

EVOLUTION OF LIFE HISTORIES ALONG ELEVATIONAL GRADIENTS: TRADE-OFF BETWEEN PARENTAL CARE AND FECUNDITY

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Abstract. Life history responses to environmental conditions include a combination of fecundity–survival schedules and behavioral strategies that yield the highest fitness in a given environment. In this study, we examined the pattern of covariation in avian life history strategies along an elevational gradient by comparing variation in life history traits, including most components of parental care, between phylogenetically paired taxa from low- and high-elevation sites. We found that high-elevation species had significantly lower annual fecundity but provided greater parental care to their offspring. However, a strong negative relationship between offspring number and duration of parental care along the elevational gradient suggested that high-elevation species were shifting investment from offspring number toward offspring quality. Although adult survival did not differ between high- and low-elevation species, higher juvenile survival may have compensated for lower annual fecundity in high-elevation species. The elevation at which breeding strongly influenced the partitioning of parental behavior between sexes. Male participation in nestling provisioning was significantly greater in high-elevation species. In turn, altitudinal variation in the frequency of biparental care closely covaries with the intensity of sexual selection, ultimately resulting in the strong elevational pattern of sexual dimorphism. Moreover, elevational variation in costs of development and maintenance of secondary sexual traits constitutes an additional effect on fecundity–survival schedules along elevational gradients. Thus, a trade-off between fecundity and parental care, and associated interactions among morphological, life history, and behavioral traits play important roles in the evolution of life history strategies in birds.

Key words: *birds; breeding elevation; environmental gradient; fecundity; life history; nest predation; parental care; sexual dimorphism; trade-offs.*

INTRODUCTION

A central goal in the study of life history evolution is understanding the ecological factors that favor different life histories (e.g., Williams 1966, Partridge and Harvey 1988, Southwood 1988). Comparisons of species and isolated populations occupying different environments often reveal extensive variation in life history traits (reviewed in Roff 1992, Stearns 1992). Theoretical models and empirical evidence suggest that the most important selection pressures favoring differences in life histories are those affecting age-specific mortality (e.g., Law et al. 1977, Charlesworth 1980, Crowl and Covich 1990, Reznick et al. 1990, 1997, Martin 1995, Martin and Clobert 1996), or the opportunity for organisms to grow and reproduce (e.g., Berven 1982*a, b*, Wyngaard 1986*a, b*, Adolph and Porter 1993, 1996).

Yet, selection rarely acts on single life history traits, but rather on suites of traits that respond to selection in a correlated manner (e.g., Endler 1995). For ex-

ample, in response to increased predation on adult fish, Trinidad guppies (*Poecilia reticulata*) evolve life history strategies characterized by a combinations of fast growth, early maturation, increased reproductive allocation, high numbers of small offspring, and the presence of a diversity of antipredator behaviors (Seghers 1974, Reznick and Endler 1982; reviewed in Endler 1995). Furthermore, differences in predation risk strongly affect the population variation in intensity of sexual selection, which in turn influences another suite of morphological and behavioral traits (Endler 1995, Svensson and Sheldon 1998, Höglund and Sheldon 1998; reviewed in Badyaev and Hill 1999). Thus, locally adapted phenotypes arise through interactions between natural and sexual selection that favor a suite of life history, behavioral, and morphological traits. Such multiple-trait co-adaptation along environmental gradients is thought to be a common phenomenon in nature, but few empirical examples exist (Endler 1995, Badyaev 1997*a*).

Elevation is one environmental gradient in which natural and sexual selection interact to influence a suite of morphological, behavioral, and life history traits (e.g., Cody 1966, Boyce 1979, Berven 1982*a*, Grant and Dunham 1990, Mathies and Andrews 1995, Badyaev 1997*a, c*). Ecological conditions at high elevations, such as colder temperatures, greater seasonality,

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shorter breeding seasons, and greater fluctuations in food availability (e.g., Abdusalyamov 1964, Kovshar 1981c), favor increased investment per offspring as a strategy to increase offspring survival (e.g., Berven 1982a, b, Badyaev 1993, 1997b, c, Blackenhorn 1997). Indeed, across a wide diversity of terrestrial and aquatic ectotherms, high-elevation populations are characterized by smaller clutches of larger eggs, whereas low-elevation populations have larger clutches of smaller eggs (Berven 1982a, b, Howard and Wallace 1985, Blackenhorn 1997, Rohr 1997, Hancock et al. 1998). Likewise, some endotherms occurring along elevational gradients exhibit a similar pattern of decreasing clutch size with increasing elevation (e.g., Zang 1980, 1988, Kremetz and Handford 1984, Badyaev 1997b), although no concomitant change in egg size has been reported. However, some evidence suggests that birds and mammals may compensate for reduced fecundity at high elevation by increasing the amount of parental care, especially male parental care, provided to offspring (Badyaev 1997c, Wynne-Edwards 1998). Thus, variation in behavioral strategies, such as aspects of parental care, could play an important role in the interaction between ecological pressures and species' fecundity and survival.

Changing ecological conditions along elevational gradients may also influence a species' mating system, intensity of sexual selection, and development of sexual ornamentation (Kovshar 1981c, Badyaev 1993, 1997a, c, Badyaev and Ghalambor 1998; reviewed in Badyaev and Hill 1999). For example, in high-elevation species of birds, the expression of secondary sexual traits may be affected in several ways. First, successful reproduction at higher elevations requires greater biparental investment because of colder, less predictable climatic conditions and the disjunct distribution of feeding and nesting habitats (Frey 1989a, b, Badyaev 1993, 1994). Thus, males of high-elevation species may require greater assurance in their own paternity, which in turn could constrain paired males and females from seeking extrapair fertilizations, thereby lowering the intensity of sexual selection (e.g., Badyaev 1997c). However, predation risk associated with increased paternal activity at the nest covaries with the expression of conspicuous traits such as plumage and song (e.g., Shutler and Weatherhead 1990, Martin and Badyaev 1996; reviewed in Badyaev and Hill 1999). Indeed, studies suggest that the intensity of sexual selection and the differences between sexes in selection pressures may be reduced at high elevations, thereby accounting for a strong negative relationship between sexual dimorphism and elevation in birds and mammals (Saino and De-Bernardi 1994, Dobson and Wigginton 1996, Badyaev 1997c). In addition, development of greater sexual ornaments is commonly associated with reduced juvenile survival (e.g., Owens and Bennett 1994), constituting an additional, indirect effect of an environment on life histories. Thus, ele-

vation-induced variation in life history traits could result from both direct effects (such as variation in predation risk and food availability) and indirect effects (such as variation in intensity of sexual selection and corresponding changes in biparental care). Yet, the interactions among life history, behavioral, and morphological traits along an ecological gradient have not been studied across species.

In this study, we examine the pattern of covariation in avian life history strategies along an elevational gradient by comparing how life history traits, including most components of parental care, differ among phylogenetically paired species of passerine birds from low- and high-elevation sites. This paper consists of three parts. First, we establish that reduced fecundity coupled with increased parental care is a common phenomenon among avian species breeding at high elevations. Second, because the interaction of nest predation and food limitation has been shown to strongly influence avian life histories (Kulesza 1990, Martin 1992, 1995, Martin and Clobert 1996, Julliard et al. 1997), we test whether elevational variation in these factors can account for differences in life history strategies between high- and low-elevation species. Finally, we discuss the integration of parental behavior with other life history traits, and specifically address how environmentally induced variation in parental strategies can affect the evolution of social systems and life histories in birds.

METHODS

Data collection

We collected published data on life history variables related to investment in reproduction. These variables include annual adult survival, length of the nest-building period, clutch size (number of eggs per nest), number of broods per year, length of the incubation period, length of the nestling period, and duration of postfledging care. We also collected all published data on components of parental care including male participation in nestling feeding (percentage of total trips), nestling provisioning rate (number of trips per hour per each nestling) separately by female and male parents, nest provisioning rate (number of trips per hour for the entire nest) by female and male, and female nest attentiveness during incubation (ratio of the number of minutes on the nest divided by the sum of minutes on and off the nest) (Tables 1 and 2). We examined variation in nestling provisioning patterns to evaluate the importance of food limitation on variation in fecundity (e.g., Martin 1996, Badyaev 1997b). Variation in the risk of nest predation has been shown to strongly influence avian life histories (Martin 1992, 1995, 1996, Martin and Clobert 1996). Thus we also collected published data on the percentage of nest success and nest predation. Predation rates are reported on a per nest basis because of possible biases in determining causes

TABLE 1. Breeding parameters, including elevation, clutch and brood size, duration of nesting cycle stages, levels of predation and nesting success, and annual adult survival for pairs of bird species analyzed (the high-elevation member of the pair is listed first).

Pair no.	Species	Elevation (m)	Clutch (no. eggs per nest)	No. broods/year	Duration of period (d)			
					Nest-building	Incubation	Nesting	Post-fledgling
1	<i>Anthus spinoletta blakistoni</i>	3050	5.3	1.5	...	14.5	14.5	...
	<i>Anthus spinoletta spinoletta</i>	100	5.5	2.0	4.5	14.5	14.5	12.0
2	<i>Anthus trivialis harringtoni</i>	2100	4.3	1.0	...	12.3	12.0	14.0
	<i>Anthus trivialis trivialis</i>	200	4.7	2.0	5.0	11.1	12.5	9.5
3	<i>Motacilla alba personata</i>	2700	5.1	2.0	18.0	11.9	15.6	16.0
	<i>Motacilla alba alba</i>	100	5.5	2.0	10.0	12.4	13.5	8.0
4	<i>Motacilla cinerea caspica</i>	2000	5.0	1.5	10.5	11.8	13.2	14.0
	<i>Motacilla flava flava</i>	100	5.3	1.0	6.0	12.4	11.7	10.0
5	<i>Troglodytes t. tianschanicus</i>	2225	5.6	2.0	...	15.8	16.8	8.0
	<i>Troglodytes t. troglodytes</i>	50	6.7	2.0	...	14.0	15.5	7.5
6	<i>Prunella f. fulvescens</i>	3200	4.1	1.5	10.0	11.2	13.0	12.5
	<i>Prunella atrogularis huttoni</i>	2600	4.0	2.1	16.0	12.3	12.6	9.0
7	<i>Calliope pectoralis ballioni</i>	2700	4.4	2.0	4.5	14.0	16.0	13.0
	<i>Luscinia luscinia</i>	50	4.9	1.0	4.0	10.5	9.5	16.0
8	<i>Phoenicurus erythronotus</i>	2600	4.6	2.0	9.5	15.0	16.2	13.0
	<i>Phoenicurus caeruleocephalus</i>	1900	3.9	2.0	8.0	14.5	16.2	11.5
9	<i>Phoenicurus p. phoenicurus</i>	2100	6.2	1.0	4.0	12.8	15.6	17.0
	<i>Phoenicurus p. phoenicurus</i>	560	6.2	2.0	5.0	13.0	14.5	7.5
10	<i>Saxicola torquata maura</i>	2400	5.2	1.5	...	14.0	12.0	16.0
	<i>Saxicola torquata rubicola</i>	700	5.3	2.0	...	13.5	13.5	4.5
11	<i>Turdus merula intermedia</i>	1600	4.2	1.5	4.0	13.0	15.0	25.0
	<i>Turdus merula merula</i>	150	4.4	2.0	4.0	13.0	13.6	19.6
12	<i>Turdus viscivorus bonapartei</i>	1900	3.7	2.0	4.0	13.5	15.7	18.0
	<i>Turdus v. viscivorus</i>	150	4.2	2.0	7.5	13.5	14.5	12.0
13	<i>Phylloscopus griseola</i>	2700	4.8	1.0	7.5	15.3	15.9	15.0
	<i>Phylloscopus collubita</i>	150	5.5	2.0	7.0	14.0	15.0	14.5
14	<i>Phylloscopus inornatus humei</i>	2600	4.8	1.0	6.0	12.6	12.9	13.0
	<i>Phylloscopus trochilus</i>	125	6.3	1.0	5.5	13.0	13.2	11.0
15	<i>Phylloscopus t. viridanus</i>	2050	4.7	1.0	5.5	12.8	13.1	15.0
	<i>P. trochiloides viridanus</i>	0	5.5	1.0	...	12.5	13.0	...
16	<i>Regulus regulus tristis</i>	2100	8.1	1.0	18.5	16.7	19.5	...
	<i>Regulus r. regulus</i>	200	9.7	2.0	11.0	16.0	19.0	13.5
17	<i>Parus songarus</i>	2050	5.2	1.0	20.0	14.8	21.1	21.0
	<i>Parus montanus</i>	100	7.5	1.0	12.5	14.0	18.5	12.0
18	<i>Parus ater rufipectus</i>	2050	7.3	1.0	10.0	14.0	19.3	11.5
	<i>Parus ater ater</i>	50	8.6	...	4.5	13.5	19.0	9.0
19	<i>Certhia f. tianshanicus</i>	2000	5.0	1.0	12.0	15.5	18.5	...
	<i>Certhia familiaris familiaris</i>	75	5.3	2.0	9.5	14.0	15.3	14.0
20	<i>Serinus pusillus</i>	2700	3.7	1.0	13.0	12.8	15.5	16.0
	<i>Serinus pusillus</i>	2000	4.2	1.0	10.0	11.4	14.6	7.0
21	<i>Carduelis carduelis carnipes</i>	2020	4.3	1.0	12.0	12.0	12.0	16.5
	<i>Carduelis carduelis</i>	0	4.9	1.0	...	11.7	14.7	10.0
22	<i>Carpodacus e. ferganensis</i>	2300	4.2	1.0	10.0	13.5	12.0	18.0
	<i>C. erythrinus erythrinus</i>	0	4.8	...	3.0	11.5	11.5	12.5
23	<i>Mycerobas carnipes</i>	3500	2.9	1.0	12.0	17.5	20.5	47.0
	<i>Mycerobas carnipes</i>	2000	3.6	1.0	8.0	15.0	17.5	20.0
24	<i>Cinclus cinclus leucogaster</i>	1500	4.0	1.0	5.5	17.0	23.0	20.0
	<i>Cinclus c. cinclus</i>	700	4.8	1.0	...	16.0	22.0	12.5

† 1, Kovshar (1979); 2, Gubin and Gubina (1976); 3, Kochanov et al. (1970); 4, Cramp (1992) and references therein; 5, Ptushenko and Inozemtsev (1968); 6, Kovshar (1966); 7, Badyaev et al. (1996) and references therein; 8, Abdusalyamov (1973); 9, Ivanov (1969); 10, Abdusalyamov (1964); 11, Kovshar (1972); 12, Badyaev et al. (1998) and references therein; 13, Rodionov (1968); 14, Potapov (1966); 15, Kuznetsov (1962); 16, Badyaev (1987); 17, Gavrilov (1973); 18, Gavrilov and Kovshar (1970); 19, Yanushevich et al. (1970); 20, Kuzmina (1970); 21, Kovshar (1964); 22, Gavrilov and Kovshar (1972); 23, Kovshar and Levin (1975); 24, Popov (1959); 25, Gavrilov (1970); 26, Kovshar and Gavrilov (1973); 27, Cramp and Perrins (1993) and references therein; 28, Kovshar et al. (1974); 29, Cramp and Perrins (1994) and references therein; 30, Kovshar (1976); 31, Kovshar and Malceva (1978); 32, Kovshar (1981b); 33, Badyaev (1993); 34, Borodichin (1974); 35, Badyaev (1994); 36, Borodichin (1970a); 37, Borodichin (1970b); 38, Bozko and Andreevskaya (1960); 39, Inozemtsev (1961).

of partial brood losses, and because predation usually causes loss of the entire brood (e.g., Ricklefs 1969, Martin 1995). Species were assigned to one of four general nest placement categories (crevice, ground,

shrub, subcanopy/canopy; after Martin and Badyaev 1996). Nests were classified as crevice nests if they were in the crevice of an uprooted tree, under the roots, or in a rock crevice (e.g., the *Troglodytes* species pair

TABLE 1. Extended.

Nest success (%)	Nest predation (%)	Adult survival (%)	References†
46.8	39.2	...	1,2
58.0	24.0	...	3,4
70.7	26.8	19.6	1,4
62.8	22.2	57.1	4,5
86.9	0.0	62.5	1,6,7,8
52.7	23.6	56.3	4,7
55.0	22.6	40.0	1,9,10
51.3	29.2	63.0	4,12
85.7	13.9	42.9	1,13
65.0	35.0	42.0	4,5,13
76.7	16.5	48.5	6,8,14–16
55.7	38.6	15.8	1,11,17
68.6	22.4	18.8	6,15,18–20
76.8	23.2	...	4,5
63.5	32.5	32.5	11,15,19–22
59.0	33.3	26.0	1,23
78.9	0.0	30.0	1,4
74.9	25.0	43.5	1,4
50.0	37.5	...	9,10,19,24
64.0	17.0	...	4,5
55.2	44.8	...	6,19,25
39.5	39.9	...	4
59.1	38.8	50.0	1,17,26
...	...	52.0	4
45.4	38.6	...	6,8,10,16
43.8	17.0	...	27
68.2	23.4	28.0	16,28
55.8	32.4	32.7	27
70.3	20.0	33.4	1,6,28,31
...	27
81.8	18.2	...	1
50.0	36.0	...	5,27
75.0	10.7	30.3	1,28,29
54.0	46.0	...	27
70.0	10.0	34.7	1,27
86.0	14.0	33.2	27,39
38.5	23.1	33.3	1,36
58.0	14.6	...	27,38
57.0	43.0	45.0	16,33
40.0	49.0	61.2	16,33
33.3	60.0	38.0	6,20,34
38.0	62.0	43.0	29
38.4	51.3	47.3	1
76.0	24.0	66.0	29
87.5	12.5	45.0	16,35
37.0	63.0	37.5	16,35
100.0	0.0	...	1,6,20,37
51.4	18.4	57.5	4,37

and the *Leucosticte* pair; Table 1), ground nests if on the ground (e.g., the *Phylloscopus* pair), shrub nests if off the ground but generally <3 m high (e.g., the *Prunella* pair), and as subcanopy/canopy nests if higher (e.g., the *Carduelis* pair). Effects of nest placement on variation in life history were controlled for in the analysis of nest predation (see Martin 1995). Female body mass was used as a measure of body size.

To test the influence of elevation on life history variation among species, we calculated the mean elevation where breeding had been recorded (across all study sites). All available data were collected for 48 species

(24 pairs) of the most closely related species or subspecies (with sample sizes of >10 nests) that differed in breeding elevation, but were similar in diet, nest placement, migratory behavior, and other aspects of biology. The use of groups that have a certain degree of genetic isolation (especially species and subspecies) allowed us to assume that observed differences in life histories represent independent and recently evolved strategies (Schmalhausen 1949, Williams 1966). Most of the data used in this paper came from a very limited range of latitudes in mountains of Central Asia and lowlands of Central Europe (Table 1). Thus, variation in latitudes of species distribution is negligible compared to differences in elevations.

Data analyses

Phylogenetic relationships potentially create a problem of statistical non-independence among species (Felsenstein 1985, Harvey and Pagel 1991). To control for possible phylogenetic effects, all data were analyzed using the modification of the independent contrast method of Felsenstein (1985) and incorporating the method of Martin and Clobert (1996). Contrasts were calculated as differences in elevation and in life history traits between high- and low-elevation taxa within each pair (Table 1). We used pairwise *t* tests to assess significance of the obtained contrasts. This method provides the most direct test of concordance between elevation and life history traits, because it does not make any assumptions about phylogenetic relationships beyond that of examined sister taxa (Møller and Birkhead 1992, Martin and Clobert 1996). All relationships utilizing obtained contrasts were regressions in which the regression line was forced through the origin (see Garland et al. 1992). Regression models were used on the independent contrasts to test the influence of nest predation and elevation on life history traits after potential covariates (nest placement and body size) were entered into the model (Garland et al. 1992, Martin and Badyaev 1996, Badyaev 1997a). All data were square-root or log-transformed, percentage data were arcsine-transformed, and body mass was cube-root transformed before statistical analyses.

Differences in behavioral and life history traits within pairs of related species are likely to be relatively recent, and are assumed to be caused by present selection pressures. Thus, this variation is not likely to be strongly confounded by phylogenetic effects (Ricklefs and Starck 1996, Price 1997). For ease of interpretation, we provide results of analyses of phylogenetically untransformed data (i.e., taxa means—"species" values; Table 1) in addition to analyses of phylogenetically transformed data (i.e., "contrasts" values).

RESULTS

High-elevation species had significantly smaller clutches, fewer broods per year, longer nest-building

TABLE 2. Data for species pairs on male participation in nestling feeding, nest provisioning rate, nestling provisioning rate by female vs. male parent, and the overall provisioning rate by pair, as well as the duration of female incubation on-bout and off-bout.

Pair no.	Feeding by male (%)	Nest provisioning (no. trips/h)			Nestling provisioning (no. trips/nestling)			Incubation by female (min)†	
		By female	By male	By pair	By female	By male	By pair	On-bout	Off-bout
1	53.00	5.405	6.095	11.500	1.029	1.161	2.190
	50.00	1.800	1.800	3.600	0.300	0.300	0.600	15.30	5.70
2	48.00	2.808	2.367	5.175	0.559	0.691	1.250	58.20	14.75
	50.00	2.550	2.550	5.100	0.510	0.510	1.020	52.50	31.00
3	50.00	6.986	7.480	14.670	1.500	1.900	3.400	21.00	10.00
	50.00	1.731	1.731	3.463	0.315	0.315	0.630	22.10	8.20
4	60.10	3.373	5.395	8.740	0.708	0.994	1.760	40.00	40.00
	43.00	13.900	10.535	24.500	3.491	2.640	6.125	80.00	30.00
5	43.00	4.217	4.813	8.400	0.703	0.802	1.505	57.00	9.16
	25.00	11.685	3.895	15.580	2.737	0.912	3.650	12.50	29.73
6	47.20	3.379	3.021	6.400	1.118	1.053	2.230	46.25	9.00
	38.00	4.833	3.531	8.365	1.112	0.624	1.860
7	...	5.749	4.395	10.144	1.241	0.849	2.090
	46.00	9.30
8	58.20	4.149	4.920	9.070	0.958	1.032	1.990
	40.50	3.844	3.425	6.400	0.961	0.856	1.817	82.74	37.00
9	32.20	10.000	4.769	14.790	1.860	1.140	3.000	33.00	12.75
	37.00	13.830	8.128	21.970	2.067	1.214	3.281	16.50	...
10	57.67	2.250	3.063	5.310	0.750	1.469	2.219
	42.00
11	61.30	1.812	2.875	4.687	0.453	0.719	1.172	59.00	5.75
	50.00	1.351	1.351	2.703	0.450	0.450	0.901
12	46.92	2.100	1.837	5.000	0.649	0.559	1.419	57.50	9.00
	...	3.000	3.000	6.000	0.710	0.710	1.420	90.00	20.00
13	53.44	3.719	4.279	7.999	0.970	1.042	2.012	25.00	21.40
	25.00	28.50	13.50
14	59.64	12.000	17.700	29.680	2.499	4.331	6.830	36.00	15.33
	42.00	13.30	4.60
15	49.16	6.498	6.371	12.788	0.999	1.224	3.213	105.3	7.25

16	62.17	3.530	5.800	12.010	0.589	0.967	1.771	221.5	18.50
	50.00	12.000	12.000	24.000	1.237	1.237	2.474
17	59.90	6.625	9.938	16.560	1.440	2.159	3.600
	50.00
18	62.05	8.420	13.031	18.886	1.616	2.539	3.529
	50.00	4.000	4.000	8.000	0.665	0.665	1.333
19	50.00	20.000	20.000	40.000	4.000	4.000	8.000	16.00	6.50
	50.00	27.70	10.60
20	72.00	0.160	1.140	1.300	0.098	0.253	0.351	130.0	2.50
	62.00	0.520	0.850	1.420	0.125	0.204	0.329	75.50	9.50
21	60.00	0.280	0.720	1.200	77.33	2.67

22	68.00	0.410	0.589	0.867	0.077	0.163	0.239	71.17	8.83
	51.60	0.750	0.800	1.550	0.204	0.217	0.421	48.50	9.20
23	68.00	1.024	2.176	3.200	0.358	0.761	1.119	88.00	32.00
	55.00	0.900	1.100	2.000	0.251	0.306	0.557	95.00	27.00
24	58.20	3.271	4.540	7.811	0.818	1.135	1.953
	52.00	2.908	3.150	6.058	0.608	0.659	1.267	77.75	...

Note: See Table 1 for pair numbers and references; the high-elevation member of the pair is listed first.

† On-bout is the time period that the female spends on the nest; off-bout is the amount of time, during incubation, that the female spends off the nest.

periods, longer incubation periods, longer nestling periods, and longer postfledging periods compared to their low-elevation counterparts (Table 3). A comparison of both species means and phylogenetically corrected contrasts shows that clutch size and numbers of broods strongly decreased with increasing breeding elevation (Table 4, Fig. 1a, b; contrasts, clutch size $b_{ST} = -0.75$, $P = 0.000$; numbers of broods $b_{ST} = -0.39$,

$P = 0.06$, where b_{ST} is a standardized partial regression coefficient). At the same time, the duration of nest-building, incubation, and nestling periods strongly increased with elevation (Table 4, Fig. 1c–e; contrasts, nest-building period $b_{ST} = 0.62$, $P = 0.006$; incubation period $b_{ST} = 0.57$, $P = 0.003$; nestling period $b_{ST} = 0.51$, $P = 0.009$), as did the duration of postfledging care (Table 4, Fig. 1f; contrasts, $b_{ST} = 0.66$, $P = 0.001$).

TABLE 3. Reproductive biology parameters (untransformed means \pm 1 SD) of high- and low-elevation avian taxa.

Variable	Elevation category		Contrast (High – Low)	P
	High	Low		
Nest building, d	9.825 \pm 4.910	7.421 \pm 3.400	2.47 \pm 3.89	0.022
Clutch size	4.864 \pm 1.125	5.480 \pm 1.459	-0.62 \pm 0.61	0.000
Number of broods	1.333 \pm 0.434	1.591 \pm 0.503	-0.23 \pm 0.52	0.052
Total no. offspring/season	6.423 \pm 2.242	8.601 \pm 3.745	-2.114 \pm 3.29	0.005
Incubation length, d	13.929 \pm 1.735	13.221 \pm 1.443	0.71 \pm 1.06	0.003
Nestling period, d	15.787 \pm 3.142	14.808 \pm 2.801	0.98 \pm 1.76	0.012
Postfledging care, d	17.119 \pm 7.744	11.439 \pm 3.783	6.35 \pm 5.78	0.000
Nest success, %	65.104 \pm 17.585	56.803 \pm 13.348	8.34 \pm 21.97	0.089
Nest predation, %	25.241 \pm 16.377	31.245 \pm 14.068	-6.38 \pm 19.31	0.136
Adult survival, %	40.228 \pm 10.875	44.950 \pm 15.003	-4.66 \pm 16.87	0.319
Male feeding, %	55.659 \pm 9.074	45.655 \pm 9.257	10.55 \pm 8.22	0.000
Provisioning by female, no. trips/h	4.924 \pm 4.409	4.975 \pm 4.877	-1.16 \pm 4.44	0.312
Provisioning by male, no. trips/h	5.721 \pm 4.950	3.865 \pm 3.400	0.56 \pm 3.78	0.561
Provisioning, no. trips/h	10.674 \pm 9.005	8.794 \pm 8.077	-0.51 \pm 7.39	0.785
Prov. by female, no. trips/nestling	1.087 \pm 0.849	0.984 \pm 0.974	-0.17 \pm 0.99	0.515
Prov. by male, no. trips/nestling	1.345 \pm 1.044	0.739 \pm 0.601	0.25 \pm 0.79	0.218
Provisioning, no. trips/nestling	2.471 \pm 1.812	1.730 \pm 1.532	0.08 \pm 1.64	0.858
Female on-bouts, min	67.192 \pm 49.976	48.993 \pm 30.379	5.89 \pm 28.16	0.483
Female off-bouts, min	13.258 \pm 10.051	17.524 \pm 11.166	-2.17 \pm 10.62	0.514

Notes: Linear contrasts between high- and low-elevation taxa (High – Low) and corresponding t statistics are calculated from the pairwise comparisons (Tables 1 and 2; see *Methods* for more details). Boldface P values indicate significance at $\alpha < 0.1$ level.

Indeed, high-elevation species fed offspring after they had left the nest for an average of 6–7 d longer than did their low-elevation relatives (Table 3). These results point to an apparent trade-off between fecundity and parental care along the elevational gradient: high-elevation species produced fewer offspring, but provided greater parental care per offspring than did low-elevation species.

Nest predation affected variation in both life history traits and parental care, although its overall influence was smaller in comparison to elevation effects (Table 4; Badyaev 1997a, b). Species that were subject to greater nest predation had shorter incubation and nestling periods (Table 4, Fig. 2). Across all species, nest visitation decreased with increased nest predation. The duration of incubation on-bouts and nest attentiveness increased, whereas the frequency of nestling provisioning decreased with an increase in nest predation

($b_{ST} = 0.39$, $t = 2.18$, $n = 29$, $P = 0.04$; $b_{ST} = 0.37$, $t = 2.06$, $P = 0.04$; and $b_{ST} = -0.45$, $t = -3.06$, $n = 38$, $P = 0.004$; Fig. 3). However, nest predation rate, overall nest success, and adult survival did not differ between low- and high-elevation species (Table 3, Fig. 4). Thus, although nest predation strongly influenced variation in life history traits within each elevation category (Table 4, Figs. 2 and 3), it could not explain observed elevational patterns of life history traits.

Low- and high-elevation species did not differ in incubation regime, nestling provisioning rate, or provisioning rate per nestling (Table 3), suggesting a limited influence of possible food fluctuations on elevational variation in life history traits (Martin 1996). However, the percentage of male provisioning of nestlings strongly increased with elevation (for species, $b_{ST} = 0.46$, $t = 3.26$, $n = 40$, $P = 0.002$; for contrasts, $b_{ST} = 0.77$, $t = 5.09$, $n = 20$, $P < 0.0001$; Fig. 5).

TABLE 4. Effect of elevation and nest predation on variation in life history traits. Shown are standardized partial regression coefficients (b_{ST}) and associated t values for data uncorrected (Species) and corrected (Contrasts) for possible phylogenetic effects using the independent-contrasts method.

Dependent variables	Elevation						Nest predation					
	Species			Contrasts			Species			Contrasts		
	b_{ST}	t	P	b_{ST}	t	P	b_{ST}	t	P	b_{ST}	t	P
Clutch size	-0.42	-3.02	0.004	-0.75	-5.51	0.001	-0.12	-0.54	0.59	-0.44	2.28	0.03
Number of broods	-0.28	-1.90	0.060	-0.39	-1.93	0.058	0.11	0.74	0.47	0.12	0.30	0.76
Nest-building period	0.36	2.32	0.020	0.62	3.14	0.006	0.05	0.33	0.74	-0.31	-1.24	0.24
Incubation length	0.31	2.23	0.030	0.57	3.36	0.003	-0.31	-2.12	0.03	-0.13	-0.62	0.54
Nestling period	0.25	1.73	0.09	0.51	2.84	0.009	-0.32	-2.24	0.03	-0.45	2.29	0.02
Postfledging care	0.33	2.24	0.03	0.66	3.80	0.001	-0.07	-0.51	0.61	-0.08	-0.60	0.55

Notes: The effect of nest predation is examined while controlling for effects of body mass and nest placement (see *Methods*). Boldface P values indicate significance at $\alpha < 0.1$ level.

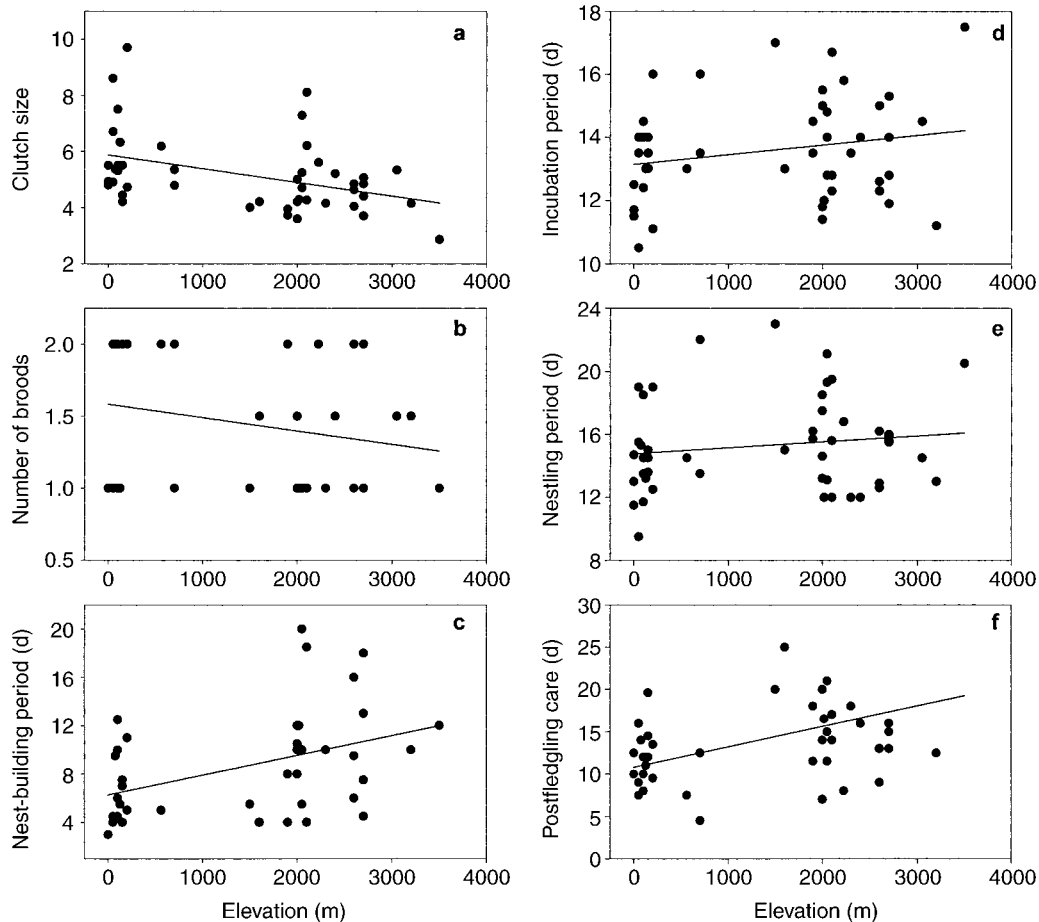


FIG. 1. Regression plots of raw data (taxa means) illustrating the relationship between elevation and (a) clutch size (standardized partial regression coefficient $b_{ST} = -0.42$, $P = 0.004$), (b) numbers of broods ($b_{ST} = -0.28$, $P = 0.05$), (c) nest-building period ($b_{ST} = 0.36$, $P = 0.02$), (d) incubation period ($b_{ST} = 0.31$, $P = 0.03$), (e) nestling period ($b_{ST} = 0.25$, $P = 0.09$), and (f) postfledgling care period ($b_{ST} = 0.33$, $P = 0.03$).

Males of high-elevation species fed nestlings, on average, 10.55% more than did males of related low-elevation species, and provisioning rates of males were higher than those of females in high-elevation species (Table 3).

DISCUSSION

General patterns in life history strategies

In comparing avian life history strategies of phylogenetically paired groups from low and high elevations, we found a general and strong pattern of covariation among traits. High-elevation species and subspecies have smaller clutch sizes and fewer broods, but longer nest-building, incubation, and nestling periods, and provide longer postfledgling care than do their low-elevation counterparts (Table 3, Figs. 1 and 2). These results suggest a trade-off between the number of offspring produced and the amount of parental care. Indeed, despite reduced annual fecundity at high elevations (see also Zang 1980, 1988, Badyaev 1997b), estimates of adult survival did not differ significantly

between low- and high-elevation pairs (Table 3). This raises a possibility that the total amount of time and energy allocated toward reproductive effort may not differ between high- and low-elevation groups (Kovshar 1981c, Badyaev 1997b; see also Bennett and Harvey 1988, Sæther 1988, Martin 1995, 1996, Martin and Clobert 1996). Instead, it appears that high-elevation birds are shifting their investment away from offspring number and toward offspring quality. For example, parental effort, measured as the time required to raise one offspring to independence, was significantly greater at high elevations (Fig. 6). We found no data on juvenile survival rates from either high or low elevations for species used in this study, but we expect that juvenile survival would be higher at high elevations because of greater parental investment. Indeed, greater parental care and delayed postfledgling dispersal at higher elevations increase the probability of offspring recruitment in high-elevation species (Badyaev 1993, 1994, 1997b, see also Ricklefs 1992). Moreover, delayed postfledgling dispersal in high-elevation species, facil-

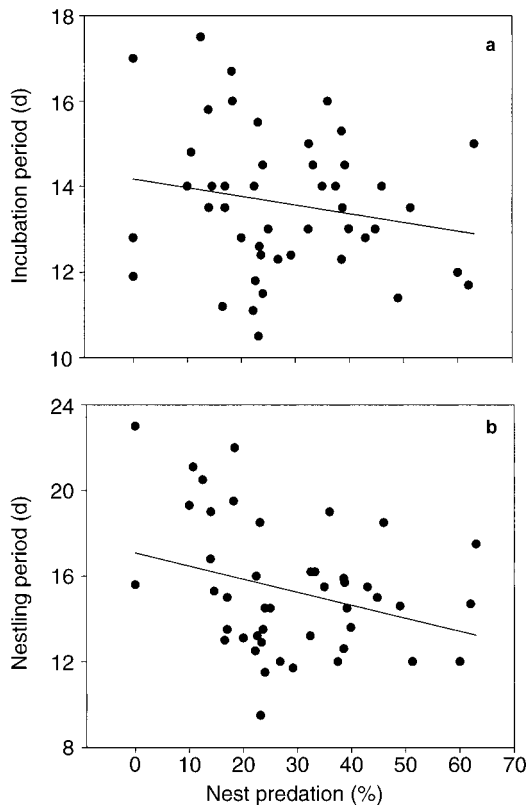


FIG. 2. Regression plots of raw data (taxa means) illustrating the relationship between nest predation and (a) incubation period ($b_{ST} = -0.31$, $P = 0.03$) and (b) nestling period ($b_{ST} = -0.32$, $P = 0.03$).

itated by reduced aggression of territorial adults toward juveniles (Kovshar 1981c), enables longer periods of growth in fledglings of high-elevation species compared to their low-elevation counterparts (e.g., in cardueline finches: Badyaev 1993, 1994, Badyaev and Martin 2000, Badyaev et al. 2001). For example, the widespread occurrence of compensatory growth during an extended postfledging period and the longer period of postfledging parental care in high-elevation finches allow smaller fledglings to achieve adult size, further increasing their survival (Badyaev 1993, 1994).

Observed differences in fecundity and parental care of birds from high and low elevations may have a genetic basis or they may represent phenotypic adjustments to local environmental conditions at different elevations. Transplant experiments or common garden approaches would shed light on the degree to which differences between groups have a genetic basis. However, pairing genetically diverged species and subspecies (rather than populations only) increased our inference of a genetic basis for observed differences in life history strategies between high- and low-elevation taxa (Schmalhausen 1949, Price 1997). Moreover, a population genetics study of natal down distribution patterns revealed a high degree of genetic isolation

between high- and low-elevation populations of several avian species (including pairs 20 and 23 of this study) in the Pamir Mountains of Central Asia (A. V. Badyaev 1987).

Environmental basis for differences in life history strategies

Increased parental care is assumed to evolve under adverse environmental conditions that reduce offspring survival (Clutton-Brock 1991). Species with extensive parental care may offset the effects of unpredictable and seasonal environments by modifying their care of young and increasing their reproductive effort (e.g., Perrins 1965, Low 1978, Lyon and Montgomerie 1987). Increased parental care and smaller clutch sizes at high elevations may therefore represent a strategy to increase offspring survival in response to increased nest predation, low food availability, or changing abiotic conditions (e.g., Martin 1995; see also Lyon and Montgomerie 1987, Nilsson and Smith 1988). In-

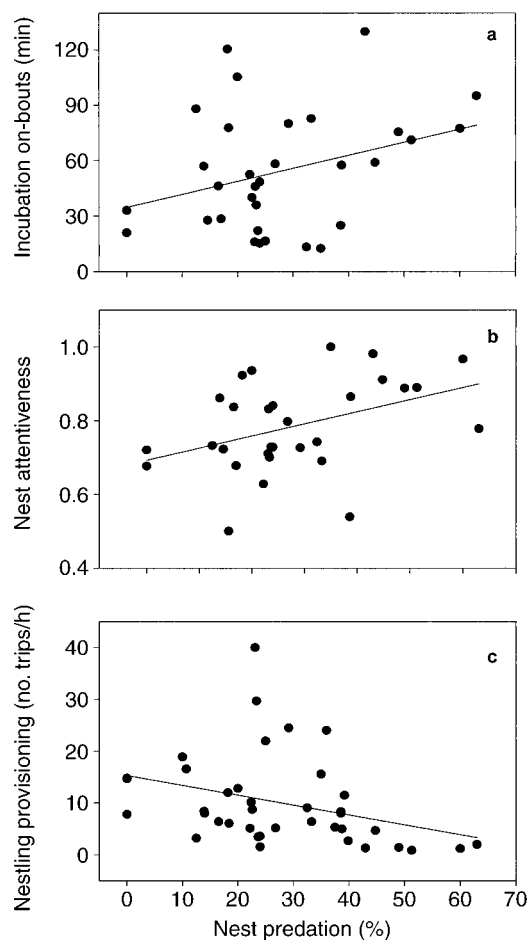


FIG. 3. Regression plots of raw data (taxa means) illustrating the relationship between nest predation and (a) incubation on-bout duration ($b_{ST} = 0.39$, $P = 0.04$), (b) nest attentiveness ($b_{ST} = 0.37$, $P = 0.04$), and (c) nestling provisioning rate ($b_{ST} = -0.45$, $P = 0.004$).

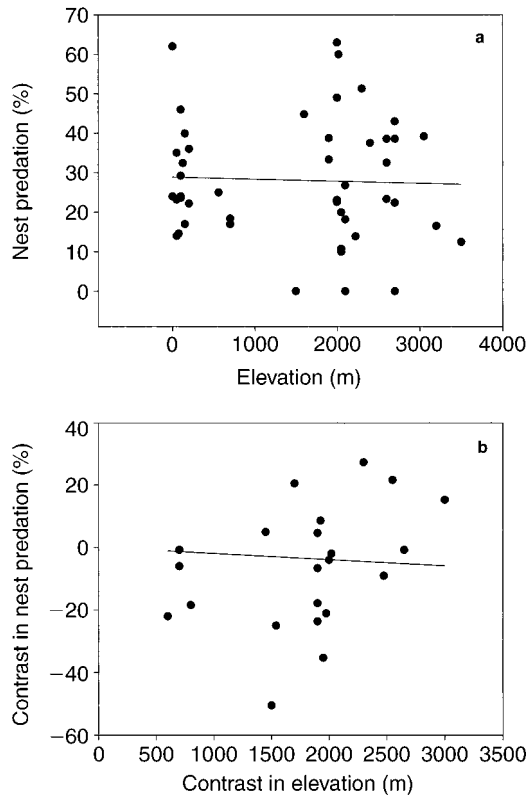


FIG. 4. Regression plots illustrating the relationship between nest predation and elevation for (a) raw data ($b_{ST} = -0.17$, $n = 47$, $t = -1.13$, $P = 0.26$), and (b) data transformed by the method of independent contrasts, which controls for possible phylogenetic effects ($b_{ST} = -0.21$, $n = 23$, $t = -0.97$, $P = 0.34$).

creased nest predation has been shown to influence a number of life history traits in birds, including nestling growth rates (Ricklefs 1968, Bosque and Bosque 1995), annual fecundity (Martin 1995, Martin and Clobert 1996), and the amount of parental activity at the nest (Ghalambor and Martin 2001). Yet, we found no difference between high and low elevations in the risk of nest predation (Table 3, Fig. 4), suggesting that nest predation is not responsible for the observed differences in life histories across the elevational gradient. Across all species, however, nest predation was negatively correlated with nestling visitation rates and the length of the incubation and nestling periods (Table 4, Fig. 2). Nest predation was also positively correlated with the duration of incubation on-bouts and nest attentiveness (Fig. 3). Thus, although nest predation does not explain variation between high and low elevations, it does account for a significant part of the variation in many life history traits within elevation categories (Table 4).

Low food availability favors reduced brood size, and frequent and longer time away from the nest during incubation could result in a longer incubation period and reduced nestling provisioning (Martin 1996). In

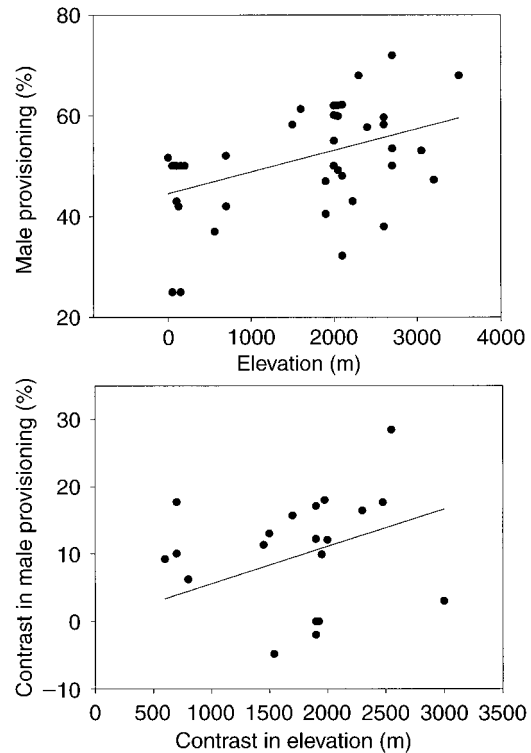


FIG. 5. Regression plots illustrating the relationship between elevation and the percentage of nestling provisioning by the male parent for (a) raw data ($b_{ST} = 0.46$, $P = 0.002$), and (b) data transformed by the method of independent contrasts, which controls for possible phylogenetic effects ($b_{ST} = 0.77$, $P < 0.0001$).

turn, reduced nestling provisioning could result in a longer nestling period (e.g., Ricklefs 1976). Thus, variation in food availability could potentially explain smaller clutches and longer development in high-elevation species (Martin 1996, Badyaev 1997b). However, we found no evidence for elevational variation in

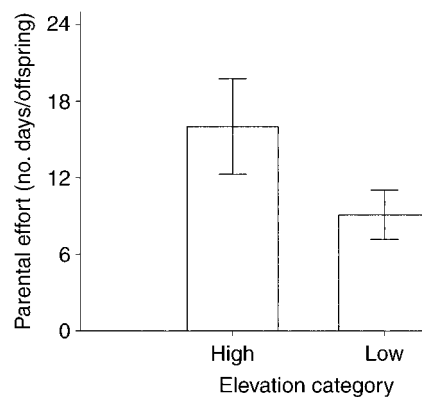


FIG. 6. Parental efforts per offspring (mean \pm 1 SD, calculated as a sum of nest-building, incubation, nestling, and postfledgling care periods divided by the number of offspring produced during one breeding season) for high- and low-elevation taxa ($F = 7.45$, $df = 1, 48$, $P = 0.009$).

either nest attentiveness or nestling provisioning rates (Table 3). Additional data on nestling growth rates, provisioning differences among nestlings, and food load per visit are necessary to further address the effect of food availability on elevational variation in life histories. However, the analysis of nestling provisioning suggests that food availability by itself is unlikely to explain the variation in avian life histories along an elevational gradient (Badyaev 1997b).

Some environmental factor other than nest predation and food availability must be favoring differences in life history strategies with increasing breeding elevation. Previous work on life history strategies of ectotherms such as frogs (Berven 1982a, b, 1987), skinks (Rohr 1997), snails (Baur and Raboud 1988), and freshwater shrimp (Hancock et al. 1998) along elevational gradients have stressed the importance of colder temperatures, reduced food availability, shorter breeding seasons, and greater climatic unpredictability at high elevations in favoring smaller clutch sizes and larger eggs to compensate for reduced juvenile survival and growth rates. Endotherms are also subject to similar selection pressures at high elevations, but rather than increasing egg size, the increased investment comes in the form of parental care. Previous work on cardueline finches has found increased parental care with increasing elevation (Frey 1989a, b, Badyaev 1993, 1994, 1997c), and studies of dwarf hamsters have shown that only mothers provide care at low elevations, whereas biparental care is provided at high elevations (Wynne-Edwards 1998). Increased parental care may therefore be analogous to increasing egg size, particularly among species in which individual fitness is largely determined by parental behavior rather than by the number of offspring produced. It would be interesting to compare altricial and precocial bird species along an elevational gradient and to test whether precocial species that lack extensive parental care decrease their clutch size and increase their egg size in a manner similar to that of ectotherms, which also lack parental care.

Elevation, parental behavior, and sexual selection

We found that variation in environmental conditions associated with changes in elevation strongly influences the partitioning of parental behavior between sexes, and especially male parental care (Table 3, Fig. 5). Males of high-elevation species provided, on average, 55.6% of all parental care compared to 45.6% in closely related low-elevation species (Table 3). Similarly, among cardueline finches, the number of days when males provided most of the parental care strongly increased with breeding elevation (Badyaev 1997c). Moreover, studies suggest that successful breeding is strongly dependent on male parental care at high elevations (Frey 1989a, b, Badyaev 1993, 1994; see also Lyon et al. 1987). High investment in parental activities reduces mating opportunities and also requires greater assurance of social paternity, i.e., it lowers solicitation

of extrapair fertilizations by both social partners (Andersson 1994). Both of these consequences of greater biparental care reduce the differences in selection pressures between males and females and lower the intensity of sexual selection on males (Andersson 1994). Thus, in monogamous species, the intensity of sexual selection should covary with the breeding elevation. This association has been documented across 126 extant species of cardueline finches; species occupying lower elevations are more sexually dimorphic in plumage than species at higher elevations, largely through increased sexual ornamentation of males at lower elevations (Badyaev 1997c).

In turn, elevational variation in sexual ornamentation by itself can have important implications for the evolution of life histories (Höglund and Sheldon 1998, Svensson and Sheldon 1998). First, because low-elevation species are more sexually ornamented (Badyaev 1997c), males and females of these species can suffer additional mortality associated with greater sexual ornamentation (Promislow et al. 1992, 1994; reviewed in Badyaev and Hill 1999). However, greater ornamentation of males in low-elevation species co-occurs with their lower activity near the nest (Table 3; see also Qvarnström 1997), thus reducing the mortality associated with parental care. As a result, the sexes experience more similar predation risks in high- than in low-elevation species (Badyaev 1997a: Table 8). Second, although conditions at low elevations favor increased and more elaborate sexual ornamentation, the development of such traits commonly results in reduced juvenile survival (e.g., Owens and Bennett 1994; see also Saino and Møller 1996). Thus, juvenile survival may be anticipated to be greater in high-elevation species, not only because of the behavioral strategies and greater parental care that we have discussed, but also because of the reduced mortality costs of development and maintenance of secondary sexual ornamentation (e.g., Owens and Bennett 1994, Badyaev 1997c; see also Höglund and Sheldon 1998).

In summary, our analyses of avian life-history strategies of phylogenetically paired taxa from low and high elevations have produced three principal conclusions. First, we found strong elevational variation in life history traits, including many measures of parental care: high-elevation species had significantly lower annual fecundity, but provided greater parental care to their offspring. Second, the strong negative relationship between offspring number and duration of parental care along elevational gradients suggests that high-elevation species are shifting their investment from the number of offspring toward offspring quality. Third, variation in the elevation of breeding strongly influences the partitioning of parental behavior between sexes; males of high-elevation species provided most of the parental care. Elevational variation in biparental care can strongly influence the intensity of sexual selection, ultimately resulting in previously described elevational

patterns of sexual dimorphism. Elevational variation in costs of development and maintenance of secondary sexual traits can also influence the evolution of life histories along an elevational gradient in birds.

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