DIET INFLUENCES LIFE SPAN IN PARROTS (PSITTACIFORMES)

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Abstract.—Evolutionary hypotheses regarding longevity predict that life span should increase as extrinsic mortality rates decrease. Specifically, a decline in age-specific survival and fertility should evolve and decrease life span in proportion to the magnitude of the mortality risk. We examined these ideas using a new data set on maximum longevity, ecology, and life history of 162 parrot species (Psittaciformes). Parrots are generally long-lived but exhibit remarkable variation in life span between similar-sized genera, with particularly long-lived species occurring in the *Cacatua*, *Calyptorhynchus*, and *Amazona*. After controlling for both body size and phylogenetic ancestry using a phylogenetic supertree of all 352 parrot species, type of diet and communal roosting explain significant variation in parrot life span, but the influence of communal roosting is statistically dependent on an association with diet type. We suggest that extreme longevity in parrots has evolved in response to species-specific characteristics of diet, habitat, and behavior that influence extrinsic mortality rates. *Received 24 July 2004, accepted 8 June 2005.*

Key words: life history, longevity, parrots, Psittaciformes.

La Dieta Influencia la Longevidad en los Psittaciformes

Resumen.—Las hipótesis evolutivas relacionadas con la longevidad predicen que la duración de la vida debe incrementarse cuando las tasas de mortalidad extrínseca disminuyen. Específicamente, se esperaría una disminución evolutiva en la supervivencia y la fertilidad a edades específicas, causando una disminución en la longevidad proporcional a la magnitud del riesgo de mortalidad. Examinamos estas ideas empleando una base de datos nueva sobre la longevidad máxima, la ecología y las historias de vida de 162 especies de Psittaciformes. Los Psittaciformes son generalmente longevos pero existe amplia variación en la longevidad entre géneros con especies de tamaño corporal similar; las especies particularmente longevas pertenecen a los géneros *Cacatua*, *Calyptorhynchus* y *Amazona*. Luego de controlar por el tamaño corporal y la ancestría filogenética empleando un superárbol filogenético de las 352 especies de Psittaciformes, el tipo de dieta y el uso de perchas comunales explicaron significativamente la variación en la longevidad, pero la influencia del uso de perchas comunales depende estadísticamente de una asociación con el tipo de dieta. Sugerimos que la extrema longevidad de los Psittaciformes ha evolucionado como respuesta a características de la dieta, el hábitat y el comportamiento específicas de las especies que influencian las tasas extrínsecas de mortalidad.

Evolutionary theories of longevity predict that average life span should increase as the rate of extrinsic mortality decreases (Austad and Fischer 1991). For example, the ability to fly may contribute to long life span in birds and bats through decreased vulnerability to environmental contingency (Holmes and Austad 1994). Probability of dying from extrinsic factors, such as predation, disease, or accidents, is believed to influence life span because the force of natural selection decreases with age. If extrinsic sources

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of mortality are important, then late-acting deleterious mutations in the population will not be exposed to selection, thus accumulating over time. Late-acting deleterious mutations that also have beneficial effects early in life result in antagonistic pleiotropy, and can further influence the evolutionary relationship between aging and extrinsic mortality (Partridge 2001). Under either the mutation-accumulation or antagonistic-pleiotropy mechanism, a decline in age-specific survival and fertility (i.e. senescence) should evolve and decrease life span in proportion to the magnitude of the mortality risk (Austad 1997). In support of this view, the rate of aging has been directly related to the risk of mortality for birds and mammals (Ricklefs 1998, Ricklefs and Scheuerlein 2001).

We present the first comparative examination of the evolution of longevity within the parrots (Psittaciformes). Parrots have been poorly studied in the wild, and a history of association with humans has only recently provided reliable longevity data for many species in captivity (Brouwer et al. 2000). The anecdotal reputation of parrots as very long-lived is not undeserved; they are the longest-lived order of birds for their body size (Prinzinger 1993). Psittacids also exhibit striking variation in life span between similar-sized taxa. We examined the evolution of life span in parrots using modern comparative methods and an extensive new database of longevity, life history, and ecological variables that seemed likely to reflect species differences in the rate of extrinsic mortality. Given this assumption, we predicted that mortality risk is associated with body size, foraging group size, communal roosting, diet type, aridity of habitat, latitude, and restriction to islands.

We predicted that the mortality risk from predation should be lower for larger-bodied species because they should have fewer predators than small-bodied species. Because many parrots are restricted to islands where predation or interspecific competition may be lower than in mainland habitats (Miller et al. 2000), we also predicted that insular species should exhibit greater longevity. We expected parrots with large foraging-group sizes and communal roosting to exhibit longer life spans, because flocking and communal roosting should reduce the per-capita risk of predation through predator dilution, enhanced vigilance, or both. Nesting habits that provide protection from predators

(such as cavity- or colonial-nesting) are associated with lower mortality rates (Martin 1995), lower fecundity, and the evolution of longer life span in birds (Owens and Bennett 1995) and bats (cave-roosting; Wilkinson and South 2002). Sociality has been implicated in the extended life spans of some taxa (Carey and Judge 2001), with eusocial insects providing the most convincing case (Keller and Genoud 1997). The gregarious nature of most parrots while foraging or roosting may result in lower extrinsic mortality in unpredictable environments. We also examined the influences of diet type, latitude, and aridity of habitat on longevity, because social behavior and the risk of starvation may be associated with diet, habitat, and foraging behavior (Cannon 1984, Jullien and Clobert 2000).

Diet type and annual fecundity may be associated with life span because of trade-offs between allocation of resources to somatic maintenance (e.g. repairing oxidative damage) and reproduction. Life span evolves as a consequence of joint selection for current reproduction along with survival and future reproduction. These evolutionary pressures may be influenced by seasonal food availability. Therefore, variation in diet type and annual fecundity may be associated with longevity even if these variables do not directly influence the risk of extrinsic mortality. We examined the influence of annual fecundity on longevity, and the influence of diet type on annual fecundity, to see whether costs associated with reproduction are implicated in the evolution of life span in parrots.

We also report comparisons between longevity and each ecological or life-history variable using analysis of phylogenetically independent contrasts, because closely related species are likely to share life-history characteristics as a result of recent common ancestry. No phylogeny of all the species included in our study was available, so we combined 53 phylogenetic trees from 28 studies into a single data set to create a phylogenetic "supertree" (Bininda-Emonds et al. 1999) of all parrot species.

Methods

Data collection.—Life-history and ecological data were compiled from primary and secondary literature for 162 parrot species for which Brouwer et al. (2000) reported maximum life span in captivity. We used captive longevity

records exclusively because these data are collected in the relative absence of extrinsic mortality and are closer to theoretical maximum life spans (Ricklefs and Scheuerlein 2001). We excluded maximum longevities under five years because all such records represented single individuals that died within a few months of entering captivity (n = 11 records excluded).

We used the following life-history variables: adult body mass (g; n = 142) and annual fecundity (number of clutches per year × clutch size; n = 149). We used the following ecological variables: aridity of habitat (n = 162), communal roosting (yes or no; n = 162), diet type (n = 159), feeding-group size (maximum; n = 115), latitude (middle of species range; n = 155), and restriction to islands (yes or no; n = 162). Aridity was ranked according to degree of precipitation (1 = arid, 2 = mesic, 3 = variable, and 4 = humid). Type of diet was ranked according to protein content (1 = frugivorous, nectarivorous, or both; 2 = omnivorous; and 3 = granivorous).

Phylogenetic methods.—Species data cannot be treated as statistically independent, because species are related through descent from common ancestors (Felsenstein 1985). Hence, we used CAIC (Comparitive Analysis by Independent Contrasts) software, version 2.6.9 (Purvis and Rambaut 1995) to convert species data into evolutionarily independent contrasts. We created a phylogenetic "supertree" (Sanderson et al. 1998) of all 352 parrot species by combining information from 53 phylogenetic trees from 28 systematic studies published since 1970 (Appendix). The supertree matrix was constructed using Matrix Representation with Parsimony (MRP; Baum 1992, Ragan 1992) where studies overlapped in species included in the analysis. We took measures to ensure the independence of the phylogenetic trees entering the final supertree analysis, because many single studies reported more than one tree calculated using the same data set (Bininda-Emonds et al. 2004). Nonindependent trees from the same study were first combined in one matrix using MRP. Then a single strict consensus tree was calculated from the most parsimonious trees found using the branch-and-bound algorithm in PAUP*, version 4.0b10 (Swofford 2001). Only this single consensus tree entered the final supertree matrix. Additionally, only trees that used unique data sets were included as independent entries in the supertree matrix. All source trees received equal

weighting in the analysis, and methods of tree combination followed those used previously for carnivores (Bininda-Emonds et al. 1999) and bats (Jones et al. 2002). We followed the species nomenclature of Juniper and Parr (1998) throughout the analysis.

All parrot species were not analyzed simultaneously because performance of the MRP method decreases with large numbers of taxa (Bininda-Emonds and Sanderson 2001). We analyzed the following clades separately: Cacatuidae (n = 21 species), Loriidae (n = 55), New World Psittacidae (n = 147), and Old World Psittacidae plus the three other higher-level clades (n = 132). Parrot systematists have long considered the Cacatuidae and Loriidae to represent monophyletic clades, though not always separate families (Forshaw 1989, Sibley and Ahlquist 1990). The New World parrots have been separated from Australasian parrots on the basis of shared morphological characters (Tribe Arini; Smith 1975), and Sibley and Ahlquist (1990) further argued that parrots could be separated by continental distribution (e.g. South America, Africa, Australia).

We found the most parsimonious trees for the Cacatuidae matrix using the branch-and-bound algorithm in PAUP*. For the three larger matrices, we calculated a strict consensus of the most parsimonious trees found using 10 replicate runs of the Parsimony Ratchet with 1,000 iterations each. The ratchet is a heuristic search strategy that moves around tree space more quickly than many traditional searching methods by reweighting a random subset of 25% of the characters at the beginning of each iteration (Nixon 1999). We used the PAUPRat computer program to implement the ratchet in PAUP* (Sikes and Lewis 2001). We set all branch lengths equal because branch lengths were not available. CAIC performs reasonably well under this assumption, even when the phylogeny is poorly resolved (Purvis et al. 1994). The data matrices used to create the supertree, and the supertree topology, are available electronically from TreeBASE (study accession no. S1219 and matrix accession nos. M2107–M2110; see Acknowledgments).

Statistical methods.—Continuous variables (body mass, longevity, annual fecundity, feeding-group size, and latitude) were log-transformed ($\log_{10}$) prior to analysis to improve normality. We controlled for body size in analyses using species data by taking

the residuals from a least-squares regression of log-transformed body mass on log-transformed longevity, because most life-history traits in homeotherms are highly correlated with body size (Lindstedt and Calder 1981). We controlled for body size in analyses using independent contrasts by taking the residuals from a least-squares regression forced through the origin (Garland et al. 1992) of the independent contrasts of log-transformed body mass on log-transformed longevity. We then analyzed these data using two different approaches. First, we examined the effects of life history and ecology on longevity using least-squares regression (continuous variables) and one-way analysis of variance (ANOVA; categorical variables: aridity, diet type, communal roosting, and island restriction). Second, we used least-squares regression forced through the origin to examine relationships between phylogenetically independent contrasts of residual longevity and continuous independent variables. We tested whether contrasts between residual longevity and categorical variables differed significantly from zero in the hypothesized direction using one-tailed t-tests (Purvis and Rambaut 1995). We also analyzed fecundity in relation to diet type using both species data and independent contrasts to examine the hypothesis that energy availability influences longevity through effects on fecundity.

We conducted a multiway ANOVA on species data to examine more complex statistical relationships between residual longevity and communal roosting, diet type, and island restriction, including the interaction between diet and island restriction. We further examined associations between diet and island restriction, and diet and communal roosting, using chi-square contingency-table analysis, and one-way ANOVA of diet on longevity and communal roosting on longevity for each communal-roosting and diet category, respectively. We used a significance level of $P \leq 0.05$ for all statistical tests. Analyses were conducted using the software package SAS, version 8.02 (SAS Institute, Cary, North Carolina).

Results

Longevity was not evenly distributed taxonomically among the Psittaciformes. Parrots in the family Cacatuidae exhibited generally greater mean longevity (39.5 years, n = 19) than species in the Psittacidae (22.7 years, n = 120) or Loriidae (17.0 years, n = 23). This same pattern was observed after factoring out body mass (Cacatuidae: mean residual longevity = 8.7 years, n = 19; Psittacidae: mean residual longevity = 0.7 years, n = 111; Loriidae: mean residual longevity = –1.5 years, n = 18). The two genera with the most long-lived species before and after factoring out body mass were also cacatuids: *Calyptorhyncus* (mean longevity = 46.0 years, n = 3; mean residual longevity = 11.7 years, n = 3) and *Cacatua* (mean longevity = 39.5 years, n = 12; mean residual longevity = 8.7 years, n = 12). The genus with the next most long-lived species was a Neotropical genus: *Amazona* (mean longevity = 33.5 years, n = 11; mean residual longevity = 5.1 years, n = 9). The Pink Cockatoo (*Cacatua leadbeateri*) exhibited the most extreme longevity ever recorded after factoring out body size: 35.0 residual years. The Salmon-crested Cockatoo (*C. moluccensis*; 28.7 residual years) and Yellow-crowned Amazon (*Amazona ochrocephala*; 26.4 residual years) have also exhibited extreme life spans for their body sizes.

Larger psittacid species live longer than smaller species (F = 120.86, df = 1 and 146, $P <$ 0.0001, adjusted r^2 = 0.45), and parrots also have longer life spans in captivity compared with other birds of the same body size (Fig. 1). After controlling for body size, only diet type and restriction to islands explained a significant proportion of variation in life span (Table 1 and Fig. 2). Parrots that form communal roosts tended to exhibit higher residual longevity, a difference that approached significance (P = 0.065). However, contingency-table analyses confirmed that diet was significantly associated with both island restriction (χ^2 = 24.45, df = 2, $P <$ 0.0001) and communal roosting (χ^2 = 8.06, df = 2, $P <$ 0.05). Multiway ANOVA revealed that the island effect was attributable to an interaction between diet type and island restriction rather than island restriction by itself (diet * island interaction: F = 3.19, df = 2 and 136, $P <$ 0.05; Fig. 2).

One-way ANOVAs of diet on residual longevity were significant for each communal roosting category (communal roosting = no, F = 4.06, df = 2 and 59, $P <$ 0.05; communal roosting = yes, F = 5.58, df = 2 and 78, $P <$ 0.01). By contrast, one-way ANOVAs of communal roosting on residual longevity for each diet category were not significant (diet = nectarivory–frugivory, F = 0.40, df = 1 and 25, P = 0.53; diet = omnivory, F = 1.53, df = 1
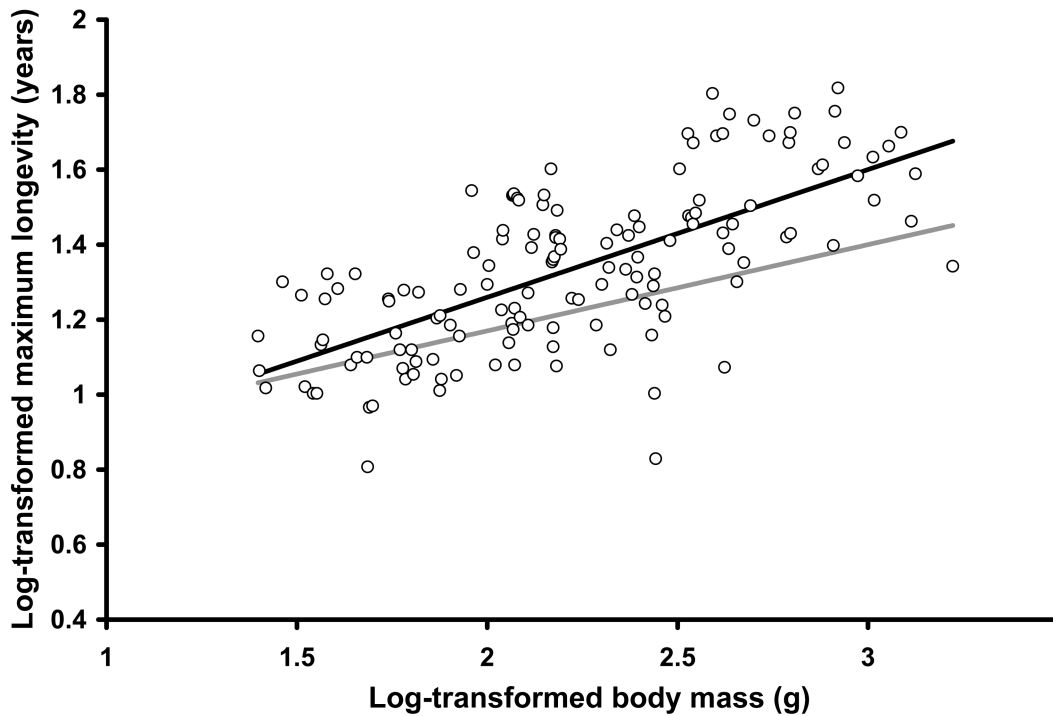
Fig. 1. Least-squares regression of log-transformed body mass (g) on log-transformed life span (years) in parrots. Open circles represent record longevities for individual species in captivity (n = 141). Black line represents the regression equation for parrots (years = 3.79 × mass$^{0.34}$). Gray line represents the regression equation of maximum longevity versus body mass for 131 bird species in captivity, including 13 parrot species (years = 5.10 × mass$^{0.23}$; Prinzinger 1993).

Table 1. Results of linear regression (continuous variables) or t-tests and ANOVAs (categorical variables) on log-transformed longevity in parrots (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). See text for details of analyses.

| Independent variables	Longevity controlled for body mass		Longevity controlled for body mass and phylogeny		
	F	df	F	t	df
Continuous variables					
Annual fecundity	0.01	1, 135	0.52		1, 45
Feeding-group size	1.71	1, 108	0.05		1, 34
Latitude	0.01	1, 144	0.62		1, 47
Categorical variables					
Aridity	1.37	3, 144		−0.45	29
Communal roosting	3.45	1, 146		1.71*	25
Diet type	11.02***	2, 140		2.95**	16
Island versus mainland	14.05***	1, 146		−0.87	8
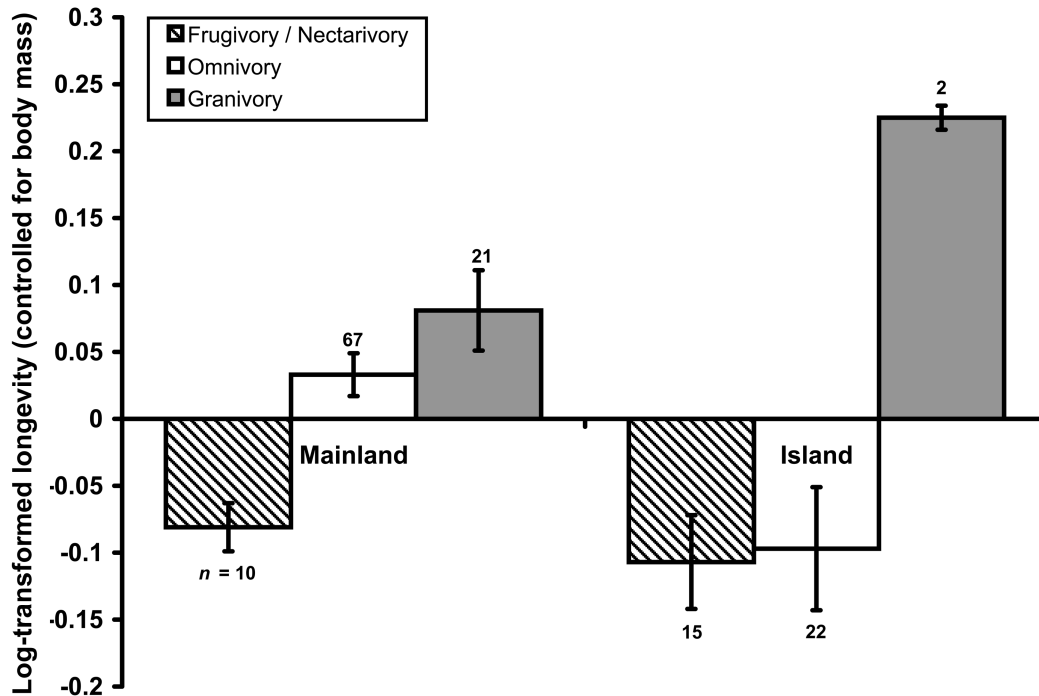
Fig. 2. Mean residual longevity (controlled for body mass) of parrots by restriction to islands and diet types. Error bars represent one standard error of the mean residual longevity. Numbers above columns represent sample sizes (n = number of species) for each diet and island combination.

and 91, $P = 0.22$; diet = granivory, $F = 0.13$, df = 1 and 21, $P = 0.72$), confirming that diet is primarily responsible for the significant association between longevity and communal roosting.

After controlling for both body mass and phylogenetic ancestry using independent contrasts, communal roosting and type of diet significantly predicted longevity in parrots. Specifically, evolution of communal roosting and evolution of a granivorous diet were associated with the evolution of longer life span (Table 1). Diet also explained a significant proportion of variation in annual fecundity after controlling for body size ($F = 7.40$, df = 2 and 126, $P < 0.001$; Fig. 3). Progeny per year was not significantly associated with diet type after factoring out both body mass and phylogenetic effects ($t = –0.19$, df = 15, $P > 0.8$).

Discussion

Although larger parrots live longer than smaller parrots (Fig. 1), change in dietary specialization was the primary factor associated

with the evolution of life span after controlling for both body size and phylogenetic ancestry. Specifically, evolution of granivory was associated with the evolution of longer life span. Our analyses do not support previous predictions that high-quality diets result in higher fecundity, and thus shorter life spans, because of higher costs of reproduction (Lack 1968). Studies of southern African passerines found that mean adult life expectancy of insectivores and nectarivores (3.1 years) is nearly twice that of granivores (1.6 years) after factoring out body size and phylogeny (Peach et al. 2001). These granivorous passerines lay larger clutches than insectivores and nectarivores, which prompted Peach et al. (2001) to argue that the shorter life spans of granivorous species are attributable to costs associated with reproduction. Similarly, marsupial species that specialize on energy-poor herbivorous diets exhibit lower fecundity and greater longevity than marsupials with relatively faunivorous diets (Fisher et al. 2001).

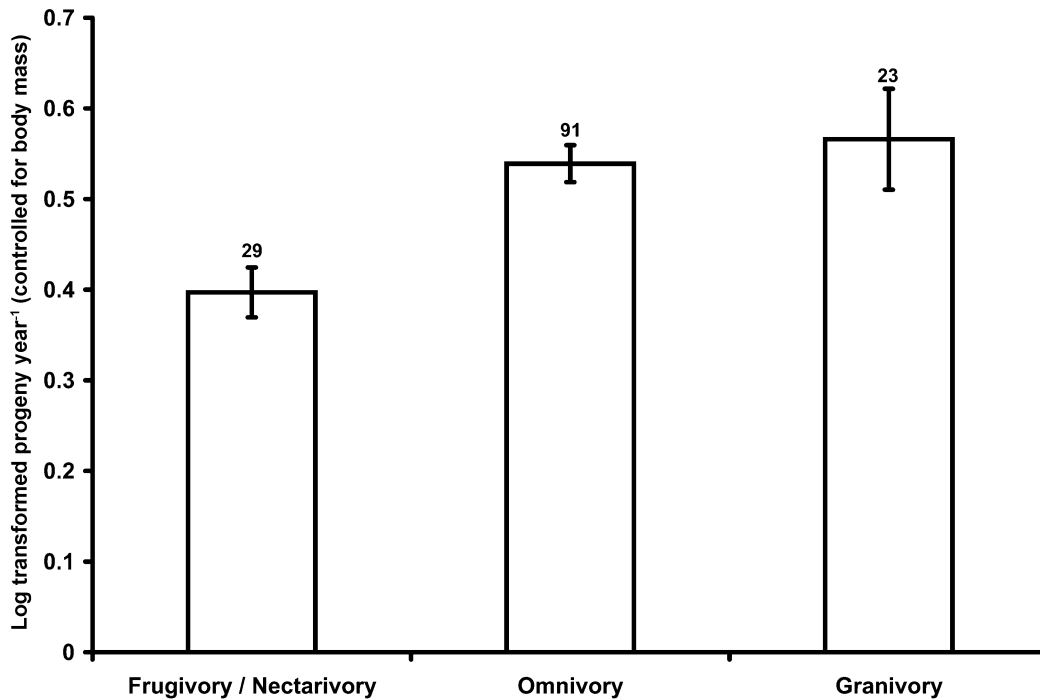The positive relationship between communal roosting and longevity found here was primarily

Fig. 3. Mean residual progeny per year (controlled for body mass) by diet type of parrots. Error bars represent one standard error of the mean residual longevity. Numbers above columns represent sample sizes (*n* = number of species).

explained by the influence of diet type. However, parrots are one of the most gregarious groups of birds, and communal roosting may have an additional influence on longevity in lineages specialized for granivory by reducing extrinsic mortality rates (Partridge and Harvey 1988, Keller and Genoud 1997). Seed-eating parrots often inhabit relatively arid environments with unpredictable resources and form large flocks during periods of patchily distributed food or water (Cannon 1984). Communal roosting and flocking may increase survival rates by improving detection of scarce resources (Jullien and Clobert 2000, Peach et al. 2001), facilitating social transfer of information about foraging sites (Chapman et al. 1989), or reducing predation through increased vigilance (Westcott and Cockburn 1988, South and Pruett-Jones 2000).

Alternatively, periodic resource shortages faced by granivorous parrots may extend longevity through caloric restriction. This mechanism has been implicated in extending the life span of laboratory rodents that face short periods of famine, perhaps because resources are shifted away from reproduction in favor of increased somatic maintenance (Shanley and Kirkwood 2000). Female life span was also extended when Mediterranean fruit flies were experimentally switched from a sugar-only to protein-containing diet, most likely because of increased allocation of resources to somatic maintenance (Romanyukha et al. 2004).

Nutritional pressures are an alternative explanation for the influence of dietary specialization on parrot longevity. Protein content represents the major nutritional difference among nectar-, fruit-, and seed-based diets in parrots (Pryor 2003). Strict frugivory or nectarivory is relatively uncommon in parrots, most likely because dietary protein deficiency is a major nutritional constraint despite adaptations for low-protein diets in some species (Pryor et al. 2001). The highly specialized frugivorous Pesquet's Parrot (*Psittrichas fulgidus*) and nectarivorous Red Lory (*Eos bornea*) have much lower protein requirements than the fully granivorous Budgerigar (*Melopsittacus undulatus*; Pryor 2003). However, the two former species also have both shorter

life spans for their body size and fewer progeny per year than *M. undulatus*. The Budgerigar has recently been employed as a cellular and genetic model of senescence in birds (Ogburn et al. 2001), but comparative research on parrots specialized for frugivory or nectarivory is needed to identify a potential diet-mediated mechanism of life-span variation in parrots.

Biases associated with keeping parrots in captivity cannot be completely discarded as explanations for the relationship between maximum longevity and diet. Natural granivorous diets may be much easier to replicate in captivity than diets based on fruit or nectar, resulting in routine chronic stress on frugivorous and nectarivorous species. If granivorous and omnivorous species have also been kept in captivity more frequently or for a longer period, then they are again likely to have longer reported life spans. The database used for this study does not seem to be biased by variable sample sizes of species with different dietary specializations (Brouwer et al. 2000). Also, records for nectarivorous and frugivorous species are not generally more recent than records for other parrots. Frugivorous and nectarivorous parrots readily breed and appear to be healthy in captivity (Pryor 2003). Unfortunately, far too few data are available from wild parrot populations to examine possible biases associated with using captive data (Juniper and Parr 1998).

The composite supertree of the Psittaciformes was generally poorly resolved, containing only 98 nodes, or 28% of a fully bifurcating solution. By contrast, recent supertrees of seabirds (Procellariformes; 62.0%; Kennedy and Page 2002) and bats (Mammalia: Chiroptera; 46.4%; Jones et al. 2002) that used tree-construction methods similar to those used here exhibited higher resolution. Systematic studies have not been distributed evenly across the Psittaciformes: the number of characters per taxon in each matrix ranged from 1.73 for the Cacatuidae and 1.41 for the Old World Psittacidae to 0.74 for the New World Psittacidae and 0.64 for the Loriidae. The large polytomies and lack of resolution in the parrot supertree is likely attributable to a lack of information for many clades rather than conflict among source trees. A benefit of the MRP supertree method is the ease with which topologies from new phylogenetic studies can be incorporated into the supertree for future analyses. Given the large sample size (162 out of ~352 parrot species) and the high concordance in the present study between analyses based on species data and independent contrasts, we expect that improved resolution in the parrot supertree would increase sample size for independent contrast analysis and increase support for the results presented here.

Our analyses indicate that the evolution of long life span in parrots is influenced by ecological factors. The evolution of dietary specialization on fruit or nectar appears to be related to reduced longevity in parrots, whereas the evolution of communal roosting and granivory are associated with extended life span. These results support evolutionary hypotheses of longevity, because extrinsic mortality rates are likely to vary depending on the characteristics of a species' behavior, habitat, and diet.

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Appendix: Literature Sources for Phylogenetic Trees Used to Construct a Supertree of the Psittaciformes

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