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Survival on the ark: life-history trends in captive parrots

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Abstract

Members of the order Psittaciformes (parrots and cockatoos) are among the most long-lived and endangered avian species. Comprehensive data on lifespan and breeding are critical to setting conservation priorities, parameterizing population viability models, and managing captive and wild populations. To meet these needs, we analyzed 83 212 life-history records of captive birds from the International Species Information System (ISIS) and calculated lifespan and breeding parameters for 260 species of parrots (71% of extant species). Species varied widely in lifespan, with larger species generally living longer than smaller ones. The highest maximum lifespan recorded was 92 years in *Cacatua moluccensis*, but only 11 other species had a maximum lifespan over 50 years. Our data indicate that while some captive individuals are capable of reaching extraordinary ages, median lifespans are generally shorter than widely assumed, albeit with some increase seen in birds presently held in zoos. Species that lived longer and bred later in life tended to be more threatened according to IUCN classifications. We documented several individuals of multiple species that were able to breed for more than two decades, but the majority of clades examined had much shorter active reproduction periods. Post-breeding periods were surprisingly long and in many cases surpassed the duration of active breeding. Our results demonstrate the value of the ISIS database to estimate life-history data for an at-risk taxon that is difficult to study in the wild, and provide life-history data that is crucial for predictive modeling of future species endangerment and proactively management of captive populations of parrots.

Introduction

Earth is facing a biodiversity crisis of enormous proportions, with extinction rates estimated to be 1000–10 000 times greater than normal background rates (Wilson, 1991; Brooks *et al*., 2006). Zoos and aquariums play a critical role in conserving biodiversity (Miller *et al*., 2004) through research, education, conservation of habitat and genomic materials, and captive breeding (Fischer & Lindenmayer, 2000; Price & Soorae, 2003; Foose & Wiese, 2006; Mace *et al*., 2007; Walters *et al*., 2010). Captive breeding maintains viable populations and in some notable cases provides the only source of individuals for reintroductions (Beck *et al*., 1994; Seddon, Armstrong & Maloney, 2007), as with the black-footed ferret *Mustela nigripes* (Biggins *et al*., 1999), California condor *Gymnogyps californianus* (Snyder & Snyder, 1989), Przewalski's horse *Equus caballus przewalskii* (Bouman, 2000) and Arabian oryx *Oryx leucoryx* (Rahbek, 1993). Another important, albeit less widely recognized, role for captive populations is to provide behavioral, physiological and life-history data that are difficult, costly or time consuming to obtain in field studies (see Ricklefs & Cadena, 2007). These data are useful for predictive modeling and management of wild populations and for setting management priorities for captive populations (Conde *et al*., 2011).

One important step in managing captive populations is to assess conservation priorities at the larger taxonomic scales of family or order. Zoos and aquariums have organized Taxon Advisory Groups (TAGs) to set priorities for maintaining and managing captive populations across higher-level taxa. TAGs determine which species to propagate based primarily on captive population numbers and conservation status (Wilkinson, 2000; Hutchins, 2003; Association of Zoos and Aquariums (AZA), 2007). The TAGs further divide species into Regional Collection Plans (RCBs) which are represented worldwide. All of these programs were initiated in the 1980s to track and manage the genetics and demographics of captive animal populations in studbooks so as to meet overall management goals for that species (Hutchins & Wiese, 1991). A critical role for TAGs is to prioritize efforts across different species because both space and funding for captive animals are limited (Hutchins & Wiese, 1991; Smith *et al*., 2002; Hutchins, 2003; Baker, 2007).

TAGs face the issue of surplus animals, animals that have already made a genetic contribution to the program either

directly or via kin (Hutchins & Wiese, 1991; Lindburg & Lindburg, 1995), and are now consuming resources that could otherwise be invested in breeding animals that would further enhance genetic diversity. To allocate limited zoo resources optimally, TAGs should work with RCPs to predict and control numbers of surplus animals (Lacy, 1995; Lindburg & Lindburg, 1995; Graham, 1996), a task which requires comprehensive data on a species' lifespan, breeding parameters, IUCN status, current numbers and demographics. Demographic and reproductive data are especially important for captive breeding programs (Hutchins & Wiese, 1991; Hutchins, 2003), and authors of captive-management manuals have been advised to incorporate data on lifespan and duration of active reproduction to improve breeding and reintroduction efforts (Jackson, 2003; Seddon *et al*., 2007). These recommendations have been followed in a few cases, most notably for elephants (Wiese & Willis, 2004; Wiese & Willis, 2006; Hutchins & Thompson, 2008). However, the comprehensive life-history data needed for optimal management of captive populations are not readily available for most taxa (Baker, 2007; Hutchins & Thompson, 2008).

Here we provide comprehensive lifespan and reproductive data for the order Psittaciformes (parrots and cockatoos, hereafter 'parrots'). The parrots are an important group in which to investigate general patterns of captive longevity and breeding. The order contains a high proportion of endangered species, with 36% of the 365 extant species of parrots (Forshaw & Knight, 2006) listed as being at risk (IUCN, 2009) and at least 18 confirmed extinctions by the end of the 20th century, making parrots the most threatened speciose order of birds (Forshaw & Knight, 2006). They are also the longest-lived order of birds for their size (Prinzinger, 1993) with some reported lifespans exceeding 50 years (Brouwer *et al*., 2000). Furthermore, they are commonly held in captivity, with upwards of 20 000 parrots housed in zoos and other animal holding facilities [International Species Information System (ISIS), 2009] and millions more held in private hands (World Parrot Trust, 2009). Successful reintroductions with captive bred parrots are challenging (Snyder *et al*., 1996), but feasible (Sanz & Grajal, 1998; Collazo *et al*., 2003; Brightsmith *et al*., 2005; White Jr, Collazo & Vilella, 2005). The majority of bird supplementation in the wild has come from captive breeding programs (Fischer & Lindenmayer, 2000), but these efforts are stymied by a lack of captive breeding populations for many species of high conservation concern. Instead, the current zoo population of parrots is biased toward large species that are more attractive to humans (Frynta *et al*., 2010). While the conventional role of zoos in the past has been entertainment (Hatchwell *et al*., 2007), the World Association of Zoos and Aquariums recently asserted that the ''major goal of zoos and aquariums will be to integrate all aspects of their work with conservation activities'' (WAZA, 2005). Overall, the large numbers, long lifespans and high level of endangerment of parrots results in a high burden on space in zoos and a critical need to set breeding and husbandry goals on the basis of conservation priorities.

Efforts to set conservation priorities for parrots have been hampered by a lack of life-history data. While there are a few exemplary studies of life-history and reproduction in wild populations (Saunders, 1982; Buckland, Rowley & Williams, 1983; Rowley, 1983; Powlesland *et al*., 1992; Sandercock *et al*., 2000; Heinsohn & Legge, 2003; Murphy, Legge & Heinsohn, 2003; Renton & Salinas-Melgoza, 2004; Beissinger *et al*., 2008; Koenig, 2008; Holdsworth, Dettmann & Baker, in press), it is difficult to age adults and field studies are generally short in duration relative to lifespans. While data from captive individuals may not precisely predict lifespans in wild animals given the different stresses faced by each, a significant positive relationship between captive and wild maximum lifespans has been demonstrated generally in birds (Wasser & Sherman, 2010) as have similar rates of actuarial senescence (Ricklefs, 2000). Previous studies in parrots have provided some data on captive lifespans: Brouwer *et al*. (2000) reported maximum recorded ages for 176 species and subspecies of parrots, while Vanstreels *et al*. (2010) examined lifespans of confiscated wild-caught parrots in a Brazilian zoo. Neither study reported reproductive parameters. Parrot studbooks are maintained regionally and internationally, but less than 10% of all parrot species and subspecies housed in zoos are currently represented by studbooks worldwide (L. Bingaman Lackey, pers. obs.). In sum, these sources provide valuable information for some species, but there remains a pressing need for comprehensive life-history data for the order as a whole.

The ISIS database contains thousands of records of parrot births, deaths and reproduction contributed by zoos and other animal holding collections from *c*. 845 member institutions in 80 countries (ISIS, 2009). This database represents a wealth of valuable information on parrots, and many other taxa, which has been largely untapped by the zoological and scientific community.

We provide a species-level analysis of ISIS records to present comprehensive life-history data for parrots. We collated data from over 87 000 individuals representing over 260 species of parrots from the ISIS database to characterize lifespan and breeding parameters for each species, examine general patterns across major clades of parrots, and test the effects of mass and sex on lifespan.

Methods

Data coding

We compiled individual lifespan records representing all available parrot species from ISIS. We used Forshaw & Knight (2006) as the taxonomic authority for common and scientific names. Our only departure from the classification of Forshaw & Knight (2006) was to elevate the three subspecies of rosellas under *Platycercus elegans* to full species based on Joseph *et al*., (2008): the crimson rosella *P. elegans*, the yellow rosella *Platycercus flaveolus* and the orange-red and yellow rosella *Platycercus adelaidae*; otherwise we did not distinguish between subspecies. Individual birds that hatched in an ISIS facility received a HATCH

date, while those that were transferred into an ISIS facility from a non-ISIS institution received an IN date. Birds transferred out of an ISIS facility received an OUT date, whereas birds that died in an ISIS facility received a DEATH date. We eliminated individuals with records that had an IN or HATCH date before the 1800s, or which were missing these dates entirely. We excluded individuals recorded as surviving less than one day from further analysis. Sorting and formatting of the data were conducted with Access 2003 (Microsoft Inc., Redmond, WA, USA), and statistical analyses were run using JMP 8.0 (SAS Institute, Cary, NC, USA).

Lifespan across species

To reveal trends in basic lifespan data across species, we first calculated the median lifespan and maximum lifespan for each species. Preliminary analysis indicated that many species followed a Type III survivorship curve (Ricklefs, 2008), with high initial mortality that reached an asymptote at 4 years of age. Thus we calculated lifespan statistics on two different datasets: (1) all individuals who lived past their first day; (2) individuals who survived to age 4 years or older. Four years exceeds the age of first reproduction for many species included in the analysis, but preliminary analyses found this age to be the best single threshold for avoiding juvenile mortality across all 260 species analyzed. We also calculated the median living adult age for individuals that were still alive as of 24 March 2008 as a measure of lifespan for the currently living captive population.

We calculated the median instead of the mean as an indicator of central tendencies because the lifespan data were non-normally distributed and exhibited a positively skewed unimodal distribution (Zar, 1999). While we report these summary statistics for all species, for the purpose of statistical tests of life-history relationships we excluded species with fewer than 20 individual records to increase reliability of the data and ensure that general trends would not be distorted by a few aberrant individuals. We tested the effect of sex on the maximum and median lifespan by performing the non-parametric Wilcoxon signed-rank test, which treated the two sexes of each species as a paired comparison (Zar, 1999). We then examined the relationship between body size and lifespan with least-squares regressions of log of mass versus log of maximum lifespan, median adult lifespan and median adult age. Least-squares regressions of maximum lifespan versus median adult lifespan and median adult age were performed on log transformed data. Positive residuals from these regressions indicated species with a single individual, represented by the maximum lifespan, that lived substantially longer than their conspecifics, represented by median adult lifespan or age; negative residuals indicated species with a median adult lifespan or age that was closer to the maximum lifespan within that species.

Lifespan trends for clades

In addition to the summary statistics described across species, we examined data for species within selected clades of particular interest to zoos and captive population managers. These clades were (1) *Cacatua* and allies (*Cacatua*, *Callocephalon, Eolophus*); (2) *Trichoglossus* and allies (*Chalcopsitta*, *Eos*, *Trichoglossus*); (3) *Platycercus* and allies (*Barnardius*, *Platycercus*, *Psephotus*, *Purpureicephalus*); (4) *Ara* and allies (*Ara*, *Orthopsittaca*, *Propyrrhura*); (5) *Aratinga*; (6) *Amazona*. We again excluded species that had fewer than 20 individual records from these analyses. A generalized linear model (GLM) was performed to test for the joint effects of mass and clade on the means of maximum lifespan, median adult lifespan and median adult age and Tukey–Kramer HSD was used for *post hoc* comparison between pairs of clades.

Breeding parameters

To describe breeding parameters for each species, we analyzed ISIS breeding information for female parrots. Males were not included in this analysis because paternity could not be unambiguously determined. For these analyses we excluded species with fewer than five individuals to maintain an adequate sample size while minimizing the effect of aberrant individuals. Several other types of exclusions were performed on the breeding data to balance maximizing the number of records available for analysis with maintaining accurate and conservative estimates of reproductive parameters (summarized in Table 1). We calculated medians of the age of first breeding, age of last breeding, duration of active breeding and duration of post-breeding. Values for

Table 1. Criteria for calculation of breeding parameters

	Parameters used	Types of individual records included in analysis
Age of first breeding	Known HATCH date, age at first breeding >0	Birds that reproduced within an ISIS facility
Age at last breeding	Both HATCH and IN date used if age at last breeding >0	Birds whose last reproduction was after their transfer into an ISIS facility
Duration of active reproduction	Both HATCH and IN date used if age of first reproduction >0	Birds that reproduced within an ISIS facility, included durations = 0, where an individual reproduced only once
Duration of post-active reproduction	Both HATCH and IN date used if age at last breeding >0, both DEATH and OUT date used	Birds whose last reproduction was after their transfer into an ISIS facility, included durations = 0, where an individual died on the day of last reproduction

ISIS, International Species Information System.

age of last breeding are conservative estimates as birds with an IN date were treated as newly hatched birds. Values of the post-breeding period are also conservative because we treated individuals transferred out of the system as deaths. A one-way ANOVA was performed to test for differences in the means of these four breeding parameters among the six major clades.

Conservation status

To determine whether conservation status is associated with particular demographic parameters, one-way ANOVAs were conducted to test for an effect of IUCN status on lifespan (maximum and median adult) and median breeding variables (age of first and last breeding, duration of active breeding and post-breeding).

Results

Lifespan across species

We compiled 87 777 individual parrot records representing 262 species (72% of all parrot species) from ISIS. After excluding those individuals hatched before the 1800s or that failed to survive their first day, and species in which no individuals lived past a year, 83 212 individuals representing 260 species remained for analysis. Parrot species in captivity ranged dramatically in their maximum and median lifespans. The highest maximum lifespan recorded was 92 years for the salmon-crested cockatoo *Cacatua moluccensis*. Only 12 species ($<5\%$ of the 260 species) had an individual live past 50 years of age. Of all the species held in ISIS institutions, 50% never had an individual live beyond 22 years of age, and only 30% of these species had a median adult lifespan ≥ 10 years, even after limiting data to individuals who survived juvenile mortality (≥ 4 years). In contrast, when only living animals were considered, 58% of species had a median age ≥ 10 years (Table 2, see supporting information Table S1 for medians with quartiles).

When further excluding species that do not have at least 20 individual records, 82 777 individuals from 199 species remained in the dataset used for the following lifespan analyses. Matched pairs analysis indicated that living adult median age is significantly different than median adult lifespan (age $= 11.12 \pm 4.79$, lifespan $= 8.81 \pm 2.62$; $z_{97} = 2036.00$, $P < 0.0001$) with living adults today surviving longer on average than adults collectively over the last 200 years. Least-squares regressions of log maximum lifespan and log median adult lifespan on log body mass revealed that mass was a significant predictor of maximum lifespan ($F_{1,195} = 148.79$, $P < 0.0001$, $R^2 = 0.43$; Fig. 1) median adult lifespan ($F_{1,167} = 182.65$, $P < 0.0001$, $R^2 = 0.52$) and median adult age ($F_{1,96} = 71.11$, $P < 0.0001$, $R^2 = 0.43$; supporting information Fig. S1) such that larger species were generally longer lived than smaller species.

Matched pairs analysis revealed that sex affected maximum lifespan (males $= 24.79 \pm 12.58$, females $= 23.05 \pm 12.52$; $z_{196} = 3027.00$, $P < 0.0001$), median adult lifespan (males $= 9.12 \pm 3.19$, females $= 8.93 \pm 3.09$; $z_{168} = 1671.50$, $P = 0.0049$) and median living adult age (males $= 11.37 \pm 5.00$, females $= 11.15 \pm 4.91$; $z_{97} = 488.00$, $P = 0.0490$) with males living longer on average (Fig. 2).

Least-squares regressions of log maximum lifespan on log median adult lifespan and log median adult age revealed that both were significant predictors of maximum lifespan (lifespan: $F_{1,167} = 78.56$, $P < 0.0001$, $R^2 = 0.32$; age: $F_{1,96} = 42.75$, $P < 0.0001$, $R^2 = 0.31$; Fig. 3). For both regressions the cockatoos were the most notable positive outliers.

Lifespan trends for clades

Our selected clades of parrots differed in most lifespan parameters. A one-way ANOVA testing for differences among clades in the means of maximum lifespan ($F_{5,77} = 13.27$, $P < 0.0001$), median adult lifespan ($F_{5,69} = 15.65$, $P < 0.0001$) and median adult age ($F_{5,37} = 112.14$, $P < 0.0001$) indicated that clades differed significantly in these parameters (Fig. 4). To assess whether these differences could be attributed to the size differences among clades, both clade and weight were run as factors in a GLM. There was no significant interaction between clade and weight for maximum lifespan ($\chi_{5,71} = 5.35$, $P = 0.3741$); when this interaction term was removed and the GLM rerun, both clade ($\chi_{5,68} = 32.07$, $P < 0.0001$), and weight ($\chi_{1,68} = 21.66$, $P < 0.0001$), had a significant effect on maximum lifespan. In contrast, there was a significant interaction for median adult lifespan ($\chi_{5,63} = 16.86$, $P = 0.0048$), but neither weight ($\chi_{1,63} = 3.69$, $P = 0.0547$) nor clade ($\chi_{5,63} = 5.71$, $P = 0.3357$) had significant effects with this interaction term in the model. There were insufficient degrees of freedom to run a GLM with an interaction for median adult age, but the effect of clade was significant ($\chi_{5,36} = 101.88$, $P < 0.0001$) while that of weight was not ($\chi_{1,36} = 0.56$, $P = 0.4544$). The *Cacatua* clade (cockatoos) showed the greatest mean of maximum lifespan at 50.78 years. In contrast, the *Ara* clade had the highest mean of median adult lifespan at 14.31 years. Overall, the *Cacatua* clade included some of the longest-lived individuals in the entire database, but out of the species held in captivity, 65% of them never had an individual live past 50 years old. Mean median adult lifespan for this clade was notably low in captivity (10.36 years), significantly less than the *Ara* clade, and did not differ from the *Aratinga* or *Amazona* clades whose mean maximum lifespans were 15–25 years less than that of the cockatoos. The median age of living birds is higher than the median lifespan of all birds for all six clades, but this increase is much less dramatic in the cockatoos than in *Ara*, *Aratinga* and *Amazona* (Fig. 4).

Breeding parameters

Breeding parameters in captivity varied greatly across the 193 species for which breeding data was available (supporting information Table S2). When restricted to species with data for ≥ 5 individuals, the lowest median age at first

Table 2. Lifespan summary across species (in years)

			Lifespan: all[a]		Lifespan: adults ≥4		Age: adults ≥4[b]		
Species common name	Scientific name	Lifespan: maximum	*n*	Median	*n*	Median	*n*	Median	IUCN status[c]
Palm cockatoo	*Probosciger aterrimus*	39.97	522	5.29	299	11.60	144	13.30	LC
Yellow-tailed black cockatoo	*Calyptorhynchus funereus*	47.41	324	2.84	136	9.78	63	10.95	LC
Red-tailed black cockatoo	*Calyptorhynchus banksii*	55.26	354	4.20	180	11.84	82	13.02	LC
Glossy black cockatoo	*Calyptorhynchus lathami*	37.72	41	5.32	22	8.15	13	9.07	LC
Gang gang cockatoo	*Callocephalon fimbriatum*	27.57	291	2.07	96	9.73	25	13.77	LC
Galah	*Eolophus roseicapilla*	72.82	1889	2.00	687	9.33	249	10.08	LC
Sulfur-crested cockatoo	*Cacatua galerita*	72.95	1668	3.71	804	10.92	309	12.38	LC
Yellow-crested cockatoo	*Cacatua sulphurea*	39.97	977	4.15	497	8.90	221	11.23	CR
Blue-eyed cockatoo	*Cacatua ophthalmica*	37.95	84	7.78	50	11.66	21	11.60	VU
White-crested cockatoo	*Cacatua alba*	32.24	967	3.49	460	9.76	228	11.15	VU
Salmon-crested cockatoo	*Cacatua moluccensis*	92.55	1675	4.56	896	9.51	314	11.07	VU
Major Mitchell's cockatoo	*Cacatua leadbeateri*	74.86	949	2.95	419	9.64	135	12.00	LC
Slender-billed corella	*Cacatua tenuirostris*	43.45	333	1.93	126	11.70	52	12.09	LC
Little corella	*Cacatua sanguinea*	44.01	455	2.45	189	11.52	56	12.49	LC
Ducorps's corella	*Cacatua ducorpsii*	57.81	73	3.75	36	9.58	23	9.58	LC
Goffin's corella	*Cacatua goffini*	30.39	581	3.90	289	10.65	131	13.46	NT
Red-vented corella	*Cacatua haematuropygia*	33.59	125	5.30	67	11.76	28	12.02	CR
Cockatiel	*Nymphicus hollandicus*	35.92	2850	2.53	949	7.06	241	8.98	LC
Black lory	*Chalcopsitta atra*	17.58	140	2.78	56	7.66	15	9.64	LC
Yellow-streaked lory	*Chalcopsitta scintillata*	25.01	176	2.13	60	9.48	20	9.03	LC
Brown lory	*Chalcopsitta duivenbodei*	26.54	248	1.66	69	8.90	30	10.07	LC
Cardinal lory	*Chalcopsitta cardinalis*	18.23	64	4.72	37	9.70	23	10.23	LC
Dusky lory	*Pseudeos fuscata*	19.59	568	2.76	239	7.34	100	7.46	LC
Black-winged lory	*Eos cyanogenia*	22.53	142	1.67	43	7.06	5	5.98	VU
Violet-necked lory	*Eos squamata*	18.23	166	2.28	58	6.57	20	6.82	LC
Blue-streaked lory	*Eos reticulata*	27.83	353	2.16	121	7.91	33	11.41	NT
Red and blue lory	*Eos histrio*	16.08	56	6.14	35	9.58	18	10.48	EN
Red lory	*Eos bornea*	29.48	881	2.78	380	6.92	145	7.86	LC
Blue-eared lory	*Eos semilarvata*	12.23	14	4.06	7	10.02	6	10.82	LC
Ornate lorikeet	*Trichoglossus ornatus*	18.49	143	3.27	62	6.45	30	7.91	LC
Rainbow lorikeet	*Trichoglossus haematodus*	37.94	6805	2.39	2424	6.47	1325	6.70	LC
Scaly-breasted lorikeet	*Trichoglossus chlorolepidotus*	24.17	187	2.60	72	6.62	25	6.62	LC
Olive-headed lorikeet	*Trichoglossus euteles*	18.74	167	2.59	63	7.40	23	8.15	LC
Yellow and green lorikeet	*Trichoglossus flavoviridis*	12.28	33	2.27	11	5.36			LC
Mindanao lorikeet	*Trichoglossus johnstoniae*	17.77	81	1.85	28	7.27	12	8.79	NT
Varied lorikeet	*Psitteuteles versicolor*	12.47	173	1.42	48	6.64	2	8.47	LC
Iris lorikeet	*Psitteuteles iris*	27.04	147	1.58	39	7.71	22	10.01	NT
Goldie's lorikeet	*Psitteuteles goldiei*	24.13	605	1.61	161	7.01	31	8.90	LC
Musk lorikeet	*Glossopsitta concinna*	19.30	467	2.22	141	5.88	22	5.69	LC
Little lorikeet	*Glossopsitta pusilla*	20.11	153	1.41	34	5.27	6	9.75	LC
Purple-crowned lorikeet	*Glossopsitta porphyrocephala*	12.67	476	1.28	81	5.47	6	5.35	LC
Blue-crowned lorikeet	*Vini australis*	37.36	241	2.05	74	6.62	31	9.51	LC
Kuhl's lorikeet	*Vini kuhlii*	2.21	1	2.21					EN
Blue lorikeet	*Vini peruviana*	21.12	91	1.21	30	11.66	1	17.95	VU
Collared lorikeet	*Phigys solitarius*	18.23	106	3.66	50	9.22	36	9.99	LC
Purple-bellied lory	*Lorius hypoinochrous*	18.13	12	10.66	11	11.09	6	11.19	LC
Black-capped lory	*Lorius lory*	30.83	482	3.13	219	7.56	107	7.50	LC
Purple-naped lory	*Lorius domicella*	19.23	181	2.79	77	7.16	29	9.00	VU
Yellow-bibbed lory	*Lorius chlorocercus*	13.81	134	5.27	87	8.88	47	13.81	LC
Chattering lory	*Lorius garrulus*	27.24	586	2.43	220	7.59	65	7.89	EN
Red-fronted lorikeet	*Charmosyna rubronotata*	2.34	3	2.30					LC
Red-flanked lorikeeet	*Charmosyna placentis*	19.59	198	1.47	56	5.91	28	6.91	LC
Fairy lorikeet	*Charmosyna pulchella*	20.78	71	1.43	21	6.65	3	15.58	LC
Duchess lorikeet	*Charmosyna margarethae*	4.00	4	4.00	4	4.00			NT
Josephine's lorikeet	*Charmosyna josefinae*	10.20	22	3.57	10	5.26			LC

Table 2. Continued.

			Lifespan: all[a]		Lifespan: adults ≥4		Age: adults ≥4[b]		
Species common name	Scientific name	Lifespan: maximum	*n*	Median	*n*	Median	*n*	Median	IUCN status[c]
Papuan lorikeet	*Charmosyna papou*	22.43	552	1.38	140	6.80	33	8.23	LC
Whiskered lorikeet	*Oreopsittacus arfaki*	1.56	2	1.56					LC
Musschenbroek's lorikeet	*Neopsittacus musschenbroekii*	26.54	73	2.34	26	7.23	4	16.89	LC
Kea	*Nestor notabilis*	50.53	773	2.88	339	10.49	114	10.80	VU
Kaka	*Nestor meridionalis*	35.46	191	2.13	64	12.55	17	12.25	EN
Pesquet's parrot	*Psittrichas fulgidus*	27.63	159	4.84	87	8.29	39	9.73	VU
Orange-breasted fig parrot	*Cyclopsitta gulielmitertii*	12.23	1	12.23	1	12.23	1	12.23	LC
Double-eyed fig parrot	*Cyclopsitta diophthalma*	14.35	287	1.81	83	6.54	16	6.47	LC
Desmarest's fig parrot	*Psittaculirostris desmarestii*	17.46	136	1.06	25	5.29	2	13.24	LC
Edwards's fig parrot	*Psittaculirostris edwardsii*	20.40	122	1.66	36	7.34	8	9.81	LC
Salvadori's fig parrot	*Psittaculirostris salvadorii*	14.89	14	3.69	7	9.73	3	9.73	VU
Guaiabero	*Bolbopsittacus lunulatus*	1.99	3	1.86					LC
Blue-rumped parrot	*Psittinus cyanurus*	15.23	28	2.60	9	6.85	2	11.04	NT
Red-cheeked parrot	*Geoffroyus geoffroyi*	5.54	2	3.07	1	5.54			LC
Blue-crowned racquet-tailed parrot	*Prioniturus discurus*	1.64	4	0.06					LC
Golden-mantled racquet-tailed parrot	*Prioniturus platurus*	24.65	17	4.79	9	15.78	4	24.65	LC
Eclectus parrot	*Eclectus roratus*	40.76	2521	1.92	949	9.00	416	10.08	LC
Great-billed parrot	*Tanygnathus megalorhynchos*	14.56	24	1.97	8	6.86	1	14.56	LC
Blue-naped parrot	*Tanygnathus lucionensis*	13.19	36	2.52	10	5.90	1	13.19	NT
Blue-backed parrot	*Tanygnathus sumatranus*	26.30	10	6.81	6	7.18	3	7.18	LC
Alexandrine parakeet	*Psittacula eupatria*	29.06	562	5.06	308	6.23	181	5.23	LC
Rose-ringed parakeet	*Psittacula krameri*	33.63	1719	3.58	797	7.69	274	9.58	LC
Mauritius parakeet	*Psittacula echo*	12.35	6	6.72	4	7.63	2	10.43	EN
Malabar parakeet	*Psittacula columboides*	14.08	15	5.18	8	7.24			LC
Emerald-collared parakeet	*Psittacula calthorpae*	10.59	2	10.41	2	10.41			LC
Plum-headed parakeet	*Psittacula cyanocephala*	19.86	410	4.22	209	5.62	117	5.23	LC
Blossom-headed parakeet	*Psittacula roseata*	17.15	21	6.07	13	9.07	6	10.12	LC
Slaty-headed parakeet	*Psittacula himalayana*	18.46	19	6.82	13	7.77	11	7.77	LC
Derbyan parakeet	*Psittacula derbiana*	28.22	408	2.24	167	9.07	62	9.81	LC
Nicobar parakeet	*Psittacula caniceps*	6.54	14	0.46	4	5.79			NT
Red-breasted parakeet	*Psittacula alexandri*	20.24	282	3.03	119	8.13	47	10.23	LC
Long-tailed parakeet	*Psittacula longicauda*	13.05	55	1.68	12	8.83	7	10.23	NT
Gray-headed lovebird	*Agapornis canus*	16.01	120	2.79	45	7.12	20	7.12	LC
Red-faced lovebird	*Agapornis pullarius*	19.23	123	4.22	62	7.55	13	7.73	LC
Black-winged lovebird	*Agapornis taranta*	15.82	164	2.38	59	7.01	2	6.16	LC
Peach-faced lovebird	*Agapornis roseicollis*	34.10	1943	2.33	663	6.74	120	8.23	LC
Masked lovebird	*Agapornis personatus*	24.24	997	1.46	282	5.73	106	5.56	LC
Fischer's lovebird	*Agapornis fischeri*	32.24	1402	1.75	397	5.94	203	7.80	NT
Nyasa lovebird	*Agapornis lilianae*	19.20	227	3.63	108	7.44	4	6.38	NT
Black-cheeked lovebird	*Agapornis nigrigenis*	13.75	675	1.71	224	6.83	152	6.88	VU
Vernal hanging parrot	*Loriculus vernalis*	13.00	50	6.93	39	8.10	11	9.62	LC
Ceylon hanging parrot	*Loriculus beryllinus*	3.56	2	2.71					LC
Philippine hanging parrot	*Loriculus philippensis*	13.33	21	4.14	12	5.05	1	10.23	LC
Blue-crowned hanging parrot	*Loriculus galgulus*	21.25	837	2.18	253	6.33	65	9.00	LC
Maroon-rumped hanging parrot	*Loriculus stigmatus*	13.03	24	4.37	12	7.93			LC
Green hanging parrot	*Loriculus exilis*	3.45	3	3.10					NT
Yellow-throated hanging parrot	*Loriculus pusillus*	2.23	1	2.23					NT
Moluccan king parrot	*Alisterus amboinensis*	29.20	112	1.94	41	7.56	17	8.16	LC
Papuan king parrot	*Alisterus chloropterus*	22.35	77	6.06	45	10.26	10	11.66	LC
Australian king parrot	*Alisterus scapularis*	31.32	699	1.53	171	7.63	59	7.75	LC
Olive-shouldered parrot	*Aprosmictus jonquillaceus*	14.84	7	11.12	6	11.18			NT
Red-winged parrot	*Aprosmictus erythropterus*	27.30	390	1.83	137	9.03	41	10.69	LC
Superb parrot	*Polytelis swainsonii*	24.21	421	2.86	166	7.18	47	6.81	VU
Regent parrot	*Polytelis anthopeplus*	27.49	365	2.51	125	7.23	36	7.21	LC

Table 2. Continued.

			Lifespan: all[a]		Lifespan: adults ≥4		Age: adults ≥4[b]		
Species common name	Scientific name	Lifespan: maximum	*n*	Median	*n*	Median	*n*	Median	IUCN status[c]
Princess parrot	*Polytelis alexandrae*	23.98	614	2.55	210	7.36	76	7.45	NT
Red-capped parrot	*Purpureicephalus spurius*	17.90	138	1.06	29	8.00	4	12.91	LC
Mallee ringneck parrot	*Barnardius barnardi*	31.62	181	1.05	52	6.75	8	4.84	NA
Port Lincoln parrot	*Barnardius zonarius*	17.96	140	3.66	68	7.81	13	8.06	LC
Green rosella	*Platycercus caledonicus*	7.98	37	3.37	15	6.35	4	6.61	LC
Crimson rosella	*Platycercus elegans*	20.14	1010	1.03	139	6.50	36	7.53	LC
Yellow rosella	*Platycercus flaveolus*	13.31	59	2.50	21	6.18	1	4.23	LC
Adelaide rosella	*Platycercus adelaidae*	17.35	58	0.26	11	8.44	5	7.23	LC
Eastern rosella	*Platycercus eximius*	37.44	1302	1.61	334	6.58	93	6.81	LC
Pale-headed rosella	*Platycercus adscitus*	25.03	267	1.76	75	6.35	23	7.18	LC
Northern rosella	*Platycercus venustus*	21.57	191	2.57	69	6.81	4	7.81	LC
Western rosella	*Platycercus icterotis*	31.64	274	1.03	64	6.58	7	5.87	LC
Bluebonnet	*Northiella haematogaster*	15.40	173	1.44	40	6.06	2	10.42	LC
Red-rumped parrot	*Psephotus haematonotus*	17.74	792	1.93	238	5.27	107	5.23	LC
Mulga parrot	*Psephotus varius*	11.79	116	1.93	25	5.61	3	4.81	LC
Golden-shouldered parrot	*Psephotus chrysopterygius*	20.96	812	1.38	221	7.91	32	9.49	EN
Swift parrot	*Lathamus discolor*	14.18	184	1.26	28	6.28	11	6.24	EN
Antipodes green parakeet	*Cyanoramphus unicolor*	12.66	147	2.77	60	6.61	7	5.37	VU
Red-fronted parakeet	*Cyanoramphus novaezelandiae*	36.45	510	1.73	129	7.23	51	10.05	VU
Yellow-fronted parakeet	*Cyanoramphus auriceps*	16.48	171	1.30	51	6.54	20	6.96	NT
Orange-fronted parakeet	*Cyanoramphus malherbi*	12.28	17	1.87	4	7.56	1	12.28	CR
Horned parakeet	*Eunymphicus cornutus*	12.90	30	2.75	11	6.93	6	11.98	EN
Masked shining parrot	*Prosopeia personata*	17.73	4	11.46	4	11.46			NT
Red shining parrot	*Prosopeia tabuensis*	23.67	35	5.42	21	9.89			LC
Blue-winged parrot	*Neophema chrysostoma*	15.85	165	0.60	30	5.47			LC
Elegant parrot	*Neophema elegans*	14.91	207	1.72	54	6.22			LC
Rock parrot	*Neophema petrophila*	16.92	68	2.17	25	6.36			LC
Orange-bellied parrot	*Neophema chrysogaster*	13.27	426	0.81	81	6.29	47	7.23	CR
Turquoise parrot	*Neophema pulchella*	26.54	461	2.15	142	6.65	15	7.52	LC
Scarlet-chested parrot	*Neophema splendida*	25.41	1284	1.05	202	5.91	32	13.05	LC
Bourke's parrot	*Neopsephotus bourkii*	19.40	511	2.11	155	6.06	43	6.56	LC
Budgerigar	*Melopsittacus undulatus*	18.01	4840	0.97	819	5.64	324	5.20	LC
Ground parrot	*Pezoporus wallicus*	1.17	1	1.17					LC
Brehm's tiger parrot	*Psittacella brehmii*	1.92	1	1.92					LC
Vasa parrot	*Coracopsis vasa*	29.06	190	5.20	109	9.76	49	11.57	LC
Black parrot	*Coracopsis nigra*	37.69	132	4.89	73	8.95	22	9.90	LC
Gray parrot	*Psittacus erithacus*	48.26	4742	2.66	1979	8.23	882	8.75	NT
Brown-necked parrot	*Poicephalus robustus*	36.00	377	3.08	172	8.15	89	8.36	LC
Jardine's parrot	*Poicephalus gulielmi*	20.20	227	4.30	118	6.81	44	9.20	LC
Brown-headed parrot	*Poicephalus cryptoxanthus*	16.20	169	2.27	63	6.61	30	8.58	LC
Niam-niam parrot	*Poicephalus crassus*	10.06	2	10.06	2	10.06	2	10.06	LC
Meyer's parrot	*Poicephalus meyeri*	31.02	275	4.53	150	8.05	60	9.63	LC
Rüppell's parrot	*Poicephalus rueppellii*	20.54	49	5.23	35	5.23	21	5.23	LC
Red-bellied parrot	*Poicephalus rufiventris*	22.23	192	1.92	65	7.49	34	7.72	LC
Senegal parrot	*Poicephalus senegalus*	27.16	736	3.88	361	6.60	186	5.47	LC
Hyacinth macaw	*Anodorhynchus hyacinthinus*	54.26	568	12.52	422	18.23	141	21.77	EN
Lear's macaw	*Anodorhynchus leari*	43.57	13	14.56	11	17.86			CR
Spix's macaw	*Cyanopsitta spixii*	32.22	9	6.18	7	15.18	3	20.21	CR
Blue and yellow macaw	*Ara ararauna*	48.52	2124	6.60	1297	12.55	273	20.78	LC
Blue-throated macaw	*Ara glaucogularis*	32.79	23	12.55	17	18.20	12	18.66	CR
Scarlet macaw	*Ara macao*	48.26	1360	8.36	896	14.59	188	21.24	LC
Green-winged macaw	*Ara chloroptera*	63.04	981	9.51	670	14.44	180	19.19	LC
Military macaw	*Ara militaris*	54.43	581	8.57	385	14.16	110	20.12	VU
Great green macaw	*Ara ambigua*	34.75	78	10.73	56	19.88	16	24.83	EN
Red-fronted macaw	*Ara rubrogenys*	36.21	241	6.48	143	13.84	42	19.77	EN
Chestnut-fronted macaw	*Ara severus*	39.67	135	5.73	80	10.57	13	19.80	LC

Table 2. Continued.

			Lifespan: all[a]		Lifespan: adults ≥4		Age: adults ≥4[b]		
Species common name	Scientific name	Lifespan: maximum	*n*	Median	*n*	Median	*n*	Median	IUCN status[c]
Yellow-collared macaw	*Primolius auricollis*	25.21	153	3.03	68	9.58	9	19.60	LC
Blue-headed macaw	*Primolius couloni*	13.30	2	13.30	2	13.30	2	13.30	EN
Blue-winged macaw	*Primolius maracana*	24.95	93	6.87	61	14.48	23	18.23	NT
Red-bellied macaw	*Orthopsittaca manilata*	9.72	43	2.01	16	6.89			LC
Red-shouldered macaw	*Diopsittaca nobilis*	22.91	157	2.51	59	11.64	15	18.98	LC
Thick-billed parrot	*Rhynchopsitta pachyrhyncha*	35.24	359	6.21	202	15.60	40	20.74	EN
Golden conure	*Guaruba guarouba*	60.90	373	4.59	190	14.10	34	21.68	EN
Blue-crowned conure	*Aratinga acuticaudata*	22.49	99	2.89	42	8.81	4	19.23	LC
White-eyed conure	*Aratinga leucophthalmus*	28.45	93	2.28	28	10.15	6	23.35	LC
Green conure	*Aratinga holochlora*	21.06	44	0.89	8	7.96			LC
Hispaniolan conure	*Aratinga chloroptera*	30.84	14	18.23	14	18.23	13	18.23	VU
Cuban conure	*Aratinga euops*	14.71	15	1.79	6	7.63			VU
Finsch's conure	*Aratinga finschi*	14.16	1	14.16	1	14.16			LC
Red-fronted conure	*Aratinga wagleri*	24.86	35	8.32	30	8.32	2	15.58	LC
Mitred conure	*Aratinga mitrata*	27.83	93	3.45	41	8.44	11	27.83	LC
Red-masked conure	*Aratinga erythrogenys*	26.64	108	4.40	56	8.93	2	21.02	NT
Golden-capped conure	*Aratinga auricapillus*	18.85	25	6.73	19	8.43	1	18.85	NT
Jandaya conure	*Aratinga jandaya*	22.24	165	1.92	69	9.53	7	19.98	LC
Sun conure	*Aratinga solstitialis*	29.70	529	2.07	200	10.98	23	18.98	EN
Dusky-headed conure	*Aratinga weddellii*	24.57	12	5.39	8	9.27	1	24.57	LC
Brown-throated conure	*Aratinga pertinax*	19.73	31	1.42	10	8.58	1	13.73	LC
Olive-throated conure	*Aratinga nana*	7.12	5	2.09	1	7.12			LC
Orange-fronted conure	*Aratinga canicularis*	28.62	131	0.87	23	8.80	2	23.42	LC
Peach-fronted conure	*Aratinga aurea*	15.34	124	2.19	25	6.58			LC
Cactus conure	*Aratinga cactorum*	9.08	15	6.26	10	6.47			LC
Nanday conure	*Nandayus nenday*	30.24	411	3.39	185	9.00	19	20.79	LC
Patagonian conure	*Cyanoliseus patagonus*	34.12	439	7.11	294	11.19	62	18.56	LC
Monk parakeet	*Myiopsitta monachus*	24.78	455	3.76	217	6.65	5	22.24	LC
Slender-billed conure	*Enicognathus leptorhynchus*	20.17	23	3.87	11	9.28			LC
Maroon-bellied conure	*Pyrrhura frontalis*	17.42	40	1.52	13	11.05			LC
Green-cheeked conure	*Pyrrhura molinae*	8.34	3	8.22	3	8.22			LC
Maroon-tailed conure	*Pyrrhura melanura*	12.05	3	1.24	1	12.05			LC
Crimson-bellied conure	*Pyrrhura perlata*	22.34	21	7.41	15	8.44			LC
Fiery-shouldered conure	*Pyrrhura egregia*	12.16	2	12.13	2	12.13			LC
White-eared conure	*Pyrrhura leucotis*	10.61	2	6.57	1	10.61			NT
Painted conure	*Pyrrhura picta*	17.75	77	0.57	12	11.26			LC
Black-capped conure	*Pyrrhura rupicola*	6.09	6	0.01	2	6.09			LC
Blue-throated conure	*Pyrrhura cruentata*	20.38	29	10.57	17	16.85	4	18.53	VU
Barred parakeet	*Bolborhynchus lineola*	6.03	3	3.73	1	6.03			LC
Andean parakeet	*Bolborhynchus orbygnesius*	9.65	28	2.24	9	7.53			LC
Mexican parrotlet	*Forpus cyanopygius*	12.02	35	6.37	22	8.10			LC
Green-rumped parrotlet	*Forpus passerinus*	11.58	22	2.42	7	4.72			LC
Blue-winged parrotlet	*Forpus xanthopterygius*	27.90	15	3.03	7	9.16	2	27.90	LC
Spectacled parrotlet	*Forpus cospicillatus*	7.12	2	4.18	1	7.12	1	7.12	LC
Pacific parrotlet	*Forpus coelestis*	30.38	145	1.27	28	6.07	2	24.26	LC
Yellow-faced parrotlet	*Forpus xanthops*	10.50	22	4.47	12	6.18			VU
Plain parakeet	*Brotogeris tirica*	4.21	24	1.74	3	4.21			LC
White-winged parakeet	*Brotogeris versicolurus*	17.84	89	1.88	29	6.82			LC
Gray-cheeked parakeet	*Brotogeris pyrrhopterus*	13.78	20	3.48	9	8.03			EN
Orange-chinned parakeet	*Brotogeris jugularis*	22.79	43	0.04	5	7.05			LC
Tui parakeet	*Brotogeris sanctithomae*	15.15	6	1.86	2	10.01			LC
Black-capped parrot	*Pionites melanocephala*	27.07	96	3.40	45	13.21	8	20.71	LC
White-bellied parrot	*Pionites leucogaster*	23.14	34	4.97	26	5.79	3	20.28	LC
Pileated parrot	*Pionopsitta pileata*	19.51	29	8.27	22	9.20	1	19.51	LC
Caica parrot	*Pionopsitta caica*	28.24	1	28.24	1	28.24	1	28.24	LC
Blue-headed parrot	*Pionus menstruus*	23.03	79	3.07	37	7.36	1	18.90	LC

Table 2. Continued.

Species common name	Scientific name	Lifespan: maximum	Lifespan: all[a] *n*	Lifespan: all[a] Median	Lifespan: adults ≥4 *n*	Lifespan: adults ≥4 Median	Age: adults ≥4[b] *n*	Age: adults ≥4[b] Median	IUCN status[c]
Red-billed parrot	*Pionus sordidus*	5.70	3	2.83	1	5.70			LC
Scaly-headed parrot	*Pionus maximiliani*	23.86	31	8.47	21	10.25	2	16.63	LC
Plum-crowned parrot	*Pionus tumultuosus*	13.76	8	4.37	4	11.29			LC
White-capped parrot	*Pionus seniloides*	7.60	1	7.60	1	7.60			LC
White-crowned parrot	*Pionus senilis*	13.45	7	12.63	4	13.02			LC
Bronze-winged parrot	*Pionus chalcopterus*	18.98	36	2.15	13	15.23	5	18.23	LC
Dusky parrot	*Pionus fuscus*	9.10	16	1.50	7	7.26			LC
Yellow-billed amazon	*Amazona collaria*	11.61	7	7.91	6	8.10			VU
Cuban amazon	*Amazona leucocephala*	30.83	292	4.09	165	7.77	24	21.24	NT
Hispaniolan amazon	*Amazona ventralis*	29.06	117	3.61	53	6.30	1	14.15	VU
Black-billed amazon	*Amazona agilis*	8.00	2	8.00	2	8.00			VU
Puerto Rican amazon	*Amazona vittata*	27.23	63	1.50	28	9.03			CR
Tucuman amazon	*Amazona tucumana*	26.19	109	5.08	66	5.41	10	18.96	NT
Red-spectacled amazon	*Amazona pretrei*	24.23	18	1.26	5	23.54	4	23.69	VU
White-fronted amazon	*Amazona albifrons*	35.24	133	3.76	64	8.76	9	20.05	LC
Yellow-lored amazon	*Amazona xantholora*	22.05	11	12.33	10	12.33	1	22.05	LC
Green-cheeked amazon	*Amazona viridigenalis*	39.45	311	5.24	180	11.59	33	20.68	EN
Lilac-crowned amazon	*Amazona finschi*	30.73	133	4.47	74	11.13	15	25.29	VU
Red-lored amazon	*Amazona autumnalis*	37.84	192	7.28	127	11.75	26	18.44	LC
Festive amazon	*Amazona festiva*	30.31	35	9.66	28	18.11	11	21.10	LC
Red-tailed amazon	*Amazona brasiliensis*	23.20	16	18.89	15	21.93	8	22.34	VU
Red-crowned amazon	*Amazona rhodocorytha*	26.94	39	14.75	32	15.37	11	24.25	EN
Blue-cheeked amazon	*Amazona dufresniana*	22.42	15	8.43	15	8.43	6	19.48	NT
Yellow-shouldered amazon	*Amazona barbadensis*	34.62	46	8.77	38	10.45	8	9.46	VU
Yellow-faced amazon	*Amazona xanthops*	24.73	28	6.92	23	11.90	4	24.73	NT
Blue-fronted amazon	*Amazona aestiva*	37.44	646	5.37	395	10.22	73	19.32	LC
Yellow-crowned amazon	*Amazona ochrocephala*	34.45	401	5.18	240	10.46	50	17.75	LC
Yellow-naped amazon	*Amazona auropalliata*	66.81	185	7.91	124	11.45	38	19.48	LC
Yellow-headed amazon	*Amazona oratrix*	41.50	620	3.37	285	10.48	54	20.78	EN
Orange-winged amazon	*Amazona amazonica*	39.02	289	5.43	174	8.44	30	18.15	LC
Scaly-naped amazon	*Amazona mercenaria*	6.57	2	4.52	1	6.57			LC
Mealy amazon	*Amazona farinosa*	42.90	100	6.11	62	10.40	11	16.93	LC
Vinaceous amazon	*Amazona vinacea*	26.94	43	4.28	22	12.15	6	21.65	VU
St Vincent amazon	*Amazona guildingii*	36.58	32	17.30	29	19.87	3	34.70	VU
St Lucia amazon	*Amazona versicolor*	38.75	27	13.57	17	19.92	7	32.04	VU
Red-necked amazon	*Amazona arausiaca*	29.65	3	29.61	2	29.63			VU
Hawk-headed parrot	*Deroptyus accipitrinus*	38.25	163	6.50	101	13.57	15	21.30	LC
Purple-bellied parrot	*Triclaria malachitacea*	15.14	12	5.80	9	7.99			NT
Carolina parakeet	*Conuropsis carolinensis*	15.55	4	10.02	3	15.03			EX

[a]Does not include chicks that died day of hatch.

[b]Individuals that were still alive as of 24 March 2008.

[c]2009 Red List status.

LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CE, Critically Endangered; EX, Extinct; NA, not available.

breeding was 1.10 years for the orange-bellied parrot *Neophema chrysogaster*. The highest median age of last breeding was 19.75 years for the St Vincent amazon *Amazona guildingii*. The blue-eyed cockatoo *Cacatua ophthalmica* had the longest median breeding duration at 5.92 years. The longest median post-breeding duration was recorded at 5.16 years for Pesquet's parrot *Psittrichas fulgidus* (supporting information Table S2).

A one-way ANOVA testing for differences in the means of reproduction data among the six selected clades indicated that they differed in the median age of first breeding ($F_{5,27} = 5.39$, $P = 0.0015$), median age of last breeding ($F_{5,49} = 17.77$, $P < 0.0001$), median duration of active reproduction ($F_{5,49} = 4.18$, $P = 0.0031$) and median duration of post-reproduction ($F_{5,45} = 5.66$, $P = 0.0004$). Notably, the mean median duration of post-reproduction was longer

than the mean median duration of active reproduction for *Trichoglossus*, *Cacatua*, *Amazona* and *Platycercus* (Fig. 5).

Life-history and IUCN status

After classifying species using the 2009 IUCN Red List, we found 68% of species were of Least Concern (LC), 10% were Near Threatened (NT), 11% were Vulnerable (VU), 7% were Endangered (EN) and 3% were Critically Endangered (CR; Table 2). One-way ANOVAs of lifespan and breeding parameters by IUCN status revealed that there was a detectable difference in adult median lifespan ($F_{4,163} = 9.00$, $P < 0.0001$), median adult age ($F_{4,93} = 6.44$, $P = 0.0001$), median age of last breeding ($F_{4,125} = 3.55$, $P = 0.0088$) and median duration of active breeding ($F_{4,125} = 4.65$, $P = 0.0016$) among the IUCN status groups. The species with VU, EN or CR (the classifications of highest threat) had greater average values for maximum lifespan, median adult lifespan, median age of last breeding and median duration of active breeding than did species classified as LC or NT.

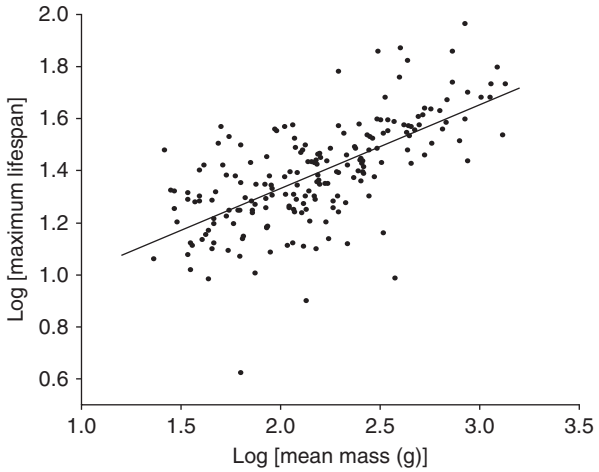

Figure 1 The regression of log of maximum lifespan on log of adult mass by parrot species with $n \geq 20$ individuals. The slope of the fit line is 0.3215 ± 0.0213.

Discussion

Parrots have a reputation for being one of the longest-lived avian taxa (Prinzinger, 1993). This analysis of 260 species of captive parrots spanning the order Psittaciformes demonstrates that even closely related clades of parrots can differ dramatically in lifespan and duration of reproduction. While a few individual parrots have lived for nearly a century, the majority of parrots in captivity did not live much beyond two decades. Even when accounting for juvenile mortality, only 30% of the 260 species had median adult lifespans ≥ 10 years. Clearly, most captive parrots are not living as long as generally thought. However, we found

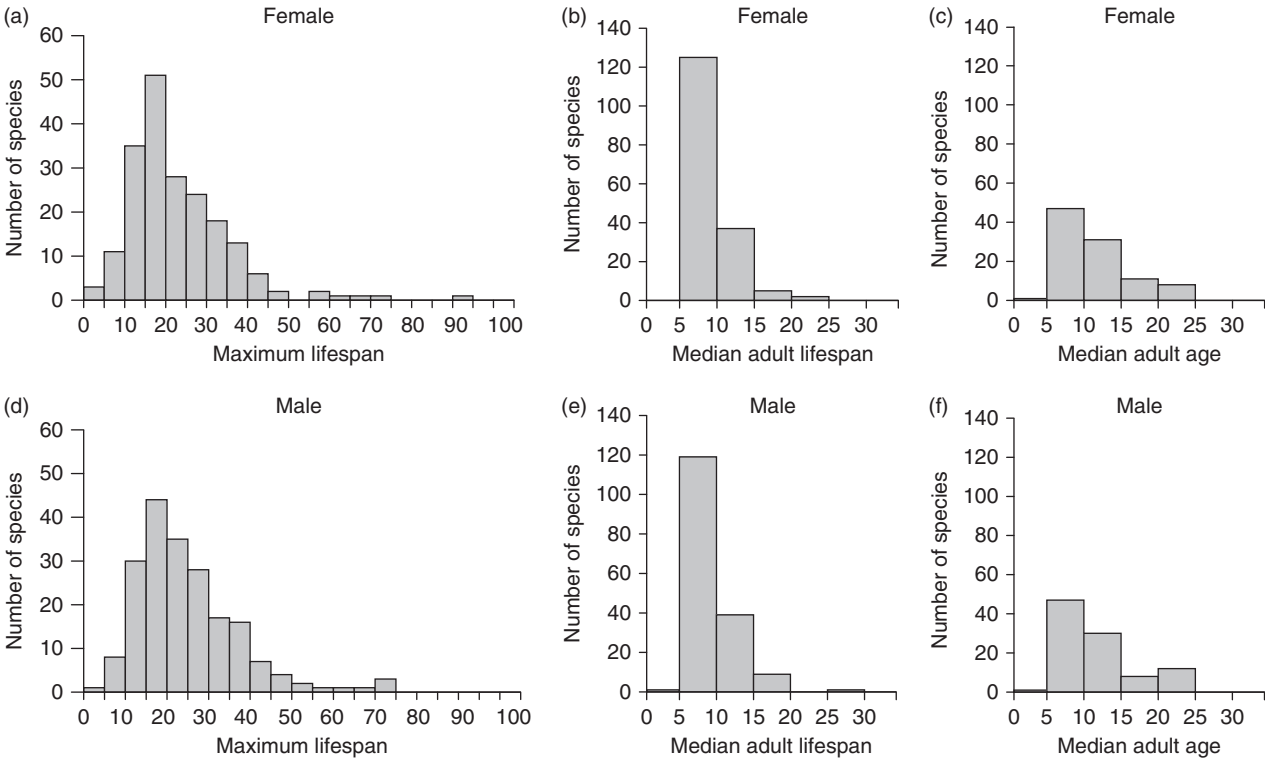

Figure 2 Histograms of lifespan by parrot species with $n \geq 20$ individuals of female (a) maximum and (b) median adult lifespan and (c) median adult age, and of male (d) maximum and (e) median adult lifespan and (f) median adult age.

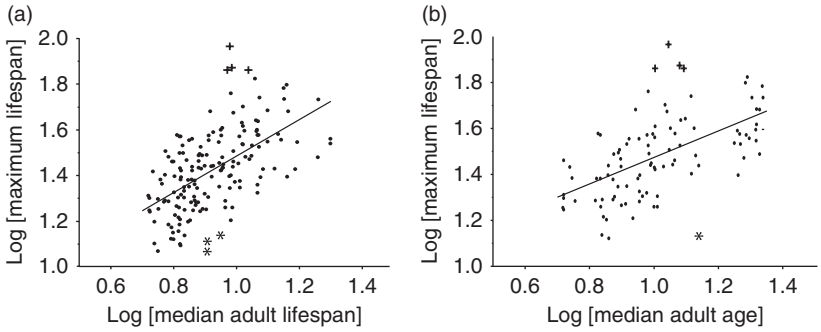

Figure 3 Regression of log of maximum lifespan on (a) log of median adult lifespan (slope = 0.7975 ± 0.0223) and (b) log of median adult age (slope = 0.5759 ± 0.0303). Points represent individual parrot species, plus signs indicate the species with a residual value > 0.3, and asterisks indicate the species with a residual value < −0.3.

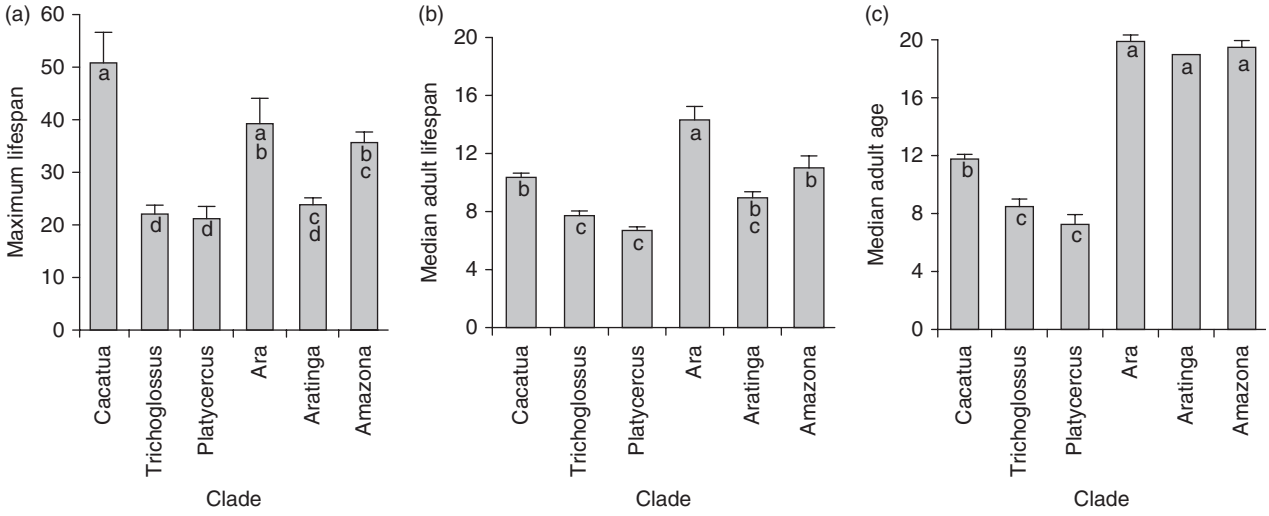

Figure 4 Mean and SE of (a) maximum lifespan, (b) median adult lifespan and (c) median adult age for major clades of parrots. Clades that do not share the same letter within the bar are significantly different based on a Tukey–Kramer HSD *post hoc* test.

that lifespan in captivity appears to be increasing, as the median age of living adult birds is significantly greater than the median lifespan of all birds in the database, despite the truncating effect on lifespan of considering only living birds. This increase is likely due to advances in animal husbandry and indicates that modern zoos have improved their care and maintenance of parrots. Below we discuss these general trends and their implications for the conservation of parrots.

Life-history trends in parrots

As found in a smaller analysis of parrot lifespan (Munshi-South & Wilkinson, 2006), we found that larger parrots had longer lifespans than smaller parrots. Even though parrots with a larger body mass generally lived longer than smaller bodied parrots, on average the difference in mean median adult lifespan and age was only about a decade within the six clades examined. When body mass was included as a covariate in the analysis, mass and clade had a significant interaction for median adult lifespan, suggesting the effect of body mass on median adult lifespan varied with different clades. In contrast, body mass and clade independently affect maximum lifespan.

Male parrots had statistically longer maximum and median lifespans than females. However, this difference was small (1.74 years longer max lifespan, 0.22 years longer median lifespan) and may not be biologically important. In general, there is no consistent pattern of sex differences in avian lifespans; some sources report that in many species of birds, males live longer than females (Holmes *et al.*, 2003), but other sources cite females as the sex with the typically longer lifespan (Christe, Keller & Roulin, 2006).

Breeding parameter patterns for captive female parrots vary greatly across species. Some smaller species were able to breed before they were a year old, while many larger species still bred when they were past 40 years old (supporting information Table S2). Notably, several species also had

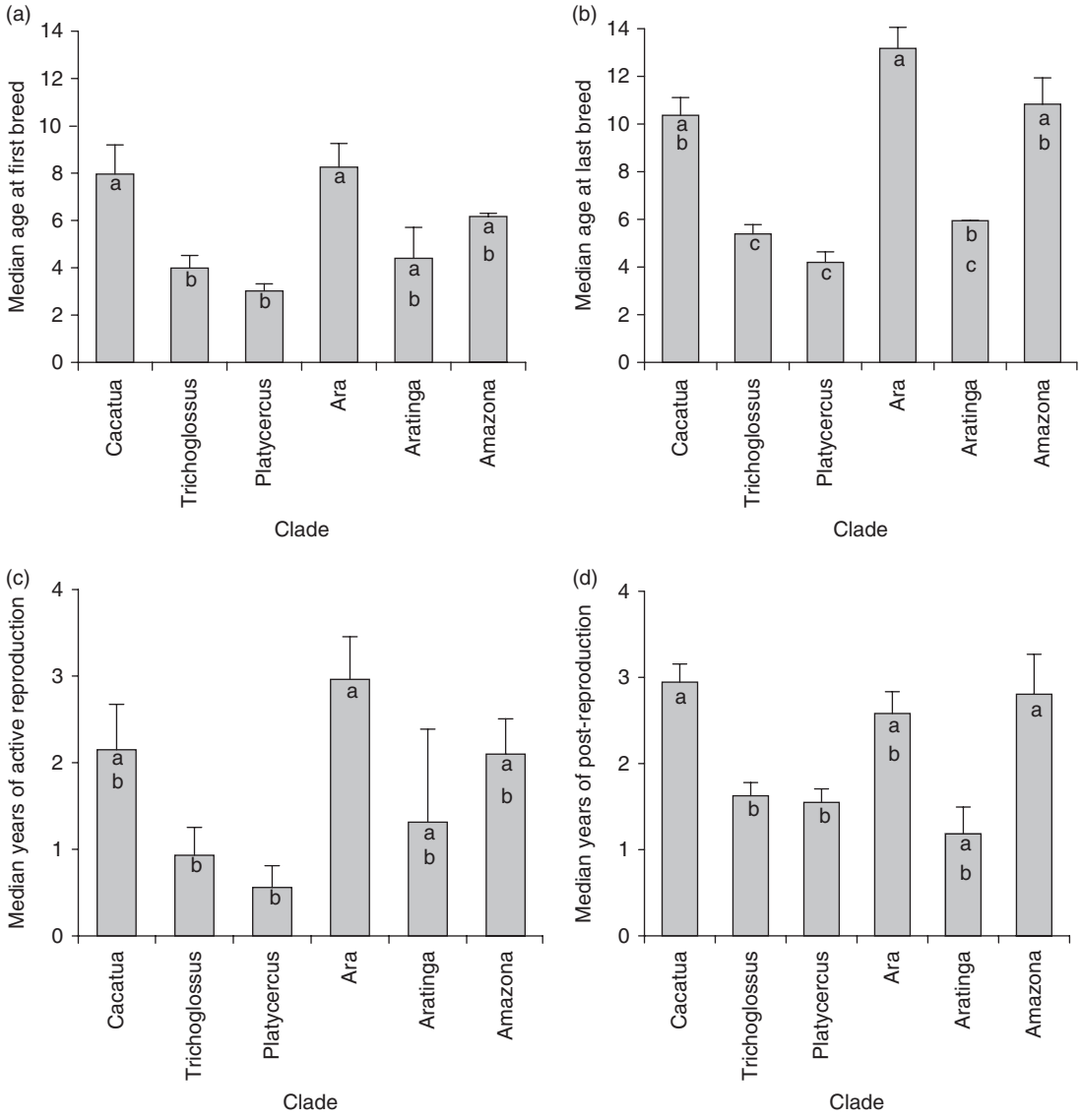

Figure 5 Mean and SE of (a) median age at first breeding, (b) median age at last breeding, (c) median duration of active breeding, (d) median duration of post-breeding for major clades of parrots. Clade bars that do not share the same letter are significantly different based on a Tukey–Kramer HSD *post hoc* test.

very long post-breeding periods, and clade means of the median duration of active reproduction were similar to the median duration of the post-reproductive period. This similarity suggests that either (1) parrots are not being housed in situations where they can realize their breeding potential fully; (2) parrots have an unusually early reproductive senescence compared to other birds (Holmes *et al.*, 2003); (3) female parrots have an extended lifespan in captivity relative to wild parrots and can live past the constraints on egg production (as seen in domestic quail; Vom Saal, Finch & Nelson, 1994). Housing is likely influencing the breeding data as not all zoo parrots have access to a sexually mature, opposite-sex conspecific in ideal breeding conditions, but this effect cannot be teased apart from the other factors until data on opportunity to breed is also recorded. While this is not always feasible, especially in monomorphic species, it would be beneficial for zoos to enter as much of these data as possible into ISIS, so the impact of biological factors could potentially be assessed.

Caveats

While our analysis provides an important demonstration of the utility of the ISIS database for providing lifespan data on long-lived species, there are important caveats concerning the reliability of the data. The ISIS database is composed of data contributed by many different institutions that do not necessarily adhere to the same standards of accuracy,

reliability, diligence and comprehensiveness in record keeping. While we tried to eliminate clearly erroneous records during our initial compilation of the data, some questionable values remain (e.g. the age at first breeding of 0.29 years from *Cyanoramphus novaezelandiae*, supporting information Table S2). Data accuracy can depend on the species, as parentage is harder to ascertain in group-living species than for species housed in pairs. In many cases, individual records may also represent an incomplete account of the entire lifespan due to transfers of animals in and out of ISIS member institutions. Overall, we suggest that the greatest care be exercised in generalizing from breeding data, as captive breeding is dependent on opportunities provided by housing arrangements and thus most subject to biases introduced by captivity. Renewed commitment of all ISIS members to record keeping protocols would improve the value of this large database for species maintenance, reproduction and conservation. A more fundamental issue is that ISIS data are from captive animals. While captive animals rarely suffer levels of predation and starvation seen in wild populations, they may experience higher rates of inbreeding, unusual social group composition and captive conditions that produce physical and psychological stress (Meehan & Mench, 2006). It is difficult to assess the relative importance of these factors, but there are some indications that lifespan data from captive animals are a generally reliable predictor of lifespan in the wild (Ricklefs, 2000; Wasser & Sherman, 2010).

Conservation implications

This taxon-wide analysis of parrot lifespan and breeding parameters has several implications for conservation. First, survival in captivity should be taken into account when deciding which species to propagate. For example, the swift parrot *Lathamus discolor* had low residuals in the maximum lifespan on median adult lifespan regression (supporting information Table S3), meaning that many individuals of that species live nearly as long as the oldest surviving members. In contrast, the cockatoos had the highest residuals, and patterns in lifespan data that suggest while cockatoos have the biological potential to live for a very long time, few individuals are realizing that potential in captivity. We suggest that in the short term, zoos focus resources on propagating endangered species that fare well in captivity in order to create populations for potential reintroductions. International or regional studbooks should be created for the species that fit these requirements, which includes the swift parrot *L. discolor*, golden-shouldered parrot *Psephotus chrysopterygius* and sun conure *Aratinga solstitialis*. Long-term goals should include research aimed at improving husbandry and welfare so that endangered species that currently do not survive well in captivity, such as some cockatoos, can become better candidates for captive propagation programs.

Second, our data are the most comprehensive to date regarding lifespan and breeding in parrots. Such data are critical for parameterizing population viability models for wild populations. It is difficult to compare our captive data to data from wild populations, as the life-history traits of interest have been studied for relatively few species over a limited scope of time in comparison to parrot lifespan and reproduction. The majority of these studies estimate survival rates or fecundity (Saunders, 1982; Buckland *et al.*, 1983; Rowley, 1983; Powlesland *et al.*, 1992; Sandercock *et al.*, 2000; Heinsohn & Legge, 2003; Murphy *et al.*, 2003; Renton & Salinas-Melgoza, 2004; Beissinger *et al.*, 2008; Koenig, 2008). A study on wild orange-bellied parrots reported life-history measures comparable to our captive data (Holdsworth, Dettmann & Baker, in press). Furthermore, two of the general trends we detected have particular importance for the viability of wild parrot populations, namely the shorter median lifespans than generally considered, and the long periods of post-reproductive lifespans. Taken together, these trends suggest that wild populations may be more vulnerable to rapid declines than previously thought.

Third, our results suggest that the suitability of older individuals for captive breeding should be carefully assessed. Many species in our dataset exhibited long post-breeding durations (see supporting information Fig. S2 and Table S2); it is not clear whether this phenomenon also occurs in wild parrots or is an artifact of captive conditions. Efforts to house pairs together could potentially increase the duration of active breeding and thereby maximize their value for conservation. On the other hand, if these long post-breeding durations are generally characteristic of parrot life-history, then many individuals will be surplus animals for as long a period as they were contributing active breeders. If true, this trend would put additional pressure on TAGs to refine their prioritization efforts.

Fourth, these data on average lifespan and breeding parameters may be used by TAGs as a rough guide for predicting future endangerment of species and proactively planning captive management priorities. We found that larger-bodied species that lived longer and bred later in life tended to be more threatened according to IUCN classifications. These trends suggest that TAGs should add lifespan and breeding measures to their existing criteria of number of individuals in captivity and IUCN status (AZA, 2007) in prioritizing the management of captive parrot populations for conservation.

Finally, this study demonstrates the general value and utility of the ISIS database and provides a baseline for demographic comparisons with wild populations. Even though caution must be exercised, ISIS provides a tremendous source of unrivaled information which can be used to parameterize population viability models for wild populations and adaptively manage captive populations according to conservation priorities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. (a) Scatterplot of median adult lifespan vs. adult mass, (b) the regression of log of median adult lifespan on log of adult mass (slope = 0.2217 ± 0.0133), (c) scatterplot of median adult age vs. adult mass, (d) the regression of log of median adult age on log of adult mass by parrot species (slope = 0.2683 ± 0.0266) with $n \geq 20$ individuals.

Figure S2. Mean and SE of (a) mean minimum age at first breeding, (b) mean minimum age at last breeding, (c) mean duration of active breeding, (d) mean duration of post-breeding for major clades of parrots. Clade bars that do not share the same letter are significantly different.

Figure S3. Scatterplot of maximum lifespan vs. adult mass by parrot species with $n \geq 20$ individuals.

Table S1. Lifespan summary across species (age in years)

Table S2. Female breeding parameters across species

Table S3. Residuals of lifespan regression on log transformed data

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