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SEXUAL SELECTION IN BIRDS: INFLUENCE OF AMBIENT LIGHT AND CONSPICUITY ON THE REPRODUCTIVE SUCCESS OF MALES

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ABSTRACT

Sexual selection postulates that the evolution of certain conspicuous physical traits in animals may lead to a greater success in obtaining mates. The majority of bird species are under strong sexual selection pressure which promotes the generation of flashy, ornamented plumage. In addition, males may also use ambient light to become more conspicuous to females as a way of increasing their chances of being selected. We reviewed sexual selection regarding birds and discussed how ambient light and background colors could affect the reproductive success of males. We recorded 17 bird species belonging to 10 families that display in periods of the day that increase their conspicuity to conspecifics, or actively modify the background to enhance plumage contrast during the display. We recommend further investigation, particularly with a behavioral and phylogenetic approach, on the influence of abiotic factors, such as ambient light, on bird courtship displays and its consequent reproductive success, in order to find patterns.

Keywords: background contrast; courtship displays; lek systems; visual signals.

INTRODUCTION

The perception that the members of a species can define who will reproduce and who will not, led Charles Darwin to propose that evolutionary change could be guided by sexual selection, which he described as "the advantage that some individuals have upon others of the same sex and species, exclusive in relation to reproduction" (Darwin 1871). Darwin delineated sexual selection to explain the evolution of costly characters that reduce survivorship. He argued that while some attributes that help individuals to find partners reduce the male's lifespan, they could enhance the reproductive success over an individual's lifetime by ensuring mates to well-ornamented males when competing with others (Johnstone 1995).

Competition for mates exerts great selective pressure upon males and sexual selection emerges as a result of that dispute for females or gaining access to favorable areas to mate (Stockley 1997). Studies have shown that females tend to prefer partners with vibrant colors (Zahavi 1975, Moller & Thornhill 1998). The most accepted hypothesis is that only well adapted males could survive to reproduce despite their flashy ornaments, or handicaps, as they are called (Moller & Thornhill 1998). The exuberant characters of sexual selection may represent a demonstration of good health and proof that animals are parasite-free since significant negative correlation between parasite infestation, singing and plumage exuberance has been found (Hamilton & Zuk 1982). The Hamilton-Zuk hypothesis, as this idea became known, was the first one in this line of investigation, enabling many studies related to the theme (Thornhill *et al*. 1990, Torio 1992, Lozano 1994).

Reproductive costs are greater for females that pair to males under sexual selection pressure, since, besides being responsible for nesting and parental care, the only resource they usually gain from the males is semen, what is particularly true to lekking species but not applicable for monogamous species (Prum 1998, Liker *et al*. 2013). Therefore, sexual selection pressure upon males is very high, which drives the evolution of increasingly elaborate strategies to attract female attention (Stockley 1997). Changes in ambient light could alter both the conspicuity and contrast of an individual with background features (Heindl & Winkler 2003a, 2003c). Thus, the habitat in which an individual display could affect signaling by the use of arenas with contrasting colors and differential illumination

(Anciães & Peterson 2009). Males that can maximize their conspicuity to conspecifics also increase their visibility to predators, which shows that these individuals have even greater abilities to avoid predation, which makes them more attractive to potential mates (Heindl & Winkler 2003b).

Despite the great availability of information about behavioral courtship repertoires among bird species, little is known about the influence of abiotic factors on these rituals. Therefore, the goal of the present review was to determine how ambient light and background colors could affect the reproductive success of bird males by influencing female choice.

MATERIAL AND METHODS

We used the research tool *Web of Science* from the data basis Thompson ISI (Thompson Institute for Scientific Information) and also the Google Scholar from 1986 until 2016. We used the following key words: sexual selection, birds, lek systems, visual signals, contrast and ambient light.

SEXUAL SELECTION: AN OVERVIEW

In evolutionary terms, the success of individuals depends on their ability to survive and also to reproduce successfully and produce more offspring than their counterparts. This can lead to competition between individuals over reproductive opportunities; individuals that are successful in this competition will produce more descendants that are successfully recruited. This differential reproductive success can give rise to sexual selection: for behavioural, morphological or physiological characteristics that increase reproductive success (Henshaw *et al.* 2016).

The theoretical framework for the different roles of the sexes was laid down by Bateman (1948), who found that multiple copulations led to a greater increase in the number of offspring produced by males than by females in *Drosophila melanogaster*. Hence, he concluded that there is a greater advantage for males by copulating with several partners than there is for females, leading to stronger competition between males over mates and stronger selection on males.

Intense sexual selection pressure upon birds has resulted in a great variety of plumages and ornaments among the males (Prum 1990, Dale *et al.* 2015). Many studies have shown the influence of female choice on the evolution of courtship displays and secondary sexual characters (Uy & Endler 2004, Janicke *et al.* 2015). Additionally, the association between habitat and plumage coloration has been indicated as an important factor in morphological evolution for birds in general (Uy & Endler 2004, Stein & Uy 2006). However, displaying for conspecifics could enhance the chance of predation. Thus, colors and patches used for signaling represent a balance between these two contrasting selective factors (Endler 1993).

The way these ornaments could indicate genetic quality has led to a great number of studies about the handicap principle (Zahavi 1975, Johnstone 1995) and the costs of baring these ornaments (Evans & Thomas 1992, Moller & de Lope 1995). The handicap principle suggests that the elaborated secondary sexual characters of the males act as handicaps, that is, ornaments that bring costs to survivorship. The fact that a male can survive baring a handicap indicates to a female that he has a superior genotype (Zahavi 1975, Dakin *et al.* 2015). Anderson (1982) carried out a simple, but well performed experiment that illustrates this principle. He shortened the tails of some long-tailed widowbird males (*Euplectes progne*) by cutting feathers, and then he elongated the tails of others by gluing these feathers on. The males with elongated tails attracted significantly more females than those with shortened or unchanged tails.

Variations in ambient light and color patterns can give an animal conspicuousness to conspecifics, what can influence the female mate choice (Endler & Théry 1996). Lekking species are an excellent system to test this idea because lek sites (arenas) are fixed and displays only occur under specific conditions (Endler & Théry 1996, Heindl & Winkler 2003, Stein & Uy 2005). Lekking species are generally characterized by strong sexual dimorphism and elaborate courtship displays (Prum 1990). Behavioral studies carried out with lekking birds show the great diversity of displays and the peculiarities of the arenas (Prum et al. 1996, Castro-Astor *et al.* 2004, 2007, Durães *et al.* 2009).

These displays can involve a great variety of courtship behaviors such as choreography, vocalizations, mechanical sounds and exposition of ornamentation (Prum 1994b). Fusani *et al.* (2014) highlighted that elaborate courtship displays may or may not require an intense expenditure of energy, but many displays do appear to require proficient neuromuscular control. Thus, females seem to choose males based on their motor skills, suggesting that neuromuscular specializations possessed by these males are driven by female choice.

A lek is a mating system in which males of the same species use an area (arena) where they copulate (Durães 2009). There are no long-term social bonds between males and females, since male reproductive involvement ends with copulation (Durães 2009, Ryder & Sillet 2016). This system maximizes the reproductive success of females by enabling them to access and compare the males that gather together (Bradbury & Gibson 1983). We summarized the bird families that present lek (Table 1). Information on presence/absence of lekking behavior in Pipridae species, including number of males that congregate, and lek category can be found in Snow (2004) and Prum (1994a).

Table 1. Summary of bird families and species that present lekking behavior and sources, resulting of the present review.

Family	Lekking species	Sources
Phasianidae	*Centrocercus urophasianus*	Bush *et al.* (2010)
	Tetrao urogallus	Rolstad *et al.* (2009)
	Tetrao parvirostri	Bain & Farley (2002)
	Tetrao tetrix	Kruijt *et al.* (1972)
	Tetrao mlokosiewiczi	Bain & Farley (2002)
	Tympanuchus cupido	Nooker (2007)
	Tympanuchus pallidicinctus	Bain & Farley (2002)
	Tympanuchus phasianellus	Lack (1940)
	Pavo cristatus	Sherman (1999)
Otididae	*Otis tarda*	Alonso *et al.* (2012)
	Tetrax tetrax	Jiguet *et al.* (2000)
	Chlamydotis undulata undualata	Hingrat *et al.* (2007)
	Chlamydotis macqueenii	Riou & Combreau (2014)
Scolopacidae	*Tryngites subruficollis*	Strauch (1978)
	Philomachus pugnax	Lank *et al.* (2002)
	Gallinago media	Kalas *et al.* (1995)
Psittacidae	*Strigops habroptilus*	Merton *et al.* (1984)
Trochilidade	*Phaethornis superciliosus*	Nicholson (1931)
	Phaethornis guy	Snow (1972)
	Phaethornis augusti	Ramjohn *et al.* (2003)
	Pygmorni longuemareus	Lack (1940)
	Amazilia candida	Atwood *et al.* (1991)
	Eupetomena macroura	Pizo & Silva (2001)
	Stephanoxis lalandi	Pizo (2012)
	Selasphorus calliope	Hutto (2014)
Dendrocolaptidae	*Dendrocincla tyrannina*	Willis & Yoshika (1993)
Tyrannidae	*Mionectes oleaginous*	Westcott & Smith (1997)
	Mionectes macconnelli	Hoglund & Sillen-Tullberg (1994)
	Mionectes rufiventris	Pizo & Aleixo (1998)

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Family	Lekking species	Sources
Cotingidae	*Lipaugus unirufus*	Lanyon (1985)
	Lipaugus vociferans	Fitzsimmons *et al.* (2008)
	Lipaugus fuscocinereus	Lanyon (1985)
	Pyroderus scutatus	Lanyon (1985)
	Rupicola rupicola	Trail (1985)
	Rupicola peruviana	Lanyon (1985)
	Phoenicircus carnifex	Lanyon (1985)
	Phoenicircus nigricollis	Lanyon (1985)
Pipridae	*Machaeropterus pyrocephalus*	Lanyon (1985)
	Machaeropterus deliciosus	Prum (1994a)
	Pipra aureola	Lanyon (1985)
	Pipra fasciicauda	Lanyon (1985)
	Pipra erythrocephala	Ryder *et al.* (2006)
	Pipra mentalis	Lanyon (1985)
	Pipra cornuta	Prum (1994a)
	Pipra pipra	Ryder *et al.* (2006)
	Pipra coronata	Lanyon (1985)
	Pipra chloromeros	Lanyon (1985)
	Pipra filicauda	Schwartz & Snow (1978)
	Pipra rubrocapilla	Prum (1994a)
	Manacus manacus	Cestari & Pizo (2013)
	Manacus candei	Prum (1994a)
	Chiroxiphia caudata	Francisco *et al.* (2007)
	Chiroxiphia pareola	Snow (1977)
	Chiroxiphia linearis	McDonald & Potts (1994)
	Chiroxiphia boliviana	Prum (1994a)
	Chiroxiphia lanceolata	Prum (1994a)
	Corapipo gutturalis	Endler & Théry (1996)
	Corapipo leucorrhoa	Prum (1994a)
	Oxyruncus cristatus	Lanyon (1985)
	Dixiphia pipra	Prum (1994a)
	Lepidothrix serena	Endler & Théry (1996)
	Lepidothrix coronata	Prum (1994a)
	Ilicura militaris	Prum (1994a)
	Masius chrysopterus	Prum (1994a)
	Heterocercus flavivertex	Prum (1994a)
	Heterocercus aurantiivertex	Prum (1994a)
	Machaeropterus regulus	Prum (1994a)
	Machaeropterus pyrocephalus	Prum (1994a)
	Machaeropterus striolatus	Prum (1994a)
	Neopelma aurifrons	Prum (1994a)
	Neopelma pallescens	Prum (1994a)
	Tyranneutes stolzmanni	Prum (1994a)
	Tyranneutes virescens	Prum (1994a)
Thraupidae	*Volatinia jacarina*	Almeida & Macedo (2001)
Paradisaeidae	*Astrapia rothschildi*	Sibley & Ahlquist (1985)
	Astrapia mayeri	Sibley & Ahlquist (1985)
	Astrapia nigra	Sibley & Ahlquist (1985)
	Paradisea raggiana	Sibley & Ahlquist (1985)
	Paradisea apoda	Sibley & Ahlquist (1985)

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Family	Lekking species	Sources
Paradisaeidae	*Paradisea minor*	Sibley & Ahlquist (1985)
	Paradisea rubra	Sibley & Ahlquist (1985)
	Paradisea guilielmi	Sibley & Ahlquist (1985)
	Paradisea decora	Sibley & Ahlquist (1985)
	Ptiloris paradiseus	Sibley & Ahlquist (1985)
	Ptiloris magnificus	Sibley & Ahlquist (1985)
	Parotia lawesii	Pruett-Jones & Pruett-Jones (1990)
	Pteridophora alberti	Oakes (1992)
	Cicinnurus regius	Beehler & Pruett-Jones (1983)
Ploceidae	*Euplectes jacksoni*	Oakes (1992)
Viduidae	*Vidua macroura*	Oakes (1992)
	Vidua parladisae	Oakes (1992)

LUMINOSITY, CONSPICUITY AND THE FEMALE CHOICE

The perception of a color pattern is a function of the ambient light, reflectance spectra of each color pattern element, transmission spectrum of the medium (in this case air) and optical and neurophysiological properties of eyes and brain (Endler 1990, Pike 2012). If one color pattern is more similar to the background in any respect than another pattern, then the former will be relatively more difficult to detect. To be more conspicuous, a color pattern need only deviate from the visual background under certain light conditions and with respect to the intended receiver's color vision and visual acuity (Endler 1986). Before copulation, males and females must communicate in a way in which they can recognize each other as similar species, determine each other's sex, ascertain the degree of receptiveness and, especially in relation to females, determine whether the mate has adequate attributes to be chosen. Environmental conditions such as luminosity during signaling could affect the transmission efficiency of information, affecting visual communication between animals, which is reflected in survivorship and reproduction (Wilgers & Hebets 2011).

If visual signals are used in mate choice, then forest geometry and weather will affect reproductive behavior and reproductive success. Variation in ambient light and color patterns can interact in a way that can make an animal conspicuous to conspecifics but relatively inconspicuous to predators. Thus, the degree of conspicuity could be maximized in some moments and minimized in others (Endler 1990, 1991, 1992, 1993). The contrast of an animal with background colors could vary significantly, depending on the similarity between spectrum of radiation, reflection of a color pattern and distance in which the animal lies from its observer. Thus, even though an animal's color remains constant, its appearance and conspicuity could change when it moves between environments with different light conditions or if it is seen at different distances (Endler 1986, 1990, 1991).

The Light Environment Hypothesis (LEH) proposes that different species use different colors because they inhabit different light environments (Marchetti 1993). Thus, it can be used to predict what specific colors or levels of brightness would maximize (or minimize) the contrast against the background, according to the amount of ambient light available in a particular habitat (Hernández-Palma 2016). The conspicuousness of a visual signal depends on the spectra of the ambient light, the signal and its background. Maximal conspicuousness is achieved for colors which are rich in the wavelengths present in the ambient light and poorly reflected by the background (Endler 1990).

Males can enhance their conspicuity by using postures that display specific colors during a display (Dakin & Montgomerie 2009), displaying in places or hours that best complement their colors (Gross *et al.* 2010, Francis *et al.* 2011) or actively modifying the environment around them to enhance the contrast of their colors with the background (Johnsgard 1994). We made a review of bird species that use ambient light and/or background colors to enhance their conspicuity to females during courtship (Table 2).

Birds seem to take advantage of the variation in the appearance of the same color pattern in different ambient lights (Hernández-Palma 2016). Endler & Théry (1996) studied *Rupicola rupicola*, *Corapipo gutturalis* and *Lepidothrix serena* and noticed that the three species use a non-random subset of the ambient light available during lek performances. *Rupicola rupicola* only displayed when the sun was not blocked by clouds, which was also observed by Gilliard (1962). In all cases, each male only performed when part of its body was illuminated by the sun and the rest of its body was in the shadow. When one or more males tried to display on a perch occupied by another male, they fought for the privileged position that allowed the sun to illuminate only part of the body. For *C. gutturalis*, displays were more common at noon, when the sun illuminated part of the perch. If the sunrise was experimentally blocked, the males stopped displaying, and when it was unblocked, the performances returned. Copulation occurred when the sunrise was brighter and the male contrast with the background was higher (Endler & Théry 1996). *Lepidothrix serena* seems to prefer to display in darker environments, where the sky is 50% covered by clouds (Endler & Théry 1996). Medeiros (2012) did not find the same results for *L. serena*, since the species did not select specific habitat or hours to display, although the period of the year with the most bird activity was that which promoted the greatest contrast for males and the least for the females. This behavior was also found in *Corapipo gutturalis*, but not in *Ilicura militaris* and *Masius chrysopterus* (Anciães & Prum 2008).

A solution for the trade-off between signaling to females and escaping predation is the evolution of hidden secondary characters that would only be shown when necessary, such as the erection of a peacock's tail or the exhibition of the Magnificent frigatebird (*Fregata magnificens*) throat pouch, both non-lekking species. However, most birds have a relatively fixed color pattern, at least during the reproductive period (Moodie 1972). Some species have evolved less conspicuous colors in response to the stress of predation (Endler 1980). Although it is also important to highlight that many bird species can see UV wavelengths due to the presence of a fourth cone cell type in the retina that is receptive to UV light (Odeen & Hastaad 2003). Therefore, avian color discrimination can be different from their predators (Burns & Shultz 2012).

The blue patches on the throat of the bluethroat (*Luscinia svecica*), a non-lekking bird, have high UV reflection and are actively shown during displays (Johnsen *et al.* 1998). Studies show that females could discriminate between males with and without artificially reduced color reflection (Anderson & Amundsen 1997). In experimental conditions, Andersson and Amundsen (1997) covered the throat plumage of a group of males with a substance that absorbs UV rays. The attractiveness of these males was compared with a control group, whose patches were left unaltered. Females associated significantly less with manipulated males which had reduced UV reflection. In natural environments, light conditions could affect how much the plumage color of these males is reflected. Thus, males that are able to enhance their conspicuity by displaying in places that favor plumage reflection for conspecifics would have higher reproductive success.

The Blue Tit, *Parus caeruleus* is a non-lekking bird known to use colour for intra and inter-sexual communication because of their UV-reflecting crown (Griffith *et al.* 2003). Gomez & Théry (2006) tested whether male Blue Tits use the light environment variability to optimize intraspecific conspicuousness. They found that male Blue Tits display more often at dawn than during the day or at dusk. By choosing to display mainly at dawn, the probability of detectability by predators is minimized. In addition, dawn may constitute a better environment for transmission of acoustic signals to conspecifics (Staicer *et al.* 1996). Thus, dawn and the early/late light environment would allow better transmission of both acoustic and color signals to conspecifics.

The environment is spatially and temporally heterogeneous and its physical properties could affect the quality of the signaling (Endler 1986, 1990). Some studies have suggested that display arenas are not selected randomly, and an arena's physical properties, particularly luminosity, make communication during the display more efficient (Westcott 1993). Additionally, the vegetation structure in the location of or around the arena is a variable that could affect the risk of predation (Boag & Sumanik 1969), the space for flying displays (Westcott 1993), the ability for a female to see the display (Théry 1990) or the quantity of males that are illuminated during the display (Théry 1990).

Heindl & Winkler (2003a) studied the Wire-tailed manakin*, Pipra filicauda,* to determine how variations in luminosity could affect the conspicuity of adult males. They found that *P. filicauda* seems to benefit from displaying in the shade, because when males are observed at long distances, as they could be by predators, their colors are able to blend in with their background since their plumage was less bright. However, when observed closely, their plumage becomes more conspicuous in the shade, an ideal situation for displaying. They also found that the contrast with the background was greater in sunny day shade, which could explain why males were more active when the sun was not blocked by the clouds.

To test whether the contrast between plumage and background affects female choice, Heindl & Winkler (2003b) studied the Atlantic canary *Serinus canaria,* a non-lekking bird, composed of two races: yellow and white. In the experiment, the females could choose between two yellow males shown in a yellow and a white background, respectively. Then, the males were exchanged by white males shown in the same backgrounds. As expected, in both cases, the females chose the one that contrasted the most with a given background.

Heindl & Winkler (2003c) studied the interaction of ambient light and plumage color in four closely related manakin species: *Pipra filicauda*, *P. erythrocephala*, *Lepidothrix coronata*, and *Dixiphia pipra*. The males are black and differ mainly in the color of their plumage signals. They examined the effects of vertical variations in ambient light on the vertical distribution of manakin leks in tropical forests. It was found that manakins place their leks at that position along the vertical gradient where ambient light increases chromatic and/or achromatic contrast of their color signals against the background and/or within their coloration patterns. *Pipra erythrocephala* displays at all times of the day in forest shade. *Pipra filicauda* and *P. erythrocephala* are also active when the sun is blocked by clouds and *D. pipra* diplays throughout the day and always in forest shade. *Lepidothrix coronata* males guide females to the nuptial perch during the first hour in the morning.

The court cleaning behavior was well described for *Manacus vitellinus* (Chapman 1935) and *Manacus manacus* (Darnton 1958, Snow 1962). The males clean the litter from around the arenas where they will display (Chapman 1935, Darnton 1958, Snow 1962). To evaluate whether the cleaning of the arenas could enhance the conspicuity of the males *Manacus vitellinus*, Uy & Endler (2004) carried out a study using scanners that measure plumage reflection, the reflection of objects lying around and the luminosity of the environment during the display. The chromatic contrast and plumage brightness were higher against the litter-free area than against the surrounding vegetation. These results suggest that this behavior of actively modifying the surrounding environment could enhance the conspicuity of a bird's plumage, which could increase its chances of attracting a female's attention.

Cestari & Pizo (2012) reported the use of auxiliary courts by males of *Manacus manacus* and discussed its probable function in attracting females for mating. They registered a male that maintained one of its auxiliary courts as clean as its main court. The court cleaning favors the attraction of females to its auxiliary court because optimize the light incidence on courts to improve male plumage contrast against background during the display (Uy & Endler 2004). Cestari & Pizo (2012) also pointed out that the court cleaning behavior, observed in *Manacus manacus*, also serves as an anti-predation strategy by facilitating the detection of predators, such as lizards and snakes that lurk on or near the courts.

Dakin & Montgomerie (2009) studied the Blue peafowl (*Pavo cristatus*), focusing particularly on male orientation relative to the position of the sun. They noticed that during the "wing-shaking" display, females were generally behind the displaying male, and male orientation with respect to the position of the sun was not significantly different from random. However, during the pre-copulatory "train-rattling" display, males were usually directed at about 45° to the right of the sun azimuth with the female positioned directly in front, suggesting that this behavior is involved in the communication of a visual signal. Dakin & Montgomerie´s study underscores the importance of visual signaling in peafowl courtship, suggesting that an angle of about 45° relative to the sun may allow males to enhance the appearance of their iridescent eyespot feathers.

Olea *et al*. (2010) tested the hypothesis that orientation of sexual displays in great bustard (*Otis tarda*) males depends on the position of the sun, i.e., males direct their uplifted white tails towards the sun in order to maximize signal detectability to distant females. They recorded the orientation of 405 male displays in relation to the sun and to females at seven leks. Great bustard males signaled towards the sun more often than expected by chance in early morning. The hypothesis was supported by the fact that displays were more directed towards the sun when the sun was most visible.

Moreover, the courtship and territorial dive displays made by male Anna's hummingbirds (*Calypte anna*) are oriented in the general direction of the sun so that the reflecting value of the iridescent, rose-colored gorget plumage is maximized towards the target female (Hamilton 1965). Also, the snowy owl, *Bubo scandiacus,* a non-lekking bird, used a specific posture oriented toward the sun preferentially on sunny days (Bortolotti *et al*. 2011). Owls with the whitest (least spotted) plumage displayed more and signaled more frequently from perches on the ground, where their colors were more conspicuous, since they did not blend in with the snow.

The eagle owl (*Bubo bubo*), a non-lekking bird, has a white badge on the throat that is especially visible during vocal displays, when the throat is repeatedly inflated and deflated (Penteriani 2002). Penteriani *et al*. (2006) investigated the communication function of this badge and found that the period in which its brightness is highest coincides with the time when territorial and courtship displays are at their peak, which is at sunset and sunrise (Penteriani 2002). That is because the light reflected by a white patch has a higher contrast against dark backgrounds (Endler & Théry1996). Achromatic plumage patches (*i.e.*, white feathers) are the best candidates for crepuscular signaling, when contrast is more important than color (Aragonés *et al.* 1999).

To determine the importance of color in a lekking species, Stein & Uy (2006) monitored the mating success of male golden-collared manakins, *Manacus vitellinus*, and related this to spectral measures of their colorful plumage, as well as other morphological and behavioral traits shown to be important in other lekking species. They found that lek centrality, male body size, and plumage brightness were associated with male mating success. Only plumage brightness entered a multiple regression model, indicating that plumage is the overall best predictor of mating success. These results provide evidence that the spectral properties of colorful plumage predict male mating success in a lekking species and provide important insight into why many lekking birds are dichromatic and have elaborate coloration associated with specific postures.

The appearance of iridescent colors can change depending on the visual angle and luminosity (Maia *et al.* 2012a). When directly illuminated, an iridescent plumage is brighter than when illuminated by diffuse light (Maia & Macedo 2010). The amount of incident light can also influence the intensity of the plumage brightness (Maia *et al.* 2012b). Sicsú *et al.* (2013) combined visual models and behavioral observations to test whether the multimodal display of the blue-black grassquit (*Volatinia jacarina*) is influenced by environmental conditions, predicting that males should display more often in moments with high sunlight incidence upon their bodies. They recorded the rates of both complete displays (leap with singing) and incomplete ones (singing while perched) for males during repeated 30-min focal observations in varying environmental situations in the field. They found that when bathed directly in sunlight, males increased their rates of displays, tending to exhibit more complete rather than incomplete displays in this condition and suggesting a potential trade-off between display types. The results suggest that birds may adjust the timing and precise location of signal activity to improve the efficiency or likelihood of detection of some signal elements.

Table 2. Summary of bird species that use ambient light and/or background colors to enhance their conspicuity to females during the courtship, resulting of the present review.

Family	Species	Behavior	Source
Cotingidade	*Rupicola rupicola*	Display when directly illuminated by the sun	Endler & Théry (1996)
Pipridae	*Corapipo gutturalis*	Display when directly illuminated by the sun	Anciães & Prum (2008)
	Lepidothrix serena	Display when directly illuminated by the sun	Endler & Théry (1996)
	Pipra filicauda	Display in the shade	Heindl & Winkler (2003a)
	Lepidothrix coronata	Display in the dawn	Heindl & Winkler (2003c)
	Pipra erythrocephala	Display in the shade	Heindl & Winkler (2003c)
	Dixiphia pipra	Display in the shade	Heindl & Winkler (2003c)
	Manacus vitellinus	Clean the litter from around the display arenas	Uy & Endler (2004)
Fringilidae	*Serinus canaria*	Display in a contrasting background	Heindl & Winkler (2003b)
Muscicapidae	*Luscinia svecica*	Display in places that favor plumage reflection	Andersson & Amundsen (1997)
Phasianidae	*Pavo cristatus*	Display directed at about 45° relative to the sun	Dakin & Montgomerie (2009)
Otididae	*Otis tarda*	Uplift white tails towards the sun	Olea *et al.* (2010)
Trochilidae	*Calypte anna*	Display when directly luminatedy the sun	Hamilton (1965)
Strigidae	*Bubo scandiacus*	Display when directly illuminated by the sun	Bortolotti *et al.* (2011)
	Bubo bubo	Display against dark backgrounds	Penteriani *et al.* (2006)
Thraupidae	*Volatinia jacarina*	Display when directly illuminated by the sun	Sicsú *et al.* (2013)
Paridae	*Parus caeruleus*	Display mainly in the early/late light environment	Gomez & Théry (2006)

FINAL CONSIDERATIONS

The information shown in the present review indicates that abiotic factors such as ambient light may be one of the variables that influence the sexual selection and, thus, the reproductive success of bird males, which are under strong sexual selection pressure and then should use all possibilities to attract female attention. These results may also have implications for conservation biology because ambient light depends critically on forest geometry (Endler 1993), thus, the disturbance of a forest can therefore have great effects on both the availability and properties of the light. For example, selective logging, and even the apparently less disruptive activity of trail construction, has affected the placement of *C. gutturalis* display logs, causing males to abandon the vicinity of the disturbed areas and move 1 km to new sites (Endler & Théry 1996). In general, disturbance to a forest may destroy the critical conditions for visual displays, which would make it difficult for the birds to reproduce (Ross *et al.* 2016). In addition, it may alter the visual environment sufficiently that visibility to predators is greatly increased. This possible scenario would be especially critical to lekking species because lek sites last for decades and are well-known to predators (Endler & Théry 1996). Despite the relatively extensive information on sexual selection, especially in lekking birds, the influence of abiotic factors on courtship displays, and also on the consequent reproductive success, remain under studied, which emphasizes the need for more behavioral and phylogenetic studies focusing on this subject, in order to find patterns.

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REFERENCES

Almeida, J. B., & Macedo, R. H. 2001. Lek-like mating system of the monogamous blue-black grassquit. The Auk, 118(2), 404-411.

Alonso, J. A. 2000. The breeding system of the Orange-crowned Manakin. The Condor, 102(1), 181-186.

Alonso, J. C., Álvarez-Martínez, J. M., & Palacín, C. 2012. Leks in ground-displaying birds: hotspots or safe places? Behavioral Ecology, 23(3), 491-501.

Anciães, M., & Prum, R. O. 2008. Manakin display and visiting behavior: a comparative test of sensory drive. Animal Behavior, 75(3), 783-790.

Anciães, M., & Peterson, T. 2009. Ecological niches and their evolution among Neotropical manakins (Aves: Pipridae). Journal of Avian Biology, 40(6) 591-604.

Anderson, M. 1982. Female choice selects for extreme tail length in a widowbird. Nature, 299(5886), 818-820.

Anderson, S., & Amundsen T. 1997. Ultraviolet color vision and ornamentation in bluethroats. Proceedings of the Royal Society of London. B, 264(1388), 1587-1591.

Aragonés, J., de Reyna, L., & Recuerda, P. 1999. Visual communication and sexual selection in a nocturnal bird species, *Caprimulgus ruficollis*, a balance between crypsis and conspicuousness. Wilson Bulletin, 111(3), 340-345.

Atwood, J. L., Fitz, V. L., & Bamesberger, J. E. 1991. Temporal patterns of singing activity at leks of the White-bellied Emerald. Wilson Bulletin, 103(3), 373-386.

Bain, M. R., & Farley, G. H. 2002. Display by apparent hybrid prairie-chickens in a zone of geographic overlap. The Condor, 104(3), 683-687.

Bateman, A. J. 1948. Intra-sexual selection in Drosophila. Heredity, 2(3), 349-368.

Beehler, B. & Pruett-Jones, S.G. 1983. Display dispersion and diet of birds of paradise: a comparison of nine species. Behavioral Ecology and Sociobiology, 13(3), 229-238.

Beehler, B. M., & Foster, M. S. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. American Naturalist, 131(2), 203-219.

Boag, D. A., & Sumanik, K. M. 1969. Characteristics of drumming sites selected by ruffed grouse in Alberta. Journal of Wildlife Management, 333(3), 621-628.

Bortolotti, G. R., Stoffel, M. J., & Galván, I. 2011. Wintering snowy owls *Bubo scandiacus* integrate plumage color, behavior and their environment to maximize efficacy of visual displays. Ibis, 153(1), 134-142.

Bradbury, J. W., & Gibson, R. M. 1983. Leks and mate choice. In: P. Bateson (Ed.), Mate choice. pp. 273-289. Cambridge: Cambridge University Press.

Burns, K. J., & Shultz, A. J. 2012. Widespread cryptic dichromatism and ultraviolet reflectance in the largest radiation of Neotropical songbirds: implications of accounting for avian vision in the study of plumage evolution. The Auk, 129(2), 211-222.

Bush, K. L., Aldridge, C. L., Carpenter, J. E., Paszkowski, C. A., Boyce, M. S., Coltman, M. S. 2010. Birds of a feather do not always lek together: genetic diversity and kinship structure of greater sage-grouse (*Centrocercus urophasianus*) in Alberta. The Auk, 127(2), 343-353.

Castro-Astor, I. N., Alves, M. A. S., & Cavalcanti, R. B. 2004. B. Display behavior and spatial distribution of the red-headed manakin in the Atlantic Forest Brazil. The Condor, 106(2), 320-335.

Castro-Astor, I. N., Alves, M. A. S., & Cavalcanti, R. B. 2007. Display behavior and spatial distribution of the White-Crowned Manakin in the Atlantic forest Brazil. The Condor, 109(1), 155-166.

Cestari, C., & Pizo, M. A. 2012. The use of auxiliary courts by the lek-forming White-bearded Manakin *Manacus manacus* (Aves, Pipridae). Acta Ethologica, 15(1), 73-79.

Cestari, C., & Pizo, M. A. 2013. Seed dispersal by the lek-forming white-bearded manakin (*Manacus manacus*, Pipridae) in the Brazilian Atlantic forest. Journal of Tropical Ecology, 29(5), 381-389.

Chapman, F. M. 1935. The courtship of Gould's manakin (*Manacus vitellinus*) on Barro Colorado Island, Canal Zone. Bulletin of the American Museum of Natural History, 68(3), 471-525.

Dakin, R., & Montgomerie, R. 2009. Peacocks orient their courtship displays towards the sun. Behavior Ecology and Sociobiology, 63(6), 825-834.

Dakin, R., Lendvai, A. Z., Ouyang, J. Q., Moore, I. T., Bonier, F. 2015. Plumage color is associated with partner parental care in mutually ornamented tree swallows. Animal behavior, 111(1), 111-118.

Dale, J., Dey, C. J., Delhey, K., Kempenares, B., Valcu, M. 2015. The effects of life history and sexual selection on male and female plumage coloration. Nature, 527(7578), 367-370.

Darnton, I. 1958. The display of the manakin *Manacus manacus*. Ibis, 100(1), 52-58.

Darwin, C. 1871. The descent of man and selection in relation to sex. Princeton University Press, Princeton, New Jersey.

Durães, R. 2009. Lek structure and male display repertoire of blue-crowned manakins in eastern Ecuador. The Condor, 111(3), 453-461.

Durães, R., Loiselle, B. A., & Blake, J. G. 2009. Female mate choice across spatial scales: influence of lek and male attributes on mating success of blue-crowned manakins. Proceedings of the Royal Society of London B, 276(1663), 1875-1881.

Durães, R., Blake, J. G., Loiselle, B. A., Ryder, T. B., Tori, W. P., Hidalgo, J. R. 2011. Vocalization activity at leks of six manakin (Pipridae) species in eastern Ecuador. Ornitologia Neotropical, 22, 437-445.

Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata.* Evolution, 34(1), 76-91.

Endler, J.A. 1986. Defense against predation. In: Feder, M.E. & Lauder, G.V. eds. Predator-prey relationships: perspectives and approaches from the study of lower vertebrates. University of Chicago Press, Chicago. 109-134.

Endler, J. A. 1990. On the measurement and classification of color in studies of animal color patterns. Biological Journal of the Linnean Society, 41(4), 315-352.

Endler, J. A. 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. Vision Research, 31(3), 587-608.

Endler, J. A. 1992. Signals, Signal Conditions, and the Direction of Evolution. The American naturalist, 139, S125-S153.

Endler, J. A. 1993. Some general comments on the evolution and design of animal communication systems. Philosophical Transactions of the Royal Society of London B, 340(1292), 215-225.

Endler, J. A., & Théry, M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. American Naturalist, 148(3), 421-452.

Evans, M. R., & Thomas, A. L. R. 1992. The aerodynamics and mechanical effects of elongated tails in the scarlet-tufted malachite sunbird: measuring the costs of a handicap. Animal Behavior, 43(2), 337-347.

Fitzsimmons, L. P., Barker, N. K., & Mennill, D. J. 2008. Individual variation and lek-based vocal distinctiveness in songs of the screaming piha (*Lipaugus vociferans*), a suboscine songbird. The Auk, 125(4), 908-914.

Francis, C. D., Ortega, C. P., & Cruz, A. 2011. Different behavioral responses to anthropogenic noise by two closely related passerine birds. Biology Letters, 7, 850-852.

Francisco, M. R., Gibbs, H. L. Galetti, M., Lunardi, V. O., Júnior, P. M. G. 2007. Genetic structure in a tropical lek breeding bird, the blue manakin (*Chiroxiphia caudata*) in the Brazilian Atlantic Forest. Molecular Ecology, 16(23), 4908-4918.

Fusani, L., Barske, J., Day, L. D., Fuxjager, M. J., Schlinger, B. A. 2014. Physiological control of elaborate male courtship: female choice for neuromuscular systems. Neuroscience and Biobehavioral Reviews, 46(4), 534-546.

Gilliard, E. T. 1962. On the breeding behavior of the cock-of-the-rock (Aves, *Rupicola rupicola*). Bulletin of the American Museum of Natural History, 124(2), 31-68.

Gomez, D., & Théry, M. 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community. Ecology Letters, 7(4), 279-284.

Gomez, D., & Théry, M. 2006. Interacting effects of signalling behaviour, ambient light and plumage colour in a temperate bird, the blue tit *Parus caeruleus.* Revue d'Écologie, 61(4), 367-382.

Griffith, S. C., Örnborg, J. Russell, A. F., Andersson, S., Sheldon, B. C. 2003. Correlations between ultraviolet coloration, overwinter survival and offspring sex-ratio in the Blue Tit. Journal of Evolutionary Biology, 16(5), 1045-1054.

Gross, K., Passinelli, G., & Kunc, H. P. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. American Naturalist, 176(4), 456-464.

Hamilton, W. J. 1965. Sun-oriented display of the Anna's hummingbird. Wilson Bulletin, 77(1), 38-44.

Hamilton, W. D., & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? Science, 218(4570), 384-387.

Heindl, M., & Winkler, H. 2003a. Interacting effects of ambient light and plumage color patterns in displaying Wire-tailed Manakins (Aves, Pipridae). Behavior Ecology Sociobiology, 53(3), 153-162.

Heindl, M., & Winkler, H. 2003b. Female Canaries (*Serinus canaria*) associate more with Males that Contrast Strongly against the Background. Ethology, 109(3), 259-271.

Heindl, M., & Winkler, H. 2003c. Vertical lek placement of forest dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. Biological Journal of the Linnean Society, 80(4), 647-658.

Henshaw, J. M., Kahn, A. T., & Fritzsche, K. 2016. A rigorous comparison of sexual selection indexes via simulations of diverse mating systems. Proceedings of the National Academy of Sciences, 113(3), 300-308.

Hernández-Palma, A. 2016. Light matters: testing the "Light Environment Hypothesis" under intra and interspecific contexts. Ecology and Evolution, 6(12), 4018-4031.

Hingrat, Y., Saint-Jalme, M., Ysnel, F., Le Nuz, E., Lacroix, F. 2007. Habitat use and mating system of the houbara bustard (*Chlamydotis undulata undulata*) in a semi-desertic area of

North Africa: implications for conservation. Journal of Ornithology, 148(1), 39-52.

Hoglund, J. & Birgitta, S.T. 1994. Does lekking promote the evolution of male-biased size dimorphism in birds? On the use of comparative approaches. The American Naturalist, 144(6), 881-889.

Hutto, R. L. 2014. Time budgets of male Calliope Hummingbirds on a dispersed lek. Wilson Journal of Ornithology, 126(1), 121-128.

Janicke, T., Haederer, I. K., Lajeunesse, M. J., & Anthes, N. 2015. Darwinian sex roles confirmed across the animal kingdom. Science Advances, 2(2), e1500983.

Jiguet, F., Arroyo, B., & Bretagnolle, V. 2000. Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. Behavioral Processes, 51, 63-82.

Johnsen, A., Andersson, S., Örnborg, J. , Lifjeld, J. T. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): a field experiment. Proceedings if the Royal Society of London B, 265(1403), 1313-1318.

Johnsgard, P. A. 1994. Arena birds: sexual selection and behavior. Washington, DC: Smithsonian Institute Press.

Johnstone, R. A. 1995. Sexual selection, honest advertising and the handicap principle: reviewing the evidence. Biological Reviews of the Cambridge Philosophical Society, 70(1), 1-65.

Kalas, J. A., Fiske, P., & Saether, S. A. 1995. The effect of mating probability on risk taking: an experimental study in lekking great snipe. The American Naturalist, 146(1), 59-71.

Kruijt, J. P., Vos, G. J., & Bossema, I. 1972. The arena system of the black grouse (*Lyrurus tetrix*). Proceedings of the *International* Ornithological *Congress*, 15, 399-423.

Lack, D. 1940. Pair-formation in birds. The Condor, 42(6), 269-286.

Lank, D. B., Smith, C. M., Hanotte, O., Ohtonen, A., Bailey, S., Burke, T. 2002. High frequency of polyandry in a lek mating system. Behavioral Ecology, 13(2), 209-215.

Lanyon, S. M. 1985. Molecular perspectives on higher-level relationships in the Tyrannoidea (Aves). Systematic Zoology, 34(4), 404-418.

Liker, A., Freckleton, R. P., & Székely, T. 2013. The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications,* 4, 1587.

Lozano, G. A. 1994. Carotenoids, Parasites, and Sexual Selection. Oikos, 70(2), 309-311

Maia, R., &. Macedo, R. H. 2010. Achieving luster: prenuptial molt pattern predicts iridescent structural coloration in Blue-black Grassquits. *Journal of Ornithology,* 152(2), 243-252.

Maia, R., Macedo, R. H., & Shawkey, M. D. 2012a. Nanostructural self-assembly of iridescent feather barbules through depletion attraction of melanosomes during keratinization. Journal of the Royal Society Interface, 9(69), 734-743.

Maia, R., Brasileiro, L., Lacava, R. V., Macedo, R. H. 2012b. Social environment affects acquisition and color of structural nuptial plumage in a sexually dimorphic tropical passerine. Plos One, 7(10), e47501.

Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. Nature, 362(6416), 149-152.

McDonald, D. B., & Potts, W. K. 1994. Cooperative display and relatedness among males in a lek-mating bird. Science New York then Washington*,* 266(5187), 1030-1032.

Medeiros, R. W. 2012. Efeito do contraste da plumagem com ambiente de fundo: o caso do Dançador-estrela (*Lepidothrix serena*, Aves: Pipridae) na Amazônia Central. Instituto Nacional de Pesquisas da Amazônia. p. 104.

Merton, Don V., Rodney, B. M., & Atkinson, I. A. 1994. Lek behavior in a parrot: the kakapo *Strigops habroptilus* of New Zealand. Ibis, 126(3), 277-283.

Moodie, G. E. E. 1972. Predation, natural selection, and adaptation in an unusual three spine stickleback. Heredity, 28(2), 155-167.

Moller, A. P., & de Lope, F. 1995. Differential costs of a secondary sexual character: an experimental test of the handicap principle. Evolution, 48(5)1676-1683.

Moller, A. P., & Thornhill, R. 1998. Male parental care, differential investment by females and sexual selection. Animal Behavior, 55(6), 1507-1515.

Nicholson, E.M. 1931. Communal Display in Hummingbirds. Ibis, 73(1), 74-83.

Nooker, J. K. 2007. Factors affecting the demography of a lek-mating bird: the Greater Prairie-Chicken. Division of Biology, College of Arts and Sciences, Kansas State University, Manhattan, Kansas.

Oakes, E. J. 1992. Lekking and the evolution of sexual dimorphism in birds: comparative approaches. The American Naturalist, 140(4), 665-684.

Odeen, A., & Hastaad, O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. Molecular Biology and Evolution*,* 20(6), 855-861.

Olea, P. P., Casas, F., Redpath, S., Viñuela, J. 2010. Bottoms up: great bustards use the sun to maximize signal efficacy. Behavior Ecology, 64(6), 927-93.

Penteriani, V. 2002. Variation in the function of eagle owl vocal behaviour: territorial defence and intra-pair communication? Ethology, Ecology & Evolution, 14(6), 275-281.

Penteriani, V., Delgado, M. D. M., Alonso-Alvarez, C., Sergio, F. 2006. The importance of visual cues for nocturnal species: eagle owls signal by badge brightness. Behavioral Ecology, 18(1), 143-147.

Pike, T. W. 2012. Preserving perceptual distances in chromaticity diagrams. Behavioral Ecology, 23(4), 723-728.

Pizo, M.A., & Aleixo, A. 1998. Lek behavior of the Gray-hooded Flycatcher. The Condor, 100(72), 726-731.

Pizo, M. A., & Silva, W. R. 2001. The dawn lek of the swallow-tailed hummingbird. The Wilson Bulletin, 113(4), 388-397.

Pizo, M. A. 2012. Lek behavior of the Plovercrest (*Stephanoxis lalandi*, Trochilidae). Wilson Journal of Ornithology, 124(1), 106-112.

Pruett-Jones, S. G., & Pruett-Jones, M. A. 1990. Sexual selection through female choice in Lawes' parotia, a lek-mating bird of paradise. Evolution. 44(3), 486-501.

Prum, R.O. 1990. Phylogenetic analysis of the evolution of display behavior in the Neotropical manikins (Aves: Pipridae). Ethology. 84(3), 202-231.

Prum, R.O. 1994a. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). Evolution. 48(5), 1657-1675.

Prum, R. O. 1994b. Species status of the white-fronted manakin, *Lepdothrix serena* (Pipridae), with comments on conservation biology. The Condor, 96(3), 692-702.

Prum, R. O., Kaplan, J. A., & Pierson, J. D. 1996. Display behavior and natural history of the yellow crowned manakin (*Heterocercus flavivertex*: Pipridae). The Condor, 98(4), 722-735.

Prum, R. O. 1998. Sexual selection and evolution of mechanical sound production in manakins (Aves: Pipridae). Animal Behavior, 55(4), 977-993.

Ramjohn, C. L., Lucas, F. B., Hayes, F. E., Ballah, S. T., Johnson, N. C., Garcia, K. M. 2003. Lek mating behavior of the Sooty-capped Hermit (*Phaethornis augusti*) in the Paria Peninsula of Venezuela. Journal of Field Ornithology, 74(3), 205-209.

Riou, S., & Combreau, O. 2014. Male territories and the lek-like mating system of MacQueen's Bustard *Chlamydotis macqueenii*. Journal of Ornithology, 155(4), 959-967.

Rolstad, J., Erlend, R. ,& Wegge, P. 2009. Capercaillie *Tetrao urogallus* lek formation in young forest. Wildlife Biology. 13(1), 59-67.

Ross, B. E., Haukos, D. A., Hagen, C. A., Pitman, J. C. 2016. Landscape composition creates a threshold influencing lesser prairie-chicken population resilience to extreme drought. Global Ecology and Conservation, 6, 179-188.

Ryder, T., Blake, J. G., & Loiselle, B. A. 2006. A test of the environmental hotspot hypothesis for lek placement in three species of manakins (Pipridae) in Ecuador. The Auk, 123(1), 247-258.

Ryder, T., & Sillet, T. S. 2016. Climate, demography and lek stability in an Amazonian bird. Proceedings of the Royal Society B, 283(1823), 20152314.

Schwartz, P., & Snow, D. M. 1978. Display and related: behavior of the wire-tailed manakin. Living Bird, 17(1978), 51-78.

Sherman, P.W.1999. Birds of a feather lek together. Nature, 401(6749), 119-120.

Sibley, C. G., & Ahlquist, J.E. 1985. Phylogeny and classification of the new world suboscine passerines (Passeriformes: Oligomyodi: Tyrannides). Ornithological Monographs, 36(1), 396-428.

Sicsú, P., Manica, L. T., Maia, R., Macedo, R. H. 2013. Here comes the sun: multimodal displays are associated with sunlight incidence. Behavior Ecology and Sociobiology, 67(10), 1633-1642.

Snow, D. 1962. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. Zoologica, 47, 65-104.

Snow, B. K. 1972. A field study of the calfbird *Perissocephalvs tricolor.* Ibis, 114(2), 139-162.

Snow, B. K. 1977. Comparison of the leks of Guy's hermit hummingbird *Phaethornis guy* in Costa Rica and Trinidad. Ibis, 119(2), 211-214.

Snow, D. 2004. Pipridae: family account. In: J. del Hoyo, A. Elliot & D. A. Christie *(Eds.), Handbook of the birds of the world. Pp.* 110-169. Barcelona, Spain: Lynx Editions.

Staicer, D. E., Spector, C. A., & Horn, A. G. 1996. The dawn chorus and other diel patterns in acoustic signaling. In: D. E. Kroodsma & E. H. Miller (Eds.), Ecology and evolution of acoustic communication in birds. pp. 426-453. Cornell: Cornell University Press.

Stein, A. C. J., & Uy, J. A. C. 2006. Plumage brightness predicts male mating success in the lekking golden-collared manakin. Behavioral Ecology, 7(1), 41-47.

Stockley, P. 1997. Sexual conflict resulting from adaptations to sperm competition. Trends in Ecology and Evolution, 12(4), 154-159.

Strauch, J. G. 1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. Transactions of the Zoological. Society of London. 34(3), 263-345.

Théry, M. 1990. Influence de la lumiere sur la choix del habitat et le comportement sexuel des Pipridae (Aves: Passeriformes) en Guyane Franqaise. Revue d'Ecologie, 45(3), 215-236.

Thornhill, R., Ligon, J. D., & Johnson, K. 1990. Parasites and mate choice in the red jungle fowl. American Zoology, 30(2), 235-244.

Torio, A. J. 1992. Effect of parasitic infection on male color pattern and female choice in guppies. Behavioral Ecolog, 3(4), 346-351.

Trail, P. W. 1985. Courtship disruption modifies mate choice in a lek-breeding bird. Science, 227(4688), 778-780.

Uy, J. A. C., & Endler, J. A. 2004. Modification of the visual background increases the conspicuousness of golden-collared manakin displays. Behavioral Ecology, 15(6), 1003-1010.

Westcott, D. 1993. Habitat characteristics of lek sites and their availability for the ochre-bellied flycatcher, *Mionectes oleagineus*. Biotropica, 25(4), 444-451.

Westcott, D., & James, N. M. S. 1997. Lek size variation and its consequences in the ochre-bellied flycatcher, *Mionectes oleaginous.* Behavioral Ecology, 8(4), 396-403.

Wilgers, D., & Hebets, S. 2011. Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. Current Zoology, 57(2), 175-186.

Willis, E. O., & Yoshika, O. 1993. On *Dendrocincla tyrannina*: morphology, behavior and conservation of a shy lek-type insectivore. Caldasia, 18(86), 131-140.

Zahavi, A. 1975. Mate selection- a selection for a handicap. Journal Theoretical Biology, 53(1), 205-214.

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