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NEOTROPICAL MODEL SYSTEMS: SOCIAL AND MATING BEHAVIOR OF BIRDS

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Resumo. – Modelos Neotropicais: Comportamento social e de acasalamento de aves. – A diversidade taxonômica de aves Neotropicais é notável, incluindo cerca de 3100 espécies, o que representa aproximadamente um terço de todas as aves do mundo. Estudos também têm mostrado que certos sítios nos Neotrópicos contêm duas vezes mais espécies do que áreas tropicais comparáveis na Africa e Asia. Justificadamente, um grande esforço tem sido dedicado à documentação, identificação e avaliação da diversidade taxonômica dos Neotrópicos, crucial frente às atuais tendências de destruição de habitat. No entanto, têm-se ignorado um outro tipo de diversidade associada às aves, que também encontra sua maior taxa de ocorrência em regiões tropicais, e que inclui a multiplicidade de interações biológicas, comportamentos, e sistemas sociais e de acasalamento. Essa diversidade de modelos comportamentais e interações está também rapidamente desaparecendo com o desmatamento e a fragmentação de habitats. Visto que fenômenos comportamentais em aves são muito mais variados nos trópicos do que em regiões temperadas, torna-se crucial que mais estudos sejam dedicados ao conhecimento da ecologia comportamental de aves Neotropicais. Neste trabalho sintetizo alguns tópicos que ilustram a diversidade de sistemas sociais e de acasalamento de aves Neotropicais e faço também um breve relato de alguns estudos conduzidos pelo meu grupo de pesquisa, que envolvem o sistema de reprodução social do Anu Branco (*Guira guira*), o sistema de acasalamento flexível do Quero-quero (*Vanellus chilensis*), e a prevalência de fertilizações extra-par no sistema socialmente monogâmico do Tiziu (*Volatinia jacarina*).

Abstract. – The taxonomic diversity of birds in the Neotropics is truly remarkable, encompassing some 3100 species that represent over one third of the world's birds. Additionally, Neotropical sites typically contain twice as many species as comparable sites in tropical Africa and Asia. Much effort has been invested in assessing avian diversity in the Neotropics, motivated largely by current trends in habitat destruction. By contrast, considerably less attention has been given to another type of bird diversity that also peaks in tropical regions, namely behavioral ecology (i.e., biological interactions, social behavior, and mating systems). Because this behavioral diversity is also quickly vanishing with habitat fragmentation and deforestation, it is crucial that more research be undertaken to document the behavioral ecology of Neotropical birds. In this paper I illustrate some of the diverse behavior and social systems of Neotropical birds, focusing mainly on studies carried out by my research group in Brazil, specifically the communal breeding of Guira Cuckoos (*Guira guira*), the flexible mating patterns of Southern Lapwings (*Vanellus chilensis*), and the extrapair fertilizations of socially monogamous Blue-black Grassquits (*Volatinia jacarina*). *Accepted 9 October 2007.*

Key words: Cooperative breeding, mating systems, extrapair paternity, Neotropics, sociality, V*anellus chilensis*, *Guira guira*, *Volatinia jacarina*, Southern Lapwing, Guira Cuckoo, Blue-black Grassquit..

INTRODUCTION

The latitudinal gradient of increasing species richness towards the tropics is a well recognized pattern that has existed for at least a quarter of a billion years, and a plethora of hypotheses have been proposed to explain the pattern (reviewed in Willig *et al.* 2003), though no consensus has been reached. This model holds for most animal taxa, and has been well verified for birds. Species richness for birds is especially high in the Neotropics. There are over 3000 bird species in South America, which is about one third of all birds in the world (Ridgely & Tudor 1989), a very high number given that the land area of the continent represents only about 10% of the planet's total. The latitudinal gradient across the Americas in diversity of genera for different bird groups increases dramatically at the lower latitudes (reviewed in Stutchbury & Morton 2001). For the Accipitridae, the number of genera rises from six, in eastern Canada, to 23 in central Brazil. There also are similar increases in diversity in other taxa, such as Troglodytidae (one genus in Canada; nine in Brazil) and Tyrannidae (five in Canada, 79 in Brazil). And of course, there are whole clades in the Neotropics that have no representatives to the north (e.g., Formicariidae). Tropical latitudes across the globe differ in species richness, with sites in the Neotropics having roughly twice the diversity of birds compared to similar latitudes in Africa and Asia (Ridgely & Tudor 1989).

Among the plausible explanations for why the Neotropics exhibits such a high diversity, one hypothesis currently favored is that species richness in Neotropical birds may be linked to habitat heterogeneity, and the latter results from heterogeneity in topography (Rahbek & Graves 2001). This probably explains, for example, why areas that are mountainous in the humid tropics, such as Colombia and Peru, have higher species richness than the Amazonian lowlands. However, other plausible explanations for high tropical diversity exist, but are not necessarily applicable to the Neotropics. One assessment revealed that bird diversity decreases when ambient energy drops, whereas when energy is high, the amount of water becomes a limiting factor for diversity (Hawkins *et al.* 2003).

Considerable effort has been invested in documenting and evaluating diversity of avian taxa in the Neotropics. There is a great emphasis on estimating numbers of bird species, their distributions, and their relative frequencies. Given the realities of habitat destruction placing these species at risk, such work must continue to be a priority. For example, tropical forests are disappearing at a rate of approximately 17 million ha per year (Ricklefs 2003). Other tropical habitats are also being lost rapidly. For example, the Brazilian savanna biome, known as Cerrado and considered one of the world´s hotspots, has lost more than 50% of its original 2 million km^2 during the last 35 years (Klink & Machado 2005).

However, there is a second type of bird diversity that peaks in tropical regions, but which has been largely ignored, namely, behavioral ecology. This encompasses the more multifaceted levels of biological interactions, types of behaviors, and the variety of social and mating systems, all of which also reach their highest points in the tropics (Stutchbury & Morton 2001). Obviously, as species disappear or are influenced by the loss of their natural habitats, this richness also declines or is modified. Unfortunately, there is much less effort at present to document and understand these complex systems than there is simply to document bird diversity.

The study of tropical birds presents a remarkable opportunity to explore crucial differences in their behaviors and systems relative to temperate birds. Moreover, because tropical latitudes support greater numbers of bird species than higher latitudes (Rosenzweig 1995, Balmford 2002), these studies will provide more general explanations for almost all biological facets of this group of animals.

Tropical birds are thought to differ from temperate birds mainly as the result of some major life history strategies that constitute evolutionary responses to at least three interrelated properties of lower latitudes: climate (e.g., variation in day length, higher temperatures), nest predation, and differences in food availability. These factors presumably promote or are associated with prolonged breeding periods for many tropical species, many nesting attempts per breeding season, with small clutches, long developmental periods, and lower adult mortality (Lack 1947, 1948, 1968; Skutch 1949, 1985; Ricklefs 1969, Fogden 1972). More recently, an experiment with nestling Stonechats (*Saxicola torquata*) from four different latitudes hand-reared under the same conditions revealed that those taken from tropical latitudes had intrinsically lower energy expenditure compared with those from the temperate areas (Wilkelski *et al.* 2003). This has important implications when considering life-history strategies of tropical birds. However, existing evidence, especially for Neotropical birds, suggests that many of the professed differences in life history characteristics between tropical and temperate birds may not exist or are unclear (Martin 2006). Only further studies in the field will ultimately provide the necessary data to compare alternative hypotheses and clarify what may be the real differences between temperate and tropical species in life history attributes.

The list of topics that could yield significant insights on the behavioral ecology of tropical birds is long and the study of these topics has been much neglected. Some research areas (e.g., lekking systems, cooperative breeding, ant-following behavior) have attracted more attention than other less conspicuous topics that are only now being approached. Among these overlooked topics are extrapair mating systems in socially monogamous birds, hormonal patterns associated with year-round territoriality and extended breeding periods and associated physiological costs, resistance to endo-parasitism and disease, and singing patterns, among others. Below I discuss two phenomena that occur more frequently in the tropics and that, with further investigation, could provide valuable insights through comparison with temperate birds. I then briefly review some of the findings of my research group that illustrate behavioral studies applied to three common Neotropical species.

COOOPERATIVE BREEDING

Cooperative breeding has been the focus of substantial research during the last 40 years (reviewed in Koenig & Dickinson 2004). The definition of cooperative breeding varies across authors and usually reflects the variability of helping behaviors and mating strategies (Ligon & Burt 2004). Many consider cooperative breeding to occur when offspring help their parents to rear a brood of young, but do not reproduce. Other definitions include cases where offspring stay in their parents' territory but do not help rear younger siblings. A third group accommodates cases where individuals help rear unrelated nestlings while simultaneously breeding themselves. Despite the diverse patterns exhibited by birds with more than two adults providing brood care (reviewed in Brown 1987), most researchers agree on the defining characteristic of cooperative breeders, namely that there are "helpers-at-the-nest" (Brown 1987, Edwards & Naeem 1993), usually presumed to be non-breeding adults, but which may also be breeders, depending on the species in question. Cooperative breeding is also rare, and occurs in only about 220 species of the

9000 or so birds in the world (Brown 1987).

Despite the diversity of types of cooperative breeders, patterns of dispersion and mating, they exhibit some common ecological and phylogenetic correlates (reviewed in Stacey & Koenig 1990). Cooperative breeders have been found more frequently in regions with tropical and mild climates rather than in cold temperate or highly seasonal climates (Rowley 1968, 1976). There is a strong phylogenetic component that accounts for the occurrence of cooperative breeding (reviewed in Ligon & Burt 2004). Additionally, there are some ecological attributes that have been frequently associated with cooperative breeding, such as high survivorship of adults (Stacey & Ligon 1987), and sophisticated systems of sentinel behavior (Gaston 1977, McGowan & Woolfenden 1989, Hailman *et al.* 1994).

Approximately 20 species of cooperative breeders had been studied for a minimum of 10 years at the time that Stacey & Koenig published their review in 1990, and some of these species have now been under study for two or more decades. Among these, only three species fall outside the subtropical and tropical zones, and a full 50% occur exclusively within the tropics. Considering that a large portion of the world's tropical land mass is represented by Latin America and Africa, it becomes clear why there have been relatively few long-term studies of cooperative breeders: these regions have few professional field biologists that work in behavioral ecology. Studies of cooperative breeders in these regions have been conducted mostly by North American and European researchers. So it is quite safe to assume that there are still many undescribed cooperative breeders remaining to be studied.

COMMUNICATION THROUGH SONG

Vocal communication is another neglected topic that is especially relevant in the study of tropical birds. Song is of special interest because there are a number of differences between tropical and temperate birds as to its function, structure and context.

Communication signals such as song, plumage or postural displays, are a means to an end, whereby the sender may influence the behavior of the receiver, but cannot control the outcome of the interaction. The sender can only control when, where and what type of signal it sends. The receiver can interpret the message and decide to act, based on the information content of the song.

Why would Neotropical bird song differ from that of temperate birds? The first major reason derives simply from the phylogenetic origin of birds in the Neotropics. As far as has been described, the true songbirds, the passerine Oscines, have more complex and longer songs, whereas the Sub-oscines have simpler and shorter songs (Kroodsma 1984, 1989). A quick overview of the geographic distribution of Sub-oscines shows that 9 of the 15 Sub-oscine families are mostly in South America (Welty & Baptista 1988). Thus, the abundance of unstudied Sub-Oscines in the Neotropics relative to temperate regions should present an opportunity for the study of song.

There are also many ecological differences between tropical and temperate birds that suggest that they should exhibit strikingly different song patterns. Whereas temperate species tend to establish and defend territories briefly, for the purposes associated with breeding, the more characteristic pattern for tropical birds, especially in rainforests, is to maintain year-round, all-purpose territories (Morton 1996). Tropical territories appear to be stable for long periods and are generally larger, as they have to provide resources year-round (Stutchbury & Morton 2004).

There is a wide range of subjects associated with singing behavior in the tropics that may offer striking contrasts to temperate regions, such as song structure, rate of output, attenuation in different vegetations, just to name a few. But two very unusual aspects of tropical bird song merit special mention and increased research attention, namely the much greater number of taxa in which female adults participate actively in singing and the related phenomena of duetting (Farabaugh 1982, Morton 1996, Slater *et al.* 2002, Slater & Mann 2004). Although several hypotheses have been advanced to explain these features, careful testing remains in its infancy. For instance, Langmore (1998) suggested female song may have evolved in species where females compete for resources (e.g., mates, space) and also to coordinate activities within the family. She also suggests that these activities should be more common in species where territories are defended year-round. Although the interest in studying female singing has increased considerably, current hypotheses have not been evaluated formally for tropical birds in general because information does not exist for most species.

Among several hypotheses for duet singing, three seem especially pertinent. One is that duetting could keep the male and female in touch with each other in dense vegetation (Thorpe 1972). A second proposes that because tropical species have more prolonged breeding periods, duetting has developed to synchronize physiological reproductive readiness between paired birds (Sonnenschein & Reyer 1983). Finally, duet singing may involve the pair bonding process and mutual mate guarding (Wickler 1980). Again, all of these hypotheses remain relatively untested for tropical birds.

BEHAVIORAL ECOLOGY OF TROPICAL BIRDS: THREE MODEL SYSTEMS

Below I review some of my work in behavioral ecology of three Neotropical species, the Guira Cuckoo (*Guira guira*), the Blue-black Grassquit (*Volatinia jacarina*) and the Southern Lapwing (*Vanellus chilensis*). The study of these birds illustrates that even the most abundant and common species have much to contribute toward the understanding of social and mating systems of tropical birds. All field work in these studies was conducted near the city of Brasilia, Brazil (15°47'S, 47°56'W), in areas dominated by tropical savanna, known as Cerrado, but that have been largely modified for agriculture. These three species are commonly associated with open vegetation types, and have adapted well to habitat disturbance.

Guira Cuckoo. In general, the Guira Cuckoo research has been shaped by questions about cooperative breeding in this species. The methods generally included monitoring active nests, individually color-marking adults and chicks, assessing genetic relatedness through molecular techniques, and behavioral observing during the chick-feeding phase of breeding.

The early years of study revealed that Guira Cuckoos are cooperative breeders with shared reproduction, wherein the group uses a joint nest. During the breeding season, groups range from 3 to 15 birds that defend the territory and produce a communal clutch of as many as 25 eggs (Macedo 1992). However, clutches or broods seldom survive intact, as they are subjected to intensive egg ejection and infanticide (Macedo & Melo 1999, Macedo *et al.* 2001). Because it was evident that much competition occurred, it became crucial to understand female reproductive strategies associated with shared breeding. The study of female reproductive skew within joint nests was only possible with the application of a molecular tool – protein yolk electrophoresis – that allowed maternal identification of eggs within communal clutches (Cariello *et al.* 2002). This technique also allowed us to answer the question of whether individual females produced eggs unique in size, shape and shell color patterns, external features that could provide a mechanism for individuals to eject eggs selectively, so as to avoid evicting their own. For some species, such as the Village Weaverbird (*Ploceus cucullatus*) (Lahti & Lahti 2002), the female habit of laying uniform eggs allows them to eject eggs from parasitic conspecifics. However, our analyses of Guira Cuckoo egg characteristics yielded a low percentage of correct classification of eggs to their mothers, ranging from 22 to 75% (mean of 44%) for 17 groups analyzed (Cariello *et al.* 2004). In fact, there were only six groups where more than 50% of the eggs were classified correctly, and these were typically groups with few females, hence relatively few eggs. We concluded that the high within-individual egg variability of female Guira Cuckoos allows the scrambling of egg identity, and decreases egg ejection because females are seldom able to identify their own eggs. Maintenance of communal breeding in this species may partly derive from individual variability in egg traits.

Blue-black Grassquit. This common, granivorous Emberizid has a wide Neotropical distribution, occurring abundantly in open habitats (Sick 1997). Several striking features of this bird pointed toward a polygynous mating system: (1) unusually conspicuous and elaborate male premating displays; (2) accentuated dichromatism during the breeding season; and (3) lek-like aggregations. On the other hand, it showed some features (e.g., biparental care) indicative of monogamy (Carvalho 1957, Costa & Macedo 2005, Carvalho *et al.* in press).These incongruities suggested the possibility of complex and variable mating behavior that might be hard to detect through traditional field observation and indicated the need to rely on molecular methods. For this we amassed a modest set of nestling and putative-parent blood samples which revealed a remarkable diversity of paternity and maternity. In particular, 7 of the 11 broods (63%) showed extra-pair paternity (involving 10 of the 20 total chicks) (Carvalho *et al.* 2006). These included one chick resulting from intraspecific parasitism (both putative parents excluded) and two cases of "quasiparasitism" (social father genetically related to the brood, but chicks related to more than one female), in addition to the seven chicks resulting from extra-pair paternity. Possible ecological factors that may promote such a high rate of extrapair fertilization include the species' extremely small territories (making effective mate-guarding more problematic), the aggregated distribution of territories during breeding, degree of breeding synchrony (Stutchbury & Morton 2001), and a possible anti-predation strategy that could include "spreading" nestlings over various nests. However, future studies are needed to gain further insight.

Southern Lapwing. Southern Lapwings are also common in the open habitats in all of South America. In central Brazil, the species is notable for occurring in groups varying in size from 2 to 4 adults. Such group members share in territorial defense, incubation and tending of chicks. Thus, this species appeared potentially to be a cooperative breeder, but there was also the possibility that groups of more than two individuals shared reproduction (polygyny/polyandry). We examined the genetic mating system through DNA fingerprinting of 41 chicks from 14 broods, and found evidence of mixed paternity involving four chicks (9.8%) from three broods (21.4%), all from social groups of 3 to 4 adults (Saracura *et al.* in prep.). Since we were unable to catch the supernumerary adults, it remains to be shown whether these extra adults sired some of the chicks. Behavioral observations revealed that isolated pairs (with no supernumerary adults in their unit) maintained smaller distances between themselves than the primary pairs within larger groups. Possibly, primary pairs in groups have a looser pair-bond association, which may either be the causal factor for group breeding or a resulting condition due to the presence of extra adults in the territory. The closer association adopted by isolated pairs may constitute a form of mate-guarding, and possibly prevents extra adults from establishing themselves in the territory, which could lead to shared breeding. Further work is in progress to determine the extant of shared breeding in the species and the adaptive value of reproduction in groups versus pairs.

CONCLUDING REMARKS

In general, tropical birds represent an underutilized opportunity for behavioral ecologists, as such subjects exhibit behavioral patterns that are quite distinctive from those of their better-studied temperate counterparts. In some cases, whole phenomena are restricted to the tropics; in other cases, they are simply much more common in this region. At any rate, it is crucial that more research be undertaken to document the behavioral ecology of Neotropical birds, since these represent such a high proportion of the world´s avifauna. Within such a framework, there are a number of interesting topics in behavioral ecology that have long been neglected and that urgently need more empirical work. In the next couple of decades, deforestation and global changes in weather patterns will produce unpredictable pressures upon avian species, and the conservation of tropical diversity will constitute one of the most challenging tasks for future biologists. Knowledge concerning the basic behavioral ecology of Neotropical birds will prove invaluable in their conservation.

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