

RECENT ADVANCES IN THE BEHAVIORAL ECOLOGY OF TROPICAL BIRDS

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ABSTRACT.—Tropical birds offer unique opportunities to test ecological and evolutionary theory because their life history traits are so diverse and different from temperate zone models upon which most empirical studies are based. We review recent studies on the behavioral ecology of tropical birds, studies that explore new advances in this field. Life histories and their evolution remain the focus of research on tropical birds. Clutch size manipulations in two species showed that food limitation does not explain small clutch size. In antbirds, enlarged clutches decreased post-fledging survival whereas in thrushes, enlarged broods were costly due to high nest predation. Small clutches may be favored via different ultimate selective forces and shared underlying tradeoffs between the immune, metabolic, and endocrine systems in the body may account for the commonly observed ‘slow pace of life’ in tropical birds. The physiological tradeoff between testosterone and immunocompetence may explain the evolution of low testosterone levels in tropical passerines where adult survival is paramount. In contrast to life history theory, few studies have explored temperate-tropical differences in territoriality, mating systems, and song function. The idea that low breeding synchrony in tropical birds is associated with low levels of extra-pair fertilizations was supported by several new paternity studies conducted on tropical passerines. Seasonally breeding tropical birds have higher testosterone levels than tropical birds with prolonged breeding seasons, although it is unclear if this pattern is driven by mating systems *per se* or selection from pathogens. Recent work on relations between pair members in permanently paired tropical passerines focuses on the question of mate defense versus territorial defense and the extent of cooperation versus selfish interests in inter-sexual relations. *Received 29 January 2007. Accepted 15 July 2007.*

Theory and empirical tests in the behavioral ecology of birds are generally constrained by a distributional problem. Whereas 80% of passerine birds reside in tropical latitudes, studies of temperate latitude species dominate our world view of avian biology. For example, does breeding occur when food for raising young is most abundant? Is the mating system of most passerine birds dominated by extra-pair behavior? Is song driven by sexual selection because it functions to attract mates for males? Does testosterone underlie the maintenance of aggression in territoriality? Well, this is what we think. But this is based on temperate passerines, popular test subjects for much of behavioral ecology theory. Studies of temperate birds outnumber those of tropical birds by a margin >100:1 (Stutchbury and Morton 2001).

What if an equivalent research effort had been spent on studying the same phenomena, but with birds in the tropics instead of birds

in the temperate zone? Alexander Skutch (1985) provided a preview when he stated that the question of latitudinal clutch size variation should not be “why do tropical birds lay so few eggs?” but, rather “why do temperate zone birds lay so many?” Studies of tropical birds test existing theory, but they also lead to entirely new questions that would otherwise not be asked. Several years ago, we reviewed research on the behavioral ecology of tropical birds to show how run-of-the-mill tropical birds have fundamentally different adaptations for life history strategies, mating systems, territory defense, and communication (Stutchbury and Morton 2001). Here we highlight recent studies to illustrate how tropical birds can be used to test and develop new theories for understanding the evolution of bird behavior.

Temperate zone birds converge in their adaptations to the overwhelmingly huge and predictable temperature and resource swings of temperate latitudes, and the vast majority of temperate breeding passerines have highly seasonal territorial defense and breeding. This creates a high level of male-male competition for territories, an intense period of social mate choice, and a sudden rush of nesting and egg-

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laying activity among females. Thus, many temperate species face a common suite of selection pressures on breeding adaptations that are imposed by climate and short breeding season. Most tropical birds are free from the constraints of the spring rush to establish territories and find mates; they typically have access to mates, territories, and food year round. Many tropical birds, often both males and females, keep singing whether breeding or not, whereas temperate zone birds stop singing when breeding wanes and females sing in only a few species (Morton 1996). One might ask, in the Skutchian vein, not “why do so many female birds sing in the tropics?” but, rather, “why do so few females sing in the temperate zone?”

Temperate-tropical comparisons are fundamental to understanding the different selective pressures acting on birds, and have been applied most frequently to the question of life history evolution (Wikelski et al. 2003a, Tieleman et al. 2005). The great diversity in life histories among tropical birds should also be viewed as a resource, one that can be used to document the full evolutionary potential of avian adaptation. Within one study area it is straightforward to find tropical passerines that are highly seasonal breeders and others that are territorial and paired year-round and have a prolonged 6 to 8 month breeding season. Seasonal effects on food availability and breeding can occur even in the same forest, depending upon whether the species forages on the ground or in the bushes and vines above (Ahumada 2001). Similarly, in a single study site one finds species that breed in the dry season as opposed to the wet season, species in which males build nests and incubate eggs as opposed to only feeding young, and species in which adults rely primarily on fruit as opposed to insects. This diversity is the largely untapped resource offered by tropical birds, a powerful tool for testing behavioral ecology theory and developing new ideas that have a broad evolutionary scope (Stutchbury and Morton 2001). Our review focuses on recent advances in life history traits of tropical birds, their slow pace of life, their mating systems, and territoriality.

Life History Traits.—Tropical birds have a much smaller clutch size than their temperate zone counterparts, a fundamental latitudinal

difference that has long been recognized (Skutch 1949), and still generates a great deal of theoretical and empirical study (Ghalambor and Martin 2001, Martin et al. 2001, Ricklefs and Wikelski 2002). There is little agreement, however, on whether small clutch sizes of tropical birds are favored because of food limitation, high predation risk, limited recruitment opportunities for juveniles, pathogens, or some combination of these selective factors (Ricklefs and Wikelski 2002). Clutch size manipulations have been a standard tool for testing optimal clutch size theory in temperate species, but few such experiments have been done with tropical birds (Stutchbury and Morton 2001).

Styrsky et al. (2005) experimentally reduced and enlarged clutches of Spotted Antbirds (*Hylophylax naevioides*) to created clutches of one, two, or three eggs. They found that parents of enlarged broods could successfully feed additional young by increasing their provisioning rate and the young fledged at normal weight. Furthermore, increased parental activity at the nest did not result in increased nest predation. Instead, the cost of having a large brood occurred after the young fledged by reducing juvenile survival. Broods of three had only 30% post-fledging survival compared with 70% for broods of one chick. Even natural broods of two eggs had lower juvenile survival (45%) than reduced clutches of one egg. Brood division after fledging normally results in each chick from a brood of two being cared for by a single parent. In enlarged clutches a single parent had to care for two chicks, but one of these chicks usually died in the first few days of the post-fledging period (Styrsky et al. 2005). This cost of a large clutch may be a general phenomenon because tropical passerines have a longer period of fledgling care and a longer delay before juvenile dispersal than temperate zone species (Russell et al. 2004).

Ferretti et al. (2005) manipulated clutch size in two populations of the Rufous-bellied Thrush (*Turdus rufiventris*) in subtropical Argentina to test whether lower food availability or high nest predation best explained inter-population variation in average clutch size (3.2 vs. 2.7 eggs). Clutch size in both populations was experimentally standardized at three eggs, and manipulated so the eggs

hatched synchronously. If low food availability results in selection for small clutch sizes, one would predict the population with the smaller natural clutch size would experience low provisioning rates, slow nestling growth, and high starvation of nestlings. However, the opposite was true; the population with the larger initial clutch size apparently had less food available because nestlings experienced more starvation and slower growth rate. No starvation was observed in the population where clutches were enlarged, suggesting that food supply was not constraining clutch size. Instead, differences in nest predation (50 vs. 75%) appear to shape life history traits in this species because the population with the highest predation had small clutch sizes, longer incubation bouts, faster nestling growth, and lower parental visitation rates to the nest.

These two examples illustrate how the direct selective influence of environmental factors on clutch size can differ among species. We can also add to the mix an earlier clutch manipulation study on Clay-colored Thrushes (*Turdus grayi*) in Panama in which parents could not raise additional young during the dry season when there were abundant fruit resources for adults but arthropod food for nestlings was scarce (Stutchbury and Morton 2001). Clay-colored Thrushes bred at a poor time for feeding nestlings because predation was lower in the dry season (Morton 1971).

A comparative study of tropical passerines in Africa found that seasonality of food resources had a strong influence on life history traits (Peach et al. 2001). Nectarivores and insectivores had high survival (72%) and low clutch size whereas granivores had low annual survival (54%) and large clutch sizes. The unpredictable and highly seasonal rainfall, which directly affects seed availability, may reduce the survival of granivores and select for larger clutch sizes. The diversity of tropical avian adaptations to food availability is exemplified by a recent study of the endangered Hawaiian Akepa (*Loxops coccineus*) (Freed et al. 2007). This specialized bird, feeding only on insects and spiders in the foliage of ohia trees (*Metrosideros polymorpha*), illustrates “nestling overgrowth” where, at peak weight, nestlings weigh more than their parents. To attain this overgrowth, Akepa nestlings are fed more than they need thus banking this food for use

during the 4-month fledgling period when food resources are declining. Akepa fledglings actually lose weight as they grow! Clay-colored Thrushes illustrate the opposite strategy. They fledge at much lower weights than the adult weight (e.g., at 35 vs. 80 g for adult weight) and continue to grow for long periods after fledging, even replacing remiges and rectrices in a complete molt so these will match their increasing size. Fledglings of the largest species of robin, the Great Thrush (*Turdus fuscater*) (33 cm long), are similar in size to fledgling robins of normal size for the genus (20–25 cm) but continue growing for an unknown length of time after fledging (E. S. Morton, unpubl. data).

Slow Pace of Life.—Tropical birds exhibit a lower basal metabolic rate than temperate birds (Wikelski et al. 2003a). Ricklefs and Wikelski (2002) argue that life history variation falls on a slow-fast continuum in all birds and that basic physiological tradeoffs can explain why tropical birds generally converge on one end of this continuum, despite a wide array of environments and selective forces. Under their model, different environmental factors act on separate physiological systems (immune, metabolic, and endocrine systems). Internal tradeoffs between the physiological systems result in a uniform life history (low clutch size, long life span) and ‘slow pace of life’ among tropical birds.

More resources may be allocated to adult survival than reproductive effort given a slow pace of life (Ricklefs and Wikelski 2002, Tieleman et al. 2005). Tropical birds appear to have a slower pace of life because they lay smaller clutches, hatchlings grow more slowly, and adults live longer than temperate zone birds, all of which suggest a lower resting metabolic rate (RMR) in tropical birds (reviewed in Wikelski et al. 2003a). The basic question is whether latitudinal relations between RMR are genetically based or whether local climate affects metabolic rates through acclimation. Weathers (1997) showed that RMR may vary by habitat in tropical birds with birds in open, sunny areas having higher metabolic rates than birds in shady forests. Eurasian Stone Chats (*Saxicola torquatus*) showed population-specific RMRs with birds from Kenya, Austria, Ireland, and Kazakhstan differing in RMR even though all were housed

under identical conditions in captivity. The tropical birds from Kenya had lower RMR (Wikelski et al. 2003b). They suggested that it was not migration or year-round territoriality but rather adaptation to temperature fluctuations that influences RMR. For example, birds from northern areas can experience cold temperatures during breeding and a higher RMR would be favored. The important point of the Eurasian Stone Chat study is that adaptation to local habitat may be under genetic control (Wikelski et al. 2003b).

A comparison of temperate-breeding and tropical House Wrens (*Troglodytes aedon*) found that Panamanian wrens had a lower field metabolic rate during reproduction, a smaller number of total provisioning trips to the nest (but not fewer trips per nestling), and fewer chicks per brood (Tieleman et al. 2006). Overall field metabolic rates during breeding were reduced by about 35% in tropical wrens, suggesting a slower pace of life, although some of this reduction may be the result of the much shorter day length in the tropics. In contrast to the temperate-breeding population, the tropical wrens did not show temporal variation in field metabolic rates while breeding which is likely due to their long breeding season.

The physiological tradeoff between testosterone and immune function is the best studied interaction among physiological systems that impacts life history evolution. This is often called the immunocompetence handicap hypothesis (Folstad and Karter 1992, Hillgarth and Wingfield 1997) and there is considerable variation among studies, and taxa, in the strength of evidence supporting this tradeoff (Roberts et al. 2004). Testosterone is important in the breeding biology of temperate male passerines, as plasma testosterone titers increase enormously during the breeding season and influence important reproductive processes such as song, courtship, sperm maturation, and territoriality (Balthazart 1983, Wingfield et al. 1990, Wingfield and Hahn 1994). Tropical birds, however, break this temperate zone rule because even during the peak of the breeding season males have low levels of testosterone (Levin and Wingfield 1992, Hau 2001). Testosterone plasma titers in temperate zone passerines are in the range of 2.1 to 5.5 ng ml⁻¹, whereas breeding tropical passerines

have values such as 0.2 ng ml⁻¹ in Spotted Antbirds (Hau et al. 2000) and 0.3 ng ml⁻¹ in White-bellied Antbirds (*Myrmeciza longipes*) (Fedy and Stutchbury 2006). In Spotted Antbirds, brain sex steroid receptor expression is increased in the non-breeding season when testosterone levels are reduced (Hau 2007), a different pattern from temperate zone birds where circulating testosterone levels and sex steroid receptors are temporally linked (e.g., both highest during the breeding season). Traditional ideas about the role of testosterone in mediating aggression seem not to apply to tropical species, especially those with year-round territoriality (Wiley and Goldizen 2003).

The pace of life model proposes the great importance of immune function in tropical birds has a cascading effect; it reduces basal metabolic rate and reproductive effort to save energy and reduces testosterone to maintain immunocompetence, all of which result in a longer adult life span. The idea is that high testosterone can be tolerated in birds with short breeding seasons (e.g., temperate zone breeders) because the short time intervals alleviate the fitness-lowering effects of testosterone such as interference in parental care and possibly impaired immune function (Wingfield et al. 2001). Tropical birds that live at high altitudes may be able to sustain higher concentrations of testosterone than lowland birds because parasite loads are low in the highlands (Goymann et al. 2004). There is support for higher prevalence of hematozoan parasites in lowland than in highland tropical birds, but it may also be true that infections occur at a higher rate in temperate than in tropical birds, arguing against the tradeoff between testosterone and hematozoan prevalence as a causal factor underlying differences in the levels of testosterone (Ricklefs 1992, Durrant et al. 2006)

Even with almost undetectable levels of testosterone (Hau et al. 2000, Fedy and Stutchbury 2006), tropical male passerines vigorously defend territories, sing, attack intruders, and pair with females (Wikelski et al. 1999). Female tropical birds can be fiercely territorial yet have low testosterone levels (Levin 1996). It is not fully understood whether female aggression in general is mediated by testosterone (Ketterson et al. 2005) and studies of female

tropical birds would provide good subjects for resolving these questions. The general pattern for tropical passerines that defend territories throughout the year is low levels of testosterone during most of the year (Levin and Wingfield 1992, Hau et al. 2000, Wikelski et al. 2003b, Day et al. 2006, Fedy and Stutchbury 2006). Tropical birds may not be able to maintain high androgen levels due to their negative effects on immunocompetence and, instead, elevate testosterone only when needed; when territorial conflicts and instability arise (Wikelski et al. 1999). Testosterone did not increase in White-bellied Antbirds after simulated territorial intrusions or during temporary removal experiments that created territorial conflicts among males (Fedy and Stutchbury 2006).

If tropical birds have a slower pace of life, is it caused by a heightened immune function resulting from low levels of testosterone? Partial support for this causal relationship was found in House Sparrows (*Passer domesticus*). House Sparrows living in Panama laid smaller clutches over a long breeding season relative to a population in temperate New Jersey. Martin et al. (2006) found that in tropical House Sparrows, secondary antibody response to an administered novel antigen was faster and “energetic investment in immune activity” was greater than in temperate House Sparrows, as predicted by differences in pace of life. However, cell-mediated immune response was greater in the fast-living temperate birds. They concluded the relation of testosterone to a reduction in immune function is equivocal because different components of the immune system differ in their relative costs and benefits and only some differences may complement variation in life histories (Martin et al. 2006). Furthermore, a laboratory study of male House Sparrows from New Jersey found that testosterone did not suppress immune function during the nonbreeding season, so seasonal variation in immune function could not be explained by seasonal changes in testosterone levels (Greenman et al. 2005).

Comparisons of the role of testosterone in temperate and tropical populations of the Eurasian Stone Chat have been influential because of the depth of study in both field and captive situations. The Stone Chat has a large breeding range that includes migratory north-

ern populations with a short breeding season to tropical populations that are resident and have year-long territoriality. Begun by Dittami and Gwinner (1985), the levels of testosterone and gonadal cycles have been studied recently in both the laboratory (Rodl et al. 2004) and in field situations (Goymann et al. 2006). Direct measurements of extra-pair mating behavior have not been published but the length of the breeding season and changes in testosterone suggest that extra-pair mating is common to all populations (Goymann et al. 2006). Stone Chats illustrate a reversal in breeding synchrony with temperate populations breeding over 5 months and tropical birds for a shorter period. Equatorial Stone Chats are single-brooded with individual pairs raising a clutch of three within a period of less than 3 months. Northern birds, in contrast, raise up to three clutches of five young each within a breeding season of 5–6 months (Helm et al. 2005, Schwabl et al. 2005). Equatorial Stone Chats, like other tropical birds, showed lower levels of testosterone (0.5 ng ml^{-1} or less) than their temperate counterparts, except during the stage when females were fertile (nest-building and laying), when testosterone levels were higher than those of European populations. This surge in testosterone was related to the relatively short time of female fertility (Goymann et al. 2006).

Another latitudinal comparison of testosterone has been accomplished within the genus *Zonotrichia*; northern populations of the White-crowned Sparrow (*Z. leucophrys*) and the tropical, but high altitude-living, Rufous-collared Sparrow (*Z. capensis*) (Moore et al. 2002, 2004a, 2004b; Wada et al. 2006). The tropical species of *Zonotrichia* can have levels of testosterone similar to northern latitude species (Moore et al. 2002). Moore et al. (2004a) report that testosterone in Rufous-collared Sparrows was higher during the main breeding period than the early breeding period (before incubation had begun), the opposite of the situation in the White-crowned Sparrow, whose testosterone levels are highest during territory establishment and decrease when they are feeding young (Morton et al. 1990). Rufous-collared Sparrows showed an elevated plasma testosterone when challenged by playbacks early in the breeding season. Oddly, testosterone was elevated much more in response

to playbacks of a heterospecific song (a sympatric seedeater) than by playback of the local conspecific dialect (4.2 vs. 2.0 ng ml⁻¹)! Testosterone-implanted Rufous-collared Sparrows exhibited enhanced testosterone concentrations but were no more aggressive than blank-implanted controls (Moore et al. 2004a). The opposite experiment, blocking testosterone pharmacologically, also did not affect territorial aggression in Rufous-collared Sparrows (Moore et al. 2004b). Moore et al. (2004a) suggested that high altitude Rufous-collared Sparrows likely have an extra-pair mating system and the sustained levels of testosterone may reflect a genetically polygynous population where males would be favored to have elevated concentrations of testosterone throughout the breeding season (Moore et al. 2004a).

We predicted that high testosterone is due to competition for extra-pair fertilizations (EPFs) in birds (Stutchbury and Morton 2001), regardless of latitude, and this view is supported by recent reviews (Hirschenhauser et al. 2003, Goymann et al. 2004, Garamszegi et al. 2005). We emphasized that extra-pair mating systems result in increased male-male competition, but more than simply male/male aggression and territoriality. Part of the enhanced performance provided by testosterone likely includes influencing female choice of extra-pair mates. Studies of testosterone in birds to date have not been accompanied by study of the mating system and breeding synchrony of the target species, making it difficult to evaluate the relative roles of immune function and mating system.

Breeding Synchrony and Extra-pair Mating.—Breeding synchrony among fertile females is generally much higher for temperate breeding than tropical birds due to the dramatic differences in the length of the breeding season (Stutchbury and Morton 1995). For Nearctic-neotropical migrants, breeding synchrony (% of females simultaneously fertile) typically ranges from 20 to 40% among species (Stutchbury et al. 2005a). The breeding synchrony for tropical passerines studied to date ranges from 8 to 30% with most species <15% (Table 1). Low values are typical for species that are territorial and paired year-round with long breeding seasons, and the highest values (25–30%) occurred in species

TABLE 1. Frequency of extra-pair fertilizations and extent of breeding synchrony in socially monogamous tropical passerines. Values give % of extra-pair young and broods that contained at least one extra-pair young (sample size in parentheses), and the breeding synchrony index (Kempnaers 1993).

Species	EPF frequency, %		Breeding synchrony (%)
	Young	Broods	
<i>Cercomacra tyrannina</i> ^a	0 (15)	0 (12)	8
<i>Tachycineta albilinea</i> ^b	15 (98)	26 (30)	8
<i>Elaenia flavogaster</i> ^c	4 (24)	8 (13)	9–10
<i>Thryothorus leucotis</i> ^d	4 (53)	3 (31)	10
<i>Zosterops lateralis</i> ^e	0 (122)	0	12
<i>Loxiodes bailleui</i> ^f	0 (20)	0 (12)	low
<i>Geospiza scandens</i> ^g	8 (159)	15 (66)	low
<i>Elaenia chiriquiensis</i> ^h	37 (14)	67 (15)	15–18
<i>Turdus grayi</i> ⁱ	38 (37)	53 (19)	25
<i>Volatinia jacarina</i> ^j	50 (20)	64 (7)	30

^a Fleischer et al. 1997; ^b Moore et al. 1999; ^{c,h} Stutchbury et al. 2007; ^d Gill et al. 2005; ^e Robertson et al. 2001; ^f Fleischer et al. 1994; ^g Petren et al. 1999; ⁱ Stutchbury et al. 1998; ^j Carvalho et al. 2006.

that defend seasonal territories and have a relatively short breeding season (Table 1).

Many variables can affect extra-pair effort in breeding birds, but we have long argued that breeding synchrony is an important predictor of extra-pair mating systems at the species level (Stutchbury and Morton 1995, Morton et al. 1998, Stutchbury 1998). The frequency of EPFs is closely correlated with breeding synchrony among New World passerines (Stutchbury 1998, Stutchbury et al. 2005b) and is an important predictor of extra-pair mating systems in more general comparative analyses (Møller and Ninni 1998). We predicted that extra-pair mating systems would not be the norm because most tropical passerines are paired and territorial year round, and have long asynchronous breeding seasons. Due to the scarcity of paternity studies, our first evidence for low EPFs in tropical passerines came from their low testes size (Stutchbury and Morton 1995) and then from a handful of tropical passerines that were found to have few or no EPFs (Stutchbury and Morton 2001).

Given that mating systems may so thoroughly affect a species' biology, it is disconcerting that only three studies on tropical passerines have been published in the last 5 years, adding only four species to the tropical list (Gill et al. 2005, Carvalho et al. 2006, Stutch-

bury et al. 2007). To be fair, this is partly due to the logistical challenges of obtaining a decent sample size when faced with small brood sizes and high nest predation. There are now 10 species of tropical passerines, all from the Neotropics, where paternity data are available (Table 1). Half have fewer than 5% extra-pair young, and can be considered genetically monogamous.

Tropical species with relatively high synchrony, like the Lesser Elaenia (*Elaenia chiriquensis*), Clay-colored Thrush, and Blue-black Grassquit (*Volatinia jacarina*), have abundant EPFs (Stutchbury et al. 1998, 2007; Carvalho et al. 2006). Blue-black Grassquits are sexually dimorphic granivores that have high breeding synchrony due to rapid and synchronous maturation of grass seed crops in the rainy season. Males have a distinctive jump display from the grass accompanied by a complicated, but short, buzzy song. Females seem to prefer to mate with males having the highest jumps and this highly synchronized breeding is coupled with an extra-pair mating system (Carvalho et al. 2006).

Studies of closely related species that differ in breeding synchrony offer a more powerful test of the tie between synchrony and extra-pair behavior. One study compared EPF frequency in two *Elaenia* flycatchers that differ in breeding synchrony (Stutchbury et al. 2007). The Lesser Elaenia and the Yellow-bellied Elaenia (*Elaenia flavogaster*) breed during the dry season but the former is migratory and more synchronous whereas the latter is permanently paired and defends territories throughout the year. Both species are monogamously paired, share the same habitat, and have a fruit-influenced territorial system (Stutchbury and Morton 2001), but the Lesser Elaenia had a high level of extra-pair fertilizations (67% of broods, 37% of nestlings) while we detected only a single instance of extra-pair paternity in the Yellow-bellied Elaenia (8% of broods, 4% of nestlings). We hope the common occurrence of near-genetic monogamy in tropical passerines, and the intriguing differences among species documented thus far, will spur others to incorporate paternity analyses into their studies.

Testosterone and Mating System.—We suggested that testosterone appeared to relate more to achieving success in extra-pair mating

than as a normal and necessary component of breeding behavior, which explains why temperate species have such high levels of testosterone compared with tropical passerines (Stutchbury and Morton 2001). Testosterone functions to maintain the exhausting aggression and displays that are associated with strong sexual selection and mate choice common to extra-pair mating systems (Raouf et al. 1997). Tropical species that do breed synchronously and have extra-pair matings are expected to have high testosterone levels, which is the case for the Clay-colored Thrush (1.8 ng ml⁻¹) (Wikelski et al. 2003a). Testosterone is also important in lekking species, like the Golden-collared Manakin (*Manacus vitellinus*), where testosterone increases display behavior (Day et al. 2006).

Testosterone has recently been tied specifically to extra-pair mating systems in temperate zone passerines (reviewed in Garamszegi et al. 2005). The model that best explains levels of testosterone suggests a primary relationship between relative testis size and extra-pair fertilizations with a secondary consequence on levels of testosterone (Garamszegi et al. 2005). An extra-pair mating system causes higher levels of testosterone, presumably because testosterone enhances behavior involved in the relative success of extra-pair fertilizations. Goymann et al. (2004) confirmed that average levels of testosterone were higher in northern temperate species than tropical species (2.8 ± 0.4 vs. 1.3 ± 0.2 ng ml⁻¹, $P < 0.0002$). They also showed that birds with short breeding seasons, including high altitude breeders, had high testosterone relative to those with long breeding seasons. Seasonally-breeding tropical birds with breeding season territoriality like temperate birds, had >2.0 ng ml⁻¹ testosterone whereas birds with year-round territories had <1.0 ng ml⁻¹. They concluded that high testosterone can evolve in the tropics under conditions of short breeding seasons and high altitudes (Goymann et al. 2004). Short breeding seasons are associated with higher breeding synchrony and more intense pressure to establish a territory and find a mate. Short breeding seasons also appear to be associated with extra-pair mating systems in tropical birds (Table 1) which clearly would generate intense male-male competition. Analysis of testosterone relative

to type of territoriality and mating system was hampered by low statistical power—we don't know enough about tropical birds!

Whether the mating systems of lowland breeders or the high cost of lowered immunocompetence explains the evolution of low testosterone requires studies that uncouple the two variables. Many species in the lowland are seasonal breeders and have extra-pair mating systems, and presumably there are also high altitude breeders with relatively long breeding seasons. Comparisons of testosterone function in congeneric tropical birds that share the same habitat but differ in mating system, for instance the *Elaenia* example (Stutchbury et al. 2007) would be a powerful way to control for exposure to parasites and explore the role of testosterone in territory defense and immune function.

Territoriality and Song.—High adult survival is expected to result in relatively low turnover of territories, which could constrain opportunities for territory and mate switching by adults, as well as territory and mate choice by juveniles (Morton et al. 2000). In Dusky Antbirds (*Cercomacra tyrannina*), experimentally created vacancies are filled rapidly (<24 hrs), usually by neighboring territory holders (Morton et al. 2000). Both males and females of several species will quickly divorce their mates to fill vacant territories, likely to obtain a higher quality territory. Other species in similar habitat and the same study area in central Panama show a pattern of voluntary mate fidelity. In White-bellied Antbirds, for instance, experimentally-created vacancies were filled slowly (2–3 days) or not at all, and divorce was uncommon (Fedy and Stutchbury 2004).

Annual survival of territory holders in Buff-breasted Wrens (*Thryothorus leucotis*) is 68% for females and 76% for males. Natural vacancies occur regularly and are filled rapidly (<24 hrs), but in this species divorce did not occur between pairs which already bred together (Gill and Stutchbury 2006). A widowed bird is conspicuous to neighbors because it sings only its half of the duet and one can presume that neighbors are aware of vacancies but choose not to move. Once a pair breeds together they remain paired until one member dies, so “til death do us part” actually applies. In contrast, divorce was relatively

common in young birds that had been paired <5 months and had not yet bred together. The interesting twist is the propensity for divorce only applied to young birds that immigrated into the population. Juveniles which lived on their parent's territory before acquiring a territory nearby (1–2 territories away) generally did not divorce once paired, even when there were opportunities to switch territories. This suggests that local recruits can successfully assess territory and mate quality prior to acquiring a territory, whereas outsiders fill a vacancy first and then begin to assess other opportunities on neighboring territories. We do not yet know why mate fidelity is so advantageous for experienced pairs.

Male and female Dusky Antbirds exhibit sex-specific territory defense (Morton and Derrickson 1996). Male song playbacks elicit a stronger response from the male than the female (Bard et al. 2002), whereas female residents are more aggressive than their mates in response to female song playback. A recent study of another antbird, the Warbling Antbird (*Hypocnemis cantator*) went much further by showing that females sang more and more quickly, thus initiating more duets, when responding to female solo playbacks than to duet or male solo playbacks (Seddon and Tobias 2006). This supports the idea that duets are in defense of the mate rather than a form of cooperation in joint defense of the territory. Male White-bellied Antbirds responded more aggressively than females regardless of whether the stimulus was male song, female song, or duetting (Fedy and Stutchbury 2005). Both genders were more aggressive to playbacks during the non-breeding (dry) season than the breeding (wet) season, perhaps because the low arthropod abundance during the dry season increases the benefits of exclusive use of the territory. Duetting did not appear to function in territory defense since pairs did not duet more during playbacks, even when duet songs were used as a stimulus.

A typical White-bellied Antbird pair sang only several (1–3) duets/hr, <10 male songs/hr, and <3 female songs/hr (Fedy and Stutchbury 2005). There was no dawn chorus (e.g., elevated song rate) during the dry or wet season. In contrast, the Chestnut-backed Antbird (*Myrmeciza exsul*) has a dawn chorus (Stutchbury et al. 2005b). Possibly, the acoustic dif-

ferences between scrubby edge (White-bellied habitat) and shaded forest (Chestnut-backed habitat), in combination with habitat differences in food availability, have influenced the tendency to sing at dawn (Morton 1977, Seddon 2005).

Antbirds do not learn songs and their duets are simple relative to the elaborate repertoires of duets found in song-learning oscine passerines (Seddon and Tobias 2006). Perhaps the best example of how complex dueting can become is found in the Plain-tailed Wren (*Thryothorus euophrys*) where groups of birds sing in synchronized choruses, coordinating their repertoires of 20 phrases of sex-specific songs for up to 2 min (Mann et al. 2007)! Buff-breasted Wrens have a conspicuous dawn chorus following daybreak, when pairs typically sing over 50 duets in 30 min, often switching to different duet combinations (Gill et al. 2005).

The role of duet singing in territorial defense has taken on new significance with the discovery of a “duet code” in Black-bellied Wrens (*Thryothorus fasciatoventris*) (Logue and Gammon 2004, Logue 2006). As in most dueting bird species, males and females differ in their responses to intra- and inter-sexual playbacks with greater responses to same-sex songs. Female Black-bellied Wrens respond more to female songs but males do not differentiate to the same extent. However, the song contributions by pair members to each duet are not random. For each pair there exists a specific pairing of songs which is somewhat reciprocal. For example, if a male sings song A, his mate duets with her song W, and if her song W is played back, her mate responds with his song A. These couplings between songs in each duet constitute the duet code in this species and serve to identify specific individuals, useful information in defending territories. Rufous-and-white Wrens (*Thryothorus rufalbus*) sing mainly solo songs with males singing much more than females and males only singing in a dawn chorus. Playback experiments using stereo speakers imitating an intruding pair showed that Rufous-and-white Wrens also have a duet code that functions in territorial defense (Mennill and Vehrencamp 2005, Mennill 2006).

There are exciting new aspects of neotropical avian biology that have developed in the

last 5 years with the traditional focus on passerine birds (Stutchbury and Morton 2001). The use of the diversity of tropical birds to evaluate and test ideas about general avian adaptations is still a largely untapped resource. We hope this mini-review encourages others to step outside the temperate zone bias and into the field to study tropical birds.

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