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Examining Ashmole's hypothesis: are life-history parameters of resident passerines related to the proportion of migrants?

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ABSTRACT

Ashmole's hypothesis predicts that clutch size of birds is related to competition with migrants. This is because higher competition with migrants leads to greater winter mortality among residents, and the resultant lower competition in the breeding season enables the remaining birds to lay larger clutches. We examined the predictions of Ashmole's hypothesis by comparing the life-history parameters of passerines inhabiting Australia, Southern Africa and India, three regions where the proportion of migrants increases in the above order. Since the proportion of migrants is higher in open habitats (grassland and semi-desert) than in closed ones (forest and rainforest), we examined the predictions of Ashmole's hypothesis in both habitats after controlling for phylogeny. We found that body mass was positively correlated with the length of the breeding season, egg mass and the length of both incubation and fledging periods, but not with clutch size. Contrasts controlled for body mass showed that clutch size in both closed and open habitats was significantly larger in India than in both Australia and Southern Africa, as predicted by Ashmole's hypothesis. Furthermore, the reproductive effort (clutch size multiplied by egg mass) of genera inhabiting two or all three regions showed that it was significantly larger in India than in the other two regions, thus supporting Ashmole's hypothesis. The length of the breeding season in closed habitats was significantly different (Australia > South Africa > India) between the regions. We attribute the differences in clutch size to ecological factors, mainly the larger proportion of Palearctic migrants wintering in India. The differences in the length of the breeding season may be attributed to the different climates of the regions examined.

Keywords: Australia, breeding season, clutch size, India, passerines, Southern Africa, southern hemisphere.

INTRODUCTION

It has long been the impression of ornithologists that life-history parameters of tropical and southern hemisphere birds differ from those of their northern hemisphere counterparts (for a review, see Martin, 1996). Tropical and southern hemisphere birds are said to have smaller

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clutches (Moreau, 1944; Lack, 1968) and longer incubation and fledging periods (Martin, 1996) than northern hemisphere birds. These claims were recently examined by Geffen and Yom-Tov (1999), who confirmed that tropical and southern hemisphere passerines have smaller clutches; however, they refuted the claim that northern hemisphere and tropical passerines differ in length of incubation and fledging periods.

Clutch size may be related to other breeding parameters. Ricklefs (1980) claimed that clutch size is negatively related to the length of the breeding season. Another factor that may contribute to the small clutch size of southern hemisphere birds is the proportion of migrants in their avifauna. Ashmole (1961, 1963) pointed out that migrants reduce populations of residents through competition for winter resources, and that surviving residents have access to more resources during the breeding season and lay larger clutches (Ricklefs, 1980; Yom-Tov, 1994).

Many species of Palearctic passerines spend their winter in southern continents, but their proportion differs between the regions. The number of wintering species in a particular area depends on several factors, including the distance from the breeding ground and the availability of food and water. Hence, many Palearctic species winter in India, but almost none winter in Australia. The number of Palearctic species wintering in Africa declines from north to south, being the smallest in Southern Africa (Moreau, 1972). Wintering passerines tend to inhabit open habitats, such as grassland, and to avoid closed ones, particularly rainforest.

Australia occupies a land area of about 7.6 million km^2 and ranges between 11° and 44° S. The continent is of low relief, with only a negligible area higher than 1000 m. Australian rainfall comes from two weather systems, a summer monsoonal system and a winter Antarctic system that comes from the south (Keast, 1981a). The centre of the continent lies towards the limits of penetration of both systems, either or both of which can fail in a particular year. As a result, most of Australia is arid or semi-arid and the variability of rainfall is greater than the world average (Leeper, 1970). Although most of Australia is arid or semi-arid, it contains many habitats, including rainforests, open forests, woodlands, heaths, grasslands and shrublands (Specht, 1981). Australia is a part of the Australasian zoogeographical region, which also includes Papua New Guinea and other islands in the Indonesian archipelago.

The Australian avifauna is composed of three components: birds of Australasian origin (termed 'old endemics'), which evolved in Australia and Papua New Guinea in isolation when it separated from Antarctica about 40 million years ago; birds of Afro-Eurasian origin (called 'new invaders'), which migrated to Australia from the north at various times; and species introduced by Europeans during the last two centuries (Keast, 1981b,c). 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). About 2% of the Australian avifauna are migrants (Yom-Tov, 1995). Blakers *et al.* (1984) recognized four bioclimatic zones on the basis of a growth response of dominant plants to temperature. These zones closely parallel the faunal divisions of early avian zoogeographers: the Bassian in the temperate south-east and south-west of the continent, the Eyrean in the arid centre, the Torresian in the monsoonal north and the Irian in the tropical region of Cape York peninsula. The breeding season of birds in Australia is known to differ according to their distribution, being shortest in the highly seasonal Torresian zone and in Tasmania, and longest for birds breeding in both the Eyrean and Bassian zones (Thomas, 1974; Yom-Tov, 1987).

The Southern African region is defined, for our purposes here, as the mainland region of the African continent south of the Cunene/Zambezi rivers. It includes Namibia, South Africa, Botswana, Zimbabwe and that part of Mozambique which lies south of the Zambezi River, an area of about 3.7 million km^2, which ranges between latitudes 27° and 35° S. The climate ranges from extreme desert and semi-desert, mainly in the west, through Mediterranean in the south and a warmer, humid climate in the east towards the Indian Ocean, to montane in the Natal Drakensberg and the mountains of Lesotho. The main habitats (comprising about 40%) are desert (Namibia) or semi-desert (Kalahari and Karoo), while the rest are grasslands, savannas, fynbos and woodlands. The avifauna is composed of about 900 species, about 500 of which are passerines. The overall percentage of Palearctic migrants among these birds is 10%, but it declines from north to south. Until about 7 million years ago, there was a connection between the forests of Africa and Asia, hence the present affinities of the avifaunas of these two regions (Snow, 1980).

The Indian subcontinent, including India, Pakistan, Bangladesh and the islands of Sri Lanka, the Andamans, Nicobar and Lakshadweep, occupies an area of about 4.3 million km^2 and ranges between latitudes 6° and 35° N. The most significant climatic event in the Indian subcontinent is the appearance of the monsoon rains, beginning in June and continuing until September. These rains contribute most of the precipitation over most of India. The wide geographical and topographical variability of the Indian subcontinent, together with the effect of the monsoonal rains, create a great variety of habitats, such as tropical wet and dry rainforest, savanna, grasslands, semi-desert, desert and high altitude habitats. The Indian subcontinent is a part of the zoogeographical Oriental region, which shares several bird families with the Australasian region. However, most Indian passerines belong to families whose main diversity is reached either in the Palearctic or in tropical Africa (Ali, 1985). Its avifauna comprises about 1000 species, of which about half are passerines (Ali and Ripley, 1968–74). About 20% of Indian bird species are migrants (Y. Yom-Tov, unpublished data).

Ashmole's (1961, 1963) hypothesis predicts that clutch size is positively related to the proportion of migrants in an avifauna. The above differences in the proportions of migrants between the three regions and habitats provide an opportunity to test Ahmole's hypothesis. We predicted that clutch size in India would be larger than in the other two regions. Following Ricklefs (1980), we also predicted that there would be a negative association between clutch size and the length of the breeding season.

MATERIALS AND METHODS

Data

Data on body mass, clutch size, egg volume and breeding season were gathered for the passerines of the Indian subcontinent from Ali and Ripley (1968–74), which provides data for most species breeding in this area. For Southern Africa we used Maclean (1985), Keith *et al.* (1992) and Urban *et al.* (1997). For Australian passerines, we used data mainly from the Appendix in Yom-Tov (1987); this was supplemented with data on body mass from Dunning (1993) and with data on clutch size from the *Reader's Digest Complete Book of Australian Birds* (1983) and Pizzey (1980). All species introduced into Australia and Southern Africa by Europeans during the last two centuries were excluded from the analysis.

Body mass

When available we used female mass. If the above sources did not provide female mass, we used the data available (mass of males or unspecified sex). This approach is justified because sexual dimorphism among passerines is generally small (Campbell and Lack, 1985).

Clutch size, breeding season, incubation period, fledging period and egg volume

The above sources provide data on clutch size, egg size, breeding season, incubation and fledging periods. 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 egg; that is, if a clutch size was said to be 2, sometimes 1, it received a value of 1.7. Similarly, a clutch of 2, sometimes 3, is scored 2.3. The data on egg length and width were supplemented by Schönwetter (1967–83). 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). For genera that are represented in more than one region, we also compared reproductive effort, defined as clutch size multiplied by egg volume.

Habitat

Using the above regional sources – as well as Grimmet *et al.* (1998) for the Indian subcontinent – we assigned every species to one of the following habitats: aquatic (living near water, reedbeds, etc.), high mountains, desert, grassland (any other open habitat, including open savanna), forest and rainforest. Each species was also categorized as resident, summer breeder, wintering or vagrant (or rare). The few species that have both resident and wintering populations were not included in the analysis. Species categorized as aquatic and high mountain (there were very few of these) were not included in the analysis because they were considered too specialized. We then combined species categorized as grassland and desert species into 'open' habitat, and those categorized as forest and rainforest into 'closed' habitat.

Statistical analysis

We examined regional changes in egg mass, clutch size, breeding season, incubation and fledging periods of passerines. We examined regional differences between Australia, Southern Africa and India in each of the five variables using *t*-tests on log-transformed data. Logarithmic transformation of size data fits the assumption that different lineages are equally likely to go through the same proportional change in scale. In the next step, we removed the effect of body mass before testing for regional differences by using residuals from a regression of each of the five variables on body mass. Last, to control for the effect of phylogeny, we used the CAIC program (Purvis and Rambaut, 1995), which implements the independent contrasts method (Felsenstein, 1985). The methods implemented in the CAIC program work best when the variables used are continuous or categorical (preferably dichotomous). Polytomies (nodes with more than two daughter branches) that express ignorance of the true branching structure are treated in CAIC according to Pagel (1992).

A dendrogram (topologies and branch lengths) based on DNA–DNA hybridizations, provided by Sibley and Ahlquist (1990: 856–869), was used to determine phylogenetic relationships among species. Species not mentioned or specified (represented only by their genus) in Sibley and Ahlquist's (1990) dendrogram 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 branch lengths in CAIC are used as a measure of the expected variance, which allows standardization of the contrasts. Contrasts between distant species will have higher expected variance (i.e. branch lengths) than contrasts between sister taxa. Furthermore, simulation studies have shown that the independent contrasts method is valid even with very inaccurate branch lengths (Martins and Garland, 1991). Because of the relative insensitivity of the contrasts method to the distance between taxa, the branch length data from Sibley and Ahlquist (1990) is a reasonable measure of the expected variance component between taxons.

For each group of birds we examined the relationship between: (1) body mass (independent variable) and five other dependent variables (egg mass, clutch size, breeding season, incubation period and fledging period) by linear regression, and (2) contrasts of body mass (independent variable) and the contrasts of the other five dependent variables by linear regression through the origin. We performed these initial steps to examine the effect of body mass on other variables before and after the phylogenetic component was removed. All analyses were performed on log-transformed data.

For our regional comparisons, we assigned a value of 0 to all species in one region and a value of 1 to all species in the other region, thus creating a categorical character with only two states. Using the Brunch option in CAIC, we compared all four dependent variables between regions. The null hypothesis is that evolution in the dependent variable (e.g. egg mass) is not linked to region; thus we should expect half the contrasts in the dependent variable to be positive and half to be negative, and the mean value of the contrasts to be zero. We tested the null hypothesis using a *t*-test on the mean of the contrasts (Purvis and Rambaut, 1995). A mean significantly greater than 0 indicates that, in the region assigned as 1, the values of the dependent variable are larger, whereas a mean significantly below 0 indicates larger values of the dependent variable in the region assigned as 0.

Several genera are represented in all three regions and some in two of them. We performed paired *t*-tests on the means of all breeding parameters of the genera that inhabit two or three regions to check if the above results occur also when carried out on common genera.

RESULTS

Proportion of wintering species

The proportion of wintering passerines relative to breeding birds in open habitats was 0% ($n = 72$), 5.3% ($n = 140$) and 30.8% ($n = 191$) for Australia, Southern Africa and India, respectively; these differences were highly significant. The proportion of wintering passerines relative to breeding birds in close habitats was 0% ($n = 199$), 3.5% ($n = 209$) and 3.6% ($n = 372$) in Australia, Southern Africa and India, respectively. In close habitats, the differences in these proportions were significant between Australia and the other two

regions, but not between Southern Africa and India ($\chi^2 = 7.04$, d.f. = 2, $P = 0.03$). The proportions of wintering to breeding species in the open habitat were significantly different between all three continents ($\chi^2 = 37.75$, d.f. = 2, $P < 0.001$).

Life-history parameters

In the first stage of the analysis, we found that body mass was positively correlated with the length of the breeding season, egg mass and the length of both incubation and fledging periods, but not with clutch size (Table 1). Hence, for all comparisons of life-history parameters, we also controlled for body mass. The differences in life-history parameters between the three regions by closed and open habitat are presented in Tables 2 and 3.

Contrasts analyses show that clutch size was significantly larger in India than in Australia and Southern Africa in both open and closed habitats, but there was no difference in clutch size in Australia and Southern Africa. The length of the breeding season in closed habitats was significantly different between the regions, but not in open habitats. For most other parameters, there were no significant differences between the regions. Only two other significant differences were detected in other breeding parameters: fledging period was longer among passerines inhabiting open habitats in Southern Africa than in India, and incubation period was longer in closed habitats in Australia than in India. We cannot provide an explanation for these latter differences, but note that sample size for the incubation period was very small (six contrasts). Furthermore, applying sequential Bonferroni correction for multiple comparisons rendered all tests with P-values >0.0025 insignificant. Taking this conservative approach, the only valid differences among continents are in clutch size.

For both closed and open habitats, mean clutch size for the whole sample was smallest in Australia, intermediate in Southern Africa and largest in India (open habitat: Australia 2.79 ± 0.66, $n = 50$; Southern Africa 3.07 ± 0.53, $n = 51$; India 4.09 ± 0.98, $n = 46$; closed habitat: Australia 2.53 ± 0.76, $n = 149$; Southern Africa 2.69 ± 0.55, $n = 112$; India 3.5 ± 1.06, $n = 106$) (mean ± standard deviation).

In our sample, 12 genera inhabit all three regions (*Acrocephalus*, *Anthus*, *Cisticola*, *Coracina*, *Corvus*, *Dicrurus*, *Hirundo*, *Mirafra*, *Nectarinia*, *Oriolus*, *Pitta* and *Zosterops*); others inhabit two of the three regions. We performed paired *t*-tests on the common genera between combinations of two regions to determine if results similar to the above would be found for these common genera. The results of these tests are presented in Table 4. They show that mean clutch size was largest in India (3.549 ± 0.951, $n = 53$), slightly smaller in Australia (3.128 ± 0.894, $n = 23$) and considerably smaller in Southern Africa (2.788 ± 0.573, $n = 45$). The difference in clutch size (controlled for body mass) between India and Southern Africa was significant ($P < 0.0001$), but that between India and Australia only approached significance ($P = 0.056$). The largest differences between India and Southern Africa were observed in the genera *Pitta*, *Coracina*, *Seicercus* and *Oenanthe*, between India and Australia in the genera *Acrocephalus*, *Coracina*, *Megalurus* and *Monarcha*, and between Australia and Southern Africa in the genera *Pitta*, *Hirundo*, *Cisticola* and *Coracina*. However, contrary to the results in the contrasts analysis, the difference in clutch size between Australia and Southern Africa was also significant. The other two significant differences in the contrasts analysis, in incubation and fledging periods (for which we cannot provide an explanation), remained significant in the paired *t*-tests. In addition, this analysis showed

Table 1. Regression coefficients of body mass (independent variable) on five reproduction-related dependent variables (breeding season, clutch size, egg mass, incubation period and fledging period) in 386 Indo-Australian passerines, 425 Southern African-Australian passerines and 464 Indo-Southern African passerines

	Raw data						Contrasts				
	Slope	Intercept	*r*	*F*	d.f.	*P*	Slope	*r*	*F*	d.f.	*P*
India and Australia											
Breeding season	−0.053	0.753	0.168	10.70	367	0.001	0.069	0.147	4.13	187	0.044
Clutch size	0.002	0.458	0.006	0.01	373	0.907	−0.033	0.103	2.02	187	0.157
Egg mass	0.712	−0.546	0.962	4504.99	365	<0.001	0.630	0.909	892.74	187	<0.001
Incubation period	0.103	1.030	0.551	63.36	145	<0.001	0.094	0.443	26.32	108	<0.001
Fledging period	0.198	0.932	0.702	120.70	124	<0.001	0.291	0.637	65.53	96	<0.001
Southern Africa and Australia											
Breeding season	−0.032	0.737	0.091	3.37	406	0.067	0.080	0.159	5.23	204	0.023
Clutch size	−0.003	0.423	0.010	0.04	413	0.836	0.002	0.005	0.01	206	0.937
Egg mass	0.716	−0.562	0.952	3865.93	401	<0.001	0.628	0.900	868.46	205	<0.001
Incubation period	0.094	1.047	0.488	52.22	181	<0.001	0.070	0.315	13.33	122	<0.001
Fledging period	0.196	0.947	0.641	124.03	179	<0.001	0.196	0.539	49.19	121	<0.001
Southern Africa and India											
Breeding season	0.008	0.626	0.019	0.12	357	0.723	0.100	0.185	5.68	162	0.018
Clutch size	0.024	0.458	0.079	2.24	358	0.135	−0.032	0.092	1.40	163	0.239
Egg mass	0.733	−0.624	0.973	6186.66	354	<0.001	0.654	0.953	1579.66	161	<0.001
Incubation period	0.066	1.058	0.434	34.99	152	<0.001	0.053	0.274	7.89	98	0.006
Fledging period	0.163	0.990	0.544	63.79	153	<0.001	0.297	0.654	75.34	102	<0.001

Note: Linear regressions were performed on the raw data (log-transformed) and on the independent contrasts (regression through the origin).

Table 2. Differences in five reproduction-related variables (breeding season, clutch size, egg mass, incubation period and fledging period) between Indian, Southern African and Australian birds in closed and open habitats

	Closed habitats (forests)								Open habitats (deserts and grasslands)							
	Contrasts				Contrasts controlled for body mass				Contrasts				Contrasts controlled for body mass			
	Mean	*t*	d.f.	*P*	Mean	*t*	d.f.	*P*	Mean	*t*	d.f.	*P*	Mean	*t*	d.f.	*P*
India and Australia																
Breeding season	−0.013	2.53	17	0.021	−0.014	2.56	17	0.020	−0.007	0.80	10	0.443	−0.008	0.86	10	0.413
Clutch size	0.008	2.60	17	0.019	0.008	2.59	17	0.019	0.013	6.37	10	<0.001	0.013	6.39	10	<0.001
Egg mass	−0.009	1.83	17	0.086	−0.003	0.88	17	0.392	−0.007	1.28	10	0.231	−0.003	1.37	10	0.201
Incubation period	−0.005	2.78	6	0.032	−0.005	4.00	6	0.007	−0.003	0.92	6	0.395	−0.002	0.93	6	0.370
Fledging period	−0.006	2.09	7	0.075	−0.006	2.30	7	0.055	−0.011	0.98	6	0.366	−0.009	1.08	6	0.320
Southern Africa and Australia																
Breeding season	−0.009	2.71	16	0.015	−0.009	2.71	16	0.015	0.004	0.87	9	0.780	0.006	0.53	9	0.606
Clutch size	−0.004	2.06	16	0.056	−0.004	2.09	16	0.053	−0.004	0.89	9	0.398	−0.005	1.12	9	0.292
Egg mass	−0.006	1.02	15	0.322	−0.002	0.67	15	0.511	0.008	1.18	9	0.269	−0.004	0.76	9	0.466
Incubation period	0.002	0.41	5	0.697	0.001	0.35	5	0.743	−0.001	0.82	6	0.444	−0.002	1.30	6	0.240
Fledging period	0.004	0.89	8	0.402	0.003	0.72	8	0.489	0.005	0.93	6	0.388	0.004	1.13	6	0.302
Southern Africa and India																
Breeding season	0.006	2.12	33	0.042	0.006	2.12	33	0.042	0.010	1.43	22	0.166	0.011	1.67	22	0.109
Clutch size	−0.013	5.69	33	<0.001	−0.013	5.71	33	<0.001	−0.017	5.28	22	<0.001	−0.018	5.47	22	<0.001
Egg mass	0.002	0.53	32	0.530	0.000	0.04	32	0.969	0.008	1.43	22	0.166	−0.002	1.00	22	0.327
Incubation period	0.001	1.02	18	0.321	0.001	1.07	18	0.298	0.002	1.21	12	0.251	0.001	0.67	12	0.517
Fledging period	0.005	1.60	17	0.129	0.004	1.30	17	0.212	0.012	2.74	13	0.017	0.010	2.49	13	0.027

Note: *t*-tests were performed on independent contrasts and on contrasts controlled for body mass (see text for details). A mean contrast significantly greater than 0 in the first comparison indicates that, in India the values of the dependent variable are larger, whereas a mean contrast significantly below 0 indicates larger values of the dependent variable in Australia. Correspondingly, a mean greater than 0 in the second and third comparisons indicates larger values for Southern Africa.

Table 3. Comparison of clutch size, length of breeding season, incubation and fledging periods, and egg volume of Indian, Southern African and Australian passerines in closed and open habitats (mean ± standard deviation)

	India		Southern Africa		Australia	
	mean ± *s*	*n*	mean ± *s*	*n*	mean ± *s*	*n*
Closed habitats (forests)						
Clutch size (*n*)	3.46 ± 1.04	100	2.69 ± 0.55	112	2.54 ± 0.76	151
Breeding season (months)	4.08 ± 1.44	100	4.53 ± 1.91	112	5.53 ± 1.34	148
Incubation (days)	14.36 ± 2.31	29	14.88 ± 2.54	48	16.66 ± 5.31	67
Fledging (days)	18.00 ± 7.05	24	17.29 ± 4.94	54	17.30 ± 6.85	57
Egg volume (cm^3)	3.94 ± 3.79	100	3.13 ± 2.45	108	5.24 ± 6.94	146
Open habitats (deserts and grasslands)						
Clutch size (*n*)	4.07 ± 0.98	45	3.08 ± 0.56	53	2.76 ± 0.66	52
Breeding season (months)	5.38 ± 2.66	45	5.35 ± 2.01	54	5.25 ± 1.13	50
Incubation (days)	13.69 ± 1.88	24	14.08 ± 2.10	28	14.35 ± 2.87	17
Fledging (days)	15.74 ± 4.72	21	18.52 ± 5.90	29	16.00 ± 8.17	15
Egg volume (cm^3)	3.21 ± 3.11	45	3.33 ± 4.77	54	3.17 ± 3.16	49

that there are significant differences in egg volume between Australia and the other two regions (Australia 1.6 ± 1.1, $n = 20$; India 2.8 ± 2.5, $n = 53$; Southern Africa 3.0 ± 3.0, $n = 45$) (Table 4). The largest differences in egg mass between India and Australia were observed in the genera *Mirafra*, *Corvus*, *Artamus* and *Pitta*, and between Australia and Southern Africa in *Mirafra*, *Corvus*, *Pitta* and *Acrocephalus*. Reproductive effort (clutch size multiplied by egg volume, controlled for body mass) in these species was highest in India (10.3 ± 11.8, $n = 49$), less in Southern Africa (9.1 ± 12.7, $n = 41$) and considerably less in Australia (4.8 ± 3.8, $n = 20$) (Table 4).

As noted above, the length of the breeding season in closed habitats differed significantly between the regions and was longest in Australia, intermediate in Southern Africa and shortest in India (Table 3). No significant differences were found in open habitats (Table 3). The length of the breeding season also differed significantly among the common genera between any two regions: 5.6 ± 1.3 ($n = 19$), 4.6 ± 1.6 ($n = 47$) and 4.7 ± 2.0 ($n = 41$) for Australia, India and Southern Africa, respectively.

Clutch size was significantly associated with the length of the breeding season in Southern Africa only (linear regression, raw data: $r = 0.14$, $F_{190} = 4.1$, $P = 0.04$, slope = 0.29; raw data controlled for body mass: $r = 0.18$, $F_{188} = 6.0$, $P = 0.01$, slope = 0.36). However, analysis of contrasts showed that this association was fully accounted for by phylogeny (linear regression through the origin, contrasts: $r = 0.07$, $F_{104} = 0.6$, $P = 0.46$; contrasts controlled for body size: $r = 0.12$, $F_{103} = 1.4$, $P = 0.23$). We repeated this analysis by splitting the data for each continent into open and closed habitats. No significant relationship between breeding season and clutch size was detected ($P > 0.2$ and number of contrasts ≥34 in all comparisons). In summary, after controlling for phylogeny, habitat type and body mass, we detected no significant association between clutch size and breeding season within any region.

Table 4. Results of paired *t*-tests between continental genera means in six breeding parameters (clutch size, breeding season, incubation period, fledging period, egg volume and reproductive effort)

	Raw data			Data controlled for body size		
	t	d.f.	*P*	*t*	d.f.	*P*
Australia and India						
Clutch size	1.94	21	0.066	2.02	21	0.056
Breeding season	2.11	18	0.049	2.13	18	0.047
Incubation period	2.98	8	0.018	2.33	7	0.052
Fledging period	1.91	6	0.105	1.45	5	0.206
Egg volume	6.89	19	<0.001	9.06	19	<0.001
Reproductive effort	7.22	19	<0.001	9.21	19	<0.001
Australia and Southern Africa						
Clutch size	4.33	13	<0.001	4.93	12	<0.001
Breeding season	2.39	12	0.034	1.98	11	0.073
Incubation period	0.07	4	0.948	0.22	3	0.836
Fledging period	1.13	4	0.321	0.98	3	0.399
Egg volume	4.24	11	0.001	4.22	10	0.002
Reproductive effort	3.30	11	0.007	3.12	10	0.011
India and Southern Africa						
Clutch size	8.41	43	<0.001	8.56	37	<0.001
Breeding season	0.06	40	0.949	0.83	34	0.413
Incubation period	1.94	27	0.062	1.20	22	0.242
Fledging period	2.76	26	0.010	3.84	22	<0.001
Egg volume	2.01	44	0.051	0.50	37	0.622
Reproductive effort	4.66	40	<0.001	6.21	34	<0.001

Note: The species that were introduced into Australia and Southern Africa were excluded from the analysis (*Acridoteres tristis*, *Passer domesticus*, *Pycnonotus*, *Sturnus vulgaris* and *Turdus merula* for both regions and *Alauda arvensis* and *Pycnonotus jocosus* for Australia).

DISCUSSION

Clutch size

Ashmole (1961, 1963) claimed that migrants reduce populations of residents through competition for winter resources, and that surviving residents have access to more resources during the breeding season and lay larger clutches (Ricklefs, 1980; Yom-Tov, 1994). The proportion of wintering species of the local avifauna declines with increasing distance from the breeding grounds of migrants. Hence, according to Ashmole's hypothesis, among the three regions examined here, clutch size should be largest in India.

We found that clutch size in both open and closed habitats was significantly larger in India than in Southern Africa and Australia. Furthermore, clutch size in each of the two habitats increased in relation to the proportion of wintering bird species in it, from Australia through Southern Africa to India. In addition, among genera that inhabit more than one region, clutch size and egg volume, as well as reproductive effort, were larger in

India than in the other two regions (although the difference in clutch size between India and Australia was on the verge of significance). All the above results provide strong support for the predictions of Ashmole's hypothesis. However, Martin *et al.* (2000) have shown that food abundance does not differ between Argentinean and North American passerines. This indicates that the mechanism determining the smaller clutch size among southern hemisphere passerines is not food abundance.

Finally, Ricklefs (1980: table 1) claimed that there is a worldwide negative association between clutch size and the length of the breeding season. Our results do not show such a relationship in any of the three regions studied here.

Length of the breeding season

Lack (1968) suggested that the breeding season of birds coincides with the period of maximum food availability for rearing young. In all three regions studied here, the growing season of plants is related to seasonal rains. Pramod and Yom-Tov (1999) have shown that the breeding season of Indian passerines is strongly related to a single climatological event, namely the monsoon, and usually peaks in May to June, a month before the arrival of the monsoon rains, so that the peak food demand of chicks coincides with the arrival of the monsoon. That breeding season was significantly longer in Australian closed habitats is apparently a result of the difference in climate between the three regions. Rains in Australia are caused by either the summer monsoon, which comes from the north, or by winter Antarctic depressions from the south. In large areas of Australia (but rarely in the desert and other open habitats), rains may fall both in winter and summer, resulting in a longer growing season of plants and a longer breeding season of birds in Australia in relation to India.

In summary, passerines inhabiting the Indian subcontinent tend to have a larger clutch size than their Australian and Southern African counterparts; we attribute this to the small proportion of migrants in these two southern temperate regions. The longer breeding season in Australia than in India is attributed to the fact that, in large areas of Australia, rains may fall both in winter and summer, resulting in a longer growing season of plants and a longer breeding season of birds.

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