

CLUTCH SIZE IN PASSERINES OF SOUTHERN SOUTH AMERICA¹

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Abstract. Clutch size of the passerines of southern South America was studied by comparing data taken from the literature for 331 species (177 genera), which breed in Chile, Argentina, Uruguay, and southern Brazil. Mean overall clutch size was 2.98 eggs, appreciably smaller than clutch size of passerines at similar latitudes in the northern hemisphere.

There was a highly significant difference between mean clutch size of the two sub-orders represented in the study area, with the Deutero-Oscines having on average smaller clutches (2.73) than the Oscines (3.32). This difference between the two sub-orders was maintained in each of the five zoogeographical regions of the study area. There were also significant differences in clutch size between the five main zoogeographical regions: overall mean clutch size was smallest in the Amazonian region (2.67) and largest in the Chaco (3.29). Deutero-Oscines eggs were proportionally larger than those of Oscines (14% and 11% of body mass, respectively).

There was no correlation between clutch size and body mass, nor was clutch size related to either nest type or migration. There is no evidence for latitudinal gradient in clutch size in the area studied.

Key words: Clutch size; Passeriformes; South America.

INTRODUCTION

Clutch size varies both between and within species, and the reasons for these variations have been the subject of many studies. Clutch size is constrained by several factors, which can be grouped into two main categories—ecological and phylogenetic or taxonomic (Klomp 1970; Lack 1947, 1968; Perrins and Birkhead 1983). The most commonly discussed factors in the first category are latitude and habitat, while relatively little has been done concerning the connection between phylogeny and clutch size.

The trend of increase in clutch size of passerines with latitude is one of the most striking variations between and within species of birds, and is especially marked in multibrooded passerines (Perrins and Birkhead 1983, Murray 1985). Clutches of tropical passerines tend to have two to three eggs (Moreau 1944, Skutch 1985), those breeding in middle latitudes laying four or five eggs, and those in the Arctic five to seven (Ricklefs 1969). This trend was studied extensively in the northern hemisphere, where it was shown to occur in both the Old (Lack 1968) and New (Cody 1971) worlds and Klomp (1970) claimed that

clutch size increases by as much as one egg per 6–10° latitude. Information about the occurrence of this phenomenon in the southern hemisphere is scarce, but Moreau (1944) showed that clutch sizes of populations in South Africa average less than one egg more than those of populations in equatorial Africa, about 30° to the north. Similarly, Yom-Tov (1987) has shown that a very weak but significant trend exists in eastern Australia, where mean clutch size of passerines increases by about 0.8 egg over 30°. Hence, it seems that although a latitudinal trend in clutch size exists in both northern and southern hemispheres, it is much more marked in the northern hemisphere, where clutch size increases at a much steeper rate. Clutch size is also related to habitat: within the tropics, clutches tend to be larger in savanna and grassland than in the rain forest (Lack and Moreau 1965), and in temperate regions clutches of great tits are larger in deciduous woodland than in pine forests (Klomp 1970), and blackbirds lay larger clutches in rural than in urban sites (Snow 1958). Other ecological factors such as population density (Perrins 1965) and type of nest (Klomp 1970) have also been shown to influence clutch size.

Several hypotheses have been suggested to explain the latitudinal trend and habitat type influence (herein termed as “ecology”) on clutch

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size. Murray (1985) distinguished between two alternative general hypotheses regarding the evolution of clutch size, per se. The view developed by Lack (1947, 1968) and his followers (Ashmole 1961, Cody 1966, Ricklefs 1980) states that birds reproduce up to the maximum energy that the parents can devote to laying eggs and rearing the young. Excess reproduction is eliminated by subsequent density-dependent mortality. A second group of views comprising the ideas often referred to as "adjusted reproduction," according to which the clutch size is adjusted to the mortality rate of the species, with those having long life expectancies also having small clutches and vice versa. There is, however, little agreement on how this adjustment evolves (Stresemann 1927-1934, Rensch 1938, Skutch 1969, Wynne-Edwards 1962, Murray 1985).

Although the single most important factor producing variation in clutch size between species is their ecology (i.e., food availability and predation; Perrins and Birkhead 1983), there are major differences in clutch size between taxonomic groups. Lack (1968) noted that some orders have a typical clutch size which is common to most of their species. For example, Procellariiformes lay only one egg, Columbiformes mostly two. The songbirds (Passeriformes) have a variable clutch size, and relatively little research has been carried out on the effect of phylogeny on clutch size in this group. However, even within this order some families have larger clutches than others. For example, among the Australian passerines, the "old endemics" families (i.e., Meliphagidae, Maluridae and Acanthizidae) have clutches of 2-3 eggs, while the "new invaders" (i.e., Hirundinidae, Ploceidae and Corvidae) lay 3-6 eggs (Yom-Tov 1987). Hence, phylogenetic differences might also be important in determining clutch size.

Most studies on variation in clutch size have been carried out in the Northern Hemisphere (for review, see Klomp 1970) and comparisons have been carried out between these regions and the tropics (Skutch 1985). Little has been done on this subject in the Southern Hemisphere (but see Moreau 1944 and Yom-Tov 1987), and there is no study of clutch size in mid-latitudes in South America. We studied the clutch size of passerines breeding in the southern cone of South America, to determine whether the clutch size of these birds was small, like those in other two southern continents. We try to relate our results to both

phylogeny and ecology. However, because there are almost no published data on clutch size in relation to latitude in this vast region, we studied clutch size in relation to habitat type, which probably has a major effect on the ecology of the birds. Clutch size is known to be affected by type of nest (Perrins and Birkhead 1983), and we examined this as well as our hypothesis that migratory passerines should have larger clutches than residents.

More than 460 species (about 240 genera) of passerine birds belonging to 25 families breed in southern South America. Eight of these (Dendrocolaptidae, Furnariidae, Formicariidae, Rhinocryptidae, Cotingidae, Pipridae, Tyrannidae and Phytotomidae) belong to the infraorder Tyranni (Sibley and Ahlquist 1985) of the suborder Deutero-Oscines (Voous 1977), and the rest belong to the suborder Oscines (Passeres). The Tyranni evolved in South America after it was separated from the Old World portions of Gondwanaland during the Cretaceous period, about 80 million years ago. The Oscines evolved in parallel. Some groups (i.e., Emberizidae, Icteridae, Parulidae) in the New World, either in South America (i.e., Thraupidae, Icteridae, Vireonidae) or North America (i.e., Emberizidae), while others (i.e., Hirundinidae, Corvidae, Cinclidae, Turdidae) evolved mainly in the Old World and dispersed to North America and then South America (Sibley and Ahlquist 1990).

Our study area includes Chile except for the Tarapaca region in the tropical north, Argentina, Uruguay, and Rio Grande de Sul, the southeast province of Brazil, and excluding all oceanic islands. This region (about 3.95 million sq. km) stretches about 4,000 kms between 22°S-56°S. We have divided it into five main zoogeographical regions, namely the Amazonian, Chaco, Andean, Patagonian, and Araucanian (Cabrera and Willink 1980, Narosky and Yzurieta 1989), which occupy approximately 7%, 54%, 14%, 14% and 11% of the total area, respectively. The Amazonian region occupies the northern half of Rio Grande de Sul and two small areas of north eastern and north western Argentina and comprises subtropical forest; the Chaco region comprises subtropical deciduous xerophytic woodland, scrub and grasslands covering central Chile, most of lowland north and central Argentina, all of Uruguay and the southern half of Rio Grande de Sul; the Andean region covers the Andes of Argentina and Chile from latitude 36°S to the

north, including the Puna and the lowlands of northern Chile, mostly subtropical to temperate deserts, xeric scrub and montane grasslands. The Patagonian region comprises the cold scrub and grass steppes of southern Argentina and Chile. The Araucanian region occupies the temperate and cold forests of southern Chile and southwestern Argentina. The Andean and Patagonian regions could be considered as sub-units of a larger Andino-Patagonian region.

MATERIALS AND METHODS

We studied several factors related to clutch size of passerines by comparing clutch sizes in relation to taxonomic relationships, habitat, body size, mode of migration, and type of nest. All these factors have been shown to be related to clutch size in one or more studies.

BODY MASS

Most data on body mass were gathered from published literature (Belton 1985, Fiora 1933, 1934; Contreras 1983a, 1983b, 1975, 1979; Mason 1985; Salvador 1988), with some additional data provided by two of the authors (MC and GI). Sample size varied greatly between these sources and between species. In cases where data for a species were given by more than one source the largest sample was chosen.

CLUTCH AND EGG SIZE

There are few sources which give data on the clutch size, egg size, and nest type of the passerines of the study area. We used data from several works (Belton 1984, 1985; Cavenari et al. 1991; De la Pena 1987, 1988, 1989; Fraga and Narosky 1985; Johnson 1967; Narosky et al. 1983; Mason 1985), which generally give a range of the common clutch sizes or in which a value is given with the comment that sometimes a clutch size is smaller or larger by one egg. Whenever we had data from more than one source for the same species, we selected data based on the largest sample. We calculated a mean from the common range and the word "sometimes" received a score of 0.3 egg; e.g., 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. Data on egg length and width are usually given as means of a sample, and the largest sample was selected for this work. Egg volume was calculated using the equation $\text{Volume} = 0.5 \times \text{Length} \times \text{Width}^2$ (van Noordwijk et al. 1981). This index is a good

approximation of both egg volume and egg mass (van Noordwijk et al. 1981).

TYPE OF NEST

All nests were divided into four types: cup nests made of vegetational matter; nests in a hole in the ground or a tree; enclosed nests made of vegetational matter; or enclosed mud nests, typical to the genus *Furnarius* and some Hirundinidae.

ANNUAL MOVEMENTS

Although most birds of the study area are year-round residents, some species migrate or move from one region to another during the year. Three types of annual movements are distinguished by Narosky and Yzurieta (1989) and Belton (1984, 1985): A) Birds that breed in the Northern Hemisphere and winter in South America. Birds belonging to this type were excluded from the analysis as they do not breed in the study area. B) Birds which breed in the study area and migrate to the neotropics for the austral winter. C) birds which breed in Patagonia or southern Chile and migrate to other parts of the study area or further north for the austral winter.

DISTRIBUTION

All species were allocated to one or more of the five main zoogeographical regions of the study area (Amazonian, Chaco, Andean, Patagonian and Araucanian) using the distribution maps in Belton (1984, 1985), Narosky and Yzurieta (1989) and Johnson (1967). Introduced species (the house sparrow and two *Carduelis* species) were not included in the analysis.

STATISTICS

Ordinary least square regression equations and their statistics were calculated for the relationships between body mass and clutch size. Mean clutch size of the various families, regions, nest types, and migration types were compared by Student *t*-tests and analysis of variance (ANOVA).

The use of species within a taxon for comparative analyses of animal variables has been criticized, because such species may share common genetic information and therefore do not provide independent values (Harvey and Mace 1982). Ideally, the most satisfactory comparative analysis should be based on comparing phylogenies, but because accurate evolutionary histories of species are scarce, taxonomic classifications can

TABLE 1. Mean clutch size (\pm SD) of passerine families in the study area, calculated from means of genera.

| Family | <i>n</i> | Mean | SD |
|---------------------|----------|-------|-------|
| Dendrocolaptidae | 7 | 2.547 | 0.718 |
| Furnariidae | 27 | 3.099 | 0.626 |
| Formicariidae | 8 | 2.225 | 0.256 |
| Rhinocryptidae | 7 | 2.357 | 0.341 |
| Cotingidae | 7 | 2.703 | 0.751 |
| Pipridae | 4 | 2.000 | 0.000 |
| Tyrannidae | 41 | 2.697 | 0.551 |
| Phytotomidae | 1 | 3.000 | |
| All Deutero-Oscines | 102 | 2.728 | 0.615 |
| Hirundinidae | 6 | 4.583 | 0.516 |
| Corvidae | 1 | 4.000 | |
| Troglodytidae | 2 | 5.000 | 0.000 |
| Cinclidae | 1 | 4.000 | |
| Mimidae | 1 | 4.060 | |
| Turdidae | 1 | 3.000 | |
| Motacillidae | 1 | 3.500 | |
| Sylviidae | 1 | 3.000 | |
| Vireonidae | 2 | 3.500 | 0.707 |
| Parulidae | 4 | 2.725 | 0.320 |
| Coerebidae | 2 | 2.750 | 0.354 |
| Tersinidae | 1 | 3.500 | |
| Thraupidae | 13 | 2.858 | 0.560 |
| Emberizidae | 26 | 3.179 | 0.376 |
| Fringillidae | 1 | 3.670 | |
| Icteridae | 12 | 3.297 | 0.896 |
| All Oscines | 75 | 3.322 | 0.746 |
| Total | 177 | 2.980 | 0.733 |

form an ad hoc basis of comparative studies (Harvey and Purvis 1991). Hence, in the present work, we analyze data allometrically at the genus level by calculating means for each character for each genus for which we had data.

RESULTS

We gathered data on clutch size for 331 species of 177 genera which constitute 72% and 73% of the total number of species and genera breeding in the study area.

Overall mean clutch size is 2.98 (SD = 0.73, $n = 177$). Mean clutch size by family is given in Table 1. There was a highly significant difference ($t = 5.66$, $P < 0.001$) in clutch size between the two suborders of passerines represented in the study area, with the Deutero-Oscines having on average smaller clutches (2.73, $n = 102$) than the Oscines (3.32, $n = 75$). There was no significant relationship between body mass and clutch size in the sample as a whole ($R^2 = 0.005$, $P = 0.3837$, $n = 160$) or in either of the suborders (Deutero-Oscines: $R^2 = 0.01$, $P = 0.353$, $n = 90$; Oscines: $R^2 = 0.002$, $P = 0.739$, $n = 70$).

TABLE 2. Mean clutch size (\pm SD) in relation to type of migration. B—breed in the study area and migrate to the Neotropics; C—breed in Patagonia and migrate within the study area; D—residents.

| Migration type | <i>n</i> | Mean | SD |
|----------------|----------|-------|-------|
| B | 32 | 2.976 | 0.956 |
| C | 29 | 3.283 | 0.790 |
| D | 145 | 2.954 | 0.667 |

Our sample includes 61 genera which have migratory species. Mean clutch size of migratory birds and residents are given in Table 2. Although genera that breed in Patagonia and migrate to northern parts of the study area for the winter have on average larger clutches than residents, there was no significant difference between the groups in clutch size in relation to migration type (ANOVA: $F_{2,203} = 2.444$, $P = 0.0894$, ns). Of the total number of 472 species of passerines observed in the study area and for which we have data, only 2% are Northern Hemisphere migrants, 11% migrate to the Neotropics and 10% are Patagonian species which migrate within the study area. There were no significant differences in clutch size in relation to nest type (Table 3; ANOVA: $F_{3,167} = 1.629$; $P = 0.1845$).

To test the hypothesis that clutch size is influenced by both systematic position (suborder) and region we performed a two-factor ANOVA on the five main regions. There were highly significant differences in mean clutch size between the two suborders ($F_1 = 20.303$; $P = 0.0001$) and between the regions ($F_4 = 4.198$; $P = 0.003$), without interaction between the two factors (Tables 4 and 5). Mean clutch size of Deutero-Oscines is smaller than that of the Oscines in every region. Overall mean clutch size is smallest in Amazonian genera (2.67) and largest in the Chaco (3.29).

Mean body mass and absolute egg volume did not differ between the two suborders (mean body mass was 30.94 and 33.34 g, ANOVA: $F_{1,192} =$

TABLE 3. Mean clutch size (\pm SD) in relation to type of nest.

| Nest type | <i>n</i> | Mean | SD |
|--------------------|----------|-------|-------|
| Cup | 96 | 2.941 | 0.605 |
| Hole | 35 | 2.892 | 0.917 |
| Enclosed nest | 38 | 3.144 | 0.841 |
| Enclosed mud nests | 2 | 3.750 | 0.354 |

TABLE 4. Mean (\pm SD) clutch size of passerines suborders in southern South America in relation to their main distribution regions.

| Region | Deutero-Oscines | | | Oscines | | | All | | |
|-----------------|-----------------|--------|-------|----------|--------|-------|----------|--------|-------|
| | <i>n</i> | Clutch | SD | <i>n</i> | Clutch | SD | <i>n</i> | Clutch | SD |
| Amazonian (A) | 41 | 2.515 | 0.719 | 17 | 3.029 | 0.822 | 58 | 2.666 | 0.780 |
| Chaco (B) | 32 | 3.078 | 0.647 | 33 | 3.496 | 0.689 | 65 | 3.290 | 0.676 |
| North Andes (C) | 9 | 2.432 | 0.504 | 4 | 3.625 | 0.479 | 13 | 2.799 | 0.745 |
| Patagonian (E) | 6 | 2.750 | 0.392 | 3 | 3.667 | 0.289 | 9 | 3.056 | 0.572 |
| Araucanian (D) | 10 | 2.675 | 0.450 | 3 | 3.267 | 0.929 | 13 | 2.812 | 0.167 |

0.2594, $P = 0.6111$; egg volume 3.56 and 3.20 cm³, $F_{1,164} = 0.7644$, $P = 0.3832$; Deutero-Oscines and Oscines, respectively), but Deutero-Oscine eggs were proportionally larger than those of Oscines (14.13% and 11.26% of body mass, respectively. Mann-Whitney U test: $n_1 = 104$, $n_2 = 44$, $U = 1,375.5$, $P = 0.0001$). However, body mass explains only 9% of the variation of this character.

DISCUSSION

Our results indicate that mean clutch size of southern South America passerines is considerably smaller than would have been expected from the latitude range of most of the study area and that in all five main biogeographic regions mean overall clutch size is about three eggs. Small clutch size is expected for the Amazonian region which is closest to the tropics, but not for the rest of the regions which extend to much higher latitudes. Even in the southernmost regions of our study area (Patagonia and Araucanian region) overall mean clutch sizes are 3.0 and 2.8, respectively. Because there is no trend of increase in clutch size from tropical (Amazonian) to temperate (Patagonia and Araucanian) regions, it does not appear that in this region clutch size of passerines changes in relation to latitude in the same way that it does in the northern hemisphere. This conclusion was also reached by Johnson (1965) for the birds of Chile. He stated that "there is no evidence that clutch size tends to increase with

latitude. . . . Not only do species nesting south of the 50th parallel lay the same number of eggs to the clutch as other members of the same families nesting further north, but no difference in the number is discernible even where the same species nests both in the extreme south and in the semi-tropical north."

The small clutch size of the southern South American passerines (2.98; 177 genera) is similar to that of the other two Southern Hemisphere continents: mean clutch size of 299 species of Australian passerines is 2.69 (Yom-Tov 1987) and that of 353 species of South African passerines is 2.8 (Rowley and Russell 1991). We suggest that Ashmole's (1961) hypothesis as formulated by Ricklefs (1980) can account for the difference in clutch size between the Northern and Southern Hemispheres. According to this hypothesis geographical trends in clutch size are caused primarily by factors that limit populations during the nonreproductive period. Birds which do not endure long migrations or severe winters survive better, and by the end of the nonreproductive period they could be faced with stronger competition from conspecifics than birds in which mortality during the nonreproductive period is high. Hence, the former birds would be capable of feeding fewer young than the latter, and thus lay smaller clutches. The high and mid-latitude areas of northern hemisphere continents form large land masses where much of the area has a continental climate and the moderating effect of the surrounding seas is not pronounced. Birds living in these areas face harsh winters or migrate south to avoid them, and consequently may suffer from heavy winter losses and produce large clutches. On the other hand, the winter climate in southern continents is much milder than that of the Northern Hemisphere due to: (1) the triangular shape, with the tip pointing south, of southern Africa and South America, which enables the moderating effect of the sea to influence

TABLE 5. Two factor analysis of variance of clutch size of the passerines of southern South America. The test was carried out on the groups included in Table 4.

| Source | df | Sum of squares | Mean square | <i>F</i> -test | <i>P</i> -value |
|-------------|-----|----------------|-------------|----------------|-----------------|
| Suborder | 1 | 9.173 | 9.173 | 20.303 | 0.0001 |
| Region | 4 | 7.588 | 1.897 | 4.198 | 0.003 |
| Interaction | 4 | 1.717 | 0.429 | 0.950 | 0.4371 |
| Error | 148 | 66.872 | 0.452 | | |

large areas; and (2) most of the area of the three southern continents lying in mid- rather than high latitude (i.e., below 40°). Consequently, the majority of passerines are residents and relatively few species are migratory, as those that are migrant travel shorter distances than Northern Hemisphere migrants (Rowley and Russell 1991). Hence, the resident birds may suffer fewer losses than Northern Hemisphere passerines, and so face more competition from conspecifics during the breeding season and lay smaller clutches.

That passerines breeding in southern continents lay on average smaller clutches than Northern Hemisphere does not necessarily mean that they lay fewer eggs per breeding season. Breeding seasons of birds are longer in the Southern Hemisphere (Baker 1938), partly because of their milder climate. Thus, Southern Hemisphere passerines may lay more clutches per season than do their Northern Hemisphere counterparts. However, very little was published on breeding frequency of passerines in our study area.

Another result of this study is that clutch size of passerines in the study area is related not only to ecological, but also to phylogenetic (taxonomic) factors. In each of the regions, Deutero-Oscines lay smaller clutches than the Oscines. This result is quite similar to the finding that among Australian passerines "old endemics" lay smaller clutches than "new invaders" (Yom-Tov 1987). Deutero-Oscines lay also relatively larger eggs, and both results indicate that they lie more towards the "K-selected" end of the K and r-selection continuum (Pianka 1974). It is interesting to note that on both continents the group which lays smaller clutches evolved there—the Deutero-Oscines (or, according to another division, infraorder Tyranni, Sibley and Ahlquist 1990) in South America and parvorder Corvida (sensu Sibley and Ahlquist 1990) in Australia. Most other families of South American passerines evolved elsewhere, either in North America or in the old world, and invaded South America later. It seems that their laying of larger clutches is one of the characteristics which enabled the latter birds to expand their range in the past to regions where they had not formerly been found.

Each of the two suborders of passerines is represented in all regions of the study area, and the Deutero-Oscines consistently have smaller clutches than the Oscines. This seems to be contrary to the conventional adaptationist wisdom, which predicts that for a particular set of envi-

ronmental conditions there is one solution. However, this is a simplistic approach to evolution (Lewontin 1979), and adaptation and selection might occur with no selective basis for differences among adaptations (Gould and Lewontin 1979). In Lewontin's words "There are multiple selective peaks when more than a single gene is involved in influencing a character. The existence of multiple peaks means that for a fixed regime of natural selection there are alternative paths of evolution and the particular one taken by a population depends upon chance events. Thus, it is not meaningful to ask for an adaptive explanation of the difference between two species that occupy alternative peaks. Hence, related taxa often develop different adaptations as solutions to the same problem. When multiple adaptive peaks are occupied, we usually have no basis for asserting that one solution is better than another" (Gould and Lewontin 1979). It seems that there is no adaptive explanation for the existence of small clutch size in the Deutero-Oscines and a larger one in the Oscines. Rather, they are alternative outcomes of the same general selective forces, and each of these two groups has reacted within its own genetic framework, and reached a different adaptive peak.

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