ORNITOLOGIA NEOTROPICAL 19 (Suppl.): 151–163, 2008

ADVANCES IN SEXUAL SELECTION THEORY: INSIGHTS FROM TROPICAL AVIFAUNA

Wendy P. Tori[1], Renata Durães[1], Thomas B. Ryder[1], Marina Anciães[2,8], Jordan Karubian[3], Regina H. Macedo[4], J. Albert C. Uy[5], Patricia G. Parker[1], Thomas B. Smith[3,6], Adam C. Stein[5], Michael S. Webster[7], John G. Blake[1], & Bette A. Loiselle[1]

[1]Department of Biology, University of Missouri-St. Louis and Whitney R. Harris World Ecology Center, 1 University Blvd., St. Louis, Missouri 63121-4400, USA.
E-mail: WendyTori@umsl.edu

[2]Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, USA.

[3]Center for Tropical Research, Institute of the Environment, University of California, Los Angeles, Box 951496, California 90095-1496, USA.

[4]Departamento de Zoologia, Universidade de Brasília, Brasília, DF, 70910-900, Brazil.

[5]Department of Biology, 108 College Place, Lyman Hall, Syracuse University, Syracuse, New York 13244, USA.

[6]Department of Ecology and Evolutionary Biology, University of California,Los Angeles, Box 951606, California 90095-1606, USA.

[7]School of Biological Sciences, Washington State University, PO Box 644236, Pullman, Washington 99164-4236, USA.

Resumen. – Avances en la teoría de la selección sexual: contribuciones de la avifauna tropical. – En los últimos 30 años, la selección sexual se ha convertido en una de las áreas de mayor crecimiento e influencia de la biología evolutiva y la ecología de comportamiento. La teoría de la selección sexual tiene efectos importantes en la evolución de las características de historia de vida, sistemas de cortejo y morfología, y ha sido sugerida como un factor que promueve la especiación. Las aves han jugado un rol esencial en su desarrollo. Sin embargo, la mayoría de estudios se han enfocado en especies de zonas templadas, a pesar que ellas comprenden menos de un cuarto de las especies de aves del mundo. Por lo tanto, antes de aplicar universalmente las teorías existentes, se recomienda cautela, especialmente considerando las tendencias latitudinales en las características de historia de vida y las estrategias evolutivas. Aquí, hemos seleccionado cinco estudios con aves tropicales que cubren diferentes aspectos de la teoría de la selección sexual. Dos estudios detallan los procesos evolutivos involucrados con signos de plumaje; uno de ellos estudia la influencia del "sensory drive" de las hembras en la evolución del plumaje de los machos, y el segundo investiga como la selección no azarosa de apareamiento puede promover la introgreción genética a lo largo de una zona de hibridación. Un tercer estudio examina como la diferencia de dieta entre sexos puede llevar a la asincronía temporal entre el periodo pico de actividad de despliegue de machos y el anidamiento de hembras. Un cuarto estudio detalla como diferencias en la estructura espacial de las asambleas

---

[8] *Current address:* Bird Collection, Instituto Nacional de Pesquisas da Amazônia – INPA, Av. André Araújo 2936, Petrópolis, Manaus-AM 69060-001, Brazil.

de cortejo y la organización social influencian el grado de sesgo reproductivo de machos saltarines. El quinto estudio examina las diferencias en la intensidad de selección sexual en taxones de zonas templadas y tropicales, y evalúa, entre regiones, nuestro conocimiento actual sobre la frecuencia de la paternidad extra-pareja. Se discuten las contribuciones de estos estudios a nuestro entendimiento actual de la selección sexual.

Abstract. – Over the last 30 years, sexual selection has become one of the most influential and rapidly growing areas within evolutionary biology and behavioral ecology. Sexual selection has important effects on the evolution of life history traits, mating systems and morphology, and also has been suggested as a factor that promotes speciation. Avian systems have played an essential role as models in the development of sexual selection theory. However, most studies have focused on temperate species, although they account for less than one quarter of avian species worldwide. Therefore, before applying existing theories universally, caution is advised, especially considering latitudinal trends in life history traits and evolutionary strategies. Here, we brought together five tropical bird studies covering different aspects of sexual selection theory. Two studies detail the evolutionary processes involved with plumage signals; one of these deals with the influence of female sensory drive on the evolution of male plumage, and the second investigates how non-random female mate choice can promote genetic introgression along a hybrid zone. A third study examines how sex differences in diet can lead to temporal asynchrony between periods of peak male display activity and female nesting. A fourth study details how differences in lek spatial structure and social organization influence the degree of male reproductive skew among manakins. The fifth study examines differences in the intensity of sexual selection in temperate and tropical taxa and assesses current knowledge regarding the frequency of extra-pair paternity among regions. The contributions of these studies to our current understanding of sexual selection are discussed. *Accepted 14 October 2007.*

Key words: Extra-pair paternity, hybridization, lekking, mate choice, reproductive skew, sexual selection, tropical birds, tropical-temperate comparisons, visual signals.

INTRODUCTION

Since initially proposed by Charles Darwin (1859, 1871), the theory of sexual selection has generated considerable interest and controversy among evolutionary biologists. Broadly speaking, sexual selection theory concerns the evolution and selection of traits that affect mating success (Andersson 1994). Elaborate and often costly phenotypic traits are hypothesized to arise through differences in reproductive success as a function of competition for mates. This variance in reproductive success is promoted by two distinct selective processes. The first is the intra-sexual component of sexual selection, which results from direct competition among individuals of the same sex (usually males) for mates. The second is the inter-sexual component of sexual selection, in which individuals of one sex (usually females) drive evolution of traits in the opposite sex through non-random mate choice. Establishing the relative importance of such intra- and inter-sexual components in empirical studies is often difficult and complicated by the interaction between these two processes.

Over the last 30 years, sexual selection theory has become one of the fastest developing areas in evolutionary and behavioral ecology (Gross 1994). Sexual selection is now recognized as an essential evolutionary factor shaping behavior, morphology, life history, and mating systems, both in animals and plants (Searcy 1982, Andersson 1994), and can also be an important force driving speciation (Lande 1981, Ptacek 2000, McDonald *et al.* 2001, Stein & Uy 2006). Birds have played a central role as subjects for the study of sexual selection. However, the vast majority of birds that have been studied are from the temperate zone. Temperate species comprise less than 25% of all bird species worldwide (Martin 2004), and among passerines, 80% (~4000) of species are in the tropics (Stutchbury & Morton 2001). This begs the question of whether the important findings we are rapidly accumulating in the field of sexual selection are universally applicable or not. Although the current lack of data on tropical species makes comparisons difficult, there are reasons to be wary before directly applying concepts developed from studies of temperate species to tropical systems. For example, several life history components are known to show latitudinal variation (e.g., Martin 1996, Martin *et al.* 2000, Ghalambor & Martin 2001), and we can expect that differences in characteristics such as survival, investment in reproduction, territoriality, breeding synchrony, and frequency of extra-pair paternity will lead to variation in the opportunity for sexual selection.

The diversity of mating systems and complex social behaviors observed among tropical species presents excellent opportunities to develop model systems for both empirical and theoretical sexual selection research. Here, we outline five examples of current research on tropical birds, and discuss how these studies have contributed to a more general understanding of sexual selection among lekking and socially monogamous species. Two studies examine how sexually selected signals in the family Pipridae are driven by signal perception in variable habitats via sensory drive in the *Illicurinii* tribe and by genetic introgression and frequency-dependent female choice in the *Manacus* clade. A third study explores how sex-related differences in diet may cause temporal asynchrony between male courtship behavior and female nesting in Long-wattled Umbrellabirds (*Cephalopterus penduliger*), and discusses the potential role for leks as information exchange centers. A fourth study examines how variation in spatial structure and social organization in the family Pipridae influence the intensity of sexual selection as measured by male reproductive skew. The fifth study reviews our current knowledge about differences in the frequency of extra-pair copulation among tropical and temperate avian species and possible explanations for such differences.

PLUMAGE CONSPICUOUSNESS IN DISPLAYING MANAKINS (PIPRIDAE) FROM THE *ILICURA–CORAPIPO* CLADE: A COMPARATIVE TEST OF THE SENSORY DRIVE HYPOTHESIS

Sexual selection by female choice has promoted the evolution of exaggerated male phenotypes among lekking birds (Kirkpatrick & Ryan 1991, Anderson 1994). However, competing hypotheses suggest different roles for how ecological specializations act on mate choice, and ultimately shape the evolution of male phenotypes, both morphological and behavioral (Prum 1997). Among them, sensory drive (Endler & McLelland 1988) predicts the evolution of conspicuous phenotypes because of reduced costs associated with mate search. In order to evolve by sensory drive, signals should be produced within sensory conditions that favor conspicuousness. Among polygynous lekking birds, the hypothesis predicts that males should display in light conditions at display sites, and at non-random subsets of sites within the habitat, that favor signal detection by females; and that females should visit males displaying under light environments that favor detection. These predictions were tested among five closely related species within the manakins from the *Ilicura-Corapipo* clade [Pin-tailed Manakin (*Ilicura militaris*), White-throated Manakin (*Corapipo gutturalis*), White-ruffed Manakin (*Corapipo leucorrhoa*), Pacific White-ruffed Manakin (*C. heteroleuca*), White-bibbed

Manakin (*C. altera*), and Golden-winged Manakin (*Masius chrysopterus*)].

Visual signals produced by males during displays were modeled based on ambient light (Endler 1990, 1993) and plumage spectra measured with spectrometers (Ocean Optics, Inc.) in the habitat of studied populations and from captured individuals and museum specimens, respectively. Female sensory systems were modeled with estimates of spectra sensitivities based on the opsin genes sequenced for the species, following Ödeen & Håstad (2003), and on the likely composition of carotenoids present in the oil droplets from the cone photoreceptors found in bird retinas (Goldsmith *et al.* 1984, Goldsmith & Buttler 2003). Contrast was estimated for both close (within plumage contrast) and far (between plumage and background) distances, based on modeled thresholds from the receptor-noise model equations (Vorobyev & Osorio 1998). Within plumage contrasts were estimated and compared using the LSED-MRPP method (Mielke & Berry 2001, Endler & Mielke 2005), and contrasts between plumage and background were estimated in values of just noticeable differences (Osorio & Vorobyev 1986, Vorobyev *et al.* 1998, Siddiqi *et al.* 2004, Eaton 2005), compared through nonparametric and parametric analyses of variance.

Our results support a role of sensory drive in the evolution of conspicuous male phenotypes within populations, based on chromatic contrast during male displays in all species, and on achromatic contrasts in the White-throated Manakin, suggesting that changes in behavior enhanced signal conspicuity. More specifically, all species but the Pin-tailed Manakin showed increased within-plumage contrast or contrast between plumage and background in the light category most used during male display (i.e., cloudy, shade, sunny gaps). In the case of the Pin-tailed Manakin, the within-plumage contrast was more contrasting during all light categories used for displays, when compared to periods without displays at display sites. Moreover, the Pin-tailed Manakin, White-bibbed Manakin and Pacific White-ruffed Manakin display sites provided light conditions that increased contrast in comparison to light conditions measured at sites not used for displays (i.e., non-display sites). Female visits, however, were not more frequent during displays in ambient light conditions of increased male plumage contrast, in comparison to the average contrast of male displays.

Our results indicate that the behavioral novelty observed in the White-throated Manakin – a male preference for displaying under sunny conditions (Endler & Théry 1996, Anciães & Prum in prep.) – is associated with a new sensory environment available for the species (Anciães & Prum in prep.) and corresponds to an increase in plumage contrast within the studied population. However, these associated changes were preceded by the evolution of the glossy blue-black plumage typical of the genus, which arose in the ancestor of *Corapipo*, indicating that this plumage has not evolved for conspicuousness. Furthermore, plumage contrast was highly decreased in *Corapipo* when compared to the other species from the clade, *Ilicura* and *Masius*, either in their own habitat or in simulations using the ambient light available to the other species, indicating that yellow and red plumages are more contrasting under any of the light environments sampled here, which are mainly green even during cloudy conditions. Lastly, the data indicate a weak association between changes in plumages and ambient light among species an a strong correlation between sensory environments and ecological niches (Anciães 2005), showing considerable plumage differentiation among species with relative similar ecologies.

SEXUAL SELECTION AND THE DYNAMICS OF DISPLAY TRAIT INTROGRESSION ACROSS HYBRID ZONES

Hybridization among individuals from distinct species typically results in less fit offspring but it can also be a creative evolutionary process by acting as a conduit for the exchange of novel traits between populations (Anderson & Stebbins 1954). When understanding the origin of elaborate traits and female preferences, studies often assume that the trait and preference emerge within the population and eventually reach fixation (see Andersson 1994). Alternatively, display traits and female preferences may have originated from another population and spread secondarily into a given population. Although this does not address the ultimate origin of a trait and preference, it does provide a mechanism for the evolution of elaborate displays and preferences for a given population.

The closely related Golden-collared (*Manacus vitellinus*) and White-collared (*M. candei*) manakins form a hybrid zone characterized by several concordant genetic and morphometric clines centered near Rio Robalo in Western Panama. A cline for yellow plumage, however, is displaced by 50 km to the west, into the white-collared population, where it forms a similar steep cline near Rio Changuinola (Brumfield *et al.* 2001). Adult males in the 50 km region between Rio Robalo and Rio Changuinola therefore carry predominantly white-collared alleles but look similar to Golden-collared Manakins due to the introgressed yellow plumage (Brumfield *et al.* 2001).

At the edge of the plumage cline, yellow- and white-collared males form common mating arenas (“mixed leks”). We monitored yellow and white males in these mixed leks to determine the underlying mechanisms that favor the spread of yellow plumage. In addition, we used a spectrophotometer to measure the color properties of male plumage, the visual background and the ambient light at the hybrid zone, and at pure golden and white populations. This allowed us to determine if a variable visual habitat can influence the attractiveness and hence the patterns of yellow plumage introgression.

We found that yellow males had significantly higher mating success than white males at mixed leks, suggesting that sexual selection favoring yellow males drives the unidirectional spread of yellow plumage across the *Manacus* hybrid zone (Stein & Uy 2006). In addition, we found that yellow and white males did not differ in body size, position in leks and levels of aggressiveness, suggesting that male-male competition cannot explain the yellow male mating advantage. However, we found that females visited both yellow and white males, and rejected white males for yellow males. This suggests that the yellow male mating advantage may be driven by female preference for yellow males.

The yellow male mating advantage is large. Yellow plumage is therefore expected to sweep through the white-collared population; however, the plumage cline seems stable near Rio Changuinola. This suggests that some factors may be constraining its rapid spread. We found that at least two factors may slow the rate of trait introgression. First, we found that the yellow male mating advantage only occurs in mixed leks where yellow males are in high frequencies. At the leading edge of the plumage cline, yellow males are rare and so would not experience a significant mating advantage over white males until they reach higher frequencies, thus slowing the spread of yellow plumage into the white population (Stein & Uy 2006). Second, as measured by the perceived difference in color between male plumage and the visual background, we found that yellow plumage appears more conspicuous than white plumage in the hybrid zone and allopatric golden-collar habitats, while white plumage appears more conspicuous than yellow plumage in the allopatric white-collared habitat (Uy & Stein 2007). This pattern suggests a mechanism for the unidirectional spread of yellow plumage across the hybrid zone but slowed movement beyond it.

The role of hybridization as a source of genetic variation for adaptive traits has long been appreciated (e.g., Grant & Grant 1994), but its potential role in the evolution of elaborate display traits is relatively unexplored. Given that over 10% of avian species hybridize with little to no costs (Grant & Grant 1992), hybridization can be important in the origin of novel display traits.

LEK DYNAMICS AND SEXUAL SELECTION IN THE LONG-WATTLED UMBRELLABIRD

In lek breeding species, males and females follow dramatically different reproductive strategies. Typically, males defend territories on leks and attempt to attract multiple mates whereas females focus on nesting and parental care (Wiley 1991, Höglund & Alatalo 1995). This leads to a very different set of evolutionary pressures on the sexes and is the primary cause of the behavioral and morphological sexual dimorphism typical of lek-breeding species (Andersson 1994, Dunn *et al.* 2001). The ecological implications of these sex-related differences, however, are less well understood. Here, we provide an overview of lek dynamics of the Long-wattled Umbrellabird, with special emphasis on the potential implications of ecological and behavioral variation between the sexes.

Long-wattled Umbrellabirds are large, frugivorous birds endemic to the humid Chocó rain forests of northwestern Ecuador and western Colombia (Snow 1982). As with many members of the family Cotingidae, male Long-wattled Umbrellabirds aggregate in leks to display to females but provide no parental care (Jahn *et al.* 1999, Karubian *et al.* 2003), suggesting that the opportunity for sexual selection may be high. In our study population in Bilsa Biological Station, northwestern Ecuador (Berg *et al.* 2000), we found that males were approximately 1.5x larger than females and had wattles and crests approximately four times larger than those of females. Variance in these traits was similar between the sexes. Juvenile males spent at least one year with crests, wattles, and body size intermediate between adult males and females.

Lek size ranged from 1–15 males, and males exhibited at least two strategies during the breeding season. Some males (usually 5–10 per lek) held fixed territories while other "floating" males moved between leks without holding territories. These floating males may have been younger, competitively inferior males moving in response to spatial and temporal variation in fruit availability. Territorial males were observed departing and returning to leks in a coordinated manner and foraging in groups away from leks. One un-tested possibility is that leks may serve some role in information-sharing as well as mate choice. In this sense, individuals may find patchily-distributed food resources by following other males when leaving the lek (Wagner & Danchin 2003).

Lek activity was strongly seasonal. Number of males at the lek, average song rate, and rate of female visitation were highest during the dry season (August–December), whereas the period of lowest lek activity corresponded to the wettest part of the year. Even during periods of lowest lek activity, however, at least some males were present at each lek. Surprisingly, most female nesting occurred when lek activity was at its lowest, leading to a temporal disconnect between activity at leks and female nesting (which peaked six months after peak lek activity). This incongruous pattern may be driven by the fact that males and females track different resources. Males may rely on fruit to maintain the physiological state required for energetically costly song and displays at the lek, whereas females may rely on insects for nesting, egg production, and provisioning of the young. Consistent with this idea, we found that males ate more fruit than did females, and that male fruit consumption during low lek activity periods was approximately one-half that of high lek activity periods. A further prediction, which remains to be tested, is that fruit availability will be highest during periods of high lek activity, while insect abundance will peak concurrently with female nesting.

How the birds manage to fertilize eggs and reproduce given this unusual asynchrony between lek activity and nesting is an open question. Females may be capable of storing male sperm for long periods of time. Alternatively, only a subset of the fittest males may be able to maintain year-round presence at the lek sites, and it is during periods of lowest lek activity that these males–monopolize matings with females.

SPATIAL STRUCTURE AND SOCIAL ORGANIZATION OF MANAKINS: POTENTIAL IMPLICATIONS FOR MALE REPRODUCTIVE SKEW

Lekking is a promiscuous mating system in which males congregate in display arenas that females visit to mate. Males do not provide parental care and do not monopolize resources essential to females. This leads to strong sexual selection and variance in male-mating success (hereafter male reproductive skew). The degree of male reproductive skew is hypothesized to vary as a function of temporal (e.g., female breeding synchrony, Shuster & Wade 2003), spatial (e.g., female crowding, Schuster & Wade 2003, inter-lek spacing, Foster 1983), and social characteristics (e.g., dominance, Foster 1983). Sexual selection theory suggests that, when given a choice, females may maximize their fitness by mating preferentially with high quality males (Andersson 1994, Höglund & Alatalo 1995, Shuster & Wade 2003). To do so, females must have the opportunity to assess potential mates. The degree of temporal synchrony and spatial overlap among sexes constrains female access to males, and has potential implications for male reproductive skew. Moreover, social organization of males (e.g., dominance hierarchies) may have repercussions on male mating success by limiting female choice (Foster 1983).

In this study, we examined spatial and social factors that may influence reproductive skew for three co-occurring lekking manakin species: the Wire-tailed Manakin (*Pipra filicauda*), the Blue-crowned Manakin (*Lepidothrix coronata*), and the White-crowned Manakin (*Pipra pipra*). These species share many ecological (e.g., diet) and morphological traits (e.g., body size, sexual plumage dichromatism). Moreover, they overlap broadly in their breeding period and, thus, are expected to show few inter-specific differences in temporal factors. In contrast, these manakins differ in spatial structure and social organization (Loiselle *et al.* 2007), making them ideal for a study on the effects of these factors on reproductive skew. Here, we specifically examined the effects of three factors, with the following predictions: 1) Female crowding, measured as the degree of female spatial aggregation: species with clumped female dispersion were predicted to have higher reproductive skew because males will have differential access to females depending on where their territories are located in relation to the areas of high female concentration; 2) Male encounter rate, measured as the proportion of males in the population potentially encountered by females: in species with greater male encounter rate, females have the ability to compare and assess a greater number of mates (assuming females have similar mating preferences, certain males will have higher reproductive success than others leading to high reproductive skew); 3) Dominance, measured as the degree of male associations and the presence of dominance hierarchies among males: in species with dominance hierarchies, top-ranking males may control access to females and are expected to have higher reproductive success than subordinate males, thus increasing reproductive skew.

Male mating success was measured using microsatellite paternity analyses based on DNA collected from chicks and mothers at nests and from potential fathers at leks. Reproductive skew was measured using λ index (Kokko & Lindström 1997) and binomial skew index (Nonacs 2000). Species were ranked according to their degree of female crowding (i.e., spatial overlap using Moran's I, Moran 1950), male encounter rate and dominance; reproductive skew predictions were generated based on these factors. The Wire-tailed Manakin had relatively low levels of female crowding, intermediate male encounter rates, and facultative associations among males (strongest association among the three species). The White-crowned Manakin had an intermediate degree of female crowding, intermediate male encounter rate and a loose association among males. The Blue-crowned Manakin had a low degree of female crowding, low male encounter rate and the weakest association among males. Given these spatial and social characteristics, our overall prediction (including the three factors) was that the Wire-tailed Manakin should have the highest reproductive skew, followed by the White-crowned Manakin; the Blue-crowned Manakin was predicted to have the lowest reproductive skew.

Our results generally supported our predictions as we found a relationship between the targeted spatial and social factors and male reproductive skew. Species differed in degrees of reproductive skew and those differences matched our overall prediction. In particular, male encounter rate by females and dominance were the two factors that best explained skew differences between species. Further studies are needed to differentiate the relative importance between these two factors. In a broader context, our results provide information about how population-level processes have the potential to influence the variance in male reproductive success, and ultimately the direction and strength of sexual selection.

SEXUAL SELECTION AND MONOGAMY IN TROPICAL AND TEMPERATE BIRDS

Many socially monogamous bird species are subject to strong sexual selection, a fact that has baffled biologists since Darwin (1871). Evidence is mounting that extrapair paternity (EPP) are common in socially monogamous species (reviewed in Griffith *et al.* 2002) and can potentially generate strong sexual selection (Webster *et al.* 1995). However, the vast majority of this evidence comes from studies of temperate zone species, yet 80% of all passerine birds are tropical. Indeed, it has been suggested that EPC are uncommon and therefore unimportant to sexual selection in tropical birds (Stutchbury & Morton 2001). Thus, we face two important questions with regard to the role of EPP in sexual selection: is EPP less common in the tropics than in the temperate zone? And, if so, what drives sexual selection in tropical monogamous species?

Three lines of evidence have been used to suggest that EPP is less important to sexual selection in tropical monogamous systems, but each has problems. First, testes size is thought to be positively associated with rates of EPP (Møller & Briskie 1995, Dunn *et al.* 2001) and some studies have indicated that tropical species generally have smaller testes than temperate species (Stutchbury & Morton 2001), thus suggesting that tropical birds have low rates of EPP. However, the relationship between testes size and EPP rates is unclear (Calhim & Birkhead 2007), and other studies have indicated that there is no latitudinal trend in testes size (Dunn *et al.* 2001, Pitcher *et al.* 2005). Second, the breeding synchrony hypothesis (Stutchbury & Morton 2001), which posits a positive relationship between breeding synchrony and rates of extrapair paternity, suggests lower EPP rates in the tropics because, in many cases, tropical birds breed less synchronously than do temperate birds. However, the effects of breeding synchrony are controversial and may not be associated with EPP rates (Saino *et al.* 1999, Yezerinac & Weatherhead 1997). Finally, some genetic studies of tropical birds have shown low EPP rates, and this has been extrapolated to a conclusion of generally low rates of EPP in tropical species (Stutchbury & Morton 2001). However, to date data are available for only seven tropical species, of which three show no EPP, three exhibit rates of 8 to 15% of the brood, and one species exhibits a high rate of EPP (Stutchbury & Morton 2001).

We do not want to reject the possibility that EPP is rare in tropical birds, but we would like to challenge this view. We believe that a first crucial step would be to critically assess the assumptions (e.g., breeding synchrony hypothesis) and data (e.g., EPP rates, testes size) underlying the concept that EPP in tropical birds is rare. Additionally, the question of whether tropical birds have EPP rates similar to that of temperate birds, and whether EPP in these birds contributes to sexual selection are issues that can only be resolved with more data. Our studies of two tropical and socially monogamous species, the Red-backed Fairywren (*Malurus melanocephalus*) and the Blue-black Grassquit (*Volatinia jacarina*) show that extrapair copulations are important to the sexual selection process for at least some tropical species. Both of these species exhibit high EPF rates (Red-backed Fairywrens: 51.1% of 514 nestlings sired by extra-pair males; Blue-black Grassquit: 50% of 20 nestlings) and a highly skewed distribution of male reproductive success. Moreover, the relationship between total male reproductive success and number of extra-pair mates (i.e., the "Bateman gradient") was strongly positive for both species, with number of mates accounting for 71% (Fairy-wrens) and 57% (Blue-black Grassquits) of the total variance in male reproductive success. These cases illustrate that EPP can be high in tropical birds, and we suggest that sexual selection can operate via different mechanisms in many tropical species.

Thus, more data are needed before we can draw general conclusions about the mechanisms of sexual selection in monogamous birds. If EPP is indeed rare in tropical birds, then a comparison of tropical to temperate species should yield important insights into the ecological factors leading to variation in EPP rates, such as breeding synchrony or migration (reviewed in Petrie & Kempenaers 1998 and Griffith *et al.* 2002). Moreover, a generally low frequency of EPP in the tropics would suggest that sexual selection operates via different mechanisms in the temperate zone and in the tropics, and this might have important implications for the sort of sexual signals that might have evolved. In contrast, if EPP is as common in the tropics as it is in the temperate zone, then there may be a common and general mechanism driving the process of sexual selection in monogamous systems across latitudes.

CONCLUDING REMARKS

In 1871, Darwin introduced the concept of sexual selection to describe differences in morphological and behavioral characteristics among individuals that could have an impact upon their reproductive success. Since then, the study of sexual selection has come a long way, theoretically and empirically, despite the fact that many of its core concepts remain unchanged (Andersson 1994). The tropics, with its incredible diversity of species, complex social behaviors and mating systems, provide exceptional opportunities to conduct research and increase our current knowledge of sexual selection. In this symposium, we brought together five examples of current research on tropical birds to examine what insights tropical taxa provide to sexual selection theory. These studies make four general contributions to our current understanding of sexual selection.

First, they shed light on the origins and evolution of exaggerated male display, a topic that has been controversial for a long time. Two studies provided evidence that male display traits evolved in response to environmental conditions and one of them that display traits can originate via hybridization. These findings are important because they reveal two potential mechanisms that may play an important role in the evolution of the spectacular diversification of male secondary sexual traits in the tropics.

Second, these studies demonstrated that a single trait rarely is implicated as the sole factor that explains female choice. Rather, mate choice is demonstrated to be context-dependent where selection on particular traits may differ or be constrained by environmental or social context. For example, environmental features, such as insect abundance, may affect female reproductive behavior in umbrellabirds, while fruit abundance may influence male display activity at leks. Further, environmental features at leks appear to influence contrast in male plumage, and thus determine whether Yellow- or White-collared Manakin males are preferred by females. Although males of three other manakin species were shown to display at sites and under light conditions that heightened plumage contrast and supposed detection by females, such behavior did not always result in more female visits. Failure to find increased female visitation under favorable light conditions does not necessarily indicate that plumage contrast is not an important cue in female choice. Rather, female visits may be influenced by spatial overlap of females with male display sites and attractive males may be located at sites that intercept few females. Moreover, population-level analyses of variance in male reproductive success showed that spatial and social aspects of lek organization are important factors influencing female choice, male reproductive success and, ultimately, the strength of sexual selection.

Third, one study demonstrated that sexual selection also operates, and can be a strong evolutionary force, in socially monogamous birds. Data are currently limited, but it is clear that this is true for at least some tropical species as well as for temperate species. While extra-pair paternity suggests that, even in monogamous systems, females may have relatively free choice of mating with multiple partners, in reality female mating options may be limited by male behaviors (e.g., male guarding) and also by ecological factors (e.g., breeding synchrony). The extent to which these factors can account for variation in EPP rates across species remains an open question, and comparisons of tropical species in different environments, as well as between tropical and temperate species, should be revealing.

Fourth, these studies demonstrated how recently developed methods and equipment are now used to characterize sexually-selected traits in biologically meaningful ways, and are helping to advance our understanding of female choice and its impact on male reproductive variance and sexual selection. Paternity analysis using molecular markers has become increasingly important to provide direct measures of female choice and variance in male mating success, and understand the complexities and evolution of mating systems in birds. Molecular tools also allow us to understand how female choice can influence genetic introgression and hybridization. Finally, reflectance spectrometry revealed previously hidden sexual dichromatism and allowed quantitative measures of plumage coloration.

It is our opinion that established paradigms should be viewed cautiously if we want to understand how sexual selection acts on tropical species. The remarkable diversity of the tropics challenges generalizations, both among species that dwell in these regions and in comparison to their temperate counterparts. For example, paradigms suggesting that tropical species engage less frequently in EPFs than temperate species seem not to hold up in face of the limited empirical data available (e.g., *Malurus, Volatinia*). In the past 30 years, we have accumulated a wealth of knowledge on sexual selection processes, but testing predictions on tropical systems still lags behind. The good news is that we now have the analytical and theoretical tools to pursue this objective and, as shown in this symposium, the process is already underway.

ACKNOWLEDGMENTS

We would like to thank the Neotropical Ornithological Society and the organizers of the VIII Neotropical Ornithological Congress, specially Carlos Bosque, Jorge Pérez-Eman and Joe Wunderle, for giving us the opportunity and support to run this symposium. Major funding for the different studies presented was provided by National Science Foundation, the Disney Foundation, Conservation Food and Health Foundation, Wildlife Conservation Society and National Geographic Society. WPT and RD would like to thank the Neotropical Ornithological Society for student travel awards. We are grateful to many people who assisted in collecting field data and/or provided logistic support for the development of these studies.

REFERENCES

Anciães, M. 2005. Evolution of visual signals and the ecological niches among manakins from the tribe Ilicurinii (Aves: Pipridae). Ph.D. diss., Univ. of Kansas, Lawrence, Kansas.

Anderson, E., & G. L. Stebbins. 1954. Hybridization as an evolutionary stimulus. Evolution 8: 378–388.

Andersson, M. 1994. Sexual selection. Monographs in behavior and ecology, Princeton Univ. Press, Princeton, New Jersey.

Berg, K. S. 2000. Field notes on the biology of the Long-wattled Umbrellabird *Cephalopterus penduliger* in west Ecuador. Cotinga 14: 26–29.

Brumfield, R. T., R. W. Jernigan, D. B. McDonald, & M. J. Braun. 2001. Evolutionary implications of divergent clines in an avian (*Manacus* : Aves) hybrid zone. Evolution 55: 2070–2087.

Calhim, S., & T. R. Birkhead. 2007. Testes size in birds: quality versus quantity—assumptions, errors, and estimates. Behav. Ecol. 18: 271–275.

Darwin, C. 1859. On the origin of species by means of natural selection. J. Murray, London, UK.

Darwin, C. 1871. The descent of man and selection in relation to sex. J. Murray, London, UK

Dunn, P. O., L. A. Whittingham, & T. E. Pitcher. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. Evolution 55: 161–175.

Eaton, M. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. Proc. Natl. Acad. Sci. 102: 10942–10946.

Endler, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns. Biol. J. Linn. Soc. 41: 315–352.

Endler, J. A. 1993. The color of light in forests and its applications. Ecol. Monogr. 63: 1–27.

Endler, J. A., & T. McLellan. 1988. The process of evolution: toward a new synthesis. Annu. Rev. Ecol. Syst. 19: 395–421.

Endler, J. A., & P. W. Mielke Jr. 2005. Comparing entire colour patterns as birds see them. Biol. J. Linn. Soc. 86: 405–431.

Endler, J. A., & M. Théry. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. Am. Nat. 148: 421–452.

Foster, M. 1983. Disruption, dispersion and dominance in lek-breeding birds. Am. Nat. 122: 53–72.

Ghalambor, C. K., & T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292: 494–497.

Goldsmith, T. H., & B. K. Butler. 2003. The roles of receptor noise and cone oil droplets in the photopic spectral sensitivity of the Budgerigar, *Melopsittacus undulatus.* J. Comp. Psychol. 189: 135–142.

Goldsmith, T. H., J. S. Collins, & S. Licht. 1984. The ultraviolet receptors of avian retinas. Vision Res. 24: 1661–1671.

Grant, P. R., & B. R. Grant. 1992. Hybridization of bird species. Science 256: 193–197.

Grant, P. R., & B. R. Grant. 1994. Phenotypic and genetic-effects of hybridization in Darwin's finches. Evolution 48: 297–316.

Griffith, S. C., I. P. F. Owens, & K. A. Thuman. 2002. Extra pair paternity in birds: a review of interespecific variation and adaptive function. Mol. Ecol. 11: 2195–2212.

Gross, M. R. 1994. The evolution of behavioural ecology. Trends Ecol. Evol. 9: 358–360.

Höglund, J., & R. Alatalo. 1995. Leks. Monographs in behavior and ecology. Princeton University Press, New Jersey.

Jahn, O., E. E. Vargas-Grefa, & K. L. Schuchmann. 1999. The life history of the Long-wattled Umbrellabird *Cephalopterus penduliger* in the Andean foothills of north-west Ecuador: leks, behaviour, ecology and conservation. Bird Conserv. Int. 9: 81–94.

Karubian, J., G. Casteneda, J. F. Freile, T. Santander, & T. B. Smith. 2003. Breeding biology and nesting behavior of the Long-wattled Umbrellabird *Cephalopterus penduliger* in northwestern Ecuador. Bird Conserv. Int. 13: 351–360.

Kirkpatrick, M., & M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. Nature 350: 33–38.

Kokko, H., & J. Lindström. 1997. Measuring the mating skew. Am. Nat. 149: 794–799

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA 78: 3721–3725.

Loiselle B. A., J. G. Blake, R. Durães, T. B. Ryder, & W. P. Tori. 2007 Environmental segregation in lek sites among six co-occurring species of manakins (Aves: Pipridae) in eastern Ecuador. Auk 124: 420–431.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? J. Avian Biol. 27: 263–272.

Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright future? Auk 121: 289–301.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, & J. J. Fontaine. 2000. Parental care and clutch size in North and South American birds. Science 287: 1482–1485.

McDonald, D. B., R. P. Clay, R. T. Brumfield, & M. J. Braun. 2001. Sexual selection on plumage and behavior in an avian hybrid zone: experimental tests of male-male interactions. Evolution 55: 1443–1451.

Mielke, P. W. Jr., & K. J. Berry. 2001. Permutation methods: a distance function approach. Springer-Verlag, New York, New York.

Møller, A. P., & J. V. Briskie. 1995. Extra-pair paternity, sperm competition and the evolution of testis size in birds. Behav. Ecol. Sociobiol. 36: 357–365.

Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. Biometrika 37: 17–23.

Nonacs, P. 2000. Measuring and using skew in the study of social behavior and evolution. Am. Nat. 156: 577–589.

Ödeen, A., & O. Håstad. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. Mol. Biol. Evol. 20: 855–861.

Osorio, D., & M. Vorobyev. 1996. Colour vision as an adaptation to frugivory in primates. Proc. R. Soc. Lond. 263: 593–599.

Petrie, M., & B. Kempenaers. 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol. Evol. 13: 52–58.

Pitcher, T. E., P. O. Dunn, & L. A. Whittingham. 2005. Sperm competition and the evolution of testes size in birds. J. Evol. Biol. 18: 557–567.

Prum, R. O. 1997. Phylogenetic tests of alternative intersexual selection mechanisms: trait macroevolution in a polygynous clade (Aves: Pipridae). Am. Nat. 149: 668–692.

Ptacek, M. B. 2000. The role of mating preferences in shaping interespecific divergence in mating signals in vertebrates. Behav. Processes 51: 111–134.

Saino, H., C. R. Primmer, H. Ellegren, & A. P. Møller. 1999. Breeding synchrony and paternity in the Barn Swallow (*Hirundo rustica*). Behav. Ecol. Sociobiol. 45: 211–218.

Searcy, W. A. 1982. The evolutionary effects of mate selection. Annu. Rev. Ecol. Syst. 13 :57–85.

Shuster, S. M., & M. J. Wade. 2003. Mating systems and strategies. Monographs in behavior and ecology, Princeton Univ. Press, Princeton, New Jersey.

Siddiqi, A., T. W. Cronin, E. R. Loew, M. Vorobyev, & K. Summers. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio.* J. Exp. Biol. 207: 2471–2485.

Snow, D. W. 1982. The cotingas. Cornell Univ. Press, Ithaca, New York.

Stein A. C., & J. A. C. Uy. 2006. Unidirectional introgression of a sexually selected trait across an avian hybrid zone: a role for female choice? Evolution 60: 1476–1485.

Stutchbury, B. J. M., & E. S. Morton. 2001. Behavioral ecology of tropical birds. Academic Press, San Diego, California.

Uy, J. A. C., & A. C. Stein. 2007. Variable visual habitats may influence the spread of colorful plumage across an avian hybrid zone. J. Evol. Biol. 20: 1847–1858.

Vorobyev, M., & D. Osorio. 1998. Receptor noise as a determinant of colour thresholds. Proc. R. Soc. Lond. 265: 351–358.

Vorobyev, M., D. Osorio, A. T. D. Bennett, N. J. Marshall, & I. C. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colours. J. Comp. Physiol. A 183:621–633.

Wagner, R. H., & E. Danchin 2003. Conspecific copying: a general mechanism of social aggregation. Anim. Behav. 65: 405–408.

Webster, M. S., S. Pruett-Jones, D. F. Westneat, & S. J. Arnold. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. Evolution 49: 1147–1157.

Wiley, R. H. 1991. Lekking in birds and mammals: behavioral and evolutionary issues. Adv. Stud. Behav. 20:201–291.

Yezerinac, S. M., & P. J. Weatherhead. 1997. Extra-pair mating, male plumage coloration and sexual selection in Yellow Warblers (*Dendroica petechia*). Proc. R. Soc. Lond. B. 264 : 527–532.