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ORIGINAL ARTICLE

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Old endemics and new invaders: alternative strategies of passerines for living in the Australian environment

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Abstract Life history parameters of "old endemics" and "new invaders" among the Australian passerines were compared, controlling for phylogeny by using current, phylogenetic research methods. Old endemics were found to have significantly smaller clutches and demonstrated significantly more cooperative breeding than the new invaders, whose fledging periods are significantly longer than those of the old endemics. We argue that breeding under conditions of a small annual food increment during the breeding season, as is probably the situtation in Australia, is possible only when clutch size is small, or while breeding cooperatively, or by extending the fledging period. Our data show that the old endemics use the first two options, while the new invaders employ the third.

Key words Clutch size · Fledging · Incubation · Life history parameters · Passerines · Australia

Introduction

Ornithologists have long had the impression that life history parameters of tropical and southern hemisphere birds differ from those of their northern hemisphere counterparts (reviewed by Martin, 1996). Tropical birds are said to have smaller clutches (Moreau 1944; Lack 1968), and longer incubation and fledging periods (Martin 1996). These claims were recently examined by Geffen and Yom-Tov (in press). Using the comparative method, they confirmed that tropical and southern hemisphere passerines have smaller clutches, but refuted the claim that northern hemisphere and tropical passerines differ in length of incubation and fledging periods.

The demographic difference between the tropics and northern temperate regions were often related to environmental factors (see Klomp 1970 for review). Due to lack of seasonality, tropical birds are potentially able to breed throughout the year, and produce several clutches annually. However, they are more heavily affected by predation and competition, and these two factors may favor small clutches and cooperative breeding (Lack 1947, 1968; Skutch 1949). Recently, Arnold and Owens (1998) showed that living in a relatively stable climate, such as the tropics, is associated with cooperative breeding, low mortality rate, and low population turnover.

Similar demographic differences also occur between southern and northern temperate regions (Moreau 1944; Yom-Tov 1994; Yom-Tov et al. 1994). Although "climatic conditions are not symmetrical about the cartographic equator, but rather are centered about 3.4 degrees north" (France 1998), temperate regions in both the southern and northern hemisphere have a similar climate. However, this factor cannot account for the differences in life history between them, and other explanations have been suggested. Following Ashmole (1961, 1963), several authors (Ricklefs 1980; Yom-Tov 1994; Yom-Tov et al. 1994) suggested that the relative absence of northern migrants contributes to the stability of bird populations in the tropics and the southern hemisphere, and this stability results in smaller clutch size. All the above hypotheses which concern differences between the northern temperate region on the one hand and the tropics and southern temperate regions on the other are related to avian ecology, without reference to phylogeny.

Communicated by R. Montgomerie

Supplementary material Data on body mass, clutch size, incubation and fledging periods, length of breeding season, frequency of breeding, origin (old endemics, new invaders and European introductions), and on the occurrence of cooperative breeding among Australian passerines (Table S1) are available in electronic form on Springer Verlag's server at http://link.springer.de/link/service/journals/00265/index.htm. These data relate to a paper originally published in *Australian Wildlife Research* 14:319-330

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The Australian avifauna is composed of three components: birds of Gondwanan origin, ("old endemics") which evolved in Australia in isolation when it separated from Antarctica about 40 million years ago; birds of Afro-Eurasian origin which migrated to Australia from the north ("new invaders"), and species introduced by Europeans during the last two centuries ("introductions"). Of the 338 species of passerines found at present in Australia, 258 almost certainly belong to the old endemics, while 64 and 16 belong to the other two groups, respectively (Rowley and Russell 1991).

Several characteristics of the Australian avifauna include small clutches, a high incidence of cooperative breeding, helping at the nest, nomadism, a 48-h interval in egg laying, protracted molt, long breeding seasons, and great longevity (Rowley 1965; Keast 1968; Thomas 1974; Fry 1980; Woinarski 1985; Wyndham 1986; Yom-Tov 1987; Rowley and Russell 1991). The average clutch size of Australian birds is smaller than that of their counterparts in North America (Woinarski 1985) or North Africa (Yom-Tov 1987). However, the small average clutch size of Australian passerines is due to the fact that the old endemics have small clutches, while the new invaders and the introduced species have clutches of comparable size to passerine species of the north temperate region (Yom-Tov 1987). In parallel, small litters, long gestation and weaning periods, and late maturity characterize the Hydromyinae rodents which invaded Australia 5–10 million years ago, while the opposite is true for the Murinae, which invaded Australia during the Pleistocene (Yom-Tov 1985). Most of the above studies compared species or genera means, and thus might be biased because these taxa may share common genetic ancestry and are therefore not necessarily independent values (Harvey and Mace 1982).

Cooperative breeding is one of the characteristics of the Australian avifauna, and Dow (1980) has shown that a high proportion of Australian birds are either obligatory or opportunistic cooperative breeders. Rowley (1965) and Harrison (1969) maintained that this phenomenon was an adaptation to an erratic climate, but Dow (1980) concluded his review by noting: "it is most unlikely that a single ecological variable, or even a few, can account for the widespread incidence of cooperative breeding in Australia." Russell (1989) suggested that although the high level of cooperative breeding in Australia is generally related to ecological factors, past history should also be taken in account, as many Australian taxa have evolved in dense tropical forest where cooperative breeding is favored. Recently, Cockburn (1996) pointed out that cooperative breeding is very common among the parvorder Corvida, a taxon which comprises all cooperatively breeding Australian passerines. This suggests that cooperative breeding is an ancestral trait among Australian passerines. Cockburn's (1996) finding was further supported by Arnold and Owens (1998) who found that cooperative breeding is not randomly distributed but concentrated in certain families.

In summary, the above characteristics of the Australian avifauna have been attributed to both environmental and phylogenetic factors. The aim of this work was to re-examine the data on various life history parameters, including cooperative breeding, while controlling for phylogeny by using current, phylogenetic research methods.

Methods

Species and study areas

Data on body mass, clutch size, incubation and fledging periods, length of breeding season, and frequency of breeding were taken mainly from the Appendix in Yom-Tov (1987) and complemented with body mass data from Dunning (1993), and clutch size data from the Reader's Digest (1983) *Complete Book of Australian Birds*. When a range of clutch size was given, a mean was calculated from the common range and the word "sometimes" received a score of 0.3 eggs; i.e., if a clutch size was said to be 2–3, sometimes 1, it received a value of 2.2. Similarly, a clutch of 2, sometimes 3, is scored 2.3. When more than one value was given for one of the other parameters, a mean was calculated from the given range. Data on cooperative breeding were from Dow (1980), the Reader's Digest (1983), and Ford et al. (1988).

Data on egg length and width were taken from the Reader's Digest (1983) *Complete Book of Australian Birds*, and Schönwetter (1967–1983). Egg volume was calculated using the equation $\text{volume}=0.5\times\text{length}\times\text{width}^2$, which is a good approximation of both egg volume and egg mass (van Noordwijk et al. 1981).

A possible source of error in our data is the parameter of mean body mass, which is affected by various factors. Sexual dimorphism among passerines is generally small (Campbell and Lack 1985) and in several passerines it varies within species; in some samples, males are heavier while in others, females are heavier (Cramp and Perrins 1993, 1994a, 1994b). Breeding birds may lose a considerable proportion of their mass while incubating or feeding their young, and even outside the breeding season, body mass may fluctuate by as much as 10% within 1 day (Yom-Tov and Hilborn 1981).

We compiled data for 322 Australian passerines; however, the following analysis was carried out on only 233 species for which phylogenetic and breeding information were available.

Statistics

A phylogenetic tree (topologies and branch lengths) based on DNA-DNA hybridizations (Sibley and Ahlquist 1990; Fig. 371–373, 380–382, 384–385) was used to determine phylogenetic relationships among species. Although some of the Sibely and Ahlquist (1990) conclusions are criticized by several authors (Parkes 1992; Storer 1992), for passerines they are the most comprehensive to date, and most of their results are supported by other work (for example Baverstock et al. 1991). Species not mentioned or specified (represented only as genus) in Sibley and Ahlquist (1990) were treated as sister taxa within their genus. Branch lengths for such species were estimated as mean branch length within the genus (in cases where other species within the genus were indicated) or as the mean branch length within all genera outlined in the dendrogram (in cases where no other species within the genus were indicated). The tree in Sibley and Ahlquist (1990) was converted to a matrix of divergences (the sum of the branch lengths separating each pair of species on the tree) using the program DISTANCE (part of COMPARE 2.0; Martins 1997), which was then used in the analysis below.

All size and life history data were log-transformed prior to analysis. To estimate phylogenetic correlation in the data, we used Moran's (1950) I statistic, a measure of autocorrelation. In applying this statistic to comparative problems, Gittleman and Kot (1990) provided an equation for the maximum I, and suggested scaling I relative to the maximum value (i.e., observed values are scaled between –1 and 1). Moran's I may be taken to be normally or randomly distributed (Cliff and Ord 1971, 1981). Using randomiza-

tion, we tested the null hypothesis of no phylogenetic autocorrelation at the 0.05 level by using a *Z*-test to examine whether *I* varies from an expected value by more than 1.96 SDs (Gittleman and Kot 1990). Using a correlogram, which shows how autocorrelation (I/I_{max}) varies with phylogenetic (genetic) distance, we located where in the tree traits are phylogenetically correlated. Using molecular phylogenetic information, we averaged over all species within some fine interval of distance, set in accordance with the distribution of values of the original genetic distance matrix (Purvis et al. 1994), and then calculated correlations at those distance intervals. The observed intervals were 3, 6, 9, 12, 15, and 18. Correlograms showing the correlation of each trait at these intervals are given in Fig. 2. We then used Cheverud et al.'s (1985) autoregressive model to remove the observed phylogenetic autocorrelation. The model takes the form: $\mathbf{y}=r\mathbf{W}\mathbf{y}+e$ where **y** is the vector of standardized trait values, $r\mathbf{W}\mathbf{y}$ is the phylogenetic component (i.e., the observed relationship between phylogenetic distance and the trait values among taxa), and *e* is the residual vector that is free of phylogenetic correlation. This technique uses a maximum-likelihood function to fit the observed trait values on the phylogenetic tree, as presented in Gittleman and Kot (1990). Recent simulation studies indicate that the autoregressive approach is statistically robust when (1) phylogenetic correlation is indeed observed in the comparative data and (2) phylogenetic information is based on appropriate molecular data (Gittleman and Luh 1992, 1994; Purvis et al. 1994). Both conditions are met in the present analysis.

After accounting for phylogenetic effects, the data were standardized to a mean of 0 and SD of 1, and then used to investigate associations of life histories with body weight via least-squares linear regression. We controlled for the effect of body weight by using the residuals generated from the regressions of this trait as the independent variable and the other traits as the dependent variables. The program PA 1.1 for the Apple Macintosh was used for the above calculations (Luh et al. 1994).

Specifically, we examined the relationship between body mass (independent variable) and six other dependent variables (egg mass, clutch size, incubation period, fledging period, length of breeding season, and breeding frequency) by linear regressions using both raw data and data controlled for phylogeny. We performed these initial steps to examine the effect of body mass on other variables before and after the phylogenetic component was removed. We used *t*-tests to examine origin and breeding mode differences in the dependent variables.

We have plotted the presence or absence of cooperative breeding in each species on the phylogenetic tree using MacClade 3.03 (Maddison and Maddison 1992). The phylogenetic reconstruction of cooperative breeding evolution was based on 65 taxa that had a reliable record confirming cooperative breeding. All other species were classified as lacking it. We selected this conservative approach to reduce bias associated with the lack of data for many species.

Results

Significant autocorrelation (Z=1.96) was observed in all the seven variables we have examined (Fig. 1). Therefore, all the dependent variables were subjected to the autoregressive correction.

Body mass was significantly correlated with all other variables examined, excluding clutch size (Table 1). Removal of the phylogenetic component maintained the significant correlations of body mass with egg volume, fledging period, and incubation period (Table 1). The proportion of the variance accounted for by phylogeny was high in egg volume and clutch size, and low in the other variables (Table 1).

Clutch size of the old endemics was significantly smaller than that of the new invaders (Table 2). For species for which we had phylogenetic information, mean clutch size was 3.2 (SD=1.0, n=36) and 2.5 (SD=0.7, n=192) eggs for the new invaders and old endemics, respectively. [For the full sample, mean clutch size was 3.8 (SD=1.1, n=53) and 2.5 (SD=0.6, n=245) eggs for the new invaders and old endemics, respectively]. There was no significant difference between the groups in incubation period, length of breeding season, breeding frequency, or egg volume prior the removal of the phylogenetic and body mass effects (Table 2). These results confirm Yom-Tov's (1987) findings. However, the present analysis revealed that the fledging period of new invaders was significantly longer than that of the old endemics (Table 2). This difference was also apparent after we controlled both raw and phylogenetically free variables for clutch size (t=3.5, df=78, P<0.005 and t=4.8, df=78 and P<0.005, respectively). For species for which we had phylogenetic information, mean fledging period was 15.8 (SD=6.0, n=67) and 24.4 (SD=10.6, n=13) days for the old endemics and new invaders, respectively. [For the full sample, mean fledging period was 15.8 (SD=5.5, n=74) and 23.4 (SD=8.3, n=21) days for the old endemics and new invaders, respectively]. The longer fledging period of the new invaders is to a large extent due to long fledging periods of the Ploceidae and Corvidae.

Mean fledging to incubation length ratio (F/I) is 0.99 (SD=0.18, n=73) and 1.6 (SD=0.34, n=18) among the

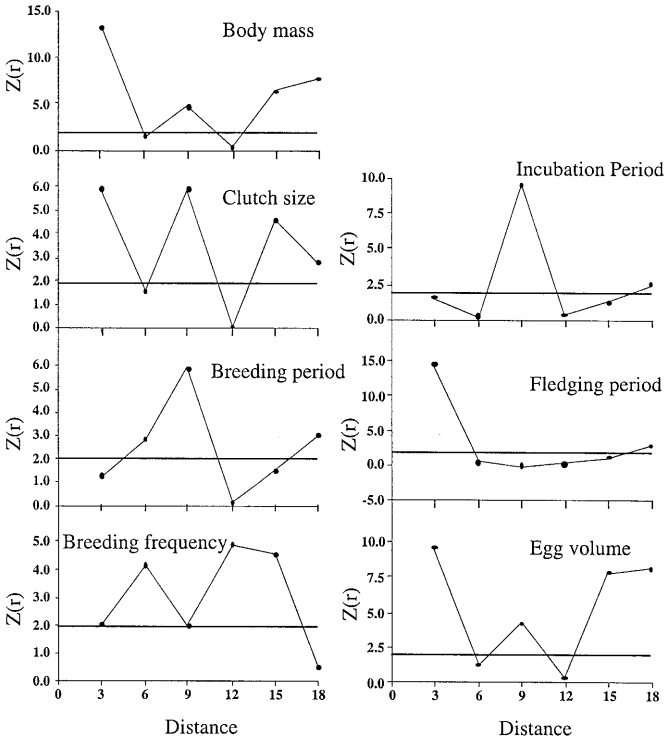

Fig. 1 Correlograms for all seven life history traits examined. The null hypothesis of no phylogenetic autocorrelation at the 0.05 level is tested here using a $Z(r)$ test to examine whether Moran's I varies from an expected value by more than 1.96 SDs. All traits, excluding litter size, show Z values higher than 1.96 (or lower than –1.96) at one or more phylogenetic distances

Table 1 Linear least-square regressions of six raw and phylogeny-controlled life history variables with body mass. Proportion of total variance accounted for by the phylogeny component is presented in the last column

Variable	r^2	Slope	Intercept	*df*	*F*	*P*	Proportion of total variance accounted for by phylogeny
Raw data							
Clutch size	0.003	–0.013	0.420	222	0.57	0.453	
Breeding period	0.076	–0.063	0.813	216	17.65	<0.001	
Breeding frequency	0.106	–0.066	0.199	215	25.46	<0.001	
Incubation period	0.343	0.114	1.039	91	47.06	<0.001	
Fledging period	0.553	0.213	0.919	79	96.42	<0.001	
Egg volume	0.921	0.704	–0.508	216	2507.70	<0.001	
Data controlled for phylogeny							
Clutch size	0.017	0.226	0.004	222	3.82	0.052	0.327
Breeding period	0.000	–0.025	0.010	216	0.03	0.859	0.056
Breeding frequency	0.001	–0.054	0.010	215	0.16	0.687	0.181
Incubation period	0.053	0.400	0.014	91	5.03	0.027	0.114
Fledging period	0.148	0.638	0.039	79	13.59	<0.001	0.169
Egg volume	0.644	0.785	–0.002	216	388.14	<0.001	0.773

Table 2 Comparisons (*t*-tests) between old endemics and new invaders for six life history variables

Variable	Raw data			Raw data controlled for body mass			Data controlled for phylogeny			Data controlled for phylogeny and body mass		
	t	*df*	*P*	*t*	*df*	*P*	*t*	*df*	*P*	*t*	*df*	*P*
Clutch size	4.16	226	<0.001	4.26	221	<0.001	2.89	226	0.004	2.54	221	0.012
Breeding period	0.55	219	0.585	0.31	215	0.759	0.02	219	0.985	0.05	215	0.958
Breeding frequency	0.52	218	0.606	1.56	214	0.121	1.18	218	0.239	1.18	214	0.238
Incubation period	0.39	90	0.696	1.91	90	0.058	1.65	90	0.102	1.10	90	0.273
Fledging period	3.99	78	<0.001	2.08	78	0.041	5.41	78	<0.001	4.59	78	<0.001
Egg volume	2.01	220	0.046	3.49	215	<0.001	1.32	220	0.187	0.51	215	0.601

Table 3 Comparisons (*t*-tests) between cooperative breeders and non-cooperative breeders for six life history variables. The tests were performed on the raw data, raw data controlled for body mass, data controlled for phylogeny, and data controlled for phylogeny and body mass

Variable	Raw data			Raw data controlled for body mass			Data controlled for phylogeny			Data controlled for phylogeny and body mass		
	t	*df*	*P*	*t*	*df*	*P*	*t*	*df*	*P*	*t*	*df*	*P*
Clutch size	1.49	226	0.137	1.41	221	0.160	1.37	226	0.172	1.43	221	0.155
Breeding period	3.34	219	0.001	3.20	215	0.002	2.65	219	0.009	2.70	215	0.007
Breeding frequency	2.56	218	0.011	2.38	214	0.018	1.79	218	0.074	1.82	214	0.070
Incubation period	0.16	90	0.880	0.61	90	0.540	0.50	90	0.616	0.61	90	0.541
Fledging period	0.93	78	0.357	0.52	78	0.605	1.25	78	0.216	1.66	78	0.101
Egg volume	2.11	220	0.036	1.68	215	0.094	0.13	220	0.896	0.53	215	0.595

old endemics and new invaders, respectively. Ar and Yom-Tov (1978) have shown that average *F*/*I* among altricial birds is 1, similar to that among the old endemics, but smaller than among the new invaders.

Some Australasian species such as bowerbirds, birds-of-paradise and lyrebirds have evolved a unique breeding system of display-site-defense promiscuity which might affect the results of the analysis. To test this, we repeated the analysis after omitting these species, and found that the results were the same as before.

Our data show that cooperative breeding is common in Australia, and reported for 32% of Australian passerines (81 out of 322 species), all of which are old endemics. Cooperative breeders in Australia have a significantly

Fig. 2 Phylogenetic tree for 233 Australian species compiled from Sibley and Ahlquist (1990). *Black branches* indicate species with cooperative breeding, *white brances* indicate non-cooperative species, and *stippled branches* represent ambiguity (branches where ancestry state cannot be determined). Clades no. 1 and 2 are indicated ▶

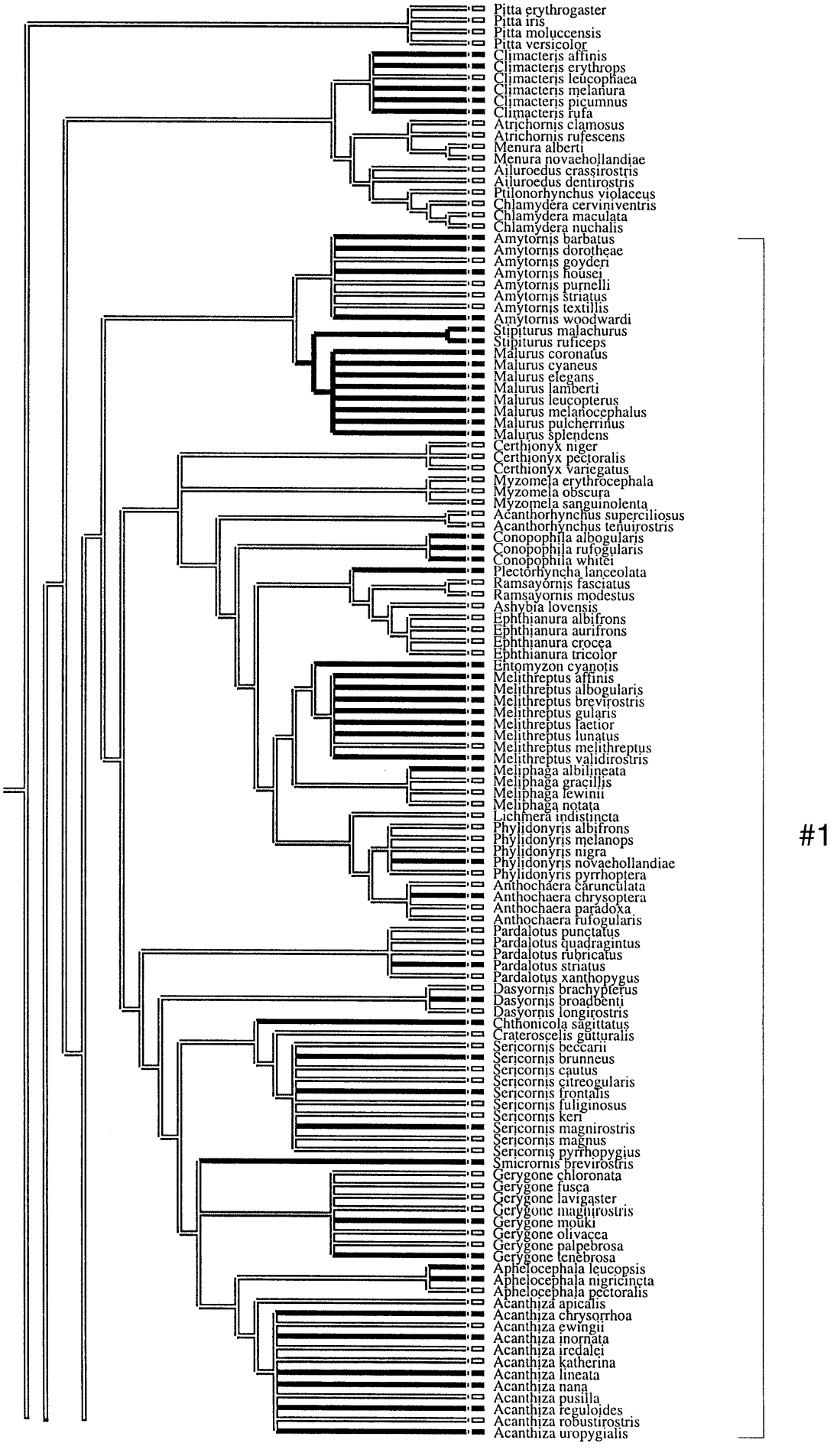
Pitta erythrogaster
Pitta iris
Pitta moluccensis
Pitta versicolor
Climacteris affinis
Climacteris erythrops
Climacteris leucophaea
Climacteris melanura
Climacteris picumnus
Climacteris rufa
Atrichornis clamosus
Atrichornis rufescens
Menura alberti
Menura novaehollandiae
Ailuroedus crassirostris
Ailuroedus dentirostris
Ptilonorhynchus violaceus
Chlamydera cerviniventris
Chlamydera maculata
Chlamydera nuchalis
Amytornis barbatus
Amytornis dorotheae
Amytornis goyderi
Amytornis housei
Amytornis purnelli
Amytornis striatus
Amytornis textillis
Amytornis woodwardi
Stipiturus malachurus
Stipiturus ruficeps
Malurus coronatus
Malurus cyaneus
Malurus elegans
Malurus lamberti
Malurus leucopterus
Malurus melanocephalus
Malurus pulcherrimus
Malurus splendens
Certhionyx niger
Certhionyx pectoralis
Certhionyx variegatus
Myzomela erythrocephala
Myzomela obscura
Myzomela sanguinolenta
Acanthorhynchus superciliosus
Acanthorhynchus tenuirostris
Conopophila albogularis
Conopophila rufogularis
Conopophila whitei
Plectorhyncha lanceolata
Ramsayornis fasciatus
Ramsayornis modestus
Ashbyia lovensis
Ephthianura albifrons
Ephthianura aurifrons
Ephthianura crocea
Ephthianura tricolor
Entomyzon cyanotis
Melithreptus affinis
Melithreptus albogularis
Melithreptus brevirostris
Melithreptus gularis
Melithreptus laetior
Melithreptus lunatus
Melithreptus melithreptus
Melithreptus validirostris
Meliphaga albilineata
Meliphaga gracillis
Meliphaga lewinii
Meliphaga notata
Lichmera indistincta
Phylidonyris albifrons
Phylidonyris melanops
Phylidonyris nigra
Phylidonyris novaehollandiae
Phylidonyris pyrrhoptera
Anthochaera carunculata
Anthochaera chrysoptera
Anthochaera paradoxa
Anthochaera rufogularis
Pardalotus punctatus
Pardalotus quadragintus
Pardalotus rubricatus
Pardalotus striatus
Pardalotus xanthopygus
Dasyornis brachypterus
Dasyornis broadbenti
Dasyornis longirostris
Chthonicola sagittatus
Crateroscelis gutturalis
Sericornis beccarii
Sericornis brunneus
Sericornis cautus
Sericornis citreogularis
Sericornis frontalis
Sericornis fuliginosus
Sericornis keri
Sericornis magnirostris
Sericornis magnus
Sericornis pyrrhopygius
Smicrornis brevirostris
Gerygone chloronata
Gerygone fusca
Gerygone lavigaster
Gerygone magnirostris
Gerygone mouki
Gerygone olivacea
Gerygone palpebrosa
Gerygone tenebrosa
Aphelocephala leucopsis
Aphelocephala nigricincta
Aphelocephala pectoralis
Acanthiza apicalis
Acanthiza chrysorrhoa
Acanthiza ewingii
Acanthiza inornata
Acanthiza iredalei
Acanthiza katherina
Acanthiza lineata
Acanthiza nana
Acanthiza pusilla
Acanthiza reguloides
Acanthiza robustirostris
Acanthiza uropygialis
#1

Fig. 2

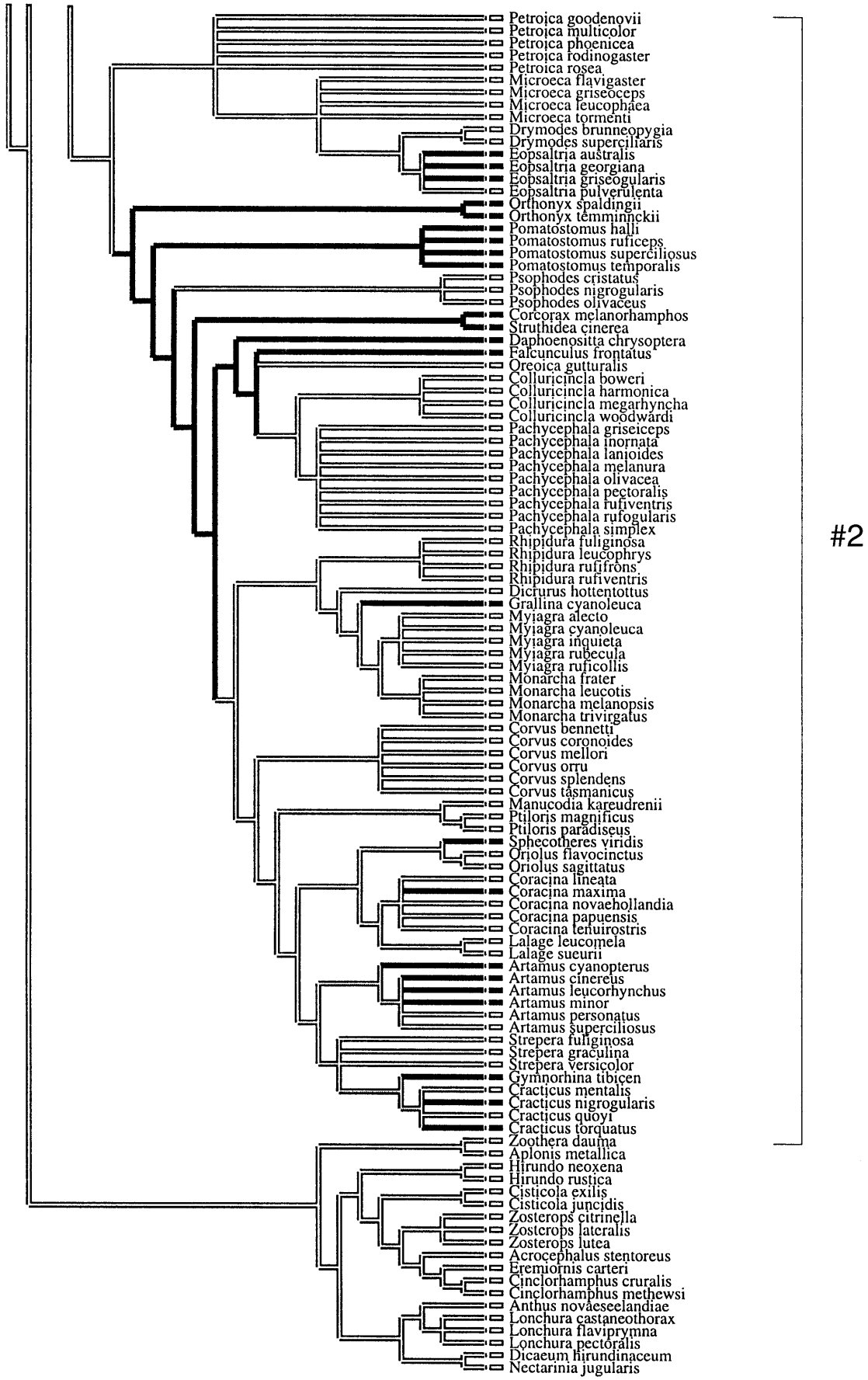
Petroica goodenovii
Petroica multicolor
Petroica phoenicea
Petroica rodinogaster
Petroica rosea
Microeca flavigaster
Microeca griseoceps
Microeca leucophaea
Microeca tormenti
Drymodes brunneopygia
Drymodes superciliaris
Eopsaltria australis
Eopsaltria georgiana
Eopsaltria griseogularis
Eopsaltria pulverulenta
Orthonyx spaldingii
Orthonyx temminnckii
Pomatostomus halli
Pomatostomus ruficeps
Pomatostomus superciliosus
Pomatostomus temporalis
Psophodes cristatus
Psophodes nigrogularis
Psophodes olivaceus
Corcorax melanorhamphos
Struthidea cinerea
Daphoenositta chrysoptera
Falcunculus frontatus
Oreoica gutturalis
Colluricincla boweri
Colluricincla harmonica
Colluricincla megarhyncha
Colluricincla woodwardi
Pachycephala griseiceps
Pachycephala inornata
Pachycephala lanioides
Pachycephala melanura
Pachycephala olivacea
Pachycephala pectoralis
Pachycephala rufiventris
Pachycephala rufogularis
Pachycephala simplex
Rhipidura fuliginosa
Rhipidura leucophrys
Rhipidura rufifrons
Rhipidura rufiventris
Dicrurus hottentottus
Grallina cyanoleuca
Myiagra alecto
Myiagra cyanoleuca
Myiagra inquieta
Myiagra rubecula
Myiagra ruficollis
Monarcha frater
Monarcha leucotis
Monarcha melanopsis
Monarcha trivirgatus
Corvus bennetti
Corvus coronoides
Corvus mellori
Corvus orru
Corvus splendens
Corvus tasmanicus
Manucodia kareudrenii
Ptiloris magnificus
Ptiloris paradiseus
Sphecotheres viridis
Oriolus flavocinctus
Oriolus sagittatus
Coracina lineata
Coracina maxima
Coracina novaehollandia
Coracina papuensis
Coracina tenuirostris
Lalage leucomela
Lalage sueurii
Artamus cyanopterus
Artamus cinereus
Artamus leucorhynchus
Artamus minor
Artamus personatus
Artamus superciliosus
Strepera fuliginosa
Strepera graculina
Strepera versicolor
Gymnorhina tibicen
Cracticus mentalis
Cracticus nigrogularis
Cracticus quoyi
Cracticus torquatus
Zoothera dauma
Aplonis metallica
Hirundo neoxena
Hirundo rustica
Cisticola exilis
Cisticola juncidis
Zosterops citrinella
Zosterops lateralis
Zosterops lutea
Acrocephalus stentoreus
Eremiornis carteri
Cinclorhamphus cruralis
Cinclorhamphus mathewsi
Anthus novaeseelandiae
Lonchura castaneothorax
Lonchura flaviprymna
Lonchura pectoralis
Dicaeum hirundinaceum
Nectarinia jugularis
#2

Fig. 2

longer breeding season than non-cooperative breeders, but this was the only significant difference between the groups in all examined life history parameters (Table 3). The mean difference (0.7 months) is 11.7% of the mean length of the breeding season of the cooperative breeders.

Figure 2 presents a reconstruction of the evolution of cooperative breeding in the Australian passerines we have examined. The analysis suggested that cooperative breeding has evolved independently six to ten times in clade no. 1 (containing the Maluridae, Pardalotidae, and the Meliphagidae; Fig. 2). In clade no. 2, only the Orthonychidae, Pomastostomidae, and Corcoracidae were consistent, with a common ancestor possessing the cooperative breeding trait. This trait has evolved independently in clade no. 2 at least four times (Fig. 2). However, many of the taxa we have classified as lacking cooperative breeding have never been studied. We have repeated the analysis, but this time we have classified any unstudied species as having cooperative breeding if other species in its genera were confirmed cooperative breeders. The outcome of this modification suggested that cooperative breeding was a trait in the ancestor of the clade no. 1, and that it has evolved independently at least twice in clade no. 2 (i.e., Campephagidae and Artamidae).

Discussion

The results of the present study indicate that small clutches and a high incidence of cooperative breeding are characteristic of the old endemics among the Australian passerines. This generalization does not apply to the new invaders, among whom clutch size is similar to passerines in the northern hemisphere, and cooperative breeding is absent, but they have a relatively long fledging period. We suggest that the differences in clutch size and fledging period between the old endemics and new invaders are different adaptive responses to local conditions in Australia. On the other hand, the high incidence of cooperative breeding may stem from a common Gondwanan ancestor of the old endemics, as claimed by Cockburn (1996). Cooperative breeders in Australia have a significantly longer breeding season than non-cooperative breeders (Table 3). Although Poiani and Jermiin (1994) showed that cooperative Corvida in Australia have a similar demography to the non-cooperative taxa, they claimed that matched-pairs analysis between cooperative and non-cooperative congeners showed that cooperative breeders tend to have a higher probability of rearing a second brood in the season. This trend, if general, may stem from the longer breeding season of cooperative breeders found by us, and adds to the advantage of breeding cooperatively in Australia.

The old endemics and new invaders differ in clutch size, but not in length of breeding season or laying frequency (Yom-Tov 1987; this study). Hence, if their fledging success and survival are similar, one would expect frequent population explosions or a continuous increase in populations of new invaders. However, neither phenomenon normally takes place, indicating a higher survival rate for old endemics. However, Yom-Tov et al. (1992) have shown that there is no difference in adult survival between the two groups.

The following hypothesis may explain why there are no population explosions of new invaders, and the difference in clutch size between the old endemics and new invaders to Australia. Several authors (Woinarski 1985; Ford et al. 1988; Yom-Tov 1987) have suggested that low seasonality and the small annual increment in food availability which enables breeding are the main factors determining the small clutch size of Australian passerines. Breeding under conditions of a small annual food increment is possible only when one or more of the following options are taken: (1) laying a small clutch, (2) breeding cooperatively, with several birds participating in feeding the young, (3) extending the fledging period. Our data show that the old endemics use the first two options, while the new invaders employ the third. The long fledging period of the new invaders may indicate difficulty in raising a large brood successfully, and suggests that survival of young birds is lower among new invaders. To date, there are no data to support this hypothesis, which future work on survival of young birds among old endemics and new invaders may provide. The old endemics among Australian rodents used the first and third options (Yom-Tov 1985). It is interesting to note that none of the introduced European passerines (and the three species of rodents – *Mus musculus*, *Rattus rattus*, and *R. norvegicus*) to Australia have any of the above adaptations to Australia, yet they still flourish there. However, most if not all these species are restricted to manmade habitats in Australia, and are not fully exposed to the natural conditions of this continent.

Finally, it is interesting to compare life history parameters between Australia and South America, another relatively isolated southern hemisphere continent. Like Australia, the passerine avifauna of temperate South America is also composed of two, phylogenetically different, groups – the Tyranni (suborder Detutro-Oscines) which evolved in South America after separated from the Old World portions of Gondwanaland during the Cretaceous period, about 80 million years ago, and the suborder Oscines, which evolved in parallel and invaded southern South America from the north. Yom-Tov et al. (1994) have shown that the clutch size of passerines in this region is significantly smaller than in the northern hemisphere, and that the older group (Deutro-Oscines) has a significantly smaller clutch size, similar to the situation in Australia.

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