

Extrapair Paternity and Sexual Selection in Socially Monogamous Birds: Are Tropical Birds Different?

Authors: Macedo, Regina H., Karubian, Jordan, and Webster, Michael S.

Source: *The Auk*, 125(4) : 769-777

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/auk.2008.11008>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

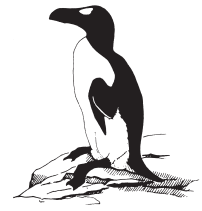
Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The Auk

An International
Journal of Ornithology

Vol. 125 No. 4 October 2008



The Auk 125(4):769–777, 2008

© The American Ornithologists' Union, 2008.

Printed in USA.

PERSPECTIVES IN ORNITHOLOGY

EXTRAPAIR PATERNITY AND SEXUAL SELECTION IN SOCIALLY MONOGAMOUS BIRDS: ARE TROPICAL BIRDS DIFFERENT?

REGINA H. MACEDO,^{1,4} JORDAN KARUBIAN,² AND MICHAEL S. WEBSTER³

¹Departamento de Zoologia-IB, Universidade de Brasília, Brasília, D.F., 70910-900, Brazil;

²Center for Tropical Research, Institute of the Environment, University of California, Los Angeles, La Kretz Hall, Suite 300,
Box 951496, Los Angeles, California 90095, USA; and

³School of Biological Sciences and Center for Reproductive Biology, Washington State University, Pullman, Washington 99164, USA

SEXUALLY ELABORATE TRAITS, such as bright plumage and courtship signals, are generally thought to evolve through sexual selection (Andersson 1994), which requires variance in male mating success to operate (Arnold 1994). More than 90% of all birds are socially monogamous (Lack 1968) and, therefore, are expected to exhibit low variance in mating success and weak sexual selection; yet, paradoxically, many socially monogamous birds show the stamp of strong sexual selection in such traits as exaggerated plumage ornamentation and courtship displays. Although Darwin (1871) suggested alternatives (Webster et al. 2007), numerous recent genetic studies have suggested that extrapair paternity (EPP) may be the most likely resolution of this apparent paradox: if copulations outside of the pair bond

are common, then variance in mating success may be far larger, and sexual selection much stronger, than suggested by social pairing success alone (Webster et al. 1995). Indeed, <25% of birds studied to date are genetically monogamous (Griffith et al. 2002), and studies have shown that EPP can generate strong sexual selection in socially

monogamous systems (e.g., Albrecht et al. 2007, Webster et al. 2007). However, despite two decades of work, we have only rudimentary understanding of the factors that lead to variation in EPP rates across populations (Griffith et al. 2002, Westneat and Stewart 2003, Neudorf 2004).

Conclusions regarding the role of EPP in sexual selection, however, must be taken with a large and important caveat, the so-called “temperate zone bias” (Stutchbury and Morton 2001): most studies have focused on temperate-zone birds, only a handful looking at tropical species. Given that most birds, by far, live and breed in the tropics, this omission is critical (see Martin 1996, 2004). Without a better understanding of the prevalence of factors contributing to EPP in tropical species, our ability

to generalize about EPP and its role in sexual selection among socially monogamous species will remain limited.

Despite the widely recognized lack of empirical data, tropical species are generally considered to have lower rates of EPP than temperate species. For example, Stutchbury and Morton

“Studies of temperate species have failed to resolve the... ecological and life-history factors that are hypothesized to affect EPP rates.... [T]ropical species will allow phylogenetically robust tests of these hypotheses on a scale that cannot be matched by studies of temperate species alone.”

⁴E-mail: rhmacedo@unb.br

(2001:39) stated that “while extra-pair mating systems are the norm for temperate zone passerines, this is not true for tropical birds.” If this is true, a lower rate of EPP in tropical systems has important implications for our understanding of the role of EPP in sexual selection and of the ecological and life-history factors that drive interspecific variation in EPP. Here, we critically review the evidence and conclude that general statements about the relative frequency of EPP in tropical birds are premature, given the small amount of data currently available, as well as the breadth of life histories and habitat types encompassed in the tropics. We argue that rigorous studies of EPP in both tropical and temperate systems will lead to a better understanding of the ecological causes and evolutionary consequences of these mating patterns and the operation of sexual selection (see also Stutchbury and Morton 2001, 2008). Indeed, there are good theoretical reasons to expect EPP rates to be lower in at least some tropical systems, and a comparison of temperate and tropical systems could shed considerable light on the factors driving variation in EPP across populations.

ARE TROPICAL BIRDS DIFFERENT?

First, we will critically review the evidence used to infer that rates of EPP are lower in tropical birds than in species that breed in the temperate zone. We define “tropical region” as the area lying between the Tropic of Cancer (23°26'N latitude) and the Tropic of Capricorn (23°26'S latitude).

Direct measures of extrapair paternity rates.—In stark contrast to the many studies of temperate-zone birds, rates of EPP have been directly measured in only a small handful of tropical species. Stutchbury and Morton (2001) reviewed the available evidence ($n = 7$ tropical species) and concluded that EPP is less common in the tropics than in the temperate zone (see also Spottiswoode and Møller 2004). However, as Stutchbury and Morton themselves emphasized, this sample size is far too small for firm conclusions because it represents <0.1% of the ~5,000 species of tropical terrestrial birds (passerines and nonpasserines; Hawkins et al. 2003), as compared with ~130 temperate-zone species (10% of ~1,270 species; Hawkins et al. 2003) that have been studied with genetic markers.

We have conducted a slightly expanded review that includes recent and unpublished studies, bringing the total number of socially monogamous tropical species for which data are available to 12. These data (Table 1; see also Stutchbury and Morton 2008) suggest that EPP rates in tropical birds span a broad range and may be roughly equivalent to those found among temperate-zone species: on average, 17.9% of young are sired by extrapair males and 26.0% of broods contain such young in tropical species, versus 11.3% of young and 17.6% of broods in temperate species (data on temperate species from appendix 1 in Griffith et al. 2002). Indeed, although EPP rates are very low in some tropical passerines (e.g., Dusky Antbird and Palila), in others (e.g., Red-backed Fairy-wren, Lesser Elaenia, and Blue-black Grassquit) rates are as high as, or higher than, those documented in most studies of temperate-zone species (see Table 1 for scientific names of species). However, it is important to consider the means calculated for tropical birds cautiously, because few tropical species have been studied and because most studies of

tropical species are based on very small sample sizes (Table 1), which has an important effect on the statistical confidence of EPP rate estimates (Griffith et al. 2002). Further, the few species that have been studied are taxonomically restricted and, in some cases, may have been chosen for study because of *a-priori* expectations about their level of promiscuity and are, therefore, not a representative subset of the entire suite of species found in the tropics. Thus, currently it is impossible to draw firm conclusions of general patterns based on studies that have directly measured EPP rates in tropical birds.

Indirect evidence from testes size data.—Relative testes size has been found to correlate with EPP rates across a number of species, likely because sexual promiscuity can lead to increased sperm production (Møller and Briskie 1995). Accordingly, testes size has been used as an index of EPP in several comparative analyses in birds (e.g., Dunn et al. 2001, Pitcher et al. 2005). In an early and influential analysis, Stutchbury and Morton (1995) found that males of tropical species have relatively smaller testes than males of temperate species (see also Garamszegi et al. 2005), which suggests that EPP rates are lower in the tropics than in the temperate zone (Stutchbury and Morton 2001, 2008). Similarly, a study of seven lowland Neotropical passerines also found that these generally have lower testosterone concentrations and smaller gonads than temperate-zone birds (Wikelski et al. 2003a). Indeed, testosterone levels appear to be generally low in tropical birds and may also reflect low levels of EPP (Garamszegi et al. 2005). However, the link between testes size in tropical species and EPP remains weak, and there are good reasons to question the use of testes size in tropical birds as an indication of EPP level.

First, the physiology that regulates reproduction and other activities in tropical birds has yet to be understood. There is good evidence that metabolic parameters differ markedly between tropical and temperate organisms, such that sedentary tropical birds exhibit intrinsically low energy-expenditure levels in comparison with temperate birds (Wikelski et al. 2003b). Accordingly, gonad size may not define the expression of behaviors typically exhibited by temperate birds in this context, and tropical birds may maintain low testosterone levels and small gonads as an energy-conserving strategy (Wikelski et al. 2003b) without reductions in EPP effort (see van de Crommenacker et al. 2004). In this vein, detailed studies of the mechanisms underlying extrapair mating behavior in tropical birds, comparable to those conducted with temperate birds (e.g., Raouf et al. 1997, Peters 2002), are badly needed.

Second, evidence for a general latitudinal trend in testes size is equivocal. Since Stutchbury and Morton's (1995) study, more extensive analyses have been conducted on the relationship between testes size and latitude. The most comprehensive analyses to date (Pitcher et al. 2005) used data from >1,000 species of birds distributed across the world and did not find a general latitudinal pattern in testes size. Moreover, Pitcher et al. (2005) found that geography may confound simple analyses of latitudinal trends: testes size was larger in taxa from Eurasia and smaller in those from Australasia and South and Central America, and earlier analyses of testes size did not control for this geographic effect. Pitcher et al. (2005) also uncovered other correlates of testes size that may confound conclusions about latitude. For example, testes size was also positively correlated with clutch size, which famously varies with latitude (Lack 1947).

TABLE 1. Direct estimates of extrapair paternity (EPP) rates in tropical species and associated life-history and ecological traits (BRSY = breeding synchrony index, and BRSL = breeding-season length; references cited refer to other traits).

Species	Percent EPP			Synchrony				Year-round			Reference ^a
	Young (n)	Broods (n)	Brood size	BRSY	BRSL	Territory	Pair bond	Dichromacy	Guild, habitat		
Red-backed Fairy-wren (<i>Malurus melanocephalus</i>) ^b	51 (517)	62.7 (185)	2-4	?	5 months	No	Yes	Yes	Insectivorous, grassland	1	
Dusky Antbird (<i>Cercomacra tyrannina</i>)	0 (15)	0 (12)	Small	8%	?	Yes	Yes	Yes	Insectivorous, rainforest	2	
Mangrove Swallow (<i>Tachycineta albilinea</i>) ^c	15 (98)	26 (30)	4	8%	5 months	No	No	No	Insectivorous, open water	3	
Clay-colored Thrush (<i>Turdus grayi</i>) ^d	38 (37)	53 (19)	2-4	25%	3 months	No	No	No	Omnivorous, open areas	4	
Palila (<i>Loxioides bailleui</i>) ^e	0 (20)	0 (12)	2	Low	9 months	?	?	Yes	Granivorous, dry forest	5	
Cactus Finch (<i>Geospiza scandens</i>) ^f	8 (159)	15 (66)	?	Low	?	?	?	Yes	Granivorous, dry forest	6	
White Eye (<i>Zosterops lateralis</i>) ^g	0 (122)	0 (?)	?	12%	?	?	?	No	Insectivorous, open forest	7	
Green-rumped Parrotlet (<i>Forpus passerinus</i>) ^h	8 (827)	14 (160)	3-12	Low	?	No	Yes	No	Seeds and fruits, grassland	8	
Lesser Elaenia (<i>Elaenia chiriquensis</i>) ⁱ	37 (38)	67 (15)	2.5	15-18%	?	No	No?	No	Frugivorous, open and scrubby	9	
Yellow-bellied Elaenia (<i>Elaenia flavogaster</i>) ^j	4 (24)	8 (13)	1.7	9-10%	?	Yes	No?	No	Frugivorous, open and scrubby	9	
Buff-breasted Wren (<i>Thryothorus leucotis</i>)	4 (53)	3 (31)	1-3	10-11%	7 months	Yes	Yes	No	Insectivorous, humid forest	10	
Blue-black Grassquit (<i>Volatinia jacarina</i>)	50 (20)	63 (11)	1-3	16-28%	5 months	No	?	Yes	Granivorous, open and scrubby	11	

^aReferences: (1) Webster et al. 2008, (2) Fleischer et al. 1997, (3) Moore et al. 1999, (4) Stutchbury et al. 1998, (5) Fleischer et al. 1994, (6) Petren et al. 1999, (7) Robertson 1996, (8) Melland 2000, (9) Stutchbury et al. 2007, (10) Gill et al. 2005, (11) Carvalho et al. 2006 and R. H. Macedo (unpubl. data).

^bAustralian, cooperative breeder, large relative testes mass.

^cCavity nester, small relative testes mass.

^dLarge relative testes mass.

^eHawaii, endangered.

^fExhibits delayed plumage maturation.

^gOceania.

^hGrassland and forest edges, average brood = 7, cavity nester, extreme hatching asynchrony.

ⁱTwo clutches season⁻¹, intra-tropical migrant.

^jOne clutch season⁻¹.

In addition, recent methodological concerns have cast doubt on the accuracy of data used in many of the comparative analyses discussed above. Calhim and Birkhead (2007) compared published results generated by analyses of relatively large data sets that have used various methods of measuring testes size with results of identical analyses using a smaller, higher-quality data set compiled by the authors. They found numerous inconsistencies in the qualitative results of these analyses, including the basic finding of Møller and Briskie (1995) that species with higher EPP levels have larger testes. In sum, it is not clear that testes size correlates with either latitude or EPP rates, so this evidence should not be used (yet) to make inferences about the latter.

Indirect evidence from patterns of sexual dichromatism.—In a similar vein, broad patterns of sexual dichromatism might be used to argue that tropical species have lower rates of EPP. First, some interspecific comparative analyses (Møller and Birkhead 1994, Dunn et al. 2001) have indicated that male plumage brightness and sexual dichromatism are positively associated with frequency of EPP. An analogous pattern has also been found within several species (i.e., more brightly colored males obtaining more EPP; reviewed in Griffith et al. 2002). Finally, sexual dichromatism appears to be less pronounced in tropical birds than in temperate species (Bailey 1978, Badyaev and Hill 2003), and also less pronounced in resident than in migratory species (Fitzpatrick 1994). Taken together, this evidence would suggest that EPP is less common in (resident) tropical species than in (migratory) temperate species.

However, for several reasons, firm conclusions about rates of EPP are difficult to draw from analyses of sexual dichromatism. First, in a large-scale comparative study, Dunn et al. (2001) found that sexual dichromatism was more closely tied to social mating system than to EPP, calling into question the causal connection between EPP and plumage ornamentation. Latitudinal differences in sexual dichromatism may also reflect variation in the action of natural selection, rather than sexual selection—for example, if predation rates on adults vary systematically (Martin and Badyaev 1996, Badyaev and Hill 2003). Indeed, in some avian taxa, female plumage coloration (dull vs. bright) is more evolutionarily labile than that of males (usually bright), which suggests that it is selection acting on females, rather than sexual selection acting on males, that determines the degree of sexual dichromatism (Irwin 1994, Burns 1998). Moreover, many early studies that reported a latitudinal trend in sexual dichromatism did not control for phylogeny. Cardillo (2002) analyzed 69 phylogenetically independent pairs of species that differed in breeding range and found no relationship between degree of sexual dichromatism and latitude,

which indicates that there is no consistent pattern in the variation of dichromatism between temperate and tropical species. Finally, there are reasons to be concerned about the interpretation of data used in earlier comparative studies: Eaton (2005) demonstrated that a large number of species that appear, to human observers, to be sexually monochromatic are actually sexually dichromatic when viewed through the avian visual system, and most previous studies had not taken this into account. Thus, as with analyses of testes size, patterns of sexual dichromatism cannot currently be used to reach any conclusions about the importance of EPP in tropical systems compared with those at higher latitudes.

SHOULD TROPICAL BIRDS BE DIFFERENT?

Above, we have argued that it is premature to conclude that EPP is less common in tropical than in temperate birds. That being said, several hypotheses have posited that various ecological factors should have a strong influence on EPP rates (below). Given the substantial ecological and life-history variables that correlate with latitude (Martin 1995, Stutchbury and Morton 2001), some of these hypotheses would indeed predict differences in EPP rates between some tropical and temperate systems.

It is important to recall, however, that the tropics encompass a diverse array of habitat types (Green 1994), ranging from tropical rainforests (typically between about 10°S and 25°N) with heavy rain throughout the year, through monsoon climates with rainfall concentrated in the hottest parts of the season, to highly seasonal regions (e.g., most tropical savannas) where there is variation in daylight hours and monthly temperatures as well as pronounced rainy and dry periods. The tropics also encompass desert biomes, generally between 18° and 28° in both hemispheres, where reproduction of plants and animals tends to be highly synchronized with the rains, and resident and nomadic species may differ in their reproductive strategies. Finally, the tropics also include alpine habitats reaching up to permanent glaciers where strong seasonality in weather regimes and breeding can be expected.

In addition to outlining how the hypotheses described below predict latitudinal variation in EPP rates, we also focus on how they predict differences between relatively seasonal versus relatively aseasonal tropical systems. Although other contrasts are certainly possible among tropical species, this broad division into seasonal versus aseasonal systems can be seen as a first step toward acknowledging the diversity contained within the tropics.

Five key hypotheses attempt to link EPP rates to underlying ecology or life-history traits (Table 2). Below, we summarize how each

TABLE 2. Predictions for five hypotheses that relate ecological or life-history traits of birds to extrapair paternity (EPP) rates for two tropical environments (low versus high seasonality) and the temperate region.

Hypothesis	Low-seasonality tropics		High-seasonality tropics		Temperate region		Reference ^a
	Value	EPP rates	Value	EPP rates	Value	EPP rates	
Breeding-synchrony	Low	Low	High	High	High	High	1
Rapid-pair-formation	Not rapid?	Low	Rapid?	High	Rapid	High	2
Breeding-density	Low	Low	High?	High?	High	High	3
Adult-mortality	Low	Low	Low	Low	High	High	4
Female-constraint	High	Low	Low	High	Low	High	5

^aReferences: (1) Stutchbury and Morton 1995; (2) Westneat et al. 1990; (3) Birkhead 1979; (4) Mauck et al. 1999, Wink and Dyrce 1999; and (5) Gowaty 1996.

might predict broad-scale differences between tropical and temperate species. Our intent is not to thoroughly review the hypotheses for variation in EPP rates, because this has been done elsewhere (e.g., Griffith et al. 2002, Neudorf 2004). Rather, we wish to highlight some possibly important contrasts between tropical and temperate birds, as well as among tropical species, to spur further research. Even among temperate species where they have been relatively well tested, none of these ecological hypotheses has found universal support, and there is little general understanding of the relative importance of each hypothesis or the interplay between them. We suggest that the increased breadth of life-history and ecological variation found in the tropics can be exploited, via phylogenetically robust comparative studies among tropical species and between tropical and temperate species, to help distinguish between these currently unresolved hypotheses (see also Stutchbury and Morton 2008).

The breeding-synchrony hypothesis.—The breeding-synchrony hypothesis proposes that EPP rates should correlate with breeding synchrony (Stutchbury and Morton 1995; Table 2), perhaps because females are better able to compare males in highly synchronous species (Stutchbury 1998a, b) or because male parental care conflicts with seeking EPP (Schwagmeyer and Ketterson 1999). Because many tropical species in relatively aseasonal tropical habitats (e.g., rainforests) typically have more extended breeding seasons (Wyndham 1986), breeding synchrony is likely to be lower than that of many temperate-zone breeders and, accordingly, EPP is expected to be lower (Stutchbury and Morton 2001).

Support for the breeding-synchrony hypothesis among temperate species has been mixed. Although some empirical studies have supported the breeding-synchrony hypothesis by showing that extrapair matings increased with breeding synchrony (Stutchbury 1998a, b; Chuang et al. 1999; Stutchbury et al. 2007), other studies and more extensive comparative analyses have failed to uncover this relationship (Yezerinac and Weatherhead 1997, Westneat and Gray 1998, Saino et al. 1999, Westneat and Mays 2005). Moreover, a meta-analysis of 12 studies found that the level of EPP actually decreased significantly when synchrony increased (Møller and Ninni 1998). Thus, the breeding-synchrony hypothesis has not gained general acceptance as a single and broad explanation for the varying degrees of EPP in monogamous birds of temperate regions (Westneat and Sherman 1997, Griffith et al. 2002, Westneat and Stewart 2003).

The widespread premise that tropical species are less synchronous than temperate-breeding species has frequently been used when applying the breeding-synchrony hypothesis to tropical birds. Although this assumption is logical for birds breeding in aseasonal tropical habitats, for birds breeding in more seasonal tropical habitats there is little reason to expect that synchrony would differ from that of temperate species (Stutchbury and Morton 2001). For example, a study of 18 bird species in montane forest in Argentina found that the average breeding-season duration was only 50 days, which is comparable to that of many northern temperate birds (Auer et al. 2007). The broad range of habitats and species found in the tropics highlights the error of attempting to generalize about “tropical” species as if they were a homogeneous group; for example, breeding synchrony varies substantially (by 8–28%) among the few studied tropical species (Table 1).

Importantly, this substantial variation among tropical species could be exploited in a comparative framework to test the hypothesis and assess the influence of breeding synchrony on EPP

rates. Initial studies of this sort have begun. For example, Stutchbury and colleagues (Stutchbury et al. 1998, 2007) found relatively high EPP rates in two tropical species (Clay-colored Thrushes and Lesser Elaenias; Table 1), both of which were predicted, *a priori*, to have high EPP rates owing to relatively synchronous breeding. Unfortunately, too few tropical species have been studied, to date, for robust comparative tests and, similarly, it is not yet possible to control for the possible effects of other factors (see below).

The rapid-pair-formation hypothesis.—Extrapair paternity rates may also be related to latitude if migratory species (which mostly breed at high latitudes) are forced to find reproductive partners rapidly after settling on the breeding grounds, because this could lead to pairing “mistakes,” with many females paired to low-quality males (Westneat et al. 1990, Spottiswoode and Møller 2004; Table 2). Although this rapid-pair-formation hypothesis has been suggested as an alternative explanation for the relationship between EPP and breeding synchrony (Yezerinac and Weatherhead 1997), it has been criticized because, in monogamous species, rapid pairing will likely not alter the proportion of females paired to low-quality males (Stutchbury and Morton 2001). However, this hypothesis may hold if female mating preferences are not consistent across females—for example, if females choose on the basis of genetic similarity to their potential reproductive partners (Mays and Hill 2004), in which case females may have difficulty in finding suitable partners if pairing occurs rapidly. To the extent that this hypothesis is valid, we expect it to predict lower rates of EPP among birds from aseasonal tropical habitats than among migratory species that are found in both highly seasonal tropical habitats and in the temperate zone (Table 2).

Both the breeding-synchrony and rapid-pair-formation hypotheses predict lower rates of EPP in tropical birds than in temperate species, because the former tend to be resident (non-migratory) species with extended breeding seasons (Spottiswoode and Møller 2004). Variation among tropical species could be used to test and tease apart these hypotheses. For example, the Red-backed Fairy-wren is a nonmigratory tropical species with an extended breeding season, but pair formation appears to be rapid in this species (unpaired females attract unpaired helpers from nearby territories and typically pair within a few hours; Karubian 2008; see also Pruett-Jones and Lewis 1990). Extrapair paternity rates in this species are very high (Webster et al. 2008), and rapid pair formation is one possible explanation. Altitudinal migrants in tropical forests may also prove informative in attempting to distinguish between these hypotheses, because they likely will exhibit marked variation in length of breeding seasons, speed of pair formation, and rates of EPP.

The breeding-density hypothesis.—The breeding-density hypothesis proposes that as the density of breeding individuals increases, there will be more opportunities for interactions among individuals and, possibly, also reduced search costs for females, leading to a higher frequency of extrapair fertilizations (Birkhead 1979, Møller and Birkhead 1993). This hypothesis has received mixed support from studies of temperate species (*sensu* Westneat and Sherman 1997). Tropical species of lowland rainforest communities tend to breed at lower densities than temperate-zone species (Terborgh et al. 1990, but see Robinson et al. 2000) and, accordingly, this hypothesis predicts generally lower rates of EPP in aseasonal tropical habitats. However, because many species form relatively

dense aggregations in seasonal tropical habitats, this hypothesis predicts relatively high rates of EPP in these habitats (Table 2). In agreement with this, some of the tropical species in Table 1 from highly seasonal environments (e.g., Blue-black Grassquit and Red-backed Fairy-wren) breed at relatively high densities and have high rates of EPP.

Adult-mortality hypothesis.—It has been suggested that adult male survival should be negatively correlated with variance in male reproductive success, which, by extension, suggests that species with high annual mortality rates should have higher rates of EPP (Mauck et al. 1999, Wink and Dyrce 1999). There are several inter-related reasons to expect a connection between longevity and EPP. First, in species with high annual mortality, females are less likely to suffer retaliations from their social mates if they seek extrapair copulations (Mauck et al. 1999), because males that desert their social mates because of uncertain paternity will have limited chance of breeding in future reproductive events. Second, basic life-history theory also indicates that, in longer-lived species, each single breeding attempt is less valuable and, hence, individuals should invest less effort into breeding, possibly including less effort in seeking EPP, than shorter-lived species (Martin 2004). Finally, the value of long-term cooperative pair bonds will be relatively high in species with low adult mortality if mutual experience leads to higher reproductive success for the pair, and this may result in a higher degree of fidelity and lower EPP in such species than in those with high adult mortality (T. E. Martin pers. comm.).

An association between longevity and EPP has been supported by comparative analyses (Arnold and Owens 2002, Bennett and Owens 2002). Although biotic factors such as disease, competition, and parasitism are expected to increase mortality among tropical species (Moreau 1944), it is generally accepted that adults of tropical species have higher survival, on average, than their temperate-zone counterparts (Martin 2004). Thus, the adult-mortality hypothesis would predict a higher rate of EPP in the temperate zone than in the tropics, though how widely this would extend to montane and other seasonal habitats in the tropics is unknown. However, we should again underscore that there is considerable variation in longevity in the tropics (T. E. Martin unpubl. data), which would also allow this hypothesis to be tested through comparisons across tropical species.

The female-constraint hypothesis.—Gowaty (1996) proposed that female pursuit of EPP may be constrained by the necessity of male parental assistance. If so, EPP rates should be low in populations where male parental assistance is important and high where females rely less on male parental assistance (Albrecht et al. 2006). This hypothesis has been supported in some studies of temperate species (Mulder et al. 1994, Hoi-Leitner et al. 1999, Whittingham and Dunn 2001). Tropical systems show a wide diversity of parental-care patterns, but typically parental feeding rates (per nestling) appear to be higher in the tropics than in the temperate zone (e.g., Martin et al. 2000). This, in turn, suggests that male parental assistance may be more important in the tropics than in temperate-zone systems and, accordingly, this hypothesis generally predicts lower rates of EPP in the tropics. This may be especially true for tropical species inhabiting lowland rainforests with little seasonality of resources, where high adult survival may lead to resource limitation during breeding (see Ashmole 1963). Tropical species inhabiting more seasonal habitats typically breed when resources peak, similarly to temperate-region birds.

Comparative tests of the female-constraint hypothesis are complicated by the fact that the relative benefits to males of parental care versus EPP also will likely vary across species (Magrath and Komdeur 2003). Consequently, an interspecific correlation between EPP rates and male parental assistance might arise not because of constraints on females, but rather because males are selected to shift investment from one reproductive activity to the other. Strong tests of this hypothesis, therefore, will most likely come from intraspecific studies of tropical as well as temperate species—for example, through careful calculations of fitness benefits of alternative behaviors to both males and females. Similarly, in cooperatively breeding monogamous species, the presence of auxiliary helpers may reduce constraints on females, and possibly also fitness consequences for males, which may explain why the presence of helpers appears to affect EPP rates in some species of fairy-wren (Mulder et al. 1994, Webster et al. 2004). Finally, experimental approaches can be used to manipulate constraints imposed by reduced parental assistance by males (e.g., Hoi-Leitner et al. 1999).

CONCLUSIONS

We know remarkably little about mating systems of tropical birds. For this reason, it is premature to make any generalizations about the relative prevalence and importance of EPP in these systems. This is especially true when one considers the tremendous breadth of habitats and life histories found in the tropics. There is an urgent need for additional research on tropical species, not just because of the basic information it will provide, but also because it has the potential to significantly advance our understanding of the factors affecting EPP and sexual selection in birds (Stutchbury and Morton 2001, 2008; Tori et al. 2008). Interestingly, many of the hypotheses put forth to explain interspecific variation in EPP predict generally lower levels of EPP in the tropics (Table 2), but also considerable variation among tropical species (e.g., species in highly seasonal habitats versus those in relatively aseasonal habitats). Finding high levels of EPP in species expected to have low levels, as predicted by several hypotheses for species that occur in the “low-seasonality tropics,” may be surprising. In fact, most of the hypotheses predict similar rates of EPP for tropical species in highly seasonal habitats and for species in the temperate region, and divergence from these predictions in tests of the various hypotheses should spur the development of further models.

A rigorous examination of the hypotheses described above could be approached in several ways. One approach is to examine whether EPP rates differ between tropical congeners that vary fundamentally in only one key aspect—for example, the study by Stutchbury et al. (2007) that examined EPP in two species of tropical elaenia that differ primarily in breeding synchrony. Alternatively, one might examine a single species that occupies a wide range of latitudes, seasonality regimes, and habitats. For example, a species such as the Blue-gray Tanager (*Thraupis episcopis*), which occurs from southern Mexico to northeast Bolivia and in all of the Amazon basin, is found in a variety of habitats, including forest edge, open woodland, and cultivated areas (Hilty 2002). An alternative approach would be to examine specific groups of tropical birds that share a common key life-history parameter. For example, thamnophilids, formicariids, and furnariids exhibit extensive male parental care, which may be associated with reduced rates

of EPP, independent of breeding synchrony. Species that breed in montane tropical habitats would provide excellent opportunities to test many of the above hypotheses, because they exhibit large variations in their social and mating systems while having a high degree of breeding synchrony (e.g., Niklison et al. 2008) and high nesting density, in addition to high adult survival (e.g., 70–90% annual adult survival estimates based on a six-year study in montane Venezuela; T. E. Martin unpubl. data). It is certainly possible to examine populations of the same species breeding in different altitudes that may vary in several breeding parameters that could be used to test the various hypotheses. Finally, single-species field studies of tropical as well as temperate species that, for example, experimentally manipulate key ecological variables, are needed to adequately tease apart the alternative hypotheses (Spottiswoode and Møller 2004).

Studies of temperate species have failed to fully resolve the relative importance of, or interactions among, ecological and life-history factors that are hypothesized to affect EPP rates, likely because of the limited ecological variation exhibited by these species. Tropical birds show considerable variation in a number of key ecological parameters and will likely vary greatly in genetic mating systems as well (Stutchbury et al. 2007). Further study of tropical species will allow phylogenetically robust tests of these hypotheses on a scale that cannot be matched by studies of temperate species alone.

ACKNOWLEDGMENTS

We are grateful to the organizers of the symposium “Advances in Sexual Selection Theory with Tropical Birds as a Model System” (VIII Neotropical Ornithological Congress, Venezuela) for stimulating us to address these ideas. We thank R. Durães, R. I. Dias, R. Maia, and T. E. Martin for the many thought-provoking discussions about sexual selection in tropical birds. We acknowledge the suggestions made by T. E. Martin, B. Stutchbury, and an anonymous reviewer, which greatly improved the manuscript. This work was supported by National Science Foundation grants to M.S.W. (no. 0213075) and to J.K. (OISE-0402137), by a scientific fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (grant no. 302063), and by National Geographic Society grants to both R.H.M. and J.K.

LITERATURE CITED

- ALBRECHT, T., J. KREISINGER, AND J. PIÁLEK. 2006. The strength of direct selection against female promiscuity is associated with rates of extrapair fertilizations in socially monogamous songbirds. *American Naturalist* 167:739–744.
- ALBRECHT, T., J. SCHNITZER, J. KREISINGER, A. EXNEROVÁ, J. BRYJA, AND P. MUNCLINGER. 2007. Extrapair paternity and the opportunity for sexual selection in long-distant migratory passerines. *Behavioral Ecology* 18:477–486.
- ANDERSSON, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, New Jersey.
- ARNOLD, K. E., AND I. P. F. OWENS. 2002. Extra-pair paternity and egg dumping in birds: Life history, parental care and the risk of retaliation. *Proceedings of the Royal Society of London, Series B* 269:1263–1269.
- ARNOLD, S. J. 1994. Bateman's principles and the measurement of sexual selection in plants and animals. *American Naturalist* 144 (Supplement):S126–S149.
- ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473.
- AUER, S. K., R. D. BASSAR, J. J. FONTAINE, AND T. E. MARTIN. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. *Condor* 109:321–333.
- BADYAEV, A. V., AND G. E. HILL. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics* 34:27–49.
- BAILEY, S. F. 1978. Latitudinal gradients in colors and patterns of passerine birds. *Condor* 80:372–381.
- BENNETT, P. M., AND I. P. F. OWENS. 2002. *Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction*. Oxford University Press, Oxford, United Kingdom.
- BIRKHEAD, T. R. 1979. Mate guarding in the Magpie *Pica pica*. *Animal Behaviour* 27:866–874.
- BURNS, K. J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): The role of female versus male plumage. *Evolution* 52:1219–1224.
- CALHIM, S., AND T. R. BIRKHEAD. 2007. Testes size in birds: Quality versus quantity—Assumptions, errors, and estimates. *Behavioral Ecology* 18:271–275.
- CARDILLO, M. 2002. The life-history basis of latitudinal diversity gradients: How do species traits vary from the poles to the equator? *Journal of Animal Ecology* 71:79–87.
- CARVALHO, C. B. V., R. H. MACEDO, AND J. A. GRAVES. 2006. Breeding strategies of a socially monogamous Neotropical passerine: Extra-pair fertilizations, behavior, and morphology. *Condor* 108:579–590.
- CHUANG, H. C., M. S. WEBSTER, AND R. T. HOLMES. 1999. Extrapair paternity and local synchrony in the Black-throated Blue Warbler. *Auk* 116:726–736.
- DARWIN, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.
- DUNN, P. O., L. A. WHITTINGHAM, AND T. E. PITCHER. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55:161–175.
- EATON, M. D. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually “monochromatic” birds. *Proceedings of the National Academy of Sciences USA* 102:10942–10946.
- FITZPATRICK, S. 1994. Colourful migratory birds: Evidence for a mechanism other than parasite resistance for the maintenance of ‘good genes’ sexual selection. *Proceedings of the Royal Society of London, Series B* 257:155–160.
- FLEISCHER, R. C., C. L. TARR, E. S. MORTON, A. SANGMEISTER, AND K. C. DERRICKSON. 1997. Mating system of the Dusky Antbird, a tropical passerine, as assessed by DNA fingerprinting. *Condor* 99:512–514.
- FLEISCHER, R. C., C. L. TARR, AND T. K. PRATT. 1994. Genetic structure and mating system in the Palila, an endangered Hawaiian honeycreeper, as assessed by DNA fingerprinting. *Molecular Ecology* 3:383–392.
- GARAMSZEGI, L. Z., M. EENS, S. HURTREZ-BOUSSÈS, AND A. P. MØLLER. 2005. Testosterone, testes size, and mating success in birds: A comparative study. *Hormones and Behavior* 47:389–409.

- GILL, S. A., M. J. VONHOF, B. J. M. STUTCHBURY, E. S. MORTON, AND J. S. QUINN. 2005. No evidence for acoustic mate-guarding in duetting Buff-breasted Wrens (*Thryothorus leucotis*). *Behavioral Ecology and Sociobiology* 57:557–565.
- GOWATY, P. A. 1996. Battles of the sexes and origins of monogamy. Pages 21–52 in *Partnerships in Birds: The Study of Monogamy* (J. M. Black, Ed.). Oxford University Press, Oxford, United Kingdom.
- GREEN, D. R. 1994. *The Eyewitness Atlas of the World*. Dorling Kindersley, London.
- GRIFFITH, S. C., I. P. F. OWENS, AND K. A. THUMAN. 2002. Extra pair paternity in birds: A review of interspecific variation and adaptive function. *Molecular Ecology* 11:2195–2212.
- HAWKINS, B. A., E. E. PORTER, AND J. A. F. DINIZ-FILHO. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* 84:1608–1623.
- HILTY, S. L. 2002. *Birds of Venezuela*. Princeton University Press, Princeton, New Jersey.
- HOI-LEITNER, M., H. HOI, M. ROMERO-PUJANTE, AND F. VALERA. 1999. Female extra-pair behaviour and environmental quality in the Serin (*Serinus serinus*): A test of the 'constrained female hypothesis'. *Proceedings of the Royal Society of London, Series B* 266: 1021–1026.
- IRWIN, R. E. 1994. The evolution of plumage dichromatism in the New World blackbirds: Social selection on female brightness? *American Naturalist* 144:890–907.
- KARUBIAN, J. 2008. Changes in breeding status are associated with rapid bill darkening in male Red-backed Fairy-wrens *Malurus melanocephalus*. *Journal of Avian Biology* 39:81–86.
- LACK, D. 1947. Significance of clutch-size, parts I and II. *Ibis* 89: 302–552.
- LACK, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London, United Kingdom.
- MAGRATH, M. J. L., AND J. KOMDEUR. 2003. Is male care compromised by additional mating opportunity? *Trends in Ecology and Evolution* 18:424–430.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- MARTIN, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* 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., AND A. V. BADYAEV. 1996. Sexual dichromatism in birds: Importance of nest predation and nest location for females versus males. *Evolution* 50:2454–2460.
- MARTIN, T. E., P. R. MARTIN, C. R. OLSON, B. J. HEIDINGER, AND J. J. FONTAINE. 2000. Parental care and clutch sizes in North and South American birds. *Science* 287:1482–1485.
- MAUCK, R. A., E. A. MARSCHALL, AND P. G. PARKER. 1999. Adult survival and imperfect assessment of parentage: Effects on male parenting decisions. *American Naturalist* 154: 99–109.
- MAYS, H. L., JR., AND G. E. HILL. 2004. Choosing mates: Good genes versus genes that are a good fit. *Trends in Ecology and Evolution* 19:554–559.
- MELLAND, R. R. 2000. *The genetic mating system and population structure of the Green-rumped Parrotlet*. Ph.D. dissertation, University of North Dakota, Grand Forks.
- MØLLER, A. P., AND T. R. BIRKHEAD. 1993. Cuckoldry and sociality: A comparative study of birds. *American Naturalist* 142:118–140.
- MØLLER, A. P., AND T. R. BIRKHEAD. 1994. The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution* 48:1089–1100.
- MØLLER, A. P., AND J. V. BRISKIE. 1995. Extra-pair paternity, sperm competition and the evolution of testis size in birds. *Behavioral Ecology and Sociobiology* 36:357–365.
- MØLLER, A. P., AND P. NINNI. 1998. Sperm competition and sexual selection: A meta-analysis of paternity studies of birds. *Behavioral Ecology and Sociobiology* 43:345–358.
- MOORE, O. R., B. J. M. STUTCHBURY, AND J. S. QUINN. 1999. Extrapair mating system of an asynchronously breeding tropical songbird: The Mangrove Swallow. *Auk* 116:1039–1046.
- MOREAU, R. E. 1944. Clutch size: A comparative study, with special reference to African birds. *Ibis* 86:286–347.
- MULDER, R. A., P. O. DUNN, A. COCKBURN, K. A. LAZENBY-COHEN, AND M. J. HOWELL. 1994. Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proceedings of the Royal Society of London, Series B* 255:223–229.
- NEUDORF, D. L. H. 2004. Extrapair paternity in birds: Understanding variation among species. *Auk* 121:302–307.
- NIKLISON, A. M., J. I. ARETA, R. A. RUGGERA, K. L. DECKER, C. BOSQUE, AND T. E. MARTIN. 2008. Natural history and breeding biology of the Rusty-breasted Antpitta (*Grallaricula ferrugin-eipectus*). *Wilson Journal of Ornithology* 120:345–352.
- PETERS, A. 2002. Testosterone and the trade-off between mating and paternal effort in extrapair-mating Superb Fairy-wrens. *Animal Behaviour* 64:103–112.
- PETREN, K., B. R. GRANT, AND P. R. GRANT. 1999. Low extrapair paternity in the Cactus Finch (*Geospiza scandens*). *Auk* 116:252–256.
- PITCHER, T. E., P. O. DUNN, AND L. A. WHITTINGHAM. 2005. Sperm competition and the evolution of testes size in birds. *Journal of Evolutionary Biology* 18:557–567.
- PRUETT-JONES, S. G., AND M. J. LEWIS. 1990. Sex ratio and habitat limitation promote delayed dispersal in Superb Fairy-wrens. *Nature* 348:541–542.
- RAOUF, S. A., P. G. PARKER, E. D. KETTERSON, V. NOLAN, JR., AND C. ZIEGENFUS. 1997. Testosterone affects reproductive success by influencing extra-pair fertilizations in male Dark-eyed Juncos (*Aves: Junco hyemalis*). *Proceedings of the Royal Society of London, Series B* 264:1599–1603.
- ROBERTSON, B. C. 1996. *The mating system of the Capricorn Silvereye*. Ph.D. dissertation, University of Queensland, St. Lucia, Brisbane.
- ROBINSON, W. D., J. D. BRAWN, AND S. K. ROBINSON. 2000. Forest bird community structure in central Panama: Influence of spatial scale and biogeography. *Ecological Monographs* 70:209–235.
- SAINO, N., C. R. PRIMMER, H. ELLEGREN, AND A. P. MØLLER. 1999. Breeding synchrony and paternity in the Barn Swallow (*Hirundo rustica*). *Behavioral Ecology and Sociobiology* 45:211–218.
- SCHWAGMEYER, P. L., AND E. D. KETTERSON. 1999. Breeding synchrony and EPF rates: The key to a can of worms? *Trends in Ecology and Evolution* 14:47–48.

- SPOTTISWOODE, C., AND A. P. MÖLLER. 2004. Extrapair paternity, migration, and breeding synchrony in birds. *Behavioral Ecology* 15:41–57.
- STUTCHBURY, B. J. M. 1998a. Breeding synchrony best explains variation in extra-pair mating system among avian species. *Behavioral Ecology and Sociobiology* 43:221–222.
- STUTCHBURY, B. J. M. 1998b. Female mate choice of extra-pair males: Breeding synchrony is important. *Behavioral Ecology and Sociobiology* 43:213–215.
- STUTCHBURY, B. J. [M.], AND E. S. MORTON. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* 132:675–690.
- STUTCHBURY, B. J. M., AND E. S. MORTON. 2001. *Behavioral Ecology of Tropical Birds*. Academic Press, San Diego, California.
- STUTCHBURY, B. J. M., AND E. S. MORTON. 2008. Recent advances in the behavioral ecology of tropical birds. *Wilson Journal of Ornithology* 120:26–37.
- STUTCHBURY, B. J. M., E. S. MORTON, AND W. H. PIPER. 1998. Extra-pair mating system of a synchronously breeding tropical songbird. *Journal of Avian Biology* 29:72–78.
- STUTCHBURY, B. J. M., E. S. MORTON, AND B. WOOLFENDEN. 2007. Comparison of the mating systems and breeding behavior of a resident and a migratory tropical flycatcher. *Journal of Field Ornithology* 78:40–49.
- TERBORGH, J., S. K. ROBINSON, T. A. PARKER III, C. A. MUNN, AND N. PIERPONT. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60:213–238.
- TORI, W. P., R. DURÃES, T. B. RYDER, M. ANCIÃES, J. KARUBIAN, R. H. MACEDO, J. A. C. UY, P. G. PARKER, T. B. SMITH, A. C. STEIN, AND OTHERS. 2008. Advances in sexual selection theory: Insights from tropical avifauna. *Ornitologia Neotropical* 19 (Supplement):151–163.
- VAN DE CROMMENACKER, J., D. S. RICHARDSON, T. G. G. GROOTHUIS, C. M. EISING, A. L. DEKKER, AND J. KOMDEUR. 2004. Testosterone, cuckoldry risk and extra-pair opportunities in the Seychelles Warbler. *Proceedings of the Royal Society of London, Series B* 271:1023–1031.
- WEBSTER, M. S., S. PRUETT-JONES, D. F. WESTNEAT, AND 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.
- WEBSTER, M. S., K. A. TARVIN, E. M. TUTTLE, AND S. PRUETT-JONES. 2004. Reproductive promiscuity in the Splendid Fairy-wren: Effects of group size and auxiliary reproduction. *Behavioral Ecology* 15:907–915.
- WEBSTER, M. S., K. A. TARVIN, E. M. TUTTLE, AND S. PRUETT-JONES. 2007. Promiscuity drives sexual selection in a socially monogamous bird. *Evolution* 61:2205–2211.
- WEBSTER, M. S., C. W. VARIAN, AND J. KARUBIAN. 2008. Plumage color and reproduction in the Red-backed Fairy-wren: Why be a dull breeder? *Behavioral Ecology* 19:517–524.
- WESTNEAT, D. F., AND E. M. GRAY. 1998. Breeding synchrony and extrapair fertilizations in two populations of Red-winged Blackbirds. *Behavioral Ecology* 9:456–464.
- WESTNEAT, D. F., AND H. L. MAYS, JR. 2005. Tests of spatial and temporal factors influencing extra-pair paternity in Red-winged Blackbirds. *Molecular Ecology* 14:2155–2167.
- WESTNEAT, D. F., AND P. W. SHERMAN. 1997. Density and extra-pair fertilizations in birds: A comparative analysis. *Behavioral Ecology and Sociobiology* 41:205–215.
- WESTNEAT, D. F., P. W. SHERMAN, AND M. L. MORTON. 1990. The ecology and evolution of extra-pair copulations in birds. Pages 331–369 in *Current Ornithology*, vol. 7 (D. M. Power, Ed.). Plenum Press, New York.
- WESTNEAT, D. F., AND I. R. K. STEWART. 2003. Extra-pair paternity in birds: Causes, correlates, and conflict. *Annual Review of Ecology, Evolution, and Systematics* 34:365–396.
- WHITTINGHAM, L. A., AND P. O. DUNN. 2001. Male parental care and paternity in birds. Pages 257–298 in *Current Ornithology*, vol. 16 (V. Nolan, Jr., and C. F. Thompson, Eds.). Plenum Press, New York.
- WIKELSKI, M., M. HAU, W. D. ROBINSON, AND J. C. WINGFIELD. 2003a. Reproductive seasonality of seven Neotropical passerine species. *Condor* 105:683–695.
- WIKELSKI, M., L. SPINNEY, W. SCHELSKY, A. SCHEUERLEIN, AND E. GWINNER. 2003b. Slow pace of life in tropical sedentary birds: A common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London, Series B* 270:2383–2388.
- WINK, M., AND A. DYRCZ. 1999. Mating systems in birds: A review of molecular studies. *Acta Ornithologica* 34:91–109.
- WYNDHAM, E. 1986. Length of birds' breeding seasons. *American Naturalist* 128:155–164.
- YEZERINAC, S. M., AND P. J. WEATHERHEAD. 1997. Extra-pair mating, male plumage coloration and sexual selection in Yellow Warblers (*Dendroica petechia*). *Proceedings of the Royal Society of London, Series B* 264:527–532.

Received 9 April 2008, accepted 2 July 2008