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Are songbird-tyrannid success and nonincubating males related to cuckoldry and seasonal habitats? (Aves: Passeriformes)

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RESUMO. **Possível associação de aves canoras, a falta de incubação pelo macho, infidelidade sexual e ambientes sazonais (Aves: Passeriformes).** O sucesso e a falta de incubação pelo macho de aves canoras podem ser devidos aos seus cantos complexos e reconhecíveis, que estão bem adaptados para rapidamente utilizar os ambientes sazonais ou novos, de sucessão secundária, onde muitas outras aves cantam ao mesmo tempo. Em ambientes constantes, as aves mantêm seus territórios por períodos longos e cantam pouco, favorecendo mais a incubação e menos o canto ou a defesa da fêmea pelo macho. O primeiro argumento parece aplicar-se aos Tyrannidae, de zonas semiabertas, que desenvolveram o grito para abafar a competição ao invés do canto; mas os cantos complexos usam menos energia e produzem outras novas possibilidades como dialetos, avaliação da degradação e a variabilidade de canto, permitindo a expansão novamente para os hábitats maduros à custa de aves menos canoras. Outras hipóteses são possíveis, também, especialmente que ambientes sazonais têm picos de alimento que deixam a fêmea incubar mais e o macho cantar e perseguir outras fêmeas mais.

PALAVRAS-CHAVE: canto, incubação, Passeres, promiscuidade, sazonalidade, Tyrannidae.

KEY WORDS: cuckoldry, incubation, Passeres, seasonality, song, Tyrannidae.

Songbirds are successful, if judged by the criterion of number of species: no other suborder of vertebrates has more than 4000 species. Wyles *et al.* (1983) and Fitzpatrick (1988) suggested one possible reason, that learning of complex songs led to larger and more intelligent brains as an incidental by-product. I am not sure that increase in song-related brain nuclei has any necessary connection with general intelligence, though I agree with these authors that possible increase in general intelligence should be investigated. Here, I suggest an alternative hypothesis for songbird success, as well as for success of convergent Tyrannidae (Keast 1972).

Could one explain songbird success by looking at the main differences between songbirds and other birds, notably the facts that they have a specialized syrinx, learn complex songs, and sing well? Birds of the other passeriform suborder, Tyranni, have a variety of simple syringes and songs are relatively invariable, probably innate (Kroodsma 1984). It may be that complex, learned songs are better in some respect than less complex songs, or that there is some environmental factor favoring song complexity and learning.

A second difference between songbirds and many other birds is that the male often does not help incubate (Appendix). Male incubation in songbird families is mainly recorded in paleotropical forest-interior birds or, at the other extreme, in seminomadic desert birds. Lack of male incubation might seem unrelated to song, but Skutch (1976) noted that this pattern might be due to male "absorption in singing and defending territory" and "division of labor" in migratory birds. He was dubious about these suggestions, but I suggest that they can be combined with the specialized syrinx to explain songbird success: songbirds are successful because they sing well in new (successional) or seasonal environments that favor singing and mate guarding or seeking other females (cuckoldry or polygyny) rather than male incubation.

Actually, I arrived at this hypothesis indirectly, by examining a successful and ecologically convergent (favoring successional and seasonal habitats) nonsongbird group, the tyrant-flycatchers (Tyranni, Tyrannidae) of the New World. This and related Pipridae and Cotingidae (perhaps just derived subfamilies) are the only families of Tyranni where males do not help incubate; they have developed a wide variety of syringes, plus loud voices. The convergence with songbirds is so striking that one begins to think of selection. The argument is as follows:

1. Tyrannidae capture food at a distance, by flying, and hence tend to occupy environments where leaves or insects are distant from the perch – i.e., semiopen or open-understory environments, not dense herbs, shrubs, or trees. Some genera do sally in dense foliage or peck insects off foliage, but these are probably secondary radiations within the family.

2. Semiopen environments are, in most cases, seasonal, new or scattered, restricted to patches of poor or recently exposed substrates or to zones that are dry or cold part of the year. Where environments are not unfavorable, dense-foliaged growth soon takes over. Tyrannids, as a consequence, are often migratory (Robbins *et al.* 1966, Willis 1988) or travel-prone.

3. Seasonal or successional habitats favor development of strong and syringeally diverse tyrannid voices because of intense and concurrent territorial noise, birds suddenly taking advantage of the habitats as soon as they appear in the spring or when they appear distant in primary habitats, with storms, earthquakes, or (recently) with human disturbance. (The canopy of forest, scrub, or even grassland is more seasonal than within vegetation, even if less so than many extratropical or edge habitats, and is also favored by Tyrannidae.)

4. Song and territorial activity occur early in the short breeding cycle, at exactly the time birds are incubating; waiting for males to help incubate would delay laying and reproductive success. Males that incubate rather than guarding females would run risks of being cuckolded (extra-pair copulations, EPC's) or forego opportunities to copulate with neighboring, extra or wandering females, given that the confusion but predictable timing of concurrent reproduction seems to favor EPC's in nontropical species or ones of seasonal habitats. (The study of EPC's is recent, and study of tropical species and of Tyrannidae needed; but cuckoldry is unrecorded even in tropical species studied well, as by Willis 1967, 1972, 1973).

5. While loud tyrannid calling is one way to colonize new or seasonal semiopen habitats, despite noise from other birds, complex songs could waste less energy, be less tiring or tiresome (see below), and be less likely to be confused with other species.

6. The complex syringes of songbirds and, to some extent, the varied if less complex syringes of Tyrannidae, permit complex and recognizable (Nelson 1989) songs and could enhance successful invasion of seasonal or other semiopen environments, where many individuals sing loudly and at the same time. Both Tyrannidae and Passeres center in such habitats (but, see below for Old World songbirds). On islands, where fewer species occur, simpler songs may evolve (Marler 1960).

7. Additionally, nonincubating tyrannid and songbird males may gain extra females (cuckoldry or polygyny). Moreover, the seasonal or new environments often have food surpluses that allow females to incubate alone.

8. In a seasonal environments, the obverse seems to hold: large territories with fewer cuckolding intruders are established in food-stable but competitively (many species) food-partitioned areas at any time of year, requiring less overlap of song and territorial activity among species and individuals of a species. Territories may be stable, passing unchanged to a new owner (Willis 1972, Greenberg and Gradwohl 1986). Cuckoldry is not recorded, although more study of tropical or male-incubating species is needed. Complex or loud songs are less needed, and song, territorial establishment and outside cuckoldry are less likely to overlap with incubation.

9. It is true that closed environments (not open-understory forests) may be unfavorable for complex songs because of song degradation (Gish and Morton 1981), especially since territories are often large due to food competition with large numbers of species, need to join mixed flocks (Powell 1989) or dispersed food (Sorjonen 1988 registers decrease in song complexity with more closed zones in one species). However, a simple song should also be good in an open environment unless there are noise problems with small territories or other birds singing at the same time.

Neotropical birds, especially forest ones, generally do not show spring or dawn choruses and are often poor singers. These facts indicate reduced song competition, favoring less song and more male incubation. Slud (1976) and others have noted the increase in songbirds relative to suboscines away from the neotropical forest, although one must note that tyrannids and songbirds also increase at forest borders and in the somewhat seasonal canopy.

Presence of male incubation in certain nomadic songbirds, notably in Estrildidae (Goodwin 1982) but also in other families (Appendix), might seem difficult to explain under the hypothesis presented here. I consider male incubation derived within the Passeres, most likely to occur (or male feeding the female as a substitute for incubation) in forest-interior songbirds like Pycnonotidae, Monarchidae, Sylviidae, and Malaconotidae, which in the Old World take the ecological places of neotropical pair-incubaters. (Timaliidae should have many pair-incubaters too, but one detects a certain laxity about recording incubation in the available literature, perhaps because northern ornithologists think male incubation abnormal due to their experience mainly with migratory songbirds.) Perhaps seminomadic species, settling in very depauperate and thus less songful environments, do not need songs so much, have to protect eggs from midday heat, or have to nest too quickly (reducing cuckoldry rates or making constant incubation better) to allow males not to incubate. The suboscines seem to have been relatively unable to develop nomadism, perhaps due to lack of intermediate stages of songful birds with female-only incubation (except Tyrannidae).

An alternative or complementary hypothesis, however, is that males are "emancipated" from nesting duties wherever food is abundant (Snow 1963). If females are able to feed rapidly, time away from incubation can be brief, and other male activities become selectively more important. Males themselves, in the frugivores and nectarivores considered by Snow, could feed in brief sessions and spend much time trying for extra-pair copulations or in lek behavior. These activities would increase the selective value of songs among other displays, especially in migratory or edge-living birds. I find little evidence of lek activity in such birds, except certain migratory Scolopacidae; but extra-pair activity is very common. The difficulty may be feeding numerous young without male help, plus short seasons for breeding; the male that abandons young as well as incubation has fewer offspring per nest and per year.

Another hypothesis for lack of male help at nests (Willis and Oniki in press) is that predators may catch males that try to follow mobile females in closed or dense habitats, favoring nonmonogamy. However, this would explain only some exceptional cases where forest birds with wandering females do not pair at all, resulting in lek behavior or intermediate stages, as in the Dendrocolaptidae studied or in Trochilidae, Pipridae, Cotingidae and Paradisaeidae.

Ornithologists generally suggest that, in the Old World tropics, songbirds have pushed their way into tropical forest interiors, leaving only a few relict Tyranni. D. F. Stotz (pers. comm.) suggests that the few there may not be relicts, but one still has to explain their lack of speciation there compared to songbirds. The success of some songbirds in tropical forests suggests that they can do more with their voices after they have complex syringes. The following suggestions from the literature are, to some extent, alternative or complementary to hypotheses of habitat-linked song complexity and incubation patterns.

Complex songs and repertoires may, in some birds, demonstrate male quality to females and be favored by sexual selection (Catchpole 1988). Birds can judge distance of a competitor by foliage-caused song degradation, which should be more obvious in a complex song and which should allow the birds to save energy if the singer is obviously too far away to be on the local territory (Richards 1981, Shy and Morton 1986). Payne (1985) has shown that viduines can have complex series of songs and learn the local song "language", perhaps fitting in with the local males and attracting local females. Monotony and habituation (Hartshorne 1958) can also be avoided if complex syringes allow variation in song. The anti-exhaustion hypothesis (Lambrechts and Dhondt 1988) suggests that varying songs tires out the syrinx muscles and neurons less. The "Beau Geste" hypothesis (Krebs 1977), of a male singing various songs to make it seem that several birds are already present, works better if songs are complex and easily modified by a complex syrinx. Learning may be associated with complex and variable songs; songbirds learn and tyrannids (at least) do not (Kroodsma 1984). It may be that learning songs led to large brains that increased success in other ways (Wyles *et al.* 1983, Fitzpatrick 1988); neuroanatomy influences speciation rates among anurans (Ryan 1986). With complex songs and learning, song dialects become possible, permitting adaptation to the local song environment or physical environment (Nottebohm 1975). In some cases, this may permit birds to increase their range to other sound environments and thus run less chance of extinction, a potentially important factor in difficult or variable semiopen zones; extratropical birds and those of secondary habitats tend to have wide geographic distributions ("Rapoport's Rule", Stevens 1989). (The literature [Payne and Guttinger 1988] tends to emphasize a second possibility, of vocal dialects leading to speciation, but the large geographical range of many dialect species could even indicate a reverse correlation. Speciation of local populations, with reinvasion as in Galapagos finches, may be facilitated by song variation, as suggested by Fitzpatrick [1988]). Complex songs, once started to favor use of semiopen zones, can allow invasion of forest zones because of these and other subsidiary advantages.

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APPENDIX

Male incubation in Passeriformes

Male does not help

– **Passeres:** Menuridae, Atrichornithidae, Alaudidae (1), Hirundinidae (1), Laniidae (1), Bombycillidae (1), Ptilogonatidae (1), Campephagidae (1), Cinclidae, Troglodytidae, Mimidae (1), Sturnidae (1), Prunellidae (1), Turdidae, Muscicapidae (2), Remizidae, Paridae, Aegithalidae, Salpornithidae (2), Climacteridae (2), Sittidae, Neosittidae, Tichadromadidae, Certhiidae (1), Motacillidae, Dicaeidae, Nectariniidae (2), Meliphagidae, Emberizidae (1,2), Parulidae, Drepanididae, Fringillidae (2), Icteridae, Vireonidae (1), Ploceidae (1), Oriolidae (1,2), Cracticidae, Ptilonorhynchidae (2), Paradisaeidae, Corvidae (2), Callaeidae, Maluridae.

– **Tyranni:** Tyrannidae (1), Pipridae, Cotingidae.

Male helps

– **Passeres:** Pycnonotidae (3), Malaconotidae, Prionopidae, Dulidae (?), Vangidae, Zosteropidae (4), Estrildidae (4), Epthianuridae (4), Grallinidae, Artamidae (4), Sylviidae (3), Paradoxornithidae, Monarchidae (3), Dicruridae, Pachycephalidae (3), Corcoracidae.

– **Tyranni:** Eurylaimidae, Dendrocolaptidae (3), Furnariidae (3), Thamnophilidae, Formicariidae, Conopophagidae, Rhinocryptidae, Pittidae, Acanthisittidae.

Not registered (5)

– Philepittidae, Irenidae (1), Timaliidae, Acanthizidae, Petroicidae, Orthonychidae.

(1) Males help in some species, at times merely covering eggs until females return. A notable case is nomadic *Phainopepla nitens*, Ptilogonatidae, where the male incubates more than the female.
(2) Male feeds incubating female in at least some species.
(3) Male fails to help in one or more species.
(4) Extensively wandering or nomadic species, neither migratory nor sedentary.
(5) Information from Harrison (1978), Campbell and Lack (1985) and Forshaw (1991).