subalpine species further stresses the limitation of breeding season duration on nesting in high-elevation species.

Alternative explanations of elevational variation in life histories

Higher adult survival is associated with lower current reproductive effort (Williams 1966, 1992; Charlesworth 1980). Therefore, lower fecundity of high elevation species could be accounted for by higher adult survival (Charlesworth 1980; Martin 1996). Estimates of annual adult survival for low- versus high-elevation finches do not suggest a difference. Adult survival of most low-elevation resident carduelines ranges from 39 to 43%: serin (*Serinus serinus*) 40%, greenfinch (*Carduelis chloris*) 43%, European goldfinch (*C. carduelis*) 40%, both siskin (*C. spinus*) and linnet (*C. cannabina*) 39%) (Cramp and Perrins 1994). These data are similar to the limited data on high-elevation species: white-winged grosbeak 38%, red-mantled rosefinch (*Carpodacus rhodochlamys*) 47% (Kovshar 1981). In addition, high-elevation species typically show higher fidelity to their previous nesting locales and shorter natal dispersal compared to low-elevation species (Kovshar 1981; Badyaev 1987). This could result in overestimating of survival in high-elevation species, further reducing support for the prediction that high-elevation species would have higher adult survival.

If reduced fecundity of high-elevation species results from lower reproductive effort, longer time between nesting attempts is expected (Martin 1992). In conditions of limited breeding season, however, renesting intervals are much shorter for high elevation species and different phases of the nesting cycle frequently overlap (i.e., provisioning first brood and incubation of a subsequent one overlap) (Kovshar 1981; Badyaev 1987). Moreover, in repeated nesting attempts, high-elevation species frequently overlap the energetically-stressful post-breeding molt period with food provisioning (Kovshar 1981). These data suggest that reproductive effort of high-elevation species may not be lower compared to low-elevation finches. More data are needed to examine whether adult survival and reproductive effort vary with elevation of breeding.

Reduced fecundity of high-elevation species could be compensated by higher juvenile survival (Charlesworth 1980). Higher juvenile survival could result from greater development of the immune systems following longer incubation and/or greater parental investment in young after they leave the nest (Breitwisch 1988; Ricklefs 1992; Martin 1996). Indeed, high-elevation carduelines provision fledged young with food for longer time than low-elevation finches (Kovshar 1981; Badyaev 1987). For example, in European populations of common rosefinch (*Carpodacus erythrinus*), adults feed fledglings for 10–15 days after leaving the nest (Ptushenko and Inozemtsev 1968) compared to 24–27 days in subalpine of Tien Shan (Kovshar 1981). Adults in low-elevation populations of common bullfinch (*Pyrrhula pyrrhula*) provide food for young for 14–16 days (Cramp and Perrins 1994), compared to 20–28 days in subalpine populations of red-mantled rosefinch (Kovshar 1981; Badyaev 1987). In low-elevation hawfinch (*Coccothraustes coccothraustes*), adults supplement young with food for 20–30 days (Cramp and Perrins 1994), compared to 34–60 days in subalpine populations of white-winged grosbeak (Badyaev 1994).

In addition to longer care of fledgings, shorter post-fledgling movements appear to be common in high-elevation species. Post-fledgling movements were much shorter for subalpine populations of gold-fronted serins and white-winged grosbeaks compared to forest populations of these species (Badyaev 1993, 1994). Families stay within 800 m of their nest for up to 60 days in white-winged grosbeaks, 10–20 m from nests for up to 27 days in red-mantled rosefinch, and within 366 m of nest for 26 days in subalpine populations of common rosefinch (Kovshar 1981). Such reduced post-fledgling movements are thought to contribute to higher familiarity with local conditions in high-elevation finches and ultimately account for reduced natal dispersal typical for high-elevation birds (Kovshar 1981). Prolonged care for young and low natal dispersal in high-elevation finches can result in higher juvenile survival which can compensate for lower fecundity of high-elevation species and account for differences in life history strategies across elevations.

In sum, I found a strong association between cardueline finch life histories and breeding elevation. High-elevation species had smaller clutches, produced fewer broods, and had longer incubation periods than low-elevation species. Variation in neither food availability, nest predation, or adult survival appear to fully account for elevational pattern in cardueline life histories. However, juvenile survival may be greater at higher elevations as a result of prolonged parental care and lower natal dispersal, and could compensate for apparent reduced fecundity in high-elevation finches.

References

Badyaev AV (1987) Composition and distribution of the Pamir-Alay Mountain avifauna (98 spp.) and peculiarities of avian biology in conditions of subalpine juniper bush belt. Thesis, Moscow University, Moscow

Badyaev AV (1993) Breeding biology of the gold-fronted serin (*Serinus pusillus*) in conditions of subalpine bush zone of the Phansky Mountains. (In Russian) Biol Nauk 348:89–99

Badyaev AV (1994) Breeding biology of white-winged grosbeak (*Mycerobas carnipes*) in the Phansky Mountains. (In Russian) Bull Mosk. Obch. Ispit. Prir. Biol Div 99:20–28

Badyaev AV (1997a) Covariation between sexually selected and life history traits: an example with cardueline finches. Oikos 80:1–11

Badyaev AV (1997b) Altitudinal variation in sexual dimorphism: a new pattern and possible underlying causes. Behav Ecol (In Press)

Banin DA (1987) Probable ways of avifauna formation in subalpine belt of the southern USSR mountains. Ornithologia 22:124–134

Berven KA (1982) The genetic basis of altitudinal variation in the wood frog *Rana syvatica*. I. An experimental analysis of life history traits. Evolution 36:962–983

Boehme RL (1975) Birds of the South Palearctic Mountains. Moscow University Press, Moscow

Boyce MS (1979) Seasonality and patterns of natural selection for life histories. Am Nat 114:569–583

Breitwisch R (1988) Mortality patterns, sex ratios, and parental investment in monogamous birds. Curr Ornithol 6:1–50

Brooks DR, McLennan DA (1991) Phylogeny, ecology, and behavior: a research programs in comparative biology. University Chicago Press, Chicago

Charlesworth B (1980) Evolution in age-structured populations. Cambridge University Press, Cambridge

Clement P, Harris A, Davis J (1993) Finches and sparrows: an identification guide. Princeton University Press, Princeton

Cody ML (1966) A general theory of clutch size. Evolution 20:174–184

Cramp S, Perrins CM (eds) (1994) The birds of the western Palearctic, vol VIII. Oxford University Press, Oxford

Endler JA (1977) Geographic variation, speciation and clines. Princeton University Press, Princeton

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15

Garland T Jr, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst Biol 41:18–32

Grafen A (1992) The uniqueness of the phylogenetic regression. J Theor Biol 156:405–424

Grant BW, Dunham AE (1990) Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus meriami*. Ecology 71:1765–1776

Harvey P, Pagel MD (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford

Hoffmann AA, Watson M (1993) Geographical variation in the acclimation responses of *Drosophila* to temperature extremes. Am Nat 142:S93–113

Krementz DG, Handford P (1984) Does avian clutch size increase with altitude? Oikos 43:256–259

Kovshar AF (1981) Peculiarities of the bird reproduction in subalpine: on the material of Passeriformes in the Tien Shan (In Russian). Academy of Sciences of the Kazakh SSR, Alma-Ata

Kulesza G (1990) An analysis of clutch-size in New World passerine birds. Ibis 132:407–422

Lack D (1948) The significance of clutch size, part 3. Some interspecific comparisons. Ibis 90:25–45

Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

Lima SL (1987) Clutch size in birds: a predation perspective. Ecology 68:1062–1070

Mathies T, Andrews RM (1995) Thermal and reproductive biology of high and low elevation populations of the lizard *Sceloporus scalaris*: Implications for the evolution of viviparity. Oecologia 104:101–111

Martin TE (1992) Interaction of nest predation and food limitation in reproductive strategies. Curr Ornithol 9:163–197

Martin TE (1993) Nest predation among vegetation layers and habitat types: revising the dogmas. Am Nat 141:897–913

Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation and food. Ecol Monogr 65:101–127

Martin TE (1996) Life history evolution in tropical and south temperate birds: what do we really know? J Avian Biol 27:263–272

Martin TE, Badyaev AV (1996) Sexual dichromatism relative to nest height and nest predation: contributions of females versus males. Evolution 50: 2454–2460

Møller AP, Birkhead TR (1992) A pairwise comparative method as illustrated by copulation frequency in birds. Am Nat 139:644–656

Owens IPF, Bennett PM (1995) Ancient ecological diversification explains life-history variation among living birds. Proc R Soc Lond B261:227–232

Price T, Liou L (1989) Selection of clutch size in birds. Am Nat 134:950–959

Ptushenko ES, Inozemtsev AA (1968) Biology and economic importance of birds of Moscow Area and adjacent territories (In Russian). Nauka, Moscow

Purvis A, and Garland T Jr (1993) Polytomies in comparative analyses of continuous characters. Syst Biol 42:569–575

Purvis A, Rambaut A (1995) Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analyzing comparative data. Comp Appl Biosci 11:247–251

Ricklefs RE (1976) Growth rates of birds in the humid New World Tropics. Ibis 118:179–207

Ricklefs RE (1992) Embryonic development period and the prevalence of avian blood parasites. Proc Natl Acad Sci USA 89: 4722–4725

Schmalhausen II (1949) Factors of evolution. Blakiston, Philadelphia

Skutch AF (1949) Do tropical birds rear as many young as they can nourish? Ibis 91:430–455

Skutch AF (1985) Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithol Monogr 36:575–594

Slagsvold T (1982) Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia 54:159–169

Stearns SC (1986) Evolution of phenotypic plasticity in life history traits: reduction of reaction norms for age and size of maturity. Evolution 40:893–913

Williams GC (1966) Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton

Williams GC (1992) Natural selection: domains, levels, and challenges. Oxford University Press, Oxford

Via S, Gomulkiewicz R, De Jong D, Scheiner SM, Schlichting CD, et al. (1995) Adaptive phenotypic plasticity; consensus and controversy. Trends Ecol Evol 10:212–217